Light and electron microscope observations of the type species of Syracosphaera, s. pulchra (Prymnesiophyceae)

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Light and Electron Microscope Observations of the Type Species of Syracosphaera, *S. pulchra* (Prymnesiophyceae)

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*Syracosphaera pulchra*, the type species of the genus was isolated into unialgal culture and studied with both the light and electron microscope. A conspicuous coiling haptonema is present containing seven microtubules in the shaft and eight in the basal region; features shared with many taxa in the order Prymnesiales. The proximal and distal coccoliths differ in shape but resemble each other structurally: the outer elements alternate to make the rim. The proximal coccoliths possess an organic base-plate scale which is absent in the distal coccoliths. The uncalcified organic scales are ornamented by a radial, more or less concentric, fibrillar pattern and are arranged in several layers between the proximal coccoliths and the plasmalemma. The ultrastructure of the cell is typical of prymnesiophycean algae. The flagellar apparatus is characterized by the absence of secondary microtubular bundles which are usually well developed in other coccolithophorids with two microtubular roots. This feature is also rather similar to that found in members of the Prymnesiales.

This investigation has indicated that *S. pulchra* has, in some respects, a closer affinity with members of the Prymnesiales than with the coccolithophorids.

A number of microanatomical studies have been undertaken using cultures of many taxa of the class Prymnesiophyceae. Most of these studies have been carried out on members of the orders Isochrysidales, Prymnesiales and Pavlovaiales, and it has been clearly demonstrated that certain ultrastructural features have taxonomic significance (for bibliography see Hibberd, 1980). The Coccosphaerales *sensu* Parke and Green (in Parke & Dixon, 1976) is the largest order of the Prymnesiophyceae and includes most coccolithophorids. Earlier electron microscopical studies on coccolithophorids, however, have been restricted to coccolith morphology. Detailed ultrastructural studies on coccolithophorid cells have been limited to a few littoral representatives. Many taxa are still proving to be extremely difficult to culture and consequently their ultrastructure has not been studied.

This paper deals with a very common coccolithophorid *Syracosphaera pulchra* Lohmann (1902), designated the type species of the genus by Loeblich & Tappan (1963). In spite of its common occurrence, *S. pulchra* has not been studied in sufficient detail. Lohmann (1902), when describing the genus, drew illustrations of a coccosphere with two chloroplasts and a single flagellum. The presence of two flagella was later mentioned by Schiller (1925). Kamptner (1941) found that the coccolith case of this organism was made up of a double layer.

In 1977, Gaarder & Heimdal revised the genus and, using the difference in the coccolith ultrastructure, split it into three genera, viz. *Syracosphaera* Lohmann *sensu stricto*, *Coronosphaera* Gaarder and *Caneosphaera* Gaarder. As a result of their work, *Syracosphaera* has become a
recognized genus that is characterized by a double-layered coccolith case (dithecatism). The purpose of the present paper is to present some new observations on the micromorphology of coccoliths and the ultrastructure of the cells of the type species of Syracosphaera.

MATERIALS AND METHODS

Sea-water samples were collected weekly from May to December, 1981 at Durban, Republic of South Africa. *S. pulchra* was one of the common coccolithophorids found throughout the period and many cells were observed in September and October. A sample collected on 6 October 1981 was treated as follows. Nanoplankton species were concentrated by filtering seawater through a Nuclepore filter of 0.8 µm pore size. Swimming cells of *S. pulchra* were isolated into sterilized PES medium (Provasoli, 1968). The resulting unialgal cultures were grown at 20°C and exposed to 25 µE m⁻² s⁻¹ in light-dark 12:12.

For shadowed preparations, drops of medium containing actively swimming cells were placed on formvar-coated grids and exposed to the vapour of a 4% aqueous solution of osmium tetroxide for 30 s. After drying, the salt was removed by rinsing the grids with neutralized distilled water. The grids were then shadowed with gold/palladium. Both living and neutralized formalin-fixed material was used for scanning electron microscopy. Cells were concentrated on to Nuclepore filters, rinsed with neutralized distilled water and dried at room temperature. Small pieces of the filter were mounted on specimen stubs and sputter-coated with gold to a thickness of 30 nm.

