# NOTES ON NANNOPLANKTON SYSTEMATICS AND LIFE-CYCLES - *CERATOLITHUS CRISTATUS, NEOSPHAERA COCCOLITHOMORPHA* AND *UMBILICOSPHAERA SIBOGAE*

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**Abstract:** *Ceratolithus cristatus* is known to produce both ceratoliths and hoop-shaped heterococcoliths. More recently, evidence has been given that a planolith-bearing heterococcolithophore, conventionally referred to the separate species *Neosphaera coccolithomorpha*, is an alternate life-cycle phase of *C. cristatus*. The evidence for this is outlined, and supported by new examples of associations of the different lith types. The type description of *N. coccolithomorpha* is reassessed and it is shown that the name is a junior synonym of *Umbilicosphaera sibogae* rather than a senior synonym of *C. cristatus*. The diversity of lith types produced by *C. cristatus* is reviewed and the structure and geological range of the planolith heterococcoliths is discussed.

## Introduction

One of the most interesting developments of recent research on nannoplankton has been the recognition of an increasing number of associations of supposedly different species, related apparently to complex life-cycles (Kleijne, 1991; Thomsen *et al.*, 1991; Billard, 1994; Alcober & Jordan, 1997; Cros *et al.*, in press). These are providing invaluable new perspectives on nannoplankton biology (Cros *et al.*, in press), but also create new taxonomic problems. We discuss here the rather complex implications of an association involving *Ceratolithus cristatus* and *Neosphaera coccolithomorpha*.

Alcober & Jordan (1997) described unusual coccospheres consisting of *N. coccolithomorpha* coccoliths together with the hoop-shaped coccoliths of *C. cristatus*. They suggested that this was not a chance association but rather evidence of a complex life-cycle with the one algal species being capable of producing three different types of lith: (1) The robust horseshoe-shaped ceratoliths well known to palaeontologists; (2) the delicate hoop-shaped heterococcoliths described by Norris (1965) and, since, frequently recorded both in association with ceratoliths and as separate coccospheres (*e.g.* Norris, 1971; Alcober & Jordan, 1997); (3) the larger more robust heterococcoliths of *N. coccolithomorpha*. These are often described as circular placoliths with the distal shield missing, but following the terminology of Young *et al.* (1997) they may more usefully be termed planoliths.

Alcober & Jordan (1997) believed that the *N. coccolithomorpha - C. cristatus* association was biologically meaningful but finally concluded that, owing to the absence of definite evidence (they only had one unambiguous specimen), nomenclatural changes would be premature. They noted, however, that *N. coccolithomorpha* Lecal-Schlauder, 1950 had priority over *C. cristatus* Kamptner, 1950 since the actual publication dates were, respectively, 30th March, 1950 (recorded printing date, from inside cover of the journal part) and later than 30th April, 1950 (the journal part includes weather records for April, 1950).

Cros *et al.* (in press) discovered a further combination coccosphere clearly showing the *N. coccolithomorpha - C. cristatus* association. From this, they concluded that this association can now be considered established. In addition, we have since found further combination coccospheres showing the association (Plate 2, Figures 2, 3) in plankton samples taken off SW Puerto Rico in February and April, 1995. Clearly nomenclatural clarification is now necessary.

## Identity of the species described by Lecal-Schlauder (1950) as *N. coccolithomorpha*

Re-examination of Lecal-Schlauder (1950) led us to realise that the species described by her as *N. coccolithomorpha* might not be the taxon usually termed *N. coccolithomorpha,* but in fact *Umbilicosphaera sibogae* var. *sibogae* Weber-van Bosse, 1901. This interpretation was also given by Gaarder (1970); when proposing the new combination *Umbilicosphaera sibogae,* she wrote „*Neosphaera coccolithomorpha* Lecal-Schlauder (1949, p.165, figs 4-6) should also be included in this species".

The type illustrations of Lecal-Schlauder (1950) are reproduced here as Plate 1, Figures 1-4. The common species concept of *N. coccolithomorpha* has been based on the drawing (Plate 1, Figure 3). However, the photograph of the coccosphere (Plate 1, Figure 4) should be regarded as the holotype and this specimen resembles *U. sibogae* var. *sibogae*. A comparative micrograph of an *U. sibogae* var. *sibogae* coccosphere is given in Plate 1, Figure 5 (courtesy of Prof. Inouye) and shows the striking similarity. The following additional points support the interpretation of *N. coccolithomorpha* as a junior synonym of *U. sibogae*:

1. In the LM, it is not easy to make accurate observations on coccospheres. In particular, with placoliths and similar coccoliths, the tube is usually prominent but the shields are hard to distinguish, even with modern microscopes. The problems caused by this are obvious in the publications of many early workers, for instance Wallich (1877) and Lohmann (1902). So, schematic cross-sections of coccoliths based on LM observations of coccospheres require careful interpretation.

