Hillichnus lobosensis: a behavioural revolution in Bathonian Tellinacean bivalves

JEHOVA L. DARNGAWN, SATISH J. PATEL* & JAQUILIN K. JOSEPH

JPSI

Hillichnus lobosensis, a multi-morphological preserved trace fossil represents the combined locomotion and feeding behavioral activities of the tellinacean bivalves. Several specimens of this complex well preserved, endogenic structures are found in the mixed siliciclastic-carbonate rocks of the Middle Jurassic (Bathonian-Callovian) of the Island Belt Zone of Kachchh, India. The structures show different morphological levels of *Hillichnus* from Level E to Level A. The earliest paleontological evidence of the deposit-feeding tellinacean bivalves is known from the Early Cretaceous. Here we interpret the locomotory and deposit-feeding activity of tellinacean bivalves during the Bathonian-Callovian age based on ichnological evidence. The preserved dual behavioural and functional activities suggest a pronounced change in siphonal function which has switched over partly/completely from infaunal suspension-feeding mode to deposit-feeding mode marking the revolution in tellinacean bivalves coinciding with the global transgression.

INTRODUCTION

The Mesozoic Marine Revolution (MMR) marks large-scale evolutionary episodes giving rise to the dominance of modern evolutionary fauna (Buatois *et al.*, 2016). The faunal turnover occurred by the Early Jurassic, as indicated by the taxonomic composition and increased diversity of bioturbation structures and the complexity of infaunal tiering (Buatois *et al.*, 2016). The suspension-feeding tellinacean bivalves evolved from the suspension-feeding cardiid bivalve which later develop deposit-feeding behavior during the Cretaceous in a fully marine setting during the Cretaceous (Pohlo, 1982). However, the present study provides evidence of preadaptive behaviour in the mode of feeding in tellinacean bivalves during Bathonian-Callovian based on ichnological data.

Hillichnus lobosensis is a complex trace fossil originally described from the Palaeocene of the USA which is preserved as five distinct morphological levels (E-A) produced by deposit-feeding tellinacean bivalve (Bromley *et al.*, 2003), barely reported in the literature due to its lack of recognition on account of its morphological complexity rather than to its actual rarity (Ekdale and Ekdale, 2018). The *Hillichnus* ichnogenera do not fit into a single traditional behavioral category (Seilacher, 1953, 1964; Ekdale, 1985 and Frey, 1978); as a result of the combination of behaviors of the trace maker at the same time in chronological order.

Five morphological categories levels E to A identified in the holotype specimens which are well preserved in the submarine canyon setting of the Carmelo Formation (Paleocene age) and Point Lobos California (Bromley *et al.*, 2003). It is also reported from shallow marine nearshore setting, Middle Eocene Scripps Formation, La Jolla Group, San Diego County, California (Ekdale and Ekdale, 2018). A similar feathered form of complex trace fossils *Hillichnus agrioensis* with multi-level morphological structure has been reported from the Lower Cretaceous Agrio Formation of the marginal marine environment with a difference in their mode of feeding and defecation (Pazos and Fernández, 2010). *Hillichnus*-like trace fossils have also been reported from Jurassic tidal deposits of the Samkamoto Formation, Kumamoto Prefecture Southwest Japan but lack distinct vertical tubes and lateral lamellae showing a flabellate (Nara *et al.*, 2014).

In the present study, *Hillichnus lobosensis* is abundantly observed at two different stratigraphic levels: Bathonian (Jurassic) in the Chorar Island and Callovian (Jurassic) in the Bela and the Khadir Islands of Island Belt of Kachchh showing dual behavioral activities of the trace makers. These specimens vary in dimension and preserved morphological levels at different exposures, mainly dominated by Level C and Level D with few Level B and Level E. The present study focuses on morphological analysis representing a functional and behavioral interpretation of trace fossil *Hillichnus lobosensis* and discusses its environmental implication.

LOCATION AND GEOLOGICAL SETTING

The Kachchh Basin is located in the westernmost part of India between latitude 22° 44' to 24° 18' N and longitude 68° 09' to 71⁰ 42' E. It comprises more than 2175 m thick of marine and deltaic deposits ranging in age from Aalenian to Albian (Biswas, 1993) and is exposed in the Kachchh Mainland, the Island Belt Zone, and the Wagad Highland. The Mesozoic succession of the Eastern Kachchh basin is represented by inter-related rock units exposed in the disconnected outcrops of the Wagad Highland, the Khadir, the Bela, and the Chorar Islands (Biswas, 1993). The Mesozoic rocks of the northeastern part of the Kachchh basin (Fig. 1) are grouped under the Khadir and the Gadhada formations. They show variations in thickness, composition, fossils content, and lateral and vertical continuities among these islands. The Khadir Formation represents the oldest stratigraphic unit exposed in the Eastern Kachchh which is a facies variant of the Kaladongar and the upper part of the Goradongar formations of Patcham Island.

