Trace fossil associations in the Swedish Mickwitzia sandstone (Lower Cambrian): Did trilobites really hunt for worms?

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Abstract: The spatial and temporal associations between *Cruziana*, trace fossils dug by foraging trilobites, and back filled burrows made by infaunal "worms" in a Lower Cambrian sandstone are described and discussed. In three large slabs and several smaller pieces, all from the same bedding plane in the lowermost part of the Mickwitzia sandstone (File Haidar Formation) at Kinnekulle, Västergötland, Sweden, *Cruziana* and worm burrows coincided more frequently than would be expected by chance. Overall, however, the association was weak and independent of the size of the worm trace. In 24 out of 29 cases, the worm burrow had deformed the *Cruziana*, implying that the arthropod was first on the spot. No clear case of the opposite situation was found. It is concluded that for an unknown reason the infaunal worms preferentially dug in places which had been visited earlier by foraging trilobites, or, possibly, that worms and trilobites preferred to dig in the same spots independently of each other. There is no evidence from this surface that the trilobites had been searching for worms or predated on them.
Keywords: *Cruziana*, palaeoecology, predation, *Rusophycus*, sandstone, trilobites, Västergötland, Sweden.

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It was in the early Cambrian that the marine benthic communities acquired the ecological characteristics, including predator–prey relationships, which still characterize most of them today. During the Vendian–Cambrian transition the benthic biota were permanently and more or less abruptly transformed from two-dimensional "matground" communities, with little or no bioturbation of the sediment, to three-dimensional "mixground" communities (Seilacher 1997). This transition almost certainly involved the evolution of predation, as it is known today, and the Cambrian explosion was perhaps even driven by it.

The anomalocaridids provide unambiguous examples of predatory animals from the early Cambrian (Hou et al. 1995), and there are two lines of evidence suggesting that at least some of the larger Cambrian trilobites also were among these early predators. Firstly, larger species of the family Olenellidae probably possessed gnathobases and spines on the appendages, structures that may have been used to handle large prey animals (Fortey & Owens 1999). Secondly, the occasional co-occurrence of *Cruziana*-type trace fossils (specifically *Rusophycus dispar*), that were probably made by trilobites (Goldring 1985; Fortey &

Seilacher 1997), and infaunal "worms" in the lower Cambrian Mickwitzia sandstone of Sweden, have been interpreted as direct evidence of predation (Bergström 1973; Jensen 1990).

The Mickwitzia sandstone of southern Sweden, forming the lower part of the File Haidar Formation (defined by Bergström & Gee 1985; see also Jensen 1997), has been studied more or less intensively for more than a century (Linnarsson 1869; Torell 1870; Nathorst 1881), and this member has become known for its richness in well-preserved trace fossils, including various forms of *Cruziana* and other arthropod traces. The Mickwitzia sandstone also contains the inarticulate brachiopod *Mickwitzia monolifera* and it is known for some enigmatic body fossils such as the sand corals *Spatangopsis* and *Protolyellia* (e.g. Seilacher & Goldring 1996).

The purpose of the present study was to evaluate the general validity of Bergström's (1973) and Jensen's (1990) observations. If the predator–prey relationships between trilobites and infaunal worms, that they described, are general features of the Mickwitzia sandstone, they should also occur on bedding planes that they did not examine. We therefore performed a detailed statistical analysis of the spatial and temporal associations between *Cruziana* and the worm burrows on a bedding plane of the Mickwitzia sandstone at Kinnekulle, Västergötland, Sweden.

Materials and methods

We used three slabs (Fig. 1), each with an area of 0.1–0.2 m^2 (Table 1), from the lowermost part of the Mickwitzia sandstone ("interval A" in Jensen 1997). The slabs were collected at the natural exposure at Trolmenshamn on the shore of Lake Vänern on the western slope of Kinnekulle. Interval A also includes a basal conglomerate, which in turn rests on Precambrian gneisses (Jensen 1997). The slabs are either deposited at the Zoology Department, Göteborg University (slab 1) or belong to the private collection of H. Buentke, Lugnås (slabs 2 and 3).

The investigated layer is 4–15 cm in thickness (Jensen 1997). The upper surface typically shows ripple marks and occasional trace fossils, while the underside is very rich in well preserved trace fossils, including *Rhizocorallium* and *Cruziana* of various types, as well as "worm" burrows of various sizes.

