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An interesting association between *Neosphaera coccolithomorpha* and *Ceratolithus cristatus* (Haptophyta)

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Phytoplankton studies in the North Atlantic have revealed coccoliths of *Neosphaera coccolithomorpha* and *Ceratolithus cristatus* occurring on the same cell. This may indicate that each of these species represents a stage of one coccolithophorid life cycle, in which each phase possesses a different heterococcolith type. However, definitive evidence for this is lacking.

Key words: Life cycle, coccolithophorid, *Neosphaera*, *Ceratolithus*, taxonomy

Introduction

Information on the taxonomy and distribution of living coccolithophorids has steadily increased over the last 100 years (see Jordan & Green (1994) and Winter *et al*. (1994), respectively), but knowledge of their life cycles is still modest (see Billard, 1994). Life cycles involving heterococcolithophorid/holococcolithophorid phases have now been documented from cultures and from natural populations, whilst cultures of the coastal genera exhibit a planktonic, motile or non-motile coccolith-bearing phase and a benthic, pseudothallus (non-motile) phase which lacks coccoliths. In the genera *Emiliania* Hay *et* Mohler and *Gephyrocapsa* Kamptner the non-motile, coccolith-bearing phase is replaced by a motile, naked phase.

Apart from life-cycle relationships, less convincing combinations involving the coccoliths of separate taxa include reports of mixed coccospheres, where cells appear to bear coccoliths of two species, each covering one half of the coccosphere, or of coccoliths of one species appearing to adhere to or be incorporated into the coccosphere of another species. These coccolith combinations are usually considered to be due merely to agglutination (Okada & McIntyre, 1977). There is also a growing literature concerning the possible symbiosis between *Reticulofenestra sessilis* (Lohmann) Jordan *et* Young (basionym *Pontosphaera sessilis*) and a diatom of the genus *Thalassiosira* Cleve (see Jordan & Kleijne, 1994).

In this paper we present a unique association involving two well-known heterococcolithophorids – *Neosphaera coccolithomorpha* Lecal-Schlauder and *Ceratolithus cristatus* Kamptner – which are currently classified in separate families (Jordan & Green, 1994).

In extant assemblages both *N. coccolithomorpha* and *C. cristatus* are found in subtropical and tropical waters, where they are associated with the upper photic zone (approx. 0–100 m). This zone is characterized by high light, warm temperature, low nutrient concentrations and low productivity, and may be considered as oligotrophic. The zone is a relatively permanent feature all year round and is therefore a stable ecological niche (see Winter *et al*., 1994).

Neosphaera Lecal-Schlauder was originally described from the coast of North Africa by Lecal-Schlauder (1950) to accommodate a single species, *N. coccolithomorpha*. The coccospheres were covered by 16–20 overlapping coccoliths (regarded by some as placoliths), each composed of a single shield of elements and a collar on the distal side surrounding the large central opening. Variability in collar structure and the size of the central opening have led some workers to distinguish two morphotypes (see Kleijne, 1993).

Ceratolithus Kamptner was inadequately, but validly, described in 1950, although subsequently redescribed a few years later by the same author (Kamptner, 1954) from the sediments of the South Atlantic and Red Sea. The genus was created to accommodate one species, *Ceratolithus cristatus*, which bore horseshoe-like coccoliths, termed ceratoliths (see definition in Jordan *et al*., 1995). Later, Norris (1965) found living cells in the surface waters of the Indian Ocean and for the first time reported the position of the ceratolith with respect to the cell, the nature of the cell components, and an additional structure, a mass of hoop-like coccoliths, which sometimes surrounded the cell and its single ceratolith. He also noticed that the coccolith case of hoops may surround more than one cell, whereby each cell possesses a ceratolith. Norris (1965) described a second extant species, *C. telesmus* Norris, which differed from *C. cristatus* in its ceratolith morphology. Borsetti & Cati (1976) assigned morphotype status to a new form of *C. cristatus* which bore a rostrum

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or beak at the suture end of the ceratolith, but as they did not provide a formal description the epithet '*rostratus*' is invalid.

Materials and methods

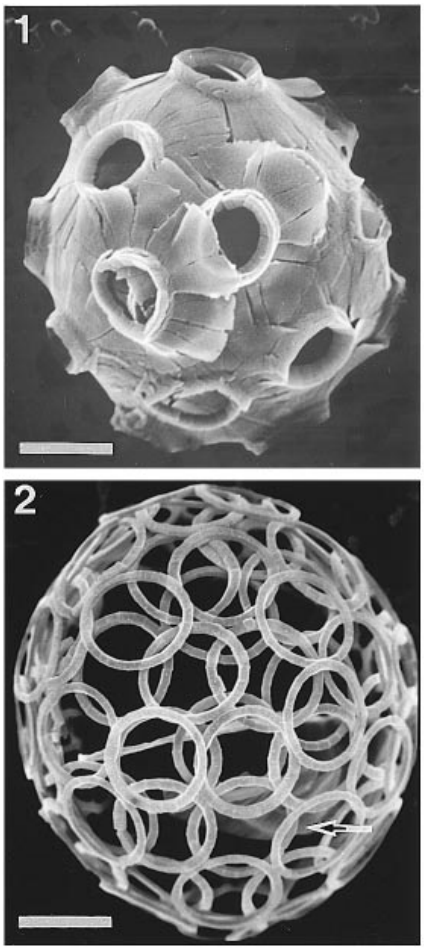
Samples were collected from the Central North Atlantic during the World Ocean Circulation Experiment (WOCE) 92 (section A-5) campaign by the oceanographic vessel *Hesperides* (July–August 1992) along the 24°30′N line of latitude from the Canary Islands to Florida (Table 1). Water samples were obtained using a rosette of 24 Niskin water bottles attached to a Conductivity, Temperature, Depth (CTD) rig. The bottles were closed electronically at selected depths and then brought back on board. About 200 ml of water from each bottle was mixed with formol and sealed in glass storage bottles. At the University of Valencia the water was then filtered through a Millipore filter (47 mm diameter, 0·65 μm porosity) using a common venturimeter. The filters were washed in distilled water to remove salt, dried and stored in plastic cases. A piece from each filter (*c.* 5 × 5 mm) was then mounted on a brass slide using a silver colloidal suspension, coated with gold, and examined in a Hitachi S2500 scanning electron microscope.

