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Possible Functional Interpretations of Coccolith Morphology

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With 2 Figures

Haptophyta
Coccoliths
Paleobiology
Functional morphology

Contents

Zusammenfassung

Die funktionelle Bedeutung der Coccolithen ist bis zum heutigen Tage noch nicht klar; jedoch weist die Fachliteratur, die sich mit lebendem und ausgestorbenem Nannoplankton sowie mit der Biologie der Haptophyten befaßt, einige Interpretationen auf. Wenn man den Literaturquellen glauben darf, so ist eine protektive Funktion am wahrscheinlichsten, insbesondere, was die Homologie mit organischen Schuppen angeht. Die überzeugendste Erklärung gibt es für die Form der einfachsten Coccolithen. Die weiterentwickelten Coccolithen reflektieren wahrscheinlich eine zweite Angleichung bezüglich zusätzlicher Funktionen, insbesondere die Angleichung an Flotation und die Wechselwirkung mit dem das Lebewesen umgebenden Wasser.

Abstract

The functional significance of coccoliths is not clearly established, however, a review of the literature on living and fossil nannoplankton, and on the biology of haptophytes suggests several possibilities. Of these a protective function seems most likely in view of their homology with organic scales, and provides the most convincing explanation for the form of simple coccoliths. More specialised coccolith forms probably reflect secondary adaptation for additional functions, notably regulation of flotation, and of interaction with the surrounding water.

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1. Introduction

Since coccoliths were first observed, by EHRENBERG in 1832, a very considerable literature has accumulated on them. There has, however, been little published on their possible functional significance, other than scattered marginal discussions. I have attempted here to draw together the various ideas and relevant evidence, to show what is known, and what we can reasonably infer. Additionally I have made some rather flimsily founded, but hopefully not unreasonable, speculations of my own. I do not expect this to be a lasting statement on the subject but I rather hope it may promote more work in this area, which I believe is not only intellectually satisfying for nannofossil workers, but also of potential importance for taxonomic and palaeoecological work.

There are three principle bodies of information on calcareous nannoplankton. The largest of these is nannopalaeontology, which is useful for indicating phylogenetic relationships, ancestral morphotypes, range of variation, homoeomorphic forms and so on. PERCH-NIELSEN (1985a,b) provides an invaluable synthesis, BLACK (1968) some important thoughts.

Work on living nannoplankton is the best source of data on morphology, particularly since the form of coccospheres, as well as of their constituent coccoliths is

visible. There are no real syntheses of this work but many major beautifully illustrated papers are available: for instance LOHMANN (1902), OKADA & MCINTYRE (1977), WINTER et al. (1978), NISHIDA (1979), HEIMDAL & GAARDER (1980, 1981).

In addition to this work on the distribution and taxonomy of living and fossil nannoplankton, biologists have, more or less independantly, done much work on coccolithophores and related uncalcified haptophytes. MANTON, PARKE and other phycologists have used light microscopy and the TEM to observe their behaviour, life cycles, cytology and physiology. This work is reviewed in BONEY (1970) and TAPPAN (1980). Also the group has proved valuable for experimental research into the controls, processes, and chemistry of biosynthesis. Useful reviews are given in PAASCHE (1968), and in KLAVENESS & PAASCHE (1979). This biological work has not been directly concerned with function, and it has concentrated on the few species easy to culture – *Coccolithus pelagicus, Emiliania huxleyi, Pleurochrysis carterae* [syns. *Syracosphaera carterae, Hymenomonas carterae, Cricosphaera carterae*, (not *Helicosphaera carteri*!)], and the uncalcified genus *Chrysochromulina*. Nonetheless it has provided pertinent information and concepts, particularly on the relationship of coccoliths to the other cell components.

Finally comparisons with other groups, particularly dinoflagellates and diatoms can provide invaluable extra perspectives. The literature here is vast, useful synthetic works include DODGE (1973) and MORRIS (Ed., 1980).

2. Basic Function of Simple Coccoliths

Coccolithophores are highly successful members of the marine phytoplankton, possibly contributing over fifty percent of total primary production (RAYMONT, 1980). Also they predominate over the closely related uncalcified haptophytes in virtually all environments. These strongly suggest that coccoliths do have a valuable function. Previous speculations, although scattered, have probably covered all the likely primary functions of coccoliths , and so it is convenient to start by reviewing them.

