

***Navilithus altivelum*: a remarkable new genus and species of deep photic coccolithophores**JEREMY R. YOUNG¹ & HARALD ANDRULEIT²¹Palaeontology Department, The Natural History Museum, London SW7 5BD, UK (e-mail: j.young@nhm.ac.uk)²Bundesanstalt für Geowissenschaften und Rohstoffe (Federal Institute for Geosciences and Natural Resources), Postfach 510153, 30631 Hannover, Germany (e-mail: h.andruleit@bgr.de)

ABSTRACT – A very distinctive new deep-photoc coccolithophore is described from the NE Indian Ocean. The new species is trimorphic with: 200–300 body coccoliths bearing low spines attached by narrow stems to a basal narrow-rimmed placolith structure; up to 18 circum-flagellar coccoliths with tall sail-like spines; and up to 22 coccoliths with moderately elevated spines occurring both around the circum-flagellar coccoliths and antapically. These features make the coccolithophore unique and require placement in a new species and genus. The basal structure, however, shows similarities to a recently recognized group of narrow-rimmed placoliths. Hence, the new coccolithophore provides some support for this grouping as a significant addition to our understanding of coccolithophore biodiversity, and potentially an explanation for a set of anomalous molecular genetic results. In addition the new taxon provides further evidence that the deep-photoc coccolithophore community is more diverse than has been assumed. *J. Micropalaeontol.* 25(2): 141–151, November 2006.

KEYWORDS: *coccolithophore, extant, Indian Ocean*

INTRODUCTION

Extant coccolithophores have been intensively studied over the past two decades and their taxonomy is probably better established than that of any other phytoplankton group. Nevertheless, new taxa continue to be recorded, especially from the deep-photoc zone (Jordan *et al.*, 1991; Kleijne *et al.*, 1991; Jordan & Chamberlain, 1993; Hagino & Okada, 1998; Cros & Fortuño, 2002; Young *et al.*, 2003). The number of very distinctive but rare coccolithophores is a curious feature of the deep photic zone. Another such unusual new coccolithophore species was found during examination of samples from the Indian Ocean off SW Indonesia. The ecological study of these samples will be described in detail elsewhere; this paper describes the new species, discusses its affinities and its implications for understanding of coccolithophore diversity.

MATERIAL AND METHODS

The samples were collected during a geological cruise, So139, of the R/V *Sonne* in the Eastern Indian during January–February 1999 (Beiersdorf *et al.*, 1999). Samples were collected at seven stations southwest of Sumatra and Java, over the Java Trough (Fig. 1). At each station depth transects of six or seven samples were collected using a rosette sampler with attached CTD device for recording salinity, temperature and depth (Fig. 2). Nutrient and chlorophyll data were not collected on this cruise. Sample depths were varied based on the temperature data in order to ensure good sampling, especially of the thermocline population. For each sample 5 l of seawater were filtered onto fleece-supported regenerated cellulose filters (Sartorius[®], 50 mm diameter, 0.45 µm pore width). The samples were counted using a standard electron microscope at the BGR, with more than 300 specimens being identified and counted per filter, except in the deepest samples, where a smaller number was counted due to the scarcity of coccospheres. In total 33 coccospheres of the new species were found during the routine counts. Selected filters on which the new species was more common were then re-examined

at the NHM using a field emission SEM (Phillips XL-30 FEG) in order to obtain high resolution images; a further six specimens were found during this examination. Measurements on the digital images were made using NIH-Image software.

SYSTEMATIC DESCRIPTIONS

Division **Haptophyta** Hibberd, 1972
Class **Prymnesiophyceae** Hibberd, 1976
Order **Coccolithales** Schwarz, 1932
Family **incertae sedis**

Navilithus gen nov. Young & Andruleit

Type species. *Navilithus altivelum*.

Derivatio nominis. From the Latin *navis* (boat) and Greek *lithos* (stone), reflecting the boat-like form of the coccoliths.

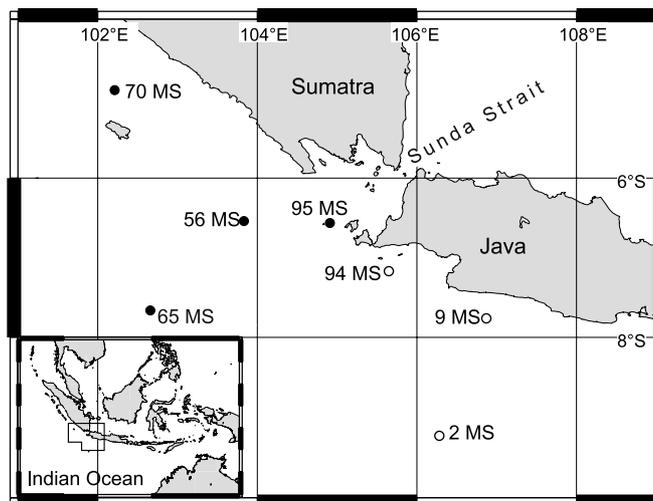


Fig. 1. Map of sample stations. Filled circles are sample stations with *N. altivelum*, open circles are sample stations without *N. altivelum*.

