Phycologia

ISSN: 0031-8884 (Print) 2330-2968 (Online) Journal homepage: www.tandfonline.com/journals/uphy20

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PHYCOLOGIA
2023, VOL. 62, NO. 2, 179–193
https://doi.org/10.1080/00318884.2023.2172841

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Taxonomic re-evaluation of *Ericiolus* and *Mercedesia* (Prymnesiophyceae) and description of three new species

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ABSTRACT
The genera *Ericiolus* and *Mercedesia* are distinctive extant coccolithophores that are characterized by monothecate, monomorphic coccospheres with one type of triradiate star-shaped nannoliths. The two genera were described from the Danish coastal waters, the surface waters of the Arctic, and the Southern Oceans. During a study of samples from the low photic zone of the Mediterranean and Sargasso Seas, and from the subtropical gyres of the South-eastern Pacific and the South Atlantic Oceans, 44 collapsed coccospheres with triradiate star-like nannoliths were observed via scanning electron microscopy. Observations on the morphologies and biometric assessments of these specimens revealed that three distinct sets of nannoliths can be distinguished and that these were morphologically differentiated from all currently known species of *Ericiolus* and *Mercedesia*. The new forms and the previously described species of *Ericiolus* and *Mercedesia* were, however, similar, as they all demonstrated a distinctive set of collectively shared morphological characters and almost identical size ranges. On the basis of this, and instead of describing a third genus for the same group of nannoliths, we preferred to taxonomically synonymize *Mercedesia* with *Ericiolus* and revise the definition of *Ericiolus*. Therefore, we describe three new species, *Ericiolus bendifii sp. nov., Ericiolus sheldoniae sp. nov*. and *Ericiolus mattioliae sp. nov*., and an incompletely defined taxon, as *Ericiolus* cf. *bendifii*, and establish the new combinations *E. aspiphorus comb. nov., E. multistellatus comb. nov*. and *E. pusillus comb. nov*.

ARTICLE HISTORY
Received 22 September 2022
Accepted 23 January 2023
Published online 14 March 2023

KEYWORDS
Biodiversity; Coccolithophores; Extant; Morphology; Nannolith; Phytoplankton

INTRODUCTION

The taxonomy of extant coccolithophores (Prymnesiophyceae, Haptophyta) has arguably been more comprehensively monographed and reviewed than that of any other phytoplankton (Jordan *et al.* 1995; Young & Bown 1997; Cros & Fortuño 2002; Jordan *et al.* 2004; Malinverno *et al.* 2008; Chang 2019) and most living coccolithophores can be readily identified to species-level with a high degree of confidence (Young *et al.* 2003; Jordan *et al.* 2004; Young *et al.* 2023). In addition, the isolation into culture of a diverse set of coccolithophores has enabled the revision of taxonomy through precise molecular sequencing and phylogenetic evaluations for diversity and evolutionary history (e.g. Sáez *et al.* 2004; Probert *et al.* 2007; Bendif *et al.* 2011; Edvardsen *et al.* 2011; Filatov *et al.* 2021; Bendif *et al.* 2023). Observations on coccolithophore life cycle associations, where coccoliths of different phases (diploid and haploid) and morphologies are found to co-occur (e.g. Cros *et al.* 2000; Archontikis & Young 2020; Keuter *et al.* 2021), have provided further valuable contributions to 1) understanding relationships of diverse morphotypes, 2) uniting taxa that were previously considered separate, and therefore, 3) resolving complex taxonomic and nomenclatural issues. All of the above-mentioned factors combined with their abundant fossil record make coccolithophores an ideal group for studying evolutionary patterns and processes in phytoplankton and the robust interpretation of their biodiversity patterns. Nonetheless, many species are yet to be successfully cultured, their life cycle is still unknown, and therefore, studies of coccolith morphology and ultrastructure, including identification of taxa in natural populations using microscopical techniques, remain prime tools for taxonomy.

An intriguing aspect of coccolithophore biodiversity is the presence of many seemingly rare but globally distributed species, especially in the low photic zone (LPZ). Many of these coccolithophores have only been informally proposed, but description of these and of entirely new forms has greatly progressed over recent years (e.g. Kleijne & Cros 2009; Andruleit & Young 2010; Young *et al.* 2014; Thomsen & Østergaard 2015; Thomsen *et al.* 2015; Andruleit & Jordan 2016; Andruleit *et al.* 2016; Thomsen *et al.* 2016; Andruleit & Jordan 2017; Archontikis & Young 2020; Archontikis *et al.* 2020; Archontikis & Young 2021; Keuter *et al.* 2021), in which many of the practical nomenclatural issues faced by taxonomists have been resolved. Here, we use electron micrographs from our individual collections to describe further elements of this biota.

The genera *Ericiolus* H.A. Thomsen and *Mercedesia* H.A. Thomsen & J.B. Østergaard are minute (3–5 μm) planktonic

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/00318884.2023.2172841

protists that produce coccospheres consisting of numerous monomorphic, star-shaped nannoliths (Thomsen *et al.* 1995; Thomsen & Østergaard 2015). The cells bear two long similar, naked flagella and a haptonema, so they are unambiguously haptophytes. *Ericiolus* and *Mercedesia* were separated on the grounds of showing nannoliths with, respectively, four and three spine-like elements. In *Ericiolus* the nannoliths are formed of four radiate spine-like elements, three of them arranged broadly parallel to the cell surface, and the fourth perpendicular to it. Conversely, in *Mercedesia* the nannoliths are formed of only three units, all arranged parallel to the cell surface, forming a triangular or triradiate nannolith. The nannoliths are calcified, but lack the annular structure of heterococcoliths, i.e. instead of being formed by a ring of crystal units, they are made from radially arranged units. This feature separates them from other living coccolithophores, and so they are regarded as *incertae sedis* nannoliths (Young *et al.* 2003; Young *et al.* 2023). Two species of *Ericiolus* (*E. frigidus* H.A. Thomsen and *E. spiculiger* H.A. Thomsen) and three of *Mercedesia* (*M. aspiphora* H.A. Thomsen & J.B. Østergaard, *M. multistellata* H.A. Thomsen & J.B. Østergaard and *M. pusilla* H.A. Thomsen & J.B. Østergaard) have been described. All five species were described from Danish waters and/or the surface waters of the Arctic and Antarctic, using transmission electron microscopy (Thomsen *et al.* 1995; Thomsen & Østergaard 2015).

Using high-resolution scanning electron microscopy (SEM) we have imaged minuscule (*c.* 2–5 μm) and well-preserved star-like nannolith specimens with morphologies comparable to *Ericiolus* and *Mercedesia* that were collected from samples originating in the LPZ of the Mediterranean and the Sargasso Seas, and the subtropical gyres of the South-eastern Pacific and the South Atlantic Oceans (Fig. 1). We report on observations and morphometric assessments of these specimens that suggest the circumscription of three new morphospecies and discuss their taxonomic implications for the genera *Ericiolus* and *Mercedesia*.

MATERIAL AND METHODS

Sample collection and SEM analyses

The observed specimens originate from a collection of samples that are summarized as follows: 1) Two water samples collected from stations 69–6 (37°25.8′N, 0°25.2′W; 90 m depth) and 69–11 (37°25.8′N, 0°25.2′W; 42.5 m depth from the deep chlorophyll maximum (DCM)) in September–October 1999 on cruise MATER II of the R/V *Hesperides* in the North-western Mediterranean and Alboran Seas (Font 1999); 2) A pair of samples from the low photic waters of stations CTD184 (32° 40.8′S, 84°4.20′W; 105 m depth; 2 December 2004) and CTD192 (33°21.6′S, 78°6.60′W; 80 m depth; 4 December 2004) during the BIOSOPE cruise of the R/V *L'Atalante* to the Southern-eastern Pacific Ocean (Claustre & Sciandra 2004); 3) Three seawater samples collected during the AMT18 cruise of the R/V *James Clark Ross* to the South Atlantic gyre (Woodward 2009), from station CTD089 (32°10.8′S, 29°49.8′W; 2 November 2008) and from depths of 72 m, 84 m, and 96 m, all within an expanded DCM; 4) Nine samples from Hydrostation 'S' (32°10.2′N, 64°30.0′W, October 2020, depths 130 m, 135 m, 155 m and 175 m; and 32°12.7′N, 64°31.5′W, November 2022, depths 80 m, 100 m, 120 m, 140 m and 160 m) that were collected below the DCM during a monthly BATS-BIOS cruise of the R/V *Atlantic Explorer* to the Sargasso Sea, North Atlantic Ocean. Information on the sample source and environmental parameters can be found in Table 1.

