Alisphaera crostae sp. nov. (Prymnesiophyceae), a new extant coccolithophore from the Southwest Indian Ocean

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ABSTRACT: The analysis of water samples collected during the MD218 CROTALE expedition (February–March, 2019), and the 4th Indian Southern Ocean Expedition (SOE) (January–February, 2010) (re-visited samples) resulted in the occurrence of a new coccolithophore species belonging to the genus *Alisphaera*, and is named *Alisphaera crostae* sp. nov. This new species appears monomorphic and shows distinctive morphological differences in terms of its coccolith size, flange structure, and nodules, compared to other known *Alisphaera* species. In this study, morphological differences between *A. crostae* and other *Alisphaera* species are illustrated and compared. We suggest that the genus *Alisphaera* may have a higher diversity and may possess a wider distribution than previously evidenced, which requires more careful observation.

Keywords: Calcareous nannofossils, Coccolithophore, Indian Ocean, taxonomy, new species

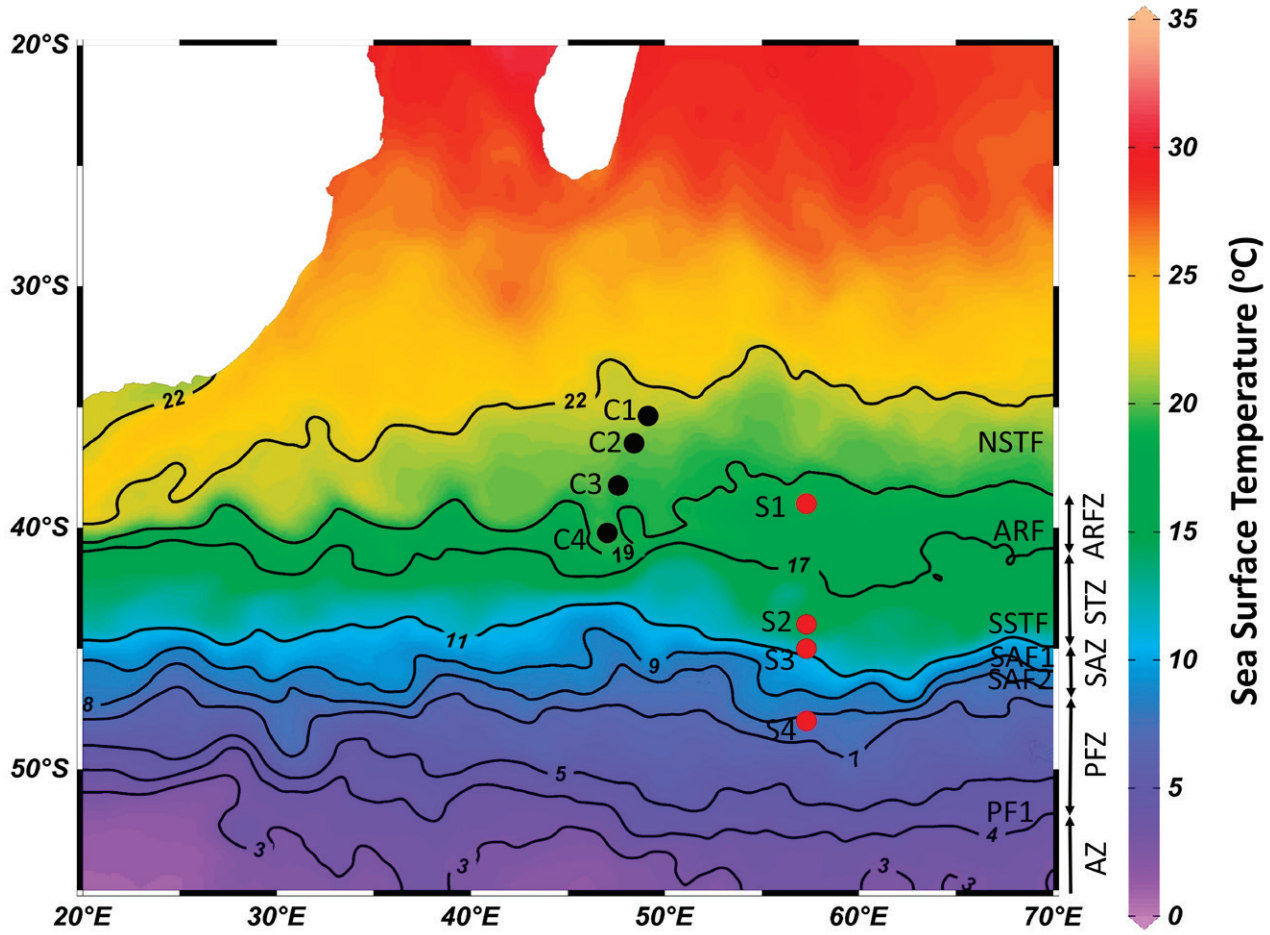
INTRODUCTION

Although studies on extant coccolithophores have been carried out in most major oceanic realms, the Southern Indian Ocean is still under-sampled. In the past decade, several new programs/projects were launched to investigate the impacts of global climate change on the polar oceans and associated ecosystems, which provided the opportunity to sample some parts of the Southern Indian Ocean. As a result, the ecology and biogeography of coccolithophores in this region were better documented (Mohan et al. 2008; Patil et al. 2013, 2014a, 2017, 2020, 2021) and several new species/varieties/new occurrences of coccolithophores/haptophytes were observed (e.g., Patil et al. 2014b, 2015, 2019; Jordan et al. 2015).

The investigation of the samples collected for coccolithophore enumeration during the MD218 CROTALE expedition (https://doi.org/10.17600/18000886) and 4th Indian Southern Ocean Expedition (SOE) resulted in the occurrence of several new fully mineralized/weakly mineralized nannoplankton taxa. In this manuscript, we describe the new species '*Alisphaera crostae* Patil and Jafar n.sp.', and compare its ultrastructural details to other *Alisphaera* species documented from the subantarctic zone of the Southwest Indian Ocean.

History of the genus *Alisphaera*

The genus *Alisphaera* (Heimdal) is moderately diverse and comprises small coccospheres. Despite their limited fossil record and lower abundance in the total coccolithophore assemblage, they hold considerable phylogenetic intrigue. So far, ten *Alisphaera* species were described from the diverse oceanic regions, with however large inter-specific ultrastructural morphological variations. The first description of the genus *Alisphaera* (*Acanthoica ordinata*) was provided by Kamptner in 1941 from the Adriatic Sea. The morphology of *A. ordinata* was characterized by its monomorphic coccoliths arranged in rows, without flagellar opening on the