Ericiolus gen. nov. (Prymnesiophyceae), a new coccolithophorid genus from polar and temperate regions

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During late August 1985, a significant coccolithophorid contribution to phytoplankton biomass and diversity was evident in the inner Danish waters of the southern Kattegat and the Isefjord. The material included new taxa, one of which, *Ericiolus spiculiger* gen. et sp. nov., is now formally described together with a second, Antarctic species from the same genus, *E. frigidus* sp. nov. The genus comprises small, apparently heterotrophic species with a single type of calcified structure reminiscent of caltrops.

Key words: Coccolithophorids, *Ericiolus* gen. nov., Isefjord, Kattegat, marine nanoplankton, Weddell Sea.

Introduction

Coccolithophorids are generally considered to be of little importance in inner Danish waters and therefore collection of material for phytoplankton monitoring programmes is most often carried out without attention being paid to preserving delicate, calcified structures. However, significant blooms of coccolithophorids [viz. *Emiliania huxleyi* (Lohmann) Hay *et* Mohler] are repeatedly reported from the Oslo Fjord and the Skagerrak area (Holligan *et al.*, 1989), for example; satellite data from the Coastal Zone Colour Scanner clearly indicate that an extensive bloom of coccolithophorids is a recurring phenomenon in the North Sea and the Skagerrak (Holligan *et al.*, 1989).

Results from a major survey of protist plankton from the Kattegat area (Thomsen, 1992) and "Belt Project" data (Thomsen, 1979*a* and unpublished data) show that *Emiliania huxleyi* at least may occur throughout the Kattegat, the Belt Sea and the western Baltic at salinities down to 8–10‰ S. Bloom quantities have not been reached, although cell concentrations in excess of 10^6 cells l^{-1} do not appear to be unusual in the southern part of the Kattegat (Hansen, 1992).

Emiliania huxleyi is beyond doubt the single most important coccolithophorid species in inner Danish waters. A number of other species have been found sporadically in samples prepared for transmission electron microscopy (Christensen *et al.*, 1985; Thomsen, unpublished data). Among these are some of the enigmatic types of weakly calcified and heterotrophic coccolithophorids that have recently been described from polar waters (see e.g. Thomsen *et al.*, 1988; Garrison & Thomsen, 1993; Marchant & Thomsen, 1994). These particular types of coccolithophorids are not distributionally confined to the more saline parts of the Baltic Sea, but can be found at salinities down to 3‰ S (Thomsen, 1979*b* and unpublished data).

An unusual nanoplankton community, in terms of abundance and diversity of coccolithophorids, was encountered in Isefjord samples from late August 1985. These particular samples included at least 8 different taxa, some of which were new to science.

The present paper comments briefly on this particular coccolithophorid community, and additionally describes the genus *Ericiolus* gen. nov. with two species: *E. spiculiger* sp. nov. from the Isefjord, Denmark, and *E. frigidus* sp. nov. from the Weddell Sea, Antarctica. The latter species has previously been illustrated as Coccolithophorid sp. 2 (Thomsen *et al.*, 1988). In both species the calcified structures resemble the caltrops or "crows-feet" used in ancient warfare. For the sake of simplicity these structures will therefore be referred to below as "caltrops".

Materials and methods

Material from the Isefjord, Denmark (*Ericiolus spiculiger* sp. nov.), originates from a nanoplankton survey undertaken during 1984–5 at several stations throughout the fjord and in the southern Kattegat (Fig. 1*A*) (Kristensen, 1986; Thomsen, 1988*a,b*). The samples used for this particular investigation were collected on 29 August 1985 from stations 3, 4, 7 and 12 (Fig. 1*A*). A manually operated valve pump was used to collect the samples. Water depths at these particular stations ranged from 9 to 15 m. Surface salinities varied from 16·5 (station 7) to 19·0‰ S (station 3). The surface temperature was *c.* 18°C at all stations.

