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The coccolithophore family *Calciosoleniaceae* with report of a new species: *Calciosolenia subtropicus* from the southern Indian Ocean

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ABSTRACT: The families Calciosoleniaceae, Syracosphaeraceae and Rhabdosphaeraceae belong to the order Syracosphaerales and constitute a significant component of extant coccolithophore species, sharing similar ultrastructural bauplans. The literature on Calciosoleniaceae is reviewed and combined light- and scanning electron microscope studies of four extant species including *Calciosolenia subtropicus* sp. nov. described herein, reveal the unique interpretative V/R structure of the Calciosoleniaceae. *Calciosolenia subtropicus* sp. nov. is primarily distinguished from previously well documented extant species, *Calciosolenia murrayi*, *Calciosolenia brasiliensis* and *Calciosolenia corsellii*, by the consistent presence of prominent clockwise imbricated wedge shaped R-elements at the inner margin and in distal view of both ordinary and apical scapholiths, distinctly tapering in size towards the major axis of the scapholiths, as observed under the scanning electron microscope. Prompted by the contrasting birefringence displayed by the rim, central area, apical and ordinary coccoliths under crossed-polarized illumination in earlier publications, the Energy Dispersive Spectrometry of *Calciosolenia subtropicus* sp. nov. reveals the presence of (a) calcite + high silica in the ordinary coccoliths showing dark appearance and (b) high calcite + negligible silica in the apical coccoliths showing bright appearance; besides the c-axis orientation of calcite, the different elemental composition of coccoliths seems to control birefringence. Molecular genetic studies are necessary to provide insight on the relationship between the Calciosoleniaceae and other coccolithophore families including reasons for its successful invasion in contrasting ecological regimes.

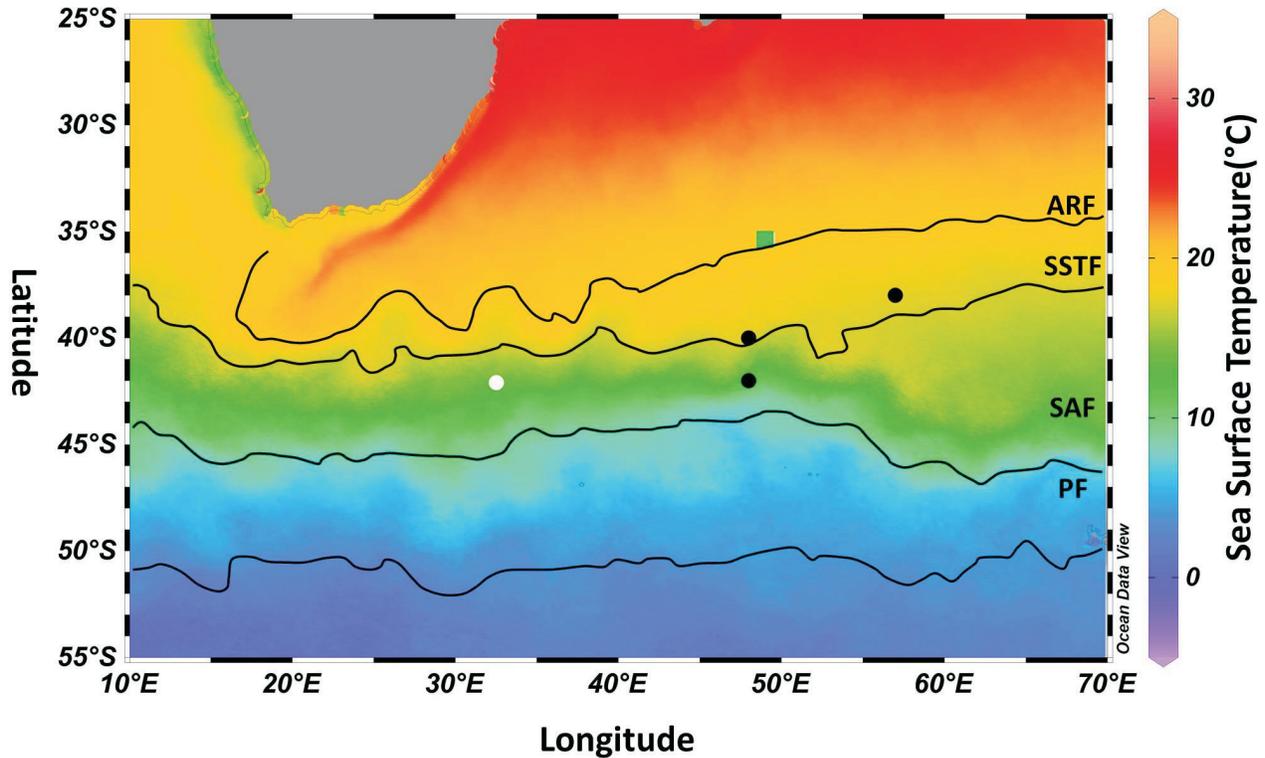
Keywords: Coccolithophores, Calciosoleniaceae, *Calciosolenia*, Energy Dispersive Spectrometry, Indian Ocean.

INTRODUCTION

Most living coccolithophores are known to form coccospheres of spherical or pseudo-spherical configuration, and in extreme cases certain extant species of *Syracosphaera* display long tubular coccospheres (cf. *Syracosphaera prolongata* Gran, 1912 ex Lohmann, 1913). The family Calciosoleniaceae comprising of a solitary genus *Calciosolenia*, is somewhat unique in displaying a fusiform coccosphere, abruptly or gradually tapering at both ends, and instead of being covered with coccoliths of circular or elliptical outline, is decorated with closely packed, spirally arranged varimorphic coccoliths showing an outline of a parallelogram, without gaps or overlap. *Calciosolenia* is a long ranging genus (earliest record ca. 135 Ma in the Hauterivian) so far only known from sporadic fossil records of isolated fossil coccoliths matching broad to narrow parallelogram with remote chances of ever encountering a complete coccosphere. However, extremely rare fossil specimens of collapsed coccospheres of *Calciosolenia fossilis* (Deflandre in Deflandre and Fert 1954) Bown in Kennedy et al. 2000, have been reported without much detail. Such fossil specimens can best be described as *Calciosolenia* sp. as commonly apical coccoliths are preserved and documented in literature, which perfectly match the dimensions of apical coccoliths of extant *Calciosolenia brasiliensis* (Bown et al. 2017, figs. 4–21). *Calciosolenia fossilis* seems redundant and its suggested occur-

rence as extant must be ruled out (Young et al. 2014, Nannotax3). Other two extinct fossil species have been described: *Calciosolenia alternans* Bown and Dunkley Jones, 2006 and *Calciosolenia aperta* (Hay and Mohler 1967) Bown, 2005, both in the Eocene.

