



The first record of the genus *Lamellibrachia* (Siboglinidae) tubeworm along with associated organisms in a chemosynthetic ecosystem from the Indian Ocean: A report from the Cauvery–Mannar Basin

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Here, we report for the first time, the genus *Lamellibrachia* tubeworm and associated chemosynthetic ecosystem from a cold-seep site in the Indian Ocean. The discovery of cold-seep was made off the Cauvery–Mannar Basin onboard *ORV Sindhu Sadhana* (SSD-070; 13th to 22nd February 2020). The chemosymbiont bearing polychaete worm is also associated with squat lobsters (*Munidopsis* sp.) and Gastropoda belonging to the family Buccinidae. Relict shells of chemosynthetic *Calyptogena* clams are ubiquitous at the seep sites. The *Lamellibrachia* tubes were found to be firmly anchored into the authigenic carbonate crusts. The authigenic carbonate crusts (chemoherm) are packed with large *Calyptogena* shells (whole shell and fragments). Very high concentrations (3800–12900 μM) of hydrogen sulfide (H_2S) in the interstitial waters (40 cmbsf) is responsible for the sustenance of chemosymbiont bearing tube-worms. The posterior end of the tube penetrates downwards into the H_2S -rich zone. The high concentration of H_2S at ~ 40 cmbsf is attributed to sulfate reduction via anaerobic oxidation of methane (AOM) pathway. Methane hydrate was observed within the faults/fractures in the sediments. The presence of ethane and propane along with methane in the headspace gases and $\delta^{13}\text{C}_{\text{CH}_4}$ values (-28.4 to -79.5% VPDB) suggest a contribution of deep-seated thermogenic methane.

Keywords. Cold-seep; gas flares; methane hydrate; methane; hydrogen sulfide; chemosymbiont; tubeworm.

1. Introduction

Marine cold-seep ecosystems are characterized by the buildup and/or emission of methane across the sediment–water interface and accumulation of very high interstitial hydrogen sulfide concentrations near the sediment–water interface at low-temperature sea-bed conditions (Levin 2005; Levin *et al.* 2016). The cold-seep ecosystem occurs as patches of variable shape and size across the ocean floor depending upon the areal extent of hydrocarbon conduits like fractures and faults (Panieri *et al.* 2017). The biotic communities thriving at the cold-seeps are characterized by an endemic ecosystem comprised of chemosynthetic and heterotrophic fauna. H_2S and CH_4 fluxes at the sediment–water interface (Portail *et al.* 2015) primarily controls the faunal diversity and spatial distribution of cold-seep ecosystems. On the other hand, a steady flux of methane and hydrogen sulfide gases control the growth and sustenance of cold-seep ecosystems.

Cold-seeps and associated ecosystems are recorded from numerous sites across the world ocean (Sibuet and Olu-Le Roy 2002; Levin 2005; Vanreusel *et al.* 2009; Olu *et al.* 2010; Mazumdar *et al.* 2019; Feng *et al.* 2020), including Hikurangi basin (off New Zealand); Congo-Angola and Nigeria margins (off West Africa), Nankai Trough (Japan); upper, middle and lower Louisiana slope/Florida escarpment (Gulf of Mexico); Gulf of Cádiz and areas of Nile deep Sea site (Eastern Mediterranean); Barbados Trench; Nordic margin; Makran coast (off Pakistan); off Papua New-Guinea; South China Sea; Queen Charlotte Basin (off the Pacific north coast of British Columbia); Krishna–Godavari basin (Mazumdar *et al.* 2019); Arctic sediment (Astrom *et al.* 2020) and below the Larsen Ice Shelf off the Antarctic (Niemann *et al.* 2009). The global attention to the genesis and sustenance of methane cold-seeps is attributed to interest in evolutionary biology, bioprospecting of extreme ecosystems, the contribution of methane emissions to global warming, and application in methane hydrate exploration (Le Bris *et al.* 2016).

Here we report for the first time association of *Lamellibrachia* tubeworm with methane seep related chemosynthetic ecosystem from the Indian Ocean. The seep site is identified off Mannar Basin (within the EEZ of India). The observed ecosystem

was developed on a carbonate chemoherm without active gas flares. However, methane flares were observed at other locations (Peketi *et al.* under review). The sites are also characterized by chemosymbiont bearing and associated heterotrophic biotic assemblages and shallow methane hydrates (2–3 mbsf). The seep site is located at 1644-m water depth (pressure: 13.9 MPa and temperature: 4.95°C).

