

Predation by early Cambrian trilobites on infaunal worms – evidence from the Swedish Mickwitzia Sandstone

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LETHAIA



Jensen, Sören 1990 01 15: Predation by early Cambrian trilobites on infaunal worms – evidence from the Swedish Mickwitzia Sandstone. *Lethaia*, Vol. 23, pp. 29–42. Oslo. ISSN 0024-1164.

Evidence of early Cambrian predation is found in trace fossils from the Mickwitzia Sandstone of Västergötland, Sweden. The arthropod burrow *Rusophycus dispar* was dug down to spreite burrows in such a manner that mere coincidence of place is unlikely. The predator is identified as an olenellacean trilobite, mainly through the presence of a cephalic impression. The prey, a worm that may have been a priapulid, was localized visually or chemically at the spreite-burrows apertures. The predator lacked legs specialized for seizing prey, as indicated by the parallel, but laterally displaced position of the *Rusophycus* above the spreite burrow. In this stance prey could be gripped by flexing the supposedly spinose legs of one side around it. When a spreite burrow of limited horizontal extension was encountered, parallel orientation was obtained prior to digging, probably through chemical sensing, whereas parallel orientation to an extended burrow required a number of diggings. These traces are important evidence of early Cambrian predation and of the predatorial capability of trilobites. □ *Lower Cambrian, Sweden predation, trilobites, priapulids, Rusophycus.*

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Trilobite feeding habits have been mostly inferred from morphological comparisons with extant arthropods and from the study of trace fossils. Most trilobites have been considered primarily microphagous, because of the absence of mouth parts and chelate legs and the similarity between the outer ramus of some trilobites and the limbs of filter-feeding crustaceans (Seilacher 1985). Nutrients could have been obtained from particles in suspension (Clarkson 1966; Stitt 1976) or from particles in the sediment (Schmalfuss 1981; Seilacher 1985). The latter activity has usually been coupled with elongated burrows (*Cruziana*) made by continuous horizontal digging. However, burrows representing stationary digging (*Rusophycus*), traditionally thought of as resting or sheltering burrows (see Seilacher 1955; Osgood 1970), may also reflect sediment feeding (Schmalfuss 1981; Seilacher 1985).

However, some trilobites had highly spinose coxae and ventral leg surfaces that could have been used in predation on soft-bodied animals (Seilacher 1962; Stürmer & Bergström 1973; Whittington 1975, 1980), and direct signs of predation have been found in trace fossils where *Rusophycus*-type burrows intersect worm bur-

rows. In these the trilobite burrow is positioned above and in contact with another trace fossil in such a way that it is unlikely they should be mere chance associations. These trace fossils may be referred to as 'hunting burrows' (Bergström 1973a), i.e. arthropod trace fossils interpreted as representing intentional digging into the sediment in the search for infaunal animals. The most detailed reports of hunting burrows have been given by Bergström (1968:500; 1973a:54, Fig. 16, Pl. 5; 1973b:158, Fig. 2) on material from the Lower Cambrian Mickwitzia Sandstone in Västergötland, Sweden. Other references to possible hunting burrows include: Hall (1852:24, Pl. 9:1; Hall interpreted them as marine plants with the worm burrows being stems or floating appendages); Walcott (1918:174, Pl. 42:3); Seilacher (1955:110, Fig. 5:8); Martinsson (1965:211, Fig. 20); Osgood & Drennen (1975:330, Pl. 1:1).

Although the existence of early Cambrian predators is meeting increasing acceptance, convincing candidates for macrophagous predators are rare. Some plausible predators (most notably *Anomalocaris*, see Whittington & Briggs 1985) or parts of predators (e.g. *Protohertzina*; Bengtson 1977, 1983) have been found, but more often their

presence is seen by their impact on other animals. This includes animals with injuries (e.g. in trilobites, see Conway Morris & Jenkins (1985) for examples and a review) or bored shells (e.g. in *Mobergella*, see Bengtson (1968)). It is, however, very difficult to connect these with any single attacker. The same is true of antipredatory adaptations, such as protective spines (e.g. in *Halkieria* and *Wiwaxia*; Bengtson & Conway Morris (1984), Conway Morris (1985)), to which is added the hazards of interpreting function from form.

Trace fossils are reflections of animal behaviour and it is sometimes possible to identify the trace makers. Thus, predation on trilobites by sea anemones has been documented in early Cambrian trace fossils (Alpert & Moore 1975; Birkenmajer 1977).

This paper deals with the evidence of predation on infaunal worms by trilobites found in hunting burrows of *Rusophycus dispar* Linnarsson, 1869, from the Lower Cambrian Mickwitzia Sandstone of Västergötland, Sweden. The main objectives of the study have been: (1) to establish identities of predator and prey, and (2) to find out how the predator behaved in locating and capturing prey.

Material and localities

The material studied is from the collections in the Swedish Museum of Natural History, Stockholm (SMNH); the Geological Survey of Sweden, Uppsala (SGU); the Department of Historical Geology and Palaeontology, University of Lund (LM); the private collections of Jan Johansson, Sköllersta and Allan Karlsson, Hjälmåsäter, and from my own field work in Västergötland. In all, 27 specimens showing arthropod-worm interactions were available. With the reservation that the locality is unknown for some museum specimens, three localities have yielded all the material. The positions of localities are given according to the UTM grid of the topographical map of Sweden (*Topografisk karta över Sverige*). (1) Hjälmåsäter-Trolmen: 13 km northeast of Lidköping. At the western foot of Kinnekulle, adjacent to the shore of Lake Vänern (see Westergård 1943), VE 032953. (2) Hällekis: 18 km northeast of Lidköping. Pile of sandstone blocks within industrial territory, 1.6 km north-northeast of Hönsäter church. VF 090008. (3) Lugnås: 11 km southwest of Mariestad. Millstone quarries at Lugnås (see Westergård 1931), VE 255966. The

illustrated specimens were coated with a thin layer of ammonium chloride before being photographed.

The Mickwitzia Sandstone

The trace fossils are from the Lower Cambrian Mickwitzia Sandstone, which is exposed in Närke and Västergötland (see Martinsson (1974) and references therein). The following summary is largely based on Martinsson (1974).

