Significance of *Lockeia* and associated trace fossils from the Bada Bagh Member, Jaisalmer Formation, Rajasthan

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A *Lockeia*-*Protovirgularia* ichnofauna representing the *Cruziana* ichnofacies is reported from a calcareous sandstone horizon of the Callovian Bada Bagh Member, Jaisalmer Formation, Rajasthan. The ichnoassemblage is characterized by *Lockeia cunctator*, *L. siliquaria*, *Protovirgularia* ?*bidirectionalis*, *P. rugosa*, *Ptychoplasma vagans* along with *Palaeophycus tubularis*, *P. striatus*, *Heliophycus* isp. and ?*Lophoctenium* isp. Use of numerical analysis yielding length to width ratio, slopes and coefficient of determination helps in confirming identification of ichnospecies of *Lockeia*. Fine morphological details of *Lockeia* and *Protovirgularia*, especially sharp and closely spaced chevrons of *Protovirgularia*, indicate that the substrate in which they were emplaced was stiff, resistant, dewatered and better consolidated. Therefore, it construes that this ichnoassemblage belonging to the classical *Cruziana* ichnofacies occurs in stiff softground and not a typical softground. Though the ichnofacies of this calcareous sandstone bed indicates low-medium energy condition under subtidal environment of deposition, underlying strata containing *Arenicolites*, *Skolithos* and *Curvolithus* of *Skolithos* ichnofacies indicate intertidal sandy shore environment with high energy conditions. Thus, it is concluded that this area was undergoing continuous, gradual deepening. However, the percentage of *Thalassinoides*, *Ophiomorpha* and *Phycodes* in the overlying bed is quite high suggesting an increase in the energy conditions resulting from a probable shallowing.

1. Introduction

Ichnology comprises of processes involved in organism–substrate interaction and their resulting products, the traces themselves (Buatois and Mángano 2011). Hence, they are excellent indicators of sedimentation rates, substrate coherence, salinity, oxygen levels, turbidity, light, temperature and hydrodynamic energy. Also, they are good proxies for palaeoenvironmental interpretations as they are emplaced *in situ*.

The current paper reviews the ichnological data of one bed from Bada Bagh Member, exposed near Bada Bagh village on Jaisalmer–Ramgarh

road (figure 1), and discusses on its palaeoecological and palaeoenvironmental interpretations. The current trace fossil suite is characterized by an exceptional assemblage exhibiting three ethological expressions of wedge and cleft footed bivalves. The three ethological classes, viz., cubichnia, repichnia and pascichnia are represented here by *Lockeia*, *Protovirgularia*, *Ptychoplasma* and ?*Lophoctenium*.

A similar trace fossil assemblage, representing deposition in foreshore to offshore environment, has been reported earlier from the coeval Middle Jurassic sediments of adjoining Kachchh basin (Joseph *et al.* 2012).

Keywords. *Lockeia*; *Protovirgularia*; *Cruziana* ichnofacies; Callovian; Jaisalmer Formation; Rajasthan.

Figure 1. Location map. Collection site is marked by asterisk.

2. Geological setting

The Jaisalmer Formation lies in the southeastern part of the Jaisalmer Basin and is assigned a Callovian to Oxfordian age. Its thickness is 400 m (Das Gupta 1975; Singh 2006). Blanford (1877) and Oldham (1886) were amongst the first to study these marine Mesozoic rocks occurring in this region. The oldest sediments of the marine Mesozoic succession, now designated as the Jaisalmer Formation, were initially referred to as the 'Jaisalmer limestone' by Blanford (1877), who had divided it into four subdivisions, viz., Joyan, Fort, Bada Bagh and Kuldhara.

The first systematic account of trace fossils from the marine Mesozoic sediments was given by Kumar (1979). Ichnofaunal studies were followed by Gupta *et al.* (1966), Chiplonkar *et al.* (1981), Sudan *et al.* (2000), Borkar and Kulkarni (2001, 2002) and Pandey *et al.* (2010).