Sectioned material was prepared as follows: a glutaraldehyde solution (5%) in 0.2 M sodium cacodylate buffer (pH 7.2) containing 0.5 M sucrose was prepared just prior to fixation. An equal volume of this fixative and the culture medium contained cells were rapidly mixed at room temperature. One hour later cells were collected by gentle centrifugation and washed twice with fresh culture medium (15 min each). Cells were then post-fixed in 2% aqueous osmium tetroxide for 2-4 h, washed twice with buffer and dehydrated in a graded ethanol series. Cells were embedded in Spurr's low viscosity resin (Spurr, 1969) and Epon 812. Sections were cut with a diamond knife and stained with uranyl acetate followed with lead citrate (Reynolds, 1963). A JEOL JSM T200 scanning electron microscope and JEOL 100CX and 100C transmission electron microscope were used to view specimens.

OBSERVATIONS

Light microscopy

General features of *S. pulchra* have been studied previously with the light microscope (e.g. Lohmann, 1902; Schiller, 1925; Kamptner, 1941), so only a brief review with some new observations obtained from unialgal cultures is included here.

The organism is usually teardrop-shaped, obpyriform or spherical (Figs 1–3), 12–39 µm x 12–18 µm, and surrounded by a double-layered coccolith case consisting of distal and proximal coccoliths which differ in shape (Figs 1, 2, 5). The proximal coccoliths are basket-shaped discoliths and dimorphic. Those located around the flagellar insertion (stomatal coccoliths) have a central stalk, unlike those covering the rest of the cell surface (ordinary coccoliths). The distal coccoliths are dome-shaped and possess a central projection which extends toward the cell surface (Fig. 2). The arrangement of the coccoliths observed in the cultured material is the same as that found in wild material. In older cultures, however, the stomatal coccoliths are not restricted to the flagellar pole and have been observed covering other parts of the cell surface.

Like many other coccolithophorids and members of the Prymnesiales, *S. pulchra* has two flagella of nearly equal length, measuring 34–51 µm, and a prominent haptonema (Figs 3–6). The haptonema is 15–28 µm long and capable of coiling as shown in Fig. 5. This was observed when the cells ceased swimming.

Reproduction is by binary fission. Firstly the flagella and haptonema replicate and chloroplasts divide; then each set of flagella and haptonemata separate and move to opposite poles (Fig. 6). Mitosis then proceeds. Finally the cell constricts medianly to produce two daughter cells (Fig. 7) which are spherical or slightly obovoid and often lack stomatal coccoliths.

In young cultures, the cells have two parietal chloroplasts. In old cultures pleomorphic cells were often observed. These cells are spherical, much larger than usual
Microscopy of *Syracosphaera pulchra*

**Electron microscopy**

**External structure.** A single type of uncalcified organic scale was observed arranged in several layers between the coccolith casing and the cell membrane (Figs 17, 18). These are circular to slightly elliptical (0.8-1.10 μm diam.) and have a radiating and more or less concentric pattern of ridges on both the proximal and distal surfaces (Fig. 8). No rim to the scale was observed. Both the radial and concentric pattern of ridges can be seen in sectioned material (Figs 17, 18).

The coccolith structure has been described by several authors (Halldal & Markali, 1955; Black & Barnes, 1961; Leadbeater & Morton, 1973; Gaarder & Heimdal, 1977). The following includes a review and some new observations based on cultured material. The proximal coccoliths are of two types, viz. ordinary coccoliths (which cover the entire cell surface except at the region of flagellar insertion) and stomatal coccoliths (which occur only at the flagellar pole; cf. Figs 1, 2, 5). The ordinary coccolith has an elliptical organic base-plate scale and three kinds of calcified elements. The base-plate scale is similar but much larger than the previously described uncalcified scale, measuring 3.5-3.8 μm × 4.8-5.6 μm. On the distal surface of the base-plate are radially

