XENOSPHERES – ASSOCIATIONS OF COCCOLITHS RESEMBLING COCCOSPHERES

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Key words: xenospheres, coccospheres, nannoplankton, biology, taxonomy

Abstract: A set of images of xenospheres are presented. These are anomalous coccospheres bearing coccoliths of two or more coccolithophore species. Unlike combination coccospheres, these are almost certainly the products of *post mortem* processes. Possible mechanisms of formation are discussed, and comparative examples of unambiguous agglutination by tintinnids and foraminifera, and in pellets, are illustrated. The need for caution in interpreting putative combination coccospheres is highlighted.

Introduction

There have been occasional records of anomalous coccospheres bearing coccoliths of two or more apparently discrete species almost since the beginning of study of coccospheres (Lohmann, 1902; Kamptner, 1941; Lecal-Schlauder, 1961). These have attracted a range of speculations on possible causes but recently it has become clear that many examples record life-cycle transitions. Most of these life-cycle transitions record change between heterococcolith-bearing and holococcolith-bearing stages (Kleijne, 1991; Thomsen *et al*., 1991; Cros *et al*., 2000a; Geisen *et al*., submitted), whilst others combine heterococcoliths and nannoliths (Cros *et al*., 2000b; Sprengel & Young, 2000). These combination coccospheres are providing invaluable evidence of life-cycle associations and so valuable insights into the ecology, phylogeny and fine-scale taxonomy of coccolithophores. However, as Cros *et al.* (2000a) noted, there are other ways in which different coccoliths can end up on single coccosphere. So, careful assessment of each individual case is needed before an interpretation of a life-cycle association is accepted.

The phenomenon was discussed during the terminology workshop at the 1991 INA Conference in Prague, where the term ‘xenosphere’ was proposed (by Jackie Burnett) and consequently formally recommended in the terminology guide which eventually followed (Young *et al*., 1997). It was defined there in (p.877) as follows: “*Xenosphere* {new, from Greek *xenos*, stranger} - anomalous coccosphere containing coccoliths normally regarded as forming on quite discrete species (e.g. *Emiliania huxleyi* and *Gephyrocapsa oceanica*; Winter *et al*. 1979). N.B. These are very probably artefacts, the term is suggested specifically to suggest the abnormal nature of these structures.” This definition does not clearly exclude combination coccospheres, so xenospheres may be better redefined as “specimens resembling coccospheres but which include coccoliths of discrete species which are unlikely to have been produced as a result of a life-cycle change or hybridisation event”. By contrast, true coccospheres may be defined as “an association of coccoliths produced by a single coccolithophore cell, or inherited from the cells which gave rise to it”. This concept includes combination coccospheres.

Possible causes for xenospheres include: (1) *accidental incorporation* of loose coccoliths onto a genuine coccosphere. This might occur in the water-column if there are large numbers of loose coccoliths. It could also obviously occur during sample preparation, especially in high-density samples; (2) *agglutination* of coccoliths by a small protist. This can potentially occur either in the water-column (*e.g.* by tintinnids: Broerse, 2000; Winter *et al.*, 1986) or in the sediment (*e.g.* by agglutinating foraminifera: Murray, 1991; Widmark & Henriksson, 1995); (3) incorporation of coccoliths in *faecal pellets*. We illustrate here a few examples of xenospheres, both as curious anomalies which may yet provide information on certain processes, and as examples of the real need for caution. In addition, we illustrate a few tintinnids and faecal pellets and an agglutinating foraminifera for comparative purposes.

Examples

Emiliania huxleyi and *Gephyrocapsa oceanica*

Plate 1, Figures 1-2

This specimen was found in a plankton sample from the Alboran Sea, western Mediterranean. It consists of numerous specimens of *E. huxleyi* and a single specimen of *G. oceanica*. Although this looks at first glance like a regular coccosphere, two features support the interpretation of it as a xenosphere. Firstly, the *E. huxleyi* coccoliths show an anomalously wide range of variation in degree of calcification, size, and central-area structure. Secondly, the coccosphere also includes a piece of tubular debris which underlies one of the *E. huxleyi* coccoliths and extends between the shields of the *G. oceanica* coccolith. It is not possible to determine whether this is a coccosphere which has accumulated additional material, or a pseudo-coccosphere produced by some other organism, but it seems very unlikely to be a true coccosphere, *i.e.* a sphere of coccoliths produced by a single coccolithophore cell, or inherited from the cell which gave rise to it.

A few other spheres have been illustrated, including coccoliths of these two species (Clocchiatti, 1971; Winter *et al*., 1979). Since these are closely-related species, and since this association has been found a few times, a biological cause has been suggested. One suggested possibility was hybridisation. This can be categorically ruled out since hybridisation involves fusion of gametes, haploid-phase cells. Flow cytometry has shown that heterococcoliths are produced on the diploid phase of *E. huxleyi* (Green *et al*., 1996), whilst the haploid phase is non-calcifying. So, even though hybridisation between *G. oceanica* and *E. huxleyi* is conceivable, it would give rise to a cell containing organic scales characteristic of these two species, not heterococcoliths.

