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Fluvial trace fossils in the Middle Siwalik (Sarmatian-Pontian) of Darjeeling Himalayas, India

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Trace fossils that record animal and plant activity are described for the first time from the Middle Siwalik, Neogene deposits of Darjeeling Himalaya. Sedimentary facies association attests to a channel-interchannel floodplain fluvial setting. The intimate association of the burrows with phytoliths, rhizoliths, leaf compressions and coal lenses suggest that the tracemakers dominated a floodplain habitat. Point bar deposits host a low diversity *Planolites-Naktodemasis-Macanopsis-Cylindricum* equilibrium ichnocoenosis in the heterolithic fine sandstone-siltstone-shale facies that alternates with dense, monospecific colonization of *Planolites* as opportunistic pioneers relocating under stressed condition. Interlayered floodplain deposits in the fluvial successions preserve enigmatic large diameter, vertical tubes within thin to thick-bedded, dark silty shale facies. These tubes bear mixed characters assignable to both crayfish burrows and large-diameter rhizoliths. Further work on these tubes is necessary to make more accurate interpretations of those structures. Shallow to moderate burrow depths; intermittent, short-lived colonization events and preservation of rhizoliths and rhizohalos under fluctuating moisture content indicate short-term fluctuations of a relatively high water table (close to the paleosurface) in an imperfectly drained proximal floodplain setting. Ichnotaxa distribution and their inferred ethology provide significant faunal data that may put constraints on the reconstruction of Middle Siwalik depositional environment.

1. Introduction

The Siwalik basin contains a thick pile of alluvial deposits formed in a long, narrow, east-west trending foreland basin lying to the immediate south of Himalayan orogenic belt (Valdiya 1998; Vaidyanadhan and Ramakrishnan 2008). The study area (figure 1a) is in the foothills of eastern Darjeeling Himalayan segment where it exposes the Middle Siwalik Successions (Mallet 1875; Gansser 1964; Raju 1969; Chaudhri 1972; Banerjee and Banerjee 1982). Essentially continental, fluvial

Siwalik deposits (Kumar *et al.* 2004) are overridden in the north by Precambrian metamorphites (Dahling Group) across a thrust. A thin slice of coal-bearing Gondwana deposits is exposed as a tectonic window in between Precambrian rocks and the Siwaliks, which is traceable from Kalijhora in the west and Bagrakot in the east.

One road-cut section at Sevoke road (Section-I; N26 54'2.49"/E088 28'15.07") and two river sections along Leesh river (Section-II; N26 55'16.3"/E088 32'34.8") and Gheesh river (Section-III; N26 54'19.6"/E088 36'46.5") in the study area have

Keywords. Trace fossils; Cenozoic; fluvial; molasse deposits; Middle Siwalik; Geology; biogeosciences.