coccosphere, which placed it in the genus *Acanthoica* (Lohmann). In 1973, after close observation under the Scanning Electron Microscope (SEM), Heimdal (1973) assigned this species to the new genus *Alisphaera*, with *A. ordinata* as the type species. All species belonging to the genus *Alisphaera* possess elliptical coccoliths with an asymmetrical distal flange with an extension. All *Alisphaera* specimens presenting spines were originally included in *A. unicornis*. However, SEM observations and re-examination allowed to subsequently separate the specimens with spines into several species. In 1994, Jordan and Green transferred the genus *Alisphaera* to the family Syracosphaeraceae (Lohmann). However, Kleijne (2002) compared the coccolith ultrastructure of *Alisphaera* species to that of the caneoliths (elliptical coccoliths, characteristic of family Syracosphaeraceae) and suggested that this *Alisphaera* should be classified outside family Syracospheracea



TEXT-FIGURE 1
Location of surface water sites in the Southern Indian Ocean where *Alisphaera crostae* sp. nov. and other *Alisphaera* spp. are documented. Map background: average sea surface temperature (January-February, 2019) obtained from www.giovanni.gsfc.nasa.gov. [NSTF-North Subtropical Front, ARF- Agulhas Retroflection Front, SSTF- Southern Subtropical Front, SAF- Subantarctic Front, PF- Polar Front]. Black dots indicates sample locations during CROTALE Expedition and red dots showing sample locations during 4th SOE.

Coccospheres combining calcite-based coccoliths of *Alisphaera* spp. with aragonite-based coccoliths of the genus *Polycrater* (Manton and Oates) were documented from the northwest Mediterranean Sea (Cros et al. 2000a, Plate 87, figs 1-6). It was then hypothesized that *Polycrater* coccoliths might substitute holococcoliths in *Alisphaera* life cycle, and that several *Alisphaera* species may have a life cycle consisting of *Polycrater* phase. However, combination spheres with coccoliths of *Polycrater* and *Canistrolithus* were also documented (Cros 2001; Plate 88, figs 1-6), with *Alisphaera* and *Canistrolitus* been identified as very close genera in the earlier literature (Jordan and Chamberlain 1993), even though they were of different morphological types. Since these three genera (*Alisphaera, Canistrolithus,* and *Polycrater*) possess common characteristics in terms of coccolith morphology (e.g., presence of horns, spines, and extended protrusions) as well as coccosphere arrangement (e.g., longitudinal asymmetry of coccoliths, and general coccolith arrangement), it was assumed that they may belong to the same sub-group of coccolithophores where aragonitic *Polycrater* coccoliths substitute holococcoliths in their life-cycle stage (Cros et al. 2000b). Thus, Cros and Fortuño (2002) eventually moved the genus *Alisphaera* from the family Syracosphaeraceae to Incertae sedis. Young et al. (2003) created a new family *Alisphaeraceae* and moved the genus *Alisphaera* along with the genus *Canistrolithus* and *Polycrater* phase into the family.