On each cruise, sampling was performed using Niskin Bottles attached to rosette samplers. Seawater samples were filtered using three types of filters: 1) Whatman membrane track-etched filters (0.8 μm porosity, 25 mm diameter); 2) Isopore hydrophilic, nonsterile membranes (0.8 μm porosity, 47 mm diameter); and 3) Pall Life Sciences Supor-800 filter membranes (0.8 μm porosity, 25 mm diameter). During BATS-BIOS cruise, samples were pre-filtered through a membrane of 50 μm porosity to remove larger zooplankton and contaminants. A low-pressure vacuum pump was used in all expeditions

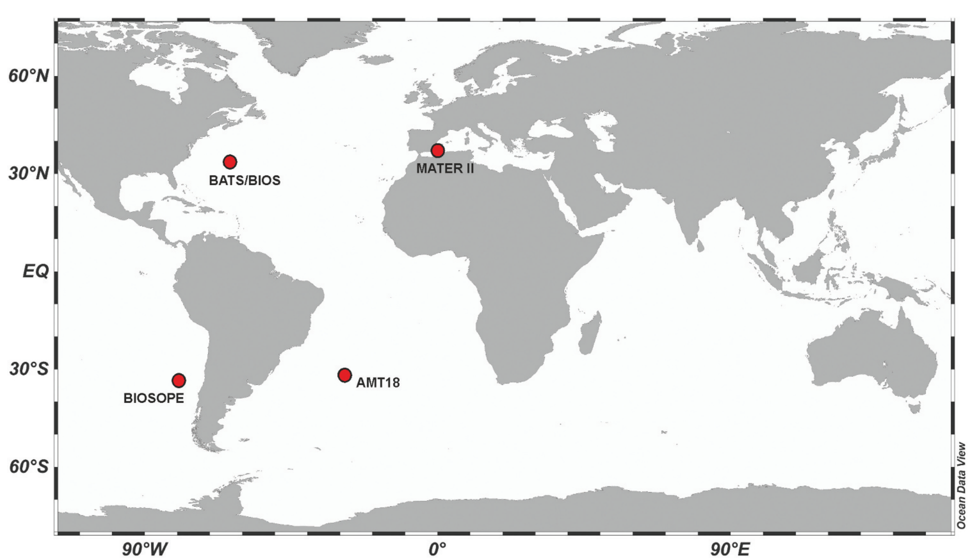


Fig. 1. Map showing localities from which specimens of *Ericiolus bendifii sp. nov.*, *E. mattioliae sp. nov.*, *E. sheldoniae sp. nov.*, *Ericiolus* cf. *bendifii* and *E. multistellatus comb. nov.*, were observed. The figure was created using the software OceanDataView v5.5 (Schlitzer 2021).

Table 1. List of sampling localities, including environmental data, from which *Ericiolus* specimens were obtained.

Study Area	Station	Sampling Date	Latitude	Longitude	Sampling Depth (m)	Temperature (°C)	Salinity (psu)	Dissolved Oxygen (µmol kg^{-1})	NO^{3-} (µmol^{-1})		Number of Specimens Studied: *E. bendifii* sp. nov.	*E. sheldoniae* sp. nov.	*E. mattioliae* sp. nov.	*E. multistellatus* comb. nov.	*E. aspiphorus* comb. nov.	*Ericiolus* cf. *bendifii*	Figures
Mediterranean & Alboran Seas																	
MATER II	69–6	10–1999	37°25.8′N	0°25.2′W	90										1		34
	69–11	10–1999	37°25.8′N	0°25.2′W	42.5						10						8, 9, 10, 14, 15
Sargasso Sea																	
BATS-BIOS	Hydrostation 'S'	14-10-2020	32°10.2′N	64°30.0′W	130	20.14	36.73	209.27				1					
	Hydrostation 'S'	26-10-2020	32°9.96′N	64°29.9′W	135	19.55	36.67	204.59				2					
	Hydrostation 'S'	26-10-2020	32°9.96′N	64°29.9′W	155	19.37	36.66	205.96				2					
	Hydrostation 'S'	26-10-2020	32°9.96′N	64°29.9′W	175	19.24	36.66	206.59						2			35
	Hydrostation 'S'	22-11-2022	32°12.7′N	64°31.5′W	80	21.02	36.74	208.94				3					22, 26
	Hydrostation 'S'	22-11-2022	32°12.7′N	64°31.5′W	100	20.38	36.72	205.99				2					29
	Hydrostation 'S'	22-11-2022	32°12.7′N	64°31.5′W	120	20.28	36.71	204.03				2					
	Hydrostation 'S'	22-11-2022	32°12.7′N	64°31.5′W	140	19.80	36.68	204.61				3					
	Hydrostation 'S'	22-11-2022	32°12.7′N	64°31.5′W	160	19.48	36.67	204.66				1	1				19, 21, 22, 23, 24, 28
South Atlantic Ocean																	
AMT18	CTD089	02-11-2008	32°10.74′S	29°49.56′W	72	16.45	35.62	251.2	0.07				3				6, 16, 17, 18, 20
	CTD089	02-11-2008	32°10.74′S	29°49.56′W	84	16.15	35.60	248	0.22		2						13
	CTD089	02-11-2008	32°10.74′S	29°49.56′W	96	15.85	35.59	241	0.17		3			1		1	5, 11, 12, 27, 36
South-eastern Pacific Ocean																	
BIOSOPE	CTD184	02-12-2004	32°40.8′S	84°4.20′W	105	13.89	34.12	241.35			1	1				1	25, 26, 30, 31
	CTD192	04-12-2004	33°21.6′S	78°6.60′W	80	13.94	34.05	249.10								1	32, 33
										Total	16	17	4	3	1	3	

Table 2. Morphological comparison of *Ericiolus bendifii sp. nov., E. mattioliae sp. nov., E. sheldoniae sp. nov*. and *Ericiolus* cf. *bendifii* with all other currently known *Ericiolus* species (including those formerly assigned to *Mercedesia*). Data for *E. spiculiger* are from Thomsen *et al.* (1995) and for all other previously published species from this study and/or Thomsen & Østergaard (2015).

Species	*Ericiolus bendifii sp. nov.*		*Ericiolus mattioliae sp. nov.*		*Ericiolus sheldoniae sp. nov.*		*Ericiolus* cf. *bendifii*		*Ericiolus spiculiger*		*Ericiolus frigidus*		*Ericiolus aspiphorus comb. nov.*		*Ericiolus multistellatus comb. nov.*		*Ericiolus pusillus comb. nov.*	
	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View	Plan View	Side View
Diagnostic features	Three bifurcate rays, equally positioned and angled; bifurcation near the nannolith center	Central long and elongate spine with a terminal robust knob	Three rays, equally positioned and angled; small bifurcation near the tip of the rays	Calyx of delicate laths developed on the rays. The calyx is slightly thicker along its distal edge	Three rays, equally positioned and angled; bifurcation near the nannolith center	Calyx of delicate laths developed in between the rays. The calyx is slightly thicker along its distal edge	Three bifurcate rays, equally positioned and angled; bifurcation near the nannolith center	Central short spine(?)	Four rays; three coplanar and one more robust, longer and thicker. All rays with longitudinal ridges.	One ray is slightly longer and with a more robust and rounded tip distally	Four rays; all equally positioned and angled. Rays with no longitudinal ridges	All rays equally long; one slightly more robust and longer	Subtriangular nannoliths with three rays showing membranous material in between	Flat nannolith surface with a central nodule	Y-shaped nannoliths; three rays. Proximal surface of nannolith is narrower compared to *E. pusillus comb. nov.*	Flat nannolith surface with a central nodule	Small Y–shaped nannoliths; three rays. Proximal view of nannolith with a small and circular central pore.	Flat nannolith surface
Coccosphere diameter, µm	2.6–4.3		4.3–5.2		2.6–5.3		5.5–6.2		3.0–3.8		3.6–4.4		7.5		5.5		4.5	
Nannolith size, µm	0.25–0.6		0.6–1.3		0.4–0.8		0.25–0.55		0.30–0.51		0.29–0.53		0.37–0.85		0.37–0.60		0.17–0.33	
Ray length, µm	0.12–0.33		0.38–0.58		0.2–0.40		0.2–0.3		0.25–0.48		0.24–0.7		0.15–0.43		0.24–0.37		0.09–0.20	
Ray width, µm	0.02–0.09		0.04–0.10		0.04–0.10		0.07–0.13		0.03–0.10		0.05–0.07		0.05–0.08		0.02–0.04		0.02–0.03	

to avoid breakage of coccosphere specimens. The filters were then washed with either buffered distilled water (adjusted with NaOH; pH *c.* 8.0) or a 20 mM sodium carbonate solution (Na_2CO_3, 2 g l^{-1}; pH *c.* 10) to remove salt, placed individually in plastic Millipore Petri-dishes, and oven-dried at 40°C for at least an hour. A portion of each filter was subsequently cut out and mounted on an aluminium stub using double-sided adhesive tape. The stubs were then sputter-coated with gold-palladium for 1–2 min. Observations and imaging were conducted at the Natural History Museum London (NHM), UK, on a Phillips XL-30 FEG Field Emission SEM or a Zeiss Ultra Plus Field Emission SEM, and on a VEGA3 TESCAN SEM at the Department of Earth and Environmental Systems, Indiana State University, USA.

Morphology, terminology and biometry

Terminology and morphological observations largely followed the guidelines of Young *et al.* (1997) and the approaches of Thomsen & Østergaard (2015) on star-shaped nannoliths. Morphometric measurements were conducted via ImageJ software (Schneider *et al.* 2012) and frequency plots were produced using the R package ggplot2 (Wickham 2009).

