

# On the ichnofossil *Treptichnus pedum*: inferences from the Nagaur Sandstone, Marwar Supergroup, India

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Sandstone-mudstone interfaces offer an excellent medium for the preservation of the burrows. This study discusses the morphology, ecological niche and correlation based of 291 *Treptichnus pedum* specimens of the lower Cambrian Nagaur Sandstone, western Rajasthan, India. Petrological attributes of the host sediment are also addressed. Statistical analyses of size (length, width and gap of each segment of *T. pedum*) were conducted to determine the inter-specific variation. Data suggest that the entire Nagaur assemblage was made by one major group of makers. Overall morphology suggests that these burrows were probably made for shelter and trapping small epibenthic or endobenthic organisms. An overview of the global occurrence of *T. pedum* shows broad environment tolerance. The Nagaur specimens are compared with various recorded occurrences of *T. pedum* to assess the nature of the plausible producer organism, its behaviour and taphonomical aspects. • Key words: *Treptichnus*, Priapulid, Cambrian, Nagaur Group, Marwar Supergroup.

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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 sediment 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  $771 \pm 5$  Ma (Gregory *et al.* 2009). The Tunklian Sandstone is the youngest formation of the Marwar Supergroup. The underlying 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

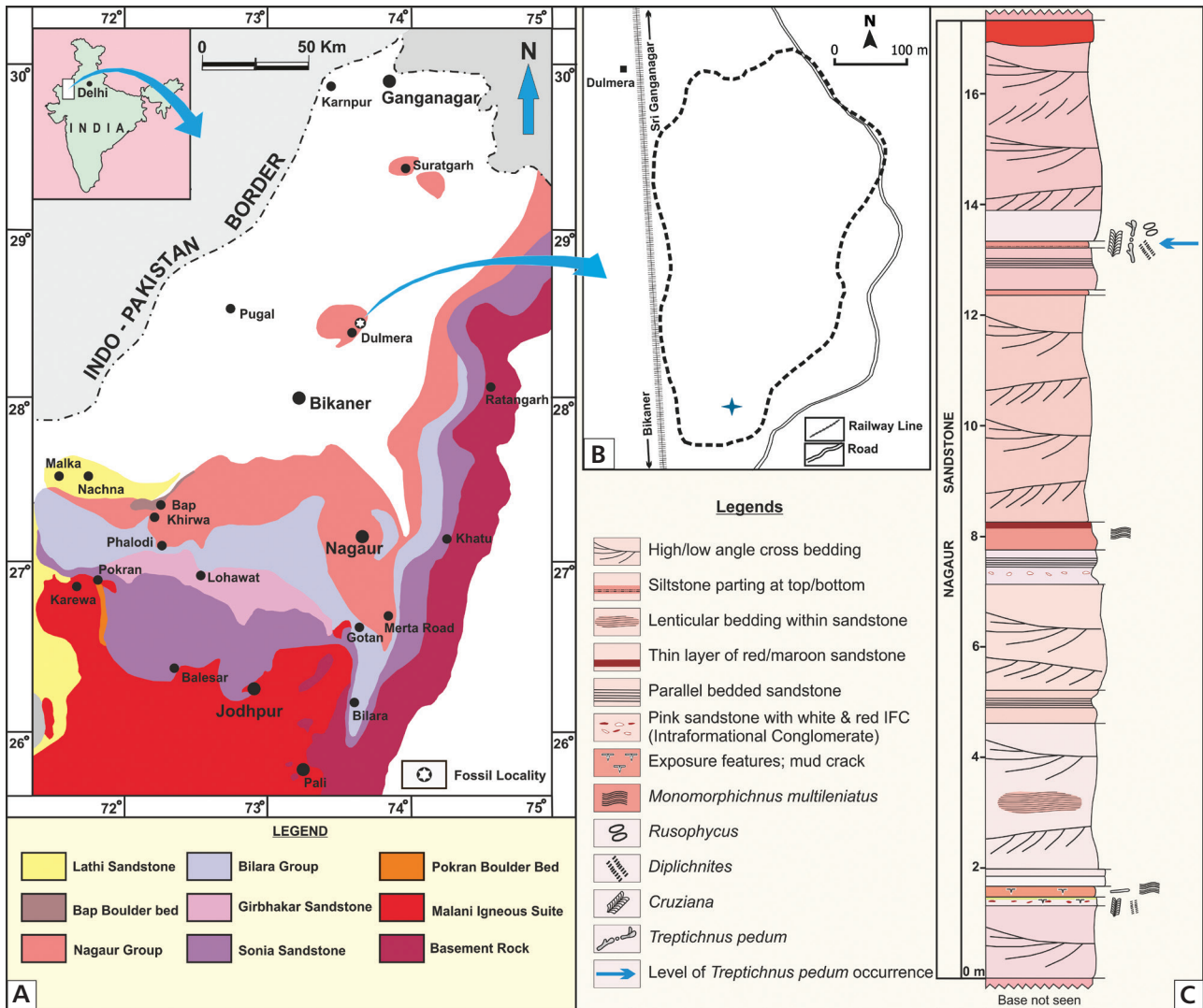
*et al.* 2011), which is the maximum age of the Nagaur Sandstone. Pandey *et al.* (2014) and Singh *et al.* (2014a) considered that the ichnofossil assemblage recorded from the Nagaur Sandstone belongs to Stage 2 of the Terreneuvian Epoch. However, the beds containing these trace fossils are not conformably 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
Ediacara to Stage 4 of the Cambrian	Marwar Supergroup	Unconformity	
		Nagaur Group (75–500 m)	Tunklian Sandstone Nagaur Sandstone
		Bilara Group (100–300 m)	Pondlo Dolomite Gotan Limestone Dhanapa Dolomite
		Jodhpur Group (125–240 m)	Girbhakar Sandstone Sonia Sandstone Pokaran Boulder Bed
		Unconformity	
		Malani Igneous Suite	
779–681 Ma			