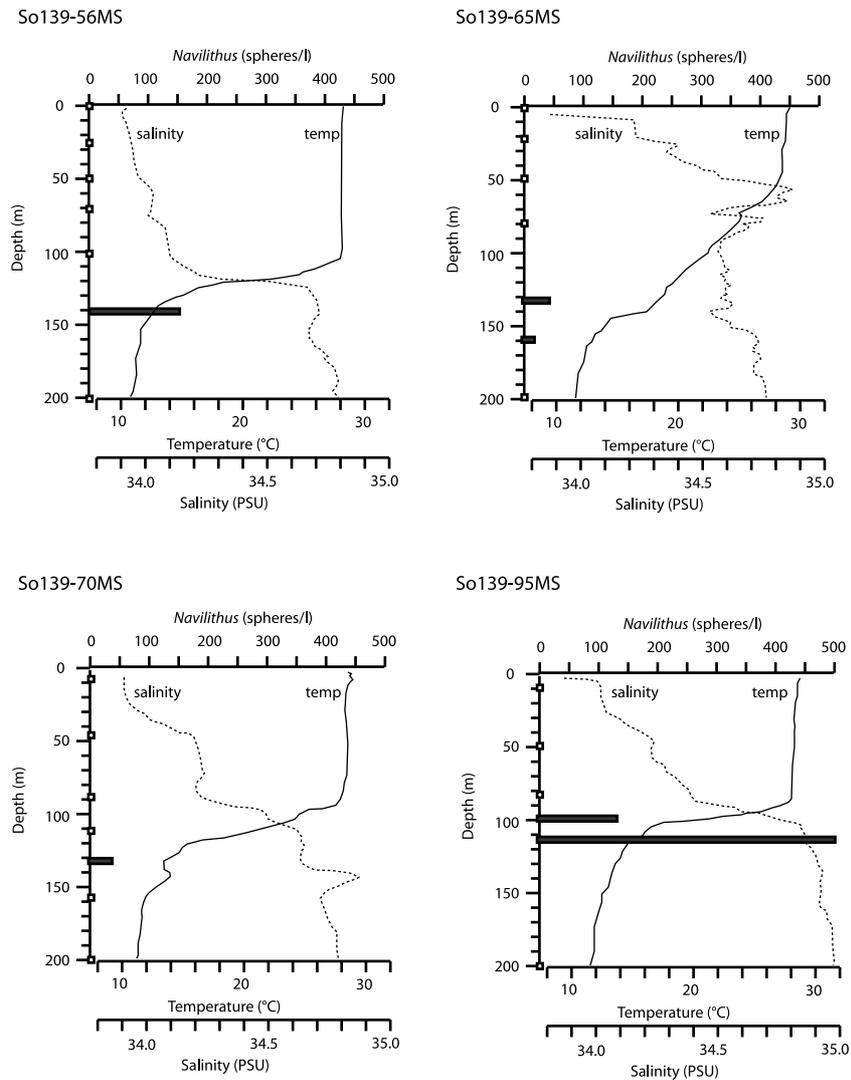


Fig. 2. Sample depths, salinity and temperature profiles for the sites at which *Navilithus altivelum* was recorded. Horizontal bars indicate calculated abundances of *Navilithus* in the samples. Open squares indicate samples without *Navilithus*.

Diagnosis. *Cellula coccolithifera polymorpha cum coccosphaera composita ex coccolithis angustimarginatis placolithis cum plano areae centralis convexo proximale et cum spinis robustis suffultis ab caule humili.*

Polymorphic coccolithophore with coccosphere formed of narrow-rimmed placolith coccoliths with central area plate which is convex proximally and with robust spines supported by a low stem.

Navilithus altivelum sp. nov. Young & Andruleit
(Pls 1–3; Fig. 3)

Derivatio nominis. From the Latin *altus* (high) and *velum* (sail) reflecting the distinctive sail-like form of the spines of the circum-flagellar coccoliths. Note that since this a noun, not an adjective, its case should not be changed to agree with that of the genus.

Diagnosis. *Species Navilithus cum coccosphaera composita ex circa 200–300 corporis coccolithis cum spinis humilibus*

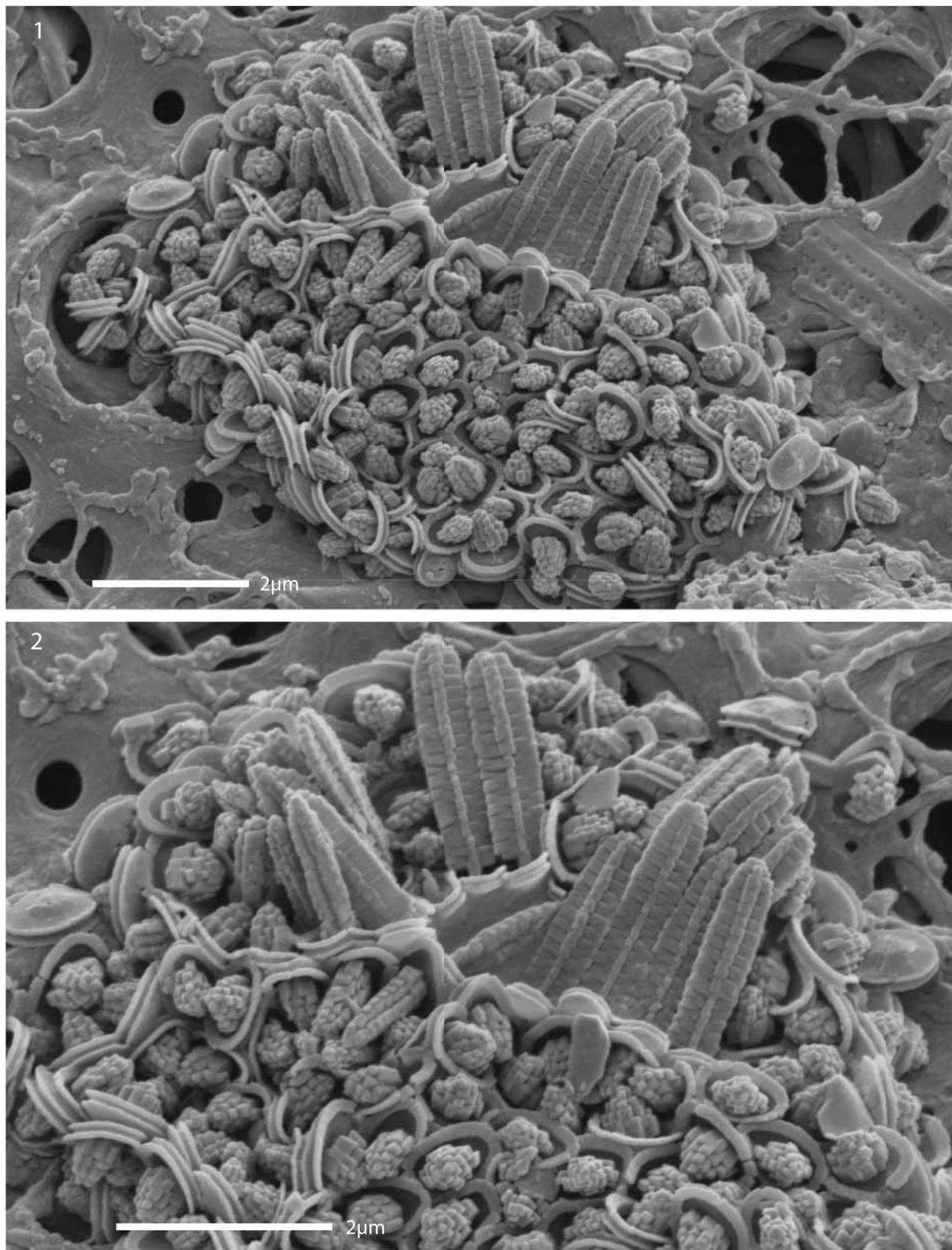
triangularibus, 10–20 coccolithis cum spinis altis ad instar veli navis et cum numero variabili coccolithorum cum spinis altis triangularibus.