Calciosolenia along with only a few coccolithophorid species survived the K-Pg mass extinction (Perch-Nielsen 1985). Meticulous light- and electron microscopic studies display a subvertical elevated rim with a well-developed lath cycle in the central area. The c-axis of calcite crystallites has been well correlated with the dark and bright appearance of ordinary and apical coccoliths and coccosphere parts under crossed-polarized illumination (Kamptner 1954, p. 39-40, abb. 40a-b; Deflandre and Fert 1953, figs. 12, 17; Manton and Oates 1985; Malinverno 2004, text-fig. 2; Bown et al. 2017). Although antiquity of *Calciosolenia* has been suggested to extend down into the Mesozoic by the analogy of its rim ultrastructure with that of stephanolithids, a continuous fossil record and better documentation is needed to confirm it (Bown et al. 2017). It is rather remarkable that the morphology of *Calciosolenia* coccoliths and coccospheres have practically remained unchanged through its ca. 135 Ma history. The extant species occur in both shelf (Andrulleit et al. 2003) and open ocean regimes (Patil et al. 2017). *Calciosolenia brasiliensis* occurs in bloom proportions in Neogene sediments of the deep Black Sea Basin (Alekseev et



TEXT-FIGURE 1

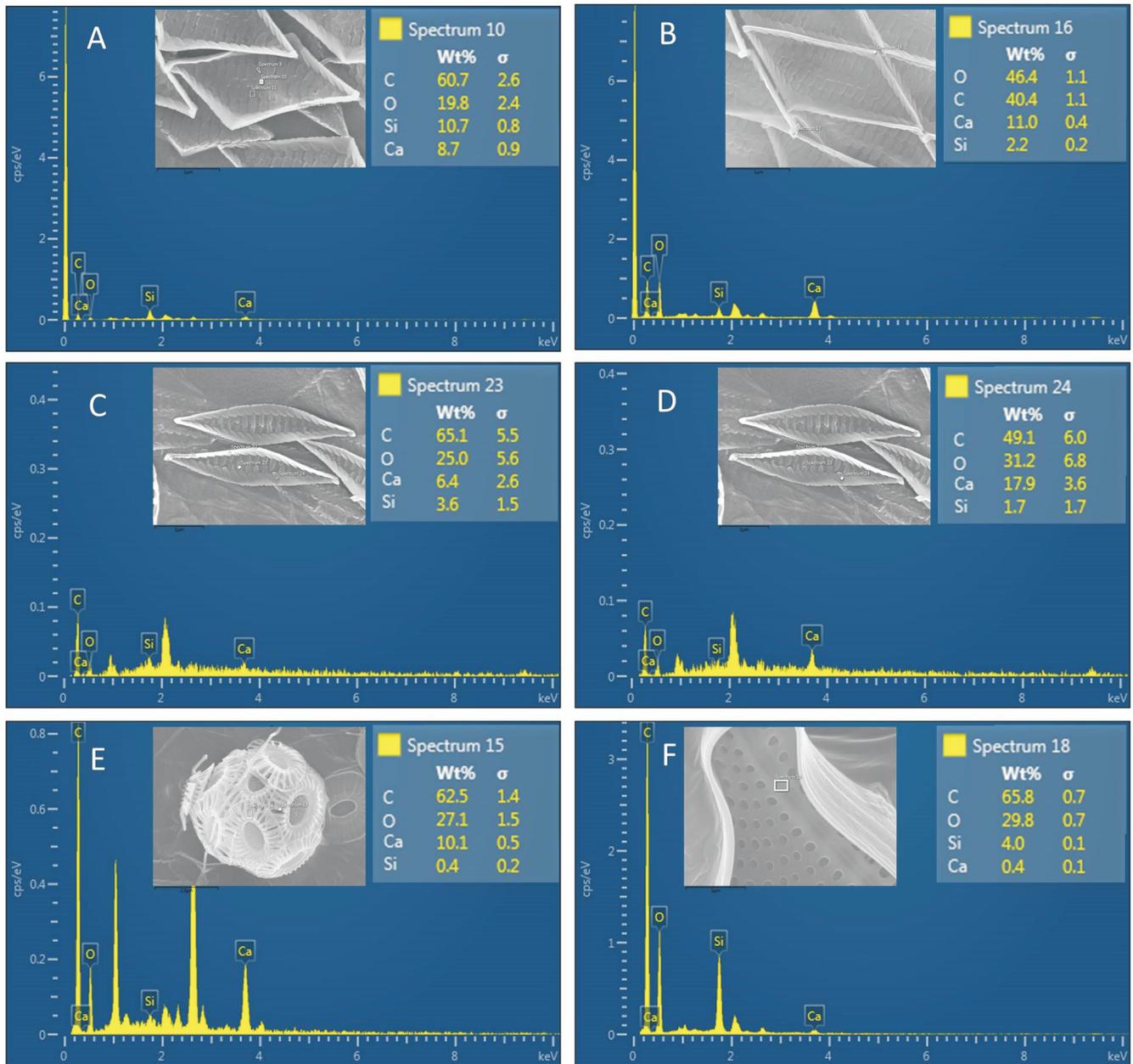
Location of surface water samples in the Southern Indian Ocean. White dot indicates documented location of *Calciosolenia subtropicus* sp. nov.; Green square indicates location of *Calciosolenia corsellii*; Black dots indicate locations of *Calciosolenia murrayi* and *Calciosolenia brasiliensis* documented in abundance. [ARF- Agulhas Return Front; SSTF- Southern Subtropical Front; SAF- Subantarctic Front; PF- Polar Front; locations of fronts after Orsi et al. 1995; Map background- annual average sea surface temperature of 2011-2014 obtained from www.giovanni.gsfc.nasa.gov]

al. 2012) and during the late Turonian, the species *Calciosolenia fossilis* flourished deep into the heartland of the Indian peninsula, >300 km from the western coast along Narmada lineament in an estuarine setting, apparently representing the oldest stratigraphic record from India (Jafar 1982, pl. 1, fig. 26, Nannofossil Zone CC 12). Molecular genetic studies in future would establish whether extant species possess a Pan Genome akin to that found in *Emiliania huxleyi*, permitting its invasion in contrasting ecological regimes (Read et al. 2013).

A BRIEF HISTORY OF THE GENUS *CALCIOSOLENIA*

The literature on this genus is cluttered with inappropriately published documentation, which has caused much confusion in taxonomy and nomenclature. The earliest published record seems to be that of Pelletan (1891, p. 202, fig. 107), which provided only a sketch of a fusiform extant species of an apparently weakly silicified diatom: *Cylindrotheca gracilis* Grun, displaying an outline of typical narrow parallelogram body elements, not seen in the type specimen of *Cylindrotheca gerstenbergeri* Rabenhorst, which shows double spirally arranged beaded thread like pattern giving false impression of a genuine parallelogram outline of coccolith commonly seen in specimens of *Calciosolenia*. Gran (1912, p. 332, fig. 239-5) described the type species *Calciosolenia murrayi* as possessing a fusiform coccosphere, abruptly tapering at both ends to bear typical apical spines, which are not seen in any other extant species. However, it was erroneously suggested to somewhat re-