**Figure 1.** Geological map, area of study and lithology of the *Treptichnus pedum* yielding succession. • A – geological map of the Marwar Supergroup, the western Rajasthan showing fossil locality exposed in Dulmera Village (after Pareek 1984). • B – geographical extent of the Dulmera quarry along the Dulmera Railway Station. • C – generalised lithology of the Nagaur Sandstone succession bearing *T. pedum*.

*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 Zaskar 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 sizable population of polycrystalline grains (5%). Square shaped opaque magnetite inclusions are noted in a few grains, while others contain inclusion of zoisite

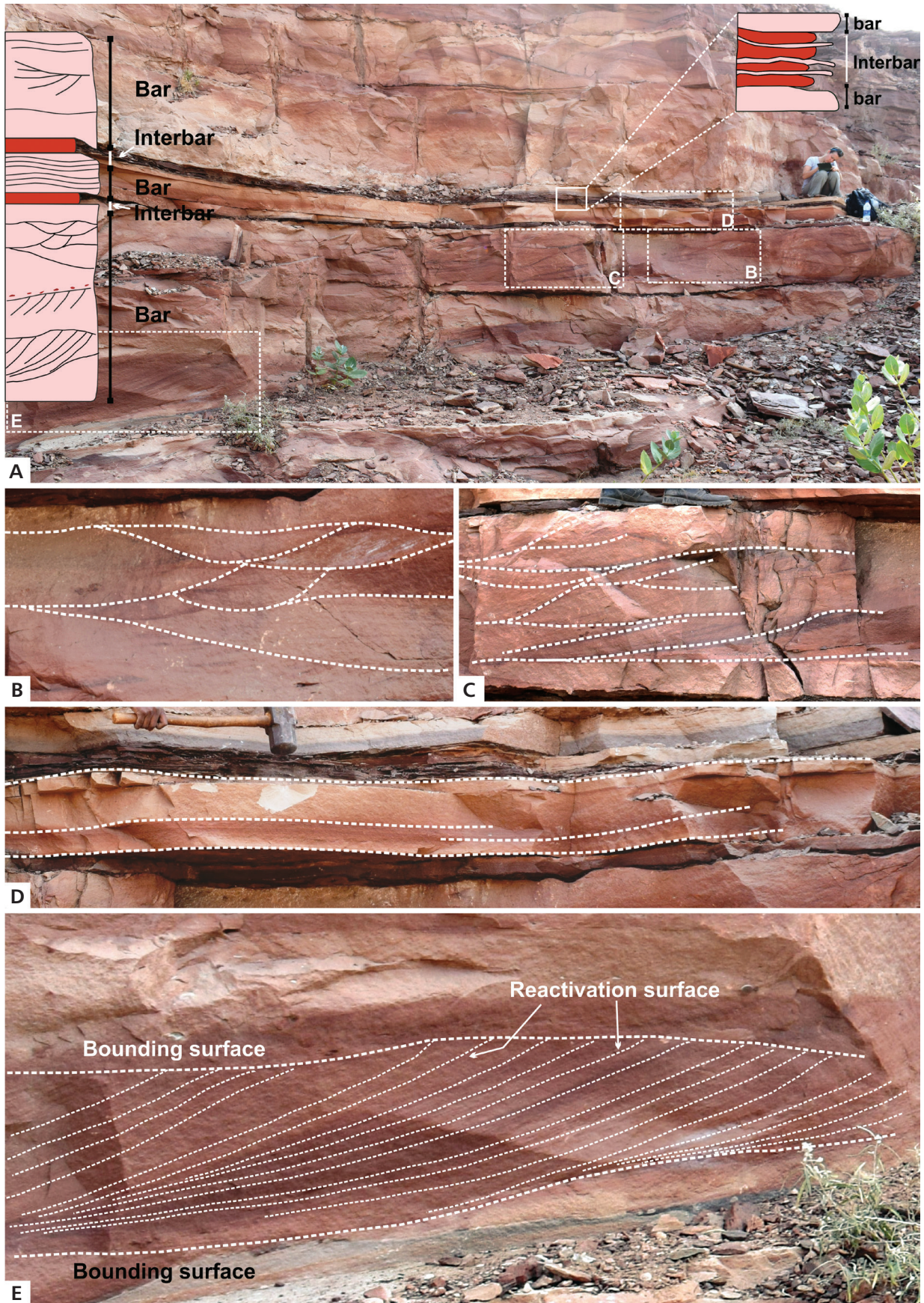
and clinozoisite. Feldspar constitutes 5% of the entire grain population. Potassium feldspars consist of tabular grains of microcline and orthoclase with characteristic cross hatched twinning, orthoclase grains, also tabular in shape, show first order grey colour. Medium-grained fresh Na feldspar consisting 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