The Antarctic material of *E. frigidus* sp. nov. mostly originates from the R/V *Melville* AMERIEZ March 1986 cruise (Fig. 1*B*) to the Weddell Sea. Additional material from the same area (Fig. 1*B*) was collected during the

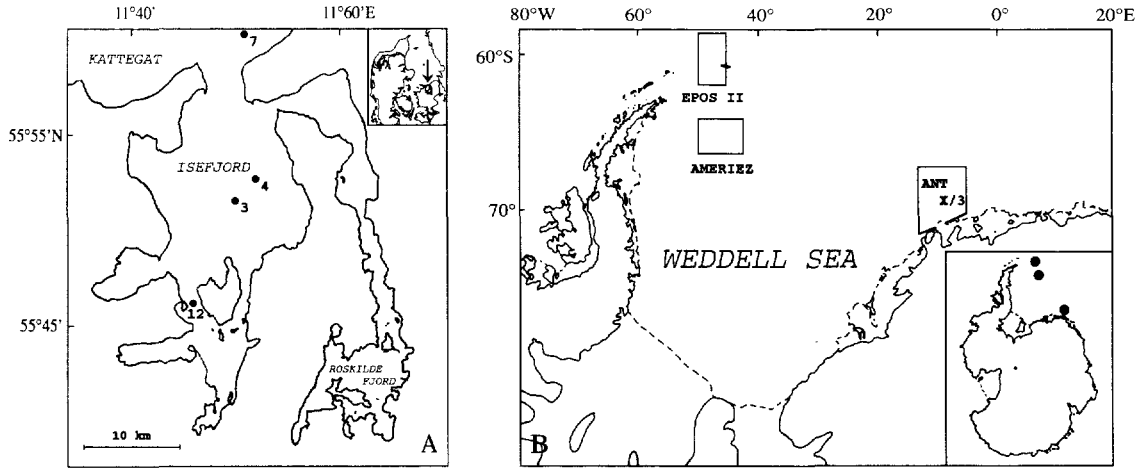


Fig. 1. Maps showing the Danish (*A*) and Antarctic sampling sites (*B*).

R/V *Polarstern* cruises EPOS leg II (Nov. 1988–Jan. 1989) and ANT X/3 "Herbst im Eis" (April–May 1992).

The nanoplankton was concentrated by means of filtration and/or centrifugation of prefiltered samples. Small droplets of resuspended material were placed on formvar/carbon coated grids for transmission (TEM) and scanning (SEM) electron microscopy or on rinsed coverslips for light microscopy. Both grids and coverslips were carefully washed in order to remove salt crystals. For a more detailed description of the techniques used see Moestrup & Thomsen (1980) and Thomsen (1982). Prior to examination in a JEOL 100SX, the grids were shadowcast with chrome or gold/palladium. Selected grids were subsequently sputter-coated with gold and examined in a JEOL 100CX microscope with scanning attachment.

The X-ray elemental analysis of the new genus was carried out at the Geological Institute of the University of Copenhagen, using a Cambridge Stereoscan 180 scanning electron microscope, equipped with a Kevex energy dispersive X-ray analyser backed by a Link system.

Measurements were made using a Leitz ASM68K picture analysis system.

Observations

Coccolithophorid community

Emiliania huxleyi was by far the most abundant coccolithophorid species encountered in the August 1985 samples from the Isefjord. Each whole mount examined included numerous complete cells and single coccoliths were scattered all over the grid surface. Other less frequently observed taxa include *Acanthoica quattrospina* Lohmann, *Homozygosphaera* sp. (undescribed species), *Sphaerocalyptra* sp. (undescribed species), *Syracosphaera* spp. (2 species), *Balaniger balticus* Thomsen *et* Oates, and *Ericiolus* gen. nov. (described below).

Ericiolus Thomsen gen. nov.

Etymology: Latin *ericius*: hedgehog; *-ol-*: diminutive suffix.

Diagnosis

Cellula coccolithophora, parva, biflagellata, heterotropha, haptonermate brevi in spiram contractili. Periplastus e squamis e substantia organica formatis et spiculis quadribranchiatis calcificatis brachiis quoqueversum exeuntibus constitutus.