The Mickwitzia Sandstone, in Västergötland reaching a thickness of about 10 m, is a fine-grained, hard, locally mica-rich sandstone with thin layers of grey-green argillaceous material. The sandstone beds are often only a few centimetres thick, rarely more than 10 cm, and are of limited lateral continuity. Ripples and dragmarks ('*Eophyton*') are common. At its base is a thin transgressive conglomerate which overlies Precambrian gneiss and it is divided by a paraconformity from the overlying, purer and whitish Lingulid Sandstone. Sedimentation occurred in shallow water and was dominated in time, but not in thickness of succession, by argillaceous material. The clay sedimentation was interrupted by periodical influx of sand. As seen from mudcracks, it was occasionally exposed subaerially. Correlation of the Lower Cambrian in Scandinavia is difficult because of the paucity of fossils, particularly trilobites. However, recent analyses based on macro- and microfossils (acritarchs) have placed the Mickwitzia Sandstone in the *Schmidtellus mickwitzi* or *Holmia inusitata* Biozones, near the bottom of the Siberian Atdabanian Stage (see Bergström & Gee 1985; Moczyłowska 1989; Moczyłowska & Vidal 1988; and references therein).

Body fossils consist of the inarticulate brachiopod *Mickwitzia* sp. (two species, *M. monilifera* (Linnarsson, 1869) and *M. pretiosa* Walcott, 1908 have been recognized, but they are probably synonymous; Lars Holmer, Uppsala, pers. comm. 1988), the problematica *Mobergella* sp. and *Volborthella tenuis* Schmidt, 1888, the hyolithelminth *Torellella laevigata* (Linnarsson, 1871) and rare finds of the arthropod *Paleomerus* (or *Strabops*) *hamiltoni* Størmer, 1956. A better indication of the richness of life is given by the occurrence of diverse and numerous trace fossils including species of the ichnogenera *Cruziana*, *Rusophycus*, *Diplocraterion*, and *Teichichnus*. Also

found are the problematic sand-bodies, *Spatangopsis costata* and *Protolyellia princeps*.

Rusophycus dispar

The main diagnostic feature of *Rusophycus dispar* is the bidirectional scratch-marks (Fig. 1). In the anterior, somewhat wider, part of the burrow they are proverse, the scratch-marks of the two lobes forming a series of V's with the apices pointing to the anterior. The posterior scratch-marks are retroverse. In the anteriormost part of *Rusophycus dispar* burrows, the two lobes of scratches are often separated, resulting in a heart-shaped form (Fig. 1).

Rusophycus dispar is restricted to Lower Cambrian strata; in the Baltic Faunal Province more specifically to the *Schmidtellus mickwitzi* Biozone (correlation based on macrofossils, e.g. Bergström 1981). It is best known from the Mickwitzia Sandstone, Sweden (Linnarsson 1869, 1871; Torell 1870; Bergström 1968, 1973a, 1973b), but similar forms have also been reported from the Norretorp Formation, Scania (Bergström 1973a); the Duolbasgaissa Formation of Finnmark, Norway (Banks 1970), unit 1a-alpha of Mjøsa, Norway (Bergström 1981a); the White-Inyo Mountains, California (Alpert 1976); Inglefield Land, Greenland (Bergström & Peel 1988); the Rispebjerg Sandstone, Bornholm, Denmark (Poulsen 1967); and the Holy Cross Mountains



Fig. 1. A *Rusophycus dispar* with characteristic anterior indented and bidirectional scratch-marks, $\times 0.7$. Lugnås. SMNH X53.

of Poland (Orłowski, Radwański & Roniewicz 1970).

Besides the Mickwitzia Sandstone specimens, hunting burrow *Rusophycus dispar* have only been reported from Poland (Bergström 1973a).

A *Rusophycus dispar* hunting burrow often consists of a series of more or less superimposed burrows formed through the animal's forward movement and rotation along its vertical axis (Figs. 2–5). Thus, the bidirectionality of the scratch-marks and the anterior lobe separation are often indistinct.

The leg marks vary from straight to gently curved ridges with the convex side facing forwards. There are no impressions that might imply that an appendage similar to a trilobite outer ramus was used in digging.

The scratch-marks can be paired, indicating that each leg had (at least) two claws. The distance between the claw marks of a leg may be as much as 7 mm but is normally between 2 and 4 mm. It has not been possible to determine the number of legs used in digging, but a minimum of seven pairs is likely.

Maximum width of the burrows is from 40 to 130 mm, with an average width of about 80 mm. Length varies from 75 to 200 mm, with an average length of about 120 mm. The length is usually difficult to determine because the animal often shifted positions while digging; the values given are the total extent of the burrow regardless of overlaps. Depth is normally between 20 and 30 mm.

The worm burrow

The *Rusophycus dispar* hunting burrows are associated with flat (length to depth ratio from 3:1 to 5:1), retrusive spreite burrows. Some specimens are wall-shaped, whereas others are little more than U-shaped or L-shaped cylindrical tunnels, probably reflecting different stages in spreite burrow formation.

The spreite consists of stacked, flatly U-shaped laminae of little textural difference from the surrounding arenaceous rock. These sandy laminae are separated by very thin layers of silty or argillaceous material.

A few specimens have tubes with rounded button-like endings, possessing radiating patterns of more or less straight ridges (Fig. 6A, B). On the two specimens where this is best seen, there are 10 and 12 ridges covering respectively, 190° and 200° . However, on the same slab as one hunting