**Figures 1-7.** *Syracosphaera pulchra* light microscopy (phase contrast). Fig. 1. Cell coated by proximal and distal coccoliths. One stomatal coccolith is seen (arrowhead). Fig. 2. Cell showing typical side view of distal coccolith (arrow head). Fig. 3. Cell with two flagella and a prominent haptonema (H). Fig. 4. Cell possessing coiling haptonema. Fig. 5. Cell with entirely coiled haptonema (H) and coiling flagellum (arrow head). Fig. 6. Dividing cell showing two new flagella and a short haptonema (H). Fig. 7. Dividing cell constricting medially.
FIGS 8-14. *Syracosphaera pulchra* Electron microscopy (SEM and shadowed preparations). Fig. 8. Uncalcified scales with radial and fibrous patterns. Fig. 9. Side view of ordinary proximal coccolith. Horizontal ridge is seen (arrow head). Fig. 10. Side view of stomatal proximal coccolith. Horizontal ridge is seen (arrow head). Fig. 11. Proximal coccolith composed of three kinds of elements: outer (O), inner (I) and lamellate elements. Fig. 12. Stomatal proximal coccolith consisting of outer, inner and lamellate elements and a central rod. Fig. 13. Rim of ordinary coccolith. Outer and inner elements alternate to construct the rim. Fig. 14. Proximal coccolith comprising outer (O), inner (I) and two kinds of lamellate elements.

arranged ridges (Figs 17, 18) and no concentric fibrillar pattern was observed. Inner and outer calcified elements, are arranged along the margin to produce the coccolith rim. The general appearance of these elements is illustrated in Fig. 15(a). The two types of calcified elements alternate in such a way that the slender lower halves of the outer elements are positioned between the inner elements [Figs 11, 13, 15(a)]. Both
Microscopy of *Syracosphaera pulchra* 209

The stomatal coccoliths are identical to the ordinary coccoliths except for possessing a central rod (Figs 10, 12). Radially orientated lamellate elements are arranged on an organic base-plate scale and the rim is made up of inner and outer elements (Fig. 12). A ridge is also seen outside the rim (Fig. 10). Although the detailed structure of the rod is still not clear, it seems to be hollow and made up of small spirally arranged lamellate elements.

The distal coccolith is monomorphic. It is dome-shaped and 5.6–6.3 μm in diameter. This coccolith has no associated organic scale similar to the base-plate scale of the proximal coccoliths. In spite of the fact that the distal coccoliths differ considerably in shape from the proximal coccoliths, they have a similar structure. The distal coccolith consists of four different types of calcium carbonate elements. The rim of the coccolith consists of outer and inner elements, the shapes of which are illustrated in Fig. 15(b). The distal half of the outer elements are attached end to end to form the distal half of the coccolith rim. The proximal half of both the outer and the inner elements, which are almost identical in width, alternate to form the proximal half of the rim [Figs 14, 15(b)]. There are approximately 50 of each type of element making up the rim. The proximal surface of both elements bend upwards. Parallel lamellate elements showing a regular spacing between each element are attached to the inner elements. On top of these elements are different lamellate elements. These are broader than the former elements and are attached one by one by their long sides so that there is no empty space between them. The broader element can also be distinguished from the other lamellate element by possessing a ridge on the longitudinal axis (Fig. 14). Numerous broader elements form a dome-like roof and a central projection on the concave surface of the coccolith (Fig. 14). As has been shown by Gaarder & Heimdal (1977), the width and number of these elements decrease...
Figs 16–18. *Syracosphaera pulchra* Ultrathin sections. Fig. 16. Median longitudinal section of cell showing major cell components: chloroplast (C), Golgi apparatus (G), mitochondria (M), pyrenoid (P), peripheral endoplasmic reticulum (PER). A membranous band enclosing pyrenoid matrix is indicated by arrow heads. Fig. 17. Peripheral region of the cell. Proximal coccoliths (PC) and uncalcified organic scales (S) situated outside the cell. Vesicle producing a distal coccolith (DC) is also seen. Fig. 18. Organic scales (S) coating the cell and a vesicle producing a proximal coccolith (PC) with associated base-plate scale (arrow heads) are seen.
Microscopy of Syracosphaera pulchra

gradually as they progress from the outer to inner region. A diagrammatic representation of the distal coccolith is given in Fig. 15(b). A comparison of Fig. 15(b) (distal coccolith) with Fig. 15(a) (proximal coccolith) enables one to compare the two types of coccoliths.

