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# Significance of the trace fossil *Zoophycos* in Pliocene deposits, Antarctic continental margin (ANDRILL 1B drill core)

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## Abstract

*Zoophycos* is a complex three dimensional trace fossil that is abundant in deep ocean sediments worldwide, but has not been described previously from Cenozoic continental margin deposits of Antarctica. In the ANDRILL 1B core drilled through the north-west McMurdo ice shelf, *Zoophycos* occurs in a 17m thick unit of interglacial sediments bounded above and below by glacial surfaces of erosion. This unit was deposited during the transition from the relatively warm Early Pliocene characterized by productive open waters to the cooler Late Pliocene with fluctuating subpolar ice sheets. Globally, Late Cenozoic *Zoophycos* are most abundant at great depths (>1000 m), and where sedimentation rates and TOC levels are low; the *Zoophycos* producer, probably a worm-like animal, was (is) a slow colonizer. Application of these preferences to the ANDRILL 1B core indicates that the *Zoophycos*-bearing unit was deposited episodically, with sufficient time between events to allow for the slow processes of colonization and construction. The foray of *Zoophycos* producer into the relatively shallow ANDRILL 1B depths (200–1000 m) during the Pliocene documents “emergence” of benthic animals, supporting suggestions that the unique modern Antarctic and Southern Ocean faunas result from both “emergence” and “submergence” during the Cenozoic.

**Key words:** biogenic structures, continental shelf, McMurdo Sound, modern fauna

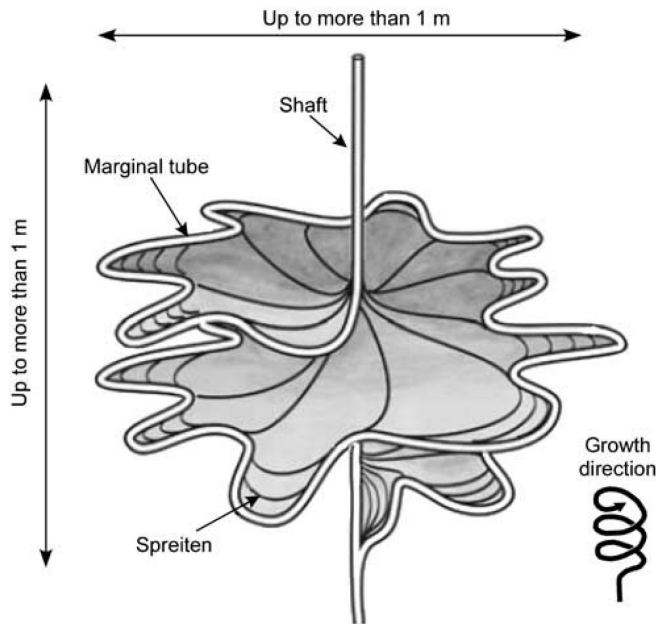
## Introduction

*Zoophycos* is a broad type of 3-dimensional structure constructed by marine infaunal animals. Palaeontologists and geologists have noted and described the structure in rocks for over 250 years (e.g. Ha'nitzschel 1975) and it is now known from deposits ranging in age from Cambrian to Holocene (Alpert 1977, Ekdale & Berger 1978). The basic form is a spreite (also termed “spreiten” or “lamina”) wound around a central axis (Fig. 1). However, the morphology of the trace fossil varies widely (e.g. Wetzel & Werner 1981, Miller 1991, Lo'wemark & Scha'fer 2003, Bromley & Hanken 2003), as does its size, with both maximum diameter and maximum depth ranging from a few cm to . 1 m; some include small forms in a separate ichnogenus, *Spirophyton* (Simpson 1970; but see Ekdale 1977). This variation and complexity has resulted in diverse reconstructions of *Zoophycos* producing behaviour(s) (Kotake 1989, 1992, Bromley 1991, Miller & D'Alberto 2001, Lo'wemark & Scha'fer 2003, Olivero & Gaillard 2007) and identification of multiple potential producers including “worms” (Seilacher 1967), echiurans (Kotake 1992), and sipunculids (Ekdale 1977, Olivero & Gaillard 2007). Given the

range in morphology and age, it is likely that over time *Zoophycos* has been constructed by different animals with a range of behaviours that are sufficiently similar to result in the broad *Zoophycos* type of structure.

Palaeozoic *Zoophycos* occurs in marine margin, shallow water, and deep water deposits (Chamberlain 1971, Osgood & Szmuc 1972, Miller 1991). Mesozoic *Zoophycos* are reported from both shelf and deeper facies (e.g. Locklair & Savrda 1998, Olivero 2003); Tertiary and younger *Zoophycos* occur predominately in deeper water deposits (e.g. Blom 1984, Manley & Lewis 1998, Bromley & Hanken 2003, Pervesler & Uchman 2004).