MATERIALS AND METHODS

Water sample collection and filtering

During the MD218 CROTALE expedition, surface water samples were collected from the southwest Indian Ocean (text-fig. 1) between 23rd February 2019 and 11th March 2019 on board the R/V *Marion Dufresne*. The water samples were obtained from a depth of 7 m using the ship's hull pumping system.

Sea surface temperature (SST) and sea surface salinity (SSS) were obtained using Sea-Bird SBE21 located at the same depth (see Patil et al., submitted, for more information). During the 4th SOE, surface and deep water samples (surface to 110 m) were collected between 31st January and 18th February 2010 onboard the ORV *Sagar Nidhi*. The water samples were obtained from different vertical depths using 5l capacity Niskin bottles attached to a CTD rosette (12 bottles) (Sea-Bird-Electronics).

During both expeditions, two litres of seawater were filtered onto Whatman polycarbonate track-etched membrane filters of 0.8 µm pore size and 47 mm diameter for enumeration of coccolithophores at each sampling site-depth. We used natural gravity to allow the passage of water through the filters to ensure good preservation of coccospheres. The filters were transferred to Pall sterile petri dishes, oven dried at 40ºC for 24 hours, and kept sealed until SEM analysis.

Coccolithophore evaluation and repository

At the National Centre for Polar and Ocean Research (NCPOR), a small piece of filter (~ 5 mm^2) was placed on a 1.5 cm diameter aluminium stub using a carbon adhesive tape, sputter coated with platinum (for 60 seconds; ~ 2 nm thickness) and observed under a JEOL JSM 7610F FE-SEM at 1 KV acceleration voltage. The stub was initially scanned at 2000× to observe coccolithophores. A variable magnification of 2000× to 100,000× was used for the identification and characterization of Alisphaera taxa and to capture high-resolution images. The micrographs of the described species were stored for record in the FE-SEM-EDS laboratory at NCPOR. Measurements on the digital images were carried out using a pre-installed in-built package version 4.0.0.2. The details of sample locations where *Alisphaera* spp. were documented are given in Table 1. The filters in which the new taxa were most common are stored in the desiccator, under a vacuum in the FE-SEM-EDS laboratory of NCPOR, Goa, India. The copies of digital files taken on FE-SEM and SEM will be deposited in the National Polar Data Centre, and the same will be shared with other re-searchers through the Mikrotax.org website.

RESULTS

Terminology

Heimdal (1973) transferred *A. ordinata* from the genus *Acanthoica* (Kampter 1941) based on SEM investigations and morphometric characteristics. The coccoliths were described as monothecate, monomorphic, and elliptical, showing caneolith-like construction. So far, three species belonging to the genus *Alisphaera* have been recorded from the southern Indian Ocean (*A. spatula* (now *A. unicornis*), *A. gaudii*, and *A. unicornis*) (Patil et al. 2017, 2020). Here we describe a new species *A. crostae* sp. nov. from the southern Indian Ocean based on its morphological differences in terms of its coccolith size, flange structure, and nodules. Detailed descriptions of the genus *Alisphaera* and of *A. crostae* sp. nov. are given below.

FAMILY ALISPHAERACEAE Young et al., 2003
Genus *Alisphaera* Heimdal emend. Kleijne, Jordan, Heimdal, Samtleben, Chamberlain and Cros

Type species: Alisphaera ordinata (Kamptner 1941) Heimdal 1973.

Background: species of genus *Alisphaera* generally form a minor component of the coccolithophore assemblages. They show considerable morphological variations. The key features of the genus *Alisphaera* are (1) two flagella and an apical opening; (2) narrowly elliptical monomorphic coccoliths arranged in nearly regular meridian rows, and a short coccolith axis arranged in the polar direction; (3) coccoliths consist of a proximal flange, a distally widening tube, a distal flange that divides into a flat part and an obliquely raised part in some species; (4) most species show the presence of nodules on the inner side of the distal flange, and a median longitudinal slit in the central area with partly zigzag borders.

