Trace fossils provide key insights into benthic faunas and their distribution in space and time (Seilacher 2007). They not only document the lifestyle of the producers but also help in the interpretation of the associated environments. In the absence of geochronological data, certain trace/body fossils are critical for determining the age of fossil-bearing litho units, as well as depositional environment and palaeoecology. The Precambrian–Cambrian boundary and its Global Standard Stratotype Section and Point (GSSP) have been established at the base of the trace fossil Treptichnus pedum zone at Fortune Head, Newfoundland (Narbonne et al. 1987, Brasier et al. 1994, Landing 1994). Previously known as Phycodes pedum (Seilacher, 1955), the First Appearance Datum (FAD) of Treptichnus pedum is accepted as the index fossil representing the Precambrian–Cambrian boundary and has been reported from several Precambrian–Cambrian transitional successions worldwide (Seilacher 2007, Buatois 2018). Formed possibly by priapulid worms (Vannier et al. 2010), T. pedum is essentially a branching, feeding burrow structure resulting from systematic probing and backfilling. Priapulids are basically considered as endobenthic predators (Vannier et al. 2010), suggesting that T. pedum may indicate the presence of predation behaviour at the Precambrian–Cambrian boundary. Morphologically these worm burrows are subdivided into modular segments, resembling buds on a twig, which follow a straight, sinusoidal or coiled course. They arguably represent the first record of complex metazoan behaviour at the onset of the Cambrian (Grotzinger et al. 1995, Jensen et al. 2006, Mángano et al. 2012). The burrowing method gradually became more complex, i.e. from horizontal to vertical in nature during this period as the priapulids probed deeper into the sediment in various ways. Such patterns distinguish it from other ordinary burrows, i.e. sub-horizontal burrows produced in the sub-surface (Vannier et al. 2010).

The Nagaur Group, as exposed at the Dulmera section (Fig. 1A, B), is well known for its trace fossil content (Kumar & Pandey 2008, 2010; Sharma & Pandey 2011; Srivastava 2012a, b; Singh et al. 2013, 2014a; Ahmad & Kumar, 2014; Pandey et al. 2014). Except a solitary claim by Singh et al. (2013), no convincing body fossil has yet been documented to date. Due to limited exposure of the Nagaur Sandstone, the FAD for the earlier reported T. pedum could not be assigned to any specific stratum at the Dulmera section (Srivastava 2012a). Furthermore, as previously pointed out with respect to Indian sections...
(Hughes et al. 2013, Hughes 2016), *T. pedum* has a stratigraphical range that extends from the base of the Cambrian into the Early Ordovician and so, its presence is not diagnostic of any particular age within the Cambrian. In this paper, we provide the details on the morphology, ecological niche, and distribution; petrological attributes of the host sediments are also provided. *Treptichnus pedum* reported from the Dulmera section is also evaluated for the possibility of the unit representing the FAD in the Nagaur Formation. The behaviour of the organism producing these burrows, as well as taphonomy of the ichnofossils, is also discussed.

**General Geology and Age**

The 1000 m thick Marwar Supergroup is represented by argillo-arenaceous and carbonates facies in the Jodhpur-Khatu-Bikaner-Phalodi areas of the western Rajasthan (Pareek 1984). The lithologies represented are conglomerate, sandstone, siltstone, shale, dolomite and limestone. The Marwar Supergroup has been stratigraphically divided into the three groups (Table 1). In stratigraphically ascending order, these are the Jodhpur Group, the Bilara Group and the Nagaur Group. These groups are further subdivided into different formations. The Jodhpur and Nagaur groups are arenaceous to argillaceous, whereas the Bilara Group is mainly calcareous in nature. The Marwar succession rests unconformably above the Malani Igneous Suite that is dated 771 ± 5 Ma (Gregory et al. 2009). The Tunklian Sandstone is the youngest formation of the Marwar Supergroup. The underling Nagaur Sandstone has yielded the ichnofossils discussed in the present paper. Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry (LA-ICP-MS) analysis calibrations of the detrital zircons recovered from the Nagaur Sandstone yielded ~540 Ma ages (McKenzie et al. 2011), which is the maximum age of the Nagaur Sandstone. Pandey et al. (2014) and Singh et al. (2014a) considered that the ichnofossil assemblage from the Nagaur Sandstone belongs to Stage 2 of the Terreneuvian Epoch. However, the beds containing these trace fossils are not conformably overlain by diagnostic short-ranged earliest Cambrian fossils and there are no convincing evidence that these sediments are Stage 2. Hughes (2016) considered these specimens to indicate Cambrian Series 2, late Stage 4 age (~509 Ma age) for the Dulmera outcrops. Therefore, the minimum age of the Nagaur Sandstone is constrained to be ~509 Ma.