The lithostratigraphic classification of the Jaisalmer Formation proposed by Das Gupta (1975) is widely accepted. He divided it into five members, viz., Hamira, Joyan, Fort, Bada Bagh and Kuldhara. The predominant lithologies are limestones and calcarenites, deposited under shallow-marine conditions. The Jaisalmer Formation is underlain by the fluvial Lathi Formation

comprised of sandstones and shales with abundant wood fragments and overlain by Baisakhi Formation predominantly of shales belonging to nearshore to shallow-marine environments.

The Bada Bagh Member begins with a thin layer of sandstone and an intrabasinal conglomerate, followed by shale, oolitic limestone and calcarenites. The calcarenites are yellowish buff in colour and highly fossiliferous. They show a lot of variation all through its thickness with regard to sand, fossil and carbonate content. The calcarenites are intercalated with numerous thin sandy and silty layers and show a diverse collection of trace fossils. The youngest bed of the Bada Bagh Member shows thin laminated layers with interference ripples, indicating close vicinity to the coast.

The Bada Bagh Member corresponds to zone 5 or the *Limatula jaini*, *Falcimyltilus* sp., *Coelastarte* sp. zone of Kachhara and Jodhawati (1999) and is considered to be of Middle Callovian age. It is believed to be conformable with the underlying Fort Member and overlying Kuldhara Member (figure 2).

3. Trace fossil assemblage

3.1 Studied material

The ichnofauna dealt within the present communication comes from a stratum 27.25 m above the base of the Bada Bagh Member and is an integral part of the calcarenite litho-unit (figures 1 and 2). It is a coarse grained calcareous sandstone exhibiting low angle cross bedding.

The type specimens are housed in the fossil repository of the Agharkar Research Institute bearing the acronym MACS G (Maharashtra Association for the Cultivation of Science, Geology).

3.2 Systematic taxonomy

Ichnogenus *Heliophycus* Miller and Dyer 1878
Heliophycus isp. Miller and Dyer 1878
 Plate 1(a)

Material: One specimen.

Plesiotype: MACS G 5186

Description: Star-like trace with five radiating arms preserved in convex hyporelief. Total diameter of the trace is 21 mm. The central portion is circular, bulbous and undifferentiated with a diameter of 6 mm. Five arms project radially outwards from it. They are 9–10 mm in length, triangular, broad at the base and tapering outwards. Width of the arms at the base is 4 mm. The arms lack ornamentation.

Remarks: The present specimen small in size, with star-like triangular arms exhibits similar

Figure 2. Litholog of Bada Bagh Member. Enlarged is the *Lockeia* bearing calcareous sandstone bed.

diagnostic features as *Asteriacites lumbricalis* Schlotheim 1820 (Seilacher 1953) as well as *Heliophycus* Miller and Dyer 1878 (Schlirf 2012). Schlirf (2012) considered *Asteriacites* to be a *nomen dubium*, the major reason in its defence being the unavailability of its type specimens. The authors agree with Schlirf (2012) and Bertling *et al.* (2006) that the diagnosis of an ichnotaxon should be independent of the producer and its interpretation. Also, a valid ichnotaxon name should be preferred over a popular nomenclature while identifying any trace fossil (Schlirf 2012). Thus, the authors favour the use of the ichnotaxon *Heliophycus* over *Asteriacites*.

Most of the earlier reported *Asteriacites* (now *Heliophycus*) occur in fine to silty sandstones with the exception of silty limestone (Wilson and Rigby 2000). But in the Bada Bagh Member, the trace is preserved in coarse-grained calcareous sandstone.

This could be the possible reason for the transverse striations not being preserved.

Two small ophiuroids found in the same bed (plate 1b) could have been the possible creators of this trace. Its close association with other bivalve traces, viz., *Lockeia* and *Protovirgularia* suggests predation on small molluscs (Mángano *et al.* 1999).

Ichnogenus *Lockeia* James 1879

Lockeia cunctator Schlirf and Uchman 2001

Plate 1(c-f)

Material: Two slabs containing 77 specimens.

