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PALAEOENVIRONMENTAL IMPLICATIONS OF MIDDLE JURASSIC TRACE FOSSILS FROM THE JAISALMER FORMATION, INDIA, WITH EMPHASIS ON THE ICHNOGENUS *ASTERIACITES LUMBRICALIS* VON SCHLOTHEIM, 1820

Shweta S. GURAV, Kantimati G. KULKARNI, Amruta R. PARANJAPE & Vidyadhar D. BORKAR

Geology and Palaeontology Group, Agharkar Research Institute, G.G. Agarkar Road, Pune 411 004, India;
e-mails:shwtgrv@gmail.com, kantimatik@gmail.com, amrita.paranjpe@gmail.com, vidyadharborkar@yahoo.co.in

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Abstract: The Hamira Member (Bathonian) of the Jaisalmer Formation records the first marine transgression within the Jaisalmer Basin. It also contains the ichnogenus *Asteriacites* von Schlotheim, 1820, as documented here for the first time. This was used to refine interpretations of the palaeoenvironment. Crowded ophiuroid resting traces, *Asteriacites lumbricalis,* occur in a silty limestone unit 1 m thick. This is preceded by a monospecific assemblage of *Diplocraterion parallelum* towards the base of this unit, while towards the top there is an assemblage, comprising *Gyrochorte comosa*, *Protovirgularia rugosa*, *Rhizocorallium commune* and *Rosselia socialis*. Colonisation by the *Asteriacites* trace makers occurred in a shallow-water, marginal-marine, normal-salinity, fully oxygenated, high-energy setting with steady rates of sedimentation. From an ichnological perspective, the sequence investigated shows a shift in environmental conditions from the middle shoreface to the offshore transition zone. Addressing the *Asteriacites/Heliophycus* nomenclatorial dilemma, Knaust (2012) suggested that the generic designation *Asteriacites* should be retained. His view was found to be appropriate and supported to avoid further confusion.

Key words: *Asteriacites, Heliophycus*, Bathonian, opportunistic colonisation, Jaisalmer Basin, Rajasthan.

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INTRODUCTION

The Jaisalmer Basin, situated in the northwestern part of the Indian Craton (Fig. 1), is also referred to as the Western Rajasthan Shelf (Das Gupta, 1975). It is a northward-sloping shelf basin (Pandey *et al*., 2009), and comprises sediments ranging from Mesozoic to Palaeogene in age. The Jurassic rocks of the Jaisalmer Basin are lithostratigraphically designated as the Lathi, Jaisalmer, Baisakhi, and Bhadasar formations, ranging in age from Liassic to Tithonian (Das Gupta, 1975). The rocks of the Jaisalmer Formation represent the first marine Mesozoic transgression in this part of India. This formation is divided into the Hamira, Joyan, Fort, Bada Bagh and Kuldhar members (Das Gupta, 1975).

The star-shaped trace fossil *Asteriacites* described here was discovered in the mixed siliciclastic and carbonate sediments of the Hamira Member (Bathonian), exposed in a section about 1 km south-southwest of Suleiman Pir (Fig. 1). The lower beds of the Hamira Member are well exposed at this location. Though Das Gupta (1975) had mentioned the contact between the Hamira Member of the Jaisalmer Formation and the underlying Lathi Formation as interfingering, recent studies suggest that this contact is marked by a discontinuity that represents a sequence boundary. The siliciclastic-carbonate succession of the Hamira Member belongs to the transgressive systems tract, with the limestones at the top of the member representing the maximum flooding zone (Agarwal *et al*., 2014).

A 1-m-thick silty limestone unit in the Hamira Member of the Jaisalmer Formation displays an interesting succession of ichnoassemblages. Towards the base of this unit there is a monospecific assemblage of *Diplocraterion parallelum*. The middle part exhibits a prolific development of *Asteriacites lumbricalis*. An ichnoassemblage of *Gyrochorte comosa, Protovirgularia rugosa, Rhizocorallium commune* and *Rosselia socialis* occurs towards the top. It was realized that such a succession of ichnoassemblages would prove useful in refining the palaeoevironments.

