

Animal-Sediment Relationship of the Crustaceans and Polychaetes in the Intertidal Zone Around Mandvi, Gulf of Kachchh, Western India

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Abstract: Animal-sediment relationships of two benthic communities (Crustaceans and Polychaetes) were studied around Mandvi coast in the Gulf of Kachchh, Western India. This coast consists of many micro-geomorphic landforms in which benthic communities are inhabited and select their niches and produce endemic biogenic structures. Five intertidal subfacies have been described and four types of grounds are identified, based on substrate consistency. 18 species of crustaceans, 15 species of polychaetes and unsegmented worm nemertea have been identified. Crustacean behavioural activities were observed in dunes, beaches and ridge-runnel in the form of burrowing, pellet making, feeding and crawling traces. Pelleted wall lining burrows of the suspension feeder stomatopodean species of *Oratosquilla striata* are also abundant in runnels. Motile, deposit feeder polychaetes are abundant on the ridges and are occasionally found on the lower reaches of the beaches, while suspension and filter feeders are found in the runnels. Lagoons consist of mainly grouped funnel branched burrows of *Oniphus eremita* which is identical to ichnogenus *Balanoglossites*. Nemertea, which are opportunistic algal grazers, have exploited restricted niches for dwelling-feeding purposes and constructed vertical burrow with pentamerous conical mound. The shore platform consists of cemented, calcareous tubes of filter feeder *Serpula* along with symbiotic encrusters like *Ostrea* and barnacles. Ichnocoenoses are discussed and three-dimensional ichno-sedimentologic models are reconstructed for Beach, Ridge, Runnel and Lagoon of the Mandvi intertidal zone.

Keywords: Bioturbation structures, Intertidal facies, Substrate consistency, Mandvi coast, Kachchh.

INTRODUCTION

Animal-sediment relationship is the study of interaction between the organisms and sediments, where the organisms alter the original sediment fabric to serve a wide spectrum for essential requirements of their life, like respiration, feeding, reproduction and protection (Bromley 1996). These sediment-processing activities of animals in turn form bioturbation structures (tracks, trails burrows and borings), in which animals may spend the entire or part of their life. These structures are autochthonous in nature, having wide environmental implications that help in understanding the behavioral and ecological pattern of endemic animals. The behavioural activities of the two benthic animal groups, viz. crustaceans and polychaetes were studied which clearly demarcate their usefulness in understanding the neoichnologic constraint of the intertidal environment. A close examination of the biogenic sedimentary structures helps in determining the various micro-environments within the intertidal zone.

The previous workers have studied about sedimentation, geomorphology and neotectonic activity of the Kachchh coastline (Glennie and Evans, 1976; Kar, 1993; Chauhan et al, 1993) and passing remarks were made on occurrence of crustacean burrows (Glennie and Evans 1976, and Kar 1993). Patel and Desai (1999) and Desai (2002) have documented the various biogenic structures of crustaceans and polychaetes from the tidal flat environment of Mundra and Manvi area. Patel et al. (2001) and Desai and Patel (2008) have also given ichnological evidences for delineating the seismic and tectonic activities of the coastal area. The prime objective of the present work is to observe, record, examine and analyze the bioturbation structures in the light of their trace makers (Crustaceans and Polychaetes), from the different micro-geomorphic units of the intertidal zone.

LOCATION

The study area is near the historic port of Mandvi

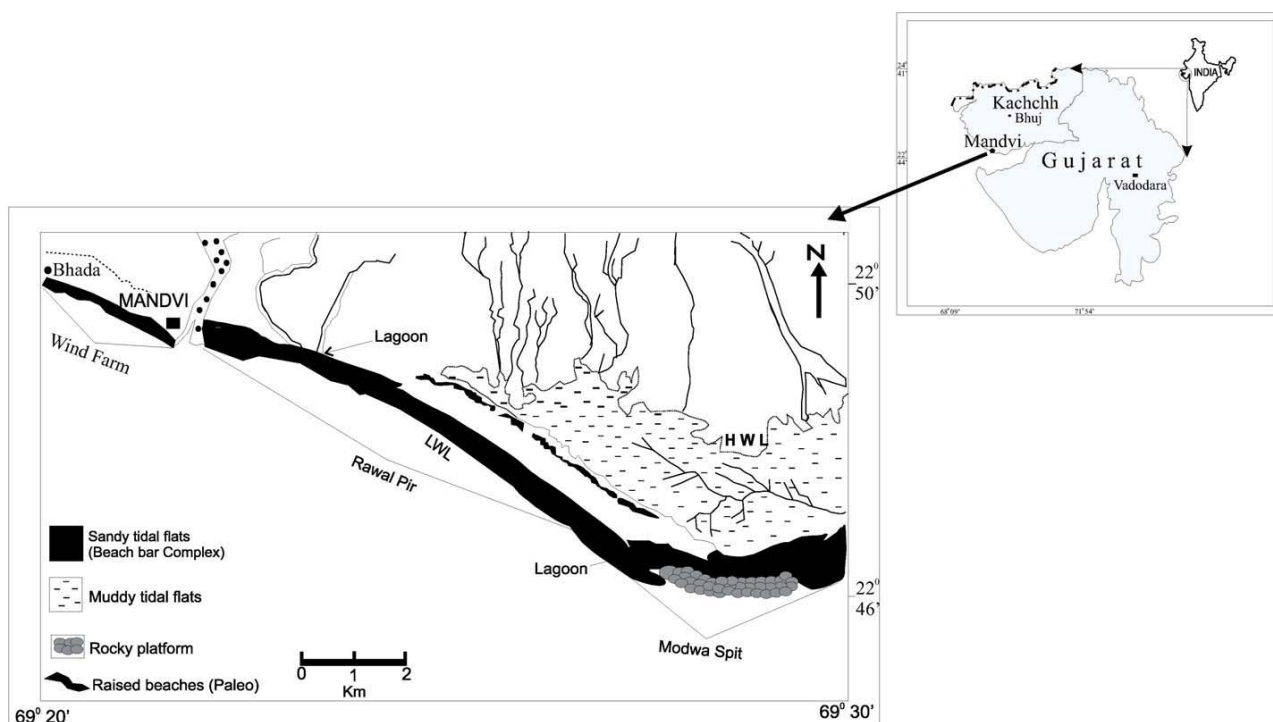


Fig.1. Location map and site map showing general geology of the study area.

(Fig.1), stretching between 22°50' N and 22°46' N latitude and 69°18'E and 69°30' E longitude. Mandvi intertidal zone is reasonably wide and situated on the mouth of the Gulf of Kachchh; the western part is influenced by open sea while the gulf environment influences the eastern part. Due to differential control of the marine agencies and offshore bathymetric configuration, the intertidal zone registers different micro-geomorphic facets. Considering the geomorphologic features, the area is divided into three zones which include- Wind Farm, Rawal Pir and Modwa Spit sites (Fig.1).

TECHNIQUES

An important approach in studying animal-sediment relationship is 'Natural History Approach' which involves field observation of the burrowing organisms. The second approach is similar to the first but is related to function of the animals that alter the sediments. Apart from these two approaches, a variety of experimental approaches have also been made for studying bioturbational and physical sedimentary structures. Various techniques employed for this study include: grain size analysis, relief peels, coring (PVC tube cores, box cores and plate cores), X-ray radiography, burrow cast and photographic documentation.

GEOMORPHOLOGY

The study area falls in the crescent shaped coastline where a variety of coastal landforms are developed, viz., tidal mudflats, raised beaches, and sealed river mouth, spits, ridge-runnel systems, stabilized and non-stabilized dunal area, lagoons and alluvial plains. The coastline consist of minor cusps along the seaward margin of the beach and beach cusp features, which are produced by superposition of the processes operating in the intertidal zone with different scale of motions (Dolan et al., 1974). The developed features are governed by the reactivation of the E-W regional fault in the Gulf of Kachchh and reflect the regional trend of the shelf edge (Chauhan et al. 1993). Other factors that are responsible for the development of the crescent coastal landforms are the waves, which are normal to the straight coast and make an impact against the curved coast.

SEDIMENTOLOGY

Exposure Index

In Mandvi region, tides are of semi-diurnal type, the intertidal zone is separated into five distinct zones known as critical tide levels -CTL's (Doty, 1946, Swinbanks and Murray; 1981), based on discrete exposure. There are four CTL's defined by higher high water (HHW), lower high water (LHW), Higher Low Water (HLW) and lower low

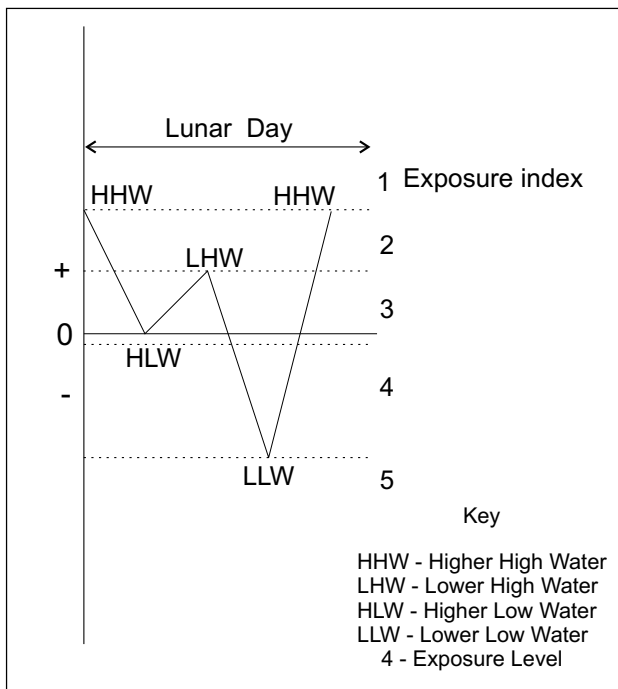


Fig.2. Five levels of exposures possible for semi-diurnal tides (after Swinbanks and Murray, 1981).

water (LLW), which subdivide the intertidal region on that day into five (Level-1= above HHW; Level-2= between HHW and LHW; Level-3= between LHW and HLW; Level-4= between HLW and LLW; Level-5= below LLW) discrete levels (Fig.2).

Grain Size Variations

Striking differences are observed in grain sizes across the coast but it displays uniformity along the coastline. Grain size decreases across the intertidal zone from beach to lowest exposed bar in the CTL's level-5. The beach samples show coarse to medium sand size which decreases from fine sand to coarse silt. No sediment variation occurs along the coast from Mandvi to Modwa Spit site but the locally high proportion of silt-clay, is due to exposure of paleo-mud in the runnels of the intertidal zone. There is a marked difference in the grain size of the ridges and runnels. The ridges show decrease in grain size across the intertidal zone and are moderately sorted while runnel sediments are poorly sorted and show wide range of grain size from gritty to fine silty mud.

Intertidal Facies

A particular suite of sediment textures along with physical sedimentary structures and geomorphic settings distinguish the intertidal facies. Across the intertidal

zone, the waves and currents play an important role for transporting and redistributing the sediments along the coast and help in forming distinct boundary between the facies. Broadly, based on micro-geomorphic features, the intertidal zone comprises beach sub facies, ridge sub-facies, runnel sub facies, lagoonal sub facies and supratidal sub-facies which are described below.

Beach subfacies: Beach environment corresponds to the CTL's exposure level 1 and 2, with sediments ranging from sandy gravel to gravel. The dominant structures are planar laminations dipping gently seaward, with low-angle discordance representing adjustment of the beach to changes in wave regimes or sediment supply. In high wave energy regimes, parallel laminated sand is deposited under intense bottom shear (Kumar and Sanders, 1976). Heavy minerals tend to be concentrated in discrete laminae, often alternating with other sand layers. Cores from the beach of Modwa Spit site show development of crude laminations, with 55-65% moderately sorted coarse sand. Inclusive graphic standard deviation of the beach sands varies from very poorly sorted 0.202 to moderately well sorted-0.6. Beach facies also consist of various structures that include air trap structures, sand dome, bubble sand layers etc (Patel et al. 2002), mega ripples with planar cross-stratification and larger scattered burrows of beach-dwelling adult crustaceans.

Ridge subfacies: Ridge environment is very similar to the beach environment, except that in CTL's exposure index it corresponds to the levels 2, 3, 4, in accordance to the nearness to the low water line. This sub-facies is found where fine clastic sediment influx into the littoral zone is high and occurs as linear, mound-shaped ridges, roughly paralleling the coast (Stapor, 1975). In the study area, such conditions are met at Rawal Pir site where there is a sudden decrease of the flow conditions as compared to the Wind Farm sites, resulting in high influx of sediments. Planar laminations are essential components, formed as a result of upper or lower flow regime conditions, depending upon the water depth and wave conditions with fluctuating tidal cycles. The proportion of fine grained sands and silts increases towards the seaward ridges. Occasionally, it also consists of armored mud balls. Clean, medium grained sands are the essential components for the ridge; the graphic mean size ranges from coarse to fine sand (-0.1 Mz to 2.2 Mz); inclusive graphic standard deviation varies from -0.394 (poorly sorted) to -0.6 (well sorted). Physical structures are obscured due to intense bioturbation by the crustaceans, polychaetes, bivalves, gastropods, etc.

Runnel subfacies: Runnel system is unique, interfringing with the ridges and often behaves as a unidirectional flow system during low tide conditions. During high tide conditions, it is dominated by bi-directional and oscillatory flow conditions. The runnel facies can be delineated by poorly sorted grain size (-0.053 to 0.16) often ranging from muddy to gravelly sediments. This is on account of the fines settling during the draining of the runnels at low tides, coarser accumulating during high tides and by rill erosion of the beaches/ridges. It is characterized by accumulation of the pebble lag deposit in the neck of the channel and is assumed to be the result of strong current velocity, enough to plane off the bottom (Carter, 1986). When runnel turns to meet an outlet channel, a triangular zone can occur in which a sequence of seaward asymmetric oscillatory ripples have formed. Sometimes due to saturation of the grains of the ridges, the steep side collapses and forms a micro-delta, which also contributes sediments into the runnels. Runnels also preserve various types of ripple marks in the form of stratification and also large scale, ebb oriented, megaripples and flaser beddings. With decreasing water depth (increasing flow regime), the following bedforms are observed, (1) straight crested, asymmetrical wave ripples, (2) undulatory crested wave ripples and (3) lunate ripples towards the center of the runnels. The bioturbational structures are chiefly of suspension and deposit feeding organisms and tubicular animals often aligning themselves to the flow directions.