Species of *Navilithus* with coccosphere composed of *c.* 200–300 body coccoliths with low triangular spines, 10–20 coccoliths with tall sail-like spines and a variable number of coccoliths with tall triangular spines.

Type specimen. Specimen illustrated in NHM SEMs JRY205-21, 22 (Pl. 1, figs 1–2; Pl. 3, figs 6, 7, 9, 13, 14, 15; Pl. 4, figs 3, 4). This specimen is located on NHM coccolithophore collection SEM stub 483.

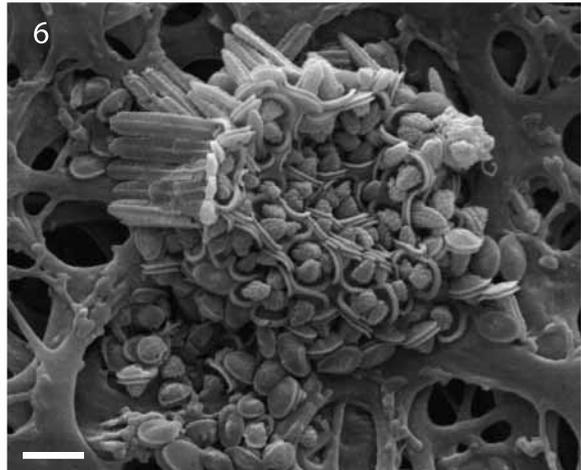
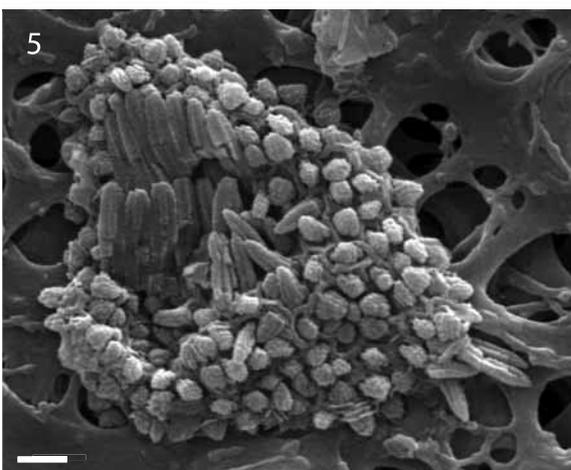
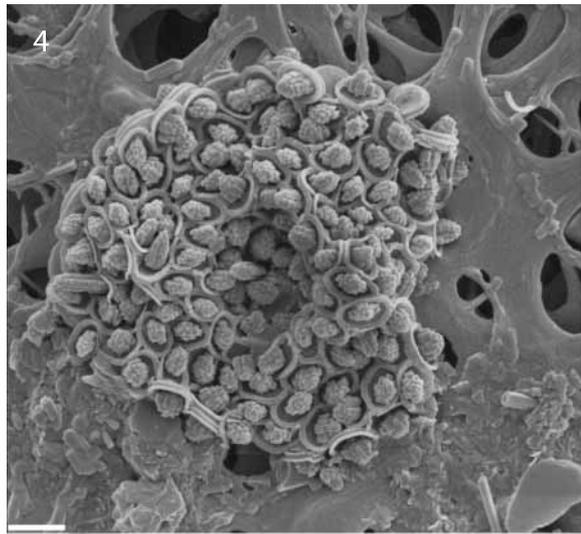
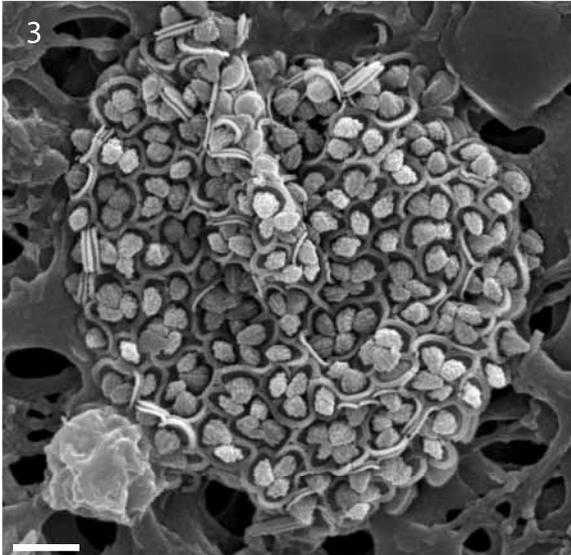
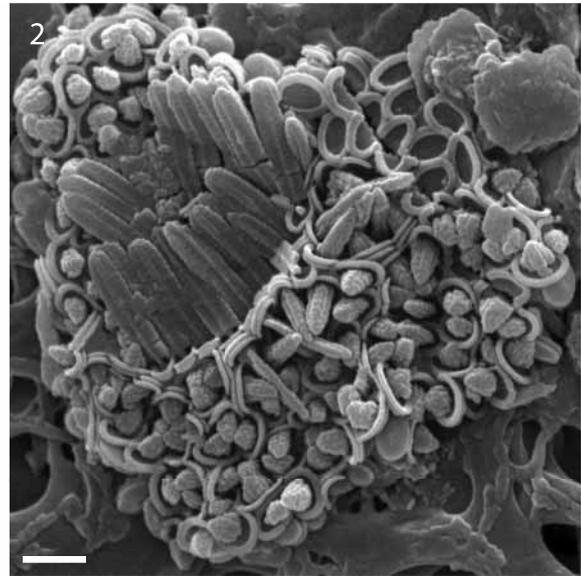
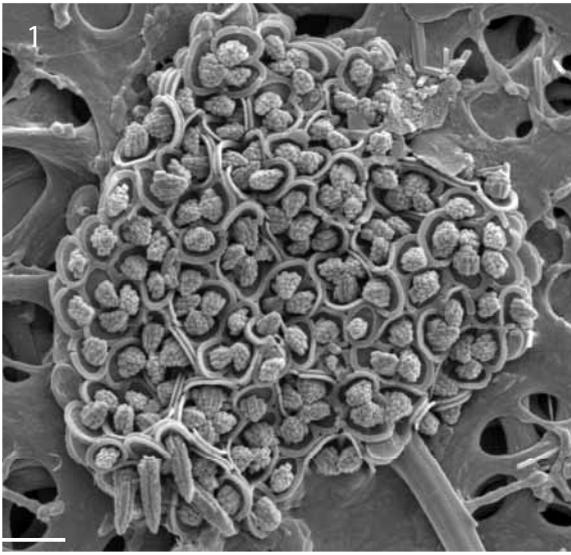
Type sample. So139-95MS, 114 m, collected from NE Indian Ocean, Latitude 6.57° S 104.90° E, 25 February 1999 by BGR.