The lower surfaces of the three slabs were copied on transparent paper. The positions of all *Cruziana* and worm burrows were marked. Measurements of all *Cruziana* (length and width in millimetres) and worm burrows (diameter, nearest 0.1 mm) were taken, using callipers. We also measured the distance between the midpoint of each *Cruziana* and the centre of the nearest visible part of a) the nearest worm burrow, and b) the nearest worm burrow that exceeded 6 mm in width ("large worm burrows"). To minimize problems with edge effects, we excluded *Cruziana* with midpoints located <50 mm from the edge of the slabs.

We examined the *Cruziana* on the slabs, and also those of another 29 smaller pieces that we found at Trolmenshamn. For
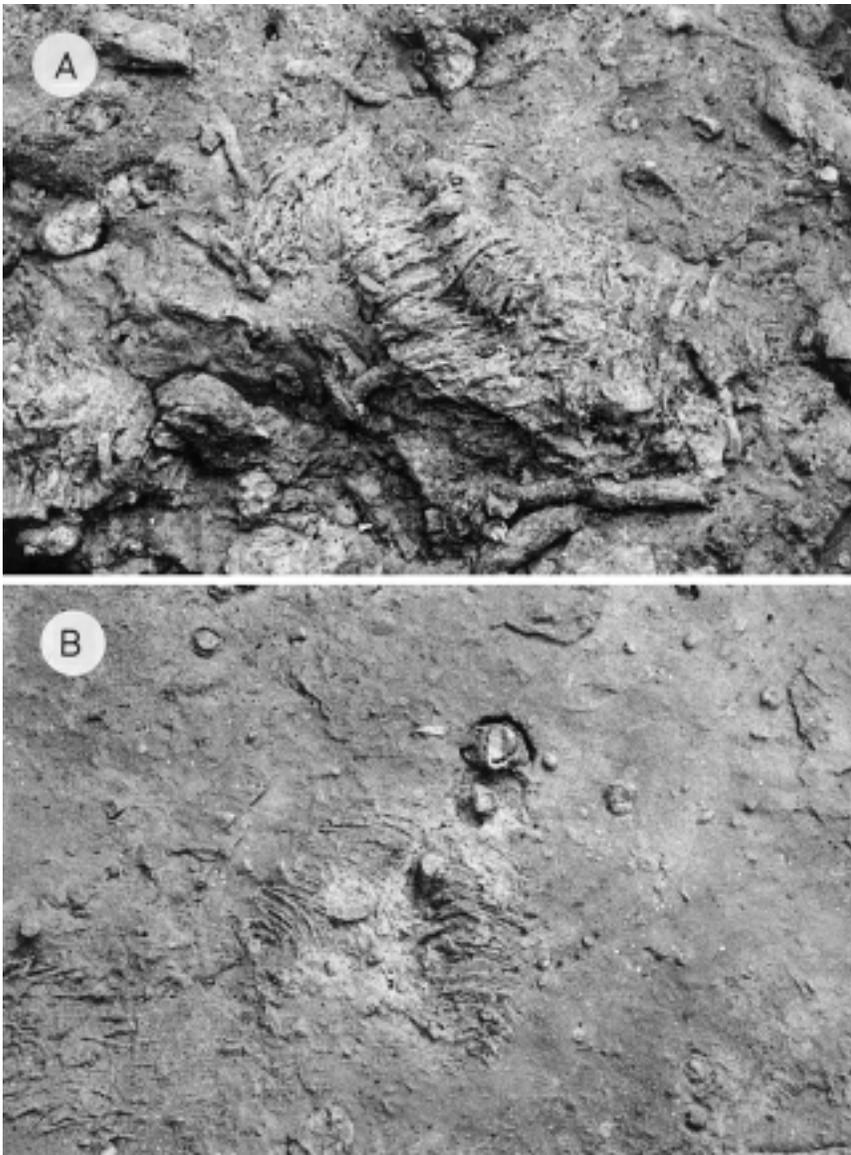
Fig. 1. Examples of (**A**) a relatively deep *Cruziana* (*Rusophycus*) *dispar*, intersected by worm burrows, from slab 1, and (**B**) a relatively shallow one from slab 2. Both are from the Mickwitzia sandstone, collected at Trolmenshamn, Kinnekulle, south Sweden. For scale, the *Cruziana* are 5 cm wide in both cases.

