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Evolution and molecular phylogeny of *Cibicides* and *Uvigerina* (Rotaliida, Foraminifera)

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Evolution and molecular phylogeny of *Cibicides* and *Uvigerina* (Rotaliida, Foraminifera)

Evolutie en moleculaire fylogenie van *Cibcides* en *Uvigerina* (Rotaliida, Foraminifera)

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A Dario

Pour son ouverture d'esprit

Contents

These organisms are no more "one-celled animals and one-celled plants" than people are shell-less multicellular amebas.
Lynn Margulis, 1990

Chapter 1
General introduction

1.1. What is a foraminifer?

Foraminifers (often abbreviated to 'forams') are unicellular organisms distributed worldwide. Traditionally, foraminifers were studied by paleontologists and for that reason they are mainly known as organisms bearing a shell (called a test) and living in marine environments. However, recent publications showed that naked (without a test) and/or fresh water protists such as *Reticulomyxa filosa* (Pawlowski et al., 1999a; 1999b), *Toxisarcon synsuicidica* (Cedhagen & Pawlowski, 2002; Wilding, 2002) or the terrestrial *Edaphoallogromia australica* (Meisterfeld et al., 2001) are also foraminifers. These results demonstrate that the definition of foraminifers has to be based rather on other features, such as the nature of the pseudopodia than on the occurrence in marine environments or the presence of a shell (Pawlowski et al., 1999a; 1999b; Pawlowski & Holzmann, 2002). Foraminifers have rather thin pseudopodia, which are called granuloreticulopodia, because they contain granules and form a network. Because of their reticulopods, foraminifers were traditionally placed in the class Granuloreticulosea and grouped with lobose and filose amoebae in the superclass Rhizopoda, subphylum Sarcodina (Lee et al. 1985). However, the first molecular data, mainly ribosomal DNA sequences, challenged the monophyly of Rhizopoda (Clark & Cross, 1988; Cavalier-Smith, 1993, 1998). New classifications, based on molecular phylogenies of several genes show that the foraminifers are closely related to the Cercozoa (Keeling, 2001; Simpson & Roger, 2002; Archibald et al., 2003; Baldauf, 2003; Berney & Pawlowski, 2003; Longet et al., 2003), a heterogeneous group recognized only by molecular techniques and including chlorarachnean algae, euglyphid filose testate amoebae, some zooflagellates and plasmodiophorid plant pathogens (Cavalier-Smith, 1998; Cavalier-Smith & Chao, 2003). These taxa together with Radiolaria are currently included in the supergroup of Rhizaria, one of the six major groups of eukaryotes (Cavalier-Smith, 2002; Nikolaev et al., 2004; Simpson and Roger, 2004; Adl et al., 2005).
Contrary to many other protists, foraminifers have a particularly complex reproduction cycle, with alternating sexual and asexual generations (e.g. Lee et al., 1991; Goldstein, 2002 for details). The alternation of generations may be facultative or even disappear in some taxa, whereas others practice self-fertilization (Goldstein, 2002). The life cycle may also vary within one species according to the environmental conditions (Lee et al., 1991; Gooday & Alve, 2001). Foraminifers may have a benthic or planktonic mode of life. Benthic foraminifers live on or in the sea floor sediments and represent the vast majority of foraminiferal species: approximately 99.5% of the extant species recognized are benthic (data from Sen Gupta, 2002). Planktic species originated from the benthic ones during the middle Jurassic (Culver, 1993) and inhabit the water column.

Among the shelled foraminifers, ones with an organic, agglutinated and calcareous test are distinguished. The last group is separated in three subgroups: microgranular (fusulinids, extinct at the Permian-Triassic boundary), porcellaneous (miliolids) and hyaline (rotaliids and several related orders). The genera studied here belong to the rotaliids.

1.2. Species concept

The species is the fundamental concept in systematics, and it is the only one supposed to be clearly defined. However, several definitions of the species coexist, depending on available information.

The biological species concept

The biological species concept is the following: all the individuals that can interbreed are considered as belonging to the same species. This definition was defended by several founders of the modern synthetic theory of evolution as Dobzhansky, Mayr or Huxley, but this concept goes back prior to Darwin's time (Ridley, 1996). Problems in studying species appear when no interbreeding can be observed, for instance when species are extinct or reproduce asexually. Both cases may

concern the study of foraminifers. Because the knowledge of foraminifers is principally based on fossils, the main species concept used to classify them is morphological.

The morphospecies concept

The morphology remains the main feature to study extinct organisms[1]. Therefore, the species concept traditionally used in paleontology is the typological definition of the species or the morphospecies concept. In this case, the species is defined by a type, generally represented by the holotype, sometimes accompanied by one or more paratypes. This species concept can be quite rigid and the specimens deviating from the type morphology will be given a new species name and a new type. To smooth this typological species concept and decrease the number of newly described species, some authors working on foraminifers have introduced the assemblage concept, where the species is defined by a homogeneous group of individuals, considered more representative of the population (e.g. Zachariasse, 1975; Van der Zwaan, 1982). In the assemblage concept the morphological range covered by one species may be considerable, although it has to remain gradual and easily distinguishable from other species units (Van der Zwaan, 1982). Therefore, a species can house several morphotypes connected by morphological intermediates.

The phylogenetic species concept

A third definition of the species, used in phylogenetic analyses is the phylogenetic or genealogical species concept (Freeman & Herron, 2004). The species as well as higher taxa are defined as monophyletic groups, which include all the descendants of a common ancestor. The recognition of groups implies their genetic isolation and consecutive divergence. Unlike the biological species concept, the phylogenetic concept can also apply to extinct or asexually reproducing species.

The molecular or genetic species concept

Within the molecular phylogenetic analyses, monophyletic groups representing species may be detected with the help of clones[2] or defined through a sequence divergence threshold (e.g. 5% in Pawlowski et al., 2002b). For the time being, this concept is not well established.

1.3. Selection of *Cibicides* and *Uvigerina*

This work focuses on the evolution, phylogeny and microhabitat occupation of two rotaliid genera, *Cibicides* and *Uvigerina*. As seen before, the order Rotaliida includes benthic hyaline calcareous foraminifers. Because of their good fossil record and their sensitivity to environmental factors rotaliids are important tools for the reconstruction of paleoenvironments and paleoclimates. Representatives of *Cibicides* and *Uvigerina* are and have been important elements of the marine meiofaunal community and are employed in, for instance, micropaleontological and stable isotope studies to reconstruct past environmental change, despite the fact that there is little knowledge on their evolution. A better insight in their evolutionary history will certainly help to understand their (paleo)ecological functioning and thus improve their proxy value in paleoecological and paleoclimatological studies. Even more important is the fact that the success or failure in using them as proxies rests on the assumption that taxa can be properly distinguished on morphological grounds.

1) In exceptional cases DNA is still available from Quaternary remains, but no DNA older than 50,000-100,000 years has been found until now (Lindahl, 1993; Austin et al., 1997).
2) Clones allow for investigation of the intra-individual variations and therefore for the exploration of the limits of populations.

1.4. Selection of bioprovince and time slice

The most recent of the three major Cenozoic turnovers affecting benthic foraminifers occurred during the middle Miocene. Earlier episodes were the Paleocene-Eocene boundary, characterized by an extinction of benthic foraminifers (BEE, benthic extinction event, e.g. Speijer, 1994; Schmitz et al., 1996; Alegret et al., 2005), and the late middle Eocene-earliest Oligocene (e.g. Miller et al., 1992; Zachos et al., 2001). The research reported here focuses on benthic foraminiferal evolution since the middle Miocene cooling. This is the time when modern oceanic conditions originated, and the present water mass circulation took shape with prevailing cool bottom waters (Douglas & Woodruff, 1981). A large part of the extant deep-sea rotaliid species arose around the middle Miocene (Douglas & Woodruff, 1981; Miller et al., 1992), which reduces taxonomical bias that is introduced by differing nomenclatures for different time slices. Moreover, many of the taxa that evolved since the middle Miocene are alive today.

At the same time, the proto-Mediterranean was subject to important tectonic events, such as the closure of the connection between the Tethys and the Indian Ocean by the northward movement of the African plate. These changes transformed the well-ventilated Tethys into a poorly ventilated and even periodically stagnating Mediterranean basin since 14 Ma (Chamley et al., 1986; Seidenkrantz et al., 2000 and references herein), ultimately leading to the Messinian salinity crisis. Extensive studies in the area have led to the development of an extremely detailed and well-constrained time frame (e.g. Krijgsman et al., 1999; Abels et al., 2005). Next to a detailed time scale research in the Mediterraenan area has focused on paleonevironmental reconstruction, including anoxic and dysoxic environments. This has led to rather good insight in the relation between benthic foraminifers and specific environments. Moreover, the taxonomy of Mediterranean-Atlantic benthic assemblages is rather well constrained, although there are minor differences between schools. This allows minimizing taxonomical problems such as encountered when different bioprovinces are compared (see for instance Chapter 4: *Uvigerina akitaensis* and *U. peregrina* are the same species when molecular phylogeny is considered).

1.5 Molecular tools provide a new perspective in the phylogeny of foraminifers

Until now, all foraminiferan classifications (Haynes, 1981; Loeblich & Tappan, 1988, 1992; Sen Gupta, 2002) are based on morphological criteria of the test only. One of the problems encountered is, whether the criteria used at different taxonomic levels are relevant or not. The choice of the best characteristics has long been under debate (e.g. Towe & Cifelli, 1967; Hansen, 1979; Cifelli & Richardson, 1990; Haynes, 1990; Sen Gupta, 2002), and the different classifications have placed emphasis on such different criteria as the composition of the wall, its crystallographic nature through polarized light, the shape of the aperture, and the number or the arrangement of chambers (d'Orbigny, 1826; Williamson, 1858; Cushman, 1928; Galloway, 1933; Hofker, 1951; Loeblich & Tappan, 1964, 1988, 1992; Haynes, 1981; Mikhalevitch & Debenay, 2001). These classifications, however, are mainly typological and do not always represent relations between living organisms. A better understanding of the living species through genetic data would improve the phylogenetic background knowledge of foraminifers.

The ribosomal RNA (rRNA) genes have the advantage of being present in several hundreds of copies in each cell. For this reason, it is possible to amplify ribosomal DNA (rDNA) from one single foraminifer specimen. However, rRNA gene phylogenies are often biased by heterogeneity of substitution rates (Pawlowski et al. 1997; Philippe, 2000) and they give a low resolution of higher-level relationships (Flakowski et al., 2005).The study of other genes was restrained by the difficulty to cultivate foraminifers, because many more specimens (at least 50-100) are needed for amplification. For a limited number of species four foraminiferal proteins have been obtained: actin (Pawlowski et al., 1999a; Keeling, 2001; Flakowski et al., 2005), RNA polymerase II largest subunit (Longet et al., 2003), ubiquitin (Archibald et al., 2003) and tubulin (Linder et al., 1997; Habura et al., 2005). Revised analysis of the SSU (small subunit) rDNA omitting long-branching lineages confirmed the results found with these other genes (see above) and showed that SSU

rDNA data remained a valuable source of information for phylogenetic purposes (Berney & Pawlowski, 2003).
These rDNA studies (SSU and LSU (large subunit) have focused on the position of foraminifers in the tree of life (Pawlowski et al., 1994, 1996, 1999a, 1999b; Wade et al., 1996), links between the foraminiferal orders (Darling et al., 1997; Pawlowski et al., 1997, 2002a; Flakowski et al., 2005), and on species concepts in planktonic foraminifers (Darling et al., 1996, 1999, 2000; de Vargas et al., 1997, 1999, 2001, 2002; Huber et al., 1997; Stewart et al., 2001) and the benthic foraminifer *Ammonia* (Pawlowski et al., 1995; Holzmann et al., 1996; Holzmann & Pawlowski, 1997, 2000; Holzmann, 2000; Hayward et al., 2004). Several studies have concerned benthic taxa in general (Ertan et al., 2004) or have focused on specific groups, such as large foraminifers (Holzmann et al., 2001, 2003) and Glabratellidae (Tsuchiya et al., 2000, 2003). The low number of papers having the DNA of deeper-water benthic foraminifers as a subject can be explained by the difficulties encountered in obtaining living material from these locations.

1.6. Obtaining DNA

Obtaining DNA from benthic foraminifers is not an easy task. The specimens have to be alive at the moment they are grinded for DNA extraction. It is not yet known how long exactly after death the DNA is destroyed; however, this happens probably within hours or days. For this reason, the Rose Bengal staining method is not precise enough to indicate whether a specimen is dead or alive. The method we used to isolate live individuals was the direct observation of the specimens in sea water, under a dissection microscope and without any staining. Most of the collected specimens came from fully marine, relatively deep-water (>200m) environments and no pseudopodial activity was observed under the microscope. The color of the protoplasm, a good condition of the test (not damaged or broken), and detritus near the aperture were positive signs of life.
One of the main limiting factors to keep foraminifers alive as long as possible, particularly the deep-sea specimens, is temperature (Lutze & Altenbach, 1988; Altenbach et al., 2003). The cold chain has to be maintained from the sampling point until the moment the foraminiferan is dried or grinded for DNA extraction. There is no possibility to interact during the return of the boxcore or multicore, which can take a few hours, depending of the sampling depth[3]. This time interval can be rather critical, particularly if the sample is derived from deep waters and if the temperature difference between the sea floor and the sea surface is high (up to 10-15°C). Consequently, sampling for live specimens is generally much more successful at high latitudes or during mid-latitude winters, than at low latitudes or during summer in mid-latitudes. From this point of view, perfect places to sample deep-sea species are the Scandinavian fjords where these species are found at shallow depths. When the sample is on board, it is important to sieve the sediment immediately, if possible with bottom water at ambient temperature, but at least with cold sea water. Afterwards, the sieved sample will be stored in the refrigerator, and kept under the (preferentially cold) light of the microscope for the shortest possible time, and on ice or in a cold room.
An additional problem may be the huge pressure difference experienced by the specimens collected at deep-sea locations. Decompression may not be a great problem for foraminifers sampled at 1000-2000m water depth (Altenbach et al., 1992). Nevertheless, the pressure difference between deep-water and surface-water environments becomes critical below 2200m and appears to be lethal for most deep-sea foraminifers (Kitazato, 1994). Deep-sea specimens are also more difficult to sample because the total number of foraminifers decreases with the increase of depth, perhaps due to a diminution of the amount of food (Corliss, 1991).
Even though drying is inevitable to obtain SEM pictures, it considerably reduces the quality of DNA. Once the specimen is dried, the delay before DNA extraction is also critical. Two examples can illustrate this. In 2002, we sampled in the Oslo Fjord and found promising material; within one month (a maximum of 23 days), the specimens were picked, dried, SEM pictured and DNA

3) The hauling speed is about 1m/s. It will take around half an hour to obtain a multicore from 2000m.

was extracted. The percentages of positive results were excellent (62%, 37 positive out of 60 extractions). One year later, in the same season, we collected samples on the west coast of Sweden, not far away from the Oslo Fjord and under the same conditions. The delay between drying and extraction of the material was longer (31 to 43 days, depending when it was sampled during the cruise). The percentage of positive results decreased dramatically (12%, 7 positive out of 60 extractions). The second example comes from Mediterranean samples. A few specimens of *Cibicides* were collected near Marseille. Four living individuals were immediately extracted after cleaning and picking and all of them gave DNA; four other specimens were dried, SEM pictured and DNA extracted two months later. Only one individual gave a positive result but the quality of its DNA was much worse than for the freshly extracted specimens.

1.7. This study

The aim of this study is to compare classical phylogenies of *Cibicides* and *Uvigerina* based on morphology and the fossil record with the new ones derived from molecular analyses. Synthesis of these two approaches may lead to new insights in the evolutionary history of the two genera. We hope to connect steps in this evolutionary history with large scale changes in the paleoenvironmental or paleoceanographic setting of the Mediterranean area. Specifically, we hope to connect the evolutionary history with the known microhabitat preferences of the various species. Although research over the past decades has brought together many data on microhabitat occupation and regulation, it is virtually unknown why and when taxa started to inhabit them.
In the three following chapters the molecular results are presented: the phylogeny of the rotaliids based on the complete SSU rDNA (Chapter 2), the phylogeny of *Cibicides* based on two fragments, representing 2/3 of the SSU rDNA (Chapter 3), and the phylogeny of *Uvigerina* based on the 3' end fragment of the SSU rDNA (Chapter 4). The subsequent chapters concern the classification, taxonomy, morphology and the microhabitats of *Cibicides* (Chapter 5) and *Uvigerina* (Chapter 6), respectively. In these chapters we also compare the molecular and morphological phylogenies and build new ones. The final chapter discusses the main findings and compares the phylogenies and evolutionary histories of both genera (Chapter 7).

Chapter 2

Molecular phylogeny of the Rotaliida (benthic calcareous foraminifers) based on the complete small subunit of ribosomal DNA

2.1. Introduction

The order Rotaliida comprises calcitic hyaline perforate species and represents a considerable part of the benthic foraminifers. They are important elements of the meiofaunal community and are extensively used to reconstruct past environmental changes (Debenay et al., 1996; Van der Zwaan et al., 1999).

Williamson (1858) was the first author who based his foraminiferal classification on the wall composition (Cifelli & Richardson, 1990); the three groups he created are still in use today as textulariids (arenaceous foraminifers), miliolids (porcellaneous foraminifers) and rotaliids (hyaline foraminifers). Later, the rotaliids were separated from the agglutinated and the porcellaneous foraminifers. However, this distinction was not always adhered to in the classifications produced before the publications of Cushman (1928) and Galloway (1933). For example, Reuss (1861), Carpenter et al. (1862), Brady (1884), Rhumbler (1895) or Cushman (1922) placed arenaceous textulariids and hyaline bolivinids (sometimes with buliminids and cassidulinids) within the same group. Several more recent publications still grouped agglutinated with calcareous foraminifers.

Hofker (1951, 1956) created the order Dentata for foraminifers bearing a tooth-plate. His classification is deviating from the mainstream since it is based on the aperture: the presence of a proto- and/or a deuteroforamen permits to separate three different suborders. The basal family giving rise to the suborders consists of agglutinated taxa, whereas the other groups comprise calcareous perforate foraminifers. Within the suborders, the arrangement of the chambers, the shape of the tooth-plate, the size, and the position of the pores and the shape of the aperture discriminate the various families. In line with Hofker's point of view, the classification elaborated by Mikhalevich (Mikhalevich & Debenay, 2001) is based on the morphology of the apertural structures and includes agglutinated and calcareous foraminifers within the same groups, assuming that parallel evolution from agglutinated to calcareous foraminifers happened several times. Therefore, in their scheme, the Class Rotaliata included the Subclasses Textulariana and Rotaliana. Five Superorders are distinghuished within the Rotaliana: the Robertinoida, the Buliminoida, the Discorboida, the Nonionoida and the Seabrookinida.