Type depositary. Type images and stub are archived in the Natural History Museum, Micropalaeontology Division; topotype material is archived in the BGR (Bundesanstalt für Geowissenschaften und Rohstoffe) coccolithophore collection.



Explanation of Plate 1.

Navilithus altivelum holotype specimen, 205/21: **fig. 1.** whole specimen. **fig. 2.** detail of upper part of coccosphere, showing probable flagellar pole surrounded by sail coccoliths. Scale bars 2 μ m.



Description – Coccospheres. All observed coccospheres (Pls 1, 2) are collapsed so the original shape cannot be determined with certainty; however, these scatters have length to width ratios of 1.5 to 1.0, average 1.15 (30 measurements) so it is reasonable to infer that the original coccospheres were sub-spherical in shape. The collapsed coccospheres are 5 to 11 μm across, average 7.8 μm , suggesting an original coccosphere diameter of *c.* 5–8 μm , assuming some of the variation is due to variable degree of scatter of coccoliths during collapse of the coccospheres. The coccospheres are trimorphic with body coccoliths, moderately elevated coccoliths and sail coccoliths (Pl. 3).

The number of body coccoliths observed range from 100 to 170 (counts on seven specimens, including the largest and smallest observed coccospheres). This suggests that the coccospheres contain 200–300 body coccoliths, on the assumption that about half the coccoliths are visible on a collapsed coccosphere. Tall sail-coccoliths are always clustered together on the coccosphere but the number observed is highly variable, from 18 to 0 (average 7.6, 30 counts). This variation is interpreted as being largely due to variable orientation of collapse of the coccospheres, with minimum values when the sail-like coccoliths are on the concealed side of the coccosphere and maximum values when they are all visible. The typical number of sail coccoliths per coccosphere is thus likely to be about 15. The number of moderately elevated coccoliths observed is highly variable, from 0 to 22 (average 4.1, 30 counts). They mostly occur around the outside of the group of sail-coccoliths but there are also often a few of these coccoliths well-separated from the circum-flagellar area and in at least some cases they appear to form a cluster of antapical coccoliths.

On the collapsed coccospheres, fields of coccoliths seen in proximal view are normally very obscured. This is probably a result of the cell membrane and other organics from the cell coating the coccoliths. No evidence of flagella was seen, but this is not necessarily significant, since they are only occasionally visible in SEMs of coccolithophores.

Description – Body coccoliths (Pl. 3, figs 7–16). These are elliptical in plan view with narrow placolith rim formed of sub-horizontal distal and proximal shields connected by a low tube. The coccolith is floored by a central area plate which supports a low robust spine. Length 0.7–1.0 μm (average 0.86 μm , from 55 measurements). Width 0.5–0.7 μm (average 0.67 μm , from 28 measurements).

The rim is narrow (0.08–0.12 μm). Elements in the distal shield are not usually imaged clearly but there seem to be 15–20. Sutures are sub-radial, with weak clockwise obliquity; the elements do not appear to be imbricated. The tube is narrow, height (0.09–0.15 μm) approximately equal to the distal shield

width. The proximal shield is similar in width to the distal shield or slightly narrower. Both shields are essentially horizontal. The central area plate is not imaged clearly in any specimens, possibly because of an organic coating, but appears to be composed of numerous irregular elements, often with a small central pore. The proximal surface of the coccolith is convex, i.e. curves toward the cell. This morphology is unusual, as coccoliths normally have concave bases, but it occurs in too many specimens for it to be a result of deformation.

The spine is low (0.4–0.7 μm), triangular in profile. It is attached to the central area plate by a very narrow basal stem. Above this it immediately widens to its maximum width then tapers upward. It is formed of numerous rhombic, vertically elongated elements arranged in irregular tiers, the lowermost tier is higher than the others. The elements show flat rhombic faces and are probably modified calcite rhombohedra. In plan view the spine is approximately diamond-shaped, aligned parallel to the axes of the coccolith.

Description – Moderately elevated coccoliths (Pl. 3, figs 3–6). These are similar to the body coccoliths but have higher spines (0.7–1.4 μm). The spines have similar structure to those of the body coccoliths, including the presence of a basal cycle of relatively tall elements and attachment by a basal stem. They are diamond-shaped in plan view and elongated parallel to the long axis of the coccolith. The spine structure becomes more regular upwards and cross-shaped in plan view. The basal structure appears to be identical to that of the body coccoliths.

Description – Circum-flagellar sail-coccoliths (Pl. 3, figs 1–2). These have similar bases to the other coccoliths but the spine is much taller (1.3–2.2 μm , average 1.84 μm , from 15 measurements) and is flattened perpendicular to the long axis of the coccolith. The spine is cross-shaped in plan view but the arms extending parallel to the long axis are very short. The basal stem of the spine is rather higher than in the other coccolith types so that the base of the sail is elevated slightly above the rim. The spine structure is regular, with each blade of the sail being formed of two series of elements originating from either side of the blade and interfingering toward the outer margin of the sail (Fig. 3).

The basal structure is similar to that of the body coccoliths but perhaps slightly smaller, and the central pores are larger and more consistently developed.