2.1. Previous Theories

– General protection
The concept that coccoliths might act as a protective shell does not seem to have been developed in detail. Many authors have however implicitly assumed such a function, or mentioned it as a possibility (e. g. DIXON, 1900, TAPPAN, 1980).

– Light diffusing
This was first proposed as a possible function by BRAARUD et al. (1952). They suggested that coccoliths would reflect and diffuse light. In low latitudes this could enable coccolithophores to live higher in the water column than other phytoplankton, and so could explain their great abundance at these latitudes.
This theory is no longer generally tenable since coccolithophores are now known to occur at depths and latitudes with very low light levels.

– Light concentrating
GARTNER & BUKRY (1969) argued that as the refractive index of water is lower than that of calcite, light should be diffracted into the protoplast. This could enhance photosynthesis, and be useful at any depths and latitudes.
The theory may be viable, althought the light gains might be cancelled out by losses through reflection. However, apart perhaps from placoliths, there is no clear adaptation of coccolith form, or crystallography, toward this function. Nor is there support from coccolithophore distribution.

– Buoyancy control
Staying within the photic zone is obviously vital for all phytoplankton. Also within it there are strong gradients in nutrient content, temperature, light etc. Modern studies (HUTCHINSON, 1967; SMAYDA, 1970; WALSBY & REYNOLDS, 1980) suggest that the vertical distribution of phytoplankton is controlled by turbulence, differential reproduction rates, and sinking. Moreover, motion relative to the surrounding water is thought to be important to avoid the production of a nutrient depleted zone around the cell. Thus a slight positive buoyancy is thought to be adaptive.
HONJO (1976) applied this work to coccoliths and suggested that they were used as ballast for the cell. He also proposed that coccolithophores might be able to actively control their density by shedding excess coccoliths. A ballasting function had also earlier been suggested for heavy coccoliths, by HAY (1968).

– Non functional / produced as a by-product of photosynthesis
PAASCHE (1962) demonstrated experimentally that a very close relationship exists between photosynthesis levels and coccolith formation in *E. huxleyi*. The extreme view from this would be that calcification occurs solely in order to act as a sink for the hydroxyl ions produced during photosynthesis. The form of coccoliths being simply the most convenient available, occurring by the deposition of calcite on organic scales. As summarised in the equations below photosynthesis produces hydroxyl ions (OH^-) as a result of converting bicarbonate ions (HCO_3^-) to carbon dioxide, and calcification requires hydroxyl ions to produce carbonate (CO_3^{2-}) from bicarbonate ions:

Photosynthesis: $HCO_3^- \rightarrow CO_2 + OH^-$

Calcification: $HCO_3^- + OH^- \rightarrow CO_3^{2-} + H_2O$

Subsequent investigations (reviewed in KLAVENESS & PAASCHE, 1979) have shown that coccolithogenesis is light-dependent, but they have not supported a simple relationship to photosynthesis. For instance coccolith formation can continue under conditions which prevent photosynthesis. Also, of course, many haptophytes do not produce coccoliths, and isolated strains of coccolith producing species tend to lose this ability to produce coccoliths (e. g. PAASCHE & KLAVENESS, 1970).
These observations suggest that other mechanisms must exist for neutralising the hydroxyl ions. Moreover the form of coccoliths is much more complex than a non-functional origin would suggest, and their morphology is not closely controlled by the underlying scales. So this suggestion does not seem reasonable.

– An unidentified function
In the absence of a single clearly accepted function there has been the possibility that coccoliths perform a different function, related to some other aspect of the protist's physiology.
As discussed relative to the previous suggestion, *and in more detail below, there is much evidence* that coccoliths are optional components of haptophytes. This tends to eliminate functions which postulate an intimate interaction between coccoliths and other parts of the cell, and so limits the potential for unidentified functions.

Summary

Of these functions only two seem viable and widely applicable, and so likely as a basic function of coccoliths: flotation control and protections. Of them I favour protection on fairly strong, though circumstantial, evidence from coccolith morphology and from their relationship to the other parts of coccolithophores, as discussed below.