*Zoophycos* is widespread and regionally abundant in Late Cenozoic bathyal and abyssal sediments of the world's oceans (Ekdale 1977, Lo'wemark & Scha'fer 2003), and occurs in bathyal and abyssal sediments of the Southern Ocean (e.g. Pudsey *et al.* 1988). In spite of the fact that the continental shelves of Antarctica are isostatically depressed (500–1000 m) and probably have been since development of large ice sheets in the mid-Cenozoic (Siegert *et al.* 2008), *Zoophycos* has not been described from Antarctic shelf deposits; the single brief listing of *Zoophycos* does not illustrate or document occurrence of characteristic features of the trace fossil

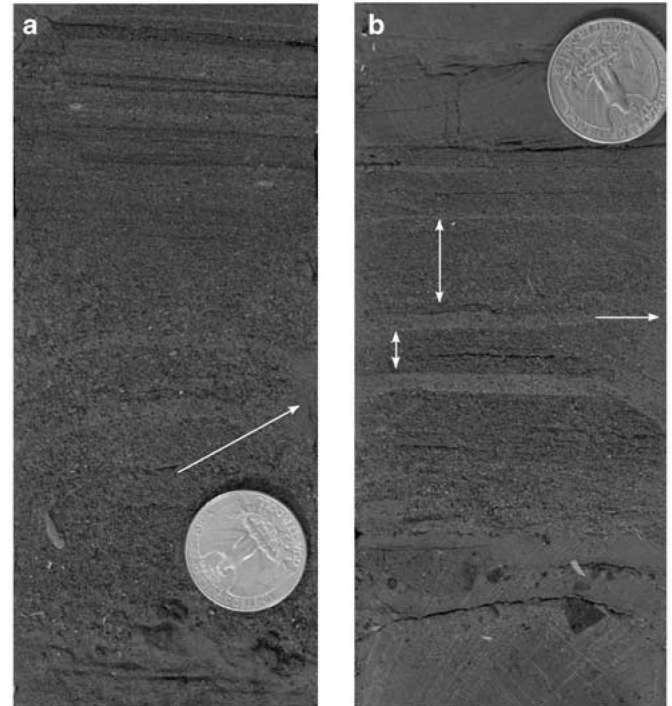


**Figure 1.** Major features of the trace fossil *Zoophycos* from Löwemark *et al.* (2006). The dark lines within the spreiten are the lamellae; alternative terms for spreiten are “spreite” and “lamina”.

(Fielding *et al.* 2000).

In this paper we describe *Zoophycos* from Pliocene deposits in the ANDRILL 1B core drilled under the Ross Ice Shelf at a water depth of 917m in summer 2006–07 (Falconer *et al.* 2007). The *Zoophycos* occurs at 352–354m below sea floor (mbsf) in a unit of interglacial marine sediments that is bounded above (346.94 mbsf) and below (364.18 mbsf) by glacial surfaces of erosion (Krissek *et al.* 2007). This interval was deposited during a major climatic transition from open water conditions in the Early Pliocene when sea surface temperatures were higher than today to cooler conditions that supported a fluctuating subpolar ice sheet during the Late Pliocene (Naish *et al.* 2007). Estimates of water depth range from 200 to 1000 m. The environmental conditions of the *Zoophycos*-bearing unit can be interpreted at a higher resolution than would otherwise be possible by comparison with well-known *Zoophycos*-bearing sequences worldwide.

This occurrence of *Zoophycos* also has implications for the origin of the unique Antarctic benthic marine fauna. Whether the fauna developed from deep water species that migrated into shallower water (“emergence”) or by expansion into deeper water of shallow water forms that survived glacial advances in protected shallow-water havens (“submergence”) has been debated, and it is likely that multiple processes have been involved (e.g. Brandt *et al.* 2007). Paucity of a Cenozoic rock record on the continent, as well as of body fossils of macro-benthic animals in cores of Cenozoic sediments around Antarctica hampers reconstructing the biogeographic history. In the absence of shelled fossils, this *Zoophycos*



**Figure 2.** *Zoophycos* in ANDRILL 1B. **a.** Spreite extending outward from portion of axial structure; arrow point to axial structure. No lamellae are visible within the spreite. Top is 352.57 mbsf. **b.** Several spreite (vertical arrows) extending outward from axial structure at right (horizontal arrow). Note diffuse boundary of axial structure. Granules at base are volcanic rock fragments. Base of coin is at 353.29 mbsf.

suggests that organisms moved from the deep sea to the Antarctic continental shelf during the extended warm period during the Early Pliocene.