An alternative suggestion is that, since *E. huxleyi* has evolved relatively recently from *Gephyrocapsa* (*c*.250kyr ago: Thierstein *et al*., 1977), the genotype might somehow have retained the potential to produce coccoliths with the ancestral morphology. This type of phenomenon is known in dogs, pigeons, and other intensively-bred domesticated species. However, in those cases, time-scales are tens of years rather than hundreds of thousands of years, so this is biologically a rather bizarre suggestion. Moreover, although *E. huxleyi* has been cultured in numerous laboratories, and enormous numbers of coccoliths observed in LM, SEM and TEM, no examples of *Gephyrocapsa* coccolith-production have been recorded.

So, we do not think these examples are likely to be true coccospheres. We conclude that the most likely reason for the recurrence of this association is simply that *E. huxleyi* and *G. oceanica* are the two most common coccolithophores, and so are the most likely two species to co-occur as a result of artefact. They also often co-occur on, for instance, tintinnids.

Cribrocentrum reticulatum and *Coccolithus pelagicus*

Plate 1, Figure 3

This coccosphere was found in a Late Eocene DSDP sample from the Indian Ocean, studied in collaboration with Sivaramakrishnan Rabindranath. It resembles a normal coccosphere but contains heterococcoliths from different families, the Coccolithaceae and Noelaerhabdaceae, which are interpreted on both conventional stratophenetic grounds and from molecular genetic research as only distantly related (Perch-Nielsen, 1985; Young, 1998; Edvardsen *et al*., 2000; Fujiwara *et al*., 2001). There is some breakage of the coccoliths but no other obvious evidence to support an origin by accidental means. In particular, it is noticeable that the coccoliths imbricate tightly. No other specimens showing this association have been reported or were found in the sample, indeed no other coccospheres were found in the sample at all.

Obviously, it is not possible to come up with a definitive explanation of this xenosphere but one possibility is that it is the proloculus (first chamber) of an agglutinating foraminifera. Agglutination of coccoliths by foraminifera is not an especially common phenomenon but many examples have been documented (Wallich, 1877; Murray, 1991; Widmark & Henriksson, 1995). The coccosphere illustrated by Gard (1987) seems comparable, and a similar origin might be suggested for it.

Acanthoica quattrospina, Syracosphaera bannockii (in the holococcolithophorid phase of the life-cycle, or HOL), and ?*Calyptrolithophora gracillima*

Plate 1, Figures 4-6

This specimen was found in a plankton sample from off the Canary Islands. It consists of: (1) numerous heterococcoliths of *A. quattrospina*, including both coccoliths and apical, spine-bearing coccoliths; (2) numerous holococcoliths of *S. bannockii*. *NB* These coccoliths were previously assigned to the holococcolithophorid species, *Zygosphaera bannockii*, but following observation of several combination coccospheres with a previously undescribed *Syracosphaera* species, the combination *S. bannockii* has been proposed (Cros *et al*., 2000a); (3) a few specimens of another holococcolith (on the lower left part of the specimen). These coccoliths show hexagonal, perforate wall-structure and a flat top. They most closely resemble *C. gracillima* but might alternatively be *Calyptrolithophora papillifera*.

The specimen superficially resembles a holococcolith-heterococcolith combination coccosphere but there are several reasons for doubting this interpretation. Firstly, two discrete holococcolith types are included. Secondly, the heterococcoliths are rather irregularly arranged. In particular, three of the spine-bearing coccoliths are arranged with spines directed into the coccosphere. Thirdly, two discrete holococcolith types occur. Fourthly, the two main coccolith morphotypes involved are known to form other associations - *A. quattrospina* with a previously undescribed holococcolith, and *S. bannockii* HOL with a previously undescribed *Syracosphaera* species (Cros *et al*., 2000a). This set of anomalies leads us to conclude that this specimen should be regarded as a xenosphere rather than as a combination coccosphere. A possible explanation of the specimen is that it is a small faecal pellet.

Helicosphaera carteri and *Syracolithus dalmaticus*

Plate 1, Figure 7

This specimen was found in a plankton sample from the Gulf of Mexico. It was sampled by Vita Pariente and imaged by Claire Findlay. It consists predominantly of *H. carteri* heterococcoliths and *S. dalmaticus* holococcoliths. Since *H. carteri* has previously been shown to form unambiguous associations with *Syracolithus catilliferus* and *S. confusus* (Cros *et al*., 2000a; Geisen *et al*., submitted), it would not be surprising if it also formed associations with the very closely similar holococcolith, *S. dalmaticus*. However, there are several reasons for regarding this as an unconvincing combination coccosphere. Firstly, other coccoliths occur on this specimen, including an *E. huxleyi* heterococcolith, several *Calciosolenia* heterococcoliths, and one unidentifiable holococcolith. Secondly, diatom and other debris also occurs on the specimen. Thirdly, the *H. carteri* and *S. dalmaticus* coccoliths are not in direct contact but separated by debris. So, there are clearly at least two alternative interpretations of this specimen: either it is a combination coccosphere onto which a range of other material has fallen during sample collection, or that it is an entirely accidental agglomeration of heteromict material. Given this ambiguity, the specimen cannot be used as evidence of an association of *H. carteri* and *S. dalmaticus*.

