# The environmental significance of the trace fossil *Rhizocorallium jenense* in the Lower Triassic of western Spitsbergen

David Worsley & Atle Mørk

The 500 m thick Lower Triassic succession of western Spitsbergen comprises two shale-dominated formations, which both show upward-coarsening motifs. These reflect repeated coastal progradations into a basin dominated by low energy fine-clastic sediments. The trace fossils *Rhizocorallium jenense* and *Skolithos* are found in the coarser parts of these units and variations in size and orientation of *R. jenense* give important palaeoenvironmental information.

*Rhizocorallium jenense* occurs in storm-generated siltstones and sandstones, whose deposition interrupted prevailing intermediate energy levels. Size variations and trace fossil abundance suggest an optimal habitat in the shoreface zone, with poorer adaptation to both more offshore and shallower environments. Age-equivalent marine sediments on north-eastern Greenland also contain local abundant occurrences of *Rhizocorallium*. These Arctic occurrences contrast with the same trace fossil's distribution in the Jurassic of Britain and France, where it characterizes shallower and higher energy environments; such sequences on Spitsbergen show an ichnofauna dominated by *Skolithos* and bivalve escape shafts.

Orientations shown by the *R. jenense* U-tubes show a generally, but not solely, unimodal distribution, with the curved distal ends usually oriented toward onshore. Presumed aperture lineations show strongly unimodal trends, probably related to longshore currents. Burrows in beds at the top of individual storm lobe units show more complex patterns, probably reflecting both current and wave reworking following lobe abandonment. All finds suggest early colonization by the burrowing organisms. These were not followed by other burrowers, either because of the nutrient-poor nature of the sediment or because of high sedimentation rates.

*D. Worsley, Norsk Hydro ASA , Box 200, NO-1321 Stabekk, Norway; A. Mørk, SINTEF Petroleum Research, N-7465 Trondheim, Norway.*

Marine shales dominate the Lower and Middle Triassic sequences that are assigned to the Sassendalen Group in the Svalbard Archipelago (Buchan et al. 1965; Mørk, Knarud et al. 1982; Mørk, Dallmann et al. 1999). Exposures in eastern and central areas of Svalbard show moderately thick sequences (in the range of 200 to 300 m) that contain only minor amounts of coarser clastic interbeds. When traced westwards, the group thickens to approximately 700 m and shows an increasing silt- and sandstone content. Exposures in western Spitsbergen (Figs. 1, 2) are assigned to

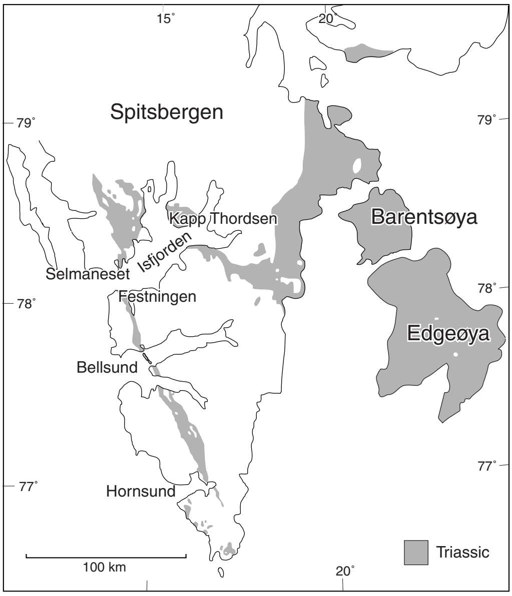

*Fig. 1.* Map showing the outcrop areas of Triassic rocks and localities mentioned in the text.

three formational units (in ascending order): the Vardebukta, Tvillingodden and Bravaisberget formations. Each of these formations shows marked upward-coarsening trends, reflecting repeated coastal progradations of a hinterland situated to the west of the present archipelago. Formational bases represent regionally significant transgressive episodes, which punctuated this long-term progradational trend (Mørk, Embry et al. 1989). Upwards coarsening sequences in western exposures show an abundance of trace fossil assemblages that document increasing energy levels upwards within each formation. The aim of this paper is to discuss the occurrence and environmental implications of trace fossils in the Vardebukta and Tvillingodden formations. The much richer trace fossil fauna of the overlying Middle Triassic Bravaisberget and Botneheia formations will be discussed elsewhere.

The most common single trace fossil in this sequence is the U-shaped burrow of *Rhizocorallium jenense.* Although this is the type species of the ichnogenus *Rhizocorallium,* many and varied forms of burrows have been assigned to the genus since Zenker (1836) first described it. All have in common a U-shaped form with spreiten between more or less parallel arms; otherwise the great variety of forms has been assigned to a total of 15 ichnospecies. Great variety in total burrow form and the proliferation of "species" names led to increasing confusion as to the origin of these burrows until Fürsich's critical review (1974). Fürsich pointed out that all previously described "species" of *Rhizocorallium* ought to be reassigned to three groups on the basis of the functional significance of the burrows themselves. Of these, only the short and obliquely dipping burrows of *R. jenense* are considered to be domichnid tunnels formed by suspension-feeders. Long horizontal and more complex forms assigned to *R. irregulare* and *R. uliarense* are interpreted as fodinichnid burrows inhabited by deposit-feeders. This simple classification is under some debate, as discussed by Jensen (1997), who regards *R. jenense* as a form typically found in high-energy shallow marine conditions. In the Wandel Sea basin of north-east Greenland, the Permian to Triassic Parish Bjerg Formation consists of 300 m of sandstones, shales and conglomerates containing *Rhizocorallium* at certain levels in its upper parts (Håkansson 1979). The overlying Dunken Formation of Early to Middle Triassic age also contains abundant *Rhizocorallium* at many horizons (Håkansson 1979; Håkansson & Stemmerik 1984).