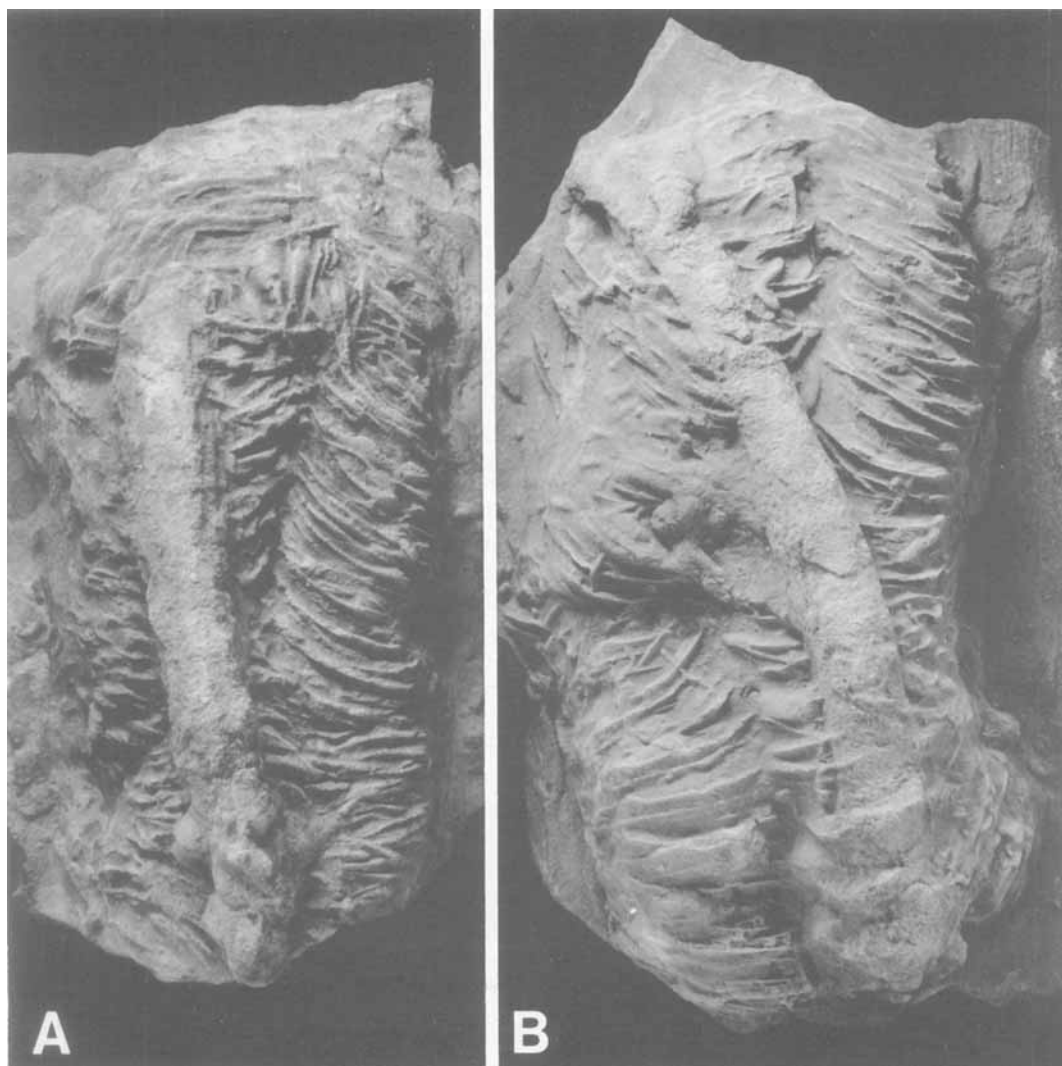


Fig. 2. *Rusophycus dispar* hunting burrows, $\times 0.7$ □ A. Hjälmåter. SMNH X722. □ B. Lugnås, SMNH X633.

burrow there is a small (5 mm wide, 15 mm long) cylindrical burrow with much the same kind of radiating ridges (Fig. 6C). Here the ridges are seen to occur on the entire surface, possibly with the exception of the central area. Because of poor preservation, few ridges are seen posteriorly, but individual ridges can be traced for up to 10 mm. The burrow is preserved as a shallow hypichnion, slightly inclined to the bedding plane, and it might well be related to the spreite burrows.

On the walls of most worm burrows there are up to 15 mm long scratch-marks. These were

probably made by the trilobite rather than the 'worm'. The reason for this is: (1) most can be paired into scratches with similar direction and curvature, the distance within the set reaching 3 mm or more; (2) although there are scratches in every direction, most are parallel to the scratches in the trilobite burrow; (3) some scratches can be laterally traced into the trilobite burrow; and (4) some scratches cross several laminae.

These are teichichnion-type burrows, most of which could be referred to *Teichichnus*. However, the radiating ridges on rounded terminal parts are