RESULTS

Morphological observations

Our examination of SEM micrographs yielded, in total, 44 collapsed coccospheres each consisting of numerous monomorphic triradiate nannoliths. The nannoliths showed three bifurcate rays in plan view, all equally positioned and angled, with tapering ray-tips. In side view, the nannoliths had a central process on one side, while their ray-tips were deflected upward. The nannoliths around the edge of collapsed coccospheres typically showed their process oriented outward, making clear that the side with the process is distal. On the proximal side the nannoliths appeared flat, but with a small central pore. Through our analyses, it also became apparent that there is considerable variability in our specimens, as these differed consistently in the ultrastructure of their nannolith centre and the degree of bifurcation. We distinguished three sets of specimens (Figs 2, 3, 4): (a) nannoliths with the bifurcation occurring near the centre of the nannoliths, and with a long and elongate central spine with a terminal knob (Fig. 2); (b) nannoliths with a similar bifurcation to the first, but with, instead of a spine, a calyx of three vertically-oriented laths, extending between the bifurcations (Fig. 3); and (c) nannoliths showing bifurcation near the tip of their rays, and a calyx formed by delicate laths (Fig. 4); the laths, however, were seen to develop along the rays or across their axis, and they extended from the nannolith centre to approximately one-quarter from the tip of the ray, as in (b). In addition, we observed a limited number of specimens with morphologies similar to (a), bearing, however, a short central spine on the distal side. Based on these morphological differences, we propose three new species, namely *Ericiolus bendifii sp. nov.*, *E. sheldoniae sp. nov.* and *E. mattioliae sp. nov.*, and describe an incompletely defined taxon under the designation of *Ericiolus* cf. *bendifii*.

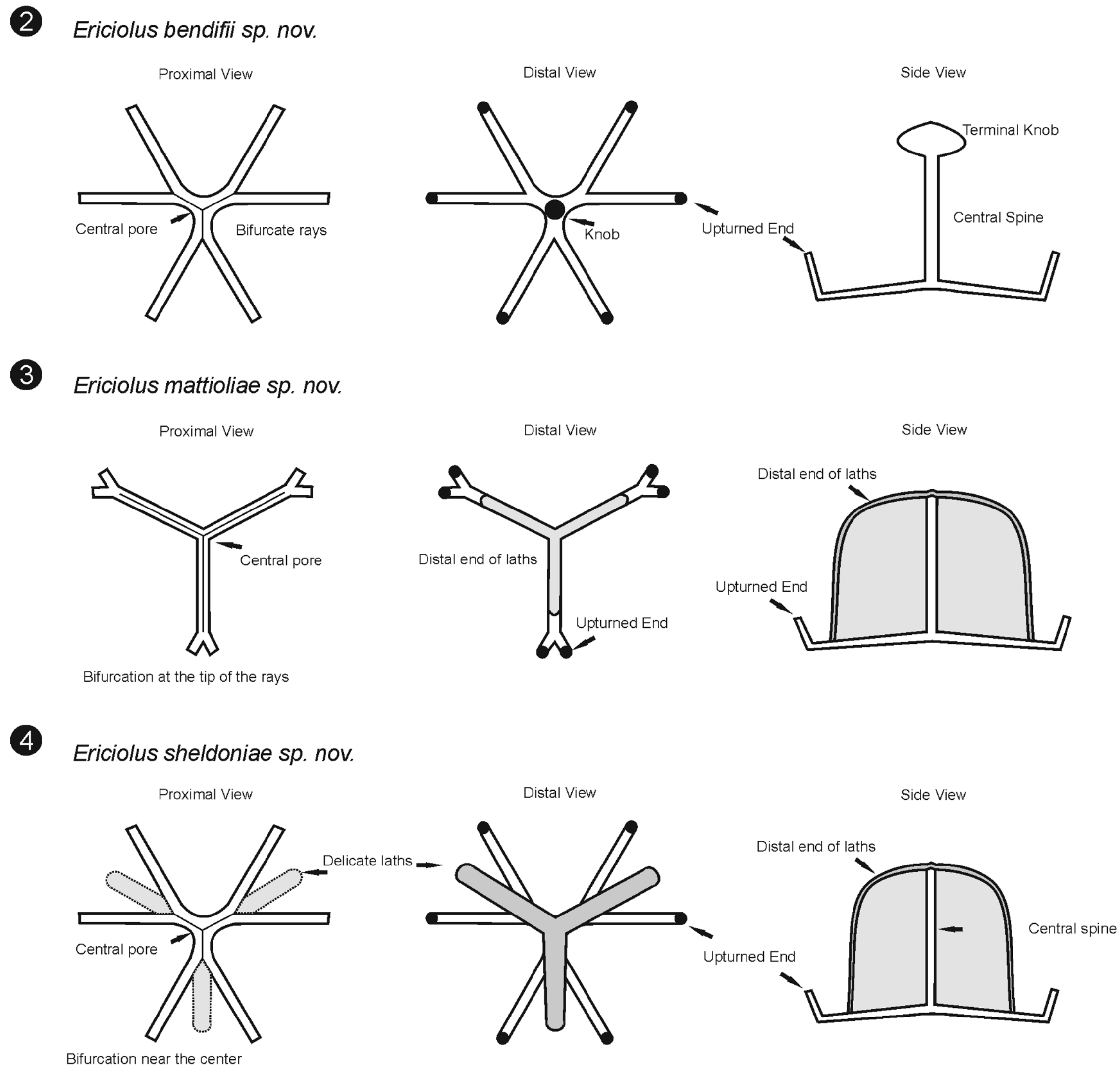
Biometric analyses

To test for morphometric differences between our new forms and the previously published species of *Ericiolus* and *Mercedesia*, we carried out biometric measurements on 728 star-shaped nannoliths originating from specimens from our collections and/or other available sources (Thomsen *et al.* 1995; Thomsen & Østergaard 2015; Table S1). To minimize subjectivity in the resulting dataset, we measured only nannoliths in plan view, and given their three-fold dimension, we considered the distance between the tips of the rays (Figs 5, 6) as representative of the nannolith size/diameter.

The frequency histogram plots (Fig. 7) highlighted that all species exhibited a (broadly) unimodal distribution pattern of their nannolith size, with our new forms, *E. bendifii sp. nov.*, *E. sheldoniae sp. nov.*, *E. mattioliae sp. nov.*, and *Ericiolus* cf. *bendifii*, demonstrating, respectively, a cluster at 0.30–0.60 μm (mean value 0.45 μm), 0.35–0.80 μm (mean value 0.55 μm), 0.60–1.30 μm (mean value 0.80 μm) and 0.25–0.55 μm (mean value 0.35 μm). The species *E. spiculiger* and *E. frigidus* showed an obvious clustering at, respectively, 0.35–0.55 μm and 0.25–0.55 μm (both with a mean value of 0.40 μm). Similarly, the species *E. pusillus comb. nov.*, *E. multistellatus comb. nov.* and *E. aspiphorus comb. nov.* (see below for taxonomic discussion and treatments) displayed, respectively, clusters at 0.18–0.34 μm (mean value 0.22 μm), 0.25–0.80 μm (mean value 0.40 μm) and 0.35–0.85 μm (mean value 0.50 μm). We thus observed that all nannolith morphotypes fell within the size range 0.2–1.3 μm with the individual morphotypes showing more restricted, but overlapping, size ranges.

Synonymization of *Mercedesia* with *Ericiolus*

As highlighted from our morphologic and biometric analyses, our new species and the genera *Ericiolus* and *Mercedesia* demonstrate numerous collectively shared features (see Table 2). They are all characterized by coccospheres 2–7 μm in size with numerous monomorphic nannoliths that are triradiate and show three symmetrically arranged, similar rays radiating from a common centre. The nannoliths vary 1) in the presence and development of the central process; 2) in whether the rays are coplanar or arranged in a low angle cone; 3) in the presence or absence of bifurcations; and 4) in details of size and shape. These common features make this a distinctive group that is well-separated from all other extant coccolithophores. As noted above, *Ericiolus* and *Mercedesia* differ in the ray angle and the process development, i.e. in *Ericiolus* the process is well-developed and the rays are arranged conically, whilst in *Mercedesia* the rays are coplanar, and the process is absent or rudimentary. Our specimens have coplanar rays and a well-developed process, and do not, therefore, readily fit in either genus. Consequently, we could either emend the generic definitions to accommodate our species, or alternatively, create a third genus exclusively for the new forms that are distinguished by the presence of bifurcations. However, we consider the



Figs 2–4. Schematic representation of the diagnostic morphological features of nannoliths of the newly described species of *Ericiolus* as observed in proximal, distal and side views. Drawings are not to the same scale.
Fig. 2. *Ericiolus bendifii sp. nov*.
Fig. 3. *Ericiolus mattioliae sp. nov*.
Fig. 4. *Ericiolus sheldoniae sp. nov*.

similarities amongst the taxa more important than their differences and that proliferation of paucispecific genera being separated on minor differences in nannolith morphology is unhelpful. Based on the above, we prefer to place all forms in a single genus, *Ericiolus*, with an emended diagnosis.

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)
Nannolith families *Incertae sedis* J.R. Young *et al.* (2003)

Genus *Ericiolus* H.A. Thomsen *emend*. Archontikis & Jer. R. Young

= *Mercedesia* H.A. Thomsen & J.B. Østergaard (2015, p. 157)

EMENDED DESCRIPTION: Coccosphere monomorphic and monothecate bearing triradiate or triangular nannoliths. The base of the nannolith is formed of three rays, which bifurcate in some species. A distally directed process is present in the centre of the nannolith in most species, with a triradiate calyx in some species.

TYPE SPECIES: *Ericiolus spiculiger* H.A. Thomsen in Thomsen *et al.* (1995).