(Fig. 1A and B, respectively). Nevertheless, all the *Cruziana* represented stationary foraging at various levels below the surface, and hence conform with *Cruziana* (*Rusophycus*) *dispar*.

The worm burrows were either running along the surface of the bedding plane or, more frequently, they were three-dimensional, often cutting through the bedding plane nearly vertically. Clearly the worms had dug in the sand as well as in the softer sediment underneath. The burrows were always backfilled and hence belong either to *Planolites* or *Teichichnus*, depending on how the backfill was made. This was not investigated, however. We found no case where the worm burrows ran parallel to the arthropod traces for an extended length, as was sometimes the case on the slabs studied by Jensen (1990).

Slab 2 had a lower frequency of larger worm burrows than the other slabs (P<0.001, Kruskal-Walls test; Fig. 2), but otherwise there was no obvious difference between the worm burrows of the three slabs. The differences in frequency of larger worm burrows and in the form of the *Cruziana* on the three slabs could be at least indirectly related to horizontal variations in the sediment structure (e.g. in grain size). Because of these heterogeneities between the three slabs we measured and analysed them separately.

Spatial association between Cruziana and worm burrows

The distance between a *Cruziana* and the nearest worm burrow, measured from the midpoint of the *Cruziana* to the midpoint of the nearest visible part of the worm burrow on the bedding plane, varied between 0 and 50 mm (Fig. 3). On each of the three slabs the mean distance between *Cruziana* and the worm burrow was as short as or shorter than the mean distance between a random point (assigned by random co-ordinates on each slab) and the nearest worm burrow. In one case (slab 3) the distance was significantly shorter (Table 3). This means that *Cruziana* and worm burrows were in fact spatially associated at least on slab 3, i.e. the two types of traces occurred closer to each other than expected by chance.

It remains possible that the *Cruziana* were more closely associated with big worm burrows than with small ones. For example, this may have been the case if the trilobite was searching specifically for larger worms, as suggested by Jensen (1990). Therefore, we repeated the analy-

each *Cruziana* that coincided with a worm burrow, we recorded whether the trace of the trilobite or that of the worm was made first. If the *Cruziana* was deformed, while the worm trace was not, at the place of contact, we scored the arthropod as having been there first, and vice versa.

Results

The three slabs (samples 1, 2 and 3) were collected at the same locality and repre-

sent the same bedding plane. They were of similar size and also had a comparable number of *Cruziana* and worm burrows (Table 1). The *Cruziana* were of approximately the same width (5 cm) on all three slabs, suggesting that they could have been made by the same animal species or even by the same individual animal. However those of slab 2 were all (N=10) relatively shallow (<1 cm deep), some being nearly two-dimensional, while those on slabs 1 and 3 (N=9) were 2–3 cm deep

sis, excluding all worm burrows with a width <6 mm. However, the result was qualitatively the same as in the previous tests; on all slabs the mean distance between *Cruziana* and the nearest worm burrow was slightly shorter than the distance between a random point and the nearest worm burrow, although it was significantly shorter only on one slab (in this case slab 2; Fig. 4 and Table 2). This means that the *Cruziana*–worm burrow association, which was weak in any case, was also independent of the size of the worm burrow.

Of the nineteen *Cruziana* present on the three slabs, as many as sixteen (84%) coincided spatially with at least one worm burrow. To see if this frequency was higher than expected, i.e., if the two types of trace occurred independently of each other, we compared the frequencies of such "hits" (80, 80, and 100% for the three slabs, respectively) with the frequencies of hits obtained by randomly placing *Cruziana*-sized pieces of transparent paper on the surface of each slab (N=100). The frequency of hits was higher for the real *Cruziana* than for randomly placed papers on two of three slabs but not significantly higher in any case (P>0.05, X^2-tests). Hence, *Cruziana* and worm burrows frequently coincided, predominantly because there were so many burrows, and not because of a casual association between the two.