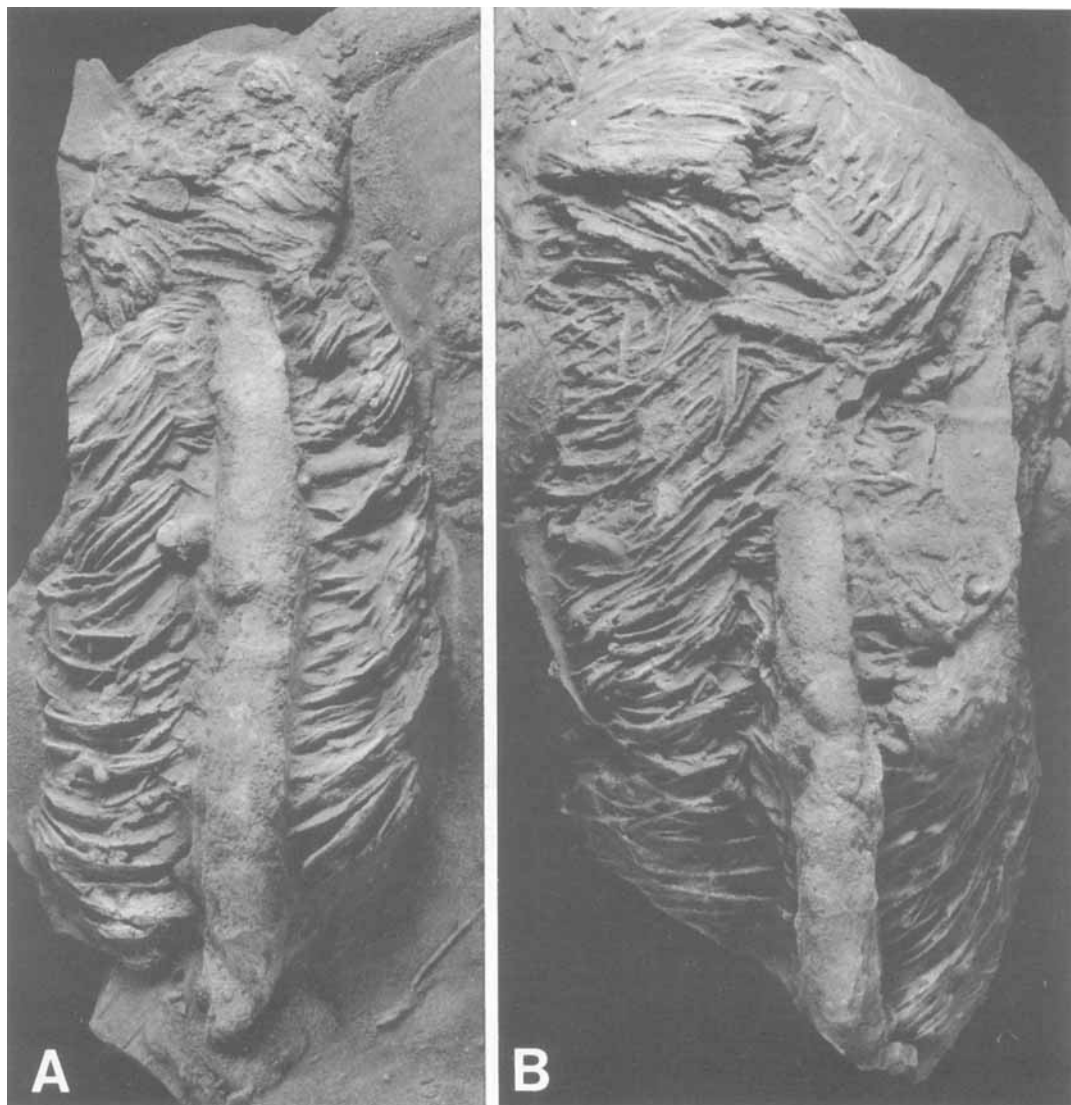


Fig. 3. *Rusophycus dispar* hunting burrows, $\times 0.7$. \square A. Hjälsäter. SMNH X712. \square B. Hjälsäter. SMNH X713.

not typical of *Teichichnus*, and rather resemble those of *Trichophycus* (cf. Osgood 1970). Unlike *Trichophycus*, there are no well-developed scratches on the lower surface of the burrows. Because of incomplete preservation it cannot be determined whether there are two separate forms present. They are here referred to collectively as worm burrows.

The diameter of the worm burrows is 6–17 mm, with an average diameter of 14 mm, but they are normally dorso-ventrally flattened owing to

compaction. The length is normally indeterminate because of incompleteness, but usually exceeds 100 mm. The depth is up to 40 mm.

The trilobite burrow–worm burrow association

Twenty-three associations of *Rusophycus* and teichichnian-type worm burrows have been found. As most of the material belongs to older museum

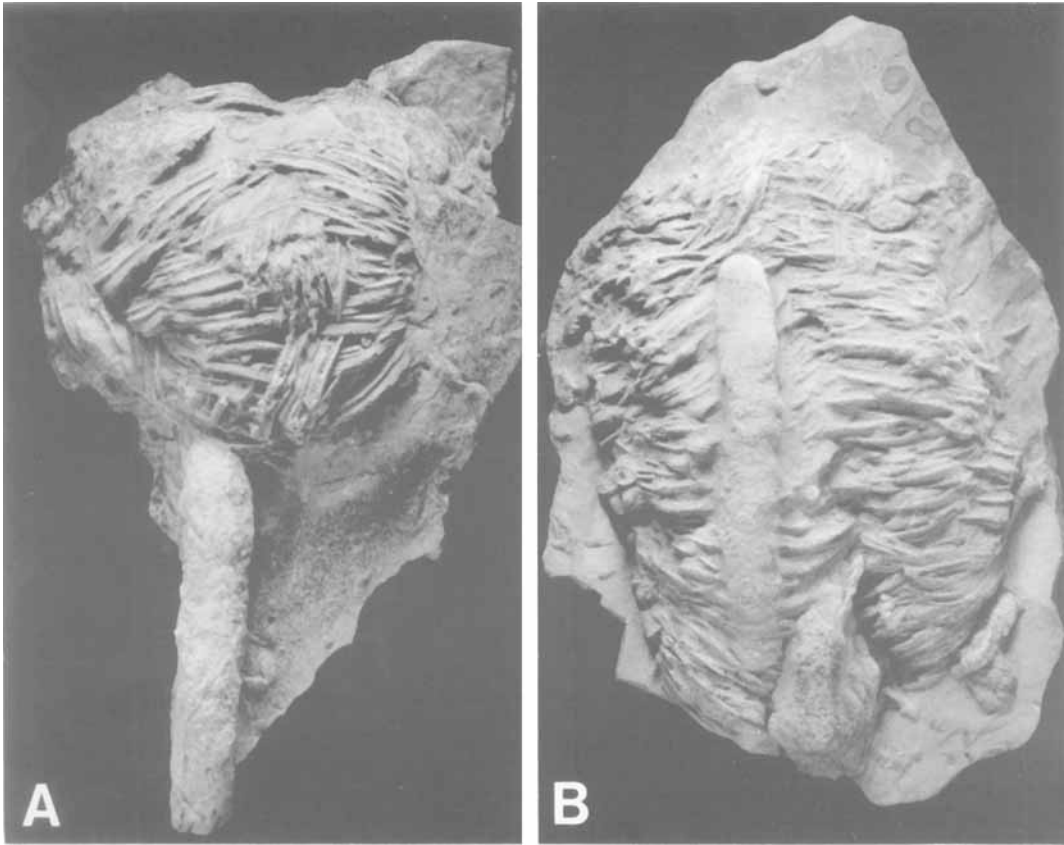


Fig. 4. *Rusophycus dispar* hunting burrows, $\times 0.7$ □ A. Lugnáš. SMNH X33. □ B. Lugnáš. SMNH X77a.

collections, and good exposures are scarce, it has not been possible to determine the frequency of *Rusophycus dispar* associated with worm burrows. At Trolmen few *Rusophycus* are of the hunting burrow type.

As pointed out by Bergström (1973a) the orientations of the associated trilobite and worm burrows are strikingly similar. Using the position of the worm burrow as a reference it was found that in the 22 measurable specimens, the orientation of the arthropod burrow deviates by more than 30° in only four cases (Fig. 7A). Of these latter specimens, two have a deviation of 90° ; but also these seem to be hunting burrows, as the *Rusophycus* is deepest where it is in contact with the worm burrow. However, on more extended worm burrows a number of connected arthropod burrows with different orientation can be seen (Figs.

2, 3, 5A, C). The initial part of the *Rusophycus* complex, which also has the greatest deviation from the worm burrow, seems to be positioned at one of the apertures of the latter. In the course of successive digging, alignment increased until the two were nearly parallel. In less extended worm burrows there is only one, although usually aligned arthropod burrow (Fig. 8C).

The arthropod burrow is typically positioned such that contact with the worm burrow is with only one lobe of leg marks (e.g. Fig. 8C). On this side the *Rusophycus* is deeper, giving the mould a lopsided transverse section (Fig. 8B). The arthropod burrow often follows the curvature of the worm burrow very closely (Fig. 8A). This is not due to compaction of the sediment, because arthropod scratches can be continued into the worm burrow.