The Khadir Island is the type area for the Khadir Formation (Biswas, 1971, 1977, 2016), comprising of 318 m thick Mesozoic succession which is divided into the Cheriya Bet, the Hadibhadang Shale, and the Hadibhadang Sandstone members. The Cheriya Bet Member (Aalenian) is the oldest unit, 45 m in thickness, and mainly consists of clast-supported polymictic (pebbly) conglomerates, deposited in an alluvial fan environment (Biswas, 1977). The Hadibhadang Shale Member (Bajocian) is 180 m thick and has a shale-dominated succession with three prominent sandstone bands exposed in the foothills of the northern escarpment. The Hadibhadang Sandstone Member (Bathonian) is exposed on the northern cliff as well as the higher back slope of the Island. It is 85 m in thickness and mainly comprises mixed siliciclastic carbonate sediments and is capped by sandy allochemic limestone which is correlatable to the Raimalro limestone of the Goradongar Formation of the Patcham Island (Biswas, 1977, 2016). The Gadhada Formation (Callovian) is 385 m thick and is divided in two members, namely the Ratanpur Sandstone and the Bambhanka. The Ratanpur Sandstone member comprises of 195 m thick, mixed siliciclastic-carbonate sequence intercalated with shales, exposed along the back slope of the island; the micritic sandstone of this member contains abundant *H. lobosensis*. The Bambhanka Member is a 190 m thick shale-dominated sequence with few fossiliferous ferruginous sandstone and limestone bands mainly exposed in the southern tip of the Khadir Island and the Kakinda bet.

The Bela Island succession comprises the upper part of the Hadibhadang Shale Member, the Hadibhadang Sandstone, and the Ratanpur Sandstone members. The Hadibhadang Shale Member is 46 m thick, exposed along the base of the northern escarpment, and mainly consists of shales intercalated with hard sandstone bands. The Hadibhadang Sandstone Member is 79 m thick, characterized by micritic sandstone with a sandy allochemic limestone band. The Ratanpur Sandstone Member is 138 m thick, and comprises mixed siliciclastic-carbonate sediments, limestone, and shales; the thinly bedded sandy allochemic limestone (SAL) bears the *H. lobosensis*.
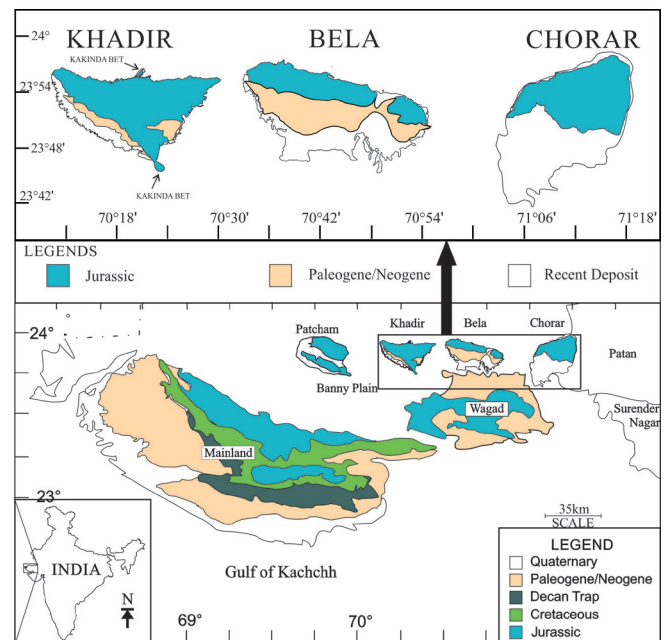

Figure 1. Generalized geological map of Kachchh showing the studied locations (Modified after Biswas and Deshpande, 1975).

The Mesozoic succession of the Chorar Island is 109 m thick (Patel *et al.*, 2018) and comprises rocks of the Khadir and the Gadhada formations. The Hadibhadang Shale and Hadibhadang Sandstone members of the Khadir Formation, and the Ratanpur Sandstone Member of the Gadhada Formation are developed in an elliptical dome near the Avaal village (Patel *et al.*, 2018). The Hadibhadang Shale Member is a 23 m thick shale-dominated sequence intercalated with thin bands of micritic sandstone. The Hadibhadang Sandstone Member is 31 m thick and comprises fossiliferous mixed siliciclastic-carbonates rocks with a 2.7 m thick coralline limestone band at the top. The sandy allochemic limestone band contained abundant well-preserved burrows of *H. lobosensis*is (Darngawn *et al.*, 2019). The Ratanpur Sandstone Member is exposed on the periphery of the dome. It is 55 m thick and comprises thick white friable cross-bedded sandstone overlain by thickly bedded ferruginous sandstone (Patel *et al.*, 2018, Darngawn *et al.*, 2018, 2019).

MATERIALS AND METHODS

Specimens of *Hillichnus lobosensis* are abundantly observed on the weathered rock surfaces of the Middle Jurassic rocks from the Khadir, Bela, and Chorar Islands. The materials described in the present work are from two different stratigraphic levels, the sandy allochemic limestone of the Hadibhadang Sandstone and the Ratanpur Sandstone members of the Chorar and the Bela Islands and micritic sandstone of the Ratanpur Sandstone Member of the Khadir Island.

Different levels of the *H. lobosensis* are exposed abundantly on bedding surfaces. The identification,

correlation, and comparison of each trace with neighboring burrows are easy owing to dissolution and erosion. The different levels of morphological features of the *Hillichnus lobosensis* are photographed in the field and in some cases, the *H. lobosensis* bearing samples and rock samples are collected for sedimentological and ichnological analysis. Each of the preserved levels is observed, and morphologically aided categories are assigned to their respective level, compared, described, interpreted, and discussed with their paleoenvironmental significance.

