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Recent deep-sea nematodes and agglutinated foraminifera select specific grains and bioclasts from their environments: Ecological implications

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ABSTRACT

The high-latitude regions are known for a diverse array of benthic meiofauna, yet our understanding of these communities remains limited, particularly in the deep ocean. This study aims to assess the variability and adaptation of nematodes and agglutinated foraminifera in the modern sediments of the Southern Pacific Ocean at >3500 m water depth. Seawater and sediment slurry from the first piston cores (i.e., mudline samples) from International Ocean Discovery Program Sites U1539, U1540, U1541, and U1543 were analyzed for Rose Bengal stained nematode and agglutinated benthic foraminifera. During the microscopic study seven nematode specimens belonging to the genus *Desmoscolex*, with 16–17, 36 or 38 main rings were found. Scanning electron

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microscopy study suggest that one morphotype with 17 main rings used only coccoliths of the species *Calcidiscus leptoporus* while the other specimens used fine-grained siliciclastic material on their concretion ring. Besides nematodes, a few benthic agglutinated foraminifera specimens exclusively used a single species of planktic foraminifera (*Globoconella inflata*) and/or robust coccoliths, in addition to other fine-grained siliciclastic material, for their test construction. These patterns appear to be highly selective. Specimens of the same benthic nematode *Desmoscolex* genus and agglutinated foraminifera that have diverse grain types show that these specimens can adapt to their environments, choose specific grains as per their preference, and have no relationship with the grain/particle abundance. This study of *Desmoscolex* and agglutinated foraminifera species suggests low to moderate organic matter flux and increased ventilation in the abyssal depth of the Southern Pacific Ocean.

1. Introduction

Nematodes are the most abundant group among meiobenthic metazoans (Platt and Warwick, 1980). They occur in all aquatic environments (freshwater, marine, and estuarine), terrestrial habitats, and polar regions (Giere, 2009) and often constitute 70–90 % of meiobenthic metazoans (Heip et al., 1982; Mokievskii et al., 2007; Miljutin et al., 2010). The Desmoscolecidae are a distinct family of mainly marine nematodes characterized in general by somatic setae and serial concretion rings/desmens (Cesaroni et al., 2017). There are 311 species present to date, belonging to 21 different genera (Decraemer, 1998; Lim and Chang, 2006). Out of all the genera in this family, the *Desmoscolex* genus stands out as the most common. Its 136 nominal species make up 43 % of the total number of species that are known to scientists (Lim and Chang, 2006). From the deep sea to the seashore or salt marshes, this genus is reported to be found globally and often living in marine sediments at water depths of over 3000 m (Decraemer, 1985). *Desmoscolex* genus (family Desmoscolecidae) contains four subgenera, showing differences in the body cuticle covering: (i) *Desmoscolex* with mainly rounded main rings (desmen or concretion rings); (ii) *Desmolorenzenia* with concretion rings with triangular outline (anterior rings with posteriorly directed slope, posterior rings with anteriorly directed slope) with abrupt reversal in slope at the level of a larger inversion ring; (iii) *Pareudesmoscolex* with concretion rings only complete anteriorly and posteriorly, rest of body with warts or papillae and (iv) *Protricomodes* similar to *Desmoscolex* in appearance, but distinct from it by the presence of interzones with scales made of tiny patches of “concretion” material (i.e., secretion and foreign particles; Decraemer and Rho, 2014). One of the most interesting features of *Desmoscolex* nematodes is their unique structure of particle accumulations on the concretion rings. Representatives of this sediment dwelling genus move by looping and firmly attach themselves to a substratum or organic material present in the sediments (Raes and Vanreusel, 2006; Riemann and Riemann, 2010). This adaptation allows them to survive in the harsh conditions of the deep sea where food can be scarce and possibly contributing to nutritional advantages for the Desmoscolecids (Schratzberger et al., 2008; Riemann and Riemann, 2010; Armenteros et al., 2010; Semprucci et al., 2016). Many factors such as organic flux, oxygenation, food availability, salinity, and temperature control the abundance and diversity of the deep-sea *Desmoscolex* genus, and the nature of their concretion rings depends on the sedimentological environment (Platt and Warwick, 1980; Heip et al., 1985; Miljutin et al., 2010). The *Desmoscolex* genus has the ability to form three-dimensional body by selecting grains of different shapes and sizes and a few of them are able to sort out the grains of their choice (Riemann and Riemann, 2010). The distribution of adhering particles is influenced by the vigorous undulatory movements of the organism, which leads to the formation of concretion rings, as observed by Riemann and Riemann (2010) in their study of living Desmoscolecids.

The North-Eastern Atlantic, Mediterranean, and Central Pacific regions have been extensively studied for deep-sea nematode species (Timm, 1970; Riemann, 1974; Freudenhammer, 1975; Riemann and Schrage, 1977; Dinet and Vivier, 1979; Decraemer, 1983a, 1983b, 1983c; Soetaert and Decraemer, 1989; Decraemer and Soetaert, 1989; Soetaert and Heip, 1995; Soltwedel et al., 1996; Sebastian et al., 2007; Tchesunov et al., 2012; Leduc et al., 2016; Zhao et al., 2020). However, the remaining parts of the deep ocean have received considerably less attention, as highlighted by Miljutin et al. (2010). Although there is a lack of research on desmoscolecids in the Central and Eastern South Pacific Ocean, existing studies have demonstrated their substantial abundance in deep-sea sediments and their critical contribution to the regional food web (Platt and Warwick, 1980; Heip et al., 1985). They are significant predators that consume microscopic organisms, including bacteria and fungi. Taxonomic research on *Desmoscolex* nematodes and its ecological interpretation is sparse in the Southern Ocean and the southern Pacific Ocean (Gambi et al., 2003; Sebastian et al., 2007; Neira et al., 2013; Guilini et al., 2013; Lins et al., 2015).

Similar to nematodes, agglutinated benthic foraminifera form their tests using sedimentary particles available in the substratum, which they bind together (Kaminski, 2014). Some agglutinated foraminifera select suitable sedimentary grains as well as biogenic material (such as planktic foraminifera, coccoliths, or fragments of calcareous and siliceous microfossils), and arrange them very methodically to form intricate three-dimensional tests (Murray, 1971; Gooday, 1990; Pearson et al., 2018; Capotondi et al., 2019). Some of these agglutinated benthic foraminifera are highly selective of size and composition and pick heavy minerals like ilmenite, rutile, and garnet (Allen et al., 1999; Makled and Langer, 2010; Capotondi et al., 2019) or biogenic clasts like echinoderm plates (e.g., Heron-Allen and Earland, 1909). Multiple factors control the abundances and assemblages of agglutinated foraminifera and the nature of their test. Stefanoudis et al. (2015) suggested variations in the community composition of agglutinated benthic foraminiferal tests’ topographical relationship, which influences the test morphology. The agglutinated benthic foraminifera are well-established and widely used meiofauna in comparison to nematodes. However, particle selection and its relationship with the environment in the abyssal plain is sparse. Further ecological interpretation of abyssal plain agglutinated benthic foraminifera and nematodes from the Southern Pacific Ocean is limited.

Hence, this research is an attempt to present a novel and distinct assessment of species belonging to the *Desmoscolex* genus and agglutinated benthic foraminifera from the Southern Pacific Ocean, accompanied by photomicrographs and scanning electron microscope (SEM) photos. Additionally, it offers a fresh perspective and probable ecological interpretation based on the *Desmoscolex* genus and agglutinated foraminifera found in the abyssal plain below 3500 m at International Ocean Discovery Program (IODP) Sites U1539, U1540, U1541, and U1543 in the Central and Eastern South Pacific Ocean.

2. Material and methods

IODP Sites U1539 (56°09.06′ S 115°08.05′ W, 4071 m water depth), U1540 (55°8.47′ S, 114°50.52′ W, ~3584 m water depth), and U1541 (54°12.76′ S, 125°25.54′ W, ~3603 m water depth) were drilled during IODP Expedition 383 (Dynamics of the Pacific Antarctic Circumpolar Current) in the Central South Pacific (CSP) / Pacific sector of the Southern Ocean (Fig. 1; Lamy et al., 2021a).