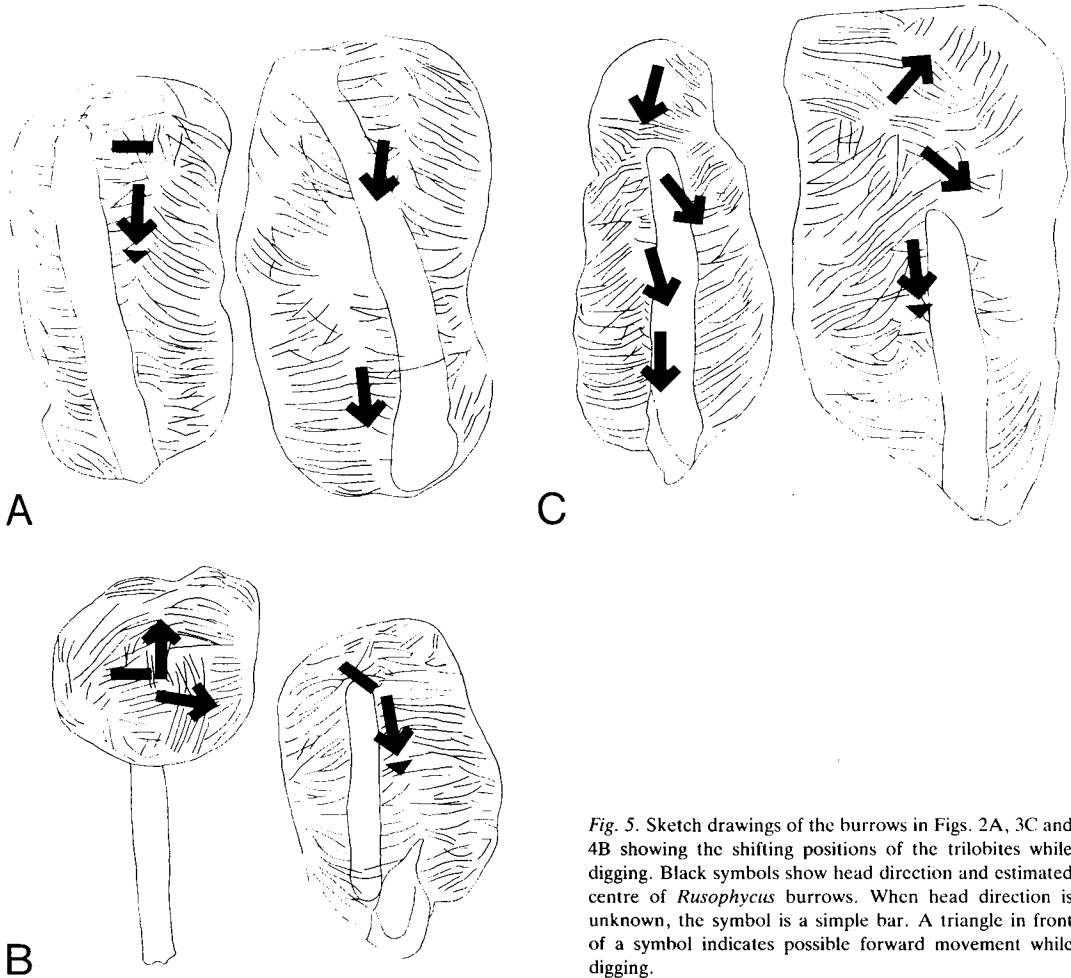


Fig. 5. Sketch drawings of the burrows in Figs. 2A, 3C and 4B showing the shifting positions of the trilobites while digging. Black symbols show head direction and estimated centre of *Rusophycus* burrows. When head direction is unknown, the symbol is a simple bar. A triangle in front of a symbol indicates possible forward movement while digging.

Plotting the maximum width of the worm burrow against the maximum width of the arthropod burrow (Fig. 7B) reveals a positive correlation, with the larger arthropod burrows being associated with the larger worm burrows ($r = 0.80$, $p < 0.001$, $n = 22$).

In the material studied there are four specimens in which arthropod burrows are associated with vertical, cylindrical shafts (Fig. 9A). These are set medially in the deepest part of the *Rusophycus* and are broken off with its lower surface. It is notable that they are positioned at the boundary between proverse and retroverse digging. With few exceptions the arthropod scratch-marks do not continue into the vertical burrow (Fig. 9B).

Similar round structures associated with arthropod burrows have been mentioned and figured by Seilacher (1955:366, Figs. 5:1, 5:8) and Hall (1852:24, Pl. 9:2).

Formation and preservation of the trace fossils

Rusophycus and *Cruziana* are generally considered to be trilobite trace fossils (e.g. Bergström 1973a:52; Seilacher 1985:232–233), but it is possible that other arthropods may have been involved. The Mickwitzia Sandstone has yielded the merostomoid (Bergström 1971) or aglaspidd

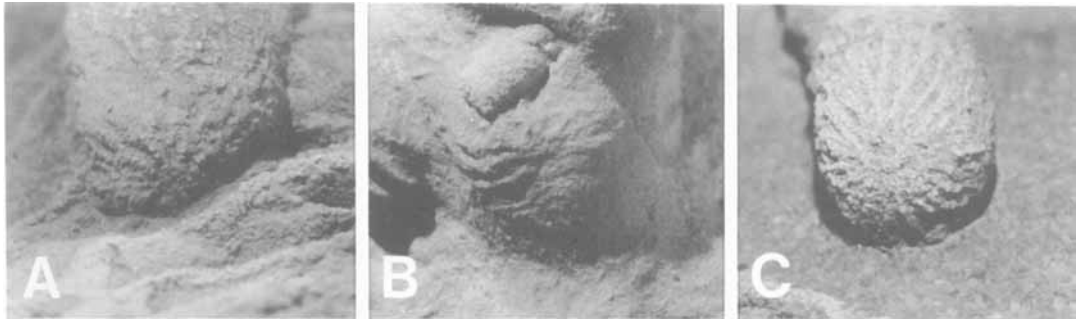


Fig. 6. Radiating ridges found on worm burrows, possibly impressions of a digging apparatus. A and B associated with hunting burrows. □ A. Lugnås. SMNH X77a, ×3. □ B. Lugnås. SMNH X3198, ×3. □ C. Hjälsåter. SMNH X712, ×5.