Plesiotypes: MACS G 5188, MACS G 5189a

Description: Circular to oval traces in convex hyporelief. Each structure is 7–8 mm long and about 5 mm wide. Thickness is about 3–4 mm. Except for a few, all other traces are attached to each other and seem to diverge in different directions from the same axis. The clusters (plate 1c),

Plate 1. (a) *Heliophycus* isp. Miller and Dyer 1878 (MACS G 5186), (b) Fossil Ophiuroids (white arrows) (MACS G 5187), (c) *Lockeia cunctator* Schlirf and Uchman 2001 in cluster (MACS G 5189), (d) Close up of *Lockeia cunctator* Schlirf and Uchman 2001 (MACS G 5188), (e) Serially arranged *Lockeia cunctator* Schlirf and Uchman 2001 diverting away from a single axis (MACS G 5188), (f) Club-like arrangement of *Lockeia cunctator* Schlirf and Uchman (2001) (MACS G 5188), (g) *Lockeia siliquaria* James 1879 in side view exhibiting a prominent ridge (MACS G 5192), (h) *Lockeia siliquaria* James 1879 in top view displaying typical almond shape (MACS G 5192), (i) Close up of same slab with *Lockeia siliquaria* James 1879 exhibiting a prominent keel (MACS G 5194), and (j) Entire slab with keeled, stout *Lockeia siliquaria* James 1879 (MACS G 5194). (Bar scale: 1 cm.)

at places, exhibit club-shaped arrangement (plate 1f).

Remarks: The specimens agree with the diagnostic features of *Lockeia cunctator* (Schlirf *et al.* 2001) such as club or almond-shaped probes arranged in a row, diverging away from the main axis (plate 1e). According to Schlirf *et al.* (2001), the club-shaped arrangement of *L. cunctator* is attributed to the movement of the bivalve in different directions. In our specimens, as some small solitary *Lockeia* are found surrounding *Lockeia cunctator*, it is suggested that they may have been produced either by young bivalves or smaller genera. By their movement in directions away from the main central axis, these traces can be easily differentiated from *Ptychoplasma vagans*. Their morphology and shape distinguish them from *L. siliquaria*.

Lockeia siliquaria James 1879

Plate 1(g–j), Plate 2(a–h)

Material: Twenty two slabs with total 127 specimens.

Plesiotypes: MACS G 5192–5196, MACS G 5197b, MACS G 5198b, MACS G 5204b

Description: These are convex, hypichnial, almond-shaped traces. The size varies greatly but the shape remains more or less the same. The traces are broadly symmetrical, elongated and tapering at both ends which are blunt. They show the presence of a central median ridge or crest (plate 1g and h). The crest is less prominent in the small specimens. The sides of the casts are usually smooth, with few exceptions showing corrugation.

In addition, a morphological variant of *L. siliquaria* was found. These forms are stout; they taper towards one end while the other end is rounded (plate 2c and d). Many of these forms show a prominent keel at the top, in place of the ridge (plate 2e and f). It shows corrugated sides whereas the rest of the cast is smooth (plate 2g and h).

The traces are 10–40 mm long, 4–17 mm wide and 2–18 mm thick. They do not show any preferred orientation on the bedding, and are commonly gregarious.

Remarks: Diagnostic characters such as elongate to stout, almond-shaped, smooth hypichnial ridges generally showing high-relief, suggested by Schlirf *et al.* (2001), help in identifying our specimens as *Lockeia siliquaria*. This ichnospecies has been interpreted as casts of the foot of a bivalve during the protraction phase or the cast of the impression of the shell by Seilacher (1953), Osgood (1970) and Seilacher and Seilacher (1994). The corrugations observed on the sides of the traces may be due to compression of sediments during compaction or the movement of the foot during penetration and

anchorage (Mángano *et al.* 1998). In case of the stout forms at Bada Bagh, only the keel-like portion exhibits corrugations, whereas the rest of the cast is smooth. Hence, we suggest that the basal portion is impression of the shell, while the keel with corrugations is impression of the foot compressing the sediments during anchorage. Seilacher and Seilacher (1994), Schlirf *et al.* (2001) and Mángano *et al.* (2002) have argued *L. amygdaloides* as a preservational variant of *L. siliquaria*. We concur with them and hence identify the stout Bada Bagh specimens under *L. siliquaria*. This variation in the morphology may reflect difference in the expansion of the bivalve foot during burrowing as interpreted by Radley *et al.* (1998). More or less all specimens occur isolated. In cases where they have been arranged in a linear fashion, they are better identified as *Ptychoplasma vagans*.