2. Geology

The Mannar basin (figure 1A), located between India and Srilanka, is a pull-apart sub-basin of the Cauvery–Mannar Basin along the eastern continental margin of India. The basin came into existence in the Late Jurassic/Early Cretaceous due to fragmentation of the Gondwanaland and drifting of the India–Srilanka landmass system away from Antarctica/Australia continental plate (Yoshida *et al.* 1992; Premarathne *et al.* 2016). Numerous deep extensional faults developed in the NE–SW direction during rifting had initiated active subsidence that resulted in the formation of graben and horst blocks (Bastia and Radhakrishna 2012; Yanqun *et al.* 2017). Differential subsidence resulted in the formation of sub-basins within the Cauvery basin. The Gulf of Mannar sub-basin is further divided into western and eastern segments by the NE–SW-aligned Mandapam–Delft ridge (Rao *et al.* 2010). Curray (1984) opined that the first rifting between India, Sri Lanka, and Antarctica occurred through the Cauvery–Palk Strait–Gulf of Mannar zone but this rift did not progress into the seafloor spreading stage.

Sediment thickness of more than 6 km has been reported from the deep-waters of the Mannar basin (Ratnayake *et al.* 2017). Seismic and drill well studies indicate six sedimentary sequences including a thick Early Cretaceous rift fill sequence (principal source horizon) overlain by a complete succession of Tertiary sequence (Rao 2006; Biswas 2012).

3. Methodology

The expedition (SSD-070) was carried out in the Mannar basin onboard *ORV Sindhu Sadhana* from 13th to 22nd February 2020. The multi-beam bathymetry shows several pock-mark-like features in the Mannar basin; one

