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NOTES AND CORRESPONDENCE

Ethology of the *Zoophycos*-Producer: Arguments against the Gardening Model from $\delta^{13}C_{org}$ Evidences of the Spreiten Material

Ludvig Löwemark[1,*], In-Tian Lin[1], Chung-Ho Wang[1], Chih-An Huh[1],
Kuo-Yen Wei[2] And Chih-Wei Chen[2]

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ABSTRACT

Recently proposed ethological explanations for the trace fossil *Zoophycos* include gardening of microorganisms. Because microorganisms are known to fractionate strongly against ^{13}C, especially under low oxic to anoxic conditions, it is argued that any gardening activity in the trace would result in a noticeable shift in $\delta^{13}C_{org}$ between spreiten and adjacent host sediment. In order to test this hypothesis, $\delta^{13}C_{org}$ of the Spreiten Material and directly adjacent host material was measured. Measured $\delta^{13}C_{org}$ in a glacial section of the core ranges from -22.6 to -22.9‰ for host sediment and between -22.8 and -23.2‰ for *Zoophycos* material. In an interglacial section the *Zoophycos* material measures -21.9‰, whereas the host material ranges from -21.2 to -21.4‰. The minimal difference between *Zoophycos* and host material suggests that gardening plays an insignificant role. The gardening hypothesis is therefore rejected in favor of a cache model, where food is squirreled away for poorer times.

(Key words: Chemosymbiosis, Isotope fractionation, Sulfur-oxidizing bacteria, Sulfate reducing bacteria, Methanogenesis)

1. INTRODUCTION

Zoophycos is a group of trace fossils that embraces a large variety of three-dimensional,

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[1] Institute of Earth Sciences, Academia Sinica, Taipei, Taiwan, ROC

[2] Department of Geosciences, National Taiwan University, Taiwan, ROC

[*] *Corresponding author address:* Dr. Ludvig Löwemark, Institute of Earth Sciences, Academia Sinica, Taipei, Taiwan, ROC; E-mail: ludvig@earth.sinica.edu.tw

often helically coiled spreiten structures (Fig. 1a). The spreiten are usually more or less horizontal and their outline may vary from semi-circular to highly lobate. Most varieties include a central shaft connecting the burrow with the sediment surface and a marginal tube that constitutes the outer border of the spreite (Häntzschel 1975). The construction of the spreiten follows through the successive lateral displacement of the marginal tube resulting in numerous lamellae representing previous positions of this tube (Figs. 1b and c) (Wetzel and Werner 1981). Trace fossil *Zoophycos* has long been considered an archetypical trace for deposit-feeding behavior (Fig. 2a) (Seilacher 1967; Wetzel and Werner 1981; Ekdale and Lewis 1991; Gaillard and Olivero 1993). The important discovery that at least some types of *Zoophycos* actively introduce surface material into a burrow (Kotake 1989; Kotake 1991; Kotake 1992) sparked new interest in alternative ethological explanations. Kotake (1989) interpreted the introduced surface material to be the result of surface detritus feeding behavior where the feces are excreted as spreiten deep in the sediment (Fig. 2b). In addition to this model, Bromley (1991) introduced three new models to explain the downward transport of surface material: the refuse dump model, the cache model, and the gardening model. The detritus-feeding model (Kotake 1989) seems unlikely mainly on the grounds of that too much energy is consumed to dispose of the fecal material (Bromley 1991; Löwemark and Schäfer 2003). According to the refuse dump model (Fig. 2c), the producer is a deposit feeder that excretes its feces on the sediment surface, and the surface material is introduced into the burrow to buttress the cavity that is created during the feeding process (Bromley 1991). This model was refuted for modern deep-sea *Zoophycos*, as the introduced surface material was shown to be more nutritious than the alleged food source-the surrounding host sediment (Löwemark and Schäfer 2003).

The cache model (Fig. 2d), where food is squirreled away for poorer times, and the gardening model (Fig. 2e), where organic rich material is introduced into the burrow as substrate for the cultivation of microorganisms, have been considered as possible explanations for the *Zoophycos* trace in several recent studies (Fu and Werner 1995; Bromley et al. 1999; Miller and D'Alberto 2001; Bromley and Hanken 2003). The introduction of organic-rich surface material in the late Quaternary deep-sea *Zoophycos* (Löwemark and Schäfer 2003) agrees well with both the cache and the gardening models.