SEDIMENTOLOGY OF *HILLICHNUS LOBO-SENSIS* BEARING HORIZON

The compositional and textural analysis of the *H. lobosensis* bearing horizon of the three separate localities revealed mixed siliciclastic-carbonate sediments. It comprises sandy allochemic limestone in the Bela and the Chorar Islands and micritic sandstone in the Khadir Island. A detailed investigation was carried out on sedimentology and stratigraphy by Patel *et al.* (2018) and ichnology and sequence stratigraphy by Darngawn *et al.* (2018, 2019) of the Chorar Island.

The sandy allochemic limestone (SAL) is part of the Hadibhadang Sandstone Member (Bathonian) of the Khadir Formation in Chorar Island. It is 1.5 m thick, hard, and massive; light yellow to dark brown, highly fossiliferous (bivalves, gastropods, echinoid spines and shell fragments) and bioturbated, containing *Hillichnus* and *Protovirgularia* (Darngawn *et al.*, 2018). Petrographically, it shows allochemic components (~40%; shell fragments, algae, pellets and ooids, echinoids spines, foraminifera, and brachiopods), micrite constitutes about ~30%, and siliciclastic component (~30%). The siliciclastic component comprises fine to medium quartz grains which are angular, and moderately sorted floating in a carbonate matrix. Digenetic modification of micrite and shell fragments forms sparite to large-size cleavable calcite crystals; occasionally micrite is replaced by ferruginous material.

The *Hillichnus* is also observed in SAL and micritic sandstone of the Ratanpur Sandstone Member (Callovian) of Gadhada Formation in Bela Island and Khadir Island respectively. SAL of Bela Island is flaggy in nature and intercalated with thin shales. It is hard, compact, and dirty yellow in colour. Each flaggy layer is centimeters thick, poorly fossiliferous, consisting of shell fragments of bivalves. The *Hillichnus*-bearing beds are highly bioturbated by different traces consisting of *Arenicolites, Diplocraterion, Helicolithus, Hillichnus, Lockeia, Monocraterion, Palaeophycus, Phycodes, Planolites, Rhizocorallium, Skolithos,* and *Taenidium*. Petrographically, it shows >60% carbonate (allochems: ~20%, micrite: ~40) and clastic grains, (~40%). Quartz is fine-grained, well-sorted, subangular to subrounded floating in a carbonate matrix.

The *Hillichnus* bearing micritic sandstone of Khadir Island is 0.5 to 1m thick, hard, compact, and dirty yellow in colour and consists of abundant fossil fragments of bivalves and trace fossils (*Diplocraterion, Monocraterion, Ophiomorpha,* and *Skolithos*). Three samples are analyzed petrographically, which shows compositional variations; quartz 60-70%, micrite, 25 to 30%, and allochems, 3%-10%. Quartz is medium-grained, well sorted, subangular to subrounded with point contact, or occurs as floating grains.

SYSTEMATICS

Ichnogenus: *Hillichnus* Bromley et al. 2003

Diagnosis: Complex trace fossil comprising several contrasting parts. Two concentric structures, a basal segmented structure and within this a basal tube, run axially along the base and give rise to lateral spreiten or feather-like structures. The individual spreiten or feather-like structures arise alternately on either side of the basal segmented structure. Arising by branching from the basal tube, a series of sand- and mud-lined tubes curve upward into a nearly vertical position. These rising tubes may stand in a straight line, as a zigzag line, or in irregular groups. The general course of the trace fossil is horizontal, straight to curving, or rarely looping (Bromley *et al.*, 2003).

Remarks: The complex trace fossil *Hillichnus* is characterized by lateral lamellae and tubules that can be differentiated from *Jamesonichnites heinbergi* by the presence of narrow splayed rising tubes. It also differs from *Lophoctenium,* by basal tube and associated vertical structure. The presence of bilateral branches and irregular main stem in *Lobichnus* and the branches that join to form the main stem in *Phycodes* differentiate them from *Hillichnus* (Bromley *et al.*, 2003). *Hillichnus lobosensis* of Bromley *et al.* (2003) comprises five distinctive morphological levels that differentiate it from *Hillichnus agrioensis* of Pazos and Fernández (2010) which is composed of 4 morphological levels. The feather-like branch with basal tubes is characteristic of Level C in *Hillichnus lobosensis* while similar structures are observed at level B in *Hillichnus agrioensis*.

Ichnospecies: *Hillichnus lobosensis* Bromley *et al.* 2003
(Plate I-IV)

Diagnosis: Same as ichnogenus
Description: Complex multilevel morphological structure exhibits five morphological Levels from E to A; Level D-C in Khadir Island, Level E-A in Bela Island, and Level D-B in Chorar Island. The specimens observed at two different stratigraphic levels show variation in dimension and preservation.

Level A

Level A consists of a series of delicate horizontal, discontinuous arcs arranged in line but alternate with the opposite side of the tube (Pl. I, Fig.1). The structures are devoid of lining and are preserved as arcuate depression.

EXPLANATION OF PLATE I

Figure 1. Level A of *Hillichnus lobosensis* showing horizontal, discontinuous arcs in SAL of the Bela Island. Fig. 2. *H. lobosensis* showing the basal tubes of Level B. Fig. 3. Level B of *H. lobosensis* showing dark brown lined, undulated, wrinkled, irregular and elongated tubes overlapping with leaf-like branches of Level C.

It is the lowermost part of the structure and is occasionally exposed to erosion. The structure is preserved parallel to the bedding plane and occurs in association with Level E which is a vertical tube (Pl. I, Fig.1). The occurrence of such multi-level trace fossils is fairly common within the same bedding plane (Bromley, 2003).