2.2. Biological Evidence for a Protective Function

As shown in Figure 1 coccoliths are only one component of a complex cell wall. The innermost component is the bounding membrane of the protoplast – the plasmalemma. By analogy with other plant groups this should be a semi-permeable membrane, with the principal function of regulating the passage of materials into and out of the cell. Above the plasmalemma is the columnar layer – *which is of rather uncertain character.* Between these and the coccoliths there is typically a layer of organic scales which although unmineralised are composed of resistant polysaccharides, including cellulose. Finally there is the outer layer or layers of coccoliths which themselves typically have organic baseplates similar to the organic scales below, and are surrounded by a more amorphous organic matrix.

This is the general structure, and is typical of most coccolithophores examined in detail, notably *Coccolithus pelagicus* and *Pleurochrysis carterae*. Baseplates have also been observed below the coccoliths of many other genera, for instance, *Helicosphaera* and *Umbilicosphaera* by GAARDER (1970), and *Syracosphaera, Rhabdosphaera* and *Calyptrosphaera* by LEADBEATER & MORTON (1974).

Considerable variations do, however, occur. In *Emiliana huxleyi* the organic scales, and baseplates, are missing. Most non-calcifying haptophytes, such as *Chrysochromulina*, are similar but without the coccoliths.

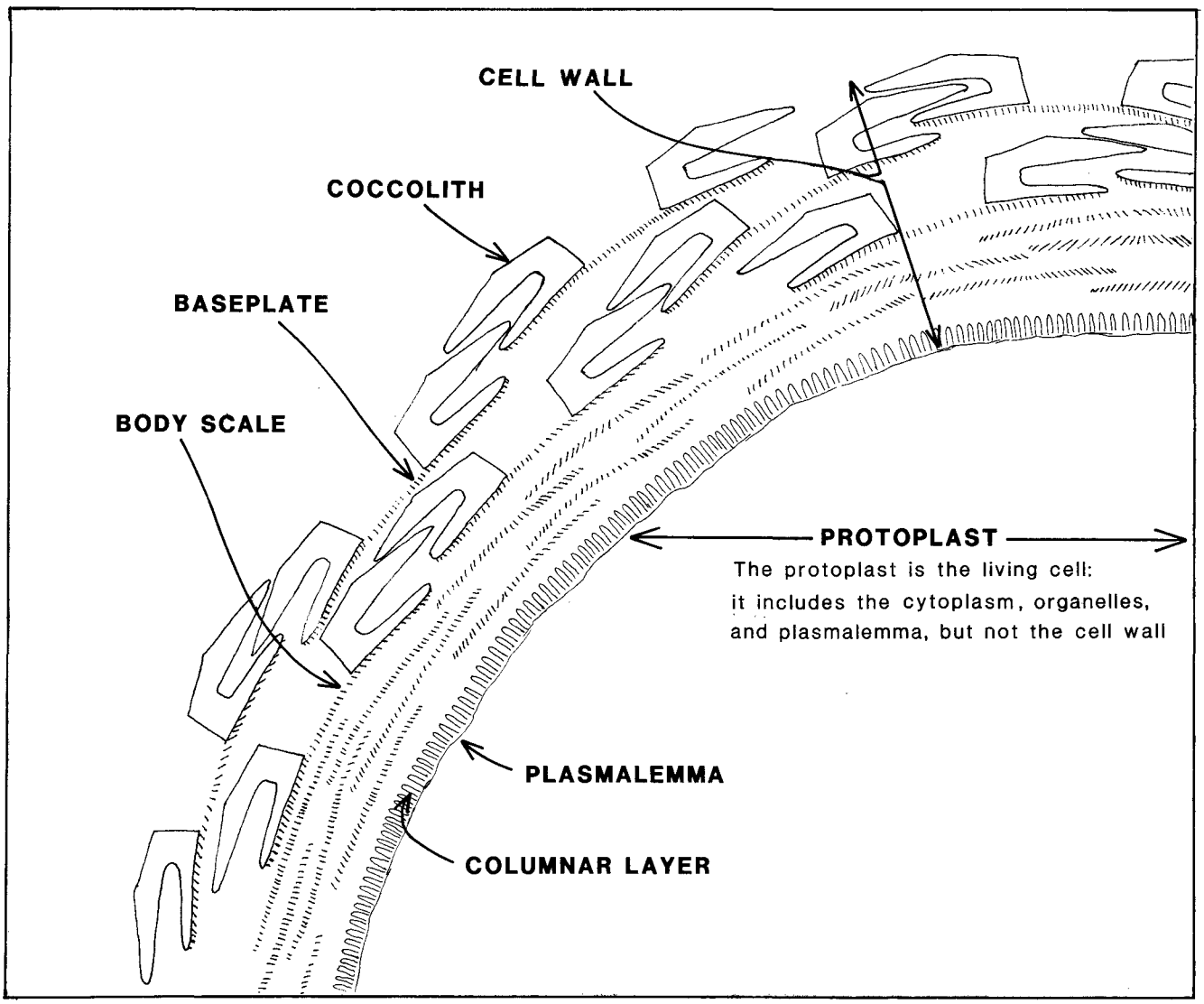


Fig. 1: Schematic cross-section of the wall of a typical coccolithoporid. Based on published TEM micrographs (e. g. in MANTON & LEEDALE, 1969).

Isolated strains of coccolithophores frequently produce cells without coccoliths. In the motile phase of *C. pelagicus (Crystalolithus hyalinus)* the cell wall sequence (columnar layer, scales, coccoliths) can be repeated several times and there is an enclosing outer cell membrane (MANTON & LEEDALE, 1963).

On the basis of these observations it would seem likely that coccospheres are not independant organelles, but rather are optional components of the cell walls. Their relationship to the organic scales is particularly significant. Various observations and lines of research have suggested that the two are analogous and interchangeable, as discussed below.

Firstly work on the morphology of organic scale bearing haptophytes by MANTON and her co-workers has revealed striking cases of homoeomorphy between organic scales and calcareous coccoliths. For instance *Chrysochromulina pringsheimi* PARKE & MANTON 1962 produces four different varieties of scales. It has an inner layer of relatively simple scales, and an outer layer of scales with rims, and spines supported by four struts – strongly reminiscent of the spines of *Eiffellithus*. It also has plates at each end with greatly elongated spines producing an overall form very much like *Acanthoica quatrispina* (Fig. 2/F).