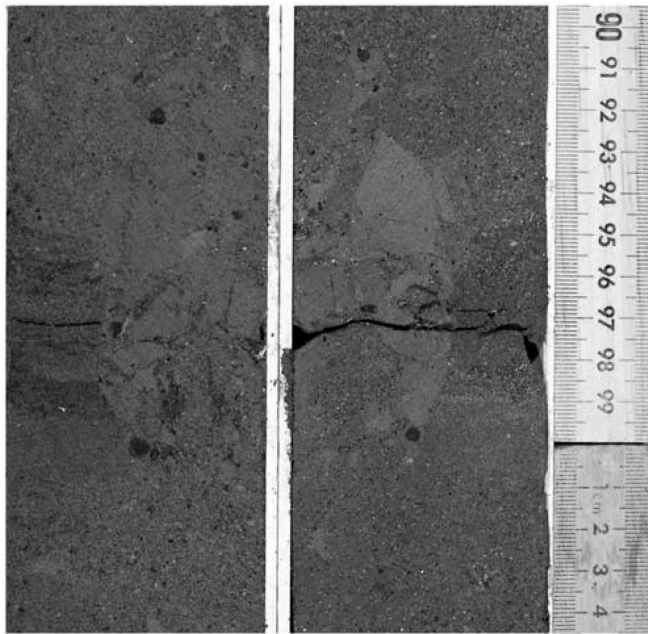
### **Zoophycos in ANDRILL 1B: morphology and depositional setting**

#### **Morphology**

Components comprising the trace fossil *Zoophycos* include a spreite or lamina coiled around a central axis, which commonly is an axial structure, lamellae within the lamina, and an open marginal tube (Fig. 1). Within this basic structure there is wide variation, and many specimens lack one or more of these components (e.g. Ekdale 1992, Löwemark & Schäfer 2003, Olivero & Gailard 2007).

In the ANDRILL 1B core, *Zoophycos* is represented by eleven cross-sections of spreite. Four of these radiate off a portion of an axial structure intersected by the core at 352.62–352.64 mbsf, and two extend from a section of axial structure at 353.30–353.36 mbsf (Fig. 2). Others are isolated or in groups of two. The spreite are horizontal, gently inclined, or slightly convex. Most of the spreite are 2 to 4mm thick. None have well defined lamellae. The spreite are composed of sediment that is lighter colored than the matrix; where connected to an axial





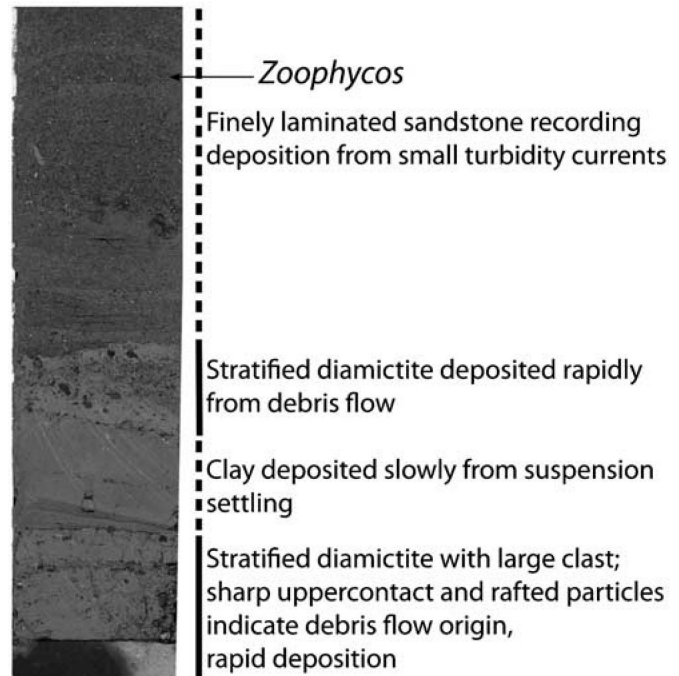
**Figure 3.** Disturbed zone that may be upper part of axial structure (Fig. 1). The images are the two halves of the core from 351.89 to 352.01 mbsf; the working half is on the right, the archival half is on the left. This is 0.5m above the highest spreiten and axial structure; although its relation to the axial structure(s) in the core is not known, its location is consistent with where an upper portion of an axial structure should occur (Löwemark & Schäfer 2003).

structure they are composed of the same material as the axial structure. In one case the spreite includes granules of volcanic rock that are similar to those occurring a few millimeters below, implying that the animal transported material upward. This has been reported elsewhere (Wetzel & Werner 1981) although downward transport of surface material reported more commonly (Kotake 1989, Miller & D'Alberto 2001). The axial structures are oriented obliquely and have diffuse boundaries. They are composed of the same sediment as the spreite to which they are connected. The axial structures are a minimum of 0.5mm in diameter (Fig. 2).

About 0.7m above the uppermost spreite (351.93 mbsf) a cone-shaped structure 1.5 cm in diameter cuts through layers of sandstone (Fig. 3). It has diffuse boundaries and is filled with fine-grained sediment. Although not physically connected to the spreite and axial structure that occur below, this may be a section through the upper part of an axial structure as described by Löwemark & Schäfer (2003). If so, and if the spreite and axial structure that occur lower are all part of the same structure, the producing animal at times lived at least 1.45m beneath the sediment-water interface.