Species typifica: *E. spiculiger* sp. nov.

Small, biflagellate, heterotrophic coccolithophorid with short, coiling haptonema. Periplast consisting of organic scales and calcified structures in the shape of caltrops, i.e. with spikes pointing in all directions.

Type species: *E. spiculiger* sp. nov.

Ericiolus spiculiger Thomsen sp. nov. (Figs 2–4)

Etymology: Latin *spiculum*: spike; *-ger*: carrying.

Diagnosis

Cellula ephippioides, 3·0–3·8 μm longa et lata, flagellis binis subaequalibus circiter 12 μm longis, haptonemate dimidiae fere eorum longitudinis. Squamae non calcificatae ovales, circiter 0·5 × 0·4 μm magnae, concentrice striatae. Spicula quadribrachiata calcificata monomorpha numerosa totam cellulam induentia; quidque e tribus brachiis paene horizontalibus subaequalibus 0·1–0·2 μm longis et brachio unico erecto 0·3–0·4 μm longo angulos paulum plus quam 90 graduum cum illis formante constitutum. Omnia brachia porcas longitudinales exhibentia.

Die 29 Augusti anni 1985 in aqua temperaturae 18·2 graduum Celsii et salinitatis 16·5‰ e summo mari

Figs 2–4. *Ericiolus spiculiger* gen. et sp. nov. from the Isefjord, Denmark; shadowcast preparations for TEM. Fig. 2. Complete specimen with curved flagella and coiling haptonema. Fig. 3. Detail of periplast showing caltrops and unmineralised scales with concentric ridges (arrowhead). Fig. 4. Caltrops; the arrowhead points to a distinct ridge. Scale bars represent 1 μm.

Sinus Codani (lat. bor. 56°00, long. orient. 11°51·0) haustus, figuris 2–4 monstratus. Holotypus a Fig. 2 constitutus.

Cell saddle-shaped, 3·0–3·8 μm, with two almost equally long flagella (*c.* 12 μm) and a coiling haptonema of about half this length. Organic base plates oval (*c.* 0·5 × 0·4 μm) and with concentric striations. Numerous calcified structures (caltrops) of one type cover the entire cell body. Each caltrop consists of 4 spikes of which the 3 proximal ones are of almost the same length (0·1–0·2 μm) and radiate in the same plane from a common centre. The angle between this plane and the outwardly projecting longer spike (0·3–0·4 μm) differs slightly from 90°. The spikes all have longitudinal ridges.

Holotype: Fig. 2.

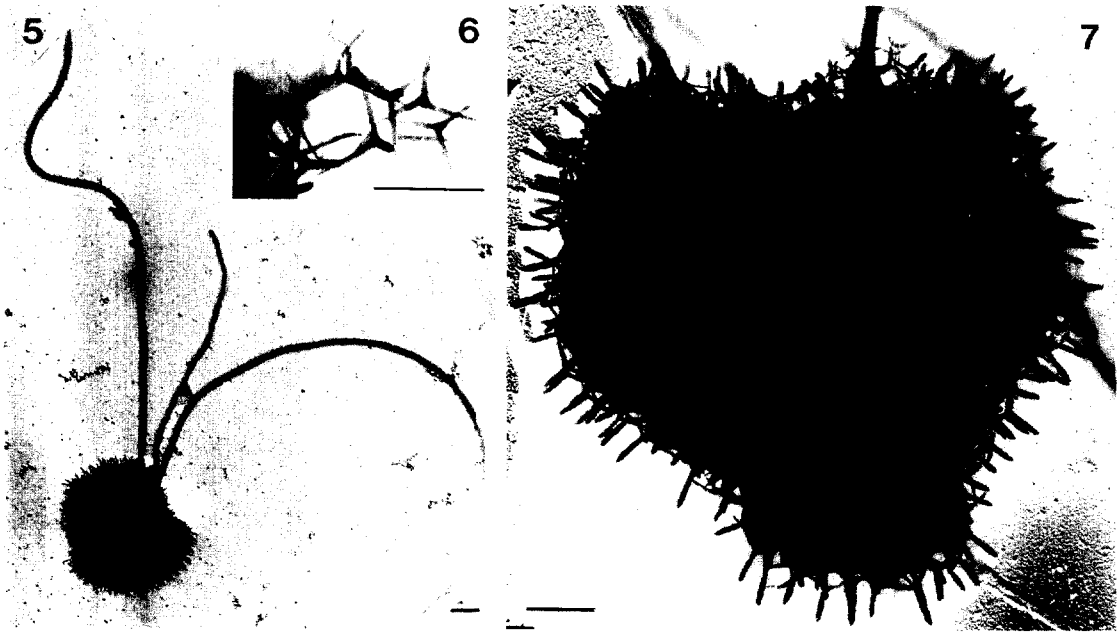
Habitat: The type material was collected on 29 August 1985 from station 7, southern Kattegat, Denmark (56°00 N/11°51·0 E; surface sample; 18·2°C; 16·5‰ S).