2. In the particular case of *U. sibogae* var. *sibogae*, the distal shield is smaller than the proximal shield and is particularly hard to observe. Lecal's drawing (our Plate 1, Figure 3) is by no means unreasonable as a cross-section of *U. sibogae* var. *sibogae* drawn from a coccosphere (cf. Plate 3, Figures 7, 8). Two features of it are indeed more characteristic of *U. sibogae* var. *sibogae* than of *N. coccolithomorpha* (auctt.): it has a flat proximal shield and a distinct distal flange. The continuation of the proximal shield across the central area is incorrect for both coccoliths.

3. Lecal's work contains many taxonomic idiosyncrasies, *e.g. Helicosphaera carteri* is variously identified as: *Coccolithus pelagicus*, *Coccolithus tesselatus* and *Coccolithus carteri*. Consequently, her taxonomic work requires critical assessment.

4. Lecal-Schlauder (1950) differentiated *N. coccolithomorpha* from *U. sibogae* on the grounds that *U. sibogae* coccoliths have an open central-area („possedant un pore veritable"), unlike those of *N. coccolithomorpha* („tremalithes à fond plein"). In fact, both forms have open central-areas, although it might be possible from LM observations to erroneously conclude that *U. sibogae* coccoliths have a closed central-area.

5. Lecal never seems to have recorded *U. sibogae* in her publications (we have checked almost all of them), even though it is usually a common component of nannoplankton assemblages. Therefore, it is quite likely that she consistently identified *U. sibogae* as *N. coccolithomorpha*.

6. The drawing of a large cell (our Plate 1, Figure 1) also resembles *U. sibogae* far more closely than it does *N. coccolithomorpha* (auctt.) - in particular, large cells with very numerous coccoliths are typical of *U. sibogae* var. *sibogae* (compare Plate 1, Figure 6).

7. Lecal-Schlauder (1950) described *N. coccolithomorpha* coccospheres as often containing several cells („Les spores se forment dans les cellules adultes: on peut en distinguer quattre, à l'interieur des plus grands stades"). This is a characteristic feature of *U. sibogae* var. *sibogae*.

**Nomenclatural conclusions**

From this, we conclude that the species described by Lecal-Schlauder (1950) was indeed *U. sibogae* var. *sibogae*, even though subsequent workers have assumed from the drawing (Plate 1, Figure 3) that it was the quite different form, conventionally identified as *N. coccolithomorpha*. So, the name *Neosphaera coccolithomorpha* is a junior synonym of *Umbilicosphaera sibogae*.

Following this, the correct name for the alga which produces ceratoliths, hoop-shaped coccoliths and ‚*Neosphaera*' planoliths is *Ceratolithus cristatus*. This conclusion avoids the nomenclatural nightmare which was possible when *Neosphaera* seemed likely to be a senior synonym of *Ceratolithus*, but leaves the relatively trivial problem of how to refer to the coccoliths and coccospheres of ‚*N. coccolithomorpha*'.

Two basic solutions are possible and, almost inevitably, both will be used. (1) As in heterococcolith-holococcolith combinations (*e.g. Coccolithus pelagicus* - ‚*Crystallolithus hyalinus*'), the original name of the alternate phase can continue to be used in an informal, non-Linnaean sense and, in this context, the nomenclatural niceties of the exact identity of the type specimen is irrelevant. This solution may be convenient to allow unambiguous communication in, for instance, nannofloral analyses. Also, it should be noted that two varieties of *N. coccolithomorpha* are conventionally distinguished: *N. coccolithomorpha* var. *coccolithomorpha* (large coccoliths and a wide central-area) and *N. coccolithomorpha* var. *nishidae* (small coccoliths with a narrow central-area). Until it is established whether and how these correlate with ceratolith varieties, the current varieties will need to be used at least informally. (2) More correctly, the cells can be identified as *Ceratolithus cristatus* (planolith phase), which can be abbreviated to *C. cristatus* (P-phase), and the coccoliths as *C. cristatus* planoliths. This solution should obviously be used in contexts where biological meaning is paramount, and hopefully will gain increasing currency.

*NB* Several workers have referred to different life-cycle phases as *forma* of a single species, *e.g. C. pelagicus* f. *pelagicus* and *C. pelagicus* f. *hyalinus*. However, this convention is contrary to basic principles of the ICBN and so is not acceptable (Paul Silva, pers comm., 1998; John Green, pers comm., 1998; Jordan *et al.*, 1995; Cros *et al.*, in press).