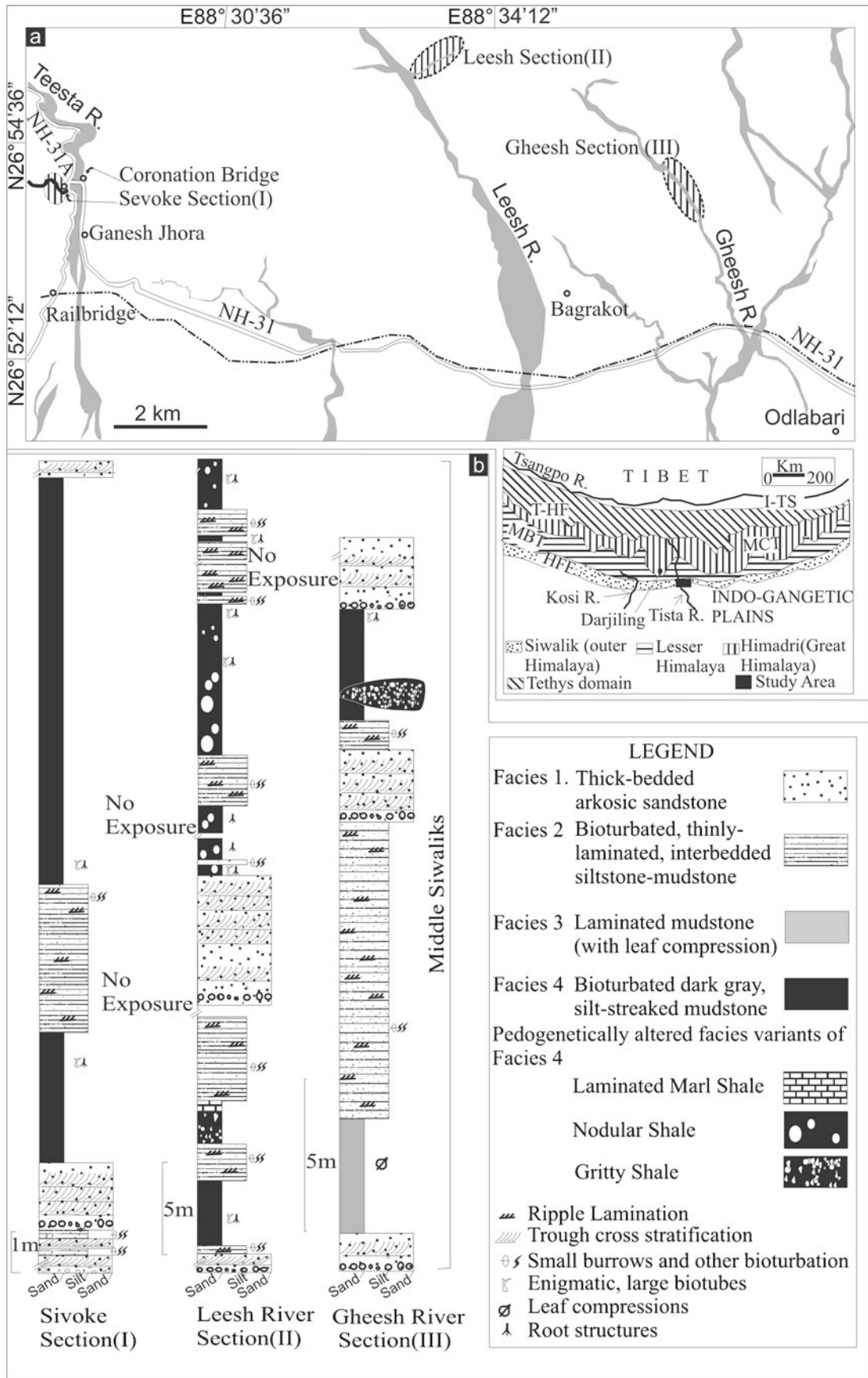


Figure 1. (a) Location map of the study area (inset regional map after Valdiya 1998) and (b) lithological successions of the Middle Siwaliks at Sevoke road cutting, Leesh River and Gheesh River sections.

been studied in detail (figure 1b) primarily for their rich ichnological content.

A dearth of robust mammalian fossils and poorly preserved macroflora in Neogene Siwalik deposits, particularly in middle Miocene strata of Darjeeling Himalayas have forced researchers to interpret paleoenvironments based largely on sedimentological studies. Depositional environments have been interpreted as continental-fluviatile, alluvial fan-braided channel and meandering channel-floodplain-lacustrine (Mallet 1875; Gansser 1964; Acharyya *et al.* 1976; Banerjee and Banerjee 1982; Jain and Sinha 2003; Sanyal *et al.* 2005; Kundu *et al.* 2012). Few ichnological assessments available on Siwalik deposits are from upper Siwalik strata of Punjab Himalayas (Tandon and Naug 1984) and from areas to the west (Agarwal and Singh 1983). Significant ichna in the deposits of the study area have been overlooked until recently.

The present work describes the trace fossils from Middle Siwalik rocks of Darjeeling Himalayan area emphasizing on their morphological variations and ethological significance that may help to constrain the reconstruction of Siwalik depositional milieu based on new faunal data.

Four sedimentary facies types have been identified in the study area (figure 1b). These are respectively, thick-bedded arkosic sandstones, with frequent pebbly inter-layers (Facies-1); bioturbated, thinly interbedded, fining up sandstone-siltstone-shale (Facies-2); laminated mudstone with abundant leaf compressions (Facies-3) and bioturbated dark gray, silt-streaked mudstone (Facies-4). The sedimentary succession in the study area is interpreted as braided river channels with inter-channel floodplain deposits in which Facies-1 represents channel deposits, Facies-2 represents point bar deposits with fining-up, ripple laminated to ripple-drift, cross-laminated intervals. Facies-3 and Facies-4 represent levee and proximal floodplain deposits, respectively. Presence of laminated marl shale and gritty and nodular marl shale are tentatively designated as facies variants of floodplain mudstone (Facies-4) that experienced varying degrees of pedogenic modification (e.g., Dubiel *et al.* 1992; Dubiel and Hasiotis 2011). The main occurrence of large-diameter, vertical tubes are in floodplain mudstones, whereas smaller burrows occur predominantly in levee and point bar deposits.

Neogene deposits of Siwalik Foreland Basin of Darjeeling Himalayas, exposed in road cuts and river sections along an east–west traverse between Sevoke (Darjeeling District) in the west and Malbazar area (Jalpaiguri District) in the east (figure 1a–b) were objectively studied in detail for their ichnological content. Facies-specific ichnotaxa were searched within thin, laminated

sandstone-siltstone-shale facies and also within dark gray, silt-streaked mudstone that were rich in ichnological content. Attributes of these ichnotaxa, their lithofacies association and common association with leaf fossils, phytoliths and rhizoliths were examined in order to glean possible paleoecological and paleohydrological information that may constrain the interpretation of the paleoenvironment and post-depositional histories of these sediments.

2. Materials and methods

Trace fossils were described as eight distinct morphotypes based on architectural and surficial morphologies and burrow-fill sediment character (Häntzschel 1975; Hasiotis 2004). Trace fossil assemblages in the present work objectively embrace all trace fossils/morphotypes occurring within a single rock unit (single bed, bed couplet, recurrent interbeds) irrespective of whether or not the traces were produced simultaneously or as temporally separated bioturbation events (following definition of Bromley 1990). Seilacher's (1964, p. 306) original English definition of the term 'ichnocoenoses' was simply as 'trace associations'. However, from their lithofacies associations (within Facies-2 and 4), trace fossil assemblages have been grouped into ichnocoenoses (e.g., Hasiotis 1990; Hasiotis and Mitchell 1993; Smith *et al.* 2008a, b). Monospecific *Planolites* isp. in Facies-2 and enigmatic tubes in Facies-4 were given status of separate trace fossil assemblages following Keighley and Pickerill (2003).

