

Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean

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Rhabdosphaerids were consistently present as a minor constituent of the 1985 summer coccolithophorid flora in surface waters of the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic. Sixteen taxa are identified, belonging to seven genera, including the two new combinations *Cyrtosphaera aculeata* and *C. cucullata* and the new species *C. lecaliae* sp. nov. of *Cyrtosphaera* gen. nov., and the new combination *Anacanthoica cidaris*. An emended description is given for the genus *Acanthoica*, of which the new species *A. biscayensis* and a type in open nomenclature are described. All species are illustrated by SEM-micrographs and their occurrences are mapped. The most frequently occurring species were *Palusphaera vandeli*, present in low numbers along the entire sampling transect, *Discosphaera tubifera* in the warm oligotrophic water of the Red Sea, *Rhabdosphaera clavigera* in the somewhat colder water of the Mediterranean Sea, and *Algirosphaera robusta* in the Indian Ocean, indicative for upwelling conditions.

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Introduction

A series of surface water samples has been collected in summer 1985 from the Indian Ocean, Red Sea, Mediterranean Sea and eastern North Atlantic, during Cruise Gx of the Indonesian-Dutch Snellius-II Expedition, the homeward voyage of the Dutch R.V. 'Tyro' (Figs. 1, 2). The species composition and coccolithophorid standing crop in these surface waters were determined to identify the relation of floral assemblages to watermasses, and the geographic intraspecific variation of the various species.

Coccolithophorid species can be roughly divided into two groups, the holococcolith-bearing species and the heterococcolith-bearing species. However, some species produce holococcoliths as well as heterococcoliths in different stages of their life cycle (Parke & Adams, 1960; Rowson et al., 1986; Samtleben & Bickert, 1990; Samtleben & Schröder, 1990; Kleijne, 1991). Species of the family Rhabdosphaeraceae Lemmerman, 1908 are known to have heterococcolith-bearing stages only.

This publication describes and illustrates species of the family Rhabdosphaeraceae, class Prymnesiophyceae; it reviews the taxonomy, records their frequency and

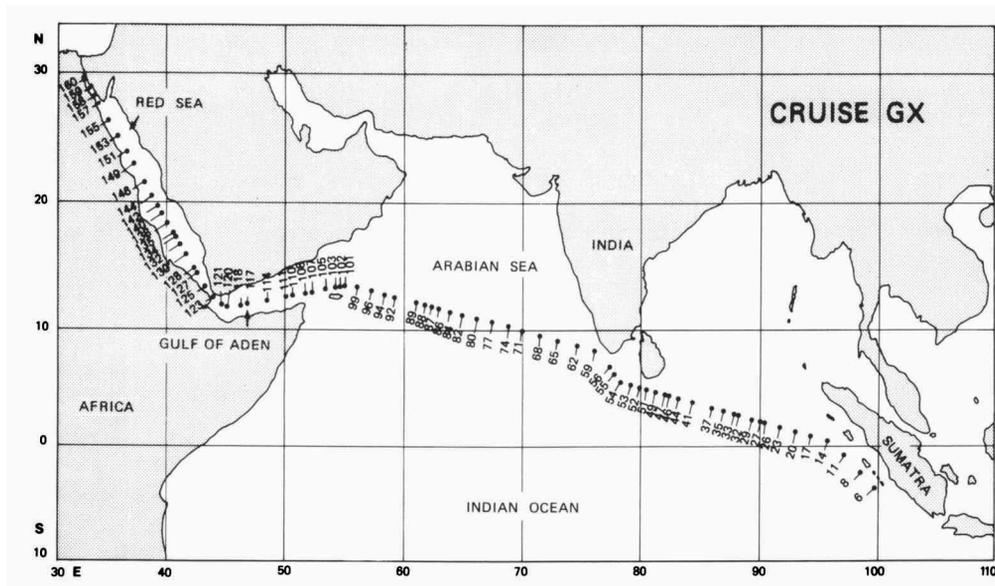


Fig. 1. Location map of selected samples of the Snellius-II Expedition, Cruise Gx, in the northern Indian Ocean and the Red Sea. See Kroon & Kleijne (1986) for coordinates.

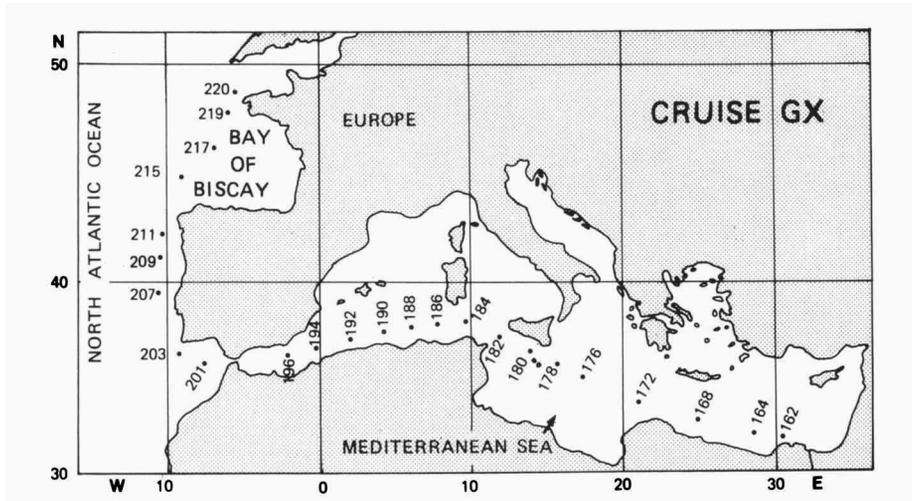


Fig. 2. Location map of selected samples of the Snellius-II Expedition, Cruise Gx, in the Mediterranean Sea and eastern North Atlantic Ocean. See Kroon & Kleijne (1986) for coordinates.

distribution and evaluates their usefulness for paleoceanography. An earlier publication reports on the holococcolithophorids (Kleijne, 1991), and reports on the families Coccolithaceae Kamptner, 1928 and Noelaerhabdaceae Jerković, 1970, collected during Cruise Gx, are in preparation.

MATERIAL AND METHODS

During Cruise Gx in June-July 1985, water samples were taken from a depth of 0-5 m (Figs. 1, 2; for coordinates see Kroon & Kleijne, 1986). From a total of 220 samples a representative selection of 101 samples were studied. Additionally the rhabdosphaerids of three samples of Cruise G0, the outward voyage of the Snellius-II Expedition (from the Netherlands to Indonesia, May-July 1984) and six samples of Cruise APNAP I (North Atlantic; Ganssen, 1986) were studied to optimize the species descriptions (Table 1).

The samples were examined with a Scanning Electron Microscope. Cocospheres and free coccoliths were counted in 25 fields under 600 \times and 1500 \times magnification, and additionally 20 fields were examined at a magnification of 800 \times to find rare species. The free coccoliths were converted to complete cocospheres on the basis of an average number of coccoliths per cocosphere for every species (see Systematic descriptions). The sum of the cocospheres is presented in Table 2 as the observed cocospheres of the rhabdosphaerid taxa per sample of Cruise Gx. Species that are represented only by some free coccoliths which do not add up to one cocosphere and rare species found at 800 \times show in Table 2 by 'p' (present). See Kleijne (1991) for more detailed information on sampling and determination of community structure and standing crop.

Table 1. Position of samples referred to in the species descriptions, taken during Cruise G0 of the Snellius-II Expedition (G0-..; Gulf of Aden and Arabian Sea) and Cruise APNAP I (T86-..; North Atlantic). D = deckwash pump; R = Rosette sampler.

Station	Date (day-month-year)	Position longitude	latitude	Sample	Depth (m)
G0-106	14-06-84	12°28.9'N	47°34.0'E	D	0-5
G0-110	15-06-84	12°41.3'N	50°57.3'E	D	0-5
G0-135	20-06-84	08°48.6'N	70°17.7'E	D	0-5
T86-C-15	19-08-86	53°29.2'N	27°08.1'W	D	0-5
T86-C-36-L	26-08-86	42°15.3'N	25°40.4'W	D	0-5
T86-8R,10,C	26-08-86	42°15.3'N	25°40.4'W	R	10
T86-C-51-A	31-08-86	34°19.9'N	34°23.8'W	D	0-5
T86-14R,20,C	02-09-86	31°26.9'N	36°14.2'W	R	20
T86-C-64	05-09-86	28°34.9'N	38°40.5'W	D	0-5

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Rhabdoliths vs. cyrtoliths

The term 'cyrtolith' was not defined until 1954 by Braarud et al. as a calotte-shaped 'spine-bearing' coccolith, without mentioning the coccoliths without a process. In recent literature all Rhabdosphaeraceae coccoliths have been regarded as 'cyrtoliths': convex disc-shaped heterococcoliths with or without a central process (Halldal & Markali, 1955; McIntyre & Bé, 1967; Okada & McIntyre, 1977; Reid, 1980; Norris, 1984). Norris (1984) used 'rhabdoliths' for process-bearing cyrtoliths, while in the early publications this term had been used for process-bearing coccoliths only, with the more or less flat coccoliths of e.g. *Acanthoica* being simply referred to as 'coccoliths'

SAMPLES	SPECIES												
		<i>Algitosphaera robusta</i>	<i>Falsusphaera vandeli</i>	<i>Rhabdosphaera clavigera</i>	<i>Acanthoica quattrosphina</i>	<i>Cyrtosphaera aculeata</i>	<i>Discosphaera tubifera</i>	<i>Acanthoica acanthifera</i>	<i>Acanthoica maxima</i>	<i>Anacanthoica cidaris</i>	<i>Rhabdosphaera xiphos</i>	<i>Acanthoica bisulcata</i>	
NORTHEASTERN INDIAN OCEAN	8	1 0.5	p -	p -									
	14												
	17												
	20												
	23	p -											
	26												
	27	p -											
	29												
	33												
	35												
	41												
	44	p -											
	46	2 0.6											
	47	1 0.5											
49	2 1.0												
SOUTH OF INDIA	52	3 1.5											
	53	p -											
	54	p -											
	55												
	55												
EASTERN ARABIAN SEA	62	1 0.5	1 0.5										
	65	p -											
	68												
	71	1 0.3											
	74	p -											
	77	2 0.5											
	80												
	82	p -											
	84	1 0.3	1 0.2										
	87	p -	1 0.3										
	87												
WESTERN ARABIAN SEA	88	1 0.3											
	89	p -											
	92	7 2.3											
	94	15 6.9	1 0.5										
	96	6 2.3											
	99	1 0.4											
	101	9 3.8											
	102												
	103	p -											
	105	1 0.5											
	107	1 0.8											
	108	2 1.1											
	108												
GULF OF ADEN	118												
	120		p -										
RED SEA	132		p -										
	134												
	135												
	138		p -										
	140		p -										
	142		p -										
	149												
	151												
	153		p -										
	155												
	157												
	158												
	159		8 3.9	p -									
159													
MEDITERRANEAN SEA	162		p -	3 0.8									
	164		p -										
	168												
	172												
	178												
	180												
	184												
	186												
	188												
	190												
	192		1 0.2										
194			6 1.5										
196		p -											
EASTERN NORTH ATLANTIC	201												
	207												
	209			1 0.5									
	211												
	215												
	217			2 0.8									
	219												

Table 2. Distribution of Rhabdosphaeraceae species along the Cruise Gx transect: (a) number of observed coccospheres, and (b) absolute frequency (10^3 cells/l). Rare occurrences, and species that are represented only by some free coccoliths that do not add up to one coccosphere, are given by 'p' (see Material and Methods).

(Schmidt, 1870; Murray & Blackman, 1898; Kamptner, 1941, p. 95). Deflandre (1952, p. 452) used 'calyptroliths' for the coccoliths of *Acanthoica* and *Anacanthoica*, a term now used for cap-shaped holococcoliths only, since the separation of holococcoliths from heterococcoliths (Braarud et al., 1955; Halldal & Markali, 1955).

During the present study it became obvious that there is no real difference between rhabdosphaerid coccoliths with or without a central process. E.g. the process-bearing pole coccoliths of *Acanthoica jancheni* ('rhabdoliths'; Pl. 5, fig. 6) closely resemble the coccoliths with a conical central area of *Anacanthoica cidaris* ('cyrtoliths'; Pl. 7, figs. 2-4).

I propose to use the original term 'rhabdolith' as a taxo-descriptive term for all coccoliths of the family Rhabdosphaeraceae, to emphasize the conformity in coccolith structure of characteristic rim and central area cycles. Cyrtoliths, then are the exothecal coccoliths that occur in the family Syracosphaeraceae (Okada & McIntyre, 1977). They are highly variable in shape and their structure differs considerably from that of rhabdoliths.

Morphological account

Overall rhabdolith morphology

Rhabdosphaeraceae are characterized by having rhabdoliths: more or less calotte-shaped heterococcoliths consisting of a rim of two cycles of elements and a central area of one to three cycles of elements arranged in dissimilar patterns (Fig. 3a-c). Many species have specialized rhabdoliths with a distally extending process in the central area. This process consists of spirally arranged lath-shaped elements of the lamellar cycle (Pl. 4, fig. 1; Pl. 8, fig. 3). The process may be helatiform, claviform, salpingiform or styliiform (see Terminology and Fig. 3). Styliiform pole rhabdoliths (synonyms polar spines/spines) are placed asymmetrically, and never at two exactly opposite poles of the coccosphere, while some specimens of *Acanthoica quattrosphina*

Fig. 3. Rhabdolith terminology. See also sections on Rhabdolith structure, Other components and Rhabdolith types. Not drawn to scale. Fig. 3a is based on a micrograph provided by Dr J.R. Young, Natural History Museum, London.

a-c. Structure of body rhabdolith of *Acanthoica quattrosphina*, in (a) distal view, (b) proximal view and (c) profile.

d-s. Drawings showing (d-l) ordinary and (m-s) process-bearing rhabdoliths:

d: discoidal/*Rhabdosphaera*, exothecal;

e: raised lamellar cycle/*Acanthoica quattrosphina*;

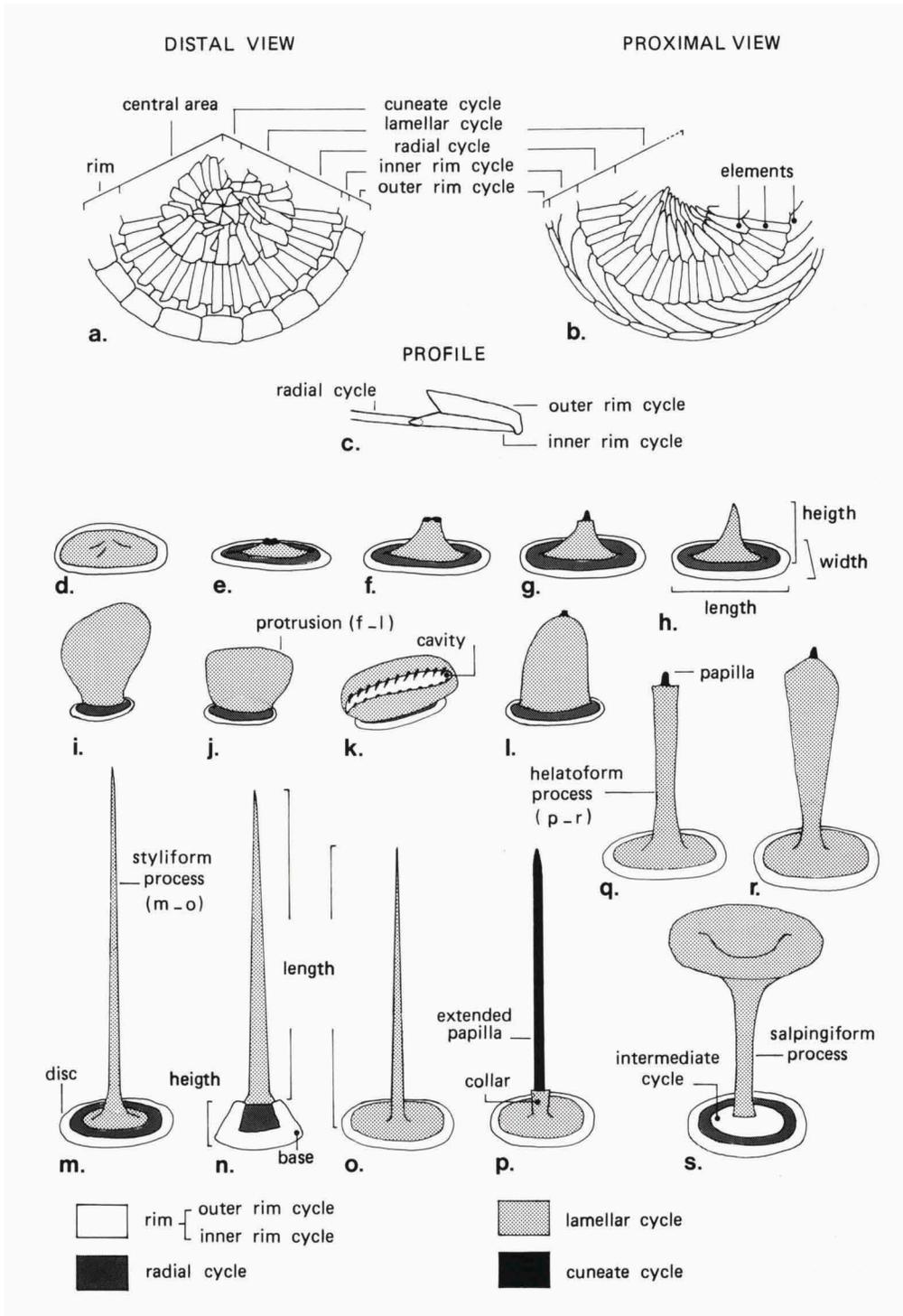
f-h: conical protrusion: (f) *Anacanthoica acanthos*, (g) *Cyrtosphaera aculeata* and (h) *Anacanthoica cidaris*;

i-l: sacculiform protrusion: (i) circum-flagellar, (j) body and (k) labiatiform in distal view/ *Algirosphaera robusta*; (l) *Cyrtosphaera cucullata*;

m-o: styliiform process: (m) apical and (n) antapical pole/*Acanthoica*; (o) *Palusphaera vandeli*;

p-r: helatiform process: (p) *Rhabdosphaera xiphos*, endothecal; rhabdoliths with (q) helatiform and (r) claviform processes of *R. clavigera*;

s: salpingiform process/*Discosphaera tubifera*, with its additional central area cycle.



even have their polar spines all placed at one side of the coccosphere (Pl. 3). Species of *Acanthoica* (emended) have four apical spines placed around the flagellar opening and two antapical spines. The 'basal disc' of the antapical pole rhabdoliths is laterally flattened and distally extended, forming a conical base (Pl. 2, fig. 7; Pl. 4, figs. 1, 2).

Other types of rhabdoliths have a hollow central area protrusion, formed by the elements of the lamellar cycle: it can be conical, or highly elevated sacculiform (*Algirosphaera*, *Cyrtosphaera cucullata* and, in a much lesser degree, *Acanthoica acanthifera*). The conical protrusions of *Cyrtosphaera aculeata* and *C. lecaliae* develop into a helatiform process towards one side of the coccosphere (Pl. 1, figs. 1-4). In *Algirosphaera* the upper part of the sacculiform protrusion may be missing, giving the protrusion a bilabiate (double-lipped) appearance.

Many rhabdoliths have a characteristic central pore (Norris, 1984), which in most species is merely present as a central axis around which the elements of all cycles are situated. In the rhabdoliths of *Anacanthoica acanthos* and the body rhabdoliths of *Acanthoica* (except *Acanthoica* sp. type A) the pore is bordered by a central cycle of wedge-shaped elements (see e.g. Pl. 2, fig. 2; Pl. 4, fig. 1, Pl. 7, fig. 1). A rhabdolith process has a channel; the opening on the proximal side of the disc is visible as a pore. The distal end of the process is closed (except in *Discosphaera tubifera*), the proximal part may be hollow and may have a conical shape (pole rhabdoliths of *Acanthoica*). Conical and sacculiform protrusions are open on the proximal side, except for *Algirosphaera* rhabdoliths which have a proximal covering of randomly arranged elongate elements (Pl. 6, fig. 3).

Rim

The marginal area of the rhabdolith consists of two overlapping cycles of elements: the rim. A prominent peripheral row of non-imbricate elements forms the distal 'outer rim cycle'. The proximal 'inner rim cycle' is partly covered by the outer rim cycle; it consists of elongate elements with an almost tangential orientation (Pl. 4, fig. 3; Pl. 8, figs. 1, 5-7). The presence of two rim cycles is clearly visible in distal view in e.g. *Anacanthoica cidaris* (Pl. 7, fig. 3) and *Cyrtosphaera aculeata* (Pl. 1, fig. 2). In *Discosphaera tubifera* the inner rim cycle is entirely covered by the outer rim cycle and not visible in distal view (Pl. 7, fig. 7; see also Systematic descriptions).