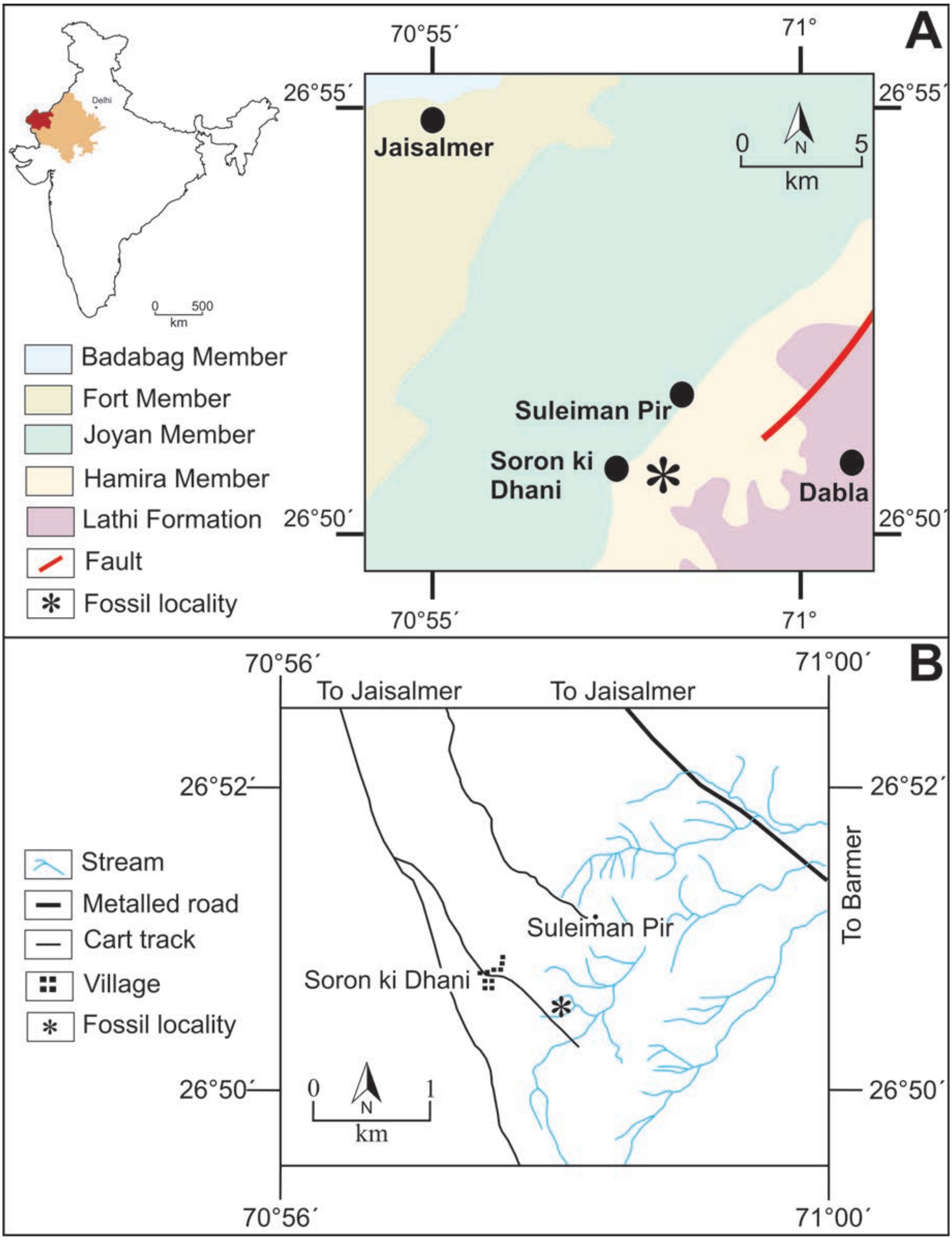


Fig. 1. Map of study area. **A.** Geological map, location indicated by asterisk. **B.** Location map, outcrop indicated by asterisk.

Moreover, the extensive development of *A. lumbricalis* was of special interest. An enquiry into the systematics of the star-shaped traces revealed that there is a debate over the nomenclature. It was imperative to see if the trace fossils occurring in this unit could assist in resolving the controversy. The outcome of these studies is presented in this paper.

The specimens described have been placed in the fossil repository of the Agharkar Research Institute (formerly the MACS Research Institute), Pune, bearing the acronym MACS G (Maharashtra Association for the Cultivation of Science, Geology) and registration numbers 5206 to 5228.