The classifications of Cushman (1928) and Galloway (1933) did not assign any taxon higher than family level within the order Foraminifera. However, their families group foraminifers with the same wall composition, and half of these families concern calcareous perforated species. The composition of the test, the arrangement of the chambers and the aperture were the main criteria used to characterize the families. Sigal (1952) divided the foraminifers into three suborders on the basis of the number and shape of the chambers (single, tubular and multiple). The classification of Reiss (1958) dealt with the hyaline (lamellar) foraminifers. It is based on the composition and texture of the wall, the aperture, the tooth-plate, the canal system, and the chamber arrangement.

Since 1964, the classifications of Loeblich & Tappan are used as the standard text in spite of some discrepancies. In their first classification (1964), Loeblich & Tappan primarily used the wall composition and microstructure of the test to distinguish their suborders; the mode of chamber and septal addition and the arrangement of the chambers also had major importance. Next important were the apertural characteristics and their modifications. Chamber form and arrangement were taken into account as final characteristic. The suborder Rotaliina included the hyaline foraminifers and was subdivided into ten superfamilies. In their next main classification, Loeblich & Tappan (1988) defined more suborders (Involutinina, Spirillinina, Carterinina, Silicoloculinina, Lagenina, Robertinina and Globigerinina were added). The suborder Rotaliina was divided into 24 superfamilies; the criteria used were the number of chambers, the presence or absence of perforations, canals and cavities in the test and the aperture (Fig. 2.1a). In 1992, to solve some of the inconsistencies reported by Haynes (1981, 1990, see below), Loeblich & Tappan raised the foraminifera from an order to a class (the foraminiferal suborders were thus given order status) and recognized the order Buliminida Fursenko, 1958. Sen Gupta (2002) slightly modified the last classification of Loeblich & Tappan (1992), for example by grouping *Cibicides* and *Cibicidoides* in the same family (Fig. 2.1b).

It was shown by Towe & Cifelli (1967) that Loeblich & Tappan put too much emphasis on the

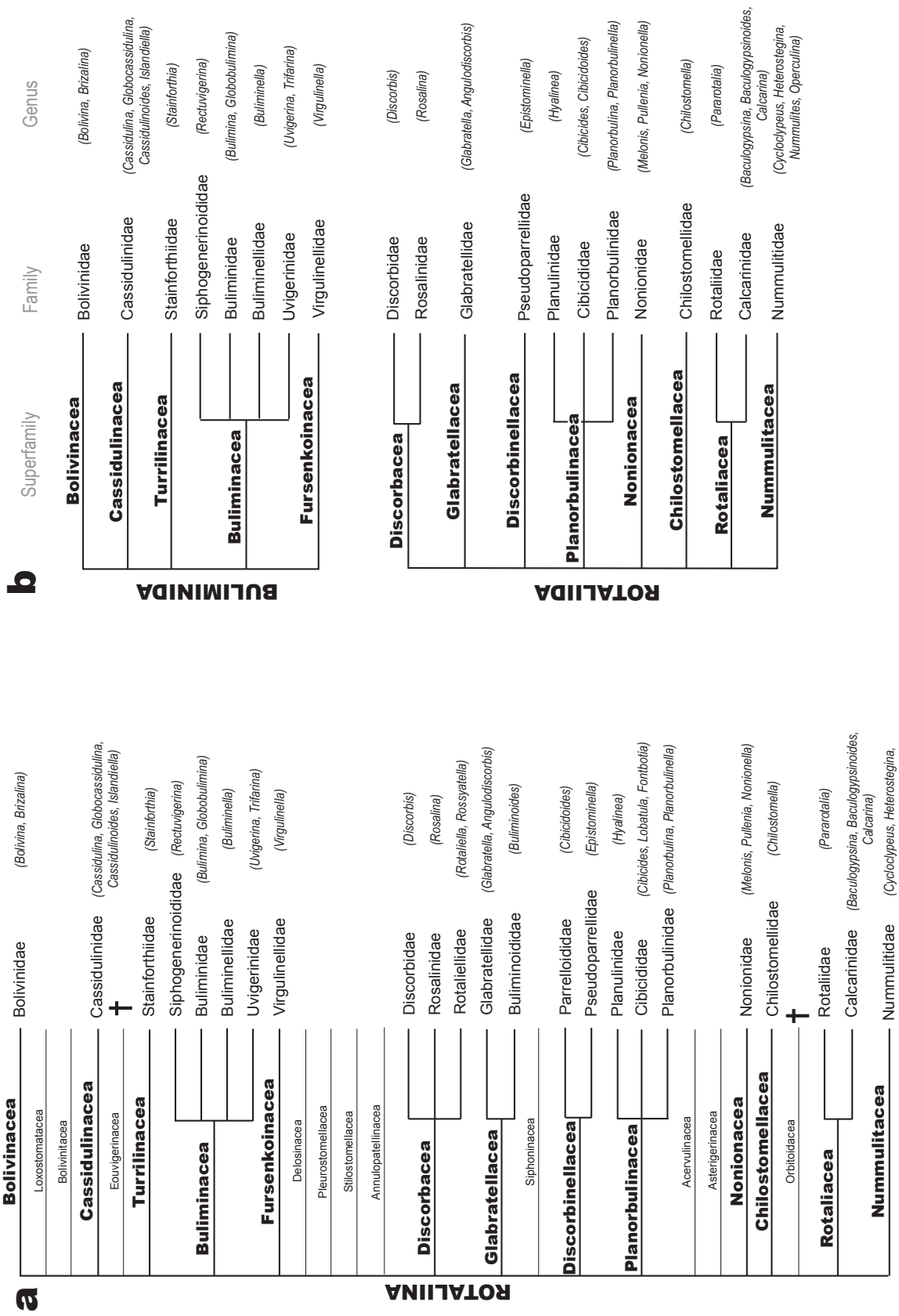

Figure 2.1. Diagrams showing the taxonomic positions of the studied genera inside the classifications of Loeblich & Tappan (1988) (a) and Sen Gupta (2002) (b).
a)The 24 superfamilies are shown with the ones represented in phylogenetic analyses in bold and a cross for the extinct ones;
b) Only the 13 superfamilies studied here are shown.

crystallographic nature of the wall in their separation of the different superfamilies: the optically granular tests were grouped in the super-family Cassidulinacea in the first classification (1964) and, therefore, closely related species were separated on the basis of this criterion. Despite the article of Towe & Cifelli (1967), the optical structure of the test remained of great importance in the revised classifications of Loeblich & Tappan (1988, 1992).

In 1981, Haynes also retained the wall structure as the primary basis of subdivision; however, the shape of the aperture was given more emphasis than in Loeblich & Tappan's classification (1964). The superfamilies were raised to orders, and the Nodosariida (Lagenina of Loeblich & Tappan, 1988), the Robertinida, the Buliminida and the Globigerinida were separated from the Rotaliida, distinguished by the structure of the test, the arrangement of the chambers and the coiling mode. In Haynes' classification (1981), the Buliminida comprised the hyaline perforate foraminifers with a toothplate and included the following superfamilies: the Buliminacea, the Bolivinitacea and the Cassidulinacea, whereas the Rotaliida contained the Spirillinacea, the Discorbacea, the Asterigerinacea and the Orbitoidacea.

To summarize the traditional classification (see Fig. 2.1), the calcareous perforate hyaline foraminifera are classified within one (Loeblich & Tappan, 1964, 1988) or two groups (Haynes, 1981; Loeblich & Tappan, 1992; Sen Gupta, 2002). The division of these groups is based on the presence (Buliminida) or absence (Rotaliida) of a tooth-plate, a loop-shaped (Buliminida) or slit-like (Rotaliida) aperture, and a high (Buliminida) or low (Rotaliida) trochospiral coil.

Since several years, the molecular approach has provided new viewpoints in the foraminiferal classification. For the moment, almost all these studies are based on the ribosomal DNA (rDNA). The first molecular results, based on a 1000 base pair (bp) fragment situated at the 3' end of the small subunit (SSU) of rDNA, showed five major clades inside the foraminifers. These confirmed only partly the morphological classifications where groups are primarily distinguished on the basis of wall composition: the molecular results suggested four groups representing the morphological orders Miliolida, Astrorhizida, Allogromiida and Globigerinida, and the fifth blending the Textulariida and the Rotaliida (Pawlowski et al., 1997). This mixed group of textulariids and rotaliids was explained by assuming a radiation occurring in a relative short time or slow rates of evolution within both groups (Pawlowski et al., 1997). Indeed, more recent analyses were able to separate the calcareous taxa from the agglutinated ones (Holzmann et al., 2003; Ertan et al., 2004; Flakowski et al., 2005) even though they did not use all the available taxa of Textulariida. The last paper was based on actin sequences and confirmed several findings of the rDNA studies like the basal position of allogromiids, astrorhizids and athalamids in the foraminiferal tree, the early divergence of miliolids, the monophyly of rotaliids, and the position of globigerinids inside the rotaliids (Flakowski et al., 2005).

Recent analyses also investigated the relationships inside the rotaliids, through the fragment at the 3' end of the SSU. Holzmann et al. (2003) examined the links between the Nummulitidae and seven other rotaliid families, Ertan et al. (2004) aimed at looking into the relationships of eleven genera of calcareous foraminifers, whereas Schweizer et al. (2005) investigated the position of uvigerinids inside the rotaliids (see Chapter 4). The two last analyses (Ertan et al., 2004; Schweizer et al., 2005) showed low statistical support for the deep nodes. Schweizer et al. (submitted, see Chapter 3), studying the cibicidids, added a supplementary fragment of about 1,000 bp, situated at the 5' end of the SSU to obtain more information. The addition of this second fragment allowed to show the monophyly of cibicidids and improved the statistical support of nodes that were not well supported in the previous analysis (Schweizer et al., 2005, Fig. 7). Further investigations of the rotaliids need to increase the number of species studied and the amount of information by adding new sequenced regions.

In phylogenetic analyses performed with the 3' fragment (14F1-B), there is no significant difference between species in the regions which are too conserved. On the other hand, the highly variable regions are too different to be properly aligned. In both cases, the signal is not powerful enough. For this reason, we decided to enlarge the studied fragment by sequencing the complete SSU to obtain a stronger signal. In the present chapter, we analyse the complete SSU sequences of foraminifers belonging to 10 of the 22 extant superfamilies present in Loeblich & Tappan's

classification (1988) and the 3' end fragment of these and three additional superfamilies. Selected specimens were amplified for the complete SSU (21 new sequences, between 3278 and 3632 nucleotides). Additionally, the fragment of 1000 nucleotides extensively used for the phylogeny of the SSU (e.g. Pawlowski, 2000; Holzmann et al., 2003; Darling et al., 2004; Ertan et al., 2004) was sequenced for all the samples we could obtain. Due to practical problems[1], it was not possible to sequence the complete SSU for all the taxa we had. However, earlier studies (Chapter 3 and 4) showed the same partition between the main clades as the complete SSU analysis. Therefore, subtrees of each clade were analysed with the 3' end fragment.

2.2. Material and methods

2.2.1. Collection of the samples

Live specimens of rotaliids were collected around the world during different expeditions from 1995 to 2003 (see Tables 2.1 and 2.2 for details). Sediment samples were either taken by hand with a scraper at the shallow sites or collected by boxcoring and multicoring at the deeper sites. The top few centimetres of sediment were collected with a spoon and immediately sieved using water from the same environment as the sampling site (fractions 500/250/125μm). The different fractions were stored at temperatures close to that of the collection site. Specimens were cleaned and picked under the dissection microscope within hours to a few days. Live individuals were distinguished from dead ones by their natural coloration, the lack of cytoplasm in the last chamber, the good preservation of the test (not eroded or broken), and the presence of debris around the aperture. Whenever possible, specimens were transferred to Petri dishes containing clean sea water and observed a few hours after picking to check whether they were alive.

2.2.2. DNA extraction, PCR amplification, cloning and sequencing

Extraction of DNA from single or multiple specimens was done with DOC lysis buffer, CTAB or guanidine buffer (Pawlowski, 2000), and, for large samples, DNeasy Plant Mini Kit (Qiagen). Fragments of rDNA were amplified with primers s14F3-sB, and reamplified with primers s14F1-sB for the 3' end fragment of the SSU. Some specimens of each available clade were selected to sequence the complete small subunit. Two supplementary fragments were added using primers s6F and s17 (s6F and s15rot for the reamplification) for the middle fragment and the primers sA10 and s13 (sA10 and s6rA for the reamplification) for the 5' end fragment. The sequences of the primers are indicated in Table 2.3 and the positions of the primers are summarized in Figure 2.2. The PCR conditions were the following: total volume of 50 μl, denaturation at 94°C during 30s, annealing during 30s at 50°C for the amplification and at 52°C for the reamplification and extension at 72°C during 2min with 40 cycles for the amplification and 35 cycles for the reamplification, final elongation for 5min at 72°C. The positive PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics). A few samples were sequenced directly within the fragment 14F1-B; all the others were cloned. Purified products were ligated in the pGEM-T Vector system (Promega) or the Topo Cloning vector (Invitro Gene), and cloned using ultracompetent

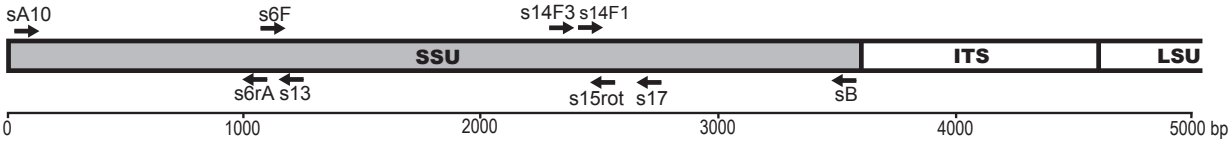

Figure 2.2. Position of the primers used to amplify the three fragments of the SSU rDNA.

1) Because sequencing of the complete SSU is time consuming, we selected some specimens from each clade identified in previous studies. However, it was not possible to obtain the complete SSU for all the selected taxa in spite of repeated attempts. The middle fragment was the most difficult to obtain because of its large size. For other samples it was impossible to clone or sequence the 5' end fragment.

Table 2.1. List of new complete SSU sequences with the origin of DNA samples, the SSU length (nt= nucleotides) and the GenBank access numbers. *Stainforthia fusiformis* SSU sequence is a hybrid of two genetically close samples; A10 (DQ205387) and 14F1 (AY934744) come from 3965 and 6F (DQ452714) from 3979. Asterisks indicate sequences previously published.

Superfamily	Species	Locality	DNA isolate	SSU length	Access number
Cassidulinacea	*Islandiella* sp.	Svalbard, Norway	2643	3278 nt	DQ408638
	Cassidulinoides porrectus	Terranova Bay, Antarctica	3924	3348 nt	DQ408639
Turrilinacea	*Stainforthia fusiformis*	Oslo Fjord,	3965	3473 nt	DQ205387*
		Norway			AY934744*
		Dunstaffnage, Scotland	3979		DQ452714
Buliminacea	*Bulimina marginata*	Oslo Fjord, Norway	3599	3462 nt	DQ408646
	Rectuvigerina phlegeri	Nazaré Canyon, Portugal	U239	3579 nt	DQ408641
	Trifarina earlandi	McMurdo Sound, Antarctica	2187	3571 nt	DQ408640
	Uvigerina peregrina	Oslo Fjord, Norway	U27	3517 nt	DQ408642
Discorbacea	*Discorbis rosea*	Florida, USA	753	3507 nt	DQ408644
Discorbinellacea	*Epistominella vitrea*	Cape Evans, Antarctica	2060	3463 nt	DQ408647
Planorbulinacea	*Hyalinea balthica*	Oslo Fjord, Norway	3604	3631 nt	DQ408645
	Planorbulinella sp.	Elat, Israel	358	3365 nt	DQ452687
	Unknown rotaliid	Culture	3675	3402 nt	DQ408643
	Cibicides pachyderma-kullenbergi	Nazaré Canyon, Portugal	C86	3409 nt	DQ408652
	Cibicides pachyderma	Nazaré Canyon, Portugal	C196	3431 nt	DQ408653
	Cibicides lobatulus	Oslo Fjord, Norway	C24	3526 nt	DQ408649
	Cibicides lobatulus	Skagerrak, Sweden	C120	3632 nt	DQ408650
	Cibicides lobatulus	Marseille, France	C170	3596 nt	DQ408648
	Cibicides sp.	North Atlantic	2524	3517 nt	DQ408651
Nonionacea	*Melonis pompilioides*	Skagerrak, Sweden	1400	3556 nt	DQ408657
	Pullenia subcarinata	McMurdo Sound, Antarctica	1148	3471 nt	DQ408656
	Pullenia subcarinata	McMurdo Sound, Antarctica	1850	3472 nt	DQ408655

cells XL2-Blue MRF' (Stratagene). Sequencing reactions were prepared using an ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analysed with an ABI-377 DNA sequencer or an ABI-PRISM 3100 (Applied Biosystems), all according to the manufacturer's instructions.

2.2.3. Phylogenetic analysis

The new sequences presented here were deposited in the EMBL/GenBank Nucleotide Sequence Database; their accession numbers are reported in Tables 2.1 and 2.2. To extend our data set, we added other sequences from the EMBL/GenBank database (mainly deposited by Ertan et al. (2004), Holzmann et al., (2001, 2003), Pawlowski et al., (1999a, 2003), Tsuchyia et al. (2003)). The accession numbers are given on the trees (see Figs. 2.3-2.7). Sequences were aligned manually by applying Seaview software (Galtier et al., 1996).

The maximum likelihood (ML) trees were obtained using the PhyML program (Guindon & Gascuel, 2003) with the HKY (Hasegawa, Kishino, Yano) model (Hasegawa et al., 1985), allowing transitions and transversions to have potentially different rates, and the GTR (General Time Reversible) model allowing all the transitions and transversions rates to be different (Lanave et al., 1984; Rodriguez et al., 1990). To correct the among-site rate variations, the proportion of invariable sites (I) and the α parameter of γ distribution (G), with eight rate categories, were estimated by the program and taken into account in all analyses. The bootstrap (BS) method (Felsenstein,

Table 2.2. List of new partial SSU sequences with the origin of DNA samples and the GenBank access numbers.

