

# Ten new extant species of the coccolithophore *Syracosphaera* and a revised classification scheme for the genus

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**ABSTRACT:** Ten new species of the coccolithophore genus *Syracosphaera* are described from temperate and sub-tropical to tropical waters: *Syracosphaera andruleitii* sp. nov., *Syracosphaera castellata* sp. nov., *Syracosphaera didyma* sp. nov., *Syracosphaera hastata* sp. nov., *Syracosphaera hirsuta* sp. nov., *Syracosphaera leptolepis* sp. nov., *Syracosphaera operculata* sp. nov., *Syracosphaera reniformis* sp. nov., *Syracosphaera serrata* sp. nov. and *Syracosphaera squamosa* sp. nov. An emended description is given for *Syracosphaera nana* Kamptner. These and other *Syracosphaera* species are placed in a revised classification scheme for the genus, based on the morphological structure of endothecal and exothecal coccoliths, and coccosphere characteristics. The *Syracosphaera noroitica* group is introduced for species with exothecal muroliths with a beaded proximal flange and varimorphic endothecal muroliths. The three new subgroups in the *Syracosphaera nodosa* group are characterised by their exothecal coccolith structure: subcircular and delicate in the *leptolepis*-subgroup, oval in the *nana*-subgroup and laminated in the *squamosa*-subgroup. The *corolla*-subgroup, with its large funnel-shaped exothecal coccoliths, is new in the *Syracosphaera pulchra* group.

## INTRODUCTION

Coccolithophores are unicellular golden-brown algae of the division Haptophyta that at least at some point in their life cycle bear coccoliths, minute calcite plates. They are a major component of the oceanic microplankton and form a significant proportion of the total primary production and carbon fixation in the pelagic area (e.g. Westbroek et al. 1994). Coccoliths are exported to the ocean floor and accumulate to form calcareous oozes and chalks, which makes them extremely valuable for stratigraphy and palaeoceanography.

The family Syracosphaeraceae (Lohmann 1902) Lemmerman 1903, and especially the genus *Syracosphaera* Lohmann 1902, shows a high diversity and a wide geographical distribution, although most species occur in low numbers (Jordan and Kleijne 1994; Young et al. 2003, 2005; Jordan et al. 2004). For taxonomic references to the *Syracosphaera* spp., see section on Species descriptions and tables 1-4. The fossil record of the family Syracosphaeraceae extends back into the Paleogene, but the delicate coccoliths have a low preservation potential and a minimal impact on the fossil biodiversity data (Perch-Nielsen 1985; Young and Bown 1997; Young et al. 2005).

Most *Syracosphaera* spp. have very small, elliptical, coccoliths - less than 3 µm in length - and can only be identified properly using scanning electron microscopy, and even then it still may be difficult to assign a specimen to one of the well-defined species. Moreover, the coccolith structure of most *Syracosphaera* species is not yet known in detail, except for the cultured species *S. pulchra* with its relatively large coccoliths (Geisen et al. 2002; Young et al. 2004). Also polymorphism, the occurrence of various kinds of coccoliths on one coccosphere, hinders species identification. Often only separate coccoliths are present in

a sample, or a species may be found without its outer layer of coccoliths, while these exothecal coccoliths are an important tool for species identification.

The development of an additional outer layer of coccoliths occurs almost exclusively in the Syracosphaeraceae - it is also found in the closely related genus *Rhabdosphaera* Haeckel 1894 - and may be a relatively recent phenomenon, resulting in a radiative evolution of the genus *Syracosphaera* and a wide range of exothecal coccolith morphologies (Young et al. 2005; Aubry 2007). Moreover, the appendages of the syracosphaerid genera *Calciopappus* Gaarder et Ramsfjell 1954 emend. Manton et Oates 1983, *Michaelsarsia* Gran 1912 emend. Manton et al. 1984 and *Ophiaster* Gran 1912 emend. Manton et Oates 1983 apparently have evolved from *Syracosphaera* species by modification of exothecal coccoliths. These appendages, as well as the chains of exothecal coccoliths that are often formed by *Syracosphaera bannockii* and related species, most likely have a defensive function, by increasing the cell size (Young et al. 2009).

Apart from their general reproduction by asexual mitotic division, coccolithophores have a complex life-cycle with morphologically distinct haploid and diploid phases, which in most cases are holococcolith- and heterococcolith-bearing phases. These phases have two distinct basic kinds of coccoliths, formed by different types of biomineralization (Billard 1994; Young et al. 2000, 2005; Houdan et al. 2004). Heterococcolithophore- and holococcolithophore-bearing phases exploit different trophic environmental situations. This indicates that the haplo-diploid versatility of coccolithophores represents a survival strategy in a changing ecological environment (Cros et al. 2000; Houdan et al. 2006). Several *Syracosphaera* species are

known to form a life-cycle association with a holococcolith-bearing 'species'. Well established combinations are known for five species, while possible associations have been found for another six species (e.g. Cros et al. 2000; Young et al. 2003, 2005; Young and Henriksen 2003; Triantaphyllou et al. 2004; see also Tables 1-4). Two *Syracosphaera* species are associated with two different holococcolith-bearing 'species', while possible hetero-holo-holococcolithophore associations have been found for another two species. This combination of morphological differentiation in the haploid holococcolith-bearing phase with no obvious differentiation in the diploid heterococcolith-bearing phase is interpreted as an example of cryptic speciation, which is also known from two other coccolithophore families (Geisen et al. 2002, 2004; Malinverno et al. 2008).

Extant coccolithophore taxonomy is primarily based on morphological characters of coccoliths. Recently it has been supplemented with information on life-cycle associations (e.g. Geisen et al. 2002; Young et al. 2003, 2004, 2005), coccolith ultrastructure (Young et al. 2003, 2004; Young and Henriksen 2003) and molecular genetic analysis (Edvardsen et al. 2000; Houdan et al. 2004; Sáez et al. 2004). This taxonomy is constantly changing and has resulted in a succession of classification schemes, ending in the recent classifications of Young et al. (2003, 2005) and Jordan et al. (2004); for an overview, see Jordan et al. (2004).

Cros (2000) revised *Syracosphaera* taxonomy based on presence/absence and structure of the exothecal coccoliths. Later, Young et al. (2003) developed this work to provide a classification scheme for all known *Syracosphaera* species including taxa in open nomenclature. This scheme was based on a combination of exothecal coccolith form, the structure of the body coccoliths, especially the number of flanges, and the presence of circum-flagellar coccoliths. Using these criteria they divided the species into three main groups, based primarily on number of flanges in the body coccoliths. These groups were further divided into smaller sets of species, the types. For example, species with two flanges on the body coccoliths were placed in the *S. molischii* group which was subdivided into the *S. molischii* type, *S. borealis* type, *S. rotula* type and *S. halldalii* type, based primarily on exothecal coccolith morphology.

In 1993 Kleijne informally described twelve *Syracosphaera* species, leaving them in open nomenclature, as *Syracosphaera* sp. type A, etc. At that time, two of these, *Syracosphaera* sp. type C and *Syracosphaera* sp. type F, already had been described by Sánchez-Suárez (1990), as *Syracosphaera tumularis* and *S. florida* respectively, and one (*Syracosphaera* sp. type A) by Kamptner (1941) as *S. nana*. Subsequently, *Syracosphaera* sp. type H was described by Knappertsbusch (1993), as *S. marginaporata*. Many years later the informal names of the other types were still being used (see e.g. Young et al. 2003, 2009). Cros (2000) and Cros (2002) also informally described a number of new taxa in open nomenclature. In the present study we describe as new ten species that were encountered in samples from temperate to sub-tropical waters while studying the geographical and vertical distribution of the coccolithophore community in the central North Atlantic Ocean, Mediterranean Sea, Red Sea and Indian Ocean (Kleijne et al. 1989; Kleijne 1991, 1992, 1993; Cros 2000, 2002; Cros and Fortuño 2002).

The introduction of ten more *Syracosphaera* species emphasizes the extensive morphological variation within the genus. It

will also facilitate the registration of life-cycle associations involving *Syracosphaera* phases that will be discovered in future. The *Syracosphaera* spp. are placed in a revised classification scheme, based on their coccosphere characteristics and detailed morphological information on their endothecal and exothecal coccoliths.

## MATERIAL AND METHODS

Surface water samples (0–5m) were taken on the transect Indian Ocean – Red Sea – Mediterranean Sea – North Atlantic during the cruises G0 and Gx of the Snellius-II Expedition (R.V. *Tyro*, May–July 1984 and June–July 1985 respectively; Kleijne 1993). Water samples from surface and subsurface layers were obtained from the North Atlantic during Cruise I of the APNAP Expedition (Actuomicropaleontology Paleoceanography North Atlantic Project, Geomarine Center, Vrije Universiteit Amsterdam; R.V. *Tyro*, August–September 1986; Kleijne 1991). From the Northwestern Mediterranean Sea water samples have been collected during several cruises of the Institut de Ciències del Mar (CSIC), on board the R.V. *García del Cid* (MESO-95, 30 May - 16 June 1995; FRONTS-95, 17-23 June 1995; MESO-96, 18 June - 3 July 1996; FRONTS-96, 16-21 September; FANS-1, 1-8 November 1996; FANS-2, 4-14 February 1997; FANS-3, 13-15 July 1997; Workshop Picasso 16 July 1998; HIVERN-99, 20 February - 14 March 1999; Cros 2002; Moran and Estrada 2005). The coccosphere shown in plate 1, figs. 5-6, was collected during Cruise So184 of the Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, at 8°47,08'S 110°29,78'E (Station GeoB10049-2, Indian Ocean off Indonesia, depth 65m, 26 August 2005).

The samples were examined in scanning electron microscopes of various types. See Kleijne (1991) and Cros (2002) for detailed information on sampling and preparation procedures. Full taxonomic citations for all *Syracosphaera* species are given in tables 1-4.

## MORPHOLOGY AND TERMINOLOGY

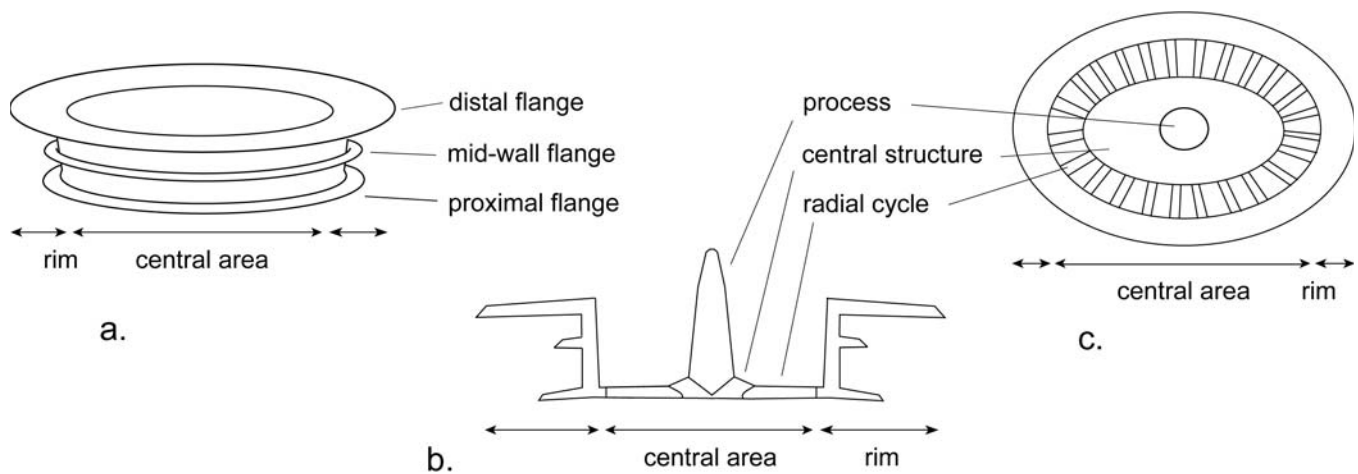
### Coccospheres

Most *Syracosphaera* species have a dithecate coccosphere; i.e. they develop distinct inner and outer layers of coccoliths. A few species have only a single layer of coccoliths; these are monothecate and lack the outer layer of coccoliths. The inner layer, or endotheca, is formed by one, two or three different kinds of endothecal coccoliths (mono-, di- or trimorphism):

- 1) body coccoliths - the ordinary coccoliths that form a complete covering of the cell; in certain species their morphology varies gradually from the apical to the antapical pole of the coccosphere (varimorphism);
- 2) circum-flagellar coccoliths – modified coccoliths, generally with a central spine, that occur around the flagellar opening;
- 3) antapical coccoliths - modified coccoliths that occur at the antapical pole of a coccosphere, opposite the circum-flagellar coccoliths; these are found in only a few species.

The outer layer, or exotheca, consists of one kind of coccoliths. These exothecal coccoliths may cover the complete endotheca, or only part of it, namely the apical side near the circum-flagellar coccoliths; in certain planolith-bearing species they may occur in a ribbon-like arrangement. Although exothecal coccoliths are known for most *Syracosphaera* species, they are often missing in individual specimens, presumably as a result of

## MUROLITH



TEXT-FIGURE 1

(a) Schematic drawings of a syracosphaerid body coccolith (muroolith) in: (a) side view, showing rim with sub-vertical wall and three flanges; (b) cross-section, showing the rim (the wall and three flanges) and the central area (the radial cycle, the central structure and the central process); (c) distal view.

the sampling procedure in case they were only loosely attached to the coccosphere.

#### Endothecal coccoliths

Endothecal *Syracosphaera* coccoliths are murooliths: i.e. bowl-shaped coccoliths with a distinct wall. They consist of two main parts:

- 1) The rim, formed by a (sub)vertical wall and one to three flanges; and
- 2) the central area, with an outer cycle of radial laths and an inner central structure (text-fig. 1).

This central structure varies from a flat plaque to a low longitudinal mound or an elevated ridge. It may bear a central process, or spine, and occasionally it is absent. The flanges are (sub)horizontal, lateral extensions from the wall. The variation in development of these flanges is one of the main characteristics used in distinguishing the *Syracosphaera* species. There is always a proximal flange and often a distal flange. Occasionally, a beaded or a continuous mid-wall flange is present somewhere in between these flanges. Previously used names for coccoliths with this structure are 'complete cancoliths' for murooliths with a distal flange or distal and mid-wall flanges, and 'incomplete cancoliths' for murooliths without these flanges (Young et al. 1997).

#### Exothecal coccoliths

The exothecal coccoliths are highly variable in shape and include planoliths, dome-shaped coccoliths and murooliths. The exothecal coccoliths are composed of similar cycles of elements to the endothecal coccoliths and are evidently modified versions of endothecal coccoliths (Inouye and Pienaar 1988; Cros 2000; Young et al. 2004). Planoliths are disc-shaped coccoliths that consist of: 1) a central area with an outer cycle of radial elements and an inner group of central elements of vari-

ous structures; and 2) a more or less flat rim (text-fig. 2). Planoliths may appear as laminated, which seems to be the result of complexly-shaped rim elements growing upwards and backwards over the central area. These rim elements seem to have a stepped profile, comparable to the blanket elements of *Helicosphaera* coccoliths; see fig. 9 in Young et al. (2004). In *Syracosphaera pulchra* and *S. histrica* the radial cycle and the central elements form a dome-shaped structure (Young et al. 2004). Finally, exothecal coccoliths may also have a muroolith structure, in which case both exotheca and endotheca consist of murooliths (Cros 2000). The large and robust exothecal murooliths of *Syracosphaera corolla* have a wide flaring wall that continues into the distal flange, forming a low and wide funnel-shaped structure (Kleijne 1993, p. 217, pl. 6, fig. 5; Young et al. 2003, pl. 19, figs. 13-15).

#### Ultrastructure

*Syracosphaera* endothecal coccoliths are constructed of units of vertical, radial and tangential crystallographic orientation, the V/R/T coccolith structure (Young et al. 1992, 1999, 2003, 2004; Young and Henriksen 2003). The rim consists of V- and R-elements, while the central area is formed by T-elements that alternate with the rim elements. In text-fig. 3 the typical *Syracosphaera* muroolith structure is represented by *Ophiaster* Gran 1912 emend. Manton et Oates 1983. Other species, such as *Syracosphaera pulchra*, may show more complexly developed R- and V-units (Young et al. 2004). The form and interlocking of the units determines the shape and thickness of the wall and flanges. Due to our lack of crystallographic data it is not possible to distinguish the R- and V-units in our specimens and, therefore, we do not use this terminology in the description of the new species. In case of distinct wall layers, we describe the inner and outer layers and e.g. the continuation of the wall into the distal flange, instead. The coccolith terminology, as used by Young et al. (1997, 2003) for species of the family Syracosphaeraceae, is summarized in text-figs. 1-3.

## SYSTEMATIC DESCRIPTIONS

We follow the classification of extant Haptophyta of Jordan et al. (2004) and the recommendations by Silva et al. (2007) and de Vargas et al. (2007) to group the calcifying haptophytes.

The descriptions of the new species are given in alphabetical order and are followed by an emended description of *Syracosphaera nana*. Their place in the classification scheme is indicated; the groups and subgroups are discussed in more detail in the section on Classification scheme. The sections on dimensions give the coccosphere diameter along the long axis and the coccolith length and width. The sections on distribution are based on illustrated records only, namely the references given in the synonymy, supplemented with our own observations.

Division HAPTOPHYTA Hibberd 1972 *ex* Edvardsen *et* Eikrem in Edvardsen et al. 2000

Class PRYMNESIOPHYCEAE Hibberd 1976 emend. Cavalier-Smith in Cavalier-Smith et al. 1996

Silva et al. (2007) re-introduced the name Coccolithophyceae Rothmaler 1951 for the class of coccolith-bearing species of the division Haptophyta, to replace the more recent name Prymnesiophyceae Hibberd 1976. They regarded the ability to calcify to be the most prominent characteristic in this group of species. Especially with the coccolith-bearing species outnumbering the other haptophyte taxa, the older name would be more appropriate. As a consequence their class Coccolithophyceae contained also the two non-calcifying orders, Prymniales Papenfuss 1955 emend. Edvardsen *et* Eikrem in Edvardsen et al. 2000, and Phaeocystales Medlin in Edvardsen et al. 2000, Jordan et al. (2004) already indicated that the priority rule is only mandatory at family level or below, and is merely a recommendation for higher levels. Since the name Prymnesiophyceae is well-established, we do not see any need to change it here.

Subclass CALCIHAPTOPHYCIDAE Probert *et* Young in de Vargas et al. 2007

To encompass the clade of calcifying haptophytes within the Class Prymnesiophyceae, de Vargas et al. (2007) introduced the subclass Calcihaptophycidae Probert *et* Young for the coccolithophores, while the non-calcifying orders remained in the subclass Prymnesiophycidae Cavalier-Smith 1986.

Order SYRACOSPHAERALES Hay 1977; emend. Young et al. 2003

This order groups species with coccoliths that consist typically of three parts:

- 1) a rim formed of two cycles of elements;
- 2) a disjunct radial lath cycle; and
- 3) a discrete central structure typically formed of one or more less regular cycles of elements.

In addition to the Syracosphaeraceae it includes the Rhabdosphaeraceae Haeckel 1894 and Calciosoleniaceae Kamptner 1937. In all three families elaborate polymorphic coccospheres are common.

Family SYRACOSPHAERACEAE (Lohmann 1902) Lemmerman 1903

Cells motile, coccospheres often showing dithecism and modified circum-flagellar coccoliths, and sometimes antapical

coccoliths. The endothecal coccoliths are muroliths, with a more or less vertical wall, one to three lateral flanges, a well-developed lath cycle and an inner central area of variable structure. The exothecal coccoliths are more variable in shape and include planoliths, muroliths and domal forms. The mono- and dithecate species are placed in the genus *Syracosphaera*, the other genera yield species with highly modified coccoliths forming appendages, instead of exothecal coccoliths.

Genus *Syracosphaera* Lohmann 1902

Coccosphere usually dithecate, with exothecal coccoliths of various shapes. Endothecal coccoliths are muroliths with one, two or three flanges, often differentiated into body and circum-flagellar coccoliths and sometimes antapical coccoliths. Exothecal coccoliths are planoliths, muroliths or dome-shaped.

Type species: *Syracosphaera pulchra* Lohmann 1902.

*Syracosphaera andruleitii* Kleijne *et* Cros **sp. nov.**

Plate 1, figures 1-6

*Syracosphaera* sp. type I, KLEIJNE 1993, p. 244, pl. 6, fig. 12.

*Non:* *Syracosphaera nodosa* auct. non Kamptner 1941. – NISHIDA 1979, pl. 8, fig. 2.

*Diagnosis:* Coccosphaera de subglobosa ad obpyriformem, dithecata, cum coccolithis endothecalibus dimorphis. Omnes coccolithi concave flexi sunt et habent similem magnitudinem. Coccolithi exothecales sunt planolithi elliptici et crassi. Coccolithi communes sunt murolithi longielliptici. Brevis paries late dilatans pergit in distale clipeum cum peripheria delicate incisa. Area centralis constat ex elementis lamellaribus radialiter tendentibus connexis in centro. Structura centralis non observata. Coccolithi circumflagellares similes sunt coccolithis comunibus sed ferunt spinam acutam.

Coccosphere subspherical to obpyriform, dithecate, with dimorphic endothecal coccoliths. All coccoliths are concavely bent and are of approximate equal size. Exothecal coccoliths are thick elliptical planoliths. Body coccoliths are long-elliptical muroliths. The extensively flaring, short wall is continued into the distal flange with delicately incised periphery. The central area consists of radial laths that connect in the centre; central structure not present. Circum-flagellar coccoliths similar to body coccoliths but they bear a pointed spine.

