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Morphological variability of menardiform globorotalids in the Atlantic Ocean during Mid-Pliocene

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ABSTRACT

The morphological variation of the planktonic foraminifera plexus of *Globorotalia* (*Menardella*) (Bandy, 1972) has been studied in a Pliocene time-slice at 3.2 Ma. Using a combination of size, linear shell measurements and shape analysis, an extended morphological protocol is explored in order to define morphological subgroups within the *Menardella* subgenus (Bandy, 1972). Isochronous samples at 3.2 Ma have been selected at five ODP/IODP Sites in the low latitude Atlantic Ocean, in which up to 600 specimens per sample have been oriented, imaged and analyzed using a new automated prototype for morphological analysis called AMOR. Multimodal size frequency distribution is related to the occurrence of several distinct populations. Three main ubiquitous populations of such menardellids are isolated, next to two additional biogeographically limited subgroups. These populations strongly differ in abundance and size. Using morphological classifiers, subpopulations are distinguished among these populations, leading to the establishment of seven different morphotypes informally named: MA, MB, MC1, MC2, MC3, SH1 and SH2. These morphotypes are assigned to formal species, i.e., MA corresponds to *Globorotalia* (*Menardella*) *menardii*, MB to *G.* (*M.*) *limbata*, SH1 to *G.* (*M.*) *exilis*, and SH2 to *G.* (*M.*) *pertenuis*. In contrast, the species *G.* (*M.*) *multicamerata* is interpreted as being composed of three distinct morphotypes, sharing a similar size range, but differing in shell morphology.
Morphotype MC1 shows thin and elongated chambers, whereas morphotype MC2 is characterized by a thick and robust test. MC3 is inflated with a distinct flexure in the final chamber. Size differences are linked to variations in habitat temperature and oxygenation, with the exception of *G.* (*M.*) *multicamerata* morphotypes, which are probably adapted to a productivity gradient.

1. Introduction

Since recent outcomes of combined morphometry and molecular studies have revealed that subtle morphological differences could reflect cryptic genetic diversity (Huber et al., 1997; de Vargas et al., 2001; Morard et al., 2009; Aurahs et al., 2011), planktonic foraminifera have been the focus of many biometric investigations (for example: Huber et al., 2000; Renaud and Schmidt, 2003; Eynaud et al., 2009; Regenberg et al., 2010; Moller et al., 2011). Traditionally defined morpho-species are actually composed of biogeographically and ecologically distinct populations (Kucera and Darling, 2002; Darling and Wade, 2008). Morphological variability, within these populations, has been inferred as evidence of genetic diversity, thus opening a new field for biometrical investigations.

Only a few studies have tracked morphological variability as possible evidence of species level diversity in ancient forms rather than in living specimens (Kucera, 1998; Kelly et al., 2001; Renaud and Schmidt, 2003; Knappertsbusch, 2007; Eynaud et al., 2009; Georgescu et al, 2009; Hull and Norris, 2009; Rossignol et al., 2010). Although the fossil record of planktonic foraminifera contains many examples of morphological gradation that are possibly including several cryptic species, the definition of the species boundary within a fossil planktonic population remains problematic. The establishment of significant differences through biometry, without molecular analysis, involves several constraints that must be surmounted. Above all, the tenuous morphological differences between cryptic species make their recognition difficult (de Vargas et al., 2001; Morard et al., 2009; Aurahs et al., 2011), and induce the analysis of hundreds of specimens (Fatela and Taborda, 2002).

Usually, specimen imaging is carried out manually, which limits sampling size due to technical constraints and efficiency. A few studies have overcome this issue by applying automated techniques for the collection of morphological parameters such as size, area, or roughness (e.g. Schmidt et al., 2006; Eynaud et al., 2009; Moller et al., 2011), applied only on randomly oriented tests. Since outline coordinates are sensitive to orientation (Sokal and Rohlf, 1969; Rohlf, 1990), the use of non-oriented tests is not suitable for geometric morphometry.

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Furthermore, morphometric studies that involve oriented tests are restricted to a limited number of specimen of the >250 μm size fraction per sample (inferior to 500 individuals to less than 100 if several times intervals are analyzed (Kucera and Widmark, 2000; Kelly et al., 2001; Renaud and Schmidt, 2003; Hull and Norris, 2009)).

This paper describes a new approach, combining size frequency distributions and morphological measurements of large size samples with the use of an automated imaging robot: the *Automated Measurement system for shell mORphology* (AMOR) (Knappertsbusch et al., 2009). We investigate morphological variability of *Globorotalia* (*Menardella*) *menardii*, and related species, through the Pliocene period in the low latitude Atlantic Ocean. This group was chosen because of its high diversity during this period (Bolli and Saunders, 1985). The use of an automated device provides the opportunity to significantly increase the necessary number of individuals. Using contoured frequency distributions allows the identification of clusters within morphological populations. As a biogeographic experiment, shell variation is evaluated by comparing morphological variability from five selected localities corresponding to different environmental settings within the tropical North Atlantic: the Caribbean Sea, the Canary Current, the Equatorial Counter Current, the Mauritanian upwelling, and the Brazilian margin (see Fig. 1).