#### Depositional setting

ANDRILL 1B recovered 1285m of core from beneath the north-west corner of the Ross Ice Shelf. The uppermost



**Figure 4.** Large variation in rates of deposition within a 24 cm thick interval (352.83–352.59 mbsf) within the *Zoophycos* bearing unit. Arrow points to *Zoophycos* in Fig. 2a. Dashed line denotes sediments deposited slowly; solid line indicates those that were deposited rapidly.

600m of core records the Pliocene to Pleistocene history of a marine-based ice shelf that waxed and waned seemingly in response to orbital cycles (Naish *et al.* 2007). In the Early Pliocene when sea surface temperatures were 58 higher (Whitehead & Bohaty 2003), the ice retreated from the Ross embayment onto land in West Antarctica and diatomite accumulated under open water conditions at the ANDRILL 1B site (Naish *et al.* 2007). The warm period ended at 3.3 Ma as temperatures dropped and the ice sheet advanced. The time interval between 3.5 Ma and 2.5 Ma was a period of high latitude cooling that heralded the expansion and change in style of both the West Antarctic Ice Sheet (WAIS) and East Antarctic Ice Sheet (EAIS) (Naish *et al.* 2007). The *Zoophycos* occurs in sediments deposited during the transition from ice-free open marine conditions to a fluctuating subpolar ice sheet suggesting that the *Zoophycos*-producing animal colonized the seafloor during this transition.

The 1.5m thick interval in which *Zoophycos* has been found (351.93–353.38 mbsf) occurs in 17.24m thick unit, bounded by glacial surfaces of erosion and comprised of silty claystone, sandstone, and clast-poor muddy diamictite thought to have been deposited under proximal to distal glaciomarine conditions (Krissek *et al.* 2007, Naish *et al.* 2007). Thin bedded stratified muddy diamictites below the *Zoophycos*-bearing interval are interpreted as debris flow deposits and the sandstones as deposited from turbidity currents; both processes are associated with a proglacial setting adjacent to the ice

Leg	Site	Latitude/ Longitude	Depth (m)	Age	Facies	Organic Carbon	Sedimentation Rate
28 <sup>a</sup>	267	59°16'S 104°29'E	4564	Oligocene (mid-late)	Nanno ooze, chalk	0.55 cm ka <sup>-1</sup>	1.4–6.8 cm ka <sup>-1</sup> (for Mid-Miocene and later)
28 <sup>a</sup>	269	61°41'S 140°04'E	4285	Miocene (early-mid)	Clay, silty clay	+	
35 <sup>b</sup>	323	63°41'S 97°60'W	5004	Cretaceous (Maastrichtian)	Claystone		
113 <sup>c</sup>	689	64°31'S 03°06'E	2080	Eocene (late)–Miocene (late)	Diatom, nannofossil ooze		0.3–0.8 cm ka <sup>-1</sup>
113 <sup>c</sup>	690	65°09'S 01°13'E	2914	K–Pliocene (early)	Nannofossil ooze	0.02–0.26%	0.55–1.2 cm ka <sup>-1</sup>
113 <sup>c</sup>	693	70°50'S 114°34'W	2359	Oligocene (late)	Nannofossil ooze, mudstone		0.7 cm ka <sup>-1</sup>
113 <sup>c</sup>	696	61°51'S 42°56'W	650	Eocene–Miocene (mid)	Mudstone, diatomite	0.23–0.57%	0.5–4.1 cm ka <sup>-1</sup>
119 <sup>d</sup>	746	56°33'S 85°52'E	4059	Miocene (late)	Clay, silty clay		3.0 cm ka <sup>-1</sup>
119 <sup>d</sup>	737	50°14'S 104°29'E	564	Eocene (mid)–Oligocene (late)	Calcareous claystone	0.01–0.19%	2.8 cm ka <sup>-1</sup>
119 <sup>d</sup>	738	62°43'S 82°47'E	2252	K (Turonian)–Eocene	Limestone, chalk	0.04–0.13%	0.44–1.2 cm ka <sup>-1</sup>
178 <sup>e</sup>	1095	66°59'S 78°29'W	3842	Miocene (late)–to Pliocene (late)	Silty clay	0.02–0.49%	2.5–11 cm ka <sup>-1</sup>
178 <sup>e</sup>	1101	64°23'S 70°16'W	3280	Pliocene (late)–Pleistocene (late)	Massive silty clay	0–0.2%	4.1–6.9 cm ka <sup>-1</sup>
178 <sup>e</sup>	1096	67°34'S 76°58'W	3152	Pliocene (early-late)	Silty clay (mottled; hemipelagites)	0.29–0.41%	9–16 cm ka <sup>-1</sup>
RRS	15	NW Weddell Sea	> 4500	Pleistocene			
<i>Discovery<sup>f</sup></i>							