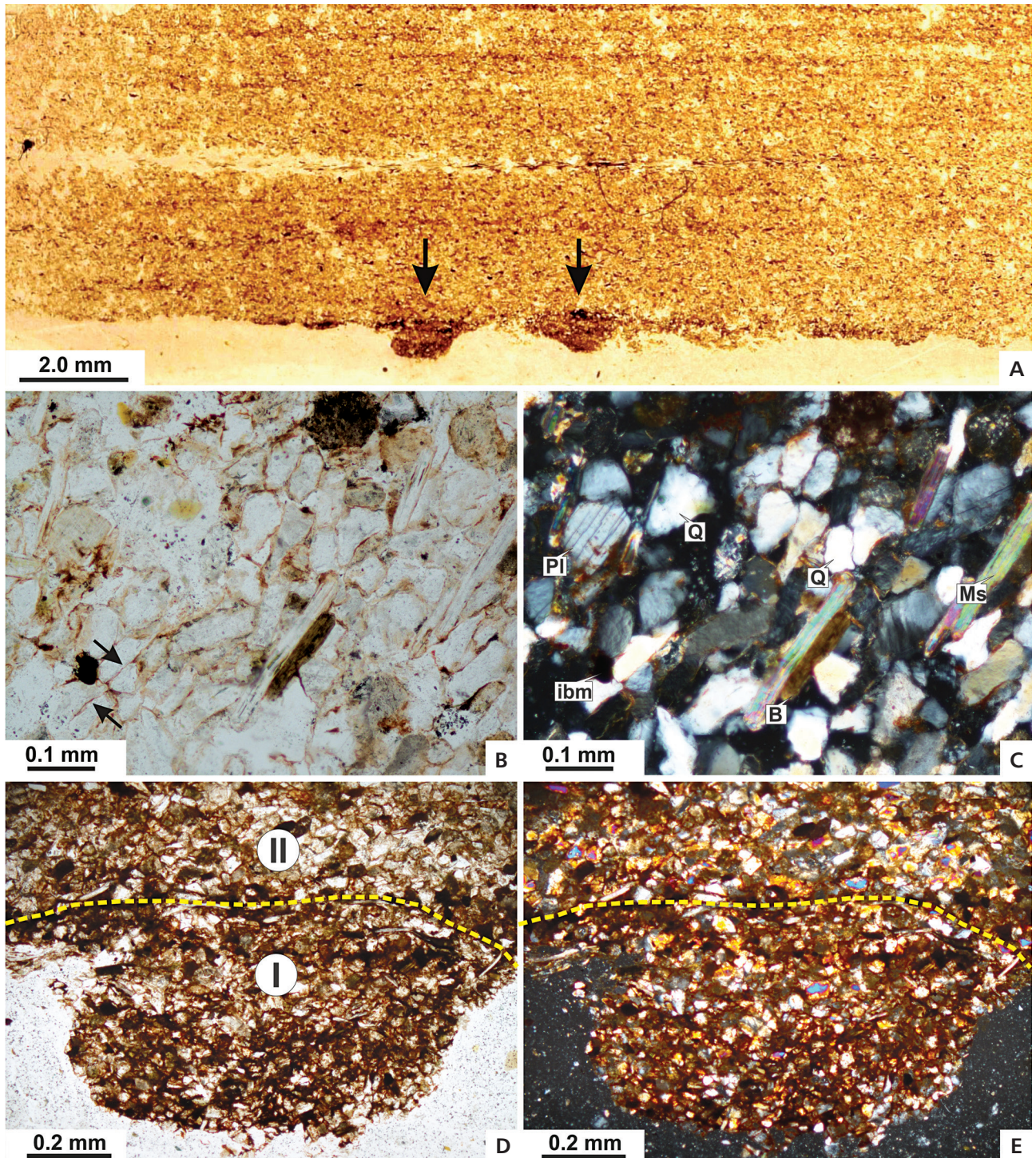
Lowermost *T. pedum*-bearing horizon is encountered 13 m from the base of the section exposed in the quarry. The trace fossil-bearing facies (~2-metre-thick unit) is brown to red in colour, medium-grained sandstone with intercalations of centimetre-thick mudstone (Fig. 2). The succession can be divided 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

**Figure 2.** Outcrop expression of *Treptichnus pedum* bearing Nagaur Sandstone. • A – typical components of *Treptichnus* ichnofacies of Nagaur Sandstone on the quarry face at Dulmera, Rajasthan which is divisible into two lithofacies namely sandstone facies and mudstone facies. Extreme right corner depicts blow-up of mudstone facies with interspersed streaks of sand; on the left edge is shown interpretative diagram of two depositional facies representing bar and interbar; detailed sedimentary features of boxes marked as b, c, d and e are shown in respective subsequent figures. • B – trough cross-bedding in sandstone facies. • C – low angle cross-bedding and trough cross-bedding. • D – planar and undulated cross-bedded strata indicating influence of waves sandwiched between two mud dominated interbar facies. • E – probable tidal bundles with reactivation and bounding surfaces marked on sandstone in bar facies.