L. siliquaria is associated with *Protovirgularia rugosa*, *Palaeophycus tubularis* and *Ptychoplasma vagans*.

When associated with chevron traces of *Protovirgularia*, they have been considered by Seilacher and Seilacher (1994) and Mángano *et al.* (1998) to be the work of a cleft-footed bivalve. *L. siliquaria* had been previously interpreted as a cubichnion (Osgood 1970; Häntzschel 1975), but Mángano *et al.* (2002) have indicated that they represent dwelling traces (domichnia) of suspension feeders or fugichnial responses to changes in the environmental conditions.

?*Lophoctenium* isp. Richter 1850

Plate 2(i)

Material: One specimen.

Specimen: MACS G 5198a

Description: The trace represents an irregular surface exhibiting undulatory humps and depressions, displaying a feeble spreiten-like structure developed around *Lockeia*. The trace is preserved in hyporelief.

Remarks: The trace resembles *Lophoctenium* of Ekdale and Bromley (2001) to a certain extent. They suggested its emplacement due to the movement of palpal tentacles of the labial palps of bivalve. Another reason for identifying the trace as *Lophoctenium* is its close association with *Lockeia*. But as the trace does not show any well preserved diagnostic feature of *Lophoctenium* its specific determination is deferred. Repetitive probing could be the reason for its spreiten-like structure not being preserved.

Ichnogenus *Palaeophycus* Hall 1847

Palaeophycus striatus Hall 1852

Plate 2(j, k)

Material: Two slabs with one specimen each.

Plesiotype: MACS G 5199a

Plate 2. (a) Cluster of *Lockeia siliquaria* James 1879 (MACS G 5195), (b) *Lockeia siliquaria* James 1879 with prominent ridge and smooth sides (MACS G 5197), (c) Stout variant of *Lockeia siliquaria* James 1879 in top view (MACS G 5194), (d) Stout variant of *Lockeia siliquaria* James 1879 in side view, tapering at one end and rounded at the other end (MACS G 5194), (e) Close up of a single specimen of stout variant of *Lockeia siliquaria* James 1879 in top view (MACS G 5194), (f) *Lockeia siliquaria* James 1879 in side view exhibiting a prominent keel (MACS G 5194), (g) *Lockeia siliquaria* James 1879 in top view with a distinct keel (MACS G 5194), (h) *Lockeia siliquaria* James 1879 in side view with keel displaying corrugations (MACS G 5194), (i) ?*Lophoctenium* isp. Richter 1850 surrounded by *Lockeia* (MACS G 5198), (j) *Palaeophycus striatus* Hall 1852 exhibiting striae on either sides (white arrows) (MACS G 5199), (k) Close up of *Palaeophycus striatus* Hall 1852 with parallel striae (MACS G 5199), (l) *Palaeophycus tubularis* Hall 1847 (MACS G 5197), (m) *Palaeophycus tubularis* Hall 1847 (MACS G 5199), (n) Cross cutting *Palaeophycus tubularis* Hall 1847 (MACS G 5200), (o) *Palaeophycus tubularis* Hall 1847 (MACS G 5201), and (p) *Palaeophycus tubularis* Hall 1847 (MACS G 5189). (Bar scale: 1 cm.)

Description: Cylindrical, slightly undulose burrow with distinct parallel longitudinal striations. The burrow is preserved as hypichnial ridge, slightly inclined to the bedding plane. It is circular in cross-section with a diameter of 13 mm while length is 17 mm. The distance between the striae is 1 mm. The wall lining is weak. The filling of the burrow is same as that of the host rock.

Remarks: As mentioned by Pemberton and Frey (1982), the trace fossil has been distinguished from other ichnospecies by longitudinal parallel striations. *Palaeophycus* is interpreted as domichnia of suspension feeders or predators, such as polychaetes (Osgood 1970; Pemberton and Frey 1982; Mángano *et al.* 2005). Its thin lining preserves the open burrow (Gámez-Vintaned *et al.* 2006).