We will first briefly review the development of the Vardebukta and Tvillingodden formations and their trace fossils in exposures from Isfjorden to Bellsund. We will then discuss a notable occurrence of large populations of *R. jenense* in the type section of the Tvillingodden Formation, near Festningen on the southern coast of outer Isfjorden.

## Trace fossil bearing sequences

Both the Vardebukta and Tvillingodden formations have their type sections in the Festningen profile (Mørk, Knarud et al. 1982). The base of the Vardebukta Formation shows bioturbated mudstones with occasional intercalated thin siltstones; the latter thicken and increase in frequency upwards in the section. Both at Festningen (Figs. 1, 2) and at Selmaneset immediately to the north (Fig. 1), the middle of the formation is marked by sand units interpreted as barrier complexes with intervening lagoonal shales and silts (Mørk, Knarud et al. 1982). The upper third of the formation then fines upwards into similar mudstone and siltstone alternations to those seen lowermost in the formation, before passing abruptly

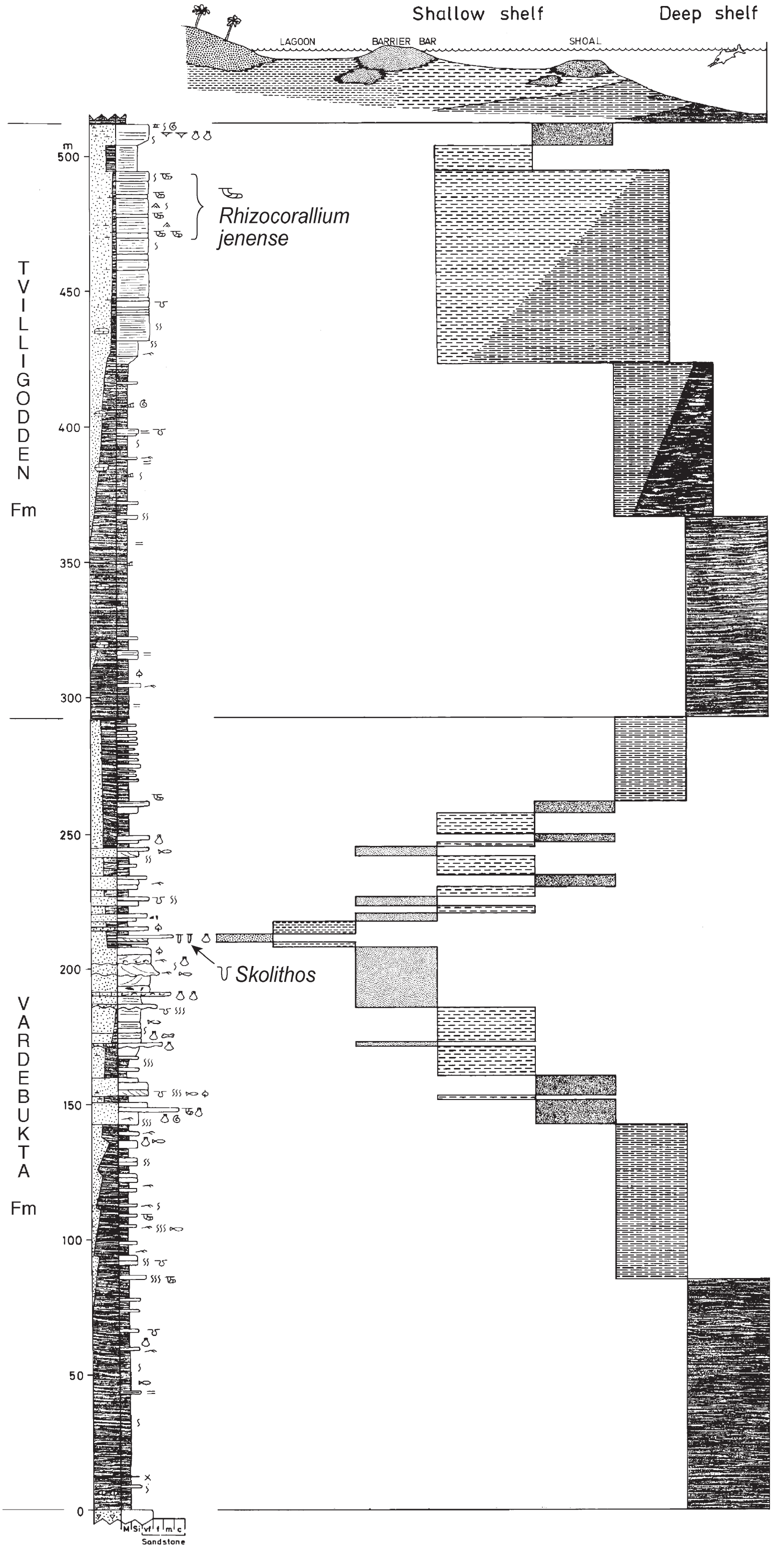

*Fig. 2.* Interpretative section of the Lower Triassic succession at Festningen. Note the presence of *Skolithos* ichnosp. in the shallowest shoreface sandstones of the Vardebukta Formation and the occurrences of *Rhizocorallium jenense* in the uppermost part of the Tvillingodden Formation (from Mørk, Knarud et al. 1982).