Central area

The central area of the rhabdoliths consists of one to three cycles of elements, viz. a radial cycle, a lamellar cycle and a cuneate cycle, all with a characteristic structure, of which the lamellar cycle is always present. The terms 'first, second and third cycle' (see e.g. Perch-Nielsen, 1985, fig. 66) must be avoided, since a species may have a central area with only one (the lamellar cycle) or two of the three cycles. *Discosphaera tubifera* has an additional cycle of elements between the radial cycle and the lamellar cycle, the intermediate central area cycle (Pl. 7, fig. 7).

The radial cycle consists of flat radial laths that may be slightly tilted (*Acanthoica acanthifera*; Pl. 1, fig. 7) or imbricated (*A. jancheni*; Pl. 5, fig. 5). The laths connect the

inner rim cycle with the central area lamellar cycle and in most species they have wedge-shaped openings between them. The radial cycle is not present in *Palusphaera*, *Rhabdosphaera* and the antapical pole rhabdoliths of *Acanthoica*.

The lamellar cycle consists of overlapping elements that may continue in the central area process or form a protrusion (e.g. Pl. 1, figs. 2-4, 7; Pl. 2, fig. 5; Pl. 4, figs. 4, 5; Pl. 6; Pl. 7, figs. 1-3; Pl. 8, fig. 3). In *Rhabdosphaera xiphos* only the lower part of the process, the 'collar', consists of lamellar cycle elements (Pl. 8, fig. 5), while in *Discosphaera tubifera* the lamellar cycle exclusively forms the salpingiform process that is loosely connected with the intermediate central area cycle (Pl. 7, figs. 6, 7). If no radial cycle is present the lamellar cycle elements directly interconnect with those of the inner rim cycle, e.g. in both the discoidal and the helatiform rhabdoliths of *Rhabdosphaera clavigera* (Pl. 8, figs. 3, 6, 7).

The cycle of cuneate elements is found as the central cycle in *Anacanthoica acanthos* and in the body rhabdoliths of *Acanthoica*, except for *Acanthoica* sp. type A. The distal part of the process in *Rhabdosphaera xiphos* consists of very long parallel elements, and is homologous to the cycle of cuneate elements occurring in *Acanthoica* and *Anacanthoica acanthos*. In other species the cuneate cycle probably is represented by the papilla, consisting of long vertical elements, on top of conical or sacculiform protrusions (*Cyrtosphaera*) and helatiform or claviform processes (*Rhabdosphaera clavigera*), and it may be present as the tooth-shaped vertical elements inside the sacculiform (labiatiform) process in *Algiosphaera* (Pl. 6, fig. 6).

Mono- and dithecatism

Most rhabdosphaerids bear one layer of rhabdoliths (monothecate). Only *Rhabdosphaera* spp. are dithecate, bearing two monomorphic layers of coccoliths: an inner layer (endotheca) of discoidal rhabdoliths and an outer layer (exothecca) of rhabdoliths with a process (Pl. 8, figs. 2-4). Okada & McIntyre (1977) and Norris (1984) considered the genus *Rhabdosphaera* to be monothecate and dimorphic, having two types of coccoliths intermixed on the coccosphere.

The genus *Cyrtosphaera* is vari-monomorphic, with one type of coccoliths increasing in height towards one pole of the coccosphere. A similar varimorphism has been found in monomorphic and dimorphic holococcolithophorids (Kleijne, 1991).

The monothecate species of the genus *Acanthoica* are polymorphic. They bear four different types of rhabdoliths: body rhabdoliths and three different types of pole rhabdoliths.

The Rhabdosphaeraceae can thus be divided in five groups:

- 1) monothecate monomorphic (*Anacanthoica*, *Discosphaera*, *Palusphaera*);
- 2) monothecate vari-monomorphic (*Cyrtosphaera* gen. nov.);
- 3) monothecate dimorphic, with differentiated rhabdoliths at one pole (*Algiosphaera*);
- 4) monothecate polymorphic, with apical and antapical spines (*Acanthoica*);
- 5) dithecate monomorphic, with two monomorphic layers of different types of rhabdoliths (*Rhabdosphaera*).

Phylogenetic relationship

Norris (1984) gave an historical overview of studies considering the family Rhabdosphaeraceae and was the first to describe its uniformity in structure. The Rhabdosphaeraceae genera *Acanthoica* and *Anacanthoica* had previously been placed in a family of their own, the Acanthoicaceae Hay, 1977 (Tappan, 1980, p. 784), while *Algirosphaera* spp., bearing heterococcoliths, were placed in the holococcolithophorid genus *Anthosphaera* (see Norris, 1985; Kleijne, 1991), or in the Syracosphaeraceae (Kamptner, 1941; Tappan, 1980; Steinmetz, 1991).

Norris (1984) concluded that the Rhabdosphaeraceae are closely related to the Mesozoic family Podorhabdaceae Noël, 1965 and he referred to the marginal area of a rhabdolite as 'podorhabdid rim', a term used for the double-shielded coccoliths of the Mesozoic family Podorhabdaceae (Rood et al., 1971). Since the rhabdolite rim can be considered as a single, bicyclic shield, that is only partly 'double-layered', the relation to the extinct podorhabdids remains doubtful. I think that the rhabdolites of the Rhabdosphaeraceae are more closely related to coccoliths of the Syracosphaeraceae (see also Jordan, 1991). This is illustrated by the following examples:

- a) pole rhabdolites of *Acanthoica* resemble the process-bearing circum-flagellar coccoliths of *Ophiaster* Gran, 1912 emend. Manton & Oates, 1983;
- b) the body rhabdolites of *Acanthoica* sp. type A resemble endothecal coccoliths of the Syracosphaeraceae (see Systematic descriptions); and
- c) processes with a blunt end, like the helatiform process in *Rhabdosphaera clavigera*, are also found in circum-flagellar coccoliths of the Syracosphaeraceae, although they seem to have a somewhat different structure. The process in *R. clavigera* merely consists of spirally arranged elements, whereas in the Syracosphaeraceae the 'helatiform process' apparently consists of parallel vertical elements, comparable with the extended papilla on the helatiform process of *Rhabdosphaera xiphos*.

As for rhabdolite development, all elements of the different cycles are separate parts, unlike those of placoliths in which elements from different cycles interconnect to form larger crystal units (Young, 1989). The location of the proto-coccolith ring seems to be the inner rim cycle, from which the outer rim cycle elements develop outward, and the radial cycle or (in case the radial cycle is not present) the peripheral row of lamellar cycle elements develop towards the centre. The development of the (remaining) lamellar cycle elements and the cuneate cycle elements is obscure.

Terminology

Our detailed terminology is based on Braarud et al. (1955), Halldal & Markali (1955), Hay et al. (1966), Okada & McIntyre (1977) and Norris (1984) and has been discussed at the INA Terminology Working Group Meeting, London, April 1992 (Young, 1991; Young et al., in prep.). The detailed description of the various cycles is based solely on SEM-observations (see Fig. 3a-c).

Coccolith types

Cyrtolith — descriptive term for a single-layered, flat to cap-shaped exothecal heterococcolith of the Syracosphaeraceae (Okada & McIntyre, 1977, pl. 8, figs. 3, 9, 11, 12; pl. 9, figs. 2, 5, 8, 11). Cap-shaped holococcoliths are calyptroliths or calyptrolith-like (Kleijne, 1991).

Placolith — heterococcolith with two shields, connected by a central tube.

Rhabdolith — taxo-descriptive term for all coccoliths of the Rhabdosphaeraceae: more or less calotte-shaped circular to elliptical heterococcolith consisting of a sub-horizontal rim of two cycles of elements, and a central area of one to three cycles of elements arranged in dissimilar patterns; a central area protrusion or process may be present.

Coccosphere characteristics

A monothecate coccosphere has a single layer of rhabdoliths. A dithecate coccosphere has two discrete layers of different rhabdolith type, an inner endotheca and an outer exotheca.

On monomorphic coccospheres all rhabdoliths are of a similar type; dithecate monomorphic species have two layers, each with a different type of rhabdolith. On a vari-monomorphic coccosphere the coccolith morphology varies continuously according to position. Coccospheres with more than one layer, all with the same type of coccoliths, are multilayered (e.g. *Emiliana huxleyi* (Lohmann) Hay & Mohler; not found in Rhabdosphaeraceae).

A dimorphic coccosphere has rhabdoliths of two types: circum-flagellar and body rhabdoliths. On a vari-dimorphic coccosphere the body coccolith morphology varies continuously according to position (not found in Rhabdosphaeraceae). Dithecate dimorphic species have a dimorphic endotheca (not found in Rhabdosphaeraceae), and thus can be regarded as 'trimorphic'.

Polymorphic coccospheres have more than three types of coccoliths; *Acanthoica* has four rhabdolith types.

Rhabdolith position on coccosphere

The apical pole is the coccosphere side with the flagellar opening; the antapical pole is the opposite side. Circum-flagellar rhabdoliths may occur around the flagellar opening; body rhabdoliths cover all, or the larger part of the cell surface (syn. 'simple cyrtoliths', Halldal & Markali, 1955; Okada & McIntyre, 1977). The six process-bearing rhabdoliths of *Acanthoica* are pole coccoliths (syn. polar spines/spines).

Rhabdolith structure

See Fig. 3.

Rim — peripheral part of rhabdolith: two largely overlapping cycles of elements.

Outer rim cycle — prominent outer, upper cycle, with radial sutures in distal view.

Inner rim cycle — inner, lower cycle, consisting of elongate elements with a sinistral precession (deflected to the left of the radial direction) in proximal view; the sutures are straight to laevogyre (Pl. 4, fig. 3; Pl. 8, figs. 1, 5-7) and the elements have an almost tangential orientation.

Central area — central part of rhabdolith.

Radial cycle — if present, the outer central area cycle, consisting of radial laths, in most species with wedge-shaped openings between them.

Lamellar cycle — structure of a highly variable number of overlapping elements that may continue in the central process, form the central process (*Discosphaera tubifera*) or form a conical or sacculiform protrusion.

Intermediate cycle — cycle between radial cycle and lamellar cycle (only in *Discosphaera tubifera*, Fig. 3s).

Cuneate cycle — if present, the central cycle of wedge-shaped vertical elements.

Other components

In alphabetical order, with references to Fig. 3.

Base (n) — laterally flattened basal part in antapical pole rhabdoliths of *Acanthoica*.

Cavity (k) — open space in sacculiform and conical protrusions.

Collar (p) — short helatiform process of lamellar cycle elements; it is surmounted by the long, distally extended papilla; *Rhabdosphaera xiphos*.

Disc/basal disc (m) — flat basal part in process-bearing rhabdolith.

Papilla (g, l, p, q, r) — narrow pointed structure of elongate, vertical elements of the cuneate cycle, on top of a protrusion or process.

Pore/proximal pore — proximal opening of channel through process.

Process (m-s) — elongate distally extending central structure of spirally arranged elements of the lamellar cycle, rod-shaped at its base, with central channel.

Protrusion (f-l) — short distally extending central structure with cavity and large opening at proximal side.

Proximal covering — layer of randomly arranged lath-shaped elements covering proximal side of sacculiform protrusion; *Algirosphaera*.

Rhabdolith types

With references to Fig. 3.

Ordinary rhabdoliths (d-l) — rhabdoliths without a process; central area flat (discoidal), with a raised lamellar cycle (e), or extended to a conical or sacculiform protrusion (body coccoliths of e.g. *Acanthoica*, *Algirosphaera*).

Discoidal (d) — flat disc-shaped; exothecal rhabdoliths of *Rhabdosphaera*.

Conical (f-h) — central area elevated to conical protrusion: (f) *Anacanthoica acanthos*, (g) *Cyrtosphaera aculeata* and (h) *Anacanthoica cidaris*.

Sacculiform (i-l) — central area elevated to sac-like protrusion with more or less rounded upper part: (i) circum-flagellar and (j) body rhabdoliths of *Algirosphaera robusta*, and (l) rhabdolith of *Cyrtosphaera cucullata*. Labiatiform: double-lipped: sacculiform rhabdolith with upper part of protrusion missing, showing two thick long

sides of protrusion and elongate central cavity: (k) distal view, *Algirosphaera robusta*.

Process-bearing rhabdolith (m-s) — rhabdolith with a process, rod-shaped at its base.

Styliform (m-o) — process gradually tapers towards the distal end (Halldal & Markali, 1955; Hay et al., 1966), consisting of lamellar cycle elements: (m) apical and (n) antapical pole rhabdoliths of *Acanthoica*; (o) *Palusphaera vandeli*. Styliform has been derived from 'stylus' (Latin), meaning style with a pointed end. Incorrect name: helatoform cyrtoliths (Okada & McIntyre, 1977).

Helatoform (p-r) — process with blunt end (Halldal & Markali, 1955; Hay et al., 1966), consisting of lamellar cycle elements, surmounted by a papilla (cuneate cycle elements): (p) endothecal rhabdoliths of *Rhabdosphaera xiphos* with an extended papilla, (q) *Rhabdosphaera clavigera*. Incorrect name: styliform cyrtolith (Norris, 1984).

Claviform (r) — club-shaped process: a special kind of helatoform process, occurring in *Rhabdosphaera clavigera*.

Salpingiform (s) — trumpet-shaped process of lamellar cycle elements; *Discosphaera tubifera*.

Geographical distribution

A total of 11 rhabdosphaerid species were found in 77 of the 100 Cruise Gx samples that contain coccolithophorids (Table 2). Five additional species were recorded from samples of Cruise APNAP I: *Acanthoica jancheni*, *Acanthoica* sp. type A, *Anacanthoica acanthos*, *Cyrtosphaera cucullata* and *C. lecaliae*. Figs. 5, 6 and the Distribution sections of the Systematic descriptions illustrate and describe the distribution of the recorded species.

In most of the 77 samples two rhabdosphaerid species were found; a maximum of 5 species was found at the northeastern Indian Ocean Station Gx-27 (Fig. 4a). The relative rhabdosphaerid frequency was on average 5 % of the total coccolithophorid standing crop, with a maximum of 18 % (*Rhabdosphaera clavigera*) at the western Mediterranean Sea Station Gx-194 (Fig. 4c).

The most frequently occurring taxa were *Palusphaera vandeli*, *Rhabdosphaera clavigera* and *Discosphaera tubifera*, along the entire or the larger part of the sampling transect, and *Algirosphaera robusta*, in the northeastern Indian Ocean and Arabian Sea (Table 2). Of these species *R. clavigera*, *D. tubifera* and *A. robusta* are cosmopolitan species with a distribution into high latitudes, while the distribution of *P. vandeli* is more restricted to tropical and subtropical regions (Figs. 5f, 6d, e, g).

During Cruise Gx the rhabdosphaerid standing crop was highest in the western Arabian Sea (maximum value 8.3×10^3 cells/l), mainly caused by high frequencies of *Algirosphaera robusta*, the species that also formed the major part of the standing crop in the area south of India and in the northeastern Indian Ocean (Fig. 4b). Other peaks were recorded in the northern Red Sea (Station Gx-159, Gulf of Suez), caused by a high frequency of *Palusphaera vandeli*, and in the Bay of Biscay (eastern North Atlantic, Stations Gx-215 – Gx-219), caused by high frequencies of *Rhabdosphaera xiphos*.

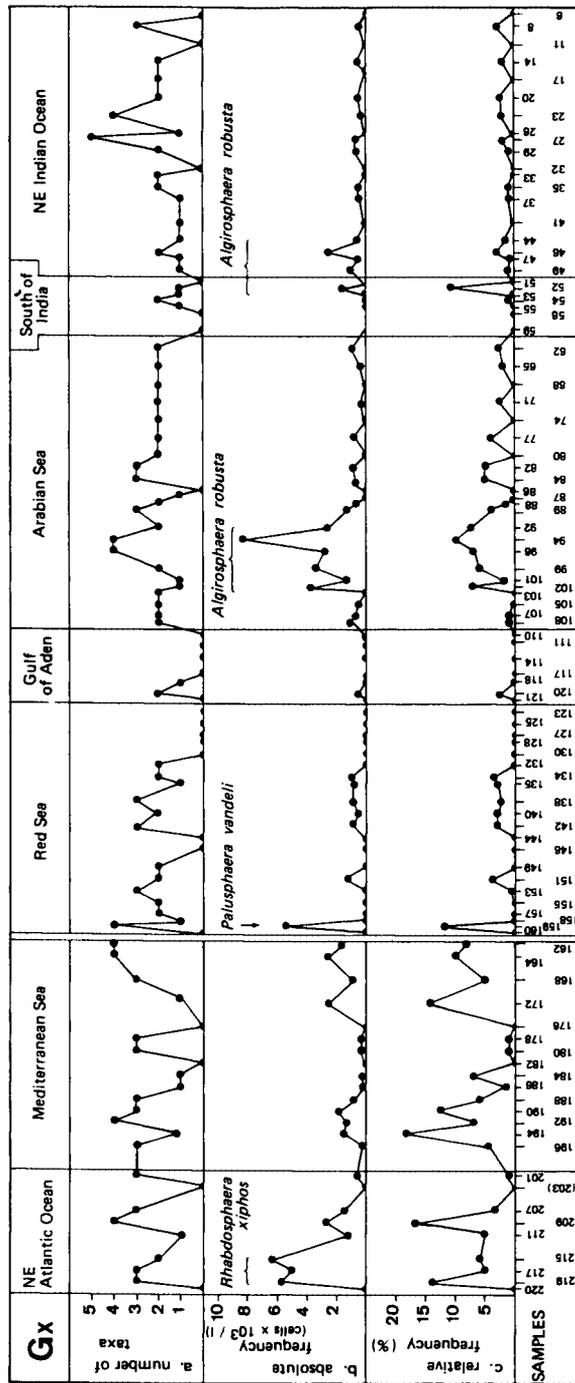
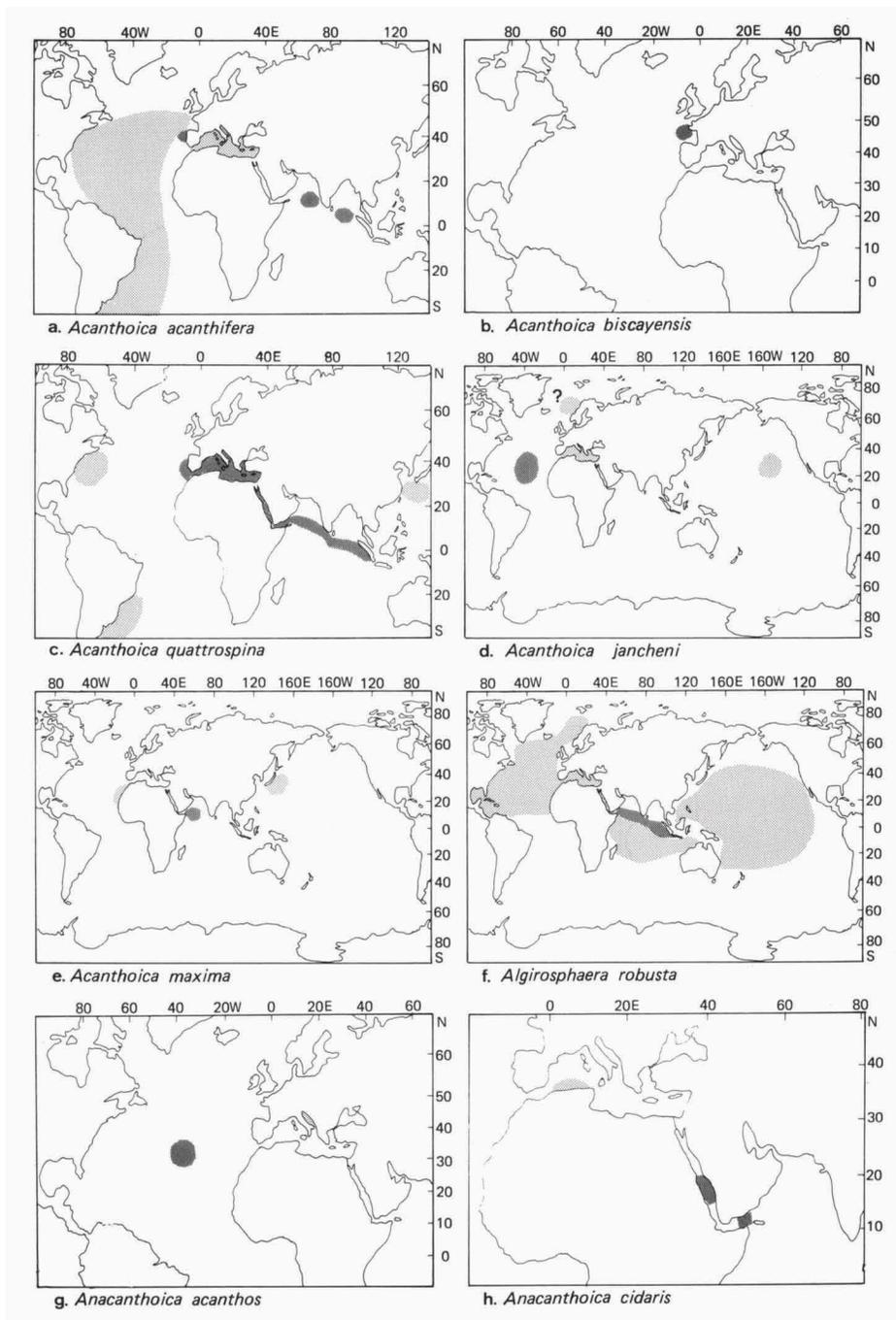
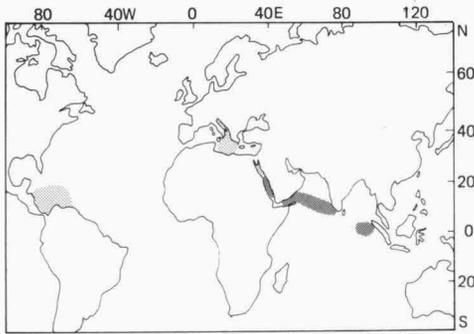


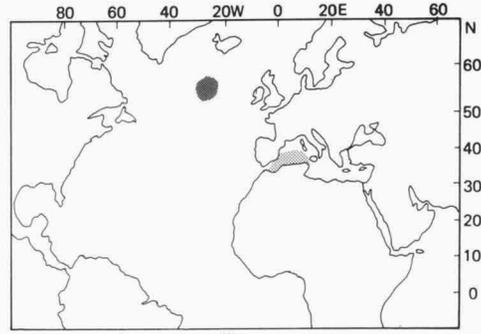
Fig. 4. Graphs showing distribution along Cruise Gx transect: (a) number of observed rhabdosphaerid taxa per sample, (b) rhabdosphaerid standing crop and (c) percentage of rhabdosphaerids in the coccolithophorid flora.



