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Syracosphaera azureaplaneta sp. nov. and revision of *Syracosphaera corolla* Lecal, 1966

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Abstract Here, we show that the extant coccolithophore *Syracosphaera corolla* Lecal, 1966 comprises two consistently different, non-intergrading morphotypes, characterised respectively by exothecal coccoliths with wide and narrow central-areas. These are interpreted as separate species, and so a new species is described—*S. azureaplaneta*—and a revised description is given for *S. corolla*.

Keywords Taxonomy, *Syracosphaera*

1. Introduction

As a result of intensive study by, and the careful taxonomic work of, many researchers, coccolithophores are one of the best-documented groups of oceanic phytoplankton, as well as having an exceptionally good fossil record. This gives them unique potential for a range of types of biodiversity studies, and also means it is particularly worthwhile completing their taxonomic documentation. Here, we document an addition to one of the most fascinating coccolithophore genera—*Syracosphaera* Lohmann, 1902.

Syracosphaera corolla Lecal, 1966 is a *Syracosphaera* species with unusually prominent exothecal coccoliths, where the distal flange is greatly expanded, giving them a resemblance to *Umbellosphaera* Paasche *in* Markali & Paasche, 1955. Indeed, the species was placed in *Umbellosphaera* by Gaarder *in* Heimdal & Gaarder (1981) and in a separate genus, *Gaarderia*, in the Umbellosphaeraceae by Kleijne (1993). However, with better images and a more detailed understanding of the coccolith structure, it became clear that the body coccoliths were typical of *Syracosphaera* and that the exothecal coccoliths, whilst distinctive, fell within the type of variation shown by *Syracosphaera*. Hence, the species was placed in *Syracosphaera* in the syntheses of Young et al. (2003) and Jordan et al. (2004). In particular, it shows close affinities to *Syracosphaera dilatata* Jordan et al., 1993 and *Syracosphaera arethusae* (Kamptner, 1941) Triantaphyllou et al., 2016 (synonym: *Syracosphaera didyma* Kleijne & Cros, 2009). For an overview of the diversity in *Syracosphaera*, see Young et al. (2003) and the Nannotax website (Young et al., 2018), and for their coccolith structure, see Young et al. (2004) and Bown et al. (2017).

2. Materials and methods

This contribution is based primarily on a review of our collections of scanning electron micrographs of extant coccolithophores. These were collected over an extended period and from diverse environments. Primarily, though, the samples were collected by the vacuum filtration of seawater onto filter membranes (typically 0.2 to 1 μm pore-size). The type material is curated in the Natural History Museum, London.

3. Results

Syracosphaera corolla is not common, but has been widely reported from all oceans and from the Equator to the sub-Arctic (e.g. Okada & Honjo, 1973; Kleijne, 1993), and our observations confirm this. A review of images of the species revealed that two distinct morphotypes were included in it. The primary differences between them are in the exothecal coccolith form—most conspicuously in the relative widths of the central-area, which may be broad (length ~2x width) or narrow (length ~4x width) (see Plate 1 and Figure 1). The form with the exothecal coccoliths with a broad central-area is the most common. In these, the central-area is floored by a flat, but rather irregular, arrangement of laths. The central-area is also often slightly constricted at the centre, and there may be openings at either end. The flange is typically strongly ridged, with both sutural and additional ridges. In the other form, the central-area in the exothecal coccoliths, as well as being narrower, is also more straight-sided and floored by regularly-arranged radial laths, which slope downwards from the edge of the central-area towards the long axis, so that the base of the central-area has a valley-like form. The flange is usually smooth, with weak sutural, but no other, ridges. In other respects, the exothecal coccoliths of the two morphotypes are similar, both having a conspicuous anticlockwise obliquity to the elements in distal view, low tubes and narrow proximal flanges.

