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A reappraisal of the taxonomy and biodiversity of the extant coccolithophore genus *Palusphaera* (Rhabdosphaeraceae, Prymnesiophyceae)

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ABSTRACT

The genus *Palusphaera* Lecal-Schlauder *emend*. R.E. Norris is a distinctive modern coccolithophore that accommodates monomorphic, monothecate coccospheres with one type of spine-bearing heterococcoliths. Having examined a set of scanning electron microscopy images from our collections, we were able to demonstrate that four distinct species of *Palusphaera* exist in the modern oceans, including the type species *Palusphaera vandelii*, an informally proposed form, *Palusphaera* sp. 1 (type robusta) that is herein taxonomically ratified as *Palusphaera crosiae sp. nov*., and a distinctive morphotype, which is formally described as *Palusphaera bownii sp. nov*. Biometric analyses and observations on the morphologies of numerous *P. vandelii* specimens revealed the existence of a further form, and its commonly distinguished coccolith morphotypes are therefore taxonomically separated from *Palusphaera vandelii* and established as a discrete species, *Palusphaera probertii sp. nov*.

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INTRODUCTION

Coccolithophores are an abundant group of eukaryotic unicellular flagellate phytoplankton in the modern-day oceans, belonging to the phylum Haptophyta, class Prymnesiophyceae. Coccolithophores precipitate a multitude of elaborately shaped scales of calcium carbonate (coccoliths) to form a distinctive mineralized cell covering known as a coccosphere (Wallich 1877; Young *et al.* 1992). Although microscopic in size, coccolithophores exert a significant influence on both oceanic biogeochemistry and the global carbon cycle (Sigman & Boyle 2000; Hutchins 2011; Monteiro *et al.* 2016), and exhibit a vast array of coccolith morphologies as a result of a substantial variety of species-level calcite production (e.g. Monteiro *et al.* 2016).

Coccolithophores are one of the most comprehensively described and reliably identifiable groups of marine phytoplankton (Jordan & Green 1994; Jordan *et al.* 1995, 2004; Young & Bown 1997), and their taxonomy and taxonomic documentation continue to greatly advance, with approximately 280 morphospecies having already been discovered (Young *et al.* 2021). This has primarily been a matter of documenting new taxa from plankton assemblages (e.g. Young *et al.* 2003; Archontikis *et al.* 2020) and/or identifying cells during their life cycle transition (Cros *et al.* 2000; Archontikis & Young 2020) but, more recently, crystallographic properties of coccolith calcite and molecular genetics have been applied to calcareous nannoplankton (Young *et al.* 2014; Hagino *et al.* 2016) to reinforce the observations on the coccolith morphologies and correspondingly rectify important taxonomic problems. Yet, there are still several cases of enigmatic taxa with inconsistent generic use and thus their taxonomic treatment is becoming increasingly important to tackle.

The family Rhabdosphaeraceae Haeckel (1894) is a diverse group of coccolithophores definitely including six extant genera (*Rhabdosphaera* Haeckel, *Acanthoica* Lohmann, *Algirosphaera* Schlauder *emend*. R.E. Norris, *Cyrtosphaera* Kleijne, *Discosphaera* Haeckel and *Palusphaera* Lecal-Schlauder *emend*. R.E. Norris), one exclusively fossil genus (*Blackites* W.W. Hay & Towe) and, more tentatively, an additional extant genus *Solisphaera* Bollmann, M.Y. Cortés, Kleijne, J.B. Østergaard & Jer.R. Young, which, however, is excluded from the subsequent discussion, because it differs in numerous ways from the other genera (see details in Bollmann *et al.* 2006). The family is characterized by the formation of planolith-type coccoliths, with a distinctive rim structure and a more variable central area (Figs 1–4), often including the presence of spines (Aubry 1988; Varol 1989; Kleijne 1992; Young *et al.* 2003; Probert *et al.* 2007; van de Locht *et al.* 2014; Bown *et al.* 2017; Table 1). The rim is almost always narrow and formed of two cycles of elements: a broad outer/upper cycle of V-units with subradial sutures and a narrow inner/lower cycle of R-units (e.g. Fig. 2; see discussion in Bown *et al.* 2017) showing strong sinistral obliquity in proximal view. The central area, excluding the process, is typically formed of two cycles of units. First, a radial lath cycle, adjacent to the rim, composed of well-formed laths often with gaps between them, whose ends interdigitate regularly with the elements of the rim. Second, a lamellar cycle of less regular elements. The lamellar cycle is present in all genera, but the radial cycle is absent in *Rhabdosphaera* and *Palusphaera*. The central process is the most variable part of the structure, showing a wide range of shapes and

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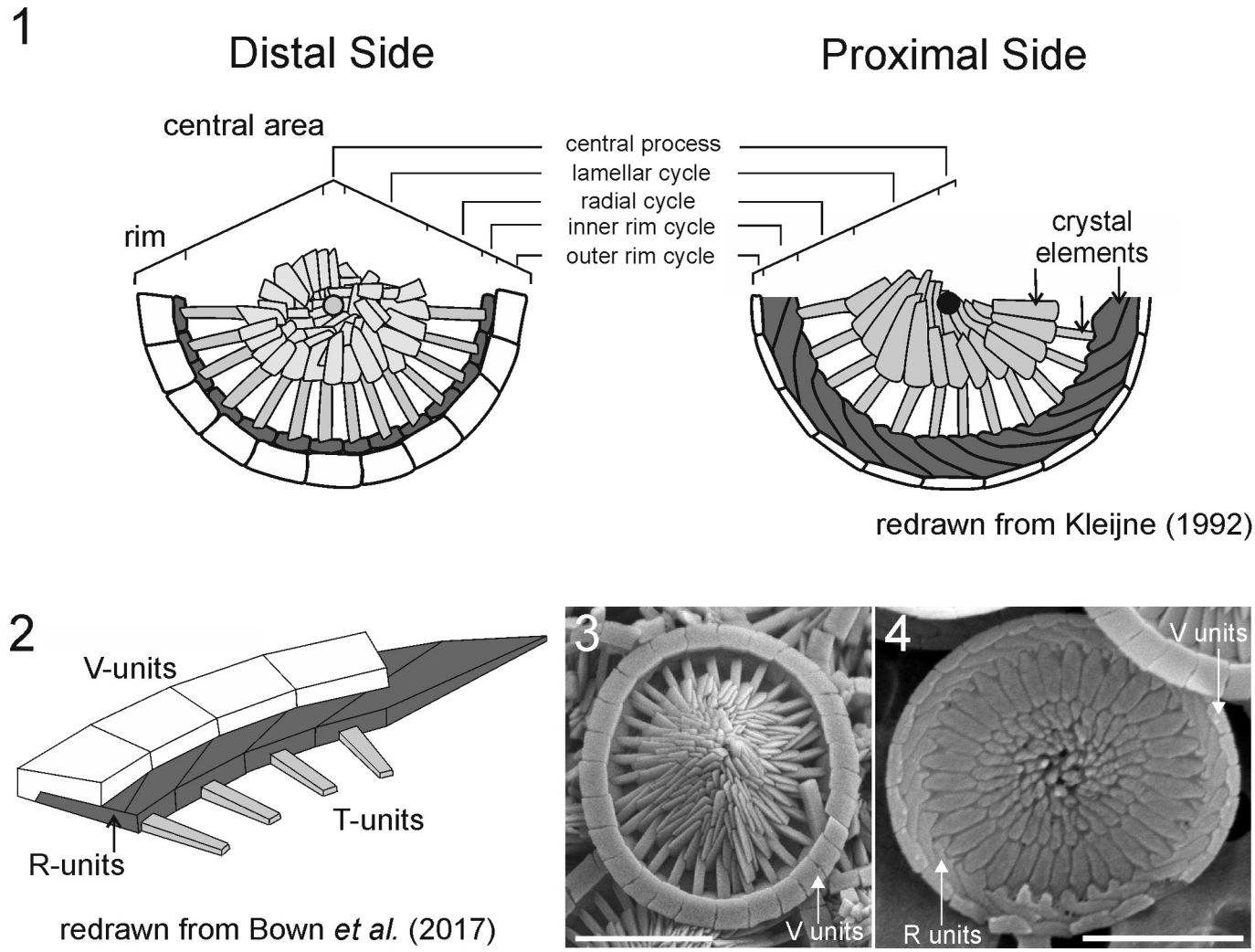


Figs 1–4. Ultrastructure of Rhabdosphaeraceae.
Fig. 1. Rhabdosphaeraceae coccolith morphological features, redrawn from Kleijne (1992).
Fig. 2. Schematic representation of the V- and R-units shown in coccoliths of *Acanthoica quattrospina* (Rhabdosphaeraceae), redrawn from Bown *et al.* (2017).
Figs 3, 4. *Acanthoica quattrospina* coccoliths in, respectively, distal (Fig. 3; scale bar = 0.5 μm) and proximal (Fig. 4; scale bar = 1 μm) views.

morphologies, and is absent from some of the coccolith types on the coccospheres of *Acanthoica* and *Rhabdosphaera*.