<sup>a</sup> Piper & Brisco (1975), Hayes *et al.* (1975)

<sup>b</sup>Hollister *et al.* (1976)

<sup>c</sup>Barker *et al.* (1988)

<sup>d</sup>Barron *et al.* (1989)

<sup>e</sup>Barker *et al.* (1999)

<sup>f</sup>Pudsey *et al.* (1988)

Data from the NW Weddell Sea is from Pudsey *et al.* 1988; for Leg 28 from Hayes *et al.* 195; Leg 35 from Hollister *et al.* 1976; Leg 113 from Barker *et al.* 1988; Leg 119 from Barron *et al.* 1989; Leg 178 from Barker *et al.* 1998.

**Table I.** Locations and water depth of Southern Ocean cores that contain *Zoophycos* and characteristics of the sedimentary units in which they occur; note the low TOC and low rates of sedimentation of *Zoophycos*-bearing sediments.

sheet (Fig. 4). Five meters above the *Zoophycos* bearing interval is the base of a diamictite that records the advance of the ice sheet and termination of open water conditions (Krissek *et al.* 2007, Naish *et al.* 2007).

The *Zoophycos*-bearing interval was deposited by sediment processes whose rates ranged from high to low (Fig. 4). Debris flow deposits accumulated rapidly whereas silty clays settled slowly from suspension. Laminated sandstones (Fig. 4) record small turbidity currents, presumably generated by processes related to the ice sheet grounding line with submarine meltwater.

### Environmental distribution of Cenozoic *Zoophycos*

*Zoophycos* is both widely distributed and locally abundant in bathyal to abyssal Cenozoic deposits. Terrestrial occurrences document the enormous size of some *Zoophycos* (>1m high and in diameter; Ekdale & Lewis 1991) and allow reconstruction of the morphology and the behavior recorded (Miller & D'Alberto 2001, Bromley & Hanken 2003). Commonly *Zoophycos* occurs in fine-grained Cenozoic limestones that were originally deposited as calcareous oozes (Miller & D'Alberto 2001, Bromley & Hanken 2003). In turbidite sequences *Zoophycos* is most abundant in the upper parts of individual turbidites and in intervening mudstones, suggesting that the producers preferred quiet water conditions (e.g. Manly & Lewis 1998). The occurrence of a small form of *Zoophycos* between turbidites where these are common, and of a larger form in the part of the same succession that lacks turbidites, has been interpreted as reflecting faster growth in less stressful environments not subjected to turbidity currents (e.g. Uchman & Demircan 1999).

*Zoophycos* is also common in cores of Cenozoic oceanic sediments (e.g. Chamberlain 1975) occurring in 30 drill sites from the Caribbean, Atlantic, and Pacific oceans (Ekdale 1977), as well as from the Kerguelen Plateau (Droser & Bottjer 1991), South China Sea (Löwemark *et al.* 2006), Sulu Sea (Wetzel 1984) and off the western coasts

of Africa and Portugal (Wetzel & Werner 1981, Löwemark & Schäfer 2003). *Zoophycos* is restricted to water depths > 1000 m. Its recognition is enhanced by radiography; it was found in 37% of 382 archived cores of upper Cenozoic sediments from the world oceans (Löwemark & Schäfer 2003). As noted from terrestrial occurrences (Ekdale 1992), *Zoophycos* is a deep tier trace fossil produced up to a metre beneath the sediment-water interface. An age difference of 9 ka has been found between the sediment within the *Zoophycos* spreite and the surrounding sediment (Leuschner *et al.* 2002). Complex structure within the axial shaft is interpreted to indicate that the *Zoophycos* structures are occupied for a long time, implying that the producer is long-lived.

*Zoophycos* occurs in sediments deposited slowly (e.g.

< 20 cm ka<sup>-1</sup>; Wetzel & Werner 1981) and is reported from hemipelagites with rates of sedimentation ranging from < 5 cmka<sup>-1</sup> to 20 cm ka<sup>-1</sup> (Stow & Tabrez 1998). Its peak abundance in the South China Sea is where rates of deposition are < 5cmka<sup>-1</sup>; this is consistent with its documented association with omission surfaces (Ekdale & Lewis 1991). Although typically occurring in muds and oozes, *Zoophycos* also has been found in slumped sediments and deposits containing ice rafted debris (IRD), as well as commonly in turbidites (Löwemark & Schäfer 2003).