Palaeophycus tubularis Hall 1847

Plate 2(l–p)

Material: Nine slabs containing 31 specimens.

Plesiotypes: MACS G 5189b, MACS G 5197a, MACS G 5199b, MACS G 5200–5202

Description: Straight to slightly curved burrows with smooth walls and thin lining, preserved as convex hyporelief. The burrows are horizontal to slightly inclined. The specimens lack branching and are rarely seen to cross each other. They are oval to elliptical in cross-section with their diameter ranging from 2–10 mm. The burrow fill shows the same lithology as that of the host rock.

Remarks: The specimens have been identified as *Palaeophycus tubularis* and are differentiated from the other ichnospecies of *Palaeophycus* by its thin wall and the absence of ornamentation (Pemberton and Frey 1982). The ethological interpretation of *P. tubularis* is similar to that of *P. striatus* (Mángano *et al.* 2005).

Ichnogenus *Protovirgularia* McCoy 1850

Protovirgularia ?bidirectionalis Mángano, Buatois, West and Maples 2002

Plate 3(a, b)

Material: One specimen.

Plesiotype: MACS G 5204a

Description: The trace shows a curved, meandering, unbranched, hypichnial ridge with chevron traces oriented in opposite directions. The chevron traces show one predominant orientation for most of its path. But at the terminal portion, the V-shaped chevrons are directed opposite to each other. The portion where the change in orientation occurs does not show chevrons. The width of the trace is 4–5 mm and the trace extends for 190 mm.

Remarks: The specimen exhibits diagnostic characters of *Protovirgularia bidirectionalis* as introduced by Mángano *et al.* (2002). The trace is differentiated from other ichnospecies by its chevrons oriented in opposite directions. Mángano *et al.* (2002)

have attributed the opposite facing chevrons within a single structure to the reorientation of the animal. It is also mentioned that the structure could have been created in the intertidal region during the flood and ebb process. This concurs with the shallow marine nature of the Bada Bagh Member.

Protovirgularia rugosa Miller and Dyer 1878

Plate 3(c–f)

Material: Four slabs with 15 specimens.

Plesiotype: MACS G 5190b, MACS G 5191b, MACS G 5204c, MACS G 5205

Description: The traces are straight to slightly curved, unbranched, hypichnial ridges with chevrons. All the trails are comparatively short, always emerging from the bivalve cubichnion *Lockeia*. The structures are horizontal to gently inclined. The chevrons appear as two bilaterally symmetrical appendages diverging from a central axis. The appendages have an arcuate appearance. The chevrons are closely spaced imparting a wrinkled appearance. The appendages show a maximum length of 4 mm. The angle of the appendages with respect to the median line varies for different individuals.

Remarks: The chevrons of *Protovirgularia* under consideration open away from *Lockeia* with which they are associated. It indicates movement of the organism away from *Lockeia*. Some of the traces are slightly inclined and indicate an upward migration. This indicates that it is an escape trace (fugichnion) and thus agrees with the diagnosis of *Protovirgularia rugosa* given by Seilacher and Seilacher (1994).

Chevrons seen in these specimens are tight and closely spaced, indicating that the substrate was stiff. Hence, the bivalve faced difficulty in locomotion (Mángano *et al.* 2002).

The association of *Lockeia* is an ample evidence that *Protovirgularia* is produced by a bivalve rather than an arthropod (in Mángano *et al.* 2002) or a scaphopod (Seilacher and Seilacher 1994).

Ichnogenus *Ptychoplasma* Fenton and Fenton 1937

Ptychoplasma vagans Książkiewicz 1977

Plate 3(g–i)

Material: Two slabs with one specimen each.

Plesiotypes: MACS G 5190a, MACS G 5191a

Description: These are elongate, serially aligned amygdaloidal traces in convex hyporelief (plate 3h). The traces are horizontal and aligned in a single plane. Individual specimens are almond-shaped, tapering at both ends, about 10 mm in length and 4–5 mm in width. They lack the characteristic median longitudinal ridge. *Prima facie*, the specimen exhibits alternate pinching and swelling (plate 3g).