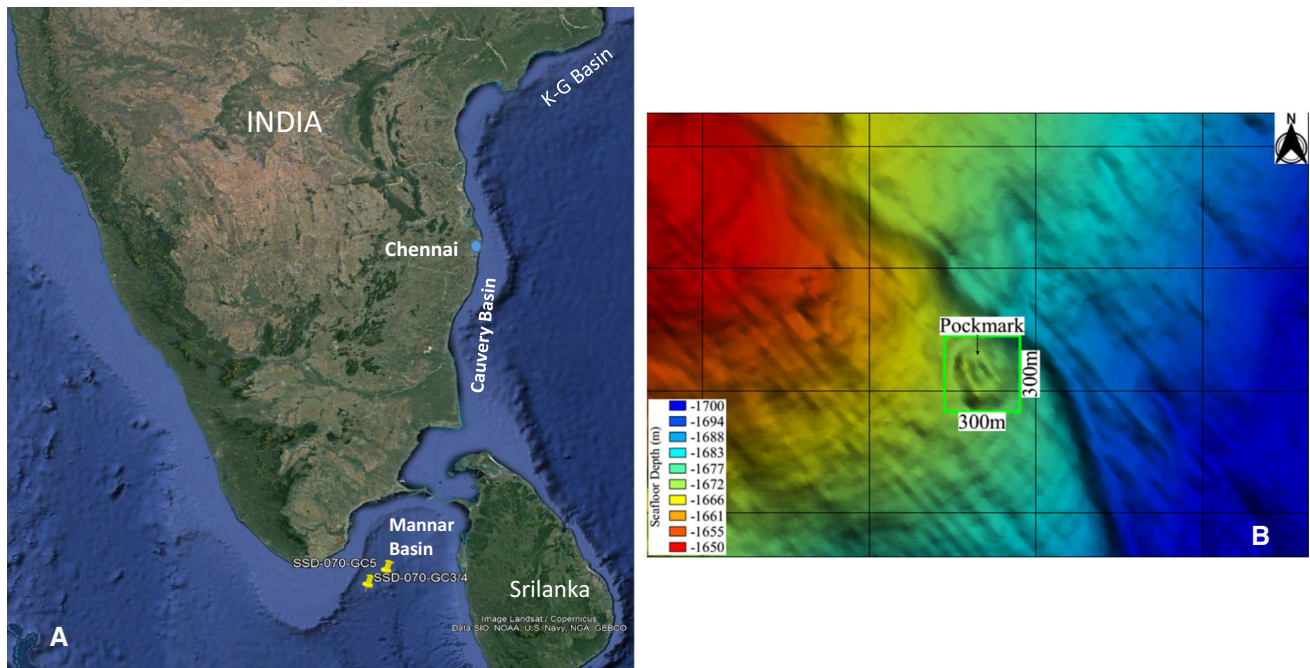


Figure 1. (A) Location of cold-seep sites in the Cauvery–Mannar Basin (image from Google Earth); (B) A doughnut-shaped pockmark observed in the Mannar basin. The inner and outer diameters of the pockmark are 50 and 300 m, respectively.

such pockmark was investigated in the expedition SSD-070 (figure 1B). The water-column (WC) images produced by the multibeam echosounder (Atlas-Hydrosweep DS) did not detect any gas flares over the pockmark. Seabird CTD profiler and sound velocity profiling (SVP) data were used to generate water column images. Salinity, temperature, and SVP data were used to carry out the depth corrections for multibeam data. We collected seabed samples at the center of the pockmark (lat: $7^{\circ}51.37086'N$; long: $78^{\circ}36.45660'E$; water depth: 1644 m) using a spade-corer (48 cm (L) \times 48 cm (B) \times 44 cm (H)) and a gravity corer (PVC liner; inner diameter: 10 cm). Handpicked organisms from the spade cores were stored in either isopropyl alcohol or in $-20^{\circ}C$ refrigerator for the shore-based analysis. Authigenic carbonates and hard shells were cleaned, dried at room temperature for petrographic/chemical analyses, and taxonomic identification. Sediment pore-fluid/gas-extraction and preservation for onshore analyses of concentrations and isotope ratios (Mazumdar *et al.* in prep.) were carried out onboard. We recovered gas hydrate samples from the gravity core, which were stored in gas-tight tubes for on-shore carbon isotope ratio measurements.

4. Results and discussion

4.1 Biotic association

4.1.1 *Polychaete tubeworm: Lamellibrachia sp. and ecological significance*

Two whitish polychaete tubeworms (*Lamellibrachia* sp.) were recovered in a spade core from the pockmark (SSD-070-5). The tubes were firmly anchored into the authigenic carbonate crust (figure 2A). The length of tube-1 and tube-2 are 93.5 and 57 cm, respectively, and are found to lie 50 and 26 cm above the carbonate crust. The posterior part of the tube is translucent and sinuous (figure 2B). The external surface of the tube is relatively smooth due to a lack of sharply projecting collars (figure 2C) and resembles (supplementary figure S1) the appearance of *Lamellibrachia columna* (Southward 1991) and *Lamellibrachia anaximandri* (Southward *et al.* 2011). The growth rings are discernible in the top 32 mm. The maximum diameter of tubes 1 and 2 are 13.4 and 15 mm, respectively. The vestimentiferan tubes are composed of giant β -chitin crystallites embedded in a protein matrix (Gaill *et al.* 1992) and the thickness of the chitin wall is ~ 2.5 mm at the anterior end. The diameter of the tubes decreases downwards and tapers at the