*Holotype:* Negative A76/9 (pl. 1, fig. 4), deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

*Type locality:* North Atlantic (42°15'3"N 25°40'4"W), depth 50m, 26 Aug. 1986 (Cruise APNAP-I, Station T86-8R).

*Etymology:* Latin *andruleitii*; referring to Dr. Harald Andruleit, coccolithophore researcher, who presented a poster with images of this undescribed species (as 'Abyssisphaera sp. B') at the Twelfth Conference of the International Nannoplankton Association, September 2008; he kindly made these images available to us for the formal description of the new species.

*Number of specimens studied:* 6, including 4 specimens from off Java (images provided by H. Andruleit and J. Young).

*Distribution:* Central North Atlantic, 50m; Indian Ocean, off Java, depth 30-120m.

**Description:** Collapsed coccospheres were found, apparently consisting of  $\pm$  80-140 dimorphic muroliths, and 1-10 planoliths (pl. 1, figs. 1, 4-5). All coccoliths are concavely bent. The body coccoliths have a prominent proximal flange, a very low wall and a well-developed distal flange of variable width (pl. 1, figs. 1-3). The outer edge of each element of the distal flange is divided into two or three angular nodes, giving the coccolith a serrated outline (pl. 1, fig. 2). The central area consists merely of the radial cycle, with 16-23 laths. The flat and elongate central part is formed by the connecting radial laths from opposite sides, occasionally with some additional elements (pl. 1, figs 2-3, 6). The coccospheres bear 1-6 circum-flagellar coccoliths, that have a wider distal flange and a pointed spine (pl. 1, figs. 1, 4-6).

The coccosphere is partly dithecate, with exothecal planoliths occurring in the apical area. The thick planoliths are broadly-elliptical, with an oblique wide rim and an almost closed central area; the distal side shows a narrow, longitudinal cleft. Their proximal side shows a clearly defined, closed and flat central area.

**Dimensions:** coccosphere, diameter  $\pm$  6.6-11.4 $\mu$ m; body coccoliths, length 1.1-2.0 $\mu$ m, width 0.8-1.2 $\mu$ m; circum-flagellar coccoliths, length 1.7 $\mu$ m, width 1.2 $\mu$ m; length of spine 0.8 $\mu$ m; planoliths, length 1.8 $\mu$ m, width 1.2 $\mu$ m.

#### Taxonomic notes

*Syracosphaera andruleitii* sp. nov. is placed in the *molischii*-subgroup of the *S. molischii* group, because of its placolith-like endothecal coccoliths, dithecatism and complex planoliths with a concave central area. Its planoliths are symmetrical, in contrast with the other species in the subgroup, that have planoliths with an asymmetrical wing-like extension.

The coccosphere shown by Nishida (1979, pl. 8, fig. 2) as *Syracosphaera nodosa* consists of coccoliths that are more elongate in outline than those of *S. andruleitii* sp. nov. and, moreover, have an obliquely raised distal flange without a fringed margin.

#### *Syracosphaera castellata* Kleijne et Cros sp. nov.

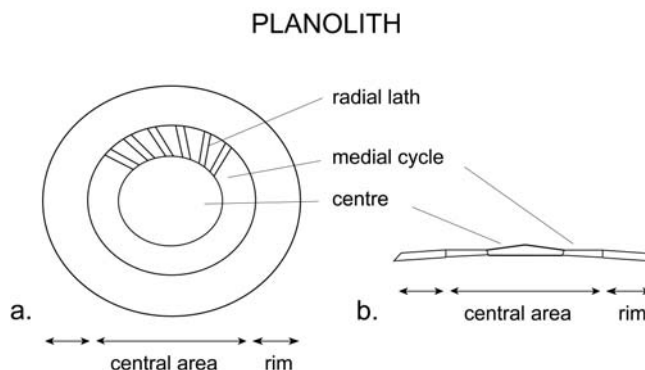
Plate 2, figures 1-6

*Syracosphaera* sp. type G, KLEIJNE 1993, p. 243, pl. 6, figs. 6, 9.  
*Syracosphaera* sp. type G of Kleijne 1993, CROS 2000, pp. 42-43, pl. 7, figs. 1-2. – CROS 2002, p. 55, pl. 29, figs. 1-4. – CROS and FORTUÑO 2002, pp. 42-43, fig. 55A-D.

*Non:* *Syracosphaera* sp. type G of Kleijne 1993, YOUNG et al. 2003, p. 44, pl. 19, fig. 10. – YOUNG et al. 2005, pl. 2, fig. 1.

*Non:* *Syracosphaera* sp. type G 'high wall', YOUNG et al. 2003, pl. 19, figs. 4-6.

**Diagnosis:** Cocco-sphaera dithecata cum coccolithis vario-formibus. Omnes coccolithi murolithi late elliptici cum unico proximali clipeo. Coccolithi exothecales habent clipeum proximale formatum nodulis globuliformibus atque altum murum cum margine delicate serrato in parte superiore. Area centralis formata structura subcirculari circumdata elementis lamellaribus radialiter tendentibus. Coccolithi communes humilem murum cum alto margine crenato habent, minuentes amplitudine ad antapicalem polum. Coccolithi communes maiores protrusionem conicam prominentem habent. Coccolithi antapicalis poli, aut nullam, aut angustam structuram longitudinalem centalem similem iugo habent. Coccolithi circumflagelares similes coccolithis comunibus sed cum bifurca et longa spina.



TEXT-FIGURE 2

Schematic drawings of a syracosphaerid exothecal coccolith (planolith) in (a) distal view and (b) cross-section.

Coccosphere dithecate, with varimorphic body coccoliths. All coccoliths are broadly-elliptical muroliths with a widening wall and only a proximal flange. Exothecal coccoliths have a beaded proximal flange and a high wall with a delicately serrated upper margin. Their central area consists of a sub-circular central structure, surrounded by radial laths. Body coccoliths have a low wall and crenellated upper margin; they diminish in size towards the antapical pole. The larger body coccoliths bear a prominent conical protrusion; coccoliths at the antapical pole have no, or only a narrow, ridge-like central structure. Circum-flagellar coccoliths similar to body coccoliths, but with a long, usually bifurcate spine.

**Holotype:** Negative A77/1 (pl. 2, fig. 1), deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

**Type locality:** North Atlantic (50°19'3"N 27°03'6"E), depth 0-5m, 21 Aug. 1986 (Cruise APNAP-I, Station T86-19D).

**Etymology:** Latin *castellatus* -a -um (adjective), castellated, built with turrets and battlements, like a castle; referring to the angular crenulations along the upper margin of the wall in the endothecal coccoliths.

**Number of specimens studied:** 5.

**Distribution:** Northeastern Indian Ocean, 0-5m; western Arabian Sea, 0-5m; Gulf of Aden, 0-5m; Red Sea, 0-5m; Mediterranean Sea, 20-75m; North Atlantic, 0-5m.

**Description:** The coccosphere shape may be ob-conical, but mostly collapsed coccospheres were found (pl. 2, fig. 1). The dithecate coccosphere consists of 35-60 varimorphic body muroliths,  $\pm$  6 circum-flagellar muroliths and an unknown number of exothecal muroliths, which are easily detached.

The exothecal coccoliths are more delicate than the endothecal coccoliths; they have a thinner wall with a finely incised upper margin, larger openings between the 25-28 radial laths and a smaller central structure (pl. 2, figs. 1, 4-5). A central opening is visible on their proximal side (pl. 2, figs. 2, 5). They bear a ring

of nodules instead of a well-developed proximal flange (pl. 2, fig. 2).

Most body coccoliths have a large sub-circular central structure that is surrounded by the 16-27 laths of the radial cycle (pl. 2, figs. 1-2, 6). The central structure is variable in shape. The large body coccoliths near the circum-flagellar area have a sub-circular conical protrusion. Coccoliths at the antapical pole have only a low ridge-like central structure or an entirely flat central area, without superposed elements (pl. 2, figs 1, 6). The central structure in the form of a protrusion probably has a small cavity, since a small opening is visible on the proximal side of the coccoliths (pl. 2, fig. 2). The protrusion appears to be formed of a single cycle of sub-vertically arranged elements. The weakly flaring wall is formed of sub-vertical polygonal elements that show an anti-clockwise imbrication in lateral view (pl. 2, fig. 2). In the uppermost part of the wall, the short horizontal sides of these elements are not connected with each other, which results in the castellated outline, (pl. 2, fig. 2, 6). The wall may vary in width; one coccolith in pl. 2, fig. 6 shows a thick wall or possibly a narrow distal flange.

The circum-flagellar coccoliths are similar in shape to the body coccoliths, although they are slightly saddle-shaped (pl. 2, figs. 1, 3-4). They bear a long spine, usually with two horn-like distal extensions (pl. 2, fig. 2).

**Dimensions:** coccosphere size  $\pm$  8-9  $\mu$ m along long axis; exothecal coccoliths, length  $\pm$  1.8 $\mu$ m; body coccoliths, length 1.1-2.1 $\mu$ m, width 1.0-1.5 $\mu$ m; circum-flagellar coccoliths, spine length 1.2-1.4 $\mu$ m.

#### Taxonomic notes

*Syracosphaera castellata* sp. nov. is placed in the new *S. noroîtica* group, and former *noroîtica*-type of Young et al. (2003), because both the endothecal and exothecal coccoliths are muraliths with only a proximal flange. In addition, both the varimorphic body coccoliths and the beaded proximal flange of the exothecal coccoliths are also found in the other species within this group, *Syracosphaera noroîtica* (Knappertsbusch 1993, p. 71-72, pl. 1, figs. 1-3; Cros 2000, figs. 5-6; Cros 2002, p. 50, pl. 23, figs. 1-6; Young et al. 2003, pl. 19, figs. 1-3) and *S. florida* (Kling 1975, pl. 3, figs. 5-6, as *Syracosphaera* sp.; Sanchez-Suarez 1990, p. 156-157, fig. 3A-F; Young et al. 2003, p. 44). *Syracosphaera castellata* sp. nov. differs from *S. noroîtica* and *S. florida* in having smaller coccoliths, with a lower wall and a larger central protrusion. Its body coccoliths have a crenellated upper margin, whereas the margin is smooth in *S. noroîtica* and undulated in *S. florida*.

Previously, two other types of coccolithophore have been assigned to this new species:

1) Coccospheres with body coccoliths with a large, longitudinally flattened central protrusion of elongate vertical elements that is considerably higher than in the endothecal coccoliths of *S. castellata* sp. nov. Moreover, the upper margin of their wall is smooth instead of crenellated. Coccoliths of this type were shown by Young et al. (2003, p. 44, pl. 19, fig. 10; as *Syracosphaera* sp. type G of Kleijne 1993) and Heimdal and Gaarder (1981, p. 67, pl. 13, fig. 65; as Unidentified heterococcolithophorid "F").

2) Coccospheres that are highly varimorphic, showing more variation in size and height of the (sub-) circular central area protrusion than in *S. castellata* sp. nov. - it may even be

rod-shaped. The coccospheres bear antapical coccoliths in which two or three radial laths are curved upwards and extend beyond the coccolith wall. Moreover, the coccoliths have a robust wall with a smooth upper margin. These coccospheres were shown by Young et al. (2003, pl. 19, figs. 4-6; as the variety 'high wall') and Young et al. 2005 (pl. 2, fig. 1; as *Syracosphaera* sp. type G of Kleijne 1993). Possibly the coccolith shown by Steinmetz (1991, pl. 18, figs. 1-2; as *Syracosphaera pirus*) also belongs to this form. These forms seem to be another two new *Syracosphaera* species belonging in the *S. noroîtica* group, or possibly variants of *S. noroîtica*.

#### *Syracosphaera didyma* Kleijne et Cros sp. nov.

Plate 3, figures 1-6

*Syracosphaera exigua* auct. non Okada et McIntyre 1977, HEIMDAL and GAARDER 1981, p. 60, pl. 8, figs. 40-41. - SÁNCHEZ-SUÁREZ 1992, p. 115-117, fig. 3A-C.

*Syracosphaera* sp. type D, KLEIJNE 1993, p. 242, pl. 6, figs. 7-8.

*Syracosphaera exigua* auct. non Okada et McIntyre 1977 var. 1, GIRAudeau and BAILEY 1995, pl. IV, fig. 3.

*Syracosphaera* sp. type D of Kleijne 1993, RIAUX-GOBIN et al. 1995, pl. 3, fig. 8. - CROS 2000, p. 42, pl. 6, figs. 3-4. - CROS et al. 2000, p. 15, pl. 8, figs. 3-4. - CROS 2002, p. 54-55, pl. 28, figs. 1-7. - CROS and FORTUÑO 2002, pp. 41-42, fig. 53A-D. - YOUNG et al. 2003, p. 44, pl. 19, figs. 9, 12.

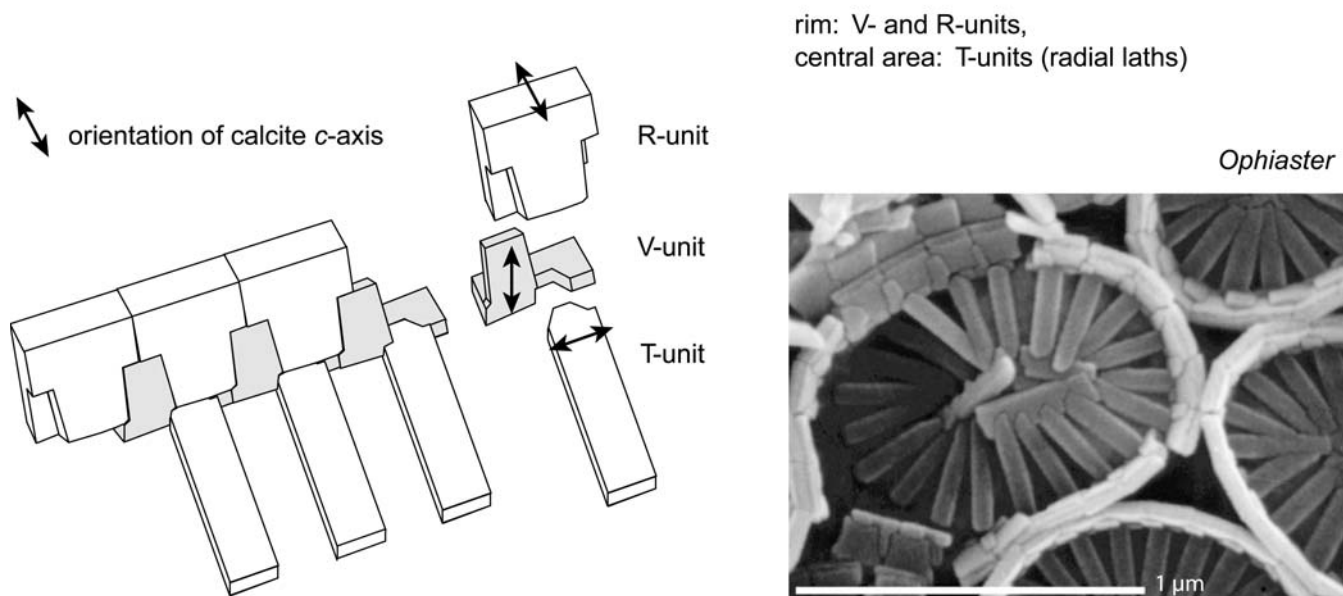
*Syracosphaera dilatata* Jordan et al. 1993, YOUNG et al. 2003 *partim*, p. 44, pl. 19, fig. 8 (non fig. 11).

**Diagnosis:** Coccosphera subglobosa ad obpyriformem, dithecata, habens dimorphos endothecales coccolithos. Omnes coccolithi sunt muralithi cum proximali clipeo angusto et distali oblique elato. Coccolithi exothecales protenti cum lateribus paene rectis et rotundatis extremis. Maiores sed fragiliores quam coccolithi comunes. Habent altum et tenuem murum augentem distaliter. Dimidium externum clipei distalis fert anulum tenuibus striis radialibus. Coccolithi comunes sunt late elliptici habentes clipeum medium parietis simile cristae. Clipeum distale fert duo concentricos anulos subtilibus striis in eorum distali superficie: interiorem striis crassis, exteriorem magis sed minoribus. Area centralis habet lamellas radialiter tendentes et structuram centram longitudinally prominentem elementis subverticalibus formatam. Circumflagelares coccolithi subcirculares ad ellipticales et ephippioidei. Ferentes clipeum, cuius paries media globulifera est, et robustam atque angularem spinam desitam in quattuor parvos nodos.

Coccosphere subspherical to obpyriform, dithecate, with dimorphic endothecal coccoliths. All coccoliths are muraliths with a narrow proximal flange and an obliquely raised distal flange. Exothecal coccoliths are elongate with flat sides and rounded ends. They are larger but more fragile than the body coccoliths. They have a high, thin wall that flares distally. The outer half of the distal flange bears a ring of fine radial ribs. Body coccoliths are broadly-elliptical, with a ridge-like mid-wall flange. The distal flange bears two concentric rings of short ribs on its distal surface: an inner ring of thick ribs and an outer ring of more and smaller ribs. The central area has radial laths and the central structure is a prominent longitudinal mound consisting of sub-vertical elements. Circum-flagellar coccoliths are subcircular to elliptical, and saddle-shaped. They bear a beaded mid-wall flange and a robust, angular, spine that ends in four small nodes.

**Holotype:** digital image 151705/TYPED (pl. 3, fig. 5), deposited at ICM (CSIC), Barcelona, Spain.

## SYRACOSPHAERALES STRUCTURE



TEXT-FIGURE 3

Syracosphaerales murolith ultrastructure; the rim is formed of V- and R-units, while additional T-units form the central area. The example shown is *Ophiaster*. From: Young et al. (2003).

**Type locality:** Western Mediterranean Sea (40°49'1"N 02°44'43"E), depth 60m, 26 Feb. 1999 (Cruise HIVERN-99, Station 25).

**Etymology:** Greek *didymos*, Latin *didymus* -a -um (adjective), twin, double, growing in pairs; referring to the two rings of nodules on the distal flange.

**Number of specimens studied:** 10.

**Distribution:** Red Sea, 0-5m; Mediterranean Sea, 25-70m; North Atlantic, 100m; South Atlantic, Southern Benguela system, 100m; southeastern Caribbean Sea.

**Description:** The dithecate coccosphere consists of up to  $\pm 37$  exothecal muroliths, and 34-58 body muroliths and 4-6 circum-flagellar muroliths in the endotheca (pl. 3, figs 1, 5). The exothecal coccoliths are very loosely attached to the coccosphere and, therefore, they are only rarely found.

The long-elliptical exothecal coccoliths are larger but more fragile than the body coccoliths. Their long sides are parallel or one side shows a slight constriction in distal view, while in proximal view many coccoliths show two constrictions (pl. 3, fig. 5). The distal flange bears only a single ring of fine ribs and lacks the inner ring of thicker ribs of the body coccoliths. The high wall seems to be single-layered (pl. 3, fig. 4).

The broadly-elliptical body coccoliths seem to have a double-layered wall: the inner layer of vertical wall elements expands in an oblique distal flange, while the outer layer is slightly curved outward, forming a ridge on the distal part of the wall that resembles a narrow mid-wall flange (pl. 3, figs 2, 6). The distal flange bears an inner ring of thick, more or less triangular, ribs and an outer ring of smaller short ribs, in almost

twice the number of the inner ribs. The central area has 20-30 radial laths and the central structure consists of sub-vertical elements (pl. 3, figs 2-3). The ornamentation of the body coccoliths may vary on one coccosphere: the inner ring of ribs on the distal flange may be less clearly developed (pl. 3, fig. 6) or may even be absent, as can be seen on pl. 3, fig. 1: the coccolith between two of the circum-flagellar coccoliths bears only a ring of small ribs on its distal surface.

The sub-circular to elliptical circum-flagellar coccoliths bear a ring of small teeth as a beaded mid-wall flange (pl. 3, figs. 2-3). The sides are slightly curved upward, resulting in a saddle-shaped form (pl. 3, fig. 3). The long, angular spine is conical and may have a constriction near its base (pl. 3, figs. 1, 3, 5-6).

**Dimensions:** coccosphere size, long axis 8-12µm; exothecal coccoliths, length 3.1-3.8µm; body coccoliths, length 2.1-3.1µm, width 1.7-1.8µm; circum-flagellar coccoliths, spine length 1.5-2.1µm.

**Taxonomic notes**

Two possible combination cells with coccoliths of *Syracosphaera didyma* sp. nov. and *Homozygosphaera arethusae* were described as a 'less well-established association' by Cros et al. (2000). Since further evidence in support of this association is needed, we prefer to describe the heterococcolithophore as a separate species.

*Syracosphaera didyma* sp. nov. belongs to the *dilatata*-subgroup of the *S. pulchra* group of Young et al. (2003). Species of this subgroup bear exothecal muroliths and their body coccoliths have three flanges of which the mid-wall flange is weakly developed, usually as a ring of bead-like nodes.

Specimens of the new species previously have been misidentified as *S. exigua*, a species with exothecal planoliths and endothecal coccoliths with a pattern of overlapping triangular elements on the distal flange (cf. Okada and McIntyre 1977; Young et al. 2003).

*Syracosphaera didyma* sp. nov. differs from *Syracosphaera dilatata* Jordan et al. 1993 (ex *Caneosphaera halldalii* f. *dilatata* Heimdal et Gaarder 1981), since their body coccoliths:

1) have a mid-wall ridge - *S. dilatata* coccoliths lack a mid-wall flange and, instead, show a slight ornamentation of short vertical ridges on the coccolith wall (Kleijne 1993, p. 238, pl. 4, fig. 10);

2) have two cycles of ribs on the prominent distal flange - *S. dilatata* coccoliths have a narrow distal flange with only one cycle of ribs (Heimdal and Gaarder 1981, p. 44, pl. 2, fig. 9; Young et al. 2003, pl. 19, fig. 11).