Level B

Level B is well preserved and comprises centrally placed thinly lined straight to curve 10cm long basal tubes with a diameter of 2 cm, preserved as shallow grooves and characterized by transversely well-developed wrinkles (Pl. I, Fig. 2); occur as straight to wavy lined tubes filled with host sediments partly eroded (Pl. I, Fig. 2) forming grooves and shows prominent lined tubes with moderately developed transverse wrinkle. The infill sediments of the tube are

similar to the host separated by the dark-colored lining of the tube (Pl. I, Fig. 3).

Level C

Level C is leaf/feather-like branching basal tubes that become distally more slender and shows maximum variation in morphological features and dimensions. It also overlaps with other morphological levels, representing the complexity of the structure. In Chorar Island, Level C is preserved as a well-developed leaf or feather-like structure with individual branches alternating on either side of the basal tube parallel to the bedding plane (Pl. II, Fig. 1, 2) and often eroded and smoothen the burrows (Pl. II, Fig. 2). The tube length varies from 16.2 to 26.4 cm. and a diameter of 2.0 cm. Some specimens of the Khadir Island show similar side branching tube patterns (Pl. II, Fig. 3) to the Chorar Island but the
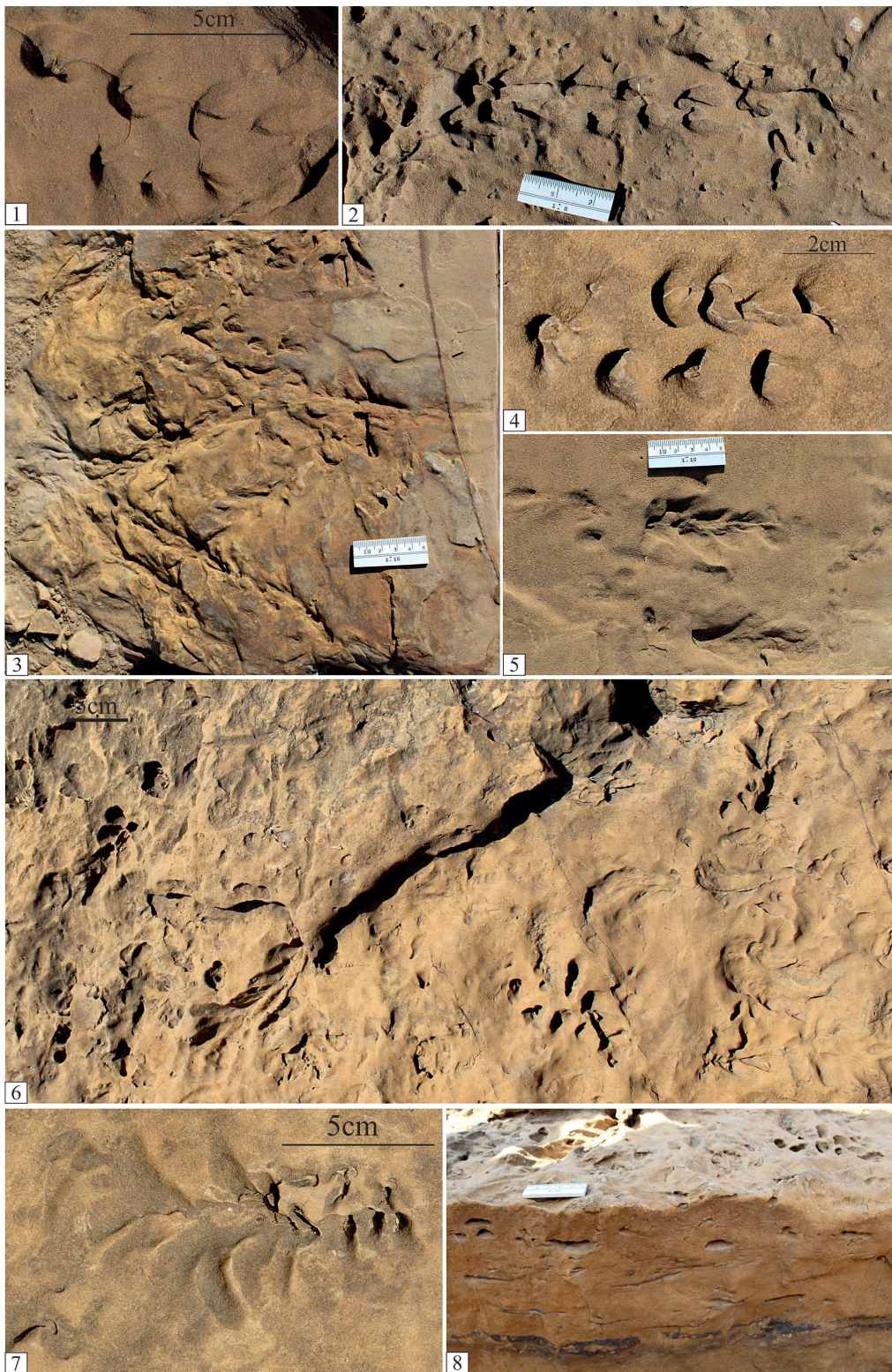
EXPLANATION OF PLATE II