Site U1543 (54°35.06′ S, 76°40.59′ W, ~3860 m water depth) is located in the Eastern South Pacific, ~204 km west of the Chilean coast

(Fig. 1; Lamy et al., 2021a). IODP Sites U1539 and U1540 are located ~2963 km west of the Magellan Strait, and Site U1541 is ~3389 km west of Magellan Strait in the CSP (Fig. 1; Lamy et al., 2021a). At these sites, present-day temperature ranges between +1 and 0 °C (Fig. 1b; Locarnini et al., 2018), the dissolved oxygen concentration is very high and varies between 200 and 220 μmol/kg (Fig. 1c; Garcia et al., 2019), and the salinity fluctuates between 34.7 and 34.8 (Fig. 1d; Zweng et al., 2019) for the bottom water column.

Seawater and sediment slurry (i.e., mudline or soupy core-top sediment material) were collected in a bucket from the first piston cores crossing the water-sediment interface at Holes U1539A, U1540B, U1541B, U1541C, and U1543A. A part of the sediment slurry was transferred into a Polyvinyl chloride bottle and a mixture of Rose Bengal and ethanol solution (2 g of rose Bengal per 1 l of ethanol) was added to identify any living benthic meiofauna specimens. The treated samples were kept for a minimum of 10 days for proper staining of the living meiofauna (Barik et al., 2019, 2022), gently washed later over a 63 μm-sieve, and dried in an oven at 50° C. The dried residues were inspected for agglutinated foraminifera. Nematode specimens of the *Desmoscolex* genus were found while analyzing the samples. The agglutinated foraminifera and nematode specimens were photographed using a table-top SEM (Hitachi TM 3000) available onboard the scientific research vessel *JOIDES Resolution* during Expedition 383. Additional photomicrographs of *Desmoscolex* nematodes and agglutinated foraminifera specimens were taken using a Leica M205A stereo microscope having three-dimensional imaging capability. Selected agglutinated nematodes of *Desmoscolex* genus were further analyzed using a Field-Emission SEM (Zeiss Ultra 55+) attached with Energy Dispersive Spectroscopy (EDS) at the Indian Institute of Technology Bhubaneswar, India. The body of these specimens were chemically characterized using the EDS at 3–5 different spots within various parts of the specimen.

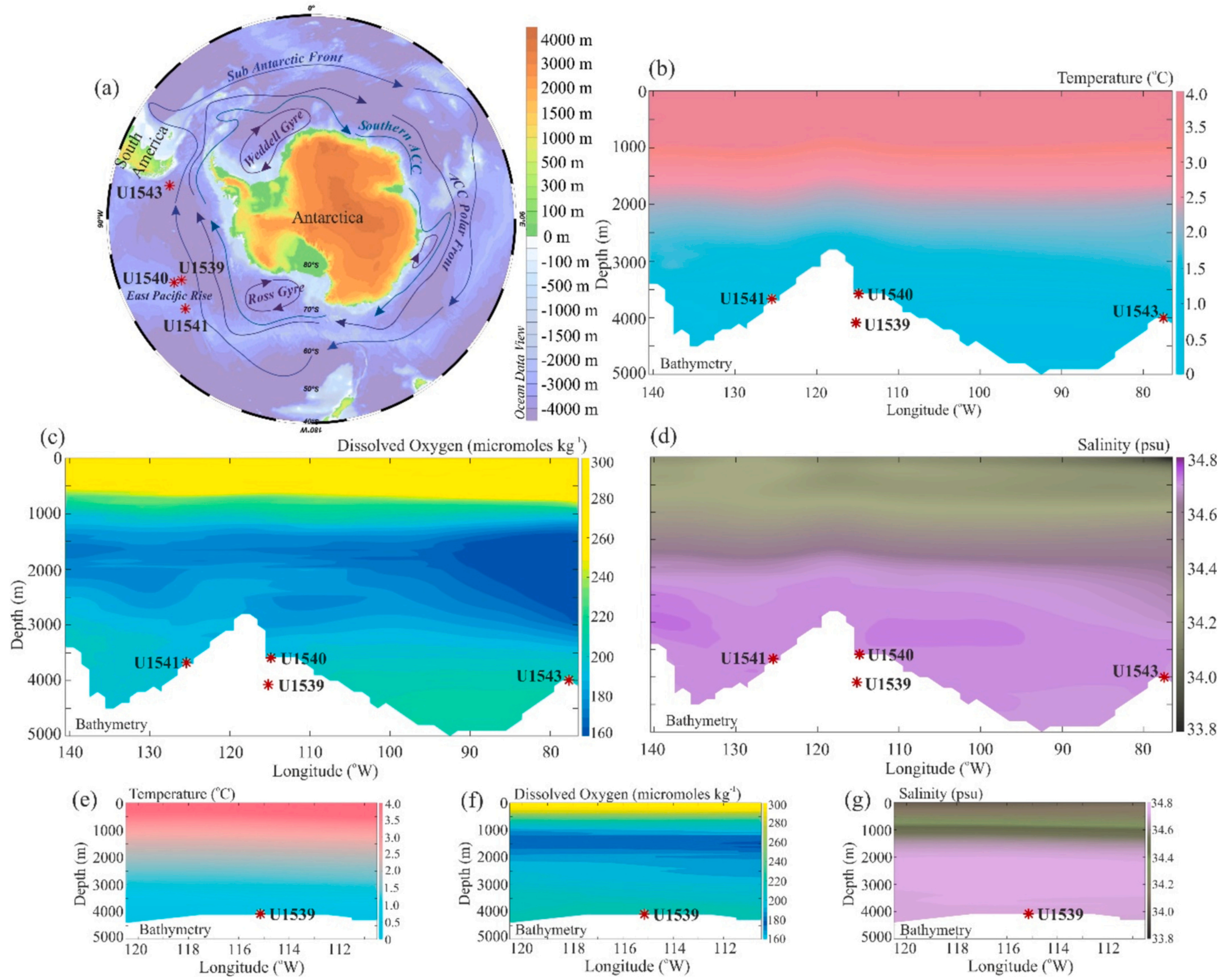

Fig. 1. (a) Southern Ocean bathymetry generated using Ocean Data View (ODV version 5.6.2; Schlitzer, 2021). Red stars indicate the IODP Sites (U1543, U1541, U1540, and U1539), oceanographic fronts (Orsi et al., 1995) are shown in solid lines: Sub Antarctic Front (SAF), Antarctic Circumpolar Current (ACC), Polar front (PF), Southern ACC fronts, Ross Sea gyre and Weddell gyre, (b, e) Vertical profile of seawater temperature (°C) (objectively analyzed annual mean; (Locarnini et al., 2018), (c, f) Dissolved Oxygen (DO; μmol/kg) (objectively analyzed annual mean; Garcia et al., 2019), (d, g) Vertical profile of seawater salinity levels (objectively analyzed annual mean; (Zweng et al., 2019), in the Central and Eastern South Pacific were generated using Matlab software (version R2023b). For (b, c, and d) latitude is fixed at 54.5 °S and for (e, f, and g) latitude is fixed at 56.5 °S, the white area represents the bathymetry surrounding the core locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results and interpretations

3.1. *Desmoscolex* nematode specimens found at the central and eastern South Pacific

Seven specimens of nematodes were found in the mudline samples over 63 μm at our study sites. The taxonomic and morphological details of these specimens are provided in Annexure A. The specimens, being inadequately fixed and shrunken (Fig. 2), not only limited us to get their actual size but also to observe the inner structures and several diagnostic features to identify them at species level (see Annexure A). The specimens are identified and belong to the genus *Desmoscolex* (Fig. 2). The specimens look similar under the stereo microscope having 16–17 concretion rings (Figs. 2a, b, d, e, g), except for two specimens one with 36 concretion rings (Fig. 2c) and another with 38 concretion rings (Fig. 2f). However, after SEM analysis, it became evident that the concretion rings of *Desmoscolex* sp. 7 was exclusively made of coccoliths (Figs. 2g, 3) and the others exclusively of fine-grained sediment particles (Figs. 2a, b, c, d, e, f; Fig. 4). We found seven stained specimens of *Desmoscolex* genus, one specimen at Site U1539 (Fig. 2a), two specimens at Site U1541 (Figs. 2c, g) and four specimens at Site U1543 (Figs.2 b, d, e, f). *Desmoscolex* sp. 7 having 17 concretion rings use coccoliths of *Calcidiscus leptoporus* subsp. *leptoporus* (from now on *C. leptoporus*) on its concretion rings (Figs. 2g, 3) is a relatively recent addition from this study to the Desmoscolecidae family.