***Ceratolithus cristatus* diversity**

Not only are ceratoliths and two types of heterococcoliths formed by *C. cristatus*, but also each of these is known in two main varieties, and a range of combination coccospheres have now been recorded. A brief summary is therefore in order, although exhaustive details do not need to be given since the literature on the species is already substantial.

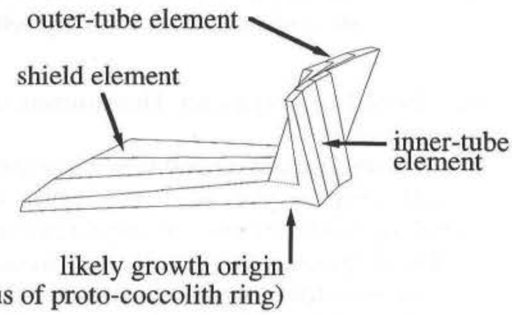
**Summary of lith types produced by *Ceratolithus:***

1. Ceratoliths Horseshoe-shaped nannoliths. Three types have been described: *Ceratolithus cristatus* var. *cristatus* - the typical form (Plate 3, Figures 5, 6); *Ceratolithus cristatus* var. *telesmus* - a form with longer arms that curve together to almost touch; *Ceratolithus cristatus* forma *rostratus* - an ornate form with an apical beak (Plate 3, Figures 1, 2, 4). (*NB* This form has not been validly described and, as discussed below, it seems likely that it is simply a more heavily calcified morphotype of *C. cristatus* var. *cristatus*, so it is referred to here informally as a *rostratus*-type ceratolith).

2. Hoop-coccoliths Simple hoop-shaped heterococcoliths. In TEM, these can be seen to be formed of alternating, large, rectangular crystal-units and much smaller, interlocking, rectangular crystal-units (Norris, 1971; Manton *et al.*, 1977; our text-figure 1B). In the SEM, only the larger crystal-units are visible. Norris (1965) describes them as forming rims to a subtending organic baseplate. Our observations suggest that two forms occur, although it is possible they intergrade: robust hoops - typically 4-5μm across with rims 0.2-0.4μm wide. These typically remain intact in SEM preparations (Plate 2, Figure

2); delicate hoops - typically 4-6μm across with rims about 0.1-0.2μm wide. These tend to disintegrate in SEM preparations (Plate 2, Figures 1, 2; Plate 3, Figures 1-7).

3. Planoliths Heterococcoliths with a single shield, formerly assigned to *N. coccolithomorpha*. They vary considerably in size and central-opening diameter but two main varieties are usually distinguished (Kleijne, 1993; Jordan & Kleijne, 1994; Jordan & Green, 1994). Measurements given below are from Kleijne (1993): var. *coccolithomorpha* with a large central-opening (opening diameter 0.4-0.5x coccolith diameter), and usually large (6-10μm), although small forms (4-5μm) also occur (Plate 2, Figures 3-6); var. *nishidae* - with a narrow central-opening (opening diameter 0.15-0.3x coccolith diameter), and small coccolith diameter (4-7μm) (Plate 3, Figure 4).




A. STRUCTURE OF PLANOLITH COCCOLITHS




B. STRUCTURE OF HOOP COCCOLITHS
(redrawn from Manton *et al.*, 1977)

**Text-figure 1:** Light micrographs of *Ceratolithus* planoliths.

**Summary of combination coccospheres observed**

A. Robust hoops surrounding ceratoliths (type indeterminable). Figured by Knappertsbusch *in* Winter & Siesser (1994) and Alcober & Jordan (1997).

B. Delicate hoops surrounding large, strongly ornamented ceratoliths, especially *rostratus*-type ceratoliths. Figured here (Plate 2, Figure 1; Plate 3, Figures 1-3, 4-6) and by Norris (1965, fig.4), Cros *et al.* (in press) and, perhaps, by Borsetti & Cati (1976, pl.17, figs 9, 13). This appears to be a very characteristic association: we have found several examples.

C. Delicate hoops with *nishidae* planoliths; either type of coccolith may form the inner layer. Figured by Alcober & Jordan (1997), Cros *et al.* (in press) and Borsetti & Cati (1972, pl.43, fig.2). Again, this appears to be a characteristic association, and we have found several examples.

D. Delicate hoops with *coccolithomorpha* planoliths. Figured here (Plate 2, Figure 3). This seems a less common association.