Predicted moisture requirement of the probable trace makers (Hasiotis 2004, 2007, 2008) of these ichnocoenoses were used, in addition to other consequential, supportive pedogenetic evidences (e.g., Glinski and Lipiec 1990), for deciphering the paleohydrologic conditions of the host sediments after deposition.

3. Result: description of morphotypes

3.1 Type 1 – *Problematica* (large-diameter, vertical tubes) (figures 2–4)

Description: These are near vertical, commonly parallel-sided, silt or mud-filled tunnels; cross-sectional diameter range between 1.05 and 7.2 cm with common terminal enlargements (up to 20.5 cm). Multiple tunnel enlargements are also present (figure 2a). Fine silt and clay lining with variable thickness along the length of tube is observable on bedding plane and in section (figure 2b), whereas some tunnels are coarse, with linings of sand (figures 2c, 3). Sediment fills of contrasted composition (clay and sand) co-exist

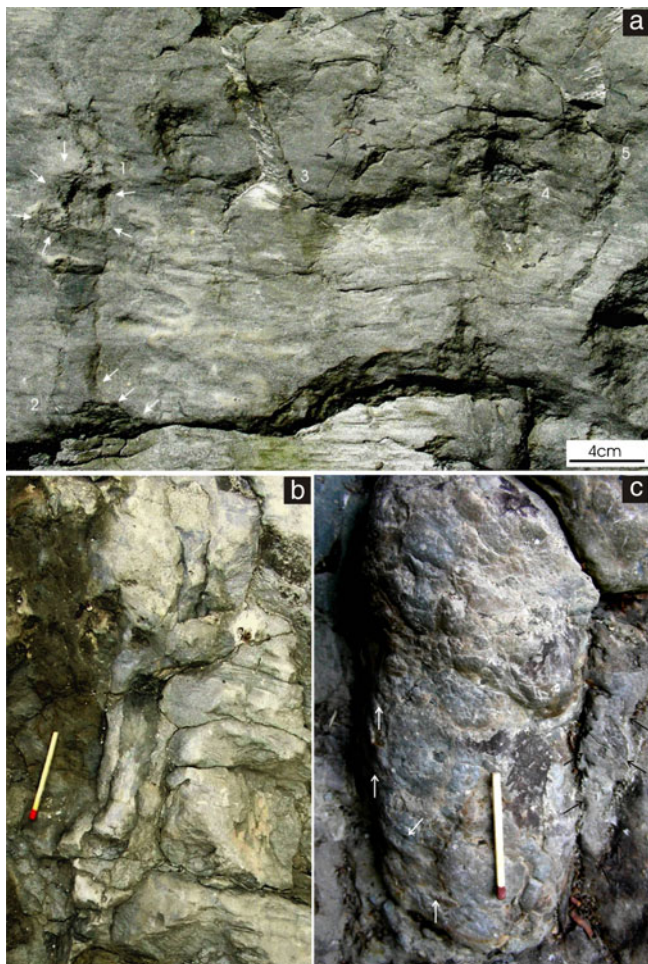


Figure 2. Biotubes (Type-1) within Facies-4 showing (a) multiple (1–2, white arrows), single (3–5) burrow enlargements and the presence of incipient rhizohalo (black arrows) in the association (Sevoke section); (b) mud liner with contrasted sediment fill in the lower (muddy) and top (sandy) part (Sevoke section, scale: Stick length 4 cm); and (c) scrape marks (white arrows) on knobby, burrow-fill sediment surface and variable width of burrow lining (black arrows) in them (Leesh section, scale: Stick length 4 cm).

even in a single tube (figure 2b). Subhorizontal, oblique ridges and furrows in the burrow-interior are inferred from corresponding negative features present on the surface of the burrow cast (figure 2c). Burrow openings are often wider, funnel shaped (figure 4a). Tube-fill sediments predominantly laminated with occasional concave-up laminae. Juxtaposed, branched upward tunnel openings in bed normal sections (figure 4a) are often seen as composite, coalesced burrow openings on plan (figure 4b). Tube density measured in plan view varies from 3–20 per m^2 (50 measurements). Clay pellets in tube-fill sediments may be of faecal origin as identified from ovoid to semi-spherical shapes with internal concentric shell

structures detected in thin sections under microscope (figure 4c–d). Common bed junction preservation rarely allows measuring of the true tube length. Maximum observed length is 47 cm at Gheesh river section and 29 cm at Sevoke section.

Associations: These large-diameter, subvertical, enigmatic tubes in Facies-4 indicate singular dominance but for the occasional presence of sediment-filled incipient rhizoliths in the assemblage.

3.2 Type 2 – *Naktodemasis* isp. (figure 5a–c)

Description: Originally described as adhesive meniscate burrows (Bown and Kraus 1983; Hasiotis and Dubiel 1994; Hasiotis 2002; Smith et al. 2008a, b); sinuous, variably oriented, unbranched and mostly unlined burrows composed of a nested series of ellipsoidal, menisci-backfilled packets. Meniscate laminae are thin, discontinuous and texturally homogeneous. Alternating colours that correspond to matrix and mottle colours of the host rock typically accentuate the meniscate backfill (figure 5a, white arrow). Burrow walls are commonly transient with the matrix. Bounding line in some inclined burrows is bulged at intervals that correspond to menisci-backfilled packets. Burrows are 1–15 cm long and have circular to elliptical cross sections, 0.3–1.4 cm in diameter.