Supratidal subfacies: Supratidal facies is developed and corresponds to the CTL's exposure level-1, which is rarely submerged, or exposed for more than 5 continuous days in a tidal cycle. The sediments are composed of fine to medium sand size, with good sorting, generally because of saltation process in dunes. This facies is very well developed all along the coast, dominated by dune accumulations. *Wind Farm site:* fore-dunes have developed in the backshore zone; comprise of fine grained and very well sorted sediments; attain a height of about 10-12 m and show multi-stage of accumulations. *Rawal Pir site:* dunes developed on the tidal plains; show large-scale cross-laminations; on leeward side cross-laminations dip 20°-30° due souths. *Modwa Spit site:* vegetated dunes attaining heights of +17 m, along with small dunes, are developed on the backshore area. The small dunes are composed of moderately to well sorted fine grain sands and unbraided bivalve shells. The supratidal facies characteristically displays three distinct dune stages including shadow dunes, foredunes and mature dunes. Low coppice dunes, bare foredunes and vast supratidal salt marsh are the characteristics of the Modwa Spit site and consist of

medium to fine grained, sand size particles of well sorted nature, low dip, parallel or aeolian type cross bedding and variation of physical structures (Frey and Howard, 1988; Howard, 1972). This sub-facies is characterized by large size isolated crustaceans burrows.

Lagoonal subfacies: Two coastal lagoons occur as shallow water bodies parallel to the coast and are separated from the sea by sandbars. The Rawal Pir site lagoon consists of coarse to fine grained sands while the Modwa Spit site lagoon is characterized by medium to fine grained sands with muddy sediments. Both the lagoons consist of black peaty layer at shallow depth which is overlain by a variable thick sandy layer. In the absence of any inflow of the rivers into the lagoons, the development of the peat layers can be attributed to the development of algal and cyanobacterial growth. The sedimentary structures comprise of sand/mud interlayer along with sequences of wavy bedding and ripple marks. The sedimentary structures show presence of hummocky and swaley cross-stratification, which can be attributed to the peak, high tidal flow conditions. Interrupting this sequence are the layers of algal deposits, indicative of low tidal current and energy. Thick algal mats attract various algal-symbiotic organisms like *Turritella*, *Cerithium* and *Telescopium* and they also give refuge to many reducing environment-loving organisms like Nemertea, Bivalves, Crustaceans and Polychaetes.

SEDIMENT SUBSTRATE CONSISTENCY

A sediment substrate is an unconsolidated surface that allows the organisms to live in or on the surface. Four types of substrate viz. soupground, softground, firmground and hardground characterize the Mandvi intertidal zone and are exposed at the depositional interface. The sediment texture and its structures of the Wind Farm site indicate its deposition under relatively high current velocities and shifting bottom sediments containing small amounts of mud and organic matter. It is characterized by the sandy and silty sand type substrate. This is in contrast to the adjoining (Rawal Pir and Modwa Spit) areas where the current velocities decrease and more amount of organic rich mud is deposited. The ridge and runnel systems are developed giving rise to the wide range of substrate characteristics ranging from pure sand to muddy gravel, silty sand and sandy gravel. The Modwa Spit is characterized by sandy to sandy gravel types. All these substrates exercise a major control over the distribution and activity of crustaceans and polychaetes. The juveniles, young and adult species of the crustaceans share the same sediment but apparent grain size of the

substrate found is different for each of them. Their burrowing strategies are modified in order to cope with the different sediments of different substrate conditions, thus resulting in different biogenic structures. Along with the grain size, water content of the sediments is also important when organisms use it as a substrate.

BIOGENIC SEDIMENTARY STRUCTURES

In marine environment, benthic animals alter the surrounding habitat by burrowing, building tubes, feeding and defecating. As a result substrate landscape is in a constant flux with disturbance rates dependent on the abundance and activity of the organisms (Wilson, 1990). Depending upon the life style of an organism, it may require a given range of grain size for burrowing, feeding or tube building (Wieser, 1959) and this sediment range represents only a portion of the fitness curve for that organism (Levins, 1968). Recent biogenic sedimentary structures are classified according to the toponomic classification, along with taxonomic, ecological and stratinomic as suggested by Seilacher (1953). The taxonomic and ecological approach helps in identifying the tracemakers and their ecological constraints, along with the morphological characteristics of the lebensspuren. The stratinomic approach involves the relation of the trace with regard to the sediment.

CRUSTACEAN ACTIVITY

The observed crustaceans' behavioural activities in the intertidal zone are in the form of locomotion, burrowing, pellet making and grazing. Among crabs, *Ocypode* species are most common and one of the primary bioturbators while the stomatopodean crustaceans are generally found in the runnels.

Pellet Making Activity

These activities of the crabs are envisaged from the surficial spreads of pellets (Fig. 3a), which are constructed mainly for feeding purposes. Pellets are in different forms, shapes and sizes and scattered around the burrows of young and juvenile *Ocypodes* on the beach and bar. The fiddler crab feeds on freshly deposited sediment surface and non-ingested materials are thrown aside as rounded pellets (up to 3 mm). The adults are restricted near the high water line while the young and juveniles are found in ridge-runnel systems as well as near the low water line. The structures made by young and juvenile crabs consist of varying sizes of vertical, cylindrical burrows surrounded by feeding and fecal pellets. They produce variety of pelleted structures

like concentric, radial, asteroid, mossy and pellet-mat design in a sequence, arranging feeding pellets around their burrow. These pellets are usually rounded (up to 12 mm diameter), elongated, and flat top-shaped and rod shaped. The young *O. ceratopthalma* generally make elongated, asteroid design during the first few minutes of the exposure of the sediments during low tide (Fig.3b). *O. platyrsis* generally makes burrowing pellets, which are characteristically flat, top-shaped and arranges them around the burrow mouth in roughly asterical pattern (Fig. 3c). The pelleted mats formed by *O. ceratopthalma* and *O. roundata* in the runnel and ridges are generally 1-8mm thick and are composed of rounded pellets of uniform size, reflecting similar age group of crustaceans. The larger the burrowing pellets (Figs.3a and d) near the burrow opening also reflects the size of the burrowers (Figs.3e, f and g). During the burrow modification (Figs.3a and d), the adult *O. roundata* and *O. platyrsis* make large, elongated burrowing pellets, this is dumped around the burrow openings. *Uca* and *Macropathalma* are also important bioturbators but their abundance is less and can be recognized on the basis of their rod-shaped fecal pellets made from mud, along with internal ramification structures (Fig.3h).

Three different types of pellets are identified, viz. feeding pellets, burrowing pellets and rod-shaped fecal pellets, of which the rod-shaped fecal pellets (Fig.3h) if preserved in fossil records can be identified as *Faverina*. The pelletal structures, when covered with sediment show structureless fills of *fossitextura deformativa* type of bioturbation. Ethologically, these structures are classed under complex pascichnia-fodinichnia types.

Burrowing Activity

The burrowing activity of the crustacean is varied and consist of three specialized techniques, viz.- the back burrowing, side burrowing and the rotating burrowing. The purpose of burrowing can vary and may range from just temporary shelter to dwelling or to hide in order to predate.

The *Ocypodes* are very efficient burrowers along the beaches of the Wind Farm, Rawal Pir and Modwa Spit sites and construct three dimensional burrow systems similar to their fossil equivalent *Psilonichnus* and *Thalassinoides*. Their burrow occurs on the coastline extending from lower part of the intertidal zone to the dunes and supratidal environments (Patel and Desai, 1999). These structures are essentially characterized by three dimensional burrow system; cylindrical component of varying diameter, with smooth, unlined wall. Branched, burrows consist of shafts and tunnels which join at Y or T junctions and may be straight to slightly curved or twisted, with more than one oblique,

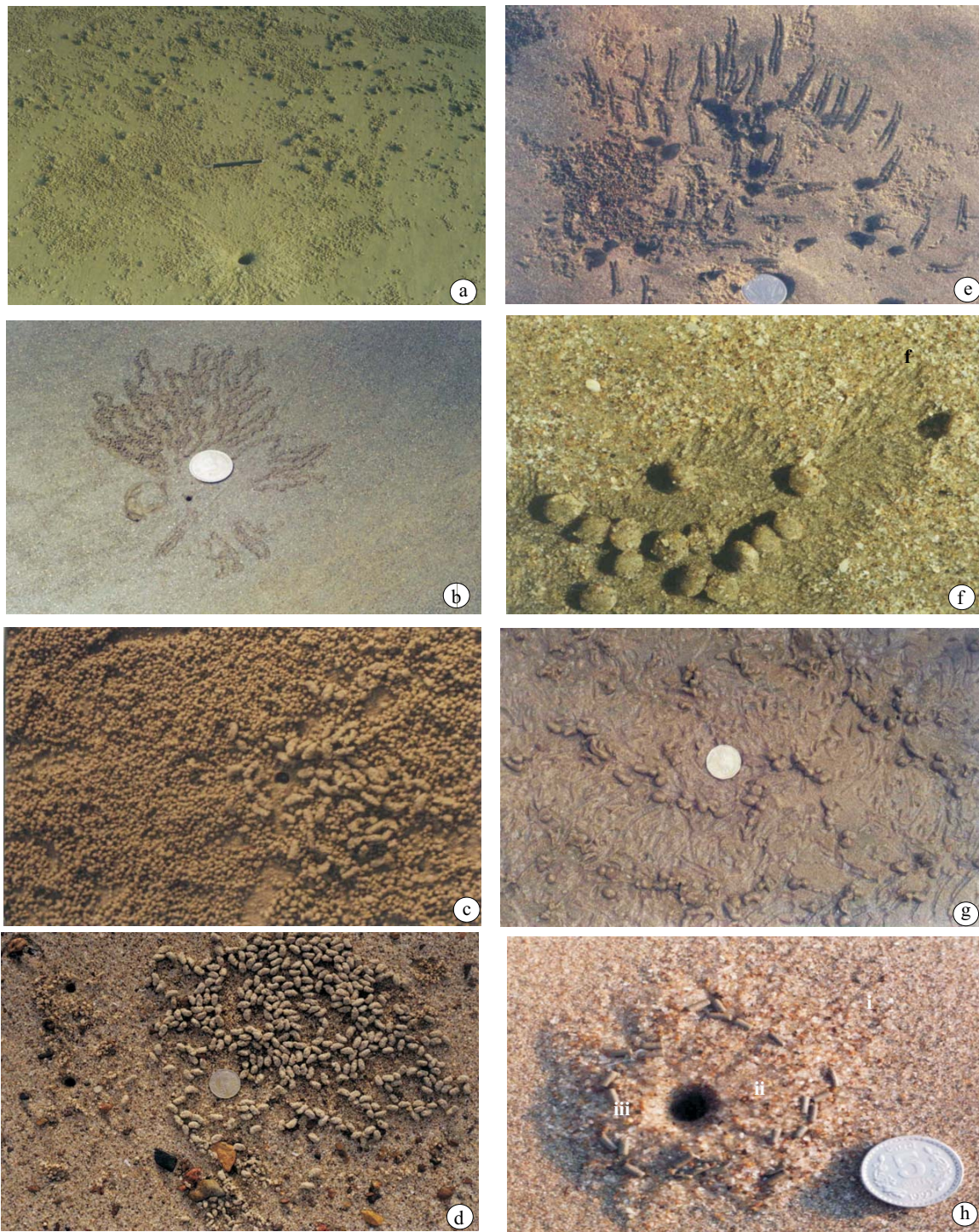


Fig.3. Different types of pellets, (a) Crustacean spread of Feeding pellets on the Intertidal zone. (b) Feeding pellets neatly arranged in strings around burrow opening. (c) Blanket of feeding pellets made by young crab species of *Ocypodes* at junction of ridge-runnel. The size and abundance of the pellets indicates population of crabs. The size of the burrowing pellets indicates two different age group of the species. (d) Cylindrical to elliptical burrowing pellets of *Uca marionis* (e) Grazing activity of crab around the burrow opening showing the scraping of the freshly deposited sediments. (f) Scratch marks of the chaela in coarse-grained sediments. (g) Paired scratch marks of the chaela during pellet making activity in the watery sediments. Note the grazing activity is more pronounced in the watery sediments. (h) Rod shaped fecal pellets, note three types of sediment (i) Surficial sediments (ii) clean sand brought and dumped around the burrow opening, (iii) fecal pellets, and a common element, which adds mud in the sand.

dead end branch. The burrow morphology of young and juvenile species are of cylindrical, smooth, unlined walled, straight and unbranched vertical shafts. *Ocypodes* burrows diameter shows considerable variation and decrease in burrow diameter towards the sea (Fig. 4a). The burrows near the sea are simple unbranched, while those near the supratidal region resemble to English letters Y, J, I and U, bifurcating in upward direction (Figs.5a and b) with their penetration, more than a meter deep.

Burrows of the *Ocypodes* consist of different types of sand mounds; the adult crabs make conical mounds along the beaches of Modwa Spit site (Fig.5c), a ridge with mound (Fig.5d) and paired mound (Fig.5e) which are nearly 45-55 cm away from the burrow opening and 10-20cm in height, and occurs on the seaward side. The inter-area of the burrow mouth and conical mound is straddled with appendage markings on account of constant movement for depositing the excavated materials (Figs.5d and e). *Uca marionis* also spread excavated materials around the burrow opening in circular fashion during the burrow modification (Figs.5f and g). Few crabs spread the sediments in the form of thin films surrounding the burrow opening (Fig.5h). The inclination of the burrow varies from 60° to 90°; observed length is of 35cm and diameter of 5cm. The young and juvenile burrows are simple, vertical, unbranched and unlined and are more densely populated (Fig.4a), near the low water line (Patel and Desai, 1999) as well as on the ridges and runnels (Fig.4b). The activity of young and juvenile crabs in the intertidal zone increases slowly (Fig. 4c) for initial 30-90 minutes of the low tide, but soon, the activity reaches a maximum of up to 400 burrows per sq meter when the low tide phase is in peak. The mound or a pyramid structures near the *Ocypode* burrow is a sort of social behavior for the territory or attracting the opposite sex, much similar to other behaviors like movement, combat and sound (Warner, 1977). The adults *Uca* build porches outside the burrow (Fig.5f), displaying its territory much more similar to the status of ownership. The species of *Uca* are also efficient burrowers and make large burrows in the muddy sediments and the surfacial activity of their young is represented by feeding pellets.