**Phycodes pedum to Treptichnus pedum:** A précis

*Phycodes* Richter, 1850 and *Treptichnus* Miller, 1889 are two ichnogenera established more than a century ago. Seilacher (1955) erected the ichnospecies *Phycodes pedum* (*pedum* = bishop’s crosier) from the Khussak Formation of the Salt Range which is early in the Cambrian Stage 4 (~514 Ma) (Hughes 2016). This ichnotaxon—shows the advent of complex behaviour and anatomy at the beginning of the Cambrian. Seilacher reconstructed *Phycodes pedum* as a flat ‘U’ tube of which one end was fixed and the other end was gradually increased by probe on the curved path emerging on the surface. In the original discussion, he did not state whether the expanding ‘U’ shaped tube was inferred or observed. An assessment of illustrations provided with the description (Seilacher 1955, p. 387, fig. 4g) suggests that *P. pedum* was formed by the addition of segments in a treptichian manner. A weakly developed alternation of direction is seen also in the holotype of *Phycodes pedum* and therefore, the ichnogenus was later placed in *Treptichnus* (see Jensen 1997, Jensen & Grant 1998, Jensen et al. 1998 for discussions).

**Table 1.** Generalized stratigraphic succession of the Marwar Supergroup (after Pareek 1984 and Chauhan et al. 2004).

| Age                  | Supergroup                  | Group          | Formation          |
|----------------------|-----------------------------|----------------|--------------------|
| Permo-Carboniferous  | Bap Boulder Bed             | Unconformity   |                    |
| Unconformity         | Tunklian Sandstone          | Nagaur Group   | (75–500 m)         |
|                      |                             | Nagaur Sandstone|
|                      |                             | Pondlo Dolomite|
|                      |                             | Gotan Limestone|
|                      |                             | Dhanapa Dolomite|
|                      |                             | Girbhakar Sandstone|
|                      |                             | Sonia Sandstone|
|                      |                             | Pokaran Boulder Bed|
| 779–681 Ma           | Malani Igneous Suite        | Unconformity   |                    |
Treptichnus consists of burrows with a straight course and with segments that regularly alternate in direction (Seilacher 1955, Geyer & Uchman 1995, Dzik, 2005). No clear morphological variations/trends are observed through its geological range (base of the Cambrian into the Early Ordovician). It is, therefore, probably correct to maintain one name – Treptichnus pedum – for such burrow structures and perhaps to distinguish the variant by informal terms (Seilacher 2007).

Global distribution

Treptichnus pedum is considered as an important fossil for demarcating the boundary between the Ediacaran and Cambrian periods (Narbonne et al. 1987, Brasier et al. 1994, Landing 1994). Concerted efforts have been made to document T. pedum from various successions in the world. Burrowing habit represents the infaunal behaviour of T. pedum which, for the first time, manifested in the Early Cambrian Period (Droser et al. 1999). Vannier et al. (2010) suggested that the priapulids were one of the earliest infaunal colonizers of the substrate that possibly interacted with epibenthic communities which played an important role in the early marine food chain and important sub-horizontal bioturbators in the Cambrian Substrate Revolution (Bottjer et al. 2000). Buatois et al. (2013) noted wide environmental tolerance in occurrences of T. pedum and supported evolutionary innovations rather than facies specific distribution. Treptichnus pedum has been recorded from all over the globe (see Table 2).
In India, *Treptichnus pedum* has been reported from the Zanskar region of the Himalaya, the Lesser Himalaya, in the Mussoorie syncline (Shah & Sudan, 1983; Singh & Rai 1983; Parcha & Singh 2005, 2010; Singh et al. 2014b), and the Nagaur Sandstone of the Marwar Supergroup in Rajasthan (Srivastava, 2012a, b; Pandey et al. 2014; Singh et al. 2017). Marwar specimens reported by Srivastava (2012a) are elongated, whereas, those reported by Pandey et al. (2014) have small projections.

**Observations on Nagaur *Treptichnus pedum***

*Treptichnus pedum*-bearing sandstone

Ichnofossil bearing, parallel-bedded sandstone and mudstone of the Nagaur Sandstone were studied in a quarry section (28° 24.228’ N, 73° 39.514’ E) Dulmera Village, close to Dulmera Railway Station ~65 km from Bikaner District on Bikaner–Ganganagar Highway (Fig. 1B) in Rajasthan, India. A 20 m thick succession of the Nagaur Sandstone is exposed in the quarry faces. The sandstone is medium to coarse grained and red to maroon in colour. Some of the beds are ferruginous. Trace fossils are present in interbedded sandstone and mudstone (Fig. 2). The quarry section reveals heterolithic bedding (Fig. 1C) along with high to low angle cross-beddings (Fig. 2C), ripple marks and mudstone drapes.