Associations: *Naktodemasis* isp. is abundant in Facies-2 heteroliths. These burrows are closely associated with *Planolites* isp. (figure 5a), probable brood chambers (figure 5b) along with *Macanopsis* isp., rhizoliths and rhizohaloes (figure 5c–d).

3.3 Type 3 – *Cylindricum* isp. (figure 6a)

Description: Vertical to nearly vertical, distinctly mud lined or unlined, straight to sinuous, unbranched burrows with unornamented surfaces. These burrows have very low width-to-length ratios that approaches 1, compared to *Skolithos* isp., which has one to two orders of higher width-to-length ratios. Burrows are found in low densities compared to other burrow occurrences. Burrow diameters up to 1.7 cm. Recorded burrow length up to 6.1 cm. Burrow terminations are rounded. Fill material is mostly structureless sandstone.

Associations: These are rare, preserved in mud dominant units of Facies-2 in which they occur in

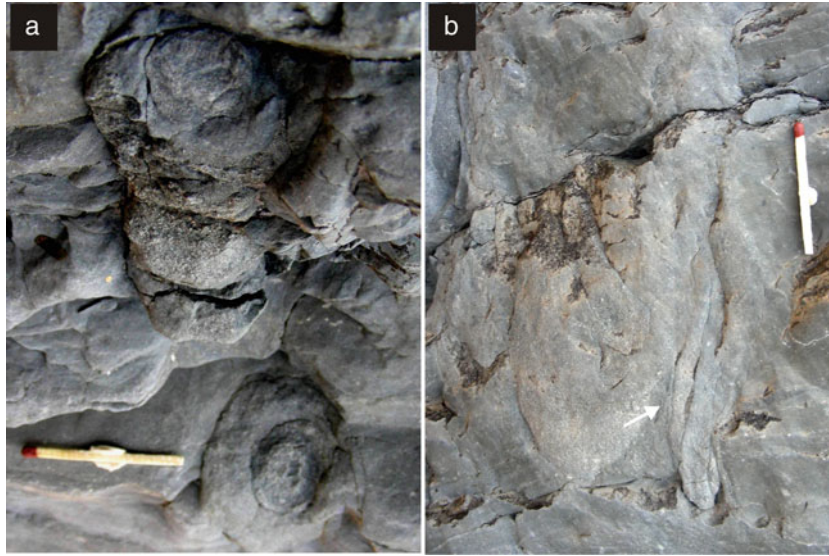


Figure 3. (a) Lag liner in Type-1 biotube around burrow-fill (visible on plan and section) and (b) distinct finer (clayey) burrow lining and coarser, sandy burrow-fill is visible in the adjacent burrows in the same outcrop (vertical section) within Facies-4 (Leesh River; scale: Stick length 4 cm).

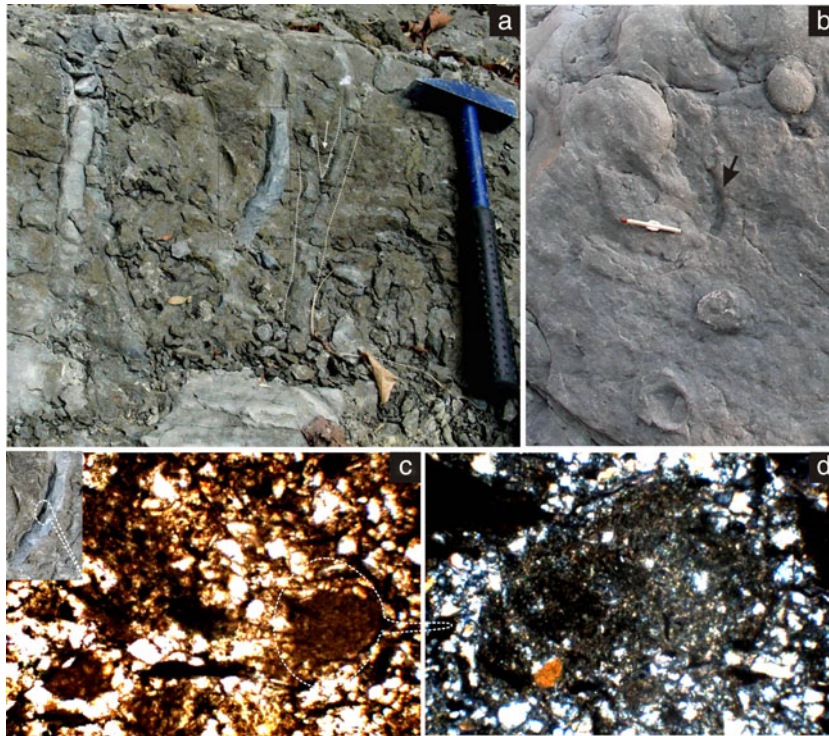


Figure 4. Type-1 enigmatic tubes within Facies-4, showing (a) branched upward tunnel opening (arrow) with funnelled top (stippled lines) (Sevoke section; scale: Hammer 30 cm); (b) Knobby appearance on bed surface with coalesced, juxtaposed burrow openings (arrow) indicating upward branching of biotubes (Leesh section, scale: Stick length 4 cm); (c) probable fecal pellets in some part (rectangle, marked in figure 4a) of burrow-fill sediment (photomicrograph, Slide No. SWK-09-1A; magnification 50 \times ; Sevoke section); and also note (d) concentric laminae in a fecal pellet under higher magnification (photomicrograph, Slide No. SWK-09-1A; magnification 100 \times).

association with dominant *Planolites* isp. and occasional *Macanopsis* isp., sparse rhizoliths and rhizohaloes. At places, thin network or lenses of coaly matter occur associated with these.