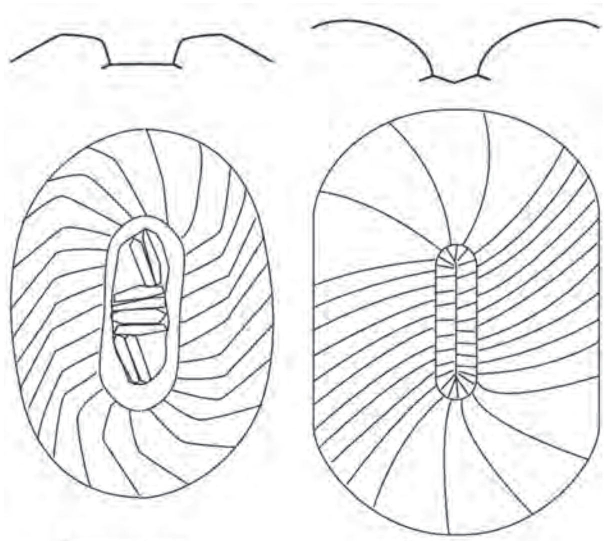

Figure 1: Drawings of the exothecal coccoliths of *Syracosphaera azureaplaneta* and *S. corolla* in plan view and cross-section, based on tracings of actual specimens

A systematic review of our images of *S. corolla* and those from published sources further showed that these two types of exothecal coccoliths could be consistently distinguished, and that they did not co-occur on the same coccosphere. The body coccoliths associated with them do not differ in any obvious way, there is no clear pattern to their biogeography (both forms occur in the Indian, Pacific and Atlantic Oceans, and in both tropical and temperate waters), and they were also found to co-occur in single samples.

3.1 Coccolith size and distribution on the coccosphere

The form with exothecal coccoliths with narrow central-areas appeared to be larger than that with broad central-area coccoliths, so we measured the exothecal and body coccoliths of 30 specimens. This confirmed the observation of a larger size for the narrow-central-area form (4.5–7.0 μm vs 3.5–6.0 μm; Figure 2). Our measurements also showed that the body coccoliths on the narrow-central-area form were slightly larger than on the broad-central-area form (typically 2.0–4.0 μm vs 1.5–3.5 μm, respectively; Figure 2). Finally, there was more variability in exothecal coccolith size in the narrow-central-area form, primarily because the individual coccospheres often had a few smaller exothecal coccoliths alongside the relatively larger ones.

In both forms, there was a tendency for the exothecal coccoliths to occur in a ring around one end of the coccosphere, with their long-axes parallel to the length of the coccosphere. This is presumably the flagellar pole, as first reported by Lecal (1966). This pattern was most consistently exhibited in the broad-central-area form, whilst in the other form, the exothecal coccoliths were found to extend further over the coccosphere or, indeed, even cover it completely.

4. Discussion

The consistency of the difference between the two exothecal coccolith forms, and the fact that the morphology was paralleled by differences in coccolith size and arrangement on the coccosphere, strongly suggest that these two forms are genotypically discrete. The absence of intermediates suggests that they should be considered to be separate species, rather than subspecies. *S. corolla* was originally described by Lecal (1966), and it is very unlikely that any type material has survived. However, his illustrations are high-quality transmission electron micrograph images of both a body coccolith and an exothecal coccolith (Lecal, 1966, pl. 1, figs 1, 2). The exothecal coccolith image distinctly shows a narrow central-area, with well-formed radial laths, and a wide flange, with only sutural ridges. Clearly, this is the narrow-central-area form, and so the name '*corolla*' must be applied to this type. A new name is therefore required for the broad-central-area species. This

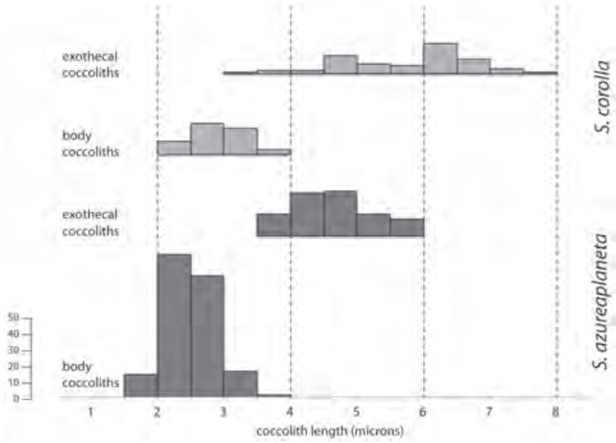

Figure 2: Coccolith size variation in *S. azureaplaneta* and *S. corolla*. Measurements made on scanning electron microscope images, with 4–20 coccoliths measured on each of 35 coccospheres. Vertical scale is count frequency

conclusion is indisputable, even though it is somewhat unfortunate because the broad-central-area form appears to be more common, and has been illustrated more often. The new species is described below, and an emended description is given for *S. corolla*.