It is known that *Desmoscolex* taxa have the capability to move by crawling and attaching themselves to substrates (Soetaert et al., 2009). This provides an ecological advantage to marine nematodes, due to their ability to clump together organic particles, which results in the formation of lumps or burrows of a few millimeters in size (Riemann and Schrage, 1978; Riemann and Helmke, 2002). They capture particles by utilizing a sticky mucus supply located in their head area. This mucus causes the particles to clump together, forming an agglutination that eventually surrounds the nematode's posterior region (Riemann and Helmke, 2002). *Desmoscolex* nematodes have somatic setae, different in length and shape between subdorsal and subventral side, an annulated body cuticle covered by thick transverse rings made up of sedimentary particles and cement (secretion). The stout body (see description in section 3.4) and specialized head region with sensory organs allow *Desmoscolex* nematodes to traverse their surroundings (Lim and Chang, 2006; Decraemer et al., 2013). The *Desmoscolex* specimens found in the deep South Pacific has narrow tails tapered towards the endring; in 17 main ring species the anus or cloacal opening is located at the end of main ring/concretion ring (Fig. 2). However, specimens with similar morphological appearance choosing different types of sedimentary particles suggest that these *Desmoscolex* nematodes have access to other types of grains available in their surroundings (Fig. 6). This may be their adaptation to evolve and survive in the challenging deep-sea habitat by using the intricate designs and structures of coccoliths, which provide protection and support. The external morphology of the nematodes in general affected by the attachment of bacteria or other microorganisms (Decraemer et al., 2013). Hence, these species managed to select and pick either coccoliths of *C. leptoporus* or siliciclastic grains depending upon the surrounding environment.

3.2. Chemical characteristics of *Desmoscolex* specimens

The chemical characterization of the *Desmoscolex* specimens, carried out using FE-SEM equipped with EDS, shows that the specimens whose concretion rings have *C. leptoporus* contain carbon, oxygen, and calcium with a minor amount of silicon (Fig. 3c; Table 1), but the amount of silicon increases at the girdle and somatic setae (Figs. 3d, e; Table 1). This represents the calcite composition of *C. leptoporus* coccoliths used by the nematodes on its concretion rings. The girdle comprising silicate grains may be an artefact, as this type of structure has never been observed in *Desmoscolex* and also not found on other specimens. The cuticle of this specimen in between the concretion rings is rich in calcium, oxygen, chlorine and iodine with a minor amount of sulphur and phosphorus (Fig. 3f; Table 1). The specimen that used fine-grained siliciclastic materials on its concretion rings have carbon, oxygen, silica, and aluminum with a minor amount of calcium, sodium, and iron (Figs. 4c, d, f; Table 2). This suggests that this nematode selected fine siliciclastic material on its concretion rings. The cuticle of this specimen in between the concretion rings is rich in calcium, oxygen, and carbon with a minor amount of silica (Fig. 4e; Table 2), suggesting its predominantly calcareous composition. The higher abundance of carbon and oxygen indicates that in both *Desmoscolex* specimens the picked grains are bounded together by calcareous cement (Figs. 3, 4; Tables 1, 2). These specimens are very delicate and were not thoroughly cleaned using ultrasonication before EDS analysis, which may be the reason for the presence of a minor amount of sodium, potassium, chlorine, and iodine within the *Desmoscolex* specimens, probably linked to the environment where they lived (Tables 1, 2).

3.3. Agglutinated foraminifera in the abyssal plain of South Pacific deep environment

Well preserved agglutinated foraminifera were found in the mudline (ocean floor) and core samples from Sites U1539 (Figs. F28, 29 in Winckler et al., 2021a), U1540 (Figs. F27–30 in Winckler et al., 2021b), Site U1541 (Figs. F26, 27 in Winckler et al., 2021c) and U1543 (Lamy et al., 2021b). The dominant agglutinated benthic foraminiferal taxa found at these sites are *Reophax* and *Rhabdammina* species, *Hormosina globulifera*, *Spiroplectommina biformis*, *Lagenammina difflugiformis*, *Ammodiscus anguillae,* and *Paratrochammina* sp. (Lamy et al., 2021a; Fig. 5). The detail taxonomy of these specimens are provided in Annexure B. These taxa generally prefer siliciclastic sedimentary grains (Gooday, 1990; Heron-Allen and Earland, 1909). However, in this study, we are focussing on the agglutinated benthic foraminifera that exhibit tests made with selected foraminifera tests and coccoliths. As shown in Fig. 5 (j), a *Reophax fusiformis* specimen used coccoliths of *Coccolithus pelagicus* subsp. *pelagicus* (from now on *C. pelagicus*), *C. leptoporus,* and *Helicosphaera carteri* -all of them very robust coccoliths- (Fig. 5j) to build its test, while a *Paratrochammina* specimen, used almost exclusively *C. leptoporus* coccoliths with a minor contribution of *C. pelagicus* to build its test (Fig. 5m). The agglutinated benthic foraminifera picking exclusively coccoliths or planktic foraminifera test is not new and reported by various workers earlier from different sea and oceans from different depths (e.g., Thomsen and Rasmussen, 2008; Mancin et al., 2015; Perner and Knudsen, 2018; Pearson et al., 2018). Perner and Knudsen (2018) reported two agglutinated foraminifera species of *Pseudobolivina islandica* and *Haplophragmoides atlanticus* from Recent and Late Holocene sediments in the north Icelandic shelf in the North Atlantic, which selected coccoliths to build their test. The trochospirally coiled trochamminid and biserial textularid were reported to have a preferential selection of almost exclusively *C. pelagicus* (Wollenburg, 1992; Young and Geisen, 2002). Thomsen and Rasmussen (2008) have reported trochospiral, planispiral, unilocular, uniserial, biserial, and triserial forms of agglutinated benthic foraminifera that build their test using exclusively made up of coccoliths of species *Watznaueria barnesae* from the Early Cretaceous marine clastic sediments deposited in the North Sea basin. The other species retrieved using coccoliths of species *W. barnesae* is *Spiroplectinella* from Upper Cretaceous deposits in the Pacific Ocean (Holbourn and Kaminski, 1997). Several other studies also retrieved agglutinated benthic foraminifera that select coccoliths for their test construction (Widmark and Henriksson, 1995; Almogi-Labin et al., 1996; Henriksson et al., 1998; Thomsen and Rasmussen, 2008). Brönnimann and Whittaker (1988) illustrated coccolith-cementing trochamminids from the Atlantic sector of the Southern Ocean (see Fig. 37 of their work). However, this is the first report of *Paratrochammina* sp. from recent sediments of the deep South Pacific having coccoliths test.