Two petrographic thin sections of the ichnofossil-bearing ferruginous sandstone were examined under the petrological microscope (Fig. 3A–E). The sandstone comprises mainly anhedral to subhedral quartz grains (80%). About 40% of the quartz grains are prismatic, but most grains are rounded to sub rounded, and few are tabular and irregular in shape. Most of the prismatic quartz grains show preferred orientation (Fig. 3B, C). These grains normally show long contact with each other whereas a few grains show convex contact, and rounded and sub-rounded grains show concave contact. Diagenetic silica overgrowth, separated by fine clay between the original grain and overgrowth, has been noticed on the rounded and sub-rounded quartz grains. Monocrystalline quartz grains dominate the assemblage (95%) with subordinate sizeable population of polycrystalline grains (5%). Square shaped opaque magnetite inclusions are noted in a few grains, while others contain inclusion of zoisite and clinozoisite. Feldspar constitutes 5% of the entire grain population. Potassium feldspars consist of tabular grains of microcline and orthoclase with characteristic cross hatched twinning, orthoclase grains, also tabular in shape, show first order grey colour. Medium-grained fresh Na feldspar consisting of albite shows first order grey colour and polysynthetic twinning. Lath/flaky shaped mica are constituted of biotite and muscovite showing preferred orientation similar to quartz grains. Under polarized light, biotite shows prominent pleochroism from light brown to dark brown. Muscovite shows second order interference colour under crossed polars. Most of these grains are altered at places; alteration of biotite in chlorite and K & Na orthoclase feldspars in kaolin has been noticed and at places kaolin is further recrystallized into sericite. Perthite grains are very rarely noticed. Quartz grains show corroded margins, which is due to clay. Iron rich (ferruginous) matrix is present in between quartz grains which are derived from alteration of biotite. Rock-fragments constitute less than 5% which are quartzite and chert fragments which are very fine grained. Diagenetic over-growth has been noted in rounded grains. In the burrowed portion, there is complete absence of prismatic quartz grains and predominance of rounded to sub rounded quartz grains; very little feldspar is noticed, with extensive alteration product and ferruginous matter as matrix. Ferruginous matrix percentage is higher at the location of burrows, with complete absence of prismatic quartz grains and increased size sorting of quartz grains in comparison to the non fossiliferous sandstones. Iron-rich opaque minerals are considerably more common in the burrowed beds. Micaceous minerals are comparatively small in size and show preferred orientation across the burrow.

*Treptichnus pedum*-bearing facies

Lowermost *T. pedum*-bearing horizon is encountered 13 m from the base of the section exposed in the quarry. The trace fossil-bearing facies (~2-metre-thick unit) is brown to red in colour, medium-grained sandstone with intercalations of centimetre-thick mudstone (Fig. 2). The succession can be divided into two lithofacies, namely the sandstone facies and the mudstone facies (Fig. 2A). The sandstone lithofacies is made up of decimetre-thick bands, showing cross-bedding, parallel lamination and
rare small ripple cross lamination. Bedding shows trough cross-bedding, planar cross-bedding and low-angle cross-bedding (Fig. 2B–D). The planar cross-bedding may show reactivation surfaces resembling tidal bundles (Fig. 2E). Some bounding surfaces in the sandstone facies are undulatory indicating influence of waves. The sandstone
facies suggests deposition similar to intertidal bars on sand shoal under the influence of tidal currents and wave actions (see Sharma et al. 2018). The mudstone facies is made up of a few millimetre-thick mud layers alternating with millimetre-to-centimetre thick sand layers. The mud layers show fine sandy streaks (Fig. 2A). The sand layers invariably show small ripple bedding. This lithofacies represents deposition in low-lying interbar areas protected from strong wave action and tidal currents. However, tidal processes controlled the fine sand-mud alternation. The trace fossils, Cruziana, Diplichnites, Monomorphichnus and Rusophycus along with Treptichnus pedum are preserved at the base of the sandstone layer as positive hyporelief (Fig. 4), overlying the mudstone facies. In this facies, Cruziana, Diplichnites, Rusophycus and Monomorphichnus are subordinate in abundance to T. pedum (Fig. 5). These burrows and resting traces were formed in unconsolidated sediments which constitute a softground. Above mentioned ichnotaxa, other than the T. pedum, are also reported from the horizons stratigraphically below this zone, which suggests that the documented T. pedum zone is unlikely to be the FAD. It is most likely that this assemblage mark the Stage 4 of the Series 2 of the Cambrian Period/System (Hughes 2016).

**Taxonomy**

Our study is based on well-preserved specimens of T. pedum recorded on the sole of seven medium-grained sandstone slabs with intercalations of mudstone. The specimens studied herein are reposited in the museum of Birbal Sahni Institute of Palaeosciences, Lucknow (collection statement number 1444).

Ichnogenus Treptichnus Miller, 1889
Ichnospecies Treptichnus pedum (Seilacher, 1955)

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**Material.** – Seven slabs of fine-grained sandstone consisting of 291 specimens preserved in hyporelief with fill identical to that of the slab.

**Description.** – Curved to slightly straight rows of short burrows. Individual burrows of equal length arranged alternating left and right at an angle; in some cases they show preferred orientation in one direction. Length of burrows varies between 1 to 17 mm (mean = 5 mm; N = 291); width varies between 1 to 3 mm (mean = 1.5 mm; N = 258), whereas 33 specimens show width less than 1 mm. The gap between the two consecutive small burrows varies between 1 mm to 7 mm. In some clusters, patterns of length of small burrows vary between 10 mm to 64 mm (mean = 34 mm; N = 9).

