Crotalia jafari: a new weakly calcified holococcolithophore genus and species from the Southwest Indian Ocean

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ABSTRACT: We here describe a distinctive weakly calcified holococcolithophore *Crotalia jafari* gen. et sp. nov. from the Southwest Indian Ocean phytoplankton. The coccospheres of *Crotalia jafari* measure 8–15 µm in diameter, and possess 430–538 coccoliths, with each coccolith measuring less than 1 µm in diameter. The coccoliths are tightly attached to each other by an organic layer. Their central area appears open. Finger-shaped extensions are present in the peripheral coccoliths, and stretch from the hexagonal surface layer towards the basal plate. The basal plate is flat and composed of irregular wall fabric. The crystallites of the coccoliths are small. These morphological features make this holococcolithophore unique among the extant and fossil coccolithophores. The described species is therefore placed into the new genus '*Crotalia*'. This study also suggests that high diversity of weakly calcified (and still undescribed) holo- and heterococcolithophores may exist in the Southern Ocean, which requires additional careful observation.

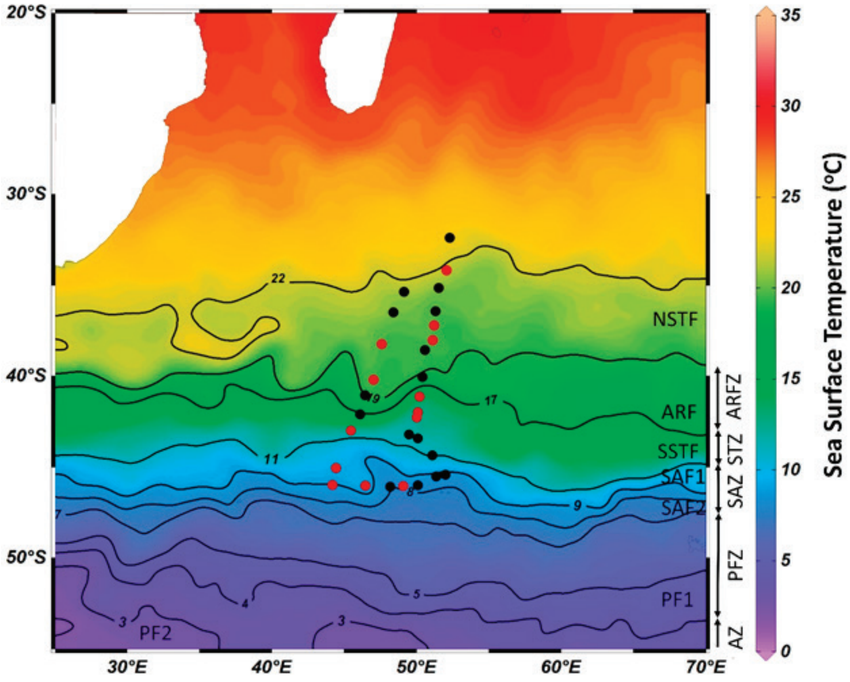
Keywords: Taxonomy, coccolithophore, new taxon, Indian Ocean.

INTRODUCTION

Over the past two decades, extant coccolithophores (haptophyte algae; Prymnesiophyceae) ecology and biogeography has been extensively studied in diverse oceanic regions. Their taxonomy, mineralization, and life cycle are relatively well established, and better known than many other phytoplankton groups (Young and Andruleit 2012). The coccolithophore life cycle consists of an alternation between diploid (a non-motile phase bearing heterococcoliths, in most specimen) and haploid (a motile phase that produces holococcoliths) (Billard 1994; Cros et al. 2000; Houdan et al. 2004) phases, which are capable of reproducing asexually for an extended period of time. However, the factors responsible for the transition from one phase to the other, and the benefits these organisms gain from switching and maintaining the haploid and diploid phases in their life cycle are not well understood. This is in part due to the limited observations on coccolithophores made from culture experiments, as these do not produce combination coccospheres, both phases are self-reproducing and transitions rarely occur in the cultures (Noël et al. 2004), and/or were unable to obtain genetic information on most heterococcolithophore and holococcolithophore taxa . In addition, limited sampling of coccolithophores in less-accessible oceanic regions [e.g., high/low latitude oceans (e.g., Southern Ocean)] and limited observations under high-resolution electronic microscope are other possible explanations behind this knowledge gap.