*Fig. 3. Skolithos* ichnosp. from the Vardebukta Formation at Festningen (ca. 210 m above base). Scale bar is 5 cm.

into the dark laminated basal shales of the overlying Tvillingodden Formation.

Burrows of *Rhizocorallium jenense* occur sporadically in siltstones above and below the uppermost shoreface or foreshore deposits of the barrier sands, but not within these bodies. Although finds of *Diplocraterion* have previously been reported from this sequence (Gazdzicki & Trammer 1978; Mørk, Knarud et al. 1982) reinvestigations of the section show that most of these traces are slightly oblique to the bedding, and they probably belong to *Rhizocorallium jenense.* The sands themselves are instead characterized by *Skolithos* and by possible bivalve escape shafts. Long parallel burrows of the fodinichnid *R. irregulare* have also been found at the transition from individual barrier sands to overlying lagoonal shales at several localities.

Two immediately adjacent sandstone beds (at 212 m; Fig. 2) are densely burrowed by vertical tubes. The burrows completely penetrate each bed, but no burrows are seen to continue through both beds. Funneling, such as seen in *Monocraterion,* is not observed in the upper part of the burrows and they have a constant thickness. The burrows follow the diagnosis of Häntzschel (1975) for *Skolithos* Haldemann 1840, being straight, subcylindrical, unbranched, sediment-filled tubes perpendicular to bedding. They often contain a muddy infilling surrounding the central sand plug and this indicates some sort of lining made by the trace producer. The sand plug probably represents passive sand filling after abandonment of the trace. The specimen in Fig. 3 is 15 cm long and the 8 - 9 mm diameter tube is surrounded by a dark brown weathering rim. The *Skolithos*-bearing sands occur between sandstones with bioclastic debris and interbedded siltstones and shales enriched in plant remains. These were interpreted by Mørk, Knarud et al. (1982) as lagoonal and shoreface facies. The low-angle cross-bedded sandstone beds with *Skolithos* represent the highest flow regimes in these sequences.

Exposures of the Vardebukta Formation further to the south around Bellsund (Mariaholmen, Akseløya and Bravaisberget; Fig. 1) show a similar coarsening and ensuing fining upwards trend. However, the coarsest parts of the sequences there show the development of sand bodies interpreted as marine offshore bars (Mørk, Knarud et al. 1982). Also in these sequences *Rhizocorallium* is generally found sporadically associated with storm-generated siltstone beds rather than with the coarser sandstone units.

Poorly exposed sequences near Kapp Thordsen (Fig. 1) show a more distal development of the Sassendalen Group than that seen on the west coast. Coarsest parts of the Vardebukta equivalents there consist of silty shales with minor thin siltstones; sporadic small burrows of *R. jenense* occur in the latter.

The Tvillingodden Formation is 215 m thick in its type section where it constitutes a single major coarsening upwards sequence (Fig. 2). The base of the formation is marked by the abrupt transition from bioturbated greyish green mudstones and intercalated thin siltstones of the Vardebukta Formation into dark grey laminated shales showing few signs of bioturbation. This formational boundary is interpreted as reflecting a marked change in depositional setting from an offshore, but still relatively well-aerated shelf into quiet and probably anoxic environments (see also Wignall et al. 1998). This transition appears to be penecontemporaneous throughout the western Spitsbergen exposure belt and represents a regional transgressive event (Mørk, Embry et al. 1989).

The basal 80 m of the formation consist of laminated shales with occasional siltstone interbeds and horizons showing large discoid carbonate concretions that range up to 3 m in diameter and 50 cm thick. From this level upwards the sequence shows an increasing sand content; thinly interlaminated silty shales and very fine sandstones show lenticular bedding disturbed by moderate to strong bioturbation.

Sporadic burrows of *R. jenense* are found in the occasional siltstones low in the sequence. Intercalated discrete siltstones and very fine sandstones are relatively common in the uppermost 50 m of the unit. A concentrated "package" of 51 such interbeds is exposed in a 12 m sequence between 170 and 182 m above formational base (marked with *R. jenense* symbols in Fig. 2). Several of these beds contain abundant burrows of *R. jenense,* but are otherwise not bioturbated. It is this sequence that has provided most data for the present study.

The top of the Tvillingodden Formation is marked by a 2.5 m thick well-sorted and strongly bioturbated bioclastic sandstone. This contains a rich but abraded fauna of molluscs and brachiopods; a notable species is the spiriferid brachiopod *Punctospirella stacheyi* considered by Dagys (1974) as typical for the Lower Anisian. A similar sandstone development has been noted at several localities along the western coast at this level (see also Worsley & Mørk 1978). The bed indicates reworking and winnowing of the topmost beds of the Tvillingodden Formation during a period of stillstand around wave base. This episode marks the onset of a regional transgression that resulted in deposition of the immediately overlying black, organic and phosphate rich shales of the Bravaisberget Formation.

A similar siltstone package has also been observed immediately beneath the top of the formation near Selmaneset, although exposures there are poor and tectonized. Two beds with abundant burrows of *Rhizocorallium jenense* have been examined. The uppermost of these also marks the top of the Tvillingodden Formation at Selmaneset. This bed also contains similar lag faunas of molluscs and brachiopods to those seen uppermost in the formation at Festningen.