Within this group, *Palusphaera* is distinguished from the other genera by forming monomorphic coccospheres with body coccoliths, all bearing spines and lacking a radial cycle. Currently, there is only one formally described species in the genus, *Palusphaera vandelii* Lecal-Schlauder *emend.* R.E. Norris, but one other morphotype has been reported informally several times. Here, we also report on two further extant morphotypes of the genus and provide formal descriptions of all currently known forms.

MATERIAL AND METHODS

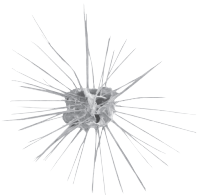
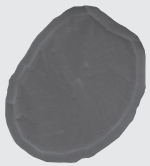
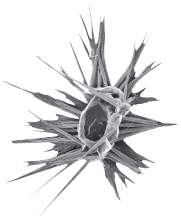
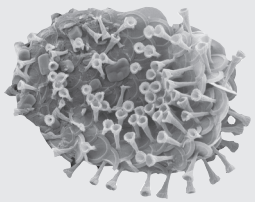
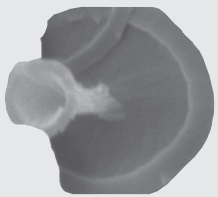
We have examined the scanning electron microscope (SEM) images of extant *Palusphaera* specimens from our collections. The material used in the present study comes from seawater samples collected in different marine basins (Fig. 5) and from several sampling projects carried out over the last two decades. The methodology used here is analytically explained below in chronological order and according to the sample source. Information about all used samples is given in Table 2.

Sample location

ATLANTIC AND PACIFIC OCEANS

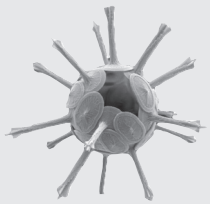
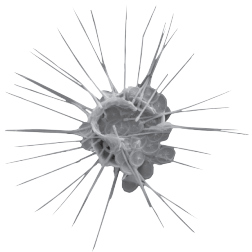
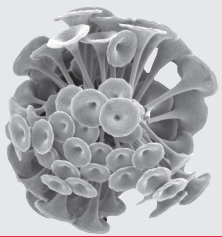
Water samples were collected aboard the R/V *Poseidon* during the P233 Expedition B (Knoll *et al.* 1998) in the Canary Islands, northeastern Atlantic Ocean in September 1997 and during the M68-03 Expedition in the Mauretania upwelling, northeastern Atlantic Ocean onboard the R/V *Meteor* in April–August 2006 (Koschinsky *et al.* 2009). Specimens of *Palusphaera* were also found in seawater samples that were obtained from the Miyake Island, western Pacific Ocean in November 1999 and from the eastern Pacific Ocean in October–December 2004 during the oceanographic cruise BIOSOPE aboard the R/V *L'Atalante* (Claustre & Sciandra 2004). Samples also originate from surface waters of the South Atlantic Ocean during the Atlantic Meridional Transect cruises AMT16 (Robinson *et al.* 2006) and AMT18 (Woodward 2009) aboard, respectively, the RRS *Discovery* in May–June 2005 and R/V *James Clark Ross* in October–November 2008.

Table 1. Description and diagnostic morphologies of all currently known extant *Palusphaera* species vs other spine-bearing taxa of the family Rhabdosphaeraceae. SEM images are not to the same scale.

Extant taxon in Rhabdosphaeraceae					
Genus	Species	*Coccosphere*	*Coccolith*	*Spine*	Diagnostic features
Palusphaera Coccosphere monomorphic and monothecate, spherical in shape. Body coccoliths are spine-bearing planoliths. Coccolith central area is well developed with a lamellar cycle but no radial cycle. Lamellar cycle elements show dextrogyral curvature in distal view and laevogyral curvature in proximal view. Spines with no collar.	*Palusphaera vandelii*				Body coccoliths that are circular in outline. Spine is styliform, long and tapering with spirally arranged crystal segments near its base.
	Palusphaera probertii				Body coccoliths that are broadly elliptical in shape. Spine is styliform and tapering with crystallites parallel oriented to its axis.
	Palusphaera crosiae				Body coccoliths that are nearly circular. Spine is styliform and markedly thicker at one-third to one-quarter height from the base of the spine.
	Palusphaera bownii				Body coccoliths that are circular in shape. Spine is salpingiform and short.

(*Continued*)

Table 1. (Continued).

Extant taxon in Rhabdosphaeraceae					
Genus	Species	*Coccosphere*	*Coccolith*	*Spine*	Diagnostic features
Rhabdosphaera Coccosphere dimorphic and monothecate, spherical in shape. Body coccoliths with a well-developed central area that does not possess a radial cycle; body coccoliths distinguished into (1) spine-bearing planoliths (inner layer) and (2) non-spine-bearing planoliths (outer layer). Lamellar cycle elements show leavogyral curvature in distal view and dextrogyral curvature in proximal view. Spines with or without collar.	*Rhabdosphaera clavigera* var. *clavigera*				Spine-bearing and non-spine-bearing coccoliths of elliptical to broadly elliptical outline. Claviform, long, robust spines with pentameral structure.
	Rhabdosphaera clavigera var. *stylifera*				Spine-bearing and non-spine-bearing coccoliths of elliptical outline. Parallel-sided, long, narrow spines with pentameral structure.
	Rhabdosphaera xiphos				Spine-bearing and non-spine-bearing coccoliths of elliptical to broadly elliptical outline. Parallel-sided, long, narrow spines with pointed tips, collar near the base but without pentameral structure.
Discosphaera Coccosphere monomorphic and monothecate, spherical in shape. Body coccoliths are planoliths bearing trumpet-shaped spines without a collar. Planolith central area with both lamellar and radial cycles.	*Discosphaera tubifera*				Body coccoliths of circular shape bearing trumpet-shaped spines. Trumpet width greater than basal width.