One practical way to test whether gardening takes place in the *Zoophycos* trace would be to look for evidence of microbial activity. Bacteria are known to fractionate strongly between ^{12}C and ^{13}C, especially under dysoxic to anoxic conditions (Whiticar et al. 1986). Therefore, gardening of bacteria in the *Zoophycos* trace would be expected to result in a significant increase in $\delta^{13}C$ values of the organic material remaining in the burrow.

In this study, the $\delta^{13}C$ values of organic material from within the trace are compared with directly surrounding host sediment.

2. METHODS AND MATERIAL

For this study, *Zoophycos*-bearing sediment from IMAGES core MD012388 (6°43,52’N, 122°55,91’E, 3340 m) from the Celebes Sea was examined. The 3402-cm-long core consists of olive green to gray nanno fossil oozes and numerous ash layers. Stable oxygen isotopes of

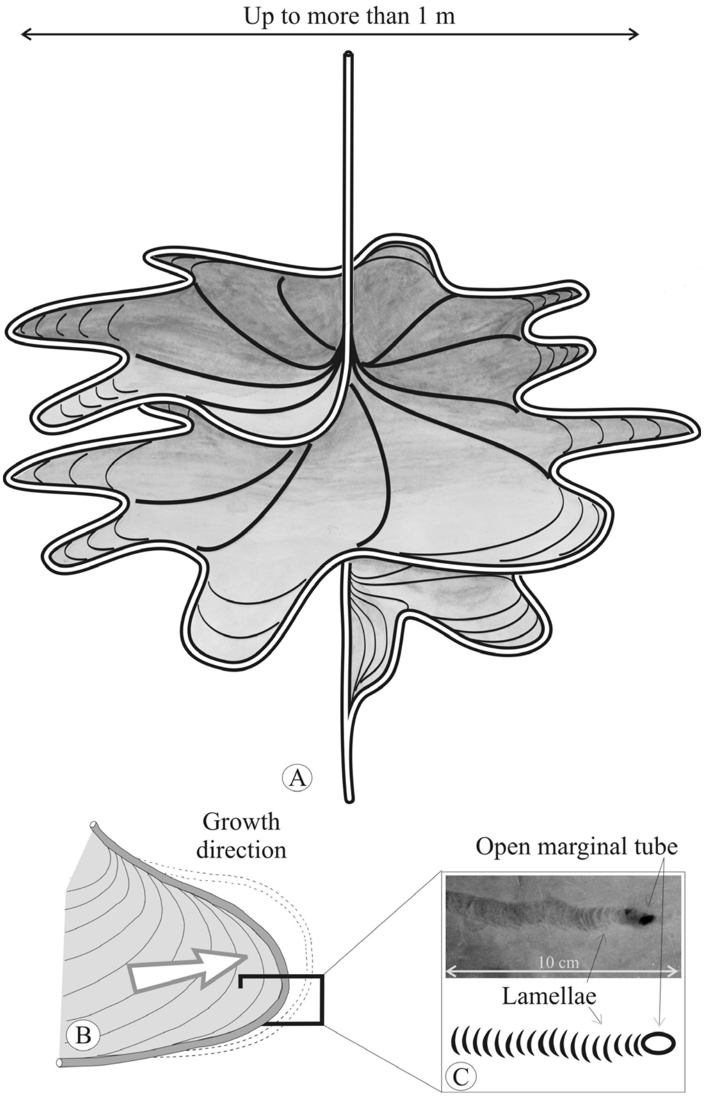
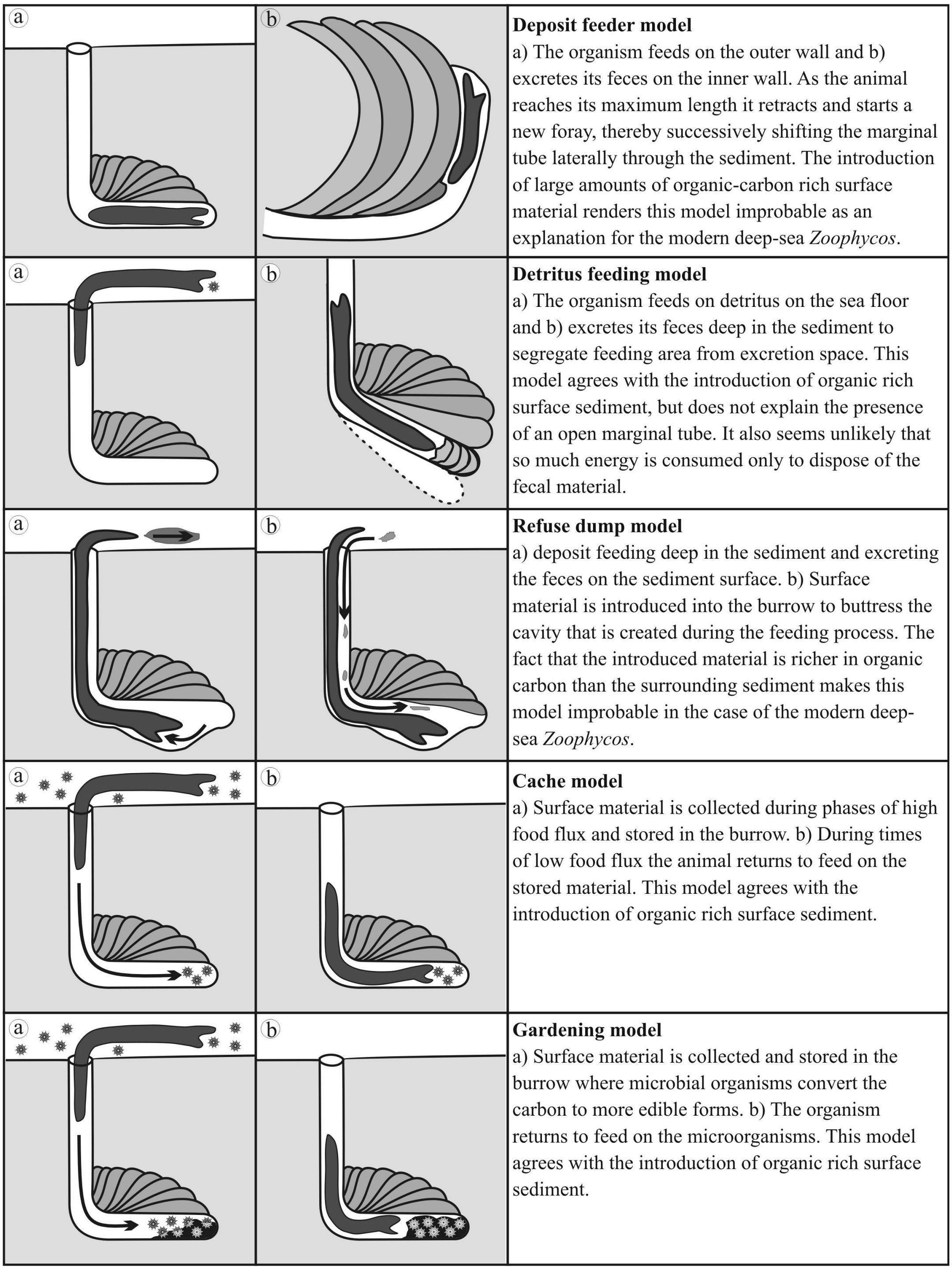