We also found a number of *Rhabdammina* specimens that have

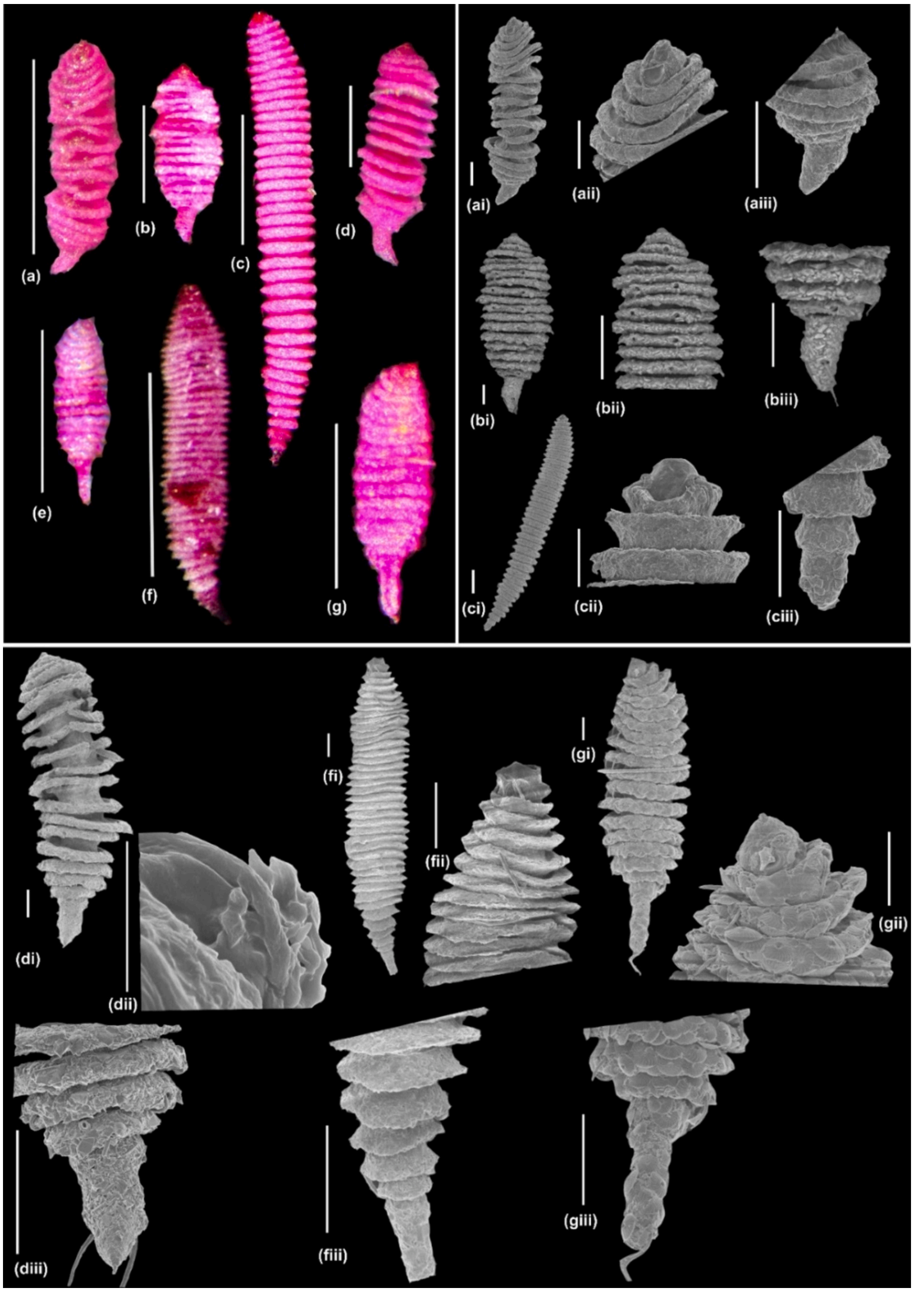

Fig. 2. Photomicrographs (Scale bars = 100 μm) of dominant living (i.e., Rose Bengal stained) *Desmoscolex* nematoda found at >3500 m water depth in the Southern Pacific. (a) *Desmoscolex* sp.1, (b) *Desmoscolex* sp. 2, (c) *Desmoscolex* sp. 3, (d) *Desmoscolex* sp. 4, (e) *Desmoscolex* sp. 5, (f) *Desmoscolex* sp.6 have siliciclastic grains on their concretion rings (also see Fig. 4), (g) *Desmoscolex* sp.7, used coccoliths of the single species *Calcidiscus leptoporus* (also see Fig. 3) on its concretion rings. (a – IODP Site U1539; c, g – Site U1541; b, d, e, f – Site U1543). Scanning Electron Microscopy (SEM, Scale bars = 10 μm) image of (ai) *Desmoscolex* sp.1 (total view), (aii) lateral view of head and 4 anterior concretion rings showing insertion of subdorsal somatic setae on rings 1 and 3, and (aiii) posterior body region in left lateral view (Site U1539), (bi) *Desmoscolex* sp.2 (total view), (bii) first 13 concretion rings, one somatic setae visible on the sixth ring, (biii) view of posterior body region, last four concretion rings showing insertion of subdorsal somatic setae on rings 14 and 17, somatic setae visible on the tail (Site U1543), (ci) *Desmoscolex* sp.3 (total view), (cii) lateral view of head showing cephalic setae and amphideal fovea and three anterior concretion rings with triangular outline and (ciii) view of posterior body region, last three concretion rings, no somatic setae visible (Site U1541), indeed in Fig. 2ciii no pair of subdorsal setae visible on the terminal main ring, however, such a pair of somatic setae is visible in Fig. 4f. The presence of a terminal pair of somatic setae is characteristic for the tribe Desmoscolecini, (di) *Desmoscolex* sp. 4 (total view), (dii) enlarged view of the apertural region of head portion, (diii) view of posterior body region, last four concretion rings showing insertion of subdorsal somatic setae on ring 16, somatic setae visible on tail (Site U1543), (fi) *Desmoscolex* sp.6 (total view), (fii) first 13 concretion rings showing insertion of subdorsal somatic setae on rings 2, 7, and 9, (fiii) view of posterior body region, last seven concretion rings showing one somatic setae on ring 38 (Site U1543), (gi) *Desmoscolex* sp.7 having *C. leptoporus* on its concretion rings, (gii) apertural, right lateral view of head and concretion rings 1–4, showing subventral somatic setae on rings 2 and 4, and (giii) view of posterior body region (Site U1541). (Taxonomic details provided in Annexure A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