Fig. 1. Level C of *H. lobosensis* showing well-developed horizontal leaf or feather branch with prominent undulated and wrinkled basal tube and Fig. 2. Leaf-like branches which are smoothened by erosion in the Chorar Island. Fig. 3. and Fig. 4. Less prominent leaf-like Level C of Khadir. Fig. 5. Overlapping of Level C of *H. lobosensis* with a prominent basal tube with the overlying sediments and the crowded nature masking the leaf-like branches in the Bela Island. Fig. 6. Level C with remnants of the broken basal tube.
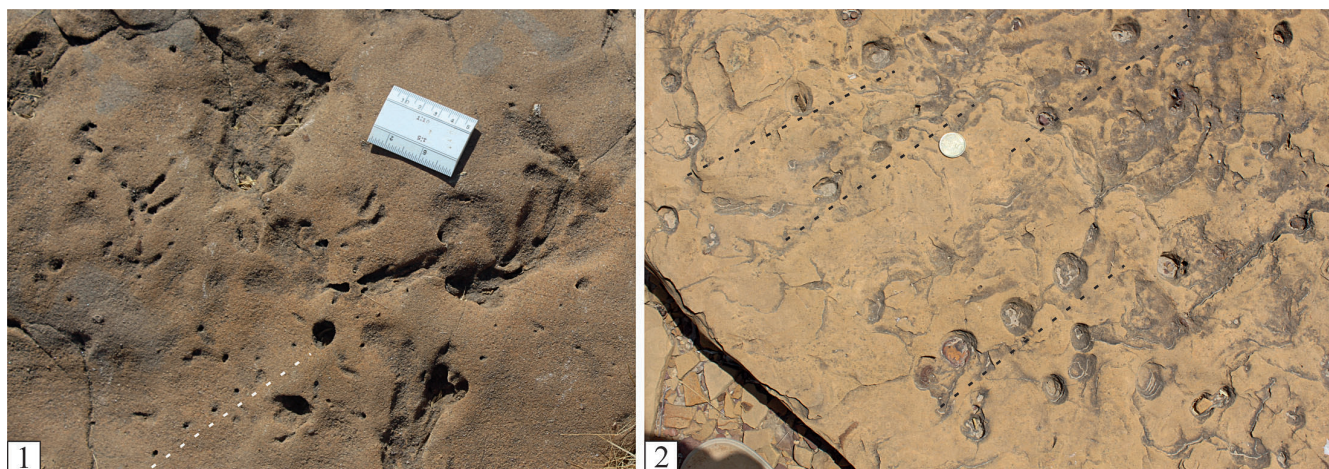
majority of specimens show comparatively less prominent (Pl. II, Fig. 4) and smoother basal tubes and lamellar branches with variation in tube length from 5.0 cm to 8.0 cm. and diameter of 1.0 to 1.5 cm. the Bela Island specimens also show overlapping feather-like structure (Pl. II, Fig. 5) however, the lateral branches are rather shorter, gently curving towards the distal end; the basal tube is prominent, length is of 19.0 cm with a diameter of 1.0 cm. The leaf/feather-like structures are graded into lined tubes without branches or inclined tubes suggesting a transition from Level C to Level B (Pl. II, Fig. 6).

EXPLANATION OF PLATE III

Level D of *H. lobosensis* Fig. 1. the rising tube arises in pairs and Fig. 2. with prominent basal tube where the rising tubes arise from the side in alternate pattern in the Khadir Island. Fig. 3. Crowded Level D of *H. lobosensis* with the prominent basal tube but eroded inclined tube, Fig. 4. Level D of *H. lobosensis* occurring parallel with a series of vertical tubes belonging to Level E. Fig. 5. Level D of *H. lobosensis* showing prominent basal tube with the inclined tube arising from the side in the Bela Island. Fig. 6 Crowded Level D of *H. lobosensis* where the basal tube is concealed while the inclined tube occurs in pair or zigzag. Fig. 7. Transition of level C to Level D. Fig. 8. Vertical view of *H. Lobosensis* in Chorar Island showing level D on top with the basal tube appearing as horizontal tubes and the feather-like protrusion from Level C appearing as thin curved lines.

Level D

Level D is characterized by rising incline tubes that are arranged in a zigzag or pair forming a straight line exposed with basal tubes in a few cases. The basal tube is often unexposed thereby revealing the incline pared tubes (Pl. III, Figs. 1,3). The structures are often crowded and overlap with one another where individual level identification becomes difficult on the Khadir Island, even though, rising tubes are observed in pairs (Pl. III, Fig.1) and alternating with each other (Pl. III, Fig. 2). The basal tubes are either covered by sediments (Pl. III, Figs. 1,4), prominently preserved (Pl. III, Fig. 2), eroded (Pl. III, Fig. 3) or faintly visible (Pl. III, Figs. 5,6). The rising tubes are eroded leaving hollow tubes (Pl. III, Figs.1,2,4). The tube diameter is ranging from 0.8 cm to 1.8 cm. In the Bela Island, the structure is often crowded (Pl. III, Fig. 3) and characterized by oblique branching tubes arising from the basal tube, rise nearly upward at higher levels and also occur alongside Level E (Pl. III, Fig. 4). At this level the feather-like branches disappear and the structure is dominated by short inclined tubes (Pl. III, Fig. 5) with a diameter of 1.0 - 1.2cm. The Chorar Island specimen shows the presence of a slightly inclined tube that shows zig-zag nature with or without a basal tube (Pl. III, Fig. 6) as well as the transition from Level C to Level D (Pl. III, Fig. 7), tube diameter ranges from 0.8cm to 1.6cm. Pl. III, Fig. 8, shows a vertical section of the *H. lobosensis* bearing host rock with variable dimensional horizontal tubes on the vertical face of SAL and inclined vertical pair burrows of Level D in series at the top surface.