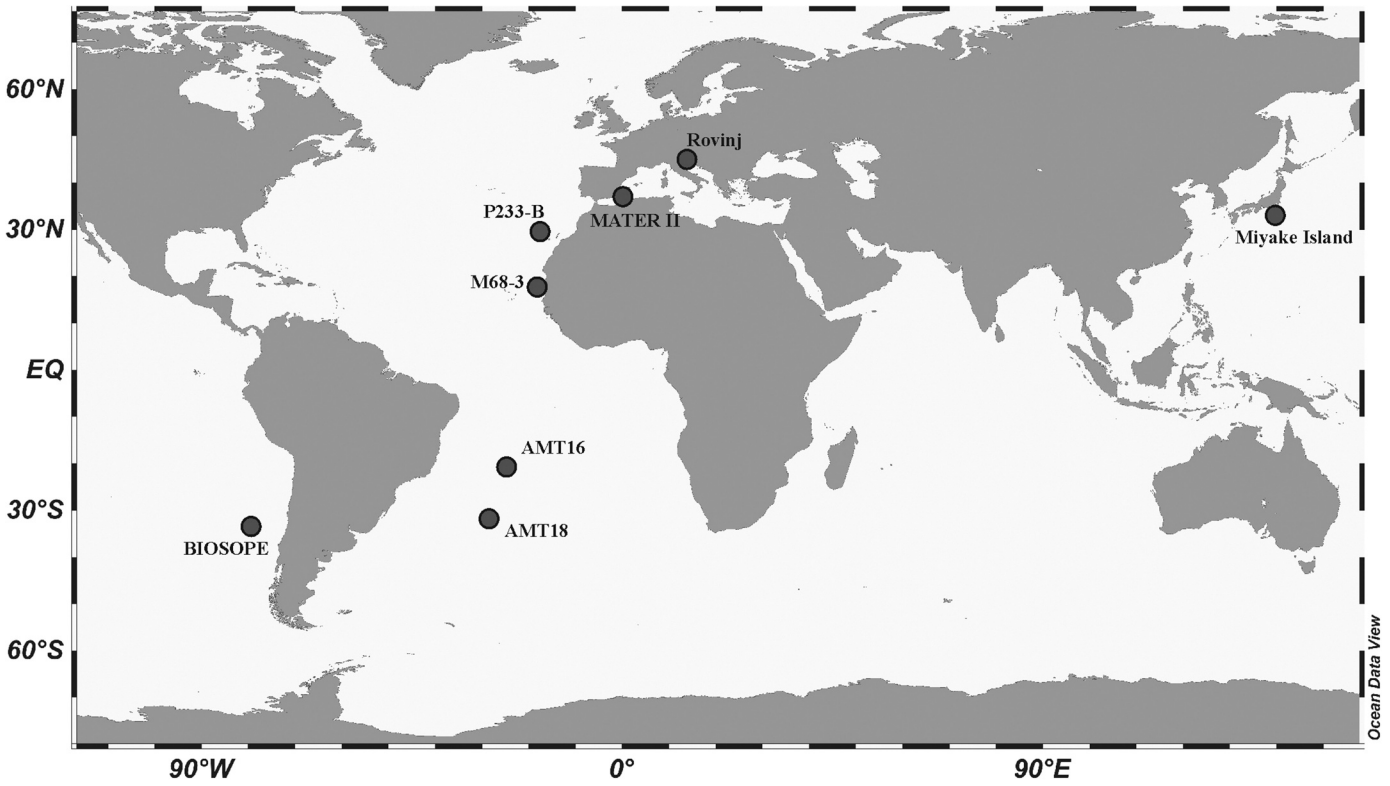


Fig. 5. Map showing the locations from which *Palusphaera* specimens were obtained.

WESTERN MEDITERRANEAN SEA

Samples have been obtained from the surface waters of the northwestern Mediterranean and Alboran Seas on board the R/V *Hesperides* during the oceanographic cruise MATER II in September–October 1999 (Font 1999).

ADRIATIC SEA

A time series sample used in the present work comes from the surface waters (5 m water depth) of a coastal station (45° 04.8'N, 13°36.6'E) off Rovinj, Croatia, in the northeastern Adriatic Sea in March 2009 aboard the R/V *Villa Velebita* (as described in Godrijan *et al.* 2018).

Filtration and SEM

Seawater samples were obtained via 5-litre Niskin bottles that were attached to CTD rosette samplers, except for samples originating from the Miyake Island that were collected using a bucket. Approximately 1 litre of seawater was filtered through 0.8-µm pore size Whatman Nuclepore polycarbonate track-etched filters of 25 mm diameter apart from P233-B cruise, during which 4 litres of seawater were filtered onto 47-mm cellulose nitrate filters (Sartorius) of 0.45 µm pore size. A low-pressure vacuum pump was used during the filtration process to prevent mechanical damage of the coccosphere specimens. The filters were subsequently oven-dried at 40°C and stored in 47-mm Millipore plastic Petri dishes; a portion of each filter was cut out and fixed onto aluminium stubs to be gold-coated. Examination of the samples was then performed on a Phillips XL-30 FEG field emission SEM at the facilities of the Natural History Museum, London.

Terminology and morphology

Morphological descriptions are given based on the guidelines of Kleijne (1992) and Young *et al.* (1997). With regards to the terminology of Rhabdosphaeraceae cycles, we follow the scheme proposed by Kleijne (1992), as also used by Young *et al.* (2003) and Bown *et al.* (2017). All morphological measurements presented in this study were obtained using the image analysis software programme ImageJ (Schneider *et al.* 2012).

RESULTS

Separation of *P. probertii sp. nov.* from *P. vandelii*

Our examination of SEM micrographs yielded in total 24 *P. vandelii*-like coccospheres (14 specimens of *P. vandelii* and 10 specimens of *P. probertii sp. nov.*; Table 2). These forms, however, were seen to display considerable variations in their coccolith morphologies and diameters. In order to assess this variability, we subjectively separated specimens with typical *P. vandelii* characteristics (i.e. circular coccolith outline, larger coccolith size and spine structure with spirally oriented elements) vs specimens that bore coccoliths of noticeably more elliptical shape, smaller size and a spine structure with elements parallel aligned to the long axis. We

Table 2. List of all sampling localities, including physicochemical data, with *Palusphaera* specimens used in the present study.

Expedition	Station	Sampling date	Latitude (°N)	Longitude (°E)	Sampling depth (m)	Temperature (°C)	Salinity (psu)	NO^{3-} (µmol/L)	Number of specimens				Figures
									P. vandelii	*P. probertii*	*P. crosiae*	*P. bownii*	
Mediterranean and Alboran Seas													
MATER II	CTD69-11	10-1999	37.430	−0.422	42.5				2	1	3	0	8, 14, 19, 20
	CTD69-08	10-1999	37.430	−0.422	70				1	0	1	0	17, 18, 21
Adriatic Sea													
Rovinj	TS 17-03-09	17-03-2009	45.040	13.630	5	13.00	36.50		1	0	0	0	11
North Atlantic Ocean													
P233-B	P233b-2	24-09-1997	29.762	−17.930	25	22.00			0	2	0	0	12
M68-3	276-20	19-07-2006	18.000	−17.000	30	24.20			2	0	0	0	*
South Atlantic Ocean													
AMT16	17	01-06-2005	−22.459	−24.991	52	25.189	37.13	0.09	1	0	1	0	*
AMT18	CTD063	26-10-2008	−8.825	−24.995	0	25.57	36.20	0.03	0	0	0	1	22
	CTD067-01	27-10-2008	−13.994	−24.995	0	24.54	36.90	0.01	0	0	0	1	23, 24
	CTD089	02-11-2008	−32.179	−29.826	0	17.33	35.58	0.02	1	4	2	0	*
	CTD089	02-11-2008	−32.179	−29.826	72	16.51	35.62	0.06	2	0	0	0	9, 10
	CTD089	02-11-2008	−32.179	−29.826	84	16.15	35.60	0.22	1	1	2	0	15
Pacific Ocean													
BIOSOPE	CTD184-2 m	02-12-2004	−32.680	−84.070	2	15.00	34.50		1	2	0	0	13, 16
	CTD184-105 m	02-12-2004	−32.680	−84.070	105	14.00	34.25		1	0	0	0	*
Miyake Jima	Miyake Jima 4	02-11-1999	34.104	139.491	0	21.00			1	0	0	0	7
								Total	*14*	*10*	*9*	*2*	

Specimens that are not illustrated but were studied are indicated with an asterisk (*).