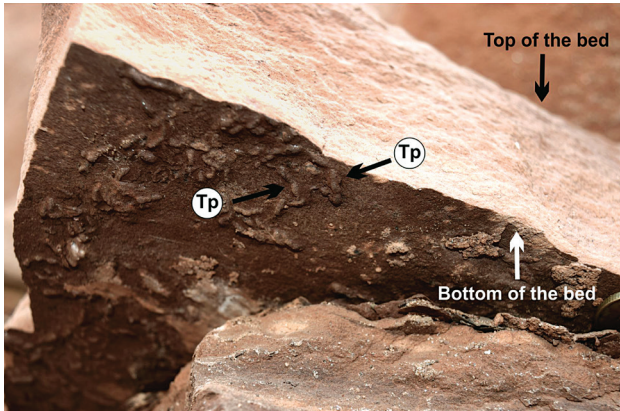


**Figure 3.** Petrographic thin section (slide number BSIP-16168) showing distinct host sediments and sediment trapped inside the burrow. • A – thin section of the Nagaur Sandstone under low power microscopy; black arrows show sole of the bedding plane with positive relief of burrow. • B – plane polarised light, black arrows indicate contact between two quartz grains. • C – cross polarised light. Abbreviations: Q – quartz; Pl – plagioclase; Ms – muscovite; ibm – iron bearing mineral; B – biotite. • D – plane polarised light, view of burrow with host sediment. Abbreviations: I – burrow whereas; II – host rock. • E – cross polarised light view of 'D'.

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





**Figure 4.** In-situ *Treptichnus pedum* noted on the sole of the fine grained sandstone, see coin for scale = 2.3 cm.

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 repositied in the museum of Birbal Sahni Institute of Palaeosciences, Lucknow (collection statement number 1444).

Ichnogenus *Treptichnus* Miller, 1889

Ichnospecies *Treptichnus pedum* (Seilacher, 1955)

Figure 5A–M

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



Table 2. continued.

No.	Ichnospecies	Stratigraphy	Facies	Depositional settings	Age	References
22.	<i>Treptichnus pedom</i>	Nama Group, Namibia	sandstone, siltstone	not mentioned	early Cambrian	Jensen <i>et al.</i> (2000)
23.	<i>Treptichnus pedom</i>	Gross Aub Formation and Nomtas Formation, South Namibia	no precise data	no precise data	early Cambrian	Germes (1972), Crimes & Germes (1982), Geyer & Uchman (1995)
24.	<i>Treptichnus pedom</i>	Death Valley, USA	sandstone, siltstone	not mentioned	early Cambrian	Corsetti & Hagadorn (2000)
25.	<i>Treptichnus pedom</i>	Bright Angel Shale, Grand Canyon, USA	no precise data	no precise data	early to middle Cambrian	Seilacher (1956), Eliot & Martin (1987)
26.	<i>Treptichnus pedom</i>	Deep Spring Formation, Campito Formation, White Mountains, USA	no precise data	no precise data	early Cambrian	Alpert (1977)
27.	<i>Treptichnus pedom</i>	Gongwusu Formation, Inner Mangolia, China	no precise data	no precise data	Middle Ordovician	Li (1993)
28.	<i>Treptichnus pedom</i>	Kaili Formation, Guizhou Province (S China)	no precise data	no precise data	middle Cambrian	Yang (1994), Wang & Wang (2006)
29.	<i>Treptichnus pedom</i>	Yu'an Shan Formation, Yunnan Province, South China	no precise data	no precise data	early Cambrian	Zhu (1997)
30.	<i>Treptichnus pedom</i>	Wisniowka Formation, Holy Cross Mountains, Poland	no precise data	no precise data	Furongian	Orlowski & Żylińska (1996)
31.	<i>Treptichnus pedom</i>	Ocieseki Formation, Holy Cross Mountains, Poland	no precise data	no precise data	early Cambrian	Orlowski (1989)
32.	<i>Treptichnus pedom</i>	Platysolenites Zone, SE Poland	no precise data	no precise data	early Cambrian	Paczesna (1985, 1986)
33.	<i>Treptichnus pedom</i>	Detrital Beds, Sierra De Guadalupe, Spain	no precise data	no precise data	early Cambrian	Liñán (1984)
34.	<i>Treptichnus pedom</i>	Vegadeo Limestone, Herreria Sandstone, Cantabrian Mountains, N Spain	sandstone	no precise data	early Cambrian	Crimes <i>et al.</i> (1977), Baldwin (1977), Legg (1985)
35.	<i>Treptichnus pedom</i>	Mickwitzia Sandstone, South Central Sweden	no precise data	no precise data	early Cambrian	Jensen (1997)
36.	<i>Treptichnus pedom</i>	Tornetrask Formation, Dividalen Group, N Sweden	no precise data	no precise data	late Ediacaran and early Cambrian	Jensen & Grant (1998)
37.	<i>Treptichnus pedom</i>	Klipbak Formation, Vanrhynsdorp Group, South Africa	sandstone	shallow marine clastic setting	early Cambrian	Buatois <i>et al.</i> (2013)
38.	<i>Treptichnus pedom</i>	Neobolus beds, Salt Range, Pakistan	no precise data	no precise data	early Cambrian	Seilacher (1955)
39.	<i>Treptichnus pedom</i>	Puerto Blanco Formation, Sonora, Mexico	sandstone	not mentioned	early Cambrian	Sour-Tovar <i>et al.</i> (2007)
40.	<i>Treptichnus pedom</i>	Melez Chorgrane Formation, Libya	no precise data	no precise data	Early Ordovician	Seilacher (1969)
41.	<i>Treptichnus pedom</i>	Rovno Formation, Ukraine	no precise data	no precise data	early Cambrian	Fedonkin (1983), Palij (1976)
42.	<i>Treptichnus pedom</i>	Breivik Formation, Finnmark, Norway	no precise data	no precise data	early Cambrian	Banks (1970), Føyn & Glaessner (1979)
43.	<i>Treptichnus pedom</i>	Lontova Formation, Estonia	no precise data	no precise data	early Cambrian	Palij (1976), Palij <i>et al.</i> (1983)
44.	<i>Treptichnus pedom</i>	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	1	0.407**	–0.051
	Sig. (2-tailed)		0.000	0.488
	N	291	258	190
Width	r	0.407**	1	–0.125
	Sig. (2-tailed)	0.000		0.112
	N	258	258	163
Gap	r	–0.051	–0.125	1
	Sig. (2-tailed)	0.488	0.112	
	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 ichnogenic 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 pictorial 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 in 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  $\pm 3$  (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