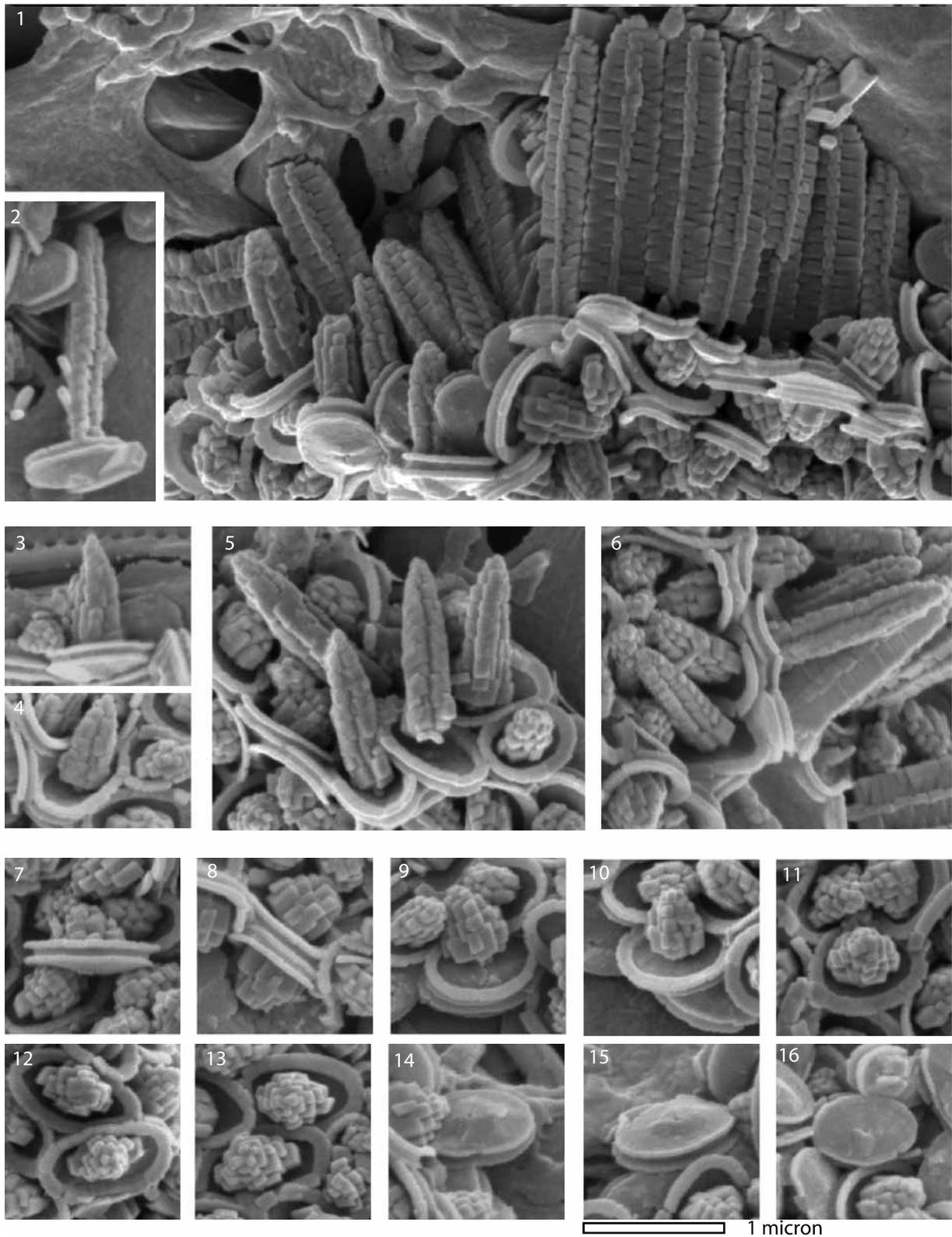
DISCUSSION

Ecological affinities

Specimens of *Navilithus* were found in four of the seven sites sampled and in a total of six samples (out of 45). All the sites

Explanation of Plate 2.

SEMs of six coccospheres of *Navilithus altivelum*, illustrating variation in exposure of the different coccolith types. Scale bars 1 μm . **fig. 1.** Specimen showing a prominent group of moderately elevated coccoliths, possibly in antapical position. SEM NHM JY205-31. **fig. 2.** Specimen with large cluster of presumably circum-flagellar sail coccoliths, and several associated moderately elevated coccoliths. Note also at upper right several body coccoliths from which the spines have been detached. SEM BGR HA2636. **fig. 3.** Nearly circular specimen showing only body coccoliths, except one moderately elevated coccolith at bottom. SEM BGR HA3868. **fig. 4.** Another specimen showing almost entirely body coccoliths, one moderately elevated coccolith at left. SEM NHM JY205-18. **fig. 5.** Specimen showing a large cluster of presumably circum-flagellar sail coccoliths, and several associated moderately elevated coccoliths. Also at bottom right several antapically positioned moderately elevated coccoliths. SEM BGR HA3837. **fig. 6.** Somewhat scattered specimen with a large cluster of presumably circum-flagellar sail coccoliths at upper left and a few associated moderately elevated coccoliths; also at bottom right one antapically positioned moderately elevated coccoliths. SEM BGR HA3850.



Explanation of Plate 3.

Details of the different types of coccoliths produced by *Navilithus altivelum*. All images have been adjusted to a common magnification. **figs 1–2.** Sail coccoliths: **1**, SEM NHM JY 209-35a; **2**, SEM NHM JY 209-30a. **figs 3–6.** moderately elevated coccoliths: **3**, SEM NHM JY 205-27e; **4**, SEM NHM JY 205-18d; **5**, SEM NHM JY 205-31d; **6**, SEM NHM JY 205-21e. **figs 7–16.** body coccoliths: **7–10** side and oblique views – **7**, SEM NHM JY 205-21c; **8**, SEM NHM JY 205-18c; **9**, SEM NHM JY 205-21i; **10**, SEM NHM JY 205-31c; **11–13** distal views – **11**, SEM NHM JY 205-31e; **12**, SEM NHM JY 205-18a; **13**, SEM NHM JY 205-21d; **14–16** proximal views – **14**, SEM NHM JY 205-21g; **15**, SEM NHM JY 205-21f; **16**, SEM NHM JY 205-27d.