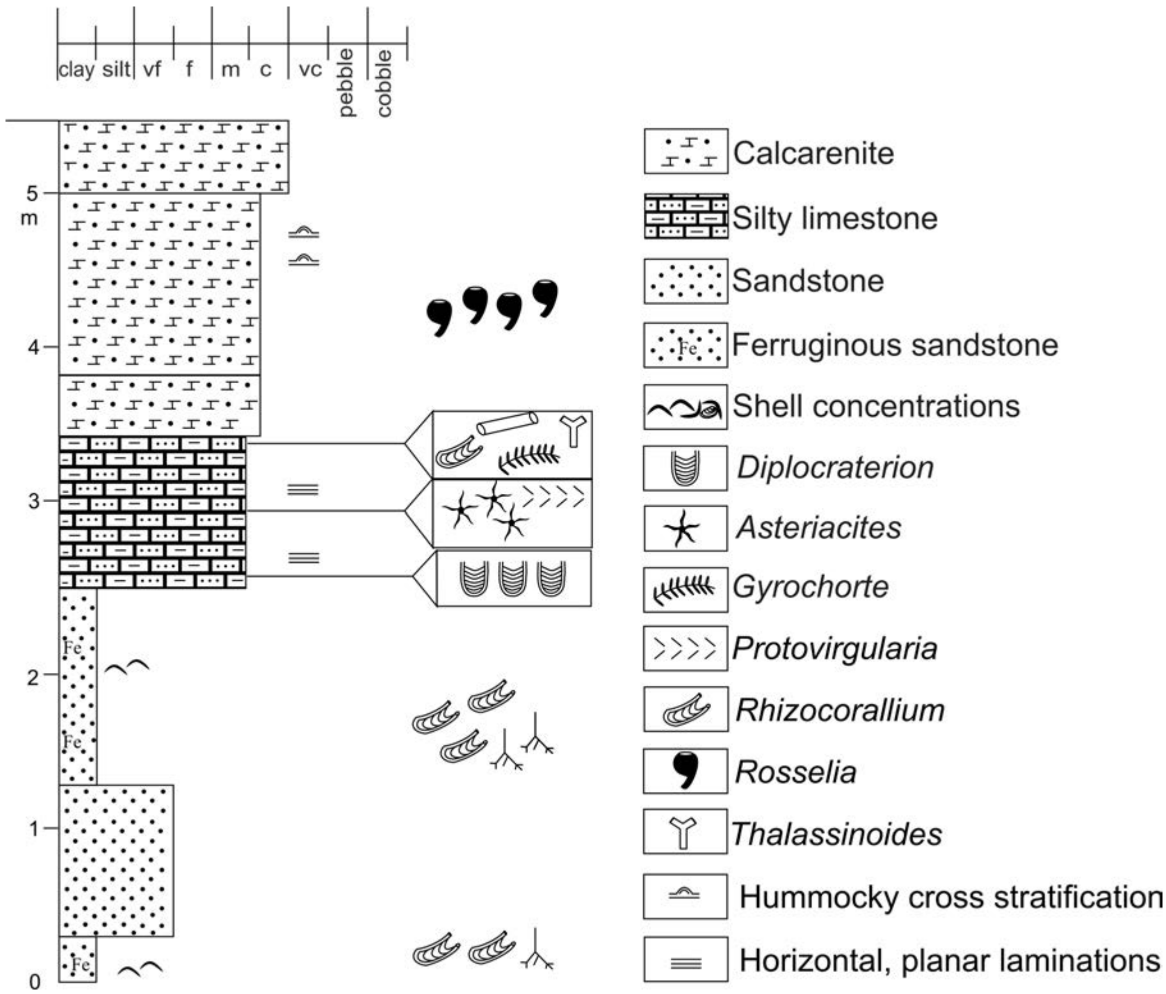


Fig. 2. Lithologic log of the exposure studied.