Secondly work on the process of biomineralisation in coccolithophores by MANTON & LEEDALE (1969), OUTKA & WILLIAMS (1971), and others, reviewed in KLAVENESS & PAASCHE (1979), has shown that coccoliths and organic scales are products of the same biosynthetic process. This seems to start with the information of golgi vesicles near the nucleus of the cell. As these migrate through the golgi body toward the outside of the cell successive biosynthetic events occur: beginning with the formation of the first components of the organic scales, proceeding through coccolith formation, and ending with extrusion of the plates, omission or enhancement of particular stages can produce a wide variety of plate types. In terms of degree of calcification these can range from simple organic scales only to coccoliths without baseplates (as in *E. huxleyi*).

Thirdly there have been some observations of weakly calcified plates that appear to be intermediate between coccoliths and organic scales. In particular MANTON et al. (1977) described from the Antarctic various haptophyte species which had complex organic plates with rims and spines which frequently, but not always, were also weakly calcified. This is quite a different case to the usual one, where although the calcareous coccolith occurs on an organic baseplate it has a form and structure almost completely independant of that of the baseplate.

Discussion

It should be clear from these observations that coccoliths and organic scales are closely related in both form and origin. It follows from this that haptophytes without coccoliths are not naked. Indeed MANTON & LEEDALE (1969) went so far as to suggest that calcification might simply "be regarded as a biochemical complication".

This strongly suggests that the organic scales and coccoliths of haptophytes perform the same basic function, although the greater success of coccolithophores would suggest that coccoliths perform this function better. In turn this makes any functions that depend essentially on the properties of calcite unlikely, specifically this makes light concentration and buoyancy regulation less likely.

This argument can be extended by comparisons with the other phytoplankton groups. Of these according to DODGE (1973) only one group, the Chloromonadophyceae, usually have naked cells. All the others have more or less elaborate wall structures, for instance thecae in dinoflagellates, frustules in diatoms, organic scales in prasinophytes, and siliceous scales or spicules in chrysophytes (including the silicoflagellates). The near universality of cell wall reinforcing strongly suggests that it has a common and significant function. Protection would seem obvious.