E. Robust hoops with *coccolithomorpha* planoliths. Figured here (Plate 2, Figure 2) and by Alcober & Jordan (1997).

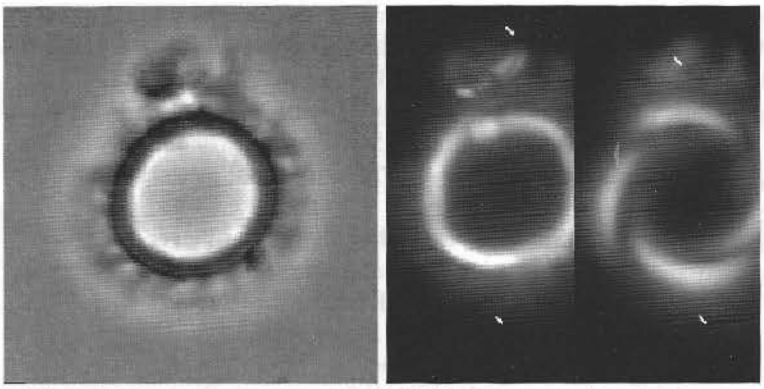
In addition, *nishidae* planoliths occur on or next to two of the five *rostratus* ceratoliths figured by Borsetti & Cati (1976, pl.17, figs 9, 10, 16), and we have found one similar possible association (Plate 3, Figure 4).

It has been speculated that heterococcolith-holococcolith associations represent a haplo-diplontic life-cycle, with heterococcoliths on the diploid phase and holococcoliths on the haploid phase (Billard, 1994; Young & Bown, 1997), although this is still unproven (Cros *et al.*, in press). The range of combinations encountered makes it difficult to fit *Ceratolithus* into this model. The simplest hypothesis, however, would seem to be that the ceratoliths are equivalent to holococcoliths and produced on haploid cells, whilst the planoliths are normal heterococcoliths produced on diploid cells, with the hoop-coccoliths being special heterococcoliths produced during, or prior to, phase changes. The frequent association of the rather rare *rostratus*-type ceratoliths with hoop-coccoliths suggests that this may be a morphotype developed in association with the phase change, rather than a genotypic variant. Obviously, further observations on this unusual species are needed.

**Notes on *C. cristatus* planoliths**
**(,*Neosphaera*' coccoliths)**

**Identification:**

*C. cristatus* planoliths are easily identified in the SEM and routinely recorded in the plankton. They are, however, harder to identify in the LM and, consequently, are less widely recorded in the fossil record. In particular, they are superficially similar to *Umbilicosphaera sibogae* and *U.*




**Text-figure 2:** Structure of *Ceratolithus* coccoliths. A. Reconstruction of the structure of *C. cristatus* planoliths. Three crystal-units drawn in oblique-view, showing interconnections of the shield, inner-tube, and outer-tube elements. B. Structure of hoop-coccoliths, redrawn from Manton *et al.* (1977). These details are only visible in TEM.

*rotula* placoliths. They can be distinguished, however, by their appearance in cross-polarised light (text-figure 2). When the coccolith is in focus, the shield is dark and the tube bright, without an obvious extinction cross. At a focal plane just above the specimen, a strong extinction cross is seen, with the arms offset by nearly 45° from radial and showing distinct curvature. By contrast in *Umbilicosphaera*, although the tube is brighter than the proximal shield, it is usually clear that the proximal shield is birefringent, and the extinction cross shows straighter and more nearly radial arms.

**Synonym - *Cyclolithella annula* (Cohen, 1964) McIntyre & Bé, 1967:**

Cohen (1964) described as a new species, ‚*Coccolithites annulus*', the *C. cristatus* planoliths. This name has been widely used by palaeontologists, although decreasingly so of late. Cohen's description is based on isolated coccoliths viewed in the LM only, but it is carefully done and the identity of the illustrated specimens is unambiguous. This epithet has been considered a junior synonym of *N. coccolithomorpha*; by our interpretation, it is a junior synonym of *C. cristatus. NB Cyclolithus anulus* Lecal (1967) is a quite different coccolithophore, probably related to *Umbilicosphaera*, see Kleijne (1993) and Young (1998).

**Fossil record:**

The fossil record of *C. cristatus* (P-phase) coccoliths is difficult to assess, since few workers have consistently identified it. Our observations suggest that it is frequently present in Quaternary deposits and occurs sporadically in the Pliocene. The earliest unambiguous records are specimens from the Early Pliocene, zone NN12, illustrated by: Perch-Nielsen (1977, pl.41, fig.7) as *Umbilicosphaera* sp. from DSDP Site 354 (S Atlantic), and by Su (1996, pl.5, fig.9) as *N. coccolithomorpha* from ODP Hole 659A, (subtropical N Atlantic). These records broadly correlate with the first occurrence of *Ceratolithus* ceratoliths, so it will be interesting to see if the fossil record of the two nannofossils shows parallels.