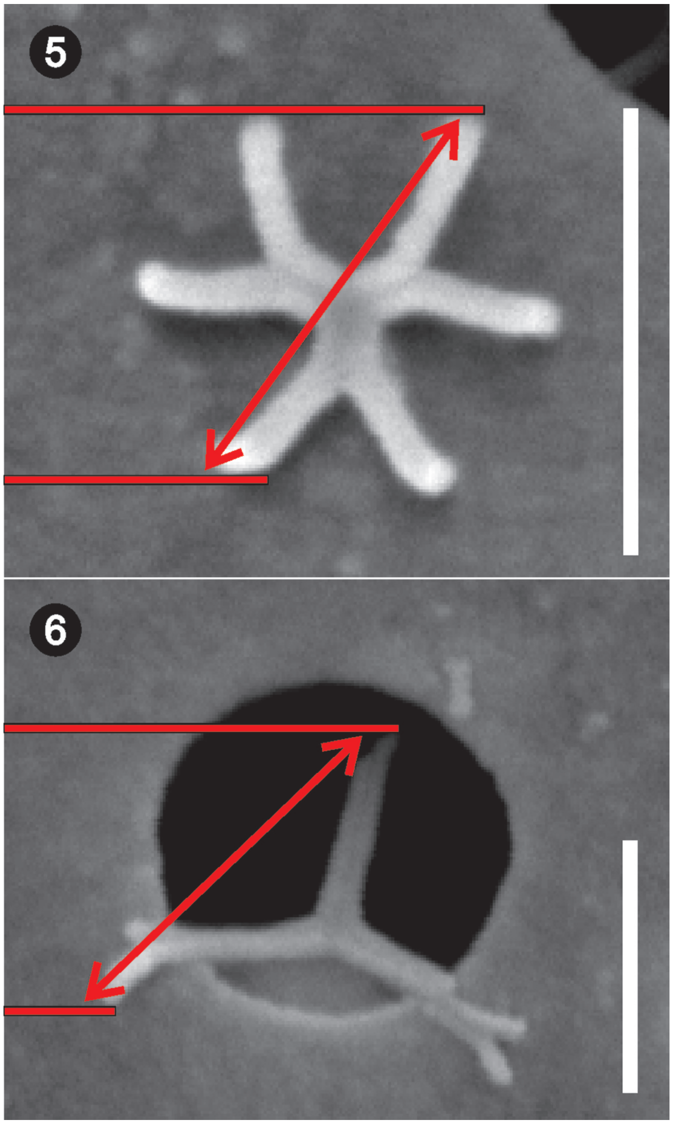
REMARKS: All known species form small monomorphic coccospheres (2–7 μm) consisting of numerous very small (<1.3 μm) nannoliths. All polar species are known to be motile with two flagella and a well-developed haptonema; equivalent observations are not available for the subtropical LPZ species.

DESCRIPTION OF NEW SPECIES

Ericiolus bendifii Archontikis, J.G. Millán, A. Winter & Jer. R. Young *sp. nov.*

Figs 8–15

SYNONYMY: *Ericiolus*? sp. *sensu* Young *et al.* (2003, p. 85, pl. 39, fig. 14).



Figs 5–6. Biometric approach for quantifying nannolith size. Given the three-fold dimension of nannoliths, we considered as nannolith size/diameter, 1) the distance between the tips of the diametrically opposite rays (Fig. 5) for *Ericiolus bendifii sp. nov*. and *E. sheldoniae sp. nov*.; and 2) the 'tip-to-tip' distance of the nannolith rays (Fig. 6) for all other species. Scale bars = 0.5 *μ*m.

Fig. 5. Distance between the tips of diametrically opposite rays, used for *Ericiolus bendifii sp. nov*. and *E. sheldoniae sp. nov*.

Fig. 6. 'Tip-to-tip' distance of the nannolith rays.

DESCRIPTION: Coccosphere shape unknown, possibly subspherical or saddle-shaped but found collapsed. It consists of *c*. 50–70 triradiate, star-shaped nannoliths probably forming a single-layered cover. Nannoliths with three coplanar bifurcate rays. The rays are symmetrically arranged (120° angle between them) and bifurcate near the centre of the nannolith with the bifurcations directed radially. The bifurcations are parallel-sided, and tips of each bifurcation are directed distally. On the distal side of the nannolith, there is an elongate central spine with a robust terminal knob. On the proximal side of the nannolith, axial grooves run along the rays from the bifurcations to the centre where they meet to form a small central pore (Fig. 12).

DIMENSIONS: Coccosphere diameter 2.5–4.5 *μ*m; nannoliths 0.3–0.6 *μ*m long and wide. Ray 0.1–0.3 *μ*m long.

HOLOTYPE: Stub no. 302/2 deposited at the facilities of NHM, UK (PM NF 4663 193–64). Specimen shown in Fig. 8.

PARATYPE: Stub no. 459/2 deposited at NHM, UK (PM NF 4814 275–53). Specimen shown in Fig. 9.

TYPE LOCALITY: North-western Mediterranean and Alboran Seas (37° 25.8′N, 0°25.3′W, depth 42.5 m (DCM), October 1999, MATER-II Cruise, Station 69–11).

DISTRIBUTION: Subtropical low-photic waters.

NUMBER OF SPECIMENS STUDIED: 16.

ETYMOLOGY: After Professor El Mahdi Bendif (Institut des Sciences de la Mer de Rimouski), in recognition of his contributions to the field of extant coccolithophore genetics.

REMARKS: Young *et al*. (2003) previously reported the holotype when examining plankton assemblages of Mediterranean waters and identified via SEM the possession of bifurcate rays in its nannoliths. The authors argued that this specimen (their p. 85, pl. 39, fig. 14, labelled as '*Ericiolus*? sp.') was reminiscent of *Ericiolus*, and although its morphology was incompatible with the generic description, the form probably represented a closely related taxon. This is now confirmed via our morphologic and biometric findings and therefore, it is established as a discrete morphospecies. The species differs in possessing nannoliths with three bifurcated rays, vertically directed ray-tips and an elongate central spine with a terminal knob. The bifurcation occurs near the nannolith centre.

Ericiolus mattioliae Archontikis, J.G. Millán, A. Winter & Jer.R. Young *sp. nov.*

Figs 16–20

DESCRIPTION: Coccosphere shape unknown, possibly subspherical or saddle-shaped but found collapsed, and with 30–60 nannoliths. Nannoliths with three coplanar rays, equally positioned, with delicate bifurcations near their tips; the bifurcations are short and have short, upturned tips. On the distal side, laths extend vertically up from each ray, developing from the centre of the nannolith to about two-thirds of the length of the ray. The laths are slightly higher at the centre giving a curved profile, and are slightly thickened along their distal edge. On the proximal side of the nannolith, grooves run along the rays from the bifurcation to the centre of the nannolith, where they unite to form a small central pore (Fig. 18, upper arrow).

DIMENSIONS: Coccosphere diameter *c*. 4.5 *μ*m; nannoliths 0.6–1.3 *μ*m long and wide. Ray 0.4–0.6 *μ*m long. Laths 0.3–0.6 *μ*m long.

HOLOTYPE: Stub no. 704/2 deposited at the facilities of NHM, UK (PM NF 5517 285–33). Specimen shown in Fig. 16.

PARATYPE: Stub no. 704/2 deposited at NHM, UK (PM NF 5517 285–31). Specimen shown in Fig. 17.

TYPE LOCALITY: 32°10.74′S, 29°49.56′W, depth 72 m, 2 November 2008, AMT18 Cruise, Station CTD089.

DISTRIBUTION: Subtropical low-photic waters.

NUMBER OF SPECIMENS STUDIED: 4.

ETYMOLOGY: After Professor Emanuela Mattioli (Université Claude Bernard Lyon 1) in recognition of her contributions to the field of Jurassic and Lower Cretaceous coccolithophore palaeoceanography.

REMARKS: The species differs in showing three coplanar rays with a small bifurcation occurring near the tips of the rays. In addition, the nannoliths bear delicate laths that form a calyx distally and they develop from the nannolith central spine towards the tips of the rays by becoming progressively shorter. The laths are also seen to develop along the nannolith rays, across their axis.