Superfamily	Species	Locality	DNA isolate	SSU fragment	Access number
Bolivinacea	*Bolivina* sp.	Guam	2341	14F1-B	DQ452688
Cassidulinacea	*Cassidulina laevigata*	Oslo Fjord, Norway	2508	14F1-B	DQ452690
	Cassidulinoides porrectus	Terra Nova Bay, Antarctica	3924	14F1-B	DQ452689
Turrilinacea	*Stainforthia fusiformis*	Dunstaffnage, Scotland	3979	14F1-B	DQ452691
Buliminacea	*Globobulimina turgida*	Oslo Fjord, Norway	3601	6F-17	DQ452711
				14F1-B	DQ452710
	Buliminella elegantissima	St-Cyr, France	459	14F1-B	DQ452702
Discorbacea	*Rossyatella* sp.	La Favière, France	3953	14F1-B	DQ452704
					DQ452705
					DQ452706
	Rotaliella sp.	Cape Evans, Antarctica	1002	14F1-B	DQ452707
Glabratellacea	*Buliminoides* sp.	Helengeli, Maldives	623	14F1-B	DQ452703
Discorbinellacea	*Epistominella vitrea*	Cape Evans, Antarctica	2060	14F1-B	DQ452696
Planorbulinacea	*Planorbulinella* sp.	Elat, Israel	358	14F1-B	DQ452687
	Planorbulina mediterranensis	Golfe du Morbihan, France	144	14F1-B	DQ452709
	Cibicides refulgens	Marseille, France	C176	14F1-B	DQ452701
Nonionacea	*Melonis pompilioides*	Skagerrak, Sweden	1400	14F1-B	DQ452697
					DQ452698
	Nonionella labradorica	Skagerrak, Sweden	1396	14F1-B	DQ452695
	Nonionella labradorica	Oslo Fjord, Norway	3600	6F-17	DQ452712
				14F1-B	DQ452692
					DQ452693
					DQ452694
	Nonionella labradorica	Skagerrak, Sweden	3966	6F-17	DQ452713
	Pullenia subcarinata	NH-Ice Hut, Antarctica	1087		DQ452700

1985) was performed, with 100 replicates, to assess the reliability of internal branches.
Bayesian analyses were made with MrBayes 3.1.1 (Huelsenbeck & Ronquist, 2001), using the GTR+I+G model. Two independent analyses were performed at the same time with four simultaneous chains run for 1,000,000 generations, and sampled every 100 generations with 1,000 of the initial trees discarded as burn-in. The posterior probabilities (PP) were calculated at the same time.
The nucleotide-nucleotide BLAST (Basic Local Alignment Search Tool) was used to find the closest relatives of sequences represented only by the 3' end fragment. This program finds regions of local similarity between sequences by comparing nucleotide sequences to sequence databases and calculates the statistical significance of matches (Altschul et al., 1997).

2.3. Results

To avoid contamination and estimate the variability inside one population or even one specimen, we have made several clones of some of our samples. Clones derived from the same sample (same individual or same population) were usually highly similar and branched closely in the trees (Figs. 2.3-2.7).
The complete SSU sequences were analysed first (Fig. 2.3). Some taxa like *Ammonia*, *Elphidium* or *Haynesina* appeared to evolve much faster than other groups and were removed from the

Table 2.3. Sequences of the primers used for the PCR amplification of the three fragments.

SSU primer	Sequence	Orientation	Specificity
sA10	CTC AAA GAT TAA GCC ATG CAA GTG G	Forward	Forams
s13	GCA ACA ATG ATT GTA TAG GC	Reverse	Forams
s6rA	GCA CCA GAC TTG CCC	Reverse	Universal
s6F	CCG CGG TAA TAC CAG CTC	Forward	Forams
s17	CGG TCA CGT TCG TTG C	Reverse	Forams
s15rot	CAT AAT CAT GAA AGG ACT AGC	Reverse	Rotaliida
s14F3	ACG CAA GTG TGA AAC TTG	Forward	Forams
s14F1	AAG GGC ACC ACA AGA ACG C	Forward	Forams
sB	TGA TCC TTC TGC AGG TTC ACC TAC	Reverse	Universal

analyses to avoid the long-branch attraction (LBA) phenomenon (Felsenstein, 1978; Philippe, 2000). The 5' end fragments (specimens 3600, 3601, 3966) or middle ones (142, 1839, C29, C172, C184) of some of the samples selected for sequencing the complete SSU could not be obtained. A second analysis including the sequences of the complete SSU and these sequences with missing data was therefore performed (Fig. 2.4). Both analyses confirmed the main groups found in earlier analyses (see Chapters 3 and 4[2]).

Three groups emerge inside the Rotaliida (the 5' end fragment is missing in species between brackets):

1) *(Globobulimina turgida), Bolivina spathulata*, *Islandiella* sp., *Cassidulinoides porrectus*, *Uvigerina peregrina*, *Rectuvigerina phlegeri* and *Trifarina earlandi*;
2) *Hyalinea balthica*, *Planorbulinella* sp., *Planorbulina mediterranensis*, *Discorbis rosea,* the Nummulitidae and *Pararotalia nipponica*;
3) *(Nonionella labradorica)*, *Bulimina marginata*, *Stainforthia fusiformis*, *Epistominella vitrea*, *Pullenia subcarinata*, *Melonis pompilioides* and *Cibicides*.

In the first analysis of the complete SSU (Fig. 2.3), the statistical support of the three groups is high: 95% BS or higher and 1.00 PP. Analyses performed with PhyML and MrBayes (data not shown) gave the same topology. The length differences observed in the various branches of the phylogenetic tree indicate that the evolutionary rates are extremely diverse in the different foraminifers studied. Within the studied taxa, *Bolivina spathulata, Hyalinea balthica*, *Planorbulinella* sp., *Planorbulina mediterranensis* and *Discorbis rosea* evolve obviously faster than other rotaliids.

The analysis of the SSU with missing data gave a phylogenetic tree with much less stability (Fig. 2.4). However, the three analyses (ML with HKY and GTR and Bayesian with GTR) gave the same topology (except for *Stainforthia*, branching with *Bulimina* in GTR analysis, data not shown). The statistical support is good for the second group, but much lower for the first and third groups (Fig. 2.4). Taxa like *Planorbulina*, *Cibicides* sp. and *C. ungerianus* have a firm position in the different analyses, whereas *Nonionella labradorica* is somewhat less stable. This species is usually placed at the basis of the third clade, sometimes grouping with *Bulimina marginata*. The other less stable taxa are *C. refulgens*, which tends to branch between *Melonis pompilioides* and *Pullenia subcarinata*, and *Globobulimina turgida* which is either branching at the basis of the first group or inside the third group (data not shown).

For the analysis of the 3' end fragment of the SSU, separated subtrees (Figs. 2.5-2.7) were built for the three datasets belonging to the groups previously distinguished with analyses of the complete SSU (Figs. 2.3-2.4). Analyses were performed with PhyML and the HKY+G+I model. Because the groups included always the same taxa throughout all analyses (Figs. 2.3-2.4, but see also Figs.

2) The clade containing *Globobulimina*, the uvigerinids, the cassidulinids and *Bolivina* was the second group described in Schweizer et al. (2005) and it was also closer to the third group than the first one. This second group became group 1 in next analyses and is less related to group 3 than group 2 (this chapter and Chapter 3).

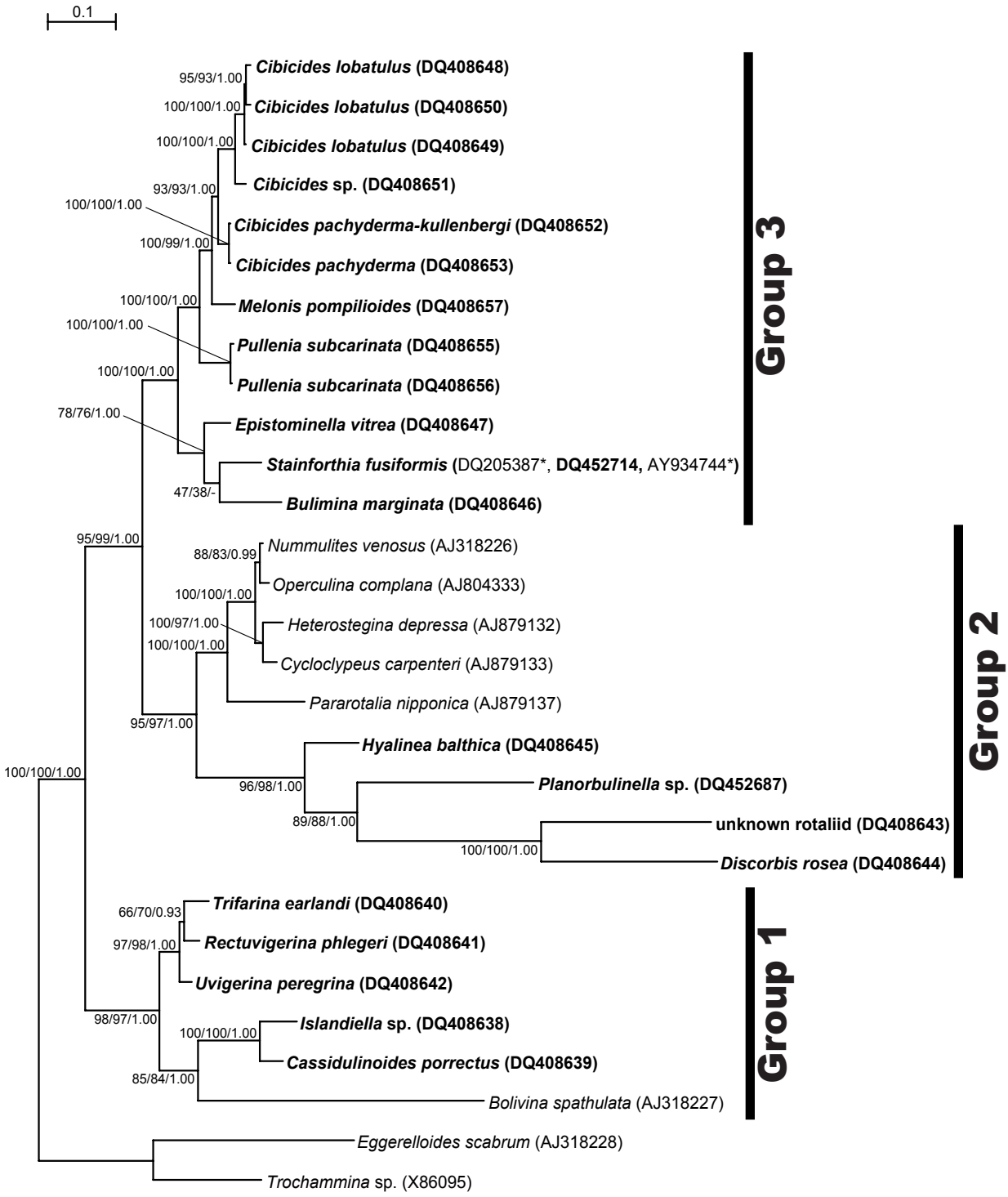

Figure 2.3. Phylogeny of Rotaliida inferred from complete SSU rDNA sequences (3702 analysed sites) using the ML method (HKY+I+G). Tree rooted on textulariids. Bootstrap for HKY and GTR (ML analysis) and PP (Bayesian analysis) indicated at the nodes. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers in brackets).

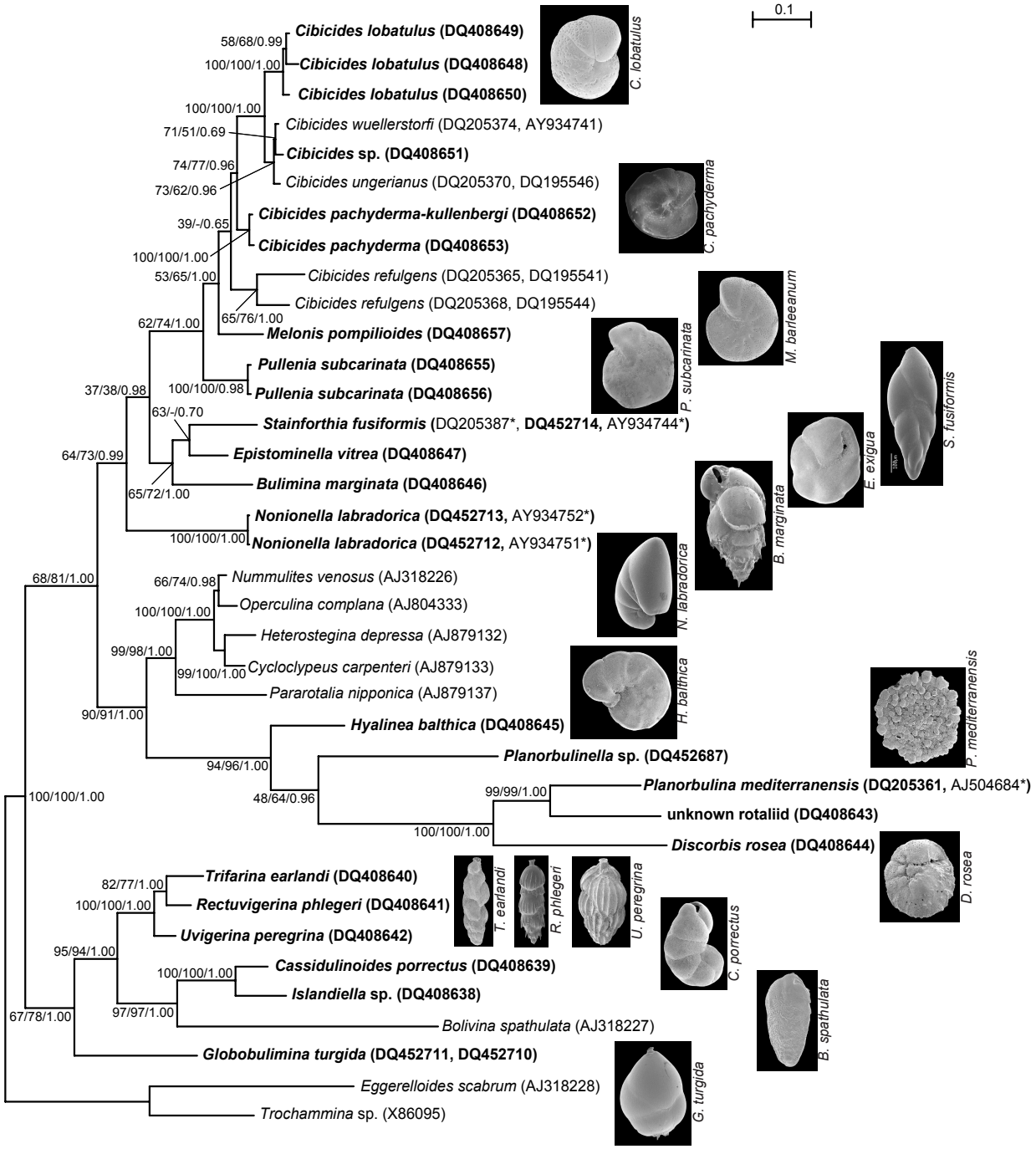

Figure 2.4. Phylogeny of Rotaliida inferred from complete SSU rDNA sequences and incomplete ones (A10 missing for *G. turgida* and *N. labradorica*, 6F missing for *C. refulgens*, *C. ungerianus*, *C. wuellerstorfi* and *P. mediterranea*); 4793 analysed sites using the ML method (HKY+I+G). Tree rooted on textulariids. Bootstrap for HKY and GTR (ML analysis) and PP (Bayesian analysis) indicated at the nodes. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers in brackets).

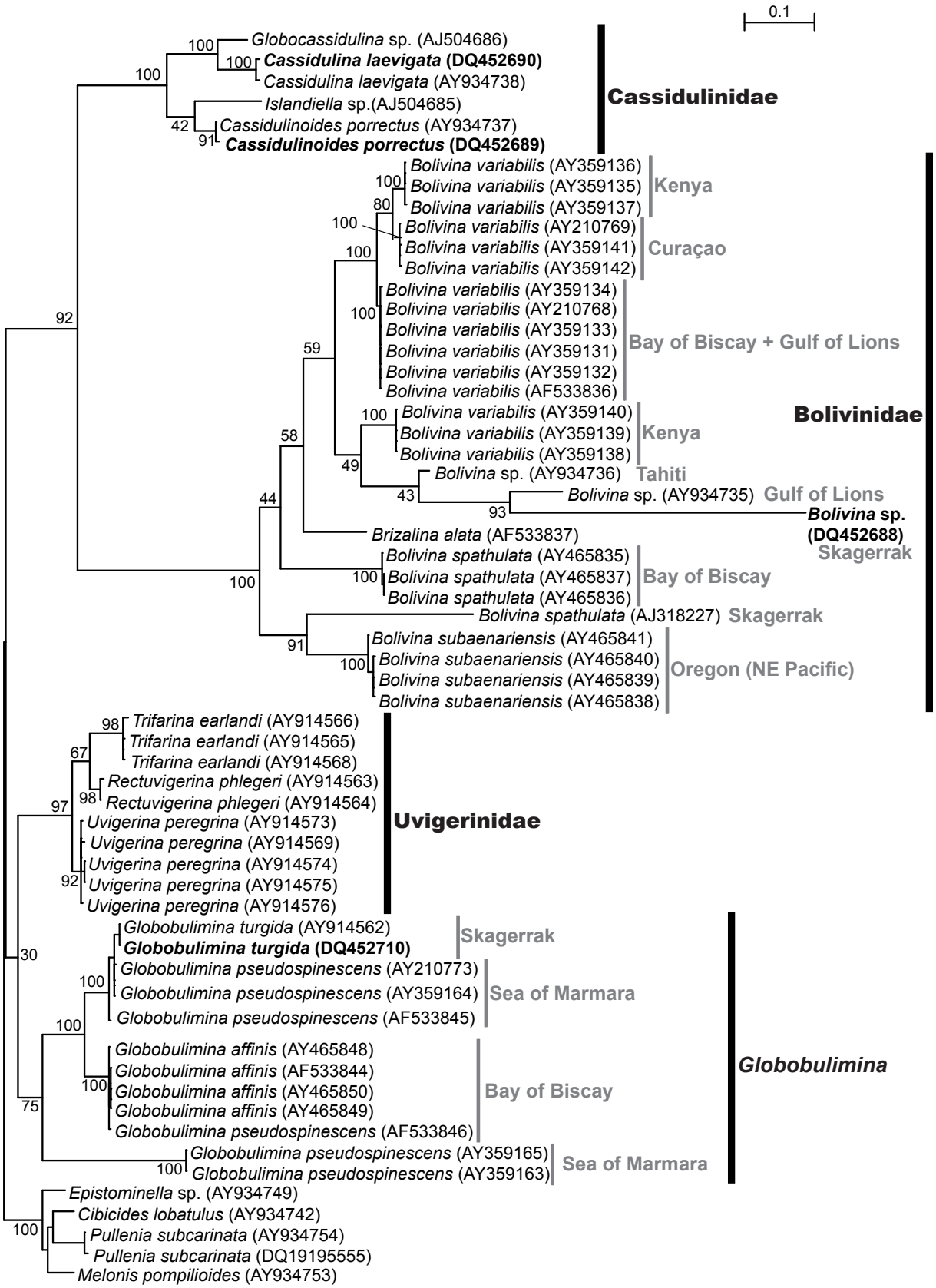

Figure 2.5. Phylogeny of the rotaliids belonging to the first group inferred from partial SSU rDNA sequences (1149 aligned sites) using the ML (HKY+I+G) method. Tree rooted on *Cibicides*, *Epistominella*, *Melonis* and *Pullenia*. Bootstrap indicated at the nodes. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers in brackets).