5. Systematic taxonomy

Syracosphaera azureaplaneta sp. nov.
Pl. 1, figs 1, 2, 6, 7

Syracosphaera corolla (Lecal, 1966): Okada & McIntyre, 1977, pl. 6, figs 1, 2; Nishida, 1979, pl. 6, fig. 4; Winter & Siesser, 1994, fig. 107; Young et al., 2003, pl. 19, figs 14, 15; Malinverno et al., 2008, fig. 76.

Umbellosphaera corolla (Lecal, 1966) Gaarder *in* Heimdal & Gaarder, 1981: pl. 6, figs 53, 57.

Gaarderia corolla (Lecal, 1966) Kleijne, 1993: pl. 6, figs 3–5; Cros & Fortuño, 2002, fig. 29A.

Derivation of name: From the Latin '*azureus*', meaning 'blue' (adjective, feminine form '*azurea*'), and '*planeta*', meaning 'planet' (noun, feminine). Named for the documentary series *The Blue Planet*, in recognition of its and its presenter Sir David Attenborough's work in promoting understanding of the marine realm. **Description — Coccosphere**: Normally seen collapsed, but coccospheres appear to be ovoid, covered with ~25–50 body coccoliths and a circlet of 6–12 exothecal coccoliths at the broader end of the sphere. On undisturbed coccospheres, the body coccoliths are mostly arranged with their long axes perpendicular to the length of the coccosphere, whilst the exothecal coccoliths have their long axes parallel to the length of the coccosphere (e.g. Plate 1, fig. 2). Possible appendages, seen on a few collapsed coccospheres, extend from the broader end of the coccosphere (e.g. Plate 1, fig. 2). **Circumflagellar coccoliths**: These are almost always covered by the exothecal coccoliths, but no specimens with spines, or any other differentiation from the regular body coccoliths, have been observed. **Body coccoliths**: Irregularly-elliptical, murolith coccoliths, 1.5–3.5 μm long, with a well-developed distal flange. The central-area is floored by a single cycle of radial laths, without a separate axial structure. The proximal flange is narrow, but always present. A mid-wall flange is absent, but a well-developed circlet of spines occurs in its place, and these are typically shorter than the distal flange width, but longer than the proximal flange width, so they are visible in proximal view, but not in distal view (e.g. Plate 1, fig. 1). The distal flange is well-developed, but the width varies and may be weakly asymmetrical. The distal flange elements have sutural ridges, and show distinct sinistral obliquity in distal view. These elements continue into the tube, where they show weak anticlockwise imbrication. **Exothecal coccoliths**: Similar to the body coccoliths, but with a much broader distal flange, making them significantly larger (3.5–6.0 μm; Figure 2). Typically oblong, with parallel sides and rounded ends, and may be slightly constricted in the middle. The central-area is broad (length ~2x the width), floored by radial laths, but these are irregularly disposed. There is no axial structure. Single laths may span the central-area (e.g. Plate 1, fig. 7), and some specimens have lunate openings at either end of the central-area (e.g. Plate 1, fig. 6). The distal flange usually shows both sutural and additional ridges, which may run either radially (e.g. Plate 1, fig. 6) or concentrically (e.g. Plate 1, fig. 2). In profile, the flange usually shows distinct flexure (Figure 1), rather than being continuously curved. Mid-wall flange spines are only very occasionally seen (e.g. Heimdal & Gaarder, 1981, fig. 57; Nishida, 1979, pl. 6, fig. 4) and only in side view. This may be because they are very short or because they are often absent. **Variation**: The exothecal coccoliths are quite variable in their ornamentation and shape, and in the arrangement of the central-area laths, but these characteristics seem to be intergradational and vary on the coccospheres, so they do not appear to define additional species. **Life-cycle**: Not known; combination coccospheres have not been observed. The closely-related species *S. arethusae* (formerly *S. didyma*), however, has been shown by Triantaphyllou et al. (2016) to form combination coccospheres with a holococcolith previously referred to as *Homozygosphaera arethusae*, so it is likely that they *do* have a holococcolith phase, and possibly with other species of *Homozygosphaera* or *Corisphaera*. **Holotype**: Plate 1, fig. 1. **Type sample**: Collected from the South Atlantic during the AMT18 research cruise of the RRS *James Clark Ross*. Sample AMT18-CTD089 48 m, image NHM-JRYSEM-288-65. Collected from 32.18°S, 29.83°W on 2 November, 2008. **Distribution**: Very broad, occurring from the tropics to the sub-Arctic and in all the major oceans.