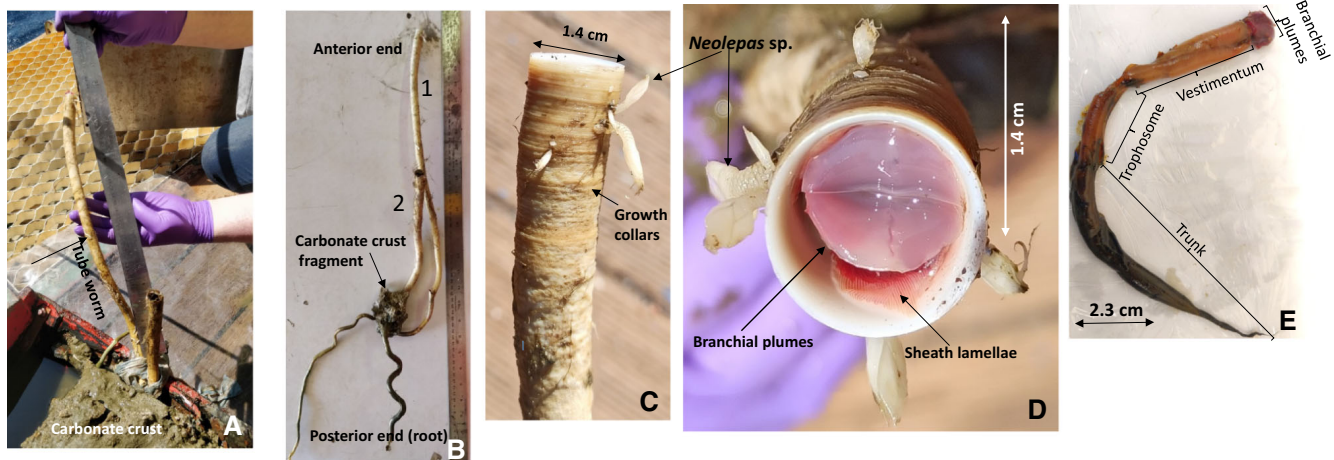


Figure 2. (A) Chitin tubes of *Lamellibrachia* sp. associated with carbonate crust recovered in a spade core from the study site; (B) anterior and posterior ends of the *Lamellibrachia* tubes; (C) a magnified view of the anterior end show growth rings or collars; (D) a magnified view of the anterior tube opening showing branchial plume and sheath lamellae. Goose-barnacles (*Neolepas* sp.) are attached to the exterior surface of the tube; and (E) soft body of the polychaete extracted from the tube.

posterior end. Goose barnacles (*Neolepas* sp.; Mazumdar *et al.* 2019) and byssus threads are attached to the outer surface of the tubes (figure 2C).

Tube-1 was dissected to observe the soft body of the worm. The different segments of the polychaete worm body like branchial plume ($l = 0.84$ cm), vestimentum ($l = 4.7$ cm), trophosome ($l = 2.89$ cm), and trunk ($l = 9.9$ cm) are marked in figure 2(D, E). The width of the branchial plume and trophosome are 1 and 0.8 cm, respectively, whereas, the trunk part tapers from 0.8 to <0.1 cm over a length of 9.9 cm. The red colour of the worm is attributed to the presence of hemoglobin within the vascular blood and coelomic fluid which can carry both oxygen and hydrogen sulfide essential for the survival of the chemosynthetic organisms (Arp *et al.* 1987; Fisher *et al.* 1988). Unlike hydrothermal vent associated tubeworms, where the H_2S enters the worm's body through the branchial plume (a set of highly vascularized gills), in the cold-seep tubeworms, H_2S is transported into the cold-seep tubeworms through the root-like posterior extension of the body (Julian *et al.* 1999) which is buried deep inside the sediment. H_2S is produced in the sediment via the sulfate reduction–AOM pathway (Vossmeier *et al.* 2012). The tubeworms lack a mouth or gut and host an endosymbiotic chemolitho-autotrophic γ -proteobacterium (S-bacteria) inside the bacteriocyte cells hosted in the vascularized trophosome sac (Duperron *et al.* 2009). The

polychaete worms acquire the symbionts from the ambient environment at the larval stage (Harmer *et al.* 2008). Through H_2S oxidation, the symbionts in the bacteriocyte cells fix CO_2 into organic molecules thus fulfilling the nutritional requirements of the polychaete worm. Sulfate ion, a by-product of HS^- oxidation, and H^+ produced via other metabolic processes are released from the coelomic fluid across the root into the sediment interstitial waters (Dattagupta *et al.* 2006). The SO_4^{2-} elimination is accompanied by anion (HCO_3^-) uptake across the root epithelium. The sulfate–sulfide recycling process is energetically economical and plays an important role in the long-term sustenance of the organisms (Dattagupta *et al.* 2006). Additionally, Thiel *et al.* (2012) reported two different carbon fixation pathways for the endosymbiont namely, the Calvin–Benson–Bassham (CBB) and reductive tricarboxylic acid (rTCA) cycles.

Vestimentiferan tubeworms associated with methane seeps are slow-growing organisms and individuals may be older than 200 years (Cordes *et al.* 2005, 2007), which may be attributed to stable environments without resource limitation and lack of lethal predation. Assuming a conservative growth rate of 0.77 $cm\ y^{-1}$ (Fisher *et al.* 1997), the estimated age of the longer tube (tube A) in our study is 121 years.