3.4 and 4.7), some taxa which are only represented by the 3' end fragment were also added to the analyses. Hundred and eighty sequences belonging to about 60 species of Rotaliida have been analysed. All the genera represented by more than one species are monophyletic except *Cibicides* and *Epistominella*. Within group 1 (Fig. 2.5), there are two clades formed by *Globobulimina* and Uvigerinidae on the one hand and *Bolivina* and Cassidulinidae on the other. The statistical support of the four groups is good (respectively 100% BS for Cassidulinidae and *Bolivina*, 97% BS for Uvigerinidae and 75% BS for *Globobulimina*). Among the two main groups, the support is high for *Bolivina* + Cassidulinidae (92% BS) but rather weak for Uvigerinidae + *Globobulimina* (30% BS). The two genera represented by an important set of sequences (*Globobulimina* and *Bolivina*) are usually well sorted by species and location, except one *B. spathulata* from the Skagerrak and one *G. pseudospinescens* from the Bay of Biscay. The second group (Fig. 2.6) keeps the same topology in the subtree as with in the tree of the complete SSU: the Nummulitidae and Calcarinidae (77% BS) on the one hand and the Discorbacea and Planorbulinacea (without *Cibicides*) on the other (93% BS). *Rosalina orbicularis* is separated in three groups. The unknown rotaliid was first identified as *Rosalina* sp., but its position in the 3' end phylogenetic tree indicates it is in fact closer to *Planorbulina*. The BLAST showed that *Glabratella, Angulodiscorbis, Buliminoides, Buliminella, Rotaliella* and *Rossyatella* were closer to group 2. For this reason, they are represented in Fig. 2.6. Their grouping shows a high support (100% BS), but the relation with group 2 needs more data. Inside group 3 (Fig. 2.7), *Chilostomella* + *Pullenia* (71% BS) and *Cibicides* (except *C. refulgens* from the Mediterranean) + *Melonis* (37% BS) cluster together with a rather low support (39% BS). Their sister group is *Epistominella, Stainforthia* + *Virgulinella, Bulimina* + *Nonionella* + *Virgulina,* with a low statistical support (47% BS). *Cibicides refulgens* (57% BS) branches as sister to these two main groups. *Chilostomella ovoidea* is separated in three different groups with good statistical supports (95% BS or higher).

2.4. Discussion

2.4.1. Contamination problems and intraspecific variability

To guarantee the absence of contamination it is important, whenever possible, to obtain several sequences from the same species. If these sequences are close to each other, it can be assumed that they actually belong to the sampled species. Contamination can occur *in situ* , when the empty test is occupied by another organism, a foraminifer in case specific foraminiferal primers are used (see Gooday, 1986; Moodley et al., 1990; Pawlowski et al., 2002). It can also take place in the laboratory, either during DNA extraction or during amplification when other DNA is present in the environment (mainly if the sample is negative). In the first and second cases, the DNA sequenced will always be the same and possibly of good quality, whereas in the third case the signal will be usually weak and the sequence of bad quality. Several sequences deposited in GenBank are obviously contaminations or mistakes due to manipulations, e.g. AF533847, AY210772, AY359145, AY641479, AY465842, AY488865.

Another reason to sequence several clones of one sample is to explore the intraspecific, or even intra-individual variability. In our case, the sequences derived from the same species and the same location never showed a high variability (see Chapter 4 for a detailed discussion on *Uvigerina peregrina*). However, sequences taken from GenBank belonging to *Bolivina variabilis, Globobulimina pseudospinescens, Rosalina orbicularis* and *Chilostomella ovoidea* showed clades of the same species with clearly separated groups coming from the same locations (see Figs. 2.5-2.7 and Ertan et al., 2004 for details). Because the genetic variation is usually low in specimens from the same species and the same origin, these differences can be explained by the presence of cryptic species (see below).

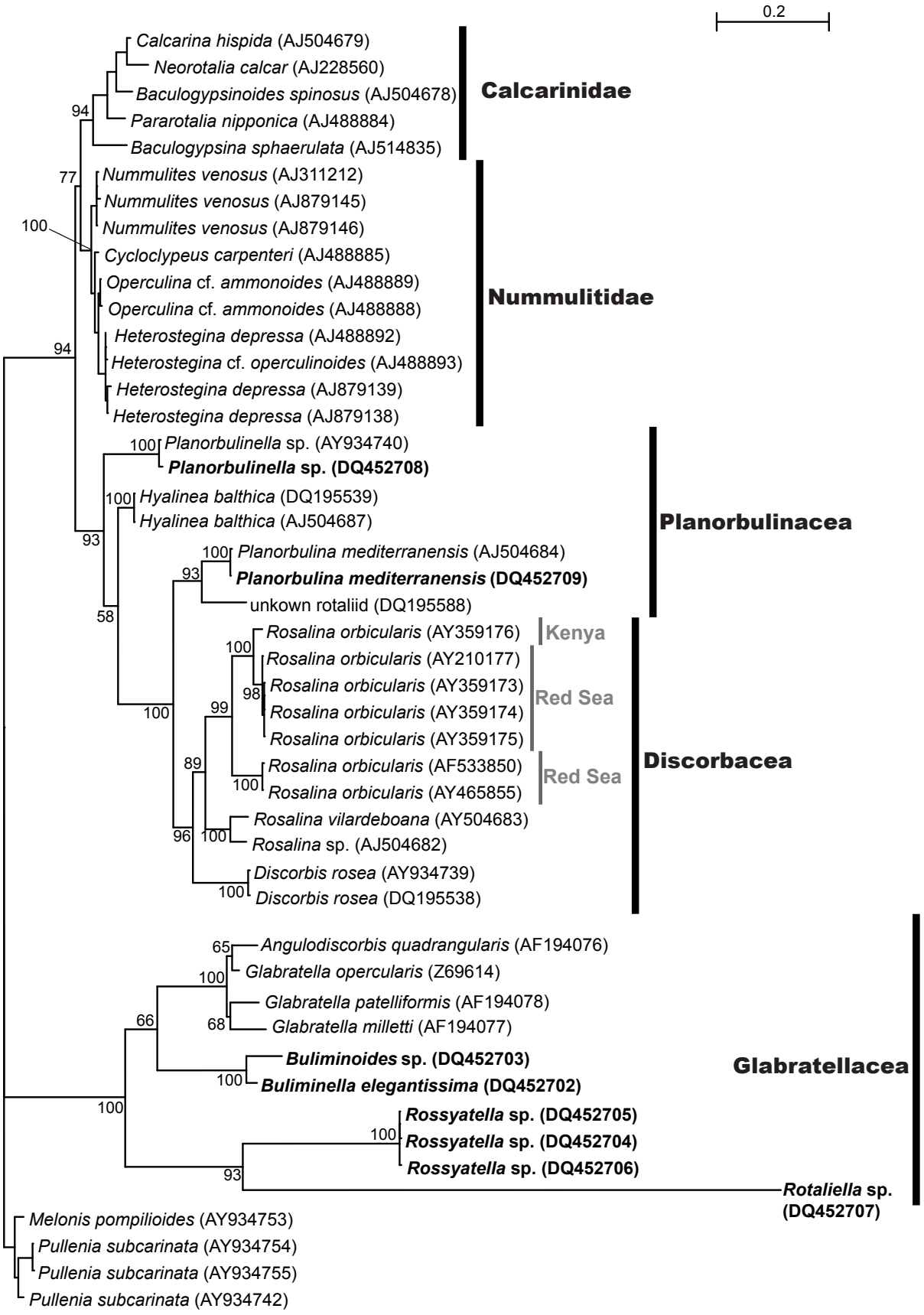

Figure 2.6. Phylogeny of the rotaliids belonging to the second group inferred from partial SSU rDNA sequences (1093 unambiguously aligned sites) using the ML (HKY+I+G) method. Tree rooted on *Melonis* and *Pullenia*. Bootstrap indicated at the nodes. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers in brackets).

2.4.2. Classification of the rotaliids

The results show that sequencing of the complete SSU greatly improved the statistical support of the deeper nodes (Fig. 2.3) and the main topology was identical in the analyses performed with PhyML (HKY and GTR) and MrBayes (GTR). The three groups identified here were already recognized in earlier analyses (Schweizer et al., 2005, Fig. 7; Schweizer et al., submitted, Fig. 4). However, the statistical supports were lower and the positions of groups (groups 1 and 2 of the first analysis permutated in the later analyses) slightly different. Here (Fig. 2.3), cibicidids show a higher statistical support (93%BS, 1.00PP) than in the analysis presented in Chapter 3 (Fig. 3.4), and the monophyly is also found with Bayesian analyses here (this was not the case with former analyses). However, we could not obtain the complete SSU for the most divergent sequences of cibicidids (*C. refulgens*).

The species studied here belong to the orders Buliminida and Rotaliida of the latest classifications (Haynes, 1981; Loeblich & Tappan, 1988, 1992; Sen Gupta, 2002). Interestingly, the two main groups observed with the phylogenetic analyses (group 1 and groups 2+3, see Figs. 2.3-2.4) roughly correspond to the morphology-based orders Buliminida and Rotaliida, except for the genera *Bulimina*, *Stainforthia*, *Virgulina* and *Virgulinella* (belonging to group 3 instead of group 1). The position of these genera inside the Rotaliida poses questions about the pertinence of the criteria used to separate the two orders. Apparently, the presence of a toothplate, which is the main feature to distinguish the two orders, is not as important as previously thought (Hofker, 1951, 1956; Haynes, 1981; Mikhalevitch & Debenay, 2001). Moreover, the fact that *Cassidulina*, a genus without a toothplate, is traditionally placed in the family Cassidulinidae (this position was confirmed by the molecular analyses), of which the other genera represented in our study do have a toothplate, shows that the presence or absence of a toothplate does not suffice to justify the inclusion into a family or a higher taxon. Besides the Bulimina-Rotaliida partition, the molecular analyses clearly show no separation on basis of wall structure as stated by Loeblich and Tappan (1964, 1988). This is particularly clearly illustrated by the classification of cibicidids, which is discussed in Chapter 3.

We compared our data with two other analyses, one based on the 3' end fragment (Holzmann et al., 2003) and the other on actin (Flakowski et al., 2005). Apart from the monophyly of rotaliids, the three studies have little in common, particularly the one using actin. The latter study obtained rather different results with *Stainforthia* + *Hyalinea* as a sister group of *Elphidium* + Globigerinida, and this larger group subsequently as a sister group of *Ammonia*, *Rosalina*, *Bulimina*, *Bolivina*, *Globobulimina* and *Nonionella* (Flakowski et al., 2005, Fig. 3). The other analysis used the 3' end fragment and in this study taxa belonging to the two first groups showed a similar topology for group 2 (Holzmann et al., 2003, Fig. 1); however, Cassidulinidae and *Bolivina* (group 1) branched inside this group. These comparisons demonstrate that more taxa are needed to stabilize the topology of the tree and that analyses with other genes are indispensable.

For the time being, our molecular results based on the complete SSU rather favor the existence of a unique order (Rotaliida) subdivided into three groups.

2.4.3. Consistency of the morphological and molecular phylogenies

The separation of *Bulimina* from other members of the Buliminacea (*Globobulimina* and *Uvigerina*) was already discussed (see Schweizer et al., 2005). The proximity of *Bulimina*, *Stainforthia, Virgulina* and *Virgulinella* is morphologically understandable; Haynes (1981, 1990) already proposed to merge the superfamilies Fursenkoinacea (*Virgulinella*) and Turrilinacea (*Stainforthia, Virgulina*) into the superfamily Buliminacea (with Buliminidae and Uvigerinidae). Moreover, he also included *Epistominella* in the Buliminacea (Haynes, 1981). Our results partially corroborate Haynes' idea, although other Buliminacea (uvigerinids and possibly *Globobulimina*) appear well separated from this group. The separation of *Bulimina* from group 1 is in contradiction with morphological classifications which have placed these taxa together (Haynes, 1981; Loeblich & Tappan, 1992; Sen Gupta, 2002). However, analysis of the complete SSU confirms the results of previous analyses with the partial 3' end fragment (Chapter 3, Schweizer et al., 2005) concerning

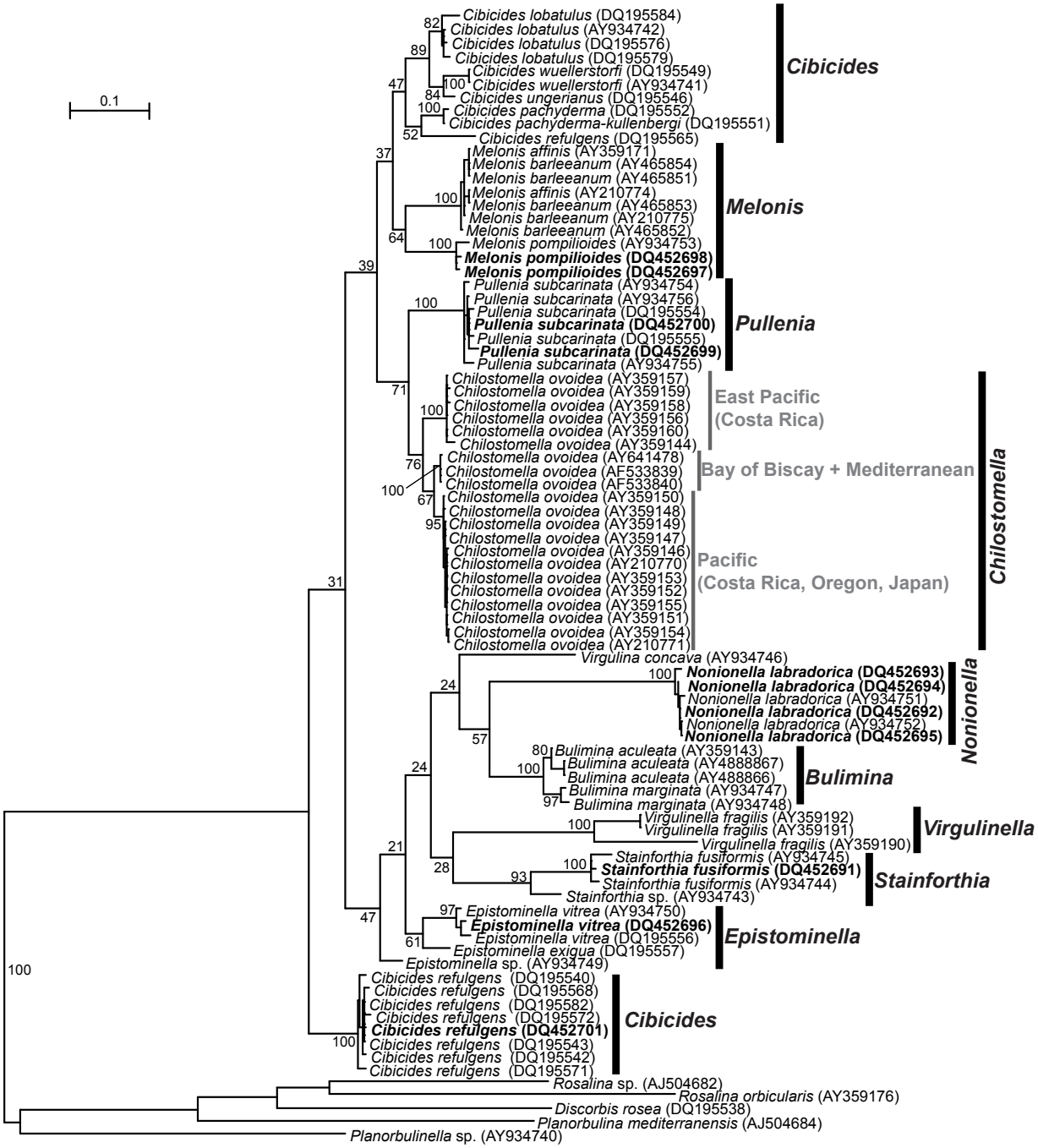

Figure 2.7. Phylogeny of the rotaliids belonging to the third group inferred from partial SSU rDNA sequences (1356 aligned sites) using the ML (HKY+I+G) method. Tree rooted on *Planorbulinella, Planorbulina, Discorbis* and unknown rotaliid. Bootstrap indicated at the nodes. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers are added).

the polyphyly of the Buliminacea. To check if this polyphyly is real or an artefact, phylogenetic studies of other genes (such as actin) involving the same taxa are needed.
Among the families containing more than one genus, the Cassidulinidae, the Uvigerinidae, the Glabratellidae, the Rotaliellidae, the Calcarinidae and the Nummulitidae are monophyletic (Figs. 2.5-2.6). Inside the Planorbulinacea, *Hyalinea* was traditionally grouped with *Cibicides* (e.g. Loeblich & Tappan, 1964, 1988; Haynes, 1981) and *Planorbulina* was thought to be a stage in the life cycle of *Cibicides* (Nyholm, 1961). Despite the superficial morphological resemblance between their members, the Planorbulinacea are a polyphyletic order. The majority of them (*Hyalinea, Planorbulinella, Planorbulina*) branch in group 2 with Discorbacea, while *Cibicides* is closer to *Melonis* and *Pullenia* inside group 3 (Figs. 2.3-2.4). The phylogenetic position of *Cibicides* is discussed in more detail in Chapter 3. Finally the Nonionacea - comprising only the family Nonionidae in our study - all belong to group 3, but *Melonis* and *Pullenia* cluster together with *Cibicides* and *Chilostomella* in the molecular analyses, whereas *Nonionella* seems more closely related to *Bulimina* (Figs. 2.4 and 2.7). The proximity of *Pullenia* and *Chilostomella* has already been proposed by Haynes (1981) who classified them in the same family.
The genera for which several species were sampled are all monophyletic (*Bolivina*, *Bulimina, Glabratella, Globobulimina*, *Melonis*, *Uvigerina*, *Rosalina*, see also Holzmann et al., 2003; Ertan et al., 2004; Schweizer et al., 2005), except *Epistominella* and *Cibicides*. Despite its identification as *Epistominella,* AY934749 probably belongs to another closely related genus. The case of cibicidids is discussed in Chapter 3. *Brizalina* and *Angulodiscorbis* seem subsumed in *Bolivina* and *Glabratella* respectively (Figs. 2.5 and 2.6). Ertan et al. (2004) already questioned the generic status of *Brizalina*. However, the other available sequences of bolivinids (*Bolivina variabilis*, *B. spathulata* and *B. subaenariensis*) are sometimes also classified in *Brizalina* and *B. subaenariensis* is the type species of this genus. A 'true' *Bolivina* is therefore needed to check whether *Brizalina* is a synonym of *Bolivina*. Some changes made in the morphological classification, such as the placement of *Buliminoides* (Loeblich & Tappan, 1988), *Rotaliella* and *Rossyatella* (Pawlowski & Zaninetti, 1993) inside the Glabratellacea (Fig. 2.7), were confirmed by the molecular results. It may be possible to add *Buliminella* to this group also. However, the sequence we obtained for this species was of bad quality.
In order to compare our molecular results with the traditional classification, we present a recapitulative tree (Fig. 2.8) based on the molecular data (Figs. 2.3-2.7). As seen before, some of the morphological families were also found in the molecular analyses.