Fig. 1. Conceptual model of the late Quaternary deep-sea *Zoophycos* based on extensive studies of X-ray radiographs from the Kiel Archives (Löwemark and Schäfer 2003). (A) The trace consists of one continuous, upwards constructed, helically coiled spreite starting from a vertical tube. A marginal tube surrounds the trace and an open vertical shaft connects it with the sediment surface. (B) Spreiten are sheet-like structures between the limbs of a U-tube that form through the successive lateral displacement of the tube. The spreiten are more or less horizontal and their outline may vary from semi-circular to highly lobate. (C) The lamellae observed in the spreiten represent previous positions of the marginal tube's inner wall.



Deposit feeder model
a) The organism feeds on the outer wall and b) excretes its feces on the inner wall. As the animal reaches its maximum length it retracts and starts a new foray, thereby successively shifting the marginal tube laterally through the sediment. The introduction of large amounts of organic-carbon rich surface material renders this model improbable as an explanation for the modern deep-sea *Zoophycos*.

Detritus feeding model
a) The organism feeds on detritus on the sea floor and b) excretes its feces deep in the sediment to segregate feeding area from excretion space. This model agrees with the introduction of organic rich surface sediment, but does not explain the presence of an open marginal tube. It also seems unlikely that so much energy is consumed only to dispose of the fecal material.