The genus *Lamellibrachia* Webb, 1969 is one of the few Siboglinidae worms with a broader geographic and habitat distribution such as seeps,

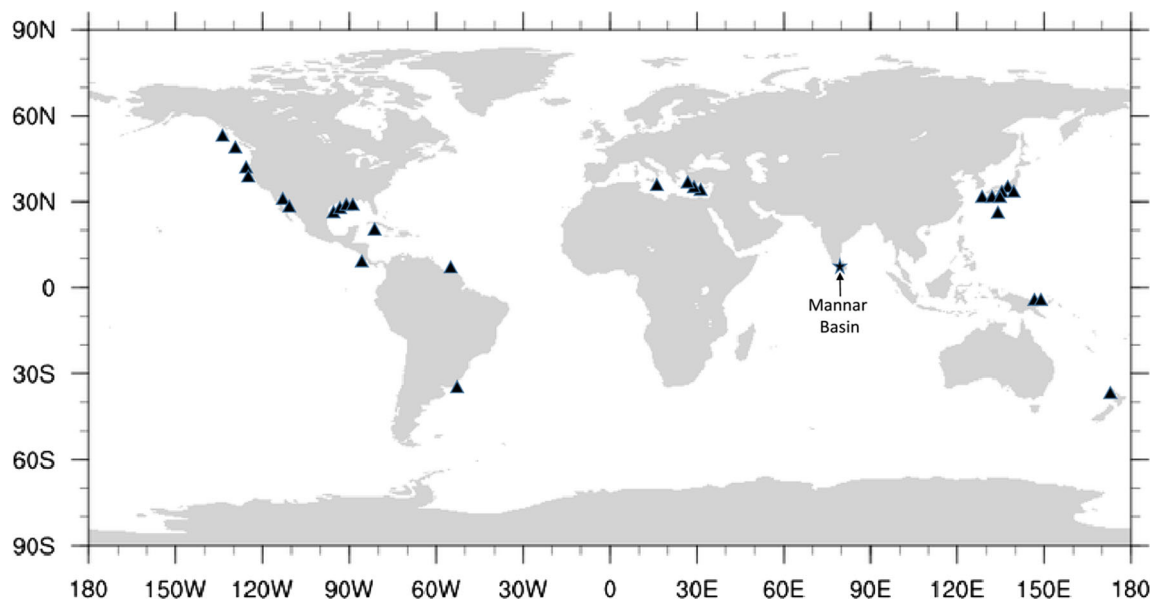


Figure 3. Global distribution of *Lamellibrachia* polychaete tubeworm (modified after Mccowin and Rouse 2018). The discovery from the Cauvery–Mannar Basin is marked by a star.

vents, and whale falls in the Pacific, Atlantic, Caribbean, and Gulf of Mexico (Feldman *et al.* 1998; Bright and Lallier 2010; Nishijima *et al.* 2010; Watanabe *et al.* 2010; Kobayashi *et al.* 2015). Before this report, there was no record of this genus from the Indian Ocean. Figure 3 shows the global distribution of eight species of the genus *Lamellibrachia* Webb polychaete tubeworms (modified after Mccowin and Rouse 2018). The present discovery (marked as a star in figure 3) is the first report of *Lamellibrachia* sp. from the Indian Ocean. Earlier Mazumdar *et al.* (2019) reported polychaete tubeworm belonging to *Sclerolinum* sp from the Krishna–Godavari methane seepage sites.

4.1.2 *Squat lobsters, gastropod and relict Calyptogena shells*

Two morphotypes (I and II) of squat lobster (figure 4A–D) belonging to the genus *Munidopsis* were recovered from the pockmark site SSD-070-5. The morphotypes reported here are distinct from those reported earlier from the K–G basin (supplementary figure S2) cold-seep sites (Mazumdar *et al.* 2019). Numerous species (~260) of the genus *Munidopsis* have been reported across the globe from cold-seeps, hydrothermal vents, deep-sea decomposing natural sunken woods, and whale carcasses (Martin and Haney 2005; Marin 2020). The morphotype I (figure 4A and B) and