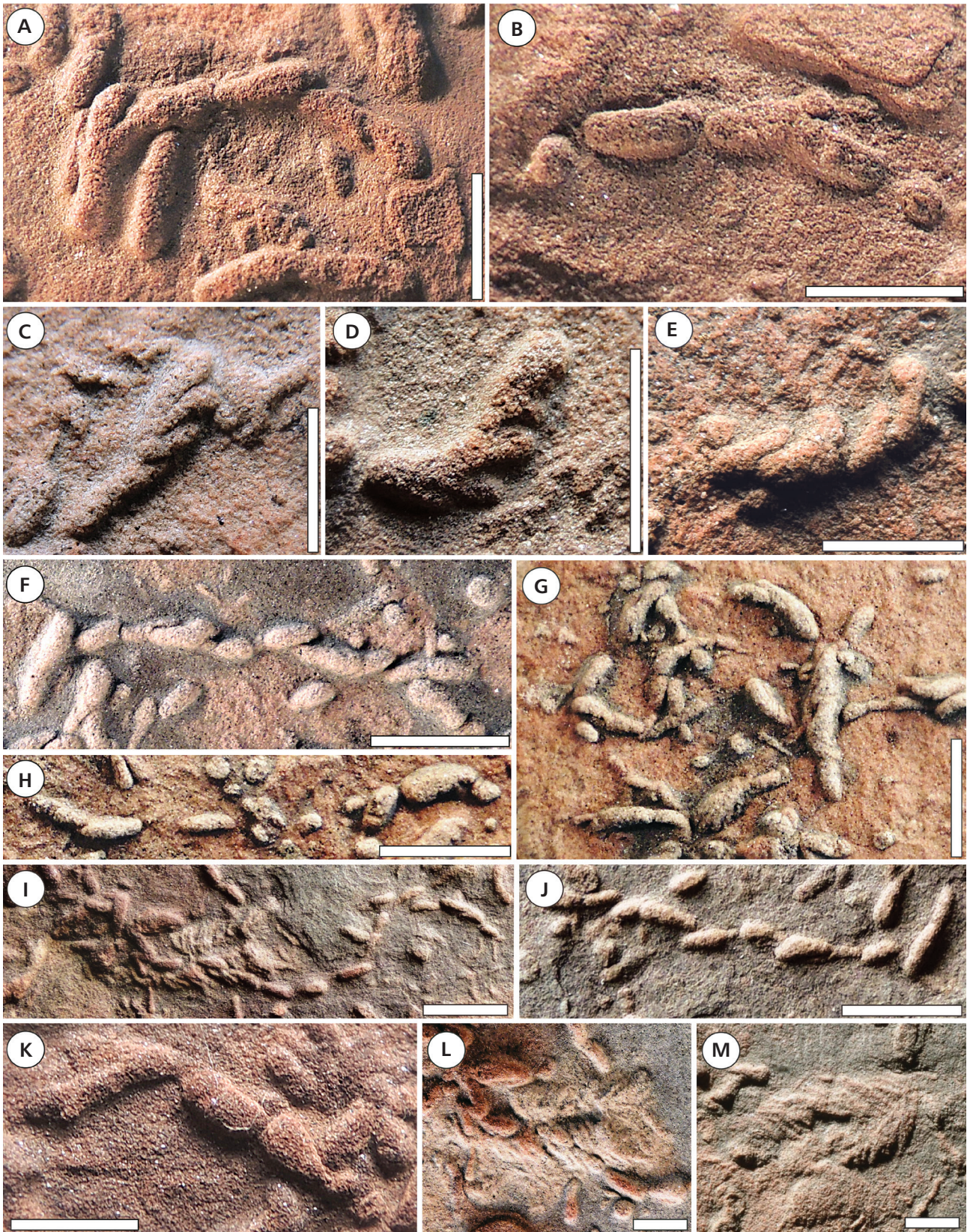
### Palaeoecology

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 *Diplichnites* 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).

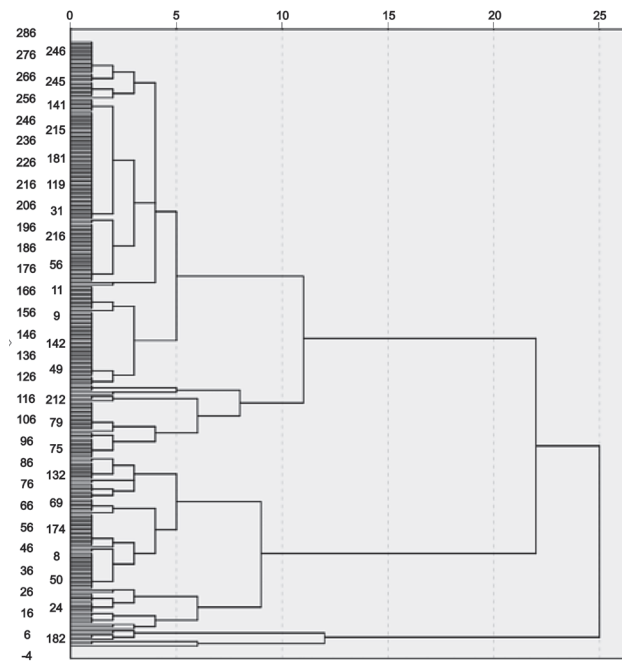
*Treptichnus pedum* is characteristically found in shallow, fully marine to marginal-marine environments