**Remarks.** – Morphometric characters of the Nagaur specimens are consistent with T. pedum (Seilacher, 1955). Various patterns formed by these specimens allow interpreting the behavioural activity and feeding mechanism of the makers (the priapulid worms) near the sediment-water interface. In the larger depositional basin, encompassing Salt Range, forms were described from the Neobolus Beds of Khussak Formation, Salt Range, Pakistan (Seilacher 1955).

**Distribution.** – Pandey et al. (2014) recorded T. pedum from the Nagaur Sandstone. Treptichnus pedum has been reported from various geological successions close to Precambrian–Cambrian boundary (Table 2) and ranges up to Ordovician (Seilacher 1969, 2007; Li 1993). Another ichnospecies of Treptichnus (e.g. T. bifurcus) has been reported up to Carboniferous (Buatois et al. 1997). Type specimen of T. pedum is from the Khussak Formation in the Salt Range (Seilacher 1955) and the stratum in which it occurs is considerably above the base of Precambrian–Cambrian boundary. Here they occur just above beds that contain the brachiopod S. rugosa, early in Stage 4 (likely about 514 Ma) (Hughes, 2016). The age of these strata are now considered 30 million years younger than the Precambrian–Cambrian boundary (Hughes 2016). It has been shown that treptichnids, not true T. pedum, occur below the Ediacaran–Cambrian boundary (Jensen et al. 2000, 2017; Högström et al. 2013; Buatois 2018). Seilacher (2007) figured specimens of T. pedum reported from South Africa to occur in Ediacaran–Cambrian age succession but it was subsequently shown to occur in Fortunian Stage (Buatois et al. 2007, Almond et al. 2008). In different regions of Laurentia, the occurrence of T. pedum coincides with the base of the Cambrian whereas the claim of diachronism in the appearance of T. pedum in Gondwanan regions needs further investigation (Babcock et al. 2014, Buatois 2018). Available evidence on the age of the Nagaur Sandstone holding T. pedum is inconclusive.
Table 2. Distribution list of *Treptichnus pedum* across the globe.

| No. | Ichnospecies     | Stratigraphy                      | Facies          | Depositional settings       | Age                  | References                  |
|-----|------------------|-----------------------------------|-----------------|----------------------------|----------------------|-----------------------------|
| 1.  | *Treptichnus pedum* | Nagaur Group, Marwar Supergroup, India | sandstone, siltstone | shallow water conditions | early Cambrian | Pandey *et al.* (2014) |
| 2.  | *Treptichnus pedum* | Nagaur Sandstone, Marwar Supergroup, India | sandstone, siltstone | shallow water conditions | early Cambrian | Srivastava (2012a) |
| 3.  | cf. *Treptichnus pedum* | Tal Formation, Lesser Himalaya, India | sandstone | not mentioned |                      | Singh *et al.* (2014a) |
| 4.  | *Treptichnus pedum* | Lolab and Tal Formation, Himalaya, India | no precise data | no precise data | early Cambrian | Shah & Sudan (1983), Singh & Rai (1983) |
| 5.  | *Treptichnus pedum* | Parahio section, Kunzum-la Formation, Spiti Valley, India | sandstone | shallow water conditions | early Cambrian | Parcha & Singh (2010) |
| 6.  | *Trychophycus; Phycodes* | Chapel Island Formation, Canada | sandstone | shallow water conditions | early Cambrian | Droser *et al.* (2002) |
| 7.  | *Treptichnus pedum* | Chapel Island, GSSP, Fortune Head, Newfoundland, Canada | siliciclastic | not mentioned | Ediacaran to early Cambrian | Gehling *et al.* (2001) |
| 8.  | *Treptichnus pedum* | E Newfoundland, Canada | no precise data | no precise data | late Ediacaran and early Cambrian | Fillion & Pickerill (1990) |
| 9.  | *Treptichnus pedum* | Chapel Island Formation (GSSP and below), Newfoundland, Canada | no precise data | no precise data | late Ediacaran and early Cambrian | Crimes & Anderson (1985), Narbonne *et al.* (1987), Brasier *et al.* (1994), Landing (1994) |
| 10. | *Treptichnus pedum* | Random Formation, SE Newfoundland, Canada | no precise data | no precise data | early Cambrian | Narbonne *et al.* (1987) |
| 11. | *Treptichnus pedum* | Boya Formation, Cassiar Mountain, Canada | no precise data | no precise data | early Cambrian | Fritz 1980, Fritz *et al.* (1983), Droser *et al.* (1999) |
| 12. | *Treptichnus pedum* | Lower Vampire Formation, Wernecke Mountains, Canada | no precise data | no precise data | early Cambrian | Nowlan *et al.* (1985), Droser *et al.* (1999) |
| 13. | *Treptichnus pedum* | Ingta Formation; Backbone Ranges Formation; Vampire Formation, Mackenzie Mountain, NW Canada | no precise data | no precise data | late Ediacaran and early Cambrian | MacNaughton & Narbonne (1999) |
| 14. | *Treptichnus pedum* | Guachos Formation, Argentina | sandstone | shallow water conditions | early Cambrian | Seilacher *et al.* (2005) |
| 15. | *Treptichnus pedum* | Balcare Formation, Buenos Aires Province, Argentina | no precise data | shallow water conditions | early Cambrian | Regalia & Herrera (1981) |
| 16. | *Treptichnus pedum* | Uratanna Formation, S Australia | sandstone | shallow water conditions | early Cambrian | Droser *et al.* (1999) |
| 17. | *Treptichnus pedum* | Parachilina Formation, Flinders Range, Australia | no precise data | no precise data | early Cambrian | Daily (1972) |
| 18. | *Treptichnus pedum* | Arumbera Formation, Dinkey Creek Beds, Amadeus Basin, Australia | no precise data | no precise data | early Cambrian | Glaessner (1969), Daily (1972), Walter *et al.* (1989) |
| 19. | *Treptichnus pedum* | Urusis Formation, S Namibia | sandstone | not mentioned | early Cambrian | Jensen & Runnegar (2005) |
| 20. | *Treptichnus pedum* | Upper Nomtsas Formation, Spitskopf Member and Urusis Formation of Nama Group, Namibia | sandstone | shallow water conditions | early Cambrian | Wilson *et al.* (2012) |
Table 2. continued.