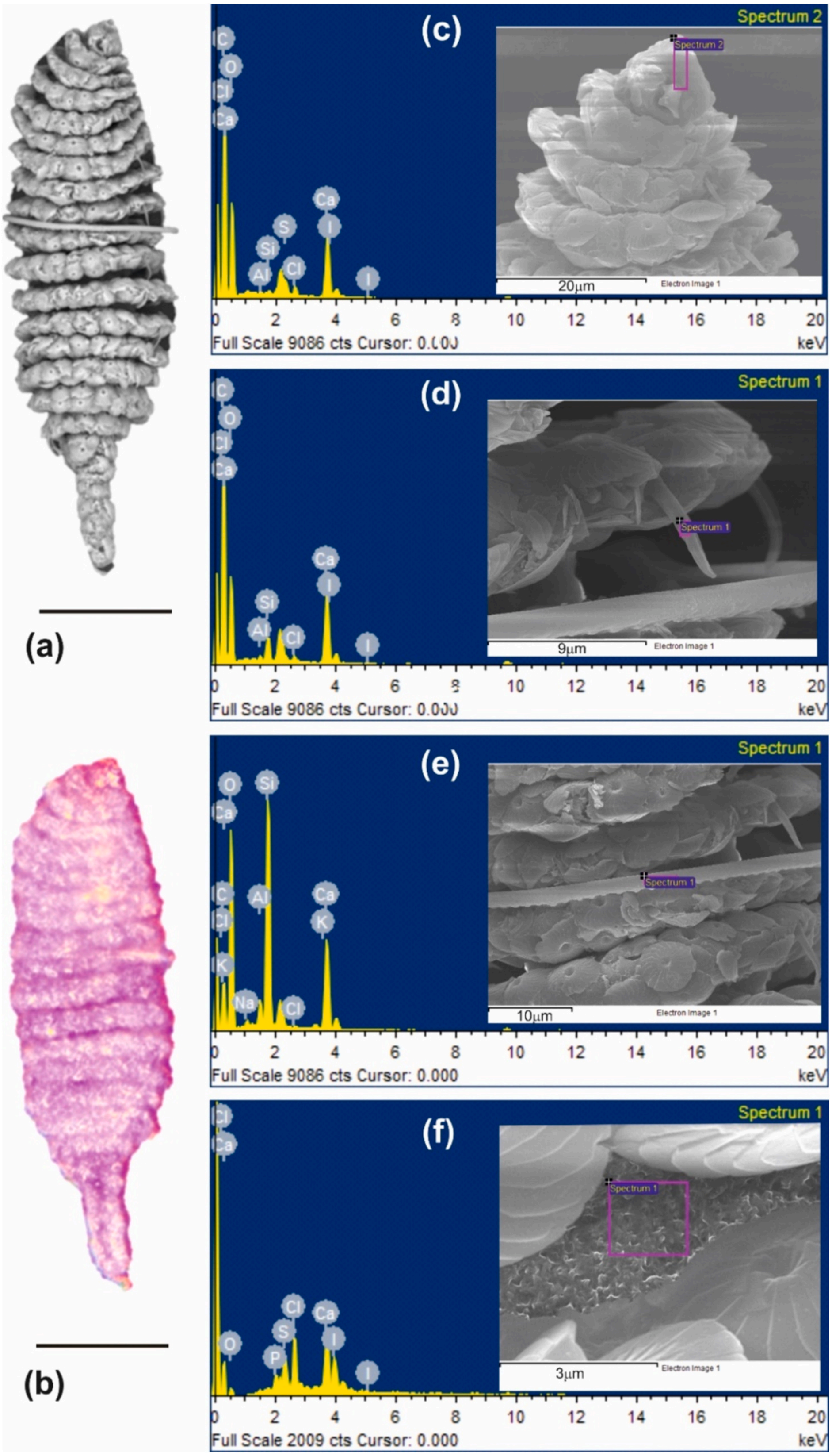

Fig. 3. Scanning Electron Microscopy (SEM) with energy dispersive spectroscopy (EDS) analysis of *Desmoscolex* sp. 7 having single species of coccolith *Calcidiscus leptoporus* on its concretion rings, (a) SEM image, (b) Photomicrograph, (c) EDS on anterior head region, (d) EDS on a subventral somatic setae on concretion ring 8, (e) EDS of girdle portion, (f) EDS of body cuticle between the concretion rings, Scale bar = 50 µm in (a) and (b).

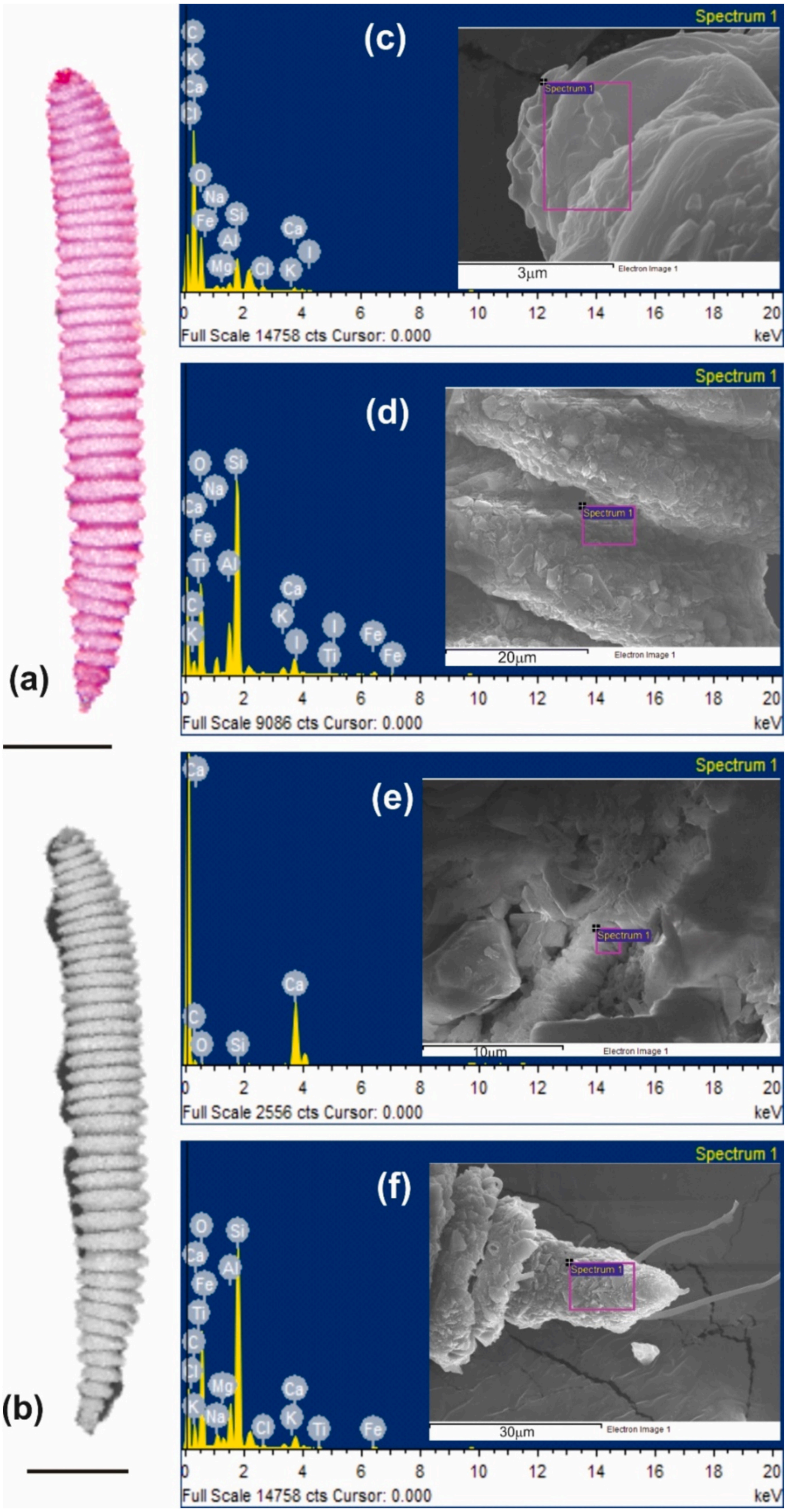

Fig. 4. Scanning Electron Microscopy (SEM) with energy dispersive spectroscopy (EDS) analysis of *Desmoscolex* sp.3 having randomly picked grains on its concretion rings, (a) Photomicrograph, (b) SEM image, (c) EDS of aperture head portion, (d) EDS of inner portions of concretion rings, (e) EDS of body cuticle between the concretion rings, (f) EDS of tail portion showing endring with pair of subdorsal somatic setae, Scale bar = 50 μm in (a) and (b).

Table 1

Energy dispersive spectroscopy (EDS) analysis of *Desmoscolex* sp.7, which selected a single species of coccolith *Calcidiscus leptoporus* on its concretion rings (Please refer to Fig. 3 for portion scanned).

	Fig. 3 (c)		Fig. 3 (d)		Fig. 3 (e)		Fig. 3 (f)	
Element	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)
C	50.47	60.44	52.07	62.24	23.11	31.84		
O	40.66	36.56	38.13	34.21	54.44	56.32	14.36	35.04
Na					0.5	0.36		
Al	0.16	0.09	0.23	0.12	1.36	0.83		
Si	0.13	0.07	1.26	0.64	12.02	7.09		
S	0.5	0.22					7.86	9.56
Cl	0.72	0.29	0.46	0.19	0.14	0.06	16.91	18.61
K					0.37	0.15		
Ca	6.11	2.19	6.96	2.49	8.07	3.33	24.12	23.49
Mn								
Fe								
Ba								
I	1.25	0.14	0.89	0.1			34.65	10.66
P							2.09	2.64
Total	100		100		100		100	

Table 2

Energy dispersive spectroscopy (EDS) analysis of *Desmoscolex* sp.3, which randomly picked grains on its concretion rings (Please refer to Fig. 4 for portion scanned).