In the past few decades, several new coccolithophore taxa [e.g., *Calciosolenia subtropicus* (Patil et al. 2019), *Solisphaera blagnacensis*, *Solisphaera emidasia* (Aubry and Kahn 2006)] as well as silicifying haptophytes [e.g., *Petasaria heterolepis* and *Prymnesium neolepis* (Patil et al. 2014; 2015; Jordan et al. 2015)] have been documented from the Southern Ocean subtropical region. Similarly, and more surprisingly, a contingent of weakly calcified (hetero- and holo-) coccolithophore taxa have been shown to be consistently present in polar waters down to latitude 60°S, which are characterized by low temperatures (e.g., -2 to +5°C), seasonal sea-ice cover, and extreme fluctuation of day-length and irradiance (e.g., Manton and Oates 1975; Thomsen et al. 1988; Thomsen et al. 1995; Findlay and Giraudeau 2000; Mohan et al. 2008; Charalampopoulou et al. 2011; Thomsen et al. 2013; Thomsen and Østergaard 2014a,b; Thomsen and Østergaard 2015a,b; Patil et al. 2020). Unlike typical photosynthetic haptophyte algae, they appear to be without chloroplast and to feed on bacteria and small-sized particles in these polar waters (Marchant and Thomsen 1994). Heterotrophy is probably an adaptation to prolonged seasonal darkness that prevails at high latitudes, and the absence of chlorophyll is, therefore, a secondary loss.

Despite their potential importance in the trophic chain and global ocean nutrient cycles, weakly-calcified coccolithophores from polar waters received very little attention, probably due to (1) their small size and fragile tests, (2) limited sampling in these largely inaccessible regions, and (3) lack of high-resolution electron microscopic investigations. The recent advances in electron microscopy and field techniques were helpful to discover and better resolve the nanno-scale fine ultrastructure of calcareous nannoplankton, including those possessing lightly calcified skeletons and organic scales. The present study is dedicated to the characterisation of the ultra-structure of a new holococcolithophore taxa found to frequently occur in surface water samples collected during the MD218 CROTALE expedition in the Southwest Indian Ocean. The ecological distribution and taxonomic affinities of this new species are described and



TEXT-FIGURE 1
Location of surface water in the Southern Indian Ocean where new coccolithophore taxa are reported. Map background: average sea surface temperature during the study period obtained from www.giovanni.gsfc.nasa.gov.

discussed. This new species with an ultrastructure which was unknown until now in any living and fossil taxon makes it an ideal example for rational analysis of affinities.

MATERIALS AND METHODS

Water sample collection and filtering:

In this study, the samples used as type material were collected between 23rd February 2019 and 11th March 2019 during the MD218 CROTALE (Crozet Archipelago Paleoceanography) expedition on board the *R.V. Marion Dufresne*. Samples were collected from 7 m water depth using the ship's hull pumping system. A total of 29 sea surface water samples were collected for enumeration of coccolithophores. In addition, Sea Surface Temperature (SST) and Sea Surface Salinity (SSS) data were obtained using a Seabird SBE21 underway thermosalinograph (TSG) mounted on the ship's hull at 7 m water depth. Water sampling locations were distributed based on the temperature and salinity data in order to ensure even sampling in each oceanic realm. At each station, two litres of seawater were filtered onto Whatman (make) polycarbonate track-etched membrane filters of 0.8 µm pore size and 47 mm diameter. We used gravity to allow passage of the water through filter papers to ensure good preservation of the coccospheres. The filters were then transferred to Pall (make) sterile petri dishes, oven-dried at 40°C for 24 hours and kept sealed until Scanning Electron Microscopy (SEM) analysis.

Coccolithophore evaluation and repository:

At the National Centre for Polar and Ocean Research (NCPOR), a filter piece of about 5 mm^2 was cut and placed on a 1.5 cm diameter brass stub using a double-sided carbon adhesive tape for each sample. The stub was then sputter coated with platinum for 60 seconds (~2 nm thickness) and observed under a JEOL JSM 7610F Field Emission Scanning Electron Microscope (FE-SEM) at 1 kV acceleration voltage. The stub was scanned at 2000×, and a variable magnification of 2000× to 150,000× was subsequently used to identify the taxa and to capture high-resolution images (up to 100 nm scale). High-resolution images were captured and stored for records.