Diagnosis: monothecate coccosphere, circumflagellar coccoliths of varying morphology. Coccoliths are elliptical and consist of a short tube. Proximal and distal flange are asymmetric in appearance. Coccolith arrangement on coccosphere in regular median rows, wider part of the flange directed towards the apical pole. The narrow distal flange usually consists of nodules on the inner periphery. Coccoliths are either monomorphic (with additional structure at the wide side of the distal flange in all coccoliths) or dimorphic (only some coccoliths bear additional structures, spines, nodules etc.). Some parts of the coccolith tube consist of interlocking elements R unit and V crystal units alternate). R units form the lower part of the tube and proximal flange, whereas V units form the distal flange, the nodules and the upper part of the tube. The central area is partly closed by plate-like extensions of the R elements. Other cycles of R elements cover the remaining part of the central area (please refer to Young et al. 2003 for the description of R and V units). In case of the absence of additional elements, the central area possess a median longitudinal S-shaped slit which shows jagged zigzag borders.

Alisphaera crostae Patil and Jafar n. sp.
Plate 1, figs A-F, Plate 2, figs A-C1

Holotype: Plate 1 A-F

Etymology: In honor of Dr. Xavier Crosta, Senior Researcher and micropaleontologist, at UMR-CNRS 5805 EPOC, University of Bordeaux, chief scientist of the MD218 CROTALE expedition.

TABLE 1.
Sample locations, water mass properties, and abundance of *Alisphaera* species in the southern Indian Ocean.

Station	Date of sampling	Latitude	Longitude	Occurrence depth	Temperature (°C)	Salinity	Total coccolitho-phore abundance (nos x 10^3cells/l)	Total *Alisphaera* abundance	*A. spatula* (abundance nos x 10^3cells/l)	*A. gaudii* (abundance nos x 10^3cells/l)	*A. unicornis* (abundance nos x 10^3cells/l)	*A. crostae sp. nov* (abundance nos x 10^3cells/l)
C1	26.02.2019	35°37'S	49°14'E	Surface	20.4	35.46	407.5	4.2		+ (4.2)		
C2	26.02.2019	36°50'S	48°42'E	Surface	20.2	35.57	940.7	3.0			+ (3.0)	
C3	26.02.2019	38°24'S	47°60'E	Surface	19.5	35.59	692.0	9.7	+ (3.1)		+ (3.4)	+ (3.2)
C4	27.02.2019	40°21'S	47°05'E	Surface	19.5	35.61	973.6	6.1			+ (3.0)	+ (3.1)
S1	31.01.2010	39°00'S	57°30'E	40 m, 60 m	17.88 at 40m; 16.75 at 60m	35.39 at 40m; 35.42 at 60m	120.5 at 40m; 82.9 9 at 60m	8.8 at 40m; 4.9 at 60m				+ (8.8 at 40m; 4.9 at 60m)
S2	02.02.2010	44°00'S	57°30'E	60m, 80m, 110m	7.5	34.25	174 at 60m; 105.7 at 80m; 46.5 at 110m	9.4			+ (5.6 at 60m, 0.07 at 80m)	+ (3.7 at 110m)
S3	04.02.2010	45°00'S	57°30'E	Surface	11.11	33.93	765.0	0.3			+ (0.3)	
S4	06.02.2010	48°00'S	57°30'E	Surface, 20, 40, 60 m	7.2 at surfaces, 20, 40 and 60m	33.72 at surface, 20, 40, and 60m	758.2 at surface; 914 at 20m; 279.3 at 40m; 234.7 at 60m	41.3				+ (11.7 at surface; 7.7 at 20m; 7.5 at 40m; 14.4 at 60m)

Type locality: 48ºS, 57.30ºE (Southwest Indian Ocean) Table 1).