Level E

It is characterized by linear or zigzag vertical tubes occurring in a single, or pairs resembling *Arenicolites*. The tubes are small, vertical, unlined, appear as single or pair burrows and arrange in series or isolated forms on the Khadir Island (Pl. IV, Fig. 1). It has variable downward extension and diameter from 0.2 cm to 1.1 cm. The 0.6-1.2 cm diameter tubes occur in series; sometimes it is parallel with inclined tubes of Level D (Pl. IV, Fig. 2) in Bela Island.

DISCUSSION

Bromley *et al.* (2003) described the five morphological levels (E to A) of *H. lobosensis* with a distinct feature of each level. The specimens described herein show different morphological levels (E- A) on the bedding surface of sandy allochemic limestone of the Bathonian age in Chorar Island, sandy allochemic limestone, and micritic sandstone of Callovian age in the Bela and the Khadir Islands respectively. This unique complex trace fossil *Hillichnus* is endogenically produced by tellinacean bivalves during locomotion and deposit feeding (Bromley *et al.*, 2003; Ekdale and Ekdale, 2018). The combined locomotion and feeding behaviour of the complex trace fossil *H. lobosensis* shed light on the possible pre-adaptive functional behavior of the trace maker. The sudden appearance of deposit-feeding mode in the trace maker, tellinacean bivalve during the Bathonian-Callovian is addressed in terms of the evolutionary and environmental aspects in the following paragraphs.

A brief overview of Tellinacean evolution

The *H. lobosensis* is interpreted as the locomotion and feeding structure of a mobile sediment-water interface deposit feeder, such as tellinacean bivalves, although its body fossils records were postdated to the trace fossils (Kondo and Sano, 2009). Nara *et al.* (2014) describe the *Hillichnus* from the Jurassic deposits of the Sakamoto Formation, Kumamoto Prefecture, Southwest Japan, and argued that the evolutionary aspects be discussed.

The relationships of Tellinoidea to other bivalves were reviewed by Pohlo (1982) who concluded that a derivation from the Astartidae was the most likely scenario. But based on molecular results, Taylor *et al.* (2007a) suggest the tellinoideans are positioned distantly on the family tree relative to the Astartidae. Taylor *et al.* (2007a) show four cardiid species that form a highly supported clade, with a long leading branch, which is sister to the Tellinoidea, and this relationship was reported by Campbell (2000), Steiner and Hammer (2000), Dreyer *et al.* (2003) and Taylor *et al.* (2005, 2007b). The status and affinities of these Early Mesozoic tellinoidean-like bivalves are not at all well resolved but for instance, it is suggested as a closer similarity of the Tancrediidae to the Cardioidea (Saul and Popenoe, 1962).

Tellinacean bivalves appeared in the Late Triassic (Cox *et al.*, 1969; Pohlo, 1982) and evolved through the remaining Mesozoic and Cenozoic Eras and developed different feeding mechanisms. The late Triassic tellinacean forms are classified as Tancrediidae, and Sowerbyidae, and later two more short-lived families Quenstedtiidae and Unicardiopsidae evolved during the Jurassic. Quenstedtiidae disappeared in the early Jurassic while Unicardiopsidae and Sowerbyidae disappeared at the end of the Jurassic. Tancrediidae continued up to the Cretaceous with more diversification of tellinoideans; Tellinidae and Icanotiidae evolved in the early Cretaceous while Donacidae and Psammobiidae family evolved during the Late Cretaceous (Pohlo, 1982).

The paleontological evidence indicates that the earliest Mesozoic Tellinacean families (Tancrediidae, Quensedtiidae, and Unicardiopsidae) were suspension feeders which lived in vertical burrows in shifting sand (Pohlo, 1982). The suspension-feeding mode continued as shown by the earliest members of the Donacidae, genus *Protodonax* from the Upper Cretaceous which bears a small pallial sinus similar to the genus *Corbicellopsi*s of the Tancrediidae (Volkes, 1945).

Bathonian revolution in behavioral mechanism in Tellinacean bivalves

Mesozoic witnessed a dramatic diversification of invertebrates due to the end-Permian and Early Triassic mass extinctions (Gregory, 2002). It is corroborated by the breaking-up of Pangea and the drifting of continents resulting in new oceans and oceanic circulation. The eustatic sea-level rise provided ample space for the flourishment of marine life resulting in the appearance of new biological entities in shallow marine settings globally. The Kachchh basin also witnessed global transgression indicated by marine shoreface sedimentary deposits of Bajocian-Callovian in far eastern parts which are well exposed in Khadir, Bela, and Chorar Islands.

The paleontological evidence suggests that the Late Triassic tellinacean bivalves were infaunal suspension feeders while deposit feeders (tellinidae) appeared in the Early Cretaceous (Pohlo, 1982). The present study documents the various morphological characteristics of the trace fossils *H. lobosensis* showing similar evidence of preadaptive behavior in the mode of feeding in tellinacean bivalve during Bathonian-Callovian (Middle Jurassic). The preadaptive

behavioral adaptation of tellinacean bivalves during Bathonian-Callovian coincides with the global eustatic sea level rise. The Bathonian-Callovian age witnessed a global eustatic sea level rise (Haq *et al.*, 1987; Hallam, 1988), and this global eustatic sea level rise is already reported by Darngawn *et al.* (2019) from the Chorar sequence from where *Hillichnus* is observed.