***Syracosphaera hastata* Kleijne et Cros sp. nov.**

Plate 4, figures 1-5

*Syracosphaera* sp. II cf. *S. epigrosa*, KLEIJNE 1993, p. 237, pl. 4, fig. 3.

*Syracosphaera* sp. II cf. *S. epigrosa* of Kleijne 1993, CROS 2000 p. 42, pl. 5, fig. 4. – YOUNG et al. 2003, p. 46, pl. 20, figs. 10-12.

*Syracosphaera* sp. 2, CROS 2002, p. 56-57, pl. 30, figs. 1-2.

*Syracosphaera* sp. 'slender', CROS and FORTUÑO 2002, pp. 31-32, fig. 33A, B.

**Diagnosis:** Coccospaera de subglobosa ad conicam, partim dithecata, cum coccolithis endothecalibus trimorphis; coccolithi circumflagellares et antapicales ferunt longam spinam. Coccolithi exothecales sunt undati planolithi apicalem aream tegentes qui constant ex depressione centrali, conica, cincta leve clipeo cum duobus extensionibus obliquis et magnis sub variis formis: altera paullulum acuta, altera plicata. Coccolithi communes sunt murolithi habentes murum tenuem et augmentem atque clipeum distalem angustum et levem. Area centralis sine stuctura centrali distincta. Coccolithi

circumflagellares sunt murolithi habentes murum rectum clipeum distalem angustum, ferentes spinam centram longam cum calyce constanti ex tribus aut quattuor elementis elongatis dilatantibus. Antapicalis poli murolithi ferunt murum altum et augmentem qui pergit in clipeum distalem ferentes longam spinam cum calyce constanti ex tribus longis ramificationibus.

Coccosphere subspherical to conical, partly dithecate, with trimorphic endothecal coccoliths; the circumflagellar coccoliths and antapical coccoliths bear a long spine. Exothecal coccoliths are undulating planoliths that cover the apical area. They consist of a central, conical depression, surrounded by a smooth flange with two large, oblique extension of different shape: one somewhat pointed and one folded. Body coccoliths are muroliths with a low, flaring wall and a narrow, smooth distal flange; their central area has no distinct central structure. Circum-flagellar coccoliths are muroliths with a straight wall and a narrow distal flange; they bear a long central spine with a calyx consisting of three or four elongate, flaring elements. Antapical pole muroliths bear a high, widening wall that continues into the distal flange; they bear a long spine with a calyx that consists of three long ramifications.

**Holotype:** Digital image 145608 (pl. 4, fig. 3), deposited at ICM (CSIC), Barcelona, Spain.

**Type locality:** Mediterranean Sea, off Barcelona (41°17'N 2°10'E), depth 0-5m, 16 July 1998 (Workshop Picasso, Station T4).

**Etymology:** Latin *hastatus* -a -um (adjective), spear-shaped, armed with a spear; referring to the long, slender spines of the apical and antapical coccoliths.

**Number of specimens studied:** 8.

**Distribution:** Northeastern Indian Ocean, 0-5m; Gulf of Aden, 0-5m; Red Sea, 0-5m; Mediterranean Sea, 0-60m; North Atlantic, 0-25 m.

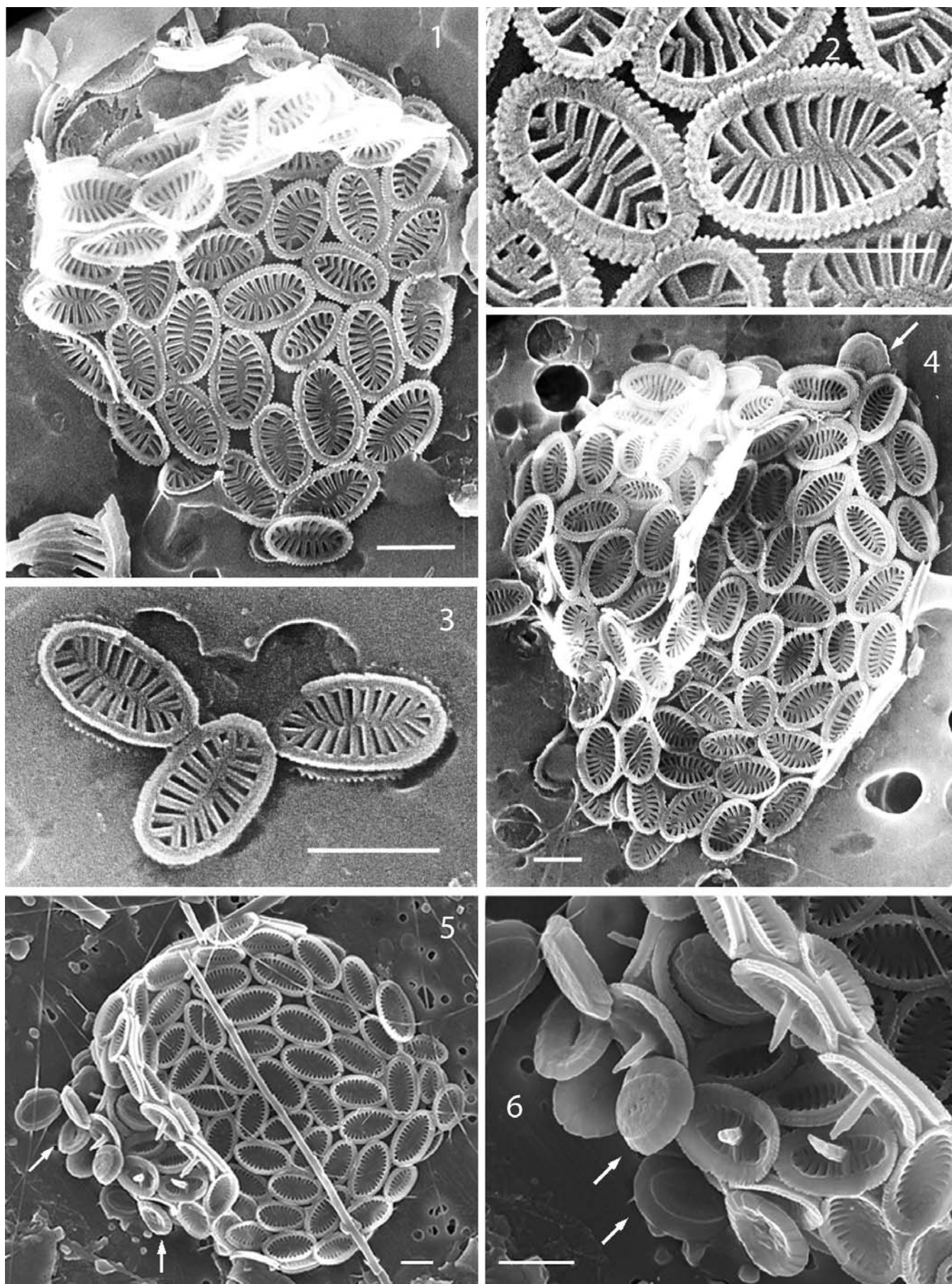
## PLATE 1

*Syracosphaera andruleitii* Kleijne et Cros sp. nov.

Scale bars = 1 µm.

Figure 1 was published previously in Kleijne (1993), as *Syracosphaera* sp. type I.

- 1 Collapsed monothecate coccosphere showing variation in size of body coccoliths and width of distal flange, concave shape of coccoliths, and circum-flagellar coccolith with slightly higher wall and pointed spine; APNAP-I/T86-8R/50m.
- 2 Detailed view of fig. 1; body coccoliths in distal view, showing extensively flaring wall, distal flange with incised periphery, radial laths and absence of central structure.
- 3 Detached coccoliths of coccosphere in fig. 1; muroliths in proximal view, showing proximal flange.
- 4 Holotype; collapsed monothecate coccosphere showing apical pole with circum-flagellar coccoliths, and one exothecal planolith in proximal view (arrow); APNAP-I/T86-8R/50m.
- 5 Collapsed coccosphere with exothecal planoliths occurring near the circumflagellar coccoliths; concave planoliths with a longitudinal cleft on the distal side (arrows); GeoB10049-2/65m.
- 6 Detailed view of fig. 6; circum-flagellar coccoliths with wider flange and spine, and planoliths in proximal view showing clearly defined closed central part (arrows).



**Description:** The circum-flagellar area is covered by 4-10 complexly folded exothecal coccoliths (pl. 4, fig. 4). Three types of endothecal muroliths occur: 1)  $\pm$  25-56 body coccoliths; 2)  $\pm$  3-6 circum-flagellar coccoliths with a slender spine and a regular, brush-shaped distal end; and 3) 1 or 2 antapical coccoliths with long spine and slender ramifications of irregular size and shape (pl. 4, figs. 2, 5; see also Young et al. 2003, pl. 20, fig. 10).

The asymmetrical exothecal coccoliths have a smooth surface. Their central conical depression is surrounded by a flange of unequal width and two oblique extensions. One extension has a wide base and pointed tip; this wing-like extension is placed in apical direction (pl. 4, fig. 4). The other, antapically directed extension is folded and has a straight upper rim (pl. 4, figs. 3-4).

The body coccoliths have an irregular elliptical outline and are variable in size (pl. 4, figs. 1-3; see also Kleijne 1993, p. 237, pl. 4, fig. 3). Their central area consists of 14-28 radial cycle laths that meet in the centre. The lack of a central structure or any kind of axial ridge is very characteristic (pl. 4, figs. 1-2).

The 3-8 circum-flagellar coccoliths have a vertical wall that shows partly ornamented sutural ridges in lateral view. The distal flange, which is present as a very narrow lateral ridge, is similar in width or narrower than the proximal flange. Their long spine ends in a calyx of 3-4 elongate, flaring elements (pl. 4, fig. 2).

The antapical pole of the coccosphere bears 1 or 2 coccoliths with a high, flaring wall and a long spine that ends in 3 long, usually slender ramifications (pl. 4, figs. 1, 3, 5; Young et al.

2003, pl. 20, fig. 10). The proximal flange is very narrow (pl. 4, figs. 4-5).

**Dimensions:** coccosphere,  $\pm$  6-10  $\mu$ m along the long axis; exothecal coccoliths, length 2.3-3.1  $\mu$ m; body coccoliths, length 1.3-2.2  $\mu$ m, width 0.8-1.4  $\mu$ m; circum-flagellar coccoliths, spine length 1.8-2.3  $\mu$ m; antapical coccoliths, spine length  $\pm$  2-3  $\mu$ m.

#### Taxonomic notes

*Syracosphaera hastata* sp. nov. is placed in the *S. molischii* group and *molischii*-subgroup of Young et al. (2003): species bearing placolith-like body coccoliths and undulated exothecal coccoliths. Other species bearing complex undulating exothecal coccoliths are *Syracosphaera ossa*, *S. molischii* and *S. marginaporata*. Like *S. hastata* sp. nov., these species have narrower flanges on the circum-flagellar coccoliths than on the body coccoliths; see e.g. Cros and Fortuño (2002, figs. 30-32, fig. 33A-B). Of these species, *S. molischii* and *S. ossa* usually bear an antapical coccolith with a short central spine, equivalent to the spine-bearing antapical coccoliths of *S. hastata* sp. nov. (see Cros 2000, pl. 5, fig. 1).

#### *Syracosphaera hirsuta* Kleijne et Cros sp. nov.

Plate 5, figures 1-6

*Syracosphaera epigrosa* auct. non Okada et McIntyre 1977. – Heimdal and GAARDER 1981, p. 60, pl. 8, fig. 38-39. – GIRAUDÉAU et al. 1993, pl. I, figs. 11-12. – WINTER and SIESSER 1994, fig. 109.

*Syracosphaera* sp. I cf. *S. epigrosa*, KLEIJNE 1993, p. 237, pl. 4, fig. 2. *Syracosphaera epigrosa* auct. non Okada et McIntyre 1977 var. 1, GIRAUDÉAU and BAILEY 1995, pl. IV, fig. 1.

*Syracosphaera* sp. I cf. *S. epigrosa* of Kleijne 1993. – CROS 2000, p. 42, pl. 5, figs. 5-6.

*Syracosphaera* sp. 3, CROS 2002, p. 57, pl. 30, figs. 3-6.

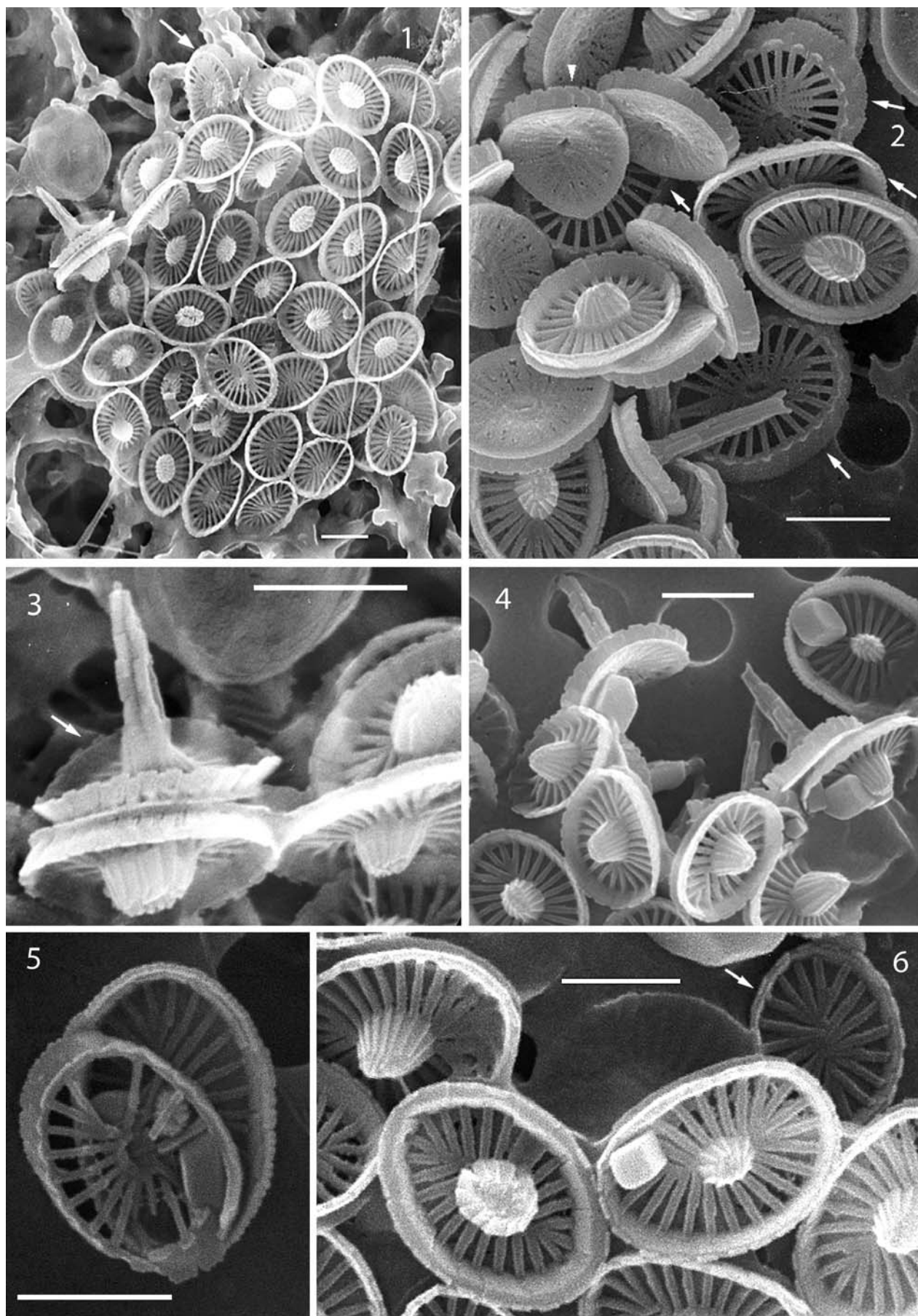
## PLATE 2

*Syracosphaera castellata* Kleijne et Cros sp. nov.

Scale bars = 1  $\mu$ m.

Figure 1 was published previously in Kleijne (1993) and figs. 2, 4 and 6 in Cros (2002) and Cros and Fortuño (2002), as *Syracosphaera* sp. type G.

- 1 Holotype; collapsed coccosphere showing varimorphic body coccoliths, one circum-flagellar coccolith with robust spine (middle left) and two exothecal muroliths in proximal view (arrows); APNAP-I/T86-19D/0-5m.
- 2 Body coccoliths in distal, proximal and lateral views, showing central structure, central opening on proximal side, polygonal wall elements with anti-clockwise imbrication (arrowhead), the castellated upper margin, one circum-flagellar coccolith with spine ending in two horns, and four exothecal muroliths with beaded proximal flange and central opening on proximal side (arrows); MESO-96/A5/70m.
- 3 Detailed view of fig. 1; body coccoliths with central structure of large sub-vertical elements, and a circum-flagellar coccolith in lateral view (arrow).
- 4 Large exothecal murolith with incised upper rim (upper right), circum-flagellar coccoliths, and body coccoliths with large central structure; FRONTS-96/013/75m.
- 5 Exothecal murolith in proximal view, showing beaded proximal flange, on top of exothecal murolith in distal view, showing finely incised upper margin of wall; FRONTS-96/013/75m.
- 6 Body coccoliths showing radial laths and variation in size of central structure, one antapical coccolith without central structure (arrow) and one coccolith with thickened inner wall; FRONTS-96/013/75m.



*Syracosphaera* sp. 'laths with rod protrusions', CROS and FORTUÑO 2002, pp. 31-32, fig. 33C, D.

*Syracosphaera borealis* auct. non Okada et McIntyre 1977 type 2. – YOUNG et al. 2003, p. 48, pl. 21, figs. 10-12.

**Diagnosis:** *Coccosphaera* subglobosa, dithecata, cum coccolithis endothecalibus monomorphis et exothecalibus simplicibus undatis, ambo fere aequales magnitudine. Coccolithi exothecales sunt structurae longae ephippioideae cum duabus rimis parenthesisformibus, una in quoque extremo ellipticalis centri. Coccolithi communes sunt murolithi ellipsoidales cum ambitu irregulari quorum parvus murus flectit et pergit in angustum clipeum. Area centralis constat ex elementis lamellaribus radialiter tendentibus quae ferunt nodos magnitudine et specimine varios.

Coccosphere subspherical, dithecate, with monomorphic endothecal coccoliths and simple undulating exothecal coccoliths. Both coccolith types are of approximate equal size. Exothecal coccoliths are saddle-shaped elongate structures, with two parenthesis-shaped slits, one at each end of the elliptical centre. Body coccoliths are elliptical muroliths with an irregular outline. Their low wall bends and continues into a narrow flange. The central area consists of radial laths that bear nodes of variable height and in a variable pattern.

**Holotype:** Negative152001/EPI2 (pl. 5, fig. 3), deposited at ICM (CSIC), Barcelona, Spain.

**Type locality:** western Mediterranean Sea (41°33'N 2°25'E), depth 0-5m, 26 Feb. 1999 (Cruise HIVERN, Station 99-30).

**Etymology:** Latin *hirsutus* -a -um (adjective) bristly, prickly; referring to the bristly central area of the body coccoliths.

**Number of specimens studied:** 13.

**Distribution:** western Mediterranean Sea, 0-60; North Atlantic, 0-5m; South Atlantic, off Namibia, 5m.

**Description:** The coccosphere consists of  $\pm$  38-70 monomorphic endothecal muroliths and up to 10 saddle-shaped exothecal planoliths (pl. 5, fig. 3). The planoliths usually occur in a low number, on one side of the coccosphere. They are very lightly attached to the coccosphere and, therefore, easily lost. Circum-flagellar coccoliths have not been found.

The elongate, undulated exothecal coccoliths are saddle-shaped. Their solid and almost smooth centre bears parenthesis-shaped slits on both ends, while it is surrounded by a narrow, distally bent rim of squarish elements. This results in a distally concave structure with an irregular margin (pl. 5, figs. 2, 4).

The narrowly to broadly-elliptical body coccoliths are irregular in outline (pl. 5, figs. 2-3). The distal flange varies in width and in shape: from nearly horizontal to obliquely raised and even slightly convex (pl. 5, figs. 1, 2, 6). The central area consists of 15-26 radial laths, that interlock in the centre (pl. 5, fig. 5). A central structure may be present as nodes that form a low and incomplete elongate ridge (pl. 5, figs. 2-3, 6). The laths of the radial cycle bear nodes, usually placed in a ring halfway the laths; sometimes they are less ordered. The nodes vary from small nodes to vertical rods between coccospheres as well as on individual coccoliths on a coccosphere (pl. 5, figs 2-3, 6).

**Dimensions:** coccosphere, diameter  $\pm$  5.5-9.0 $\mu$ m; exothecal coccoliths, length 1.7-2.4 $\mu$ m; body coccoliths, length 1.2-2.6 $\mu$ m, width 0.8-1.5 $\mu$ m.

#### Taxonomic notes

*Syracosphaera hirsuta* sp. nov. belongs to the *S. molischii* group of Young et al. (2003): species bearing body muroliths with prominent proximal and distal flanges. It is placed in the *borealis*-subgroup: species with elliptical exothecal coccoliths and without circum-flagellar coccoliths.