	Fig. 4 (c)		Fig. 4 (d)		Fig. 4 (e)		Fig. 4 (f)	
Element	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)	Weight (%)	Atomic (%)
C	62.88	70.95	20.15	29.57	18.02	34.31	27.43	37.36
O	31.67	26.83	45.1	49.69	21.68	31	47.1	48.15
Na	0.42	0.25	2.7	2.07			1.48	1.06
Mg	0.17	0.09					0.7	0.47
Al	0.49	0.24	5.14	3.36			3.39	2.05
Si	2.26	1.09	20.73	13.01	1.2	0.98	16.57	9.65
Cl	0.56	0.21					0.18	0.08
K	0.15	0.05	1.07	0.48			0.42	0.17
Ca	0.42	0.14	2.74	1.2	59.1	33.72	1.75	0.71
Ti			0.28	0.1			0.16	0.06
Fe	0.26	0.06	1.31	0.42			0.83	0.24
I	0.72	0.08	0.78	0.11				
Total	100		100		100		100	

selected specific planktic foraminifera *Globoconella inflata* species (Fig. 5n), or have used multi-species planktic foraminifera of the same size to build their test (Figs. 5o, p; see also F29. A, C, and D in Winckler et al., 2021b). Our findings match those of Pearson et al. (2018) who reported unique probable *Rhabdammina* species from 1466 m water depth in the northwest Australian margin (IODP Hole 1482B), which exclusively selected planktic foraminifera *Turborotalita clarkei* to build their test. *Turborotalita clarkei* is a subsurface dwelling species that may occur below the thermocline and occupies tropical to temperate waters. This species has a detritivorous feeding habit on exported organic matter below thermocline (Levy et al., 2023). The other studies also reported the use of dead planktic foraminifera test for constructing test of agglutinated benthic foraminifera (Brady, 1879; Cartwright et al., 1989; Gooday, 1990). However, this is the first report of such specimens from the abyssal plain of the Southern Pacific Ocean, one of which exclusively used planktic foraminifera *G. inflata* species (Fig. 5n).

3.4. Ecological Implications in Central and Southeastern Pacific Ocean

Free-living marine nematodes survive by burrowing between sediment particles, suggesting a significant relationship between the type of nematodes and the size of the surrounding sediment grains (Fleeger et al., 2011). The morphometrics, including length, diameter, biovolume, biomass, body form, tail shape, etc., of free-living marine nematodes exhibit variations in response to different environmental circumstances. The deep-sea unconsolidated muds are a common habitat for short, stout nematodes, which are particularly prevalent in the uppermost sediment levels (1–2 cm; Soetaert et al., 2002). This study shows that all the specimens of *Desmoscolex* are short and stout except *Desmoscolex* sp. 3 and sp. 6 (Figs. 2c, f).

The species composition and diversity of deep ocean nematodes are shown to be associated with variations in bottom water temperature and sediment type (Tietjen, 1976). Dinet and Vivier (1979) found that the Desmoscolecidae are more prevalent in the Bay of Biscay's deeper waters with higher clay-silt sediments and susceptible to the periodic harsh deep ocean conditions (Heip et al., 1982). The deep abyssal depths of the Southern Pacific Ocean have limited clay-silt sediments and are rich in bioclast (Lamy et al., 2021a; Fig. 6), which may be the reason for a lower abundance and diversity of *Desmoscolex* at the CSP Sites U1539 and U1541 compared to Site U1543 from the Southeastern Pacific (Fig. 6). Decreasing food availability, because of increasing water depth, might benefit smaller nematodes (Udalov et al., 2005; Soetaert et al., 2009; Fleeger et al., 2011). Further, the *Desmoscolex* nematodes abundance is linked to higher surface primary productivity and high organic matter flux to the sea floor (Lins et al., 2015). Hence the reduced organic matter transport to the abyssal depth of the Southern Ocean (Das et al., 2024) may be another reason for the smaller size and low abundance of *Desmoscolex* nematodes in the Southern Pacific Ocean.

Lamy et al. (2021a) reported several agglutinated benthic foraminifera from the deeper Southern Pacific IODP Sites U1539, U1540, U1541 and U1543. The dominant and common agglutinated foraminifera like *Siphotextularia rolshauseni*, *Cribrostomoides subglobosus*, *Eggerella bradyi* and *Hormosina globulifera*, present in the mudline samples of Sites U1539, U1540, U1541 and U1543 are preserved in the sediment sequences, but some fragile mudline agglutinated species like *Rhabdammina* spp., and *Reophax* sp. were not found in the geological

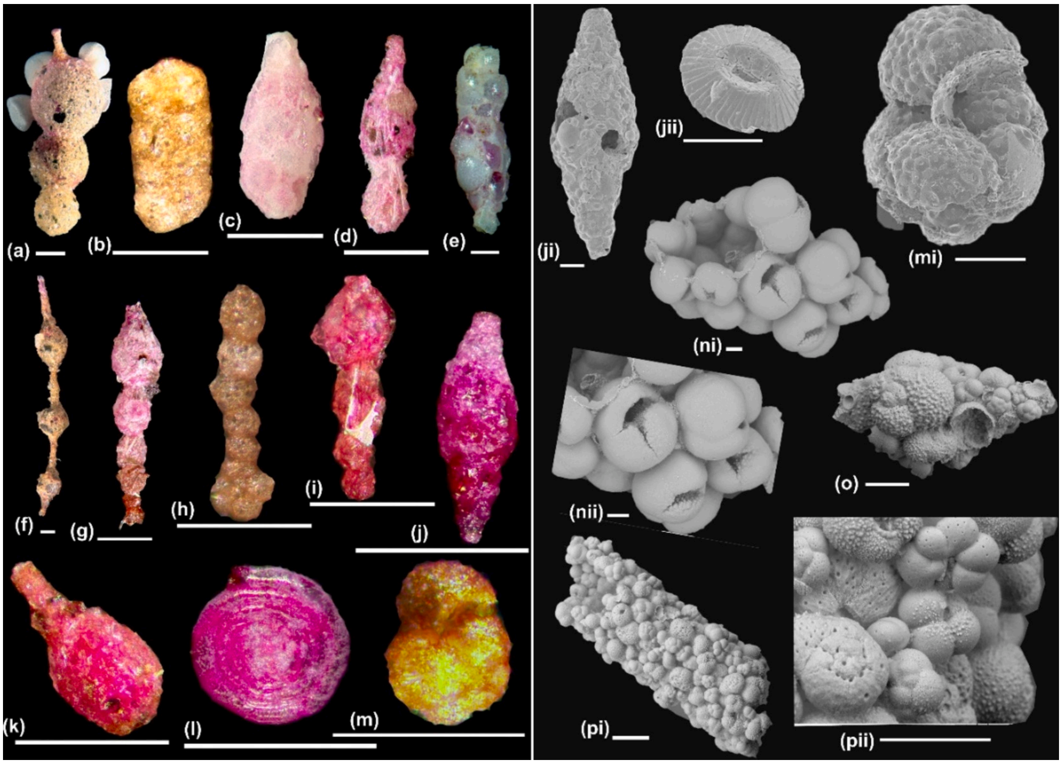

Fig. 5. Photomicrographs (Scale bars = 100 μm) of dominant living (i.e., Rose Bengal stained) agglutinated benthic foraminifera species found at >3500 m water depth in the central South Pacific. (a) *Hormosina globulifera* (IODP Site U1539); (b) *Spiroplectammina biformis* (Site U1539); (c) *Lagenammina* sp. (Site U1539); (d) *Reophax* sp. (Site U1539); (e) *Rhabdammina* sp. 1 (Site U1541); (f) *Hormosinella distans* (Site U1539); (g) *Reophax gaussica* (Site U1539); (h) *Ammobaculites exilis* (Site U1539); (i) *Reophax excentricus* (Site U1539); (j) *Reophax fusiformis* (Site U1539); (k) *Lagenammina difflugiformis* (Site U1539); (l) *Ammodiscus anguillae* (Site U1543); (m) *Paratrochammina* sp. (Site U1543). Scanning Electron Microscopy (SEM, Scale bars = 10 μm) image of (ji) *Reophax fusiformis*, (jii) enhanced view of a *Coccolithus pelagicus* from (ji) (Site U1539); (mi) *Paratrochammina* sp. (Site U1543); (ni) *Rhabdammina* sp. 2 composed of planktic foraminiferal species *Globoconella inflata* only, (nii) enlarged view (Site U1540); (o) *Rhabdammina* sp. 3 composed of differently sized planktic and benthic foraminifera (Site U1540); (pi) *Rhabdammina* sp. 4 built up using same-sized planktic and benthic foraminifera, (pii) enlarged view (Site U1540). (Taxonomic details provided in Annexure B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