GEOLOGICAL SETTING

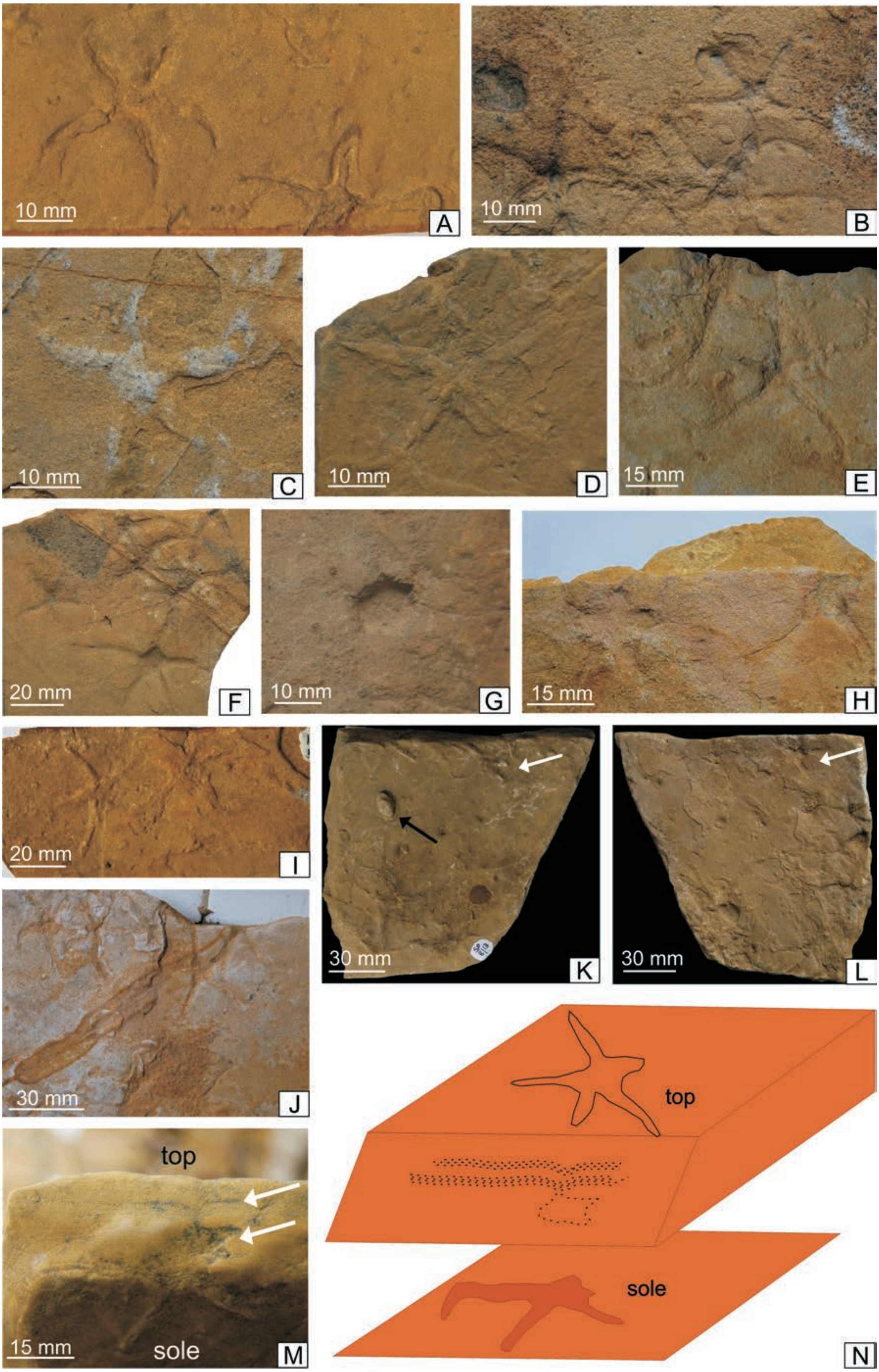
In the section near Suleiman Pir (26°50'33.90"N, 70°57' 59.90"E), the base is marked by a ferruginous, fossiliferous sandstone (0.3 m thick) with *Rhizocorallium* and *Chondrites*. This bed is overlain by white to grey, friable sandstone (1 m thick), followed by a ferruginous, fossiliferous sandstone with *Rhizocorallium* and *Chondrites* (1.30 m thick) and a 1-m-thick, flaggy, brown medium-grained silty limestone, rich in trace fossils. Its base is marked by *Diplocraterion parallelum* Torell, 1870, followed by *Asteriacites lumbricalis* von Schlotheim, 1820; *Protovirgularia* isp., *Lockeia siliquaria* James, 1879 and ?*Sagittichnus* isp. in the middle and *Gyrochorte comosa* Heer, 1865, *Protovirgularia rugosa* (Miller and Dyer, 1878), *Rhizocorallium commune* Schmid, 1876 and *Rosselia socialis* Dahmer, 1937 towards the top. The contact between the underlying ferruginous, fossiliferous limestone and the brown-coloured, silty limestone is sharp. Towards the top of the section, the lithology is carbonate-dominated consisting of limestone 2.08 m thick. The lower part (0.4 m) of this limestone is massive, medium- to coarse grained and contains *Planolites*. The middle part (1.20 m) is medium-grained, displays hummocky cross-stratification, locally flaser bedding, flame structures and lacks biogenic structures. The top (0.48 m) of this limestone unit is coarse-grained and devoid of ichnofossils.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Asteriacites* von Schlotheim, 1820
Type ichnospecies: *Asteriacites lumbricalis* von Schlotheim, 1820.

Asteriacites lumbricalis von Schlotheim, 1820
Fig. 3A–N

*1820 *Asteriacites lumbricalis* – von Schlotheim, p. 324.
1953 *Asteriacites lumbricalis* von Schlotheim – Seilacher, p. 94, figs 2–3, pls 7–9.
1968 *Asteriacites lumbricalis* von Schlotheim – Häntzschel and Reineck, p. 20, pl. 16, fig. 1.
1970 *Asteriacites lumbricalis* von Schlotheim – Osgood, p. 312.
1975 *Asteriacites* von Schlotheim – Häntzschel, p. W42–43, fig. 26 (4).
1990 *A. lumbricalis* von Schlotheim, 1820 – Mikuláš, p. 134, fig. 2.
1992 *A. lumbricalis* von Schlotheim, 1820 – Mikuláš, p. 35, pl. X, fig. 1, pl. XII, figs 3, 4; pl. XIV, fig. 4.


10 mm
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B
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C
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D
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top
sole
15 mm
M
top
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N

1999 *Asteriacites lumbricalis* von Schlotheim – Mángano, Buatois, West and Maples, p. 19–24, figs 3–4.
2000 *Asteriacites lumbricalis* von Schlotheim – Wilson and Rigby, p. 46–47, fig. 3.
2002 *Asteriacites lumbricalis* von Schlotheim – Mángano, Buatois, West and Maples, p. 25, 27, fig. 25F.
2004 *Asteriacites lumbricalis* von Schlotheim – Bell, p. 56–57, figs 4–5.
2004 *Asteriacites* – Pruss and Bottjer, p. 554, fig. 5B.
2010 *Asteriacites lumbricalis* von Schlotheim – Bernardi, Petti and Avanzini, p. 187–190, fig. 2.
2011 *Asteriacites lumbricalis* – Bernardi and Avanzini, p. 187–190, fig. 2.
2012 *Heliophycus seilacheri* Schlirf – Schlirf, p. 185–198, figs 5–7.
2013 *Heliophycus* isp. – Paranjape, Kulkarni and Gurav, p. 1360–1361, pl. 1a.