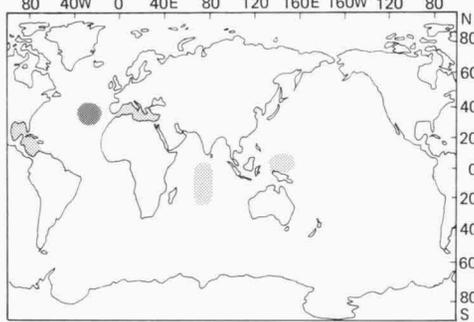
Figs. 5a-h, 6a-h. Distribution of rhabdosphaerid species recorded during the Snellius-II Expedition, cruises Gx and G0, and Cruise APNAP I (dark shading), supplemented with previous records from literature (light shading). For references see Table 3.



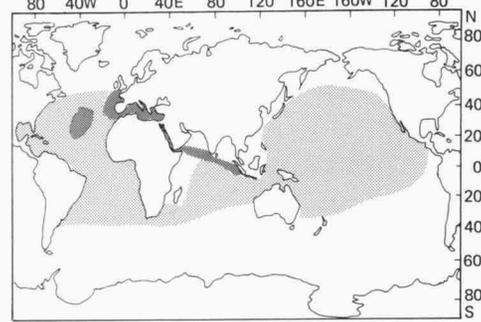
a. *Cyrtosphaera aculeata*



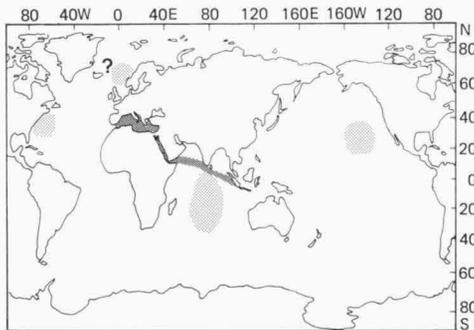
b. *Cyrtosphaera cucullata*



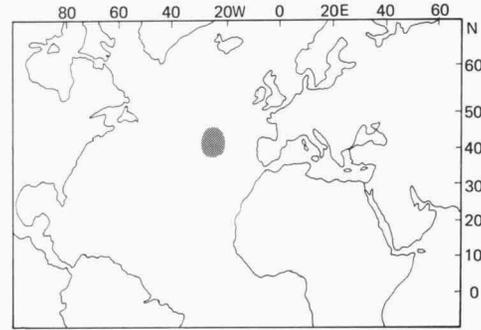
c. *Cyrtosphaera lecaliae*



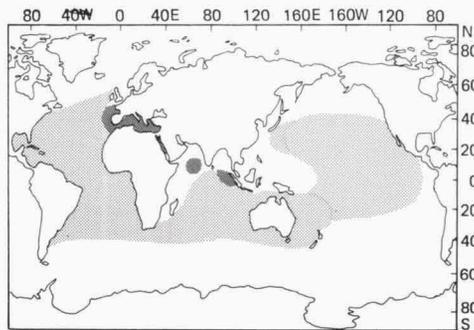
d. *Discosphaera tubifera*



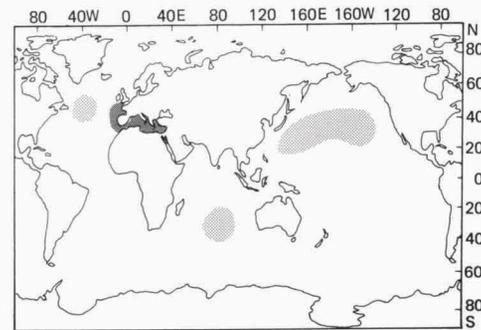
e. *Palusphaera vandeli*



f. *Acanthoica* sp. type A



g. *Rhabdosphaera clavigera*



h. *Rhabdosphaera xiphos*

Discussion

The family Rhabdosphaeraceae represents only a small part of the species recorded during this study; 16 out of approximately 115 species are rhabdosphaerids. The low absolute rhabdosphaerid frequencies correspond with earlier reports on their distribution. *D. tubifera*, *A. robusta* and *R. clavigera* are the numerically most important rhabdosphaerid species that, however, form only a minor part of the coccolithophorid flora (McIntyre & Bé, 1967; Okada & Honjo, 1973; Honjo & Okada, 1974; Okada & McIntyre, 1979; Reid, 1980; Samtleben & Schröder, 1990; for further references see Systematic descriptions).

D. tubifera and *R. clavigera* are warm water species of the upper water layers, with a subtropical temperature preference, of which *R. clavigera* (3-29 °C) has a wider temperature range than *D. tubifera* (14-30 °C, maximum concentration at 21-29 °C; Okada & McIntyre, 1979). Their relative and absolute frequencies reach maximum values of 10% and 10^3 cells/l in the Atlantic, while in the Pacific *D. tubifera* forms never more than 30% and *R. clavigera* 23% of the coccolithophorid flora, with low absolute frequency values of maximum 3.5×10^3 cells/l (McIntyre et al., 1970; Nishida, 1979; Okada & McIntyre, 1979). *Anthosphaera robusta* (syn. *A. oryza*, *A. quadricornu*) is on the other hand characteristic for the lower water layers (deeper than 100 m), and has a wider distribution range into higher latitudes (5-29 °C; Okada & McIntyre, 1979) where it can survive in water below 1 °C (Samtleben & Bickert, 1990). It merely forms less than 30% of the coccolithophorid flora, with low absolute frequency values of maximum 10^3 cells/l in the Atlantic and Pacific Oceans. Some higher percentages are known, viz. 94% for *R. clavigera* and 39% for *D. tubifera* (Honjo & Okada, 1974) and 41-80% for *A. robusta* (Samtleben & Schröder, 1990), but then their absolute frequencies as well as the total rhabdosphaerid standing crop were never higher than 10×10^3 cells/l. These low values correspond with results from the present study (Fig. 4b, c; Table 2).

The increased rhabdosphaerid abundance in the western Arabian Sea is caused by *Algirosphaera robusta*, which apparently thrives in the outer margin of the upwelling area off the Somalian Coast (Stations Gx-92 – Gx-102; Table 2; Fig. 4b, c). Towards the centre of the upwelling area *Emiliania huxleyi* (Lohmann) Hay & Mohler and *Gephyrocapsa oceanica* Kamptner dominate the coccolithophorid flora (Kleijne et al., 1989). *A. robusta* shows another small abundance peak east of the upwelling area south of India (Stations Gx-44 – Gx-52), where *Gephyrocapsa oceanica* dominates the coccolithophorid flora (Kleijne et al., 1989). The species does not occur west of Station Gx-108, in the warm oligotrophic surface waters of the Gulf of Aden and Red Sea (Kleijne et al., 1989), nor in the cooler surface waters of the Mediterranean Sea and eastern North Atlantic. Its distribution seems to be determined by temperature, as well as by nutrient levels (for nutrients and temperatures, see Kleijne et al., 1989; Kleijne, 1991), which makes *A. robusta* an indicator for relatively cold and eutrophic conditions, thus upwelling, during Cruise Gx.

Discosphaera tubifera, on the other hand, merely occurred outside the upwelling areas, in the northeastern Indian Ocean, eastern Arabian Sea, Red Sea and eastern Mediterranean Sea, thus in warmer water (see also McIntyre & Bé, 1967;

Okada & McIntyre, 1979). Compared to *D. tubifera*, *Rhabdosphaera clavigera* showed a more subtropical to transitional distribution, with highest absolute frequencies in the Mediterranean Sea, and somewhat lower values in the Red Sea and eastern North Atlantic (Table 2).

All other rhabdosphaerid species occur only in low numbers. In literature sporadic higher values have been recorded for *Rhabdosphaera xiphos* (syn. *R. longistylis*, 17% and 35%, however with less than 5×10^3 cells/l; Winter et al., 1979; Winter, 1985) and a species identified as *Acanthoica quattrosipina* that probably is *A. jancheni* (less than 20% and 10×10^3 cells/l; Samtleben & Schröder, 1990). An increased abundance of *R. xiphos* was found during Cruise Gx in the Bay of Biscay. The abundance peak in the Gulf of Suez of *Palusphaera vandeli*, the fourth frequent species on the Cruise Gx transect (Table 2), is remarkable since no high values have been reported for this species in literature.

P. vandeli and *R. xiphos* show corresponding worldwide distribution patterns (Fig. 6e, h). During Cruise Gx, however, *P. vandeli* occurred in low numbers, except for the abundance peak in the Gulf of Suez, along the entire transect (although most frequently in the Indian Ocean and Red Sea), whereas *R. xiphos* was clearly restricted to the Gulf of Suez, Mediterranean Sea and eastern North Atlantic. *R. xiphos* thus seems to thrive at somewhat lower temperatures than *P. vandeli*.

Acanthoica maxima is restricted to the outer margin of the western Arabian Sea upwelling area (Stations Gx-94 – Gx-99, Table 2). This species is also known from the upwelling area off the northwestern African coast (Heimdal & Gaarder, 1981) and from the northwestern Pacific south of Japan (Nishida, 1979).

Acanthoica acanthifera, *A. quattrosipina*, *A. jancheni*, *Acanthoica* sp. type A, *Anacanthoica acanthos*, *A. cidaris*, *Cyrtosphaera aculeata*, *C. cucullata* and *C. lecaliae* are known to have a sporadic distribution, which is reflected in our material (Table 2). *Acanthoica biscayensis* is only known from the Bay of Biscay. The distribution of these species with their low numbers and dispersed occurrences could not be related to environmental parameters (Figs. 5a-d, g, h, 6a-c, f).

Compared to the holococcolithophorid distribution along the same transect (Kleijne, 1991), the rhabdosphaerids, with considerably less species and lower relative and absolute frequencies, are more evenly distributed in number of species and showed wider individual distribution patterns. The holococcolithophorids showed their highest absolute and relative frequencies in the Mediterranean Sea and eastern North Atlantic and seemed to be indicative for oligotrophic conditions, whereas the rhabdosphaerid 'abundance peaks' were found along the entire transect, caused by different species.

The low rhabdosphaerid standing crop is reflected in sediment samples in which rhabdololiths of Recent species form only a minor component (McIntyre & Bé, 1967; Samtleben & Schröder, 1990), except for a report of 54% rhabdololiths of *Rhabdosphaera clavigera* (Cohen, 1964).

No intra-specific morphological variation has been observed for the four most frequently occurring species along the Cruise Gx transect, nor for the other rhabdosphaerid species. *Acanthoica quattrosipina*, showing variation in coccosphere shape and place of pole rhabdololiths, was found in the western Arabian Sea outside the upwelling area. The different types of coccospheres co-occurred in the same samples

(Pl. 3, Pl. 4, figs. 1-3), and thus, could not be related to environmental parameters.

Coccospheres of *Rhabdosphaera clavigera* all had rhabdoliths with a rod-shaped helatiform process. Some specimens from the eastern Mediterranean Sea had processes with small wings on the distal end, which is a form with a known worldwide distribution (see Systematic descriptions). Coccospheres that bear different types of rhabdoliths with helatiform, claviform and intergrading processes, occur less often than the 'stylifera' type coccospheres that bear only helatiform processes.

Conclusions

This study on the distribution of rhabdosphaerid species in surface waters along the transect of Cruise Gx, Snellius-II Expedition (summer 1985), shows that rhabdosphaerids were consistently present as a minor constituent of the coccolithophorid flora, with *Discosphaera tubifera*, *Algirosphaera robusta*, *Palusphaera vandeli* and *Rhabdosphaera clavigera* as the most frequently occurring species. Similar results are known from previous studies, although the prominent presence of *P. vandeli* has not been reported earlier.

Peaks in the rhabdosphaerid standing crop were caused by *Algirosphaera robusta* (northeastern Indian Ocean and Arabian Sea), *Palusphaera vandeli* (Gulf of Suez) and *Rhabdosphaera xiphos* (Bay of Biscay).

The genus *Cyrtosphaera* and the two species *Cyrtosphaera lecaliae* and *Acanthoica biscayensis* are new to science. An emended description is given for the genus *Acanthoica*, and one type is described in open nomenclature: *Acanthoica* sp. type A. Three new combinations are given: *Anacanthoica cidaris*, *Cyrtosphaera aculeata* and *C. cucullata*.

Apart from the monomorphic genera (*Anacanthoica*, *Discosphaera*, *Palusphaera*) a polymorphic genus (*Acanthoica*), a vari-monomorphic genus (*Cyrtosphaera*, with rhabdoliths increasing in height towards one pole) and a dimorphic genus (*Rhabdosphaera*) are identified.

A rhabdolith is characterised by the presence of a rim, with the outer and inner rim cycles, and a central area consisting of one to three different cycles: the radial cycle, the lamellar cycle and the cuneate cycle. *Discosphaera tubifera* has an additional cycle between the radial and lamellar cycles, the intermediate cycle, forming the central part of the basal disc.

The cuneate cycle may be present in the centre of the rhabdolith as a circle of wedge-shaped elements, a small papilla, the extended papilla on the collar in *Rhabdosphaera xiphos*, or as the vertical ridges inside the sacculiform protrusion in *Algirosphaera robusta*.

Systematic descriptions

Genera and species are listed alphabetically. The synonymy includes references to publications on extant coccolithophorid distribution, unless indicated otherwise. Data

of dimensions are based upon measurements on the SEM-micrographs, see also Fig. 3. The negatives, including the holotypes of the new species, are deposited at the National Herbarium, Leiden, The Netherlands.

Brief accounts and a map are given of the geographical distribution of every taxon, as recorded during Cruises Gx, G0 and APNAP I, as well as during previous research (Figs. 5, 6; Table 3). Only publications in which a species was illustrated have been included in the sections on distribution, except for *Discosphaera tubifera* and *Algirosphaera robusta* (species that are easy to identify).

A species is considered 'rare' when it was found in 0-20% of the samples, 'occasional' when found in 21-50%, 'frequent' when it occurred in 51-80%, and 'very frequent' when it was found in more than 80% of the samples in a particular area.

Class Prymnesiophyceae Hibberd, 1976
Order Coccolithophorales Schiller, 1926

Family Rhabdosphaeraceae Ostefeld, 1899

Haeckel (1894) introduced the invalid family name Rhabdosphaeralen (not in latinized form). The name was validated by Ostefeld (1899), who introduced the name Rhabdosphaerales, later changed to Rhabdosphaerales (Ostefeld, 1900). According to the ICBN, Art. 32.5 this family name with an improper Latin termination must be changed without change of the author's name or date of publication. Because Lemmermann (1908) was the first to use the name Rhabdosphaeraceae, the family has often been unjustly attributed to him.

Description — Coccosphere consisting of rhabdoliths: heterococcoliths with a bicyclic sub-horizontal rim and a central area consisting of one to three concentric cycles of elements. Central area more or less flat, extended to a conical or sacculiform protrusion, or bearing a central process.

Genus *Acanthoica* Lohmann, 1903 emend. Schiller, 1913

Emended description — Monothecate, polymorphic coccosphere, bearing four types of rhabdoliths: body coccoliths and three different types of in total six pole rhabdoliths. Pole rhabdoliths mostly occur in both polar regions of the coccosphere, occasionally only at one pole. If divided over two poles, one rhabdolith with a long and thick process and three rhabdoliths with a short process occur at the apical pole (long and short apical pole rhabdoliths, respectively), while two rhabdoliths with a long process and a laterally flattened base are present at the antapical pole (antapical pole rhabdoliths). Otherwise, all types are present on one side of the coccosphere. Body coccoliths are ordinary rhabdoliths: more or less flat discs. They have a cuneate cycle enclosing a central pore (see e.g. Pl. 4, fig. 1), except in *Acanthoica* sp. type A.

Type species — *Acanthoica quattrosipina* Lohmann, 1903. Since the name *A. quattrosipina* is a widely used, in contrast with *Acanthoica coronata* Lohmann, 1903, it is

		<i>Acanthoica acanthifera</i>	<i>Acanthoica guattrospina</i>	<i>Acanthoica janчени</i>	<i>Acanthoica maxima</i>	<i>Algirosphaera robusta</i>	<i>Anacanthoica acanthos</i>	<i>Anacanthoica cidaris</i>	<i>Cyrtosphaera aculeata</i>	<i>Cyrtosphaera cucullata</i>	<i>Cyrtosphaera lecaliae</i>	<i>Discosphaera tubifera</i>	<i>Palusphaera vandeli</i>	<i>Rhabdosphaera clavigera</i>	<i>Rhabdosphaera xiphos</i>
ATLANTIC	Ostenfeld 1899														
	Lohmann 1902	x										x			
	Lohmann 1912	x	x									x			
	Lohmann 1913a	x													
	Lohmann 1919	x	x												
	Halldal and Markali 1955	x				x							x ²	x	
	Lecal 1965														
	McIntyre and Bé 1967														
	Gaarder and Hasle 1971						x								
	Thronsen 1972										x				
	Kling 1975						x								
	Okada and McIntyre 1977						x		x						
	Heimdahl and Gaarder 1981					x									
	Verbeek 1989														
	Samtleben and Bickert 1990														
Samtleben and Schröder 1990				x ¹		x								x	
MEDITERRANEAN SEA	Lohmann 1902														
	Lohmann 1903		x												
	Schiller 1913		x												
	Schiller 1914		x												
	Schiller 1925	x	x	x		x	x								
	Kamptner 1937														
	Kamptner 1941		x												
	Kamptner 1944								x						
	Schlauder 1945														
	Lecal-Schlauder 1951														
	Bernard and Lecal 1960														
	Lecal and Bernheim 1960														
	Lecal 1965														
	Lecal 1966														
	Lecal 1967														
Borsetti and Cati 1972		x				x						x ¹	x		
Kimor and Wood 1975															
Borsetti and Cati 1976															
Knapperbusch 1990		x				x									
RED SEA	Bernard and Lecal 1960														
	Winter et al. 1979														
INDIAN OCEAN	Bernard and Lecal 1960														
	Norris 1971														
	Hallegraeff 1984														
	Norris 1984														
INDO-MALAYAN REGION	Friedinger and Winter 1987														
PACIFIC	Hallegraeff 1984														
	Kleijne 1990														
	Hasle 1960														
	McIntyre et al. 1970														
	Gaarder and Hasle 1971														
	Okada and McIntyre 1977														
	Nishida 1979														
	Reid 1980	x													
Hallegraeff 1984															
Nishida 1985															

Table 3. References used for compiling the distribution maps in Figs. 5a, c-h and 6a-h (1, with reservations, explained in Systematic descriptions; 2, exact sampling location not known).

preferable to use the former name, and include *A. coronata* in the synonymy.

Remarks — The genus *Acanthoica* is emended by giving a detailed description of the body rhabdoliths and the three different kinds of pole rhabdoliths.

Without recognizing the individual coccoliths Lohmann (1903) described the genus *Acanthoica* to include species that are calcareous spheres with long spines. He distinguished two species: the type species *A. coronata* with a small spherical coccosphere (6.5 µm in diameter) and long spines at one pole, and *A. quattrosospina* with a spherical to ellipsoidal coccosphere and two spines at both poles. A third species, *A. acanthifera*, was later described by Lohmann (1912) as a nomen nudum, and correctly by Lohmann (1913a), to have circular coccoliths with a highly thickened central area. Schiller (1913) gave an emended generic description, recognizing coccospheres consisting of coccoliths, bearing long spines on one or both poles. He included a new species, *A. brevispina*, characterized by its spines of variable length at both poles, but later Schiller (1925) considered this form to be a variety of *A. quattrosospina*.