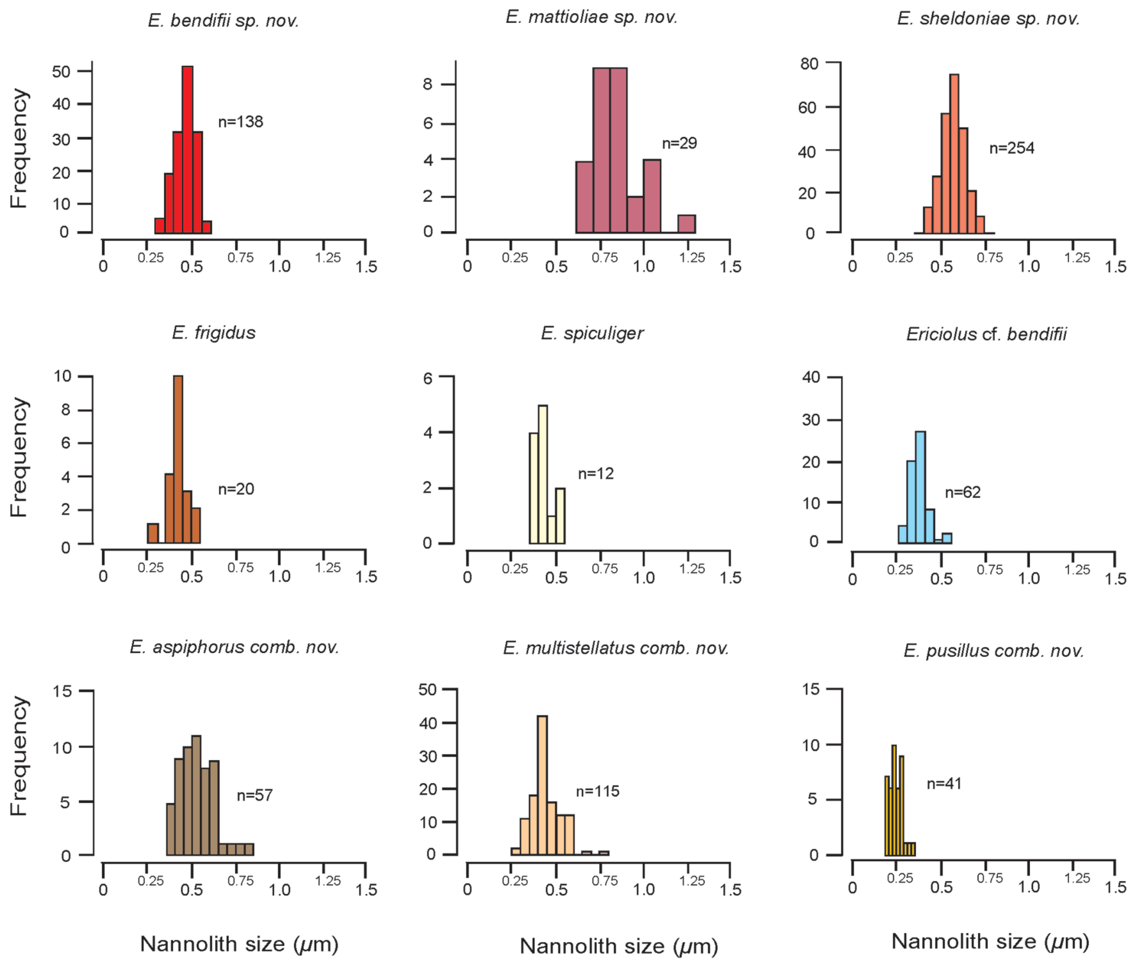


Fig. 7. Frequency histogram plots of the nannolith size data for *Ericiolus bendifii sp. nov., E. sheldoniae sp. nov., E. mattioliae sp. nov., Ericiolus* cf. *bendifii, E. spiculiger, E. frigidus, E. pusillus comb. nov., E. multistellatus comb. nov.* and *E. aspiphorus comb. nov.* Analytic biometric data are found in Table S1.

Ericiolus sheldoniae Archontikis, J.G. Millán, A. Winter & Jer. R. Young *sp. nov.*

Figs 21–29

DESCRIPTION: Coccosphere shape unknown, possibly saddle-shaped or sub-spherical but seen collapsed. It shows 30–60 star-shaped triradiate nannoliths with three coplanar bifurcate rays, equally positioned and angled. The rays are symmetrically arranged (120° angle between them) and bifurcate near the centre of the nannolith. The bifurcations are parallel-sided and directed radially, and show upturned tips that are directed distally. On the distal side of the nannolith, laths extend vertically down from the centre of the nannolith, in between the rays (Fig. 23) and to about one-quarter from their tips. The laths form a calyx that is slightly thickened along its distal edge. On the proximal side of the nannolith, axial grooves run along the rays from the bifurcation to the nannolith centre where they unite to form a small central pore (Fig. 22); laths are usually seen collapsed in proximal view.

DIMENSIONS: Coccosphere diameter 3.0–5.3 μm; nannoliths 0.4–0.8 μm long and wide. Ray 0.2–0.4 μm long. Laths 0.2–0.3 μm long.

HOLOTYPE: Stub no. AB2019 80m, deposited at the Algal Collection of the US National Herbarium (US Alg. Coll. – 238319). Specimen shown in Fig. 21.

PARATYPE: Stub no. AB2019 140m, deposited at the Algal Collection of the US National Herbarium (US Alg. Coll. – 238322). Specimen shown in Fig. 24.

TYPE LOCALITY: 32°12.72′N, 64°31.5′W, depth 80 m, 22 November 2022, BATS Cruise, Hydrostation 'S'.

NUMBER OF SPECIMENS STUDIED: 17.

DISTRIBUTION: Subtropical low-photic waters.

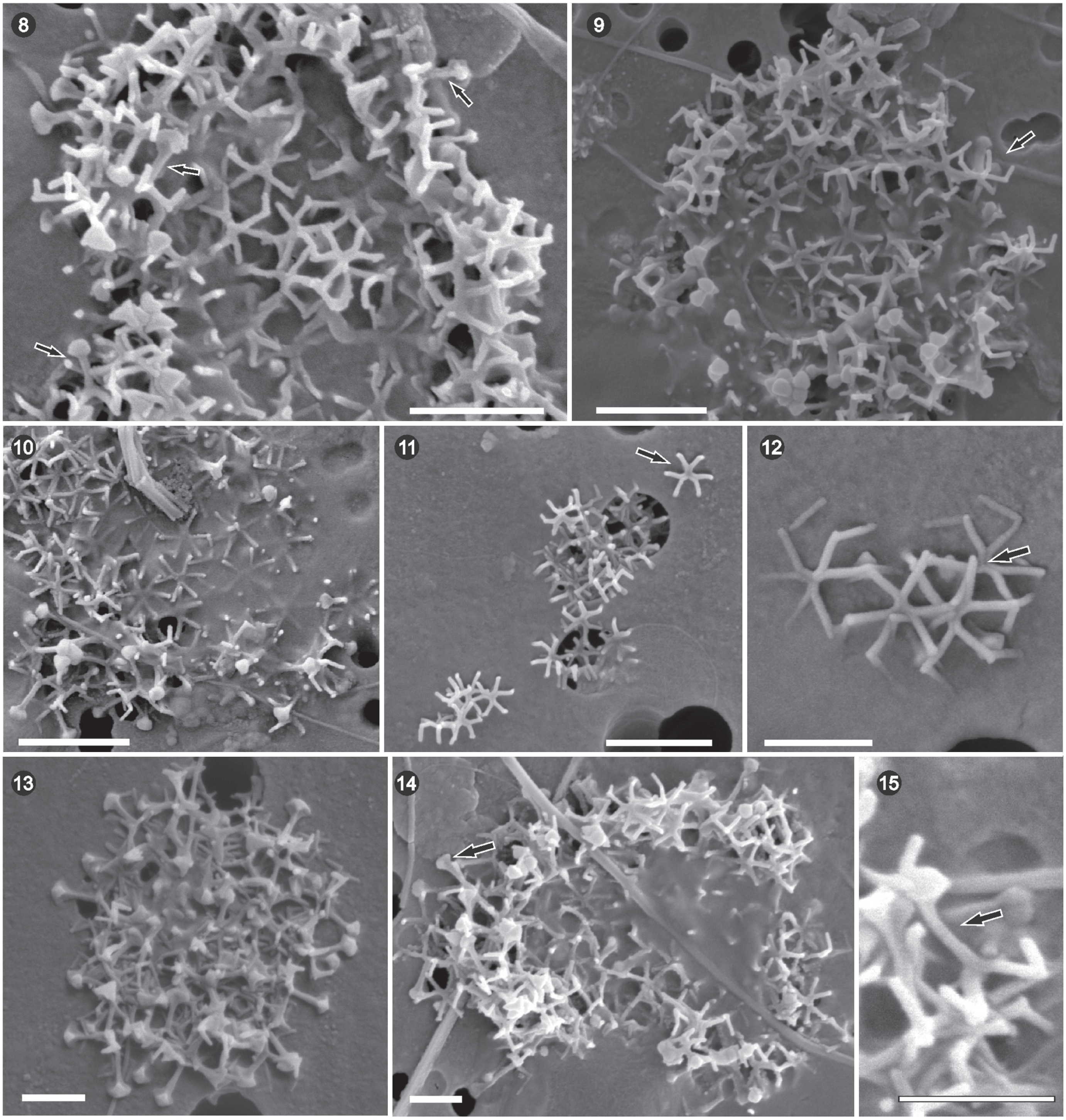
ETYMOLOGY: After Dr. Emma Sheldon (Geological Survey of Denmark and Greenland) in recognition of her contributions to the field of Cretaceous coccolithophore biostratigraphy.

REMARKS: The species shows similarities to both *E. bendifii sp. nov.* and *E. mattioliae sp. nov.* The presence of three coplanar rays with bifurcation near the nannolith centre is more reminiscent of *E. bendifii sp. nov.*, but instead of having a spine that is terminated by a knob, the species bears a calyx of three laths. The laths nearly extend to the nannolith rays but unlike in *E. mattioliae sp. nov.*, they do not rise from them. In addition, whilst the bifurcations are long and similar to *E. bendifii sp. nov.*, the ray tip extensions are short as shown in *E. mattioliae sp. nov.*

Ericiolus cf. *bendifii*

Figs 30–33

REMARKS: Three of our specimens appear similar to *E. bendifii sp. nov.*, and *E. sheldoniae sp. nov.*, but the nannoliths have only a short central spine rather than a long spine with a terminal knob or calyx. These most obviously resemble *E. bendifii sp. nov.*, but may alternatively be incompletely formed or broken specimens of *E. sheldoniae sp. nov.*, as they occurred in the same sample from the BIOSOPE cruise, and the calyces appear to be only weakly attached in that species.



Figs 8–15. SEM micrographs of *Ericiolus bendifii sp. nov*. Scale bars = 1 μm.

Fig. 8. Holotype. Coccosphere with star-shaped nannoliths showing three bifurcate rays and a central spine (arrow) with a robust terminal knob on distal side.

Fig. 9. Paratype. Central spine with a terminal knob at the centre of the nannolith and ray tips deflected upwards (arrow).

Fig. 10. Collapsed monomorphic coccosphere with star-shaped nannoliths.

