



## The ecology and biogeography of *Discospirina tenuissima* (Foraminifera) in the Atlantic and Indian Oceans



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### ARTICLE INFO

Available online 17 May 2012

#### Keywords:

Mid-Atlantic Ridge  
Benthos  
Miliolid  
Phytodetritus  
North Atlantic Ocean  
Indian Ocean

### ABSTRACT

The large ( $\geq 1$  cm diameter) miliolid foraminifera *Discospirina tenuissima* (Carpenter and Jeffreys, 1870) is common at four sites (NW, NE, SW, and SE), located on either side of the Mid-Atlantic Ridge to the north ( $54^{\circ}\text{N}$ ) and south ( $49^{\circ}\text{N}$ ) of the Charlie–Gibbs Fracture Zone. The white discoidal tests of this epifaunal species were visible in video surveys of flat and gently ( $10^{\circ}$ ) sloping, sediment-covered areas of seafloor (replicate 500-m-long transects, 1000 m<sup>2</sup> surface area) obtained using the Remote Operated Vehicle *Isis*. Average densities varied from 0.07 (SE site) to 1.12 (NW) ind m<sup>-2</sup> for sloped transects and 0.02 (NW) to 1.75 (SW) ind m<sup>-2</sup> for flat transects. Considerable variation was also evident between individual transects (0–2.25 ind m<sup>-2</sup>). The tests displayed no consistent dispersion pattern; both significantly random and clumped patterns were observed, in some cases within a single site. *Isis* was also used to make detailed *in situ* observations of *D. tenuissima* and to collect individual specimens. The delicate test margin sometimes exhibited angular notches and other signs of damage, presumably a result of megafaunal activity; in some cases the damage had been repaired. Specimens perforated by a large central hole occurred at the SE site. Smaller sessile organisms, including agglutinated foraminifera and occasional brachiopods, use *D. tenuissima* tests as a substratum for attachment. In all areas, some tests were surrounded by a ring of sediment, presumably surface material collected by pseudopodia. We interpret these features as being comparable to the feeding cysts created by other foraminiferal species. They were particularly common at the SE site, where one or two abandoned rings indicated that some tests had moved distances of several centimetres across the seafloor. Most previous records of *D. tenuissima* are from well-oxygenated sites in the NE Atlantic. We provide the first records from the Indian Ocean. Here, this species occurs at bathyal depths in the northwest (1980 m) and northeast (938 m) Arabian Sea, where bottom-water oxygen concentrations are depressed.

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### 1. Introduction

In addition to rocky substrata and hydrothermal vents, the Mid Atlantic Ridge (MAR) provides the largest area of sediment-covered bathyal seafloor in the North Atlantic, exceeding the sedimentary environments of the continental margins in terms of area (Shields et al., 2011). Nevertheless, in contrast to the continental margins, few studies have addressed the soft-sediment faunas in this central oceanic region (Levin and Gooday, 2003). The Ecosystem of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie–Gibbs Fracture Zone (ECOMAR) project was formulated in order to address this knowledge gap. The project focussed on two sections of the MAR, located around  $54^{\circ}$  and

$49^{\circ}\text{N}$  and each encompassing a site to the west (NW and SW sites) and to the east (NE and SE sites) of the MAR. The Ridge represents a geographical barrier that potentially creates faunal differences between the eastern and the western basins of the North Atlantic. Further faunal variations may arise from environmental heterogeneity generated by the considerable topographic complexity within this region, which includes the Charlie–Gibbs Fracture Zone (CGFZ), a major system of transform faults located between the northern and southern sites. In addition to investigating the MAR faunas, ECOMAR aimed to explore connectivity between faunal assemblages on the Ridge and those on the North American and European/NW African margins.

During the R.R.S. *James Cook* cruise 048, the Remote Operated Vehicle (ROV) *Isis* was deployed to make video surveys at the four ECOMAR sites, and to collect specimens and detailed *in situ* photographs of selected species in order to facilitate their identification. The *Isis* dives revealed the abundant presence at all four

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sites of small, white, discoidal structures that proved, on collection, to be tests of the foraminifera *Discospirina tenuissima* (Carpenter and Jeffreys, 1870). Apart from two early records to the north of our study sites (Jeffreys, 1876), this distinctive species is known only from continental margin settings in the North Atlantic and some relatively shallow Mediterranean sites. Moreover, little is known about its ecology. The main aims of this paper are therefore to describe (1) the abundance and dispersion of *D. tenuissima* at the four ECOMAR sites and (2) some novel observations of its ecology in the deep sea based on *in situ* photographs and collected specimens. In addition, we take the opportunity to report the first record of this species from the Indian Ocean, based on material collected in 2002 and 2003 on the Oman and Pakistan margins of the Arabian Sea.

## 2. Background

### 2.1. General features of *Discospirina* and history of study

*Discospirina* is a genus of large miliolid foraminifera characterised by a very thin, discoidal test. An interesting feature of this taxon is that ancestral growth patterns preserved in the centre of the test are clearly visible externally. The juvenile part comprises a globular proloculus followed by an aseptate, planispirally coiled tube, which develops into a subdivided *Ophthalmidium*-like coil followed by flaring flabelliform chambers and finally annular chambers that make complete circuits of the outer part of the test (Brasier, 1984). Another unusual feature is the division of both flabelliform and annular chambers into chamberlets. This pattern, from tubular non-septate, to flaring septate, to partitioned annular chambers, has provided a template for decoding foraminiferal test evolution throughout the Phanerozoic (e.g. Brasier, 1986, 2012; Loeblich and Tappan, 1988).