semble the extant diatom *Rhizosolenia*. Schiller (1914, 1925, p. 27, pl. 2, figs. 21, 22) described *Calciosolenia grani* from the Adriatic Sea and a species of *Calciosolenia* was figured by Brehm-Eger (1918, p. 53, abb. 6). Lohmann (1919, p. 187, fig. 56) described a species of *Calciosolenia*, that was erroneously assigned to a pennate diatom. Kamptner (1927, 1937) introduced the family Calciosoleniaceae and with meticulous observations and detailed description under crossed-polarized illumination and by using a Gypsum plate, deciphered the fine c-axis orientation of the crystallites (Kamptner 1954, p. 39-40, abb. 40a-b), which perfectly matched the Transmission Electron Microscope images earlier published by Deflandre (Deflandre and Fert 1953, p. 329, fig. 7). Schlauder (1945) described *Calciosolenia sinuosa* based on different shapes of body and apical coccoliths under light microscopic observations, but the species was considered as synonym of the well-known *Calciosolenia murrayi* (cf. Gaarder and Hasle 1971; Heimdal and Gaarder 1981). Black (1968, p. 803, pl. 148, figs. 1-2) dealt with the family Calciosoleniaceae highlighting the challenges in the systematics and taxonomy at the generic and specific level. Bernard and Lecal (1960) described *Calciosolenia tenuis* resembling *Calciosolenia grani* in terms of size, number of “rhomboliths” and shape of the coccosphere. Later, Malinverno (2004) published the new species *Calciosolenia corsellii* from the waters of the eastern Mediterranean, based on morphometric traits, coccosphere shape, size, ultrastructure of central and rim area of body and apical coccoliths. In the same paper Malin-



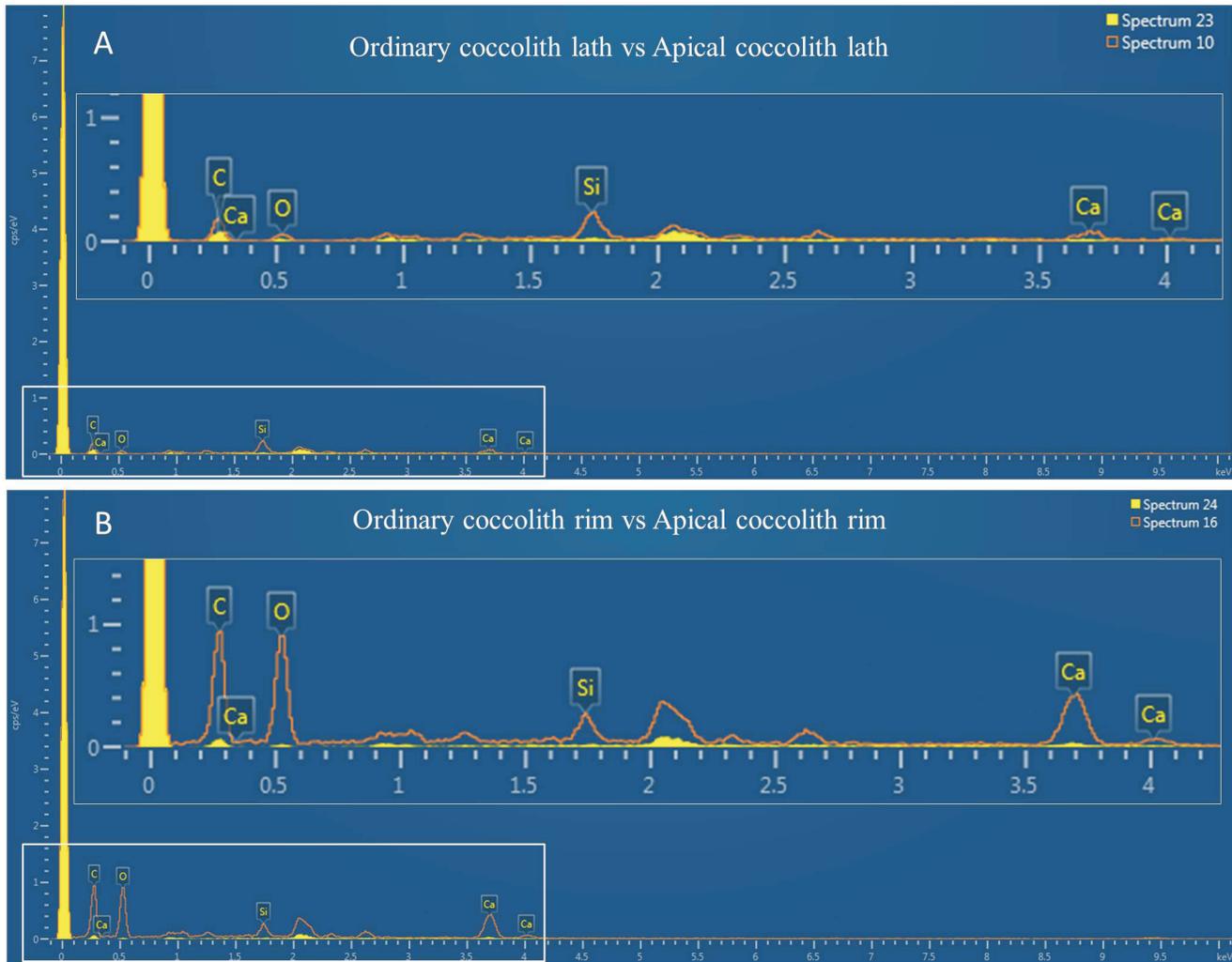
TEXT-FIGURE 2

Energy Dispersive Spectrometry results of *Calciosolenia subtropicus* sp. nov.- (A) ordinary coccolith lath, (B) ordinary coccolith rim (C) apical coccolith lath, (D) apical coccolith rim (E) *Emiliana huxleyi* coccolith and (F) Diatom.

verno differentiated four morphotypes of the type species *Calciosolenia murrayi* based on coccolith shape, ultrastructure and the degree of overcalcification of ordinary and polar coccoliths.

During the initial days, light microscopic observations with limited magnification and resolution led to confusion in the taxonomic assessment of *Calciosolenia* species. The advent of phase contrast and polarized light microscopy and subsequently Transmission- and Scanning Electron Microscopy permitted recognition of species based on fine ultrastructural details. In recent years, such studies unveiled the fine scale taxonomy of

Calciosolenia with a detailed reassessment of the species (Geisen et al. 2002; Sáez et al. 2003; Young et al. 2003; Malinverno 2004; Alekseev et al. 2012; Bown et al. 2017). In view of strong morphologic similarity, we support placing the two species *Calciosolenia brasiliensis* and *Calciosolenia murrayi* in one genus (Young et al. 2003). *Calciosolenia* continues to be the solitary genus in the family Calciosoleniaceae, but over the years several forms were published showing superficial resemblance or affinity with it. A non-calcifying extant haptophyte *Navisolenia aprili* Lecal 1965, displays a remarkable resemblance to *Calciosolenia*, but we hesitate at this stage to include it in this family for want of further details (Jordan and Green



TEXT-FIGURE 3 Energy Dispersive Spectrometry comparison of (A) Ordinary coccolith lath (orange line) vs Apical coccolith lath (yellow peak) and (B) Ordinary coccolith rim (orange line) vs Apical coccolith rim (yellow peak) of *Calciosolenia subtropicus* sp. nov.