Out of the total 29 filters scanned, >13 samples showed the occurrence of the described *C. jafari* during routine counts. The details of sample collection, analysis, and abundance of the new species are given in Table 1. The filters in which the new taxa was most common were examined again to obtain high-resolution images. Measurements on the digital images were carried out under FE-SEM using a pre-installed measurement package version 4.0.0.2.

Energy Dispersive Spectrometry:

Energy Dispersive Spectrometry (EDS) analysis was carried out to assess the elemental composition of the *C. jafari* coccoliths. For EDS, an accelerating voltage of 15 kV and a magnification up to 150,000× were used. The stub containing abundant specimens of the new taxa is archived in the FE-SEM and EDS laboratory of NCPOR with archival number FE-SEM-EDS Lab/Arch-03.

Preservation of samples:

The stubs containing holotypes and paratypes of the new species are kept in a desiccator to alleviate preservation issues of weakly calcified taxa sometimes observed on SEM stubs over a long period of time. The filter papers containing original samples were kept in the FE-SEM-EDS laboratory of NCPOR, Goa, India. Copies of the digital image files taken on SEM and FESEM, along with the EDS data files, will be deposited in the National Polar Data Centre. The images of the new specimens will be shared with other researchers through the Mikrotax.org website.

TABLE 1.
Sample locations, wind speed, sea surface temperature (SST), sea surface salinity (SSS), total coccolithophore abundance, and presence of *Crotalia jafari* documented in the study area

Station number	Date	Latitude (°S)	Longitude (°E)	Wind speed (kt)	SST (°C)	SSS (psu)	Coccolithophore abundance (x10^{-3} Cells/l)	Number of taxa recorded	*Crotalia jafari* sp. nov. (+ Present; - absent)
Station 1	26.02-2019	35°37.31'	49°14.41'	16.7	20.9	35.46	407.49	42	-
Station 2	26.02-2019	36°50.15'	48°42.41'	19.4	20.63	35.57	940.68	60	-
Station 3	26.02.2019	38°24.65'	47°59.97'	25.7	19.22	35.59	695.02	51	+
Station 4	27.02.2019	40°21.86'	47°04.96'	22.1	19.22	35.62	973.63	59	+
Station 5	27.02.2019	41°06.97'	46°45.04'	23.5	20.75	35.52	0.00	0	-
Station 6	27.02.2019	42°11.38'	46°12.25'	18	17.92	35.29	188.73	8	-
Station 7	27.02.2019	43°00.84'	45°48.12'	13.4	12.25	33.62	53.92	3	+
Station 8	28.02.2019	45°07.10'	44°45.25'	8.5	9.07	33.71	1632.70	23	+
Station 9	28.02.2019	46°00.21'	44°20.05'	12.4	8.75	33.70	227.68	5	+
Station 10	01.03.2019	46°04.56'	46°48.67'	23.1	9.66	33.66	14.98	1	+
Station 11	01.03.2019	46°10.02'	48°19.77'	15.3	7.13	33.70	8.99	2	-
Station 12	02.03.2019	46°05.34'	49°11.40'	18	7.96	33.70	473.33	3	+
Station 13	02.03.2019	46°01.63'	50°09.56'	28	8.31	33.63	0.00	0	-
Station 14	02.03.2019	45°53.04'	51°38.57'	15.2	8.2	33.65	281.60	1	-
Station 15	03.03.2019	45°44.03'	52°01.40'	30.3	8.16	33.63	41.94	1	-
Station 16	04.03.2019	44°37.39'	51°10.25'	19.6	10.61	33.58	0.00	0	-
Station 17	04.03.2017	43°43.45'	50°10.29'	25.8	11.07	33.58	0.00	0	-
Station 18	05.03.2019	43°22.67'	49°49.71'	37.3	10.65	33.58	0.00	0	-
Station 19	05.03.2019	42°29.03'	50°04.19'	18.7	10.22	33.65	5.99	1	+
Station 20	05.03.2019	42°00.15'	50°11.50'	13.9	10.29	33.65	308.57	5	+
Station 21	05.03.2019	41°15.02'	50°24.06'	17.8	11.18	33.63	707.01	9	+
Station 22	06.03.2019	40°04.98'	50°42.14'	22.4	17.55	35.30	470.34	5	-
Station 23	06.03.2019	38°57.64'	50°59.24'	18.5	18.62	35.37	515.28	17	-
Station 24	06.03.2019	38°03.83'	51°13.09'	5.6	19.54	35.51	131.81	13	+
Station 25	06.03.2019	37°22.27'	51°23.13'	16.3	19.31	35.60	104.85	8	+
Station 26	06.03.2019	36°43.20'	51°33.46'	18.8	19.1	35.55	59.92	6	-
Station 27	07.03.2019	35°15.26'	51°54.57'	25	20.76	35.43	161.77	14	-
Station 28	07.03.2019	34°18.42'	52°08.57'	24.3	21.8	35.34	203.71	13	+
Station 29	07.03.2019	32°40.31'	52°31.72'	20.8	22.65	35.39	56.92	7	-