3.4 Type 4 – *Planolites* isp. (figures 5a–c, 6c)

Description: Variable orientations (figure 5a, black arrows), straight to slightly sinuous, unlined,

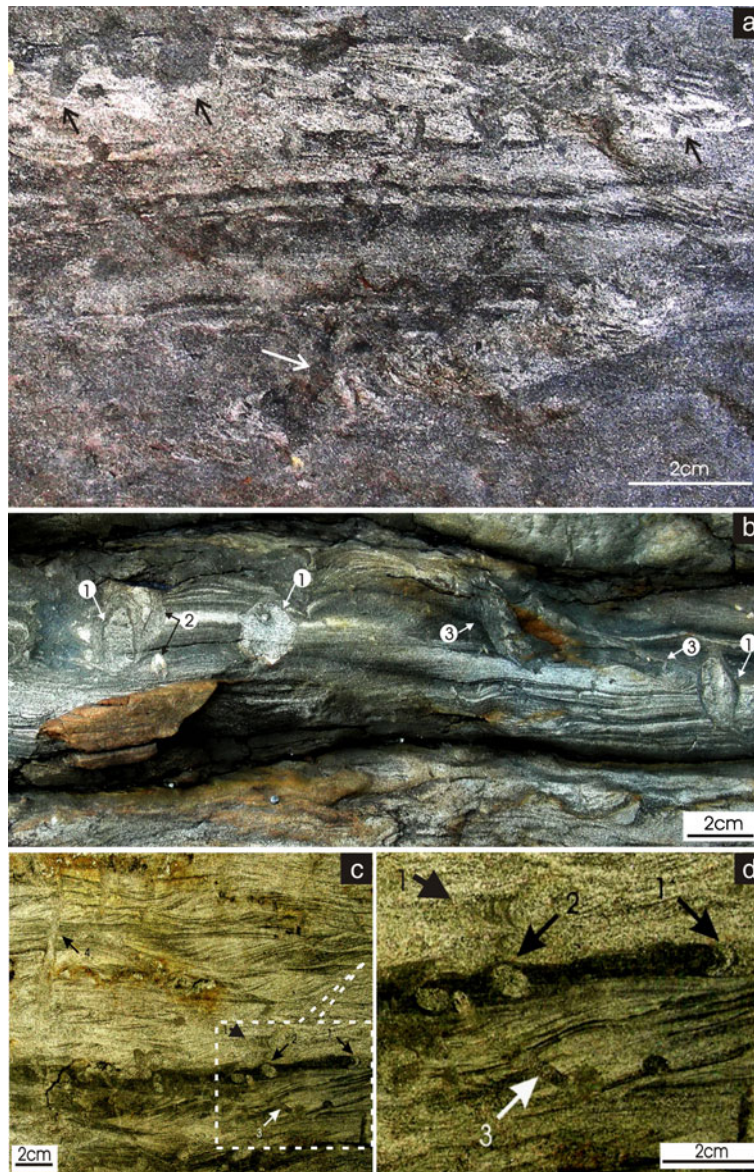


Figure 5. (a) *Naktodemasis* isp. (white arrow) in association with dominantly mud filled tubes of *Planolites* isp. (black arrows). Also note the bulging of the bounding line of the inclined burrow at intervals (Sevoke section, Facies-2); (b) Brood chambers (1) associated with *Planolites* isp. (2) and *Naktodemasis* isp. (3) and rhizohalo. Note the sharp truncation of *Naktodemasis* isp. against pupae-form brood chamber (right, middle) indicating continuous tiering by members of temporally differentiated trace fossil suites (Leesh section; Facies-2); (c) association of *Naktodemasis* isp. (1), *Planolites* isp. (2), *Macanopsis* isp. (3) and mottled, rhizohalos (4); (d) magnified view of a portion (stippled box) of figure 5(c) showing concave out backfill structures of *Naktodemasis* isp. (1), elliptical traces of sediment-filled sub-horizontal tubes of *Planolites* isp. (2) and distinct, rounded chamber at the bottom of sand-filled burrow of *Macanopsis* isp. (3) (Sevoke section; Facies-2).

unbranched burrows of constant width (within same burrow); circular to elliptical in cross section; structureless, homogeneous mud or sand-filled burrows (figure 5a–b). Burrow diameters range from 0.2 to 0.9 cm, but most are between 0.3 and 0.5 cm. Probable juveniles are associated with brood chambers (figure 5b, marked 2). Burrow orientation change from near vertical or inclined in siltstone intervals to predominantly horizontal, showing circular or elliptical cross section in mudstone intervals (figures 5, 6a; marked 2).

Associations: These traces are almost ubiquitous in all ichnocoenoses described under Facies-2 and less commonly in Facies-3 and Facies-4.