The *Zoophycos* producers' preference for sediments with moderate to relatively low total organic carbon (TOC) is well documented (< 1.5% TOC Wetzel & Werner 1981; 0.3–0.7% TOC Löwemark *et al.* 2006), as is its apparent predilection for episodic rather than continual delivery of food resources. In some areas such as the South China Sea its abundance roughly tracks glacial-interglacial cycles; this is attributed to climate-driven, interrelated changes in monsoons, ocean currents, upwelling and productivity (Löwemark *et al.* 2006). Conditions inimical to the *Zoophycos* producer(s) include high rates of sedimentation (>20 cm ka<sup>-1</sup>), sandy substrates, substrates with large amounts of IRD or high TOC (>2% TOC), and low levels of dissolved oxygen (Fu & Werner 1994).

### *Zoophycos* in the Southern Ocean

*Zoophycos* has been reported from cores taken at depths of > 3000m off of the Antarctic Peninsula, where it occurs in the upper parts of turbidites and massive muds ranging in age from Early Pliocene to Late Pleistocene (ODP Leg 178, sites 1095, 1096, 1101; Table I). It has also been reported from hemipelagic deposits 200–300 ka in age recovered from a depth of ~4500m the north-western Weddell Sea (Pudsey *et al.* 1988), as well from Cretaceous to Miocene sediments in the Weddell Sea and between Prydz Bay and the Kerguelen Plateau (Table I). However, it is not ubiquitous in the cores from sites drilled on DSDP Legs 28 (Ross Sea) and 35 (Bellingshausen Sea), or ODP Leg 113 (Weddell Sea) and 119 (Prydz Bay).

*Zoophycos* has not been documented to occur in Antarctic continental shelf deposits, in spite of the great depth (mean ~ 500m) and proximity to occurrences in the Southern Ocean. It has been mentioned as occurring in Oligocene deposits of the CRP 2/2a cores, but not illustrated or described morphologically (Fielding *et al.* 2000). The core description did not list the trace fossil; M. Miller perused core interval containing the reported *Zoophycos* and noted no well-defined structures similar to the *Zoophycos* in the ANDRILL 1B. Shelf deposits have been extensively investigated (e.g. Dunbar *et al.* 1989, Anderson 1999, Domack *et al.* 1999) so if *Zoophycos* were common, it probably would have been described. Reasons for its presumed absence or rarity are not known



but may include one or more of the following:

1) Rate of accumulation of siliceous ooze is too high. Siliceous ooze is accumulating all around Antarctica except in the Weddell Sea (Anderson 1999); accumulation rate in the Ross Sea reaches 250 cm kyr<sup>-1</sup> in coastal basins but is lower seaward (DeMaster *et al.* 1996).

2) Total organic carbon is too high. In McMurdo Sound, average TOC at depths below 600m are 1.5% and are as high as 3.5% (Dunbar *et al.* 1989), which exceed TOC levels of sediment in which *Zoophycos* is abundant.

3) Current is too strong, substrate too coarse. Irregular topography coupled with bottom currents results in current-winnowed substrates on banks and slopes which are coarser than the *Zoophycos* producers' preferred low-energy mud-dominated habitat (Taviani *et al.* 1993).

4) Too much IRD. IRD is accumulating today, particularly near the coast. In addition, glacial advance during the LGM in the Ross Sea and elsewhere removed soft sediment, leaving poorly sorted glacial deposits that subsequently have been blanketed with a veneer of ooze (Domack *et al.* 1998, 1999, Shipp *et al.* 1999).

5) Disruption by ice scour is too common. Iceberg scour disturbs the Antarctic shelf to depths > 500 m. It is estimated that every square meter of the Antarctic shelf is disturbed by ice once every 340 years (Gutt 2001), a level of disturbance that may be inimical to the *Zoophycos* producers.

### **ZOOPHYCOS constrains Pliocene conditions and Climate in ANDRILL 1B core**

On a large scale, the *Zoophycos*-bearing unit in the ANDRILL 1B core represents an environmental window of opportunity between the relatively warm Early Pliocene whose productive open ocean conditions potentially led to TOC levels too high for the *Zoophycos* producers and the much cooler Late Pliocene during which persistent glaciation and accumulation of IRD would have been inimical to the animals. The 17m thick heterolithic unit contains neither biosiliceous material signaling high productivity nor large quantities of IRD, although it is sandwiched between overlying biosiliceous diamicite and an underlying unit of intermixed diatomite and biosiliceous diamicite and mudstone that caps a .75m thick unit of diatomite (Krissek *et al.* 2007). These favorable conditions for the *Zoophycos* producers must have been extant for an extended period for them to colonize the ANDRILL 1B site. Early Pliocene ice free conditions probably allowed long-term migration of the *Zoophycos* producer toward the continent, but this and colonization of sediments were most likely slow processes; at present both Antarctic and deep sea faunas are characterized by slow rates of dispersal and thus of colonization (Lipps & Hickman 1982).