Syracosphaera noroitica and *Helladosphaera cornifera*

Plate 1, Figure 8

This specimen was found in a plankton sample off the Canary Islands. It consists of about eight exothecal coccoliths of *S. noroitica* and ten or more holococcoliths of *H. cornifera*. No other coccoliths are definitely included in the specimen, although single *E. huxleyi* and *Discosphaera tubifera* coccoliths lie nearby. However, there are problems with accepting this as a combination coccosphere. Firstly, the *S. noroitica* coccoliths are all exothecal coccoliths whilst all definitive combination coccospheres of *Syracosphaera* include endothecal heterococcoliths. Secondly, both the *S. noroitica* heterococcoliths and the *H. cornifera* holococcoliths are chaotically arranged. Thirdly, although the two coccoliths types are closely associated on this specimen, they do overlap each other and are not interspersed.

It is conceivable that this specimen is a combination coccosphere but the alternative possibility, that it is an accidental association, is at least equally possible, hence in the absence of other evidence it cannot be used to infer a life-cycle association between these species.

Tintinnids

Plate 2, Figures 1-6

Tintinnids, marine protozoans with an external organic test (lorica) between 45 and 1000μm long, are able to agglutinate particles such as coccoliths onto their loricae. In addition to the examples given by Broerse (2000) and Winter *et al.* (1986), we picture here four clear (with parts of the tintinnid lorica visible in each case: Figures 1, 3-5) and one ambiguous (tintinnid lorica not visible, but size and shape comparable: Figure 2) examples of tintinnids covered with different heterococcoliths from different plankton samples.

Faecal pellets

Plate 2, Figures 7, 8

A small (Figure 7) and a medium-sized (Figure 8) faecal pellet are illustrated in Plate 2. The medium-sized pellet includes a diverse range of coccoliths, including, *Helicosphaera carteri* holococcoliths (‘*Syracolithus catilliferus*’), *Rhabdosphaera clavigera, Syracosphaera pirus, Umbellosphaera tenuis, Ceratolithus cristatus* planoliths (‘*Neosphaera coccolithomorpha*’) and *Discosphaera tubifera*. There is also a dinoflagellate and other debris. The range of material in the pellet makes it obvious that it is a *post mortem* association but it is noticeable that the preservation is very good - a small portion of this pellet could easily cause confusion. The smaller pellet illustrates this point even more clearly, consisting of a large group of *Helladosphaera spinosa* coccoliths, a single inverted *E. huxleyi* coccolith, and a range of unidentifiable debris.

Agglutinating foraminifera

Plate 3, Figures 4-6

This is a specimen of a textulariid foraminifera which has formed its test almost exclusively from *C. pelagicus* coccoliths. Note that the initial chambers are similar in size to coccospheres (compare coccosphere in Figures 1-3). An isolated first chamber (proloculus) would be very difficult to distinguish from a coccosphere, unless the aperture was visible, or it included a range of material.

This specimen is also of some historical interest, in that it is from a slide in the G.C. Wallich collection in the Natural History Museum. It was certainly one of the specimens he observed (the slide is labelled) and possibly one he illustrated (Wallich, 1861, 1877). As discussed in Siesser (1994), specimens of this type led Wallich into speculating that coccospheres were the larval stage of foraminifera.

Conclusions

The specimens illustrated here are all intriguing, and have indeed diverted us into interesting speculations. However, in each case the balance of evidence suggests that they are unlikely to be true coccospheres. This set of examples should serve as cautionary warnings as we seek to identify combination coccospheres.

Acknowledgements

These examples are drawn form research over an extended period in collaboration with numerous colleagues, including notably Lluïsa Cros (Inst. de Ciencias del Mar, Barcelona), Claire Findlay (whilst working at the NHM), Annelies Kleijne (Free Univ., Amsterdam), Vita Pariente (Texas A&M Univ.), and Sivaramakrishnan Rabindranath and Claudia Sprengel (Alfred Wegener Inst. for Polar & Marine Research). Research funding was provided by the EU (CODENET Project) and the UK’s Natural Environment Research Council. The two reviewers are also thanked.

References

Broerse, A. 2000. *Coccolithophore export production in selected ocean environments*. Faculty of Earth Sciences, Amsterdam: 185 pp.

Clocchiatti, M. 1971. Sur l’éxistence de coccosphères portant coccolithes de *Gephyrocapsa oceanica* et de *Emiliania huxleyi* (Coccolithophoridés). *C. r. hebd. Seánc. Acad., Paris. Série D*, **273**: 318-321.

Cros, L., Kleijne, A. & Young, J.R. 2000b. Coccolithophorid diversity in the genus *Polycrater* and possible relationships with other genera. *J. Nannoplankton Res.*, **22**(2): 92.

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000a. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Mar. Micropaleontol.*, **39**(1-4): 1-34.

Edvardsen, B., Eikrem, W., Green, J.C., Andersen, R.A., Yeo Moon-van der Staay, S. & Medlin, L.K. 2000. Phylogenetic reconstructions of the Haptophyta inferred from 18S ribosomal DNA sequences and available morphological data. *Phycologia*, **39**(1): 19-35.

Fujiwara, S., Tsuzuki, M., Kawachi, M., Minaka, N. & Inouyé, I. 2001. Molecular phylogeny of the haptophyta based on the *rbc*L gene and sequence variation in the spacer region of the RUBISCO operon. *J. Phycol.*, **37**: 121-129.

Gard, G. 1987. Observation of a dimorphic coccosphere. *Abh. geol. Bundesanst.*, **39**: 85-87.

