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Zoophycos: strip mine, refuse dump, cache or sewage farm?

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In recent papers, Kotake (1989, 1991) has demonstrated that the material that comprises the spreite lamina of *Zoophycos* derives from a higher level, presumably at or near the sea floor. And because this material was emplaced as pellets, assumed to be of faecal origin, the *Zoophycos* animal is considered to have fed on detritus at the sea floor and to have deposited its excreta deeply beneath it. Ekdale and Bromley (1983) had previously shown that in both *Zoophycos* and *Chondrites*, sediment is piped down from higher levels, but they did not reach the logical trophic conclusions that Kotake (1991) has done: that the *Zoophycos* animal is a detritus feeder.

As Kotake has pointed out, his new model opposes previous interpretations of *Zoophycos* activity, which are basically those of Seilacher (1967) and Simpson (1970). These authors envisaged the spreite as representing a deposit-feeding, strip-mining activity where sediment exploitation and waste disposal occurred almost simultaneously. This is a particularly low-cost exercise in which there is minimal transport of sediment. Indeed, on this basis, the *Zoophycos* animal has been interpreted as having both mouth and anus at the same end of the body, suggesting a sipunculan worm (Wetzel & Werner 1981). Donaldson and Simpson (1962) considered mounds, *Chomatichnus*, associated with *Zoophycos* to represent faecal accumulations on the sea floor, thereby implying upward conveyor activity.

But large-scale downward conveyance has now been demonstrated, and the elegant strip mine model no longer adequately accounts for the structure of *Zoophycos*. Yet many features of the spreite lamina nevertheless meet the strip mine paradigm; and why should excrement be deposited in such a costly manner? Is *Zoophycos* just a beautiful cesspit?

Strip mine model. Features that suggest foraging at depth are shared by other spreite structures such as *Rhizocorallium* (Fürsich 1974) and are similar to many complex trace fossils (e.g. graphoglyptids) that have been interpreted as deposit feeder structures (Seilacher 1977).

1. Although spiral in construction, the lamina of *Zoophycos* is basically horizontal. Thus, it follows the primary depositional pattern of organic detritus on the sea floor, or secondary patterns produced by shallower-tier reworking of that detritus.

2. Working of the sediment shows a high degree of rigor. Lamellae of the spreite are usually closely parallel and in contact; the passage of the animal never leaves any gaps of untouched sediment. Simpson (1970) proposed a precise, repetitive, axial probing by a worm along each successive lamella (thereby producing the next lamella). This model would allow the making of mistakes, leaving holes in the lamina. If, on the other hand, the worm sweeps sideways, broadside on, through the sediment, no holes could develop, and the broad contact with the sediment would be ideal for selective processing during deposit feeding. Waste material would be correspondingly redeposited along the opposite side of the worm (Seilacher 1967). This lateral movement would also account for irregularities in the spreite, where new lamellae locally cut across and obliterate older lamellae.

3. In many forms, the margin of the spreite is lobed. Individual lobes may show a 'seeking' development, running accurately within earlier burrow fills, particularly *Thalassinoides* (Ekdale & Bromley 1983; Bromley & Ekdale 1984). *Chondrites* is renowned for the same behaviour (Frey & Bromley 1985; Bromley & Ekdale 1987). This feature suggests selective deposit feeding rather than the dumping of waste.

Detritus feeding model. The downward conveyance of sediment led Kotake (1989) to assume that the *Zoophycos* animal feeds on detritus at the sea floor and deposits excreta as a spreite at depth beneath it. This begs the question as to why so much energy is used to deposit the faecal material. Many downward conveyors excrete pellets as apparently random clumps within the sediment (Wohlenberg 1939; Reineck 1963; Reise 1981), causing compaction of the surrounding sediment. Such distortion is not seen around *Zoophycos*. This model also leaves unexplained the features that suggest strip mining and exploration.

New models for Zoophycos. I offer three possibilities that account better for the features mentioned above. However, the morphology of *Zoophycos* varies considerably and the behaviour responsible for its construction no doubt was not uniform.

Refuse dump model. The overall morphology of the spreite indicates a foraging, seeking activity, yet the material of which it is composed is derived from a higher level. It was deposited in a preconstructed cavity, as is seen from the lack of compactional distortion around the spreite.

The simplest explanation of this is that deposit feeding creates the cavity and that sediment is conveyed to the surface through the animal's gut, to be voided on the sea floor. Meanwhile, in order to maintain the narrow form of the burrow, so necessary for efficient water circulation, a corresponding amount of sediment simultaneously is passed externally along the animal from the upper level and deposited as ballast at the site of feeding. In order to manipulate this ballast sediment, it is entrained in mucus and deposited as pellets.