record (Lamy et al., 2021a; Das et al., 2024). No other specimens of agglutinated foraminifera, which exclusively built their tests using single or multiple species of coccoliths or planktic foraminifera were found in the geological strata of any of the studied sites (Lamy et al., 2021a). This suggests that the deep Southern Ocean environment is conducive for various fragile agglutinated foraminiferal species, but most of them are not preserved in sediment downcore. We argue that it may be possibly due to a stronger and seasonal corrosive bottom water current or degradation of organic cement over time (Das et al., 2024). Most of the common agglutinated foraminiferal species like *Siphotextularia rolshauseni*, *Hormosina* spp., and *Eggerella bradyi* are cosmopolitan in nature and suggest low to intermediate organic flux and better deep-sea oxygenation, whereas *Reophax* species tends to be an opportunistic form (Kaminski et al., 1988; Hess et al., 2001) indicating low quality of organic flux to the seafloor. The abundance of *Reophax* and *Rhabdammina* species, along with the other calcareous and agglutinated species reported from the mudline sample in Lamy et al. (2021a) suggest low to intermediate organic flux in the CSP sites and slightly improved conditions at Southeastern Pacific. The presence of *Oridorsalis umbonatus*, *Globocassidulina subglobosa*, *Cibicidoides mundulus,* and *Melonis affinis,* etc. calcareous benthic foraminifera in the mudline samples further confirm the better oxygenation conditions (Lamy et al., 2021a).

3.5. Selective grains and bioclasts preferences of meiofauna

The agglutinations of *Desmoscolex* nematodes and benthic foraminifera specimens with only *C. leptoporus* coccoliths is an important factor to consider. *Emiliania huxleyi* (recently renamed as *Gephyrocapsa huxleyi,* Bendif et al., 2023) is actually the dominant extant coccolithophore species in the Pacific sector of the Southern Ocean (e.g., Saavedra-Pellitero et al., 2014). However, due to the small size of its coccoliths (usually 2–4 μm in length) and its delicate structure, *E. huxleyi* is more prone to dissolution than for instance, *C. leptoporus* (with coccolith diameters usually ranging from 5 to more than 8 μm). That is why relatively higher numbers of *C. leptoporus* have been previously reported in Southern Pacific Ocean surface sediment samples (e.g., Saavedra-Pellitero and Baumann, 2015). We speculate that this particular *Desmoscolex* nematode specimen (*Desmoscolex* sp.7; Figs. 2g, 3) preferentially selected the largest and most robust coccoliths available in the surface sediments (i.e. *C. leptoporus*, Figs. 6c, Site U1541) on its concretion rings.

The dissolution resistance and higher abundance or availability of *C. leptoporus* at water depths greater than 3500 m may be one reason for its selection by one of this *Desmoscolex* specimen (*Desmoscolex* sp. 7, Figs. 2g, 6). It would appear that the coccoliths are always arranged such that the convex surfaces face outwards and the concave surfaces face inside (Fig. 3). The development of a more robust test with fewer empty areas might be the primary benefit of adapting the coccoliths (Thomsen and Rasmussen, 2008).

There are some agglutinated benthic foraminifera genus like *Paratrochammina* and *Reophax* species found at the studied sites that also selected coccoliths from the species *C. leptoporus*, *C. pelagicus,* and *H. carteri* for test construction (Figs. 5j, m). Still, some of the agglutinated benthic foraminifera, like *Rhabdammina* sp., specimens that have selected specific planktic foraminifera *G. inflata* species (Figs. 5n, 6). *Globoconella inflata* is a deep-dwelling transitional water planktic foraminiferal species, having a higher abundance between 30 and 50 $^{\mathrm{o}}$S. This

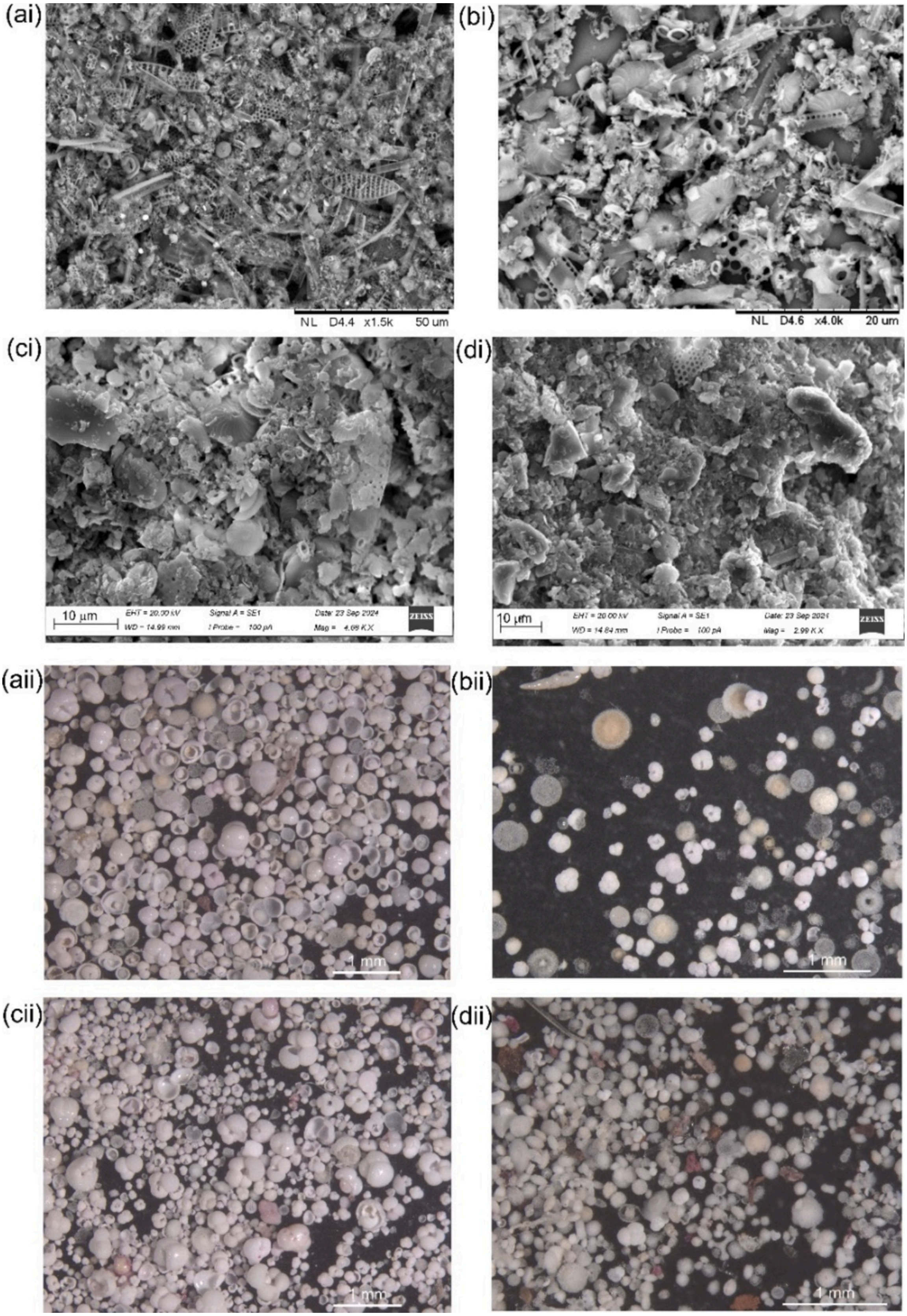

Fig. 6. Scanning Electron Microscopy image of finest fraction of the mudline samples of Sites (ai) U1539, (bi) U1540 taken onboard at *Joides Resolution* using Tabletop SEM Hitachi TM 3100 and of Sites (ci) U1541, (di) U1543 at University of Portsmouth using Zeiss Evo MA10 SEM comprising of coccolith *C. leptoporous*, various diatoms, and siliciclastic fragments; Photomicrographs (scale = 1 mm) of coarse fraction (>63 μm) of the mudline samples taken at IIT Bhubaneswar using a Leica M205A stereo microscope showing composition at Sites (aii) U1539, (bii) U1540, (cii) U1541, rich in planktic foraminifera, but not dominant by *G. inflata* and at Site (dii) U1543 rich in diatom, radiolaria and siliciclastic fragments.