Two other species that were originally included in the genus *Acanthoica* have a vari-monomorphic coccosphere with rhabdoliths increasing in height towards one pole. They are here transferred to *Cyrtosphaera* gen. nov.

Species can not be identified on the position of the spines on the coccosphere – at one or both poles – alone, since both conditions occur within one and the same species, as was found for *Acanthoica quattrosospina* and *A. acanthifera*. The pole rhabdoliths in *Acanthoica* species appear to be placed asymmetrically and never at two exactly opposite poles. This is also shown in the drawings by Schiller (1913, pl. 3, fig. 26; 1925, pl. 3, fig. 34a) and Lohmann (1913b, fig. 11). In the samples the coccospheres apparently always rest on the side with the shortest distance between both groups of pole rhabdoliths, obscuring the view of their basal discs which therefore have never been described in detail. The significance of these asymmetrically placed polar spines for the coccosphere orientation in the sea is not known.

Sometimes pole rhabdoliths of *Acanthoica* spp. recorded from sediments have been misidentified as *Rhabdosphaera longistylis* (e.g. Conley, 1979, pl. 3, fig. 18, pl. 4, fig. 9; Biekart, 1989, pl. 4, fig. 7). See remarks on *Palusphaera vandeli*, *Rhabdosphaera* and *R. xiphos*.

Acanthoica acanthifera Lohmann, 1912 ex Lohmann, 1913a
Pl. 1, figs. 5-7.

- 1912 *Acanthoica acanthifera* sp. nov. – Lohmann, p. 219 (nomen nudum). Validated by Lohmann, 1913a, pp. 358, 359, figs. 15b, c.
1913b *Acanthoica acanthifera* – Lohmann, fig. 11b.
1925 *Acanthoica acanthifera* Lohmann – Schiller, pp. 35, 36, pl. 3, fig. 35.
1925 *Acanthoica monospina* sp. nov. – Schiller, pp. 34, 35, pl. 3, fig. 33.
1955 *Acanthoica quattrosospina* Lohmann – (in part) Halldal & Markali, pp. 15, 16, pl. 18, figs. 1, 2 (non fig. 3).

Description — Ellipsoidal coccosphere consisting of 6 pole rhabdoliths and ± 40 very small sub-circular body rhabdoliths. Body rhabdoliths with radial cycle of 23-38 tilted

laths with narrow openings between them; overlapping elements of lamellar cycle form conical to somewhat sacculiform protrusion with flattened upper part, slightly compressed at its long sides (Pl. 1, figs. 5, 7). Most coccospheres bear pole rhabdoliths at both poles: three apical pole rhabdoliths with a short and one with a long and thick process, and two antapical pole rhabdoliths with a long process. They may also occur all at one pole (Pl. 1, figs. 5, 6).

Dimensions — Coccosphere $6.7 \times 5.1 \mu\text{m}$. Body rhabdoliths $1.5\text{-}2.1 \mu\text{m}$ long, $1.3\text{-}2.0 \mu\text{m}$ wide, $0.8 \mu\text{m}$ high; outer rim cycle $0.17\text{-}0.22 \mu\text{m}$ wide. Pole rhabdoliths, process $2.7\text{-}11.0 \mu\text{m}$ long.

Remarks — *A. monospina* is included in the synonymy because of its coccoliths with a highly thickened central area. According to Schiller (1925) this species has only one long spine-bearing rhabdolith, but in all probability the other pole rhabdoliths have been broken or fallen off. *A. acanthifera* has erroneously been included as a synonym in *A. quattrosolina* by Kamptner (1941), which has been followed by Heimdal & Gaarder (1981) and Norris (1984), however, not by Halldal & Markali (1955).

The protrusion formed by the lamellar cycle elements somewhat looks like the sacculiform protrusion of *Cyrtosphaera cucullata* rhabdoliths, but in that species it is constructed of very small, needle-like elements. Yet, the presence of a sacculiform protrusion in an *Acanthoica* species affirms the close relationship between the genera *Acanthoica*, *Cyrtosphaera* and *Algirosphaera*.

The coccosphere of Pl. 1, fig. 5 is smaller than the dimensions given by Schiller (1925), which probably is an artefact of the preparation methods. Drying of the cell will result in 'telescoping' of the coccosphere by overlapping of the coccoliths and thus, a decreased diameter.

Distribution (Fig. 5a) — Northeastern Indian Ocean and eastern North Atlantic, rare. Highest absolute frequency: eastern North Atlantic. Cruise G0: one specimen in the eastern Arabian Sea (Station G0-135).

Previous research — Atlantic, Mediterranean Sea.

Acanthoica biscayensis sp. nov.

Pl. 2, figs. 3-6.

Diagnosis — Coccusphaera monothecata, polymorpha, ellipsoidalis, consistens ex 6 rhabdolithis polaribus et circa 30 rhabdolithis corporeis late-ellipticis. Rhabdolithi corporei cum area centrali fere plana. Cyclus radiorum consistens ex 44-50 radiis planis sine spatiis distinctis interiacentibus. Elementa dextraliter imbricata cycli lamellaris in forma extensionis parvae noduliformis, tectae elementis cycli cuneati, tegentibus partem circa 0.13am clipei secus axem longiorem. Rhabdolithi polares inveniuntur im ambobus polis. Polus apicalis habet tres spinas cum brevi prosequo et cum clipeo, et unum rhabdolithum cum processu longo, latiore quam processus duorum rhabdolithorum polarium antapicalium.

Dimensiones — Coccusphaera $7.9 \times 6.2 \mu\text{m}$. Rhabdolithi corporei longitudine $2.7\text{-}3.0 \mu\text{m}$, latitudine $2.2\text{-}2.4 \mu\text{m}$; cyclus marginis externae latitudine $0.23 \mu\text{m}$.

Processus apicales breves longitudine 3.0-3.4 μm . Processus apicales longi longitudine 9.8 μm . Processus antapicales, basi inclusa, longitudine 15.7 μm .

Monothebate, polymorphic ellipsoidal coccosphere consisting of 6 pole rhabdoliths and ± 30 broad-elliptical body rhabdoliths. Body rhabdoliths with an almost flat central area. Radial cycle consisting of 44-50 flat laths without distinct openings between them. Dextrally imbricated elements of the lamellar cycle form a small knob-like extension, surmounted by the elements of the cuneate cycle, on ± 0.13 part of the rhabdolith along the longer axis. Pole rhabdoliths occur at both poles. The apical pole has three rhabdoliths with a short process and circular disc, and one with a long process that is thicker than the processes of the two antapical pole rhabdoliths.

Dimensions — Coccosphere 7.9 \times 6.2 μm . Body rhabdoliths 2.7-3.0 μm long, 2.2-2.4 μm wide; outer rim cycle 0.23 μm wide. Short apical spine, process 3.0-3.4 μm long. Long apical spine, process 9.8 μm long. Antapical spines, process including base 15.7 μm long.

Holotype — Pl. 2, figs. 3-6.

Type locality — 46°05.8'N, 7°19.1'W (Station Gx-217, Bay of Biscay, depth 0-5m, July 31 1985).

Derivation of name — '*biscayensis*', from the Bay of Biscay, the place of first discovery.

Number of specimens studied — 2.

Remarks — *A. biscayensis* somewhat looks like *A. janzeni* in having body rhabdoliths with a relatively small, pointed central structure and no distinct openings between the radial laths (compare Pl. 2, figs. 4, 6 and Pl. 5, fig. 5). However, it differs from *A. janzeni* and all other here described *Acanthoica* species in having relatively large, broad-elliptical body rhabdoliths, with curved ends and subparallel sides.

A. biscayensis shows some resemblance to *Acanthoica rubus* Kamptner, 1941, however, its body rhabdoliths differ in being larger and broad-elliptical and in bearing a pointed central structure, instead of being normal-elliptical and lacking the elevation on the central area. The two species cannot be distinguished on the presence of up to seven spine-bearing rhabdoliths at only one pole in *A. rubus*, since the position of the pole coccoliths alone is not a good characteristic (see remarks on *Acanthoica*).

Distribution (Fig. 5b) — Eastern North Atlantic, occasional (Bay of Biscay).

Acanthoica janzeni Schiller, 1925
Pl. 5, figs. 5-6.

- 1925 *Acanthoica janzeni* sp. nov. — Schiller, p. 36, text-fig. S. As '*Janzeni*'.
1980 *Acanthoica acanthifera* Lohmann — Reid, p. 157, pl. 3, figs. 8, 9.
1984 *Acanthoica janzeni* Schiller — Norris, p. 37.

? 1990 *Acanthoica quattrosolina* Lohmann – Samtleben & Schröder, pp. 40, 41, pl. 1, fig. 1.

Description — Sub-spherical coccosphere consisting of ± 50 circular body rhabdoliths with relatively wide outer rim cycle, and 6 pole rhabdoliths. Body rhabdoliths with radial cycle of 30-38 dextrally imbricated elements, and lamellar cycle extending into a narrow, somewhat conical protrusion with blunt end, surmounted by elements of the cuneate cycle. Three apical pole rhabdoliths with a short and one with a long process (only very small parts are visible on Pl. 5, fig. 5). Two antapical pole rhabdoliths with a long process.

Dimensions (two coccospheres) — Coccosphere $7.1 \times 6.4 \mu\text{m}$. Body rhabdoliths $1.7\text{-}2.5 \mu\text{m}$ in diameter, $0.5\text{-}0.6 \mu\text{m}$ high; outer rim cycle $0.20\text{-}0.26 \mu\text{m}$ wide. Short apical spines, process $\pm 3.3 \mu\text{m}$ long.

Remarks — According to ICBN rules the species epithet has been changed to *jancheni* by Norris (1984). The possibility of correction to *janchenii* cannot be verified, since Schiller (1925) did not give a derivation of the name.

A. jancheni is characterized by its circular body rhabdoliths (Schiller, 1925) which differ from those of the other *Acanthoica* species and the rhabdoliths of *Anacanthoica acanthos* (Pl. 7, fig. 1) in having dextrally imbricated laths in the radial cycle, instead of flat (or somewhat tilted) laths with openings between them.

The specimen given by Samtleben & Schröder (1990) probably belongs to *A. jancheni*, since its rhabdoliths have a relatively wide outer rim cycle and dextrally imbricated laths in the radial cycle.

Distribution (Fig. 5d) — Not recorded on Cruise Gx. During Cruise APNAP I two specimens in the central North Atlantic (Stations T86-14R,20,C and T86-64).

Previous research — ?North Atlantic, Mediterranean Sea, Pacific.

Acanthoica maxima Heimdal, in: Heimdal & Gaarder, 1981
Pl. 2, figs. 1, 2, 7.

1979 *Acanthoica quattrosolina* Lohmann – (err. type; in part) Nishida, pl. 13, fig. 1b (non fig. 1a).

1981 *Acanthoica maxima* Heimdal sp. nov. – Heimdal & Gaarder, p. 39, pl. 1, figs. 1, 2.

Description — Large ellipsoidal coccosphere consisting of ± 60 body rhabdoliths and 6 pole rhabdoliths. Body rhabdoliths long-elliptical, almost flat, with a radial cycle of 42-50 flat laths. Elements of lamellar cycle forming an elongate elevation with flat upper part, surmounted by elements of the cuneate cycle. Both poles bear pole rhabdoliths. One apical pole rhabdolith with a very thick and long process and large disc (Heimdal & Gaarder, 1981, pl. 1, fig. 2a), and three with a shorter process (only two are visible on Pl. 2, fig. 1) and small circular disc (Heimdal & Gaarder, 1981, pl. 1, fig. 2a). Two antapical pole rhabdoliths with a long process and laterally flattened base (Pl. 2, fig. 7).

Dimensions — Coccosphere $\pm 24 \times 18 \mu\text{m}$. Body rhabdoliths $3.4\text{-}4.0 \mu\text{m}$ long, $2.0\text{-}2.6 \mu\text{m}$ wide; outer rim cycle $0.25 \mu\text{m}$ wide. Pole rhabdoliths, process $11\text{-}25 \mu\text{m}$ long.

Remarks — The pole rhabdoliths are all relatively long, compared to the other *Acanthoica* species. *Acanthoica maxima* seems to be indicative for upwelling conditions (see Discussion).

Distribution (Fig. 5e) — Western Arabian Sea upwelling area, occasional.
Previous research — North Atlantic, Pacific.

Acanthoica quattrospina Lohmann, 1903

Pl. 3, figs. 1-6; Pl. 4, figs. 1-3.

- 1903 *Acanthoica coronata* sp. nov. – Lohmann, p. 68, pl. 2, figs. 21, 22.
1903 *Acanthoica quattrospina* sp. nov., – Lohmann, p. 68, pl. 2, figs. 23, 24.
1912 *Acanthoica quattrospina* Lohmann – Lohmann, p. 240, fig. 15d.
1913 *Acanthoica brevispina* sp. nov. – Schiller, p. 610, pl. 3, figs. 25, 26.
1925 *Acanthoica quattrospina* var. *brevispina* (Schiller) stat. nov. – (err. type) Schiller, p. 35, pl. 3, figs. 34c, d.
1941 *Acanthoica quattrospina* Lohmann – Kamptner, pp. 76, 77, 98, pl. 1, figs. 5-8.
1951 *Acanthoica quattrospina* var. *mediterranea* var. nov. – Lecal-Schlauder, p. 271.
1955 *Acanthoica acanthifera* Lohmann – Halldal & Markali, p. 16, pl. 19, figs. 1, 2.
1972 *Acanthoica acanthifera* Lohmann – Borsetti & Cati, pp. 397, 398, pl. 39, figs. 1a, b.
1972 *Acanthoica quattrospina* Lohmann – Borsetti & Cati, p. 398, pl. 39, figs. 2a, b.
1979 *Acanthoica quattrospina* Lohmann – (in part; err. type) Nishida, pl. 13, fig. 1a (non fig. 1b).
1990 *Acanthoica quattrospina* Lohmann – Knappertsbusch, p. 23, pl. 6, figs. 3, 4.

Description — Coccosphere spherical to ellipsoidal (see also Kamptner, 1941; Heimdal & Gaarder, 1981), bearing \pm 40-80 body rhabdoliths and a total of 6 pole rhabdoliths, mostly divided over both poles: one long and three short spines at one pole and two long spines at the opposite pole, as was described by Kamptner (1941). Other coccospheres have all process-bearing rhabdoliths placed at one side of the coccosphere. Body rhabdoliths sub-circular, with radial cycle of 24-32 somewhat tilted laths and openings between them. Overlapping elements of lamellar cycle form a low elevated structure in the central area, on 0.4-0.5 part of the rhabdolith.

Three rhabdoliths with a short styliform process and an oblong basal disc (Pl. 4, fig. 1) and one with a circular disc and a larger, relatively thick process are placed at the apical pole. The two antapical pole rhabdoliths have a laterally flattened base, of which the outer rim cycle elements are lengthened at the short sides of the elliptical base (Pl. 4, fig. 2). The imbricating, relatively broad elements between these short sides probably are parts of the lamellar cycle, that also forms the process.

Dimensions — Coccosphere 7-10 μm along the longer axis. Body rhabdoliths 1.5-2.3 μm long, 1.5-2.0 μm wide; outer rim cycle 0.10-0.26 μm wide. Long apical spine, process 11-12 μm long, 0.5 μm thick at proximal part; diameter disc 1.8-2.4 μm . Short apical spines, process 1.5-3.6 μm long; basal disc 2.0-2.7 μm long, 1.6 μm wide. Antapical spines, process 12-17 μm long; base 1.6 μm long, 1.1 μm wide, 0.7 μm high.

Remarks — Two forms were recorded: spherical to sub-spherical coccospheres with three short and three long spines at one pole (Pl. 3, figs. 4-6), and sub-spherical to ellipsoidal coccospheres with three short and one long spine at one pole and two long spines at the opposite pole (Pl. 4, figs. 1-3). These forms were originally described by

Lohmann (1903) as two different species, *Acanthoica coronata* and *A. quattrospina* respectively. From the present material can be concluded that the process-bearing rhabdoliths may fall off easily, thus, the number of spines, the angle between them, their thickness and their position on the coccosphere are inaccurate characteristics to distinguish species. Also forms that were described as separate varieties, bearing a variable number of polar spines and having body rhabdoliths without a distinct central area protrusion (*A. quattrospina* var. *brevispina* and var. *mediterranea*) are now synonymized with *A. quattrospina*.

Distribution (Fig. 5c) — *A. quattrospina* occurred along the entire sampling transect, with the spherical and sub-spherical forms co-occurring in the same samples: occasional in the western Arabian Sea and rare in all other areas. Highest absolute frequency: western Arabian Sea.

Previous research — Atlantic, Mediterranean Sea, Pacific.

Acanthoica sp. type A

Pl. 5, figs. 1-4.

Description — Monothecate, polymorphic coccosphere consisting of ± 40 very small flat body rhabdoliths and 6 pole rhabdoliths. Body rhabdoliths elliptical, with radial cycle of 18-26 laths, forming larger part of central area. Overlapping elements of the lamellar cycle form an almost flat, irregular central structure. No cuneate cycle. Both poles bear pole rhabdoliths. Three apical pole rhabdoliths with a long-elliptical basal disc (narrower than in the body rhabdoliths) and short process, and one with a long process that is thicker than in the antapical spines. Two antapical rhabdoliths with a long process and laterally flattened base.

Dimensions (one coccosphere) — Coccosphere probably spherical, diameter $\pm 5 \mu\text{m}$. Body rhabdoliths 1.2-1.4 μm long, 0.9-1.0 μm wide; outer rim cycle 0.1 μm wide. Short apical spines, process 1.7 μm long. Antapical spines, process including base, 5.6-6.3 μm long.

Remarks — The body rhabdoliths lack the central cycle of cuneate elements, that is present in the other *Acanthoica* species. The lamellar cycle of the central area has the form of a more or less elongate structure of irregularly arranged elements, as can be found in species of the family Syracosphaeraceae Lemmermann, 1908 (e.g. Okada & McIntyre, 1977, pl. 9, fig. 3). Moreover, the apical pole rhabdoliths with a short process show a resemblance to rhabdoliths with a styliform process of the syracosphaerid genus *Ophiaster* (Gaarder, 1967; Manton & Oates, 1983). However, coccoliths of the here described form have a flat rim – the outer and inner rim cycles – whereas in coccoliths of the Syracosphaeraceae (caneoliths) the rim consists of a cycle of vertical elements and up to three laterally extending ‘shields’. The mentioned similarity in shape of *Acanthoica* sp. type A body rhabdoliths and caneoliths with a short styliform process, however, does indicate a close phylogenetic relationship between the families Rhabdosphaeraceae and Syracosphaeraceae.

Distribution (Fig. 6f) — Not recorded on Cruise Gx. Cruise APNAP I: one specimen in the central North Atlantic (Station T86-8R,10,C).

Genus *Algirosphaera* Schlauder, 1945 emend. Norris, 1984

Description — Monothecate, dimorphic coccosphere, consisting of two types of sacculiform (to labiatiform) rhabdololiths. Protrusion, formed by lamellar cycle elements, is long-elliptical at its base; it consists of two thick curved blades that are connected by a thin layer of interlocking elements along their distal and lateral sides (Pl. 6, fig. 7). Body rhabdololiths with a low, bulging protrusion; protrusion of circum-flagellar rhabdololiths higher, wider and more laterally flattened – almost petaloid – especially at about half its height. Protrusion appears to be double-lipped (labiatiform) when the upper part is missing (Pl. 6, fig. 6). Proximal side of hollow protrusion covered by a layer of randomly arranged elements.

Type species — *Syracosphaera robusta* Lohmann, 1902. *Algirosphaera oryza* Schlauder, 1945 is a junior synonym.

Remarks — The type species of *Algirosphaera*, the heterococcolith-bearing *A. oryza* (designated by Loeblich & Tappan, 1963), was transferred to *Anthosphaera* Kamptner, 1937 by Gaarder & Hasle (1971) and *Algirosphaera* became a junior synonym of *Anthosphaera*. When the type species of *Anthosphaera* Kamptner, 1937 proved to have holococcoliths, Norris (1984) transferred all heterococcolith-bearing *Anthosphaera* species to *Algirosphaera* and gave an emended description of this originally as monomorphic described genus. An emended description of the holococcolithophorid genus *Anthosphaera* has been given by Kleijne (1991).

Halldal & Markali (1955) considered the *Algirosphaera* coccoliths to be rhabdololiths ('cyrtoliths') and according to this the genus has been placed in the Rhabdosphaeraceae in most of the recent literature, although Tappan (1980) and Steinmetz (1991) included them in the Syracosphaeraceae, following Kamptner (1941).

