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Occurrence of faecal pellet-filled simple and composite burrows in cold seep carbonates: A glimpse of a complex benthic ecosystem

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Abstract

Ichnofossils preserved in marine sedimentary records provide unique information on various activities (feeding, dwelling, excretion etc.) of benthic organisms. Here we report faecal pellet-filled tubular (simple and composite) burrow casts from cold seep carbonate layers (16-18 mbsf) deposited at least 46-58 kyr ago in the Krishna-Godavari basin, Bay of Bengal, India. Deposition of these chemosynthetic clam bearing authigenic carbonate sediments with highly depleted carbon stable isotope ratios indicates methane expulsion that resulted in the development of a cold seep ecosystem. Although cold seep communities are extensively reported from the rock record and modern seep sites, hardly any information is available on burrowing activity of the seep biota. Our findings open up a window for future investigation of the ecological significance of such burrows.

Keywords: Cold seep carbonate, Ichnofossil, Composite burrow, Faecal pellet, Krishna-Godavari Basin.

Introduction

Marine cold seeps are characterized by expulsion of fluids enriched in methane, hydrogen sulfide (HS⁻) and bicarbonate (HCO_{3⁻}) from the seafloor which results in the precipitation of calcium carbonates and pyrite at or below the sediment water interface (Hovland et al., 1987; Kulm and Suess, 1990). Enrichment in HS⁻ and HCO₃⁻ concentrations in the pore fluids is brought about by anaerobic oxidation of methane (AOM) performed by syntrophic consortia of methanogenic archaea and sulfate-reducing bacteria (Boetius et al., 2000; Orphan et al., 2001). Cold seeps constitute a complex ecosystem encompassing diverse faunal groups which include chemoautotrophs like sulfideoxidizing bacteria (Beggiatoa, Thioploca, Arcobacter, Thiothrix), chemoautotrophic symbiontbearing bivalves (from the families Solemyidae, Vesicomyidae, Lucinidae, Thyasiridae, Mytilidae), tubeworms (Vestimentifera and Pogonophora), Gastropods (e.g. Provannidae and Neolepetopsidae) and heterotrophic seep and non-seep fauna including decapod crustaceans, polychaete annelids, gastropods and echinoderms (Paull et al., 1984; Sassen et al., 1993; Barry et al., 1997; Sibuet and Olu, 1998; Fisher et al., 2000; Levin, 2005; Martin and Haney, 2005; Cordes et al 2007; Han et al., 2008; Quiroga and Sellanes, 2009). Chemoautotrophy involves oxidation of reduced inorganic compounds like hydrogen sulfide for energy and fixing of carbon molecules from CH₄ or CO₂ into organic biomass (Dubilier et al., 2008; Stewart et al., 2005). Hydrogen sulfide flux play an important role in structuring the community composition around cold seeps (Sahling et al., 2002).

Information on traces of activities (dwelling, feeding, excretion etc.) of cold seep associated benthos are sparse from present and past geological records (Campbell et al., 2002; Campbell et al., 2010). Systematic studies of such trace fossils preserved in seep-associated sediments will shed light on mutual interactions and ecological evolution of seep benthos. Recently, cold seep carbonate layers that are at least 46 to 58 kyr old, have been reported from a core (MD161/8 @16-18 mbsf: Fig.1) in the Krishna-Godavari Basin (K-G Basin), Bay of Bengal (Mazumdar et al., 2009). Genesis of these cold seep carbonates has been attributed to the anaerobic oxidation of methane (AOM) close to sediment water interface during the methane expulsion. In the present work we report occurrence of hitherto unreported pellet-filled simple and composite burrow casts from these cold seep carbonates. We have attempted to link these structures with benthic biological activities at this paleo-cold seep site.

Geology

The K-G basin is a peri-cratonic rift basin located in the middle of the eastern continental margin of India. The maximum sediment thickness in the K-G basin reaches as much as 8000 m (Prabhakar and Zutsi, 1993). The Krishna and Godavari rivers supply the bulk of the detrital

sediments to the basin. The smectite-bearing Godavari Clay Formation constitutes the Holocene-Pleistocene deposit of the K-G basin. Numerous shale diapirs, have been identified in the K-G basin offshore. Upward movement of the shale diapirs have resulted in folding and faulting of the overburden sediment facilitating movement of fluid enriched in methane and other lighter hydrocarbon gases (Rao and Mani, 1993; Mazumdar et al., 2009; Dewangan et al., 2010). The study area lies within the continental slope region of the K-G basin (Fig.1). The core (MD161/8) was collected on board *R/V Marion Dufresne* (MD-161: May, 2007) using a Giant Calypso piston corer at a water depth of 1033 m (latitude =15° 51.8624' N and longitude = 81° 50.0692' E). The core is located directly on the top of a diapiric structure.