RESULTS

Coccolithophore community at the study site

In the study area, 88 heterococcolithophore and 26 holococcolithophore taxa were reported including species, subspecies, and morphotypes. The highest hetero- and holococcolithophore abundances were recorded in the stations located in the Agulhas Retroflection Frontal Zone (ARFZ) and Subtropical Zone (STZ) (Table 1; text-figs. 1, 2). Conversely, sampling stations from the Subantarctic Zone (SAZ1 and SAZ2) showed low coccolithophore abundance and diversity. *Syracosphaera* was the most diverse coccolithophore genus with the presence of 29 taxa, whereas *Emiliania huxleyi* was found to be the most abundant coccolithophore taxon (with the presence of four morphologically distinct types) representing >47% of the assemblage at each sampling site. The new species, *C. jafari*, occurred at 13 locations with abundance ranging between 3 and 66×10^3 cells/l (Table 1). Though it is encountered in all oceanic realm covered by our sampling sites, this taxa reached its highest abundance between 6 and 66×10^3 cells/l, in the SAZ1 and SAZ2, whereas its abundance remained lower than 9×10^3 cells/l at stations from the ARFZ and STZ (text-fig. 2).

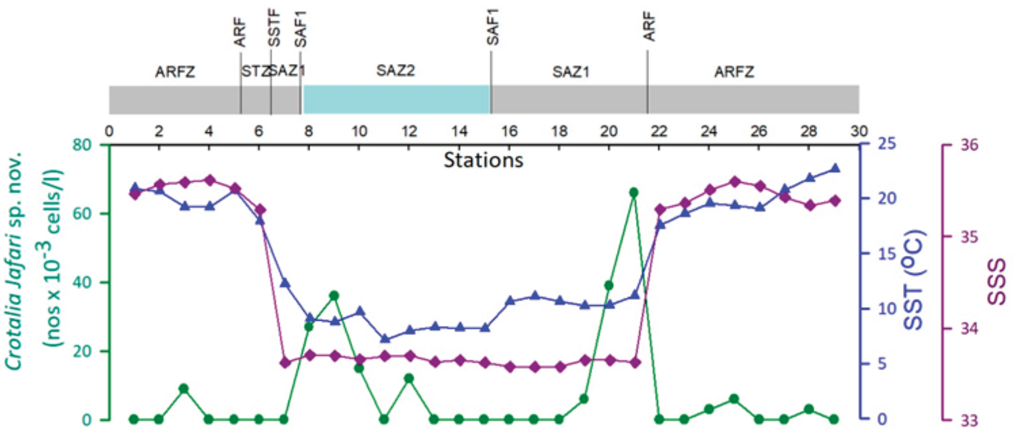
Classification and terminology

In the following section, we describe a new weakly calcified holococcolithophore genus and species *Crotalia jafari* gen. et sp. nov. To our knowledge, this taxon has not been recorded before. The description of *C. jafari* is based on its occurrence at 13 stations and detailed morphological observations of more than 10 specimens of described taxon. The descriptive terminology used in this work follows the recommendation of Jordan and Young (1990), and Young et al. (1997, 2003).

Genus ***Crotalia*** Patil gen. nov.

Etymology: Based on the acronym of the project under which this study was carried out (CROTALE: Crozet Archipelago Paleoceanography)

Diagnosis: Cell solitary, planktonic, coccosphere shape unknown. Collapsed specimens are of spherical to sub-spherical



TEXT-FIGURE 2
Abundance of *Crotalia jafari* sp. nov. recorded in the study area. (Annotations: ARFZ- Agulhas Retroflection Frontal Zone, STZ- Subtropical Zone, SAZ- Subantarctic Zone, ARF- Agulhas Retroflection Front, SSTF- Southern Subtropical Front, SAF- Subantarctic Front).

outline; and coccosphere sizes of 8–15 µm were frequently observed. Coccolith size is usually less than 1 µm, coccolith shape circular to sub-circular; central coccoliths appear hexagonal.