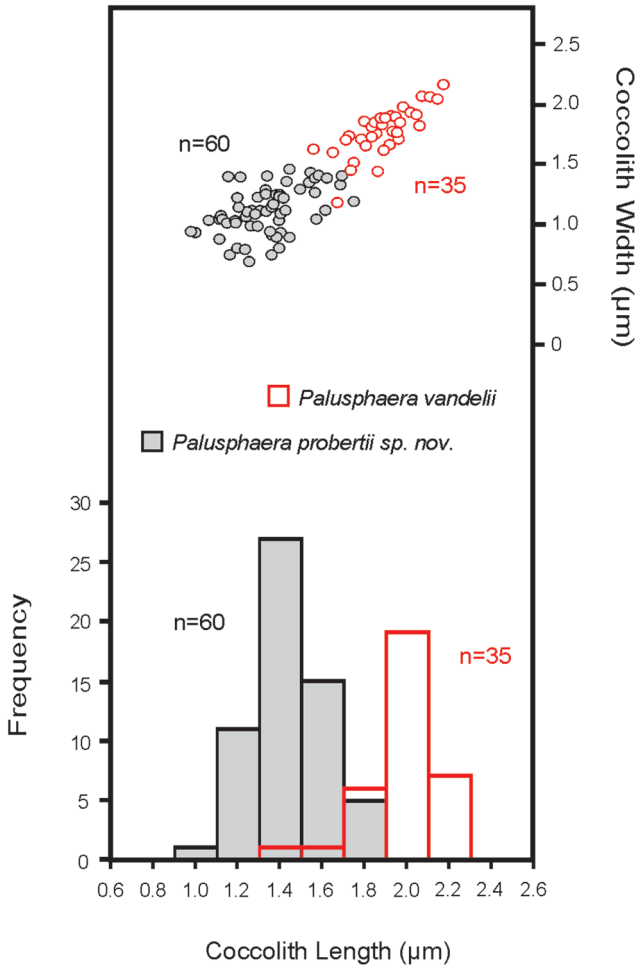


Fig. 6. Frequency and bivariate plots of the main morphological parameters (coccolith length and width) measured in specimens of *Palusphaera vandelii* (image codes 222-04, 289-62, 246-06a 262-20, 247-17 276-30, 280-14) and *Palusphaera probertii sp. nov.* (image codes 118-55, 188-03, 288-06, 297-77).

subsequently performed morphometric analyses on several of these specimens and measured 95 (in total) well-preserved body coccoliths (BCs) in plan view; these allowed a straightforward biometric analysis and correspondingly yielded more objective data (Table S1).

There were 35 typical *P. vandelii* coccoliths from five coccospheres and 60 well-differentiated forms from four well-preserved coccosphere specimens. The morphometric frequency plots (Fig. 6) indicated a clear bimodal distribution pattern of all studied specimens with an obvious clustering at 1.3 µm to 2.3 µm (mean 2.0 µm) for *P. vandelii* and a cluster group at 0.9 µm to 1.9 µm (mean 1.4 µm) for all other specimens. This well-defined separation pattern was further supported by our coccolith width data (Fig. 6), with specimens of *P. vandelii* demonstrating higher width values (>1.5 µm). Hence, two different coccolith size groups could be seen, essentially confirming our initial morphologic grouping, and we therefore taxonomically separated them and proposed them as two discrete taxa.

Taxonomy

Division Haptophyta D.J. Hibberd (1972) *ex* Edvardsen & Eikrem in Edvardsen *et al.* (2000)
Class Prymnesiophyceae D.J. Hibberd (1976) *emend.* Cavalier-Smith *et al.* (1996)
Order Syracosphaerales W.W. Hay (1977) *emend.* Jer.R. Young *et al.* (2003)
Family Rhabdosphaeraceae Haeckel (1894)

Genus *Palusphaera* Lecal-Schlauder *emend.* R.E. Norris

EMENDED DESCRIPTION: Coccosphere monomorphic and monothecate, with only spine-bearing BCs and no differentiated circum-flagellar coccoliths. BCs flat, with two rim cycles, an outer/upper cycle with near-radial sutures, an inner/lower cycle showing strong sinistral obliquity in proximal view. The radial lath cycle shown by many other Rhabdosphaeraceae is absent; instead, the lamellar cycle fills the central area. The lamellar cycle of tabular elements shows dextrogyral obliquity in distal view and laevogyral obliquity in proximal view. Central process is a spine, variable in shape but without a collar; proximal side with a central pore surrounded by several (usually three) angular nodes.

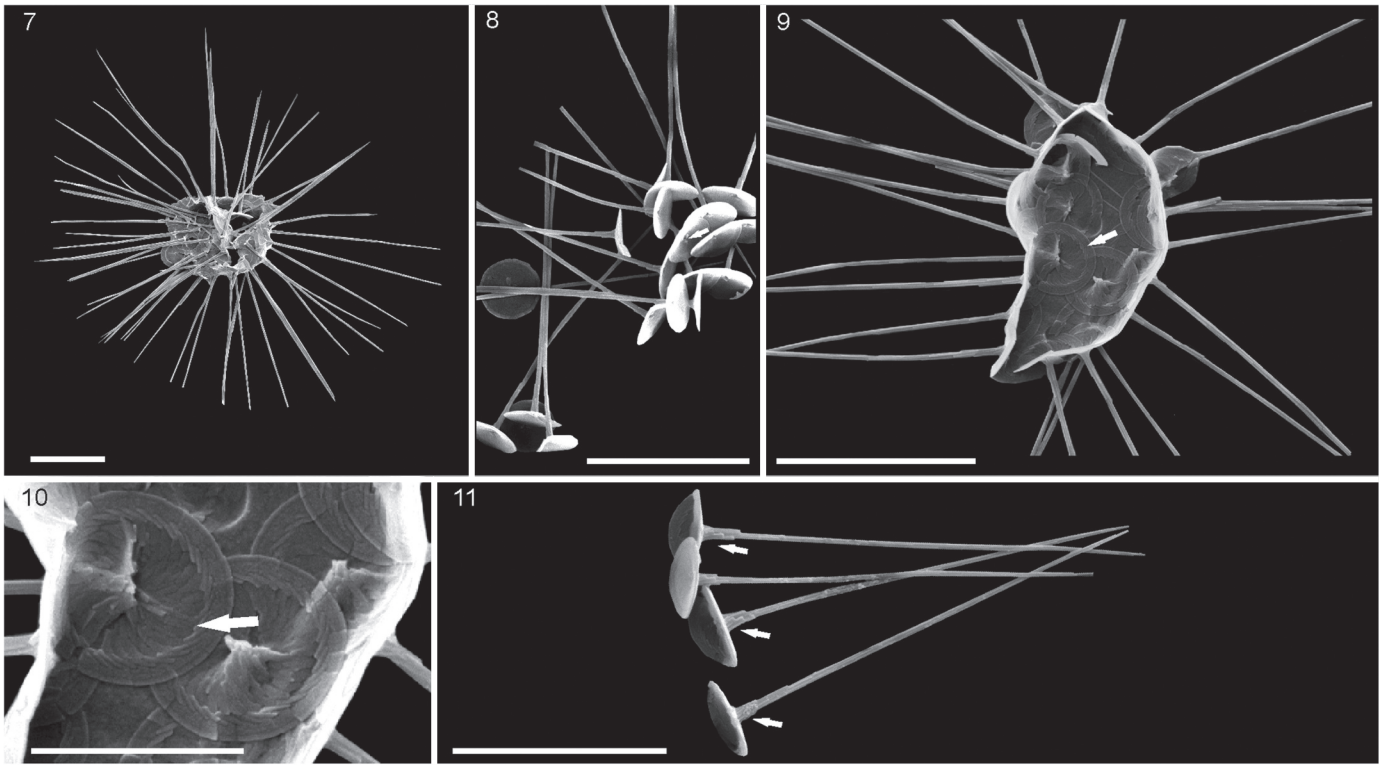
TYPE SPECIES: *Palusphaera vandelii* Lecal-Schlauder (1966) *emend.* R.E. Norris (1984). The original author published under the name Lecal.