Plate 3. (a) *Protovirgularia ?bidirectionalis* Mángano, Buatois, West and Maples 2002 (MACS G 5204), (b) Line drawing showing oppositely directed chevron structure of *Protovirgularia ?bidirectionalis* Mángano, Buatois, West and Maples 2002 (MACS G 5204), (c) *Protovirgularia rugosa* Miller and Dyer 1878 (MACS G 5191), (d) *Protovirgularia rugosa* Miller and Dyer 1878 (MACS G 5204), (e) *Protovirgularia rugosa* Miller and Dyer 1878 moving away from *Lockeia* (MACS G 5190), (f) *Protovirgularia rugosa* Miller and Dyer 1878 moving away from *Lockeia* (MACS G 5205), (g) *Ptychoplasma vagans* Książkiewicz 1977 in top view, exhibiting pichning and swelling (MACS G 5190), (h) *Ptychoplasma vagans* Książkiewicz 1977 in top view, exhibiting serially arranged almond-shaped traces (MACS G 5191), (i) *Ptychoplasma vagans* Książkiewicz 1977 in side view (MACS G 5190), and (j) Unidentified specimen A. Arrow points to the apical protruberance (MACS G 5203). (Bar scale: 1 cm.)

Remarks: This trace can be interpreted as a crawling trace rather than a dwelling structure. The specimens exhibit the diagnostic characters of *Lockeia serialis* given by Seilacher and Seilacher (1994). Schlirf et al. (2001) assigned a *nomen nudum* status to *L. serialis* explaining

that no holotype, nor illustrations or descriptions of it exists in the literature given by Seilacher and Seilacher (1994) as well as Linck (1949). Uchman et al. (2011) reassigned it to ichnogenus *Ptychoplasma* highlighting the validity of this ichnogenus over *L. serialis*. They also stated that

the ichnogenus *Lockeia* should be restricted to only the cubichnial traces of bivalves. Uchman *et al.* (2011) differentiated the three species of *Ptychoplasma* on the basis of the continuity between bodies. They have described *Ptychoplasma vagans* as ‘mostly discontinuous, *Lockeia*-like bodies in series’. Hence specimens under consideration are identified as *Ptychoplasma vagans*.

Ptychoplasma vagans has been reported from all environments ranging from continental, marginal-marine, shallow-marine to deep-sea (Uchman *et al.* 2011).

The Bada Bagh specimens are commonly associated with *L. siliquaria*, *Protovirgularia*.

Unidentified specimen A

Plate 3(j)

Material: One specimen.

Repository registration no.: MACS G 5203

Description: Subcylindrical, nearly vertical, feebly pentamerous trace, in positive hyporelief. It exhibits a protuberance at the apical end. The maximum width of the trace is 27.5 mm and its height is 15 mm. The protuberance is 10 mm in diameter.

Remarks: The specimen shows close resemblance to ichnogenus *Pentichnus*. Maerz *et al.* (1976) have interpreted *Pentichnus* as dwelling trace of an ophiuroid and they considered pentamerous symmetry to be its most important taxonomic character. The specimen under consideration does not exhibit perfect pentamerous symmetry making its generic identification difficult. All other characters in this specimen, i.e., its subcylindrical form, its

occurrence on the sole of the bedding plane and the presence of a protuberance at the apical end are alike the specimens of *Pentichnus* described by Maerz *et al.* (1976) and Mángano *et al.* (2002), respectively.

4. Numerical analysis

The use of numerical analysis for the differentiation of various ichnospecies of *Lockeia* has been attempted by Mángano *et al.* (1998). For this purpose, a graph of length against width of individual *Lockeia* specimens is plotted and the respective slopes of different ichnospecies are calculated (figure 3). This analysis serves as an additional ichnotaxonomical tool for the confirmation of different ichnospecies.

The length of *L. siliquaria* ranges from 5.5 to 63 mm, whereas that of *L. cunctator* ranges from 6.5 to 16 mm. This clearly indicates that *L. siliquaria* shows greater variation in length than *L. cunctator*. Even the width range of *L. siliquaria* (4–36 mm) is greater than that of *L. cunctator*. Thus, as the length increases there is a proportional increase in their width. This is also evident from its average length to width ratio, 1:0.88.