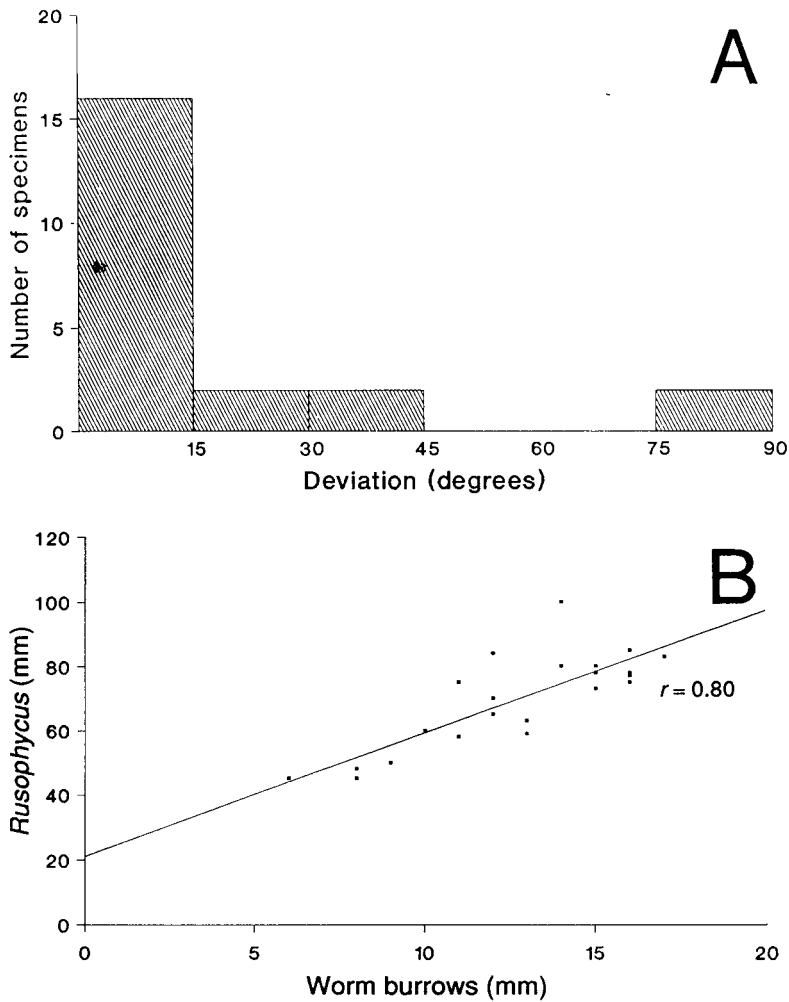


Fig. 7. □ A. Deviation in orientation between trilobite and worm burrow. In associations where the trilobite has shifted position, measurements were made on the *Rusophycus* with the least deviation. □ B. Size correlation (maximum widths) of associated trilobite and worm burrows.

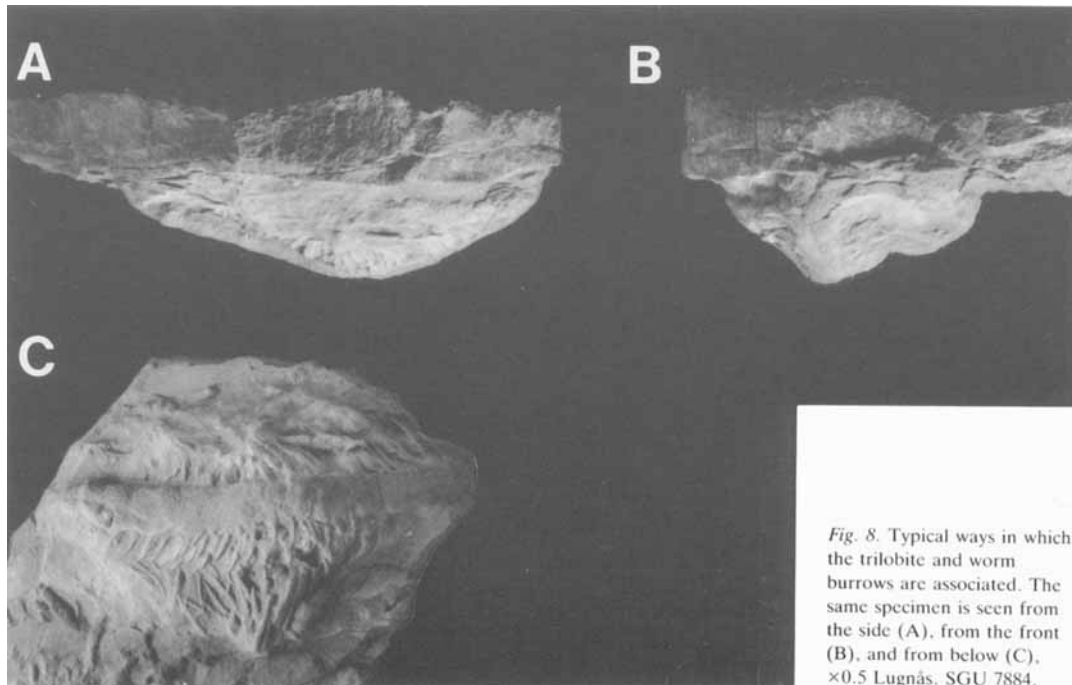


Fig. 8. Typical ways in which the trilobite and worm burrows are associated. The same specimen is seen from the side (A), from the front (B), and from below (C), $\times 0.5$ Lugnås. SGU 7884.

Paleomerus hamiltoni, a possible producer of *Rusophycus*-like burrows. Unfortunately, nothing is known about its leg morphology, but merostomoids have at least homopodous walking legs, and judging from *Aglaspis spinifer* Raasch 1939, the only aglaspidid with well-preserved legs (see Briggs *et al.* 1979), so too did aglaspidids. Bergström (1973a) argued that the morphology of *Paleomerus* prevented it from making deep convex burrows.

Additional information on the producer of this trace fossil is given by a trace fossil I found at Lugnås, where a small *Rusophycus dispar* (width 34 mm) is associated with a cephalic impression, apparently from the trace fossil producer. This impression shows that the animal had a shelf-like anterior cephalic border, as do many trilobites. *Paleomerus hamiltoni*, on the other hand, had a vertically dipping anterior margin (Størmer 1956). Thus it is most likely that *Rusophycus dispar* was made by a trilobite. It is noteworthy that the only unequivocal aglaspidid trace fossil, *Raaschichnus gundersoni* Hesselbo, 1988, is very different from *Rusophycus dispar* (see Hesselbo 1988).

Among trilobites from the Lower Cambrian Baltic Faunal Province, Bergström (1973a) considered only olenellaceans to be large enough to have produced *Rusophycus dispar*. No trilobites have been found in the Mickwitzia Sandstone, but from biostratigraphically correlative beds elsewhere in the faunal province, six species of olenellaceans have been described (Ahlberg *et al.* 1986, Fig. 1).