Type material: FE-SEM-EDS Lab/Arch- stub no. 05

Diagnosis: Coccospheres spherical or subspherical, 5.9–6.7 µm in diameter, bearing 70-95 body coccoliths (based on 8 specimens, measurements on collapsed coccospheres). Coccospheres are monomorphic, all coccoliths have similar flange development. Body coccoliths appear elliptical, 1.25–1.59 µm in length and 1.0–1.27 µm in width (measurements on 5 coccospheres, total 62 coccoliths). One side of the coccolith distal flange is laterally extended making a broad wing-like structure. The tip of the extended flange is blunt and broad (Plate 3 A a,b) and in some specimens it is not elevated (approx. 50% narrower than the elevated flange). Flange width varies from 0.30–0.55 µm. Rim smooth to indented (Plate 1, 2). Nodules are prominent and present in the narrow side of the flange (8–12 numbers in each coccoliths) (Plate 1, C-D, d). The narrow flange shows a slit running parallel, outer area of the short flange is slightly elevated and curved (Plate 1, D-E, e). Coccoliths central area presents a zigzag fissure approximately 50% area on each side in the opposite direction (Plate 1, E-F, f). Coccoliths do not show pointed end as seen in other specimens of the genus (e.g. *A. extenta*).

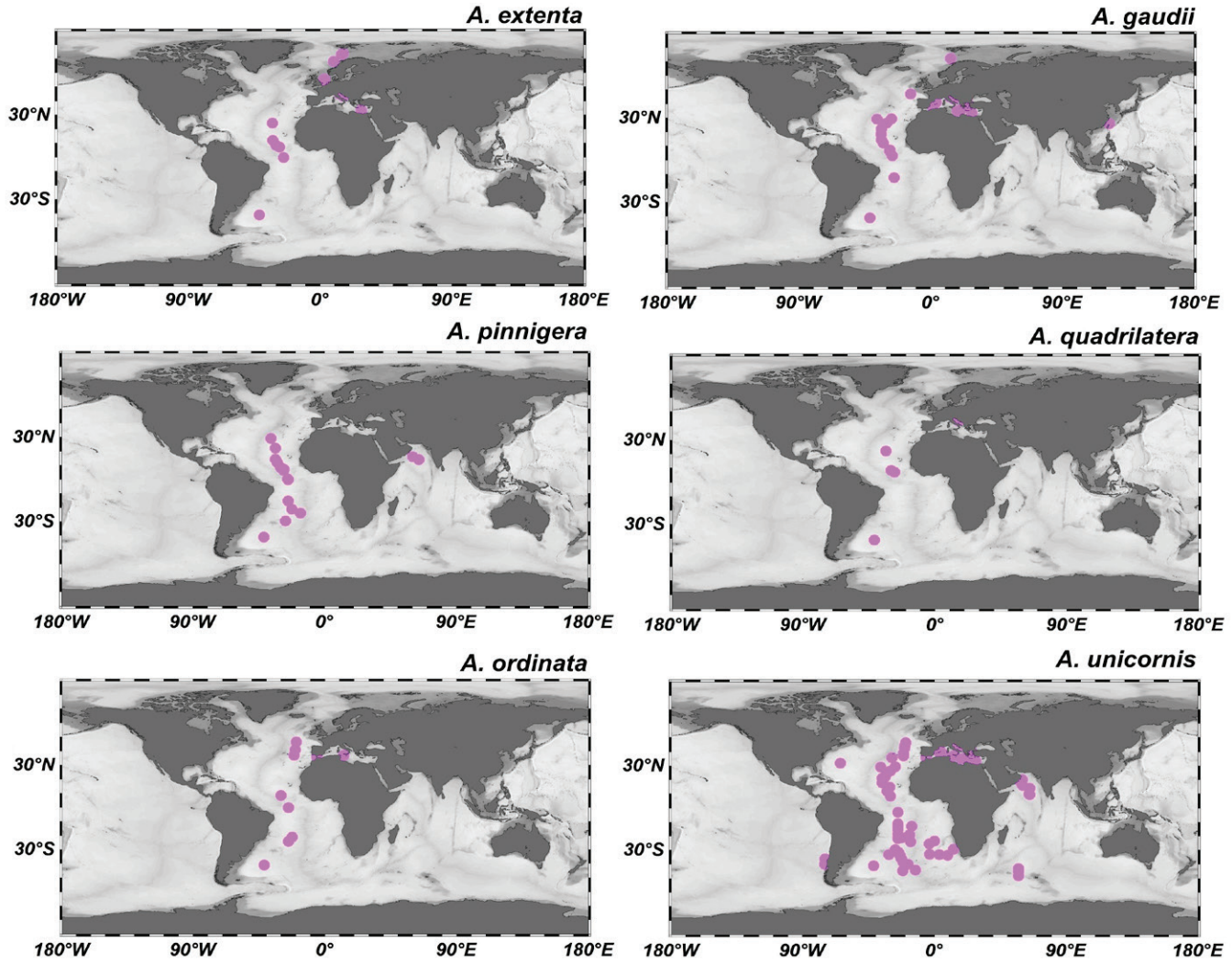
Remarks: Alisphaera crostae somewhat resembles *A. extenta*, but is significantly different in morphology. The size of the *A. crostae* (coccoliths 1.25–1.69 µm in length and 1.0–1.27 µm in width) is larger than *A. extenta* holotype (1.1–1.3 µm long, c. 0.6–1.0 µm wide), but smaller than *A. extenta* specimens illustrated by Giraudeau and Bailey (1995) (c. 2 µm long, c. 1.8 µm wide). They are however in the range of *A. extenta* specimens in Nishida (1979) (pl. 15, fig. 2a,b). In *A. extenta*, the wing on the distal flange is generally extended (but highly variable) in the lateral direction (Giraudeau and Bailey 1995; Nishida 1979), despite being obliquely raised occasionally in some phytoplankton samples from the Nordic Seas. Previous descriptions indicate that *A. extenta* coccoliths are without nodules (Giraudeau and Bailey 1995), though nodules were reported in antapical pole coccoliths from the holotype material. These nodules were not prominent and were observed in only three coccoliths at the narrow part of the flange. Previously, Nishida (1979), and Winter and Siesser (1994) observed nodules on the wide side of the flange, and the distal shield extension was not sharply pointed, i.e. had a blunt end. Therefore, the prominent and numerous nodules present in all coccoliths both at the narrow part of the flange and at the less elevated wider side of the flange are a distinctive characteristics of *A. crostae* (plate 1, 2).