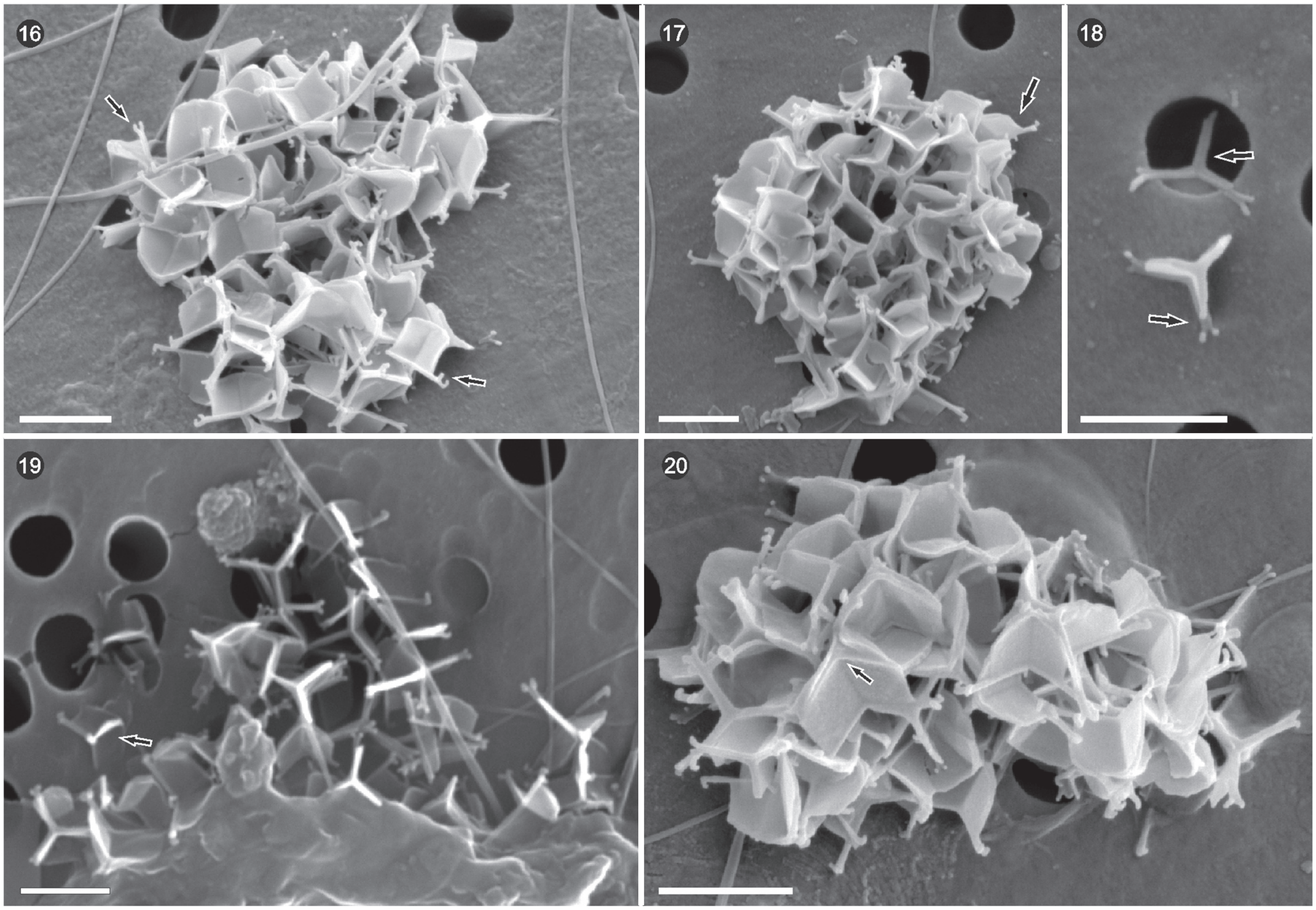
Fig. 11. Nannoliths with three coplanar rays showing bifurcation near their centre (arrow).

Fig. 12. Detail of star-shaped nannoliths in proximal view showing a central pore (arrow) made by axial grooves that run along the rays.

Fig. 13. Collapsed coccosphere showing nannoliths with a central spine that is oriented outward.

Fig. 14. Collapsed coccosphere; the nannoliths surrounding the coccosphere show their central spine outward (arrow).

Fig. 15. Detailed view of an individual nannolith showing a long (arrow) central spine that terminates in a prominent knob.



Figs 16–20. SEM micrographs of *Ericiolus mattioliae sp. nov*. Scale bars = 1 μm.

Fig. 16. Holotype. Coccosphere with star-shaped nannoliths showing three rays with small bifurcation at their tips (arrows).

Fig. 17. Paratype. Coccosphere with nannoliths showing, in distal view, delicate laths that develop from approximately one-quarter from the tip of the ray (arrow; side view) towards the nannolith centre, vertically up.

Fig. 18. Detailed view of star-shaped nannoliths of the specimen shown in Fig. 17. Proximal nannolith side with a central pore made by axial grooves (upper arrow); distal nannolith side showing a star-shaped calyx reaching approximately one-quarter of the tip of the ray (lower arrow).

Fig. 19. Collapsed individual nannoliths with bifurcation at the tip of the rays. Arrow indicates the lath-made calyx in side view.

Fig. 20. Collapsed coccosphere specimen. Nannoliths bearing delicate laths that become progressively higher towards the nannolith centre, forming a calyx. The elements of the calyx appear blockier at its distal end (arrow).

NEW COMBINATIONS

Ericiolus aspiphorus (H.A. Thomsen & J.B. Østergaard) Archontikis & Jer.R. Young *comb. nov.* Fig. 34

BASIONYM: *Mercedesia aspiphora* H.A. Thomsen & J.B. Østergaard in Thomsen & Østergaard 2015, *Acta Protozoologica* 54, p. 157, figs 3–8.

Ericiolus multistellatus (H.A. Thomsen & J.B. Østergaard) Archontikis & Jer.R. Young *comb. nov.* Figs 35, 36

BASIONYM: *Mercedesia multistellata* H.A. Thomsen & J.B. Østergaard in Thomsen & Østergaard 2015, *Acta Protozoologica* 54, p. 159, figs 9, 10, 14, 15.

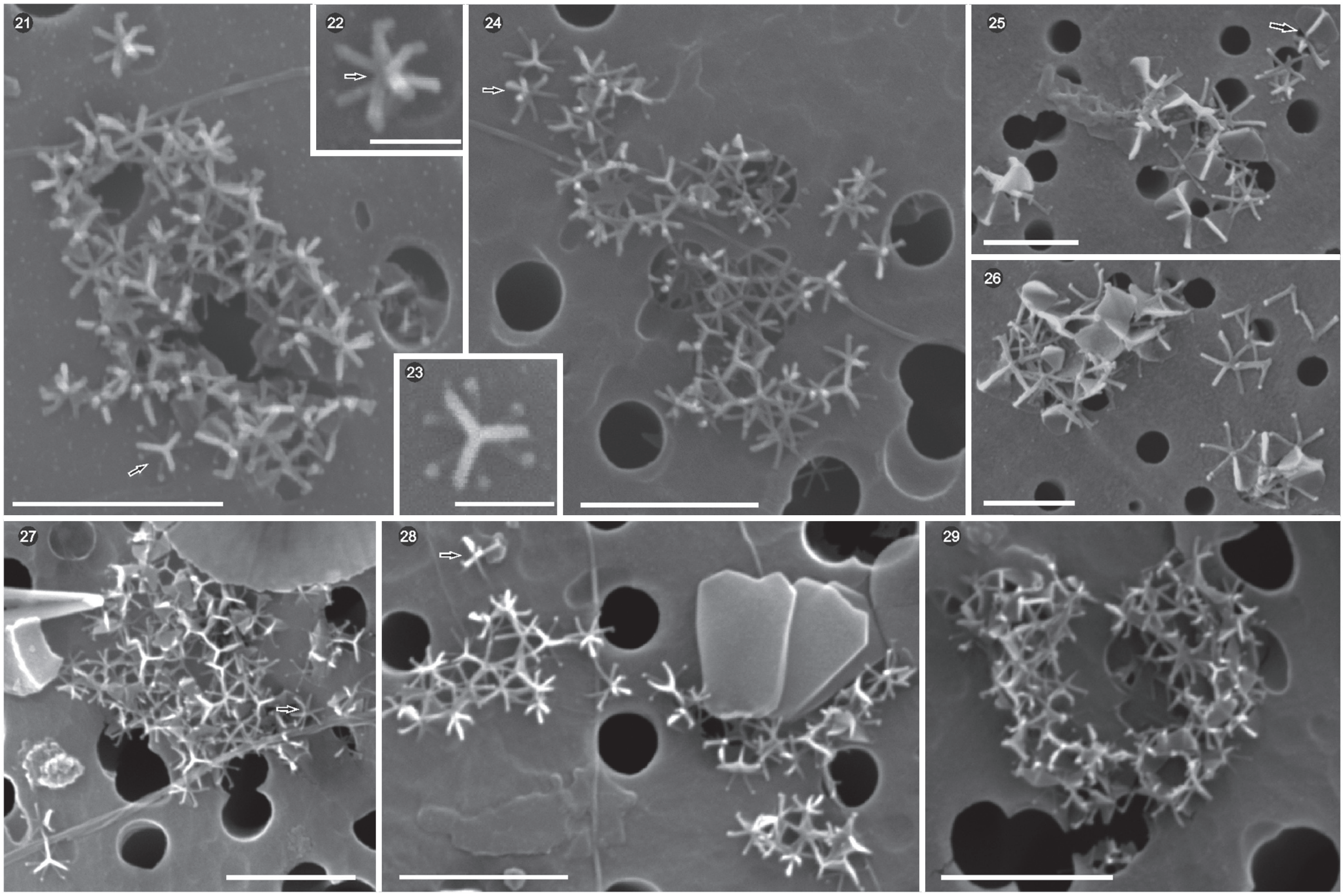
REMARKS: Thomsen & Østergaard (2015) note that "a cluster of nannoliths reminiscent of *M. multistellata* have been observed from tropical waters (Phuket, Thailand)". We have found another three such clusters (two of them shown in Figs 35, 36) from the LPZ of the subtropical South Atlantic Ocean and Sargasso Sea. This seems to confirm that the species occurs both in the surface waters of the Arctic and the LPZ of the sub-tropics. This pattern is also shown by other living coccolithophores, such as *Algirosphaera robusta* (Lohmann) R.E. Norris and *Calciopappus caudatus* Gaarder & Ramsfjell.