Palusphaera vandelii Lecal-Schlauder *emend.* R.E. Norris
Figs 7–11

PUBLISHED ILLUSTRATIONS OF THE SPECIES: Lecal (1966, pp 68-69, text-fig. K, pl. 2, fig. 9); Lecal (1967, pp 318-320, text-fig. 13, figs 19-20); Norris (1984, p. 35, figs 1f, 9, 10); Kleijne (1992, pp 38-39, pl. 8, fig. 1); Giraudeau & Bailey (1995, p. 1833, pl. 3, fig. 3); Aubry (1999, pp 298-300, figs 3-13); Yang *et al.* (2001, pp 295-296, pl. III, fig. 8); Cros (2002, p. 36, pl. 9, fig. 5); Cros & Fortuño (2002, pp 24-25, fig. 22B); Young *et al.* (2003, pp 56-57, pl. 25, fig. 9); Andruleit *et al.* (2005, p. 12, pl. 2, fig. 4); Kahn & Aubry (2006, pp 319, 334, text-fig. 2c and pl. 2, figs 1-3 *non* figs 4-6); Kahn (2007, p. 38, pl. 2, figs 1-3 *non* figs 4-6); Gravalosa *et al.* (2008, p. 21, pl. I, fig. 4); Malinverno *et al.* (2008, p. 65, fig. 36); Wang *et al.* (2012, p. 5, pl. 2, figs G, I); Guerreiro *et al.* (2014, p. 355, fig. B.17); Malinverno *et al.* (2015, p. 504, pl. 3, fig. 10); Chang & Northcote (2016, p. 8, fig. 3b); Karatsolis *et al.* (2017, p. 144, pl. 2, fig. 7); Chang (2019, p. 51, figs 20C, D).

PREVIOUS RECORDS UNDER MISAPPLIED NAMES: *Acanthoica quattrospina* Lohmann *sensu* Halldal & Markali (1955, pp 15-16, fig. 3, *non* figs 1, 2, 4). *Rhabdosphaera longistylis* J. Schiller *sensu* Norris (1971, p. 902, fig. 4); Kling (1975, p. 6, pl. 3, figs 13-14); Conley (1979, p. 30, pl. 3, fig. 18 and pl. 4, fig. 9); Reid (1980, p. 157, pl. 4, fig. 2 *non* fig. 3). *Halopappus* cf. *H. adriaticus* J. Schiller *sensu* Winter *et al.* (1979, p. 200, pl. III, fig. 5). *Palusphaera vandelii* var. *vandelii sensu* Dimiza (2006, p. 61, pl. X, figs 3-4; unpublished PhD thesis).

EMENDED DESCRIPTION: Coccosphere monomorphic, spherical but usually seen collapsed, composed of *c.* 50 BCs. BCs planoliths with a subcircular to circular outline; rim thin with typical Rhabdosphaeraceae rim structure. Lamellar cycle fills central area, convex on distal side and concave on the proximal side. Lamellar cycle elements rod shaped, overlapping and displaying dextrogyral curvature on the distal side and laevogyral in proximal view (e.g. Fig. 10). Central process with a central pore in proximal view, usually surrounded by two to three small nodes; distal side with a thin and long spine, formed of numerous spirally arranged elements at the base becoming less spiral upwards. Spine is styliform-shaped without a collar.



Figs 7–11. SEM micrographs of *Palusphaera vandelii*. Scale bar = 5 μm for Figs 7, 8, 9, 11.
Fig. 7. Complete coccosphere.
Fig. 8. Specimen with coccoliths that bear planolith bases with usually three nodes in proximal side (arrow).
Fig. 9. Collapsed coccosphere with circular coccoliths; inner rim cycle is typically wider in proximal side (arrow).
Fig. 10. Detailed view of Fig. 9; arrow shows the laevogyral curvature of the crystal elements of the lamellar cycle, observed in proximal view. Scale bar = 2 μm.
Fig. 11. Disarticulated coccoliths bearing spines with spirally arranged crystal segments, highly visible towards the central process (arrows).

DIMENSIONS: Coccosphere diameter *c*. 5–10 μm excluding processes and *c*. 25–30 μm with processes. BCs *c*. 2.0 μm long and *c*. 1.7 μm wide; rim *c*. 0.2–0.5 μm. Spine *c*. 10 μm long.

Palusphaera probertii Archontikis & Jer.R. Young *sp. nov.*
Figs 12–16

PREVIOUS RECORDS UNDER MISAPPLIED NAMES: *Rhabdosphaera longistylis* J. Schiller *sensu* Reid (1980, p. 157, pl. 4, fig. 3). *Palusphaera vandelii sensu* Cros (2002, p. 36, pl. 9, fig. 3); Cros & Fortuño (2002, pp 24-25, fig. 22A); Yang *et al.* (2003, p. 38, pl. IV, fig. 1); Young *et al.* (2003, pp 56-57, pl. 25, fig. 8); Kahn & Aubry (2006, p. 334, pl. 2, figs 4-6); Andruleit (2007, p. 43, fig. 6d); Kahn (2007, p. 38, pl. 2, figs. 4-6); Wang *et al.* (2012, p. 5, pl. 2, fig. H).

DESCRIPTION: Coccosphere, monomorphic and spherically shaped, but usually seen collapsed, composed of *c*. 45–60 BCs. BCs broadly elliptical to subcircular in plan view, with narrow rims and nearly flat bases. Rim with typical Rhabdosphaeraceae rim structure. Central area filled by a lamellar cycle of numerous rod-shaped, slightly overlapping crystal segments; no radial cycle is observed. Central process bears a thin, hollow, styliform spine with no collar; spine structure composed predominantly of numerous elongate elements arranged parallel to the axis of the spine. The spine is remarkably long compared to the coccosphere diameter. The proximal planolith side has three robust angular nodes around the central pore.

DIMENSIONS: Coccosphere diameter *c*. 7–8 μm excluding processes and *c*. 13–18 μm with processes. BCs *c*. 1.5 μm × *c*. 1.1 μm; rim *c*. 0.2 μm in length and width. Spine is typically *c*. 5–8 μm long.

HOLOTYPE: 118-55 (specimen illustrated in Fig. 12), stub no. 257/0, deposited at the collections of the Natural History Museum, London under the designation PM NF 4591 118-55.

PARATYPES: 212-09 (stub no. 511/3, designation PM NF 4875 212-09); 188-03 (stub no. 459/2, designation PM NF 4814 188-03); 297-77 (stub no. 729/0, designation PM NF 4928 297-77); 212-19 (stub no. 511/3, designation PM NF 4875 212-19). Specimens of these stubs are illustrated by Figs 13–16.

TYPE LOCALITY: North-eastern Atlantic Ocean (29°45.7'N, 17°55.8'W, depth 25 m, 24 September 1997, P233B Expedition, Station P233b-2).

DISTRIBUTION: Subtropical waters.