Burrow orientation of the crustaceans was studied following the method suggested by Frey and Mayou (1971). The burrow openings near the high water line are towards the seaward direction and also confirms with similar study done by Chakrabarti (1981). The rose diagram (Fig.6) indicates the orientation of burrow openings; supratidal zone does not show any distinct orientation (Fig.6a), while, the foreshore burrows with mound show marked orientation towards the seaward direction (Fig.6b). In some

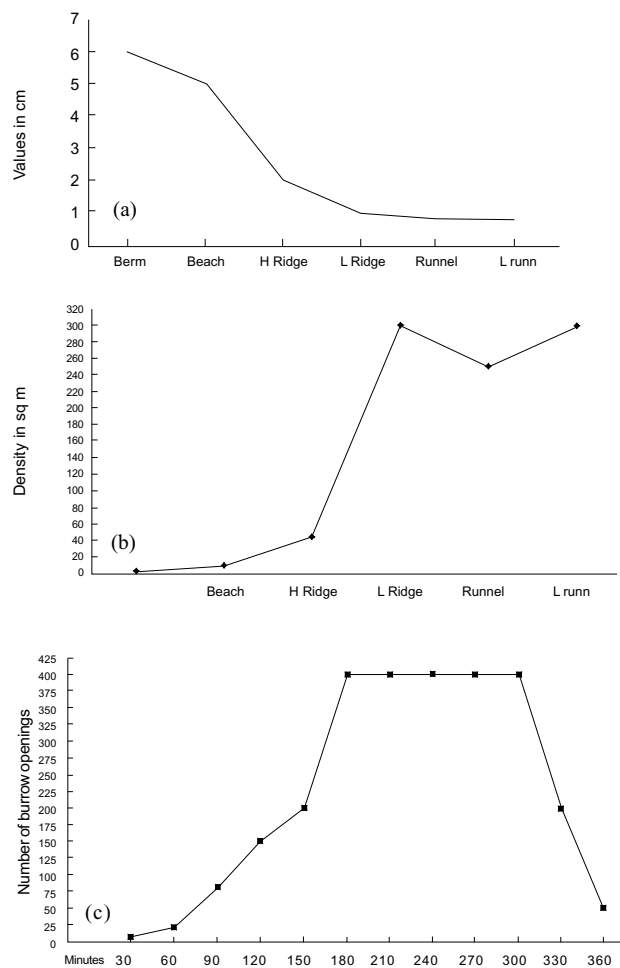


Fig.4. (a) Burrow diameter of the *Ocypode* species across the intertidal zone. (b) Crustacean burrow densities across the intertidal zone and (c) Graph showing the number of burrow openings against the minutes during low tide.

cases the mounds near the burrow opening consist of linear ridges or paired mounds (Fig.4d).

Burrowing and locomotion activity of the juvenile form of *O. platyrsis* is observed on the Wind Farm and Rawal Pir Sites. During the low tide, gently sloping beach surface becomes free from residual water flow; crab comes out from the sediments and wanders on the surface for food, after walking a few centimeters, it feeds on organic rich sediments and throws waste in the form of rounded feeding pellets. Time-lapse photographic technique was employed to study the behavior activity of the *O. platyrsis* (Figs.7a, b, c, d). Figure 7b represents initial churning of sediments at a place and pushing aside feeding pellets to a rim-like structure on the surface. This activity is repeated many times and excavated material is continuously thrown in circular fashion forming pelletoidal wall structure. Burrow deepens downward and at the same time the animal piles up pellets

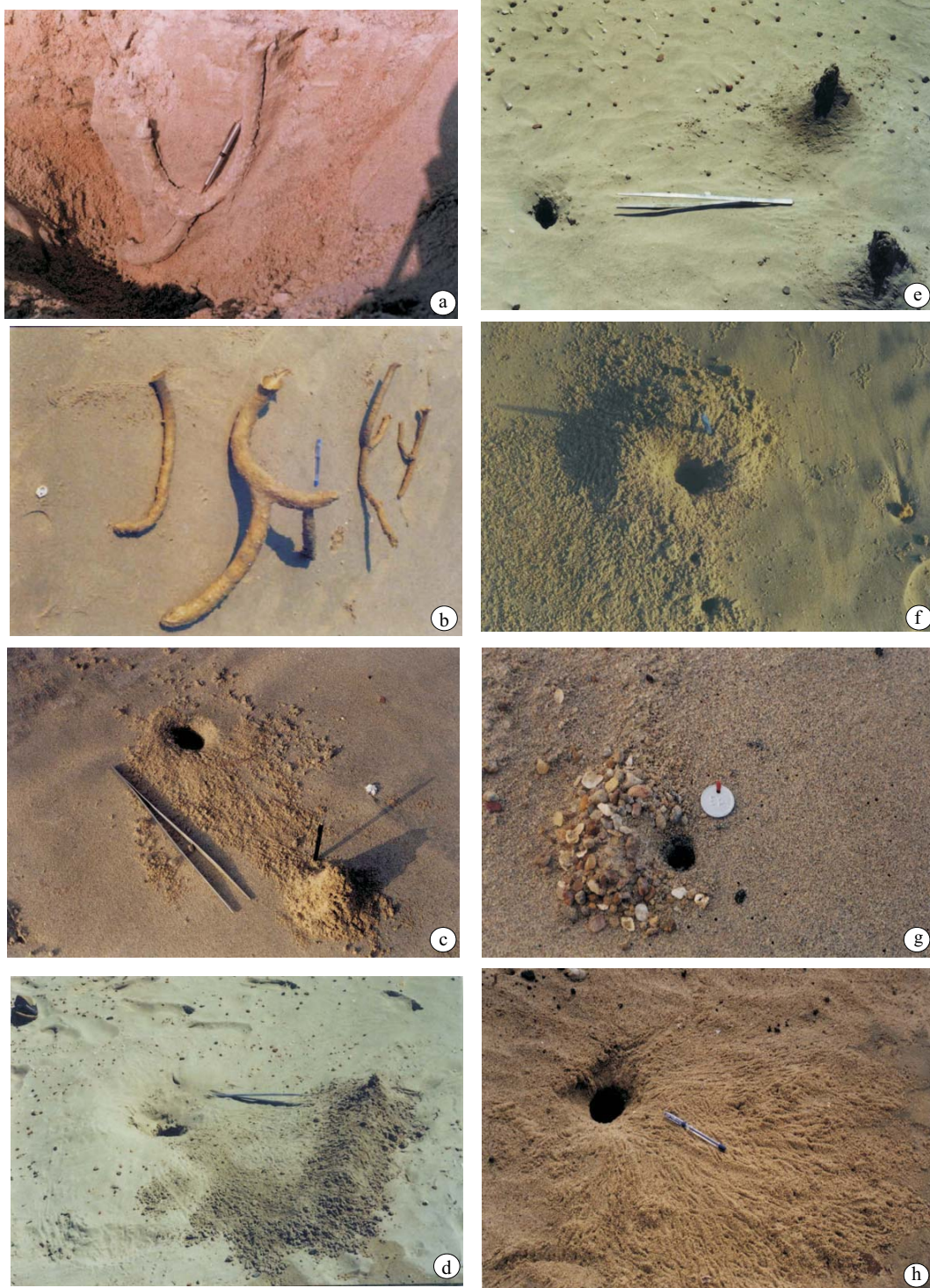


Fig.5. Crustacean Burrows, (a) Wax-Cast of Adult *Ocypode* burrows along with opening on the intertidal zone. (b) Wax cast of the burrows of adult *Ocypode ceratopathalma* showing different types of “I, J, U and Y shaped” burrow morphologies. (c) Burrow opening associated with conical mounds consisting of excavated materials, (~ 45 cm) apart from the opening. (d) Burrow with ridge of loose excavated sediments with appendage markings. Note the cone shaped structures at the extreme left side of the heap (Forceps=45 cm) also note appendage markings of *Ocypode roundata* with the heap of loose sediments. (e) Burrow with paired conical mound, equi-distance apart from the holes. (f) Thick rimmed burrow opening of *Uca marionis*. (g) Half rim near burrow opening consisting of gravels and shell fragments. (h) Burrow opening with broad, thin, rim of the loose sediments modified by the appendages.

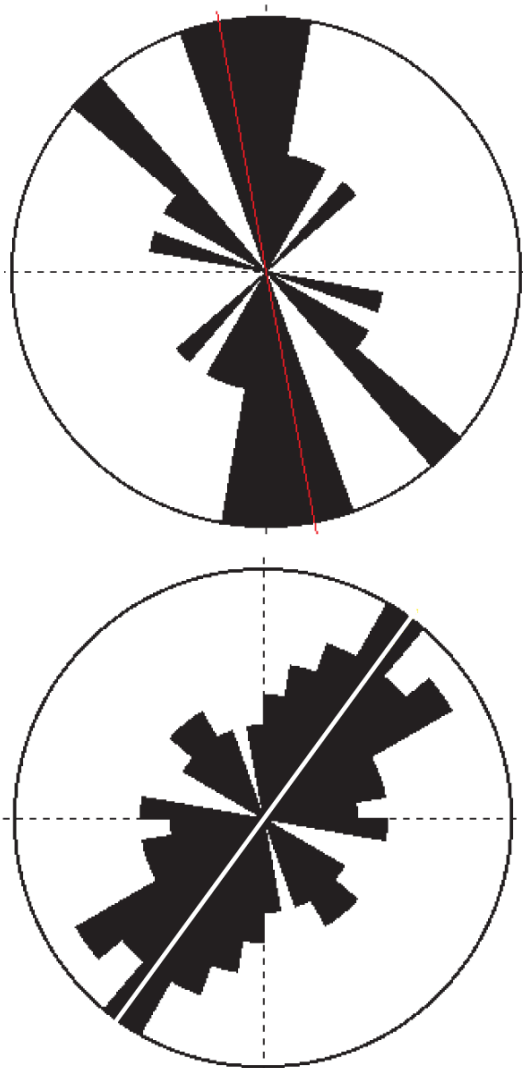


Fig.6. Burrow orientation of the *Ocypode* burrows (a) orientation of backshore burrows without mound (b) orientation of the foreshore burrows with mound.

raising the rim above the surface. Photographs (Fig. 7a) were taken 135 seconds after it starts burrowing. The burrow further deepens downward, at the same time the diameter increases and the rim is further raised (Fig.7b). For constructing this structure, the animal took another 150 seconds. After the required depth is reached (2 cm) the animal covers the burrow by adding more pellets (Fig.7c) from inside to the top of the burrow wall and forms pelleted roof-like structure. To complete this structure (Fig. 7d), the animal took another 180 seconds. During the construction of pelletoidal roof, a small hole equal to the size of the animal is left open. But due to non-cohesiveness and watery nature of the sediment, the pelletoidal roof collapses and the animal gets covered with the pelletoidal structures (Fig.7d). Repeated activity in rotating fashion at one-

place results in burrow forms which are few millimeters deep and arranged pellets in circular fashion above the surface (1-4 cm high) appear like chimney (Fig.7e).

The burrows of all the crustaceans if preserved are definitely *fossitextura figurative* and ethologically correspond essentially to the Domichnia group. The wax casts of the burrows of the adult species taken from Rawal Pir site indicates its morphological similarity to *Psilonichnus* and *Thalassinoides* ichnogenera, suggesting more of a semi-permanent nature of the burrows. The burrow morphology of the juvenile crabs is identical to *Skolithos* or *Monocraterion* and may not even last more than one tidal cycle. Several small, vertical burrows are also covered by chimneys of pelleted walls, if preserved may correspond to the ichnogenus *Ophiomorpha* and are indicative of composite fodinichnial/domichnial structures.

The stomatopodean shrimp *Oratosquilla striata* is voracious and of carnivorous nature that predate on passing prey (Cladwell and Dingle 1976), abundantly found in the runnels. It feeds on fine grained food particles in suspension-feeding mode and rarely does it come to the sediment-water interface (MacGinitie and MacGinitie, 1949). The burrows of *O. striata* are generally simple to complex, inclined to vertical (Hamano et al. 1994), three dimensional burrow systems which are lined by pellets (Figs. 7f and g), identical to ichnospecies *Ophiomorpha nodosa* (Vaugelas, 1991). The pelleted walls are nearly 2-5mm in thickness (Fig. 7f and g). Two types of pelleted wall structures can be delineated: (i) a compact packing of predominantly regularly distributed, discoid, ovoid or irregular-polygonal pellets, and (ii) loosely packed small pellets of about 0.3-1mm in diameter. They may be more than a meter deep and secrete gelatinous mucus to stabilize the loose sediments of the wall.

Crawling Traces

Two types of crawling traces were observed; one made by adults of *Ocypode* and the other made by Hermit crabs. The crawling traces of *Ocypode* are mainly confined to the beach and backshore region. *Dactylus imprints*, consisting of sets of parallel-arranged grooves, make these traces. Appendage markings are also found around the burrow during the burrow modification for throwing the sediments in the form of mounds. Such types of traces are often formed by side burrowers (Frey et al. 1984).

Hermit crabs *Clibanarus infraspinus*, preferred gastropod shells (*Turritella*, *Cerithium*, *Murex*, *Natica* and *Telescopium*) to hide themselves and used for protection and concealment. These species are mainly detritivores and may sometime prefer organic rich watery sediment (Patel



Fig.7. Decapod burrows (a, b, c & d) rotating burrowers. Time lapse photographic sequence is showing burrowing activity of young *Ocypode platyrsis*. (e) *Pseudo-Ophiomorpha* colony of the protruded, pelleted rimmed burrows. (f) Pelleted wall burrows in the tidal channel made by the *Oratosquilla striata*. (g) Abandoned burrow of *Oratosquilla striata* showing mammillated exterior wall surface.

and Desai, 1999). Ichnologically, the best evidence for the hermit crab activity is the telltale of the shell imprint left along the animal's trail, together with the tracks reflecting the peculiar style of locomotion. Locomotion may be continuous for long distances and comprises mainly of trails made by heavy gastropod shells. Their traces appear to be trails, but close examination reveals them to be track ways about 2cm wide, meandering to winding and often cross-cutting each other. They comprise of a series of oblique grooves arranged in V-shapes and gouges, along with a sharp mid-line. Ethologically, the track ways of the hermit crabs represent crawling traces (Repichnia).