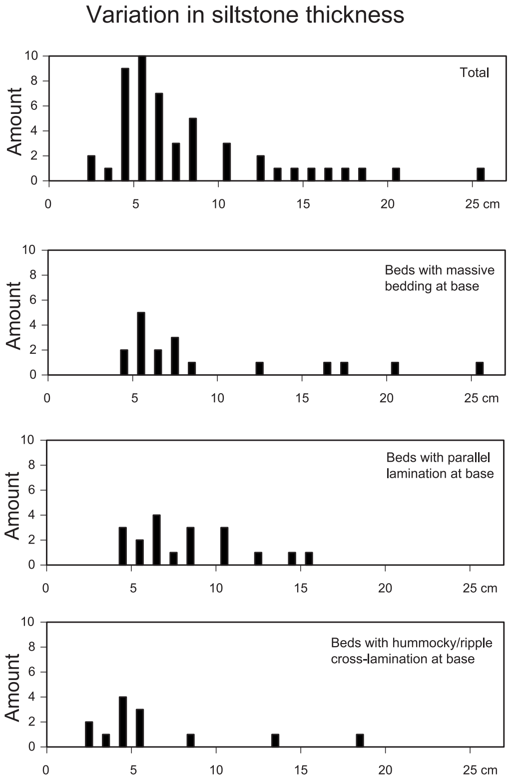

*Fig. 4.* Sedimentological features of the siltstone beds from the *Rhizocorallium*-bearing sequence at Festningen.

In contrast to the Vardebukta Formation, the upper parts of the Tvillingodden Formation show increasing proximality southwards in the western exposure belt. Exposures from Bellsund to Hornsund show laminated shales in the lower part of the formation and these pass up into highly bioturbated thick sandstone bodies interpreted as deltafront deposits. We suggest that this delta front environment either was not conducive to the establishment of burrows of *R. jenense* or that possible early post-depositional burrows of this type were later obscured by more thorough bioturbators.

## *Rhizocorallium*-rich siltstone sequences

Forty-nine of the 51 siltstone beds high in the type section of the Tvillingodden Formation are between 4 and 20 cm thick (Fig. 4 shows features

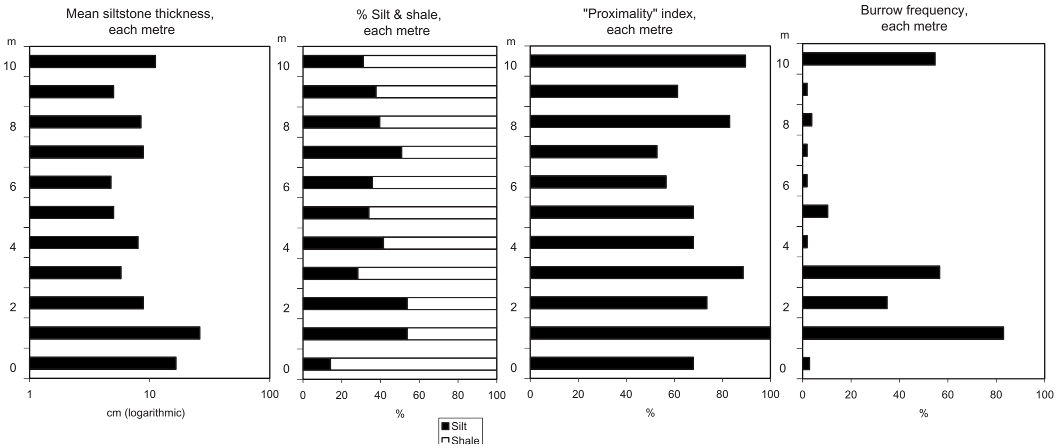

*Fig. 5.* Features of the *Rhizocorallium*-bearing sequence at Festningen. The parameters are summarized for each metre. See discussion in the text.

marked *R. jenense* in Fig. 2). Grain size varies from coarse silt to very fine sand, but most beds fall within the silt fraction; the siltstones contain effectively no clay matrix and have a carbonate cement. Most siltstone beds show sharp, usually clearly erosive bases and more diffuse upper contacts, some of which are wave reworked, passing up into silt/mud laminae. Some beds appear to lens and thin out laterally, but most show a constant development over the 10 m lateral extent of exposures (parallel to strike). *Rhizocorallium jenense* is restricted to the upper parts of individual beds, confirming that each represents a single depositional episode.

Primary structures within the siltstone beds include massive bedding, plane-parallel lamination, hummocky and ripple cross-lamination and planar-laminated mud–silt intercalations; these tend to appear upwards in each bed in the order listed. This vertical organization in individual beds suggests decreasing flow regimes upwards during each depositional episode. It is also notable that there is a significant correlation between the type of structure at the base of a bed and that bed's thickness. The order and frequency of occurrence of these structures may be used as a measure of relative "proximality" or, more correctly, of flow regimes prevailing during the deposition of each individual bed. The "proximality" index used herein is a modified form of the ABC index first used by Walker (1967) for turbidite sequences. An essentially similar index was also used by Brenchley et al. (1979) for storm-generated sandstones in Ordovician epicontinental shelf settings. As used herein, this "proximality" index is computed per metre as:

$$((M + 2/3P + 1/3H)/(M + P + H))*100$$

where M represents the number of beds with massive bedding as basal structure, P those with parallel lamination and H those with hummocky or ripple cross lamination at their bases. Results shown in Fig. 5 show variations in this index ranging from 53 % to 100 %. There is a good general correlation between this index and average siltstone bed thickness through the sequence, supporting the observation by Walker (1967) that thicker beds were deposited from currents inferred to be flowing in higher regimes. There is a poor correlation between the index and total silt content (Fig. 5), in contrast to the results of Brenchley et al. (1979); these workers noted a better correlation between sandstone content and relative proximality than between bed thickness and this index.