**Cell ultrastructure.** The cell organelles are not unlike those of many other members of the class (Fig. 16). Endoplasmic reticulum (ER) is found immediately beneath the plasmalemma enclosing the cytoplasm and associated organelles (Fig. 16). There are two laterally situated chloroplasts which possess lamellae of three thylakoids (Fig. 16). Each chloroplast contains an immersed fusiform pyrenoid. The pyrenoid matrix is surrounded by a very thin envelope as has been observed in other taxa of the class such as Phaeocystis pouchetii Lagerheim (Parke, Green & Manton, 1971), Platychrysis pienaarii Gayral et Fresnell (Gayral & Fresnel, 1983) and Umbilosphaera sibogae var. foliosa (Kampfner Okada et McIntyre (Inouye & Pienaar, 1984) and Jomonlithus littoralis Inouye et Chihara (Inouye & Chihara, 1983) is applied to S. pulchra. In Figs 24–26, transverse sections provide information on the flagellar apparatus when viewed from above. The two basal bodies can be distinguished from each other by their position relative to the haptonema base and are referred to as the right and left bodies. The terminology used in previous papers is also used here to describe the microtubular and fibrous roots. The two basal bodies are arranged at an acute angle with their proximal ends overlapping. In the lumen of the basal body, an electron dense core is observed (Figs 25, 26). The basal bodies are linked with each other by a distal and a proximal striated band (Fig. 25). In S. pulchra the proximal band is difficult to distinguish because it is obscured by amorphous electron opaque material that surrounds it. The haptonema base is associated with the flagellar basal body complex. At the level of the distal band the basal bodies and haptonema base are arranged to form a triangle, while at their proximal end they are arranged in a row. The haptonema base seems to be linked by accessory bands with both the left and right basal bodies. There are eight microtubules in the haptonema base at the level of the proximal band (Fig. 26) but it decreases to seven before reaching the level of the distal band (Fig. 25). Seven microtubules extend into the emergent region of the haptonema (Fig. 25). Like many other taxa of the class, the peripheral ER is also associated with the haptonema microtubules and extends into the emergent part of the haptonema. When viewed in transverse section (Fig. 23), the endoplasmic reticulum can be seen as a concentric structure surrounding the seven microtubules. The flagellar roots are of four types, three microtubular and one fibrous. The microtubular roots are referred to as root 1, 2 and 3. Root 1 consists of about 10 microtubules which are closely aligned and form a sheet-like structure (Figs 20, 22). It arises adjacent to the haptonema and extends to the right basal body (Figs 25, 26).
Figs 19–23. *Syracosphaera pulchra* Ultrathin sections. Fig. 19. Flagellar base and Golgi region. Fibrous root (FR) arises from right basal body (R) and Golgi apparatus (G) consisting of cisternae with intercalary dilations are seen. Fig. 20. Haptonema base with associated ER (arrow head) is situated between two basal bodies (L and R). Root 1 (R1) and fibrous root (FR) are also seen. Figs 21–22. Longitudinal and transverse sections of sheet-like microtubules of root 1 (R1) with electron-dense plate (arrow heads) associated with left basal body (L). Fig. 23. Transverse section of the haptonema containing ringlike endoplasmic reticulum and seven microtubules.
The proximal side of the sheet is connected to the left basal body (Figs 20, 21, 22). A thin electron-dense structure similar to that in *Pleurochrysis* sp. (Inouye & Pienaar, 1984) is present in *S. pulchra* and lies next to the microtubular sheet on the side facing the left basal body (Figs 21, 22). Root 1 of *S. pulchra* is not a compound root, that is, it lacks the secondary microtubular bundle which has been found in root 1 of some coccolithophorids. Root 2 consists of four stranded microtubules like *Pleurochrysis* sp. and *U. sibogae* var. *foliosa* and arises in the space between the two basal bodies and extends to the haptonema (Figs 26, 27). In contrast to other coccolithophorids, there is no secondary microtubular bundle associated with root 2. Root 3 is associated with the right basal body (Fig. 29). Immediately near the right basal body this root is seen as two pairs of microtubules situated on opposite sides of the basal body (one pair is seen in Fig. 28) each of which increase in number from two to four some distance away (Fig. 29). These two sets of microtubules extend for a short distance to the left basal body and then bend clockwise if viewed from above the basal body apparatus (Fig. 25). Finally a conspicuous fibrous root is observed associated with the right basal body (Fig. 19). This root extends along root 3 (Figs 20, 26, 29) and several microtubules of unknown origin are associated with it.