2.4.4. Relations between the species within each group

The different species of *Bulimina* (*B. aculeata* and *B. marginata*) and *Rosalina* (*R. orbicularis*, *R. vilardeboana*) are well separated (Figs. 2.6-2.7). This is also the case for *Bolivina* (*B. variabilis*, *B. alata*, *B. subaenariensis*), except *B. spathulata* which has one sequence branching closer to *B. subaenarensis* (Fig. 2.5). Because these sequences of *B. spathulata* have been deposited by different authors (the Bay of Biscay specimens by Ertan et al., 2004 and the Skagerrak one by Pawlowski et al., 1999a), there is a possibility of different species definition. In our molecular results *M. pompilioides* is well separated from *M. affinis* + *M. barleeanum*, which branch together (Fig. 2.7). The latter morphospecies are mainly distinguished by the more inflated profile of *M. affinis* and they are put in synonymy by several authors (see Van Morkhoven et al., 1986), which is confirmed here. Inside *Globobulimina*, the position of the two sequences of *G. turgida* branching together with *G. pseudospinescens* (Fig. 2.5) partly confirms the hypothesis of Fontanier et al. (2003b), who suggested that these two species are the same and have to be put in synonymy with *G. pyrula*. Sequences of *G. pyrula* are needed to confirm this hypothesis. Within the same genus, *G. pseudospinescens* is separated in two groups. The sequence from the Bay of Biscay is part of the *G. affinis* clade; this may be a misidentification, but the clear separation of two groups in the Sea of Marmara probably indicates the existence of two, possibly cryptic, species. The existence of cryptic species coexisting in the same area is also suspected for the two subgroups *of Bolivina variabilis* from Kenya (Fig. 2.5), of *Rosalina orbicularis* from the Red Sea (Fig. 2.6) and

of *Chilostomella ovoidea* from Costa Rica (Fig. 2.7).
Within the third group, the genus *Virgulina* d'Orbigny, 1826 was recognized in the classifications of Cushman (1928, 1959) and Galloway (1933) as *V. concava* but not in more recent ones (Loeblich & Tappan, 1964, 1988; Haynes, 1981; Sen Gupta, 2002). However, the species presently called *Stainforthia concava* and *S. fusiformis* obviously do not belong to the same genus (Fig. 2.7 and Fig. 4.7). Therefore, we propose to conserve the name *Virgulina concava*.

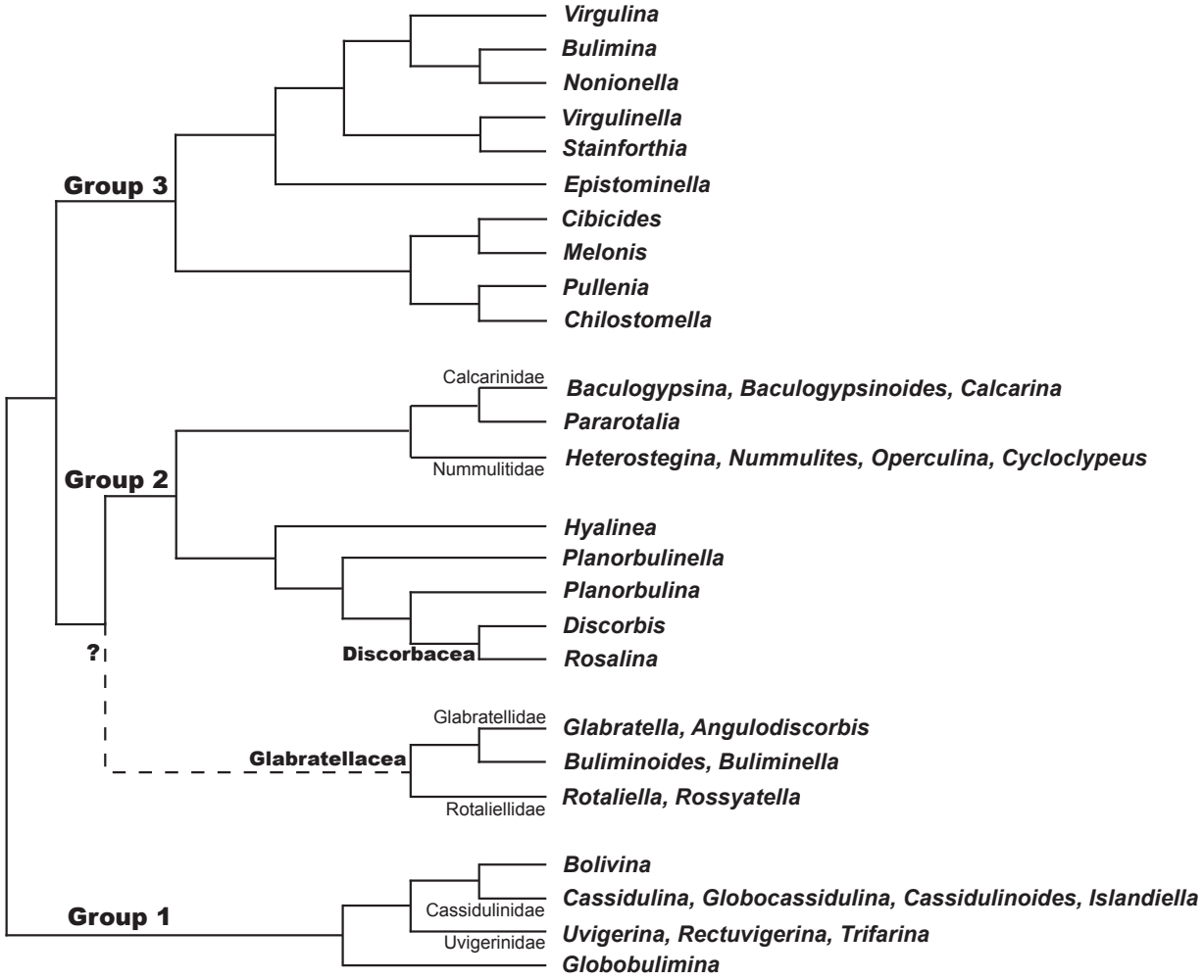

Figure 2.8. Phylogenetic tree summarizing the relations between rotaliids based on the molecular results.

2.5. Conclusions

The separation between Buliminida and Rotaliida that is often adhered to is not confirmed by our molecular results (Figs. 2.3-2.4). The only order retained for members of these two taxa is the Rotaliida, which is divided into three different subgroups (Fig. 2.8). Further molecular studies are needed to confirm this partition in three groups, including sequencing of the complete subunit of species only represented by the 3' end fragment and of representatives of other taxa not yet sequenced. The existence of several morphologically defined taxa was confirmed by molecular results, whereas other taxa appeared polyphyletic. A careful reexamination of the morphological features used to define the different higher taxa is needed to evaluate their taxonomical importance and to bring them in line with molecular results. The problematic discrepancy between the morphological and the molecular positions of *Bulimina*, *Stainforthia*, *Virgulina* and *Virgulinella*

remains unsolved and will need additional polygenic studies.
To improve the phylogenetic signal contained by the 3' end fragment, Ertan et al. (2004) used the secondary structure of the rRNA strand to obtain better alignments of the highly variable parts. We think, however, that the problem cannot be solved by increasing the number of aligned sites. The limited length of this fragment and the lack of signal observed remain problematic, even if the maximum number of sites of the 3' end fragment is used. This raises another question: is the rDNA really suitable for phylogenies of higher ranks within the foraminifers? The analysis of the complete SSU showed a clear improvement of the statistical support compared to the partial studies (see Figs. 2.5-2.6, 3.4 and 4.7). However, the variations of substitution rates between the different taxa (Pawlowski et al., 1997) are also apparent in our data and could hamper the analyses. To solve these problems, we need to sample more taxa, but also use other genes despite the technical difficulties.

Chapter 3

Molecular phylogeny of *Cibicides*, *Cibicidoides* and related genera (Rotaliida, Foraminifers): taxonomic implications

Abstract

Cibicidids comprise several species of rotaliid foraminifera that are widely used as proxies of marine paleoenvironments. On the basis of test form and structure several genera of cibicidids have been erected, of which some have been placed in different families and superfamilies. To test the monophyly of the cibicidids and to infer their phylogenetic relationships, we obtained partial small-subunit ribosomal DNA (SSU rDNA) sequences of six common species: *kullenbergi, lobatulus, pachyderma, refulgens, ungerianus* and *wuellerstorfi.* Phylogenetic analyses of our sequence data show that the cibicidids group together, albeit their monophyly is not strongly supported. Among the six species, two (*lobatulus* and *wuellerstorfi*) form well defined clades, branching together in all analyses. Two species (*kullenbergi*, *pachyderma*) form a single clade, while one (*refulgens*) splits into two clades, possibly indicating the existence of two cryptic species. The sixth species, *ungerianus*, represented by a single sequence, branches as a sister group to *wuellerstorfi.* The wide morphological variations observed in *lobatulus* seem to be due mainly to environmental factors, since regularly and irregularly shaped specimens (ecophenotypes) group together in the molecular analyses. In view of our analyses, the distinction between planoconvex *Cibicides* and biconvex *Cibicidoides* and the placement of cibicidids in different superfamilies is not justified. Our data suggest that all species examined here could be classified in one unique family, and, for the time being, in a single genus, *Cibicides* de Montfort, 1808. This genus has been defined by a low trochospiral coil with an evolute spiral side and an involute umbilical side, and a simple slit as an aperture, located near the peripheral margin and edged by a lip.

Keywords: Benthic foraminifera; Rotaliida; Cibicidids; *Cibicides; Cibicidoides*, SSU rDNA; Molecular phylogeny

3.1. Introduction

Cibicidids play an important role in the fossil record as proxies of marine paleoenvironmental conditions like trophic state (e.g. Altenbach & Sarnthein, 1989), oxygen (Kaiho, 1994), and paleodepth (e.g. Wright, 1978; Van der Zwaan et al., 1999; Van Hinsbergen et al., 2005). Furthermore, cibicidids are frequently used in stable carbon and oxygen isotopic analyses. Most species have an epibenthic or shallow infaunal microhabitat (Murray, 2003). *Cibicides wuellerstorfi* (Schwager, 1866), which is the most commonly used species in stable isotope studies (Murray, 1991), is considered to reliably reflect bottom water oxygen and carbon isotope ratios because it is an epibenthic species (Lutze & Thiel, 1989; Schmiedl et al., 2004; but see Mackensen et al., 1993). To construct proper down-core isotope curves, it is important to use one single species instead of a mix of different species (Murray, 1991; Schmiedl et al., 2004). Therefore, the status and recognition of the different species play an important role, not only for evolutionary purposes, but also in paleoecology.

The present classification of the cibicidids is entirely based on morphological characteristics and there is some confusion about the generic status of the different species. The species examined in this paper have been and still are classified in various genera (the most commonly used names are shown between brackets, see taxonomic notes in the appendix for more details): *Anomalina* d'Orbigny, 1826, *Cibicides* de Montfort, 1808 (*Cibicides refulgens* de Montfort, 1808*, C. kullenbergi* Parker, 1953*, C. lobatulus* (Walker and Jacob, 1798), *C. pachyderma* (Rzehak, 1886), *C. ungerianus* (d'Orbigny, 1846), *C. wuellerstorfi*), *Cibicidoides* Thalmann, 1939 (*Cibicidoides kullenbergi, C. pachyderma*), *Fontbotia* Gonzalez-Donoso & Linares, 1970 (*Fontbotia wuellerstorfi*), *Heterolepa* Franzenau, 1884 (*Heterolepa kullenbergi*), *Lobatula* Fleming, 1828 (*Lobatula lobatula*), *Planulina* d'Orbigny, 1826 (*Planulina wuellerstorfi*), *Truncatulina* d'Orbigny, 1826.

Among the validated generic names, *Cibicides* was the most commonly used for this group of species during the first half of the 20th century. *Cibicidoides* was initially described as a subgenus of *Cibicides* in 1936 by Brotzen and validated by Thalmann (1939) upon the designation of a subgenotype. However, *Cibicidoides* only became a widely used genus name for biconvex forms since the end of the 1970s. *Lobatula*, *Truncatulina* and *Heterolepa* were considered junior synonyms of *Cibicides* by Galloway & Wissler (1927) and Cushman (1928). *Planulina* and *Fontbotia* have been used as generic names for *wuellerstorfi* (e.g. Van Morkhoven et al., 1986; Holbourn

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& Henderson, 2002; respectively Gonzalez-Donoso & Linares, 1970; Loeblich & Tappan, 1988). However, *Planulina* differs from *Cibicides* by the partially evolute umbilical side and from *Cibicidoides* by the planoconvex shape of the test, while *Fontbotia* was regarded as a junior synonym of *Cibicides* (Sen Gupta, 1989), *Cibicidoides* (Whittaker, 1988) or *Planulina* (Revets, 1996).
Many authors have considered the cibicidids as a monophyletic group and have placed them together within the family Anomalinidae Cushman, 1927 (Cushman, 1928; Reiss, 1958), Rotaliidae Reuss, 1860 (Galloway, 1933), or Cibicididae Cushman, 1927 (Hofker, 1956). Loeblich & Tappan (1964) introduced a classification in which they placed *Cibicides* and *Cibicidoides* in two different superfamilies, distinguished by the crystallographic structure of the wall: the Orbitoidacea (radial) for *Cibicides* and the Cassidulinacea (granular) for *Cibicidoides,* together with *Heterolepa.* The placement of *Cibicidoides* and *Heterolepa* in a separate superfamily was based on the granular structure of the wall compared to the radial wall of the other cibicidids (Loeblich & Tappan, 1962). In their later classification (1988), Loeblich & Tappan maintained a division of the cibicidids over different superfamilies. The wall structure is considered of great importance in the classifications of Loeblich & Tappan (1964, 1988). Towe & Cifelli (1967), however, showed that this difference, which seems huge when observed in polarized light, is a matter of orientation of the crystals: the same crystal morphology can produce different optical orientations, and conversely, similar optical characteristics can be generated by different crystal forms. These authors (1967, p. 754) demonstrated that *C. refulgens*, which was first considered having a granular wall, and later a radial one, has in fact optical attributes of both radial and granular wall structures. They concluded that the dichotomy radial versus granular cannot be used as a major criterion for higher taxonomic levels (Towe & Cifelli, 1967, p. 755).
Summarizing, there are two concepts of the classification of cibicidids in the more recent works: they are either united in a single family (Haynes, 1981, Sen Gupta, 2002) or separated in different superfamilies (Loeblich & Tappan, 1988, 1992; Revets, 1996).
Here, we use SSU rDNA sequences to investigate the phylogeny of six Recent species of cibicidids and to establish their relationships with other rotaliids. Until now, only three sequences of cibicidids have been deposited in the EMBL/GenBank data base: *C. refulgens* (AJ514839) (Pawlowski et al., 2003), *C. wuellerstorfi* (AY934741) and *C. lobatulus* (AY934742) (Schweizer et al., 2005). These sequences correspond to the 3' end fragment of the SSU rDNA, which is widely used in foraminiferal phylogeny (e.g. Pawlowski, 2000; Holzmann et al., 2003; Darling et al., 2004; Ertan et al., 2004). We extended this dataset by the addition of 53 new sequences of the 3' end fragment and 37 new sequences of a fragment situated at the 5' beginning of the SSU. Phylogenetic analyses of these combined sequence data indicate that the cibicidids form a

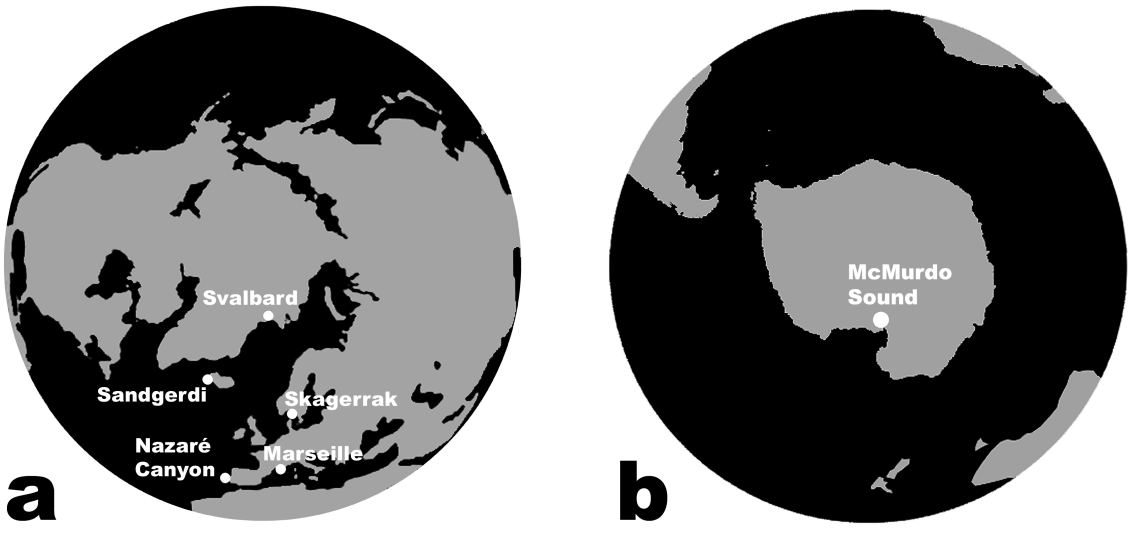

Figure 3.1. Maps showing the sampling sites of the northern (a) and southern (b) hemispheres.