Geisen, M., Billard, C., Broerse, A.T.C., Cros, L., Probert, I. & Young, J.R. submitted. Life-cycle associations involving pairs of holococcolithophorid species: intraspecific variation or cryptic speciation? *Eur. J. Phycol.*

Green, J.C., Course, P.A. & Tarran, G.A. 1996. The life-cycle of *Emiliania huxleyi*: A brief review and a study of relative ploidy levels analysed by flow cytometry. *J. Mar. Syst.*, **9**: 33-44.

Kamptner, E. 1941. Die Coccolithineen der Südwestküste von Istrien. *Ann. Naturh. Mus. Wien*, **51**: 54-149.

Kleijne, A. 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Mar. Micropaleontol.*, 17: 1-76.

Lecal-Schlauder, J. 1961. Anomalies dans la composition des coques de flagelles calcaires. *Bull. Soc. Hist. nat. Afr. N.*, **52**: 63-66.

Lohmann, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, Zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. *Arch. Protistenk.*, **1**: 89-165.

Murray, J.W. 1991. *An atlas of British recent foraminiferids*. Heinemann Educational Books Ltd., London: 244 pp.

Perch-Nielsen, K. 1985. Cenozoic calcareous nannofossils. *In*: H.M. Bolli, J.B. Saunders & K. Perch-Nielsen (Eds). *Plankton Stratigraphy*. Cambridge University Press, Cambridge: 427-555.

Siesser, W.G. 1994. Historical background of coccolithophore studies. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 1-11.

Sprengel, C. & Young, J.R. 2000. First direct documentation of associations of *Ceratolithus cristatus* ceratoliths, hoop-coccoliths and *Neosphaera coccolithomorpha* planoliths. *Mar. Micropaleontol.*, **39**(1-4): 39-41.

Thierstein, H.R., Geitzenauer, K.R., Molfino, B. & Shackleton, N.J. 1977. Global synchroneity of late Quaternary coccolith datum levels: Validation by oxygen isotopes. *Geology, Boulder, Colo.*, **5**: 400-404.

Thomsen, H.A., Ostergaard, J.B. & Hansen, L.E. 1991. Heteromorphic life histories in Arctic coccolithophorids (Prymnesiophyceae). *J. Phycol.*, **27**: 634-642.

Wallich, G.C. 1861. Remarks on some novel phases of organic life, and on the boring powers of minute annelids, at great depths in the sea. *Ann. Mag. nat. Hist.*, **8**: 52-58.

Wallich, G.C. 1877. Observations on the coccosphere. *Ann. Mag. nat. Hist.*, **19**: 342-350.

Widmark, J.G.V. & Henriksson, A.S. 1995. The “orphaned” agglutinated foraminifera - *Gaudryina cribrosphaerellifera* n. sp. from the Upper Cretaceous (Maastrichtian) Central Pacific Ocean. *In*: M.A. Kaminski, S. Geroch & M.A. Gasinski (Eds). *Proceedings of the fourth international workshop on agglutinated foraminifera*. Grzybowski Foundation Special Publication: 293-301.

Winter, A., Reiss, Z. & Luz, B. 1979. Distribution of Living Coccolithophore Assemblages in the Gulf of Eilat (‘Aqaba). *Mar. Micropaleontol.*, **4**: 197-223.

Winter, A., Stockwell, D. & Hargraves, P.E. 1986. Tintinnid agglutination of coccoliths: A selective or random process? *Mar. Micropaleontol.*, **10**: 375-379.

Young, J.R. 1998. Neogene. *In*: P.R. Bown (Ed.). *Calcareous Nannofossil Biostratigraphy*. British Micropalaeontological Society Publications Series. Chapman & Hall/Kluwer Academic, London: 225-265.

Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., Niel, B.E. van, Romein, A.J.T. & Salis, K. von 1997. Guidelines for coccolith and Calcareous nannofossil terminology. *Palaeontology*, **40**: 875-912.

Plate captions

All SEM images, with the exception of Plate 1, Figure 3, were taken with a Philips XL-30 field-emission digital SEM in the electron microscopy and mineral preparation unit (EMMA) of the Dept. of Mineralogy at the Natural History Museum, London. For Plate 1, Figure 3, a Hitachi S800 field-emission SEM was used. The files of the images have been archived and are accessible via a database; the BMNH reference numbers are given in the captions. The LM images have been captured using a Hamamatsu video camera attached to a Zeiss Axioplan light-microscope.

Plate 1

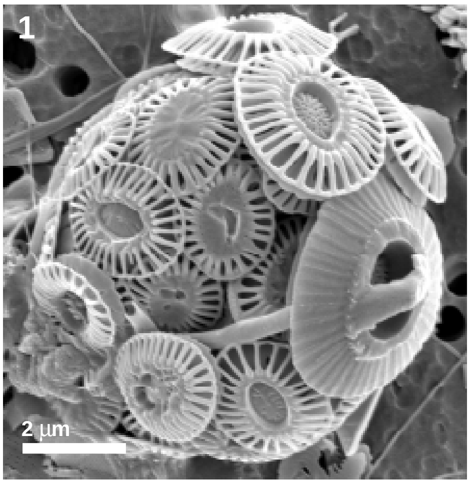
Figs 1-2: Xenosphere of *Emiliania huxleyi* and *Gephyrocapsa oceanica.* We do not have any definite explanation for this specimen but believe it is likely to be an artefact. Cruise MATER II, R/V *Hesperides*, station 56 at 37.16°N, 1.19°W, depth 34m. Fig.1: BMNH 119-33; Fig.2: BMNH 119-34.