morphotype II (figure 4C and D) show distinctly different carapace, abdominal, cheliped, telson, and sternum structures. Although the lengths of carapace and abdomen segments in morphotype I (11 and 5.5 mm) are comparable to that of morphotype II (12 and 4 mm), the rostrum in morphotype I (6 mm) is significantly bigger than that of morphotype II (3.5 mm). Morphotype I shows prominent transverse grooves and serrate granules on the carapace which is missing in morphotype II, whereas latter has setae on the carapace. The triangular abdomen part with broad ridges and groves in morphotype I is distinct from the rounded form in morphotype II. The segmentation patterns of the telson, sternum, and chelipeds are also different in the two morphotypes. The morphotype I and II are heterotrophs and their food sources include chemosynthetic bacteria, meiobenthos, and soft bodies of chemosymbiont bearing mussels (Macavoy *et al.* 2008; Thurber *et al.* 2011; Tsuchida *et al.* 2011).

Gastropod (figure 4E) belonging to the family Buccinidae (Kantor *et al.* 2013) known to be associated with cold-seeps and hydrothermal vents were recovered from the study sites. The 5 cm long gastropod sample has a 3-cm high spire while the last whorl is 2 cm long. Individual whorls (5 in number) have rounded margins with smooth axial ribs. The siphoncal canal is elongated with a broad inner lip. The foot part (soft body) is also visible. Cold-seep gastropods show multiple feeding habits

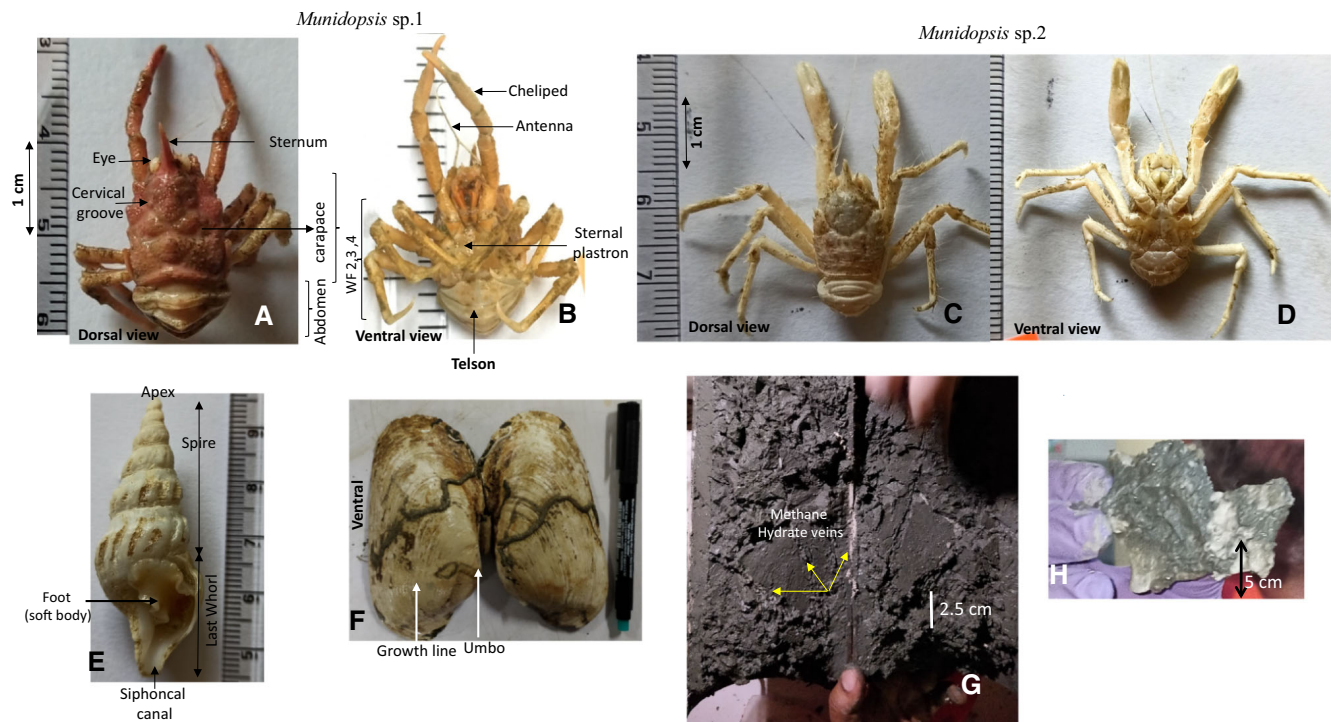


Figure 4. (A) Dorsal and (B) ventral view of squat lobster morphotype I belonging to the genus *Munidopsis*; (C) dorsal and (D) ventral view of squat lobster morphotype II belonging to the genus *Munidopsis*; (E) Gastropoda shell belonging to the family Buccinidae with the soft body (foot part); (F) whole shell of the genus *Calyptogena* showing growth layers; (G) fracture filling methane hydrate shown by arrows; and (H) methane hydrate recovered from the fractures.