3.5 Type 5 – Brood chambers (figure 5b)

Description: Sand or mud-filled, vertically elongated, cocoon-like ellipsoids; occasional thin mud lining; long diameter varying between 2.1 and 3 cm, with nearly constant height *vs.* width ratio

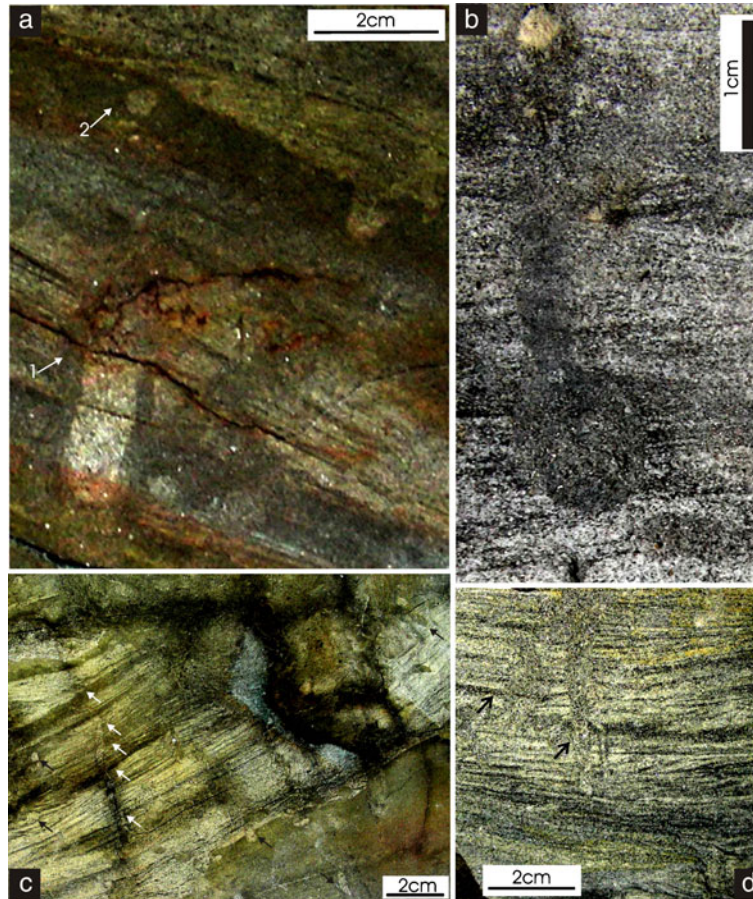


Figure 6. (a) *Cylindricum* isp. (1) and *Planolites* isp. (2). Note the distinct mud lining (arrow) and typical U-shaped, rounded bottom in *Cylindricum* isp. (Leesh section; Facies-2); (b) *Macanopsis* isp. in vertical section, showing distinct, rounded bottom and coarser sand fill near burrow opening (Sevoke section; Facies-2); (c) *Planolites* isp. (black arrows) and sediment-filled rhizolith (white arrows) in Gheesh River section (Facies-2); and (d) mottled rhizohaloes showing distinct branching downward (Gheesh section; Facies-2).

(between 1.7 and 1.9). These structures appear to be internally sediment filled and occasionally connected, with a number of very small *Planolites* isp. (figure 5b, black arrows, 2) emerging from it in different directions. Traces of *Naktodemasis* isp. deflect around these elliptical structures (figure 5b, marked 3).

Association: These burrows occur associated with *Naktodemasis* isp., *Planolites* isp. and incipient rhizoliths in the mud-dominant units of Facies-2.

3.6 Type 6 – *Macanopsis* isp. (figures 5, 6b)

Description: These are unlined, sand- or mud-filled burrows within Facies-2; near vertical with distinct, J-shaped subhorizontal bend terminating at a bulb; constant width (up to 0.5 cm) along the tunnel length; width nearly doubled (0.9 cm) at bulbous end (figure 6b).

Association: These burrows occur associated with *Naktodemasis* isp., *Cylindricum* isp., *Planolites* isp. and incipient rhizoliths in the heterolithic packages of siltstone and mudstone of Facies-2.

3.7 Type 7 – Sediment-filled rhizoliths (figure 6c–d)

Description: Nearly vertical, often associated with downward-tapering and rare incipient branching (figure 6c); up to 1.3 cm in diameter, cylindrical structures composed of homogeneous silt or mud fill within Facies-2.

Associations: Sediment-filled rhizoliths are found in the thicker clay and thinner silt laminated intervals of Facies-2 heteroliths (figure 6c–d). Associated trace fossils include predominant *Planolites* isp., *Cylindricum* isp., *Macanopsis* isp. and rhizohaloes (type 8).

3.8 Type 8 – *Rhizohaloes* (figures 2a, 6d)

Description: Vertical to subvertical; sometimes downward tapering and commonly branching (figure 6d); dark gray mottles with up to 7 cm in circular cross sections.

Associations: *Rhizohaloes* are nearly ubiquitous and occur in association with all other ichnotaxa present in Facies-2 and Facies-4.

4. Discussions

This is the first report of Middle Siwalik ichnofauna from Darjeeling–Jalpaiguri sector of eastern Himalayas. Trace fossils are reported here from a sedimentary facies association, suggesting interwoven subunits of a channel–floodplain environment. Different facies-specific and facies-transgressive ichnotaxa identified from the studied Siwalik succession include *Naktodemasis* isp., *Macanopsis* isp., *Cylindricum* isp. and *Planolites* isp., along with few brood chambers and large-diameter vertical tubes of unknown origin. Often, these are associated with sediment-filled rhizoliths and/or mottled rhizohalos.