The well-developed morphological Levels E-A indicate dual behavioral activities such as feeding and locomotion. Pohlo (1982) envisaged the earliest tellinoideans, such as Tancrediidae, were suspension feeders with short, separate siphons similar to recent *Donax*, while deposit-feeding Tellinidae with longer siphons evolved later in the Mesozoic (Cretaceous). He also opined that the trace maker *Tellinacean* bivalves developed feeding behavior during early Cretaceous (*Tellinidae*) based on paleontological evidence (shell structure) with long inhalant and exhalant siphons. The inhalant siphon is used for feeding and respiration where the siphon extended many centimeters from the aperture of its burrow, sucking up quantities of sediment and producing a trace on the seafloor (e.g., Häntzschel, 1934; Schäfer, 1962; Cadée *et al.*, 1994). The inhalant siphon may also probe horizontally within the sediments successively producing feather-like pairs or unpaired lateral lamellae (Level C). The orientation of living bivalve burrowers with sagittal plane vertical is often reflected by the siphonal region and lateral view outlines (Stanley, 1970). The vertical and horizontal life orientation of the sagittal plane in the tellinacean bivalves is an adaptation to siphonate deposit feeders (Stanley, 1970). The horizontal basal tube is envisaged to be lateral movement of the tellinacean bivalves which may be the preadaptive morphological features concurrently supported by the long siphons (Fig. 2).
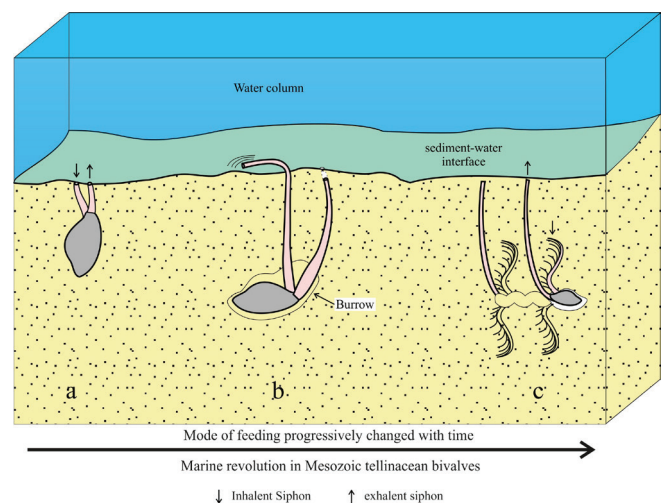

Figure 2. Illustration of tellinacean bivalves is showing the different feeding modes. a. The shallow burrowing infaunal suspension feeding early tellinacean bivalve (Late Triassic) possess short split siphons which maintain the contact with upper surface for feeding and respiration as well as for throwing the waste. b. Deep burrowing Bathonian (Middle Jurassic) tellinacean bivalve possess long split siphons and has also change their orientation, the inhalant siphon stretches out to suck the water and detrital organic particles and exhalant siphon terminate few mm below the surface to throw their waste while inhalant siphon may also ingest from within the sediments as shown in c.

The exhalant siphon lies a centimeter or so beneath the sediment surface (e.g., Hylleberg and Gallucci, 1975) to discharge faeces and respiratory water. The fast-burrowing bivalves *Tancredia* and *Corbicellopsis* were able to cope with shifting substrates and thus were also adapted to life in shallow, high-energy environments (Fürsich and Thomsen, 2005). Tancrediidaen genus *Corbicellopsis* Cox 1929 (clam) range in age from Sinemurian (196.5 Ma) (Aberhan, 1992) to Tithonian 145.5 Ma (Cox 1929) and is recorded from the Jurassic of Chile (Aberhan, 1992), Germany (Scholz, 2005), Gadhada Formation (Callovian) of the island belt zone of Kachchh India (Fürsich 2006), and Spain (Fürsich *et al.*, 2001).

The ichnological evidence of the Kachchh basin shows deposit-feeding behavior by the trace maker as early as the Bathonian indicated by well-developed Level C of *H. lobosensis. Corbicellopsis,* the predecessor of Tellinidae appeared in the Bajocian (Hallam, 1977; Quilty, 1977)*,* and might have developed deposit-feeding behavior without pronounced change in the internal shell structure using preadaptation. The term preadaptation in evolution refers to a large change in function accomplished with little or no change in structure (Ridley, 2004). Different workers have mixed opinions on the feeding behavour of *Corbicellopsis* as a suspension feeder (Pohlo, 1982; Fürsich and Thomsen 2005; Fürsich *et al.*, 2001) and considered to be a facultative mobile deep infaunal deposit feeder (Danise and Holland, 2017) of shallow marine environments (Fürsich *et al.*, 2001). The trace maker might also develop dual feeding behavior analogous to *Macoma* (Levinton, 1991) which is also reflected by Levels D and E which serve as a connection with the seafloor for water circulation (Bromley *et al.*, 2003) and can also serve as a means for suspension feeding behaviour. The documented multi-morphological trace fossil, *H. lobosensis* shows locomotion and feeding behavioural activities of the trace maker suggesting the marine revolution in tellinacean bivalves during the Bathonian-Callovian age. This behavioural revolution in tellinacean bivalves corroborates with global marine transgression during the Bathonian-Callovian which provides ample space for flourishing and diversifying in shoreface environments.