For references between 1820 to 1953 see Seilacher (1953).

Material: Nineteen slabs containing 145 specimens. Several seen in the field.

Plesiotypes: MACS G 5206A and B, 5207A to D, 5208A, 5209, 5210A and B, 5211A to F, 5212A and B, 5213A and B, 5214A and B, 5215A to D, 5216A and B, 5217A to D, 5218A, 5219A and B, 5220A to C, 5221A and B, 5222A, 5223A and 5224A to E.

Diagnosis: 'Stellate trace fossils in the form of asteroid or ophiuroid echinoderms; often but not always with transversely sculptured arms' (Wilson and Rigby, 2000).

Description: Star-shaped trace with five rays, preserved in both convex hyporelief and concave epirelief. Total diameter of the traces ranges from 23–53 mm (arm tip to arm tip). The central portion is poorly preserved in most specimens, but in many it is circular or star-shaped (Fig. 3B, F–H) with a diameter of 12–25 mm. Six impressions show a prominent central depression exhibiting pentamerous symmetry with partially preserved arms (Fig. 3F). Arms are 20–35 mm in length, straight to curved; elongated-triangular, broad at the base and tapering outwards (Fig. 3B, E, F). Length of the arms in an individual trace is variable. Width of the arms at the base is 2–6 mm. Ornamentation on the arms consists of weakly defined delicate transverse striae (Fig. 3E). Clusters of four to five traces are seen on the slabs collected. Overprinting of arms in traces points to horizontal movement (Fig. 3D) of the creator and the disturbed bed laminae supports an upward motion and vertical repetition (Fig. 3I) of the trace.

Remarks: Among the 145 star-shaped traces studied here, 120 are preserved in negative epirelief. Diagnostic features of the specimens (after Seilacher, 1953) include a star-like shape, 4 to 5 relatively narrow rays, originating from a central structure and tapering towards the tip. The specimens are larger than those described by Mángano *et al*. (2002), Wilson and Rigby (2000) and Bernardi *et al*. (2010) with regard to total diameter of the trace, size of the central part, and arm length.

A. lumbricalis is interpreted as a resting trace (cubichnion) of burrowing ophiuroids. Though no ophiuroid body fossils were recovered, the morphological characters, especially the slender arms help in assigning these specimens to *A. lumbricalis.* One of the specimens described (MACS 5206 C; Fig. 3G), displays a concave central portion with sharply outlined, pentamerous symmetry and the absence of arms, probably an outcome of poor preservation.

Six trace fossils show well-defined impressions of the central disc with partly preserved shallow traces of the arms, but without the arm tips. Such morphology is indicative of the trace maker in the life position (Fig. 3F), as argued by Mángano *et al*. (1999), the partially preserved arms indicating the sweeping action of tube feet. Overprinting of the arms is indicative of horizontal movements (Fig. 3C). Vertical movement is evident from ophiuroid traces preserved on both sides of a bed (MACS G 5215, Fig. 3K, L).The disturbed bed lamina (MACS G 5215; Fig. 3M, N) also supports upward movement by the trace producer. Discussing the behaviour of the *Asteriacites* producer, Mángano *et al*. (1999) suggested that horizontal repetition documents different accommodation positions in the search for new areas for hiding or resting, whereas the vertical structures probably indicate escape.

Ophiuroids are well adapted to a wide variety of diets, including both macrophagy as well as microphagy (Fell, 1966; Mángano *et al*., 1999). Yokoyama and Amaral (2008) observed that although ophiuroids are omnivorous, algae constitute their staple food. The specimens studied are closely associated with the bivalve trace, *Protovirgularia* (Fig. 4C, D), *Lockeia* (Fig. 3K) and ?*Sagittichnus*. Though the size of *Protovirgularia* varies greatly, the possibility of predation on smaller bivalves by the ophiuroid trace maker cannot be ruled out.

Ichnogenus *Diplocraterion* Torell, 1870
Diplocraterion parallelum Torell, 1870
Fig. 3A, B

Material: Two slabs containing 193specimens.

Figured specimen numbers: MACS G 5227, MACS G 5228.

Description: Endichnial, U-shaped tubes with spreite, perpendicular to bedding plane. Burrow diameter ranges from 1–2 mm; distance between two arms ranges from 1–1.5 mm; spreite incipient, for the most part weakly preserved, but unidirectional. Limbs parallel to each other. Burrow depth varies from 15–30 mm. On the upper bedding plane, appear as pair of circular pits.

Remarks: Though the morphological characters are similar to the type material described by Fürsich (1974), the Jaisalmer specimens are much smaller than the type material described from the Cambrian of Sweden (Westergård, 1931).

Ichnogenus *Gyrochorte* Heer, 1865
Gyrochorte comosa Heer, 1865

Material: Several trace fossils seen in the field.