Refuse dump model
a) deposit feeding deep in the sediment and excreting the feces on the sediment surface. b) Surface material is introduced into the burrow to buttress the cavity that is created during the feeding process. The fact that the introduced material is richer in organic carbon than the surrounding sediment makes this model improbable in the case of the modern deep-sea *Zoophycos*.

Cache model
a) Surface material is collected during phases of high food flux and stored in the burrow. b) During times of low food flux the animal returns to feed on the stored material. This model agrees with the introduction of organic rich surface sediment.

Gardening model
a) Surface material is collected and stored in the burrow where microbial organisms convert the carbon to more edible forms. b) The organism returns to feed on the microorganisms. This model agrees with the introduction of organic rich surface sediment.

Fig. 2. Proposed behavioral models for the *Zoophycos* producing animal.

the planktic foraminifera *Globigerinoides sacculifer* used for the stratigraphy of this core were measured on a Finnigan MAT DELTA mass spectrometer at the Department of Geosciences, NTU, Taiwan. Pairs of *Zoophycos* spreiten and surrounding host sediment were sampled from two intervals in the core. Spreite-host pairs A and B were taken from section 13-1 (1830 - 1845 cm, Fig. 3), corresponding to an age of 128 ka based on $\delta^{18}O$ stratigraphy (Fig. 2). Pair C was taken from section 22-2 (3166 - 3180.5 cm, Fig. 2), approximately corresponding to an age of 210 ka based on an average sedimentation rate of 15 cm ka^{-1}, as derived from the uppermost 20 m, where a $\delta^{18}O$ stratigraphy exists. The pair consists of one *Zoophycos* spreite and two host sediment samples directly above and below the spreite, in addition a third host sample was taken ca. 6 cm above the spreite to allow an assessment of the small scale spatial variation of the host sediment.

The X-ray radiographs for this study were produced using the method described by Bouma (1964) and Werner (1967). Plastic boxes $15 \times 8 \times 1$ cm were pushed into the sediment, cut out with a nylon string and placed in vacuum-sealed plastic pouches. The sediment slabs were placed directly on the X-ray film bags for exposure at the Department of Oceanography, NTU, Taiwan. The machine used was an ANDREX BW434 with 40 kV, 9.5 mA and exposure time 4 minutes and 30 seconds. The spreiten and the surrounding host sediments were identified in radiographs, and their outlines were transferred to transparent film templates. The outlines were cut out, and then the templates were placed on the original sediment slabs. This allowed a precise sampling of the sediment using a small spatula.

Samples were decarbonated with 2N HCl for 1 hour, centrifuged at 4500 rpm for 4 min., washed with distilled water three times and then freeze dried. About 0.250 g of the decarbonated samples were placed together with 1 g CuO and 1 g Cu in quartz combustion tubes. The tubes were evacuated (0.01 Torr), sealed, and combusted at 900°C for 3 hrs. to oxidize all carbon to CO_2 and then at 600°C for 3 hrs. to reduce NO_x to N_2 according to standard procedures described in Coleman and Fry (1991). During decarbonation and combustion carbonate and total organic carbon content were determined through weight loss and CO_2-gas volume, respectively. The CO_2 gas was separated cryogenically on a vacuum line and stable isotope ratios were measured on a VG SIRA 10 mass spectrometer at Academia Sinica, Taiwan. The precision of the mass spectrometer measurement is ± 0.04 ‰. In the measurements performed, sample preparation and mass spectrometer errors resulted in a mean error of ± 0.10 ‰, which is calculated as the root-mean-square (RMS) of the differences between duplicate measurements. The relatively small mean error indicates a high level of homogeneity in the samples and consistency during sample preparation.