Two separate protective functions are likely. First support for and protection of the plasmalemma. This must be a delicate membrane since the flagella, ingested food particles, and of course scales, are able to pass through it. Second inhibition of predation. The main cropping of phytoplankton is by small zooplankton (planktonic forams, radiolaria, mollusc veligers, copepods and other crustacea). Most of these have feeding systems capable of selective predation. There is considerable evidence from laboratory experiments that selective predation occurs, and from marine biology that zooplankton can strongly influence phytoplankton abundance and species composition (FROST, 1980; SMAYDA, 1980). Hence protective structures should be strongly adaptive.

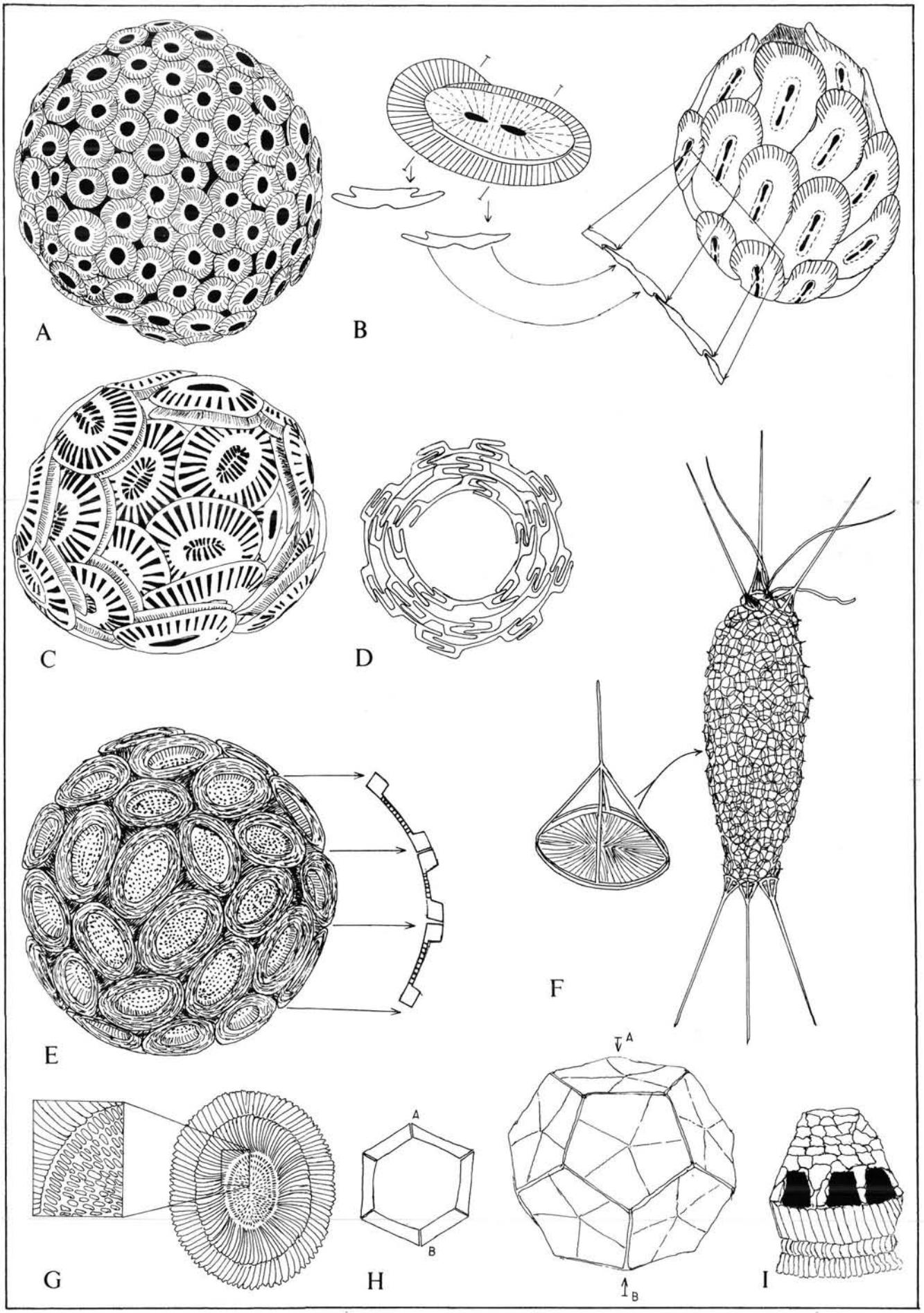
2.3. Simple Coccoliths as Protective Plates

By simple coccoliths I mean those coccoliths which have a more or less disc shaped overall morphology. This includes species with widely varying central structures and several rim types. The majority of them, however, are of one of two basic types – discoliths (sensu lato), and placoliths. The general form of coccoliths such as these seems readily explicable in terms of a protective function, as suggested above. The morphological differences between them doubtless in part reflect differing evolutionary histories, but also may in part reflect differing adaptive morphologies. Four cases are discussed below.