**Figure 5.** Distribution pattern and characteristic features of *Treptichnus pedum* recovered from Nagaur Sandstone, Dulmera quarry. • A – small segments of burrow consecutively connected which depicts the movement of the organism, BSIP-41046. • B – the interspaces between the two consecutive burrow segments indicate sediment-water interface zone where the animal was out of sediment cover, BSIP-41046. • C, D, E – multiple burrows are attached to main master burrow, BSIP-41043. • F, H – linear arrangement of burrow system, BSIP-41045. • G – randomly distributed burrow geometry, BSIP-41045. • I – in hyporelief, *T. pedum* overlapping the *Cruziana* isp., BSIP-41045. • J – little gap between the two consecutive burrows, BSIP-41045. • K – another pattern of *T. pedum* burrow, BSIP-41043. • L, M – overlapping of *T. pedum* and *Cruziana*, BSIP-41045. Scale bars: A–E, K–M = 0.5 cm; F–J = 1 cm.



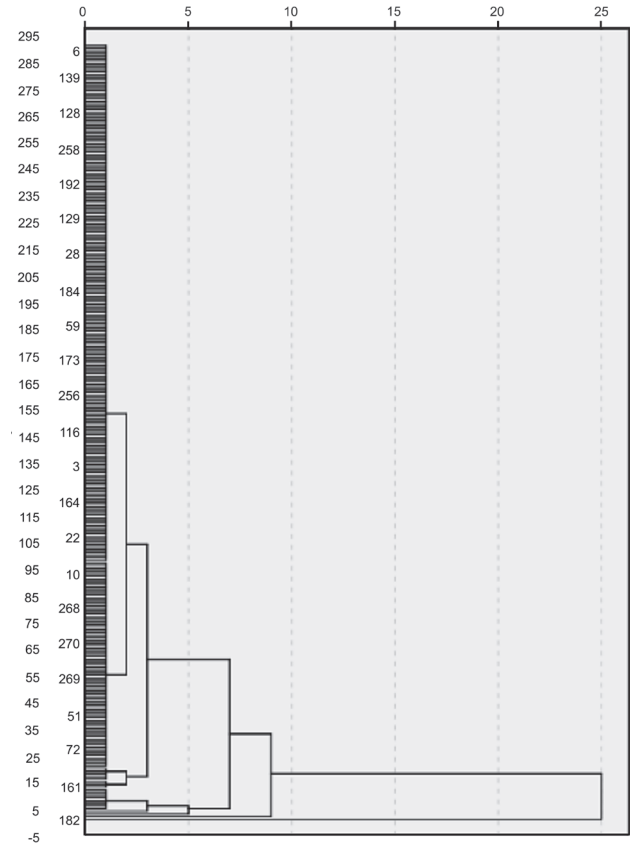






**Figure 6.** Dendrogram using Average Linkage algorithm (between groups) of *Treptichnus pedum* (N = 291), showing all the burrows were formed by single species (Priapulid). The vertical axis gives the specimen number while horizontal axis gives the distance which is a measure of closeness of clusters.

(Geyer & Uchman 1995, MacNaughton & Narbonne 1999, Mángano *et al.* 2012). *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 avail-