Cros (2002) distinguished two forms in the taxon that is presently introduced as the new species *S. hirsuta*. She described 'irregular type' specimens that bear coccoliths with irregularly

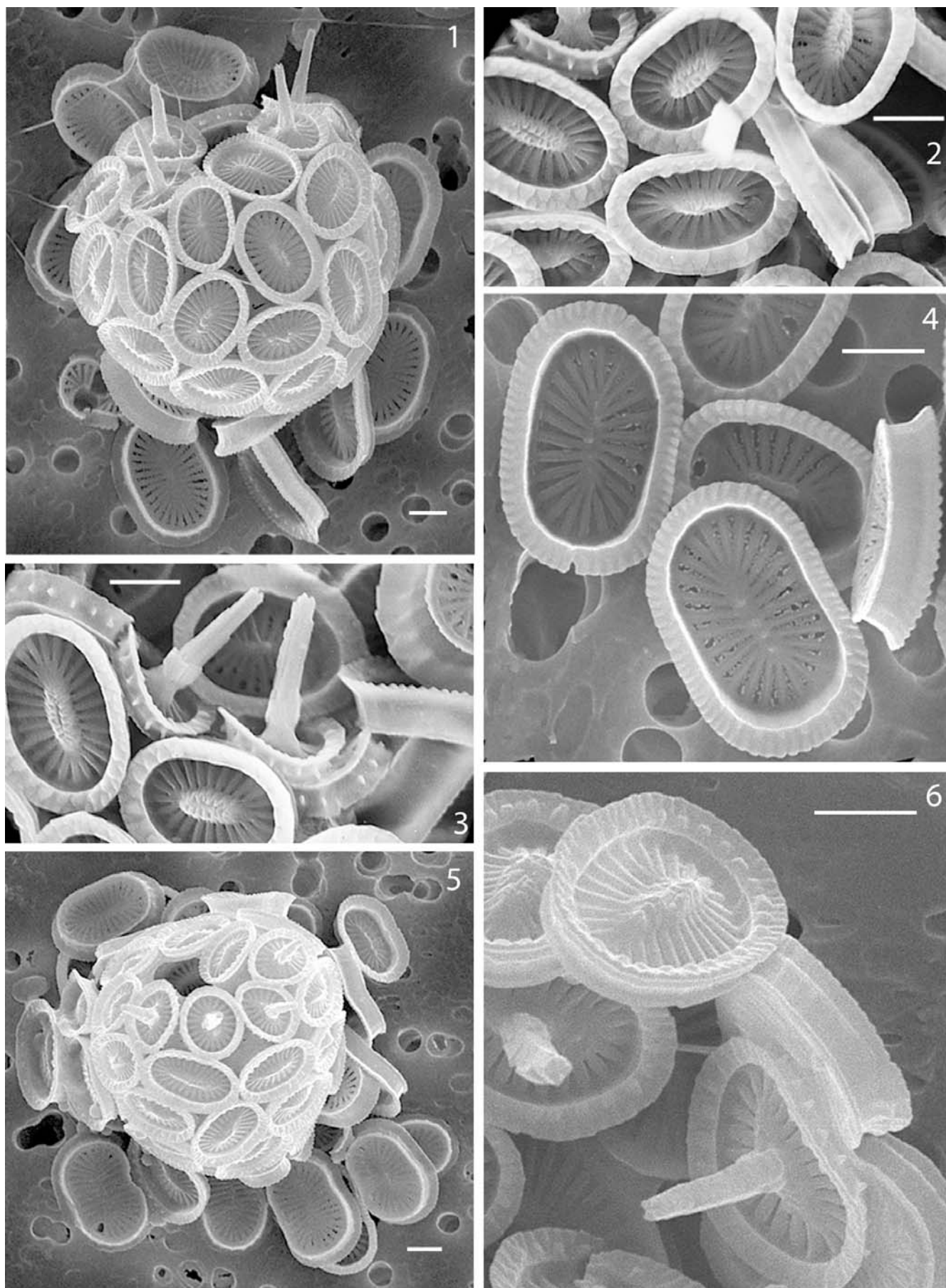
### PLATE 3

*Syracosphaera didyma* Kleijne et Cros sp. nov.

Scale bars = 1  $\mu$ m.

Figure 2 has been published previously in Kleijne (1993) and fig. 5 in Cros (2002) and Cros and Fortuño (2002), as *Syracosphaera* sp. type D.

- 1 Collapsed dithecate coccosphere showing exothecal and dimorphic endothecal muroliths; FANS-2/M07/25m.
- 2 Coccoliths in distal and lateral view, showing central structure with sub-vertical elements and ridge-like midwall flange; APNAP-I/T86-14R/100m.
- 3 Same specimen as fig. 2; body coccoliths in distal view showing variation in shield ornamentation, circum-flagellar coccoliths in lateral view showing beaded mid-wall flange and long, angular spine with constriction near its base, and exothecal muroliths with thin wall (right side of image).
- 4 Exothecal muroliths; MESO-96/I-4/70m.
- 5 Holotype; coccosphere showing variation in size and shape of the three coccolith types; most exothecal muroliths have been detached; HIVERN-99/25/60m.
- 6 Body coccoliths with mid-wall flange and two circum-flagellar coccoliths with beaded midwall flange, showing radial cycle elements and central structure; HIVERN-99/55/60m.



arranged rods (pl. 5, fig. 1; see also Heimdal and Gaarder 1981, pl. 8, fig. 39; Giraudeau et al. 1993, pl. 1, figs. 11-12; Cros 2002, pl. 30, figs. 3, 5;). The 'regular type' specimens, on the other hand, have coccoliths with regularly placed perpendicular rods (pl. 5, figs. 2-3, 6; see also Heimdal and Gaarder 1981, pl. 8, fig. 38; Cros 2002, pl. 30, figs. 4, 6; Cros and Fortuño 2002, fig. 33C-D; Young et al. 2003, pl. 21, fig. 12). Coccoliths with a more regular rod distribution are typically smaller and more irregular in outline than the ones with irregularly arranged rods.

The coccolith morphology of *Syracosphaera hirsuta* sp. nov. appears to be highly variable, since a third form has also been found: coccospheres bearing coccoliths with very small central area nodes (pl. 5, fig. 5; see also Kleijne 1993, p. 237, pl. 4, fig. 2; Young et al. 2003, pl. 21, figs. 10-11).

Coccospheres of the 'irregular type' were included in *Syracosphaera borealis* by Young et al. (2003), as *S. borealis* type 2. However, although both *S. hirsuta* sp. nov. and *S. borealis* have saddle-shaped exothecal coccoliths and lack circum-flagellar coccoliths, we now think that these taxa are different enough to separate them as distinct species. The folded exothecal planoliths of *S. borealis* have a wider rim and stronger curvature than those of *S. hirsuta* sp. nov., see e.g. Winter and Siesser (1994, fig. 106, by C. Samtleben) and their body coccoliths are notably different. In *Syracosphaera borealis* muroliths the vertical wall bends sharply into the wide distal flange, that has prominent sutural ridges, and its central area bears an elongate mound of short nodes. In *S. hirsuta* sp. nov., on the other hand, the narrower flange bears small sutural ridges on the inner side of the wall and on the more gradual bending from wall to flange, while the central area bears an elliptical cycle of nodes, or even rods, on the radial laths. Moreover, the two species are biogeographically separated, with *S. borealis* occurring in subarctic and subantarctic regions (south of Iceland, Bergen Fjord and Antarctic; J. Young, pers. comm.), whilst *S. hirsuta* sp. nov. appears to be a temperate species.

Another species with nodes or rods on the central area is *Syracosphaera epigrosa*, but that species has a wider and flat distal flange, while no exothecal coccoliths have been described yet (see Okada and McIntyre 1977, pl. 7, figs. 5-6; Kleijne 1993, p. 237, pl. 4, fig. 1; Young et al. 2003, p. 48, pl. 21, fig. 6).

***Syracosphaera leptolepis* Kleijne et Cros sp. nov.**

Plate 6, figures 1-6

?*Syracolithus variabilis* (Halldal et Markali 1955). – BORSETTI and CATI 1972, pl. 43, fig. 2.

*Syracosphaera nodosa* Kamptner. – Okada and MCINTYRE 1977 *partim*, p. 25, pl. 9, figs. 1, 3, *non* fig. 2.

?*Syracosphaera variabilis* (Halldal et Markali) Borsetti et Cati. – Winter et al. 1979 *partim*, pl. 4, fig. 7, *non* fig. 8.

*Syracosphaera* sp. type L, KLEIJNE 1993, p. 245, pl. 5, figs. 1-2.

*Syracosphaera nana* auct. *non* Kamptner 1941. – WINTER and SIESSER 1994, fig. 116.

*Syracosphaera* sp. type L of Kleijne 1993. – Cros 2000, p. 42, pl. 2, figs. 5, 7. – CROS 2002, p. 55-56, pl. 29, figs. 5-6. – CROS and FORTUÑO 2002, p. 38, figs. 43C, D. – YOUNG et al. 2003, p. 36, pl. 15, figs. 7-9.

**Diagnosis:** Coccosphaera de globosa ad subglobosam, dithecata, cum murolithis endothealibus monomorphis. Coccolithi exothecales sunt planolithi circulares plani, minores quam coccolithi endothecales. Eorum pars centralis constat ex elementis obliquis dextorsum et circumdatur margine elementorum lamellarum. Coccolithi communes sunt murolithi late ellipsoideales quorum magnitudo varia est. Habent murum tenuem distaliter latum et aream centralem leviter convexam cum structura centrali humili. Extensiones centripetae ex muri elementis efficiunt clipeum proximale interiore circum aream centralem.

Coccosphere spherical to subspherical, dithecate, with monomorphic endotheal muroliths. Exothecal coccoliths are delicate, flat, circular planoliths, that are smaller than the endotheal coccoliths. Their central part consisting of dextrally oblique elements and is surrounded by a rim of plate-like elements. Body coccoliths are broadly-elliptical muroliths of variable size. They have a distally flaring, thin wall and a slightly

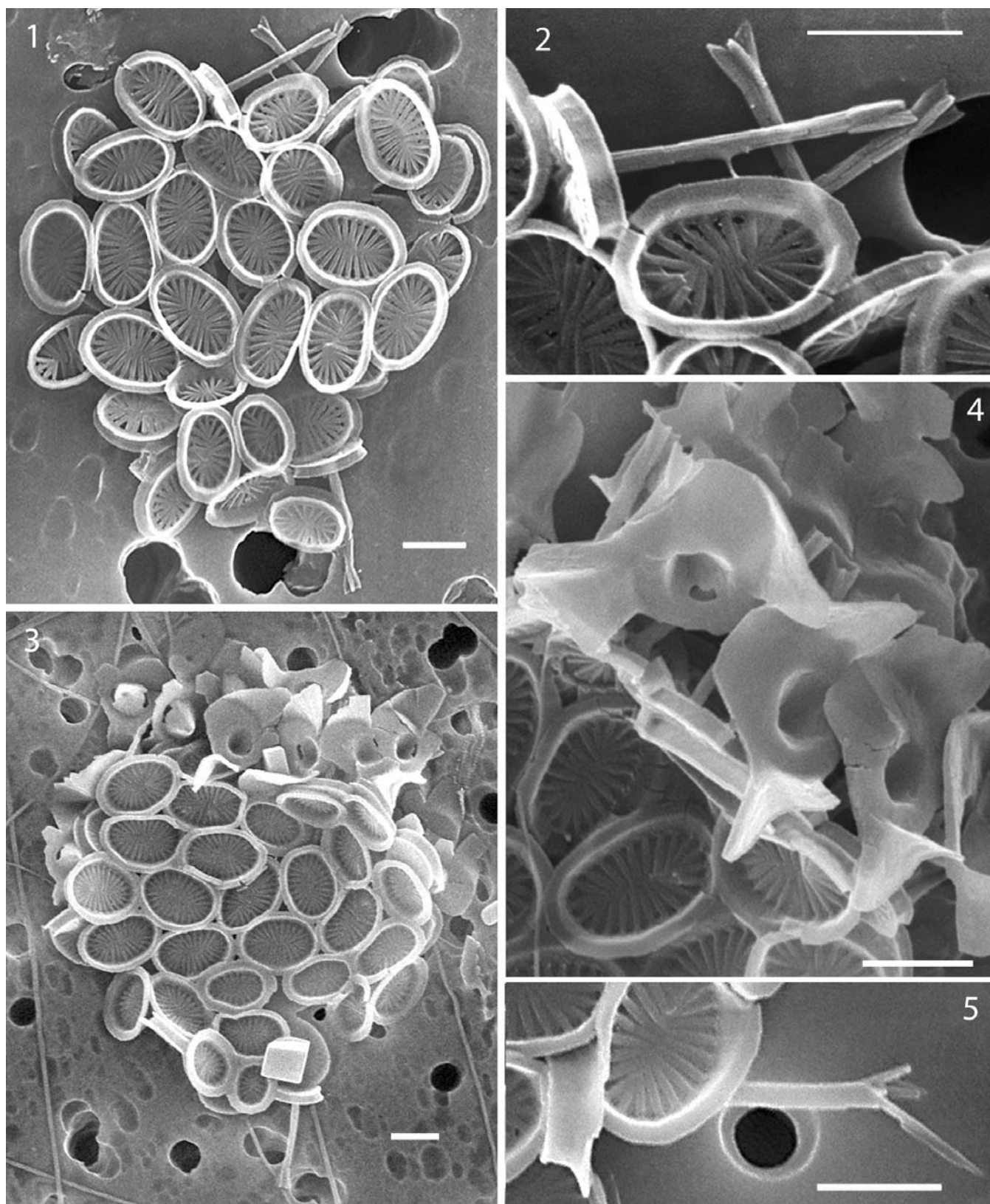
**PLATE 4**

*Syracosphaera hastata* Kleijne et Cros sp. nov.

Scale bars = 1µm.

Figure 1 was published previously in Kleijne (1993), as *Syracosphaera* sp. II cf. *S. epigrosa*, and fig. 4 in Cros (2002), as *Syracosphaera* sp. 2 'slender', and Cros and Fortuño (2002), as *Syracosphaera* sp. 'slender'.

- 1 Collapsed coccosphere showing body coccoliths, three circum-flagellar coccoliths (top) and one antapical coccolith with long spine (bottom); Snellius-II/Gx-188/0-5m (western Mediterranean Sea).
- 2 Detailed view of fig. 1; circum-flagellar coccoliths with straight wall, small distal flange and long spine ending in three triangular elements.
- 3 Holotype; coccosphere with undulating exothecal coccoliths around apical pole, and two antapical pole coccoliths; Workshop Picasso T4/0-5m.
- 4 Circum-flagellar coccoliths covered by complexly folded exothecal coccoliths that have two wing-like extensions of different shape, and central conical depression; FANS-1/123/40m.
- 5 Antapical coccolith in lateral view, showing the flaring wall and the long spine with ramifications; FRONTS-96/013/60m.



vaulted central area with a low central structure. Centripetal extensions from the wall elements form an inner-proximal flange around the central area.

**Holotype:** Negative A77/3 (pl. 6, fig. 1) deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

**Type locality:** North Atlantic (50°19'3"N 27°03'6"W), depth 0-5m, 21 Aug. 1986 (Cruise APNAP-I, Station T86-19C).

**Etymology:** Greek *lepto-*, thin, slender; Greek *lepto-*, scaly; Greek *leptolepis*, with fine scales; referring to the thin exothecal coccoliths.

**Number of specimens studied:** 8.

**Distribution:** Pacific; Northeastern Indian Ocean, 0-5m; eastern Arabian Sea, 0-5m; (?Gulf of Elat, northern Red Sea); Mediterranean Sea, 0-30m, including Alboran Sea (10 coccospheres; M. Geisen and J. Young, pers. comm.); North Atlantic, 0-5m.

**Description:** The dithecate coccosphere consists of 42-68 delicate disc-like exothecal planoliths and  $\pm$  35-68 monomorphic endothecal muroliths (pl. 6, figs. 1, 4). Differentiated circum-flagellar coccoliths do not occur.

The exothecal planoliths are delicate, circular discs that are very loosely attached to the coccospheres and, thus, easily lost. They are smaller than the endothecal muroliths (pl. 6, figs. 1, 4, 6). Their centre consists of elongate elements with dextral obliquity (pl. 6, fig. 6; Young et al. pl. 15, fig.9); it is surrounded by a narrow medial cycle of squarish elements - equivalent to radial laths - and a rim of wider elements (pl. 6, figs. 2, 6). The individual parts may be difficult to distinguish (pl. 6, fig. 4).

The broadly-elliptical muroliths have a thin, slightly flaring but straight wall, with a smooth outer surface and upper margin (pl. 6, figs. 2, 6). They are highly variable in size (pl. 6, fig. 5). The central area consists of 19-31 laths with narrow openings in between, and a broad central structure of overlapping elements, in the form of a low mound (pl. 6, fig. 3). Centripetal extensions from the wall elements alternate with the outer ends of the radial laths and form a flat, smooth inner-proximal flange around the central area (pl. 6, fig. 3; see also Young et al. 2003, pl. 15, fig. 8). The radial laths are of irregular width, see pl. 6, fig. 3 and Young et al. (2003, pl. 15, fig. 8). In fact these spokes consist of two elements, comparable to the bipartite radial laths in *Syracosphaera anthos*, as described and shown by Young et al. (2003, pl. 16, fig. 4).

**Dimensions:** coccosphere,  $\pm$  6-9 $\mu$ m along the long axis; exothecal coccoliths, diameter 1.5-2.0 $\mu$ m; body coccoliths, length 1.3-2.5 $\mu$ m, width 1.1-1.5 $\mu$ m.

#### Taxonomic notes

*Syracosphaera leptolepis* sp. nov. belongs to the *S. nodosa* group of Young et al. (2003), having exothecal planoliths and endothecal muroliths with only a proximal flange. The species is placed in the new *leptolepis*-subgroup, because of its monomorphic endotheca and its planoliths with a central part that consists of dextrally oblique elements. A similar planolith type is found in *Syracosphaera nana*, another species of the *S. nodosa* group and placed in a separate subgroup because of its dimorphic endotheca.

Endothecal muroliths of *S. leptolepis* sp. nov. have been shown previously as *S. nodosa* by Okada and McIntyre (1977, pl. 9, figs. 1, 3; the planoliths in their fig. 2 do represent exothecal coccoliths of *S. nodosa*). The new species differs from *S. nodosa* in having muroliths with a smooth wall, instead of a wall with prominent vertical ribs, while its central structure is broadly-, instead of narrowly-elliptical. Both species have cir-

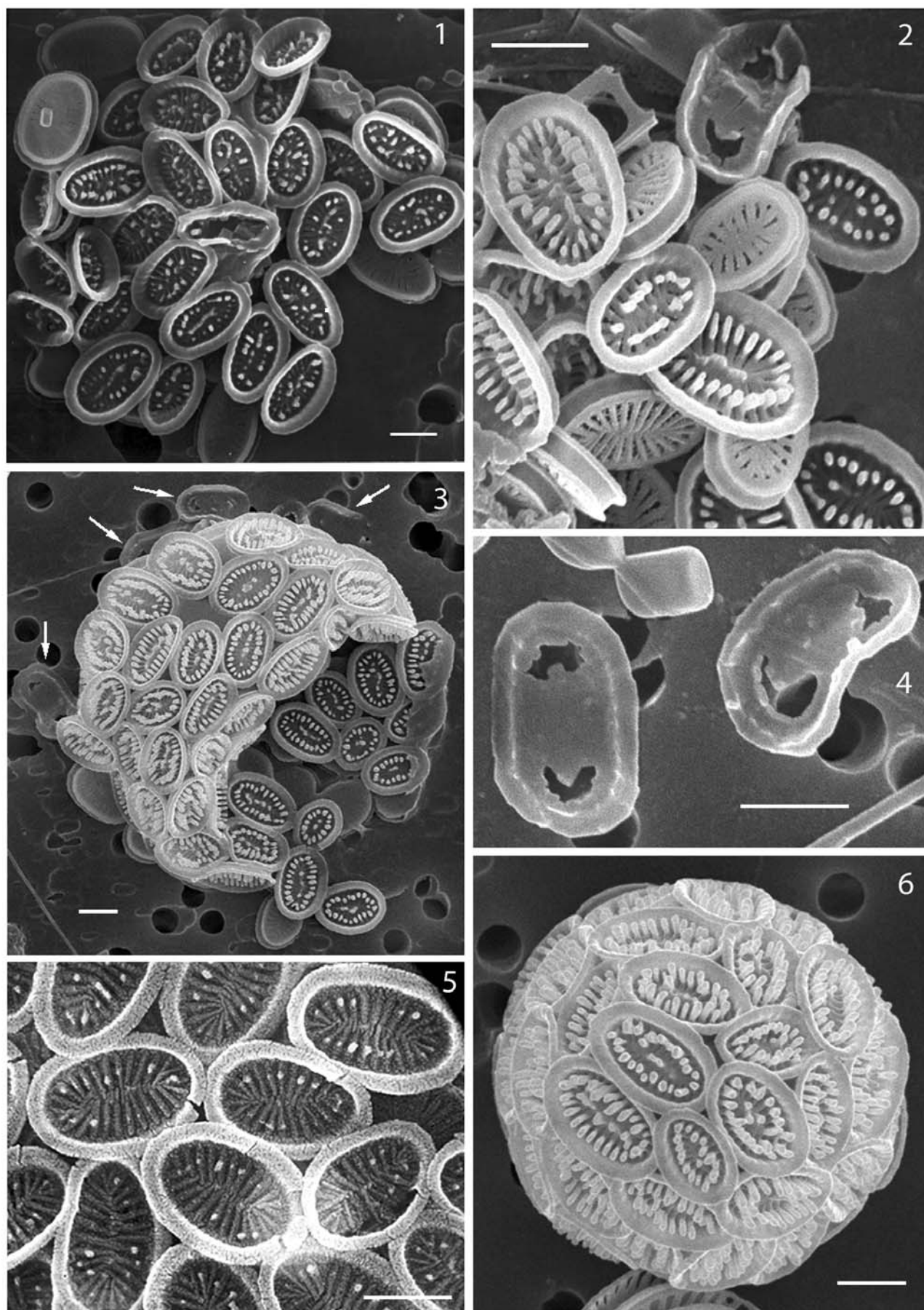
## PLATE 5

*Syracosphaera hirsuta* Kleijne & Cros sp. nov.