POLYCHAETE TRACES

Polychaetes are the second important bioturbator group, abundantly found in fine-grained watery sediments, especially in pools and runnels, but are scarce or absent on the extreme reaches of beach and dunal region. These animals further modify the substrate by employing specialized techniques like peristaltic movement of the body for feeding, grazing and dwelling purposes. The bioturbational work especially the burrowing, is dependent on the fluidity and consistency of the substrate which they inhabit. Majority of the species are burrowing and modify their structures deep into the sediment. The highest structural complexities of the polychaete taxocoenosis may be directly related to the higher environmental stability and higher degree of microhabitats like clastic oxygenated sediments and enough food (Martin et al. 1993).

Burrowing Activity

Burrowing activities of the polychaetes are found essentially on ridges, runnels and in the lagoons. Morphologically, the burrows are cylindrical, vertical to inclined, branched to unbranched and mucus bound. They usually occur as sand bounded small tubes, generally 1-15mm in diameter and up to 50 cm deep and are densely populated in runnels and lagoons. They also occur as isolated tubes on the beach, near the high water line. These forms are similar to pipes made by mucus secreting polychaetes.

Dichotomously Branched Forms

These structures occur as 3 ramifying forms consisting of vertical tubes, which are systematically branched, horizontally 2-3 cm below the sediment-water interface (Fig.8). The horizontal components further open up on surface and appear as dendritic pattern or plant root-like structures (Figs.8a-e, Fig. 9). The vertical component is cylindrical, unbranched, mucus lined tube, 40-50 cm deep,

with a diameter of 3 mm. The horizontal component is a multiple branched burrow that consists of an extensive series of short tunnels; either straight or gently curved (Fig. 8f). The X-radiograph shows first, second and third order ramifying tunnel systems, each bifurcating at an acute angle (Fig.9). These tunnels open to the surface trending upward across the sediment-water interface, each one consisting of numerous feeding grooves surrounding the opening. Very often these grooves are dichotomously branched, forming a tight network to open system and sometimes tassel like, but all these structures are similar in having internal tunnels joining the main shaft (Fig.8f). Two polychaete species, *Nephtys inermis* (Fig.8g) and *N. diabranthis* (Fig.8h) are found to be trace makers of these structures. During the receding tide, when the sediment surface is covered with a veneer of water, the animal comes out from the semi-permanent tunnels to feed (Figs. 8g and h) on freshly deposited organic rich sediments. While exploiting the surficial sediments the animal leaves behind varied forms of network. The whole ramifying structure indicates two distinct types of behavioral activity, (i) dwelling and (ii) grazing activities- exploiting the freshly deposited organic rich sediments. The complete form consists of composite burrow structure having vertical shaft, dichotomously branched tunnel (Fig. 9) and dendritic patterns identical to ichnogenera *Skolithos*, *Thalassinoides* and *Chondrites* respectively.

Fecal Strings/Mounds

The surficial activity of the polychaetes is limited and represented as fecal strings and mounds (Fig. 10a) all along the Mandvi coast. The fecal mounds, show different kind of shapes and at places are represented as multiple mounds. These structures are small, circular and conical, consisting of fecal cast; height is of up to 2 cm and diameter of a centimeter (Fig.10b). These are generally associated with vertical and with paired burrow openings. They are similar to the fossilized form first described by Donaldson and Simpson (1962) as ichnogenus *Chomatichnus*. In the Rawal Pir site lagoon, *Chloeia flava* is making mound structures consisting of fecal materials (Fig. 10b). *Nephtys inermis*, *N. diabranthis*, *Nereis diversicolour* and *Nereis* sp. also make conical mounds of fecal string. The shedding of the fecal material at the top of the burrow mouth (Fig.10c) is indicative of the worm adapted to working in anoxic conditions or in low oxygen conditions. The paired burrows made by *Arenicola* sp., consists of funnel shaped opening and mound on other end (Fig.10d) are used for irrigating the burrow and other end is used for throwing out the fecal material respectively.

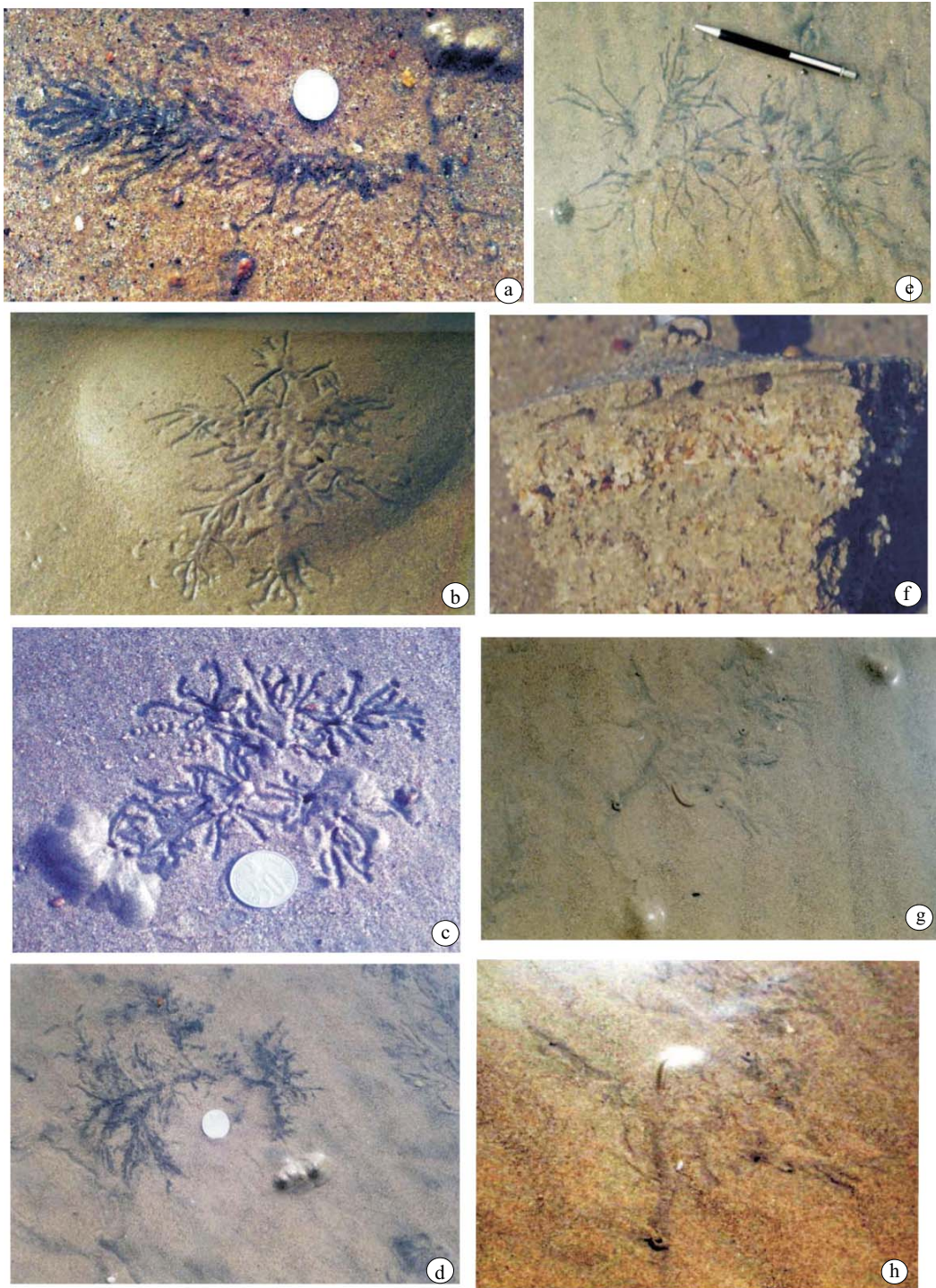


Fig.8. Complex behavioral structures of Polychaetes. **(a)** Tassel like structures in organic rich sediment, made by interface-deposit feeding polychaete *Nephtys*. **(b)** Surficial expression of *Chondrite* like trace made by polychaete *Nephtys* in the intertidal zone of Wind Farm Site. **(c)** Fully developed dichthomously branched feeding burrow showing composite structures made up of surficial feeding burrows and excreta mounds. **(d)** Large, branched feeding structures and mound of excreta made by Polychaetes *Nephtys*. Note the difference in the sediment colour, indicating structures were made in freshly deposited materials. **(e)** Branched burrow system with long, slender, straight to gently curved tunnels. **(f)** Vertical section of the mucus lined burrow showing horizontal branched network parallel to the surface. Holes indicate branching points of the burrows. Detailed burrow system has been shown in Fig.5. **(g and h)** Initial stage development of the burrow in the watery sediments; note the polychaete *Nephtys* in action.

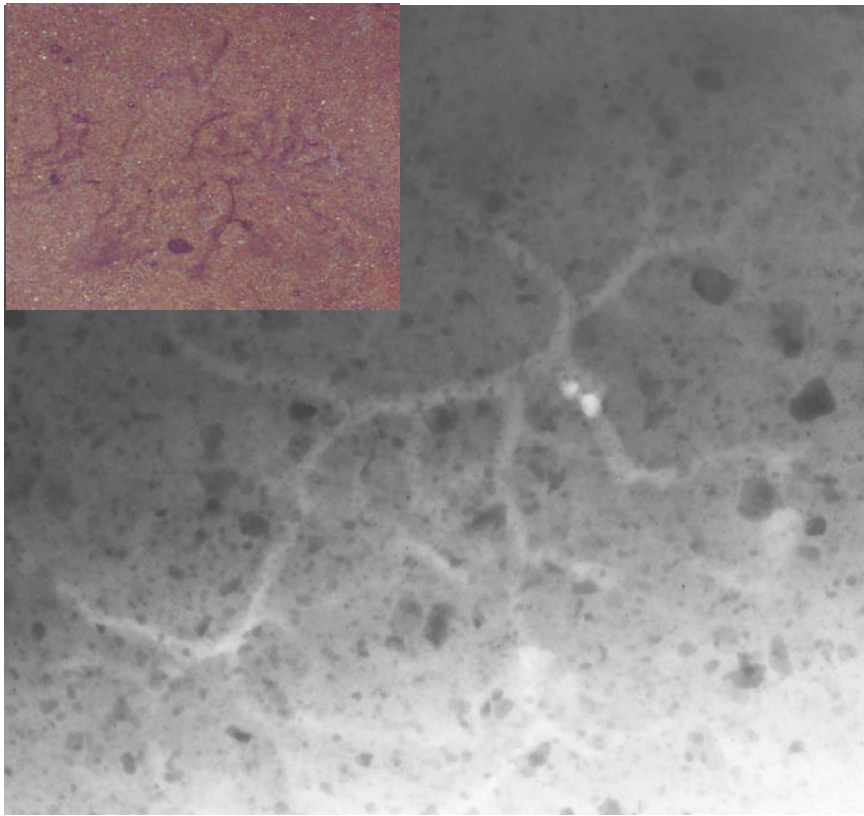


Fig.9. Inset photograph showing surficial traces of the *Nephtys* and X-radiograph of the same showing subsurface mucus lined horizontal tunnel network.

U-Shaped Forms

These structures usually consist of two vertical to inclined tubes, converging downward and forming U-shaped burrows (Fig.10e). Tubes are cylindrical, unbranched and smooth with mucus bound; also seen as paired funnel openings (Figs.10d and e). These U-shaped tubes consist of funnel-shaped opening and conical mound (base ranging from 5 to 12 mm and height up to 13 mm) at other end. The dimensions of the funnel vary in different burrow populations; the maximum diameter of 20mm and depth is 25 mm; two limbs are parallel and openings are 7-10cm apart, and diameter of 5mm. The suspension feeders *Arenicola* sp. and *Amphinome rostrata* belong to separate families (Rouse and Fauchald 1997) but their feeding behavior is similar commonly making the structures in the runnels and lagoons. Their feeding guild according to Fauchald and Jumars (1979) is CMX i.e. carnivore, mobile and mouth structure consists of usually sac-like pharynges. According to MacGinitie and MacGinitie (1949) these types of structures and animals are well acquainted with the irrigation of the burrow by the peristaltic movement. These burrow structures are identical to ichnogenus *Arenicolites franconocus*.

Agglutinated Tubes

Lined cylindrical tubes with diameter of 10-15 mm, depth 50 cm and thickness of mucus lining is up to 2 mm. Tube tops are semi rigid and protrude up to 16 cm above the surface. The protruded tube may be cylindrical to sub-cylindrical and diameter of the tube increases upward. The material (Fig. 10f) attached to the tube can range from shell fragments (80%), sand grains, marine weeds, plastic cords and coir. The average armoured length of the tube is ~10cm, remaining on the surface. *Diopatra neapolitana* is a true suspension feeder, abundantly found in runnels and undoubted constructor of these tubes. During the late stage of low tide their tubes are directed according to the flow.