| No. | Ichnospecies | Stratigraphy | Facies | Depositional settings | Age | References |
|-----|--------------|--------------|--------|------------------------|-----|------------|
| 22. | Treptichnus pedum | Nama Group, Namibia | sandstone, siltstone | not mentioned | early Cambrian | Jensen et al. (2000) |
| 23. | Treptichnus pedum | Gross Aub Formation and Nomtas Formation, South Namibia | no precise data | no precise data | early Cambrian | Germs (1972), Crimes & Germs (1982), Geyer & Uchman (1995) |
| 24. | Treptichnus pedum | Death Valley, USA | sandstone, siltstone | not mentioned | early Cambrian | Corsetti & Hagadorn (2000) |
| 25. | Treptichnus pedum | Bright Angel Shale, Grand Canyon, USA | no precise data | no precise data | early to middle Cambrian | Seilacher (1956), Eliot & Martin (1987) |
| 26. | Treptichnus pedum | Deep Spring Formation, Campito Formation, White Mountains, USA | no precise data | no precise data | early Cambrian | Alpert (1977) |
| 27. | Treptichnus pedum | Gongwusu Formation, Inner Mongolia, China | no precise data | no precise data | Middle Ordovician | Li (1993) |
| 28. | Treptichnus pedum | Kaili Formation, Guizhou Province (S China) | no precise data | no precise data | middle Cambrian | Yang (1994), Wang & Wang (2006) |
| 29. | Treptichnus pedum | Yu’anshan Formation, Yunnan Province, South China | no precise data | no precise data | early Cambrian | Zhu (1997) |
| 30. | Treptichnus pedum | Wisniowka Formation, Holy Cross Mountains, Poland | no precise data | no precise data | Furongian | Orlowski & Żylińska (1996) |
| 31. | Treptichnus pedum | Ocieseki Formation, Holy Cross Mountains, Poland | no precise data | no precise data | early Cambrian | Orlowski (1989) |
| 32. | Treptichnus pedum | Platysolemites Zone, SE Poland | no precise data | no precise data | early Cambrian | Paczesna (1985, 1986) |
| 33. | Treptichnus pedum | Detrital Beds, Sierra De Guadalupe, Spain | no precise data | no precise data | early Cambrian | Liñán (1984) |
| 34. | Treptichnus pedum | Vegadeo Limestone, Herreria Sandstone, Cantabrian Mountains, N Spain | sandstone | no precise data | early Cambrian | Crimes et al. (1977), Baldwin (1977), Legg (1985) |
| 35. | Treptichnus pedum | Mickwitzia Sandstone, South Central Sweden | no precise data | no precise data | early Cambrian | Jensen (1997) |
| 36. | Treptichnus pedum | Tornetrask Formation, Dividalen Group, N Sweden | no precise data | no precise data | Ediacaran and early Cambrian | Jensen & Grant (1998) |
| 37. | Treptichnus pedum | Klipbak Formation, Vanrhynsdorp Group, South Africa | sandstone | shallow marine clastic setting | early Cambrian | Buatois et al. (2013) |
| 38. | Treptichnus pedum | Neobolus beds, Salt Range, Pakistan | no precise data | no precise data | early Cambrian | Seilacher (1955) |
| 39. | Treptichnus pedum | Puerto Blanco Formation, Sonora, Mexico | sandstone | not mentioned | early Cambrian | Sour-Tovar et al. (2007) |
| 40. | Treptichnus pedum | Melez Chorgrane Formation, Libya | no precise data | no precise data | Early Ordovician | Seilacher (1969) |
| 41. | Treptichnus pedum | Rovno Formation, Ukraine | no precise data | no precise data | early Cambrian | Fedonkin (1983), Palij (1976) |
| 42. | Treptichnus pedum | Breivik Formation, Finnmark, Norway | no precise data | no precise data | early Cambrian | Banks (1970), Føyn & Glaessner (1979) |
| 43. | Treptichnus pedum | Lontova Formation, Estonia | no precise data | no precise data | early Cambrian | Palij (1976), Palij et al. (1983) |
| 44. | Treptichnus pedum | Buen Formation, N Greenland | no precise data | no precise data | early Cambrian | Bryant & Pickerill (1990) |
Table 3. Pearson correlation coefficients (r) of Treptichnus pedum dimensions recorded from the Nagaur Group. Abbreviations: N – number of specimens; ** – statistically significant correlation at the 0.01 level (2-tailed).