Syracosphaera corolla Lecal, 1966 emend.
Pl. 1, figs 3–5

Syracosphaera corolla Lecal, 1966: pl. 1, figs 1–4; Young et al., 2003, pl. 19, fig. 13;
Umbellosphaera corolla (Lecal, 1966) Gaarder *in* Heimdal & Gaarder, 1981: pl. 6, fig. 56.
Gaarderia corolla (Lecal, 1966) Kleijne, 1993: pl. 6, fig. 6; Cros & Fortuño, 2002, fig. 29B–D.
NB Lecal (1966) used both the names *Syracolithus corolla* and *Syracosphaera corolla*, but this was corrected by Loeblich and Tappan (1968) to *Syracosphaera* (*Syracolithus*) *corolla*.

Emended description: Following our recognition that *S. corolla*, as traditionally understood, was actually two species, the name '*corolla*' is now restricted to the species with exothecal coccoliths with narrow central-areas. **Coccosphere**: Similar to those of *S. azureaplaneta*, but exothecal coccoliths may extend over the entire surface and show significant variation in size. **Body coccoliths**: Very similar to those of *S. azureaplaneta*, but slightly larger—2–4 μm vs 1.5–3.5 μm (Figure 2). **Exothecal coccoliths**: Similar to those of *S. azureaplaneta*, but: 1) central-area narrow (breadth ~4x the length); 2) central-area base 'V'-shaped in profile, and with regularly-arranged laths; 3) distal flange smooth except for weak sutural ridges; and 4) sutural ridges also present on the proximal side of the distal flange. The ends of the distal flanges are typically formed of only 3 or 4 elements, with wide ends, as opposed to more numerous and narrower elements in this area in *S. azureaplaneta* (Figure 1). We have not observed mid-wall spines on the exothecal coccoliths of *S. azureaplaneta*—they are clearly not present on our specimens (e.g. Plate 1, fig. 4). The coccoliths are also slightly larger; in *S. corolla*, the exothecal coccoliths are predominantly 4.5–7.0 μm long, vs 3.5–6.0 μm for *S. azureaplaneta* (Figure 2). They also show a wide total range of sizes (from 3 to 8 μm), reflecting the fact that there is often a strong variation in size on single coccospheres, typically with large coccoliths in a ring at one end of the coccosphere and variable-sized coccoliths over the rest of the surface.

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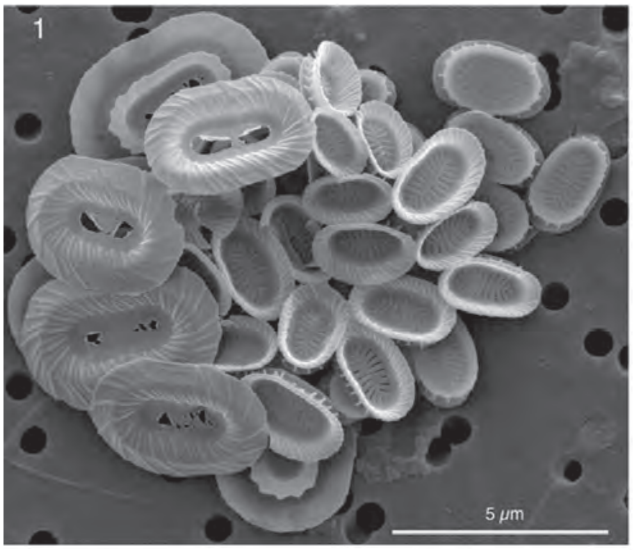
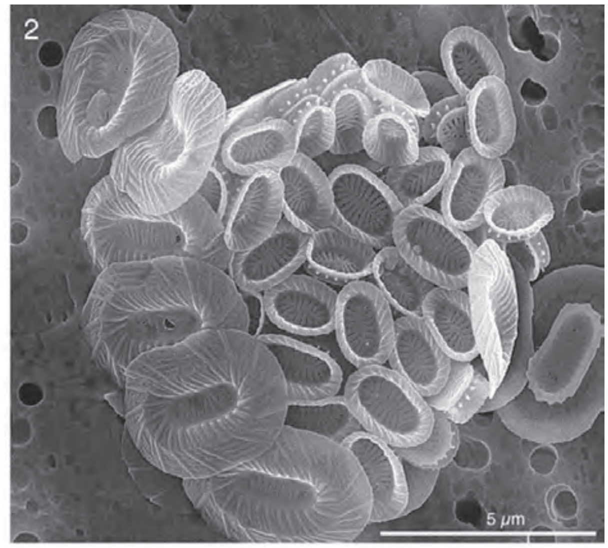
Plate 1