DISCUSSION AND CONCLUSIONS

The genus *Alisphaera* was previously considered monomorphic (Jordan and Chamberlain 1993). Kleijne et al. (2002) categorized the genus *Alisphaera* into several new species, including the introduction of five new species of which three were dimorphic. However, the *Alisphaera* species would be better described as varimorphic. The differentiation of the newly described *A. crostae* from other *Alisphaera* species is primarily based on the extension of the flange and the presence of nodules at the narrow part of the flange. *Alisphaera* crostae closely resembles *A. extenta* in terms of coccolith size but differs in morphology, e.g., flange shape and nodules. In *A. crostae* the flange end is not pointed, and the flange size is significantly smaller than that of the *A. extenta* (Mikrotax.org). Additionally, *A. extenta* is considered monomorphic, though some coccoliths were observed to possess few nodules at the antapical pole (Nishida 1979; Winter and Siesser 1994).

In the previous studies, *Alisphaera* species were sparsely documented (text-fig. 2) and information about their biogeochemical range is still not well known. *A. spatula* is documented from low latitudes in Atlantic and Indian oceans; *A. capulata*, *A. ordinata*, and *A. quadrilatera* occur in the Atlantic Ocean; *A. gaudii* is present in the Atlantic tropical zone, Mediterranean Sea and Pacific temperate zone; *A. pinnigera* is somehow ubiquitous with presence from the tropical to subtropical waters; and *A. unicornis* is present from the tropical to temperate zones. Whereas *Alisphaera extenta* is documented from the Eastern Mediterranean Sea and the northern North Atlantic. Previously, Samtleben et al. (1995) referred *A. extenta* as 'Arctic group' since this species was documented as far as polar front in low temperatures (3–14ºC). As such, *A. extenta* seems to be a characteristic of high latitudes in the North Atlantic (occurs in North Atlantic drift and Norwegian current) despite some presence in the Mediterranean Sea, upwelling waters of the Benguela system, and the Pacific temperate zone. It is also known to reach elevated abundance (up to 10^4 cells/l; eg. Samtleben et al. 1995), amounting up to 20% of the coccolithophore assemblages in the North Atlantic.

Patil et al. (2017) recorded presence of *A. extenta* coccoliths ($3.7\text{-}14.3 \times 10^3$ nos/l) in the south of the subtropical front of the Southern Indian Ocean between 39ºS and 48ºS. However, re-observation of these filters indicate that the coccoliths possess prominent nodules, which are not present in *A. extenta* but a distinctive characteristic of *A. crostae*. For this reason, and with comparison to the monomorphic coccospheres of *A. crostae* (>15 coccospheres observed in the samples), we suggest these spheres belong to the latter species. The presence of *A. extanta* in the Southern Ocean is therefore not supported by our new findings. Along with the newly described species, coccospheres of three *Alisphaera* species, viz. *A. spatula* (now *A. unicornis*), *A. gaudii*, and *A. unicornis* were documented in low abundances at northernmost stations 1-4, probably showing the southernmost distribution of these tropical-to-temperate species.