Ichnological interpretations of the varied morphotypes (1–8) observed in the studied sections may be summarized as follows:

Type-1 ichna is represented by slender, near-vertical, straight or Y-shaped, sediment-filled tunnels; distal, multiple enlargements of the tunnels; persistent mud-, sand-, or pebble-lined segments of burrows and sediment fill suggest a probable freshwater crayfish origin (Ortmann 1906; Hobbs 1974, 1988; Hasiotis and Mitchell 1993; Hasiotis and Honey 2000; Hasiotis 2002). Scrape marks interpreted from burrow margins or from more deliberate surface markings as well as the presence of faecal pellets in the burrow-fill sediments also support this prediction. Multiple tunnel enlargements throughout the length of the tubes as well as at the terminations may be interpreted as chambers. Bromley and Asgaard (1979) described similar forms with somewhat smaller dimensions as striated oblique burrow (cited in Tandon and Naug 1984). The variations of tunnel width as well as the presence of terminal tapering in some of the tunnels; incipient, apparent down-depth branching and common association with carbonate nodules, however, may also be indicative of rhizoliths. Pending detailed microscopic studies and outcrop studies in additional localities, these enigmatic tubes are held for the present as problematica showing dual characters resembling crayfish

burrows and rhizoliths. We cannot rule out probable active burrow modifications on pre-existing conduits, producing these ichna.

A comprehensive statement on the implications of these enigmatic tubes is not warranted as yet, by full proof diagnoses. Indulging a crayfish origin for these tubes, multiple distal enlargements within a single burrow may be referred as reconstructed dwellings depicting sustained burrow occupancy and successive readjustments of burrowing depth. Multiple openings are also typical of crayfish burrow morphologies (Hobbs 1988; Hasiotis and Mitchell 1993; Hasiotis and Honey 2000). Permanent nature of these structures is also indicated by persistent, thick and thin burrow lining in them. Network of interpenetrating tunnels, secondary tunnel openings and the K-selected size distribution of tunnel diameters suggest a stable colony or equilibrium assemblage of the trace makers (Ekdale 1985; Vossler and Pemberton 1988; Bromley 1996). Triassic, Jurassic and Paleogene crayfish burrows show similar development of secondary tunnel openings by cross-cutting, interpenetrating burrows (e.g., Hasiotis 2002). Preserved funnelled top is regarded as preservation bias that might have been formed by the collapse of sediment at the open burrow mouth. Alternatively, the wider opening with a thicker lining of sediment may record the initial burrow construction by removal of more material to accommodate excavated sediment produced by the deepening of the burrow (Hasiotis and Mitchell 1993; Hasiotis and Honey 2000). Tube-fill sediments of contrasted composition within a single burrow suggest passive filling and bed junction preservation. Occasional presence of incipient laminae and observed concavity in them is intriguing in this context. Both sand and mud-filled tubes in the same population may be interpreted as the mixing of temporally differentiated populations through tiering.

Type-2 ichna, identified as *Naktodemasis* isp., is interpreted as the intermittent locomotion and dwelling traces of burrowing beetles of hemipteran or coleopteran affinity (Hasiotis 2002, 2008; Smith et al. 2008b; Smith and Hasiotis 2008; Counts and Hasiotis 2009). A terraphilic to hygrophilic moisture preference and a compatible rooted A and upper B horizons of the soil profile is indicated by the association of *Naktodemasis* isp. with sediment-filled rhizoliths (Hasiotis 2008; Smith et al. 2008b; Counts and Hasiotis 2009). A relatively higher diversity association of this ichna with brood chambers, rhizoliths and *Planolites* isp. at distinct stratigraphic intervals indicates an equilibrium assemblage in this context, compatible with a short-term stable groundwater profile. Longer term stability in the groundwater conditions,

coupled with lower sedimentation rates, would have produced greater bioturbation intensity in which *Naktodemasis* would have destroyed all original primary bedding.

Type-3 ichna are almost similar to *Cylindricum*, in that they are short, smooth-walled and predominantly vertical shafts with gently rounded terminations (cf. Smith *et al.* 2008b). The lack of other diagnostic morphologies limits the assignment of these burrows to any specific group of tracemakers. *Cylindricum* can be made by a variety of different arthropods, including spiders and insects living in subaerial conditions where the water table is close to the surface (Stanley and Fagerstrom 1974; Ratcliffe and Fagerstrom 1980; Hasiotis 2002).

Predominance of horizontal burrows of *Planolites* isp. (Type-4) in mudstones and inclined to near vertical burrow segment in siltstones within Facies-2 heteroliths may indicate a preference for mud. The distinct wall and structureless fill, particularly in the vertical segment of these burrows, however, suggests passive, sediment-filled, open burrows. The presence of *Planolites* isp. in different ichnocoenoses indicates the simple character of this burrow morphology, which can be created by nearly invertebrate living above or below the water table. Low abundance of *Planolites* isp., where they occur in association with other ichna (*Naktodemasis* isp., *Macanopsis* isp. and *Cylindricum* isp.) indicate a K-selected equilibrium assemblage compatible with stable, less stressed depositional milieu. In contrast, their monospecific occurrences in distinct stratigraphic interval in good numbers indicate their colonization as an opportunist colonizer (Ekdale 1985; Bromley 1996). Millimetre-thick heterolithic layers within Facies-2 that are thoroughly riddled by relatively shallow burrows of *Planolites* isp. in this context, probably indicate a floodplain depositional milieu where temporary environmental shifts have allowed colonization (Pollard 1988). Here, typically mud-filled burrows within thin sandy-silty layers represent the passage of the burrower through a sandy unit from an overlying mud (e.g., Taylor *et al.* 2003).