The slopes calculated for the two ichnospecies help in their taxonomic distinction. The slope of the regression line calculated for *L. siliquaria* (0.47) concurs with that suggested for *L. siliquaria* from the Upper Carboniferous of Eastern Kansas (Mángano *et al.* 1998). This substantiates our identification of this ichnospecies from the Bada Bagh

Figure 3. Numerical analysis of the two *Lockeia* species found. The lines in the graph represent the regression lines for the respective species.

Plate 4. (a) Mottled appearance of the top surface of the bed and (b) *Gyrochorte* on the top surface of the bed. (Bar scale: 1 cm.)

Member. Mángano *et al.* (1998) have compared *L. siliquaria* and *L. ornata* using this method. The slope of *L. cunctator* (0.91) exhibits great variation with that of *L. siliquaria*.

Another important parameter here is the coefficient of determination, an overall measure of the accuracy of the trendline or the regression line. A regression line is most accurate when its coefficient of determination value (R^2) is at or near 1. The coefficient of determination for *L. siliquaria* (0.75) and *L. cunctator* (0.84) is high indicating that the estimated values for the regression line and the actual values are fairly similar (plate 4).

5. Discussion

It is important to note that all traces described are preserved in convex hyporelief and were collected from the lower bedding plane of single calcareous sandstone under consideration. Their epichnial equivalents could not be found even after a careful investigation. In this connection, it may be pointed out that the 7.35 m thick calcarenite litho-unit, of which the calcareous sandstone is part, is punctuated by a number of thin, silty and clayey intercalations. It is assumed that the traces, *Lockeia*, *Protovirgularia*, *Ptychoplasma* and ?*Lophoctenium*, seen at the sole of the calcareous sandstone were originally emplaced on the upper bedding plane of such a thin, silty layer. Whenever exposed, this silty layer is eroded away being vulnerable to

erosional processes of the desert. This poses difficulty in collecting the original epichnial traces. Nevertheless they are expected to occur in equally great number with satisfactory preservation in the portion hitherto unexposed.

5.1 Nature of substrate

The type of substrate and its consistency are affected by a number of factors such as water content, grain size, lithology, sorting, organic content, etc. Of these, the percentage of water present in the sediment serves the key role. With progressive loss of water and consolidation, the same sediment can get transformed serially from a soup-ground to soft-ground, firm-ground and finally with cementation into a hard-ground (Bromley 1996). Consequently, the substrate consistency along with the grain size affects the mode of emplacement of biogenic structures. The remarkable preservation of *Lockeia* and *Protovirgularia* in the Bada Bagh Member needs to be seen in this context. *L. siliquaria* show smooth, well preserved sides and a sharp central longitudinal crest. In the stout variants of *L. siliquaria* (plate 2c–h), the keel looks perfectly distinct from the main body. This indicates that the silty substrate, in which these burrows were emplaced, was compact enough, facilitating preservation of finer details. Moreover, *Protovirgularia* associated with *Lockeia* show sharp and closely spaced chevrons, an observation also made by Mángano *et al.* (2002) in specimens from the Stull Shale Member in Eastern Kansas of Late Pennsylvanian age. They have explained it by envisaging that ‘the bivalve faced difficulty and had to struggle to move ahead in a stiff, resistant and dewatered substrate, and therefore had to take short steps’, equally applicable to the Bada Bagh specimens. Earlier, Mángano *et al.* (1998) had indicated that traces with sharp, closely spaced chevrons can be attributed to a firmer soft-ground. Uchman and Pervesler (2006) are also of the opinion that the chances of preservation of morphological details increase with increase in stiffness of the substrate. Trueman (1966) and Schieber (2003) concur with the same. Though, it may be noted here that Buatois *et al.* (1997) have attributed striated trace fossils such as *Palaeophycus striatus* to a firm-ground suite. Seilacher and Seilacher (1994) stated that any hypichnial traces do not directly form from casts of the muddy substrate but are more likely to be formed when the muddy substrate has been blanketed by a coarser event deposit. Traces formed in such a manner escape destruction from the current and wave action and exhibit more details being formed in a cohesive substrate. The mechanism discussed by Seilacher

and Seilacher (1994) is also applicable to the present specimens. Based on the above factors, the authors are inclined to term the substrate as a stiff soft-ground.