Method

Carbonate tubular structures were washed in an ultrasonic bath and photographed for mesoscopic description. Petrographic thin sections of the tubules were studied with a polarized light microscope (Leica DMLP, Germany). Mineralogical identification was carried out using a Philips X-ray diffractometer (PW1840, Netherlands). 14 burrow filled carbonate samples were run from 25 to 32° 20 at 1°/min scan speed using CuK α radiation ($\lambda = 1.541838$ Å). MgCO₃ content in the carbonate samples was determined following Goldsmith and Graf (1958). A Scanning electron microscope (JEOL JSM-5800LV, Japan) was used for micro-structural studies of the carbonate pellets. Carbon and oxygen stable isotope ratio measurements of carbonates were carried out using a Thermo-Finnigan (Germany) Delta Plus continuous flow isotope ratio mass spectrometer attached with a Gas Bench II. The external precision calculated is typically 0.07–0.09 ‰ VPDB for δ^{13} C and 0.06–0.12 ‰ VPDB (Vienna Pee Dee Belemnite) for δ^{18} O. NBS-18 and NBS-19 were used as standards. Quantification of chromium reducible sulfur (primarily pyrite sulfur) was performed following gravimetric methodology (Canfield et al., 1986).

Results

Tubular casts of burrows packed with pellets are shown in figure 2. Diameters of the tubes vary from 4 to 17 mm. Most of the burrow casts are in the form of single straight tubes (Fig. 2 a-f) or interconnected paired-tubes (Fig. 2 g) with appendages (arrows in Fig. 2b to g) of diameter 0.5 to 4 mm running parallel to the primary burrow surfaces, protruding out from the burrow casts at variable angles or having root like branching. These appendages are either homogenously filled with micrite or with pellets. Bifurcated (Fig. 2 h, i) tubular burrow casts are also present. Filled tubes with speites are occasionally observed. (Fig. 2 j and k). Polished, transverse cross sections (Fig. 2 l) of the burrow casts show uniform pellets filling without any discernible inner burrow wall.

The pellets filling up the burrows are ellipsoidal (Fig.2 and Fig. 3a and b) in shape and the long axes range in size from 700 to 2000 μ m. The long/ short axis ratio (L/W) ranges from 2 to 2.5 (Avg = 2.3±0.20). Pellets show deformation due to compaction (Fig. 3a), and do not have differentiated internal structures. They are composed of microcrystalline (Fig. 3 b) high magnesian calcite (MgCO₃ content ranges from 11 to 19 mol%: Table 1). Scattered and clustered pyrite framboids (7-20 μ m) are recorded within the pellets (Fig. 3 c). The inter-pelletal void space is filled with framboidal pyrite (20-25 μ m) and carbonate cement (Fig. 3 b, d). Pellets have an external sheath like coating (Fig. 3 e, f) which apparently extends within the pelletal groundmass, forming a network (Fig. 3 f). Ribbon shaped filaments, ~400 μ m long, are found adhered to the pellet surface and associated with the pyrite crystals (Fig. 3 g, h and i). The $\delta^{13}C_{carb}$ and $\delta^{18}O_{carb}$ of the carbonate pellets varies from -45.1 to -52.4‰ and 3.3 to 4.9‰ VPDB (Table 1). Except for one sample (8/12A), chromium reducible sulfur (CRS wt %) varies from 0.02 to 0.2% (Avg. = 0.2±0.0.3%: Table-1).

Discussion

Shape, uniformity of size, composition and association with burrows (Flügel, 1982; Scholle and Ulmer-Scholle, 2003; Flügel, 2004) suggest faecal origin for the pellets reported in this study. A thin sheath, coating the pellets (Fig. 3 a, e and f) possibly represents mineralized peritrophic membrane (PTM) (Forster, 1953; Kennedy et al., 1969; Martin et al., 2006). The intrapelletal extension (Fig. 3 f) of this external sheath provides support and strength to the soft and fragile pellets.