3. RESULTS

Organic carbon content in the *Zoophycos* spreiten is notably higher than surrounding host sediment in pairs A and B but about the same as host material in pair C (Table 1). Carbonate content differs markedly between *Zoophycos* spreiten and host sediment. In section 13-1, the $CaCO_3$ content is about 50% higher in the *Zoophycos* spreiten, whereas the *Zoophycos* in section 22-2 is depleted by about 15% relative to host material (Table 1). The differences in

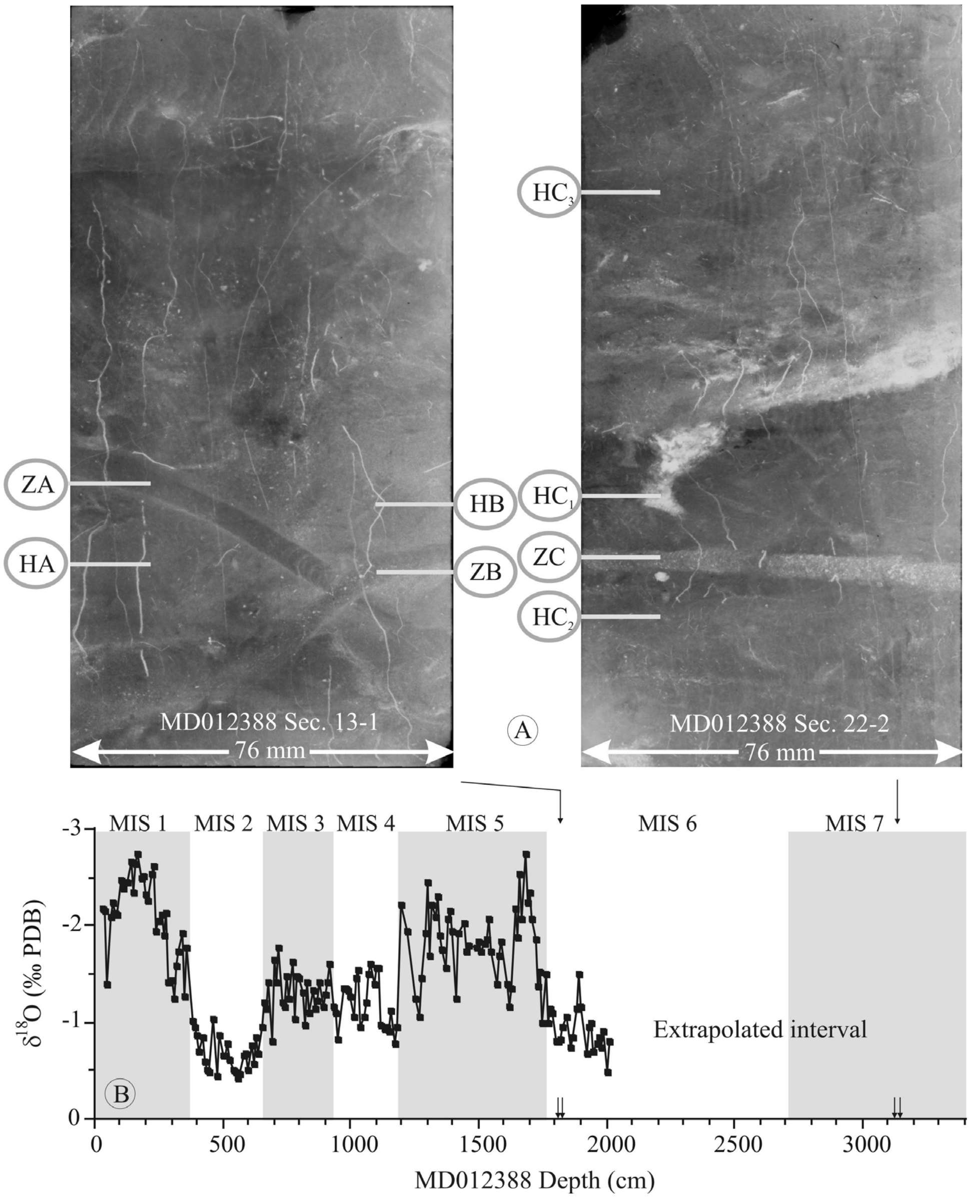


Fig. 3. Sampled X-ray radiographs and stable oxygen isotope stratigraphy. (A) X-ray radiographs from core MD012388 (6°43,52'N, 122°55,91'E, 3340 m) from the Celebes Sea showing the sampled *Zoophycos* spreiten and adjacent host sediment. Z = *Zoophycos* spreiten, H = host sediment. (B) Oxygen isotope stratigraphy based upon analysis of *Globigerinoides sacculifer*, plotted against depth of core MD012388. Gray intervals correspond to interglacials and white to glacials. MIS = Marine Isotope Stage.

carbonate content between *Zoophycos* spreiten and adjacent material point to a source outside the host sediment, presumably surface material. The enrichment in organic carbon content in the spreiten suggests a selective collection of nutritious material.