Fig.3: Xenosphere of *Cribrocentrum reticulatum* and *Coccolithus pelagicus.* This specimen is possibly the proloculus of an agglutinating foraminifera. DSDP sample 220-11-1, 70cm, Indian Ocean, Late Eocene (NP18). BMNH-088589.

Figs 4-6: Xenosphere of *Acanthoica quattrospina*, *Syracosphaera bannockii* (in holococcolithophore phase of life-cycle), and ?*Calyptrolithophora gracillima.* We suspect this is a faecal pellet. Plankton sample from cruise P233b, R/V *Poseidon*, station 2 at 29.75°N, 17.93°W, depth 50m. Fig.4: BMNH 167-10; Fig.5: BMNH 167-11; Fig.11: BMNH 167-12. Collected by C. Sprengel.

Fig.7: Xenosphere of *Helicosphaera carteri* and *Syracolithus dalmaticus.* This specimen is probably an accidental association produced during sample collection. Plankton sample from the Gulf of Mexico, cruise 93-G-01, R/V *Gyre*, station 5c at 26.68°N, 95.12°W, depth 20m. BMNH CSF0195. Collected by V. Pariente.

Fig.8: Xenosphere of *Syracosphaera noroitica* and *Helladosphaera cornifera.* Again, this specimen is probably an accidental association produced during sample collection, but conceivably could be a combination coccosphere. Plankton sample from off the Canary Islands, cruise P233b, R/V *Poseidon*, station 2 at 29.75°N, 17.93°W, depth 50m. BMNH 126-20. Collected by C. Sprengel.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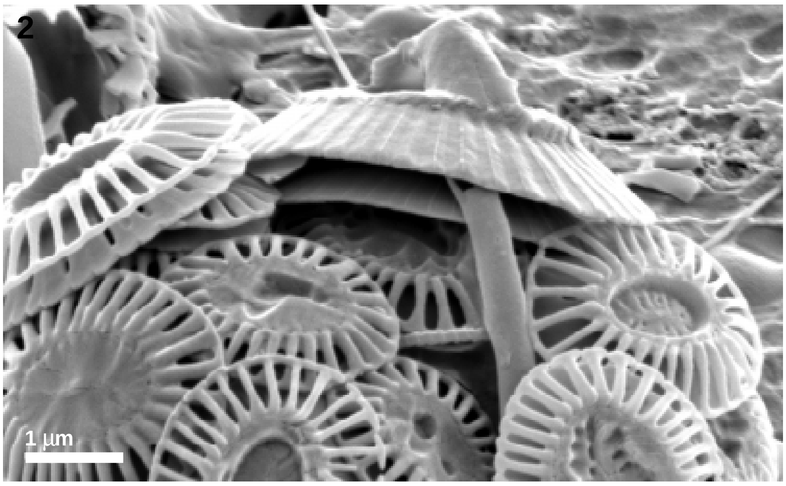