– Discoliths (s. l.)

  A wide variety of coccoliths can be characterised as having a well developed, more or less vertical, rim and a variably filled central area. Typically they occur as a single non-imbricate layer (Fig. 2/E).

Fig. 2: Sketches of various discussed species. Based on micrographs in NISHIDA (1979), PARKE & MANTON (1962), PERCH-NIELSEN (1971). Aproximate maximum dimensions in parentheses.
A = *Umbilicosphaera sibogae*, coccosphere (37 µm); B = *Helicosphaera carteri*, coccosphere (16 µm), proximal view of a coccolith, and interpretative cross-sections; C = *Emiliania huxleyi*, coccosphere (11 µm); D = *Emiliania huxleyi*, schematic cross-section of a coccosphere; E = *Pontosphaera discopora*, coccosphere (47 µm), and schematic cross-section of part of it; F = *Chrysochromulina pringsheimi*, entire cell, with flagella and haptonema (40 µm), and one scale (2 µm); G = *Reticulofenestra umbilica*, coccolith (14 µm), and detail of central area (2.5 µm); H = *Braarudosphaera bigelowi*, braarudosphaere, and schematic cross-section of it (15 µm); I = *Naninfula deflandrei*, side view of coccolith.



Complications are most common around the flagella where, as with organic scales, specialised plates are often developed.

These are usually given a variety of names, cricoliths, syracoliths, discoliths etc, but in terms of basic function it seems worth treating them as a single group. They are the simpler of the two main morphologies, and most closely related to their underlying organic scales. Also they can probably be regarded as the primitive coccolith type since the first known (Late Triassic) coccoliths are discoliths (BOWN, 1985), placoliths do not appear till considerably later (PRINS, 1969; BOWN, this vol.). Hence discolith morphology should reflect the basic function of coccoliths. This is of interest since their form does not seem adapted either for light concentration or for ballasting. It can, however, perhaps be interpreted as an economical means of giving protection. Concentration of calcification in the rim is an efficient way of strengthening the disc as a whole, and formation of a single layer of coccoliths provides a complete test with the minimum number of coccoliths.

- *Umbilicosphaera sibogae*

  U. sibogae and similar forms represent one extreme of placolith morphology, with a thin coccosphere formed of a single layer of placoliths (Fig. 2/A). In these the calcification continues to reinforce the scales but in addition the placolith form allows adjacent coccoliths to overlap thus giving the coccosphere as a whole additional strength and rigidity. The thinness of the coccolith layer makes it unlikely that it could have the alternative functions of light concentration or buoyancy control.

- *Emiliania huxleyi*

  In this and many other common species the placoliths are massive relative the protoplast and frequently occur in many layers (Figs. 2/C, D). The protective function seems more obvious for these than any other species.

  The form is also, however, one which can be related to other suggested functions. Thus the thickness of the coccosphere relative to the protoplast means that light could be concentrated from a usefully large area, whilst the lens like form of placoliths looks suited to such a function. Buoyancy control is rather likely as the mass of the coccoliths must significantly alter the cell's overall density. Also control of density by coccolith shedding may occur (HONJO, 1976).

  So for these species coccoliths have several possible functions. For the reasons discussed above I see the raison d'être of these placoliths as protection, however, it would hardly be surprinsing if they had accreted secondary functions. Conceivably thus the phenomenal evolutionary success of such coccoliths – they dominate most assemblages from the Toarcian to the Recent – is due to their being adapted to a range of functions.