An effort to distinguish the different *Algirosphaera* species resulted in the conclusion that rhabdololiths with characteristics of the individual species occur together on the same coccospheres. Since at this stage the various species are indistinguishable, I merge all recent *Algirosphaera* species into one, until more specimens from different areas have been examined in more detail.

Algirosphaera robusta (Lohmann, 1902) Norris, 1984

Pl. 6, figs. 1-7.

1902 *Syracosphaera robusta* sp. nov. – Lohmann, p. 135, pl. 4, figs. 34, 35.

1914 *Syracosphaera quatricornu* sp. nov. – Schiller, p. 6, pl. 2, fig. 19. Spelling of species epithet changed to *Syracosphaera quadricornu* by Schiller, 1925, p. 22, pl. 2, fig. 18.

1941 *Anthosphaera robusta* (Lohmann) comb. nov. – Kamptner, pp. 86, 87, 107, pl. 9, figs. 91-94.

1945 *Algirosphaera campanula* sp. nov. – Schlauder, p. 24, pl. 5, figs. 20, 20a-c.

1945 *Algirosphaera oryza* sp. nov. – Schlauder, p. 23, pl. 5, figs. 19, 19a-c.

1945 *Algirosphaera spinulosa* sp. nov. – Schlauder, p. 23, pl. 5, figs. 21, 21a-c.

- 1945 *Anthosphaera bicornu* sp. nov. – Schlauder, p. 29, pl. 4, figs. 17, 17a, b, pl. 5, figs. 17c, d, 18.
 1951 *Anthosphaera bicornu* Schlauder – Lecal-Schlauder, pl. 9, figs. 13-16.
 1954 *Anthosphaera robusta* (Lohmann) Kamptner – Halldal & Markali, pp. 117, 118, pl. 1, figs. a-g, pl. 2, figs. g, h.
 1955 *Anthosphaera quadricornu* (Schiller) comb. nov. – Halldal & Markali, p. 17, pl. 21, figs. 1-3.
 1960 *Anthosphaera aurea* sp. nov. – Bernard & Lecal, p. 11, figs. 2, 2a, b, 4.
 1960 *Anthosphaera bicornu* Schlauder – Lecal & Bernheim, p. 285, pl. 13, fig. 22.
 1971 *Anthosphaera oryza* (Schlauder) Gaarder comb. nov. – Gaarder & Hasle, pp. 523, 529, figs. 4a-e.
 1971 *Anthosphaera robusta* (Lohmann) Kamptner – Gaarder & Hasle, p. 529, figs. 4f, g.
 1972 *Anthosphaera meteora* sp. nov. – Müller, pp. 92, 93, pl. 4, figs. 4, 5, 8, 9 (sediments).
 1972 *Anthosphaera quadricornu* (Schiller) – Borsetti & Cati, p. 403, pl. 48, fig. 1.
 1972 *Anthosphaera robusta* (Lohmann) – Borsetti & Cati, p. 403, pl. 48, fig. 2.
 1975 *Anthosphaera* sp. cf. *A. quadricornu* (Schiller) Halldal & Markali – Kling, pp. 4, 5, pl. 1, figs. 13, 14.
 1979 *Anthosphaera oryza* (Schiller) Gaarder – Nishida, p. 25, pl. 17, figs. 1a, b (reference to author incorrect).
 1979 *Anthosphaera quadricornu* (Schiller) – Winter et al., p. 200, pl. 2, fig. 7.
 1979 *Anthosphaera robusta* (Lohmann) – Winter et al., p. 200, pl. 2, fig. 8.
 1980 *Anthosphaera oryza* (Schlauder) Gaarder – Reid, p. 157, pl. 3, fig. 10, pl. 4, fig. 1.
 1984 *Algirosphaera aurea* (Bernard & Lecal) comb. nov. – Norris, p. 38.
 1984 *Algirosphaera oryza* Schlauder – Norris, p. 38, figs. 1m, n, 14, 16.
 1984 *Algirosphaera quadricornu* (Schiller) comb. nov. – Norris, p. 38.
 1984 *Algirosphaera robusta* (Lohmann) comb. nov. – Norris, p. 38, fig. 15.
 1984 *Anthosphaera quadricornu* (Schiller) Halldal & Markali – Hallegraeff, p. 236, figs. 27, 28.
 1984 *Anthosphaera robusta* (Lohmann) Kamptner – Hallegraeff, p. 236, figs. 26a, b.
 1985 *Anthosphaera oryza* (Schlauder) Gaarder – Nishida, pl. 1, fig. 8.
 1990 *Anthosphaera robusta* (Lohmann) Kamptner – Samtleben & Schröder, p. 41., pl. 1, fig. 4, pl. 2, fig. 5.
 1990 *Anthosphaera robusta* (Lohmann) Norris – Knappertsbusch, p. 23, pl. 6, fig. 5 (reference to author incorrect).

Description — Coccosphere spherical to ellipsoidal, consisting of \pm 60-80 sacculiform body rhabdoliths, and three rhabdoliths with a higher, wider and more flattened sacculiform protrusion around the flagellar opening. Circum-flagellar rhabdoliths with a slightly curved protrusion, consisting of two closely set, distally protruding thick blades that may be pointed at the distal end (e.g. Pl. 6, fig. 1). Flat elliptical proximal part of rhabdoliths consisting of outer rim cycle of broad rectangular elements that partly cover the inner rim cycle, and radial cycle with 24-40 flat laths. Inner rim cycle with laevogyre sutures in proximal view (Pl. 6, fig. 3; Norris, 1984, fig. 15). Sacculiform protrusion, formed by overlapping lamellar cycle elements (Pl. 6, figs. 3, 7) is broad- to long-elliptical in distal view, and broad-elliptical to trapezoidal in lateral view. It consists of two thick blades (the long sides; Pl. 6, figs. 1, 2, 4-6), connected along the distal and lateral margins by a thin layer of interlocking elements (Pl. 6, fig. 7). A circular depression or a small nodular structure may be present on the distal part (Pl. 6, figs. 1, 2, 4). Where no upper part is formed the protrusion appears to be 'double-lipped' (labiatiform) with an elongate distal opening to the central cavity. In the labiatiform rhabdoliths the inner sides of the thick blades bear vertical ribs that slightly protrude the upper part, showing a row of very small tooth-like elements (Pl. 6, fig. 6). Sacculiform and labiatiform rhabdoliths occur together on the same coccosphere (Pl. 6, fig. 6).

Dimensions — Diameter coccosphere excluding circum-flagellar rhabdoliths 6.5-9.6 μ m. Rhabdolith proximal part 1.6-2.6 μ m long, 1.1-1.8 μ m wide; outer rim cycle 0.2 μ m wide. Body rhabdolith protrusion 0.8-1.8 μ m high, 1.1-3.6 μ m long, 0.3-1.1 μ m wide. Circum-flagellar rhabdolith protrusion \pm 4.5 μ m high, 3.0-3.2 μ m long.

Remarks — The cycle of elongate elements that is visible inside the labiatiform pro-

trusions probably is homologous to the cuneate cycle. Compare e.g. *Rhabdosphaera xiphos* with its elongate, vertical elements that form the extended papilla on the short helatiform process.

In distal view the narrow cavity between the two long sides of the protrusion is visible as a dark line through the thin layer of elements forming the upper part of the sacculiform protrusion (Pl. 6, figs. 1, 2, 4-7). Where this upper layer is missing the elongate central cavity is visible. This '*A. robusta*' characteristic has been described and illustrated as an infolding that may occur at the distal end of the protrusion, giving a labiatiform appearance (Kamptner, 1941; Halldal & Markali, 1954, 1955; Kling, 1975; Norris, 1984).

Determining the individual *Algirosphaera* species resulted in much confusion, as was also indicated by Kamptner (1941; *A. quadricornu* is included in the synonymy of *A. robusta*), Norris (1984; the separation of *A. robusta* and *A. quadricornu* is difficult) and Heimdal & Gaarder (1981; the body coccoliths of *A. oryza* and *A. quadricornu* are indistinguishable even with an EM, and the circum-flagellar rhabdololiths of *A. oryza*, *A. quadricornu* and *A. robusta* cannot be distinguished). Also the shape of the coccospere appears to be highly variable, since in all three species it varies from spherical to flattened ellipsoidal (Heimdal & Gaarder, 1981).

Difficulties in identification are also shown in the following examples. The coccosphere of Pl. 6, fig. 1 corresponds with *A. quadricornu* in Winter et al. (1979, pl. 2, fig. 7) and *A. robusta* in Hallegraeff (1984, fig. 26a), whereas *A. robusta* in Winter et al. (1979, pl. 2, fig. 8) corresponds with *A. robusta* and *A. quadricornu* in Hallegraeff (1984, fig. 26b, and figs. 27-28 respectively). The specimens given by Kling (1975, pl. 1, figs. 13, 14) as *Anthosphaera* sp. cf. *A. quadricornu*, by Nishida (1979, pl. 17, fig. 1a) as *A. oryza*, and by Borsetti & Cati (1972, pl. 48, figs. 1, 2) as *A. quadricornu* and *A. robusta* are all similar to Pl. 6, fig. 1. Winter (1985, table 1) put *A. oryza* and *A. robusta* together in the counting list, while the specimens given by Steinmetz (1991, pl. 16), as *Anthosphaera oryza*, show a similar variation in morphology as the specimens recorded during the present study.

The different species mentioned in the synonymy are here merged into one species, *A. robusta* (Lohmann) Norris, because the rhabdololith protrusion is highly variable in outline: rhabdololiths with elliptical protrusions (in distal view) may occur on a coccosphere together with those having nearly parallel long sides (Pl. 6, figs. 2, 4-6). The outline of the protrusion in lateral view may vary from rounded to trapezoidal (Pl. 6, fig. 2) and the protrusion may be somewhat pointed, which results in the inclusion of *A. bicornu* and *A. meteora* in the synonymy. The protrusion may bear a small nodular structure (Pl. 6, fig. 4, middle and lower right; see also Samtleben & Schröder, 1990, *A. robusta*, pl. 1, fig. 4, pl. 2, fig. 5). The orientation of the coccosphere on the filter determines the shape of the 'species'; the presence of a row of equatorial coccoliths (in *A. oryza*; Reid, 1980) probably is the result of partial disintegration of the coccosphere (see also Pl. 6, fig. 5). *A. oryza* and the two other species described by Schlauder (1945) on differences in coccolith ornamentation, *Algirosphaera campanula* and *A. spinulosa*, are all considered to be synonyms of *A. robusta*.

The apparent morphological variation of this species explains why so many only slightly different forms have been described as new species. It is possible that a

number of varieties can be distinguished, but then no relations to certain geographical areas seem to exist. E.g. specimens recorded by Samtleben & Bickert (1990) as *A. robusta* are typical for subarctic water and survive in water below 1 °C, while similar specimens are also known from the warm Indian Ocean (e.g. this study; Hallegraeff, 1984).

Distribution (Fig. 5f) — Northeastern Indian Ocean and south of India, occasional; eastern and western Arabian Sea, very frequent. Highest absolute frequency: western Arabian Sea.

Previous research — North Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Pacific.

Genus *Anacanthoica* Deflandre, 1952

Description — Monothecate, monomorphic coccosphere consisting of rhabdoliths in which the lamellar cycle elements form a conical protrusion. Radial cycle consisting of flat laths with openings between them. A cuneate cycle may be present.

Type species — *Acanthoica acanthos* Schiller, 1925.

Remarks — The monomorphic species of the genus *Anacanthoica* were separated from the polymorphic genus *Acanthoica* by Deflandre (1952, p. 452). Two species could be identified in the present material.

Anacanthoica differs from the monomorphic genus *Palusphaera* in having a radial cycle and a lamellar cycle that forms the protrusion (with a cavity), whereas in *Palusphaera* the central area and the styliform process (rod-shaped at its base, with a channel) consist entirely of lamellar cycle elements.

Anacanthoica acanthos (Schiller, 1925) Deflandre, 1952 Pl. 7, fig. 1.

1925 *Acanthoica acanthos* sp. nov. – Schiller, p. 34, pl. 3, figs. 32, 32a.

1952 *Anacanthoica acanthos* (Schiller) comb. nov. – Deflandre, p. 452, fig. 350d.

Description — Ellipsoidal coccosphere consisting of ± 60 elliptical rhabdoliths with a low conical protrusion. Protrusion with blunt end, surmounted by elements of cuneate cycle. Lamellar cycle elements, forming protrusion, are placed in sharp angle with radial cycle that has 24-35 flat laths. Apart from rhabdoliths with a relatively wide outer rim cycle of 0.3 μm width, also two rhabdoliths with an outer rim cycle of 0.17 μm width were found on the coccosphere (Pl. 7, fig. 1, lower left).

Dimensions — Coccosphere $8 \times 7 \mu\text{m}$. Rhabdoliths 2.0-2.5 μm long, 1.7-1.9 μm wide, 0.6-0.7 μm high; outer rim cycle (0.17 and) 0.3 μm wide.

Remarks — The small open spaces between the rhabdoliths on the coccosphere

(Schiller, 1925) were not observed, probably as a result of the difference in preparation methods (see also *Acanthoica acanthifera*).

Distribution (Fig. 5g) — Not found on Cruise Gx. One specimen was found during Cruise APNAP I, central North Atlantic (Station T86-14R,20,C).

Previous research — Mediterranean Sea.

Anacanthoica cidaris (Schlauder, 1945) comb. nov.

Pl. 7, figs. 2-4

Basionym — *Acanthoica cidaris*, Schlauder, 1945, p. 7, pl. 1, figs. 1, 1a-c.

1984 *Acanthoica cidaris* Schlauder – Norris, p.37.

Description — Spherical coccosphere consisting of ± 60 elliptical rhabdoliths with a central area with a protracted conical shape. Relatively narrow outer rim cycle. Radial cycle flat, consisting of 44-60 laths with narrow openings between them. Lamellar cycle with overlapping elements that gradually continue into the hollow, sharply pointed conical protrusion. Width at proximal part and height of this protrusion are variable (Pl. 7, fig. 2). No cuneate cycle.

Dimensions — Diameter coccosphere including protrusions 13 μm . Rhabdoliths 3.1-3.7 μm long, 2.1-2.6 μm wide, 1.9-2.3 μm high (also rhabdoliths with shorter and larger protrusions were observed but could not be measured); outer rim cycle 0.13 μm .

Remarks — The size of the coccosphere is conform the original description, although the coccoliths are larger than reported by Schlauder (1945; cf. length and height of coccoliths 1.5-1.6 μm).

Acanthoica cidaris is transferred to the genus *Anacanthoica*, because of its monomorphism. Norris (1984) excluded *A. cidaris* Schlauder from *Acanthoica*, considering its coccoliths to be rhabdoliths with a process, but he did not transfer it to another genus. Indeed, they do look like process-bearing rhabdoliths, e.g. like the short apical pole rhabdoliths in *Acanthoica janчени* (Pl. 5, fig. 6), but they must not be included in the monomorphic, process-bearing genus *Palusphaera*. The conical protrusion of *A. cidaris* as well as the styliform process of *Palusphaera vandeli* are extensions of the lamellar cycle and both species lack the cuneate cycle. However, *A. cidaris* has a lath cycle and *Palusphaera* has not.

Schlauder (1945) described *Acanthoica cidaris* having coccoliths all of the same form and dimensions, but Pl. 7, fig. 2 shows a considerable variation. No complete coccospheres were studied in detail, but possibly the species is vari-monomorphic, which implies a transfer to the genus *Cyrtosphaera*. For that, however, more specimens need to be examined.

Distribution (Fig. 5h) — One disintegrated specimen in the Red Sea, Station Gx-134. Cruise G0: one coccosphere in the Gulf of Aden (Station G0-110).

Previous research — Mediterranean Sea.

Genus *Cyrtosphaera* gen. nov.

Diagnosis — *Coccosphaera* monothecata, varie monomorpha, consistens ex rhabdolithis cum protrusione crescenti quoad altitudinem versus polum unum coccosphaerae. Elementa cycli lamellaris in forma protrusionis conicae sive sacculiformis, prolongatae per papillam elementorum cycli cuneati.

Monothecate, vari-monomorphic coccosphere consisting of rhabdoliths with a protrusion that increases in height towards one pole of the coccosphere. Lamellar cycle elements form a conical or sacculiform protrusion that is prolonged by a papilla of cuneate cycle elements.

Type species — *Acanthoica aculeata* Kamptner, 1941.

Derivation of name — ‘*cyrtolith*’, referring to the former name of the coccolith type present in this genus; ‘*sphaera*’ (Latin), sphere.

Remarks — The vari-monomorphic species *Acanthoica aculeata* is transferred from *Acanthoica*, characterized by its four types of rhabdoliths, to *Cyrtosphaera*, which has only one type of rhabdolith with a protrusion of lamellar cycle elements increasing in height towards one pole. A second species, often misidentified as *A. aculeata*, is now named *Cyrtosphaera lecaliae* sp. nov. *Acanthoica cucullata* Lecal-Schlauder, bearing rhabdoliths with a sacculiform protrusion that increases in height towards one pole, is transferred to the new genus *Cyrtosphaera* as well.

I include these three species in a vari-monomorphic genus, because body and circum-flagellar rhabdoliths, such as present in dimorphic species, cannot clearly be distinguished. *Cyrtosphaera* species seem to lack a flagellar opening, which already has been observed for *Cyrtosphaera cucullata* by Lecal-Schlauder (1951).

Cyrtosphaera aculeata (Kamptner, 1941) comb. nov.
Pl. 1, figs. 1-3.

Basionym — *Acanthoica aculeata*, Kamptner, 1941, pp. 76, 133, pl. 1, figs. 1, 2.

1972 *Acanthoica aculeata* Kamptner – (in part) Thronsen, pp. 56, 57, figs. 16-19 (non figs. 20, 21).

1979 *Acanthoica aculeata* Kamptner – Winter et al., pl. 2, fig. 6.

Description — Coccosphere consisting of \pm 25-50 elliptical rhabdoliths with a depression in one or both long sides. Radial cycle with 26-38 radial laths with openings between them. Lamellar cycle with dextrally imbricated elements, forming conical protrusion with blunt end, prolonged by small papilla of cuneate cycle elements (Pl. 1, figs. 2, 3). Rhabdoliths increase in height towards one pole of the coccosphere: rhabdoliths with a conical protrusion gradually develop into rhabdoliths with a short helatiform process.

Dimensions — Coccosphere diameter \pm 5-6.5 μ m. Rhabdolith 1.8-2.6 μ m long, 1.4-2.1 μ m wide, \pm 0.8-1.5 μ m high; outer rim cycle 0.10-0.13 μ m wide.

Remarks — The excluded figures 20 and 21 in Throndsen (1972) show a specimen of *Cyrtosphaera lecaliae*.

Distribution (Fig. 6a) — Northeastern Indian Ocean and Red Sea, rare. Highest absolute frequency: Red Sea. Cruise G0: Gulf of Aden (Station G0-106) and Arabian Sea (Station G0-135).

Previous research — North Atlantic, Mediterranean Sea, Red Sea.

Cyrtosphaera cucullata (Lecal-Schlauder, 1951) comb. nov.
Pl. 4, figs. 4-5.

1951 *Acanthoica cucullata*, Lecal-Schlauder, p. 269, figs. 6a-d.

Description — Coccosphere flattened at one pole, consisting of \pm 50 elliptical rhabdolites with a sacculiform protrusion that increases in height towards opposite pole of coccosphere. Rim cycles and radial cycle form flat area surrounding the sacculiform protrusion. Radial cycle with 50-56 radial laths with openings between them. Lamellar cycle elements forming sacculiform protrusion are needle-like, loosely arranged in a clockwise spiral with small openings between them, prolonged by a small papilla of vertical cuneate cycle elements (Pl. 4, fig. 4).

Dimensions (one coccosphere) — Coccosphere $13.7 \times 11.6 \mu\text{m}$. Rhabdolite proximal part 3.1-3.3 μm long, 2.1-2.3 μm wide; outer rim cycle 0.2 μm wide; protrusion 1.2-2.5 μm high.

Remarks — The smaller dimensions given by Lecal-Schlauder (1951, light microscope) probably are the result of measuring only the sacculiform process, instead of the complete rhabdolite including the flat proximal part consisting of rim cycles and radial cycle.

C. cucullata, with its rhabdolites that increase in height towards one pole, is vari-monomorphic instead of dimorphic and, therefore, is not included in the genus *Algirosphaera*. The form of the rhabdolite protrusion is intermediate between *Acanthoica acanthifera* and *Algirosphaera robusta* (see also remarks on *A. acanthifera*).

Distribution (Fig. 6b) — Not found on Cruise Gx. Cruise APNAP I: one specimen in the northern North Atlantic (Station T86-C-15).

Previous research — Mediterranean Sea.

Cyrtosphaera lecaliae sp. nov.
Pl. 1, fig. 4.

1960 *Syracolithus corii* (Schiller) comb. nov. — Lecal & Bernheim, p. 279, pl. 5, fig. 8.