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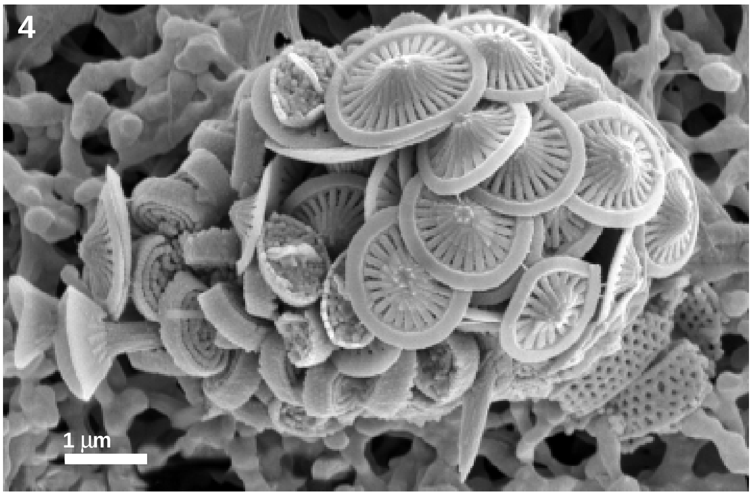
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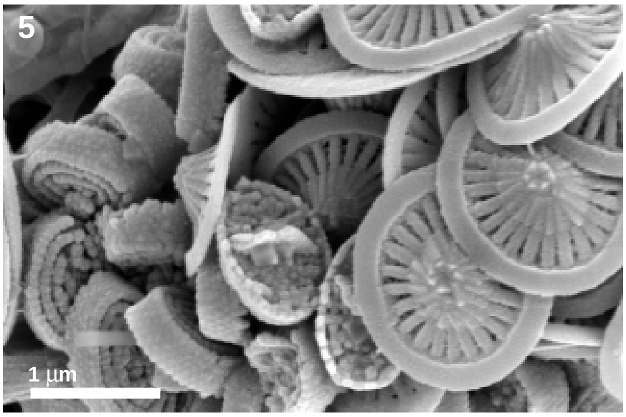
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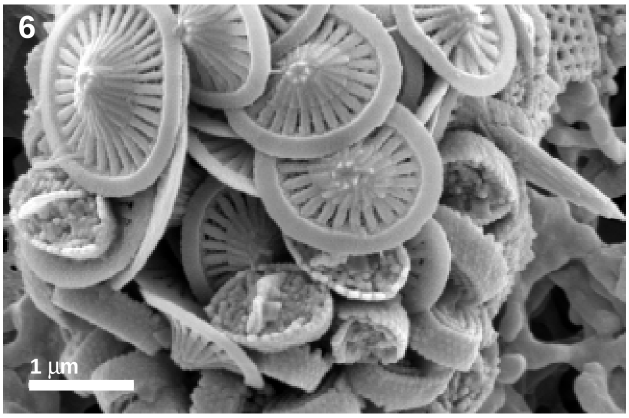
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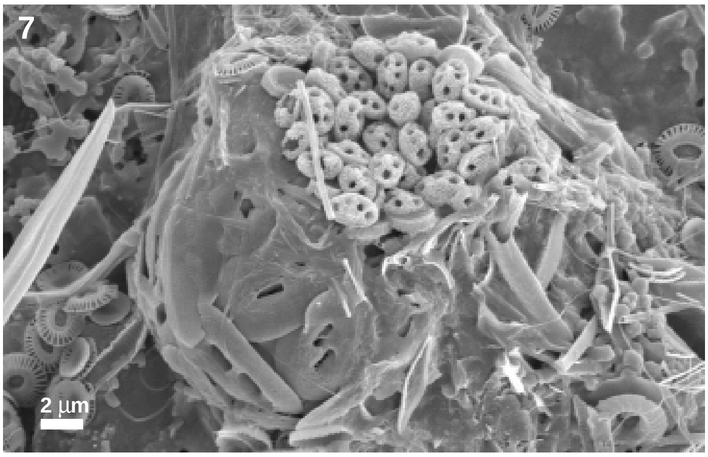
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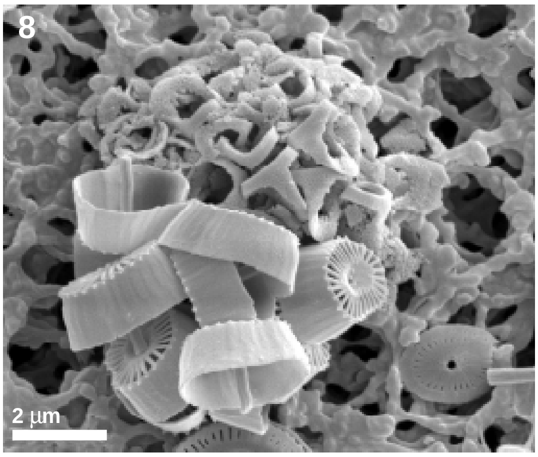
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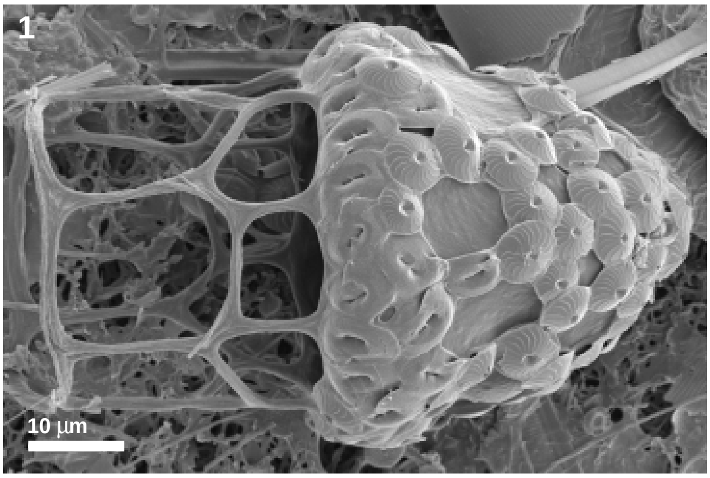
Plate 2

Figs 1- 6: Tintinnids with agglutinated coccoliths, all from plankton samples. Figures 1-4: South Atlantic Ocean, off Namibia, cruise M48-4b, R/V *Meteor.* Fig.1: station 11 at 20.6°S, 9.87°E, depth 5m; Figs 2-3: station 477 at 23.46°S, 12.62°E, depth 5m; Fig.4: station 44 at 30.15°S, 4.43°E, depth 5m. Figs 5-6: Alboran Sea, western Mediterranean, cruise MATER II, R/V *Hesperides*, station 69 at 37.43°N, 0.43°W, depth 50m. Fig.1: BMNH 136-35; Fig.2: BMNH 137-17; Fig.3: BMNH 137-18; Fig.4: BMNH 137-20; Fig.5: BMNH 145-27; Fig.6: BMNH 145-28.