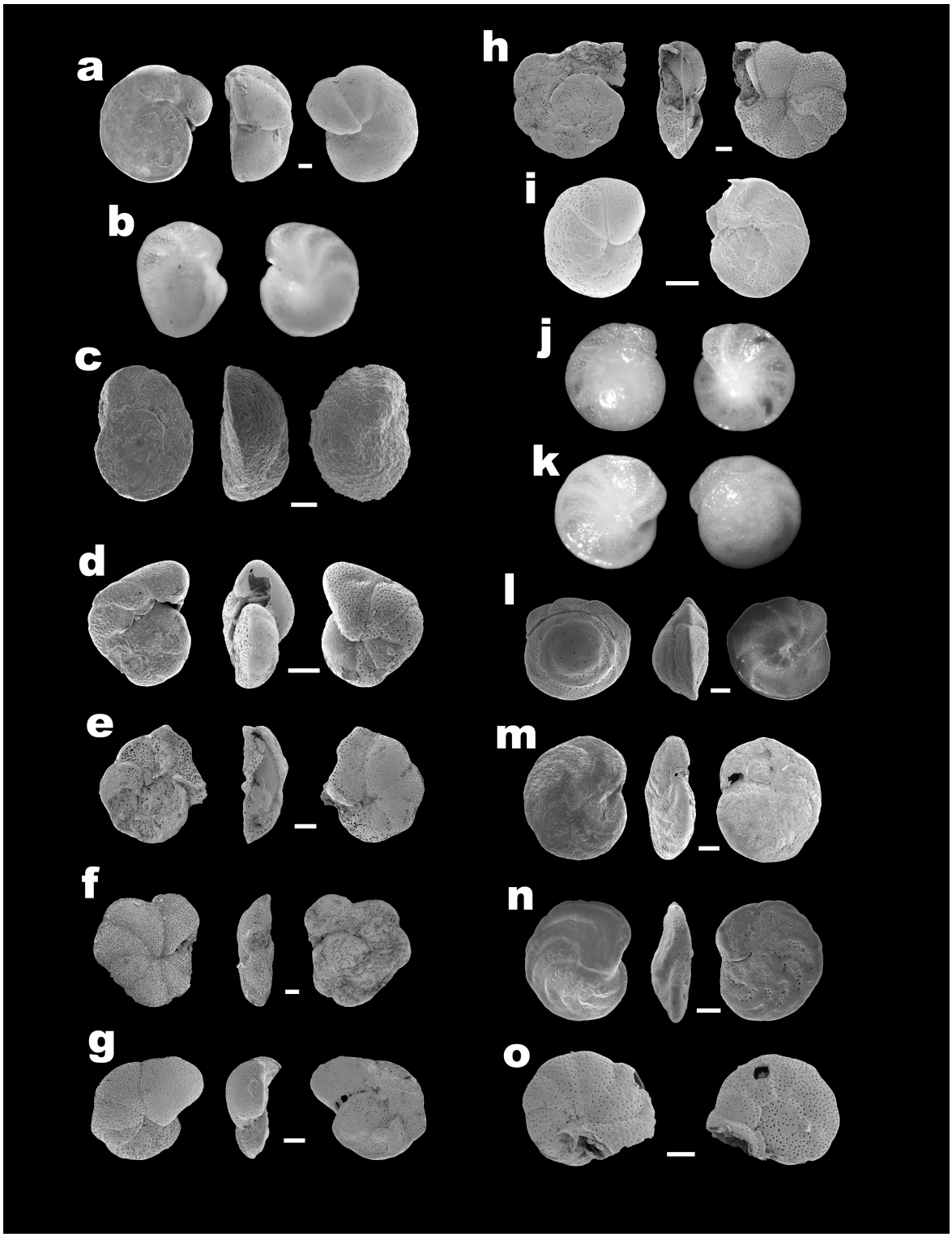

Figure 3.2. SEM pictures and light photomicrographs (b, j, k) of the studied specimens of *Cibicides* (u: umbilical side, s: spiral side, p: profile). Except (a), (c) and (m), all the pictures correspond to DNA samples (DNA number is indicated in brackets after the species name). (a) *C. refulgens* from Antarctica (u, p, s), (b) *C. refulgens* (C78) from the Mediterranean (s, u), (c) *C. refulgens* from the Mediterranean (s, p, u), (d) *C. lobatulus* (C2) from Iceland (s, p, u), (e) *C. lobatulus (*C35) from Oslo Fjord (s, p, u), (f) *C. lobatulus* (C37) from Oslo Fjord (u, p, s), (g) *C. lobatulus* (C39) from Oslo Fjord (u, p, s), (h) *C. lobatulus* (C40) from Oslo Fjord (s, p, u), (i) *C. lobatulus* (C120) from Skagerrak (u, s), (j) *C. kullenbergi* (C86) from Portugal (s, u), (k) *C. kullenbergi* (C87) from Portugal (u, s), (l) *C. pachyderma* (C196) from Portugal (u, p, s), (m) *C. wuellerstorfi* from Svalbard (u, p, s), (n) *C. wuellerstorfi* (C184) from Portugal (u, p, s), (o) *C. ungerianus* (C29) from Oslo Fjord (u, s). Scale= 100 μm

monophyletic group, which branches closely to *Melonis* de Montfort, 1808 and *Pullenia* Parker and Jones, 1862. The relationships within this group and molecular versus morphological variations in some species are discussed in this paper.

3.2. Material and Methods

3.2.1. Sample collection

Living individuals of cibicidids were obtained from the North Atlantic, the North Sea, the Mediterranean and the Southern Ocean (Fig. 3.1). Shallow water samples were collected by SCUBA diving or from intertidal rocks; they were kept at a temperature close to the one observed where they were collected. Deeper-water samples were obtained by boxcoring or multicoring. The top few centimeters of sediment were collected, immediately sieved and kept in the refrigerator at 4°C. Live specimens, identified by their natural coloration (mainly pinkish) were cleaned, picked and dried on Chapman slides (see Schweizer et al., 2005 for details). Most of the specimens were subsequently pictured with scanning electron microscope (SEM) or a camera connected to a dissection microscope, before DNA extraction (Fig. 3.2).

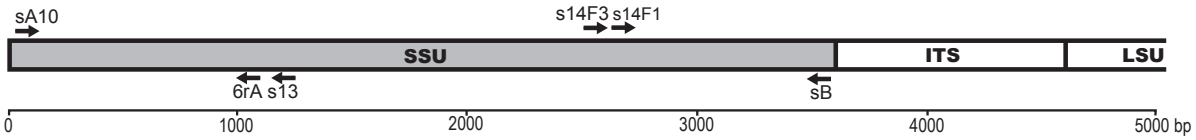

Figure 3.3. Schematic representation of the rRNA genes and the approximate position of the primers used in this study.

3.2.2. DNA extraction, PCR amplification, cloning and sequencing

DNA was extracted from single specimens using DOC lysis buffer (Pawlowski, 2000) and from samples containing multiple specimens by DNeasy Plant Mini Kit (Qiagen).
Two fragments of the SSU, each about 1,000 nucleotides in length, were examined (Fig. 3.3). The first fragment starting at the 5' end of the SSU was amplified with the primers sA10 and s13 and reamplified using primers sA10 and s6rA. The second fragment placed at the 3' end of the SSU was amplified using the primer pair s14F3 and sB and reamplified with the primer pair s14F1 and sB. The sequences of all these primers are available in Table 2.3. Both fragments were amplified by PCR (polymerase chain reaction) in a total volume of 50µl. The thermal cycle parameters consisted of 40 cycles of 30s at 94°C, 30s at 50°C and 120s at 72°C, followed by 5min at 72°C for final extension. Reamplification was carried out using 35 cycles of 30s at 52°C instead of 50°C, all other parameters remaining unchanged. Positive PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics). PCR products obtained from the 3' end fragment of DNA samples 1075, 1994, 2524, 2648, 2649, 3623, C29, C35, C37, C78, C86, C87, U27 (see Table 3.1) were sequenced directly. All other PCR products were ligated in the pGEM-T Vector (Promega) or the Topo Cloning vector (Invitro Gene), and cloned using ultracompetent cells XL2-Blue MRF' (Stratagene). Sequencing reactions were prepared using an ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analysed with DNA sequencers ABI-377 or ABI-PRISM 3100 (Applied Biosystems), all according to the manufacturer's instructions.
New sequences have been deposited in the EMBL/GenBank database; their accession numbers are indicated in Table 3.1.

Table 3.1. List of new SSU sequences and origin of DNA samples. Asterisks indicate sequences previously published.

Access # A10	14F1	Species	DNA #	Collection site	Cells
DQ205389	AY934747*	*Bulimina marginata*	3599	Oslo Fjord, Norway	130
DQ205355	AY934737*	*Cassidulinoides porrectus*	3924	Terranova Bay, Antarctica	3
DQ205369	DQ195545, DQ195583, DQ195584	*Cibicides lobatulus*	C170	Marseille, France	1
	DQ195576, DQ195585	*Cibicides lobatulus*	C2	Sandgerdi, Iceland	1
DQ205371	DQ195547, DQ195577, DQ195578, DQ195579	*Cibicides lobatulus*	C24	Oslo Fjord, Norway	1
	DQ195580	*Cibicides lobatulus*	C35	Oslo Fjord, Norway	1
	DQ195581	*Cibicides lobatulus*	C37	Oslo Fjord, Norway	1
	AY934742*, DQ195586	*Cibicides lobatulus*	C39	Oslo Fjord, Norway	1
	DQ195587	*Cibicides lobatulus*	C40	Oslo Fjord, Norway	1
DQ205372	DQ195548, DQ195561, DQ195562	*Cibicides lobatulus*	C120	Skagerrak, Sweden	1
	DQ195573, DQ195574	*Cibicides lobatulus*	576	Skagerrak, Sweden	5
DQ205377, DQ205378	DQ195552, DQ195553, DQ195563	*Cibicides pachyderma*	C196	Nazaré Canyon, Portugal	1
DQ205376	DQ195551	*Cibicides kullenbergi*	C86	Nazaré Canyon, Portugal	1
	DQ195575	*Cibicides kullenbergi*	C87	Nazaré Canyon, Portugal	1
	DQ195564	*Cibicides refulgens*	1075	McMurdo Sound, Antarctica	1
	DQ195566, DQ195567	*Cibicides refulgens*	1838	McMurdo Sound, Antarctica	1
DQ205368	DQ195544, DQ195565	*Cibicides refulgens*	1839	McMurdo Sound, Antarctica	1
	AJ514839*	*Cibicides refulgens*	2068	McMurdo Sound, Antarctica	10
DQ205367	DQ195543	*Cibicides refulgens*	C78	Gulf of Lions, France	1
	DQ195568, DQ195569, DQ195570	*Cibicides refulgens*	C171	Marseille, France	1
DQ205365, DQ205366	DQ195541, DQ195542	*Cibicides refulgens*	C172	Marseille, France	1
DQ205364	DQ195540, DQ195571, DQ195572	*Cibicides refulgens*	C173	Marseille, France	1
	DQ195582	*Cibicides refulgens*	C208	Marseille, France	1

A10	14F1	Species	DNA #	Collection site	Cells
DQ205375	DQ195550	*Cibicides* sp.	2524	North Atlantic	1
DQ205370	DQ195546	*Cibicides ungerianus*	C29	Oslo Fjord, Norway	1
	DQ195560	*Cibicides wuellerstorfi*	2648	Svalbard, Norway	
	DQ195559	*Cibicides wuellerstorfi*	2649	Svalbard, Norway	
DQ205373, DQ205374	AY934741*, DQ195549, DQ195558	*Cibicides wuellerstorfi*	C184	Setubal Canyon, Portugal	1
DQ205360	DQ195538	*Discorbis rosea*	753	Florida, USA	1
DQ205386	DQ195557	*Epistominella exigua*	3623	Weddell Sea, Antarctica	1
DQ205384, DQ205385	AY934750*, DQ195556	*Epistominella vitrea*	2060	Cape Evans, Antarctica	4
DQ205362	DQ195539	*Hyalinea balthica*	3604	Oslo Fjord, Norway	
DQ205354	AJ504685*	*Islandiella* sp.	2643	Svalbard, Norway	
DQ205379	AY934753*	*Melonis pompilioides*	1400	Skagerrak, Sweden	1
DQ205361	AJ504684*	*Planorbulina mediterranensis*	142	Golfe du Morbihan, France	1
DQ205382, DQ205383	AY934755*, DQ195555	*Pullenia subcarinata*	1148	McMurdo Sound, Antarctica	1
DQ205380, DQ205381	AY934754*, DQ195554	*Pullenia subcarinata*	1850	McMurdo Sound, Antarctica	1
DQ205357	AY914563*	*Rectuvigerina phlegeri*	U239	Nazaré Canyon, Portugal	
DQ205363	DQ195588	Unknown rotaliid	3675	Culture	100
DQ205387	AY934744*	*Stainforthia fusiformis*	3965	Skagerrak, Sweden	150
DQ205390	AY914568*	*Trifarina earlandi*	1994	McMurdo Sound, Antarctica	10
DQ205356	AY914565*	*Trifarina earlandi*	2187	McMurdo Sound, Antarctica	5
DQ408637	DQ408637	*Trochammina hadai*	95	Hamana Lake, Japan	1
DQ205359	DQ195537	*Uvigerina peregrina*	U27	Oslo Fjord, Norway	9
DQ205358	AY914571*	*Uvigerina peregrina*	U32	Oslo Fjord, Norway	2

3.2.3. Phylogenetic analysis

Sequences were aligned manually using Seaview (Galtier et al., 1996). Three sequence datasets were analysed. The first dataset includes a total of 2632 aligned sites from concatenated 3' and 5' fragments for 15 sequences of cibicidids, 27 sequences of other rotaliids and three sequences of textulariids, taken as an outgroup. The second dataset comprises 2357 aligned sites from the concatenated fragments for the 15 sequences of cibicidids, the 10 most closely related sequences of rotaliids and the Nummulitidae and *Pararotalia* as the outgroup. The third dataset includes 1013 aligned sites from the 3' fragment with 47 sequences of cibicidids and four sequences of *Pullenia subcarinata* used as an outgroup.

The maximum likelihood (ML) trees were obtained using PhyML 2.4.4 (Guindon & Gascuel, 2003). To assess the reliability of internal branches, the bootstrap support (BS) values were calculated by PhyML, with 100 replicates. Bayesian analyses were done with MrBayes 3.1.1 (Huelsenbeck & Ronquist, 2001). Two independent analyses were performed at the same time with four simultaneous chains run for 1,000,000 generations, and sampled every 100 generations with 1,000 initial trees discarded as burn-in. The posterior probabilities (PP), calculated during the Bayesian analysis, estimated the reliability of internal branches. Both ML and Bayesian analyses were performed using the GTR+I+G model as suggested by Modeltest 3.7 (Posada & Crandall,

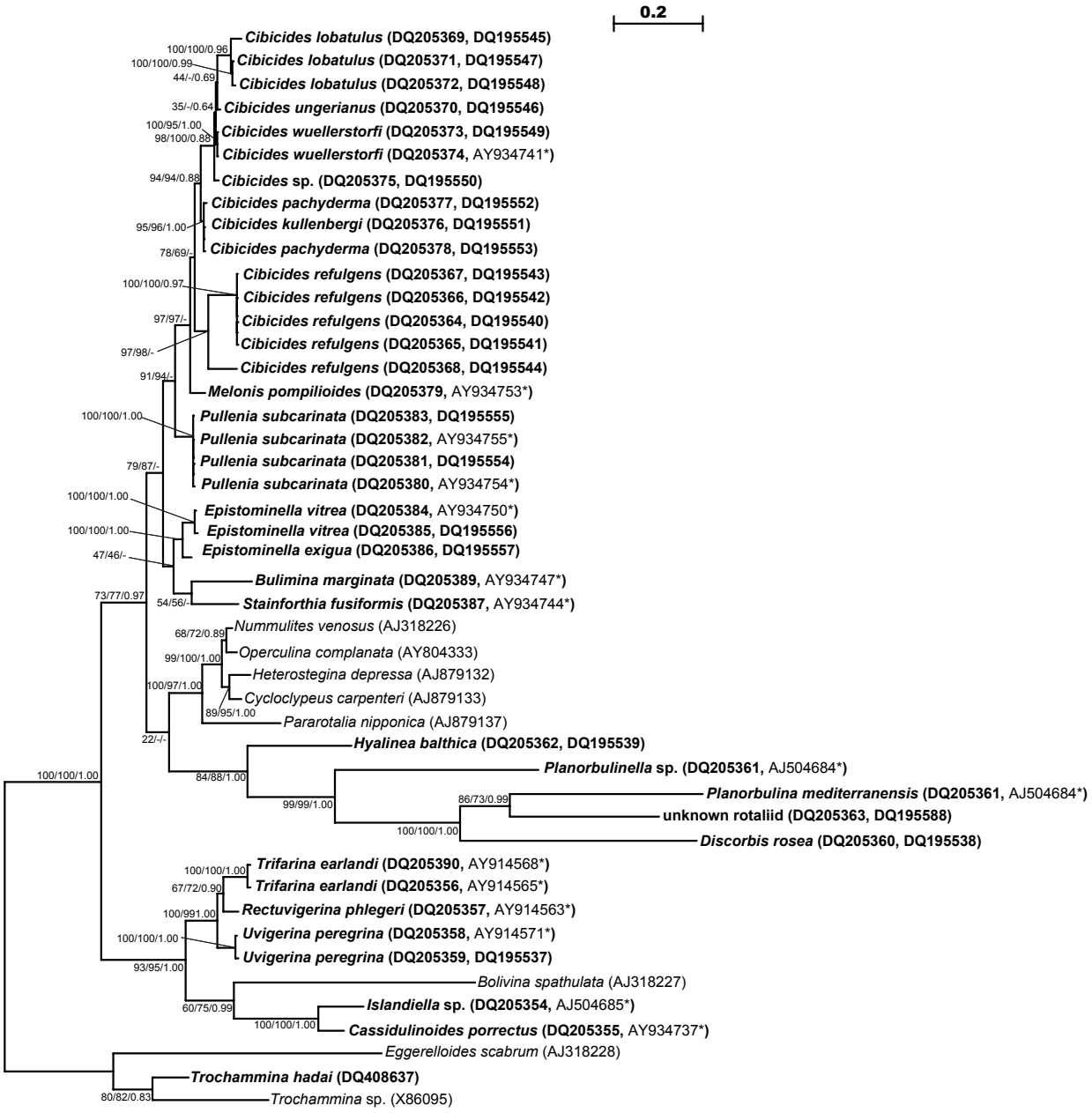

Figure 3.4. Phylogeny of Rotaliida inferred from partial SSU rDNA sequences (5' and 3' end fragments) using the ML (HKY+I+G) method (2632 aligned sites). Values are given for internal nodes for HKY, GTR and PP. Species names written in bold designate new sequences, the others were taken from GenBank (accession numbers in brackets).