Table 1. Location of collection sites and sampling depths in the Central North Atlantic

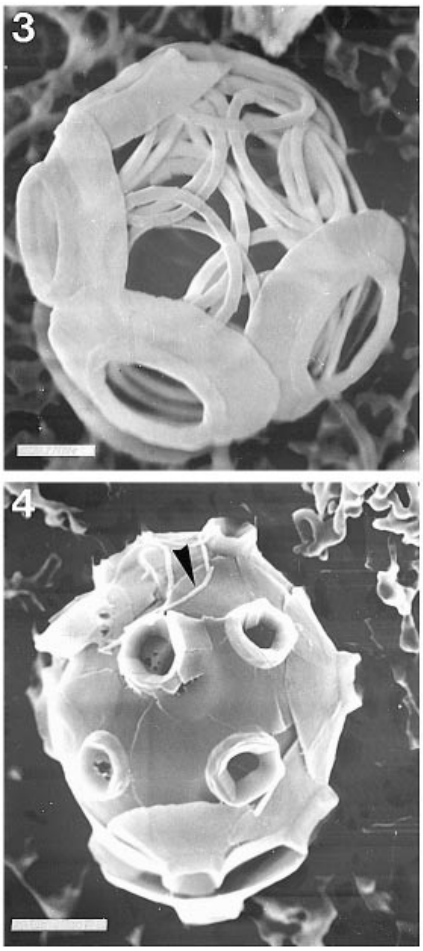
Collection site	Latitude (°N)	Longitude (°W)	Sampling depth (m)	Figs
I	24°30′	33°20′	50	4
II	24°30′	62°00′	50	1, 3
III	24°30′	72°00′	50	2

Observations and discussion

In the present study, *Neosphaera coccolithomorpha* was a common component of the upper photic zone flora (Fig. 1). *Ceratolithus cristatus* was always rare, but of those specimens encountered, many possessed an outer covering of hoop-like coccoliths (Fig. 2). Occasionally, it was noticed that the coccosphere of one species was associated with the coccoliths of the other. In particular, a cell of *C. cristatus* was observed partially covered by overlapping coccoliths of *N. coccolithomorpha* (Fig. 3), and coccoliths or



Figs 1,2. Scanning electron micrographs of coccolithophorids from the Central North Atlantic. **Fig. 1.** Coccosphere of *Neosphaera coccolithomorpha* var. *nishidae*. Scale bar represents 2 μm. **Fig. 2.** *Ceratolithus cristatus*. Mass of hoop-like coccoliths surrounding a single ceratolith (arrow). Scale bar represents 4 μm.



Figs 3, 4. Associations between coccoliths of *Neosphaera* and *Ceratolithus*. **Fig. 3.** Coccoliths of *N. coccolithomorpha* var. *coccolithomorpha* attached to the outside of a coccosphere of *C. cristatus*. **Fig. 4.** Hoop-like coccoliths of *C. cristatus* (arrowhead; variety unknown) attached to the coccosphere of *N. coccolithomorpha* var. *nishidae*. Scale bars represent 2 μm.

coccospheres of *N. coccolithomorpha* var. *nishidae* Kleijne were associated with the remnants of a hoop-like coccolith case of *C. cristatus* (Fig. 4; see also Borsetti & Cati, 1972, pl. 53, fig. 2).

The remnants of hoops on the outside of a *Neosphaera* coccosphere (Fig. 4) may be a result of agglutination. However, the micrograph shown in Fig. 3 suggests that the association between *Neosphaera coccolithomorpha* and *Ceratolithus cristatus* is more than mere agglutination and possibly represents two phases in the life cycle of a single species. The *Neosphaera* coccoliths outside the *Ceratolithus* hoop case are tightly arranged, forming an almost complete covering, and do not appear to have become attached during filtration or within the water column. Furthermore, the degree of overlapping within the underlying hoop case, and the small size of the coccosphere, suggests that the *Ceratolithus* cell is in a state of early growth. Although agglutination cannot be ruled out, it is possible that a developing *Neosphaera* cell would displace the hoop coccoliths. Thus, it is feasible that our figures represent a transition from *Neosphaera* to *Ceratolithus* (Fig. 3), or from *Ceratolithus* to *Neosphaera* (Fig. 4). However, the authors recognize that these micrographs and the few cells observed in these combinations do not represent concrete evidence and more information is needed.

If the two currently recognized species are found subsequently to represent elements of the life cycle of a single taxon, then the genus *Neosphaera* (published 30 March 1950) would take priority and *Ceratolithus* (published after paper presented at the 17 April 1950 meeting of the Österreichische Akademie der Wissenschaften) would become a later synonym. However, the family Ceratolithaceae R. E. Norris (1965) would remain valid.

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