The *Zoophycos*-bearing interval falls within a well-dated and complete stratigraphic window from 440–280 mbsf (–3.6–3.2myr) in ANDRILL 1B that is comprised of numerous advance/retreat cycles (Naish *et al.* 2007). *Zoophycos* producers were slow colonizers that preferred stable environments; its presence in the sequence implies that the grounding line position remained unchanged for an extended period within the cycle, further constraining the sedimentation rate.

On a smaller scale, the occurrence of *Zoophycos* provides information about the frequency of the debris flows recorded in this interval: they were sufficiently infrequent to allow colonization by and maintenance of the population of *Zoophycos* producers. The only quantitative estimate of time to colonize a new substrate type in the deep sea or Antarctic by *Zoophycos* producers of which we are aware is Wetzel's (1984) estimate of < 100–200 years in the deep sea. Given the *Zoophycos* producers predilection for stable conditions combined with their low rate of colonization, we infer that the debris flows and rapid sedimentation events did not occur for some period (~100–200 years) before colonization nor during production of the trace. The *Zoophycos* structure may have been excavated into debris flow deposits, but these events predated construction of the *Zoophycos*.

The proclivity of the *Zoophycos* producer for habitats characterized by episodic and limited food supply also illuminates conditions during deposition. *Zoophycos*-bearing strata in ANDRILL 1B are devoid of clear bioturbation fabrics and of discrete trace fossils formed by other deposit feeders that inhabit modern muddy sediments of the Antarctic shelf such spatangoid sea urchins, holothurians, and burrow-dwelling echinurans and whose subsurface tier activities have a high preservation potential (Smith *et al.* 2006). In modern shelf sediments off the Antarctic Peninsula, these animals have been shown to consume labile organic matter throughout the year, in spite of seasonal productivity in the water column, perhaps because summer phytodetritus forms a sediment food bank that deposits feeders draw on year round (Smith *et al.* 2006). However, in less productive settings, such as those with longer sea ice cover, or adjacent to ice shelves, food supply may be limited as well as highly seasonal. Under these conditions and similar conditions in the past, active "caching" of food resources might be the optimal survival strategy. There is growing consensus that the *Zoophycos* structure is used as a short-term cache for food (Miller & D'Alberto 2001, Löwemark & Schäfer 2003) and it has been suggested that spreite of re-ingested sediment (e.g. used cache material) are characterized by absence of lamellae (Löwemark & Schäfer 2003); lamellae are absent from all of the ANDRILL 1B spreite. The lack of biogenic structures produced by medium to deep tier animals other than the *Zoophycos* producers is consistent with the interpretation that the *Zoophycos*-bearing sediments

were deposited in a habitat with such limited food resources delivered so sporadically that active caching was necessary; perhaps the common shelf “sediment food bank” (Smith *et al.* 2006) was insufficient to support non-caching deposit feeders, leaving the *Zoophycos* producer as the sole infaunal deposit feeder.

### Origin of Antarctic fauna: relation to *Zoophycos*

There is widespread agreement that the Antarctic marine fauna is unique, particularly in its lack of shell-breaking predators, high diversity and abundance of large suspension feeders, high level of endemism, prevalence of gigantism and dwarfism and of individual longevity, and tendency toward slow growth, limited reproductive dispersion, and slow colonization (Lipps & Hickman 1982, Aronson & Blake 2001, Gili *et al.* 2006).

The history and origin of the Antarctic fauna is not well understood nor is its relation to the fauna of the Southern Ocean, which only recently has been the focus of major study (e.g. Brandt *et al.* 2007). Components of modern benthic Antarctic faunas have been shown to have Jurassic–Cretaceous affinities (e.g. isopods, molluscs, gorgonaceans, hexactinellids; Stilwell & Zinsmeister 1992, Gili *et al.* 2006) and the legacies of early Tertiary molluscs, echinoids, and polychaetes (La Meseta Formation) are represented in modern faunas (Clarke 1990, Crame 1997, Stilwell & Zinsmeister 2000). Lack of post-Cretaceous deposits and paucity of body fossils in post-Eocene sediments on the shelf hampers reconstruction of the evolution of the benthic fauna that occurred as the climate cooled starting in the late Eocene and the fauna was isolated by the opening of the Drake Passage (Aronson & Blake 2001).

### Suggested origins of the Antarctic marine fauna

In the absence of fossil data, several scenarios for the origin of the Antarctic benthic fauna have been proposed, including that the shelf faunas migrated to deep ocean basins (“submergence”), that deepwater faunas migrated upward to the continental shelves (“emergence”), and that the faunas have developed largely in place (Clarke *et al.* 2004). Evidence for submergence comes from the distribution of genetically similar populations of *Epistominella vitrea*, a benthic foram that is abundant on Antarctic shelves and has an expanded depth range in the Southern Ocean (Brandt *et al.* 2007), from present-day occurrence in deep water of molluscs found in early Cenozoic deposits on the Antarctic Peninsula, and from the eurybathic distributions of many species, interpreted to have developed by forced retreat to deep water during ice sheet advance (Brey *et al.* 1996).