**DISCUSSION**

The present investigation provides new observations on the external morphology and ultrastructure of a widely distributed but inadequately studied coccolithophorid *S. pulchra*. The cell covering of *S. pulchra* is characterized by organic scales and a double-layered coccolith case. The latter is
such an unusual characteristic among the coccolithophorids that it has been adopted as a major generic criterion (Gaarder & Heimdal, 1977). Our observations on cultured cells have confirmed that this character is very stable. We are also of the opinion that the shape and arrangement of the calcium carbonate elements making up the coccolith rim is of taxonomic significance. This was mentioned by Manton, Sutherland & Oates (1977) when they studied the peculiar coccolithophorid, Wigwamma. In S. pulchra, distinctive alternating elements make up the rim of the proximal coccolith. It is interesting that the rim of the distal coccolith shows basically the same structure as the proximal coccolith, despite the differences in the gross morphology of these coccoliths. Gaarder & Heimdal (1977), in their revision of the genus Syracosphaera, showed that the proximal coccoliths of Syracosphaera histricha Kamptner and S. pirus Halldal et Markali have a similar structure to that of S. pulchra, and that the structure of the distal coccolith of these two species is basically the same as that of S. pulchra. We agree with their observations. Further detailed investigations of other representatives of the genus Syracosphaera could prove the substructure of the coccolith to be another useful taxonomic criterion for distinguishing the genus Syracosphaera.

Another aspect of S. pulchra which needs to be thoroughly investigated is the production of the two types of coccoliths. Manton & Leedale (1969) proposed that the coccolith is an organic scale with a calcified rim. This hypothesis is supported by the proximal coccolith of S. pulchra which has an organic base plate. Calcification of this coccolith occurs on the associated organic base plate within a Golgi vesicle (Fig. 18). The distal coccolith, on the other hand, has no organic base plate and for this reason does not comply with Manton's and Leedale's theory. This coccolith is produced in a vesicle without any evidence of an organic base plate being present (Fig. 17). These observations suggest that the organic base plate scale and the coccoliths are produced independently, i.e. the calcified rim can be produced without the organic base plate. We feel that cells possessing coccoliths with associated base-plate scales are more primitive than those that do not possess base-plate scales because, within the Prymnesiophyceae, the uncalcified organic scales are much more widely distributed than coccoliths.

The cell structure of S. pulchra is not unlike other members of the coccolithophorids and the Prymnesiales. For this reason only the structure of the haptonema and the flagella apparatus are discussed. The ultrastructure of the haptonema is not well-studied in the coccolithophorids, although the number of microtubules organized in the emergent part and base of the haptonema is known in several species. The haptonema base is probably comprised of three microtubules in Hymenomonas lacuna Pienaar (Pienaar, 1976), four in Pleurochrysis carterae (Braarud) Gayral et Fresnel of Von Stosch's isolate (Leadbeater, 1970) five in Ochrosphaera neapolitana Schussnig (Gayral & Fresnel-Morange, 1971) and Jomonolithus littoralis (Inouye & Chihara, 1983), and eight in Calyptrosphaera sphaeroidea Schiller (Klaveness, 1973), H. globosa (Magne) Gayral et Fresnel (Gayral & Fresnel, 1976) and Pleurochrysis sp. (Inouye & Pienaar, 1984). The emergent part of the haptonema, on the other hand, contains six microtubules in the motile phase of Coccolithus pelagicus (Manton & Leedale, 1963) and Calyptrosphaera sphaeroidea (Klaveness, 1973). It is interesting that the number of microtubules in the haptonema is variable in different taxa of coccolithophorids, while in many taxa of the Prymnesiales it is comprised mainly of seven in the emergent part and eight in the base. In some species it eventually increases to nine at the extreme proximal end (Manton, 1964, 1967, 1968; Leadbeater & Manton, 1969). The haptonema of S. pulchra consists of seven microtubules in the emergent part and eight at the base, thus resembling that of Prymnesium and Chrysochromulina species.
rather than the coccolithophorids mentioned above. Many coccolithophorids have a vestigial or reduced haptonema with regard to length and/or number of microtubules. *Syracosphaera pulchra* is the only known coccolithophorid possessing a haptonema of the more common type. This fact suggests a close affinity between *S. pulchra* and representatives of the Prymnesiales. This is further supported by the similarity in the structure of the flagellar apparatus of *S. pulchra* and members of the Prymnesiales (see below).