Ericiolus pusillus (H.A. Thomsen & J.B. Østergaard) Archontikis & Jer.R. Young *comb. nov.*

BASIONYM: *Mercedesia pusilla* H.A. Thomsen & J.B. Østergaard in Thomsen & Østergaard 2015, *Acta Protozoologica* 54, p. 159, figs 11–13.

Ecology

Very little information can currently be extracted in relation to the ecology of *Ericiolus bendifii sp. nov., E. sheldoniae sp. nov.,*



Figs 21–29. SEM micrographs of *Ericiolus sheldoniae sp. nov*.

Fig. 21. Holotype. Collapsed coccosphere bearing nannoliths with three coplanar rays showing bifurcation near the centre (arrow) and a calyx structure on distal side. Scale bar = 2 μm.

Fig. 22. Detail of Fig. 21. Proximal view of a nannolith showing a central pore (arrow) and the interior side of broken laths. Scale bar = 0.5 μm.

Fig. 23. Detail of Fig. 21. Distal view of a nannolith showing a calyx formed of delicate laths. The calyx develops in between the bifurcated rays of the nannolith. Scale bar = 0.5 μm.

Fig. 24. Paratype. Nannoliths, each bearing a calyx; in a few nannoliths, the calyx is seen collapsed. Arrow indicates the delicate laths of the calyx in side view. Scale bar = 2 μm.

Fig. 25. Individual nannoliths with lath-made calyx completely or partially collapsed (arrow). Scale bar = 1 μm.

Fig. 26. Individual nannoliths showing partially collapsed delicate laths at their centre. Scale bar = 1 μm.

Fig. 27. Collapsed coccosphere with a dense layer of nannoliths showing a calyx of laths occasionally completely or partially collapsed (arrow). Scale bar = 2 μm.

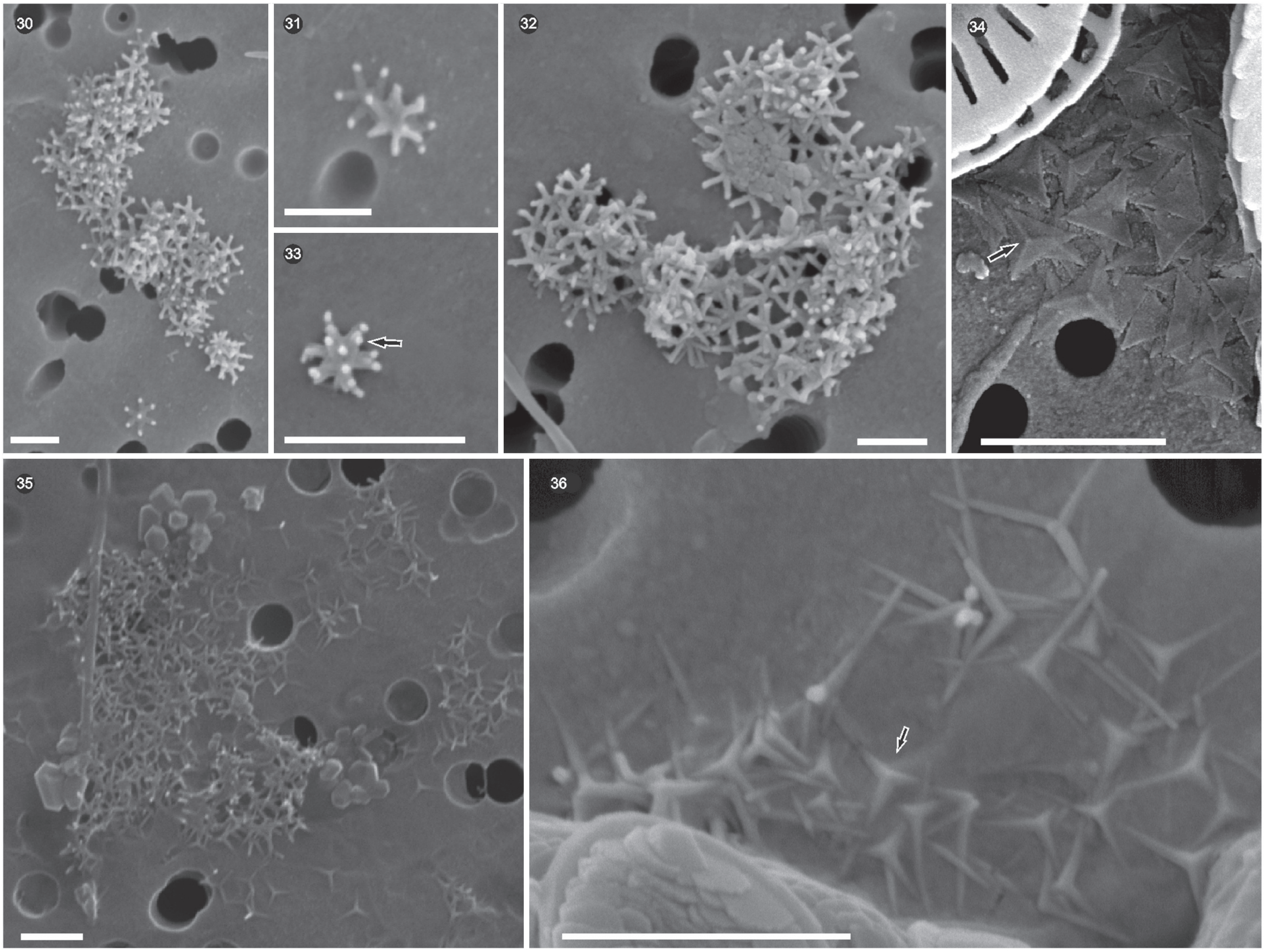
Fig. 28. Individual nannoliths that may show collapsed or partially developed calyces (arrow). Scale bar = 2 μm. Upper right side with three coccoliths of *Florisphaera profunda* His. Okada & Honjo.

Fig. 29. Collapsed coccosphere with saddle-like shape and numerous nannoliths showing lath-made calyces distally. Scale bar = 2 μm.

E. mattioliae sp. nov. and *Ericiolus* cf. *bendifii*, other than that our specimens have been obtained from the LPZ layers (within or close to the DCM) of subtropical to tropical waters. Our records, however, expand the findings of Thomsen *et al*. (1995) and Thomsen & Østergaard (2015), who noted occurrences of star-like nannolith-bearing species in the surface waters (10–40 m) of high latitude environments, namely the Arctic, Danish, Antarctic and Weddell Seas.

DISCUSSION

The genus *Ericiolus* (including now species previously classified in *Mercedesia*) is a minuscule extant coccolithophore that accommodates saddle-shaped, ovoid and/or sub-spherical monothecate monomorphic coccospheres with one type of nannoliths showing three-fold symmetry. The nannoliths are remarkably small (0.2–1.3 μm) in size and they show a star-like shape. They are convex on distal side and flat or concave in proximal view, and they demonstrate a peculiar morphology and ultrastructure, predominantly composed of an assembly of rays (Thomsen *et al*. 1995; Thomsen & Østergaard 2015; our observations). The rays overlie an organic baseplate, are almost equal in length and width, and they are seen almost equally positioned and angled across the nannolith. They develop from the centre of the nannolith distally by becoming progressively thinner with noticeably tapering ends. In addition, the nannolith rays may or may not show bifurcation; this typically occurs either near the nannolith centre or close to the tips of the rays. The ray base is narrow and usually bears a central pore in proximal view (e.g. Thomsen & Østergaard 2015, p. 158, fig. 3; our Figs 12, 18, 22). The nannolith centre may vary in showing a central structure with either: 1) a narrow and almost flat surface (e.g. *E. spiculiger*,



Figs 30–36. SEM micrographs of *Ericiolus* cf. *bendifii, E. aspiphorus comb. nov*. and *E. multistellatus comb. nov*. Scale bars = 1 μm.
Fig. 30. *Ericiolus* cf. *bendifii*. Dense layer of star-shaped nannoliths showing bifucation near their centre and a short central process on distal side.
Fig. 31. *Ericiolus* cf. *bendifii*. Detailed view of specimen in Fig. 30, with two nannoliths in, respectively, distal (upper nannolith) and proximal (lower nannolith) views.
Fig. 32. *Ericiolus* cf. *bendifii*. Collapsed and dense layer of triradiate nannoliths bearing a short central spine at the centre; the spine is usually seen collapsed.
Fig. 33. *Ericiolus* cf. *bendifii*. Detailed view of nannoliths from Fig. 32; arrow indicates the upturned end of the ray tips of the nannolith.
Fig. 34. Collapsed nannoliths of *Ericiolus aspiphorus comb. nov*.. Arrow indicates the short central knob observed at the nannolith centre in distal view.
Fig. 35. Collapsed dense layer of *E. multistellatus comb. nov*., triradiate nannoliths.
Fig. 36. Well-preserved triradiate nannoliths of *E. multistellatus comb. nov*., which bear a small knob (arrow) at their centre, in distal view. Bottom left side showing a *Solisphaera turbinella* A. Kahn & M-P. Aubry coccolith.