- *Helicosphaera*

  The numerous species of *Helicosphaera* form a monogeneric group, distinguished by their unusual coccolith type. The structure and morphology of them has been studied and discussed by various authors, notably KAMPTNER (1954), BLACK & BARNES (1961), CLOCCHIATTI (1969), and THEODORIDIS (1984). This work has shown that they have a form analogous to, but distincly different from, that of normal placoliths. Whereas normal placoliths have two clearly separated shield, giving rise to a continuous double margin, helicoliths are more complex with a helical structure giving rise to a double margin on one side but a single margin along most of the other side. SEMs of coccospheres (e. g. in BORSETTI & CATI, 1972, or NISHIDA, 1979) show that this asymmetric form allows a regular and close interlocking of the coccoliths, the single edge of one coccolith tucking into the double edge of the next one (Fig. 2/B). The prominent wing-like expansion of *H. carteri* and many other species assists this interlocking. However the wing is not present in Palaeogene species and is probably a readily evolved addition to the structure rather than an essential part of it.

  Helicoliths seem likely to have the same function as the placoliths just discussed, forming a strong single layered test. The form thus represents an alternative solution to the same end. It is also noteworthy that *Helicosphaera* coccospheres are usually elongated and have an opening at one end, this is probably a flagellar opening, as shown by LOHMANN (1902). In at least some specimens the wings of the surrounding helicoliths are expanded somewhat. These may be analogous to the specialised circum-flagella coccoliths of *Syracosphaera* and other genera.

3. Additional Homoeomorphic structures

Introduction

The discussion so far has been essentially an attempt at explaining the basic, discoidal morphology of what I have termed simple coccoliths. There are, however, other features of some simple coccoliths which seem to require functional explanations, and also other coccoliths with more complex forms. The diversity and complexity of some such structures does not make them easy to interpret, which is probably one of the main reasons why there has been little work done on the functional morphology of coccoliths.

The approach I tried to adopt was to look for structures or forms which recur independantly in different groups. Such homoeomorphic features are likely to have an adaptive significance. The cases which I discuss below are all rather obvious, but they do encompass a considerable amount of total coccolith variation. The possible functions which I give are inevitably vague and unsubstantiated, detailed experimental research would probably be necessary to provide any firm theories.

3.1. Perforations

The most striking feature of coccoliths which cannot be explained in terms of the functions discussed so far is that they are virtually all perforate. This seems to be the general case for coccoliths throughout the geological record, they nearly all have open central areas, or pores in the central plate. In many cases this seems to have involved considerable architectural effort, examples include the elaborately formed pores of *Pontosphaera* spp., subdived pores in some arkhangelskiellids (see e. g. BUKRY, 1969; HATTNER & WISE, 1977), and the

central grids of *Cribrosphaera* and particularly *Reticulofenestra* (Fig. 2/G). Interestingly, very similar grids to those of *Reticulofenestra* are also known from a few unrelated species, notably *Chiasmolithus grandis* (see PERCH-NIELSEN, 1971) and *Helicosphaera seminulum* (see GARTNER & SMITH, 1967). Interestingly, in *Umbilicosphaera* similar grids seem to be formed by the organic baseplate (see GAARDER, 1970). The near ubiquity of perforations and the frequency with which they are finely regulated in size suggests that they must have some function. I suspect that this is more likely to be related to the protist's physiology than to a physical cause of the types cited above. A similar problem seems to exist as to the function of pores on diatom frustules.

The most unambiguous exception to this rule is *Braarudosphaera bigelowi* which has a completely imperforate test (Fig. 2/H). This species, however, also has an unusual microstructure and test construction (it always has just twelve plates), and its ecological and geological distribution is aberrant. It is probably not closely related to other coccoliths, and may not be a haptophyte at all.

3.2. Spines

Spines, unlike perforations, are by no means universal. They do, however, occur in many species of coccolithophores, and of uncalcified haptophytes. Although in many families spines are characteristically either present or absent, in other families spines are present in some genera and species only. This is the case in, for instance, the Stephanolithaceae, Calciosolenaceae, Syracosphaeraceae and Biscutaceae. The Arkhangelskiellaceae are an interesting case since absence of spines was thought to be a characteristic of the group until a single spine bearing species, *Thiersteinia ecclesiastica*, was described by WISE (1983). So it seems clear that spinosity is a feature of low taxonomic significance which has recurred homoeomorphically in many groups. In terms of coccolithogenesis this is rather curious since spines are often long and complex structures whose formation might be expected to require significant modification of the coccolith production process. The functional inference is, however, clearly that they do have a useful role.