Development of the faunas *in situ* is supported by the high proportion of endemics in many groups, including pycnogonids (85% endemics, Clarke & Johnston 2003), gastropods (Crame 1997), and isopods (Brandt 2005). An

example of emergence is provided by the large agglutinated foraminifera *Astrammmina triangularis* which occurs at 25m in western McMurdo Sound but at much greater depths elsewhere (Bowser *et al.* 2002). It appears that all three processes have contributed to the origin of the Antarctic benthic fauna, an interpretation based almost exclusively on inferences from distributions of modern animals with little contribution from the limited body fossil record.

### Contribution of *Zoophycos* to understanding modern Antarctic marine fauna

Occurrence of *Zoophycos* in Pliocene sediments from the ANDRILL 1B core coupled with its distribution in cores of deep sea sediments both younger and older in age demonstrates convincingly that some benthic animals migrated from deep water onto the Antarctic shelf during glacial minima.

The oldest post-Palaeozoic occurrence of *Zoophycos* in Antarctica is from the Jurassic to Cretaceous Fossil Butte Group of Alexander Island (Antarctic Peninsula) (Taylor 1967), composed primarily of bathyal siliciclastics (Doubleday *et al.* 1993). *Zoophycos* also has been recorded from numerous deep sea cores from all sectors of the Southern Ocean (Table I) in deposits of Cretaceous and Eocene through Pleistocene age. We suspect that poor core recovery and lack of x-radiography has resulted in *Zoophycos* being under-reported; *Zoophycos* stands out in radiographs but may be difficult to see on core surfaces (Löwemark & Schäfer 2003).

We are aware of no previously published descriptions of *Zoophycos* in cores of Cenozoic deposits from Ross Sea and McMurdo Sound. The single documented occurrence is that reported herein in Pliocene deposits, where the *Zoophycos* structure stands out in lithologic contrast with the surrounding material. More specimens may well be found in SHALDRILL, ANDRILL and other cores as more are x-rayed. *Zoophycos* occurs at the end of a multi-million year period of relative warmth (Naish *et al.* 2007) that provided time for the producer, probably a slow colonizer (Lipps & Hickman 1982, Wetzel 1984), to migrate onto the shelf; in fact there was time for repeated migrations around the continent. We infer that the distribution of *Zoophycos* producers was limited to localized areas shielded from high rates of sedimentation and organic enrichment, but that seasonal influx of organic matter provided material that could be stashed in temporary caches within the *Zoophycos* structure (Jumars *et al.* 1990, Smith *et al.* 2006).

Significantly, *Zoophycos* occurs in Pliocene and Pleistocene deposits at depths > 3000m off of the Antarctic Peninsula and in the Weddell Sea in sediments 200 ka to 300 ka (Pudsey *et al.* 1988). These occurrences document the continued presence of the *Zoophycos* producer(s) in deep sea habitats during Pliocene migration into shallower water. The subsequent history is less clear,



with several possibilities: 1) the *Zoophycos* producer(s) retreated to deeper water habitats, 2) the *Zoophycos* producer(s) remained on the shelf, but the record of activity has been eroded, or 3) the *Zoophycos* producer(s) remained in isolated refuges on the shelf (e.g. Gili *et al.* 2006).

## Conclusions

The trace fossil *Zoophycos* occurs as sections of spreite and axial structures in a 1.5m thick interval in ANDRILL 1B core recovered from underneath the Ross Ice Shelf. It is found in debris flow and vertically accreted sediments deposited during the transition from warm, open marine conditions in the Early Pliocene to a colder Late Pliocene characterized by subpolar ice sheets. Application of known preferences of the *Zoophycos* producers known from worldwide occurrences to the *Zoophycos* in ANDRILL 1B suggests that rates of sedimentation and levels of TOC were low, and that food was delivered episodically. In spite of evidence of sea floor disturbance (e.g. debris flows, turbidity currents), the presence of *Zoophycos*, whose producers are slow colonizers with strong preference for stable environments indicates extended periods with little change and minimal disturbance.

Previously *Zoophycos* was known from Mesozoic deposits in the Antarctic Peninsula and Cenozoic deep sea deposits around Antarctica, but had never been described from continental shelf deposits. The apparent absence of *Zoophycos* from shelf deposits except in ANDRILL 1B near the end of an extended period of Pliocene relative warmth suggests that the producers migrated onto the shelf during climate amelioration and retreated into deeper water during cooling and ice sheet advance. Given the poor Cenozoic body fossil record of Antarctica, this occurrence of *Zoophycos* provides rare positive fossil evidence that components of the Antarctic benthic fauna have “emerged” into shallow water during ameliorating climate.

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