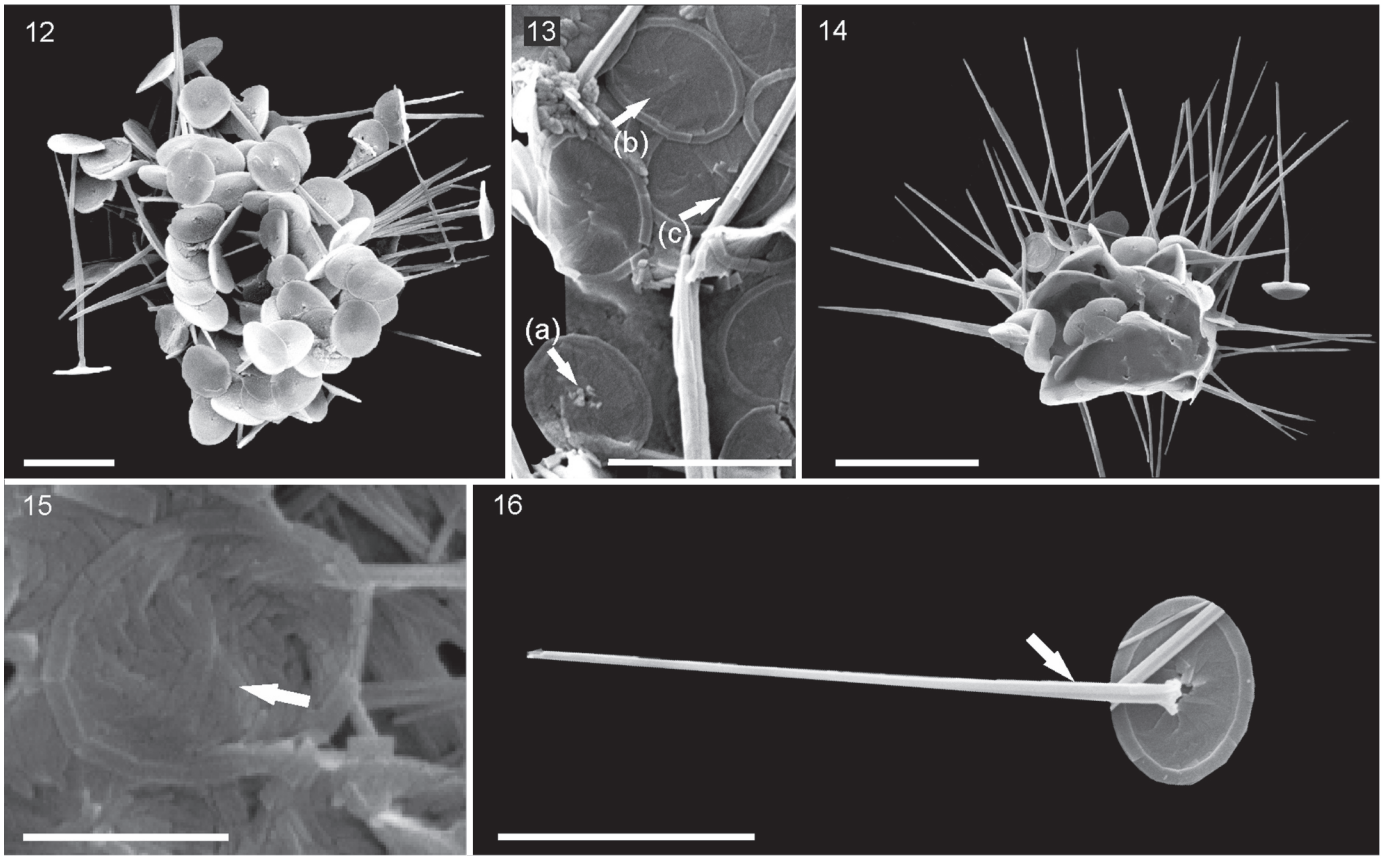
NUMBER OF SPECIMENS STUDIED: Ten.

ETYMOLOGY: After Dr. Ian Probert (Station Biologique de Roscoff) in recognition of his many contributions to extant coccolithophore biology and physiology.

REMARKS: The species is similar to *P. vandelii* but with noticeably smaller BCs that present a more broadly elliptical shape. The outer rim of the BCs on the distal side is usually narrower than that of *P. vandelii*, and the styliform central process is hollow and predominantly composed of a single set of very long elements aligned parallel to the long axis. This clearly opposes the spine structure of *P. vandelii*, which is formed by numerous shorter (*c*. 1 μm) elements in a spiral arrangement.

Palusphaera crosiae Archontikis & Jer.R. Young *sp. nov.*
Figs 17–21

PREVIOUS RECORDS UNDER MISAPPLIED NAMES: sp. aff. *Palusphaera sensu* Kleijne (1992, p. 38, described under remarks on *Palusphaera* but



Figs 12–16. SEM micrographs of *Palusphaera probertii sp. nov*.
Fig. 12. Holotype and complete coccosphere specimen. Scale bar = 2 µm.
Fig. 13. Detailed view of a specimen with broadly elliptical planoliths showing a central pore and three angular nodes on the proximal side (a) and clockwise imbrication on the distal side (b); broken spine (c) is long and thin, formed of crystallites arranged parallel to the spine axis. Scale bar = 2 µm.
Fig. 14. Collapsed coccosphere. Scale bar = 5 µm.
Fig. 15. Incomplete coccolith in distal view; crystal elements show dextrogyral curvature (arrow). Scale bar = 1 µm.
Fig. 16. Detailed view of a broadly elliptical coccolith, small in size, and its broken styliform process. The lath-like crystal segments of the spine are arranged parallel to its long axis (see arrow). Scale bar = 1 µm.

not illustrated). *Palusphaera* sp. 1 (type robusta) *sensu* Cros (2002, p. 36, pl. 9, figs 4, 6); Cros & Fortuño (2002, p. 84, figs 22C, 22D); Young *et al.* (2003, pp 56–57, pl. 25, figs 10, 11); Malinverno *et al.* (2008, p. 66, fig. 37). *Palusphaera vandelii* var. *crassa sensu* Dimiza (2006, pp 61–62, pl. X, figs 5–6 and pl. XI, figs 1–6, unpublished PhD thesis, invalid).

DESCRIPTION: Coccosphere, monomorphic and generally seen collapsed but probably spherical in shape, with *c.* 45–60 BCs. BC bases broadly elliptical in outline and slightly concavo-convex. Rim shows typical Rhabdosphaeraceae rim structure. Central area filled by the lamellar cycle; no radial cycle is present. Central process is a long, tapering spindle-shaped spine. Maximum thickness is at one-third to one-quarter of the height and it tapers to a fine point. The spine is formed from robust laths, *c.* 1.0 µm × 0.15 µm at the base, becoming smaller towards the tip; they abutt neatly to form a 6- to 8-µm sided smooth hollow structure. Adjacent laths are offset by about one-third of their length. BC proximal side with a central pore surrounded by a few angular nodes.

DIMENSIONS: Coccosphere diameter *c.* 5–9 µm without processes and *c.* 15–25 µm including processes. BCs *c.* 1.2–2.0 µm × *c.* 1.0 µm; rim is *c.* 0.2 µm. Spine *c.* 6 µm long.

HOLOTYPE: 200-07 (specimen illustrated in Figs 17–18), stub no. 470/3, deposited at the collections of the Natural History Museum, London under the designation PM NF 4917 200-07.

PARATYPES: 211-21 (stub no. 487/0, designation PM NF 4855 211-21); 211-22 (stub no. 487/0, designation PM NF 4855 211-22); 177-56 (stub no. 302/2, designation PM NF 4663 177-56). Specimens of these stubs are illustrated by Figs 19–21.

TYPE LOCALITY: North-western Mediterranean and Alboran Seas (37° 25.98'N, 0°25.3'W, depth 70 m, October 1999, MATER II Expedition, Station 69-08).

DISTRIBUTION: Subtropical waters.