**Structure:**

In the SEM, the shield of the *C. cristatus* planoliths is clearly formed of a single cycle of radial elements, whilst the tube is formed of discrete inner and outer cycles (Plate 2, Figures 4-6; Kleijne, 1993). The outer-cycle elements are easily observed to be connected to the shield elements, and show clockwise imbrication (Plate 2, Figure 5). The inner-tube elements are oriented vertically (Plate 2, Figure 6). The inner- and outer-tube elements are probably formed from the same crystal-unit as the shield and outer-tube since: (1) connections between inner- and outer-tube elements are sometimes visible in distal view; (2) in proximal view, there is no evidence of discontinuity between the inner-tube and shield elements. This structure is summarised in text-figure 1A.

LM observations support this: when seen in side-view with a gypsum plate (cf. Young, 1992), the entire coccolith appears to be formed of a single cycle of crystal-units with steep *c*-axes. Our LM observations suggest that the *c*-axes are oriented with an inclination of about 60° from the horizontal and an azimuth (*i.e.* orientation in plan-view) of about 45° from radial. The steep inclination means they can be tentatively identified as V-units, *sensu* Young *et al.* (1992). By contrast, the placoliths of *Umbilicosphaera* (including *U. rotula*) and other Calcidiscaceae have a proximal shield of R-units and a distal shield of V-units. So, Young & Bown (1997) placed *N. coccolithomorpha* in heterococcoliths *incertae sedis*.

The very distinctive structure of ‚*N. coccolithomorpha*' planoliths makes it unlikely that they were derived from any known placolith by loss of the distal shield. Instead, we may speculate that they may have been derived from the hoop-shaped coccoliths of *Ceratolithus* by development of a proximal shield.

Descriptions of the structure of the hoop-shaped coccoliths of *Ceratolithus* have been given by Norris (1971) and Manton *et al.* (1977), based on TEM observations. They apparently worked independently, but their descriptions of the structure are identical. The hoops are formed of alternating, large, rectangular crystallites and interlocking, much smaller, rectangular crystallites (text-figure 1B). If the planoliths were derived from this structure, then we might expect only the larger crystallites to develop, giving rise to planoliths almost entirely formed from a single crystal-unit. So, the structure of the hoop and planolith coccolith-types are compatible with the hypothesis that the planoliths are a modified form of the hoop-shaped coccoliths.

**Taxa cited**

*Ceratolithus cristatus* Kamptner, 1950

Synonyms: *Cyclolithella annula* (Cohen, 1964) McIntyre & Bé, 1967

*Neosphaera coccolithomorpha* var. *nishidae* Kleijne, 1993

*Ceratolithus cristatus* var. *telesmus* (Norris, 1965) Jordan & Young, 1990

*Ceratolithus cristatus* f. *rostratus* Borsetti & Cati, 1976 [Invalid, no diagnosis. We do not validate this form here since we believe the morphotype is likely to be related to the life-cycle and so should not be given any formal taxonomic status]

*Cyclolithus anulus* (Lecal, 1967)

*Coccolithus pelagicus* (Wallich, 1877) Schiller, 1930

*Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954

*Umbilicosphaera sibogae* var. *sibogae* (Weber-van Bosse, 1901) Gaarder, 1970

Synonym: *Neosphaera coccolithomorpha* Lecal-Schlauder 1950

*Umbilicosphaera rotula* (Kamptner, 1956) Varol, 1982

Synonym: *Geminilithella rotula* (Kamptner, 1956) Backman, 1980

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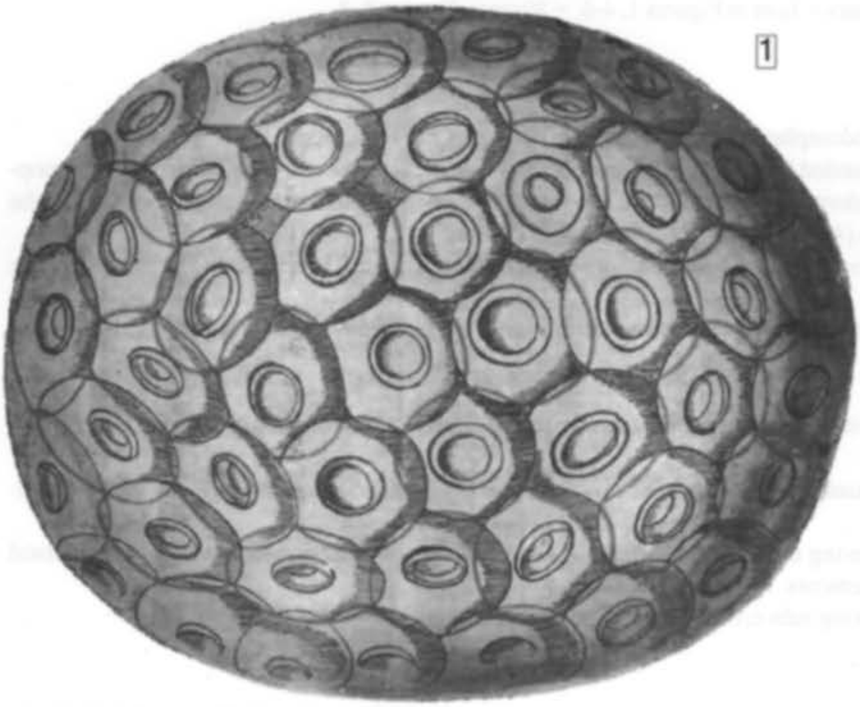
## Plate 1
### *Umbilicosphaera sibogae* var. *sibogae*