Scale bars = 1 $\mu$ m.

Figure 2 was published previously in Cros (2002), as *Syracosphaera* sp. 3 'rods on the laths', and in Cros and Fortuño (2002), as *Syracosphaera* sp. 'laths with rod protrusions', and fig. 5 in Kleijne (1993), as *Syracosphaera* sp. I cf. *S. epigrosa*.

- 1 Collapsed 'irregular type' coccosphere showing body coccoliths with relatively wide and obliquely raised distal flange and irregularly arranged rods on radial laths; FRONTS-95/18P/5m.
- 2 Body coccoliths of 'regular type' in distal, proximal and lateral view, showing radial laths with regularly arranged rods, variation in width of distal flange, and one exothecal coccolith in distal view (upper right); Station FANS-1/123/60m.
- 3 Holotype; partly collapsed coccosphere of 'regular type' showing monomorphic body coccoliths and detached exothecal coccoliths (arrows); HIVERN-99/30/0-5m.
- 4 Saddle-shaped exothecal coccoliths in proximal view (left) and in distal and side view (right) with two parenthesis-shaped openings; HIVERN-99/19/0-5m.
- 5 Body coccoliths of 'small type' showing radial cycle laths with small nodes, and central structure that is merely formed by interlocking laths; Snellius-II/Gx-196/0-5m (eastern North Atlantic).
- 6 Coccosphere consisting of body coccoliths of the 'regular type' with large spinous protrusions on the radial laths; HIVERN-99/19/0-5m.



cular planoliths, but these are differently constructed: the larger and thicker planoliths of *S. nodosa* have two large, plate-like elements in the centre, separated from the rim by a cycle of sinistrally oblique laths. Moreover, *S. nodosa* bears well differentiated circum-flagellar coccoliths with a prominent spine, while the endotheca of *S. leptolepis* sp. nov. is monomorphic.

Within *S. leptolepis* sp. nov. we can distinguish a somewhat deviating form with larger, more solid, exothecal coccoliths, and muroliths with a higher wall, fewer radial elements and a somewhat wider inner-proximal flange around the central area. Examples are the monothecate, monomorphic specimens shown by Borsetti and Cati (1972, pl. 43, fig. 2) as *Syracolithus variabilis* and Winter et al. (1979, pl. 4, fig. 7) as *Syracosphaera variabilis*; both names are junior synonyms of *Syracosphaera nodosa* (Kleijne 1993). Since the two very closely related forms within *S. leptolepis* sp. nov. are difficult to separate, we prefer to include them in the same species until more specimens have been recorded.

***Syracosphaera operculata* Kleijne et Cros sp. nov.**

Plate 7, figures 1-4

*Syracosphaera nana* auct. non (Kamptner 1941), OKADA and MCINTYRE 1977 *partim*, pp. 24-25, pl. 8, fig. 9, non figs. 7-8.

Unidentified sp. 2, REID 1980, p. 172, pl. 9, figs. 8-9.

*Syracosphaera* sp., CROS 2000, pl. 1, figs. 5-6.

*Syracosphaera* sp. 6, CROS 2002, p. 59, pl. 32, figs. 1-4.

*Syracosphaera* sp. 'with stratified coccoliths', CROS and FORTUÑO 2002, pp. 34-35, figs. 38C-D.

**Diagnosis:** Coccosphaera dithecata cum coccolithis endothealibus dimorphis. Coccolithi exothecales sunt subcirculares, planolithi magni dense stratifixi sine orificiis. Habent superficiem distalem gradatam, convexam et proximalem levem. Coccolithi communes sunt murolithi late elliptici et habent murum humilem et crassum, augentem, bistratum in parte proximali. Area centralis formata exiguis elementis lamellaribus radialiter tendentibus cum orificiis triangulis in medio et structura centrali lata et leviter convexa. Murolithi circumflagelares habent murum angustum et altum, augentem leviter et spinam brevem et rotundam in extremo.

Coccosphere dithecate, with dimorphic endotheal coccoliths. Exothecal coccoliths are subcircular, large thickly-stratified planoliths without openings. They have a stepped, convex distal surface and a smooth proximal surface. Body coccoliths are broadly-elliptical muroliths with a low and thick, flaring wall that is double-layered in the proximal part; the central area has short radial laths with triangular openings in between, and a broad and slightly convex central structure. Circum-flagellar muroliths have a thin and high, slightly flaring wall and a short spine with a rounded end.

**Holotype:** Negative 143707, (pl. 7, fig. 3), deposited at ICM (CSIC), Barcelona.

**Type locality:** western Mediterranean Sea (41°02'N 3°49'E), depth 70m, date 20 June 1996 (Cruise MESO-96, Station D8).

**Etymology:** Latin *operculatus* -a -um (adjective), operculate or operculated; referring to the shape of the exothecal coccoliths that reminds of a gastropod operculum.

**Number of specimens studied:** 3; plus 1 in Okada and McIntyre (1977) and 1 in Reid (1980).

**Distribution:** Pacific; Western Mediterranean Sea, 70m; Equatorial Atlantic (80m, A. Kleijne, unpubl. res.).

**Description:** The dithecate coccosphere is probably sub-spherical (pl. 7, fig. 1). It consists of  $\pm$  40-44 dimorphic endotheal muroliths and up to  $\pm$  34 more or less subcircular, solid exothecal planoliths with a highly asymmetrical rim (pl. 7, figs. 1, 3). The planoliths are considerably larger than the endotheal coccoliths and may cover the entire coccosphere (Okada and McIntyre 1977, pl. 8, fig. 9).

In proximal view the planoliths show a smooth surface with two distinct parts: the sub-circular central area and the surrounding rim of variable width (pl. 7, fig. 4). The distal side shows a stepped pattern that is the result of extended rim elements with a complex profile. These elements grow outward, and also backwards and upwards over the central area, and cover it completely. The most distal part of the planolith consists of several

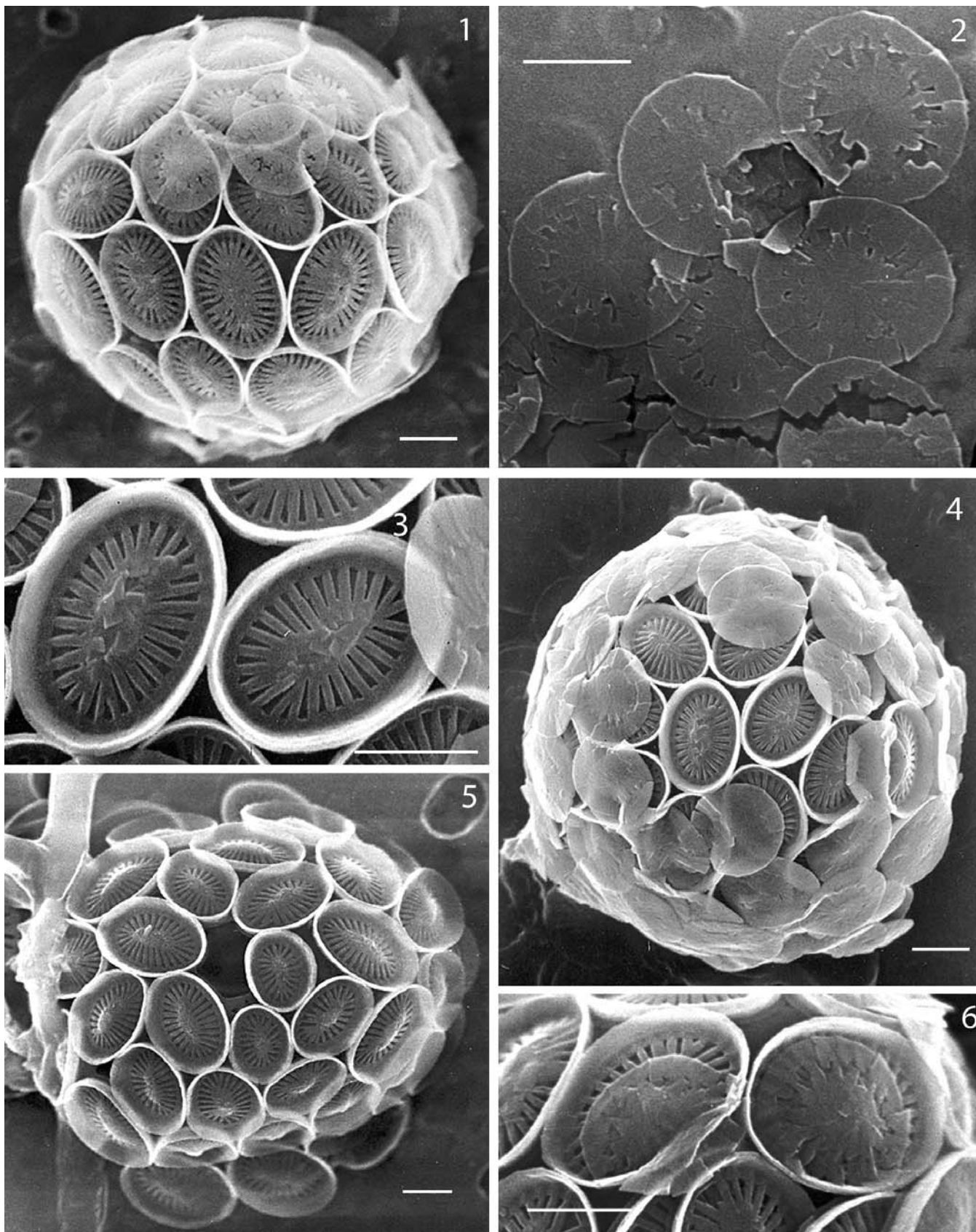
**PLATE 6**

*Syracosphaera leptolepis* Kleijne et Cros sp. nov.

Scale bars = 1  $\mu$ m.

Figure 1 was published previously in Kleijne (1993), and fig. 4 in Cros (2002) and Cros and Fortuño (2002), as *Syracosphaera* sp. type L.

- 1 Holotype; coccosphere showing complete endotheca of monomorphic coccoliths, with three exothecal planoliths; APNAP-I/T86-19C/0-5m.
- 2 Exothecal planoliths in proximal view, showing sinistrally oblique elements of centre; same specimen as fig. 6.
- 3 Detailed view of fig. 4; body coccoliths showing inner-proximal flange around central area.
- 4 Dithecate coccosphere showing exotheca of delicate planoliths; MESO-95/023/0-5m.
- 5 Coccosphere showing variation in body coccolith size; Snellius-II/Gx-209/0-5m (eastern North Atlantic).
- 6 Size comparison of body coccoliths and planoliths; planolith centre with dextrally oblique elements; APNAP-I/T86-19B/0-5m.



large elements of irregular shape. The central area and medial cycle elements are not visible. The distal surface shows one large step on the wider part of the flange (pl. 7, figs. 1, 4; Cros 2000, pl. 1, fig. 6). This probably is the place where the planoliths overlap when they occur in a ribbon-like arrangement, as described for species of this subgroup by Young et al. (2009).

The broadly-elliptical body coccoliths have a low, thick wall that shows a pattern of concentric rings in distal view. The wall is constructed of two layers: the elements of the thick outer layer are obliquely raised and about twice the height of the thinner, inner wall layer (pl. 7, fig. 4). Their central area has 23–28 radial laths that have a vertical extension along the inner wall layer (pl. 7, fig. 2). The broad, slightly convex central structure consists of wide, irregularly placed lamellar elements (pl. 7, fig. 4).

The circum-flagellar coccoliths have a thin, single-layered wall that is higher than in the body coccoliths, and a short, rod-shaped central spine (pl. 7, fig. 4).

**Dimensions:** coccosphere, diameter along long axis 6.5–7.5 µm; exothecal coccoliths, length 2.5–2.9 µm; body coccoliths, length 1.5–2.0 µm; circum-flagellar coccoliths, spine length ± 0.5 µm.

#### Taxonomic notes

Three species are described here with body coccoliths that have only a proximal flange, and exothecal coccoliths that consist of several layers of plate-like elements, *Syracosphaera operculata* sp. nov., *S. squamigera* sp. nov. and *S. reniformis* sp. nov. These are evidently closely related and are included in the *squamosa*-subgroup within the *S. nodosa* group, which is equivalent to the “laminated type” of Young et al. (2003). The differences between them are discussed below.

One of the three specimens shown by Okada and McIntyre (1977, pl. 8, fig. 9, as *Syracosphaera nana*), is included on similarity in shape of the exothecal coccoliths; the specimens in their figs. 7 and 8 are included in *S. reniformis* sp. nov., because the muroliths have smaller triangular openings between the radial laths.

#### *Syracosphaera reniformis* Kleijne et Cros sp. nov.

Plate 8, figures 1–2

*Syracosphaera nana* auct. non (Kamptner 1941), OKADA and MCINTYRE 1977 *partim*, pp. 24–25, pl. 8, figs. 7, 8, non fig. 9.

?*Florisphaera* sp. R, REID 1980, p. 168, pl. 8, figs. 6–7.

*Syracosphaera* cf. *nana*, HEIMDAL and GAARDER 1981, p. 60, pl. 8, figs. 42a, b.

*Syracosphaera* sp. type J, KLEIJNE 1993, p. 244, pl. 5, fig. 3.

*Syracosphaera* sp. type J of Kleijne 1993. – YOUNG et al. 2003, p. 40, pl. 17, figs. 11, 13, ?figs. 10, 12. – YOUNG et al. 2009, fig. 6c–d.

**Diagnosis:** *Coccosphaera globosa*, dithecata, cum coccolithis endothealibus dimorphis. Coccolithi exothecales sunt planolithi longi, lamellati, incrassati asymmetrici, cum ordinatione superpositorum stratorum magnitudinis decrescentis in uno latere. Coccolithi communes sunt murolithi late elliptici cum muro humili, augenti. Area centralis formatum structura magna et levis cum orbe peripherali elementorum lamellarum brevium radialier tendentibus cum parvis orificiis in medio. Coccolithi circumflagellares sunt murolithi cum spina acuta.

Coccosphere spherical, dithecate, with dimorphic endotheal coccoliths. Exothecal coccoliths are large, laminated, asymmet-

rically thickened planoliths, with a pattern of superposed layers of decreasing size on one side. Body coccoliths are broadly-elliptical muroliths with a low, flaring wall. The central area is a large, smooth central structure with a peripheral cycle of short radial laths with very small openings in between. Circum-flagellar coccoliths are muroliths with a pointed spine.

**Holotype:** Negative A81/43 (pl. 8, fig. 1), deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

**Type locality:** North Atlantic (34°19'2"N 34°21'3"W), depth 87m, 31 Aug. 1986 (Cruise APNAP-I, Station T86-12R).

**Etymology:** Latin *reniformis* -e (adjective), kidney-shaped; referring to the kidney-shaped outline of the exothecal coccoliths without the large wing-like extension, as it is visible in pl. 8, fig. 2.

**Number of specimens studied:** 1, plus 1 in Okada and McIntyre (1977), 2 in Heimdal and Gaarder (1981) and 2 in Young et al. (2003; 2009).

**Distribution:** Pacific; Mediterranean Sea, 37–38m; North Atlantic, 87m.

**Description:** The dithecate coccosphere consists of up to ± 50 large laminated exothecal planoliths and ± 35 dimorphic endotheal muroliths with a characteristic large, smooth and flat centre, and small peripheral openings in between the radial laths (pl. 8, figs. 1–2). The planoliths are considerably larger than the endotheal coccoliths.

The exothecal coccoliths are solid, asymmetrically thickened discs, with a flat, smooth proximal side, on which two different parts can be distinguished: an elliptical central area is surrounded by a highly asymmetrical rim (pl. 8, fig. 1, lower right). The rim bears a large square-built extension (Young et al. 2009, fig. 6c). The distal side shows a stepped pattern of elements with a complex structure: they grow backwards over the central area and cover approximately half of it. The elements that form the widest rim extensions extend back higher and further than elements that form the narrower part of the rim. The outer margin of the wider part of the rim is not continuous with the narrow rim part, which gives the planolith a more or less kidney-shaped outline. The uppermost outline of the planolith consists of large elements with a flat surface and a large step near the narrow part of the rim (pl. 8, fig. 2), where the planoliths overlap to form a ribbon, see also Young et al. (2009)

The body coccoliths have a single-layered wall and are variable in size. The slightly convex central area shows a large, smooth central part, surrounded by a radial cycle of short laths with very small openings in between (pl. 8, fig. 1; see also Okada and McIntyre 1977, pl. 8, figs. 7–8).

Spine-bearing circum-flagellar coccoliths are visible in the coccospheres shown by Heimdal and Gaarder (1980, figs. 42a, b). The structure that is visible in the centre of the holotype possibly is the rounded top of a spine (pl. 8, fig. 1).

**Dimensions:** coccosphere diameter ± 6–8 µm; exothecal coccoliths, length ± 2.2 µm; body coccoliths, length 1.4–1.8 µm, width 1.0–1.2 µm; circum-flagellar coccoliths, spine length up to 1.2 µm (Heimdal and Gaarder, 1981).

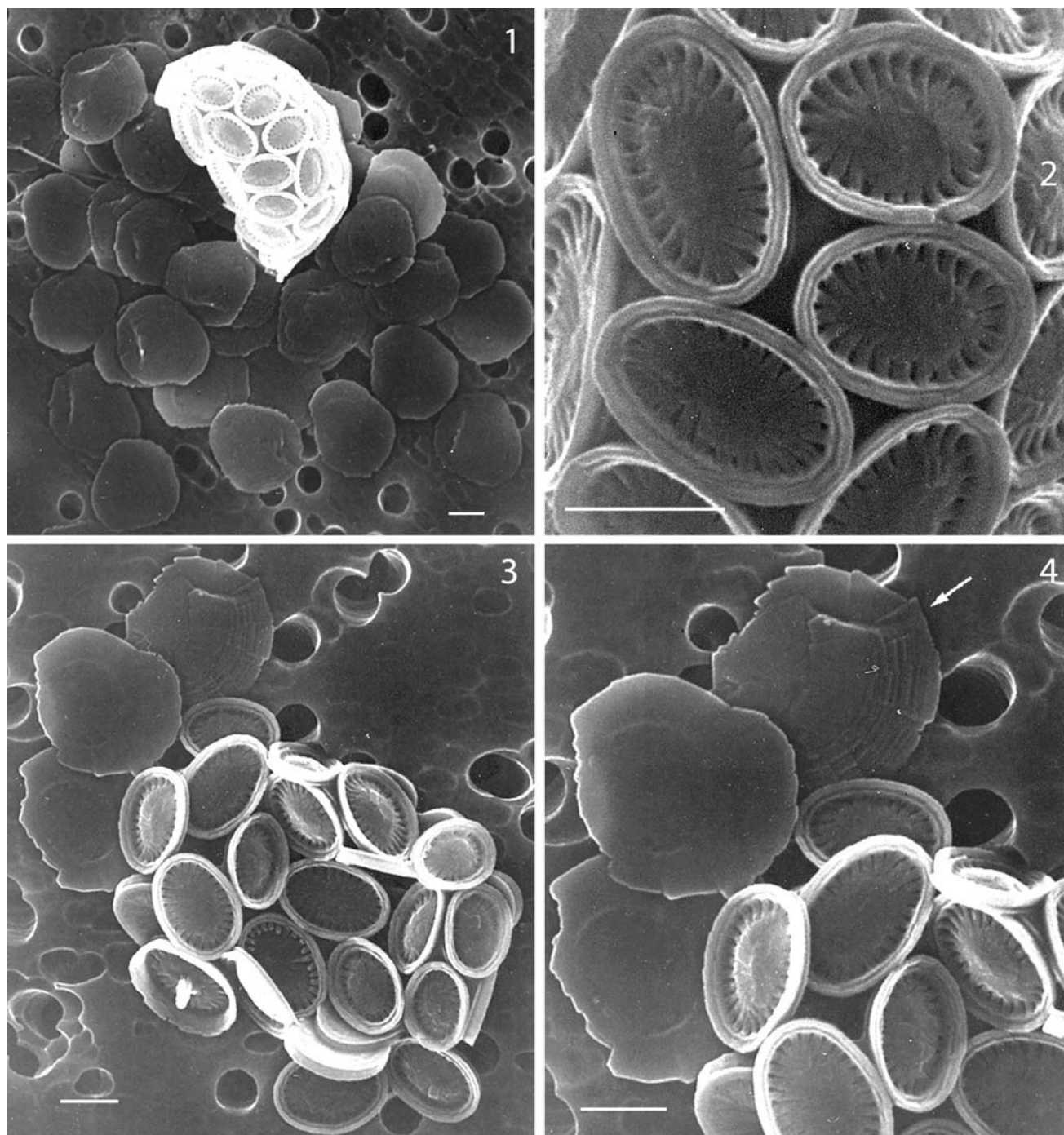
**PLATE 7***Syracosphaera operculata* Kleijne et Cros sp. nov.Scale bars = 1  $\mu$ m.

Figure 1 was published previously in Cros (2000), as *Syracosphaera* sp. with stratified coccoliths, and fig. 3 in Cros (2002) as *Syracosphaera* sp. 6 with stratified coccoliths.

- 1 Partly collapsed coccosphere showing body coccoliths, and exothecal planoliths in distal and proximal views; MESO-96/D8/70m.
- 2 Detailed view of fig. 1; body coccoliths in distal and lateral views, showing thick wall that is double-layered in proximal part.
- 3 Holotype; collapsed coccosphere showing body coccoliths with convex central area, one thin-walled circum-flagellar coccolith with spine, and three exothecal coccoliths; MESO-96/D8/70m.
- 4 Detailed view of fig. 3; operculum-like laminated exothecal planoliths have a flat proximal side (left) and convex distal side with stepped surface (arrow).