1965 *Syracorhabdus lactaria* sp. nov. — (nomen nudum) Lecal, p. 65, text-fig. D, pl. 1, fig. 2. Description by Lecal, 1966, pp. 256, 257, pl. 6, figs. 18-21, pl. 7, figs. 22-23 (invalid, ICZN Art. 11.h.iii). Changed to *Syracosphaera* (*Syracosphaera*) *lactaria* Lecal by Loeblich &

- Tappan, 1968, p. 591 (invalid, ICBN Art. 33.2).
1971 *Acanthoica aculeata* Kamptner – Gaarder & Hasle, p. 523, figs. 2e-f.
1972 *Acanthoica aculeata* Kamptner – (in part) Thronsen, pp. 56, 57, figs. 20-21.
1976 *Acanthoica aculeata* Kamptner – Borsetti & Cati, pp. 209, 210, pl. 12, fig. 1.
1979 *Acanthoica aculeata* Kamptner – Nishida, pl. 13, figs. 3a, b.
1981 *Acanthoica aculeata* Kamptner – Heimdal & Gaarder, p. 39.
1984 *Acanthoica* sp. – Norris, p. 37, fig. 13.

Diagnosis — *Coccosphaera* monothecata, varie monomorpha, consistens ex + 45 rhabdolithis ellipticis, quorum margo curvatus sursum ex area centrali. Cyclus radorum consistens ex 42-52 radiis. Elementa cycli lamellaris collocata in spira dextroversa et acute angulata versus cyclum radorum. Elementa efficiunt protrusionem conicam truncatam, protrudentem aliquo modo oblique ex area centrali. Protrusio prolongata per papillam elementorum cycli cuneati. Rhabdolithi crescentes quoad altitudinem versus unum polum, protrusione conica extendente in processum brevem helatiformem.

Dimensiones — *Coccosphaera* diametro $\pm 9 \mu\text{m}$. Rhabdolithi longitudine 2.5-3.4 μm , latitudine 2.0-2.5 μm , altitudine minimum 1.1 μm (rhabdolithi cum protrusione maxima non mensi); cyclus marginis externi latitudine 0.12 μm .

Monothebate, vari-monomorphic coccosphere consisting of ± 45 elliptical rhabdoliths in which the rim is curved upward from the central area. Radial cycle consisting of 42-52 radial laths. Lamellar cycle elements arranged in a clockwise spiral, placed at sharp angle to radial cycle; elements form a conical protrusion with blunt end that protrudes somewhat obliquely from the central area. Protrusion prolonged by a papilla of cuneate cycle elements. Rhabdoliths increasing in height towards one pole, with extension of the conical protrusion to a short helatiform process.

Dimensions — Coccosphere diameter $\pm 9 \mu\text{m}$. Rhabdoliths 2.5-3.4 μm long, 2.0-2.5 μm wide, minimum 1.1 μm high (rhabdoliths with largest protrusions could not be measured); outer rim cycle 0.12 μm wide.

Holotype — Pl. 1, fig. 4.

Type locality — 34°19.9'N, 34°23.8'W (Station T86-51-C-A, central North Atlantic, depth 0-5 m, August 31, 1986).

Derivation of name — The species name is given in honour of J. Lecal.

Number of specimens studied — 1, and previously published micrographs.

Remarks — Lecal & Bernheim (1960) introduced the subgenus *Syracorhabdus* under ICZN (zoological code) without designating a type species; the name is therefore invalid (unavailable, ICZN Art.13.b; see also Loeblich & Tappan, 1966, p. 167). Lecal (1966) introduced the species *Syracorhabdus lactaria*, without designating the holotype, which would make the name invalid according to ICBN Art.37.1, but since the zoological rules were applied again, the species is typified by the series of figures ('type series') given by Lecal (1966; ICZN Art. 72.a). However, the introduction of

Syracorhabdus lactaria must be regarded as invalid according to ICZN Art. 11.h.iii, as it was not published in combination with a generic name. Later Loeblich & Tappan (1968) incorrectly placed the species in a new subgenus without validating the species and without indication of the basionym (invalid, ICBN Art. 33.2). The new name *Cyrtosphaera lecaliae* is introduced here for this species.

The rhabdolith shown by Lecal & Bernheim (1960) was misidentified as the canelolith-bearing *Syracosphaera corii* Schiller, 1925, which they included in the subgenus *Syracolithus* Kamptner, 1941.

Cyrtosphaera lecaliae differs from *C. aculeata* in having larger rhabdoliths with higher numbers of elements in the radial and the lamellar cycles (cf. radial cycle with 42-52 laths and rhabdolith length 2.5-3.4 μm in *Cyrtosphaera lecaliae*, versus 26-38 laths and 1.8-2.6 μm in *C. aculeata*). Especially the elements in the lamellar cycle are far more numerous, and they form a conical protrusion that is somewhat asymmetrical (Pl. 1, fig. 4; Lecal, 1966, pl. 6, fig. 20) and also larger and higher than in *C. aculeata*. Moreover, the coccospheres seem to consist of a higher number of rhabdoliths than was apparent in the original specimens described as *Acanthoica aculeata* by Kamptner (1941), which was also mentioned by Norris (1984).

Distribution (Fig. 6c) — Not found during Cruise Gx. Cruise APNAP I: one specimen in the central North Atlantic (Station T86-51-C-A).

Previous research — North Atlantic, Mediterranean Sea, Indian Ocean, Pacific.

Genus *Discosphaera* Haeckel, 1894

Description — Monothecate, monomorphic coccosphere, consisting of salpingiform rhabdoliths: an almost flat disc bearing a process with a trumpet-shaped extension.

Type species — *Rhabdosphaera tubifera* Murray & Blackman, 1898.

Remarks — *Discosphaera thomsonii* Ostensfeld, 1899 and *D. tubifera* have been differentiated on basis of size of coccospheres and rhabdolith processes. Norris (1984) synonymized the two species, since the differences were caused by the incomplete description of *D. thomsonii* by Ostensfeld (1899), based on the somewhat inaccurate original illustration by Thomson (1874).

Discosphaera tubifera (Murray & Blackman, 1898) Ostensfeld, 1900 Pl. 7, figs. 5-7.

1898 *Rhabdosphaera tubifera* sp. nov. — Murray & Blackman, pp. 438, 439, pl. 15, figs. 8-10. As '*Tubifer*'; corrected to *D. tubifera* by Kamptner, 1944, p. 139.

1899 *Discosphaera thomsoni* sp. nov. — Ostensfeld, p. 436. Corr. to *Discosphaera thomsonii* by Schiller, 1930, p. 254.

1900 *Discosphaera tubifer* (Murray & Blackman) comb. nov. — Ostensfeld, p. 200.

1902 *Discosphaera thomsoni* Ostensfeld — Lohmann, p. 141, pl. 5, fig. 49.

1902 *Discosphaera tubifer* (Murray & Blackman) comb. nov. — Lohmann, pp. 141, 142, pl. 5, figs. 47, 48, 48a, 50 (invalid new combination).

- 1951 *Discosphaera tubifer* (Murray & Blackman) Lohmann, – Lecal-Schlauder, pp. 302, 303, text-fig. 39 (reference to Lohmann incorrect).
1955 *Discosphaera tubifer* (Murray & Blackman) Lohmann – Halldal & Markali, p. 17, pl. 22, figs. 1-3 (reference to Lohmann incorrect).
1965 *Discosphaera thomsoni* Ostenfeld – Lecal, p. 68, text-fig. J, pl. 2, fig. 8.
1967 *Discosphaera tubifera* (Murray & Blackman) Lohmann – McIntyre & Bé, p. 566, pl. 1, figs. a-c (reference to Lohmann incorrect).
1971 *Discosphaera tubifera* (Murray & Blackman) Ostenfeld – Gaarder & Hasle, p. 533, fig. 8.
1972 *Discosphaera tubifera* (Murray & Blackman) – Borsetti & Cati, p. 407, pl. 54, figs. 3a, b.
1975 *Discosphaera tubifera* (Murray & Blackman) Ostenfeld – Kling, p. 5, pl. 1, fig. 8.
1979 *Discosphaera tubifera* (Murray & Blackman) Ostenfeld – Nishida, pl. 12, figs. 1a, b.
1979 *Discosphaera tubifera* (Murray & Blackman) – Winter et al., pl. 2, fig. 9.
1984 *Discosphaera tubifer* (Murray & Blackman) Lohmann – Hallegraeff, p. 236, figs. 34-36 (reference to Lohmann incorrect).
1984 *Discosphaera tubifer* (Murray & Blackman) Ostenfeld – Norris, p. 35, figs. 1L, 11, 12.
1990 *Discosphaera tubifera* (Murray & Blackman) Ostenfeld – Knappertsbusch, p. 24, pl. 6, fig. 6.

Description — Spherical coccosphere consisting of ± 50 salpingiform rhabdolites with a distal extension of variable size. Basal disc sub-circular to elliptical, flat, consisting of a relatively broad outer rim cycle, the radial cycle and towards the centre an additional cycle: the intermediate central area cycle. Radial cycle with 23-30 flat, short radial laths with only small openings between them. Overlapping elements of intermediate cycle form flat, smooth surface, with a central pore of 0.15 μm diameter. Lamellar cycle elements form hollow process (rod-shaped at its base) on top of this pore. Process loosely connected to disc, consisting of imbricating elements that are lath-shaped in the proximal part and tile-shaped in the distal part of the process. Periphery of trumpet-shaped extension consists of flat elongate elements, arranged with their greatest length in tangential direction.

Dimensions — Diameter coccosphere without processes 6 μm , including processes 15-20 μm . Rhabdolith disc 1.7-2.4 μm long, 1.4-1.6 μm wide; outer rim cycle 0.3 μm wide. Diameter distal part of process 2.0-4.2 μm .

Remarks — Some coccoliths have a small elongate structure protruding through the central pore, which possibly is a remainder of the organic inner covering of the hollow process (Pl. 7, fig. 7), connecting disc and process.

The elements of the salpingiform process (lamellar cycle) meet those of the disc at a sharp angle. The disc elements do not continue in the process, unlike in other rhabdolith processes (see also McIntyre & Bé, 1967). The loose connection between the process and the disc, therefore, must be the result of the presence of the additional intermediate central area cycle. The inner rim cycle, connecting the outer rim and radial cycles, is not visible in the specimens shown in Pl. 7, figs. 5-7; in distal view it is completely covered by the outer rim cycle.

Distribution (Fig. 6d) — *D. tubifera* occurred along the entire sampling transect. Gulf of Aden, rare; northeastern Indian Ocean, eastern and western Arabian Sea, Mediterranean Sea and eastern North Atlantic, occasional; Red Sea, frequent. Cruise APNAP I: central North Atlantic. Highest absolute frequency: Mediterranean Sea.

Previous research — Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Indo-Malayan Region, Pacific.

Genus *Palusphaera* Lecal, 1965 emend. Norris, 1984

Description — Monothecate, monomorphic coccosphere consisting of rhabdoliths with a long styliiform process. Central area without radial cycle.

Type species — *Palusphaera vandeli* Lecal, 1965.

Remarks — In the North Atlantic (Cruise APNAP I) a collapsed monomorphic coccosphere with a *Palusphaera* affinity was found. It consists of rhabdoliths with a sub-circular disc of 1.5-2.2 μm in diameter, without a radial cycle, bearing a spindle-shaped pointed process of variable length, that is thickest ($\pm 0.35 \mu\text{m}$) at 1/2-1/3 height from the disc. The process seems to be entirely constructed of long, parallel cuneate cycle elements, which makes the rhabdoliths distinctly different from those of *Palusphaera vandeli*.

A similar specimen from the western Mediterranean Sea was shown by Knap-pertsbusch (1990, pl. 7, fig. 3) as *Rhabdosphaera longistylis*; coccosphere diameter without processes $\pm 5 \mu\text{m}$, process length 3-9 μm , disc diameter $\pm 1.6 \mu\text{m}$. Although *Rhabdosphaera longistylis* was described by Schiller (1925, p. 40, pl. 4, fig. 40; northern Adriatic Sea) having much larger dimensions (coccosphere diameter without processes 20-25 μm , process length 38-40 μm , disc diameter 4-5 μm), the similarity in process shape suggests that the two forms might be identical. See also Remarks on *Rhabdosphaera*.

Palusphaera vandeli Lecal, 1965 emend. Norris, 1984

Pl. 8, fig. 1.

- 1955 *Acanthoica quattrosolina* Lohmann – (in part) Halldal & Markali, pp. 15, 16, pl. 18, fig. 3 (non figs. 1, 2, 4).
1965 *Palusphaera vandeli* sp. nov. – Lecal, pp. 68, 69, text-fig. K, pl. 2, fig. 9.
1967 *Palusphaera vandeli* Lecal – Lecal, pp. 319, 320, text-fig. 13, figs. 19, 20.
1971 *Rhabdosphaera longistylis* Schiller – Norris, p. 902, fig. 4.
1980 *Rhabdosphaera longistylis* Schiller – (in part) Reid, pl. 4, fig. 2 (non fig. 3).
1984 *Palusphaera vandeli* Lecal emend. – Norris, p. 35, figs. 1f, 9, 10.

Description — Coccosphere consisting of ± 40 rhabdoliths with a long, very thin styliiform process of spirally arranged lath-shaped elements. Basal disc circular, almost flat, with central pore at proximal side. Outer rim cycle relatively wide, consisting of rectangular to slightly wedge-shaped elements, completely covering inner rim cycle in distal view. Inner rim cycle elements almost tangentially arranged, with strongly laevogyre sutures in proximal view (Pl. 8, fig. 1). Lamellar cycle elements form the central area, that is slightly convex distally and concave proximally, and the process.

Dimensions — Rhabdolith disc 2.0-2.3 μm in diameter; outer rim cycle $\pm 0.3 \mu\text{m}$ wide; process length more than 10 μm .

Remarks — The continuous second layer of elements on the proximal side of the disc, described by Norris (1984), apparently is the inner rim cycle.

The specimen given by Borsetti & Cati (1972, pl. 55, fig. 1) as *Rhabdosphaera*

longistylis probably belongs to *P. vandeli* as well, but the SEM-micrograph does not show the necessary details to be conclusive about that.

Distribution (Fig. 6e) — South of India, western Arabian Sea, Gulf of Aden, rare; northeastern Indian Ocean, eastern Arabian Sea, Red Sea, Mediterranean Sea, occasional. Highest absolute frequency: northern Red Sea (Gulf of Suez).

Previous research — North Atlantic, Mediterranean Sea, Indian Ocean, Pacific.

Genus *Rhabdosphaera* Haeckel, 1894

Description — Dithecate coccosphere, with monomorphic endotheca and exotheca, consisting of two distinctly different types of rhabdololiths. Central area composed of lamellar cycle elements; without lath cycle. Discoidal rhabdololiths form the exotheca; they partly cover the basal discs of the endothecal helatiform rhabdololiths.

Type species — *Rhabdosphaera clavigera* Murray & Blackman, 1898. As '*Claviger*'; corrected by Kamptner (1944, p. 140). Designated as type species by Hay & Towe (1962).

Remarks — *Rhabdosphaera* is the only rhabdosphaerid genus that possesses dithecatism: two layers of differently constructed rhabdololiths on the coccosphere.

Norris (1984) excluded the two species described as *Rhabdosphaera longistylis* Schiller, 1925 and *Ruginaster longistylis* (Schiller, 1925) Kamptner, 1941 (with *Rhabdosphaera ruginiensis* Kamptner, 1936 as a synonym), because they possibly are non-coccolithophorids. If future research reveals a coccolithophorid nature of these species, they may need to be transferred to the monomorphic rhabdololith-bearing genus *Palusphaera*.

Rhabdosphaera clavigera Murray & Blackman, 1898

Pl. 8, figs. 3, 4, 6, 7.

- 1898 *Rhabdosphaera claviger* sp. nov. — Murray & Blackman, p. 438, pl. 15, figs. 13-15.
 1902 *Rhabdosphaera stylifer* sp. nov. — Lohmann, p. 143, pl. 5, fig. 65.
 1935 *Rhabdosphaera stylifera* Lohmann — Gran & Braarud, p. 389.
 1937 *Rhabdosphaera stylifer* Lohmann var. *capitillifera* var. nov. — Kamptner, p. 313, pl. 17, figs. 43-45.
 1941 *Rhabdosphaera stylifer* Lohmann — Kamptner, pp. 96, 115, pl. 15, figs. 148, 149, 155.
 1955 *Rhabdosphaera stylifer* Lohmann — Halldal & Markali, p. 16, pl. 20, figs. 1-4.
 1961 *Discolithus phaseolus* sp. nov. — Black & Barnes, p. 144, pl. 26, figs. 1-4 (sediments).
 1967 *Rhabdosphaera stylifera* Lohmann — McIntyre & Bé, p. 567, pl. 4, figs. a-c (figs. b and c from sediments).
 1971 *Rhabdosphaera clavigera* Murray & Blackman — Gaarder & Hasle, p. 536, fig. 11.
 1972 *Rhabdosphaera claviger* Murray & Blackman — Borsetti & Cati, pp. 407-409, pl. 55, figs. 2-6.
 1975 *Rhabdosphaera clavigera* Murray & Blackman — Kling, pp. 5, 6, pl. 3, figs. 11, 12.
 1979 *Rhabdosphaera claviger* Murray & Blackman — Nishida, pl. 12, fig. 2.
 1979 *Rhabdosphaera clavigera* Murray & Blackman — Winter et al., pl. 2, fig. 10.
 1984 *Rhabdosphaera claviger* Murray & Blackman — Hallegraeff, p. 236, figs. 32, 33.
 1984 *Rhabdosphaera claviger* Murray & Blackman — Norris, pp. 31, 33, figs. 2-5.
 1985 *Rhabdosphaera clavigera* Murray & Blackman — Nishida, pl. 1, fig. 2.
 1990 *Rhabdosphaera clavigera* Murray & Blackman — Knappertsbusch, pp. 24, 25, pl. 7, figs. 1, 2.
 1990 *Rhabdosphaera clavigera* var. *stylifera* (Lohmann) stat. nov. — Kleijne & Jordan, p. 13.

Description — Coccosphere with exotheca of \pm 15-20 discoidal rhabdoliths and endotheca of \pm 20 helatoform rhabdoliths. The outer rim cycle elements are narrow at the proximal side and wider at the distal side, covering the inner rim cycle along the periphery and on the distal side. Inner rim cycle elements arranged in almost tangential direction (Pl. 8, figs. 6, 7). Central area constructed of a single layer of irregularly arranged lamellar cycle elements, angular on the distal side and with rounded edges on the proximal side (Pl. 8, figs. 3, 6, 7). Discoidal rhabdoliths elliptical, with narrow outer rim cycle, a depression in one or both long sides and a small central peak of overlapping elements. Helatoform rhabdoliths have an elliptical disc with a relatively wider outer rim cycle (in distal view) and a central area of overlapping lamellar cycle elements that rise towards the centre and continue in the rod-shaped process of spirally arranged elongate elements; with central pore on proximal side. Process prolonged by a papilla of cuneate cycle elements.

Dimensions — Diameter coccosphere without processes 7.9-8.6 μm , including processes 18.7-19.7 μm . Discoidal rhabdoliths 3.0-3.7 μm long, 1.8-2.4 μm wide; outer rim cycle 0.2 μm wide. Helatoform rhabdoliths, disc 3.4-3.5 μm long, 2.4-2.7 μm wide; outer rim cycle 0.4 μm wide; process \pm 5 μm long.

Remarks — In distal view the inner rim cycle is entirely covered by the elements of the outer rim cycle. Unlike Norris (1984) I think that only the marginal part (rim) of the rhabdolith disc is double-layered.

Rhabdosphaera clavigera is a highly variable species, showing intergradations of different process shapes. The process morphology varies between claviform, characteristic for specimens originally described as *R. clavigera*, and helatoform, originally described as *R. stylifera* (Kamptner, 1937; McIntyre & Bé, 1967; Borsetti & Cati, 1972; Hallegraeff, 1984; Norris, 1984; Knappertsbusch, 1990).

Coccospheres with helatoform rhabdoliths are the commonly occurring specimens (McIntyre & Bé, 1967; Hallegraeff, 1984). The less common, more robust, club-shaped (claviform) rhabdoliths also occur worldwide and are especially known as isolated rhabdoliths from sediment traps (Steinmetz, 1991) and sediments (e.g. Cohen, 1964; Cohen & Reinhardt, 1968; Bartolini, 1970; Müller, 1972; Martini & Müller, 1972; Conley, 1979; Biekart, 1989). SEM-micrographs of coccospheres bearing claviform rhabdoliths show that these coccospheres always bear also helatoform rhabdoliths and/or rhabdoliths with a process intermediate of claviform and helatoform rhabdoliths (pers. comm. Dr M. Boysen, University of California; Gaarder & Hasle, 1971; Borsetti & Cati, 1972; Nishida, 1979, 1985; Hallegraeff, 1984). The process shape seems to be a characteristic of individual rhabdoliths and not of entire rhabdospheres and, therefore, it is incorrect to distinguish coccospheres with different types of processes as the varieties *clavigera* and *stylifera*, as was done by Kleijne & Jordan (1990). Moreover, coccospheres with only helatoform, with claviform and helatoform, and with intergrading processes show no difference in geographical distribution. In case differentiation between process types is preferred, it seems better to separate the coccospheres as 'formae'.