The burrow linings are secreted as mucus by the worm and later stiffen to a thin parchment-like material. During the tube construction, the exterior is reinforced with detritus picked up by the worm from the surroundings. This reinforcement not only increases the tube strength, a necessary condition for protection and adequate flushing (Myers, 1972), but also aids in predator detection by increasing the effective tube diameter (Brenchley, 1976). Reinforcement probably also increases the feeding efficiency

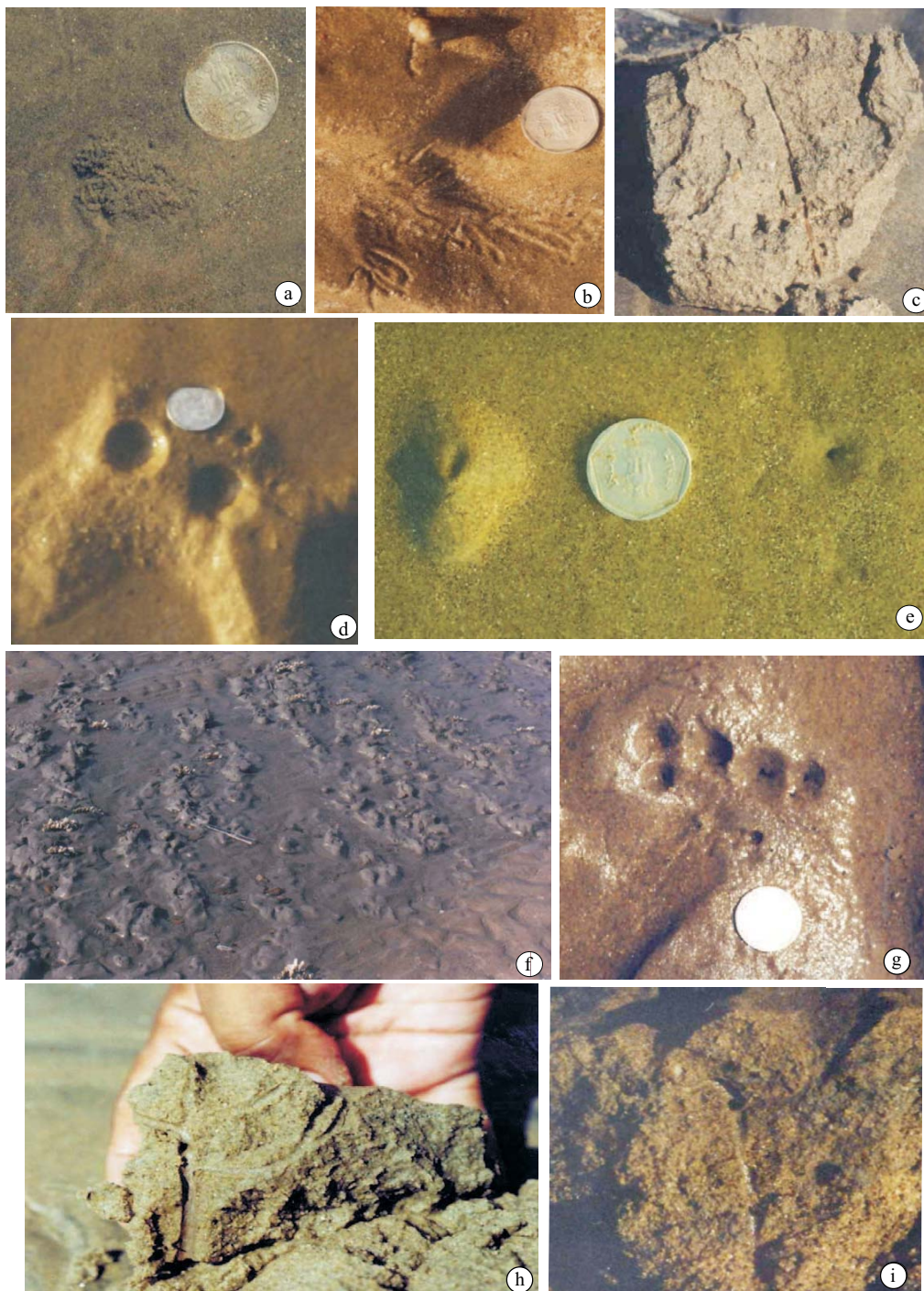


Fig.10. (a) Polychaetes activity in shallow pool near Rawal Pir site, consisting of excreted sediments in the form of pseudo-strings. (b) Cylindrical fecal mound of *Chloeia flava* associated with feeding burrows in Rawal Pir lagoon. (c) Vertical section of the mucus lined burrow with mound. (d) Paired opening burrows consisting of funnel at one end and mound with opening on other end. The funnel acts to irrigate the burrow and the used water and waste is expelled from the other end in the form of mound. (e) Paired funnel shaped burrows identical ichnospecies *Arenicolites* made by polychaete *Arenicola*. (f) *Diopatra* armored tubes oriented along the flow direction in runnel. Group funnel burrows in Rawal Pir lagoon. (g) Surficial expression of the grouped funnel burrows of the *Oniphys*. (h) Cross section of a funnel shaped burrow showing central shaft with curved, inclined to horizontal tunnels, curving upward and outward. (i) Cross section of a funnel burrow system showing central shaft with tunnels curving upward and outward, branching palmately in proximal part. Grouped funnel burrows identical to ichnospecies *Balanoglossites*.

by aiding in the trapping of edible detritus. Tube tops have inverted J -shape which helps in effective feeding (Mangum et al. 1968).

Grouped Funnel Burrows

Grouped funnel burrows represent a system with a complex spatial configuration and on the whole consist of mucus bound vertical tubes with horizontal to oblique segments, which further bifurcate in their upper parts and open in the funnel shape at the surface (Fig.10g). Individual structure therefore has many outlets on the surface, usually 4-7 funnels (Fig.10g) which are interconnected to main shaft. Each funnel converges in the middle of the structure (Figs. 10h and i); the convergence points of the burrows are 3-5 cm below the sediment-water interface. Burrows are smooth, cylindrical, lined, branched and with a diameter of 5mm. Observed depths of the structures are 50 cm and funnel diameter is up to 40 mm while depth of the funnel is about 30 mm. These structures are made by filter/suspension feeder *Oniphus eremita* and are identical to ichnogenus *Balanoglossites triadicus*. These burrows are extending up to the anoxic zone or algal/peaty layer in the lagoon sediments of the Rawal Pir site.

Y/I Shaped Burrows

These burrows are smooth, inclined to vertical, straight, cylindrical, branched/unbranched, lined, resembling English letter 'Y' and 'I'. The arm of the "Y" shaped burrow bifurcates in upward direction at 10cm below the sediment-water interface (Figs.11a and b); diameter is of 8mm and depth is 40 cm. Mucus bound 'I'-shaped burrows are vertical to steeply inclined (Figs. 11a and b) with tube diameter of 1-4 mm and variable depth (up to 50 cm). The burrows are kept open by the producer and have a permanent connection to the sediment/water interface. The acute angles of Y-shaped branching (Fig.11a) indicate that the joining did not serve as turning points for animals. These structures are very common in ridges of the Rawal Pir and Modwa Spit sites. 'Y' shaped burrow are made by *Heteromastus filiformis*, identical to fossil form *Polykladichmus irregularis* while 'I'-shaped structures of *Nereis costoe*, *Amphinome rostrata*, and *Oniphus eremita* are identical to fossil form like *Skolithos linearis*.

Calclitic Tubes

Cemented calcitic tubes are found on varied hard substrates including pebbles, bivalve shells, oyster's reefs and rocky platforms (Fig.11c). These tubes are spiral to tightly coiled, sub-cylindrical to conical in shape and consist of growth rings, ridges and ribs on the outer surface. The

diameter of these tubes is variable, generally the proto-tube diameter is less than 1mm, tube aperture is up to 10mm and length of uncoiled tube is up to 15 cm. Generally, single occupancy of the tubes is found on any sort of hard substrate, but crowding of the tubes is observed on oyster reefs (Fig.11c) and rocky platforms. *Serpula vermiculris* and *Sabellaria* sp. secrete calcareous tubes and grow by the accretion on anterior sides. These structures are suggestive of the activity of the filter-feeding animals, specialized in seston feeding or having ciliated tentacular crown by which they feed.

Polychaete Sand Reef

Sand reef (Fig.11d) building activities were observed on man-made structures along the mouth of Rukhmavati River and shore platforms of Rawal Pir sites. *Scolopos latus*, a filter feeding (Fauchald and Jumars, 1979) polychaete secretes mucus on the burrow opening and binds the sand grains during the high tide condition. Tubes usually occur in a bunch, crowded, curved and randomly oriented with a length of up to 12 cm and diameter of 2 mm. Colony grows randomly by binding size sorted grains (heavy minerals, small shell fragments and faecal pellets) and represented by number of generations. The reefs consist of individual tubes, which are concomitantly glue to each other in reef mass with same cement and their subsequent synchronous growth produces individual reefs.

NEMERTEA

Cerebratulus marginatus are unsegmented worms found abundantly in the lagoon (Modwa Spit site), live in anoxic sediments and come to the oxic surface for feeding the algal rich sediments (Fig.11). The small conical mound of extruded sediments often contain a hole at center from which the worm comes out to the surface and moves around and makes the pentamerous structures (Fig.11e). The burrows are simple, straight, vertical, deep, lined and unbranched and often extend to the anoxic zone. It is lined with iron or black coloured muddy sediments, which imply that the animal irrigates the burrow during high tide when the overlying water causes oxidation of ferrous and ferrous lining on the burrow walls of the anoxic mud (Fig.11h). *Cerebratulus marginatus* stretches out on the surface for feeding purposes and also makes the undulatory biogenic grazing laminae (Figs.11 f and g).

ICHNOCOENOSES

"An ichnocoenosis is an association of lebensspuren

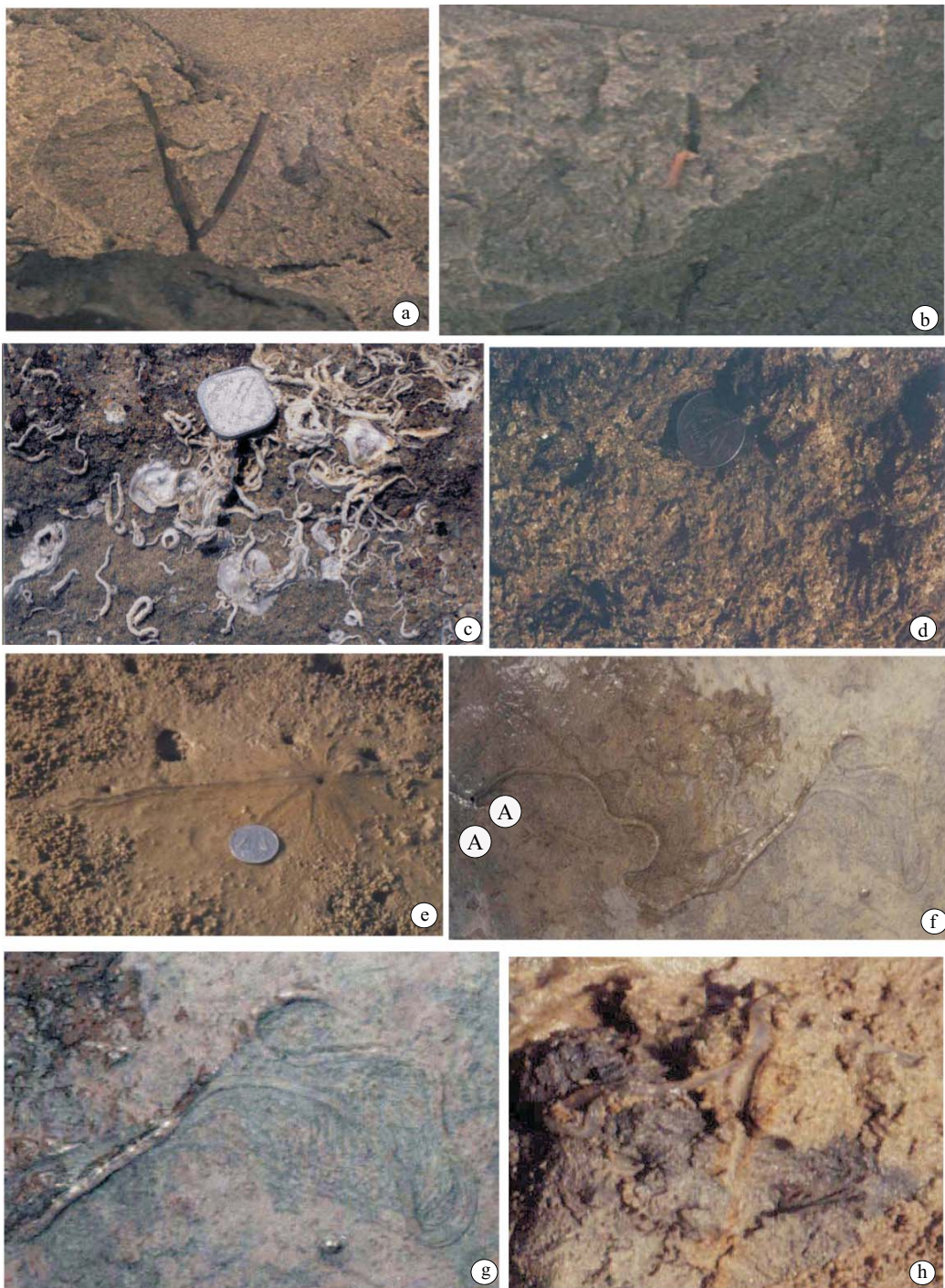


Fig.11. (a) Vertical, "Y" shaped branched burrow, very close to the upper surface. "Y" shaped polychaete burrows similar to ichnospecies *Polykladichnus irregularie* Fursich 1981. (b) Vertical burrows of *Nereis* sp. identical to ichnospecies *Skolithos linearis*). (c) Extensive development of the live oyster reefs on the shore platform (Modwa Spit). Note the association of the oyster shells with symbiotically relationship of Sabellarid polychaete. (d) Sand binded polychaete reefs of *clymene* developed on anthropogenically formed barriers along the Rukmavati river mouth. Biogenic structures of unsegmented worms. (e) Pentamerous structure on the mound formed on account of pumping of water. Unsegmented worm *Nemertea*, *Cerebratulus marginatus* stretching out from the burrow and pumping the water make the sediments watery around the burrow. (f) *Cerebratulus marginatus* stretch out in the watery, algal rich sediments for grazing. Note formation of the biogenic laminae because of peristaltic movement of the animal. (g) Close up view of the biogenic laminae. (h) Black anoxic mud of the lagoon with oxidized lined burrow wall of the *Cerebratulus marginatus* formed due to irrigation of the burrows in anaerobic condition.

reflecting life activity of the individuals of a biocoenoses” (Dorjes and Hertweck, 1975). Thus, the term is strictly confined to the neoichnologic realm, though some of the workers have used it in fossil context and have modified it as “an ecologically pure assemblage of traces and trace fossils, derived from the work of a single endobenthic community” (Ekdale et al. 1984 and Bromley, 1996). The biogenic structures of the modern intertidal zone demonstrate wide range of animal behaviour and can be interpreted with known ecology, behavioural patterns, adaptations and other physical parameters. The individual traces studied in the intertidal zone exhibit a distinct non-random pattern; some traces occur together recurrently whereas others are never found in the same geomorphic units. Naming the individual ichnocoenosis is necessary for their identification as recurring entities. The simplest method is to identify the ichnocoenosis by its characteristic dominating ichnogenus and the names of ichnocoenoses in following sections are based on “Incipient fossils” (Bromley and Fursich, 1980; Rindsberg, 1990). Six ichnocoenoses are found, which includes *Faecichnia* ichnocoenosis, *Psilonichnus* ichnocoenosis; *Skolithos* ichnocoenosis; *Ophiomorpha* ichnocoenosis; *Chondrites* ichnocoenosis and *Balanoglossites* ichnocoenosis.