|        | Length | Width | Gap |
|--------|--------|-------|-----|
| Length | r      |       |     |
| Sig. (2-tailed) | 1 | 0.407** | -0.051 |
| N       | 291    | 258   | 190 |
| Width  | r      |       |     |
| Sig. (2-tailed) | 0.407** | 1 | -0.125 |
| N       | 258    | 258   | 163 |
| Gap    | r      |       |     |
| Sig. (2-tailed) | -0.051 | -0.125 | 1 |
| N       | 190    | 163   | 190 |

Statistical analysis

In the present study, three components of each burrow, i.e. length, width and consecutive gaps between segments of *T. pedum* have been measured in order to explore the variation of these parameters at the ichnogenERIC or ichnospecies level. Statistical analyses including Pearson product-moment correlation, box-plot and hierarchical cluster analysis were performed to assess the variability. The techniques of cluster analysis are useful tools for data analysis in various situations. These techniques are commonly used to search for natural groupings in the objects based on certain variables so that similar objects are in the same cluster or group. In some situations, cluster analysis methods can also be used to produce groups that form the basis of classification. Cluster analysis can be used for predictive purpose to determine the group based on certain variables. There are various algorithms available for cluster analysis (Everitt 1978). In this case we used Ward’s minimum variance algorithm which is most appropriate for this data set and produces a dendrogram that is a pictoral representation of relationships (see Figs 6, 7). A total of 291 specimens, present on seven slabs, have been counted where length of burrows varies between 1 to 17 mm (median = 4 mm, N = 291); width varies between <1 to 3 mm (median = 1 mm, N = 291). The gap between two segments ranges <1 to 7 mm with a mean of 1 mm. Pearson product-moment correlation suggest that there was a significant positive correlation between length and width (Table 3). As the length increases, the width of each segment also increases, but no significant correlation between the length and gap as well as between the width and gap was observed. Similarly, the box-plot for the length was calculated, the median range quartile was found between of 3 to 5 while the upper quartile range was observed at approximately 7. There were few outliers, in length the specimens 181, 182, 242, 199, 112, 100. Similarly, for the width and the gap, the box-plot showed varying outliers viz. 119, 215, 118, 247, 268, 280 and inliers were 278, 276, 275, 277, while in the gap the outliers were 101, 35, 150, 189, 149, 190, 100 and 36. These outliers are calculated if the specimen characteristics (length, width or gap) falls outside mean ±3 (standard deviation) bands. Box-plots do not show any significant relationship of the gap with the length and width. The hierarchical cluster analysis was performed on the length, width and gap and it was found that all the specimens belong to one species. However, for the specimen 182, the result varied and this may possibly be due to the outlier, hence, it can be omitted (Fig. 8A–F). When all the outliers were removed, all the specimens were grouped into two: specimen numbers 35, 183, 145, 146, 182, 98, 99, 157 fall in one group and rest of the 282 specimens in the other group. Thus, it is established in the firm context that all the specimens are from one major group.

Discussion

Palaeoecology

Trace fossils reflect the behaviour of animals responsible for their formation (Seilacher 1967), but the record is biased towards activities of infaunal organisms, and their distribution is strongly controlled by environmental factors (Buatois & Mángano 2011). *Treptichnus pedum*, *Rusophycus* isp., *Cruziana* isp. and *Dilipichnites* isp. are important trace fossils in the Nagaur assemblage to ascertain the age and palaeoecology (Fig. 9A–F). A number of scratch marks and burrows, supposed to be produced by different types of trilobites or other arthropods, are reported from this unit (Kumar & Pandey 2008, 2010; Sharma & Pandey 2011; Singh et al. 2013; Ahmad & Kumar 2014).

*Treptichnus pedum* is characteristically found in shallow, fully marine to marginal-marine environments.
Rusophycus and Cruziana may occur in brackish-water environment (Mángano & Buatois 2003). Rusophycus is a typical resting form of the trilobite (Buatois & Mángano 2011; for general review see Mángano et al. 2012). Cruziana is commonly preserved as the convex hyporelief cast of the trough-shaped burrow, rather than original concave burrow. Most of Cruziana are interpreted to be crawling traces of trilobites/other arthropods, since these bear scratch traces of stiff legs as they tunnelled through the shallow sediment. With high ichno-diversity the Nagaur assemblage is dominated by horizontal traces which are formed by the ichnofauna characteristic of low energy conditions (Buatois & Mángano 2011) typically included in the Cruziana ichnofacies. Although trace fossils in the softground unit of the Nagaur Sandstone are abundant, no body fossil has been documented, such situation is rather common to note in other successions elsewhere. Burrows by animals are formed to address the four life cycle related issues: respiration, feeding, reproduction, and protection (Bromley 1990, 1996; Mángano & Buatois 1999). Life of the organisms within the substrate is insulated from environmental and biological stress (salinity fluctuations, erosion, desiccation and predation). As mentioned above, the Nagaur assemblage is preserved in sandstone–mudstone bar–interbar facies. No direct evidence is available for the reason to burrow the softground but possibly these burrows were formed in search of food.