TEXT-FIGURE 2
Documentation of *Alisphaera* species in the global oceans (figure after de Vries et al. 2020).

The discovery of several *Alisphaera* species over the last decade suggest that this genus may comprise several undescribed species in diverse oceanic regions, which calls for further careful investigations. Isolating, culturing and sequencing of *Alisphaera* species are important to further divide the *Alisphaera* species into different groups/clades and better understand their phylogeny.

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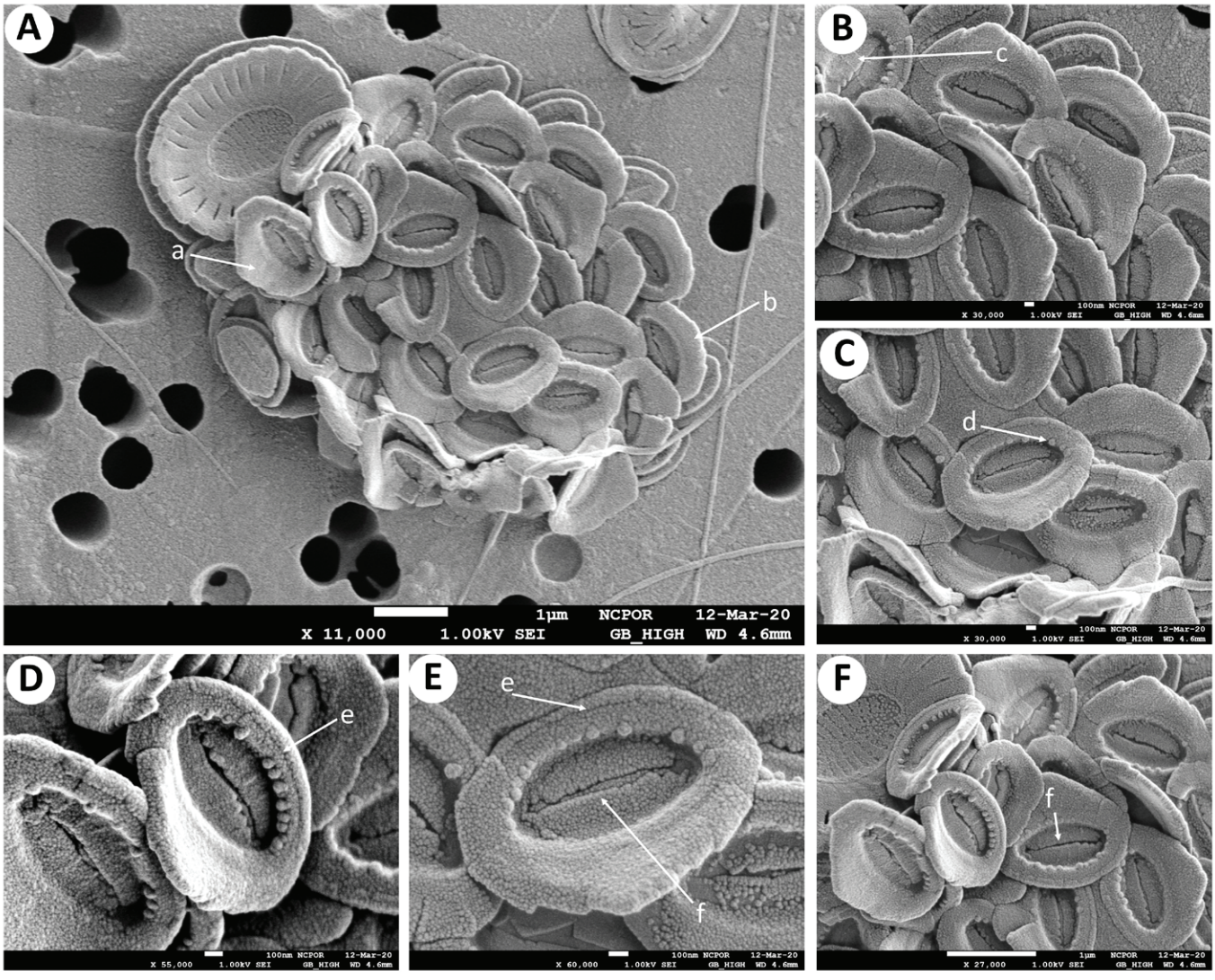

PLATE 1

(A) Coccosphere of *Alisphaera crostae* sp. nov. (holotype). Showing sub-vertical (V units) a, b; (B) showing sub-radial (R units) - c; (C) showing nodules - d; (D-E) slightly elevated short flange - e; (E-F) central area fissure - f.