**Figs 1-4:** Reproductions of the illustrations from Lecal-Schlauder (1950) illustrating the description of ‚*Neosphaera coccolithomorpha*'.
**Fig.1:** Drawing of ‚adult' cell (fig.4 of Lecal-Schlauder, 1950)
**Fig.2:** Plan-view of a coccolith (fig.5 of Lecal-Schlauder, 1950)
**Fig.3:** Cross-section („coupe optique") of a coccolith (fig.5 of Lecal-Schlauder, 1950)
**Fig.4:** Light micrograph of a cell („stade bulle en lumiére parallčle") (pl.VI, fig.4 of Lecal-Schlauder, 1950).

**Figs 5-8:** Comparative illustrations of unambiguously identified *U. sibogae* var. *sibogae*.
**Fig.5:** Light micrograph of a coccosphere of *U. sibogae* var. *sibogae* courtesy of Prof. Inouye, Tsukuba University.
**Fig.6:** SEM of a large, partially collapsed coccosphere specimen. From N Atlantic, Sample 11290/2/5 (200m water-depth). Scale-bar = 1μm.
**Fig.7:** Reconstruction of coccolith profile of *U. sibogae* var. *sibogae* from Young (in press) - note similarity with Figure 3.
**Fig.8:** Detail from same coccosphere as Figure 6. Scale-bar = 1μm.

# PLATE 1



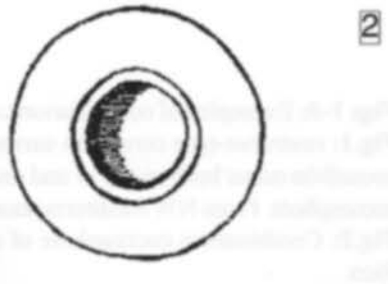




Fig. 5. – *Neosphaera coccolithomorpha* n. sp. Plaque vue de face. Grossissement: 6.000.

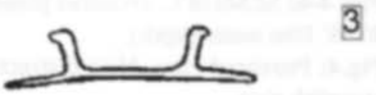
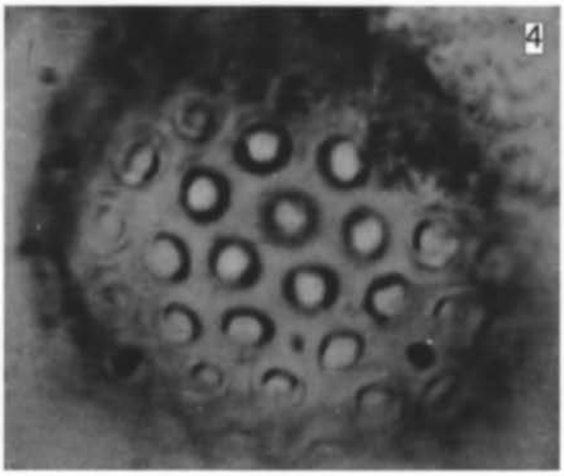
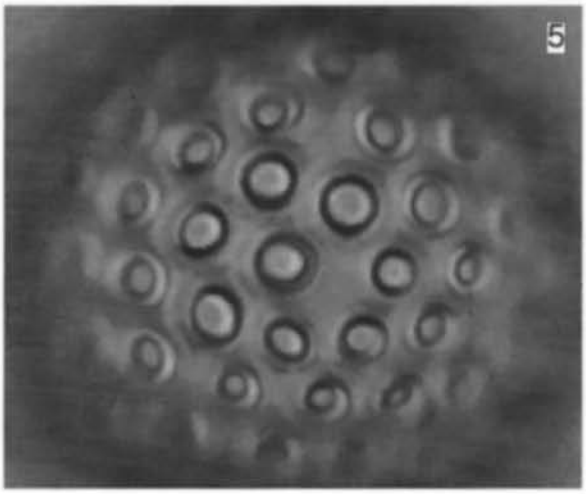
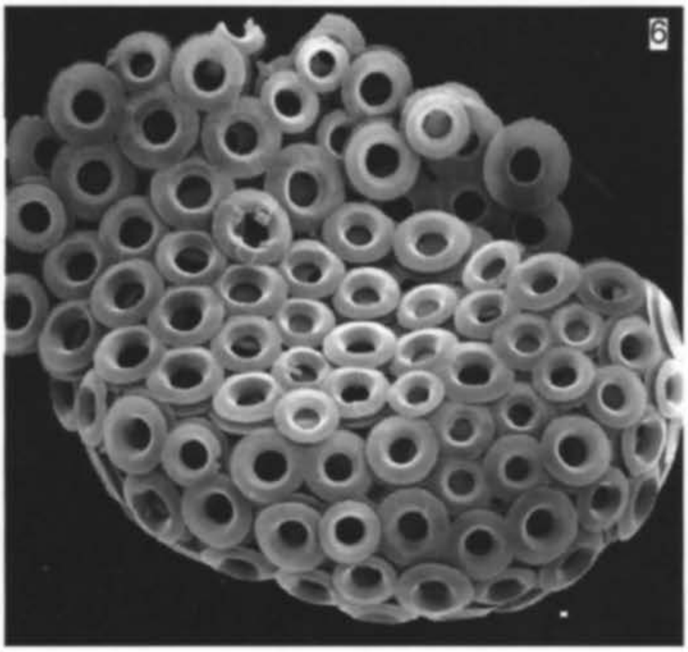