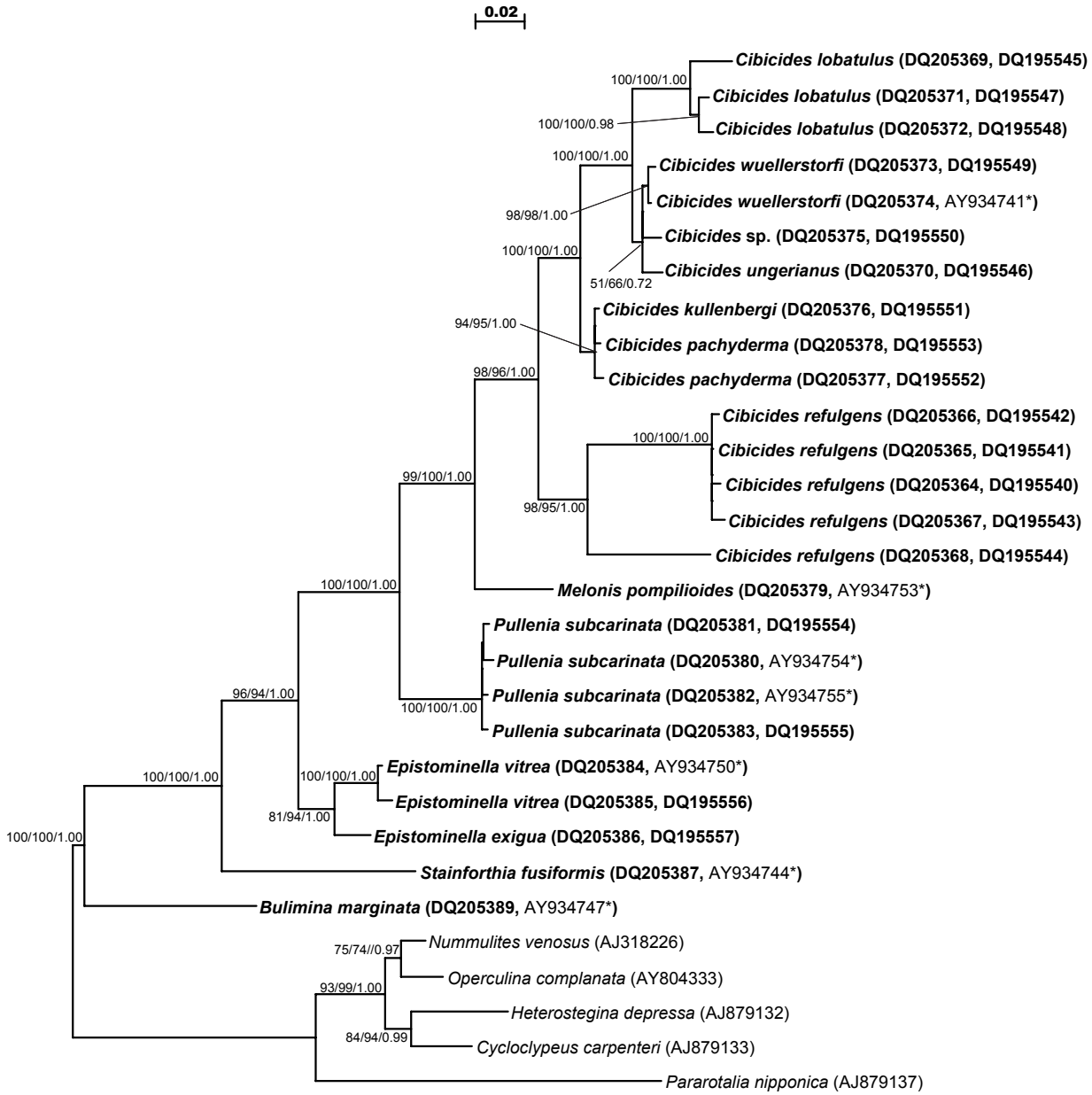

Figure 3.5. Phylogeny of *Cibicides* and closely related species inferred from partial SSU rDNA sequences (5' and 3' end fragments) using the ML (HKY+I+G) method (2357 aligned sites). Values are given for internal nodes for HKY, GTR and PP. Species names written in bold designate new sequences, the others were taken from GenBank (accession numbers in brackets).

1998). The GTR or General Time Reversible model allows the transition and transversion rates to be different (Lanave et al., 1984; Rodriguez et al., 1990). To correct for among-site rate variations, the proportion of invariable sites (I) and the α parameter of γ distribution (G), with eight rate categories, were estimated by the programs and taken into account in all analyses. Additionally, the HKY model (Hasegawa et al., 1985), allowing transitions and transversions to have potentially different rates, was applied with PhyML.

3.3. Results

First, we analysed the two concatenated fragments with all the sequences available to test the monophyly of cibicidids and to infer their position among Rotaliida Delage and Hérouard, 1896. As shown in Fig. 3.4, the 15 sequences of cibicidids group together in the ML tree, albeit the bootstrap support for this grouping is rather weak (78% BS with HKY/69% BS with GTR). This support increases up to 97% BS (HKY) if the sequence of *Melonis pompilioides* (Fichtel and Moll, 1798), which branches as a sister group to cibicidids is removed (data not shown).

The cibicidids group together with *M. pompilioides*, *Pullenia subcarinata* (d'Orbigny, 1839), *Epistominella* Husezima and Maruhasi, 1944 (*E. exigua* (Brady, 1884) and *E. vitrea* Parker, 1953), *Stainforthia fusiformis* (Williamson, 1858) and *Bulimina marginata* d'Orbigny, 1826 in a reasonably supported clade (79% BS with HKY/87% BS with GTR). Three other major groupings in the ML tree are the sub-clade of Nummulitidae de Blainville, 1827 + *Pararotalia nipponica* (Asano, 1936) (100% BS with HKY/97% BS with GTR) and the sub-clade of *Hyalinea balthica* (Schroeter, 1783) + *Planorbulinella* sp. + *Planorbulina mediterranensis* d'Orbigny, 1826 + *Discorbis rosea* (d'Orbigny, 1826) + unkown rotaliid (84% BS with HKY/88% BS with GTR) grouped together and the clade of Uvigerinidae Haeckel, 1894 + Cassidulinidae d'Orbigny, 1839 + *Bolivina spathulata* (Williamson, 1858) (93% BS with HKY/95% BS with GTR*).* In the HKY analysis, the Nummulitidae + *Pararotalia* group with the *Hyalinea* + *Planorbulinella* + *Planorbulina* + *Discorbis* + unkown rotaliid clade, whereas in the GTR analysis, they group with the *Cibicides* + *Melonis* + *Pullenia* + *Epistominella* + *Stainforthia* + *Bulimina* clade. Two groups (uvigerinids – cassidulinids - *Bolivina* and *Hyalinea – Planorbulinella – Planorbulina* - unknown rotaliid - *Discorbis*) are also recognized in Bayesian analyses, with statistical support of 1.00 PP and a structure similar to the one found in the ML analysis. In the Bayesian tree the group *Epistominella + S. fusiformis + B. marginata + P. subcarinata + M. pompilioides + Cibicides* appears as paraphyletic, with the clade Nummulitidae + *P. nipponica* branching within it. With the exception of *C. refulgens*, the cibicidids form a monophyletic clade with 0.88 PP (data not shown).

To investigate the relationships between cibicidid species, we analysed the concatenated data for the clade *Cibicides + M. pompilioides + P. subcarinata + Epistominella + S. fusiformis + B. marginata*, using Nummulitidae and *P. nipponica* as an outgroup (Fig. 3.5). The resulting tree has almost the same topology as the one in Fig. 3.4, but the bootstrap values have substantially increased in almost every case. The topology of ML and Bayesian trees is similar. The clade of cibicidids is supported by 98% BS (HKY), 96% BS (GTR) and 1.00 PP. It branches as sister group to *M. pompilioides*, with 99% BS (HKY), 100% BS (GTR) and 1.00 PP. *Pullenia subcarinata* and *Epistominella* form successive sister groups with strong BS and PP values. Within the cibicidids, three well supported clades can be distinguished: the most basal *C. refulgens* clade (98% BS (HKY), 95% BS (GTR), 1.00 PP), the *C. pachyderma + C. kullenbergi* clade (94% BS (HKY), 95% BS (GTR), 1.00 PP), and the *C. ungerianus + Cibicides* sp. *+ C. wuellerstorfi + C. lobatulus* clade (100% BS (HKY and GTR), 1.00 PP).

The third dataset, including 47 cibicidid sequences, was analysed to examine intraspecific variations (Fig. 3.6), using the fragment 14F1-B. *Pullenia subcarinata* was chosen as an outgroup, because there were several sequences available for this species. All morphospecies form well supported groups, except *C. refulgens,* which splits into two clades, one grouping the specimens from Antarctica and branching as sister to all other cibicidids and the second comprising the specimens from the Mediterranean. The statistical support is good for most of the clades, although

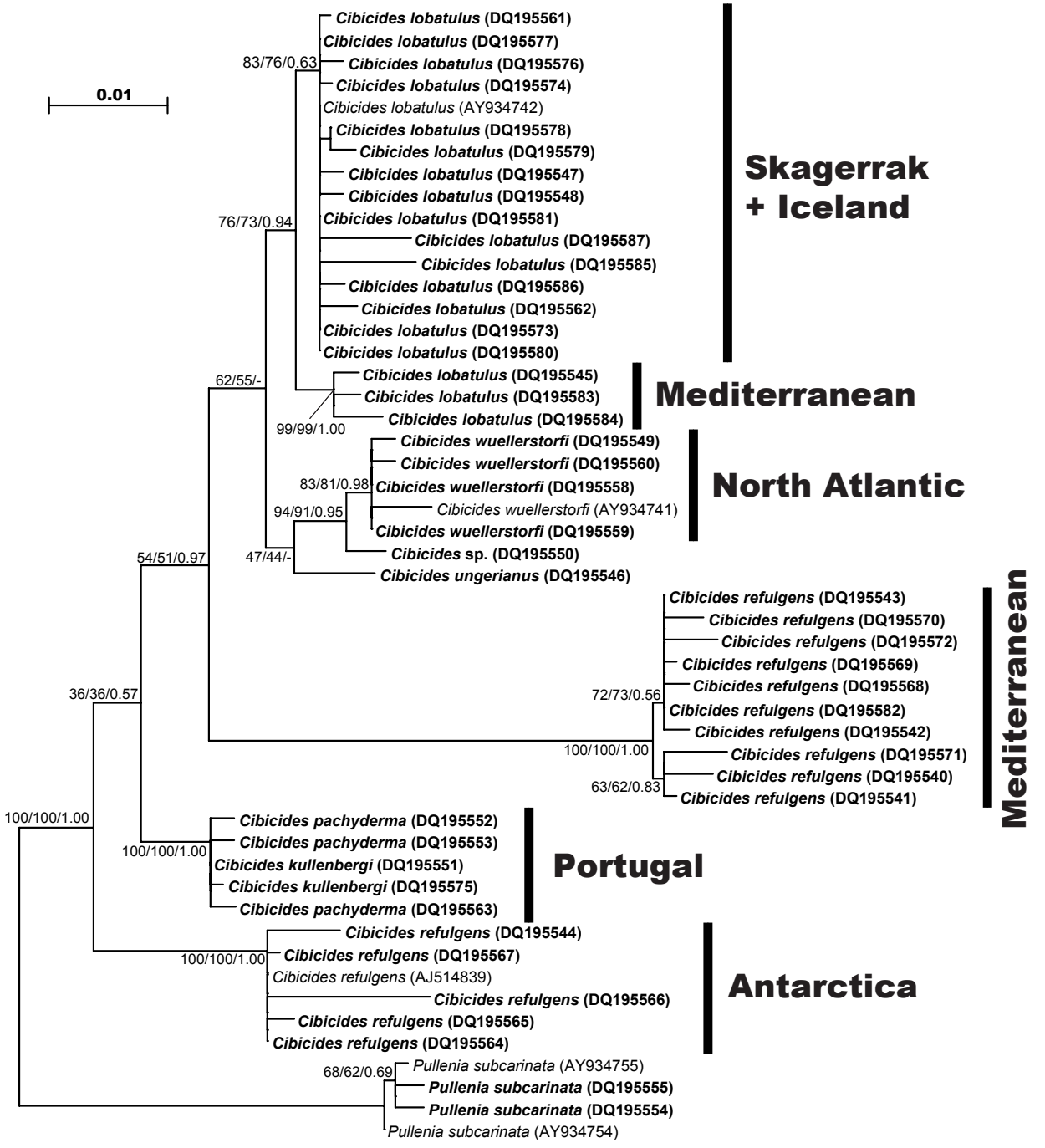

Figure 3.6. Phylogeny of *Cibicides* inferred from partial SSU rDNA sequences (3' end fragment) using the ML (HKY+I+G) method (1013 aligned sites). Values are given for internal nodes for HKY, GTR and PP. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers in brackets).

the nodes connecting the clades are not very well supported (below 75% BS in all cases). The Bayesian analysis confirms the ML topology except for the Antarctic population of *C. refulgens*, which branches as a sister group to *C. wuellerstorfi* (data not shown). *Cibicides lobatulus* forms a well defined group with clear geographical subgroups for populations from the North Atlantic and the Mediterranean. *Cibicides pachyderma* and *C. kullenbergi* branch together. The last taxa, *C. ungerianus* and *Cibicides* sp., represented by only one sequence each, group with *C. wuellerstorfi*.

3.4. Discussion

3.4.1. Are cibicidids monophyletic?

Phylogenetic analyses of our data showed that the cibicidids are monophyletic in ML trees but failed to support their monophyly in Bayesian trees. Comparing the results of analyses with different numbers of sites, we noticed that whether the clade of *Cibicides* shows up as monophyletic depends on the length of the examined sequences. When we analysed a shorter fragment of the SSU, which is traditionally used in foraminiferal phylogeny (e.g. Pawlowski, 2000; Holzmann et al., 2003; Darling et al., 2004; Ertan et al., 2004), the cibicidids neither grouped together in ML nor in Bayesian analyses (Fig. 2.7). By combining two fragments of the SSU we obtained more informative sites, and were able to establish the relationships among rotaliids more accurately. The analyses of combined fragments confirmed the phylogenetic position of the major groups and significantly increased the bootstrap support for most of the clades defined in a previous study (Schweizer et al., 2005, Fig. 7). Additional analyses show that these supports are even higher when complete SSU sequences are analysed (see Chapter 2).

Although the support for monophyly of cibicidids is not very strong, there is even less evidence to consider them as belonging to different superfamilies, as suggested by some morphology-based classifications (Loeblich & Tappan, 1964, 1988; Revets, 1996). Cibicidids share many morphological traits: the coarsely perforate wall made of hyaline lamellar calcite, the trochospiral coil with an evolute spiral side and an involute umbilical side, and the aperture, which is a simple slit edged by a lip and located near the peripheral margin on the umbilical side. Although they were split into different superfamilies on the basis of the optical properties of their wall microstructure by Loeblich & Tappan (1964, 1988), this criterion was already dismissed as inappropriate for classification of higher taxa (Towe & Cifelli, 1967, Deutsch Conger et al., 1977). Our molecular results have confirmed that and agree with the classifications which place all the cibicidids in a single family (Cushman, 1928, Galloway, 1933, Hofker, 1956, Reiss, 1958, Haynes, 1981, Sen Gupta, 2002).

The close relationship of cibicidids with *Melonis* and *Pullenia* may appear surprising in view of traditional taxonomy. *Melonis* and *Pullenia* belong to the superfamily Nonionacae Schultze, 1854 (Loeblich & Tappan, 1988). However, there are some morphological similarities between

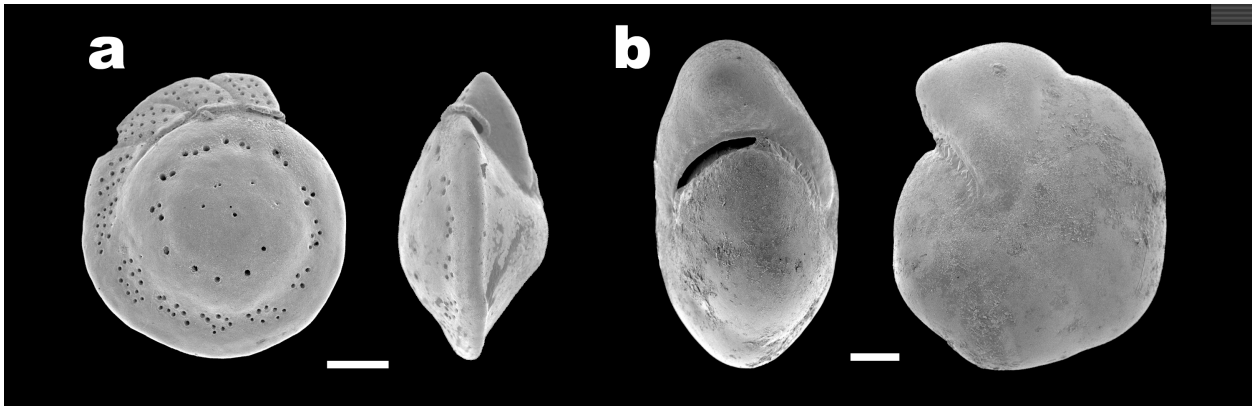

Figure 3.7. SEM picture showing the apertures of *Cibicides* (a) and *Pullenia* (b). Scale= 100μm

cibicidids and these two genera. *Cibicides* has the same kind of aperture as *Melonis* and *Pullenia*: a low interiomarginal slit with a lip (Fig. 3.7). Moreover, morphological intermediates (*Anomalina* d'Orbigny, 1826, *Anomalinoides* Brotzen, 1942) exist between the planispiral coil of *Melonis* and *Pullenia* and the trochospiral one of *Cibicides*, suggesting that a transition is possible. Therefore, the grouping of *Melonis*, *Pullenia* and *Cibicides* within the same family seems justified.

3.4.2. Relationships between the cibicidid species

Molecular data allow the distinction of three main clades within the cibicidids: clade 1 comprising Antarctic and Mediterranean populations of *C. refulgens*; clade 2 comprising *C. pachyderma* and *C. kullenbergi*, and clade 3, which includes *C. ungerianus*, *Cibicides* sp., *C. wuellerstorfi* and *C. lobatulus*.