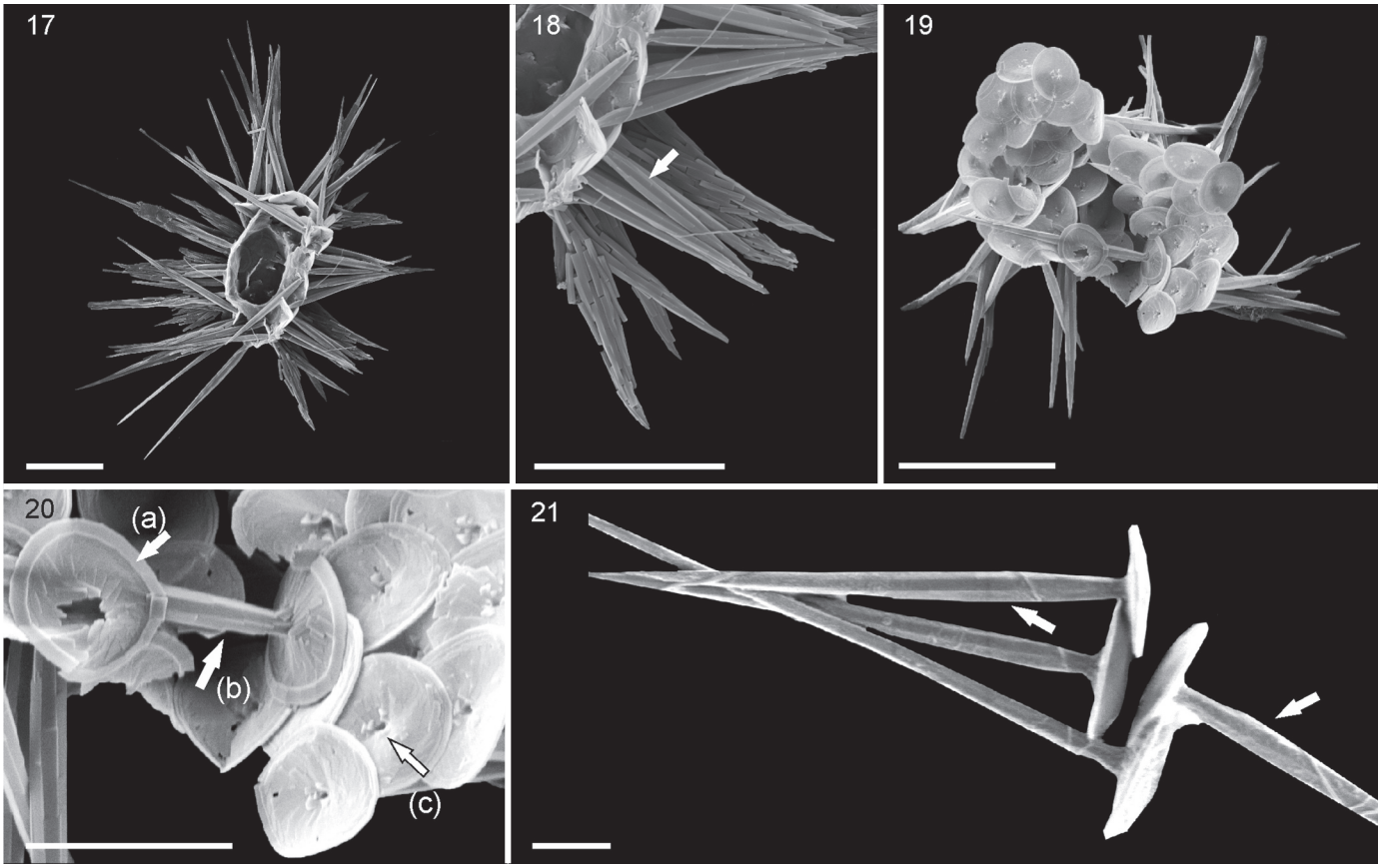
NUMBER OF SPECIMENS STUDIED: Nine, plus two published in Cros & Fortuño (2002).

ETYMOLOGY: After Dr. Lluïsa Cros (Institut de Ciències del Mar, CSIC), who first illustrated the taxon, and in recognition of her many contributions to extant coccolithophore taxonomy.

REMARKS: The species differs from the other taxa in possessing a styliform spine with robust and thick lath-like crystal segments, markedly thicker at the one-third to one-quarter height from the base of the central area. The distal side outer rim cycle is distinctly narrower compared to that of *P. vandelii*.

Palusphaera bownii Archontikis & Jer.R. Young *sp. nov.*
Figs 22–24

DESCRIPTION: Coccosphere, monomorphic of subspherical to spherical shape, usually found collapsed, with *c.* 80–120 BCs. BCs broadly elliptical to circular in outline with slightly convex planolith bases. Rim shows the



Figs 17–21. SEM micrographs of *Palusphaera crosiae sp. nov*. Scale bar = 5 μm for Figs 17, 18, 19.
Fig. 17. Holotype and complete coccosphere.
Fig. 18. Detailed view of Fig. 17; arrow indicates the part of the spine being markedly thicker at the one-third to one-quarter height from the base.
Fig. 19. Complete coccosphere with subcircular planoliths.
Fig. 20. Detailed view of Fig. 19; planoliths with (a) a relatively wide outer rim cycle, (b) a styliform spine formed at the centre of the lamellar cycle in distal side, and (c) three robust angular nodes surrounding the central pore in proximal side. Scale bar = 2 μm.
Fig. 21. Side view of styliform processes of disarticulated spine-bearing planoliths. Scale bar = 1 μm.

typical Rhabdosphaeraceae rim structure. Central area, filled by lamellar cycle, with overlapping tabular elements showing clockwise curvature in distal view. The radial cycle is absent. Central process is a trumpet-shaped spine without a collar, formed of vertically elongate elements arranged in spiralling series; the distal end is formed of blockier elements, but these appear to have developed from the spiral elements of the spine. Trumpet aperture wider than the basal spine width. On the proximal side of the coccolith there is a central pore surrounded by two to three nodes.

DIMENSIONS: Coccosphere diameter *c*. 10–15 μm. BCs 1.0–1.5 μm long and wide; rim *c*. 0.2 μm in width. Spine *c*. 1.5 μm long and trumpet aperture *c*. 0.5 μm wide, although few spines tend to bear slightly closer apertures at their outermost part.

HOLOTYPE: 302-04 (specimen illustrated in Fig. 22), stub no. 756/1, deposited at the collections of the Natural History Museum, London under the designation PM NF 4930 302-04.

PARATYPE: 308-031 (stub no. 768/0, designation PM NF 4932 308-031), 308-032 (stub no. 768/0, designation PM NF 4932 308-032). One specimen of this stub is illustrated by Figs 23, 24.

TYPE LOCALITY: Subtropical waters of the South Atlantic Ocean (8° 49.52'S, 24°59.72'W, depth 0 m, 28 October 2008, AMT18 Expedition, Station CTD063).

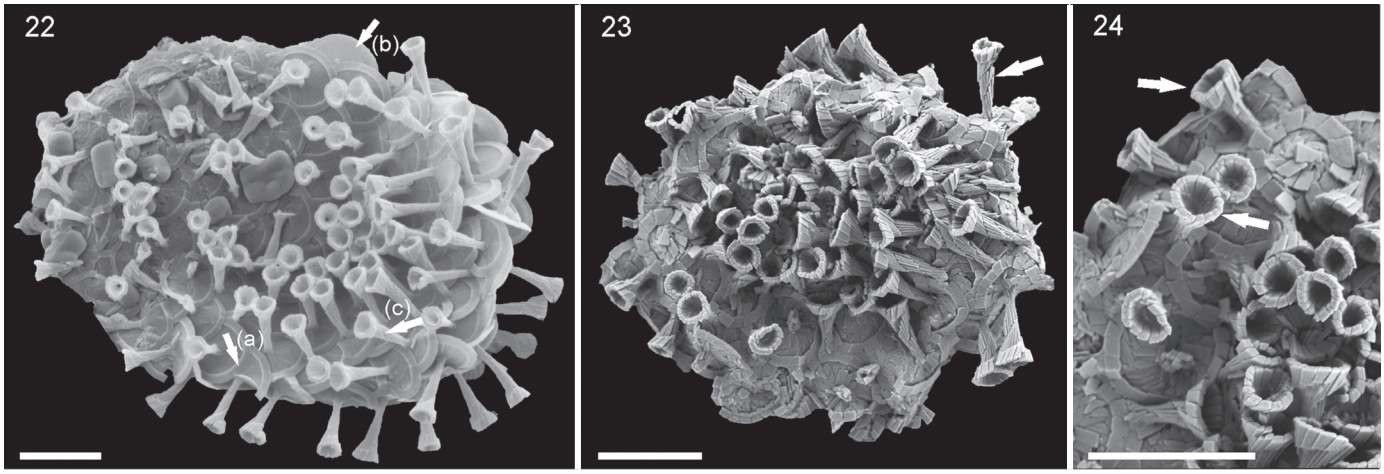
NUMBER OF SPECIMENS STUDIED: Two.

ETYMOLOGY: After Professor Paul R. Bown (University College London), in recognition of his many contributions to Jurassic, Cretaceous and Paleogene coccolithophore taxonomy.