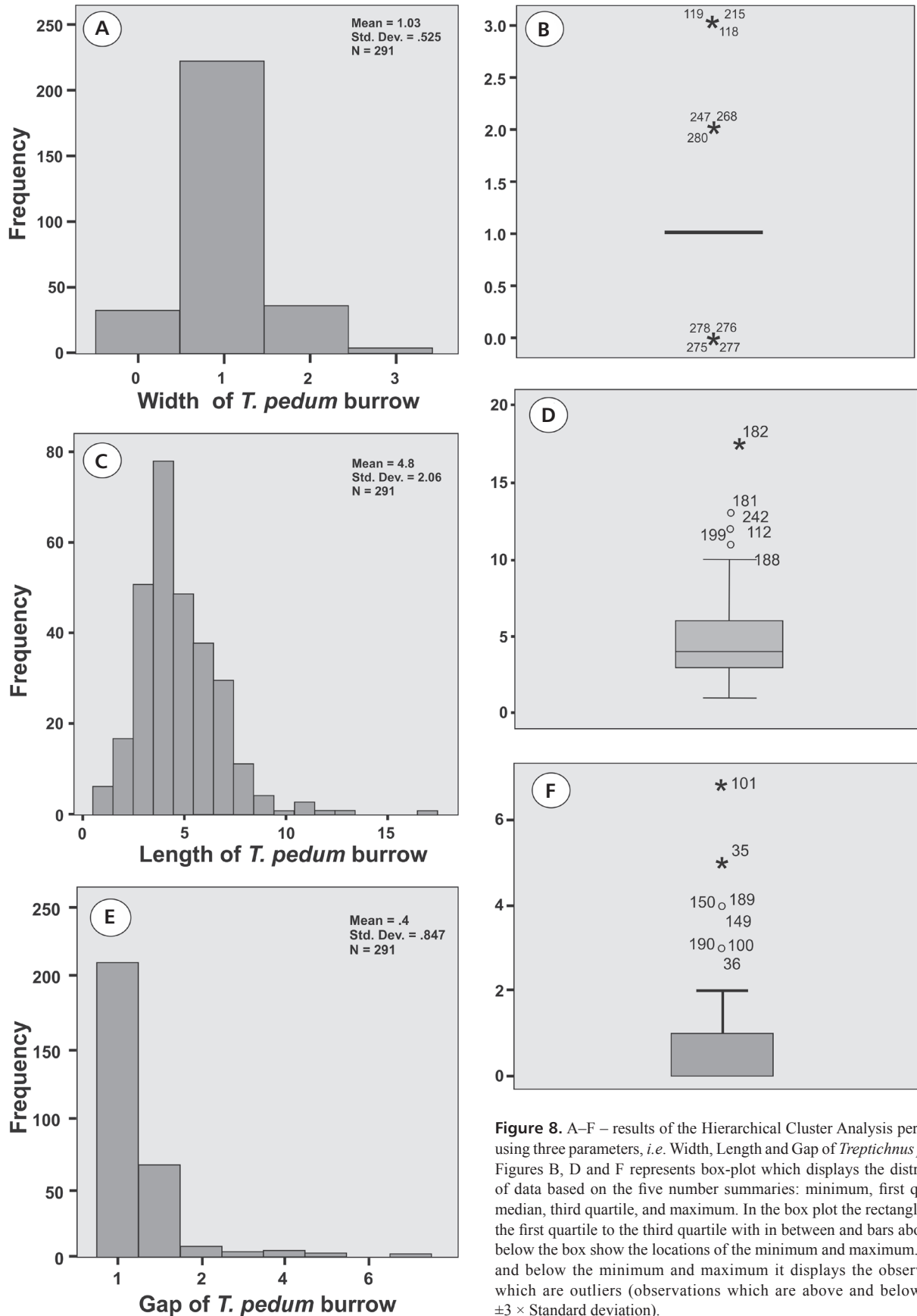
**Figure 7.** Dendrogram using Average Linkage algorithm (between groups) of *Treptichnus pedum* (N = 291) shows that all specimen comes under 1 cluster except specimen no. 182 which could be an outlier. The vertical axis gives the specimen number while horizontal axis gives the distance which is a measure of closeness of clusters.

able 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 comes 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 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  $\pm 3 \times$  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

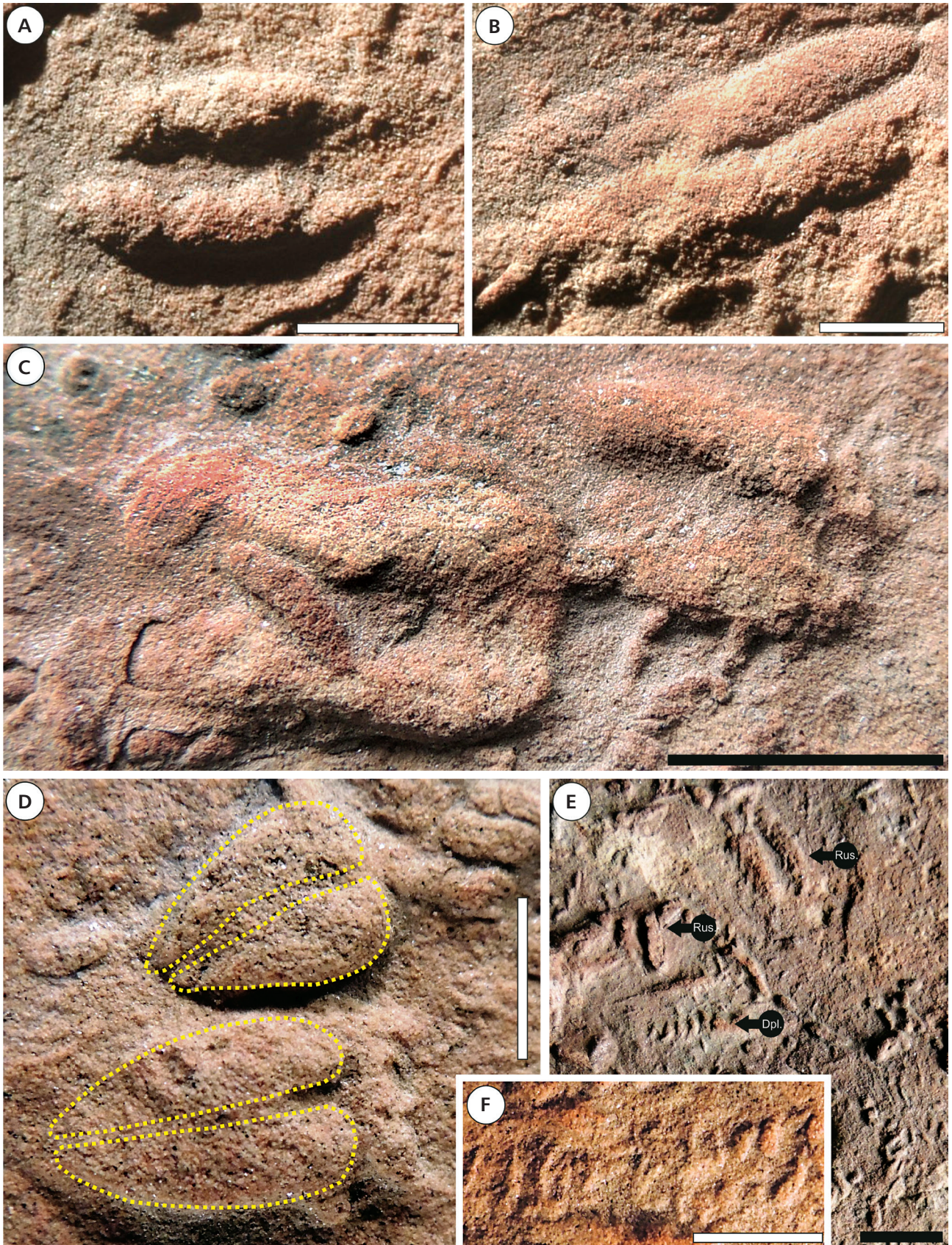
short range taxon is found in the assemblage (Fig. 9E) suggesting that the zones of *T. pedum* cross over in these strata and occur together with *Rusophycus* throughout the Cambrian (Jensen & Mens 2001, Hofmann *et al.* 2012, Srivastava 2012a, Pandey *et al.* 2014). The Agronomic Revolution (Seilacher & 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