Type species: Crotalia jafari sp. nov. (HOL)

Etymology: Named after Dr. Syed A. Jafar, Scientist (Retd.), nannofossil expert and biostratigrapher, Birbal Sahni Institute of Paleosciences, India

Diagnosis: Coccosphere shape appears to be circular, monomorphic, monothecate, bearing 430–538 coccoliths (>15 sphere counts). The coccolith distal face appears to be hexagonal near the centre of the coccosphere and sub-circular at the periphery. The coccolith surface is covered by an organic layer most of the time and coccoliths in the equatorial position on the coccosphere appear tightly attached to each other by this organic layer. The central area of the coccoliths is open. 10–12 finger shaped extensions protrude from the hexagonal surface layer towards the basal plate of the coccolith (Plate 1, text-fig. 3). These finger-shaped extensions are less visible in the coccoliths located at the centre of the coccosphere where coccoliths are tightly arranged than in the periphery where coccoliths are loosely attached. The basal plate of each coccolith is flat. Tiered with several layer of irregular wall fabric. Crystallites in the central and peripheral coccoliths are very small in size (~0.02 µm). The central area coccoliths measure 0.53–1.15 µm × 0.33–0.71 µm in length and width, respectively, while coccoliths in the periphery are smaller in size (0.45–0.62 µm × 0.38–0.51 µm, in length and width, respectively). The cell may or may not possess associated organic scales. Organic scales are not prominently visible near all *C. jafari* spheres documented in the study.

Differentiation: There are no extant coccolithophores that resembles *Crotalia jafari* sp. nov.

Remarks: In some specimens (see open arrows in Plate 1-A, c) flagellum like structures are visible close to the coccoliths. If it is a true flagella, then it is narrow and very long.

Type locality: Present at 13 stations located between 35°S–46°S and 44°E–52°E (southwestern Indian Ocean surface water samples).

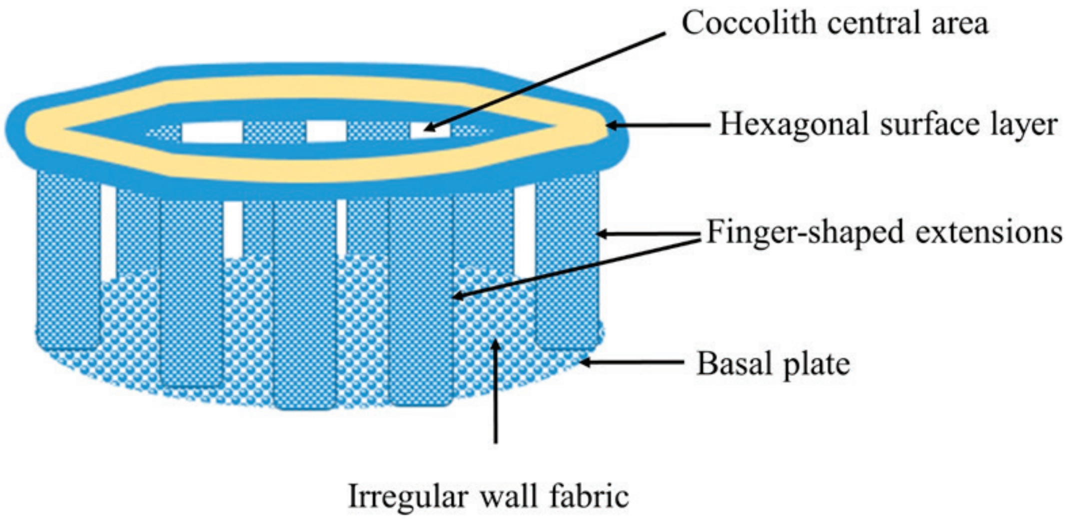
Holotype: Plate 1, A-F, Text-Figures 2 and 3.