REMARKS: We have only found two coccospheres of this species and to our knowledge no other specimens have been published. Nonetheless, this is a distinctive form and clearly separate from any other coccolithophore, so we are confident it is a discrete species. The species shows possible affinities to several genera. The trumpet-like spines resemble those of *Discosphaera*, but the base lacks a radial cycle, and the spine shows a structure that is not seen in *Discosphaera*. The spine structure is closer to that of *Rhabdosphaera*, but in *Rhabdosphaera* coccospheres are dimorphic with both spine-bearing and non-spine-bearing BCs. Finally, the species resembles *Palusphaera* in being monomorphic and lacking a radial cycle. In addition, the rows of the laminar cycle elements show the same curvature (clockwise in distal view) as that of *Palusphaera* coccoliths and the opposite of that shown by *Rhabdosphaera* coccoliths. Therefore, we place the species in *Palusphaera*.

DISCUSSION

The genus *Palusphaera* is a distinctive extant coccolithophore, known only from the heterococcolith-bearing phase, and based on our observations it now comprises four discrete taxa



Figs 22–24. SEM micrographs of *Palusphaera bownii sp. nov*. Scale bar = 2 µm.
Fig. 22. Holotype. Collapsed coccosphere bearing nearly circular planolith bases with outer rim cycles that are broader on the distal side (arrow a) than on the proximal side (arrow b); the central process displays a short trumpet-shaped process (arrow c).
Fig. 23. Collapsed specimen bearing trumpet-shaped spines with spirally arranged crystal segments (see arrow) extending outwards forming distinct apertures.
Fig. 24. Detailed view of Fig. 23 showing the ultrastructure of the spine aperture (arrows) and the dextrogyral curvature of lamellar elements in distal view.

(Fig. 25), namely, *P. vandelii, P. probertii sp. nov., P. crosiae sp. nov*. and *P. bownii sp. nov*., which show a range of shared morphological characteristics. All of these species possess monomorphic and monothecate coccospheres composed of spine-bearing BCs, without differentiated circum-flagellar coccoliths. The BCs consist of solid circular to elliptical planolith bases with a rim and an imbricate central area (see Fig. 25; Table 1). The rim, as in all typical Rhabdosphaeraceae (e.g. Fig. 1; Kleijne 1992; Bown *et al.* 2017) is formed of two cycles: an outer and upper cycle with radial sutures and an inner and lower cycle with strongly oblique sutures, showing sinistral obliquity in proximal view. Unlike *Acanthoica, Algirosphaera, Cyrtosphaera* and *Discosphaera*, there is no radial lath cycle present. Instead, the central area is closed by the lamellar cycle of subrectangular, slightly overlapping crystallites. In proximal view, these can be seen to be arranged in rows showing laevogyral curvature; i.e. they appear bent to the left as they run from the centre to the rim; the proximal surface of the central process typically shows a central pore that is surrounded by a limited number of nodes, usually two to three (e.g. Fig. 20). In distal view, lamellar cycle segments show dextrogyral curvature but this is less obvious due to overlap of elements. The central elements of the lamellar cycle extend outwards to form an imbricate spine in distal view. The spines are formed of butting segments that disintegrate into separate elements (e.g. Figs 16, 18, 21), and they do not bear collars at their bases.

Palusphaera is most obviously separated from *Rhabdosphaera* by being monomorphic; all of the BCs have spines, whereas in *Rhabdosphaera* there is an outer layer of non-spine-bearing coccoliths. In addition, however, our observations suggest that two other features consistently separate the four *Palusphaera* species from the two extant *Rhabdosphaera* species. First, spines in *Rhabdosphaera* species are robust solid structures formed of intergrown elements, whereas those of *Palusphaera* are delicate hollow structures formed of directly abutting elements. Second, the lamellar cycle elements in *Rhabdosphaera* show the opposite sense of curvature to those in *Palusphaera*; i.e. they show laevogyral curvature on the distal side and dextrogyral on the proximal side.

Consequently, the observations reported in our study conclusively supported a proposal to emend the description of both *Palusphaera* and *Palusphaera vandelii*. In parallel, based on the well-differentiated subset of taxa within the Rhabdosphaeraceae, our results provided the evidence needed to formally maintain *Palusphaera* separable from its sister taxa and consider it a clearly diagnosable and taxonomically valid genus.

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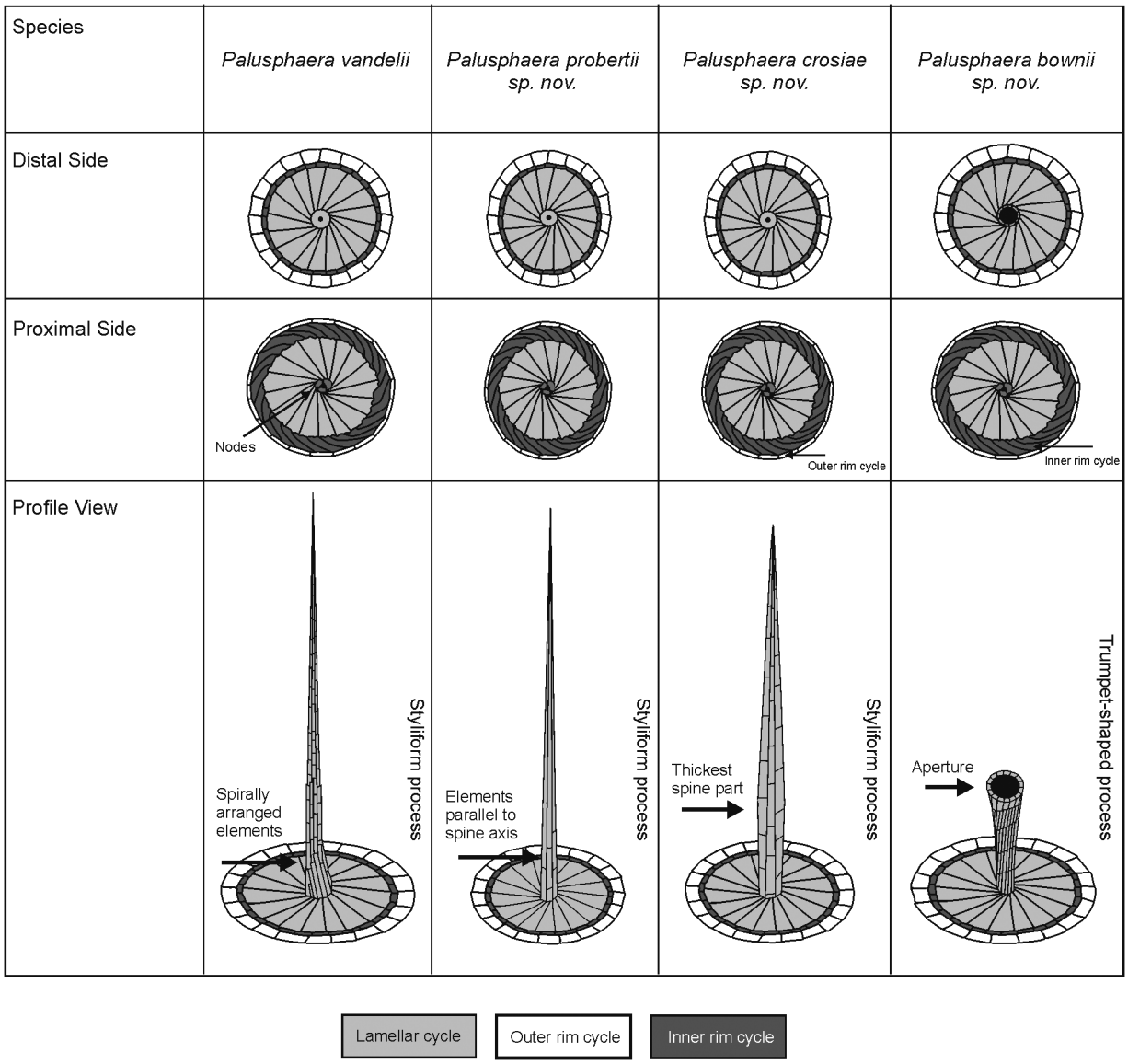

Fig. 25. Schematic representation of the coccolith morphology and ultrastructure of all currently known morphospecies in the genus *Palusphaera*.

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