In this context, it may be pointed out that the ichnogenera *Lockeia*, *Protovirgularia* and *Helio-phyucus* from the present ichnoassemblage are believed to belong to the classical *Cruziana* ichnofacies. Bromley (1996) mentioned that the *Cruziana* ichnofacies indicates loose and soft-ground substrate with silty to sandy grain size. However, observations regarding the nature of substrate of the silty layer at Bada Bagh are contrary to this generalisation. Therefore, it is suggested that the *Cruziana* ichnofacies can also occur in stiffer soft-ground.

A change in the nature of substrate is apparent in the lower silty layer and the overlying calcareous sandstone bed. The burrows assigned to *Palaeo-phyucus* in this bed, associated with *Lockeia* and *Protovirgularia* show elliptical cross-section evincing that it was not as compacted as the silty layer. The top of the calcareous sandstone bed shows intense bioturbation which has destroyed the bedding, leading to a non-descript relief. This evinces a change in conditions of deposition. A few *Gyrochorte* and certain beaded structures are the only trace fossils that could be identified in the crowded assortment of traces. These traces clearly identify upper calcareous sandstone bed to be soft-ground in nature.

5.2 Environment of deposition

Lockeia and *Protovirgularia* are recorded in environments ranging from shallow to deep water, restricting their use in determining the environment. However, in the Bada Bagh Member, they occur in great abundance. It transpires that conditions were extremely conducive for the bivalve community which emplaced them. The bivalves thrived at this locality in a large population. Several cubichnia are associated with repichnia. It implies that ambient settings including food, oxygen and ideal substrate consistency permitted them to proliferate here when the silty layer was being deposited. Dominance of horizontal traces is also indicative of a regular steady input of organic matter (Buatois and Mángano 2011). The ophiuroid resting trace *Heliophycus* (identified as *Asteriacites lumbricalis* by earlier researchers) indicates marginal-marine, tidal environment (Hakes 1976; Mángano *et al.* 1999) with clear waters (Bernardi *et al.* 2010). Although, *Asteriacites* has also been found in brackish waters, it typically indicates well oxygenated waters of normal salinity (Mángano *et al.* 1999). Hence, here it is considered that *Heliophycus* also indicates a shallow-water environment

of deposition. Maerz *et al.* (1976) have reported it from limestone wherein it occurs in quiet water conditions.

A meticulous search for *Lockeia*, *Protovirgularia* and *Ptychoplasma* in any of the younger or older beds of the Bada Bagh Member, however, was unfruitful. Thus, it construes that the *Lockeia*–*Protovirgularia*–*Ptychoplasma* assemblage described in the foregoing lines was a single colonization event.

Seilacher and Seilacher (1994) have interpreted *Protovirgularia rugosa* as the response of the organism to storm sand sedimentation, while Mángano *et al.* (2002) have attributed it to rapid tidal sedimentation. However, in the specimens studied, escape traces were not observed in vertical cross sections. This could be because of the difficulty faced by the cleft footed bivalves to move vertically (Mángano *et al.* 2002), or it could be interpreted that moderate sedimentation rates were not conducive for the organism to leave any vertical trace.

Vis-à-vis the entire succession of the Bada Bagh Member, the ichnofacies of this calcareous sandstone litho-unit points towards low-medium energy condition under subtidal environment of deposition. Strata underlying this litho-unit show traces such as *Arenicolites*, *Skolithos* and *Curvolithus* which point towards *Skolithos* ichnofacies, indicating intertidal sandy shore environment with high-energy conditions. Thus, it can be concluded that this area underwent a continuous, gradual deepening. It is also observed that the beds overlying this litho-unit show traces such as *Thalassinoides*, *Ophiomorpha* and *Phycodes*. The percentage of occurrence of these traces (*Thalassinoides* and *Ophiomorpha*) is quite large and is thus indicative of an increase in the energy conditions resulting from a probable shallowing.

Further studies on the entire trace fossil assemblage of the Jaisalmer Formation and its integration with sedimentology will favour a better understanding of the sea level dynamics.

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