The $\delta^{13}C$ values vary between -22.6 and -23.2‰ and between -21.2 and -21.9‰ in section 13-1 and section 22-2, respectively (Table 1). *Zoophycos* spreiten values are generally on the lighter side of the spectrum. The relatively large difference between section 13-1 and 22-2 can be attributed to the fact that the sediments in section 13-1 were deposited during glacial conditions (MIS 6), while the sediments in section 22-2 originated under interglacial conditions (MIS 7). Similar differences of more than 2‰ have been observed between glacial and interglacial sediments in the nearby South China Sea (Thunell et al. 1992; Kienast et al. 2001).

Although the number of studied samples is quite small, the minor differences between adjacent host sediment measurements (0.05 to 0.24‰) indicate that the data is representative of the bulk organic carbon $\delta^{13}C$ values. For comparison, $\delta^{13}C_{org}$ measurements in the nearby South China Sea often show fluctuations of up to 0.5‰ between adjacent data points (Kienast et al. 2001).

Table 1. Carbonate content ($CaCO_3$), and duplicate measurements of total organic carbon content (C_{org}), and organic carbon isotope values ($\delta^{13}C_{org}$ ‰ PDB) of *Zoophycos* spreiten material and directly surrounding host sediments.

Spreite-host pair	Sample material	Core section	Core depth cm	$CaCO_3$ %	C_{org} %		$\delta^{13}C_{org}$ ‰ PDB			
					1st	2nd	1st	2nd	Difference	Square difference
A	Host (HA)	Sec 13-1	1841	14.48	0.59	0.53	-22.64	-22.53	-0.11	0.0121
	Zoophycos ZA)	Sec 13-1	1840	21.38	0.74	0.76	-22.79	-22.74	-0.05	0.0025
B	Host (HB)	Sec 13-1	1839	13.43	0.51	0.56	-22.88	-22.65	-0.23	0.0529
	Zoophycos (ZB)	Sec 13-1	1841	19.79	0.82	0.81	-23.21	-23.12	-0.09	0.0081
C	Host (HC_1)	Sec 22-2	3176	24.41	0.69	0.71	-21.43	-21.45	0.02	0.0004
	Zoophycos (ZC)	Sec 22-2	3177	21.90	0.66	0.66	-21.86	-21.95	0.09	0.0081
	Host (HC_2)	Sec 22-2	3178	25.30	0.70	0.68	-21.20	-21.24	0.04	0.0016
	Host (HC_3)	Sec 22-2	3170	25.28	0.64	0.63	-21.25	-21.21	-0.04	0.0016
									RMS =	0.10

4. DISCUSSIONS

The gardening model postulates that the animal collects refractory organic material on the seafloor and deposits it deep in the sediment as a substrate for microorganisms to grow on. When the microbes are ripe the animal returns to feed on the now labile carbon source that the microbes represent. Therefore, if gardening of microorganisms is a major motive for the construction of the helically spiraled type of *Zoophycos* observed in late Quaternary deep-sea sediments, the producer would be expected to create optimal conditions for bacterial growth and the bacterial biomass would be high. Under favorable conditions, as much as 50% of TOC in marine sediments have been observed to consist of bacteria (Alongi 1988). However, in anoxic and oxic incubation experiments only 5 - 25% of the bacterially degraded carbon was converted to bacterial carbon (Harvey et al. 1995). Therefore, as a large portion of the carbon is lost at each trophic level through respiration during the metabolism simply to keep the organism alive, doubts have been raised as to whether microorganisms thriving on organic matter in marine sediments can provide enough food to motivate gardening behavior (Cammen 1989). Moreover, the energy yield from the metabolism of carbon decreases with increasing reducing conditions (Aller 1982), making gardening even more costly. Nevertheless, if gardening takes place in the deep-sea settings of the modern *Zoophycos*, with a massive conversion of refractory carbon into labile bacterial carbon as its purpose, we argue that a strong fractionation signal should be present in the spreiten material.