Paratype: FE-SEM-EDS Lab/Arch- stub no. 03

DISCUSSION AND CONCLUSIONS

So far, over 280 extant mineralized coccolithophore taxa have been reported globally (Mikrotax.org). Furthermore, with the multiplication of oceanographic cruises and the development of new technologies, new coccolithophore (heterococcolithophore and holococcolithophore) taxa (including new genus, species, subspecies, and varieties) are continuously being reported from the tropical to the high latitude oceans (e.g., Thomsen et al., 1995; Kleijne, 2002; Dimiza et al., 2005; Bollmann et al., 2006; Aubry and Kahn, 2006; Kleijne and Cros, 2009; Couapel et al., 2009; Andruleit and Young, 2010; Young and Andruleit, 2012; Kahn and Aubry, 2012; Thomsen et al., 2016; Andruleit et al., 2016; Andruleit and Jordan, 2017; Young et al., 2018; Patil et al., 2019). While studying the biogeographic distribution of coccolithophores in surface waters of the Southwest Indian Ocean, one new holococcolithophore genus and species *Crotalia jafari* nov. gen. et sp. nov. was identified. A close ultrastructural observation of the specimens under FE-SEM (Plate 1, text-fig. 3) confirmed the new species as a holococcolithophore. The energy dispersive spectrometry analysis revealed that the observed tests are predominantly composed of calcium (text-fig. 4).

The described genus *Crotalia* does not bear morphological resemblance with any known extant holococcolithophres in terms of coccolith and coccosphere shape and size. Owing to its peculiar morphological and ultrastructural features, it is drastically distinct from previously described holococcolithophores, and thus the observed specimens are placed in a new genus. We refrained from linking this new genus to any existing higher taxonomic level because of the absence of molecular information.
Most mineralized holococcolithophore taxa in the Southern Indian Ocean are documented from the subtropical zone (Patil et al.,



TEXT-FIGURE 3
Schematic diagram of the coccolith of *Crotalia jafari* sp. nov.

2017, 2020). In the same way, weakly calcified coccolithophores are not confined to polar waters, but mostly present in the tropical and subtropical waters (e.g., Thomsen et al., 1994). However, the documentation of weakly calcified holococcolithophores in the polar waters is still rare (e.g., Thomsen et al., 1995). This lack of information persists probably due to their low abundance in the polar waters, poor coccosphere preservation on filters and/or poor microscope resolution. Despite *C. jafari* being abundant in the SAZ we cannot ensure it is a pure "polar" species as long as its complete life cycle remains unknown.

We suspect there may be a high abundance of weakly mineralized holococcolithophores in the Southern Ocean, which needs to be further investigated. Isolating, culturing and sequencing coccolithophores from the Southern Ocean waters is extremely important in order to better understand coccolithophore ecology, standing stock and biogeography, as well as their role in the trophic web and nutrient cycles. During light and electron microscopic analysis, meticulous ultrastructural observation and documentation is essential to investigate morphological differences within species-subspecies of weakly mineralized- and small-sized coccolithophores. In addition, elemental composition on weakly mineralized species is required to confirm their characteristics.

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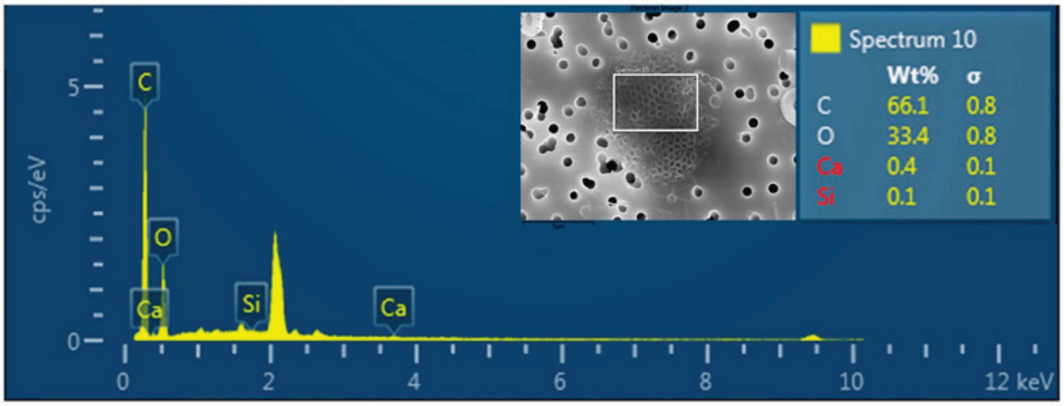

TEXT-FIGURE 4
Energy Dispersive Spectrometry results of *Crotalia jafari* gen. et sp. nov.