1994, Young et al. 2003). *Acanthosolenia* Bernard 1939, *Anoplosolenia* Deflandre 1952 and *Scapholithus* Deflandre and Fert 1954, must be considered as synonyms of *Calciosolenia* Gran 1912. *Alveosphaera bimurata* (Okada and McIntyre, 1977) Jordan and Young, 1990, was suggested to show affinity to *Calciosolenia*, however, a more recent publication on newly discovered combination coccosphere by Keuter et al. (2019) assigned it to *Syracosphaera gaarderae* comb. nov. (ex *Alveosphaera bimurata*). Another interesting species that shows remarkable similarity in the shape of coccosphere with *Calciosolenia* is *Placorhombus ziveriae* Young and Geisen in Young et al. (2003), which was earlier documented as *Incertaina sedis* – undescribed gen. et sp. (Cros and Fortuño 2002, fig. 7). It is exceedingly difficult to differentiate between narrow rimmed placoliths and muroliths with a small flange such as seen in *Placorhombus ziveriae*. Known narrow rimmed placoliths (*Calyptosphaera*, *Navilithus*, *Tetralithoides* and *Turrilithus*) have tightly compacted shields which do not fall apart like in true placoliths. The proximal side of the coccolith shows no significant feature, whereas the distal view shows two pairs of plates with a closely spaced set of needle-like elements running

subparallel to the shorter axis of the coccolith. The boundary of the plates are slightly offset and faintly crenulated. The rim is subvertical and slightly outward flaring. The visible double shield can possibly be interpreted as a murolith with a minor flange. Pending further documentation of this species, it remains excluded from the family Calciosoleniaceae.

In this study we present unique characters of the fourth newly documented extant *Calciosolenia subtropicus* sp. nov. and compare it with other known extant species: *Calciosolenia murrayi*, *Calciosolenia brasiliensis* and *Calciosolenia corsellii*, indicating morphometric, ultrastructural and elemental differences (Table 1, Plates 1–4).

MATERIALS AND METHODS

Water sample collection

Surface water samples (using ships' hull sea water pumping system) were collected during: (1) the 36th Indian Scientific Expedition to Antarctica (ISEA) (18th December 2016 – 6th January, 2017) onboard the Ivan Papanin between Cape Town and Prydz

TABLE 1

Summary of the characteristics of coccoliths and collapsed coccospheres of *Calciosolenia subtropicus* sp. nov., *Calciosolenia corsellii*, *Calciosolenia brasiliensis* and *Calciosolenia murrayi*.

| Species | C o c c o l i t h | | | C o c c o s p h e r e | |
|-----------------------------------|-------------------|----------------------------------|--|---|------------------------|
| | Coccolith type | Coccolith length and width (µm) | Laths on long: short side of parallelogram | Coccosphere Shape | Coccosphere size (µm) |
| <i>Calciosolenia subtropicus</i> | Ordinary | L= 3.14 – 3.38 W= 0.9 – 1.1 | 10:6 to 11:7 |  | L= 45-60 W= 5.4-6.6 |
| | Apical | L= 3.35 – 4.34 W= 0.7 – 0.9 | 18 – 21 | | |
| <i>Calciosolenia corsellii</i> | Ordinary | L= 3.02 – 3.24 W= 1.64 – 1.70 | 10:6 |  | L= 42-45 W= 4.7-4.9 |
| | Apical | L= 3.27 – 3.30 W= 1.19 – 1.21 | 14-15 | | |
| <i>Calciosolenia brasiliensis</i> | Ordinary | L= 5.9 – 6.1 W= 1.6 – 1.8 | 16:12 to 17:13 |  | L= 60-80 W= 8.0-8.2 |
| | Apical | L= 5.5 – 5.9 W= 1.1 – 1.3 | 28 – 30 | | |
| <i>Calciosolenia murrayi</i> | Ordinary | L= 2.7 – 3.0 W= 0.7 – 0.8 | 8:6 to 9:6 |  | L= 25-30 W= 5-6 |
| | Apical | L= 2.6 – 2.7 W= 0.5 – 0.6 | 12 – 14 | | |

Other measurements on *Calciosolenia subtropicus*: (1) Apical element width= 89.5-150 nm (2) dextrally imbricated element length=203-231 nm (3) coccolith offset element width in dorsal view= 202-208 nm

Bay; (2) the MD218 CROTALE (Crozet Archipelago Paleocyanography) (23rd February 2019 – 11th March 2019 onboard the R.V. Marion Dufresne between La Réunion Island and the Crozet Archipelago and (3) the 4th Indian Southern Ocean Expediton (23rd January – 25th February) onboard the R.V. Sagar Nidhi between Mauritius and Antarctica (text-fig. 1). For coccolithophores, two liters of sea water were filtered through Whatman 0.8 micron Nuclepore Trek-Etched membrane filters of 47 mm diameter. We allowed earth's gravity to allow passage of the water through filters, to ensure preservation of intact coccospheres. The filter papers containing samples were transferred into Pall sterile petri dishes, oven dried at 40°C for 24 hours and stored until Scanning Electron Microscopic analysis.

Coccolithophores evaluation and repository

In the laboratory at National Centre for Polar and Ocean Research (NCPOR), about 5 mm² filter paper were cut and placed on a 1.5 cm diameter brass stub using silver paste. The specimen stub was sputter coated with platinum (approx. 3–5 nm thickness) and observed under a JEOL JSM 7610F Field Emission Scanning Electron Microscope (FE-SEM) at 1 KV acceleration voltage and using 2,000-150,000x magnification. The *Calciosolenia* species were magnified and micrographs images were stored for records.

Energy Dispersive Spectrometry (EDS) was carried out on *Calciosolenia subtropicus* coccoliths to assess the elemental composition of ordinary and apical coccoliths. The real time images of each coccolith were captured using Oxford Aztec software and point analysis per spectrum on lath, broad rim and near long and short axis of ordinary and apical coccoliths were carried out. For EDS, 15 KV accelerating voltage and magnification up to 140,000x was used. The stub with abundant *Calciosolenia subtropicus* sp. nov. is archived in the FE-SEM-

EDS laboratory with an archival number *FE-SEM-EDS Lab/Arch-02/Calciosolenia subtropicus*.

SPECIES DISTRIBUTION

In the southern Indian Ocean, *Calciosolenia brasiliensis* and *Calciosolenia murrayi* were documented previously by Patil et al. (2017) in low abundance. The maximum abundance of *Calciosolenia brasiliensis* was documented in the Subtropical Frontal region (STF1) (at 43°S, 40 m depth, during January–February, 2010) was 1.1x10³ cells/l and *Calciosolenia murrayi* was 1.5x10³ cells/l. Uneven occurrence of coccoliths of *Calciosolenia brasiliensis* and *Calciosolenia murrayi* were documented as far as Polar Frontal regions (PF1 and PF2) in low abundance (<0.02 x10³). *Calciosolenia subtropicus* sp. nov., was collected at 42.09°S; 23.52°E at temperature 14.1°C and salinity 35.74 psu at the Southern Subtropical Frontal region (36th ISEA, January 2016). Other environmental parameters recorded at this location are, nitrate: 3.77 µmol, nitrite: 0.11 µmol, silicate: 0.74 µmol and phosphate: 0.36 µmol. No other extant species of *Calciosolenia* was found associated with *Calciosolenia subtropicus* sp. nov. (text-fig. 1).