Two possible scenarios can be envisaged. Either the animal pumps oxygenated water into the burrow creating favorable conditions for sulfur-oxidizing bacteria, which are known to fractionate against ^{13}C (Ruby et al. 1987), or, more probable, anoxic conditions prevail in the burrow and anaerobic bacteria feed on the introduced carbon. As free oxygen and nitrate are quickly depleted as terminal electron acceptors in marine sediments (Tyson 1995), iron-reduction, sulfate-reduction and methanogenesis remain potential ways to metabolize the introduced carbon under anoxic conditions. Iron-reduction (Zhang et al. 2003), sulfate-reduction (Morasch et al. 2001; Zhang 2002) and methanogenesis (Whiticar et al. 1986; Blair 1998) have all been shown to fractionate against ^{13}C and bacterially produced methane from marine sediments may have $\delta^{13}C$ values as light as -110‰ PDB (Whiticar et al. 1986).

In both scenarios the bacteria feeding on the introduced carbon strongly fractionate against ^{13}C, thus effectively removing ^{12}C from the system through their respiration products. When the animal then returns to feed, it ingests the microbes together with some of the residual refractory carbon. Bacterial hydrocarbons have been observed to have $\delta^{13}C$ values 5 - 60‰ lighter than source material (Woltemate et al. 1984; Gong and Hollander 1997; Hollander and Smith 2001). Whereas the ^{12}C-rich carbon from the microbes is preferentially used in the animal's metabolism and respired as CO_2 into the water column, the refractory ^{13}C-rich carbon to a large extent passes through the guts and is excreted as fecal pellets. The overall result of these two processes should be a removal of ^{12}C from the system resulting in heavier $\delta^{13}C$-values of the remaining the spreiten material (Fig. 4).

One potential problem with this approach is diagenetic overprint of the $\delta^{13}C_{org}$ signals. Two counteracting processes mainly control early diagenetic isotopic changes in marine sediment. The preferential degradation of organic compounds enriched in ^{13}C, such as hydrocarbons and proteins,

