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# Testing ethological hypotheses of the trace fossil *Zoophycos* based on Quaternary material from the Greenland and Norwegian Seas

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ABSTRACT

Despite the fact that the trace fossil *Zoophycos* has been found in rocks from most of the Phanerozoic, little consensus has been reached on how and why this intricate burrow was constructed. The Cenozoic morphotypes of *Zoophycos* typically include a helically coiled spreite arranged around a vertical shaft connected to the sediment surface.

Morphological details and environmental preferences of the *Zoophycos* producer were studied using 156 cores from the Norwegian and Greenland Seas in order to test the different ethological hypothesis proposed for this trace fossil. The spreiten were constructed during interglacial or interstadial intervals and consist of a repeated alternation of lamellae consisting of fine-grained pelleted material, and coarse-grained unpelleted material, respectively. Spreiten were encountered in vigorously bioturbated sediment, in turbidite layers, and in layers dominated by coarse ice-rafted debris. This indifference to the composition of the substrate effectively rules out ethological models based on different forms of deposit-feeding, and the large size and wide spacing of the whorls of the spreiten also make the cesspit model unlikely. Rather, the observed features best agree with a cache behaviour, where the main purpose of the deep penetration was to store food and to prevent access by other burrowers, likely combined with some gardening of microbes. However, no indubitable evidence of a reworking of the cached material could be found, and probably the answer to how the cache was accessed by the producer is to be found in the marginal tube. The difference in diameter between marginal tube and spreiten lamellae, together with the presence of both open and filled marginal tubes indicate that the marginal tube is the result of a far more complex behaviour than simply a lateral shift through the sediment.


## 1. Introduction

The trace fossil *Zoophycos* typically consist of one or more lobate spreiten arranged around a central axis, often marked by a vertical shaft (Häntzschel, 1975; Uchman, 1995). The spreite is made up of a large number of lamellae and often, but not always, bordered by a marginal tube. This complex morphology, somewhat resembling a huge, irregular corkscrew, is probably one of the most intriguing trace fossils, and despite being dealt with in a large number studies, little consensus has been reached regarding the constructional mode of operation, nor the ethological explanation for this elaborate design.

The oldest occurrence of *Zoophycos* stems from the lower Cambrian (Sappenfield et al., 2012), although lobed spreiten bordered by a marginal tube have even been recorded in sediment as old as the Late Ediacaran (Macdonald et al., 2014). In contrast, the youngest observed *Zoophycos* are found in Holocene strata, where open central shafts suggest that it is actively being constructed today (Löwemark and Schäfer, 2003; Wetzel, 2008).

Over the course of the Phanerozoic, a trend from smaller and simpler morphologies towards larger and more complex forms has been observed (Chamberlain, 2000; Kotake, 2014; Seilacher, 1967). This change in morphology runs parallel to a trend towards the occupation of gradually deeper environments (Bottjer et al., 1988; Chamberlain, 2000; Seilacher, 1986), making it questionable whether all *Zoophycos* represent the same kind of behaviour. Further complicating the study of *Zoophycos* is the considerable range in the morphologies attributed to the *Zoophycos* group by various investigators (cf. Uchman, 1995; Uchman and Demírcan, 1999). This implies that no matter how well founded interpretations may be for one type of *Zoophycos*, these ethological models may be of limited value for the interpretation of other kinds of *Zoophycos*. However, the necessary revision of the *Zoophycos* ichnogenus goes far beyond the scope of this study.

The aim of this study is to address the morphology, ethology, and environmental preferences of the modern deep-sea *Zoophycos* based on the study of a large number of Late Quaternary sediment cores from the northeastern North Atlantic, the Greenland Sea, and the Norwegian Sea. Previous studies have indicated a strong preference for calm conditions, relatively low sedimentation rates, intermediate organic carbon content, and possibly a preference for settings with a strong seasonal shift in the food flux (Löwemark, 2012; Löwemark et al., 2006; Löwemark and Schäfer, 2003; Wetzel and Werner, 1981). Especially the Greenland and Norwegian Seas are characterized by

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extremes both in the composition of the sediment, which often contains high amounts of ice rafted debris, and in the extreme differences in primary productivity between winter and summer. These conditions allow a number of questions to be addressed: How is the distribution of *Zoophycos* related to the position of the winter and summer sea ice margins and the resulting primary productivity patterns? How has the occurrence varied over time? How much influence do variations in substrate composition and consistency have on the construction and distribution of *Zoophycos*? Furthermore, from a number of cores, X-ray radiographs of vertical and horizontal serial sections of the sediment allows the comparison of details of the morphology of *Zoophycos* with Late Quaternary *Zoophycos* described from mid- and low latitudes, as well as with the morphologies of older Phanerozoic *Zoophycos*. The observations and the information obtained from the 156 cores examined in this study allows the usefulness of previously proposed ethological models to be tested as explanations for the large helicoidally coiled late Quaternary *Zoophycos*.

## 2. Material and methods

The material used for this study consists of X-ray radiographs from 156 piston, gravity, and box cores retrieved from the northeastern North Atlantic and the Nordic Seas (Fig. 1). Negatives of the X-radiographs were studied in the archives at Kiel University using light table, and scanned X-radiographs from selected cores were downloaded for further evaluation from the Pangaea server (www.pangaea.de). Cores are referred to either by their GIK (Geologisches Institut Kiel) numbers or by their PS (research vessel Polarstern) numbers. In some cases, especially when data has been published using different core numbers, both are given. Contrast, brightness and intensity of the digitized radiographs were adjusted to improve the grey scales and enhance the visibility of the studied trace fossils using the commercial software Corel Photo-Paint (cf. Dorador and Rodríguez-Tovar, 2014; Rodríguez-Tovar and Dorador, 2014).