TAXONOMIC REMARKS

Family: **CALCIOSOLENIACEAE** Kamptner 1927/1937; Kamptner 1954

The family is somewhat unique in possessing a fusiform coccosphere with varimorphic scapholiths covering the entire coccosphere without gap or overlap. This must be viewed as an elegant energy minimizing and space saving strategy. The solitary genus *Calciosolenia* belonging to this family comprises only a few extant and fossil species, which fail to survive in modern seas and the antiquity of well-established extant species remains speculative. Pending molecular genetic studies of species, affiliation with other coccolithophores remains obscured.

Combined light- and scanning electron microscope studies of species have revealed the V/R structure matching the interpretative figures published by Bown et al. (2017). Besides the c-axis orientation, the elemental composition possibly controls the differential birefringence displayed by ordinary and apical coccoliths on fusiform coccospheres under crossed polarized illumination (Malinverno 2004; Bown et al. 2017).

Genus *Calciosolenia* Gran 1912

Type species: *Calciosolenia murrayi* Gran 1912

Coccoliths of the genus *Calciosolenia* have been called 'rhomboliths' (Halldal and Markali 1955; Cros and Fortuño 2002), 'scapholiths' (Deflandre and Fert 1954) or 'rhombic muroliths' (Young et al. 1997, 2003). The initial description by Deflandre and Fert (1954) from the Miocene–Pliocene sediments of El Medhi Algeria documented coccoliths called '*Scapholithus fossilis*'. Further detailed description of the genus *Calciosolenia* and *Anoplosolenia* was given by Manton and Oates (1985) in samples collected from the Galapagos Islands. Young et al. (2003) described *Calciosolenia* coccoliths as 'rhombic muroliths', with elevated, narrow rim and central area spanned by transverse bars which alternate from the two sides and meet in the center, where they partially overlap and interlock, forming a central ridge. Instead of the term 'rhomboliths' we prefer to use the appropriate term "scapholith" displaying an outline of parallelogram for ordinary and apical coccoliths covering the entire coccosphere of *Calciosolenia* (Kamptner 1954, Black 1968).

Calciosolenia murrayi Gran 1912

Plate 3, figures A, E, I, M; Plate 4, figures M–P

Remarks: The original description of this type species mentions a dimorphic coccosphere with one or two apical spines at the extremities (Gran 1912, p. 332, fig. 239-5), whereas recent scanning electron microscope images suggest broad abruptly tapering coccosphere with multiple apical spines formed by extension of polar coccoliths not to be found in any other extant species (Malinverno 2004). In distal view, the lateral laths (T-units) in ordinary coccoliths merge to form a faintly visible central ridge, which fades towards longer axis of scapholith or completely covered with plates without forming a central ridge (pl. 3, fig. E). Malinverno (2004) based on degree of overcalcification, distinguished four morphotypes of *Calciosolenia murrayi* under the scanning electron microscope. In distal view, tiny apical spur is present like the one found on acute angles of coccoliths of other extant species. Apical coccoliths are less angular than ordinary coccoliths and on distal side display faint and thin quadrate shaped elements stacked side by side on the inner wall of the murolith (R-units; pl. 3, fig. M). Radial laths meet at the centre leaving distinct slits and are gently intertwined without forming a central ridge (T-units; pl. 3, fig. M). In proximal view, the R-units appear as tiny knobs opposite radial laths.

An enigmatic *C. murrayi* collapsed coccosphere was reported with at least three types of coccoliths from the waters off Puerto Rico (Jordan and Winter 1998).

Calciosolenia brasiliensis (Lohmann, 1919) Young et al. 2003

Plate 3, figures B, F, J, N; Plate 4, figures I–L

Remarks: Relatively large coccospheres gently taper and lack apical spines. Ordinary and apical coccoliths are distinctly dif-

ferent from other extant species in terms of size and ultrastructure. In distal view, relatively large ordinary coccoliths possess a pair of lateral laths (T-units; pl. 3, fig. F) with slit in between to join in an offset manner and intertwine to produce a prominent central ridge, which fades towards the major axis of the coccolith. Subvertical rim broadest at obtuse angles and narrows towards acute angles of the coccolith. Tiny distally protruding spur, like the one found in coccoliths of other extant species is present on the apex of acute angles of the coccolith. Outer margin of the ordinary and apical coccoliths are smooth. In distal view the ordinary coccoliths display quadrate shaped thin elements at the inner margin lying side by side and decrease in size towards acute angles of the coccolith (R-units pl. 3; fig. F). Apical coccoliths lack median ridge both in distal and proximal views, but well display V-unit, R-unit and T-unit (pl. 3; fig. N).

Calciosolenia corsellii Malinverno 2004

Plate 2, figures A–I

Remarks: Long and cylindrical varimorphic coccosphere lack polar spines, tapering at both ends in the form of long horn formed by apical coccoliths. Coccoliths can be described as "scapholiths". Ordinary coccoliths are long, the rim is thin, subvertical with smooth outer margin (V-unit; pl. 2; fig. E). Inner margin of murolith is decorated with quadrate shaped thin elements decreasing in size towards acute angles of coccoliths (R-unit pl. 2; fig. E). Relatively large and diagnostic spur is found distally and a small one proximally at the acute angles of coccolith. In distal view, 14-20 radial laths (T-unit pl. 2; fig. E) gently intertwine in the centre to produce a prominent central ridge, which fades towards major axis of the coccolith. Apical coccoliths are narrower with prominent spur at the acute angle of the coccolith and central area is devoid of central ridge but decorated with well-spaced lateral bars (T-unit pl. 2; fig. G, I).

TAXONOMY

Class Coccolithophyceae (Rothmaler 1951)

Subclass Prymnesiophycidae (Cavalier-Smith 1986)

Order Syracosphaerales (Hay 1977)

Family Calciosoleniaceae (Kamptner 1927, 1937; Kamptner 1954)

Calciosolenia Gran 1912

Calciosolenia subtropicus Patil and Jafar n. sp.

Holotype: Plate 4, figures A–D

Dimensions: Ordinary Coccoliths (Fig. A): length 3.21 µm and width 1.5 µm. Apical Coccoliths (Fig. C): length 3.52 µm and width 0.8 µm

Etymology: From the region where this species is documented: subtropical frontal region of the southern Indian Ocean.

Type locality: 42.09°S; 23.52°E (Station 36 ISEA-5, southern Indian Ocean), surface water.