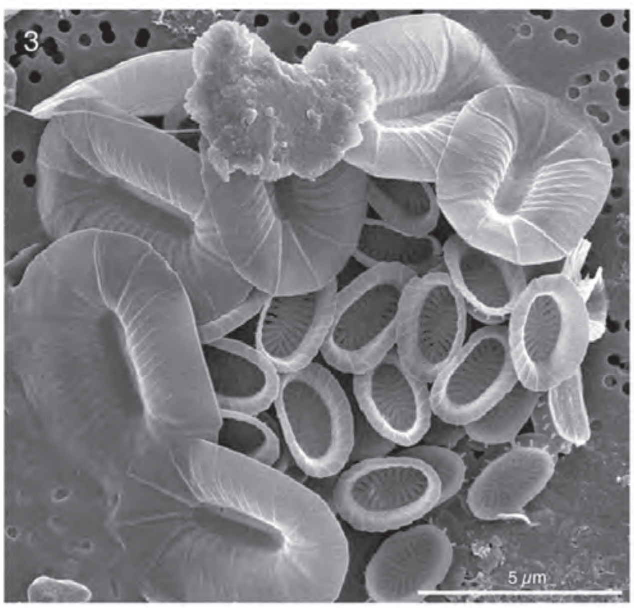
Figs 1, 2, 6, 7: *S. azureaplaneta*; Figs 3–5: *S. corolla*



Holotype, collapsed coccosphere. Image NHM-JRY288-65. Sample AMT18-CTD089, 48 m, S Atlantic

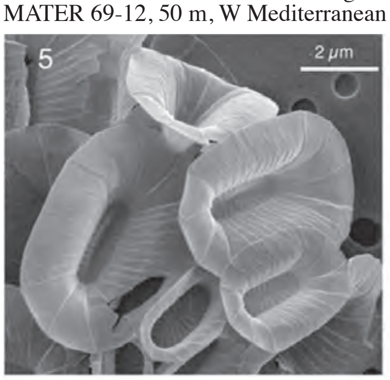


Collapsed coccosphere. Note coiled appendage (left). Image GARDCOR(F3K05-40). Sample F3K05, W Mediterranean (Alboran Sea)

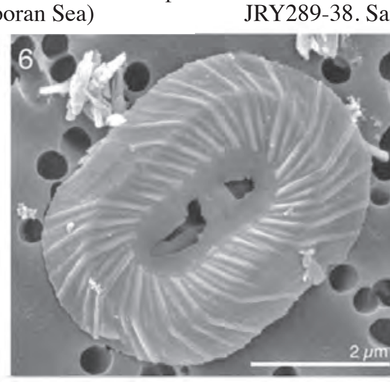


Collapsed coccosphere, scale as fig. 1, so showing larger size of *S. corolla* exothecal coccoliths. Image NHM-JRY193-80. Sample MATER 69-12, 50 m, W Mediterranean (Alboran Sea)

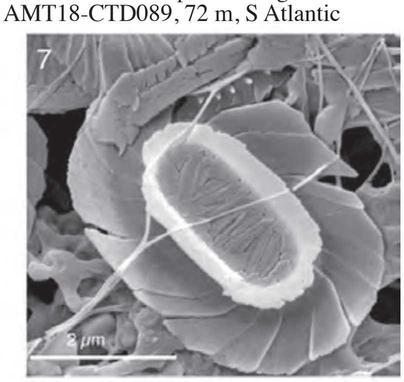
Small coccosphere almost entirely covered by exothecal coccoliths. Note absence of mid-wall spines. Image NHM-JRY289-38. Sample AMT18-CTD089, 72 m, S Atlantic



Detail of exothecal coccoliths. Note size variation. Image NHM-JRY288-39. Sample AMT18-CTD089, 48 m, S Atlantic



Distal view, isolated coccolith. Image NHM-JRY112-N10U05. N10U05, S Atlantic sediment trap



Proximal view, isolated coccolith. Image NHM-JRY114-48. Sample P233-1, 5 m, NE Atlantic (Canary Islands)