Kotake (1991) could find no indication of sorting of the pellet sediment, which exactly resembled that found at the higher level. This would not be expected if the sediment had been manipulated for food.

Thus, this model requires that the animal is a deep-tier deposit feeder, that the structure is a mine, but that the pellets in it are not faecal pellets.

Cache model. Recent advances in our understanding of deep-sea benthic environments have shown that organic material may be periodically deposited there in quantity. This creates an incentive for animals to squirrel away nutritive material for use later when food is less available. In a review of this deep-sea scenario, Jumars *et al.* (1990) actually suggested in passing that *Zoophycos* might represent such a cache, and published a radiograph of a sipunculan worm associated with a possible modern *Zoophycos*.

The model states that the *Zoophycos* animal feeds at the surface on organic-rich detritus (Kotake's model). Possibly a funnel at the sea floor might be constructed to trap such material. Faecal pellets are deposited within a previously excavated cavity at depth. In times of need, the faecal material is revisited and reworked for food (autocoprophagy). But where was the animal's anus? Feeding at the surface but excreting at depth implies mouth and anus at opposite ends as in a polychaete; but Simpson's model would benefit from having both close together as in sipunculans.

Some *Zoophycos* are not visibly pelleted. Possibly such unpelleted laminae have been reworked. If food availability at the sea floor remains good, autocoprophagy will not be necessary and the original (pelleted) spreite will be preserved.

This model explains some anomalies of *Zoophycos*. A cache of organic-rich sediment would be buried to advantage well below the sea floor, out of reach of other bioturbating animals. This explains the deep-tier position of *Zoophycos*. Furthermore, the high content of labile organic matter of the spreite would contrast chemically with its surroundings, rendering the structure diagnetically dynamic and thus conspicuous in fossil material.

It also explains the apparent occurrence of large-scale 'deposit-feeder' structures in a deep tier, far below redox level, in a situation where deposit feeding would be unattractive. These features all fit *Chondrites* equally well, which may also be considered a 'cache' structure.

Gardening model. Certain *Zoophycos* have a more complex structure, suggesting a more complicated model.

The animal excavates a gallery at depth in the sediment and simultaneously fills it with faecal pellets derived from feeding on the organic-rich detritus at the sea floor (Kotake's model). The gallery and fill extend laterally and spirally as a thin lamina, having a large interface with the surrounding sediment and its pore waters. The animal then revisits the faecal material and re-exploits it for its now mature microbial content. However, the animal does not plough through the whole lamina once more. The bacteria are cultured within the long marginal tube that runs around the perimeter of the spreite and presumably circulates oxygenated water.

Some *Zoophycos* have extra tubular structures that connect with the marginal tube and accurately follow the spreite towards the central shaft. (These have been interpreted as 'short cuts' by the animal to the surface, produced when the spiral marginal tube has become too long for effective irrigation; Ekdale & Bromley in press.)

However, the extra tubes rigorously follow the spreite lamella instead of taking the shortest path; and they connect with the marginal tube not at interlobe re-entrants but instead run centrally along lobes to their farthest extent before connecting with the marginal tube. Thus, far from answering the short-cut paradigm, they seem instead to maximize their contact with the lamina.

These extra tubes are interpreted here as additional (or periodically alternate) canals for circulating water, within which the occupant can culture a microbial crop.

Some Tertiary *Zoophycos* are dominated by numerous, straight, radial tubes (Lewis 1970; Girotti 1970), but probably these have a different function.

This model explains several features that are inadequately treated by previous models. First, the elegant and regular, spreading form of the spreite bespeaks the intention of revisiting the material with minimum energy expenditure. Second, the central shaft of *Zoophycos* is commonly a complex structure, indicating long and frequent use (Kotake 1989; Ekdale & Bromley in press). Alternate activity at the sea floor and at depth would require frequent passage up and down the shaft.

The 'seeking' behaviour, e.g. along *Thalassinoides* fills, may represent preference for less compacted, more easily worked sediment, or more probably, selection of sites that are already rich in organics or microbes.

This model requires that the animal be considered alternately detritus feeder and gardener, perhaps also deposit feeder when a favourable sediment is encountered. The pellets are true faecal pellets. Such a scenario would mean that *Zoophycos*, normally classified as a fodinichnion, should instead by considered an agrichnion.

Conclusion. Many animals show such complicated life-styles as are envisaged here, combining several trophic persuits alternately (Bromley 1990). A great variety of structures from Ordovician to Recent have been included in ichnogenus *Zoophycos* and it is likely that they represent different trophic activities. Maybe different models outlined here will be found applicable to different *Zoophycos*. The 'extra tube' form of the Danish Cretaceous chalk is interpreted here according to the gardening model, while the *Chondrites* that accompany it probably are best explained as cache structures.

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