Ericiolus frigidus Thomsen sp. nov. (Figs 5–7)

Etymology: Latin *frigidus*: cold.

Diagnosis

Cellula ephippioides, 3·6–4·1 μm longa et lata, flagellis binis subaequalibus, haptonemate contractili dimidiae fere eorum longitudinis. Spicula calcificata monomorpha totam cellulam induentia; quidque e quattuor brachiis



Figs 5–7. *Ericiolus frigidus* sp. nov. from Antarctica; shadowcast preparations for TEM. Fig. 5. Complete cell with extended haptonema. Fig. 6. High magnification of cluster of caltrops. Notice that one spike mostly seen end-on as a dot appears more solid than others. Fig. 7. Detail of periplast showing cell shape and the dense cover of caltrops. Scale bars represent 1 μm (Fig. 5) or 0·5 μm (Figs 6, 7).

subaequalibus angulos aequales inter se formantibus, in sectione transversa circularibus constitutem.

Die 14 Decembris anni 1988 in aqua temperaturae 1 gradus Celsii et salinitatis 33·9‰ inter 10 et 20 m sub aequore maris Weddellensis (lat. austr. 58°29·7, long. occ. 47°01·03) haustus, figuris 5–7 monstratus. Holotypus a Fig. 5 constitutus.

Cell saddle-shaped (3·6–4·1 μm), with two almost equally long flagella and a coiling haptonema of about half this length. Calcified structures of one type (caltrops) cover the entire cell body. Each caltrop is constructed from 4 almost equally long spikes positioned so that angles between them are equal. The spikes are circular in cross-section.

Holotype: Fig. 5.

Habitat: The type material was collected on 14 December 1988 from EPOS station 163 (Weddell Sea; 58°29·7 S, 47°01·03 W; mixed surface sample from 10 and 20 m depth; *c.* 1°C and 33·9‰ S).

Comments

The presence of calcium in the caltrops of *E. frigidus* has been verified by means of X-ray analyses of periplasts.

The main characteristics distinguishing the two species relate to the general morphology of the caltrops (presence or absence of longitudinal ridges and angles between spikes). A distinct difference in size between the outwardly pointing spike and those forming the proximal base of the individual caltrop is a characteristic feature of *E. spiculiger* (Figs 3, 4). In *E. frigidus* all spikes appear to be of the same length, although in this species the outwardly pointing spike is somewhat more heavily calcified and rounded at the tip. Other spikes attenuate into fine-pointed tips (Figs 6, 7).

Organic base plates have so far been observed only in *E. spiculiger* (Fig. 3). The periplast of *E. frigidus* does not break easily. This explains why micrographs with individual caltrops are rare and also why no information is available on the organic component of the periplast of this taxon.

The material available does not allow for conclusions concerning the actual number of caltrops attached to each organic base plate in *E. spiculiger*. However, the span of the 3 proximal spikes approximately corresponds to the width of the organic base plate, indicating that a 1 : 1 relationship may exist between caltrops and base plates. A complete understanding of the periplast must await the examination of sectioned material.