Figs 7-8: Faecal pellets. Cruise P233b, R/V *Poseidon*, station 2 at 29.75°N, 17.93°W, depth 50m. Fig.7: BMNH 118-27; Fig.8: BMNH 126-16. Collected by C. Sprengel.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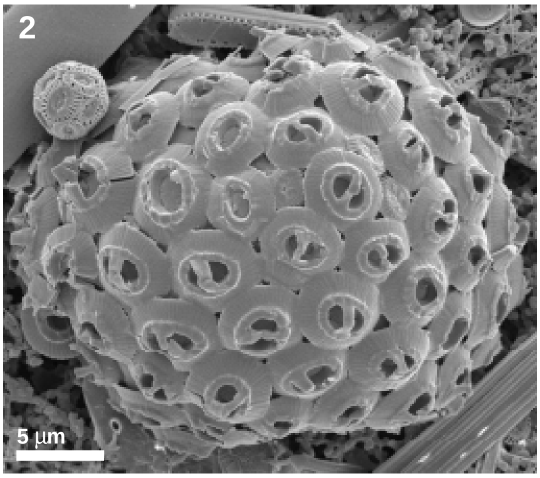
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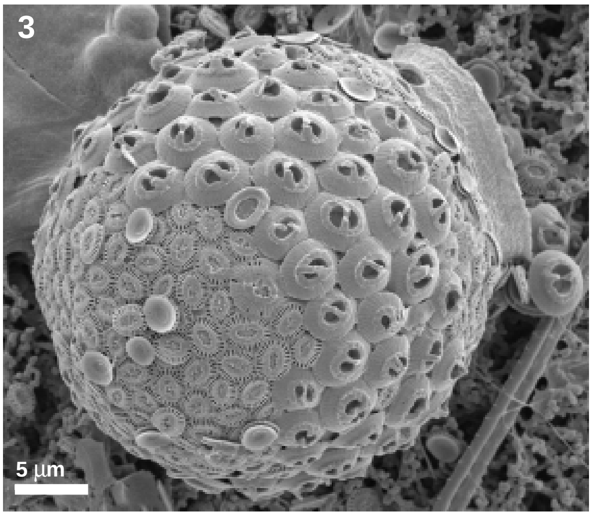
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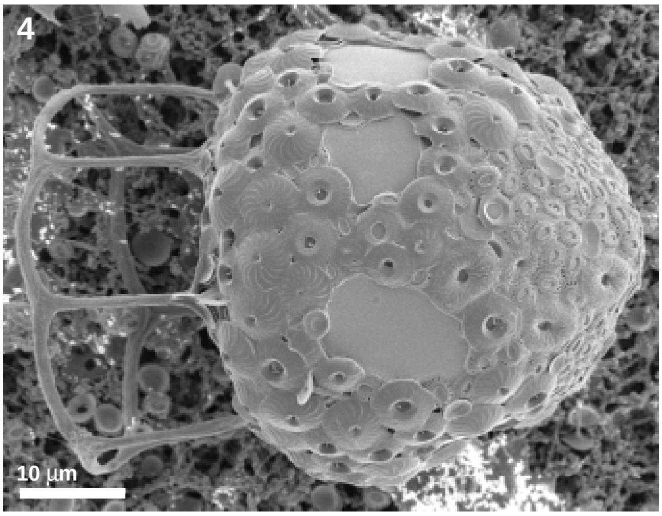
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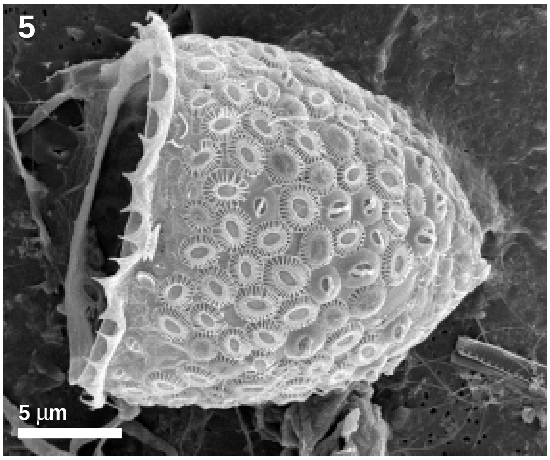
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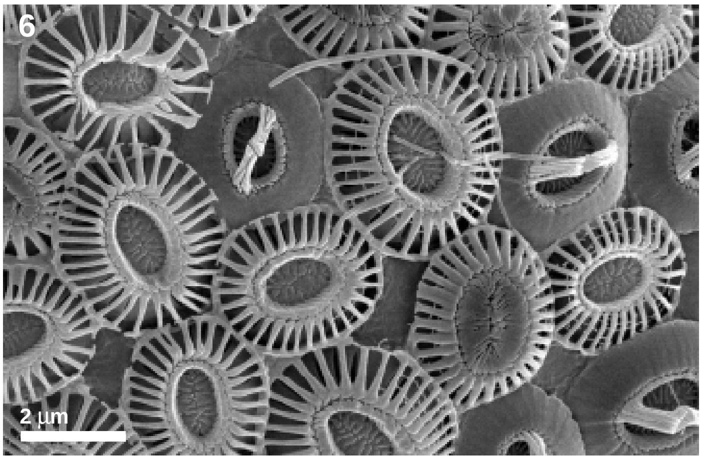
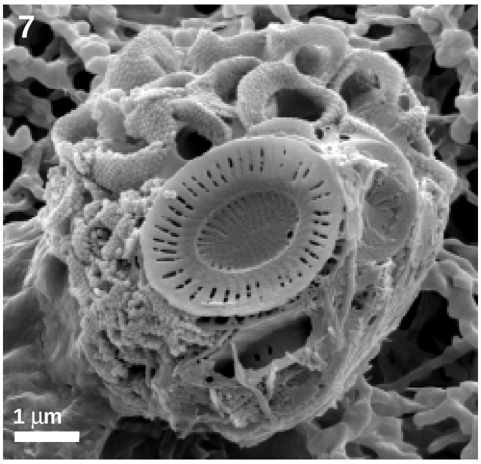
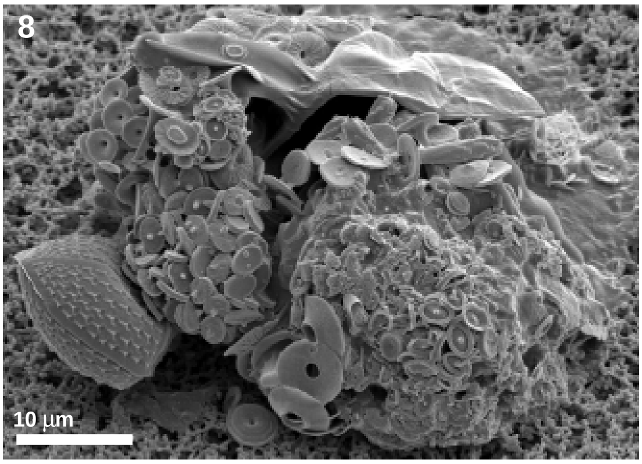