It has been proposed that chamberlets are developed in larger benthic foraminifera that contain photosymbionts in order to distribute the symbionts more efficiently around the test (Brasier, 1995). In the case of *Discospirina*, a predominately deep-sea genus, this hypothesis is clearly challenged. One possibility, not tested here, is that *Discospirina* had photosymbiotic ancestors and has since abandoned this way of life (e.g., Brasier, 2012). A second hypothesis, suggested to us by Lynn Margulis (pers. comm., 2010), is that *Discospirina* cultivates non-phototrophic (e.g. sulphur oxidising) bacteria in the same way as ciliates, molluscs and annelids living around sulphidic seeps (e.g. Levin, 2005; Rinke et al., 2007). A third hypothesis is that the chamberlets merely serve as a means of strengthening a test that is very large but very thin. This raises the question of why, in terms of ecological adaptation, the test is unusually large and thin?

The first species of *Discospirina* was described (as *Pavonina italica*) from the fossil record by Costa (1856). Costa's figures are poor and he seems to have been uncertain about what kind of organism he was describing. The first substantial work on the genus was that of Carpenter (1883a, 1883b), who described a second species, as *Orbitolites tenuissima*, in great detail and was the first to see its significance in preserving the morphologies of less advanced types of miliolid. Carpenter's material was obtained between 1869 and 1876 during the pioneering expeditions of H.M.S. *Porcupine* (Carpenter et al., 1870; Carpenter and Jeffreys, 1870; Thomson, 1874), *Valorous* (Jeffreys, 1876), and *Challenger* (Thomson, 1877) (Table 4).

Since Carpenter's work there have been only a few detailed studies of *Discospirina* and most of these have described aspects of its test morphology in order to illustrate particular scientific arguments. Munier-Chalmas (1902) named the genus and gave a brief description of its morphology. Lister (1903) first understood its true affinities, suggesting that it was related to *Ophthalmidium* rather than to *Orbitolites*. It also appeared in the

catalogues of foraminifera compiled by Liebus (1931), Galloway (1933), Davies (1935), Cushman (1928, 1948), Loeblich and Tappan, (1964, 1987) and Haynes (1981). Adams (1959) listed many references to the genus and in later papers, explored its distribution and value as a palaeobiogeographical indicator. He grouped all known species into *Discospirina italica* as he believed the differences were not great enough to merit further subdivision. Brasier (1984) carried out a detailed study on the form and possible function of the test of *Discospirina*. The most recent contribution was by Chaproniere (1991) who described the first known Pacific specimens of this genus from late Pleistocene sediments in cores taken in the Coral Sea off NE Australia, and discussed possible means of dispersal. This and other living and fossil materials have also been the subject of an unpublished Masters thesis (Marsden, 2003).

### 2.2. Species identification

Brady, (1884) drew attention to close similarities between the fossil species from the 'later Tertiaries' of Southern Italy, described by Costa (1856) as *Pavonia italica*, and modern specimens of *Orbitolites* (= *Discospirina*) *tenuissima*. He subsequently obtained specimens from Upper Miocene deposits near Messina, which he judged to be identical to *O. tenuissima* of Carpenter (Brady, 1886). Adams (1959) re-examined Brady's two specimens and a large collection of similar Miocene fossils from Cyprus and concurred with Brady's conclusion. However, a detailed biometrical study has revealed clear differences between the fossil and modern forms in the size and shape of the partitions separating the chamberlets (Marsden, 2003). We therefore retain the name *D. tenuissima* for our modern North Atlantic specimens, which are undoubtedly conspecific with those described and beautifully illustrated by Carpenter (1883a, b). A paper on the morphometry and taxonomy of fossil and living species of *Discospirina* is currently in preparation.

## 3. Materials and methods

### 3.1. Study sites and sample collection

The Mid Atlantic Ridge (MAR) was visited during R.R.S. *James Cook* cruise 48 (JC048; May to July 2010). Four sites (NW, NE, SW and SE), located at ~2500 m water depth on the eastern and western flanks of the MAR, were studied (Tables 1 and 2). The two northern sites lay to the north, and the two southern sites to the south, of the Charlie-Gibbs Fracture Zone (CGFZ). Surface current flow in this region is predominantly from the west to the east. Current flow near the floor of the CGFZ fluctuates in direction, with a slight tendency for westward flow to predominate (Saunders, 1994). The position of the Fracture Zone coincides more or less with the position of the Sub-Polar Front. Mean annual primary production is slightly higher at the northern than at the southern sites, but not significantly so (Table 1). The mean organic carbon flux measured in sediment traps moored 1000 m above the seafloor was higher at the two southern sites (SW and SE sites combined) compared to the two northern sites (NW and NE sites combined); however, the variance was large and the difference therefore not significant (Abell et al., 2013). Sediments were very soft muds at the northern sites and somewhat coarser, silty muds to the south. Variable densities of pteropod shells were visible on the sediment surface at the SW and SE sites. Bottom-water oxygen concentrations and temperatures were fairly uniform, around 282  $\mu\text{mol L}^{-1}$  (=6.3  $\text{ml L}^{-1}$ ) and 3.15 °C, respectively (Table 1).

Specimens from the Arabian Sea were collected during R.R.S. *Charles Darwin* Cruise 143 (CD143; November to December 2002) on

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