Diagnosis: The inner rim margin in distal views of both ordinary and apical coccoliths are decorated with large and prominent wedge shaped clockwise imbricated elements (R-unit) at obtuse angles tapering in size towards acute angles of scapholith. In proximal view of both ordinary and apical coccoliths, the rim is decorated with raised and prominent knobs (R-unit).

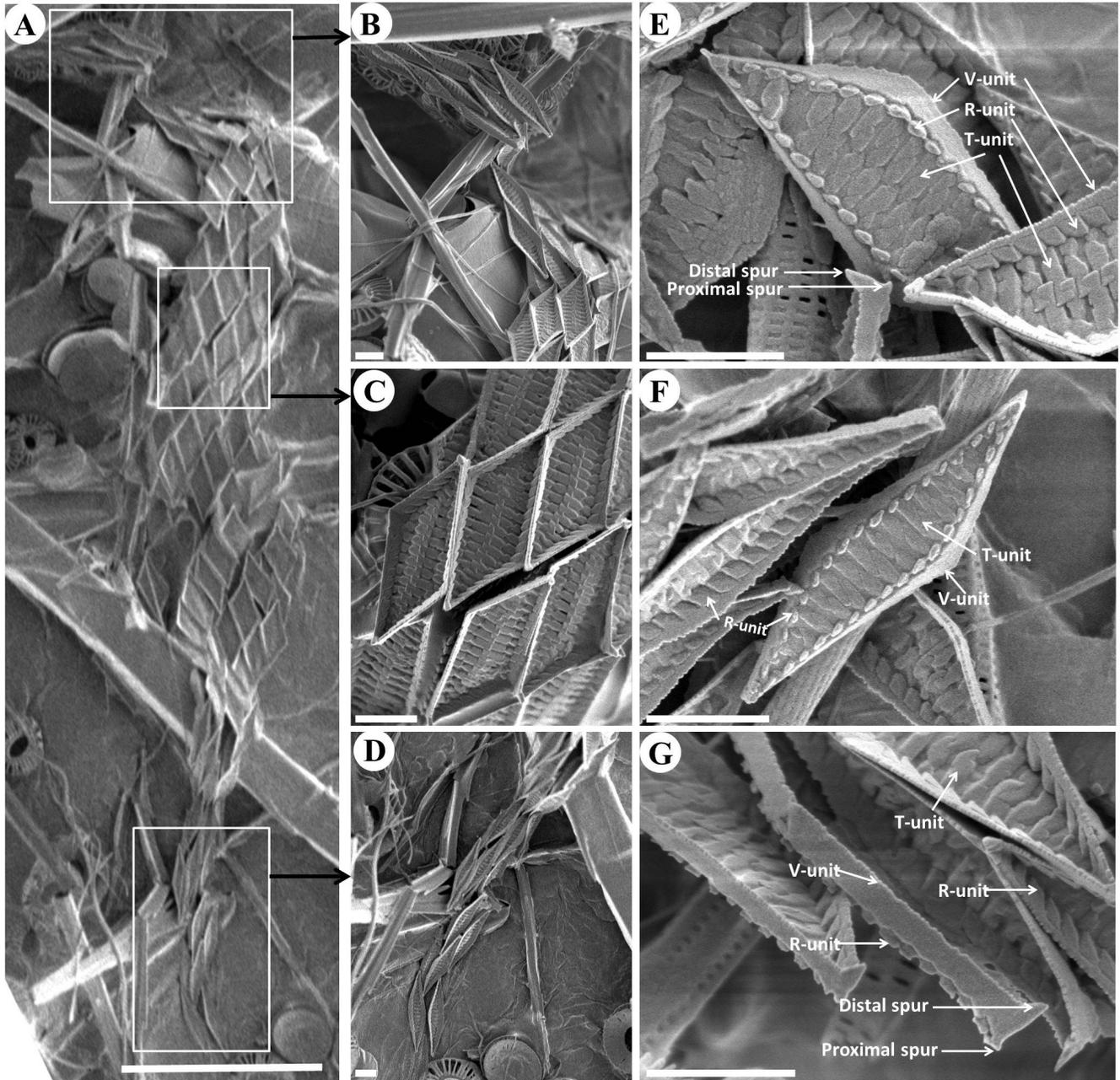


PLATE 1

Scale: A - 10 μm; B-G - 1 μm.

- | | | | |
|-----|---|---|-------------------------------------|
| A | coccosphere of <i>Calciosolenia subtropicus</i> | E | ordinary coccoliths proximal shield |
| B,D | apical coccoliths distal shield | F | apical coccoliths proximal shield |
| C | Ordinary coccoliths distal shield | G | side view of apical coccolith. |