# Taxonomic notes

*Syracosphaera reniformis* sp. nov. is placed in the *squamosa*-subgroup, because of its laminated exothecal coccoliths. The body coccoliths have a very characteristic broad smooth central area, with a peripheral cycle of triangular openings that are hardly visible (pl. 8, figs. 1-2). Similar specimens have been shown previously by Okada and McIntyre (1977, pl.8, figs.7-8), although misidentified as *S. nana*, and by Heimdal and Gaarder (1981, pl.8, figs.42a, b) as *S. cf. nana*. Unlike the large and smooth central part that is found in *S. reniformis* sp. nov., body coccoliths of *S. nana* have an elongate, narrow central structure in the form of a whale-back (pl. 11, figs. 1-2, 4).

Another species bearing large stratified planoliths and body muroliths with a large and broad central structure and no distal flange is *S. operculata* sp. nov. However, that species has subcircular exothecal coccoliths and body coccoliths with a double-layered wall, whereas in *S. reniformis* sp. nov. the planoliths consist of a more or less kidney-shaped part with a wide extension on one side, while the body coccolith wall is single-layered.

The specimen figured in Young et al. (2003) in pl. 17, figs. 10 and 12, could not be identified with certainty as belonging to this new species. This collapsed coccosphere consists of endothecal coccoliths of *S. reniformis* sp. nov., that are, on the contrary, surrounded by exothecal coccoliths that look more like those of *S. operculata* sp. nov.

## *Syracosphaera serrata* Kleijne et Cros sp. nov.

Plate 9, figures 1-6

*Syracosphaera* sp. type B, KLEIJNE 1993, p. 241, pl. 6, figs. 2-3.

*Syracosphaera nodosa* type B, YOUNG et al. 2003, p. 36, pl. 15, fig. 6.

**Diagnosis:** Coccosphaera dithecata cum coccolithis endothecalibus dimorphis. Coccolithi exothecales sunt planolithi similes rotae cum margine serrato quorum centralis area constat ex duobus magnis elementis cinctis lamelliis radialiter tendentibus. Margo constat ex elementis late dilatantibus cum acuta extensione in margine exteriore. Coccolithi communes sunt murolithi late ellipticales cum ambitu irregulari habentes tenuem et humilem murum augmentem. Eorum area centralis constat ex duobus elementis rectangularibus, subnullimis, cinctis lamelliis distinctis radialiter tendentibus. Coccolithi circumflagellares eidem sunt ac coccolithi communes sed cum spina centrali brevi et acuta.

Coccosphere dithecate, with dimorphic endothecal coccoliths. Exothecal coccoliths are wheel-like planoliths with a serrate margin; their central area consists of two large elements, surrounded by radial laths; the rim consists of broad widening elements with a pointed extension on the outer margin. Body coccoliths are broadly-elliptical muroliths with an irregular outline. They have a low and thin, flaring wall; their central area consists of two, very delicate, rectangular elements, surrounded by distinct radial laths. Circum-flagellar coccoliths identical to body coccoliths, but with a short central, pointed spine.

**Holotype:** Negative A15/98 (pl. 9, fig. 1), deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

**Type locality:** Southern Red Sea (13°51'7"N 42°52'5"E), depth 0-5m, 13 June 1984 (Snellius-II Expedition, Station G0-98).

**Etymology:** Latin *serratus* -a -um, dentate, serrate; referring to the saw-blade margin of the exothecal coccoliths.

**Number of specimens studied:** 6.

**Distribution:** Northeastern Indian Ocean, 0-5m; Gulf of Aden, 0-5m; Red Sea, 0-5m; North Atlantic, Canary Islands, 25m.

**Description:** The dithecate coccosphere is probably spherical and consists of 60-70 endothecal muroliths (pl. 9, figs. 1, 5) and  $\pm 25$  exothecal planoliths (pl. 9, figs. 1-2). On our specimens, all collapsed coccospheres, we found only one circum-flagellar coccolith, bearing a short central, pointed spine (pl. 9, figs. 3-4).

The wheel-like exothecal planoliths have a characteristic dentate periphery. The rim consists of broad, widening elements. The pointed extension on the right outer corner (seen in distal view) gives the margin its saw-like appearance (pl. 9, figs 1-2; see also Young et al. 2003, pl. 15, fig. 6). The coccolith centre appears to consist of two large, elongate elements. The medial cycle consists of  $\pm 20$  radial laths with triangular openings in between; the laths show distinctive sinistral obliquity in distal view.

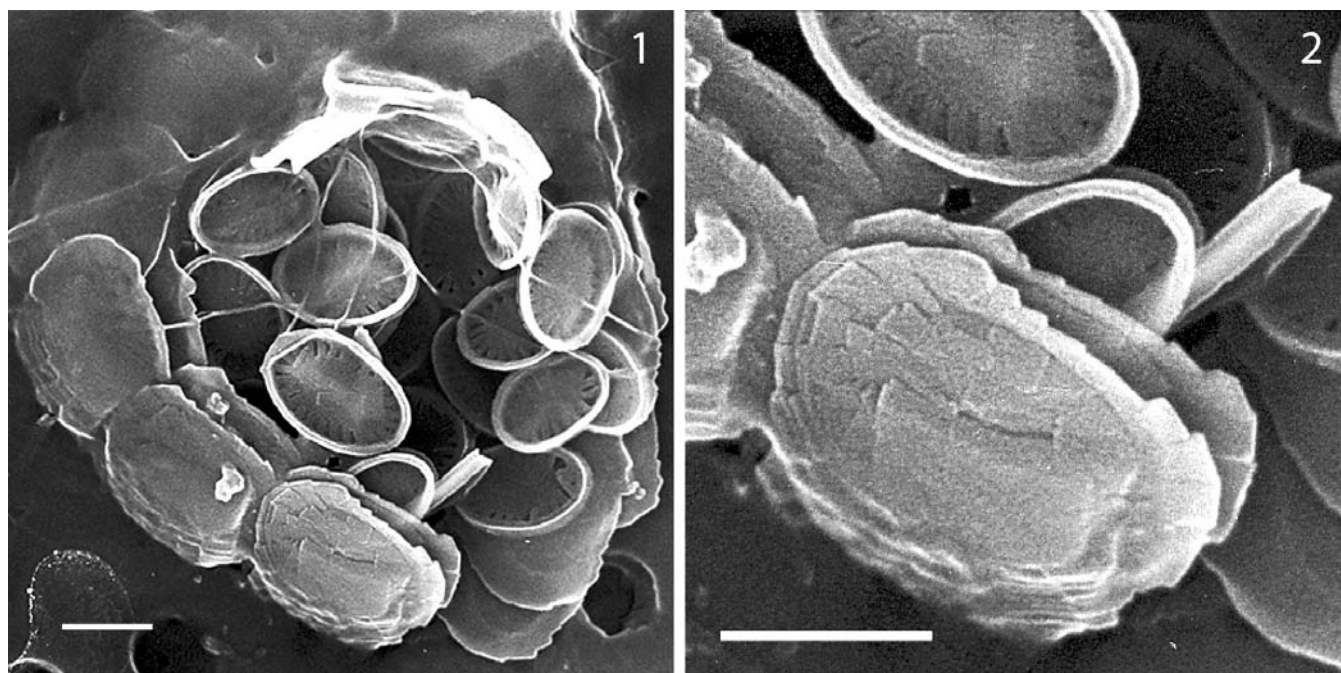
The body coccoliths are broadly-elliptical, usually with an irregular outline, and are variable in size (pl. 9, figs 1, 3-5). The wall elements are curved outward, giving the impression of a narrow distal flange (pl. 9, figs. 2, 4, 6). The central structure consists of two flat, rectangular elements, visible on the proximal side of the coccolith (pl. 9, fig. 2). The radial cycle consists of 18-31 laths, that are often irregularly placed; their ends are visible on the distal side of the flat central structure (pl. 9, figs 2, 6).

**Dimensions:** coccosphere diameter  $\pm 8 \mu\text{m}$ ; exothecal coccoliths, diameter  $\pm 2.7 \mu\text{m}$ ; body coccoliths, length 1.4-2.4  $\mu\text{m}$ , width 1.0-1.7  $\mu\text{m}$ ; circum-flagellar coccolith, spine length  $\pm 0.5 \mu\text{m}$ .

# Taxonomic notes

*Syracosphaera serrata* sp. nov. is placed in the *nodosa*-subgroup within the *S. nodosa* group of Young et al. (2003). Species included in this subgroup have body coccoliths with only a proximal flange, circum-flagellar coccoliths with a spine, and circular to elliptical exothecal planoliths that may cover the entire endotheca. The wheel-like exothecal coccoliths of *Syracosphaera serrata* sp. nov. have a dentate margin, whereas the circular planoliths of *S. nodosa* have a smooth periphery (see Kleijne 1993, p. 257, pl. 4, fig. 8). The wheel-like structure of the exothecal coccoliths lead Young et al. (2003) to include *S. serrata* sp. nov. in *S. nodosa*, as one of its three types. Now, detailed study of the body coccoliths shows that the muroliths of *S. serrata* sp. nov. are very different from those of *S. nodosa*. They lack a central mound, while their wall is very low, flaring and smooth, instead of straight and high with vertical ribs on the outer side. Moreover, the circum-flagellar coccoliths of *S. nodosa* bear robust spines.

*Syracosphaera nana* has endothecal coccoliths with a similar low wall. However, the muroliths of *S. serrata* sp. nov. differ from *S. nana* by their flat and smooth central structure, on which the ends of the radial laths are clearly visible, while *S. nana* has a longitudinal whaleback-shaped central part (see Cros et al. 2000, p. 13, pl. 5, fig. 1). Moreover, *S. nana* has broadly-elliptical, instead of circular exothecal coccoliths.



# **PLATE 8**

*Syracosphaera reniformis* Kleijne et Cros sp. nov.

Scale bars = 1 µm.

Figure 1 was published previously in Kleijne (1993), as *Syracosphaera* sp. type J.

- 1 Holotype; collapsed dithecate coccosphere showing body coccoliths, overlapping exothecal planoliths in proximal (lower right) and distal views; APNAP-I/T86-12R/87m.
- 2 Detailed view of fig. 1; body coccoliths with low wall, large smooth central structure and narrow triangular openings between short radial laths; exothecal planoliths in lateral-distal view, showing pattern of superposed layers of decreasing size.

## *Syracosphaera squamosa* Kleijne et Cros sp. nov.

Plate 10, figures 1-5

*Syracosphaera* sp. type K, KLEIJNE 1993, p. 244, pl. 6, fig. 11;  
*Syracosphaera* sp. 3, GIRAudeau and BAILEY 1995, p. 1852, pl. 5, figs. 8-9.

*Syracosphaera* sp. type K of Kleijne 1993. – YOUNG et al. 2003 *partim*, p. 40, pl. 17, fig. 14, *non* fig. 15.

**Diagnosis:** Coccosphaera subglobosa dithecata, cum coccolithis endothealibus dimorphis. Coccolithi exothecales sunt planolithi magni, asymetrici, cum extensione, incrassata et eminenti, simili alae. Extensiones ad apicalem polum intendunt. Coccolithi communes sunt muralithi elliptici lati ad angustos cum muro crasso ex duobus stratis clare separatis. Area centralis formatum elementis lamellaribus radialiter tendentibus et structura centrali elongata et leviter incrassata. Coccolithi circumflagellares sunt muralithi cum spina acuta.

Coccosphere subspherical, dithecate, with dimorphic endotheal coccoliths. Exothecal coccoliths are large, asymmetrical planoliths with a prominent wing-like extension. The extensions are directed towards the apical pole. Body coccoliths are broad- to narrow-elliptical muraliths with a thick wall of two clearly separated layers. Their central area consists of radial laths and a slightly thickened, elongate central structure. Circum-flagellar coccoliths are muraliths with a pointed spine.

**Holotype:** Negative A80/14 (pl. 10, fig. 4), deposited at the Nationaal Herbarium Nederland, Universiteit Leiden branch (L).

**Type locality:** North Atlantic (31°26'9"N 36°14'2"W), depth 100m, 2 Sept. 1986 (Cruise APNAP-I, Station T86-14R).

**Etymology:** Latin *squamosus* -a -um (adjective), covered with coarse scales; referring to the exothecal coccoliths that cover the endotheca like fish-scales.

*Number of specimens studied:* 4, plus 2 in Giraudeau and Bailey (1995).

*Distribution:* North Pacific, 0-20m; central North Atlantic, 100m; South Atlantic, off Namibia.

*Description:* The coccosphere consists of  $\pm 50$  dimorphic endothecal coccoliths; we counted up to 15 exothecal coccoliths (pl. 10, figs. 1, 3-4). The exothecal coccoliths are large asymmetrical planoliths that may occur in a ribbon-like arrangement (pl.10, fig. 3). They have a wing-like extension with a smooth periphery (pl. 10, figs. 2-4). The extensions are directed towards the apical pole and overlap the narrow and thin rim parts of the adjacent coccoliths, giving the appearance of fish-scales (pl. 10, fig. 4).

The planoliths consist of a flat to slightly convex central part of radially orientated elements, surrounded by the short elements of the medial cycle, and an obliquely raised rim with a complex structure. One long side, approximately one fourth of the rim, is narrow and delicate; it consists of small blade-like elements (pl. 10, figs. 2, 4). The elements of the remaining, wider part have a more complex shape; they seem to have a stepped profile, with several small steps on the outer part of the rim elements. In distal view, only one third of the central area is visible on that side. The other part is covered by rim elements that grow outwards, to form the wing-like extension, and also backwards over the central area (pl. 10, figs. 2, 4). One narrow end of the planolith bears a rim element with a pointed extension, while at the opposite end the rim elements are continuous with the wing-like extension (pl. 10, fig. 4).

The body coccoliths vary in size and shape, from broad- to narrow-elliptical (pl. 10, figs. 3, 5). They have a low, distally widening, double-layered wall. The inner layer consists of vertical elements with a clockwise imbrication; it is clearly separated from the outer layer by a cleft. The width of the inner wall layer is equal to, or wider than the outer layer. The coccolith central area consists of a radial cycle with  $\pm 15$ -25 laths, and a slightly thickened, narrow central structure. The radial laths extend upward along the inner wall layer (pl. 10, fig. 5).

One of our specimens bears 3 circum-flagellar coccoliths (pl. 10, fig. 1). The circum-flagellar coccoliths have a short pointed spine (pl. 10, figs. 1-2).

*Dimensions:* coccosphere, diameter  $\pm 6\mu\text{m}$ ; exothecal coccoliths, length  $\pm 2.6\mu\text{m}$ ; body coccoliths, length 1.4-1.7 $\mu\text{m}$ , width 0.9-1.3 $\mu\text{m}$ ; circum-flagellar coccoliths, spine length 0.4 $\mu\text{m}$ .

#### Taxonomic notes

*Syracosphaera squamosa* sp. nov. is placed in the new *squamosa*-subgroup and former 'laminated type' of the *S. nodosa* group of Young et al. (2003), since its exothecal coccoliths appear as having a partly laminated rim. Species of this subgroup bear planoliths with a rim that, in fact, partly or entirely consists of complexly shaped elements with a stepped profile. The surface of numerous smaller and larger steps gives the appearance of overlapping layers of elements, comparable to the blanket elements of *Helicosphaera* coccoliths, shown by Young et al. (2004, fig. 9). The planoliths of *S. squamosa* sp. nov. are partly laminated, in contrast to the entirely laminated planoliths of the other species of this subgroup, *S. reniformis* sp. nov. and *S. operculata* sp. nov.

Body coccoliths of *Syracosphaera squamosa* sp. nov. differ from those of *S. operculata* sp. nov. in having a double-layered wall with two layers of approximate equal thickness, instead of a narrow and low inner layer and a more prominent outer layer. Moreover, their mural central area structures differ in shape; it is narrow-elliptical in *S. squamosa* sp. nov. and flatter and broad-elliptical in *S. operculata* sp. nov.

The specimen shown by Young et al. (2003, p. 40, pl. 17, fig.15) as *Syracosphaera* sp. type K probably belongs to *Syracosphaera bannockii*, since the circum-flagellar coccoliths are robust and have a wall structure similar to the body coccoliths, instead of having a single-layered wall. The body coccoliths of *S. bannockii* have a different wall structure, since the inner wall layer is narrower and considerably lower than the outer layer. Moreover, these layers are not as clearly separated as in the body coccoliths of *S. squamosa* sp. nov., that have a ring-like cleft in between the wall layers. The planoliths of *S. bannockii*

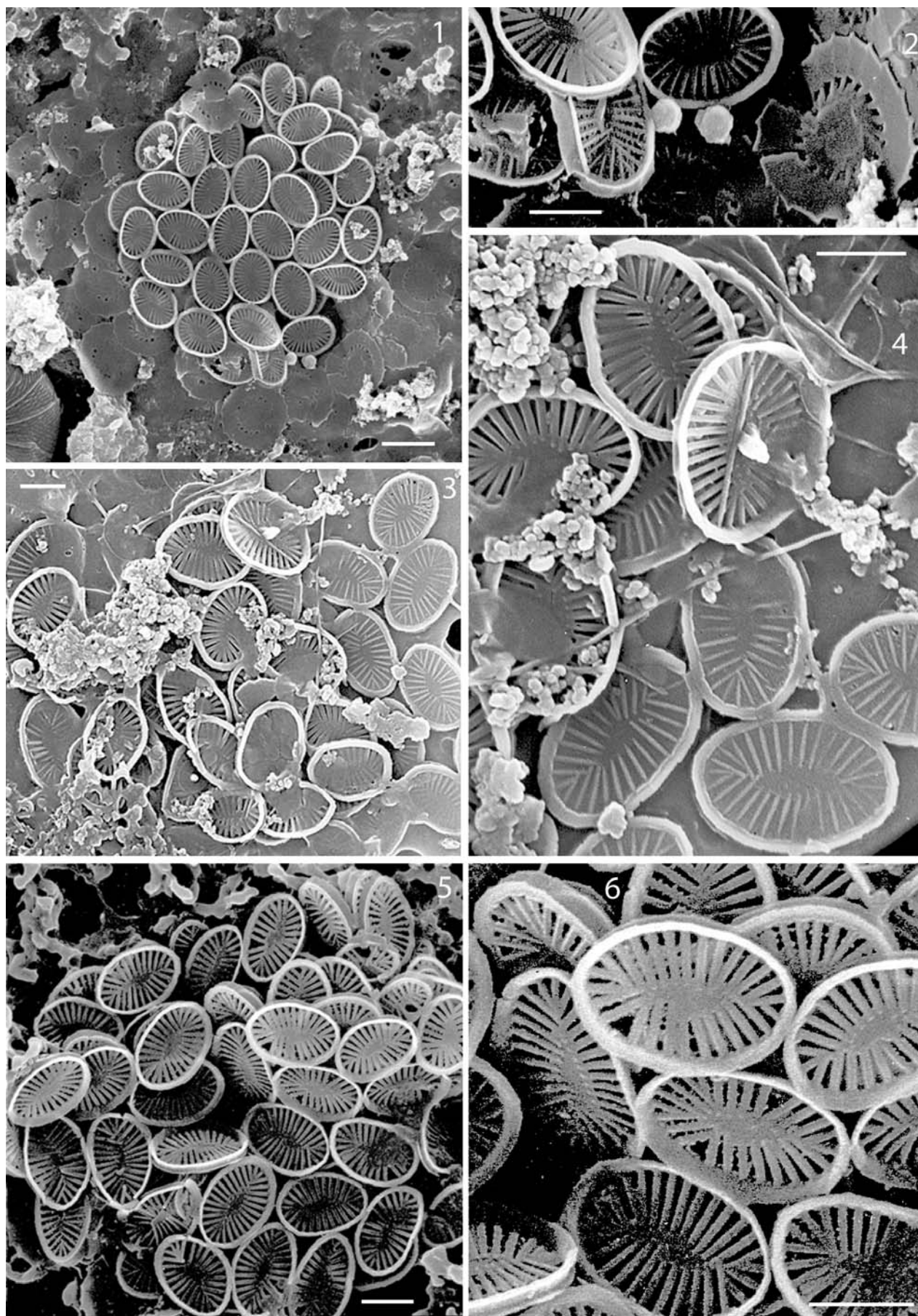
### PLATE 9

*Syracosphaera serrata* Kleijne et Cros sp. nov.

Scale bars fig. 1 = 2  $\mu\text{m}$ , figs. 2-6 = 1  $\mu\text{m}$ .

Figure 1 has been published previously in Kleijne (1993), as *Syracosphaera* sp. type B.

- 1 Holotype; collapsed dithecate coccosphere showing body coccoliths and exothecal planoliths; Snellius-II/G0-98/0-5m (Red Sea).
- 2 Detailed view of fig. 1, showing body coccoliths in distal and proximal view, part of widening coccolith wall in lateral view (left), and exothecal planolith in proximal view showing medial cycle elements with dextral obliquity, and serrated margin.
- 3 Collapsed coccosphere; Snellius-II/Gx-14/0-5m (northeastern Indian Ocean).
- 4 Detailed view of fig. 3, showing body coccoliths in proximal (lower part) and distal view, and one spine-bearing circum-flagellar coccolith.
- 5 Collapsed coccosphere showing variation in coccolith size and shape, and coccoliths in lateral view; Snellius-II/G0-106/0-5m (Gulf of Aden).
- 6 Detailed view of fig. 5, showing ends of radial laths on top of flat central structure.



are similar in outline - including the pointed extension on one end - to *S. squamosa* sp. nov., but they are different in being more or less flat and non-laminated (see Cros et al. 2000, pl. 7, fig. 1).

