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Marine Micropaleontology 57 (2005) 51–67
MARINE MICROPALEONTOLOGY
www.elsevier.com/locate/marmicro

Molecular phylogeny of the foraminiferal genus *Uvigerina* based on ribosomal DNA sequences

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Received 29 March 2005; received in revised form 11 July 2005; accepted 19 July 2005

Abstract

Uvigerina is a common genus of benthic foraminifera, often used as a proxy for paleoclimate and paleoenvironment reconstructions. Better understanding of the phylogeny of *Uvigerina* would improve its proxy value and would allow us to check whether its different morphospecies are real species or ecophenotypes only. Here, we used partial small-subunit ribosomal DNA (SSU rDNA) sequences to examine the phylogenetic relationships within *Uvigerina* and between this genus and other rotaliids. Our analyses show that the family Uvigerinidae forms a well supported clade branching as a sister group to Bolivinidae and Cassidulinidae. Studied individuals of Uvigerinidae include three species described as *Uvigerina* – *U. mediterranea*, *U. elongatastriata* and *U. peregrina* – as well as *Rectuvigerina phlegeri* and *Trifarina earlandi*. As *U. peregrina* is more closely related to *R. phlegeri* and *T. earlandi* than to the other two *Uvigerina*, the taxonomic status of these species needs to be revised. At the intraspecific level, we studied a morphologically highly variable population of *U. peregrina* from the Oslo Fjord. For the sequences obtained from this population of *U. peregrina*, we found almost no divergence inside the internal transcribed spacer (ITS), which is the most variable part of ribosomal DNA. This indicates a high morphological plasticity of *Uvigerina* species, which should be taken into consideration when using this genus as a proxy in paleoecological reconstructions.

Keywords: Benthic foraminifera; Rotaliida; *Uvigerina*; Ribosomal DNA; Molecular phylogeny; Morphometry

1. Introduction

The benthic foraminiferal genus *Uvigerina* d'Orbigny, 1826 is common in temperate and high latitude regions (Haynes, 1981). Members of this cosmopolitan taxon mainly live in muddy sediment at shallow

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doi:10.1016/j.marmicro.2005.07.001

in-sediment depths, have a vagile mode of life, and prefer relatively cold marine waters of shelf to bathyal zones (Murray, 1991).

Uvigerina is frequently used in reconstructions of Cenozoic marine environments. Initially *Uvigerina* and related morphotypes were, and in the absence of other biostratigraphic markers still are, used as stratigraphic tools for Upper Cretaceous to Neogene sediments (e.g. Lamb, 1964; Hornibrook, 1968; Papp and Schmid, 1971; Douglas, 1973; Boersma, 1984). Since the ecological information carried by benthic foraminifera in general has been recognized, various species of *Uvigerina* have been extensively used as indicator taxa in studies pertaining to marine paleoenvironment and paleoclimate (e.g. Wright, 1980; Woodruff and Douglas, 1981; Boersma, 1986; Casford et al., 2003). In fossil applications, proxy relationships of benthic taxa with environmental factors are often derived from the ecological behaviour observed in Recent representatives of these taxa (Murray, 1991, 2001). This relationship is based on covariance of species abundances and/or benthic assemblage characteristics with environmental parameters (e.g. Bernhard, 1986; Fariduddin and Loubère, 1997; Fontanier et al., 2002; Licari et al., 2003).

Incorporation of elements in foraminiferal shells provides another means to constrain physico-chemical parameters of the marine (paleo-)environment. Important proxies are stable isotopes of oxygen and carbon, which are often measured on *Uvigerina*. Since *Uvigerina* taxa incorporate stable oxygen isotopes in their shell in near-equilibrium with ambient sea water (e.g. Shackleton, 1974; Woodruff et al., 1980; McCorkle et al., 1997), marine oxygen isotope records have been based on these species (e.g. Mix et al., 1995; Zachos et al., 2001). Many *Uvigerina* species occupy a shallow infaunal habitat (e.g. Corliss, 1985; Jorissen et al., 1998; de Stigter et al., 1998). Effort has been invested in studies to establish effects of microhabitat and calcification depth (e.g. McCorkle et al., 1997; Schmiedl et al., 2004) on the carbon isotope signature of *Uvigerina* (e.g. Grossman, 1984; Wilson-Finelli et al., 1998; Tachikawa and Elderfield, 2002; Mackensen and Licari, 2004).

The genus *Uvigerina* was first recorded in sediments of Lower Eocene age (Loeblich and Tappan, 1988). Galloway (1933) proposed *Bulimina* as its ancestor, giving rise first to *Uvigerinella* and then to *Uvigerina*, of which juvenile stages have a *Bulimina*-like aperture. According to Haynes (1981), *Uvigerina* and *Trifarina* may have evolved from *Praebulimina* in two independent lineages since the Late Cretaceous.

In current classification systems, *Uvigerina* belongs to the family Uvigerinidae Haeckel, 1894, which is placed in the superfamily Buliminacea Jones, 1975 (Loeblich and Tappan, 1988). The family includes the Recent genera *Uvigerina*, *Euuvigerina, Neouvigerina* and *Siphouvigerina,* grouped in the subfamily Uvigerininae Haeckel, 1894 and the Recent genera *Angulogerina* and *Trifarina,* grouped in the subfamily Angulogerininae Galloway, 1933. Members of Uvigerinidae are characterized by a triserial test tending to biseriality or uniseriality, a terminal aperture with a neck, a phyaline lip and an internal toothplate (Loeblich and Tappan, 1988). Distinctive features of Uvigerininae are rounded and inflated chambers, while Angulogerininae are characterized by triangular sections of their tests. Another morphologically similar genus, *Rectuvigerina*, which was examined in this study, has been classified in the family Siphogenerinoididae Saidova, 1981. Specimens belonging to this family have triserial or biserial tests, showing a tendency to develop uniseriality, and an aperture with a toothplate (Loeblich and Tappan, 1988).

The genus *Uvigerina* has been divided by Van der Zwaan et al. (1986) in three morphological groups. The *U. semiornata* group is characterized by a test that is triserial throughout, a short apertural neck standing in a depression, broad and high chambers strongly overlapping the previous ones, and pores with an elongated shape. The *U. peregrina* group shows a frequent tendency to reduced seriality. The relatively long apertural neck is not in a depression, the chambers are more or less inflated and not strongly overlapping the previous ones. The pores are rounded, the sutures are straight and often the basal chamber sutures are depressed. The ornamentation is variable and can be either hispid or costate, or a combination of both. In the *U. bononiensis* group the seriality is reduced during ontogeny. This group is further characterized by a neck that is not standing in a depression, a costate ornamentation, "en crochet" sutures, and rounded pores. In our material, two species are classified inside the *U. semiornata* group (*U. elongatastriata* and *U. mediterranea*), one in the *U.*