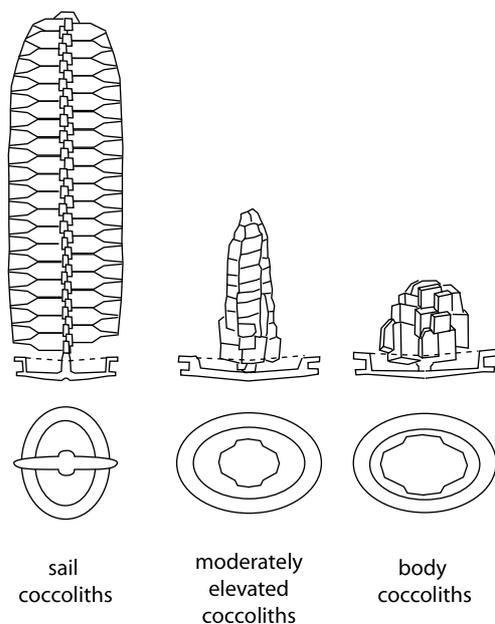


Fig. 3. Summary drawings of the three *Navilithus altivelum* coccolith morphologies: circum-flagellar sail coccoliths, body coccoliths and moderately elevated coccoliths (plan and side views). The plan views and the side view of the sail coccolith are schematic, based on numerous observations, the other side views are tracings of SEMs.

contained low abundance coccolithophore communities, with surface assemblages either dominated by *Gephyrocapsa oceanica* or *Umbellosphaera irregularis* or a diverse mixture including the two named species plus *Palusphaera vandellii*, *Ophiaster hydroideus*, *Syracosphaera* spp. and *Calciosolenia* spp. with no clear dominance of a single species. There was a well-defined thermocline in the area at *c.* 100m and below this a deep-photoc nannoplankton community was developed dominated by *Florisphaera profunda*, but also with high abundances of *Algirosphaera robusta*, *Gladiolithus flabellatus* and *Oolithotus antillarum*. In addition *Gephyrocapsa oceanica* persisted in high abundances in the deep samples, although some at least of this population was probably settling out from the upper photic zone, it is particularly noticeable that the deepest samples recovered (from *c.* 200 m) typically had reduced abundances of *Florisphaera profunda*.

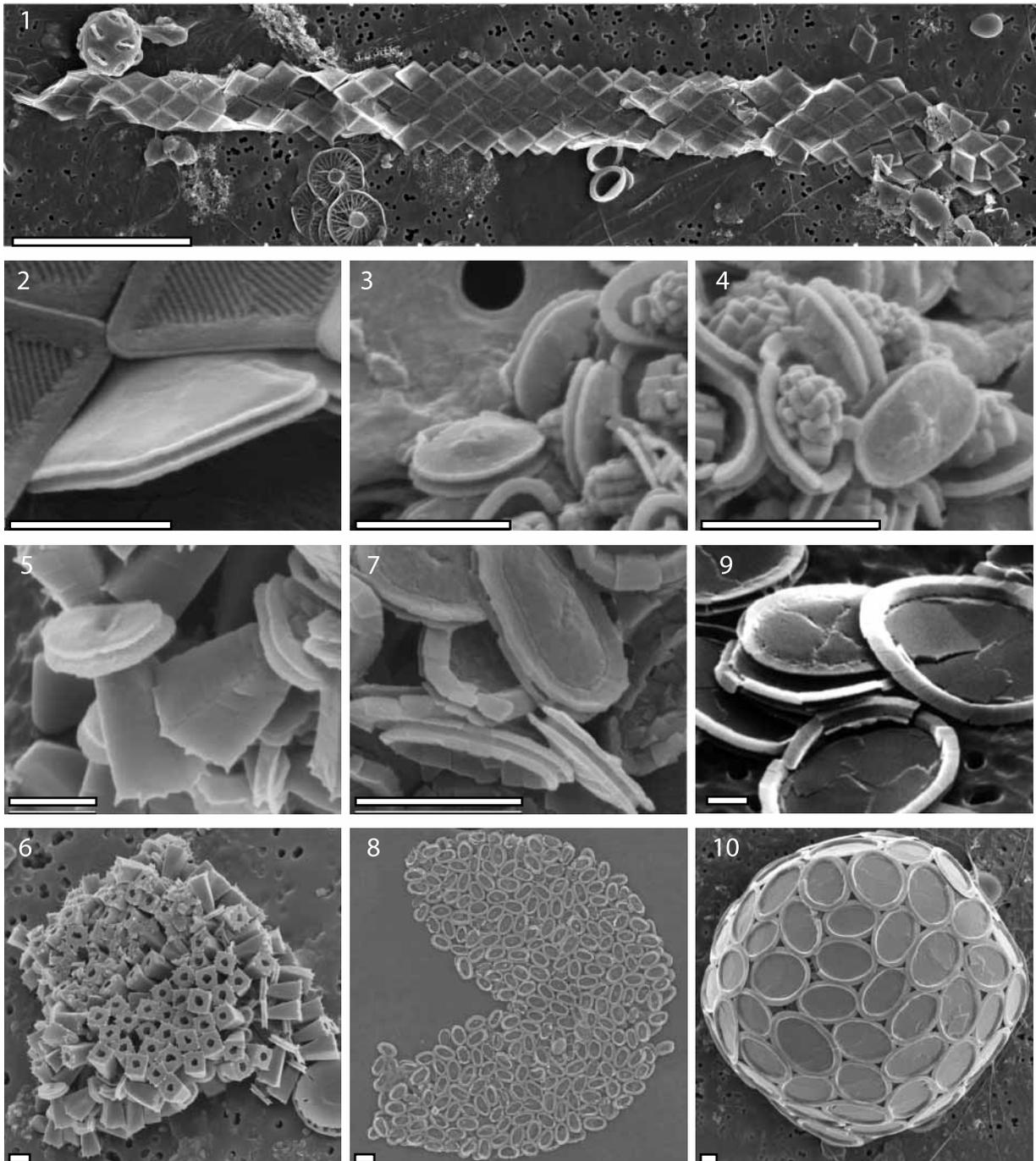
All the *Navilithus* specimens observed came from samples within or below the thermocline and with a significant abundance of deep photic zone species. Hence, one can infer confidently that this is a true obligate deep-photoc species. The thermocline is usually abrupt in this area, with temperatures dropping from the surface values of 28–30°C to deep values of 11–13°C in an interval of less than 50 m. Consequently thermocline-dwelling species inevitably encounter a wide range of temperatures. This applies to *Navilithus* and the samples containing the species came from water samples ranging in temperature from 12.8–21.6°C. Similarly the thermocline is marked by a rather abrupt increase in salinity from surface values of sometimes less than 33 PSU to deep values of *c.* 35 PSU and samples with *Navilithus* had salinities of 34.35 to 34.72 PSU. The depth of *Navilithus*-bearing samples varies from 100 m to 160 m, again this seems to be largely controlled by the

varying thermocline depth at different stations. There is no obvious difference between the communities present in the sub-thermocline samples with and without *Navilithus* specimens. In addition, *Navilithus* specimens occur at sites with rather different and even contrasting upper photic zone communities.