**Palaeobiology**

Priapulids live under the thin film of sediments and sometimes, they come to the surface or near the sediment–water interface for oxygen and nutrient; for managing so, they propel themselves in upward curving projection that breaches into the sediment surface (Seilacher 1955, Seilacher & Hemleben 1966, Vannier et al. 2010). Seilacher (1955), Jensen (1997) and Dzik (2005) considered that treptichnid burrows were mainly produced during feeding near the sediment–water interface but also intended for protection and shelter. Another important feature that adds to burrow complexity burrow is the pattern of outline morphology, i.e. straight to curved, locally discontinuous in a linear fashion. There is the main tunnel from which many small buds like projections are attached. These small bud-like projections are arranged

![Figure 6](image-url)

**Figure 6.** Dendrogram using Average Linkage algorithm (between groups) of *Treptichnus pedum* (N = 291), showing all the burrows were formed by single species (Priapulid). The vertical axis gives the specimen number while horizontal axis gives the distance which is a measure of closeness of clusters.

![Figure 7](image-url)

**Figure 7.** Dendrogram using Average Linkage algorithm (between groups) of *Treptichnus pedum* (N = 291) shows that all specimen comes under 1 cluster except specimen no. 182 which could be an outlier. The vertical axis gives the specimen number while horizontal axis gives the distance which is a measure of closeness of clusters.
Figure 8. A–F – results of the Hierarchical Cluster Analysis performed using three parameters, i.e. Width, Length and Gap of Treptichnus pedum. Figures B, D and F represents box-plot which displays the distribution of data based on the five number summaries: minimum, first quartile, median, third quartile, and maximum. In the box plot the rectangle spans the first quartile to the third quartile with in between and bars above and below the box show the locations of the minimum and maximum. Above and below the minimum and maximum it displays the observations which are outliers (observations which are above and below mean ±3 × Standard deviation).
on one side or, in some cases, they occur on both sides of the main tunnel. These projections signify the behavioural movement of the animal. Wilson et al. (2012) suggested the functional biology of priapulids in two ways: a) the animal might have lived infaunally to avoid predation or desiccation, and appeared on the surface episodically to feed and receive oxygen; and b) the animal might have been a deposit feeder that surfaced regularly to exchange gases and perhaps to disperse eggs, sperm or fertilized eggs. The latter appears more plausible because if the priapulid were able to find food on the surface then there is no valid reason for them to build three-dimensional burrows, although the safety from other predators could be the reason in that case the burrow system reflects the escape mechanism from predation.

**Taphonomy**

In the present study, a model is proposed to elaborate the taphonomical aspects of the Nagaur specimens, including burrowing (Fig. 3D, E) and movement of *T. pedum* (Fig. 10A–F). As stated earlier, there were gaps between the two segments which might have been formed during the time when the animal was out of the sediment layer (Fig. 10D, F). The length of the individual segments also varies as some segments extend up to centimetres scale, while a few hardly reach the millimetre-scale. It is presumed that when the animal moved into softer sediments it made long individual segments (see Srivastava 2012a, fig. 3f) and on the contrary when the sediments were relatively consolidated and hard, the resultant segments were small (Fig. 5D). The purpose of multiple exits noted in the burrow system still requires a suitable explanation as in an open tunnel system active ventilation would have been easier in a U-shaped structure with only two openings to the surface. Most likely, the multiple exits served the role of passive ventilation and/or for trapping small biotic elements that drifted inside the burrow from the sediment-water interface. Alternatively, they could have become actively backfilled upon completion of the next exit. *Treptichnus pedum* is prominently more three dimensional than the burrow of any other typical under mat miners.