Faecichnia Ichnocoenosis

Pellet making activities of crustaceans and polychaetes in the form of surfacial workings dominate this ichnocoenosis (Fig.12a). It is characterized by rod-shaped faecal pellets; rounded, elongated, oblong, pseudo-faecal pellets, string pellets, etc. The pseudo faecal pellets were restricted only to the top of the freshly deposited surface, created by young and juvenile *Ocypode ceratopthalma*, *O. roundata*, *O. platyrsis*, *Uca marionis*, etc. These crabs created structures in specific designs, surrounding their burrow opening and were abundant on the beach, ridge and runnels. Ethologically these traces represent the feeding activity in which the pellet is never passed from the animal body. This association often represents periodic exposures of the area. The true faecal pellets are rod and string-shaped, made up of fine mud, excreted as a result of suspension feeding activity.

Interpretation: The importance of this ichnocoenosis is that the surfacial working often disrupts completely the original sedimentary structures (Howard and Frey, 1975) which are only preserved as biodeformational structures. These workings are also important for sediment cycling and deposition of fine mud in coarse sands and especially in the deposition of argillaceous sediments in the form of biogenic pelletization (Pryor, 1975). This ichnocoenosis has poor

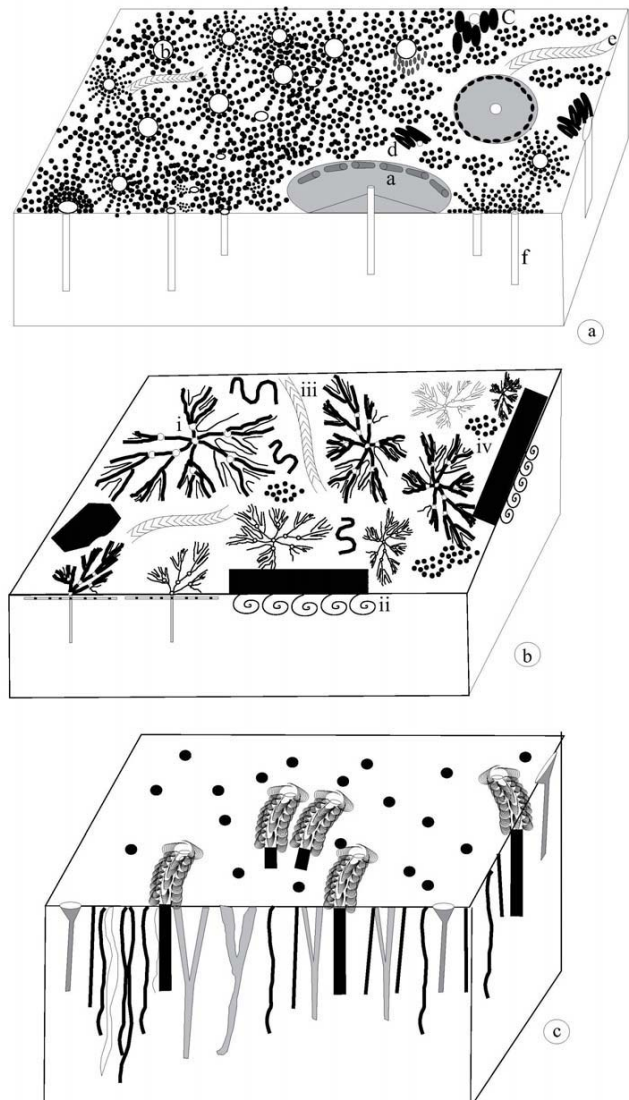


Fig.12. (a) Schematic diagram showing *Faecechnia* ichnocoenosis (i) rod shaped pellets, (ii) feeding pellets arranged in different designs, (iii) burrowing pellets, (iv) fecal string, (v) hermit crab trail, (vi) *Skolithos* burrow. **(b)** Schematic diagram of the *Chondrite* ichnocoenosis (i) *Chondrite*, (ii) gastropod siphonal burrows, (iii) gastropod trails, (iv) faecal pellets and **(c)** Schematic diagram of *Skolithos* ichnocoenosis (i) *Skolithos* (ii) *Diopatrighnus* (iii) *Polykladichnus* (iv) *Monocraterion*.

potential of preservation but can accumulate as clay lenses in sand rich horizons.

Chondrites Ichnocoenosis

This ichnocoenosis (Fig.12b) is characterized by *Chondrites*-like traces made by *Nephtys* in the silty sand and sandy substrates. This assemblage represents regularly branching burrow system constructed for combined feeding

and dwelling purposes. The burrows represent three ramifying units consisting of (i) straight vertical tunnel more than 10cm deep, (ii) straight or slightly arcuate dichotomous branched tunnel and (iii) dendritic pattern tunnels, diverging at acute angle, which are placed at SWI and are produced as deposit feeder makes repeated probing in the sediments. Each tunnel terminates at the surface by creating feeding grooves; occasionally tunnel ends are marked with faecal mounds. This indicates that the structure is made for complex ethological purposes, which include dwelling and interface feeding. According to Bromley and Ekdale (1984), *Chondrites* indicate very low level of oxygen in interstitial waters within the sediment, at the site and time of the burrow emplacement. But water samples show normal dissolved oxygen 2.1mg l^{-1} to 1.25mg l^{-1} and free CO_2 ranges from 25% to 73% at an average temperature of 88°F ; indicates that, the structures can also be made in normal conditions.

Interpretation: This ichnocoenosis is characteristic of the structures made by non-vagile, interface deposit feeder opportunistic polychaetes *Nephtys inermis* and *N. diabranchis*. Sedimentologically, they are associated with plane laminations and antidunes and are characteristically absent from the rough hydrodynamic conditions necessary for producing ripples. Ethologically, the structure represents complex fodinichnial burrows (Ekdale, 1992) whose maker's behaviour changes from deposit feeder to suspension feeder. Ekdale (1985) considered *Chondrites* as opportunistic while Bromley (1996) described the ichnocoenosis as non-vagile, deep deposit feeder structure.

Skolithos Ichnocoenosis

This ichnocoenosis (Fig.12c) consists vertical to inclined, branched/unbranched, lined or unlined dwelling burrows of polychaetes which are identical to ichnogenus *Skolithos*, *Polykladichnus*, *Monocraterion*, *Diopatrachus* etc. This assemblage is made in a variety of substrates ranging from silty sand, mature sand to muddy gravel, but is restricted at the exposure level below 2. 'I'-shaped structures made by *Amphinome rostrata*, *Nereis costoe* and *Oniphus eremita* are identical to ichnogenus *Skolithos linearis*. The small, cylindrical, funnel shaped and Y to J-shaped, branched, thinly lined burrows made for dwelling polychaetes like *Nereis costoe*, *N. unifasciata*, *N. diversicolour*, *Lycastis indica*, *Lumbriconereis pseudobifilaris* and *Heteromastus filiformis* are identical to ichnogenus *Monocraterion* or *Polykladichnus irregularis*.

Interpretation: This ichnocoenosis is characterized by dwelling tubes with mucus linings and filled with coarse-grained materials (Fig.13a). Sedimentologically, they

are found to be abundant in the plane bed laminations (*Skolithos*, *Polykladichnus* and *Monocraterion*); while they are fewer (*Diopatrachus*) in rippled, muddy graveled substrates. The biogenic structures of this assemblage is found below the exposure level 1, of CTL's and indicates medium to high-energy settings, with moderate to high degree of bioturbation in clastic shifting substrates. Similar conditions were also found favourable for *Skolithos* and its modern analogue tubes of *Diopatra cuprea* across modern tidal flats (Skoog et al. 1994).

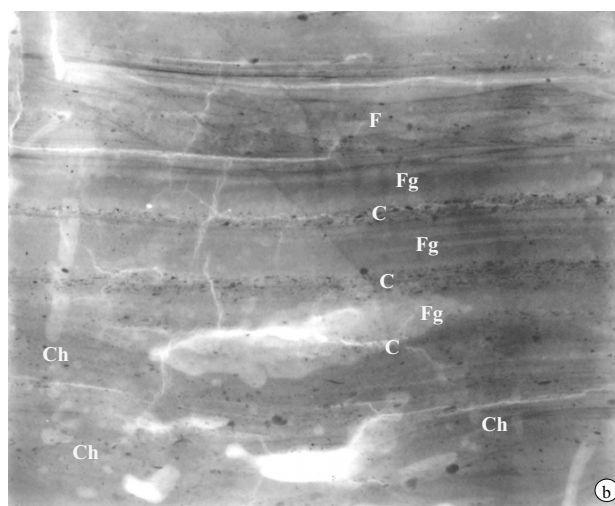
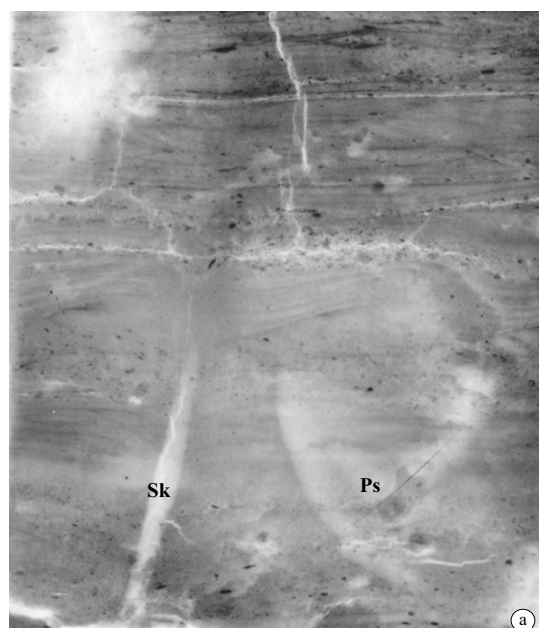


Fig.13. (a) X-radiograph of the ridge sediments showing *Skolithos* (Sk) and *Pylonichnus* (Ps), along with ripple x-laminations. **(b)** X-radiograph of the runnel sediments with *Chondrite* (Ch) and Flaser beddings (F) with alteration of coarse (C) and fine grained (Fg) intercalations.

Psilonichnus Ichnocoenosis

This is characterized by three dimensional, branched, unlined dwelling burrow systems (Fig. 14a), which are either in the shape of the English letter Y, J, or I or identical to the ichnogenus *Psilonichnus*. They are restricted in the intertidal zone up to CTL's exposure level 0 & 1 and often extend more than a meter deep into the sediment. The burrows are often renewed after high tides and the renewal processes are done by bringing the inner and deeper sediments to the surface. These excavated sediments are deposited in the form of mounds or thick rims. This process is very effective in bioturbating the beach and backshore sediments; otherwise it is not bioturbated by any other organisms.

Interpretation: *Psilonichnus* like burrows are made by *Ocypode roundata*, *O. ceratopthalma*, *O. platyrsis* and *Uca marionis*, and during their young stage, they make small unbranched, burrows identical to *Skolithos*. The process and intentions, involved in making the burrows are same, i.e. for dwelling and protection and exhibits an earlier ontogenic phase of the *Psilonichnus* burrows. The intermediate phase consists of gradation between fully developed *Psilonichnus* and *Skolithos*. Characteristically towards the low water line, the burrow diameter decreases, while density increases. In the Wind Farm and Rawal Pir sites, *Psilonichnus* burrows were low in density, far spaced, indicating, territorial behaviour of the crabs. At back shores of Rawal Pir and Modwa Spit site the burrow openings were characteristically directed towards the seaward sides. The presence of the *Psilonichnus* ichnocoenosis is clear indication of the beach-backshore environment in clastic sediments and its range extends even to the dunal areas. Curran (1992) described similar ichnocoenosis in carbonate setting; the burrows are confined to the upper foreshore and backshore zones only. The *Psilonichnus* have great potential for preservation and are good indicators of the past sea level positions and it also marks the lowest limit of the ground water fluctuation during low tide (Frey and Pemberton 1987).