The fossilized microbial structures preserved on the surface of the faecal pellets (Fig 3 g, h and i) appear similar to filamentous structures that Han et al.(2008) suggested may represent sulfide oxidizing bacteria. Association of inter-pelletal pyrite framboides and possible sulfide oxidizing bacterial fossil suggest percolation of hydrogen sulfide enriched fluid through inter-pelletal pore space. AOM results in the enrichment of HCO_3^{-1} and HS^- ions in pore fluids (Eq.1 and 2) resulting in the intimate association of isotopically depleted authigen high magnesian calcite with $\delta^{13}C$ ranges from -45.1 to -52.4‰ VPDB and pyrite (Table-1) at or below the sediment water interface (Kulm and Suess, 1990).

$$CH_4 + SO_4^2 \rightarrow HCO_3^- + HS^- + H_2O$$
(Eq. 1)
$$Ca^{2^+} + HCO_3^- \rightarrow CaCO_3 + H^+$$
(Eq. 2)

Apparently, the faecal pellets were produced by burrowing organisms thriving on the carbonate sediments for food including organic particulates, bacteria/ archaea etc. Flügel (1982), Flügel (2004)

and Tucker et al. (1990) suggested that the burrowing organisms on carbonate platforms, ingest the carbonate mud, digest required organic component from the mud and excrete the non-digested limemud in the form of well rounded pellets.

The pellet filling gives a pustular appearance to the burrow surfaces, except for the samples in figures 2 e and g, where a thin carbonate layer masks the pelleted surface. The pelleted burrows resemble Ophiomorpha (Häntzschel, 1975; Seilacher, 2007), a pellet-walled burrow created as a fodinichnial structure by deposit-feeding decapod crustaceans in particular callianasid shrimp. However, unlike *Ophiomorpha*, the burrow casts in this study do not show a discernible smooth inner burrow lining. Moreover, the homogenous faecal pellets reported here are markedly different from the internally structured crustacian pellets (Favreina and Palaxius:: Kennedy et al., 1969; Senowbari-Daryan et al., 2007). Lack of meniscus or horizontal stacking pattern of pellets suggest passive filling of the pellets in the burrows. Faecal pellets were probably thrown out of the burrow during digging and feeding activities and later got redeposited (back filling) inside the burrow once the organisms vacated the space or constructed new burrows (Seilacher, 2007). We have recorded three types of chemosynthic bivalves (Supplementary Fig. 4) belonging to the genera Calyptogena, Lucinoma and Vesicomaya from the carbonate rich layers. Chemosynthetic bivalves are known to burrow into sediments for hydrogen sulfide (Paull et al., 2005). However, it is difficult to attribute production of faecal pellets to burrowing activities of such bivalves, since they have rudimentary or no guts and survive on chemosymbiosis. In the absence of definite evidence, we tentatively attribute the burrow and pellet forming activities (dwelling and/ or feeding) to polychaete worms and/or small crabs. Fragments of *Diplocraterion* (Seilacher, 2007) like traces in Figure 2 j and k possibly represent activities of polychaetes (Cornish, 1986).

Different types of composite ichnofossils (Fig. 2 b, c, d, e, f, g) are recorded in this study. Composite ichnofossils are the result of superimposition of activities of successive or commensal communities of endobenthic organisms reworking the same sediment (Bromley and Ekdale, 1986; Gingras et al., 2002). Probing for nutrients, competition for space and adaptation to environmental conditions (sedimentation, oxygen/ H₂S availability etc.) influence the nature of composite burrows. Composite trace fossils can provide important information on behavioral ecology of primary and secondary tracemakers as well as environmental changes through time (Bromley and Ekdale, 1986; Pickerill, 1994; Gingras et al., 2002). *Chondrites* penetrating preexisting burrow fills in figure 2 e and f may be attributed to feeding activities of polychaete worms. Burrowing was probably carried out to utilize the nutrients (Vaugelas and Buscail, 1990) in the faecal pellets produced by the primary tracemaker. *Chondrites*-reburrowed *Thalassinoides* and *Diplocraterion* are known from geological records (Bromley and Frey, 1974; Seilacher, 2007). The secondary side tunnels (Fig. 2 g) connecting

the paired burrows and spike like protrusion may suggest probing for food by secondary tracemakers. Figure 2 b, c and d possibly indicate composite of multiple burrows by juveniles with a burrow of an adult (De, 2000).