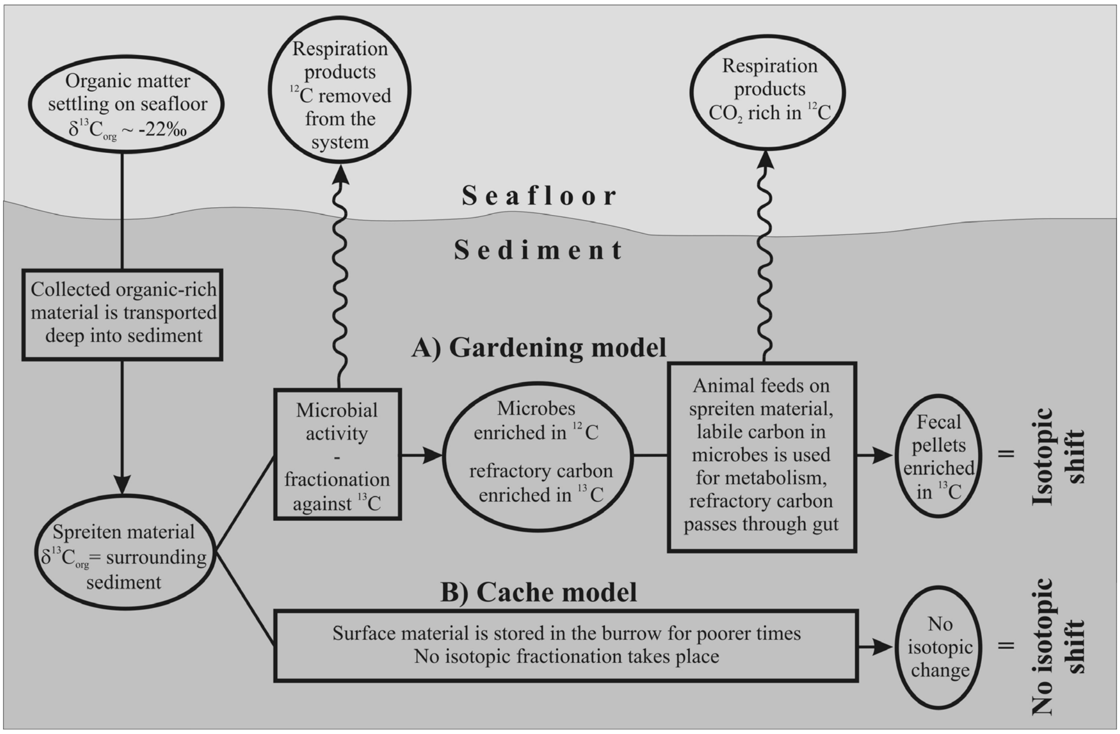


Fig. 4. Flow chart describing the fate of ^{12}C and ^{13}C in the gardening and cache models. (A) Gardening model: The organism collects organic rich particles on the surface. The labile fraction is digested and the refractory carbon is introduced deep into the sediment for cultivation of microorganisms. Bacteria growing on the introduced carbon strongly fractionate against ^{13}C, thus effectively removing ^{12}C from the system through their respiration products. The animal then ingests the microbes together with refractory carbon. Whereas the ^{12}C-rich carbon is used in the animal's metabolism and respired as CO_2 into the water column, the refractory ^{13}C-rich carbon passes through the guts and is excreted as fecal pellets, remaining in the spreite. The overall result of these two processes should be a removal of ^{12}C from the system resulting in heavier $\delta^{13}C$-values of the spreiten material. (B) Cache model: The organism collects organic rich particles on the surface. The collected material is stored in the burrow for poorer times. No isotopic fractionation takes place. Therefore there should be a minimal difference between spreiten and host material.

compared to the slower degradation of more resistant compounds depleted in ^{13}C, such as lipids and lignin, lead to a negative shift of the bulk $\delta^{13}C$. This is partly offset or exceeded by the positive shift caused by isotope fractionation in the metabolism of the organisms responsible for the degradation of the organic matter. The two processes generally result in a shift of less than 1 ‰ (Freudenthal et al. 2001). Incubation experiments under oxic as well as anoxic conditions have shown that most of the isotopic shift occurs within the first months of burial (Lehmann et al. 2002). The lack of any isotopic trend in down-core records from the nearby South China Sea (Thunell et al. 1992; Kienast et al. 2001), and the fact that a glacial-interglacial variability of about 2 ‰ is still visible, suggests a minimal influence of early diagenesis on the isotopic values observed. The difference of about 1.5 ‰ between glacial and interglacial stages in the studied core suggests a similarly small impact of diagenesis in the Celebes Sea.

Because of the lack of any substantial differences in $\delta^{13}C$ between *Zoophycos* spreiten and host sediment in the sampled material we conclude that no significant amount of gardening has taken place in the trace. Microbial activity most likely does occur to some extent in the introduced organic material but it is not the reason for the construction of this elaborate trace fossil. The fact that the difference between spreiten and host material is slightly larger (0.15 to 0.66 ‰) than the difference between adjacent data points from the host material (0.05 - 0.24‰) can be attributed to the introduction of surface material into the spreiten. Several recent studies show that the material in the spreiten partly consists of material introduced from higher levels (e.g., Leuschner et al. 2002; Löwemark and Schäfer 2003), slight differences of less than 1‰ in the $\delta^{13}C_{org}$ are therefore not surprising.

If gardening can be excluded and the introduction of organic rich surface material falsifies the deposit-feeder and refuse dump models, then only the detritus feeding model and the cache model remain plausible ethological explanations consistent with the observations of TOC, carbonate and ^{14}C-ages (Löwemark and Schäfer 2003). However, the detritus-feeding model does not explain the necessity of a helically coiled spreite or the presence of an open marginal tube, nor does it explain why the trace makers shows a preference for calm settings at water depths exceeding 1000 m (Löwemark and Schäfer 2003). In calm deep settings where food supply comes in pulses with long interceptions, a cache behavior is necessary for survival. Therefore we conclude that modern deep sea *Zoophycos* most likely is the result of cache behavior as suggested by earlier studies (Jumars et al. 1990; Bromley 1991; Miller and D'Alberto 2001; Löwemark and Schäfer 2003).

5. CONCLUSION

Because marine microbes are known to strongly fractionate against the heavier ^{13}C isotope under dysoxic to anoxic conditions, a shift in $\delta^{13}C_{org}$ of the spreite material relative to surrounding material should be present if gardening of microorganisms takes place in the *Zoophycos* trace. The strong similarity between $\delta^{13}C$ values of *Zoophycos* spreite material and the surrounding host sediment indicate that little or no isotopic fractionation takes place within the trace, and consequently that the amount of microbial activity in the spreite material is negligible. The gardening model is therefore refuted as an ethological explanation for the *Zoophycos* trace in favor of a cache model, where food collected at the surface is squirreled away for poorer times.

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