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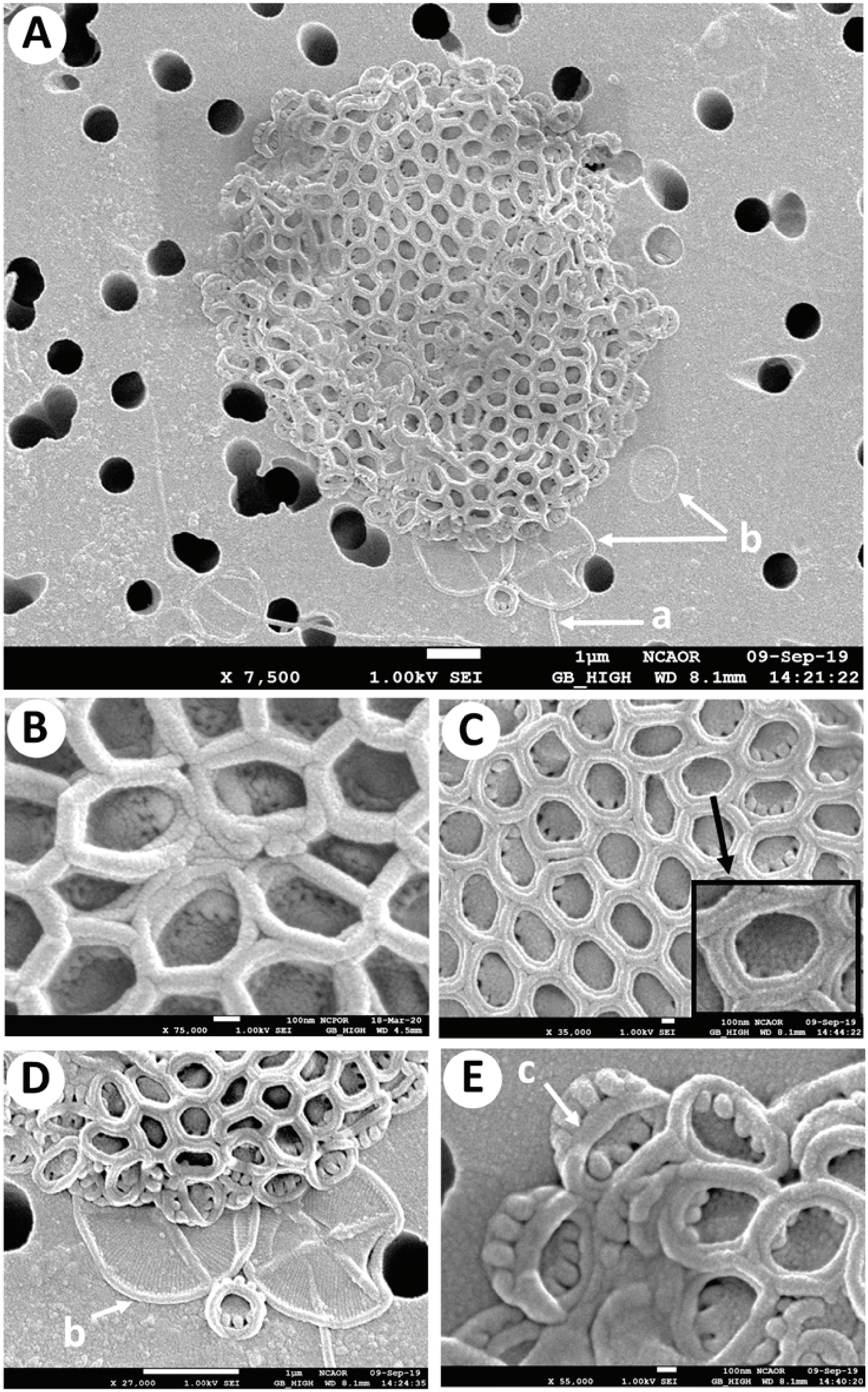
PLATE 1

A Collapsed coccosphere of *Crotalia jafari* sp. nov.; a- flagella like structure; b- organic scales.

B-C Coccoliths showing small crystallites and tired irregular wall fabric structure.

D-E Circular coccoliths in the periphery of the coccosphere, c- finger-shaped extensions in peripheral coccoliths.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