Variations in siltstone thickness and in the "proximality" index suggest slightly higher energy regimes in the lower and upper parts of the sequence than in the middle beds. Abundant occurrences of *R. jenense* are notably restricted to the thickest beds—which also show the full range of sedimentary structures, suggesting deposition in the highest flow regimes (Fig. 5).

What are the depositional environments suggested by this sequence? It occurs within the coarsest part of the entire formation. Although similar siltstones are seen intermittently throughout the unit, structures and thicknesses in this part of the succession suggest higher energy regimes than seen elsewhere. The individual siltstones show all characters typical of storm generation, reflecting offshore transport of clastic sediment from a barrier or open coastline by rip currents. The few directional structures indicate a southwest directed flow, and post-depositional storm wave reworking of some beds produced ripples with axes perpendicular to current flow. This concentrated and well-defined lithofacies association, with sharp lower and upper limits, suggests a short-lived depositional episode atypical of the rest of the formation. These features suggest deposition as a localized inner-shelf storm lobe in the main path of periodic storm-generated rip currents channelled from tidal inlets of barrier systems or from an estuarine complex (see also Brenchley & Newall 1982). The abrupt top to the sequence would suggest migration of the lobe concurrent with inlet or estuary migration. Although exposures do not permit lateral tracing of the sequence to test this model, the poor exposures at Selmaneset show essentially the same features, and are compatible with this model. We should also note that Brenchley et al. (1979) found index values of 50 % or less in sequences considered typical of open shelf or lower shoreface settings, while values similar to those observed in the Festningen section were encountered in sequences interpreted as deposited in the upper shoreface zone

## Occurrence of *Rhizocorallium jenense*

Most information on the mode of occurrence of *R. jenense* has been provided by the siltstone package in the Festningen section. Varying modes of preservation and variation in burrow form are indicated in Fig. 6. Burrows are U- to pear-shaped and extend downwards from bed tops obliquely to bedding, although the angle of burrowing varies considerably. Because of this oblique angle only parts of individual burrows are usually seen. Reasonably complete specimens indicate that both tube diameters and burrow widths increase somewhat towards the curved distal ends. More proximal parts, and especially the aperture to the sediment surface, have only rarely been observed. Minimum, mean and maximum dimensions, observed in a total population of 157 measured specimens are shown in Fig. 7. The lengths and minimum burrow widths are mostly taken from incomplete specimens with only the curved distal parts of the burrow preserved. Mean observed lengths are therefore smaller, and mean minimum widths greater than true values to be expected for complete specimens.

Size variation is therefore best expressed by either tube diameter or maximum burrow width immediately adjacent to the distal end of each burrow. The correlation between these parameters is shown in Table 1. The observed spread probably reflects a certain degree of protrusive/retrusive activity in some specimens, causing superimposition of two tubes very near to each other, leading to an overestimation of tube diameter. This tendency is also augmented by a certain amount of compaction, which has flattened the tubes somewhat. The most accurate size estimate is therefore taken as the maximum width of the entire burrow.

Histograms showing both tube diameters and maximum burrow widths in the four beds with reasonably large populations are shown in Fig. 8. Burrow width shows clearly unimodal distributions, which are slightly positive-skewed; in each case the size distributions do not suggest the presence of several populations of burrows. There is, however, a large and significant increase in burrow size from the lowest to the highest bed in the sequence.

Both beds studied at Selmaneset contain specimens intermediate in size between the extremes seen at Festningen (mean maximum burrow widths of 3.8 and 3.9 cm) and there is no significant size difference between the two populations. It is notable that in all other occurrences showing only sporadic burrows of *R. jenense*, the vast bulk of burrows are very small, approximating to the smallest size classes seen in the storm lobe sequence at Festningen.

Marintsch & Finks (1978) noted size variations in *Zoophycos* and other feeding traces from lower Devonian sequences in New York State, which were interpreted as representing a double onshore—offshore cycle. Largest sizes

*Table 1.* Dimension parameters of *Rhizocorallium jenense* at Festningen.

| | Minimum | Mean | Maximum |
|---|---|---|---|
| Length (cm) | 2.0 | 5.2 | 18.5 |
| Max. burrow width (cm) | 1.6 | 3.9 | 9.0 |
| Min. burrow width (cm) | 1.2 | 3.6 | 6.8 |
| Tube diameter (cm) | 0.3 | 0.7 | 1.5 |