Ophiomorpha Ichnocoenosis

This ichnocoenosis (Fig.14b) is characterized by monodominant species of *Ophiomorpha nodosa*. Ethologically, it represents dwelling burrows constructed by squillidean crustacean species of *Oratosquilla striata* (Patel and Desai, 2001). The burrows are abundant in the lower intertidal zone, at exposure levels 4 and 5, with substrate conditions of fine, silty sand. The thick wall of the burrow indicates stability of the structure and is often found keeping pace with the sediment-water interface. Density of the burrows varies, but high density, closely packed burrows

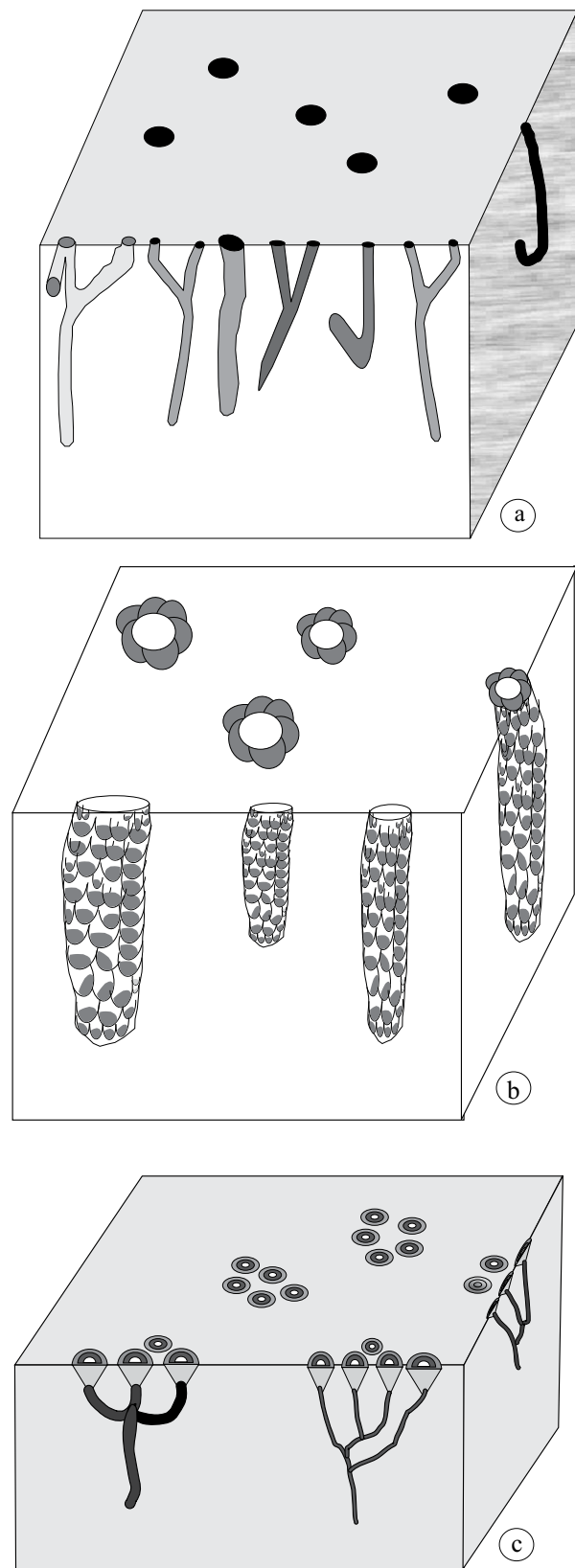


Fig.14. Schematic diagram, (a) *Psilonichnus* ichnocoenosis, (b) *Ophiomorpha* ichnocoenosis and (c) *Balanoglossites* ichnocoenosis.

are found close to the low water line or in runnels where some considerable water column is available during low tide conditions. The ichno-zonation of the recent crustacean traces of the intertidal zone shows that they are abundant near the low tide level (Desai and Patel 2008). Similar to the *Ophiomorpha* burrows, a pelleted chimney is constructed by deposit feeders (juvenile/young *Ocypodes*), above the sediment surface, to serve as tubular entrance. Similar types of chimneys were considered, if preserved, by Frey et al. (1978) to be *Ophiomorpha*.

Interpretation: This ichnocoenosis is indicating the work of suspension and deposit feeders and their association is found in runnels and ridges respectively. The *Ophiomorpha* ichnogenus is considered to be a poor environmental indicator (Ekdale, 1992), when dealing with broad environments. The Kachchh intertidal ichno-zonation suggests that the ichnogenus is a good indicator of the lower intertidal zone, where it occurs in the clastic, shifting substrates of moderate wave and current energy conditions. The structures made by deposit feeders, however, ethologically do not match with those of *Ophiomorpha* constructed by squillidean *Oratosquilla striata*.

***Balanoglossites* Ichnocoenosis**

This ichnocoenosis (Fig.14c) is characteristically developed in Rawal Pir lagoon, and constructed in alternating peat and sand layers by *Oniphus eremita*. The burrows and their tunnels extend in to the anoxic layer, devoid of any interstitial oxygen. The sediments are fine sand and substrate is purely of silty sand nature, often covered by algal mats that drastically cut the oxygen supply in the sediments (Leszczynski et al. 1996). The burrows represent complex spatial configuration, consisting of horizontal segment from which vertical or somewhat oblique segments bifurcate upward towards the surface. The surfacial expression of the burrow is a group of 5-7 funnels, connected by several U- shaped interconnecting tunnels, which are lined, are of equal diameter and converge towards a centre point. The branching and bifurcation are restricted only to the top 5 cm of the sediment. The worm is purely a suspension feeder, which feeds by irrigating the burrows and suspension feeding from the water that is circulated. Due to the presence of the numerous funnels, the water that is circulated brings additional oxygen supply to the anoxic mud. Other common structure associated with *Balanoglossites* is another funnel feeder- *Arenicolites*, which consists of a pair of funnels or a funnel and a mound, with U shaped interconnections.

Interpretation: Ethologically, this ichnocoenosis is suggestive of fodinichnial burrows, modified to adapt to the low interstitial oxygen and anoxic conditions. Sedimentologically, the biogenic structures are present on high viscosity flow deposits, indicating their adaptation to varied clastic environments of low to high-energy conditions. Palaeoecologically, the burrows are considered to be indicative of high organic matters in the sediments (Kazmierczak and Pszczolkowski, 1969). Barington (1965) and Kazmierczak and Pszczolkowski (1969) regarded the ichnogenus as indicative of lower intertidal zone. The occurrence of *Arenicolites* indicates that it must have acted as shelter only for a short period of time and not as permanent domicile (Dam, 1990). In all, the ichnocoenosis suggests major environmental changes like high water flow during spring tides in bottom substrate, followed by short period of well-aerated conditions in bottom water with no-sedimentation and abundant food supply.

ICHNO-SEDIMENTOLOGICAL MODEL

The present studies on the animal-sediment relationship, established the factors governing the distribution of the biogenic structures. Fauna and sediment distributions in many benthic habitats have been at least crudely characterized over wide spatial and temporal scales (Snelgrove and Butman, 1994). The proposed model has been studied under natural conditions, with natural flow regimes. Data on biogenic structures (Table 1) was compiled for the distribution of organisms that created the structures and correlated with the observed working depth along with functional group codes (Woodin and Jackson, 1979). This data was then compared with the published data, compiled by Thayer (1975) which showed the reworking rates and reworking zones of some organisms of the same genus from different parts of the world (Table 2). Based on these data, ichno-sedimentologic models were drawn for major geomorphic units and are discussed in the light of sediment characteristics, biogenic structures, their trace makers and working depth. The beach, ridge, runnel and lagoon ichno-sedimentologic model corresponds to the upper shoreface, shoreline models of Howard (1972) and Shoreface model of Pemberton et al. (2001).

Beach Environment and Biogenic Structures

The beach ichno-sedimentologic model displays medium to coarse grained sediments, with low angle cross stratification and plane bed laminations with characteristic biogenic structures like faecal, feeding and burrowing pellets and *Psilonichnus* burrow (Fig.15a). The nature of the

Table 1. Distribution of the organisms, their observed working depth, functional group codes and biogenic structures

Organisms	Region of Abundance						Working Depth in cm	Functional group Codes	Biogenic Structures	
	Beach	Ridge	Runnel	Lagoon	Flats	Shell Platform				
<i>Ocypode</i> (C)	x	x	x	x			-1 to -3	1a, 1b	Pellets; Burrows	<i>Psilonichnus</i>
<i>Uca</i> (C)			x	x			-1 to -3	1a, 1b	Pellets; Burrows	<i>Psilonichnus</i>
<i>Macropathalmus</i> (C)	x						-1 to -3	1a	Pellets; Burrows	<i>Thalassinoides</i>
<i>Plagusia</i> (C)		x					-1 to -3	1a	Burrows?	
<i>Graspus</i> (C)		x					-1 to -3	1a, 1b	Pellets; Burrows	<i>Psilonichnus</i>
<i>Portunus</i> (C)	x						-1 to -3	2c	Burrows	
<i>Matuta</i> (C)		x		x			-1 to -3	1a	Pellets; Burrows	<i>Psilonichnus</i>
<i>Scylla</i> (C)					x		-1 to -5	2c	Burrows	
<i>Neptunus</i> (C)			x				+5 to -3	2c	Burrows?	
<i>Clibanarius</i> (HC)			x		x		0	1a	Trails, bioturbation	
<i>Oratosquilla</i> (S)		x	x	x	x		+5 to -1	1a, 1b, 2a	Burrows	<i>Ophiomorpha</i>
<i>Squilla</i> (S)		x	x		x		+5 to -1	1a, 2a	Burrows	<i>Ophiomorpha</i>
<i>Diopatra</i> (P)			x				+10 to +3	2a, 2b	Tube	<i>Diopatrachus</i>
<i>Onuphis</i> (P)				x			+7 to -7	1a, 2a	Tube, burrow	<i>Balanoglossites</i> , <i>Skolithos</i>
<i>Lumbiconereis</i> (P)			x		x		-1 to -5	2a, 2b	Burrows	
<i>Nereis</i> (P)		x	x	x			0 to -5	1a, 2a	Burrows, pellets, mound	<i>Chondrite</i> , <i>Skolithos</i>
<i>Lycastis</i> (P)	x						0 to -5	1a, 2a, 2b	Burrows	
<i>Nephtys</i> (P)	x	x	x	x	x		0 to -5	1a, 2a, 2b 2c	Burrows, pellets, mound	<i>Chondrites</i>
<i>Serpula</i> (P)						x	0 to +3	2a, 2c	Tubes	<i>Worm Tube</i>
<i>Clymene</i> (P)				x	x		0 to -5	2a, 2c	Burrows, mound	
<i>Heteromastus</i> (P)			x	x			>-10	1a	Burrows	<i>Polykladichnus</i> , <i>Skolithos</i>
<i>Amphinome</i> (P)		x		x	x		0 to -7	1a	Burrows	<i>Arenicolites</i> , <i>Skolithos</i>
<i>Chloeia</i> (P)			x	x			+3	1a	Burrows, fecal mound	<i>Chomatichnus</i>
<i>Cerebratulus</i>				x			+3 to -7	2a	Burrow, mound, grazing	<i>Skolithos</i>

physical and biogenic sedimentary structures shows a similar pattern in all the three sites. Population of adult crustaceans like *Ocypode ceratophthalma*, *O. platytarsis*, *O. roundata* and *Uca annulipes* dominates the beaches. However polychaetes are totally absent or sparse from the beach due to its ecologically harsh environmental condition and high degree of exposure. Locally, lower parts of the beach occasionally consist of *Heteromastus* species.

Two ichnocoenoses, *Faecichnia* and *Psilonichnus* represent the biogenic structures of the beach (Fig.15a). *Faecichnia* is an important ichnocoenosis of beach

environment because it helps in bioturbating and recycling the upper layer sediments in thinly populated zones. Preservation status of the ichnocoenosis is very poor, but recycled sediments in the core/relief peels were observed as lenses of ghost/foreign sediments. The *Psilonichnus* ichnocoenosis of the beach is characterized by burrows, which disturb the sediment and sediment laminations, to a greater degree as compared to *Faecichnia* ichnocoenosis. The burrows are widely spaced, monodominant and their bioturbational index is 1-2 BI (Desai and Patel 2008). The presence of deep vertical dwelling burrows of the *Ocypode*

Table 2. Published data on reworking rates and working zones of the individual organisms

Genus/Species	Locality	Ind rewk rate (Cm ³ day ⁻¹)	Rewk Zone (Cm)	References
<i>Amphitrite ornata</i>	BarnstableHarbour, M.A.	12.7	~3	Rhoads (1967)
<i>Clymenella</i>	Bahaia paraguera Puerto rico	1	5	Magnum (1964a,b)
<i>C. Torquata</i>	BarnstableHarbour, M.A.	0.75	20	Rhoads (1967)
<i>C. Torquata</i>	BarnstableHarbour, M.A.	0.37	20	Magnum (1964 a,b)
<i>Hetromastus filiformis</i>	Waden Sea Neatherlands	0.2-1.2	15	Cadee (1979)
<i>Nephtys incisa</i>	Buzzard Bay, M.A.	-0?	2	Rhoads (1967)
<i>Nereis diversicolor</i>	N. Caspian sea	0.15		Viltischeva and Karzinkin (1970)
<i>Nereis succinea</i>	Narraganset bay, RI	0.02	0.2	Cammen (1980a,b)
<i>Scolopus robustus</i>	Narraganset bay, RI	0.06	13	Myers (1977a)
<i>Stomatopoda</i>				
<i>Squilla empusa</i>	Rhode island	11	212	Myers (1979)
<i>Ocyopode Quadrata</i>	padre island, TX	450	60	Hill and Hunter (1979)
<i>Ocyopode Quadrata</i>	Sapelo island	106	15	Frey and Mayou (1979)
<i>Ocyopode Quadrata</i>	Sapelo island	>7.6	0.3	Frey and Mayou (1979)
<i>Uca pugilator</i>	Georgia	13.3	0.2?	Kraeuter (1976)

on extreme reaches of the beach indicates shifting substrates, scarcity of food supply and maximum duration of exposure causing dryness and winnowing effect in sediments. The sediment characteristics with physical, biological and bioturbated evidences inferred moderate wave and current energy for the deposition of the sediments.

Ridge Environment and Biogenic Structures

The ridges have higher exposure time as compared to the runnel, and can be easily separated out from runnel based on primary sedimentary structures like ripple marks; megaripples may also develop on the junction of the ridge and runnel and may be preserved as lens of clean, coarse sand. Similar lenses were encountered in trenching, relief peels and X-radiography (Fig.13). The ridges consist of abundant and diverse groups of organisms, including young and juvenile crustaceans along with Anomura; Stomatopods; Prawn *Peneus japonicus* and polychaetes. Definite zonation of these animals can be observed based on the distribution of their biogenic structures (Fig.6) in the intertidal. The ridge exhibits well developed biogenic structures (Fig.15b) which comprise of four distinct ichnocoenoses: *Faecichnia* ichnocoenosis, *Skolithos* ichnocoenosis, *Chondrites* ichnocoenosis and *Ophiomorpha* ichnocoenosis.