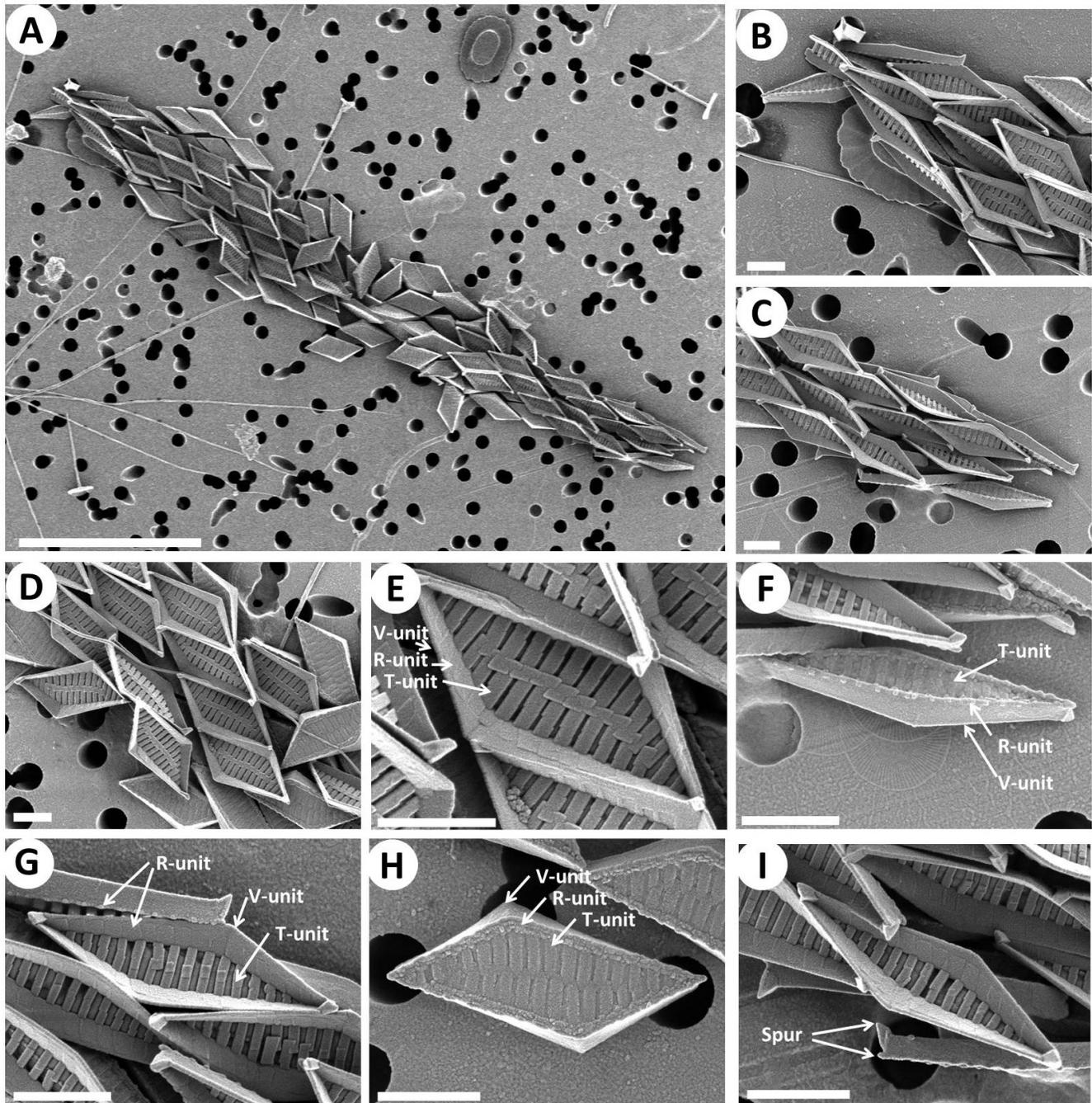


PLATE 2
Scale A: 10 µm; B–I: 1 µm.

A coccosphere of *Calcosolenia corsellii*
B, C, G Apical coccoliths distal view
F Apical coccolith distal and proximal view

D, E Ordinary coccoliths distal view
H ordinary coccolith proximal view.

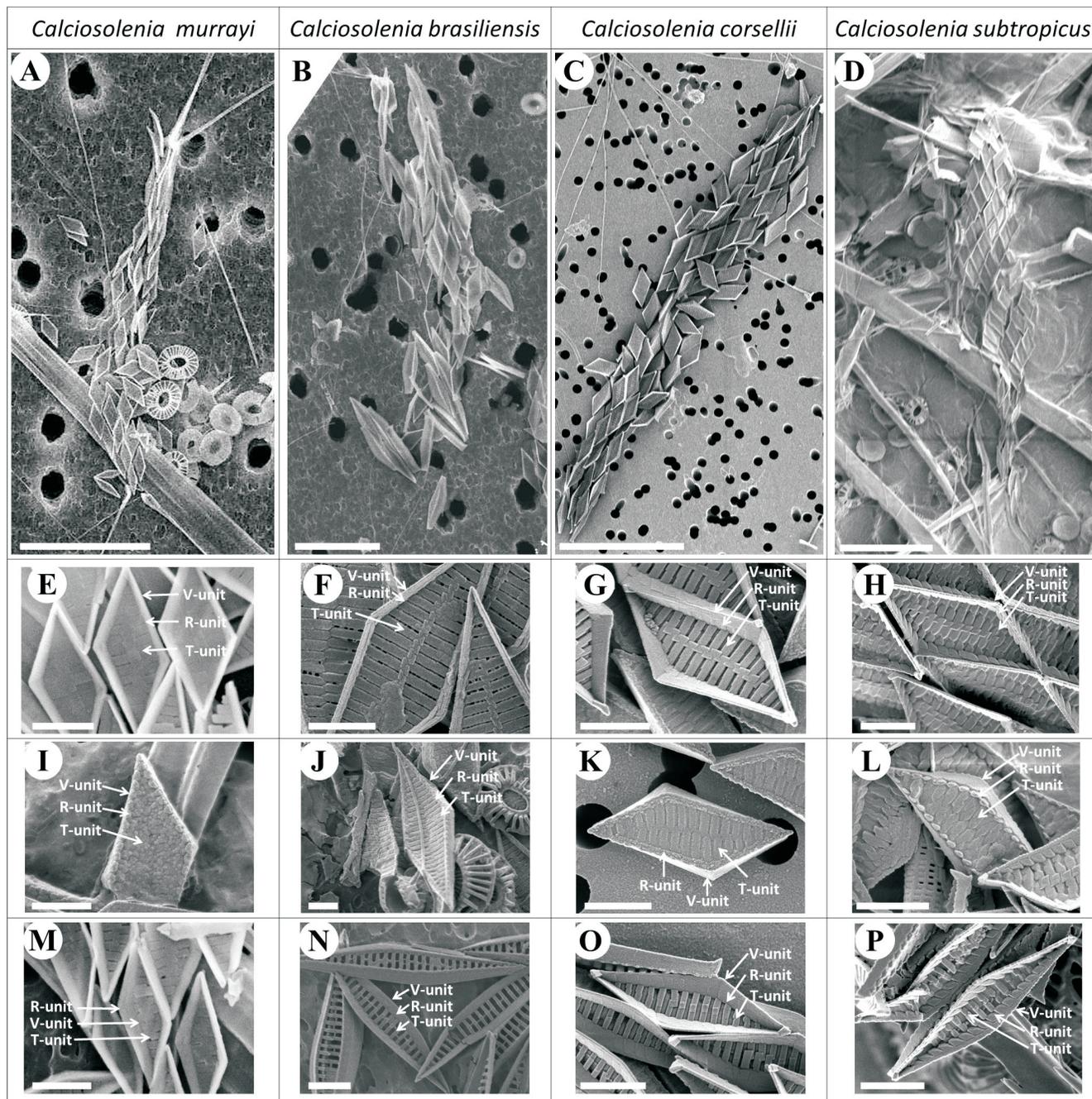


PLATE 3

Scale: A–D - 10 µm; E–P - 1 µm.

Comparative ultrastructure of coccosphere, ordinary coccoliths and apical coccoliths of *Calciosolenia murrayi*, *Calciosolenia brasiliensis*, *Calciosolenia corsellii* and *Calciosolenia subtropicus* sp.nov. observed in the southern Indian Ocean.