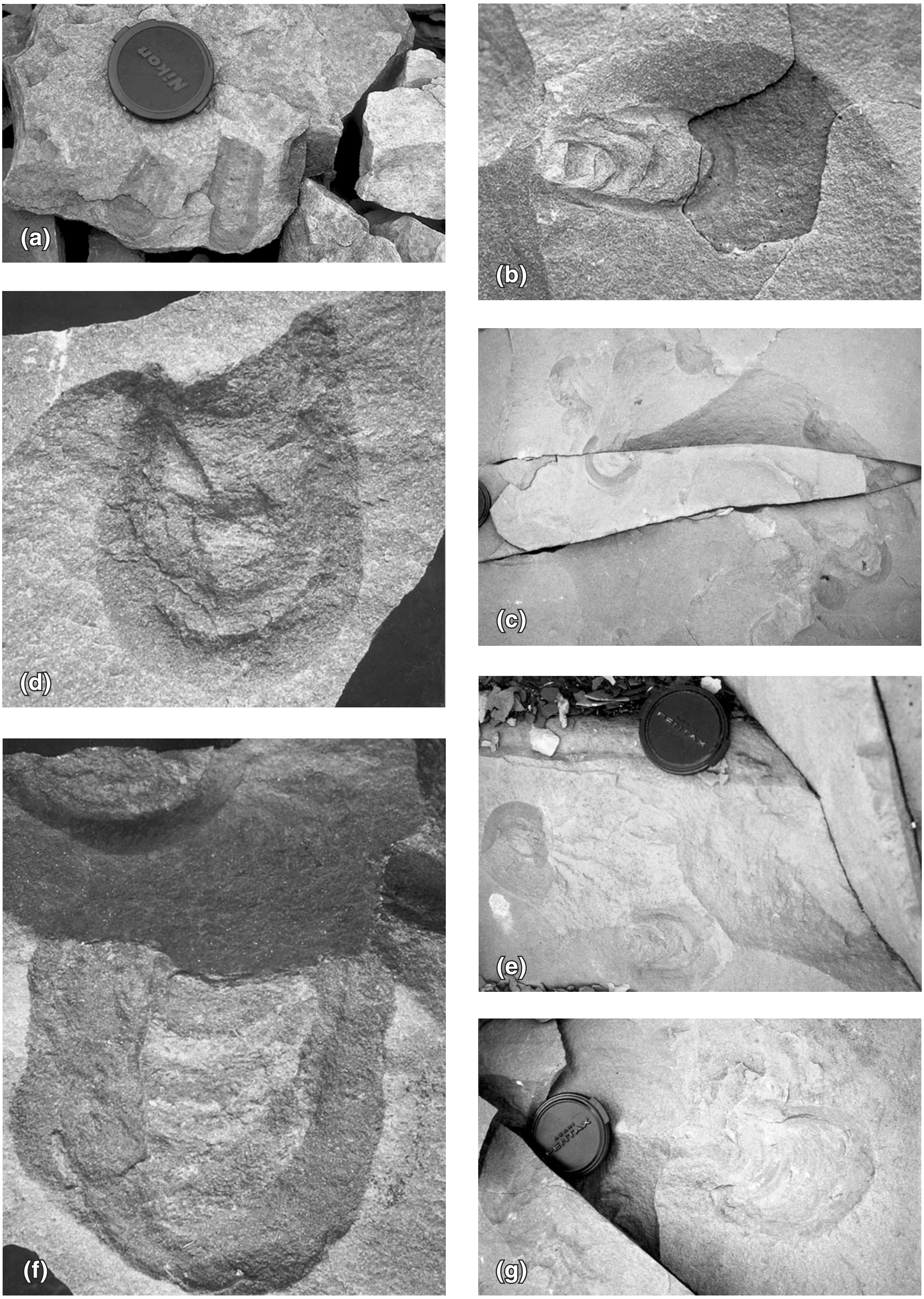

*Fig. 6.* Photos of occurrences of *Rhicozorallium jenense* at Festningen. Lens cap is 5 cm in diameter. (a), (b) and (d) show oblique traces, while (c), (e) and (g) are more flattened. (f) is nearly vertical and resembles *Diplocraterion*.

were found near the centre of each trace's environmental range, for *Zoophycos* this being in quieter, deeper water environments. Burrows became smaller in shallower water and were absent in the shallowest environments represented.

Although not in an entirely analogous environmental situation to the Festningen sequence, work by Savrda et al. (1984) in bottom sediments of silled basins of the Californian continental borderland is of great interest as it also deals with size variation in domichnid burrows. These workers found that average size of both straight and U-tube burrows (mostly dug by polychaetes) decrease markedly with increasing depth and decreasing oxygen content.

Burrows of *Rhizocorallium jenense* are interpreted as dug by suspension-feeding or scavenging organisms, which obtained their food from the water just outside the burrows. The unimodal size frequency distributions notably reflect the presence of only a single generation of the same burrower. This indicates immediately post-depositional settlement of spat on the bottom in optimal conditions, presumably still subject to wave reworking. Survival times (reflected in burrow size) were then dependent on the prevailing local environmental conditions. The Festningen sequence suggests that more and larger burrows are found in relatively shallow and higher energy environments—presumably also environments with greater amounts of nutrients in suspension.

## Burrow orientations

In all cases where there are sufficient numbers to permit analysis, the burrows show significant orientations. In the field this was measured as the direction of the U-tubes, forming the basis for Fig. 9. The lineation of the tube apertures is also plotted, assuming this to be perpendicular to burrow orientation. The pattern that emerges is that three of four beds low in the sequence at Festningen and the lowest bed studied at Selmaneset show burrows directed to the south-west, with only small peaks in the diametrically opposed quadrant. Burrows in one bed, interesting enough, show an equally significant, but opposite, major orientation and are directed towards the north-east quadrant. In all these cases, however, aperture lineations are grouped in the SE–NW quadrant, subparallel to the palaeocoastline suggested both by sedimentary structures and regional facies trends. Significantly enough, the uppermost bed (bed 50, 11 m interval) with abundant *Rhizocorallium* shows a quite different pattern. Orientations are markedly bimodal, with a major north-west and minor south-east direction, so that presumed aperture lineations are perpendicular to those seen lower in the sequence. The uppermost bed at Selmaneset shows a diffuse but still significant orientation; aperture lineation may indicate two trends: a minor one parallel, but a major perpendicular to lineations seen otherwise. The changing orientation and lineation patterns in these topmost beds clearly reflect changing current regimes accompanying abandonment of the individual depositional lobes. The especially diffuse patterns seen at Selmaneset suggest multidirectional wave and current action, passing well with the interpretation of this bed as being extensively winnowed.