It is rather curious that such a distinctive species should be found in what is a very well-studied group of organisms. The coccospheres are small and could be overlooked, especially on cellulose filters as used here, but they would be readily visible on polycarbonate filters. Moreover, there have been several very detailed studies by taxonomically interested workers of sample sets, including deep photic zone taxa (e.g. Okada & Honjo, 1973; Okada & McIntyre, 1979; Hagino *et al.*, 2000; Cortes *et al.*, 2001; Cros & Fortuño, 2002; Andruleit *et al.*, 2005) and this species has never been recorded before, even in open nomenclature. This was confirmed by showing the images to many nannoplankton specialists via the coccoliths listserver (coccoliths@morgan.ucs.mun.ca) and at the International Nannoplankton Association conference in 2004. None of the consulted specialists had ever seen this species. Similarly, several other very distinctive deep photic zone species have been described with very sporadic occurrences, notably including *Gladiolithus striatus*, *Placorhombus ziveriae*, *Tetralithoides quadrilaminata*, *Turrilithus latericioides*, numerous informally described Papposphaeraceae (Cros & Fortuño, 2002) and several small Rhabdosphaeraceae (Young *et al.*, 2003). The deep photic coccolithophore flora is characteristically dominated by *Florisphaera profunda* and this has given an impression of homogeneity in the flora. However, as Quinn *et al.*, (2005) have shown, *F. profunda* itself is morphologically highly variable and it is suspected that it may constitute a plexus of pseudo-cryptic species. This variability in *F. profunda*, combines with variability in the secondary and rare species constituting the deep-photoc assemblage. So, this assemblage may be much more taxonomically heterogeneous than has been assumed and this heterogeneity may be ecologically informative. Taken together, the new evidence of cryptic diversity in *Florisphaera*, and of a wider diversity of accessory species than has been assumed means that the deep-photoc nannoplankton assemblage should be seen as heterogeneous and attempting to discover the controls on this heterogeneity might be highly productive.

Taxonomic affinities

Extant coccolithophore taxonomy is comprehensively reviewed in Young *et al.* (2003). The majority of known coccolithophores can be assigned confidently to a few major groupings based on coccolith structure and these groupings have been well-supported by available molecular genetic data (Saez *et al.*, 2004). There are, however, a number of anomalous genera which do not fit into any of the major groupings. Young *et al.*, (2003) argued that these could be subdivided into two groups. First, narrow-rimmed muraliths, including *Vexillarius cancellifer* Jordan & Chamberlain, 1993, *Wigwamma* Manton *et al.*, 1977 (several species), *Picarola margalefii* Cros & Estrada, 2004, and an undescribed genus. These forms show some affinity to the Papposphaeraceae. Secondly, narrow-rimmed placoliths, including *Tetralithoides quadrilaminata* (Okada & McIntyre, 1977) Jordan *et al.* 1993, *Turrilithus latericioides* Jordan *et al.*, 1991, *Placorhombus ziveriae* Young & Geisen, in Young *et al.* (2003),



Explanation of Plate 4.

Comparison of *N. altivelum* and other narrow-rimmed placolith coccolithophores. Scale bars 1 µm, except fig. 1. **fig. 1.** *Placorhombus ziveriae* coccosphere, scale bar 10 µm. SEM NHM JY 144-04. **fig. 2.** *P. ziveriae*, detail of coccoliths SEM NHM JY127-03. **fig. 3.** *Navilithus altivelum*, detail of coccoliths SEM NHM JY205-21g. **fig. 4.** *Navilithus altivelum*, detail of coccoliths SEM NHM JY205-21h. **fig. 5.** *Turrilithus latericiodes*, detail of coccoliths SEM NHM JY200-13a. **fig. 6.** *Tetralithoides quadrilaminata*, detail of coccoliths (image courtesy of R. Jordan). **fig. 7.** '*Calyptosphaera*' *sphaeroidea* HET, detail of coccoliths (image courtesy of M-H Noel). **fig. 8.** '*Calyptosphaera*' *sphaeroidea* HET coccosphere (image of M-H Noel). **fig. 9.** *Turrilithus latericiodes* coccosphere SEM NHM JY SEM NHM JY200-13. **fig. 10.** *Tetralithoides quadrilaminata* coccosphere SEM NHM JY128-16.

and the heterococcolith phase of *Calyptosphaera sphaeroidea* Schiller, 1913, which was recently described by Noel *et al.*, (2004).

Navilithus certainly does not show the characteristic features of any of the main groups, such as the Syracosphaeraceae,

Rhabdosphaeraceae or Coccolithaceae, in terms of either rim or central area structure. It does, however, show the basic narrow-rimmed placolith rim morphology which Young *et al.* (2003) used as the primary basis for grouping this set of coccoliths

incertae sedis. So, it is worth considering in detail the degree to which it shows affinity with this group, and to review the degree to which this group shows sufficient common characteristics to be likely to be monophyletic. The characteristics of this group are discussed below and the other species of the group are illustrated in Pl. 4.

Rim structure. In all the species considered, the rim has a simple morphology with narrow distal and proximal shields connected by a thin sub-vertical tube. It is not possible to be sure of the exact structure but it appears in each case to be formed of a single cycle of elements, rather than two interlocked series of elements, as in the Coccolithaceae, Pleurochrysidaceae or Syracosphaeraceae. The sutures are radial or show weak clockwise obliquity on the distal shield, are vertical in the tube, and less certainly are radial in the proximal shield. Light microscope observations are only available for *Tetralithoides*, which appears to be formed of V-units (J. R. Young, personal observation).

Rim structure is normally the best single morphological indicator of affinity for heterococcoliths (e.g. Perch-Nielsen, 1985; Bown & Young, 1998; Young *et al.*, 2004), and these rims certainly appear similar to each other and unlike those of other coccoliths, but the absence of detailed structural or crystallographic observations means that this rim similarity cannot be considered decisive evidence of affinity.