E. frigidus, *E. multistellatus comb. nov*. and *E. pusillus comb. nov*.); 2) membranous material between the rays covering the nannolith surface (as shown in *E. aspiphorus comb. nov*.); 3) an elongate central spine bearing a terminal knob (e.g. *E. bendifii sp. nov*. and *Ericiolus* cf. *bendifii*); and/or 4) delicate laths that develop across the nannolith forming a calyx structure distally (*E. sheldoniae sp. nov*. and *E. mattioliae sp. nov*.).

Taxonomic affinities

Ericiolus is currently classified within the informal category 'nannolith *incertae sedis*' (Young *et al*. 2003, 2023) pending elucidation of its phylogenetic affinity in relation to other extant coccolithophores. Indeed, any attempt for higher levels of classification based exclusively on morphological observations of its nannoliths may prove challenging. However, comparisons of morphologies and ultrastructures are still meaningful attempts to infer potential taxonomic affinities. Here, we discuss several morpho-structural similarities between *Ericiolus* and other known coccolithophores – the extant *Polycrater* phase of Alisphaeraceae Jer. R. Young, Kleijne & L. Cros, the family Papposphaeraceae R.W. Jordan & Jer.R. Young *emend*. Andruleit & Jer.R. Young, the living genus *Pileolosphaera* K.J.S. Meier, Kinkel & Jer.R. Young, and the fossil genus *Discoaster* S. H. Tan.

ALISPHAERACEAE – *POLYCRATER* PHASE

The Alisphaeraceae are a group of heterococcoliths, which, in their alternate life cycle phase, produce aragonitic nannoliths that were formerly placed in the genus *Polycrater* Manton & Oates (Cros *et al.* 2000; Cros & Fortuño 2002; Šupraha *et al.* 2018). Well-developed nannoliths of the '*Polycrater*' phase are monomorphic and form monothecate coccospheres but, unlike *Ericiolus*, they are typically asymmetrical and four-sided, i.e. they are seen as quadrate in plan view and with an hour-glass shape in side view. The nannolith long axes are directed equatorially, and the nannoliths are seen to embrace the cell in regular meridian rows. The size of the nannoliths (*c.* 0.4–1.0 μm) is similar to that observed in *Ericiolus*. A range of different analogues (e.g. forms with holes, tubercles, ladle-like or petal-like forms) to the ray structures of *Ericiolus* have previously been documented (Cros & Fortuño 2002; Young *et al.* 2003), and these also partially resemble the more skeletal *Polycrater*-type species; however, the basic four-fold symmetry seems to be a significant difference between these and the *Ericiolus* forms. In addition, it is still unclear whether *Ericiolus* nannoliths are calcitic or aragonitic, although the presence of calcium in the periplast has been confirmed (Thomsen *et al.* 1988). Therefore, it would be useful to determine if *Ericiolus* nannoliths were formed of aragonite or calcite and, if aragonitic, then affinity with *Polycrater* nannoliths would be indicated.

PAPPOSPHAERACEAE

The family Papposphaeraceae includes a wide range of small coccolithophores, which, like *Ericiolus*, occur sporadically in both polar waters and in the LPZ of the tropics and subtropics. Indeed, our key samples with common *Ericiolus* specimens also contained various members of the Papposphaeraceae. However, unlike *Ericiolus*, this group is characterized by predominantly dimorphic coccospheres with unambiguous heterococcoliths that are both made by R- and V-units, not monomorphic nannoliths. The heterococcoliths predominantly show four-fold symmetry and display narrow murolith rims (see Andruleit & Young 2010 for extended discussion), whereas *Ericiolus* is characterized by a three-fold symmetry pattern and a rim is absent; instead, a narrow ray base is always seen. Therefore, affinity with the Papposphaeraceae seems unlikely.

PILEOLOSPHAERA

The extant nannolith-bearing species *Pileolosphaera longistirpes* K.J.S. Meier, Kinkel & Jer.R. Young, which is the type species of the genus *Pileolosphaera*, is composed of about six to eight circular shield-like nannoliths. The nannoliths are formed exclusively of V-units (Meier *et al.* 2014) showing on the coccosphere, radially oriented calcite axes under light microscopy (Meier *et al.* 2014). The nannoliths possess three radial segments with a central triradiate process. Light microscopy observations indicate that all three elements are formed of crystal units with their c-axes vertical relative to the nannolith, and therefore, radial relative to the coccosphere (Meier *et al.* 2014). *Pileolosphaera* shares with *Ericiolus* the key features of triradiate symmetry and radial growth of the elements from the centre, rather than around a rim. There are, however, notable differences between the two taxa: 1) *Pileolosphaera* coccospheres have far fewer nannoliths than those of *Ericiolus* (6–8 vs 30–70); and 2) the *Pileolosphaera* nannoliths are considerably larger than those of *Ericiolus* (3.0–4.0 μm vs 0.2–1.3 μm). Despite these quantitative differences, *Pileolosphaera* nannoliths are structurally the closest extant forms to *Ericiolus*, and affinity between the two genera remains likely.

DISCOASTER

Discoaster is an important genus of nannofossils that were abundant through most of the Cenozoic, especially in warm oligotrophic waters. The last two species, *D. brouweri* S.H. Tan and *D. triradiatus* S.H. Tan went extinct 1.8 million years ago, in the Early Quaternary. Like *Ericiolus, Discoaster* nannoliths have radial symmetry, being formed of rays that grow from a central axis, rather than a proto-coccolith ring as in heterococcoliths (Young *et al.* 1999). This radial growth pattern, however, is characteristic of not only *Discoaster* but several other major extinct Cenozoic nannofossil groups, notably *Fasciculithus* Bramlette & F.R. Sullivan, *Heliolithus* Bramlette & F.R. Sullivan and *Sphenolithus* Deflandre, which are now grouped together as the Discoasterales W.W. Hay *emend.* Bown (Bown 2010). Moreover, the last *Discoaster* species show three- or six-fold symmetry and have deflected ray tips. Of the eight species of *Ericiolus, Ericiolus bendifii sp. nov.*, is, in particular, remarkably reminiscent of a miniature *D. brouweri* or *D. surculus* E. Martini & Bramlette. Meier *et al.* (2014) noted that the crystallographic origin of the elements in *Pileolosphaera* was the same as that in *Discoaster*, with the c-axes vertical/parallel to the axis of rotational symmetry of the nannolith. Unfortunately, *Ericiolus* is too small to determine crystallographic orientation optically and we do not have suitable samples for X-ray diffraction studies. Nonetheless, this type of analyses would be an interesting test, as would molecular genetics, to confirm whether *Ericiolus* is instead related to another group of extant coccolithophores.

Concluding Remarks

In summary, our findings showed that *Ericiolus* is a more diverse genus than was previously known and includes at least eight morphologically different species. The radial construction with three-fold symmetry separates the genus from other extant coccolithophores except the equally poorly known species *Pileolosphaera longistirpes*. In parallel, this construction pattern suggests a possible origin from the otherwise extinct Discoasterales, and therefore the possibility that these species may prove valuable keys to past biodiversity.

ACKNOWLEDGEMENTS

We warmly thank the captains and the crews of R/V *Hesperides*, R/V *L'Atalante*, R/V *James Clark Ross* and R/V *Atlantic Explorer* for their help with seawater collection. The assistance of Leocadio Blanco-Bercial, Alexandre Broerse, Martine Couapel, Markus Geisen, Andy Howard, Daniel Vaulot, Jeffery Stone, Alex Ball and Innes Clatworthy in obtaining samples and/or with the SEM is gratefully acknowledged. We would also like to thank Mike Guiry for discussions on matters of algal nomenclature, Giles Miller and Barrett Brooks for their expert assistance in cataloguing our material at, respectively, the Natural History Museum London, UK, and the U.S. National Herbarium of the Smithsonian Institute, and Luc Beaufort for providing environmental data for the BIOSOPE samples. Helge A. Thomsen, an anonymous reviewer and the Editor-in-Chief, António J. Calado, are warmly acknowledged for their insightful suggestions on the article.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

The results presented here constitute part of the EC-TMR research project CODENET, Coccolithophorid Evolutionary Biodiversity and Ecology Network (Contract no. ERB-FRMX-CT97-0113) and the Bermuda Institute of Ocean Sciences (BIOS) Grant-in-Aid awarded to JGM by the Sydney L. Wright, the Samuel Riker, the Wolfgang Sterrer, and the Eugene & Lillian Y. Lehman Fellowships. JGM and AW acknowledge the Bermuda Atlantic Time-series Study (BATS) program (Grant no. NSF OCE-1756105). Part of this study is also a contribution to the Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Museum and Zoo, Department of Environment & Natural Resources (Special permit no. SP201201). Partial support of this work was provided by the NASA Indiana Space Grant Consortium (NASA Award no. 80NSSC20M0121) via a Doctoral Fellowship to JGM at Indiana State University. OAA acknowledges an INA Foundation Katharina von Salis Graduate Fellowship. The work was supported by the UK Natural Environment Research Council (NERC) under Grant no. NE/S007474/1 to OAA and contains data supplied by NERC.

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