#### Emended description of *Syracosphaera nana*

Although Kamptner (1941) clearly described the endotheal coccoliths of *Syracosphaera nana* with the whale-back shaped ridge in their central area, this species has long been misidentified and the name has been applied to many different *Syracosphaera* specimens. E.g. Cros et al. (2000) described as new *Syracosphaera delicata*, a species that previously had been regarded as *S. nana*. The name was also used for specimens of several other species that we describe here. Detailed information on the coccolith structure of *S. nana* has become available, after specimens were shown by Kleijne (1991, 1993; as *Syracosphaera* sp. type A) and were identified correctly by Cros (2000).

Since hetero-holococcolithophore combination coccospheres involving *Syracosphaera nana* have been observed, the species is considered as being part of a life-cycle association, of which the holococcolithophore phase has not been described as a separate species (Kleijne 1991; Cros et al. 2000; Cros and Fortuño 2002; Young et al. 2003). To avoid future misidentification, we here give an emended description of both phases of *Syracosphaera nana*.

***Syracosphaera nana*** (Kamptner 1941) Okada *et* McIntyre 1977; **emend.** Kleijne *et* Cros  
Plate 11, figures 1-6

**Basionym:** *Pontosphaera nana* KAMPTNER 1941, p. 79, pl. 3, figs. 31-33.

**Non:** *Pontosphaera nana* auct. non Kamptner. – HALLDAL and MARKALI 1955, p.14, pl. 15.

*Syracosphaera* sp. 1, BORSETTI and CATI 1972, p. 402, pl. 47, fig. 4; GIRAudeau and BAILEY 1995, pl. V, fig.6.

*Syracosphaera nana* (Kamptner). – OKADA and MCINTYRE 1977, p. 24 (as to type only), non pl. 8, figs. 7-9.

**Non:** *Syracosphaera nana* auct. non (Kamptner) Okada *et* McIntyre. – NISHIDA 1979, pl. 7, fig. 4. – WINTER and SIESSER 1994, fig. 116. Unidentified heterococcolithophorid “C”, HEIMDAL and GAARDER 1981, p. 67, pl. 12, fig. 62.

*Syracosphaera* sp. type A, KLEIJNE 1991, p. 21, pl. 20, figs. 5-6; KLEIJNE 1993, p. 241, pl. 6, fig. 1.

*Syracosphaera nana* (Kamptner) Okada *et* McIntyre. – CROS 2000, p. 46, pl. 2, figs. 6, 8. – CROS *et al.* 2000, p. 13, pl. 5. – CROS 2002, p. 48, pl. 21, figs. 1-6. – CROS and FORTUNO 2002, pp. 33-34, figs. 36-37. – YOUNG *et al.* 2003, p. 36, pl. 15, figs. 10-13, and p. 88, pl. 41, figs. 10-12.

#### Emended description

Heteromorphic life-cycle.

**Heterococcolith-bearing phase:** The dithecate ovoid coccosphere consists of 44-100 dimorphic endotheal coccoliths; we counted up to 17 exotheal coccoliths (pl. 11, figs. 1-4).

Exotheal coccoliths are slightly convex planoliths with a perfectly egg-shaped outline. Their broad rim is composed of wide elements; the elements on the wider end of the coccolith bear a small node on the inner margin (pl. 11, figs. 2, 4). Their centre is formed of 12-14 plate-like elements that are more or less triangular in shape at the ends and lath-shaped at the long sides of the coccolith (pl. 11, fig. 4). These elements almost completely cover the central area.

Body coccoliths are oval to broadly-elliptical muroliths with a low, solid wall that has a smooth upper margin. The central area is vaulted into a whaleback shape; the ends of the radial laths fuse in the centre and form a well-defined axial ridge (pl. 11, figs. 1-4).

Circum-flagellar coccoliths are muroliths that bear a very short central spine with a rounded top (pl. 11, fig. 3).

**Holococcolith-bearing phase:** The coccosphere consists of dimorphic planar holococcoliths (Young *et al.* 2003, p. 88). The 94-112 body coccoliths are flat disks with an irregular distal surface and a smooth, 2 crystallites high, peripheral rim (pl. 11, fig. 5). The 10-12 circum-flagellar coccoliths consist of a disk of one layer of crystallites and bear a relatively high transverse ridge; they are slightly smaller than the body coccoliths (pl. 11, fig. 6).

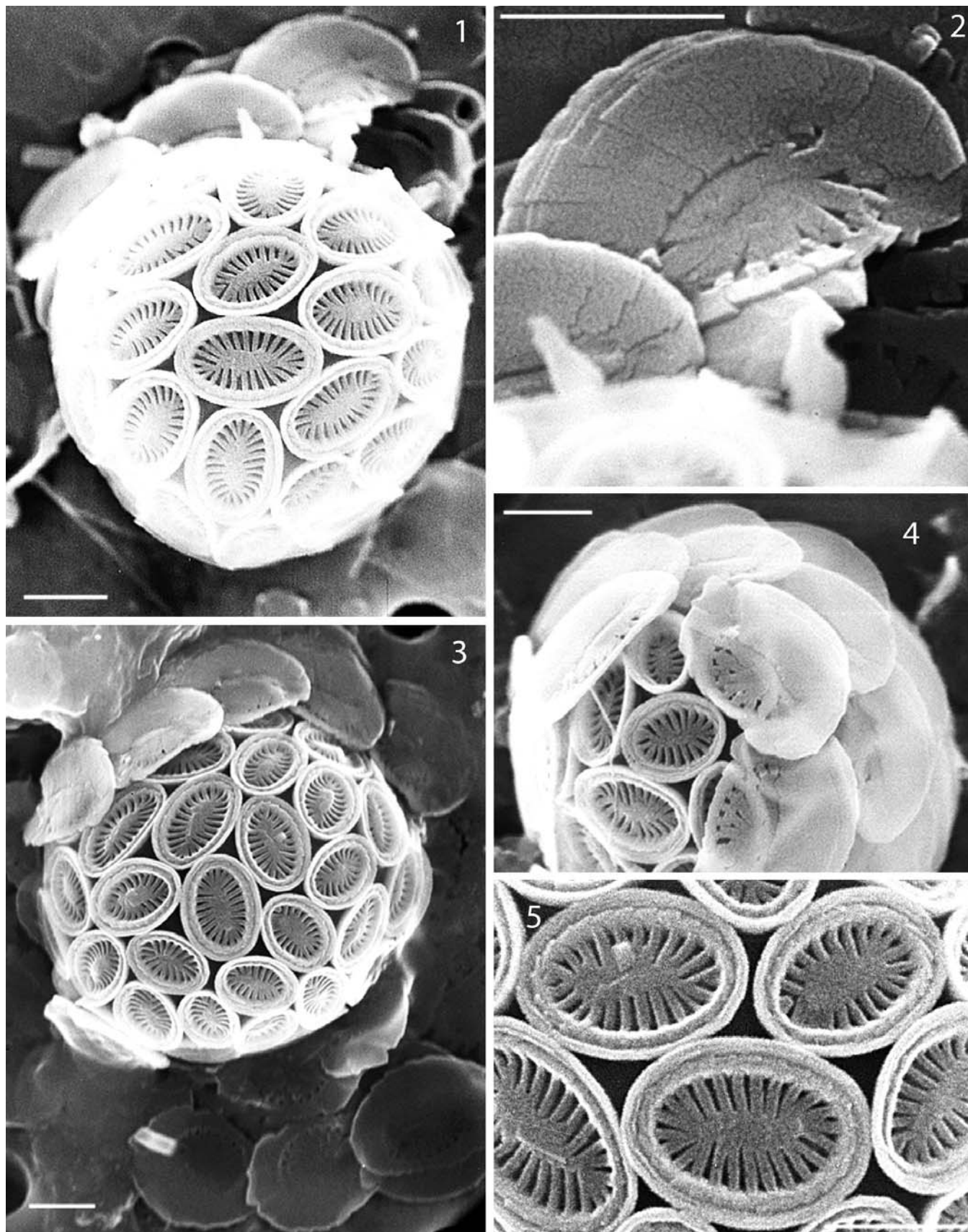
### PLATE 10

*Syracosphaera squamosa* Kleijne *et* Cros sp. nov.

Scale bars = 1 µm.

Figure 1 was published previously in Kleijne (1993), as *Syracosphaera* sp. type K.

- 1 Coccosphere showing body coccoliths, three circum-flagellar coccoliths with a short spine (upper right) and three exotheal planoliths in distal view; APNAP-I/T86-14R/100m.
- 2 Detailed view of fig. 1; exotheal planoliths with asymmetrical rim in distal view, showing one narrow single-layered side and one large, obliquely raised, multi-layered side.
- 3 Coccosphere with partly detached exotheal coccoliths in distal and proximal (bottom) views; APNAP-I/T86-14R/100m.
- 4 Holotype; coccosphere showing overlapping laminated planoliths with wing-like rim part directed towards apical pole; APNAP-I/T86-14R/100m.
- 5 Detailed view of fig. 3; body coccoliths with double-layered wall and elongate, smooth central structure.



*Dimensions heterococcolith phase:* coccosphere, diameter 5-7µm; exothecal coccoliths, length 1.8-2.2µm; body coccoliths, length 0.9-1.9µm; circum-flagellar coccoliths, spine length 0.1- 0.2µm.

*Dimensions holococcolith phase:* coccosphere, diameter 5.5-7.5µm; body coccoliths, length 0.9-1.5µm.

*Distribution HO:* western Mediterranean Sea; central North Atlantic.

*Distribution HE:* Red Sea, 0-5m; Mediterranean Sea; eastern North Atlantic; South Atlantic, off Namibia, 5m.

*Occurrence combination coccospheres:* Mediterranean Sea, 0-5m; central North Atlantic, 20m.

#### Taxonomic notes

*Syracosphaera nana*, with its endothecal coccoliths with only a proximal flange and its oval planoliths, is placed in the new *nana*-subgroup of the *S. nodosa* group.

The characteristic oviform coccosphere shape of *S. nana* (pl. 11, fig. 1) has been well figured and described as “Die Schale ist kurz eiförmig” by Kamptner (1941, p. 79, plate 3, figs. 31-32; ‘the coccosphere is short egg-shaped’). He described the vaulted shape of the muroliths as “In der Mitte des Bodens tragen sie eine längliche buckelartige Erhebung” (‘in the middle of the bottom they bear a long, hunchback-shaped elevation’). The oval, convex exothecal coccoliths, were not noticed by Kamptner (1941), but were described by Kleijne (1993, as *Syracosphaera* sp. type A), while Cros (2000) identified these specimens as belonging to *S. nana*. Cros (2002) gave a detailed discussion of the species.

Despite the early, but very clear, description of the species several *Syracosphaera* coccospheres have been wrongly assigned to *S. nana*. These coccospheres represent different species, including some of the here described species, namely: *S. reniformis* sp. nov. (Okada and McIntyre 1977, pl. 8, figs. 7-8), *S. operculata* sp. nov. (Okada and McIntyre 1977, pl. 8, fig. 9) and *S. leptolepis* sp. nov. (Winter and Siesser 1994, fig. 116).

Images of yet another, still undescribed, new *Syracosphaera* species were presented as *S. nana* by Halldal and Markali (1955) and Nishida (1979).

#### CLASSIFICATION SCHEME

Young et al. (2003) divided the *Syracosphaera* species and taxa in open nomenclature into three main groups, based primarily on the distinction on number of flanges in the body coccoliths. These groups were further divided into smaller groups of species, the types. Instead of type we prefer to use subgroup, to avoid confusion with the other meanings of the word type in taxonomy, e.g. holotype and type species. We adapt the existing classification scheme and raise the new *Syracosphaera noroitica* main group, for species bearing varimorphic endothecal muroliths with one flange, and exothecal muroliths with a beaded proximal flange. Three new subgroups are introduced to be able to place all species in the scheme: the *leptolepis*- and *nana*-subgroups are new in the *S. nodosa* group, and the *corolla*-subgroup in the *S. pulchra* group. The name *squamosa*-subgroup is introduced for the laminated type of Young et al. (2003) to avoid confusion with the name *lamina*-subgroup, since both subgroups co-exist in the *S. nodosa* main group. Complete references to the species are given in tables 1-4. The resulting classification scheme consists of four main groups, 15 subgroups and 36 species:

#### *S. nodosa* group; table 1

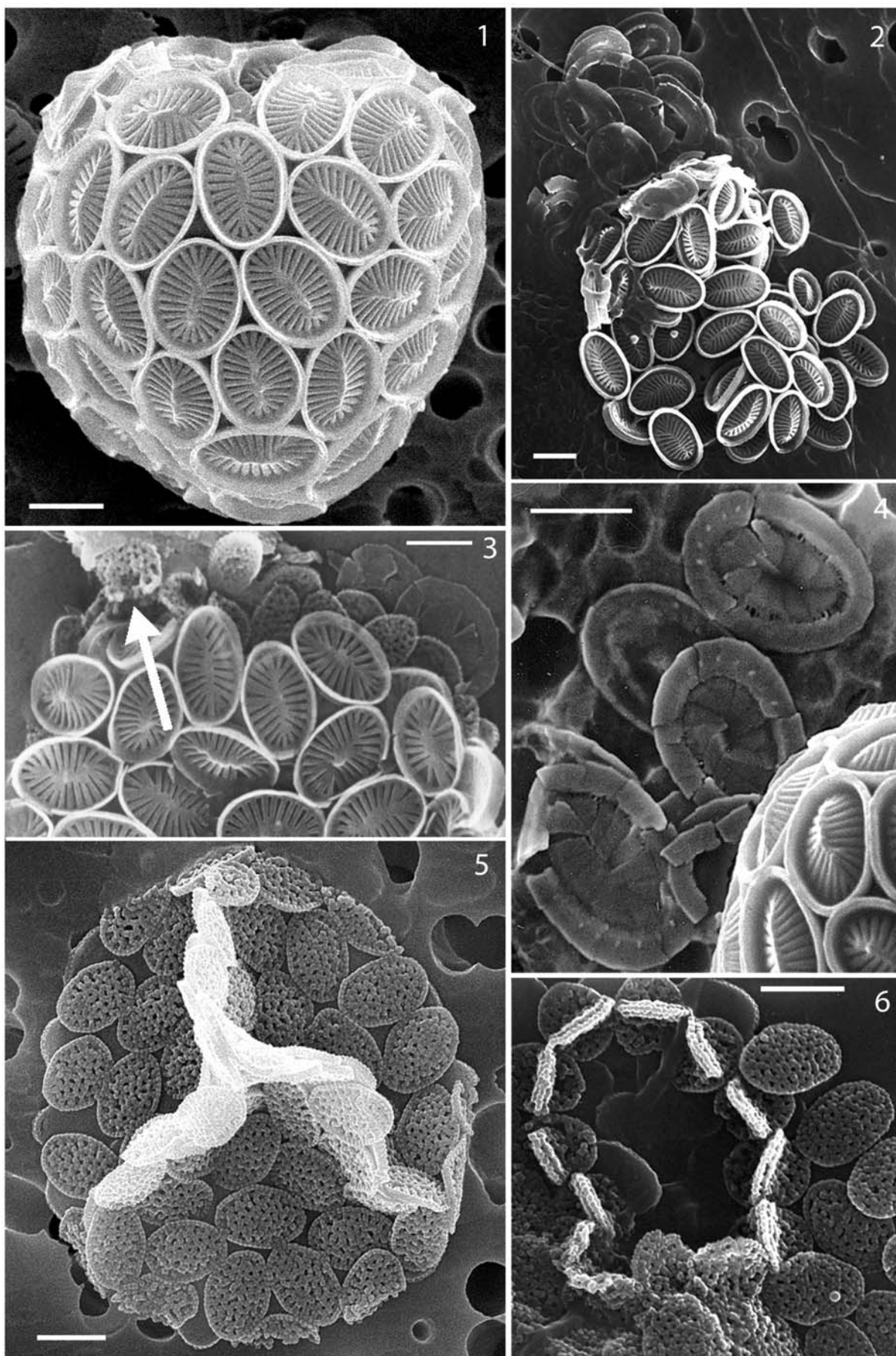
The *Syracosphaera nodosa* group of Young et al. (2003) contains dithecate species that have body coccoliths with only one, proximal, flange and without a central spine; these are the simplest kind of syracosphaerid muroliths. Their exothecal coccoliths are of the planolith-type. This group contains 13 species in seven subgroups. Five subgroups have differentiated circum-flagellar coccoliths with a spine, while their planoliths have a rim that is either symmetrical (the *nodosa*-, *anthos*- and *nana*-subgroups), or asymmetrical with a folded or laminated part (the *bannockii*- and *squamosa*-subgroups). Species of the *nodosa*-subgroup have body coccoliths with clearly defined radial laths, and exothecal planoliths that may cover the entire endotheca. Their planoliths have a prominent cycle of radial el-

#### PLATE 11

*Syracosphaera nana*; emend. Kleijne et Cros; Scale bars = 1 µm.

Figure 3 was published previously in Kleijne (1991) as *Syracosphaera* sp. type A holococcolith and heterococcolith stages, and figs. 1-2, 4-6 in Cros (2000), Cros et al. (2000), Cros (2002) and Cros and Fortuño (2002) as *Syracosphaera nana*.

- 1 Coccosphere showing body coccoliths with a central area vaulted into a whaleback shape; FANS-3/M11/60m.
- 2 Collapsed coccosphere showing two circum-flagellar coccoliths and exothecal coccoliths; FRONTS-95/23D/50m.
- 3 Detail of partly collapsed combination coccosphere, showing body muroliths and exothecal planoliths of heterococcolith-bearing phase, and planar holococcoliths with (arrow) and without bridge of holococcolith-bearing phase; APNAP-I/T86-14R/20m.
- 4 Oval exothecal coccoliths with small nodes on the rim elements and a central part of large plate-like elements; MESO-96/I3/70m.
- 5 Coccosphere of holococcolith phase, showing planar coccoliths; MESO-96/G6/5m.
- 6 Holococcolith phase; detail of apical area with flagellar opening surrounded by holococcoliths with high transverse ridge; FRONTS-95/26W/30m.



elements and a centre that consists of two large, plate-like elements. Included species are *S. nodosa* and *S. serrata* sp. nov. *Syracosphaera nana* has been transferred from the *nodosa*- to the new *nana*-subgroup, since its oval planoliths lack the two characteristic central elements of the *nodosa*-subgroup. Instead, its central area is almost entirely covered by large, plate-like radial elements. The *anthos*-subgroup, with *S. anthos*, has large circular planoliths with a broad rim and a conical central part.

The species of the *bannockii*-subgroup have simple, more or less flat, asymmetrical planoliths; their central area consists of radial elements and a small or larger part of the rim is curved upwards. The species included are *S. bannockii*, *S. delicata* and *S. orbiculus*. We found three new species with more complex asymmetrical planoliths that seem to be modifications of the more or less flat planoliths in the *bannockii*-subgroup. They are placed in the new *squamosa*-subgroup, the former 'laminated type' of Young et al. (2003). The planoliths of these new species show different degrees of lamination, that varies from one laminated long side in *S. squamosa* sp. nov., to an apparently thickly stratified centre in *S. reniformis* sp. nov., or an almost completely stratified coccolith in *S. operculata* sp. nov. These species have a rim that consists of complexly-shaped elements with a stepped profile (see section on Terminology; and Young et al. 2004, fig. 9). Cros (2000) described that the asymmetrical exothecal coccoliths of species of the *bannockii*-subgroup often occur in an imbricate, ribbon-like arrangement. Later, Young et al. (2009) reported for species of this and the *squamosa*-subgroups, that exothecal coccoliths may occur as a pair of ribbon-like chains attached to the flagellar pole.

Two subgroups contain species with a monomorphic endotheca. *Syracosphaera leptolepis* sp. nov. is placed in the new *leptolepis*-subgroup, characterised by the planoliths that have a central area of dextrally oblique radial elements. Although a similar structure is found in the *bannockii*-subgroup, the species cannot be included in that subgroup because of its flat symmetrical planolith rim and its endothecal monomorphism. The *lamina*-subgroup contains *S. lamina* and *S. tumularis*; the central part in their planoliths consists of two plates.

#### *S. noroîtica* group; table 2

The new *Syracosphaera noroîtica* group is raised to accommodate the three species that bear two layers of syracosphaerid muroliths of the simplest type. Both endothecal and exothecal muroliths bear only a proximal flange; they have neither distal nor mid-wall flanges. The endothecal coccoliths are varimorphic: their spine-like central structure decreases in size from apical to antapical pole, where it is non-existent. The murolith structure of the exothecal coccoliths was first recog-

nized by Cros (2000) for coccoliths of *S. noroîtica*. Other species in this group are *S. castellata* sp. nov. and *S. florida*.

The group is equivalent to the previous *noroîtica*-type of Young et al. (2003) that was placed inside the *S. pulchra* group and next to the *prolongata*-subgroup, because of the similarity in their exothecal coccolith structure. Since our classification scheme is based primarily on number of flanges in the endothecal coccoliths, the *S. noroîtica* group is separated from the species of the *S. pulchra* group that have endothecal coccoliths with three flanges.

#### *S. molischii* group; table 3

The *Syracosphaera molischii* group of Young et al. (2003) is a highly diverse group; it contains 13 species that show all possible variations in *Syracosphaera* coccosphere morphology, viz. mono- and dithecatism, as well as endothecal mono-, di- and trimorphism. The species bear placolith-like body coccoliths, while planoliths of various shapes may form a complete or an incomplete exotheca.