like grazing, filter-feeding, predation, and scavenging. Additionally, Sasaki *et al.* (2010) reported the presence of symbiotic bacteria intracellularly in the ctenidium, on the exterior of the gill, and fine-grained pyrite grains in the diminished digestive system indicating possible chemosynthetic feeding habit as well.

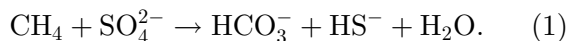
Large-sized (up to 15 cm long) relict shells of *Calyptogena* sp. (figure 4F) are recorded from the study site. *Calyptogena* shells are also present as part of carbonate chemoherm in association with the tubeworms. In contrast, *Bathymodiolus* shell fragments were scarce; *Calyptogena* sp. are chemosynthetic organisms and use H_2S for the production of energy and body mass following the haemoglobin- H_2S - O_2 - CO_2 biochemical pathway commonly observed in thiotrophic chemosynthesis as discussed for the tubeworms (Dupéron *et al.* 2013). More than 60 species of *Calyptogena* are reported from the cold-seep and vent regions (Sibuet and Olu 1998; Barry *et al.* 2007); *Calyptogena* sp. may grow at a rate >4 cm year⁻¹ at some locations (Turekian and Cochran 1981; Turekian *et al.* 1983). Earlier, Mazumdar *et al.* (2019) reported the presence of large *Calyptogena* shells from cold-seeps off the K-G basin.

4.2 Occurrence of methane hydrate, interstitial H_2S , and role of AOM

Methane hydrate was observed as fracture fillings within the sediments (figure 4G and H). The thawing of methane hydrate in the network of cracks results in the brittle and fragmented nature of the muddy sediment. The presence of ethane and propane along with methane in the hydrate phase and $\delta^{13}C_{CH_4}$ values (-28.4 to -79.5 : Mazumdar *et al.* in prep.) suggest a contribution of deep-seated thermogenic methane likely transmitted through fault-fracture systems. Thermogenic methane in the surface sediments was earlier reported by Rasheed *et al.* (2014) from the SW end of the Mannar basin. The remarkable range of the $\delta^{13}C_{CH_4}$ values of the methane-hydrates shows a complex system characterized by micro and macro fractures responsible for advection of thermogenic gases ($\delta^{13}C > -50$ ‰ VPDB: Whiticar *et al.* 1999) and production of biogenic methane (< -50 ‰) below the SMTZ (~ 30 – 35 cmbsf). The bottom water P-T conditions based on the CTD data support the stability of methane hydrate within the sediments.

High concentrations of hydrogen sulfide (3800–12932 μM : Mazumdar *et al.*, in prep.) are

reported below the sediment–water interface. The production of hydrogen sulfide in the sediment can be explained by microbially mediated sulfate reduction processes dominated by anaerobic oxidation of methane pathway (Knittel and Boetius 2009) represented by equation (1):



The HCO_3^- ion is consumed by the precipitation of CaCO_3 (equation 2) and forms the chemoherm (figure 5A and B).



The interstitial HS^- (H_2S) is consumed via multiple pathways, e.g., (i) precipitation of Fe-sulfide or sulfurized organic matter in the sediments, (ii) consumption by chemosynthetic organism including microbial mats, and (iii) reoxidation at or above the sediment–water interface via oxidative recycling to $\text{S}^0/\text{SO}_4^{2-}$ using oxidants like O_2 and NO_3^- (Fernandes *et al.* 2020; Volvoikar *et al.* 2020).