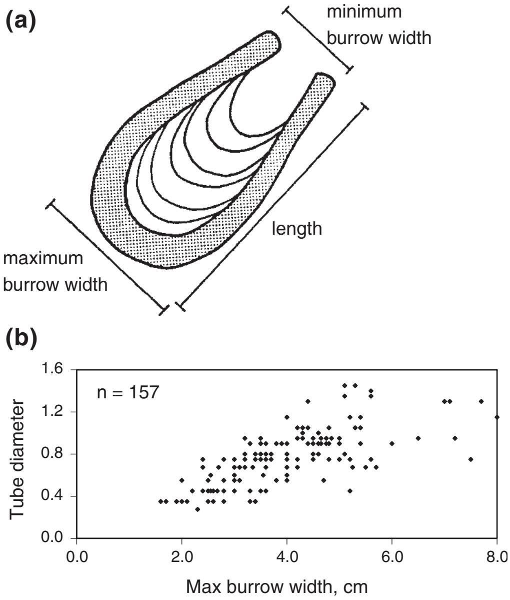

*Fig. 7.* (a) Sketch of *Rhizocorallium jenense* showing parameters measured. (b) Scatter diagram of correlation between maximum burrow width and tube diameter of *R. jenense* at Festningen.

There have been several reports of well-oriented populations of *Rhizocorallium,* but these have apparently been restricted to finds of the long U-tubes of the Jurassic fodinichnid *R. irregulare.* Farrow (1966) suggested an orientation in response to tidal currents and Ager & Wallace

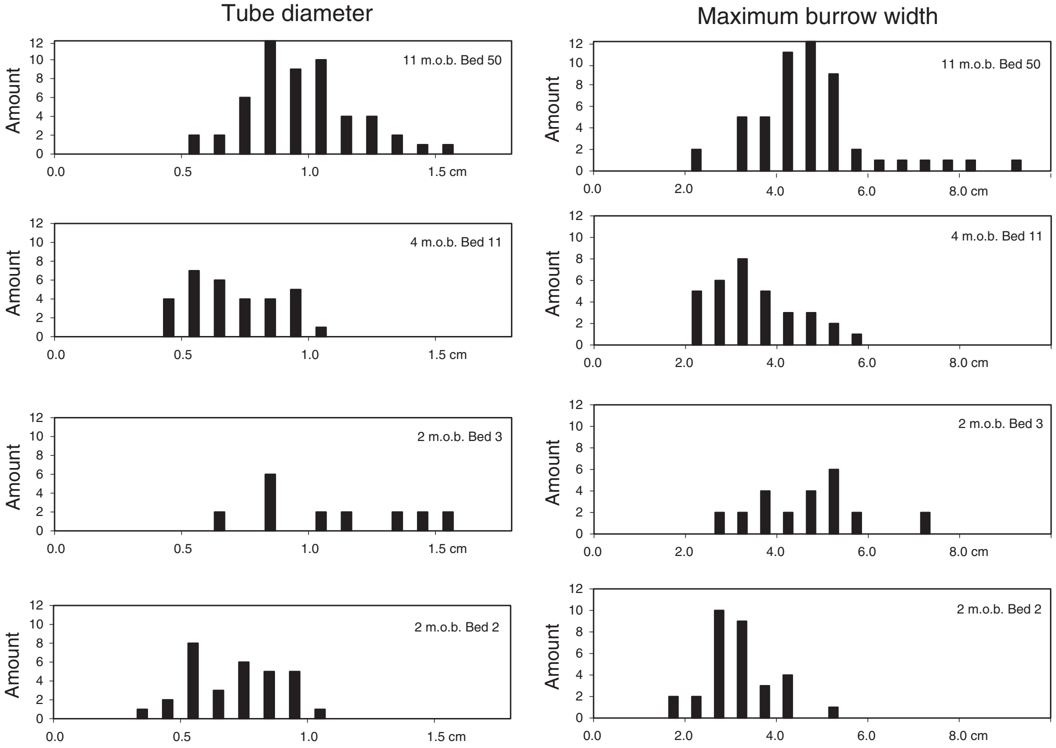

*Fig. 8.* Histograms showing variation in tube diameter and burrow width for *Rhizocorallium jenense*, at Festningen.

(1970) and Sellwood (1970) noted similar occurrences. The reasons for these orientations were somewhat obscure until Fürsich (1975) showed that the burrows occur in rippled sequences, following ripple troughs, i.e. in lee situations with higher organic content in the sediments.

Burrows made by suspension feeders are often distinctly oriented, e.g. *Diplocraterion parallelum* described by Fürsich (1975) as oriented "probably towards tidal currents". In these cases, as with *R. jenense,* orientation with regard to prevailing currents probably served the double function of continuously supplying fresh food-rich water to the burrow and removing excremental wastes.

## Ecology of *Rhizocorallium jenense*

Prior to work of Fürsich (1974) there was considerable confusion as to the nature and ethology of *Rhizocorallium*. Although several workers noted the existence of oblique and horizontal traces in different situations, they apparently assumed a common origin for these various types. It is now clear that burrows of *R. jenense* reflect domichnid traces, although like Sellwood (1970) we note that the burrows of some recent callianassids may reflect a double life function of the inhabitant—as a deposit-feeder during excavation, and later as a suspension-feeder.