Description: Horizontal, bilobate trail, mostly preserved as positive epirelief. It shows two convex lobes with median groove. Trail is 2–5 mm wide; characteristic plait-like structure poorly preserved. Crossovers are common.

Fig. 3. *Asteriacites lumbricalis* occurring in the Hamira Member, Jaisalmer Formation, Rajasthan. **A.** Convex hyporelief MACS G 5206A and B. Note five arms with arm tip and poorly preserved central part. **B.** Concave epirelief, MACS G 5207A to D, showing traces of horizontal relocation. **C.** Convex hyporelief , MACS G 5208A. Note the overlapping arms. **D.** MACS G 5209, showing weak ornamentation on arms, convex hyporelief. **E.** Concave epirelief, MACS G 5210A and B. Note tapering arms. **F.** Concave epirelief, MACS G 5211 A to F, with deep central part and absence of arm tip, indicating that trace maker was in life position. **G.** Concave epirelief, MACS G 5206C, showing deep central part. **H.** Concave epirelief, MACS G 5213A and B. Note deep, star-shaped central part. **I.** Convex hyporelief, MACS G 5212A and B. **J.** MACS G 5217, concave epirelief. **K.** *A. lumbricalis* and *Lockeia* in concave epirelief, MACS G 5217. White arrow indicates position of ophiuroid trace, black arrow indicates *Lockeia*. **L.** Reverse side of the slab in K, showing bedding plane view. Arrows indicate equivalent position of ophiuroid trace. **M.** *A. lumbricalis* on the sole of the bed, MACS G 5217. Note disturbed lamina and presence of central disc which marks vertical repetition. **N.** Line drawing of *A. lumbricalis* from M.

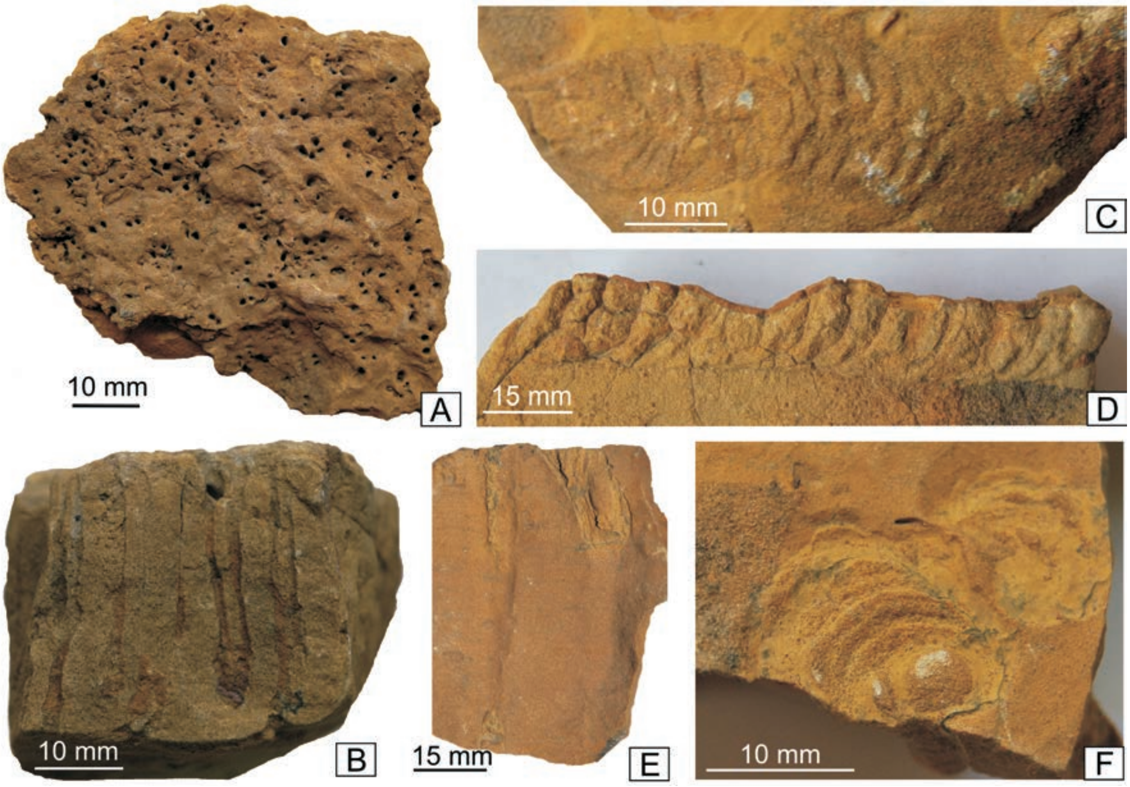

Fig. 4. Associated ichnofauna occurring in the Hamira Member, Jaisalmer Formation, Rajasthan. **A.** *Diplocraterion parallelum,* upper bedding plane view, MACS G 5227; note the abundance. **B.** *D. parallelum* seen in vertical plane, MACS G 5228. Note U-shaped burrow with spreite preserved at places. **C.** *Protovirgularia rugosa,* MACS G 5226, showing paired chevron shaped markings in hyporelief. **D.** Partially preserved *Protovirgularia* in hyporelief, MACS G 5208B. **E.** *Rosselia socialis,* MACS G 5225A and B, vertical section. **F.** *R. socialis,* MACS G 5225A and B, bedding plane view.