During Cruise Gx no specimens with claviform or intergrading processes were found, however, some specimens from the eastern Mediterranean Sea had helatoform

processes with five small 'wings' of laterally extending elements instead of a straight end. This form has been described from the Aegean Sea by Kamptner (1937, p. 313, pl. 17, figs. 43-45) as *Rhabdosphaera styliifera* var. *capitillifera*, and it has been illustrated by e.g. Borsetti & Cati (1972, pl. 55, fig. 5), Winter et al. (1979, pl. 2, fig. 10), Hallegraeff (1984, fig. 33b) and Knappertsbusch (1990, pl. 7, figs. 1-2), which shows that also this type of rhabdolith process has a wide geographical distribution.

Distribution (Fig. 6g) — Northeastern Indian Ocean, eastern Arabian Sea, rare; Red Sea, occasional; eastern North Atlantic, frequent; Mediterranean Sea, very frequent. Highest absolute frequency: Mediterranean Sea.

Previous research — Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Indo-Malayan Region, Pacific.

Rhabdosphaera xiphos (Deflandre & Fert, 1954) Norris, 1984
Pl. 8, figs. 2, 5.

1954 *Rhabdolithus xiphos* sp. nov. — Deflandre & Fert, pp. 42,43, pl. 8, figs. 1-3 (sediments).

1977 *Rhabdosphaera longistylis* Schiller — Okada & McIntyre, p. 17, pl. 5, fig. 6.

1979 *Rhabdosphaera longistylis* Schiller — Winter et al., pl. 2, fig. 11.

1980 *Rhabdosphaera longistylis* Schiller — (in part) Reid, p. 157, pl. 4, fig. 3 (non fig. 2).

1984 *Rhabdosphaera xiphos* (Deflandre & Fert) comb. nov. — Norris, pp. 33, 34, figs. 1d, e, 6-8.

Description — Coccosphere consisting of ± 50 discoidal exothecal rhabdoliths and ± 50 process-bearing endothecal rhabdoliths with a characteristic collar. Discoidal rhabdoliths elliptical, with slightly elevated central area of lamellar cycle elements; overlapping large elements form a pattern of radial spokes in the centre. Process-bearing rhabdoliths have a flat circular disc with a central area of lamellar cycle elements that protrude distally in the centre, forming a collar: a short helatiform process with a blunt end. The collar is prolonged by an elongate thin vertical structure, an extended papilla, of parallel cuneate cycle elements, that gradually tapers from a broader proximal part to a fine tip. Inner rim cycle of process-bearing rhabdoliths consists of almost tangentially arranged elements (Pl. 8, fig. 5).

Dimensions — Discoidal rhabdoliths 1.6-2.0 μm long, 1.2-1.4 μm wide. Helatiform rhabdoliths, disc diameter 1.0-1.2 μm ; collar 0.35 μm high; process (collar + extended papilla) 6.0-7.2 μm long.

Remarks — In the process-bearing rhabdoliths of *R. xiphos* the lamellar cycle elements form the central part of the disc and the lower part of the process, the collar, while the upper part of the process is formed by cuneate cycle elements (compare with the papilla in rhabdoliths of *Cyrtosphaera* and *Rhabdosphaera clavigera* and the vertical ridges inside the labiatiform protrusion of *Algirosphaera robusta*).

The pattern of 'radiating spokes' in the centre of the rhabdolith (Norris, 1984: 'superposed elements on the distal side') seem to be caused by relatively large overlapping elements, of which the distally protruding long sides form ridges on the distal surface.

In extant coccolithophorid literature *Rhabdosphaera xiphos* has been misinter-

preted as *R. longistylis*, see e.g. Okada & McIntyre (1977), Winter et al. (1979) and Reid (1980).

Rhabdoliths of *Palusphaera vandeli* differ from the process-bearing rhabdoliths of *R. xiphos* in having a styliform process instead of a collar with an extended papilla (helatiform process), and in having a basal disc that is twice as large in diameter.

Distribution (Fig. 6h) — Red Sea, rare; Mediterranean Sea, frequent; eastern North Atlantic, very frequent. Highest absolute frequency: eastern North Atlantic.

Previous research — North Atlantic, Red Sea, Indian Ocean, Pacific.

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Appendix 1: Rhabdosphaerid key

1. Cocosphere
 - a. monothecate..... 2
 - b. dithecate; *Rhabdosphaera* 8
- 2 (1a). Monothecate cocosphere
 - a. monomorphic 3
 - b. vari-monomorphic; *Cyrtosphaera* 6
 - c. dimorphic: *Algirosphaera* *Algirosphaera robusta*
 - d. polymorphic: *Acanthoica* 9
- 3 (2a). Central area of rhabdoliths with a
 - a. protrusion (with a cavity): *Anacanthoica* 4
 - b. process (rod-shaped at its base) 5
- 4 (3a). Protrusion conical
 - a. with blunt end prolonged by a papilla; lath cycle with 24-35 radial laths *Anacanthoica acanthos*
 - b. with pointed end; lath cycle with 44-60 radial laths *Anacanthoica cidaris*
- 5 (3b). Process
 - a. salpingiform: *Discosphaera* *Discosphaera tubifera*
 - b. styliform: *Palusphaera* *Palusphaera vandeli*
- 6 (2b). Rhabdoliths with protrusion
 - a. sacculiform, of needle-like elements *Cyrtosphaera cucullata*
 - b. conical with blunt end and papilla 7
- 7 (6b). Radial cycle with
 - a. 26-38 laths *Cyrtosphaera aculeata*
 - b. 42-52 laths, with rim curved upward from lath cycle; protrusion somewhat asymmetrical *Cyrtosphaera lecaliae*
- 8 (1b). Basal disc helatiform endothecal rhabdoliths elliptical; discoidal exothecal rhabdoliths
 - a. circular *Rhabdosphaera xiphos*
- 9 (2d). *Acanthoica* body rhabdoliths
 - a. circular to sub-circular 10
 - b. elliptical 12
- 10 (9a). Radial cycle with
 - a. 30-38 dextrally imbricated elements *Acanthoica jancheni*
 - b. openings between the radial laths 11
- 11 (10b). Radial cycle with
 - a. 23-38 tilted laths; central area with somewhat sacculiform protrusion *Acanthoica acanthifera*
 - b. 24-32 laths; slightly elevated central area *Acanthoica quattrosolina*
- 12 (9b). Radial cycle
 - a. with 42-50 laths and openings between them *Acanthoica maxima*
 - b. without distinct openings between laths 13
- 13 (12b). Body rhabdoliths
 - a. relatively large, broad-elliptical; radial cycle with 44-50 elements *Acanthoica biscayensis*
 - b. relatively small; radial cycle with 18-26 elements *Acanthoica* sp. type A

Plate 1

Figs. 1-4, 6, 7: bar = 1 μm ; fig. 5: bar = 2 μm .

1-3. *Cyrtosphaera aculeata* (Kamptner) comb. nov.

1. Disintegrated coccosphere bearing rhabdoliths with a conical protrusion to helatoform process (upper middle); Gulf of Aden (Station G0-106).

2. Detailed view of fig. 1, showing conical protrusion prolonged by papilla.

3. Rhabdoliths with protrusions of variable height; Red Sea (Station Gx-142).

4. *Cyrtosphaera lecaliae* sp. nov., holotype

Collapsed coccosphere of rhabdoliths with somewhat asymmetrical protrusion that may be extended to a helatoform process; central North Atlantic (Station T86-C-51-A).

5-7. *Acanthoica acanthifera* Schiller

5. Coccosphere with pole rhabdoliths at one pole; eastern Arabian Sea (Station G0-135).

6. Detailed view of pole rhabdoliths of fig. 5, showing one thick, long and three short apical spines, and one thinner 'antapical' spine (upper right).

7. Detailed view of body rhabdoliths of fig. 5, showing outer rim cycle, radial cycle with tilted elements, and thick conical to somewhat sacculiform protrusion of lamellar cycle elements.

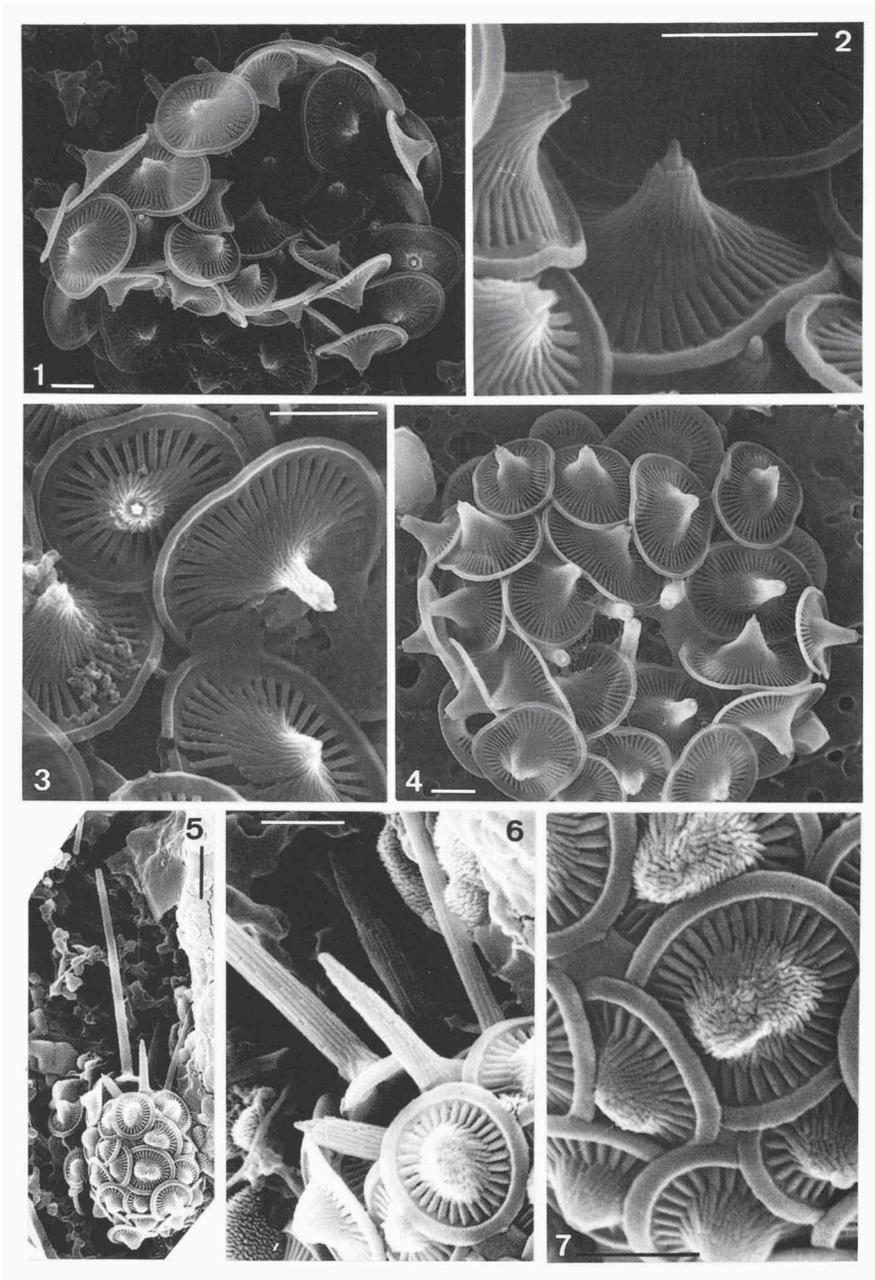


Plate 2

Figs. 1, 2, 4-6: bar = 1 μm ; figs. 3, 7: bar = 3 μm .

1, 2, 7. *Acanthoica maxima* Heimdal

1. Disintegrated coccosphere showing three apical spines (right; one with a thicker process) and two antapical spines; western Arabian Sea (Station Gx-94).

2. Detailed view of long-elliptical body rhabdoliths of fig. 1.

7. Disintegrated coccosphere with four pole rhabdoliths: one apical spine with a thick and one with a thin process, and two 'antapical' spines (left) with a laterally flattened base; western Arabian Sea (Station Gx-96).

3-6. *Acanthoica biscayensis* sp. nov., holotype

3. Coccosphere with three long and three short spines; eastern North Atlantic (Station Gx-217).

4. Detailed view of fig. 3, showing broad-elliptical body rhabdoliths.

5. Detailed view of fig. 3, showing three apical pole rhabdoliths with a short process (and circular disc) and one with a long process.

6. Detailed view of broad-elliptical body rhabdoliths of fig. 3, with a small peak of lamellar cycle and wedge-shaped cuneate cycle elements.

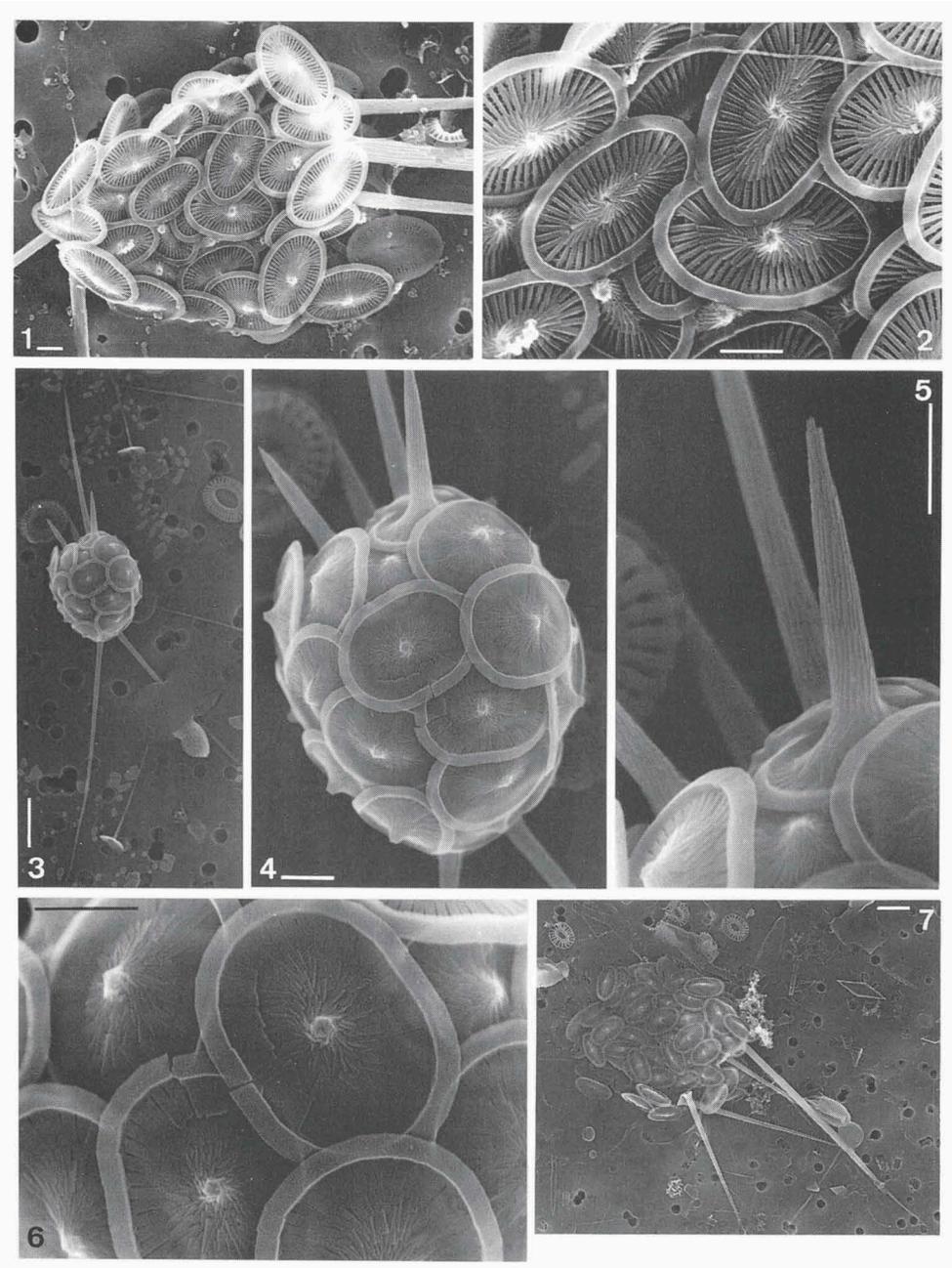


Plate 3

Figs. 1-6: bar = 3 μ m.

1-6. *Acanthoica quattrosquina* Lohmann

1. Long-ellipsoidal coccosphere of the '*quattrosquina*'-type, with spines at both poles; western Arabian Sea (Station Gx-96).
2. Ellipsoidal coccosphere with spines at both poles; Arabian Sea (Station Gx-88).
3. Sub-spherical coccosphere with spines at both poles; Arabian Sea (Station Gx-88).
4. Sub-spherical coccosphere with large opening, and all spines on one side; Arabian Sea (Station Gx-88).
5. Sub-spherical coccosphere with spines on one side; Arabian Sea (Station Gx-88).
6. Spherical coccosphere of the '*coronata*'-type with spines at one pole; western Arabian Sea (Station Gx-96).

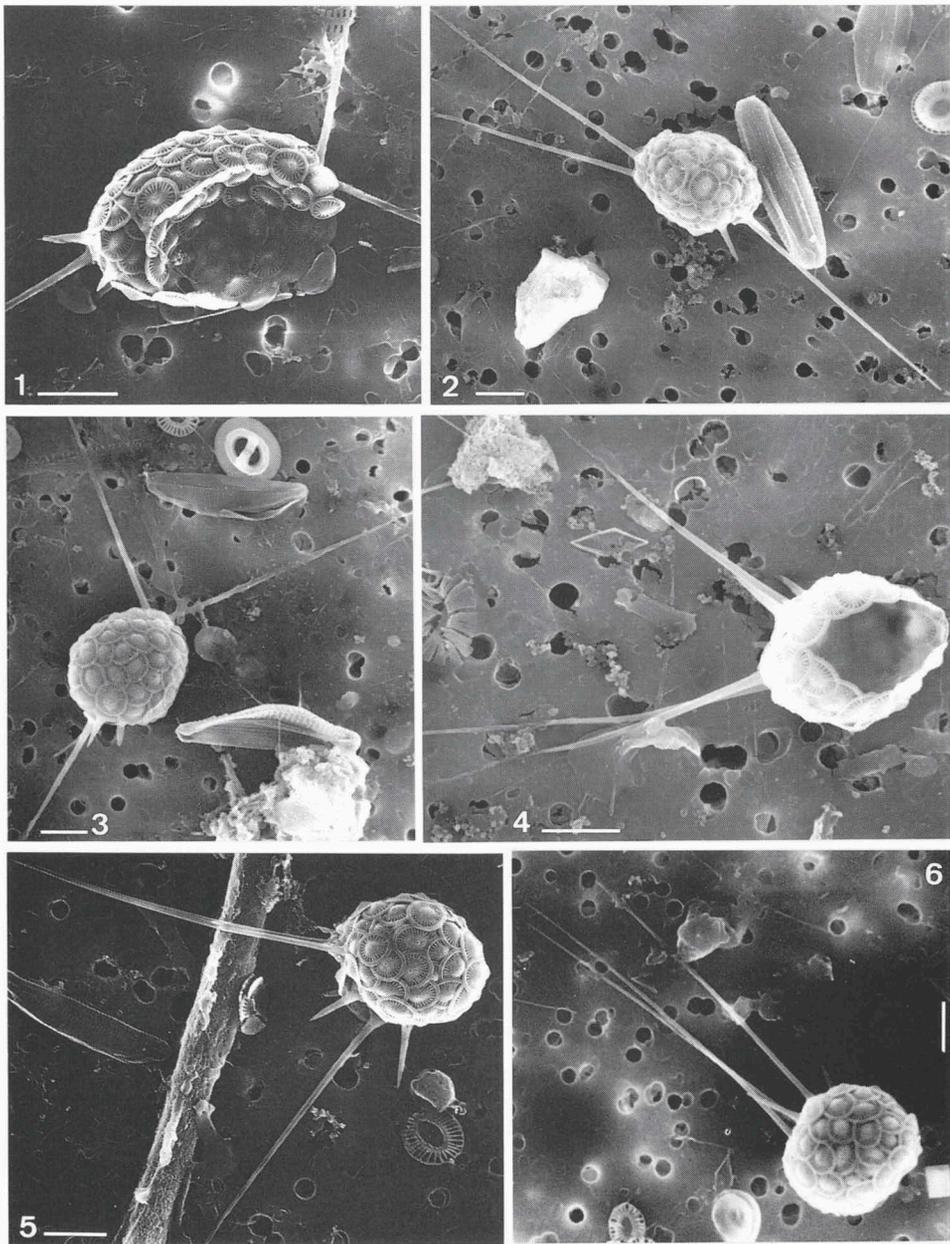


Plate 4

Figs. 1-5: bar = 1 μm .