Fürsich (1975) noted that throughout the Jurassic, *Rhizocorallium jenense* shows a distribution in unstable sedimentary regimes indicative of foreshore, high-energy regimes—probably in the uppermost subtidal zone. In the Corallian, although it does not constitute one of the characteristic members of Fürsich's three distinct associations, *R. jenense* is one of the few forms that shows a clear relation to only one or a few substrate types. It is in fact highly substrate-specific and is restricted to high-energy oolite banks. These younger occurrences are restricted to a more shallow and higher energy lithofacies than shown by the Triassic sequences of Svalbard, which are assumed to have been deposited in more intermediate depths, although still in the shoreface zone. These marked changes in lithofacies preference of the burrows with time have clear significance for environmental interpretations of Mesozoic trace-bearing sequences.

In the German Muschelkalk succession of Thuringia, Knaust (1998) reported a community of small *R. jenense* at the base of high-energy limestone beds in a middle ramp setting. It is interesting that these occurrences of *R. jenense* occupy a similar facies setting to those reported by us. Uchman (1992), in a study of Paleogene sediments from Poland, concluded that *Rhizocorallium* is a facies crossing form found both in shallow and deep water, and Fürsich & Mayr (1981) describe *R. jenense* from fresh water environments in Miocene southern Germany exposures. The wider facies occurrences of the Tertiary forms may suggest that the *Rhizocorallium* animal occupied wider niches through time. A similar phenomenom is also reported from *Zoophycos,* which is a typical shallow water form in the Late Palaeozoic but a deep water indicator in younger sediments (see discussion by Bromley 1996: 251).

## Conclusions

*Rhizocorallium jenense* is found in the Lower Triassic of western Spitsbergen in deposits of intermediate energy levels, associated with storm-generated siltstone and sandstone beds. Variations in size and abundance suggest an optimal habitat in the shoreface zone, decreasing into offshore environments. These occurrences contrast to trace fossil distributions in Jurassic sequences in England and France, where *R. jenense* is restricted to shallower high-energy environments. Such sequences in the Lower Triassic of Svalbard show an association dominated by *Skolithos* and bivalve escape shafts. They also conflict with the Tertiary records of central Europe where *R. jenense* occurs in a much wider range of environments. Similar occurrences of *Rhizocorallium* may, however, be found in north-east Greenland in time equivalent beds.

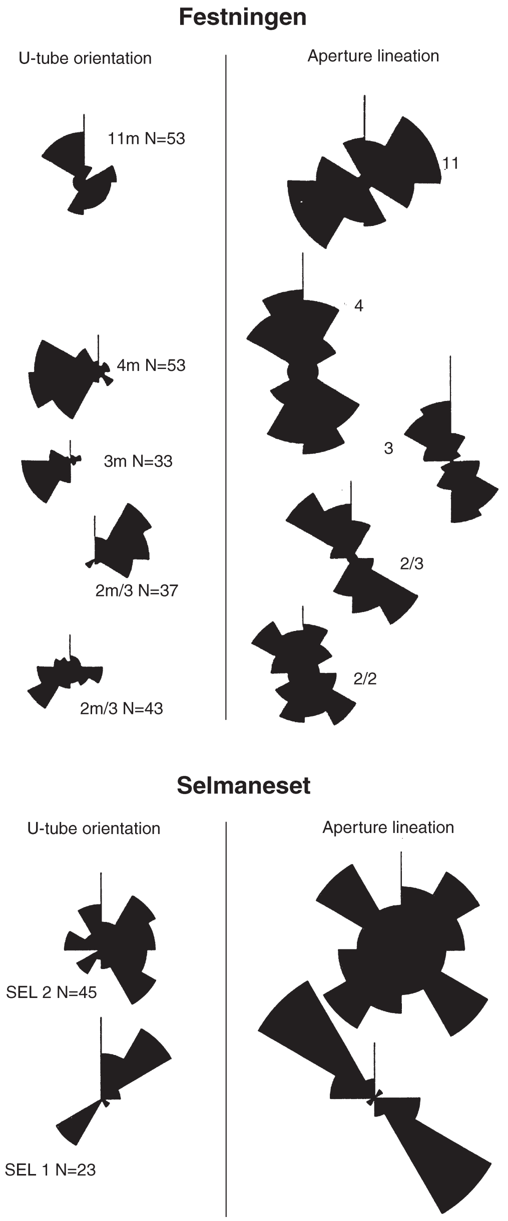

*Fig. 9.* Orientation of *Rhizocorallium jenense* at Festningen and Selmaneset.

Orientations of *R. jenese* U-tubes show a generally, but not solely, unimodal distribution, with the curved distal ends usually directed onshore. Presumed aperture lineations show strongly unimodal trends, probably related to longshore currents. Burrows in beds at the top of storm lobe sequences show more complex orientation and lineation patterns, probably reflecting both current and wave reworking following lobe abandonment.

All finds suggest early colonization by the organisms responsible for the burrows. These were not followed by other burrowers, either because of the nutrient-poor nature of the sediment (for infauna) or because of episodic high sedimentation rates (for suspension feeders).

Detailed sedimentological studies combined with trace fossil analysis are useful for environmental interpretations. Distinctions should be attempted between occurrences of *Diplocraterion*, *Rhizocorallium jenense*, *R. irregulare* and *Teichichnus.* In Triassic sequences of northern shelf regions such a distinction will be an important indicator of energy regimes, aiding environmental interpretation.

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