Remarks: The vertical dimension of the trail is not measured as only the positive epireliefs are present. *Gyrochorte* is interpreted as a structure created by worm-like deposit-feeder which commonly occurred in a shallow, nearshore marine environment in sandy facies. They are a typical component of the *Cruziana* ichnofacies. This ichnogenus ranges in age from Lower Ordovician to Pliocene, but is abundant in the Jurassic and Cretaceous (Gibert and Benner, 2002).

Ichnogenus *Lockeia* James, 1879
Lockeia siliquaria James, 1879
Fig. 3K

Material: One specimen.
Plesiotype: MACS G 5217
Description: Convex, hypichnial, almond shape, elongated structures. Broadly symmetrical and tapering to blunt terminations at both ends. Central median crest not preserved; sides are smooth. The length of trace is 16 mm, width is 10 mm and height is 3 mm.
Remarks: Mángano et al (2002) interpreted *Lockeia siliquaria* as domichnia (dwelling structures). Earlier *L. siliquaria* was interpreted as resting structure (cubichnion) of a wedge-footed bivalve by Seilacher (1953), Osgood (1970) and Seilacher and Seilacher (1994). The specimen described here is similar to those figured by Paranjape *et al.* (2013, pl. 2, fig. b) from the Bada Bagh Member of Jaisalmer Formation. The oldest record of this ichnogenus is from the Late Cambrian/Early Ordovician and ranges up to the Pleistocene (Mángano *et al.*, 2002). This trace fossil is reported from a wide range of environments, ranging from continental, tidal-flat,, shallow marine and marginal marine to deep marine (Mángano *et al.*, 2002).

Ichnogenus *Protovirgularia* McCoy, 1850
Protovirgularia rugosa (Miller and Dyer, 1878)
Fig. 3C

Material: One specimen.
Plesiotype: MACS G 5226.
Description: Straight to slightly curved, unbranched, hypichnial ridges with chevron markings. The ridges are short, emerging from partially preserved *Lockeia*. The chevron markings are bilaterally symmetrical, arcuate in appearance, and closely spaced, giving rise to wrinkles. Observed length is 60 mm.
Remarks: Though the *Protovirgularia* and the associated *Lockeia* show low relief, the diagnostic morphological characters of *P. rugosa* are clearly discernible, permitting identification. This association of chevron structures with *Lockeia* is considered as the work of a cleft-footed bivalve (Seilacher and Seilacher, 1994; Mángano *et al.*, 1998).

Protovirgularia isp.
Fig. 4D

Material: One specimen.
Plesiotypes: MACS G 5208B.
Description: Straight, unbranched, hypichnial ridges with deeply impressed, closely spaced, partially preserved chevron ribs. Observed length is 100 mm.
Remarks: As the structure is partially preserved, ichnospecific as-

sessment is not possible. However, the specimen compares favourably with the terminology described by McCoy (1950) for the ichnogenus *Protovirgularia*.

Ichnogenus *Rhizocorallium* Zenker, 1836
Rhizocorallium commune Schmid, 1876

Material: Several trace fossils seen in the field.
Description: Short, straight, horizontal to subhorizontal, unbranched, U-shaped spreite tunnel. Spreite retrusive. Limbs are 7–8 mm wide, length of tunnel is 50–65 mm, spreite structure mostly is eroded away.
Remarks: Knaust (2013) revised this ichnogenus on the basis of 14 morphological characters along with their transitional ichnotaxa, ethology, and ichnofacies, retaining only two ichnospecies *R. commune* and *R. jenense*. On the basis of morphological characters, such as horizontal, U-shaped, short, unbranched tunnels and isolated appearance, the specimens here are identified as *R. comune*. Decapod crustaceans, annelids and mayflies are three possible producers of this structure. Taking into consideration worms as the probable producer *R. commune* is now considered to show a combined suspension- and deposit-feeding activity (Knaust, 2013). *R. commune* is also a component of the trace fossil assemblage of the *Cruziana* ichnofacies.

Ichnogenus *Rosselia* Dahmer, 1937
Rosselia socialis Dahmer, 1937
Fig. 3E, F

Material: One slab containing two specimens. Several seen in the field.
Plesiotypes: MACS G 5225A and B
Description: Vertical to slightly inclined, straight, cylindrical tube. Fill consists of circular, concentric laminae of mud or silt, visible as concentric rings on bedding plane. Entire structure is 10–15 mm in diameter; maximum depth observed is 65 mm. Central tube is vertical, smooth and walled. It is 4–7 mm in diameter.
Remarks: The specimens described here are mostly funnel- shaped and surrounded by mud laminae. The funnel-like shape is result of erosion of the upper part of the spindle shape morphology (Nara, 1995). To date, no specific trace maker has been assigned to *R. socialis*. Many authors have proposed sea anemones (Curran and Frey, 1975), Terebellidae (Nara, 1995; Uchman and Krenmayr, 1995; Schlirf *et al.*, 2002; Schlirf, 2003) as probable producers.