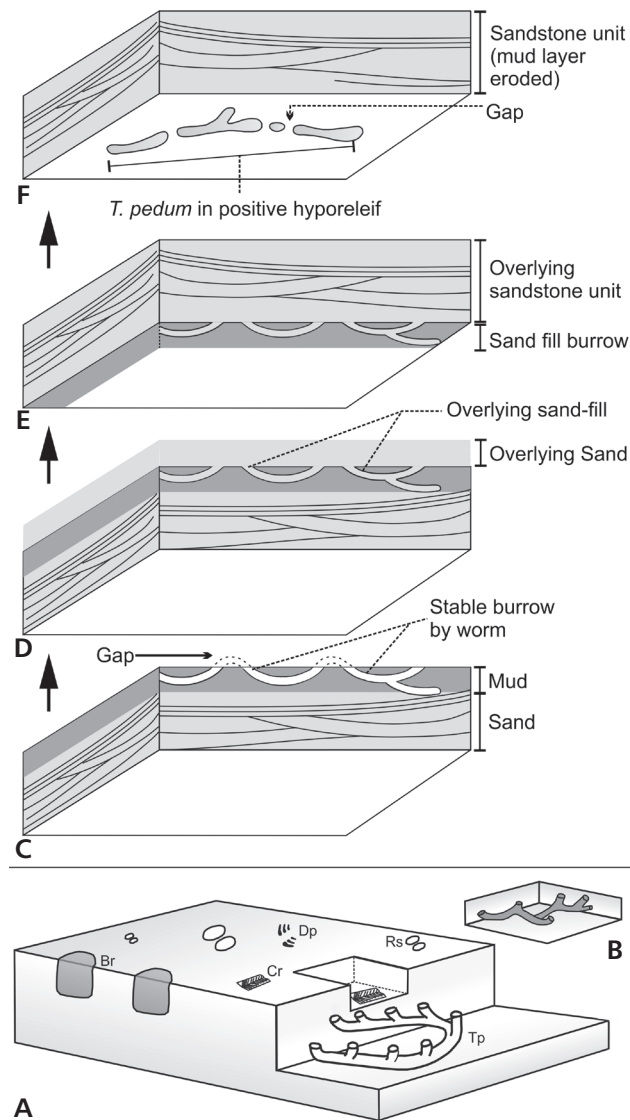
In many places, specifically Namibia and Spain, treptichnids appeared below the Ediacaran–Cambrian

**Figure 9.** Other trace fossils in the assemblage recorded from the Nagaur Sandstone (BSIP specimen no. BSIP-41046). • A–D – *Rusophycus* isp. preserved as a negative hyporelief. • E – preservation of *Rusophycus* isp. and *Diplichnites* isp. on the same bedding. • F – *Diplichnites* isp. preserved on the Nagaur Sandstone. Scale bars: 0.5 cm (white bar) and 1 cm (black bar).









**Figure 10.** Cartoons illustrating the suggested stages of formation and preservation of burrows of *Treptichnus pedum* reported from the Nagaur Sandstone. • A – block diagram showing the level of preservation of simple to complex burrow system and other miscellaneous trace fossils noted at 13 metres level of Nagaur Sandstone. Abbreviations: Tp – *Treptichnus pedum*; Br – *Bergaueria*; Cr – *Cruziana*; Rs – *Rusophycus*; Dp – *Diplichnites*. • B – mould of *T. pedum* burrow as it would appear on the sole of the sandstone bed (three-dimensional morphology of burrow after cleaning and partitioning from mudstone-sandstone interface). • C – block diagram illustrating sandstone-mudstone interface with sedimentary features and stable burrows made by *T. pedum* in mudstone unit. Gaps denoted by broken lines represent the part of the burrows where priapulid worm emerged on the surface close to sediment-water interface before re-entering the unconsolidated sediments. • D – deposition of successive thin layers of sandstone passively fills the burrows formed in the underlying mudstone. • E – continuous deposition of sandstone over the in-filled burrows seals and preserves them on the sole of the sandstone. • F – mechanical or natural exposure unearths burrows of *T. pedum* preserved as positive hyporelief whereas gaps denoting emergence of priapulid worms on the surface are merged with the sediments of overlying sandstone.

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. pedom* is strictly found in siliciclastic sediments; it also holds true for the Nagaur Group where *T. pedom* 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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