X-ray radiographs represent an integrated two-dimensional image of three-dimensional sedimentary features in a thin slice of sediment. Consequently, where narrow or thin features, such as laminae or sheet-like structures, are perpendicular to the plane of the analysed sediment slab, they will be portrayed with great accuracy in the radiograph. In contrast, where the plane of the sheet-like structure is oblique relative to the plane of the slab, the resulting image will be a palimpsest of sediment on both sides of the sheet. This is of particular importance when studying *Zoophycos*, as the lamellae of the spreiten will only be clearly visible in cases where the lamellae are perfectly perpendicular to the radiograph. In cases where the lamellae are curved or arched, they may give the impression of a shift from clearly lamellated to homogeneous-looking spreiten. For core GIK17047-1 from the NE Atlantic, computer-tomographic (CT) scans were available at www.pangaea.de. However, although *Zoophycos* spreiten could be identified in the CT slices, it was not possible to extract meaningful morphological data from the images.

The geographic distribution of *Zoophycos* was evaluated by noting presence or absence of *Zoophycos* for all 156 cores examined in this study. From several cores, radiographs of vertical serial sections or horizontal sections were available. These radiographs were used to further constrain the three-dimensional features of the morphology of *Zoophycos*. For eight cores, oxygen isotope data and published age models were available, allowing the stratigraphic distribution of *Zoophycos* in these cores to be assessed. For these eight cores, the stratigraphic distribution of the dominating trace fossils was recorded, variations in ice-rafted debris (IRD) was noted, and stable oxygen isotopes were plotted. In addition, the stratigraphic position of published age points was marked by arrows and interglacial marine isotope stages (MIS) highlighted by light grey bars in Fig. 1.

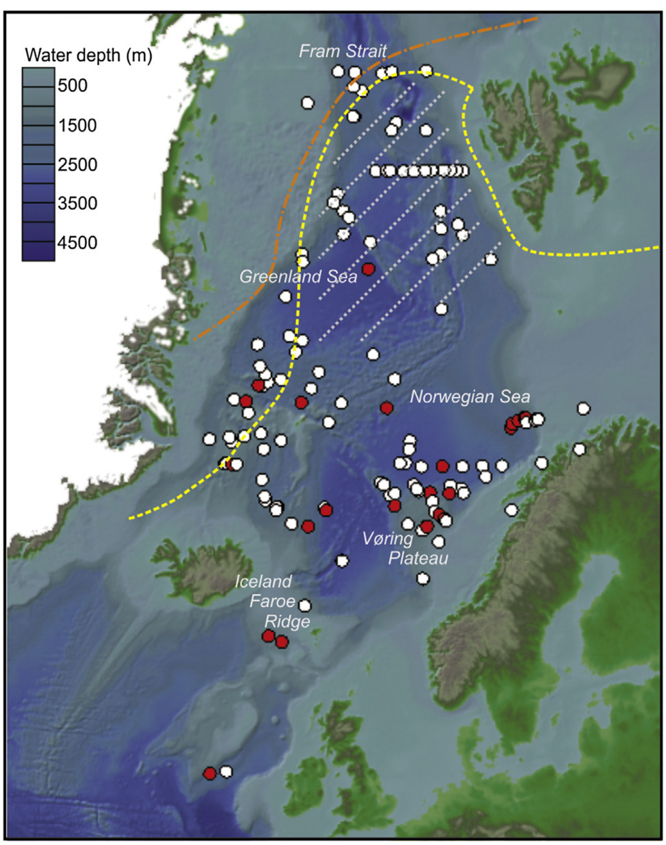


**Fig. 1.** Bathymetric map showing the position of the studied cores and the average (1981–2010) winter sea-ice extent (yellow dashed line) and average summer (orange dot-dash line) sea ice extent (National Snow and Ice Data Center, 2014; Perovich et al., 2013). It should be noted that the area between Svalbard and Iceland (hatched area with grey dashed lines) is also ice covered in winter many years, probably more often so before global warming. White circles denote cores without *Zoophycos* spreiten, red circles denote cores containing at least one *Zoophycos* spreite.

## 3. Results

### 3.1. Geographic distribution

Of the 156 cores used in this study, 30 contained at least single spreiten that could be unambiguously classified as *Zoophycos*. From the geographic distribution of cores containing *Zoophycos*, compared with cores lacking *Zoophycos*, it is obvious that *Zoophycos* is fairly abundant in the Norwegian Sea and in the southern Greenland Sea. In contrast, the cores from the northern Greenland Sea and the Fram Strait, with one exception, lack *Zoophycos*. The water depth of the *Zoophycos*-bearing cores span from 922 to 2836 m, with an average of 2076 m, while the depth of the cores without *Zoophycos* ranges from 228 to 5563 m, with an average of 2064 m. Although the average depths are practically identical, the depth distribution of *Zoophycos* indicates a strong preference for mid-slope settings, something corroborated by the bathymetric map in Fig. 1. The geographic distribution further shows that *Zoophycos* is largely absent in the cores taken in areas dominated by severe sea ice conditions (National Snow and Ice Data Center, 2014; Perovich et al., 2013).

### 3.2. Stratigraphic distribution

For eight of the studied cores, published age models were available (Fig. 2). These reveal large differences in sedimentation rates between the coring sites (Table 1). For example, while GIK23074-1 reaches back to around 27 ka with a core length of almost 7.5 m, the similarly long PS1243-1 is dated at the base to over 450 ka, resulting in a span of the linear sedimentation rates from 1.5 cm ky$^{-1}$ to 30 cm ky$^{-1}$. All