6
2 µm


7
1 µm


8
10 µm

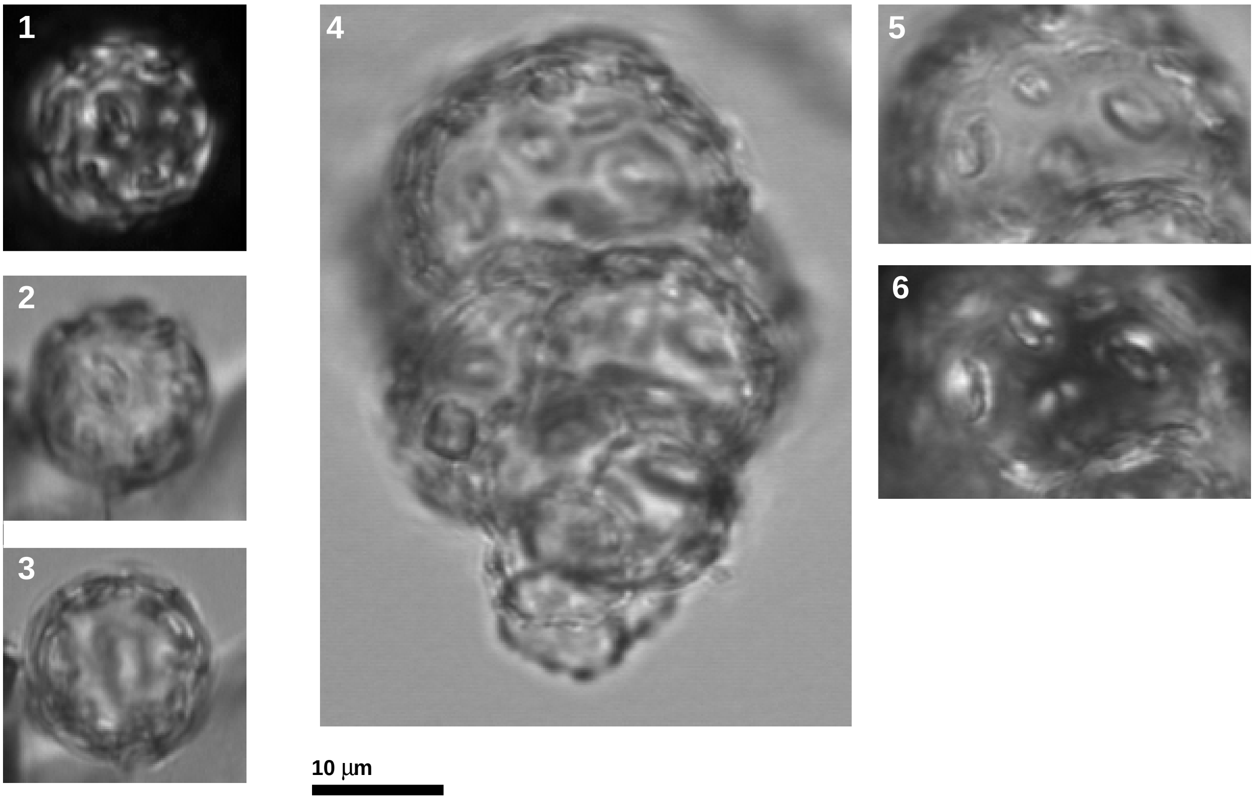


Plate 3

Foraminifera agglutinating *Coccolithus pelagicus*. Surface sediment sample from south of Iceland, collected by G.C. Wallich during *Bulldog* cruise, station 120, in 1860.

Figs 1-3: Coccosphere of *Coccolithus pelagicus*. Fig.1: crossed-polars; Fig.2: bright field, surface focus; Fig.3: Bright field, median focus.

Figs 4-6: Agglutinating foraminifera. Fig.4: complete specimen; Fig.5: terminal chamber, surface focus, bright field; Fig.6: terminal chamber, surface focus, crossed- polars.