Fig. 6. – *Neosphaera coccolithomorpha* n. sp. Coupe optique d'une plaque. Grossissement: 6.000.





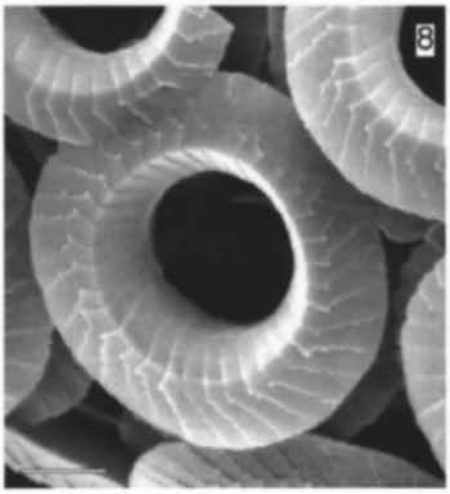


**Plate 2**

***Ceratolithus cristatus***

Scale-bars = 1μm in Figures 1, 4-6; = 10μm in Figures 2, 3

**Figs 1-3:** Examples of combination coccospheres.

**Fig.1:** *rostratus*-type ceratolith surrounded by collapsed coccosphere of delicate hoop- coccoliths. Note that the hoop-coccoliths occur both on top of and underneath the ceratolith, supporting the inference that the ceratolith was inside the coccosphere. From NW Mediterranean (40°N, 1°E), Fans-1 Stn.123(137), 25m.

**Fig.2:** Combination coccosphere of *coccolithomorpha* planoliths surrounding robust hoop-coccoliths. From Puerto Rico.

**Fig.3:** Combination coccosphere of delicate hoop-coccoliths surrounding *coccolithomorpha* planoliths. From Puerto Rico.

**Figs 4-6:** SEMs of *C. cristatus* planoliths showing the ultrastructure. All from N Atlantic, Sample 11290/2/12 (26°N, 30°W, 10m water-depth).

**Fig.4:** Proximal view. Note distinct kink in elements near inner margin. This may represent the locus of the proto-coccolith ring.

**Fig.5:** Detail of outer-tube cycle, showing clockwise imbrication and extensions running anticlockwise on the distal surface toward the inner-tube cycle elements. Inset: view of entire planolith.