1-3. *Acanthoica quattrosolina* Lohmann

1. Body rhabdoliths, two apical spines with a short process and long-elliptical disc and one with a thick process and circular disc, and two 'antapical' spines with a long process and laterally flattened base; western Arabian Sea (Station Gx-96).

2. Laterally flattened basal part of antapical spines; Arabian Sea (Station Gx-88).

3. Body rhabdoliths in proximal and lateral view, showing proximal part of outer rim cycle elements, inner rim cycle with laevogyre sutures, radial cycle laths and lamellar cycle elements; same specimen as fig. 2.

4-5. *Cyrtosphaera cucullata* (Lecal-Schlauder) comb. nov.

4. Detailed view of fig. 5, showing rhabdoliths in distal and lateral view, with sacculiform protrusion of needle-like lamellar cycle elements.

5a-b. 3D-micrographs of coccosphere bearing rhabdoliths with a protrusion that is higher on one side of the coccosphere; northern North Atlantic (Station T86-C-15).

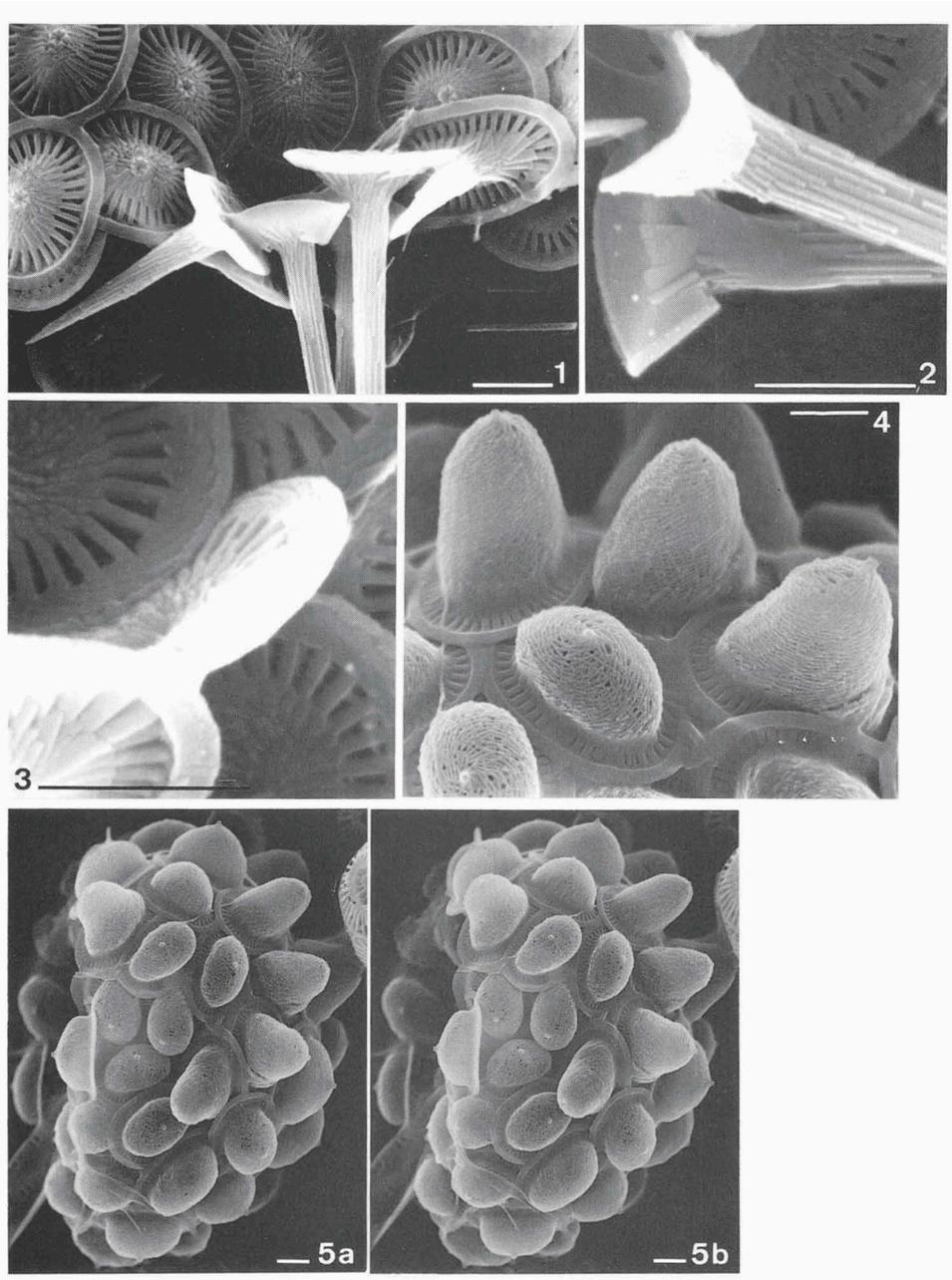


Plate 5

Figs. 1-6: bar = 1 μm .

1-4. *Acanthoica* sp. type A

1. Collapsed coccosphere with six pole rhabdoliths; central North Atlantic (Station T86-8R,10,C).
2. Detailed view of antapical pole, showing two partly disintegrated rhabdoliths with a long process; same coccosphere as fig. 1.
3. Detailed view of apical pole, showing one long and three short spines; same coccosphere as fig. 1.
4. Detailed view of elliptical body rhabdoliths of fig. 1.

5-6. *Acanthoica jancheni* Schiller

5. Coccosphere bearing body rhabdoliths with a low conical protrusion of lamellar and cuneate cycle elements, and two antapical spines. At the apical pole one long and three short spines are present; central North Atlantic (Station T86-14R,20,C).
6. Disintegrated coccosphere showing the three short apical spines; central North Atlantic (Station T86-C-64).

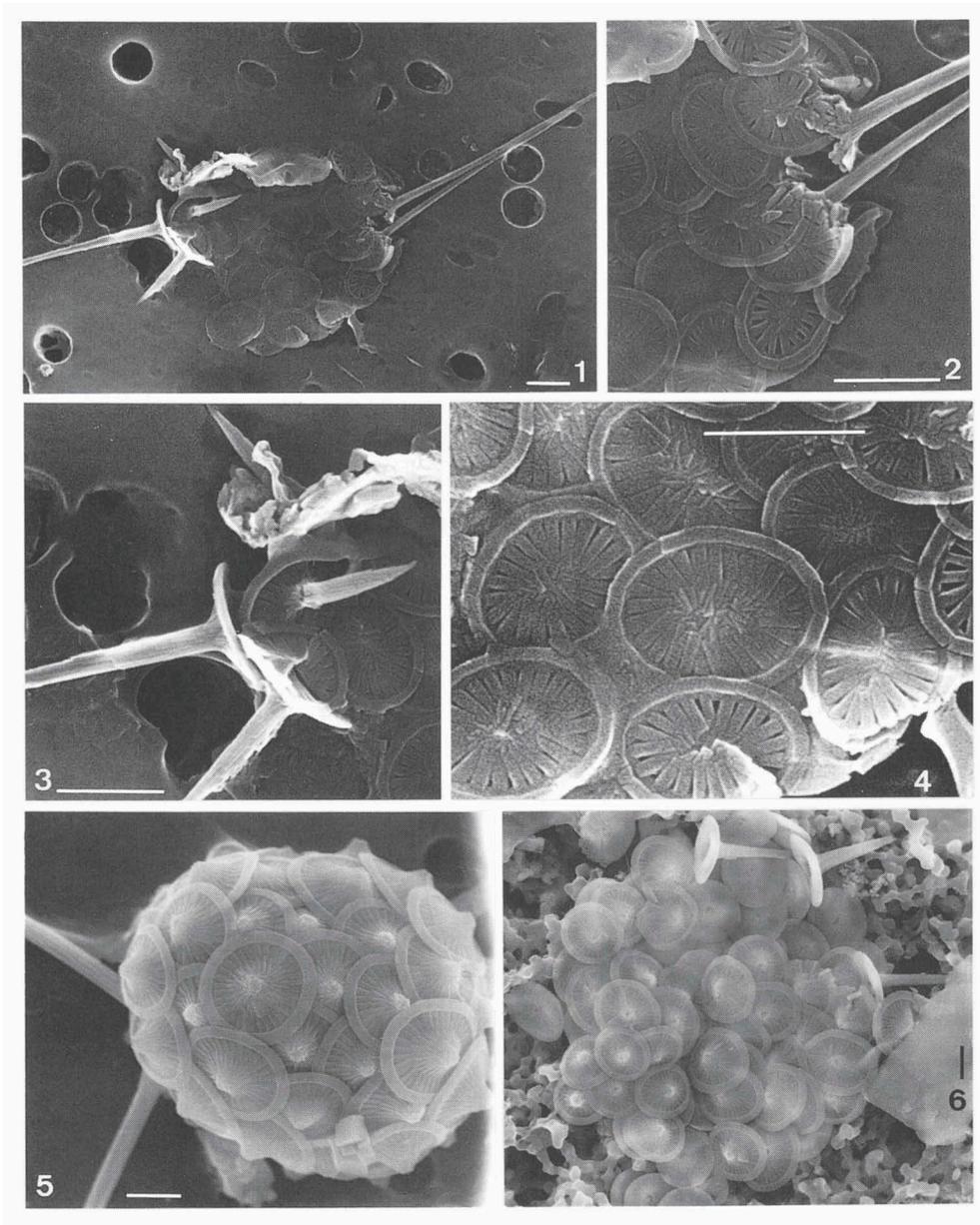


Plate 6

Figs. 1-6: bar = 1 μm ; fig. 7: bar = 0.5 μm .

1-7. *Algirosphaera robusta* (Lohmann) Norris

1. Cocosphere in apical view, showing three circum-flagellar rhabdoliths with a pointed protrusion; central North Atlantic (Station T86-C-57-A).
2. Cocosphere with three circum-flagellar rhabdoliths, and body rhabdoliths in which the elongate central cavity is visible as a dark line; western Arabian Sea (Station Gx-96).
3. Proximal view of sacculiform rhabdoliths, showing the proximal covering of elongate elements; northeastern Indian Ocean (Station Gx-8).
4. Cocosphere in antapical view; western Arabian Sea (Station Gx-96).
5. Cocosphere in lateral view; western Arabian Sea (Station Gx-96).
6. Distal view of sacculiform protrusion. Some coccoliths have an open distal part (labiatiform protrusion), showing cycle of elongate vertical ribs; northeastern Indian Ocean (Station Gx-49).
7. Distal view of sacculiform protrusion, showing interlocking elements of the distal part; Arabian Sea (Station Gx-88).

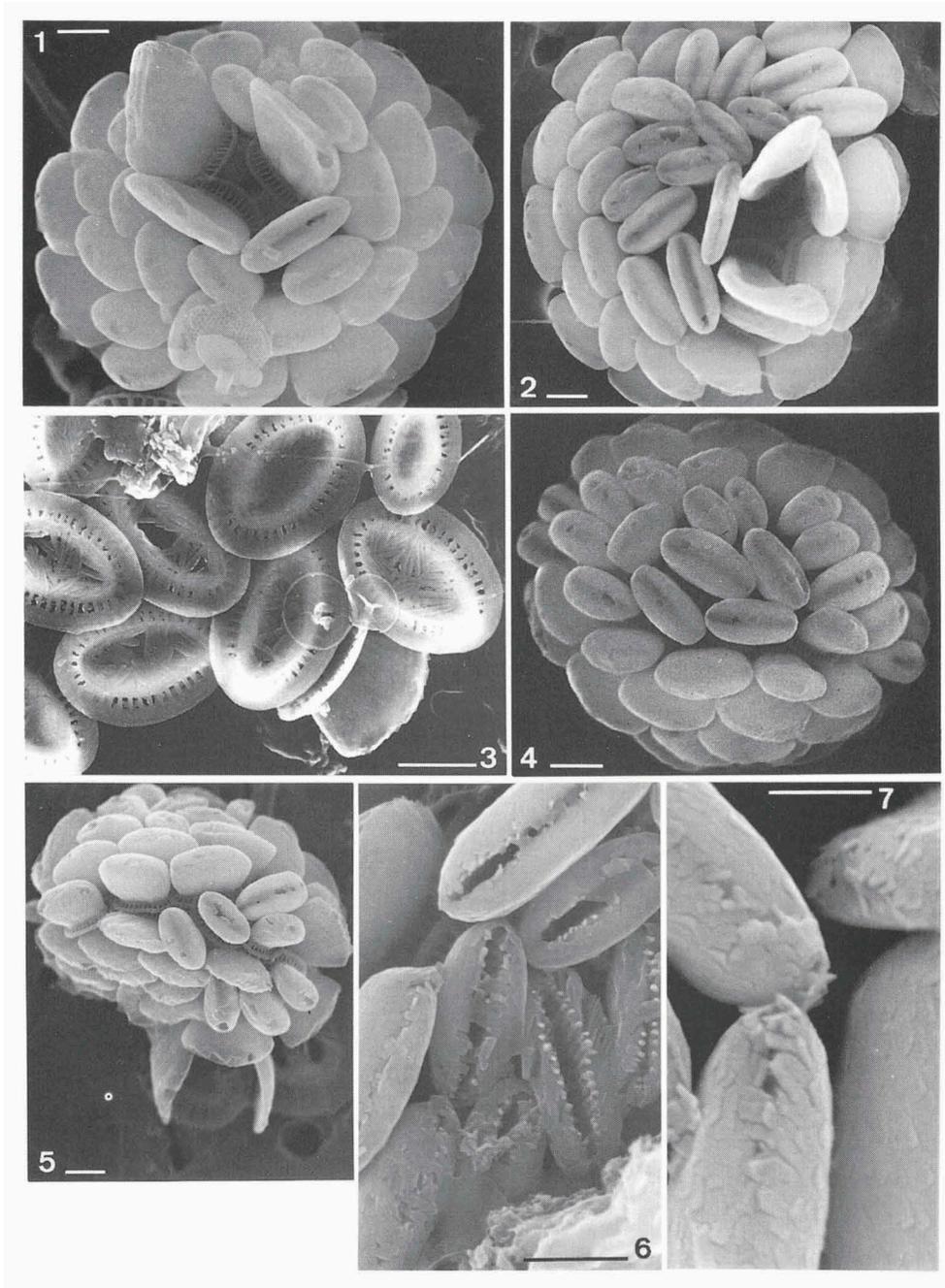


Plate 7

Figs. 1-3, 6: bar = 1 μm ; figs. 4, 5: bar = 4 μm .

1. *Anacanthoica acanthos* (Schiller) Deflandre.

Monomorphic coccosphere of rhabdoliths that have a conical protrusion with a blunt end; central North Atlantic (Station T86-14R,20,C).

2-4. *Anacanthoica cidaris* (Schlauder) comb. nov.

2. Disintegrated coccosphere of rhabdoliths with a pointed conical protrusion; Red Sea (Station Gx-134).

3. Detailed view of rhabdoliths of fig. 2.

4. Partly disintegrated coccosphere; Gulf of Aden (Station G0-110).

5-7. *Discosphaera tubifera* (Murray & Blackman) Ostenfeld.

5. Coccospheres, showing variation in size of salpingiform process; central North Atlantic (Station T86-C-57-F).

6. Rhabdoliths with many processes broken off; central North Atlantic (Station T86-C-36-L).

7. Detailed view of rhabdoliths of fig. 6, showing the wide outer rim cycle, radial cycle, intermediate cycle, broken off process (lamellar cycle) and a small elongate structure sticking through the central pore.

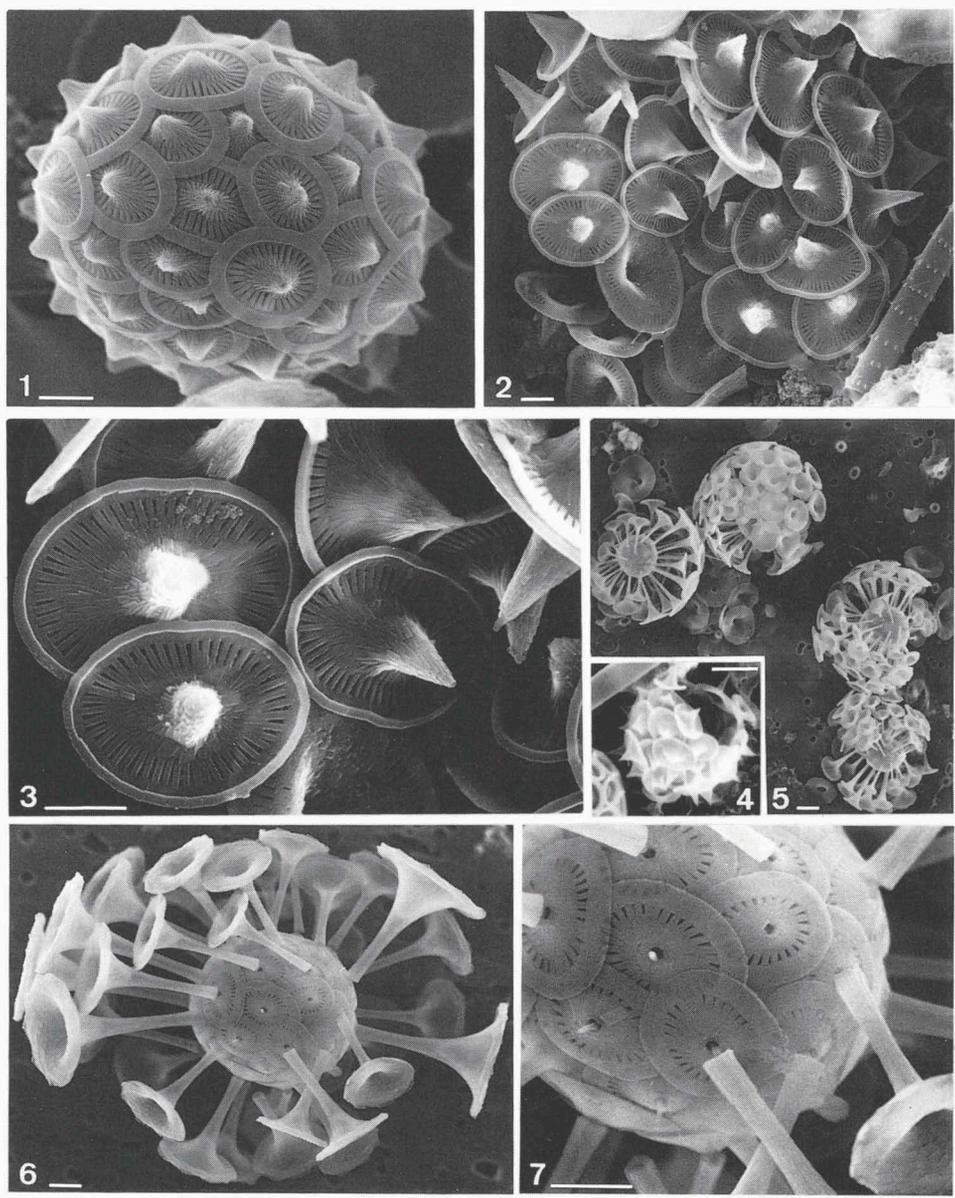


Plate 8

Figs. 1, 3, 5-7: bar = 1 μm ; figs. 2, 4: bar = 2 μm .

1. *Palusphaera vandeli* Lecal emend. Norris.

Rhabdolith with styliform process, showing outer rim cycle in lateral view (arrow 1) and inner rim cycle with laevogyre sutures in proximal view (arrow 2); northern Red Sea (Station Gx-159).

2, 5. *Rhabdosphaera xiphos* (Deflandre & Fert) Norris.

2. Collapsed coccosphere with discoidal exothecal rhabdoliths and helatoform endothecal rhabdoliths; eastern North Atlantic (Station Gx-215).

5. Detailed view of helatoform rhabdoliths, showing collar of lamellar cycle elements with an extended papilla of long, parallel cuneate cycle elements, and the proximal pore; Mediterranean Sea (Station Gx-162).

3, 4, 6, 7. *Rhabdosphaera clavigera* Murray & Blackman.

3. Detailed view of coccosphere of fig. 4.

4. Dithecate coccosphere with discoidal exothecal rhabdoliths and helatoform endothecal rhabdoliths; eastern North Atlantic (Station Gx-209).

6. Proximal view of discoidal rhabdolith, showing outer rim cycle elements (arrow 1) and almost tangentially arranged inner rim cycle elements (arrow 2). Remaining elements are of lamellar cycle; Red Sea (Station Gx-153).

7. Proximal view of helatoform rhabdolith, showing outer rim cycle elements, inner rim cycle elements (arrow) and central pore; Red Sea (Station Gx-153).