Species of *Ericiolus* cannot be recognised with certainty in any type of light microscopical preparation, without a simultaneous examination of whole mounts of cells prepared for TEM. However, having first established the presence of this genus from TEM and, secondly, listed other species with similar overall morphology, it is in most cases possible to identify with a high degree of certainty these particular types of cells from "air-mounted" coverslip preparations by light microscopy. A saddle-shaped cell, a coiling haptonema half the length of

the flagella, and a jagged outline of the cell caused by the caltrops, constitute the main morphological criteria for light microscopical identification (compare Figs 2 and 5). In the Isefjord material it was impossible to distinguish between *E. spiculiger* and *Balaniger balticus*. A similar problem existed in Antarctic material with respect to distinguishing *E. frigidus* from Coccolithophorid sp. 1 (Thomsen *et al.*, 1988). *Balaniger balticus* and Coccolithophorid sp. 1 share with species of *Ericiolus* a similar overall morphology and a jagged cell outline caused by the presence of delicate calcified structures.

The assumption of a heterotrophic nutritional mode in species of *Ericiolus* is based on the fact that none of the cells identified as *Ericiolus* aff. in the light microscope ("air-mounted" preparations; see paragraph above) showed any red chlorophyll autofluorescence when examined under blue light excitation. Other cells, mostly diatoms, present in the same fields of view were clearly autofluorescing despite the age of the preparations. In addition, recent examination of both Antarctic and Arctic samples (living material and "air-mounted" preparations), using a similar technique of switching between phase-contrast and epifluorescence microscopy, has shown that the polar contingent of coccolithophorids is entirely heterotrophic (Garrison & Thomsen, 1993; Marchant & Thomsen, 1994; Thomsen, unpublished data). It is unclear for the moment whether these organisms are osmotrophs or phagotrophs. Epifluorescence microscopy has failed to detect any evidence of remnants of photosynthetic prey present inside the cell. Non-photosynthetic prey (e.g. bacteria) is still a likely food source.

Ericiolus spiculiger was observed at all Isefjord/southern Kattegat stations sampled during late August 1985 (Fig. 1*A*). *Ericiolus frigidus* has been found in samples from three Antarctic cruises and is likely to be ubiquitous in circumpolar Antarctic waters. The genus has not been encountered in north Atlantic polar regions.

Discussion

Ericiolus gen. nov. is morphologically distinct, and calcified structures even remotely reminiscent of the *Ericiolus* caltrops are not known from any living or fossil coccolithophorid. The allocation of this genus to any existing higher taxonomic level is problematic.

It has recently been shown (Thomsen *et al.*, 1991) that complex life histories link genera of coccolithophorids in polar regions. The evidence for this is the occurrence of combination cells that in one periplast combine coccoliths from two genera, typically a holococcolithophorid genus and a heterococcolithophorid genus (viz. *Turrisphaera/Papposphaera*; *Trigonaspis/Pappomonas*). It is anticipated (Thomsen *et al.*, 1991) that most, if not all, of the heterotrophic, weakly mineralised "polar" coccolithophorids form part of such life histories. It should be emphasised that although these organisms have originally been described from polar regions, subsequent research has shown that several of these genera also occur at lower latitudes, and even in subtropical waters (see e.g. Thomsen *et al.*, 1994), and also that some of the "polar" species do indeed have a much wider geographical distribution. So far there is no evidence (i.e. periplasts with multiple types of coccoliths) in favour of linking species of *Ericiolus* with those of any other genus. Despite the fact that we strongly believe that such a link is likely to be found eventually, we consider it relevant to place these new species within a genus of their own. The formal descriptions provide the tools needed adequately to handle new information on features such as distribution and abundance. At the moment we consider this more important than avoiding future nomenclatural problems through postponing the establishment of any new genera or species of "polar" coccolithophorids until their complete life histories are unravelled.

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