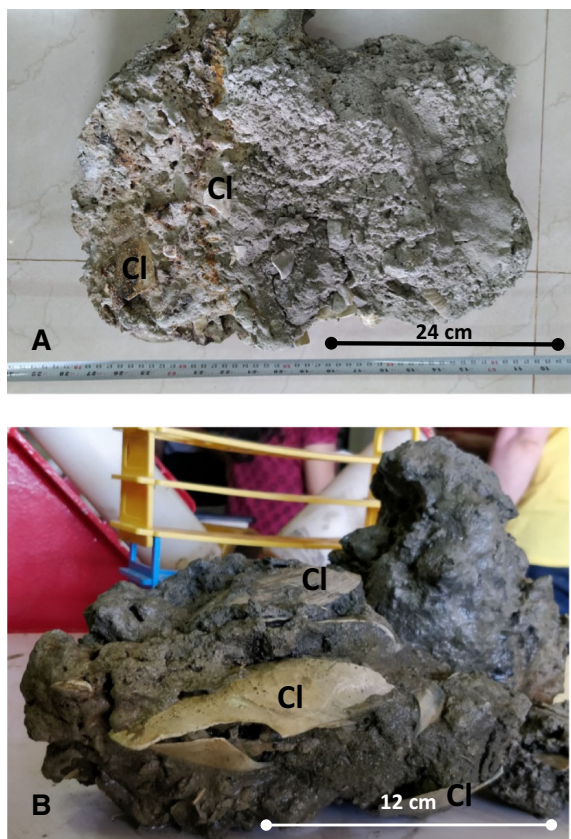


Figure 5. (A, B) Authigenic carbonate crust (chemoherm) with embedded *Calymptogena* shells (CL).

4.3 Association of tubeworm and carbonate crust

The association of the tubeworm with hard substratum (carbonate crust: figures 2A, 5A and B) may be attributed to the settling of larval vestimentiferans gregariously on exposed rocks which eventually form dense colonies (Fisher *et al.* 1997). The roots of the tubeworms extend deeper below the hard substratum, where H_2S concentrations are enough for their sustenance. The posterior end of the tubes is reported to be thin ($\sim 70 \mu\text{m}$) and quite permeable (permeability coefficient at 20°C of $0.41 \times 10^{-3} \text{cm s}^{-1}$) to H_2S (Julian *et al.* 1999). It is interesting to note that although plenty of large shells could be recovered (figure 5A and B), no live *Calymptogena* sp. could be found along with the tubeworm. The lack of live *Calymptogena* sp. and the absence of active gas flare suggest low H_2S concentration near the sediment–water interface which is essential for sustenance of the *Calymptogena* to survive and grow. However, the tubeworm's posterior part could penetrate to the depth below the seafloor ($\sim 30\text{--}40$ cmbsf) where H_2S is in sufficient concentrations for growth and proliferation of the tubeworms. Association of tubeworm, carbonate bioherm and *Calymptogena/Bathymodiolus* have also been reported globally (Teichert *et al.* 2005; Bayon *et al.* 2009; Bowden *et al.* 2013; Feng *et al.* 2013).

5. Conclusion

We report for the first time presence of *Lamelli-brachia* sp. and associated chemosynthetic ecosystem from the Indian Ocean. The chemosynthetic fauna associated with the methane cold-seeps and shallow hydrate were discovered from the Mannar basin located between India and Srilanka. The tubeworms are attached to the authigenic carbonate crust enriched with large relict shells of *Calymptogena* sp., a chemosymbiont bearing bivalve. Squat lobsters and gastropod belonging to the *Munidopsis* sp. and Buccinidae family, respectively, are integral components of the chemosynthesis-based ecosystem. The *Lamelli-brachia* polychaete also bears sulfide oxidizing endosymbionts in their trophosome which is responsible for the energy and body mass synthesis. High concentrations of H_2S at some depths below the sediment–water interface are responsible for the sustenance of the tubeworms based on the chemosynthesis based ecosystem.

Anaerobic oxidation of methane coupled with sulfate reduction in the sediment is responsible for the interstitial H₂S generation. Carbon isotope ratios of methane and the presence of ethane and propane in the headspace gas suggests a mixing of thermogenic and biogenic methane at the study site. A detailed RoV-based survey would be essential to understand the distribution of the chemosynthetic communities and their relationships to geological and chemical properties of the cold-seep sites.

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Author statement

AM carried out result interpretation, manuscript preparation; PD interpreted geophysical results and contributed to manuscript preparation; AP, FB, MS, KS, JM, AG, AZ, SPKP, UC, CKM, WF, AT, and TP participated in onboard sampling and onshore analyses.

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