The preservation of the hunting burrow *Rusophycus* in Västergötland is elucidated by its association with teichichnian-type burrows. These are usually considered to be feeding traces, resulting from the activity of a deposit-feeder, but some forms have been interpreted as more or less permanent dwelling structures, the spreite resulting from the inhabitant's response to sediment influx (Chisholm 1970). The specimens found in the Mickwitzia Sandstone are shallow and have a mainly horizontal extension, suggesting that they were made by deposit-feeders. They have a filling that is little different from the surrounding arenaceous rock and probably drifted in from a bed of sand covering the mud into which the deposit-

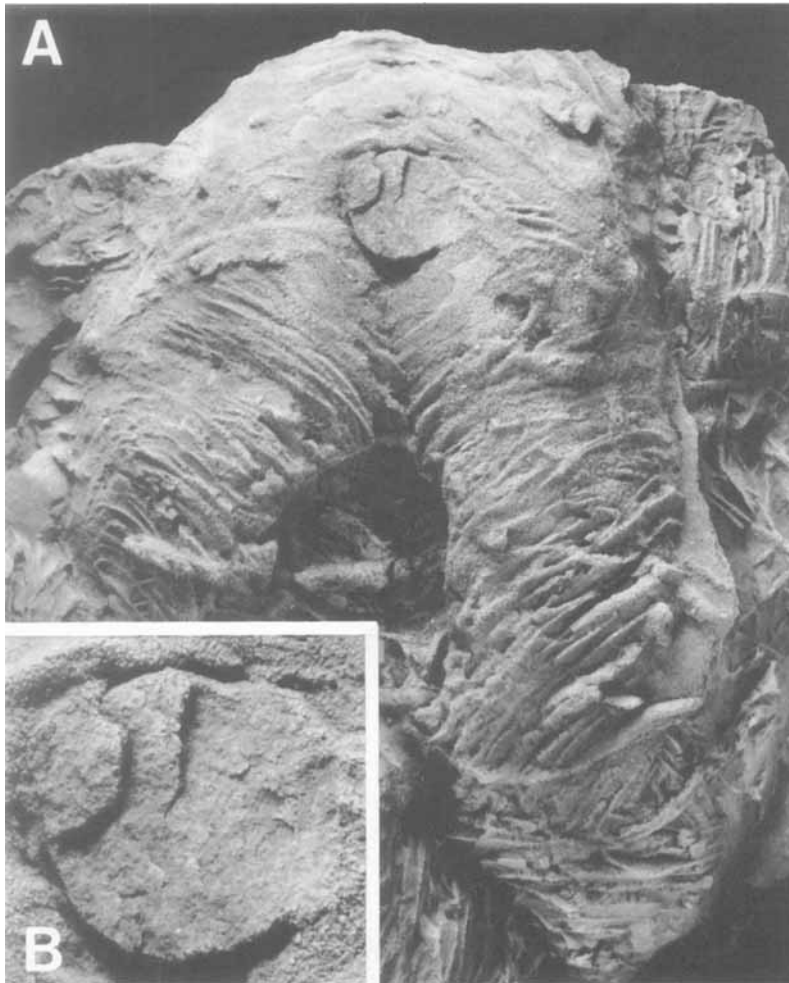


Fig. 9. Vertical trace fossils associated with trilobite burrows. □ A. Large trilobite burrow with deep and wide anterior indent. Hjälmåsaer. SMNH X713, $\times 0.7$. □ B. Enlargement ($\times 2$) of vertical shaft in A. Notice the clear boundary between the two burrows; a few trilobite scratch-marks can be traced into the vertical burrow.

feeder was digging. Both trace fossils are thus post-depositional with respect to the sandstone.

The producers of spreite burrows are largely unknown, and Martinsson (1965) among others has cautioned against making any assignments. Today, burrows with spreite are made by animals as different as crustaceans, echiurans and polychaets (Chisholm (1970) and references therein). Some suggestions on the general body plan of the trace-maker in the Mickwitzia Sandstone may be made, however.

The terminal radiating ridges indicate radial symmetry of at least the digging apparatus. This and the absence of bilobation make it less likely that the producer was an arthropod. The animal may have had a digging apparatus similar to a priapulid proboscis (cf. e.g. Conway Morris 1977,

Fig. 12). The appearance of the ridges could be accounted for by digging 'spines' on the proboscis. Thus it appears that the animal was more or less tubular, had an anteriorly situated digging apparatus with radially arranged spines and lacked extremities forming scratch-marks. Among animals living today, priapulids, echiuroids and possibly sipunculoids are possible candidates; of these, at least priapulids were relatively diverse in the Cambrian (Conway Morris 1977; see also Sun & Hou 1987).

Discussion

Evidence of predation in *Rusophycus dispar* was discussed by Bergström (1973a, b), who used



Fig. 10. *Rusophycus dispar* appearing in cluster. Although lacking the typical association of a hunting burrow, these burrows may be interpreted as representing the search for infaunal worms. Hjälsäter. SMNH X589. $\times 0.5$.

the termination of worm burrows beneath the *Rusophycus* as the clearest evidence of predation. In one specimen irregular scratch-marks at the intersection between the two burrows were interpreted as the point of capture. Localization was considered to have been done with mechanical rather than with chemical sensing, since the prey, assumed to be digging a horizontal burrow, was covered by mud, impenetrable to smell, and since the burrows are usually parallel. However, the worm burrows in the material studied here are spreite burrows.

I had the opportunity to study some of Bergström's material. Specimen LM LO 4560 t (Pl. 5:10 of Bergström 1973a) is of low relief. While no laminae can be seen, it is somewhat convex and might just as well be a spreite burrow as a cylindrical horizontal burrow. Specimen LM LO 4559 t (Pl. 5:9 of Bergström 1973a) is possibly

cylindrical, but terminates some distance from the *Rusophycus* and might have been a shallow U-shaped burrow. The preservation of these two burrows prevents a definite statement as regards their morphology, but as it cannot be proved that they were horizontal, the termination of a worm burrow beneath a *Rusophycus* is insufficient evidence of capture.

There are, however, other features that support the hunting burrow interpretation. In some burrows it can be seen that the arthropod has dug to a depth considerably above the lowest part of the spreite burrow. This would be expected if the arthropod was a predator, as it would dig no deeper than down to the prey. Furthermore, in some burrows the arthropod has shifted orientation repeatedly while remaining in the same place (e.g. Fig. 4A); this is behaviour that would not be expected from a microphagous animal.