Various functions are conceivable. Spines might act defensively by a simple "porcupine" effect as in many other spine bearing organisms, or possibly by increasing the test diameter they cause the coccolithophores to be rejected by specific filter feeding predators. Alternatively they may have a flotation related function; in species where spines only occur on certain parts of the test they could act as orientators. In others, where they occur over the entire test, they may effectively increase the diameter and thus lower the density of the organism. This seems most attractive for species in which the spines are thin and have flaring ends, notably many late Cretaceous Podorhabdaceae.

In the absence of culture studies there exists, however, at least for *Rhabdosphaera clavigera* the quite different possibility that the spines are parts of resting cysts developed inside larger cells, in a manner analogous to that of hystrichosphaerid dinoflagellates. This seems a real possibility for *R. clavigera* since its spines seem too long to have developed within the cell they enclose, and since its basal plates are imperforate. Also the obvservations of NORRIS (1965, 1971) indicate that *Ceratolithus cristatus* develops in this manner. A phase with a large coccosphere of delicate hoop-like coccoliths being followed by one with a smaller cell. This is enveloped by a single ceratolith, which initially developed within the larger coccosphere.

3.3. Asymmetric Coccospheres

Coccospheres are predominantly spherical, presumably because this is the simplest and strongest form to adopt. However, a number of living coccospheres, particularly some syracosphaerids have elaborately formed tests of different shapes.

These include discoidal (*Scyphosphaera*), tear-drop to ellipsoidal (many syracospherids, *Helicosphaera spp., C. pringsheimi* (Figs. 2/B, F, J) and tube-like coccospheres (*Syracosphaera prolongata*). All these morphologies are also commonly shown by diatoms and dinoflagellates, where they are generally interpreted as being related to flotation – in appropriate orentiations they will tend to lessen sinking rates. Interestingly such coccospheres seem always to be borne by motile phases. This is relevant since coccospheres, like dinoflagellates, but unlike many diatoms, are too small for sheer forces to orient them when sinking (HUTCHINSON, 1967). These motile forms may be able to utilise their asymmetry to vary sinking rates, and to minimise resistance to swimming. Many other motile coccolithophores are however symmetrically spherical, notably most holococcolith bearing species.

3.4. Basins, Domes and Exothecae

In addition to the predominant disc-shaped coccoliths (with or without spines) there occur throughout the geological record other more complex morphologies. These include:

- Bowl shapes, i. e. coccoliths with elevated rims and flattish bases. They include many stephanoliths, zygodiscids, and pontosphaerids.
- Domal coccoliths such as *Lapideacassis, Calciopappus*, and *Naninfula* (Fig. 2/1). These small rare coccoliths have very similar forms but quite different structures, and are unlikely to be related.
- Exothecae: Various coccolithophores have an outer layer or exotheca. In some genera this is formed by very strongly flaring umbrella like spines; a modern example is *Umbellosphaera*, a possible Jurassic homoeomorph is *Carinolithus superbus*. Various *Syracosphaera* species create the same effect by means of separate exothecal coccoliths.

These morphologies may possibly all have different functions, or permutations of functions. An alternative however suggested by MANTON (1985 oral comm.) is that they are all water-trapping adaptations. In these terms they can be thought of as producing a thickened wall zone in which trapped water is regulated, producing a buffer zone between the protoplast and the hydrosphere.

This putative function has similarities with my suggestions above for perforations and grilles. They both assume that interaction between the protoplast and the surrounding water is important and that

specialised coccoliths can help regulate these interactions. Interestingly the genera with complex forms do also tend to have more elaborate perforation systems.

4. Summary

None of the above suggestions are proven, and they do not provide a single elegant explanation of coccolith function. I feel there is, however, a reasonably strong case for the, non-radical, suggestion that the primary function of coccoliths is to enhance the protection provided by the other elements of the cell wall. The variability of coccoliths makes some secondary functions almost inevitable, of these flotation regulation seems much the most likely on theoretical grounds and can successfully explain certain features, notably the form of non-spherical coccospheres. Perhaps surprisingly, however, there also are features that defy explanations in terms of simple physical functions, particularly complex mesh structures and a variety of elaborate coccolith forms. A possible explanation is that they are adaptations for assisting in the regulation of seawater-protoplast interaction, and especially perhaps in nutrient uptake.

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