In the absence of body fossil records of deposit-feeding tellinacean bivalve before the Early Cretaceous Period (Pholo, 1982), the ichnological data provide important evidence of an early evolutionary modification. The presence of *H. lobosensis* from the Bathonian-Callovian of the Kachchh basin served as evidence for the evolution of deposit-feeding tellinacean bivalves which is much earlier than the body fossils records.

Environmental Implications

The preservation of *H. lobosensis* relies on different substrate conditions and environmental settings. To assess the paleoenvironmental interpretation, the associated sedimentological and ichnological evidence is integrated to strengthen the interpretation. *Hillichnus lobosensis* is known to be spread in a range of environments and stratigraphic positions in different parts of the world. Its earlier occurrences were reported from the deep-water turbidities (Clifton, 1981; Bromley *et al.*, 2003), deep-sea submarine

canyons and fan (Farmer and Miller, 1981; Bromley *et al.*, 2003), shallow nearshore (Deméré and Walsh, 2003), and shallow marine tidal sand deposits (Nara *et al.*, 2014). The palaeobathymetric occurrence of *H. lobosensis* is also estimated to be at 500 to 1500 m water depth (Clifton, 2008). The Kachchh specimens are observed in SAL and micritic sandstone which consists of well-sorted medium to fine-grained, subangular to subrounded quartz, allochems, and matrix indicating shoreface environment where the shifting of substrates compromise energy conditions and depth-related parameters.

A detailed study was carried out on sedimentology and stratigraphy (Patel *et al.*, 2018) and ichnology (Darngawn *et al.*, 2018) of the *Hillichnus lobosensis* bearing horizon of the Chorar Island. It is observed in sandy allochemic limestone; mostly showing Level D to B, but Level C which is well developed, large, and crowded in nature suggests intensive feeding behavior in a nutrient-rich substrate. The *H. lobosensis* associated with horizontal trace fossils such as *Protovirgularia* suggest unconsolidated, well-oxygenated, low-energy stable substrate conditions. The associated allochemic components (algae, bivalves shell fragments, echinoids spines, forams and brachiopods with ooids) and well-sorted fine clastics indicate a lower-middle shoreface environment (Patel *et al.*, 2018; Darngawn *et al.*, 2018 and 2019).

The micritic sandstone of Khadir Island shows variation in clastic and nonclastic components but is mainly dominated by medium-grained quartz, allochems, and micrite. The *Hillichnus lobosensis* structures are crowded, mainly represented by Levels E to C and are dominated by Levels D and E. The dominance of a relatively smaller diameter of vertical shafts (Level D and E) suggests a change in substrate condition or taphonomic aspects. It is also associated with *Diplocraterion, Monocraterion, Ophiomorpha,* and *Skolithos* which are the member of Skolithos Ichnofacies (Seilacher, 1967; Frey, 1978). Medium size quartz grains with ooids, Level E to C of *H. lobosensis* and associated trace fossils observed in micritic sandstone of Callovian indicate unconsolidated, shifting sediments in slightly agitating condition in shoreface environment.

The occurrence of *H. lobosensis* on Bela Island is age equivalent to the of Khadir Island, its lateral lithological variants represent by mixed siliciclastic-carbonate sediments. These structures are observed in sandy allochemic limestone and are comparatively smaller than the Chorar Island and show the dominance of Levels C and D. It is associated with *Arenicolites, Diplocraterion, Helicolithus, Lockeia, Monocraterion, Palaeophycus, Phycodes, Rhizocorallium* and *Skolithos* which are a typical member of mixed Skolithos-Cruziana Ichnofacies (Patel *et al.*, 2014; Joseph *et al.*, 2012). This ichnofacies (Seilacher, 1967, Pemberton *et al.*, 1992) indicate the soft, unconsolidated, and moderately shifting substrate. Sandy allochemic limestone comprises medium grain, poorly sorted, and angular quartz grain (30-40%) floating in the micritic matrix a carbonate-prone environment with fluctuating energy conditions in the shoreface environment.

Sedimentological and ichnological characteristics of the *Hillichnus lobosensis* bearing horizons of Khadir, Bela, and Chorar Islands suggest deposition of the sediments took place in low to moderate energy conditions in the clastic and

nonclastic prone shoreface environment.

CONCLUSIONS

The morphological analysis of the complex dual behavioural pattern of *H. lobosensis* of the Island Belt Zone of Kachchh Basin, western India, suggests the following inferences.

1. The Bathonian *H. lobosensis* of the Chorar Island suggest a marine revolution in Tellinecean bivalves, where suspension feeding mode switched over to deposit feeding mode and subsequently continued in Callovian deposits of the Khadir and the Bela Islands.
2. It is observed in sandy allochemic limestone on Chorar Island (Level D-B) and Bela Island (Level E-A) and micritic sandstone on Khadir Island (Level E-C).

3. The preserved different levels of *Hillichnus lobosensis* and their abundance is solely due to solution activities rather than the taphonomic modifications.
4. The multi-morphological structures *Hillichnus lobosensis* suggest the change in inhalant siphonal function resulted in endogenic locomotory and detritus probing habit in tellinacean bivalves.
5. The sedimentological and ichnological evidence indicates the soft unconsolidated shifting substrate in shoreface environmental settings.

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