The *Faecichnia* ichnocoenosis has structures similar to the beach but exhibits denser population of different size and shape of the pellets. The *Skolithos* ichnocoenosis consists of *Skolithos* and *Polykladichnus* burrows which are made by polychaetes and also exhibit variation in population towards the low water line. The density of the *Skolithos* and *Polykladichnus* burrows increases in seaward direction and

their structures are represented by faecal pellets surrounding the simple unbranched burrows. *Chondrites* ichnocoenosis is found at the junction of the ridge and runnel towards the LWL, where thin layer of water column allows the settling of food particles on the surface. The observed working depths of the *Nephtys* varies from 0 to -5 (Table 1) and they are also able to use the top 5 cm of the sediment for dwelling and feeding purpose and their reworking zone is 0.2 cm (Table 2). *Ophiomorpha* ichnocoenosis is developed on seaward slopping part of rides and characteristically consists of nodose lined burrows of *Oratosquilla striata*. The distinct development of the biogenic structures on the ridges helps in local zonation of the ridge ichnocoenoses. The bioturbational index of the ridges varies from 2-5 BI, i.e. BI 2 near high water line to BI 5 near low water line (Desai and Patel, 2008).

Runnel Environment and Biogenic Structures

The runnels intervene with the ridges of the Rawal Pir and Modwa Spit sites and finally merge with the tidal flat of the Modwa Spit site. They are characterized by moderately to poorly sorted sediments with hummocky and swaley cross stratification and rippled bed forms. These are deposited under the dominance of unidirectional and oscillatory flow conditions and are represented by symmetrical/asymmetrical small 2D and 3D ripples and subaqueous dunes. The X-ray analysis of the plate core from runnels indicates presence of small-scale ripples, along with hummocks and swaley kind of structures.

Runnels (Fig.15c) are the most favourable for deposit and suspension feeding animals (Table 1) like crabs

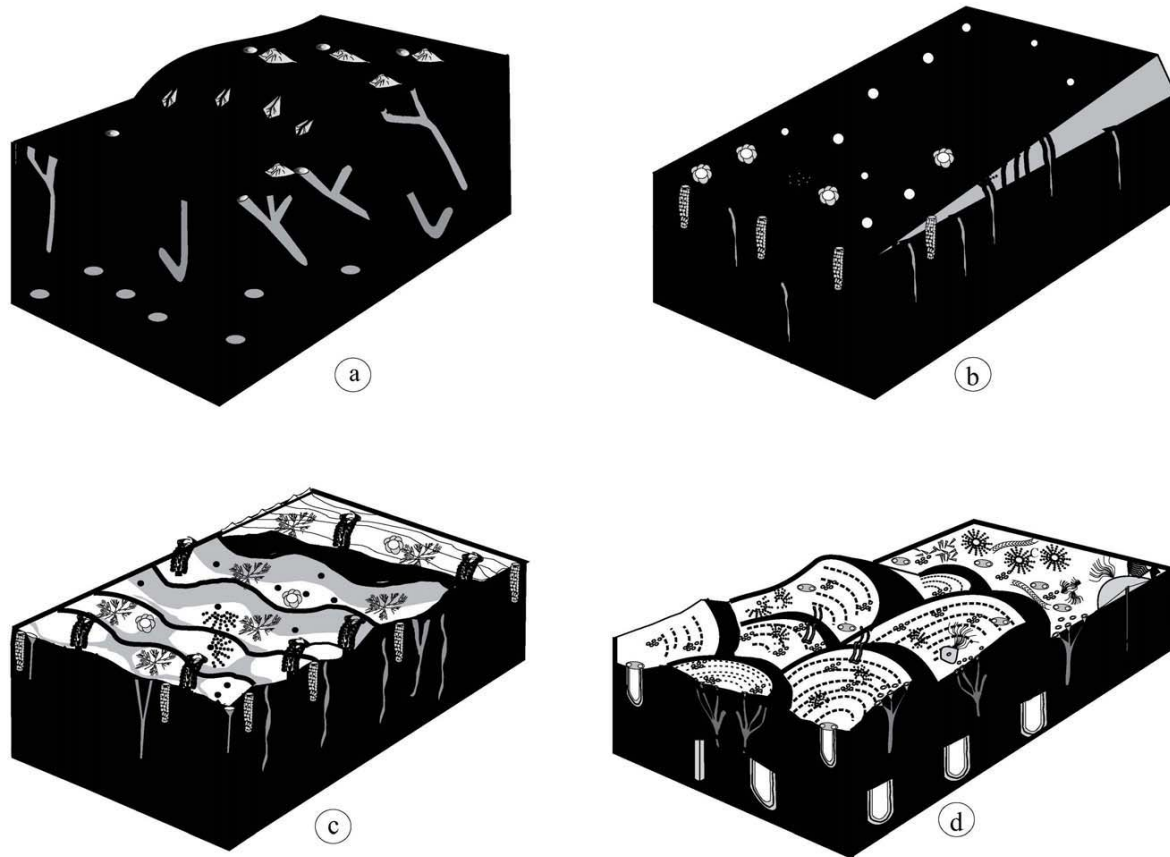


Fig.15. (a) Ichnosedimentologic model of the beach showing cross-bedded units with *Psilonichmus* and *facechina* ichnocoenoses. (b) Ichno-sedimentologic model of the ridge showing plane bed laminations with *Skolithos* and *Facechina* ichnocoenoses. (c) Ichno-sedimentologic model of runnel showing rippled, cross-bedded units with *Skolithos*, *chondrite* and *Ophiomorpha* ichnocoenoses and (d) Ichno-sedimentologic model of lagoon showing subaqueous 3D dunes and *Balanoglossites* ichnocoenosis.

(*Ocypode*, *Uca*, *Scylla*), Hermit crab (*Clibanarus*), Stomatopods (*Oratosquilla*, *Squilla*) and polychaetes (*Diopatra*, *Lumbriconereis*, *Nereis*, *Nephtys*, *Oniphus*, etc). The bioturbators of runnel are deposit and interface feeding *Nephtys diabranchis* and *N. inermis* which produce extensive network of feeding voids and grooves; surface deposition of faecal sediments surrounding *Nereis* burrows; suspension feeding by *Diopatra neapolitana* which helps in mixing of suspended, surface and subsurface sediments. Rod-shaped pellets of shrimps, mucus bound feeding and faecal pellets of small crustaceans are also deposited on the sediment-water interface. Faecal materials deposited at the sediment-water interface are readily transported as bed load during strong spring tides (Wright et al., 1997). Runnels thus depict an epifaunal suspension and deposit feeding assemblage associated with the tubes and burrows of polychaetes and small crustaceans, enhancing the potential for biodeposition of material from suspension near the bed (Schaffner, 1990). The bioturbational index of runnels is usually high (Desai and Patel 2008) as compared to ridges,

because it is characterized by finer sediments, less exposure time, filled with a thin water column and abundance of food.

The characteristic ichnocoenoses of the runnels are *Chondrites*, *Skolithos*, *Ophiomorpha* and *Faecichnia*. The *Chondrites* ichnocoenosis is by far the most dominating ichnocoenosis of the runnels, consisting of branched, horizontal structures of *Nephtys inermis* and *N. diabranchis*. The subsurface forms occur as ramifying tunnels represented as small circular rings in cross-section (Fig.13b). *Skolithos* ichnocoenosis is again dominating, but differs from ridges in having dominating structures like "*Diopatrachus*", which is an agglutinated tube, made by suspension feeder *Diopatra neapolitana*. *Ophiomorpha* ichnocoenosis is also well developed and represented by pelleted wall lining burrows of the *Oratosquilla*. *Faecichnia* ichnocoenosis exhibits denser population of smaller size of feeding pellets of young and juvenile crabs.

Lagoon Environment and Biogenic Structures

The lagoons are characterized by medium to fine grained,

moderately sorted sediments, with hummocky and swaley, cross stratification, flaser bedding and rippled bed forms. The bedform shows cross-stratification formed by larger bed forms with intra-set discontinuities that indicates periods of tidal reversal. Characteristically the lagoons constitute peat layer, overlain by sandy sediments and contains algal mats. Various deposit and suspension feeding polychaetes like *Onuphis eremita*, *Arenicola* sp., *Chloeia flava*, *Heteromastus filiformis* and unsegmented worms (Nemertea) like *Cerebratulus marginatus* dominate the lagoon. Deposit feeding crustacean like *Uca* is a mono-dominant crustacean in lagoon along with stomatopodean *Squilla*.

Rawal Pir lagoon is characterized by *Balanoglossites* and *Faecichnia* ichnocoenoses, while *Skolithos* and *Faecichnia* ichnocoenoses represent Modwa Spit lagoon. The shafts of the *Arenicolites* and *Balanoglossites* are quite resistant to sediment deformation by the sediment mixers and the presence of a lining suggests a reinforcement of the burrows. This is because of the shallow RPD layer, or low pore water oxygen and reducing environment in the lagoon, along with dense microbial mats that cause change in the substrate consistency by stiffening the surface and cutting off the influx of the bottom oxygen from the water columns in to the sediment (Leszczynski et al. 1996). The organisms develop the funnels at the burrow opening in order to circulate oxygenated water in to the burrows. The burrows thus made in the lagoons by *Oniphus* have multiple funnel opening and they have a tendency to irrigate the burrow system. *Skolithos* ichnocoenosis is represented by simple, vertical and deep burrow of *Cerebratulus marginatus* which often extends into the anoxic zone and irrigates the burrows. Crustaceans like *Uca* and *Squilla* modify their burrows by lining them with plant materials. *Faecichnia* ichnocoenosis exhibits denser population of different size and shape of the feeding and burrowing pellets.

The characteristic traces are identical to *Balanoglossites*, *Arenicolites*, and *Skolithos* with disturbed sedimentary structures (Fig.15d), which have a bioturbation index 3. Lagoonal niches are well exploited by highly specialized and an opportunistic animal that lives in high fluctuations of water levels, salinity, temperature and food supply.

Supratidal Environment and Biogenic Structures

The Supratidal zone of the Mandvi area comprises of fore dunes, berms and dunal accumulations consisting of fine grained, very well sorted sediments. The sedimentary structures are characterized by large-scale planar cross-stratification with sparse burrows of the adult *Ocypodes* and abundant plant root traces like *Rhizomorphs*. Such types of

burrows identical to the *Psilonichmus* and *Thalassinoides* structures are common element in even carbonate dunes of Bahamas (Curran, 1992) and are a result of opportunistic mature colonizer like adult *Ocypodes*. The bioturbation rate is very low and the bioturbation index is 1 (BI-1). The *Rhizomorphs* do not disturb much of the sediments, but act as good stabilizer.

Shore Platform and Biogenic Structures

The shore platforms are exposed at Modwa Spit site and in the runnel of the Rawal Pir site, which are colonized by filter feeder, hard substrate encrusters like, serpulids, barnacles, oysters, etc. Two types of shore platforms are developed in the study area (i) Rawal Pir shore platform consisting of rocks and encrusted by mainly serpulids tubes and barnacles and (ii) Modwa Spit shore platform characterized by encrusted oysters, which grow from generation to generation and provide hard substrates for younger generations after their death.

CONCLUSIONS

Mandvi intertidal zone comprises spacio-temporal dynamic landforms that host opportunistic animals. A large number of trace-making crustaceans and polychaetes inhabit the zone and occupy particular niches. These endemic organisms produce assemblages of biogenic structures that can help in understanding the various substrate conditions of the micro-geomorphic units (dune, beach, ridge, runnel and lagoon) of the intertidal zone. Certain types of biogenic sedimentary structures are found on more than one habitat because stress tolerant animals adapt to a wide range of variations (i.e. geomorphic settings, substrate preference, food resources and fluctuation in temperature, salinity and oxygen contents) when subaerially exposed.

The important observations are as follows:

1. Dune and beach zone have favoured the adult *Ocypode* species, high proportion is observed in the beach zone as compared to dunal zone, while, high level fluctuation of water levels created harsh environmental conditions for polychaetes. Young and juvenile species of crabs are found on the ridges and runnels, their proportion increases in seaward direction. Stomatopodean species *Oratosquilla striata* are found in runnels and lower reaches of the ridges.
2. Motile deposit feeder polychaetes are abundant on the ridges and are occasionally found on the lower reaches of the beaches, while suspension and filter feeders are abundant in the runnels. The sessile filter feeder polychaetes are abundant on the rocky shore platforms.

Rawal Pir lagoon consists of suspension feeders *Chloeia flava* and *Onuphis*, while Modwa Spit lagoon consists of unsegmented worm *Cerebratulus marginatus*.

3. Dunes and beaches are characterized by I, Y, J shaped dwelling burrows of adult *Ocypodes*. The crustacean burrows of the dunes are characteristically large, widely spaced and mono-dominant while on the beach the burrows are large but densely populated, often marking their territory with sand mound. The openings of the burrows on the beach are markedly oriented towards the sea, while they are randomly oriented in the dunal area. They are identical to ichnogenus *Psilonichnus*.
4. Ridges represent deposit-feeding burrows of young and juvenile crustaceans while the surfaces are completely studded with feeding, burrowing and faecal pellets.
5. The pellet making activity leads to complete obscuring of the freshly deposited sediment layer. *Nephtys inermis* and *Nephtys diabranchis* make characteristic multi-ramifying tunnel system in the lower part of the ridges, identical to ichnogenus *Chondrites*.
6. Runnels consist of three dimensional, pelleted, walled burrow system of *Oratosquilla striata*, which is identical to ichnogenus *Ophiomorpha*. Flow oriented structures of polychaetes are dominating in the runnels and includes agglutinated tubes of *Diopatra*. U-shaped

tubes of *Arenicola*, mucus bound dwelling burrows of *Heteromastus* and multi-ramifying tunnel system of *Nephtys* are also abundant.

7. Lagoons consist of mainly grouped funnel systems, branched burrows of *Oniphus* and *Chloeia flava*, identical to ichnogenus *Balanoglossites*. U-shaped burrows of *Arenicola* and straight, simple and vertical dwelling burrows of Nemertea are identical to ichnogenus *Arenicolites* and *Skolithos*. These are opportunistic and have exploited restricted niches for dwelling-feeding purposes.
8. Seven ichnocoenoses were identified: *Faecichnia* ichnocoenosis, *Entobia-Meandropolydora* ichnocoenosis, *Chondrite* ichnocoenosis, *Skolithos* Ichnocoenosis, *Psilonichnus* ichnocoenosis, *Ophiomorpha* ichnocoenosis, and *Balanoglossites* ichnocoenosis.

Study on animal-sediment relationships of the crustaceans and polychaetes of the Mandvi intertidal zone marks the profound zonation of biogenic structures that help in distinguishing the shoreline micro-environments.

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