species' maximum numbers occur within the thermocline (e.g., Groeneveld and Chiessi, 2011) and is more abundant in phytoplankton-rich and productive cold waters (Martínez-García et al., 2023). Both *T. clarkei* and *G. inflata* species have similar morphology, but *G. inflata* reach higher numbers in the sub-Antarctic frontal zone of the study sites in comparison to *T. clarkei*; hence, we argue that these *Rhabdammina* species preferred *G. inflata* at our studied central South Pacific Site U1540 due to biogeographical limitations (Figs. 5n, o, p). However, various other *Rhabdammina* species choose different species of planktic foraminifera, coccoliths, and rarely available siliciclastic grains, but have the preferences for planktic foraminifera test and coccolith (Figs. 5p, q, 6). Most of the agglutinated benthic foraminifera *Rhizammina* and *Rhabdammina* species found in mudline samples from Southern Pacific IODP Sites U1539, U1540, U1541 and U1543 built their test by randomly selecting available fragments or whole tests of different planktic foraminifera, and coccolith besides or along with siliciclastic grains (Figs. 5, 6; Lamy et al., 2021a). However, a few specimens are selectively picked a particular shape and size of planktic foraminifera or coccolith. It should also be taken into account that the variations in agglutinated foraminifera test composition can be influenced by grain availability (Hess and Kuhnt, 1996; Stefanoudis et al., 2016). Henriksson et al. (1998) suggested that certain species, such as *Spiroplectinella* sp. from the Early Cretaceous and *Gaudryina cribrosphaerellifera* from the Late Cretaceous, might not have been selective in their picking of coccoliths but rather had simply picked up the most abundant particles/grains from the seafloor. However, the mudline samples of sites U1539, U1540, and U1541 are not all dominated by *C. leptoporus* or *G. inflata*, which are picked by some of the above-mentioned meiofauna (Fig. 6). Hence, this study suggests that these meiofauna have selectively picked *C. leptoporus*, *G. inflata* and/or other planktic foraminifera and coccoliths for their test construction and has no relationship with the abundance.

3.6. Limitations

The study is based on limited retrieval of Rose-Bengal stained *Desmoscolex* nematodes (Only Seven). These specimens are shrunk and badly fixed, which may not allow us to get the main diagnostic features for reliable identification. Further limited specimen occurrences do not allow us to conduct a detailed study of these nematodes. The agglutinated foraminifera found was not quantitatively analyzed during onboard analysis at the scientific research vessel *JOIDES Resolution*, which restricted us from doing further detailed analyses. Despite this, we consider that these meiofauna will contribute to enhance our knowledge about the abyssal plain of Central and Eastern Southern Pacific Ocean.

4. Conclusions

Recent *Desmoscolex* genus nematodes and agglutinated benthic foraminiferal tests studied in mudline samples from IODP Sites U1539, U1540, and U1541 of Central South Pacific and Site U1543 in the Eastern South Pacific are made up of a range of lithic and biogenic sedimentary particles. This study reports *Desmoscolex* species, which used coccoliths from a single taxon (*Calcidiscus leptoporus* subsp. *leptoporus*) on its concretion rings. This specimen looks morphologically similar to the few other specimens of nematodes, which used fine siliciclastic grains on its concretion rings. We also found an agglutinated foraminiferal species of Rhabdamminidae family, which picked single planktic foraminiferal species, such as *Globoconella inflata* to build its test and a *Paratrochammina* specimen, which used almost exclusively *C. leptoporus* subsp. *leptoporus* coccoliths (with a minor contribution of *Coccolithus pelagicus* subsp. *pelagicus*). A *Reophax fusiformis* specimen picked robust coccoliths of *C. pelagicus, C. leptoporus, and Helicosphaera carteri* to build its test. These meiofauna specimens selectively choose and pick the bioclast grains, which are robust and available in the sediments but not linked to the dominance of bioclast grains. The deeper Southern Pacific (>3500 m water depth) shows fragile *Desmoscolex* nematode and agglutinated foraminiferal species of *Rhabdammina*, and *Reophax* in core-top (i.e. recent) sediments, but most of them are not preserved in the geological record, possibly due to a stronger and seasonal corrosive bottom water current or degradation of organic cement over time. *Desmoscolex* species and the commonly occurring agglutinated foraminiferal species mentioned in Lamy et al. (2021a) suggest low to intermediate organic flux and relatively better ventilated bottom water conditions in the modern Central and Eastern South Pacific. This study of nematodes and agglutinated benthic foraminifera enhances our ecological knowledge about the underexplored deep abyssal plain of the Southern Pacific Ocean and provides information about modern conditions of the deep ocean's oxygenation and organic matter flux. However, limited retrieval of nematodes and non-quantitative analysis of agglutinated foraminifera limit its ecological interpretations.

CRediT authorship contribution statement

Sunil K. Das: Writing – original draft, Validation, Investigation, Formal analysis, Conceptualization. **Raj K. Singh:** Writing – review & editing, Formal analysis, Data curation. **Mariem Saavedra-Pellitero:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Julia Gottschalk:** Writing – review & editing, Formal analysis, Data curation. **Carlos A. Alvarez Zarikian:** Writing – review & editing, Formal analysis, Data curation. **Lester Lembke-Jene:** Writing – review & editing, Data curation. **Frank Lamy:** Resources, Data curation. **Gisela Winckler:** Resources, Conceptualization. **Jennifer L. Middleton:** Writing – review & editing, Formal analysis, Data curation. **Helge W. Arz:** Writing – review & editing, Formal analysis, Data curation. **Chandranath Basak:** Writing – review & editing, Formal analysis, Data curation. **Anieke Brombacher:** Writing – review & editing, Formal analysis, Data curation. **Oliver M. Esper:** Writing – review & editing, Formal analysis, Data curation. **Jesse R. Farmer:** Writing – review & editing, Formal analysis, Data curation. **Lisa C. Herbert:** Writing – review & editing, Formal analysis, Data curation. **Shinya Iwasaki:** Writing – review & editing, Formal analysis, Data curation. **Vera J. Lawson:** Writing – review & editing, Formal analysis, Data curation. **Li Lo:** Writing – review & editing, Formal analysis, Data curation. **Elisa Malinverno:** Writing – review & editing, Formal analysis, Data curation. **Elisabeth Michel:** Writing – review & editing, Formal analysis, Data curation. **Simone Moretti:** Writing – review & editing, Formal analysis, Data curation. **Christopher M. Moy:** Writing – review & editing, Formal analysis, Data curation. **Ana Christina Ravelo:** Writing – review & editing, Formal analysis, Data curation. **Christina R. Riesselman:** Writing – review & editing, Formal analysis, Data curation. **Inah Seo:** Writing – review & editing, Formal analysis, Data curation. **Rebecca A. Smith:** Writing – review & editing, Formal analysis, Data curation. **Alexandre L. Souza:** Writing – review & editing, Formal analysis, Data curation. **Joseph S. Stoner:** Writing – review & editing, Formal analysis, Data curation. **Igor M. Venancio:** Writing – review & editing, Formal analysis, Data curation. **Sui Wan:** Writing – review & editing, Formal analysis, Data curation. **Xiangyu Zhao:** Writing – review & editing, Formal analysis, Data curation.

Declaration of competing interest

The contact author has declared that none of the authors has any competing interests.

Data availability

All the data used in this study are included in the Appendix.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marmicro.2024.102409.

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