Sharp deflection of *Naktodemasis* isp. around the Type-5 ichna perhaps indicate a continued tiering of the former, within a stable ichnocoenose in which, Type-5 sediment-filled structures represent a relatively earlier colonization. These are interpreted as brood chambers from the connected tiny strands of *Planolites* isp. that are in this context, interpreted to represent exit burrows of juveniles. Presence of these probable brood chambers indicates periods of well-drained subsurface condition with optimal moisture content in the sediment, allowing safe exit of juveniles.

Though the type materials of *Macanopsis* (Type-6) were described as marine, these were later

recorded in the pointbar deposits of the fluvial deposits (Bown 1982; Bown and Kraus 1983), fluvial floodplain (Hasiotis *et al.* 1993) and in braided fluvial environment (Fernandes and Carvalho 2006). These structures were attributed to a variety of invertebrate trace makers including insects, spiders, decapods and molluscs (cf. Bown and Kraus 1983). Facies association of this ichnotaxon within pointbar deposits in this context is compatible with its freshwater allegiance. Bulbous end in these burrows suggest a dwelling structure (domichnia). Structureless sand and mud fill indicate open burrows that were passively filled. Association with *Naktodemasis* isp. and incipient rhizohaloes suggests intermittent well-drained conditions that prevailed in the accumulated sediments.

Type-7 morphotypes are interpreted as root pathways, in-filled with sediments after the decay of the original roots. Overall association indicates a fluctuating hydrologic condition but root placement in the vadose zone of the groundwater profile (Glinski and Lipiec 1990). This behaviour would be referred to as terraphylic to hygrophilic in that the plant roots are seeking out areas of pore spaces filled with air and water (Hasiotis 2002, 2007).

The branching patterns and circular cross sections of Type-8 mottled structures suggest that these are formed in the depletion zones resulting from surface-water gleying within and adjacent to original roots (Schwertmann 1993; Kraus and Hasiotis 2006). Seasonal, saturated soil conditions followed by periods of better drainage and lower water tables may be suggested from this association of mottles (Bigham *et al.* 1978; Torrent *et al.* 1980).

Overall low-diversity ichno-assemblages in the studied sections is compatible with other recorded low-diversity fluvial ichnocoenoses, which is indicative of high sedimentation rates and sediment accumulation rates (e.g., Hasiotis 2004, 2007).

A low density, but relatively more diverse *Naktodemasis-Macanopsis-Cylindricum-Planolites* ichno-assemblage (occasionally with probable brood chambers) within thinly laminated heterolithic Facies-2 probably indicate an equilibrium assemblage compatible with periods of stability in the depositional environment in terms of rate of sedimentation and shifts in hydrologic surface. All these ichnotaxa (except *Planolites* isp.) are facies specific in their occurrences. A distinctly different ichnocoenosis within sandstone-dominant intervals of Facies-2 is represented by monospecific occurrence of high density population of *Planolites* that, in this context, indicate a stressed, opportunistic colony (Ekdale 1985; Bromley 1996). Still another monospecific colonization of enigmatic large diameter, vertical tubes within Facies-4 (with occasional, rare *Planolites* isp.) records

probable reburrowing events. Association of rhizoliths and rhizohalos of varying descriptions also suggests varying moisture content in the sediment matrix. Historically, Siwalik depositional milieu is reported to record phased episodic uplifts of the Himalaya and the remarkable fall of sea level in the Indian shelf, that significantly affected the sedimentation, paleoclimatic and paleohydrological conditions in the Cenozoic around the area (Johnson *et al.* 1983; Valdiya 1998; Vaidyanadhan and Ramakrishnan 2008). Subtle changes in the hydrologic surface *vis-a-vis* shifts in media (=substrate) elevation and sedimentation rate appear to put major constraints in this depositional regime. Repetitive adjustment of burrowing depths in enigmatic burrows, mud and lag liners in them; recurrence of equilibrium and opportunist colonization events; varied mode of preservation of plant roots may thus probably be interpreted as feed-back responses of middle Siwalik ichnofauna to repetitive changes in depths of water table in a floodplain environment.

5. Conclusions

Monospecific colonies of *Planolites* isp. defining a pioneer, opportunistic (r-selected) assemblage and *Naktodemasis-Planolites-Cylindricum-Macanopsis* equilibrium (K-selected) assemblage along with enigmatic, monospecific large diameter vertical burrows from the Neogene Middle Siwalik sedimentary succession of the Darjeeling Himalayas developed in a continental fluvial environment. Recurrence of monospecific colonies of *Planolites* isp. indicate stressed conditions interpreted in terms of subtle changes in the depth of paleohydrologic surface. Relative quieter periods in the depositional set-up are represented by equilibrium assemblage. Ethological interpretation of large diameter enigmatic biotubes may offer valuable information in this context, pending their formal diagnosis. Taphonomic aspects of preserved rhizoliths or rhizohaloes further indicate varied moisture level in the substrate. Addition of new faunal data from eastern Himalayas help to put constraints on middle Siwalik sedimentation milieu in the studied part of the basin and delineates an ichnological-paleoecological frame for further study on continental Siwalik sedimentation.

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