The *molischii*-subgroup contains dithecate species with di- or trimorphic endothecal muroliths, and complex planoliths occurring around the flagellar pole. The planoliths are either elliptical (table 3, *molischii*-subgroup, III), or they bear a wing-like extension (I, II). Species that were already placed in this subgroup are *S. marginaporata*, *S. molischii* and *S. ossa*, and we now include *S. andruleitii* sp. nov. and *S. hastata* sp. nov. All five species have circum-flagellar coccoliths with a prominent spine. *Syracosphaera molischii* and *S. ossa* usually bear an antapical coccolith with a central spine, equivalent to the spine-bearing antapical coccoliths of *S. hastata* sp. nov. (*molischii*-subgroup, I); see e.g. Cros and Fortuño (2002, figs. 31A, 32C). The rare species *S. epigrosa* is provisionally placed in this subgroup on resemblance of body coccolith morphology, as well as on the presence of an antapical coccolith and circum-flagellar coccoliths. No images of exothecal or circum-flagellar coccoliths have yet been published; Okada and McIntyre (1977, pl. 7, fig. 5) and Young et al. (2003, p. 48, pl. 21, fig. 6) show only endothecal body coccoliths and one antapical coccolith. However, the species is known to have circum-flagellar coccoliths with a central spine that bears very large blade-like extensions (personal communication Alexandra Zeltner, 1998, and Doan Nhu Hai, unpublished PhD thesis 2002).

Species of the *borealis*-subgroup have a monomorphic endotheca and elliptical exothecal coccoliths with a convex shape (Young et al. 2003). *Syracosphaera exigua* has planoliths with a concavo-convex shape. Okada and McIntyre (1977) described *S. borealis* without its exothecal coccoliths; later, these folded, saddle-shaped exothecal coccoliths were shown by

#### TABLES 1-4

Classification scheme for species of the genus *Syracosphaera*, based on number of flanges in the body coccoliths, shape and presence/absence of exothecal coccoliths, and endothecal coccolith morphology. This classification scheme is based on earlier schemes of Cros (2000) and Young et al. (2003) and is extended with the new species, as well as the new *Syracosphaera noroîtica* group and three new subgroups within the three other groups. BCs = body coccoliths; CFCs = circum-flagellar coccoliths; XCs = exothecal coccoliths; AAC = antapical coccolith; ass. = forms life-cycle association with the named taxon; ? ass. = possible life-cycle association; [ ] = reference to association. The holococcolith-bearing life-cycle stages are given by their (previous) holococcolithophore name. For coccolith morphology, see Terminology.

TABLE 1

Classification scheme for *Syracosphaera* species bearing body coccoliths with one flange and exothecal planoliths.


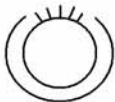
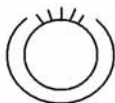
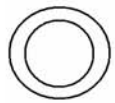
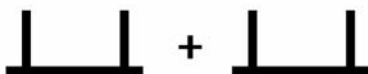
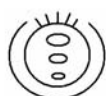
<b><i>S. nodosa</i> group</b> <ul style="list-style-type: none"> <li>• BCs with proximal flange; no spine</li> <li>• Dithcate coccospheres</li> <li>• XCs planoliths; symmetrical or asymmetrical</li> </ul> 	
endotheca dimorphic  	<b><i>nodosa</i>-subgroup</b> BCs with slightly flaring wall; clearly defined radial laths CFCs with spines XCs circular; prominent radial cycle; central structure: 2 plates  <i>S. nodosa</i> Kamptner 1941 ? ass. <i>Helladosphaera cornifera</i> (Schiller 1913) Kamptner 1937 [Cros et al. 2000] <i>S. serrata</i> Kleijne et Cros sp. nov.
planoliths symmetrical	<b><i>anthos</i>-subgroup</b> BCs with domal central area CFCs with robust spines XCs robust, circular; broad rim; central area conical  <i>S. anthos</i> (Lohmann 1912) Janin 1987 ass. <i>Periphyllophora mirabilis</i> (Schiller 1925) Kamptner 1937 [Cros et al. 2000]
	<b><i>nana</i>-subgroup</b> BCs with convex central area with axial ridge; low wall CFCs with small blunt spines XCs oval; axially elevated central area  <i>S. nana</i> (Kamptner 1941) Okada et McIntyre 1977; emend. Kleijne et Cros ass. <i>S. nana</i> HOL [Cros et al. 2000]
endotheca dimorphic  	<b><i>bannockii</i>-subgroup</b> BCs with low wall; broad and flat radial laths; flat central structure CFCs have spines with simple rounded tip XCs with asymmetric rim and narrow medial cycle; often in ribbon-like chains  <i>S. bannockii</i> (Borsetti et Cati 1976) Cros et al. 2000 ass. <i>Corisphaera</i> sp. type A of Kleijne 1991 [Cros et al. 2000] ass. <i>Zygosphaera bannockii</i> (Borsetti et Cati 1976) Heimdal 1982 [Cros et al. 2000] <i>S. delicata</i> Cros et al. 2000 ? ass. <i>Corisphaera</i> sp. type B of Kleijne 1991 [Cros et al. 2000] <i>S. orbiculus</i> Okada et McIntyre 1977
planoliths asymmetrical	<b><i>squamosa</i>-subgroup</b> BCs with low wall and flat central structure CFCs with spines XCs asymmetrical, thick; partly or entirely laminated; occasionally in ribbon-like chains  <i>S. operculata</i> Kleijne et Cros sp. nov. <i>S. reniformis</i> Kleijne et Cros sp. nov. <i>S. squamosa</i> Kleijne et Cros sp. nov.
endotheca monomorphic  	<b><i>lamina</i>-subgroup</b> BCs high and thin wall with corrugated margin; clearly defined radial laths; prominent longitudinal central structure CFCs not differentiated XCs subcircular, weakly calcified; narrow medial cycle; central structure: 2 plates  <i>S. lamina</i> Lecal-Schlauder 1951 <i>S. tumularis</i> Sánchez-Suárez 1990
planoliths symmetrical	<b><i>leptolepis</i>-subgroup</b> BCs with slightly flaring, smooth wall; clearly defined radial laths CFCs not differentiated XCs subcircular; small and very delicate; central structure: radial elements  <i>S. leptolepis</i> Kleijne et Cros sp. nov.

TABLE 2

Classification scheme for *Syracosphaera* species bearing body coccoliths with one flange and exothecal muroliths.

<b><i>S. noroitica</i> group</b> <ul style="list-style-type: none"><li>• BCs with proximal flange; usually with a spine</li><li>• Dithecate coccospheres</li><li>• XCs muroliths with proximal flange</li></ul>			
endotheca varimorphic 	BCs central structure decreasing in size towards the antapical pole; at antapical pole BCs without a central structure CFCs spine-bearing, with bifurcate tip XCs muroliths with beaded proximal flange  <i>S. castellata</i> Kleijne <i>et</i> Cros sp. nov. <i>S. florida</i> Sánchez-Suárez 1990 <i>S. noroitica</i> Knappertsbusch 1993		

Winter and Sieser (1994, image by C. Samtleben). Similar saddle-shaped planoliths are found in *S. hirsuta* sp. nov., which warrants its inclusion in this subgroup. The simple elliptical planoliths of *S. ampliata* are concave and slightly folded, with a convex central area (Cros, unpublished results). *Syracosphaera rotula*, the other species with a monomorphic endotheca, is placed in the *rotula*-subgroup. Its circular planoliths have a convexly bent rim and a funnel-shaped central area – a flat central part surrounded by obliquely raised radial laths (see e.g. Young et al. 2003, pl. 22, fig. 3).

At present, no exothecal coccoliths are known for only two *Syracosphaera* species, viz. *S. halldalii* and *S. protrudens*. They are placed in the monothecate dimorphic *halldalii*-subgroup, characterised by their vertical coccolith wall and flat distal flange; their circum-flagellar coccoliths bear a prominent spine.

#### *S. pulchra* group; table 4

The *Syracosphaera pulchra* group of Young et al. (2003) includes seven dithecate species that bear body coccoliths with three flanges and an exotheca that consists of either muroliths with two or three flanges, or dome-shaped coccoliths. Dome-shaped exothecal coccoliths occur in the well-known species *S. pulchra* and *S. histrica* of the *pulchra*-subgroup. Species of the other subgroups bear exothecal muroliths.

The species of the *prolongata*-subgroup, *S. pirus* and *S. prolongata*, are well-known for their extraordinary coccosphere shapes; see e.g. the tube-like coccospheres in Cros and Fortuño (2002, fig. 57A) and Young et al. (2003, pl. 18, figs. 9–11). Their sub-circular exothecal muroliths have a beaded proximal flange.

*Syracosphaera didyma* sp. nov. is placed in the *dilatata*-subgroup of Young et al. (2003), that also contains *S. dilatata*. Species of this subgroup bear body coccoliths with three flanges, of which the mid-wall flange is weakly developed and usually has the form of a ring of bead-like nodes. Their endothecal and exothecal coccoliths look very similar (Cros 2000; Cros 2002). *Syracosphaera corolla* bears very large funnel-shaped, elliptical exothecal muroliths. The species has been removed from the *dilatata*-subgroup and is now placed in the new *corolla*-subgroup, the only subgroup in the *S. pulchra* group with endothecal monomorphism.

## DISCUSSION

The description of the new species that were previously known in open nomenclature raise the number of formally described *Syracosphaera* species from 26, as distinguished by Young et al. (2003) and Jordan et al. (2004), to 36. Like most other *Syracosphaera* species, these ten species have a rare to very rare abundance in the plankton; they are known from only a few records. The identification of ten new *Syracosphaera* species made it necessary to modify the classification scheme by Young et al. (2003), in order to accommodate all species. Our new classification scheme has one new main group and three new subgroups, see tables 1–4. We established the *Syracosphaera* taxonomy on the newly described species and the detailed information from earlier observations (e.g. Gaarder and Heimdal 1977; Okada and McIntyre 1977; Heimdal and Gaarder 1980, 1981; Kleijne 1993; Cros 2000; Cros 2002; Cros and Fortuño 2002; Young et al. 2003; 2009).

### Body coccolith morphology

Our classification of the *Syracosphaera* species is primarily based on the distinguishing characteristics of *Syracosphaera* species: the structure of the body coccolith and the number of flanges. A classification based on number of flanges results in three instead of four of our main groups. However, in combination with differences in central area structure, we can divide the species with only a proximal flange in two main groups: species bearing body coccoliths with and without a central spine, viz. the *S. noroitica* group and the *S. nodosa* group. A classification based on the structure of wall elements, viz. the shape of the V- and/or R-units, and central area elements, the T-units, would be preferable, but is beyond the scope of this study. Molecular genetic research is limited to one species, since *Syracosphaera pulchra* is the only species of the genus that has yet been cultured (Geisen et al. 2002; Houdan et al. 2004). Due to the lack of such crystallographic and phylogenetic data we use body coccolith morphology, in combination with exothecal coccolith structure.

### Presence of exothecal coccoliths

Species are further classified by characteristics of the coccosphere: the presence or absence of exothecal coccoliths. The possession of dithecism versus monothecism can be used in characterizing subgroups. Since often only endothecal coccoliths are found, without their matching exothecal cocco-

TABLE 3

Classification scheme for *Syracosphaera* species bearing body coccoliths with two flanges.

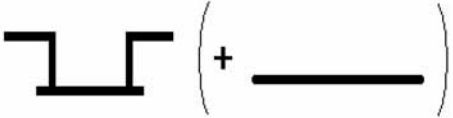
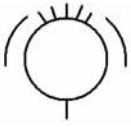
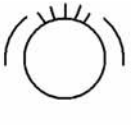
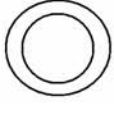
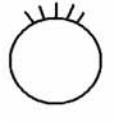
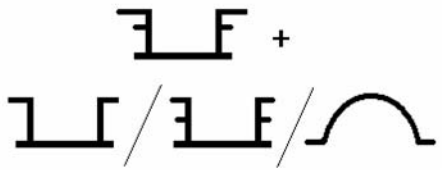
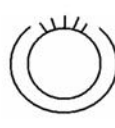
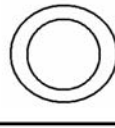
<b><i>S. molischii</i> group</b> <div> <ul style="list-style-type: none"> <li>• BCs with proximal and distal flanges (placolith-like)</li> <li>• Mono- or dithecate coccospheres</li> <li>• XCs planoliths of various shapes, or not found</li> </ul>  </div>		
dithecate	<b><i>molischii</i>-subgroup</b>	CFCs with prominent spine; distal flange usually narrow XCs complex planoliths, around flagellar pole; concave central area
endotheca trimorphic	I -	AAC(s) with spine XCs with wing-like extension, asymmetrical flange; 2 horseshoe-shaped slits in central area
		<i>S. hastata</i> Kleijne <i>et</i> Cros sp. nov. <i>S. molischii</i> Schiller 1925 ? ass. <i>Gliscolithus amitakareniae</i> Norris 1985 [Malinverno <i>et al.</i> 2008] ? ass. <i>Anthosphaera fragaria</i> Kamptner 1937 emend. Kleijne 1991 [Cros <i>et al.</i> 2000] <i>S. ossa</i> (Lecal 1966) Loeblich <i>et</i> Tappan 1968  Provisionally placed here (XCs not known): <i>S. epigrosa</i> Okada <i>et</i> McIntyre 1977
endotheca dimorphic	II -	AAC(s) not known XCs with wing-like extension, asymmetrical flange; 2 horseshoe-shaped slits in central area
		<i>S. marginaporata</i> Knappertsbusch 1993 ? ass. <i>Anthosphaera</i> sp. [Cros and Fortuño 2000]
	III -	AAC(s) not known XCs symmetrical; thick elliptical planoliths
		<i>S. andruleitii</i> Kleijne <i>et</i> Cros sp. nov.
dithecate	<b><i>borealis</i>-subgroup</b>	CFCs not differentiated XCs simple elliptical planoliths; general shape convex (may be folded into saddle-shape)
endotheca monomorphic		<i>S. ampliora</i> Okada <i>et</i> McIntyre 1977 <i>S. borealis</i> Okada <i>et</i> McIntyre 1977 <i>S. exigua</i> Okada <i>et</i> McIntyre 1977 <i>S. hirsuta</i> Kleijne <i>et</i> Cros sp. nov.
	<b><i>rotula</i>-subgroup</b>	CFCs not differentiated XCs circular, with convexly bent rim and concave central area
		<i>S. rotula</i> Okada <i>et</i> McIntyre 1977
monothecate	<b><i>halldalii</i>-subgroup</b>	BCs with vertical wall and horizontal distal flange CFCs with prominent spine XCs not found
endotheca dimorphic		<i>S. halldalii</i> Gaarder in Gaarder <i>et</i> Hasle 1971 <i>ex</i> Jordan <i>et</i> Green 1994 <i>ass. Calyptrolithina divergens</i> var. <i>tuberosa</i> Heimdal in Heimdal <i>et</i> Gaarder 1980 [Triantaphyllou <i>et al.</i> 2004] <i>S. protrudens</i> Okada <i>et</i> McIntyre 1977
		

TABLE 4

Classification scheme for *Syracosphaera* species bearing body coccoliths with three flanges.

<div> <b><i>S. pulchra</i> group</b> <ul style="list-style-type: none"> <li>• BCs with 3 flanges; robust; mid-wall flange diverse</li> <li>• Dithecate coccospheres</li> <li>• XCs muroliths with 2 or 3 flanges, or domal</li> </ul>  </div>		
<div> <b>endotheca dimorphic</b>  </div>	<b><i>pulchra</i>-subgroup</b>	BCs with 3 flanges CFCs spine-bearing, with notched tip XCs domal  <i>S. histrica</i> Kamptner 1941 ? ass. <i>Calyptosphaera oblonga</i> Lohmann 1902 [Malinverno et al. 2008] ? ass. <i>Calyptrolithophora papillifera</i> (Halldal 1953) Heimdal in Heimdal et Gaarder 1980 [Cros et al. 2000]  <i>S. pulchra</i> Lohmann 1902 ass. <i>Calyptosphaera oblonga</i> Lohmann 1902 [Cros et al. 2000] ass. <i>Calyptosphaera pirus</i> Kamptner 1937 [Geisen et al. 2000]
	<b><i>prolongata</i>-subgroup</b>	BCs with 3 flanges; central spine or boss CFCs spine-bearing, with bifurcate tip XCs muroliths with spine; beaded proximal flange  <i>S. pirus</i> Halldal et Markali 1955 <i>S. prolongata</i> Gran 1912 ex Lohmann 1913
	<b><i>dilatata</i>-subgroup</b>	BCs mid-wall flange is folded or ring of bead-like nodes CFCs spine-bearing; mid-wall flange is ring of bead-like nodes XCs muroliths, similar to BCs, but larger and thinner  <i>S. didyma</i> Kleijne et Cros sp. nov. ? ass. <i>Homozygospheara arethusae</i> (Kamptner 1941) Kleijne 1991 [Cros et al. 2000] <i>S. dilatata</i> Jordan et al. 1993
<div> <b>endotheca monomorphic</b>  </div>	<b><i>corolla</i>-subgroup</b>	BCs mid-wall flange developed as a ring of rods CFCs not differentiated XCs large, funnel-shaped muroliths  <i>S. corolla</i> Lecal 1966

liths, this character must be applied in combination with the number of flanges in the body coccoliths.

The structure of the exothecal coccoliths can be used to further subdivide the main groups; a unique combination involving a certain type of exothecal coccolith may characterize a new subgroup. Exothecal coccoliths vary in shape from flat, nearly flat and laminated planoliths, to muroliths and domal coccoliths.

#### Exothecal coccolith morphology

Exothecal coccoliths may show extreme morphologies (see e.g.: pl. 4, fig. 4; pl. 5, fig. 4; pl. 7, fig. 4; pl. 10, fig. 4). Their morphology may be a more important distinctive character than the number of flanges in the body coccoliths, where presence and number of flanges simply seems to be the result of variation in lateral extension of the V- and/or R-crystal units within a group of species. E.g. sometimes it is difficult to distinguish between a flaring wall and a wall with a distal flange. It seems plausible that within a phylogenetic lineage a straight coccolith

wall may be developed into a lateral extension, the distal flange, or that a smooth flange is developed into a flange with ornamentation, resulting in a new species. Developing a new exothecal coccolith type, on the other hand, seems to be a more significant step. The variation in exothecal coccolith morphology indicates that grouping should be based on exothecal coccolith type first and secondly on body coccolith shape, instead of the other way around. However, exothecal coccoliths are not always present – they may be detached or may be unknown for certain species – and, therefore, can only be used in combination with other characteristics of the species.

#### Presence of circum-flagellar coccoliths

Most *Syracosphaera* species possess a dithecate coccosphere with mono- or dimorphic, and occasionally tri- or varimorphic, endothecal coccoliths. However, nine species (25%) show endothecal monomorphism. Absence of circum-flagellar coccoliths in combination with endothecal and exothecal coccolith

morphology results in the identification of five subgroups: the *lamina*- and *leptolepis*-subgroups in the *S. nodosa* group; the *borealis*- and *rotula*-subgroups in the *S. molischii* group; and the *corolla*-subgroup in the *S. pulchra* group.

### Holococcolith-bearing phases

Five *Syracosphaera* species are known to be part of a life-cycle association that also includes a holococcolith-bearing phase. Of these, *S. bannockii* has two intraspecific holococcolithophore morphotypes, and *S. pulchra* is known to form associations with two different holococcolithophores, as a result of cryptic speciation (Cros et al. 2000; Geisen et al. 2002). Six other species show less well-established associations with one or two holococcolithophores (tables 1-4).

The examples of proven life-cycles occur in all main groups, except for the *S. noroîtica* group with its three species that bear exothecal muroliths. All *Syracosphaera* species involved in life-cycle associations possess a dimorphic endotheca and, thus, a circum-flagellar opening. There is no obvious correlation between holococcolith-bearing and heterococcolith-bearing stages, with regard to coccolith morphology, mono- or dithecatism, and presence of a flagellar opening in both stages.

### Available generic names

It is tempting to subdivide the large number of *Syracosphaera* species and transfer subgroups to new genera. For three of the most distinctive subgroups previously described genera are available. The genus *Deutschlandia* Lohmann 1912 could be used again for the *anthos*-subgroup; *Gaarderia* Kleijne 1993 for the *corolla*-subgroup; and *Caneosphaera* Gaarder in Gaarder and Heimdal 1977 for the *halldalii*-subgroup. If this was done then the species of the *S. noroîtica* group, with their striking combination of endothecal and exothecal muroliths that have only a proximal flange, should also be placed in a new genus. Alternatively, these genera could be used for the main groups, rather than for subgroups. I.e. *Deutschlandia* for the *S. nodosa* group; *Caneosphaera* for the *S. molischii* group; *Syracosphaera* for the *S. pulchra*-subgroup; and a new genus for the *noroîtica* group. However, the classification of *Syracosphaera* spp. is still rather artificial, based on small differences in structure of the body coccoliths, the presence/absence of circum-flagellar coccoliths and morphology of exothecal coccoliths. Therefore, it seems not justified to transfer the seven species from these subgroups, or even all species from three main groups, from *Syracosphaera* to other genera. Molecular genetics and research on coccolith ultra-structure will provide new data to allow classification of *Syracosphaera* species. And whilst we strongly suspect that it will broadly support our morphological classification, it will also inevitably change aspects of it. To avoid great nomenclatural instability we prefer to continue with the group/subgroup classification instead of making a formal generic classification.

### CONCLUSIONS

Ten new species of the highly diverse genus *Syracosphaera* have been described and an emended description has been given for *S. nana*. Like many other *Syracosphaera* species, most of these eleven taxa have a rare to very rare abundance in the plankton. Although not numerically important, they significantly increase the *Syracosphaera* species diversity. The descriptions of coccolith structure and new kinds of exothecal coccoliths increases our knowledge of the morphological variation within *Syracosphaera* and can be used in tracing phylogenies between the groups and subgroups of *Syracosphaera*

and other syracosphaerid genera. A classification based on ultra-structure of body coccolith wall elements and molecular genetics will result in a more natural classification, however, at the moment that is far from possible. Instead, we have used morphological characteristics of coccospheres and coccoliths to distinguish four main groups and 15 subgroups of *Syracosphaera* species.

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