To date, few representatives of the Prymnesiophyceae have been investigated with respect to the detailed ultrastructure of the flagellar apparatus. These include *Diacronema vlkianum* Prauser (Green & Hibberd, 1977), *Pavlova pinguis* Green (Green, 1980), *Pleurochrysis* sp. (Inouye & Pienaar, 1985), *Umbilicosphaera sibogae* var. *foliosa* (Inouye & Pienaar, 1984) and *Jomonlithus littoralis* (Inouye & Chihara, 1983). The former two are members of the Pavlovales and the latter three are coccolithophorids. The flagellar apparatuses of these two groups are distinct and their possible homology has been previously discussed (Inouye & Pienaar, 1985). In this paper *S. pulchra* is compared with the latter three species, and with other representatives of the coccolithophorids and the Prymnesiales where information on the flagellar apparatus is available.

Although the flagellar apparatus of *S. pulchra* is similar to that of *Pleurochrysis* sp. and *U. sibogae* var. *foliosa*, *S. pulchra* has an electron dense core in the basal body lumen that has not been reported in any other coccolithophorids. The Prymnesiales, however, possess a similar although less compact core in their basal bodies. *Prymnesium parvum* Carter (Manton, 1964, Figs 12, 19), *Chrysochromulina chiton* Parke et Manton (Manton, 1968, Figs 12, 18), *Platychrysis pienaarrii* Gayral et Fresnel and *Phaeocystis pouchetii* (unpubl. obs.) are species in which an electron-dense core in the basal body has been observed. Although its chemical nature and function are unknown, this electron-dense core may prove to be of taxonomic and/or phylogenetic significance. Its frequent occurrence in the Prymnesiales, and apparent absence in the coccolithophorids (with the exception of *S. pulchra*), may serve as a useful character to distinguish between these two orders.

Another interesting feature of the flagellar apparatus of *S. pulchra* when compared with other coccolithophorids is the complete absence of a secondary bundle of microtubules in roots 1 and 2. In previous papers we have shown that *Pleurochrysis* sp., *U. sibogae* var. *foliosa* and *J. littoralis* have a flagellar apparatus of a similar type which shares one common character; viz. two of three microtubular roots, roots 1 and 2, are of the compound type (Inouye & Pienaar, 1984, 1985; Inouye & Chihara, 1983). The compound flagellar root has been observed in many other coccolithophorids even though the detailed structure of their flagellar apparatus is presently unknown (for references, see Inouye & Pienaar, 1985). These observations suggest that the secondary bundle of microtubules is common to most of the coccolithophorids and, because of the absence of these bundles in roots 1 and 2 of *S. pulchra*, it seems that *S. pulchra* is a very unusual coccolithophorid with regard to the structure of its flagellar roots. Once again it should be noted that *S. pulchra* resembles members of the Prymnesiales in this respect. To date, no detailed study of the flagellar apparatus of the Prymnesiales has been made. However, some photographs of *P. parvum* given by Manton (1964, 1966) provide sufficient information to enable us to reconstruct its flagellar apparatus. The basal bodies and haptonema of *P. parvum* are arranged in the same way as in *Pleurochrysis, Umbilicosphaera, Jomonlithus* and *Syracosphaera* (See figs 11, 19, 23 in Manton 1964 and figs 7, 8 in Manton 1966). The microtubular flagellar roots are of three types corresponding to the roots 1, 2 and 3 of the above mentioned coccolithophorids (see figs 7, 8, in Manton, 1966). No secondary
bundle is detectable in any published photographs of members of the Prymnesiales. Recently Gayral & Fresnel (1983) showed that P. pienaarii possesses a bundle-like microtubular root similar to the compound roots of Pleurochrysis and other coccolithophorids. However, from our unpublished observations this root appears to be associated with the right basal body, and we believe that this root is not homologous with the compound roots of the coccolithophorids but is probably an uncommon type of root 3.

In summary, this investigation has shown that S. pulchra bears a closer resemblance to the members of the Prymnesiales than to many of the coccolithophorids. These conclusions are based on features of the haptonema, the presence of a dense core in the basal body lumen and the absence of secondary microtubular bundles in roots 1 and 2. The two types of coccoliths—one with an organic base plate and one without—make S. pulchra a unique coccolithophorid, and the method of production of these coccoliths is of particular interest. This aspect of S. pulchra requires further research and we hope to investigate it in the near future.

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