Temporal relationships

We found altogether 29 cases where *Cruziana* and worm burrows crossed each other in a way that potentially made it possible to decide which trace had deformed the other; five on the large slabs and another 24 on loose pieces laying on the lake shore at Trolmenshamn. The loose pieces were found next to where the larger slabs were originally collected. They were superficially identical to the larger slabs in texture and colour. We therefore assume that all specimens came from the same layer, and thus represent the same bedding plane. In 24 cases the worm burrow had cut through the *Cruziana* and deformed it, but we found no case where the *Cruziana* had deformed the worm burrow. In five cases we were unable to decide which trace had deformed which. The temporal relationship was significantly non-random (X^2=16.0, P<0.001). The trilobite typically dug first and the worm afterwards.
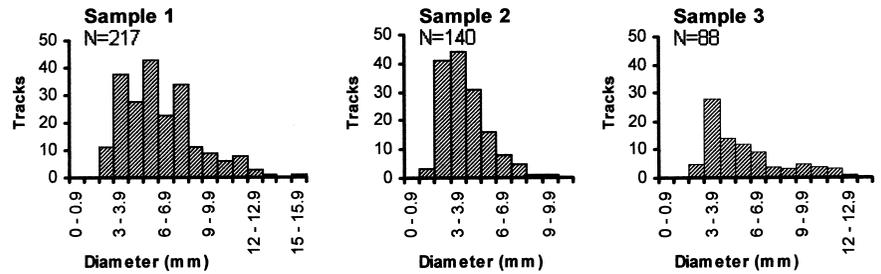

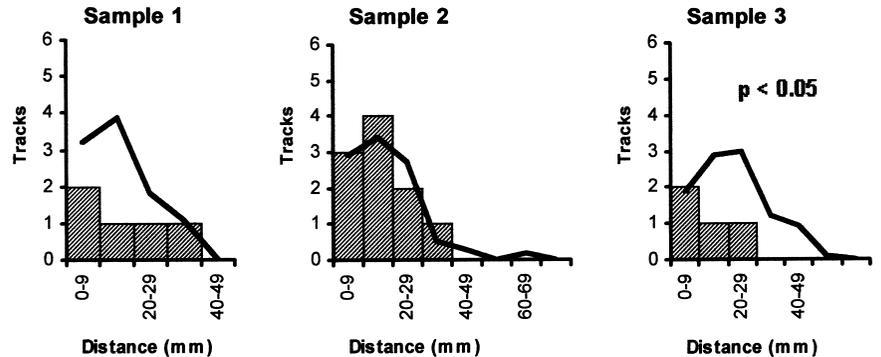Fig. 2. Distribution of widths (mm) of the worm burrows on the three slabs (samples 1, 2 and 3).

Fig. 3. Distribution of distances (mm) between the midpoint of each *Cruziana* and the midpoint of the nearest worm burrow (grey bars), and the distance between each random point (N=100 for each slab) and the midpoint of the nearest worm burrow (black line). The results are for the three slabs (samples 1–3) separately.
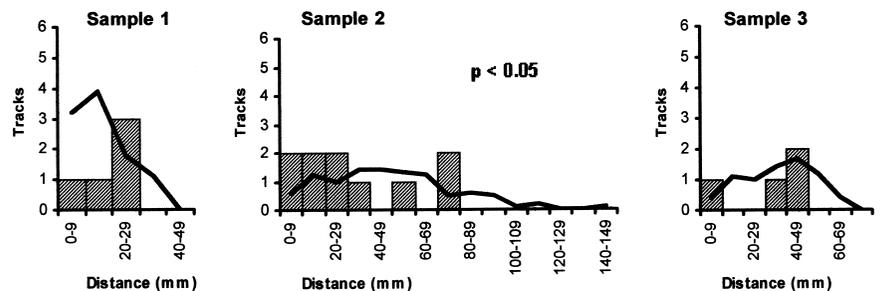

Fig. 4. Same as in Fig. 3, except that only worm burrows >6 mm wide were included.

Table 1. Basic data for the sandstone slabs (samples 1–3) used for the statistical analysis.

	Sample 1	Sample 2	Sample 3
Area (cm²)	1550	1600	1560
Number of *Cruziana*	5	10	4
Number of worm burrows	217	140	88
Number of worm burrows >6 mm diameter	97	15	29

Table 2. Distances, in mm; mean + S.D. and (N), between *Cruziana* and the nearest worm burrow on each of the three slabs (samples 1–3), compared with the distance from a random point to the nearest worm burrow. In the first test (above) all worm burrows were included, while in the second test (below) only those >6 mm in diameter were considered.