Ichnogenus *Sagittichnus* Seilacher, 1953
?*Sagittichnus* isp.

Material: Several seen on three slabs.
Plesiotypes: MACS G 5209, MACS G 5214, MACS G 5223.
Description: Hypichnial, convex, triangular structures, 1–3 mm long and 1 mm wide. Very few specimens exhibit diagnostic arrowhead shape.
Remarks: These structures exhibit morphological characters, such as triangular shape, but the diagnostic arrowhead shape was observed in very few; as such, they cannot be assigned to any ichnospecies. The absence of arrowhead shape may be due to erosion of original structure.

DISCUSSION

Taxonomy of star-shaped resting traces

By long tradition, the star-shaped resting traces described were named *Asteriacites* von Schlotheim, 1820, which is the oldest available name for a trace fossil (Knaust, 2012). Unfortunately, Schlotheim's description remains unclear as to whether *Asteriacites* is a trace fossil or a body fossil; nor does it seem to have a holotype. For that reason, Schlirf (2012) regards *A. lumbricalis* as *nomen dubium* and recommends usage of its junior synonym *Heliophycus* Miller and Dyer, 1878. Unfortunately, the ichnogenus *Heliophycus* is hardly known and its validation over *Asteriacites* would lead to ichnotaxonomical instability. To avoid such a situation, the authors here follow the suggestion of Knaust (2012) and regard *A. lumbricalis* as a valid ichnotaxon, until that issue has been resolved completely.

Implications of *A. lumbricalis*

Asteriacites lumbricalis is considered as a trace fossil, found in marginal-marine, shallow waters (Mángano *et al.,* 1999; Bernardi *et al*., 2010). In the present study, the abundance of *Asteriacites* found in the silty limestone bed is more than 100 individuals per m^2. Their occurrence in such large numbers is indicative of abundant availability of food (Aronson, 1989).This is also evident from the diverse, associated trace-fossil assemblage, such as *Gyrochorte, Protovirgularia* (Fig. 4C, D), *Rhizocorallium* and *Rosselia* (Fig. 4A, B), belonging to the *Cruziana* ichnofacies (Fig. 2). Such a diverse ichnoassemblage indicates normal salinity and fully oxygenated conditions. It does not only indicate the availability of abundant food, but also optimum conditions for a variety of organisms.

Considering other factors responsible for such a large number of individuals, lack of predation appears to be the dominant reason. In Recent coastal settings around the British Isles, Aronson (1989) observed that dense aggregations of ophiuroids are due to insignificant predation. Subsequent studies (Aronson, 1992) revealed that beds with ophiuroids are found in high-current areas without much sedimentation. He was also of the opinion that high currents are essential to meet the food demands of the large number of individuals, whereas excessive sedimentation would affect the feeding mechanism of the ophiuroids, eventually smothering them. Stating a different perspective, Warner (1971) believed that aggregation is a strategy which helps them in increasing shear stress and facilitating sedimentation; this not only gives stability to the seafloor, but also increases food supply. Moreover, Goldring and Stephenson (1972) interpreted that if ophiuroids occur in small groups, rather than as a community, they either get transported for short distances or are buried in the life position. Thus, the abundance of *Asteriacites* in the Hamira section indicates abundant availability of food, brought in by strong currents, normal oxygen and salinity conditions, and steady rates of sedimentation.

Palaeoenvironmental interpretations of the Suleiman Pir section

Shift in environmental conditions is indicated markedly by the changes in the ichnoassemblage, both in ichnofacies as well as in ichnodiversity. The monospecific ichnoassemblage of *Diplocraterion parallelum* (Fig. 4E, F) below the *Asteriacites*-bearing silty limestone indicates the *Skolithos* ichnofacies. Occurrence of these U-shaped burrows indicates an upper- to middle-shoreface environment with moderate to high energy conditions. Water with relatively strong currents, irregular rates of sedimentation and a high flux of food particles is conducive to the occurrence of suspension feeders. Gingras *et al*. (2011) also regarded the abundance of permanent U-shaped burrows and vertical tubes as indicative of shallow-marine areas with shifting sandy substrates, moderate- to high-energy conditions and food in suspension. Thus, the monospecific ichnofauna comprising *Diplocraterion* indicates colonisation by a K-strategist (Buatois and Mángano, 2011) above the fair-weather wave base.

In contrast, the bed with *Asteriacites,* along with *Protovirgularia, Lockeia* and ?*Sagittichnus,* replaced towards top by *Gyrochorte, Protovirgularia, Rhizocorallium and Rosselia*, marks the transition to an archetypal *Cruziana* ichnofacies. This suggests a position just below the fair-weather wave base (Buatois and Mángano, 2011).

In conclusion, the deposition of the silty limestone discussed here records a shift from the middle shoreface to the offshore transition zone, implying gradual deepening.

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