Perhaps the strongest indication of predation is the positive size correlation seen in Fig. 7B. This indicates that the arthropod was size-selective in its choice of prey, pointing against a mere chance encounter.

Some indication of how the arthropods behaved in locating and capturing an infaunal worm is given by the way in which the trace fossils are associated and from their morphology.

The worm may have produced the spreite by digging back and forth or by probing from a fixed position. In either case sand would have drifted in at one, probably two, apertures. Unless the worm had mined entirely up to the sand, it would have been detectable only at these apertures. The observed hunting burrows confirm this assumption, because on extended worm burrows the position of initial arthropod digging is near an aperture. The mode of detection could have been by direct sight of the worm, by sight of funnels formed when sand drifted into the worm burrow, or by chemical sensing. Of these possibilities, the first is likely only if the sand cover was thin.

The arthropod probably lacked raptorial legs – trilobites and merostomoids (sensu Bergström 1981b) were mostly homopodous (an exception is the Devonian *Cheloniellon*). Also mouth parts suitable for gripping prey were probably missing. Therefore the prey had to be seized with the same legs that were used in digging. It has been suggested that trilobites with spinose telopodites used these to capture soft-bodied animals (Stürmer & Bergström 1973; Whittington 1975, 1980). Whittington (1975:133) proposed that *Olenoides serratus* gripped prey between the telopodites. In the hunting burrows observed here, the arthropods have consistently positioned themselves so that only legs of one side were in contact with the worm burrow. This could mean that the arthropod caught the worm by flexing the legs of one side around it. This requires a large amount of flexing, and would have been aided by the presence of a 'knee' (as in *Phacops*, see Seilacher (1962)).

In the absence of true mouth parts in trilobites, it has been suggested (e.g. Stürmer & Bergström 1973) that spinose inner parts of the coxae could have served as enditic 'jaws'. Whittington (1975) suggested (for *Olenoides serratus*) that movement of the coxae, used as gnathobases, brought food forwards to the mouth where it was ingested into the gut by peristaltic action of the oesophagus. The posteriorly directed opening of the mouth

would be in full accordance with this. Shredding of the prey into suitably sized pieces could have been accomplished by motion of the coxae (Whittington 1975), or by movements of the telopodites after the prey was gripped. An alternative possibility of capture is that the arthropod lowered itself down over the exposed worm, seizing it directly with its enditic 'jaws'.

The parallel orientation of the *Rusophycus* to the worm burrow apparently resulted from somewhat different behaviour depending on the horizontal extension of the latter. In less extended worm burrows (horizontal extension less than about 12 cm) the arthropod was obviously able to align itself prior to digging, while in worm burrows of greater extension the arthropod had to dig a number of successive burrows to achieve that position. The reason for this might be related to the distance between the apertures (under the assumption that the worm burrow was U-shaped) in relation to the length of the arthropod. This relation could have been important whether orientation was achieved by chemical sensing or by sight.

Besides true hunting burrows, also *Rusophycus dispar* appearing in clusters (Fig. 10) may well have been made in the search for infaunal animals.

Arthropod burrows associated with vertical burrows

These cylindrical structures may have been tubes of vertical or U-shaped dwelling burrows. There are, however, circumstances indicating that they had already been abandoned and filled with sediment before the arthropod started digging. As seen in Fig. 9B, some of the scratches can be followed into the cylindrical burrow. This could only have happened if it was already filled with (slightly compacted) sediment, as it is unlikely that impressions would be preserved in sand falling in while the arthropod dug. A possibility is that the cylindrical burrow was a vertical dwelling burrow in an environment of rapid sedimentation. To keep track with sedimentation the inhabitant had to raise the burrow level to compensate for material falling into the burrow. The scratches could then have been formed in the lower, sediment-filled part of the burrow. Until the true nature of these cylindrical structures is known it is unwise to regard their association with arthropod traces as signs of predation.

Conclusions

(1) In the Lower Cambrian Mickwitzia Sandstone of Västergötland, Sweden, the activity of arthropods hunting infaunal animals is preserved in associations of the arthropod trace fossil *Rusophycus dispar* and teichichnian worm burrows.

(2) The arthropods were probably olenellacean trilobites, while the animals they hunted may have been priapulids.

(3) The worm burrows were made by deposit-feeders digging series of U-shaped or L-shaped tunnels in mud. The mud was covered by sand which drifted into these tunnels and enabled them to be preserved. Similarly, sand drifted into the burrows formed by the arthropod's digging, but it is less certain whether an immediate infilling of sand was a prerequisite for their preservation.

(4) A *Rusophycus dispar* hunting burrow (a) is strongly aligned with the worm burrow; (b) has only leg-marks of one side in contact with the worm burrow; and (c) is deepest where it is in contact with the worm burrow. A hunting burrow associated with an extended worm burrow (length about 120 mm or more) shows a series of diggings, starting approximately at an inferred aperture. In the successive digging, alignment between the two trace fossils gradually increased.

(5) The trilobite localized the worm by the apertures of the worm burrows. The means of localization could have been by sight of funnels formed when sand drifted into the worm burrow or by chemical sensing.

(6) The trilobite probably captured its prey by flexing the legs of one side around it or by seizing it with spinose coxae.

(7) In a few trilobite burrows remnants have been found of probable vertical cylindrical burrows positioned at the boundary between retroverse and proverse digging. These associations cannot unequivocally be referred to as hunting burrows.

Acknowledgements. – I am grateful to my supervisor, Stefan Bengtson, Uppsala, for introducing me to the topic, and for his guidance and criticism. I am also thankful to Jan Bergström for valuable correspondence and discussions and for his critique of a manuscript draft. Helpful comments were given by Peter Crimes, Liverpool, P. Roniewicz, Warsaw, and Adolf Seilacher, Tübingen. Peter Bengtson, Richard Reymont and Jürgen Schöbel, Uppsala, read and commented on an earlier manuscript draft. Jan Johansson, Sköllersta and Allan Karlsson, Hjälmåsäter

shared their knowledge of localities, assisted in field work and gave access to their trace fossil material. Christer Bäck, Uppsala, did the dark-room work. I am also grateful to the staffs of the Swedish Museum of Natural History, Stockholm, the Swedish Geological Survey Museum, Uppsala, and the Palaeontological Department, University of Lund, for access to collections and loan of trace fossil material.

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