Conclusion

The present study shows definite evidence of intense burrowing and pellet forming activities by benthic fauna thriving in paleo-carbonate sediment deposited via anaerobic methane oxidation process in Krishna-Godavari Basin, Bay of Bengal. Composite nature of the trace fossils reported here is indicative of a complex ecosystem. The burrowing organisms consumed the organic matter including bacterial/ archaeal biomass in the sediment. However, with the limited information it is difficult to attribute the burrows to specific faunal groups. We suggest that the application of techniques like polyester resin casting (Gingras et al., 2002) of burrows as well as computer aided image enhancement tools in spade-cores collected from present day cold seep sediments, may shed light on ecological relationship between components of composite traces and possibly the organisms responsible for the production of the burrows and faecal pellets.

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Figure and table captions

Figure 1. Study area in Krishna-Godavari basin, Bay of Bengal. Core location is demarcated by star.

Figure 2. Morphology of faecal pellet-filled carbonate burrow casts recovered from cold seep carbonates from Krishna-Godavari basin. (a) Single carbonate tube, (b, c & d) Carbonate tube with pellet filled tubular appendages (arrows) parallel to the burrow surface Note the composite of a wide (black arrow) and multiple narrow carbonate burrow casts in 'd'(three white arrows), (e & f) Burrow casts with *Chondrites* like structure penetrating the burrow fill, (g) Paired- burrow tubes interconnected by narrow tubules, (h) Burrow cast showing bifurcation, (i) Magnified inset in 'h' showing faecal pellets, (j & k) Carbonate tubes showing spreites like structures (arrows), (l) Polished cross section of burrow cast showing homogenous pellet filling and absence of any inner burrow wall.

Figure 3. Morphology and texture of the carbonate faecal pellets. (a) Faecal pellets showing deformation due to compaction (arrow). Partially detached thin sheath is the peritrophic membrane, (b) Photomicrograph of faecal pellets in transmitted light (crossed polars) showing pyrite feeling (arrow) in the intrapelletal space, (c) Back scatter image of intrapelletal framboidal pyrite (arrow), (d) Back scatter image of pyrite framboid cluster filling up the pore spaces between the pellets (magnified inset in a). (e) SEM image of faecal pellet showing calcite crystals (white arrow) and peritrophic membrane (black arrow), (f) Intrapelletal extension of the peritrophic membrane (magnified inset in e), (g, h & i) Filamentous bacterial fossils (arrows) resembling sulfide oxidizing bacteria.

Table-1. MgCO₃ content (mol %), carbon and oxygen stable isotopic composition of some carbonate burrow casts. nm = not measured, nd = not detectable.

Supplementary Figure 4. Chemosynthetic clam shells associated with cold seep carbonates in Krishna Goavari basin. **a & b**, *Calyptogena sp.*, **c**, **d** & **e**, *Vesicomaya sp.*, **f**, *Lucinoma sp.* Note drill hole in A and C (arrows) suggesting predatory activity by gastropods.





















Figure 2











500 μm

100 µm



50 µm

100 µm

200µm



400 μm

d

e







Figure 3













Suppl. Figure 1

Table-1

Sample Number	Depth (m)	MgCO ₃	CRS wt%	δ ¹³ C ‰	δ ¹⁸ O ‰
		Mol (%)		(VPDB)	VPDB
8/12A	11.05	11	1.1	-45.7	4.8
8/13	12.10	17	0.2	-45.5	4.3
8/15	14.05	12	0.2	-52.4	4.6
8/16B	15.00	14	0.1	-47.8	4.3
8/18A	17.05	19	0.2	-45.1	4.5
8/18B	17.05	16	0.02	-45.5	4.8
8/18F	17.40	11	0.1	-46.0	4.9
8/18H	17.50	14	0.2	-46.0	4.7
8/18K	17.65	16	0.02	-49.8	4.2
8/18L	17.70	18	nd	-51.2	4.5
8/18Q	17.95	18	0.2	-51.5	4.3
8/19A	18.05	nm	0.2	-50.2	4.2
8/19B	18.05	10	nd	-48.0	3.3
8/20A	19.55	nm	nd	-52.4	4.5