Distance measured	Sample 1	Sample 2	Sample 3
Cruziana - worm burrow	15±9 (5)	15±9 (10)	10±9 (4)
Random point - worm burrow	15±10 (100)	17±11 (100)	21±12 (100)
t-test	n.s.	n.s.	P<0.05
Cruziana - big worm burrow	19±8 (5)	33±23 (10)	32±17 (4)
Random point - big worm burrow	22±11 (100)	49±28 (100)	33±15 (100)
t-test	n.s.	P<0.05	n.s.

Discussion

Our results suggest that there was a spatial association between *Cruziana* traces and burrows made by infaunal worms. This association was weak and may not have been consistent across all the slabs. The association between the two trace fossils may perhaps have arisen because the worms preferentially dug in places that already had been bioturbated by foraging trilobites. A possible functional reason for this preference could be an accumulation of organic material in the trilobite burrows, perhaps including remains of faecal material left behind at the foraging site. Alternatively, the worms may not have had any specific preference for organic-rich places *per se*, but rather preferred to dig in the stirred up and therefore relatively soft sediment in places where the trilobite had been foraging. It also seems possible that both animals preferred to dig in places with relatively soft sediments; in this case the spatial association between the two traces may have been indirect.

Based on the morphology of the legs, it has been suggested that some larger Cambrian trilobites, such as *Olenoides serratus*, may have been predators (Fortey & Owens 1999). Likewise the frequent co-occurrence of *Cruziana* and large worm burrows on some surfaces of the Mickwitzia sandstone suggests a predator–prey relationship, in which arthropods were digging for large infaunal worms, which they subsequently killed (Bergström 1973; Jensen 1990). However, we found no evidence of predation on the surface that we studied. The *Cruziana* were c. 5 cm wide, indicating that they were made by relatively large trilobites, perhaps olenellids (Goldring 1995; Fortey & Seilacher 1997). Olenellid trilobites are known from contemporary deposits in Sweden (Ahlberg 1985; Ahlberg et al. 1986). The arthropods sometimes foraged on sediment at or near the surface and sometimes a few centimetres below.

We found no case where the worm burrow temporally preceded the *Cruziana*, only the opposite, and, therefore, we cannot say with confidence that the arthropod and the worms actually occurred in the same place at the same time. It remains possible that the worms entered the area only after it was deserted by the arthropod, and this in turn means that the arthropod may not actually have encountered worms while it was foraging. More likely, we deal with a superimposition of different tiers. Because markings made at the surface have a low fossilization potential, traces preserved on the lower surface of the sandstone were probably made after the underlying mud was covered by at least a veneer of sand. Unless the sand/mud interface became secondarily eroded, it may subsequently have become inscribed by burrowers of deeper tiers, as more sediment accumulated. Since trilobites could scratch the interface only below a thin cover of sand, it will generally be the burrows of the infaunal worms that are superimposed on the trilobite traces.

A similar situation is illustrated by an example from the Lower Silurian of Libya (Seilacher 2000), where worms belonging to a relatively deep tier (*Arthrophycus alleghaniensis*) preferred sites where trilobites had dug previously (*Cruziana acacensis*). Since, in this case, the worms also tended to follow the axes of the trilobite burrows, it was suggested that the worms were attracted by the depression in the interface, in which organic pore fluids or bacteria would have become concentrated. Further evidence that worms sometimes exploit trilobite traces while foraging was presented by Brandt et al. (1995).

It should be noted that our study was very limited in space and time and hence that the implications also are limited. We restricted our analysis to a single bedding plane and perhaps even to the traces left by a single trilobite individual. Accordingly, our conclusions only relate to this specific foraging situation and should not be used to argue about trilobite or arthropod behaviour in general. In particular, the bedding plane that we used for this study was not the same as the one that was investigated by Jensen (1990), and trilobite–worm relationships may of course vary from bedding plane to bedding plane. Nevertheless our results suggest that ecological relationships between arthropods and "worms" in the early Cambrian sea may have been complex and not restricted to the predator–prey relationship described by Bergström (1973) and Jensen (1990).

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