**Fig.6:** Detail of inner-tube cycle, showing subvertical orientation. Same specimen as Fig.5.

# PLATE 2

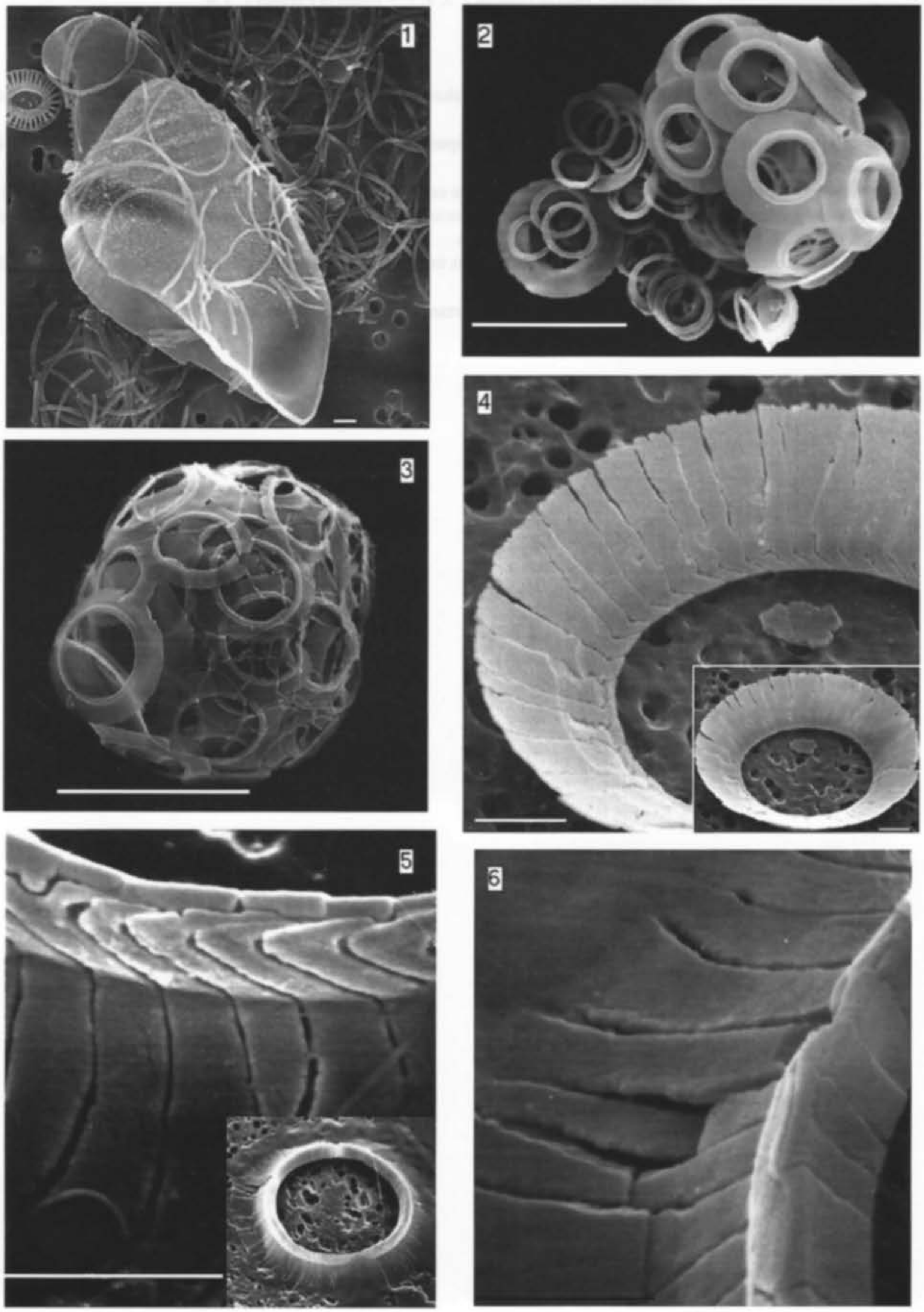


**Plate 3**

***Ceratolithus cristatus***

Scale-bars = 1μm in Figures 1, 3, 4, 7; = 10μm in Figures 2, 5, 6

**Fig.1:** *rostratus*-type ceratolith with remains of a few broken delicate hoop-coccoliths lying on it. From N Atlantic, Sample ST11311 (26°N, 45°W), 40m.

**Figs 2-3:** *rostratus*-type ceratolith surrounded by collapsed coccosphere of delicate hoop-coccoliths. From NW Mediterranean, Fronts-96, Stn. 013 (31°N, 4°E), 10m.

**Fig.4:** Association of a *rostratus*-type ceratolith, a simple ceratolith, three *nishidae*-type planoliths, and remains of delicate hoop-coccoliths (inside the planoliths). This association is suggestive but could be in part accidental. From NW Mediterranean, Fans-1, Stn. 123(137) (40°N, 1°E), 40m.

**Figs 5-6:** Association of two highly ornamented ceratoliths inside a collapsed coccosphere of delicate hoop-coccoliths. From N Atlantic, Sample ST 11314/3 (26°N, 42°W).

**Fig.7:** Detail of delicate hoop-coccoliths. From NW Mediterranean, Fans-1, Stn. 100(113) (40°N, 1°E), 5m.

# PLATE 3