The appearance of *T. pedum* in the Nagaur Sandstone of the Marwar Supergroup symbolises the change in the ecology and depositional realm and also shows the evolutionary trend in the early metazoan biosphere. The ichnogenera *Rusophycus*, *Diplichnites* and *Cruziana* are also found preserved on the same surface however, no short range taxon is found in the assemblage (Fig. 9E) suggesting that the zones of *T. pedum* cross over in these strata and occur together with *Rusophycus* throughout the Cambrian (Jensen & Mens 2001, Hofmann et al. 2012, Srivastava 2012a, Pandey et al. 2014). The Agronomic Revolution (Seilacher & Pflüger 1994, Seilacher 1999) subsequently triggered another revolution in selection of the substrate changes by the benthic organisms (Mángano & Buatois 2017). The radiation of burrowing metazoan in the early Phanerozoic is considered to involve the evolution of hardgrounds and complex organism-substrate interactions, also known as ‘Cambrian Substrate Revolution’ (Bottjer et al. 2000, Tarhan & Droser 2014). The lack of or hunt for nutrition on the substrate compelled the organisms, building simple burrows, to intrude deeper into the sediment crafting a complex burrow system. *Treptichnus pedum* accounts for the first infaunal activity in the Nagaur Sandstone of the Marwar Basin. The ichnospecies *Bergaueria cf. perata* occasionally found associated with *T. pedum* is another example of vertical burrowing. Though, the ichnospecies *T. pedum* is also reported from the various depositional environments (Buatois et al. 2013) but mostly it represents shallow marine setting; in the case of the Nagaur Group, the sedimentary structures of sandstone and mudstone facies suggest that the Nagaur Sandstone represents deposition in low-lying interbar areas protected from strong wave action and tidal currents indicating shallow marine setting. Penetration depths are 1–5 mm which indicates that the animal occupied shallow tiers. It also suggests that the sufficient nutrient saturation was available immediately below the substrate and there was no need to dig deeper burrows by the organisms. The statistical analysis also concludes that all these small projections were formed by the same priapulid as all of them falls in same hierarchy in the hierarchical cluster analysis (dendrogram) and also the box-plot analysis, which shows that the peculiar pattern of burrowing might be the end result of their behavioural activity. The gaps in between the two consecutive projections infer that the animal lived near the sediment-water interface and represents the time frame when the animal was out of the sediment.

**Implications on Precambrian–Cambrian boundary**

In many places, specifically Namibia and Spain, treptichnids appeared below the Ediacaran–Cambrian...
boundary (Jensen et al. 2000, Jensen 2003, Buatois 2018); whereas in others, Treptichnus pedum is recorded in the early Cambrian and survived up to the Ordovician (Seilacher 2007). A solitary record shows the presence Treptichnus in recent times (see Muñiz Guinea et al. 2014); therefore, the group has a long temporal range (Wilson et al. 2012). Vannier et al. (2010) demonstrated that the treptichnid burrows were made by priapulids or priapulids-like worms. A sharp decrease of T. pedum is attributed to the extinction/replacement of such priapulids (Conway-Morris 1977). In the geological history, the Precambrian–Cambrian boundary is the only stratigraphical boundary which is based on the FAD of a trace fossil (T. pedum; Brasier et al. 1994, Landing 1994, Peng et al. 2012). However, it has been advocated that T. pedum alone should not be considered as the marker trace fossil for Precambrian–Cambrian boundary/transition; rather, ‘Treptichnus pedum Ichnofossil Assemblage Zone’ would be more appropriate for demarcating the boundary (Narbonne et al. 1987, Landing et al. 2013, Laing et al. 2016, Buatois 2018).

Precambrian–Cambrian boundary/transition within the Marwar Basin is widely debated for its existence in the argillo-arenaceous succession of the Nagaur Group or in the underlying carbonate succession of the Bilara Group. On the basis of microfossils data, it was suggested that the boundary should be within the Bilara Group (Prasad et al. 2010). This has been questioned by Hughes (2016) on the basis of quality of microfossils illustrated in the paper of Prasad et al. (2010). Stable carbon isotope data has been used to argue suggesting that the Precambrian–Cambrian boundary lies within the carbonate succession, i.e. the Bilara Group of the Marwar Supergroup (Pandit et al. 2001, Maheshwari et al. 2003, Mazumdar & Bhattacharya 2004, Mazumdar & Strauss 2006, Ansari et al. 2018), however, on the basis of trace fossils assemblage, especially T. pedum, Rusophycus, Cruziana, Diplichnites, Chondrites and Monomorphichnus, it is believed that the Nagaur Sandstone is early Cambrian in age (Kumar & Pandey 2008, 2010; Srivastava 2012a; Pandey et al. 2014; Singh et al. 2014a). Data presented here suggest that the Nagaur Sandstone in the Marwar Supergroup is the most promising succession to study the Precambrian–Cambrian boundary in the peninsular India, if FAD of T. pedum and ‘Treptichnus pedum Ichnofossil Assemblage Zone’ is established in the hitherto underlying unexplored vast thickness of Nagaur Sandstone.

**Conclusions**

1) The Treptichnus pedum marks the first infaunal activity in the Nagaur Sandstone and also represent the appearance of complex burrows pattern in the early biosphere.
2) The Nagaur Sandstone has all the signatures which positively support the hierarchy of evolutionary trend as it demonstrates the succession from simple burrow to complex burrow, followed by miscellaneous track and trails of arthropods. The hierarchy order of such biozone is correlative with the Mackenzie Mountain, Canada.

3) Statistical analysis especially the hierarchical cluster analysis suggest that all the individuals (N = 291) belong to the same species.

4) The burrow-producing animal lived under the thin layer of sand and occasionally protruded out of the sediment. The gaps between the two consecutive segments denote the phase of life when it came out of the sediment covering.

5) On the global scale, ichnospecies *T. pedum* is strictly found in siliciclastic sediments; it also holds true for the Nagaur Group where *T. pedum* is confined to Nagaur Sandstone-Siltstone alteration. The present study reiterates that the First Appearance Datum (FAD) is yet to be documented in the vast thickness of the Nagaur Sandstone which underlies the exposed succession at Dulmera locality in Bikaner District of Rajasthan.

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