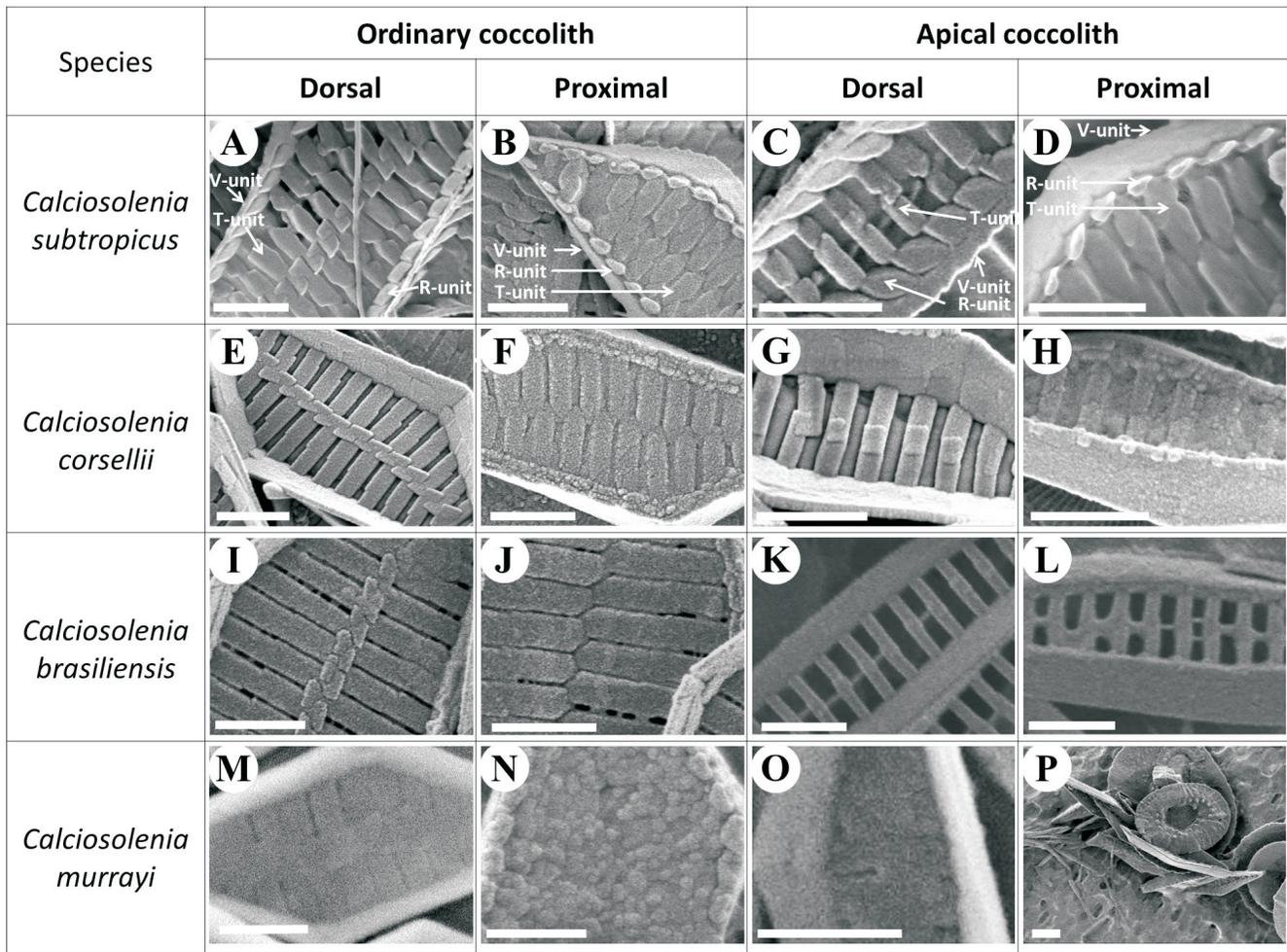


PLATE 4

Scale: A–O - 0.5 μm; P - 1 μm.

Comparative ultrastructure of *Calciosolenia* spp. ordinary and apical coccoliths observed in the southern Indian Ocean.

Remarks: Long, cylindrical, fusiform, dimorphic coccosphere, without polar spines, resembling coccospheres of *Calciosolenia brasiliensis* and *Calciosolenia corsellii*, tapering at both ends in to a long horn formed by apical coccoliths (Fig. 1, Plate 1, 3 and 4). Coccoliths for practical purpose are simply designated as “scapholiths” throughout the text, with slightly outward flaring subvertical rim, tightly packed, without overlapping and spirally arranged on coccosphere. A unique pair each of 16–18 transverse laths (T-unit) meet at offset position, intertwined and leaving characteristic geometrical gaps on either sides of the central ridge. Central ridge running subparallel to the long axis of coccolith consists of ca. 10 elevated and intertwined Calcite rhombohedra, and fades away towards longer axis of the coccolith, where only a few transverse bars are present. Ordinary coccoliths: (average length: 3.14 μm to 3.38 μm, average width: 1.14 μm to 1.6 μm), rim margin distinctly broadens to-

wards the minor axis and tapers towards the longer axis (plate 1). Rim slightly raised and terminates with a distinct and small spur at acute angles of coccolith both on distal and proximal sides. The inner rim margin displays large and diagnostic clockwise imbricated elements at the shorter axis, gradually tapering towards the acute angle of the coccolith (R-unit pl. 1, figs. E-G; pl. 4, figs. A, C), and this feature sets it apart from closely related species *Calciosolenia corsellii*. This diagnostic feature has not been observed on coccoliths or coccospheres of any other extant species of *Calciosolenia*, and the consistent presence of this trait on several specimens rules out any role of overcalcification. The outer margin of the rim is slightly serrated. In distal view, apical coccoliths are narrow (3.35 μm to 4.34 μm long and 0.59 μm to 0.90 μm wide) lacking central ridge and with prominent spurs at the acute angles of coccolith; diagnostic clockwise imbricated wedge shaped elements can be distinctly

seen on the inner wall of the murolith (R-units pl. 1; fig. E). In proximal view of apical coccoliths, broad radial laths join in offset fashion (T-unit) and the R-units appear as a row of raised knobs lining the rim margin (pl. 1, figs. E-F).

DISCUSSION AND CONCLUSIONS

Kamptner (1954) described the structure of *Calciosolenia* coccoliths under cross-polarized illumination by using a gypsum plate, wherein inner coccoliths rim is birefringent, and the central part remains dark, and based on meticulous observation he could determine the c-axis orientation of crystallites. Malinverno (2004, text-figs. 2A-B) provided crossed-polarized light images of the coccospheres of *C. brasiliensis* (polar coccoliths birefringent, ordinary coccoliths faintly birefringent) and *C. murrayi* (entire coccosphere weakly birefringent). This observation had prompted us to further probe whether c-axis orientation or something else in addition could be responsible for the contrasting behavior of birefringence in the central and apical parts of the coccosphere. Our Energy Dispersive Spectrometry on *Calciosolenia subtropicus* sp. nov., revealed a high concentration of silica in the body coccoliths which appear dark (text-figs. 2, 3); whereas negligible silica in the apical coccolith probably caused them to appear brighter under crossed-polarized illumination. Such a combination of silicon and calcium is rare in coccoliths and has previously been documented in *Petasaria heterolepis*, where calcium appears as a small peak along with the major element silicon (Patil et al. 2015). Recently, Durak et al. (2016) discovered silica in the coccolithophore species *S. apsteinii*, *C. braarudi* and *C. leptoporus*, emphasizing that the silica plays a crucial role in modulating crystallinity and calcification. Hermoso et al. (2017) further demonstrated in culture studies of *Scyphosphaera apsteinii* that extreme strontium concentration, hitherto unknown, reveals specific biomineralization pathways in certain coccolithophores. Further research is needed to understand this strange but important phenomenon.

During the analysis of sediment archives and living samples, meticulous ultrastructural documentation is essential for understanding various *Calciosolenia* forms. Elemental composition of coccolithophore families forming two or more types of coccoliths is required to understand the meaning of differential biomineralization of coccoliths on a single coccosphere.

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