1.1. Taxonomic considerations

Menardiform globorotalids constitute a subset within the genus *Globorotalia* (Cushman, 1927), in which *G.* (*M.*) *menardii* is the best known representative. To express the need to further separate *G. menardii* and its phylogenetically related forms from the remaining globorotalids, Bandy (1972) suggested the two subgenera *Globorotalia* and *Menardella*, on the basis of the hypothetical phylogenetic relationship. The clade *G. acheomenardii–praemenardii–menardii* and its related species is kept apart from the other globorotalid lineages (i.e. *Fohsella*, *Jenkinsella*, *Globoconella*, *Hirsutella*, *Truncorotalia*, *Tenuitella* and *Turborotalia*). This concept was also applied by Kennett and Srinivasan (1983), using the term menardellid to refer to the *G. menardii* clade. Following similar arguments, the terms menardiform globorotalid (Stainforth et al., 1975) or menardine (Cifelli and Scott, 1986) were applied to distinguish the *G. menardii* lineage from other globorotalids.

The present work follows the generic and specific concept of Bandy (1972) and Kennett and Srinivasan (1983). It takes into consideration the observations of Bolli and Saunders (1985). In synonymy with the term *Globorotalia* (*Menardella*) sensu Kennett and Srinivasan (1983), we apply the term menardiform of Stainforth et al. (1975) for summarizing members of the *G. menardii* lineage.

1.2. Test objects: Mid-Pliocene menardellids

We selected menardellid globorotalids as a model because of their ubiquitous occurrence in tropical sediments, their large size range, and their wide variety of morphologies. Their lenticular biconvex profile, divided in two sides by a blunt keel, makes them easy objects to model in two dimensions.

The *Globorotalia* (*Menardella*) *menardii–Globorotalia* (*Menardella*) *multicamerata* lineage originated with the appearance of *G.* (*M.*) *menardii* during the middle Miocene zone N12 (between 13.5 and 12 Ma). The species gave rise to *Globorotalia* (*Menardella*) *limbata* and *Globorotalia* (*Menardella*) *multicamerata* during the middle Miocene zone N14 and the Late Miocene zone N17b (Kennett and Srinivasan, 1983). A progressive evolution to larger size occurred between 3.11 and 2.29 Ma (Knappertsbusch, 2007). At the end of the Pliocene, all menardellids but *G.* (*M.*) *menardii* became extinct.

Extant *G.* (*M.*) *menardii* are facultative symbiont bearing species (Hemleben et al., 1989) living at the seasonal thermocline depth, but capable to adapt the depth of their habitat depending on temperature (Gasperi and Kennett, 1992). Recently, Sexton and Norris (2011) investigated the ecological preferences of *G.* (*M.*) *menardii*. According to these authors, the ventilation of the upper thermocline is the key feature controlling menardellid populations, *G. menardii* tracking poorly ventilated waters.

In contrast, the ecological preferences of *G.* (*M.*) *limbata* and *G.* (*M.*) *multicamerata* are poorly known. Chaisson and Pearson (1997) and Chaisson (2003) considered them to be thermocline dwellers whereas Pfuhl and Shackleton (2004) interpreted their oxygen isotope ratios to be indicative of shallower habitats. Gasperi and Kenneth (1993) suggested that this group changed its habitat depth from intermediate to shallow during the late Miocene.

G. (*M.*) *menardii*, *G.* (*M.*) *limbata*, and *G.* (*M.*) *multicamerata* form a phylogenetic lineage, which is expressed as a continuous morphological intergradation from *G.* (*M.*) *menardii* to *G.* (*M.*) *multicamerata* (Kennett and Srinivasan, 1983; Bolli and Saunders, 1985; Cifelli and Scott, 1986; Chaisson, 2003; Knappertsbusch, 2007). All three species share the typical menardiform test morphology; i.e. a low trochospiral circular to oval test surrounded by a prominent keel. Chambers are densely perforated, sutures are straight on the umbilical and curved on the spiral side (Blow, 1969; Kennett and Srinivasan, 1983). They differ by an increase

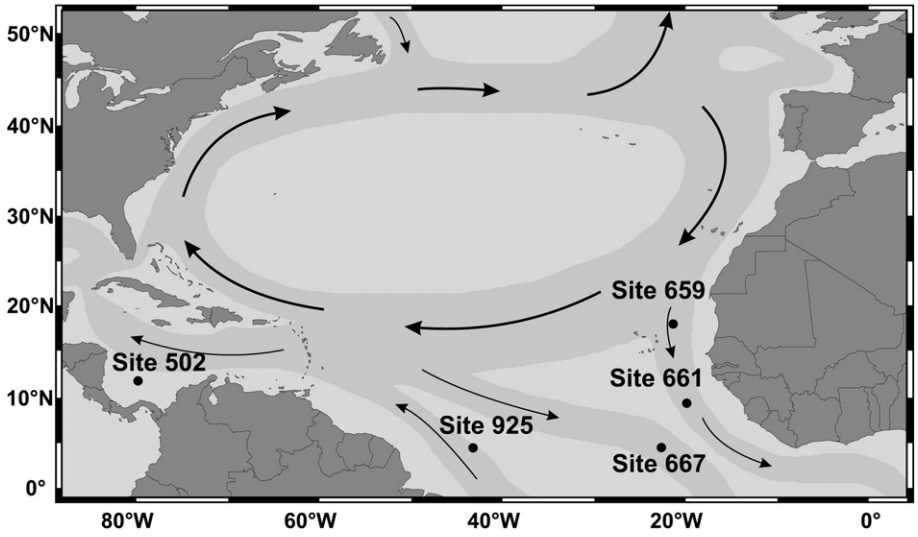

Fig. 1. Geographic distribution of ODP study Sites 502, 659, 661, 667, and 925. Approximate position of actual currents is shown. Map adapted from Dowsett and Robinson (2007).