Central area structures. All the included species have central area structures which are clearly disjunct from the rim, i.e. formed of separate crystal units. In *Placorhombus* and *Tetralithoides* the central structure is four large plates, striate in the case of *Placorhombus*. In *C. sphaeroidea* HET, *Navilithus* and probably in *Turrilithus*, the central area is floored by a mass of small irregular crystallites. This floor is remarkably similar in appearance in *Navilithus* and *C. sphaeroidea* HET, notably in proximal view, with distinct convexity being shown. This convexity of the proximal surface is very unusual and is also shown, to a lesser extent, by *Placorhombus*. Only *Navilithus* and *Turrilithus* show processes and these are different in shape but exhibit some similarities in being tall and massive in relation to a rather small coccolith base. It is noteworthy that each side of the quadrate tower spines of *Turrilithus* is formed of two offset series of sub-horizontally elongated elements, thus in total the structure is formed of eight series of offset elements, as are the sail spines of *Navilithus*, possibly indicating some structural relationship. No other coccolithophores have processes with similar structure.

Coccosphere/cell. All the species form coccospheres formed of numerous coccoliths, from 60 to 500. They show few other common characteristics, however. Most are spherical but *Placorhombus* coccospheres are tapering cylinders. Young *et al.* (2003) included monomorphism as a feature of the group, even though *Placorhombus* is weakly dimorphic (small coccoliths occur at the tapered end of the coccospheres). *Navilithus* is very different being trimorphic, with the sail coccoliths having a very different form to the body coccoliths. Related to this, it is likely that *Navilithus* is motile since polymorphism is strongly related to motility (Young, 1994; Young *et al.*, 2005) and the sail coccoliths are grouped in the characteristic manner of circum flagellar coccoliths. By contrast, the *Calyptrosphaera*

sphaeroidea HET phase is known to be non-motile from culture observations (Noel *et al.*, 2004) whilst *Turrilithus* and *Tetralithoides* form spherical monomorphic coccospheres with no obvious flagellar opening and so are probably non-motile. As noted by Young *et al.* (2003), one end of *Placorhombus* coccospheres is typically bluntly terminated, leaving a possible flagellar opening, so these are likely to be motile. In most coccolithophore families the heterococcolith phase is either consistently motile (e.g. Pleurochrysidaceae, Syracosphaeraceae, Papposphaeraceae) or consistently non-motile (e.g. Noelaerhabdaceae, Calcidiscaceae). However, there are also families with a mixture of motile and non-motile heterococcolithophores (e.g. Rhabdosphaeraceae, Pontosphaeraceae), so the variable motility in the narrow-rimmed placolith group does not prove it is an artificial grouping.

Ecology. All members of the narrow-rimmed placolith group are rare deep-dwelling species; they have been recorded only very sporadically and exclusively from deep photic zone samples. The only likely exception is the *Calyptrosphaera sphaeroidea* HET phase. This form has been observed only in culture so it is not known if it is a deep photic phase, or, as suggested by Noel *et al.*, (2004), a coastal semi-benthic phase. It also is a less distinctive form than the other species so may conceivably have been overlooked. This ecological similarity provides weak support for the grouping.

Molecular genetic evidence. Of the narrow-rimmed placolith group, only *Calyptrosphaera sphaeroidea* has been cultured, so this is the only species for which there is molecular genetic data. However, *C. sphaeroidea* fell in a somewhat surprising place in the molecular tree, occurring within the Coccolithaceae–Calcidiscaceae clade, in an intermediate position between those two families, together with a few other holococcolithophores known only from cultures (Fujiwara *et al.*, 2001; Saez *et al.*, 2004). An obvious problem of this result was that these holococcolithophores should have heterococcolith phases and it was difficult to predict which species these should be. That is, the molecular genetic data identified a group of holococcolithophores falling outside the main groups of heterococcolithophores and so predicted that there should be an associated group of heterococcolithophores. The *Calyptrosphaera sphaeroidea* HET phase described by Noel *et al.* (2004) is a narrow-rimmed placolith, so an attractive possibility is that the other narrow-rimmed placoliths are heterococcolith phases of the additional holococcolithophores associated with *C. sphaeroidea*.

The morphological evidence in support of the narrow-rimmed placolith grouping is plainly suggestive but not overwhelming or conclusive. The group is diverse and the features which unite it are all somewhat disputable. The strongest features uniting the group are the form of the rim and the central plate. In this respect it is remarkable that the two most similar forms are *C. sphaeroidea* HET and *Navilithus altivelum*. The *C. sphaeroidea* heterococcoliths are almost identical to *N. altivelum* body coccoliths which have lost their spines. This similarity is so strong that it seems very good evidence of close taxonomic affinity, especially since basal features have consistently proven much more reliable for taxonomy than spines and other appendages. Given this, it can be rather strongly predicted that

Navilithus will fall close to *C. sphaeroidea* in the molecular phylogeny and, from the tree topology (Saez *et al.*, 2004), that this group diverged from the Coccolithaceae early in the evolution of the Coccolithaceae, i.e. probably in the early Palaeogene.

Of the narrow-rimmed placoliths, only *Tetralithoides* has a documented fossil record, extending back to the Early Miocene (Theodoridis, 1984; Young, 1998). There are, however, many poorly characterized fossil coccoliths in the Cenozoic and, as these are revised, possible affinity with the narrow-rimmed placolith group should be considered.

CONCLUSIONS

This paper has described a new, highly distinctive, deep photic coccolithophore species, *Navilithus altivelum*. The continued discovery of rare and patchily distributed deep photic species suggests that this environment is more heterogeneous than has been assumed and that systematic study of this assemblage may enable an understanding of the ecology of this key environment.

The unique feature of *Navilithus* coccoliths are the spines, which are supported by narrow basal stems and, in the case of the sail coccoliths, are formed of eight rows of interdigitating elements. No obviously similar spines occur in living or fossil coccoliths. However, it is well established that basal and especially rim features of coccoliths are the most useful phylogenetic characters of coccoliths. In this respect the *Navilithus* coccoliths show striking similarity to the coccoliths of *Calyptrorphaera sphaeroidea* HET and arguable similarities to the three other species included in the informal narrow-rimmed placolith grouping of Young *et al.* (2003). Since *C. sphaeroidea* is known from molecular genetic data to belong to a group of holococcolithophore species nesting within the Coccolithales clade, it can be predicted that *Navilithus* is a member of this group.

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