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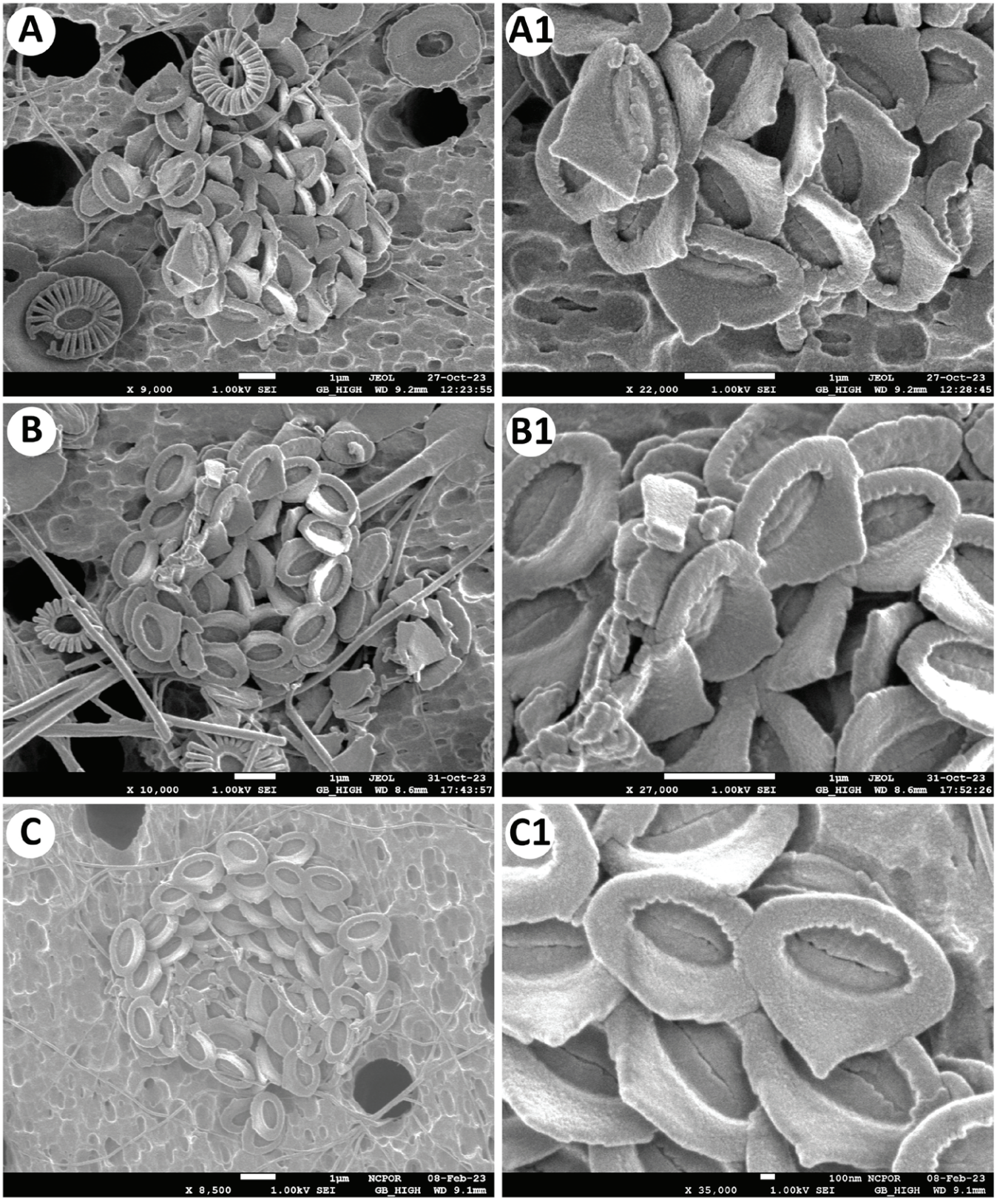

PLATE 2

(A-C1) Coccospheres and resolved portions of coccospheres of *Alisphaera crostae* sp. nov..