Molecular distinction of three clades of cibicidids contradicts the traditional taxonomic separation between *Cibicides* and *Cibicidoides*, based on test convexity. The planoconvex species *C. lobatulus*, *C. refulgens* and *C. wuellerstorfi* form two separate clades, one of which also includes the planoconvex to slightly biconvex *C. ungerianus*. The two biconvex species, *C. kullenbergi* and *C. pachyderma* form a clade, which branches closer to *C. lobatulus*, *C. wuellerstorfi* and *C. ungerianus* than to *C. refulgens*. This is in agreement with critical remarks of some authors who already noticed that the separation between plano- and biconvex forms was not always clear and that both forms occurred within the same species (Mead, 1985; Verhallen, 1991; Gupta, 1994). Our results show that this distinction is not taxonomically relevant and confirm that the plano- or biconvex shape depends on the mode of life of the specimen, explaining why this can vary within one species.

3.4.3. Species identification

Among the six studied species, only *C. wuellerstorfi* appears to be well characterized genetically and morphologically. In all examined specimens the SSU sequences are almost identical (91-99%). The genetic homogeneity of this species is also confirmed by analysis of the much more variable ITS sequences (Pawlowski et al., work in progress).

Closely related to *C. wuellerstorfi,* is *C. lobatulus*. This species is also well characterized genetically, but its morphology is much more variable. It is often difficult to distinguish *C. lobatulus* from *C. refulgens*, especially when both species are found at the same localities and in similar environments (e.g. the specimens C170 to C173, sampled at the same location in the Mediterranean). *Cibicides refulgens* is often included within *C. lobatulus* in (paleo)ecological studies (see for instance Hageman, 1979; Verhallen, 1991), because of the morphological similarity and the observation of intermediate forms between both species (Verhoeve, 1971; Hageman, 1979; Van der Zwaan, 1982; Verhallen, 1991; Jonkers et al., 2002). *Cibicides lobatulus* comprises a huge variety of morphotypes which were sometimes described as different subspecies or even different species (Wood & Haynes, 1957; Nyholm, 1961; Cooper, 1965; Schnitker, 1969). Some specimens adopt strange shapes commanded by the substrate on which they live fixed; others, vagile, have a more regular shape. The molecular analyses show that regular (C120) and irregular (C35, C37) morphotypes branch together (Fig. 3.6), confirming that the large phenotypic variation within *C. lobatulus* is not phylogenetically relevant. On the other hand, a clear geographical separation between the population of *C. lobatulus* from the Mediteranean (C170) and the populations from the North Atlantic (C2) and the Skagerrak (576, C35, C37, C39, C40, C120) suggest that this species may comprise several cryptic species (Table 3.1; Fig. 3.6).

Cryptic speciation is evident in the case of *C. refulgens*. This species splits into two clades, one grouping the specimens from the Mediterranean, living attached to seaweeds, the second grouping the specimens collected in Antarctica. The latter live attached to the scallop *Adamussium colbecki* Smith, 1902 and feed on diatoms or on the mantle of their host, and can therefore be considered as parasites or predators (Alexander & DeLaca, 1987). Consequently, on the basis of these ecological and molecular differences, both populations should be considered as separate cryptic species, even if no morphological features can distinguish them yet.

Among the remaining four cibicidids, *C. pachyderma* and *C. kullenbergi* form a single clade, and

apparently belong to the same species. They are morphologically rather close and intermediates were observed between them (see Chapter 5). This implies that the name *C. pachyderma* should be retained for this morphospecies, while *C. kullenbergi* should be considered as its junior synonym. However, discrepancies in the species concept of *C. kullenbergi* exist and further sampling of other specimens is needed to confirm this synonymy. *Cibicides* sp. and *C. ungerianus*, are each represented by a single sequence and branch as sister groups to *C. wuellerstorfi*. *Cibicides ungerianus* appears distinct from *C. pachyderma* and *C. kullenbergi* contrary to the inference of Jonkers (1984) or Van Morkhoven et al. (1986).

3.5. Conclusions

As we have seen, current classifications have split the cibicidids into different genera, families and even superfamilies despite their common morphological and ecological features. Our study clearly shows that there is no justification for classifying the cibicidids in different superfamilies. According to our data, the planoconvex (*C. lobatulus, C. refulgens, C. ungerianus, C. wuellerstorfi*) and biconvex (*C. kullenbergi, C. pachyderma*) species group together suggesting that there is no reason to separate the biconvex from the planoconvex tests in two different genera (*Cibicides* and *Cibicidoides*), nor to split *Cibicides* into *Fontbotia* and *Lobatula* or to place *wuellerstorfi* in the genus *Planulina*. It seems justified to include all these species into the same family, and, for the time being, in the same genus *Cibicides* de Monfort, 1808. However, the monophyly of this genus should be investigated by more extensive taxon sampling and further analyses of other genes.
Within the genus *Cibicides*, some morphospecies have been confirmed by molecular analyses (*C. lobatulus*, *C. wuellerstorfi*), whereas others are probably different morphotypes of the same species (*C. pachyderma* and *C. kullenbergi*) or represent several cryptic species (*C. refulgens*). The morphological distinction between *C. lobatulus* and *C. refulgens* needs to be studied in more detail and their morphological definition should be revised. Samples from other localities around the world are clearly needed to test the species definition in widely distributed cibicidids and to fully answer all the questions addressed in this paper.

Chapter 4

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

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

4.1. 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 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 & 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 & 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 & Loubere, 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 & Elderfield, 2002; Mackensen & Licari, 2004).

The genus *Uvigerina* was first recorded in sediments of lower Eocene age (Loeblich & 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,

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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 & 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

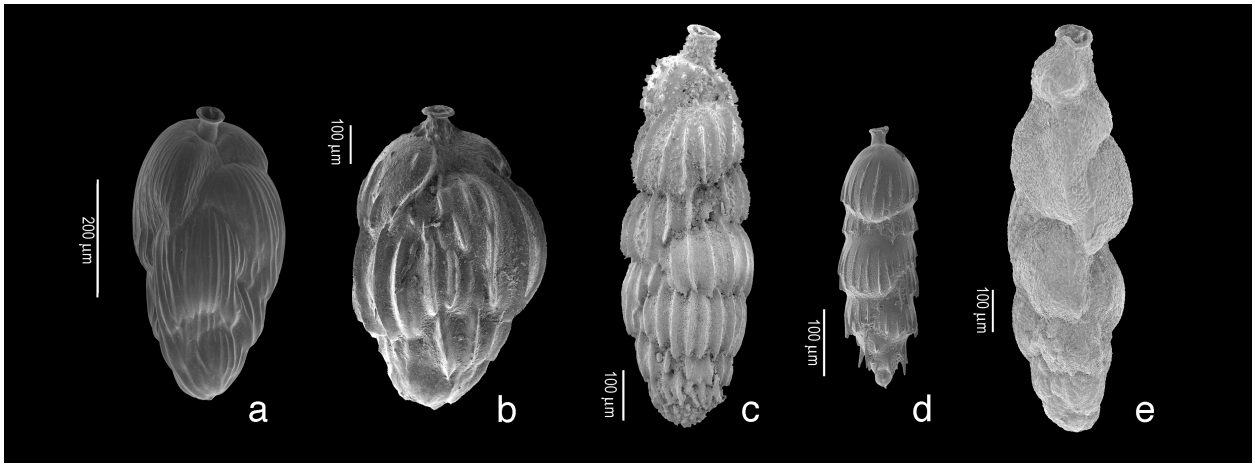

Figure 4.1. SEM pictures of the examined uvigerinids: a) *U. elongatastriata* (U273), b) *U. mediterranea,* c) *U. peregrina* (U67), d) *R. phlegeri* (U239), e) *T. earlandi*. For specimens from which DNA was extracted and sequenced, the DNA number is indicated in brackets.

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 & Tappan, 1988).

The genus *Uvigerina* has been divided by Van der Zwaan et al. (1986a) 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. peregrina* group (*U. peregrina*) and one in the *U. bononiensis* group (*R. phlegeri*) (Fig. 4.1).

The present classification and phylogeny of *Uvigerina* is based exclusively on morphological features but recently ribosomal DNA sequences of several *Uvigerina* species were published (Ertan et al., 2004). Here, we report 61 new sequences of *Uvigerina* and other rotaliids (GenBank accession numbers AY914562-AY914600 and AY934735-AY934756), which we used for phylogenetic analyses together with previously published sequences.

Our goals were to infer the phylogenetic position of *Uvigerina* among rotaliid foraminiferans, to analyse its intrageneric relationships, and to examine intraspecific variation in a population of *U. peregrina*. Our results are compared to existing molecular data on rotaliid foraminifera. We discuss the position of *Uvigerina* in the rotaliid tree, and the possible differences between genetically and morphologically based taxonomies.

4.2. Material and methods

4.2.1. Sampling and SEM identification

Live specimens of *Uvigerina* and *Rectuvigerina* were collected during three cruises: in May 2002 with the R/V Trygve Braarud (University of Oslo, Norway) in the Oslo Fjord, in May 2003 with the R/V Arne Tiselius (Kristineberg Marine Research Station, Sweden) in the Skagerrak and the Kattegat, and in October 2003 with the R/V Pelagia (Royal Netherlands Institute for Sea Research, The Netherlands) on the Portuguese coast of the Atlantic (Fig. 4.2). The specimens of *Trifarina earlandi* were collected in November 1998 and 1999 in Antarctica (Explorer Cove, McMurdo Sound).

Figure 4.2. Map of Europe indicating the three areas sampled during the cruises.
1) Oslo Fjord (Norway); 2) Swedish coast of Skagerrak; 3) Portuguese coast of Atlantic.

Sediment samples were collected by boxcoring and multicoring. The top few centimeters were sampled with a spoon and immediately sieved using cold bottom water (fractions 500/250/125μm). The different fractions were stored in the refrigerator at 4°C.
Specimens were cleaned and picked under a dissection microscope within hours to a few days. Living individuals were distinguished from dead ones by their natural coloration (e.g. greenish-brownish for *U. peregrina* and *R. phlegeri*, orange for *U. elongatastriata*), lack of cytoplasm in the last chamber, good preservation of the test (not eroded or broken), and presence of debris around the aperture. Whenever possible, specimens were transferred to Petri dishes containing clean sea water and observed a few hours after picking, to check whether they were alive. Putatively living specimens were dried on Chapman slides; later the dried specimens were coated with gold and pictured with scanning electron microscope (SEM). All the SEM pictured specimens were extracted for DNA, however the percentages of positive results were variable.

4.2.2. Morphometrical analysis

Uvigerina peregrina was very abundant in samples from the Oslo Fjord and showed a wide range of morphologies. SEM pictures of individuals from this population were used to perform morphometrical analyses. A general view of the specimens and a view of the pores at a higher magnification were used. Eight characteristics were measured or observed. Three of them are metrical criteria: the maximal length (maxL) without the neck, the maximum transversal diameter (MTD) and the number of chambers (nc). Two ratios were calculated from the metrical criteria: MTD/maxL*100 and nc/maxL*100. Five of the measured characteristics are non-metrical: the shape of the chambers (inflated, marginate, standard (not inflated nor marginate)), the number of costae (small, medium, large), the number of pores (small, medium, large), the spinosity (absent, between costae, on the last chamber), and the position of the neck (terminal, inclined, in a depression, with spines).
Bivariate graphs were made using the three metrical criteria. The software employed was Statview 4.5 (Abacus Concepts). Metrical as well as non-metrical criteria were used for multivariate analyses: Detrended Correspondence Analysis (DCA) and Canonical Variates Analysis (CVA, alias Fisher's linear discriminant analysis), using the program CANOCO (Ter Braak and Smilauer, 1998). In order to incorporate nominal variables in our analyses, they were transformed into

Table 4.1. List of new SSU sequences and origin of DNA samples.

Access #	Species	DNA #	Collection site	Cells	Cloning
AY934735	*Bolivina* sp.	JPM99	Mediterranean		direct
AY934736	*Bolivina* sp.	170	Tahiti		direct
AY934737	*Cassidulinoides porrectus*	3924	Terranova Bay, Antarctica		2
AY934738	*Cassidulina laevigata*	2508	Oslo Fjord, Norway	1	2
AY934744	*Stainforthia fusiformis*	3965	Skagerrak, Sweden	150	2
AY934745	*Stainforthia fusiformis*	3979	Dunstaffnage, Scotland	50	1
AY934743	*Stainforthia* sp.	2641	Svalbard, Norway		direct
AY934746	*Virgulina concava*	3991	Dunstaffnage, Scotland	5	1
AY934747	*Bulimina marginata*	3599	Oslo Fjord, Norway	130	1
AY934748	*Bulimina marginata*	523	Kosterfjord, Sweden	3	direct
AY914562	*Globobulimina turgida*	3601	Oslo Fjord, Norway	20	2
AY914563, AY914564	*Rectuvigerina phlegeri*	U239	Nazaré Canyon, Portugal	1	4
AY914566, AY914567	*Trifarina earlandi*	1145	McMurdo, Antarctica	5	2
AY914568	*Trifarina earlandi*	1994	NH-Ice Hut, Antarctica	10	direct
AY914565	*Trifarina earlandi*	2187	McMurdo, Antarctica	5	3
AY914577, AY914578	*Uvigerina elongatastriata*	U273	Nazaré Canyon, Portugal	1	2
AY914569, AY914570	*Uvigerina peregrina*	U26	Oslo Fjord, Norway	1	3
AY914571	*Uvigerina peregrina*	U32	Oslo Fjord, Norway	2	direct
AY914572	*Uvigerina peregrina*	U67	Oslo Fjord, Norway	1	direct
AY914573	*Uvigerina peregrina*	U169	Skagerrak, Sweden	1	2
AY914574, AY914575	*Uvigerina peregrina*	U184	Skagerrak, Sweden	1	3
AY914576	*Uvigerina peregrina*	U195	Skagerrak, Sweden	1	3
AY934739	*Discorbis rosea*	753	Florida, USA	1	2
AY934749	*Epistominella* sp.	286	Channel, France	10	direct
AY934750	*Epistominella vitrea*	2060	Cape Evans, Antarctica	4	3
AY934741	*Cibicides wuellerstorfi*	C184	Setubal Canyon, Portugal	1	3
AY934742	*Cibicides lobatulus*	C39	Oslo Fjord, Norway	1	2
AY934740	*Planorbulinella* sp.	358	Elat, Israel	4	2
AY934751	*Nonionella labradorica*	3600	Oslo Fjord, Norway	60	5
AY934752	*Nonionella labradorica*	3966	Skagerrak, Sweden	20	1
AY934753	*Melonis pompilioides*	1400	Skagerrak, Sweden		3
AY934756	*Pullenia subcarinata*	1087	NH-Ice Hut, Antarctica	2	2
AY934755	*Pullenia subcarinata*	1148	McMurdo, Antarctica	1	3
AY934754	*Pullenia subcarinata*	1850	McMurdo, Antarctica	1	2

'dummy variables', e.g. a nominal variable with three categories was split into three separate variables with values of 0 or 1.

DCA is a unimodal ordination technique (Ter Braak, 1995). In our analysis, individual specimens were treated as 'samples' (as defined in CANOCO) and their morphological characteristics as 'species'. Thus, the specimens were arranged on DCA axes, maximizing the spread of their corresponding characteristics along the axes. The method of detrending was by 2nd order polynomials. To obtain

Table 4.2. List of new ITS sequences and origin of DNA samples.

Access #	Species	DNA #	Collection site	Depth	Cells	Cloning
AY914579, AY914580, AY914581	*Uvigerina peregrina*	U37	Oslo Fjord Norway	195m	1	3
AY914582, AY914583	*Uvigerina peregrina*	U42	Oslo Fjord Norway	195m	1	2
AY914584, AY914585, AY914586	*Uvigerina peregrina*	U51	Oslo Fjord Norway	54m	1	3
AY914587, AY914588	*Uvigerina peregrina*	U66	Oslo Fjord Norway	87m	1	2
AY914589	*Uvigerina peregrina*	U67	Oslo Fjord Norway	87m	1	1
AY914590, AY914591, AY914592	*Uvigerina peregrina*	U72	Oslo Fjord Norway	87m	1	3
AY914593, AY914594, AY914595	*Uvigerina peregrina*	U86	Oslo Fjord Norway	87m	1	3
AY914596, AY914597	*Uvigerina peregrina*	U87	Oslo Fjord Norway	87m	1	2
AY914598, AY914599, AY914600	*Uvigerina peregrina*	U194	Skagerrak Sweden	60m	1	3

a CVA, we performed a special kind of canonical correspondence analysis (CCA) as explained by Ter Braak and Smilauer (1998, pp. 60-62). Again the specimens were 'samples'. The *Uvigerina* types were 'species' with an abundance of either 0 or 1, so each sample consisted of only one 'species'. The morphological characteristics are included as 'environmental parameters' (in CANOCO terminology). Thus, in CCA the axes were defined as linear combinations of the values of the morphological characteristics. The linear combination of characteristics that gave the best separation of the *Uvigerina* types was the first axis, the second best (independent of the first) was the second axis, etc. The eigenvalues in CVA (θ) could be derived from the eigenvalues in CCA (λ): $\theta = \lambda / (1 - \lambda)$. Because type 4 specimens appeared to be outliers in the analyses, we eliminated them in the CVA in order to improve the separation of the other three types.

4.2.3. DNA extraction, PCR amplification, cloning and sequencing

DNA was extracted from single specimens using DOC lysis buffer (Pawlowski et al., 1994). For the extraction of multiple specimens, DNeasy Plant Mini Kit (Qiagen) was used. Two regions of ribosomal DNA (rDNA) were examined here: a fragment of the SSU (small subunit) rDNA situated at the 3' end of approximately 1,000 base pairs, and the ITS (Internal Transcribed Spacer) region (ITS1 + 5.8S + ITS2) with a length of about 1,000-1,100 base pairs. The SSU fragment was amplified using the primer pair s14F3-sB and reamplified using the primers s14F1-sB. The ITS region was amplified with s20-2TAIC and reamplified with sBr-2TAIC. The sequences of these primers can be found in Pawlowski (2000) except s14F3 (5' ACG CAM GTG TGA AAC TTG 3') and sBr (5' GTA GGT GAA CCT GCA GAA GG 3'). SSU and ITS were amplified by PCR using a total volume of 50µl. The thermal cycle parameters consisted of 40 cycles of 30 s at 94°C, 30 s at 50°C and 120 s at 72°C, followed by 5 min at 72°C for final extension. Reamplification was carried out using 35 cycles of 30 s at 52°C instead of 50°C, all other parameters remaining

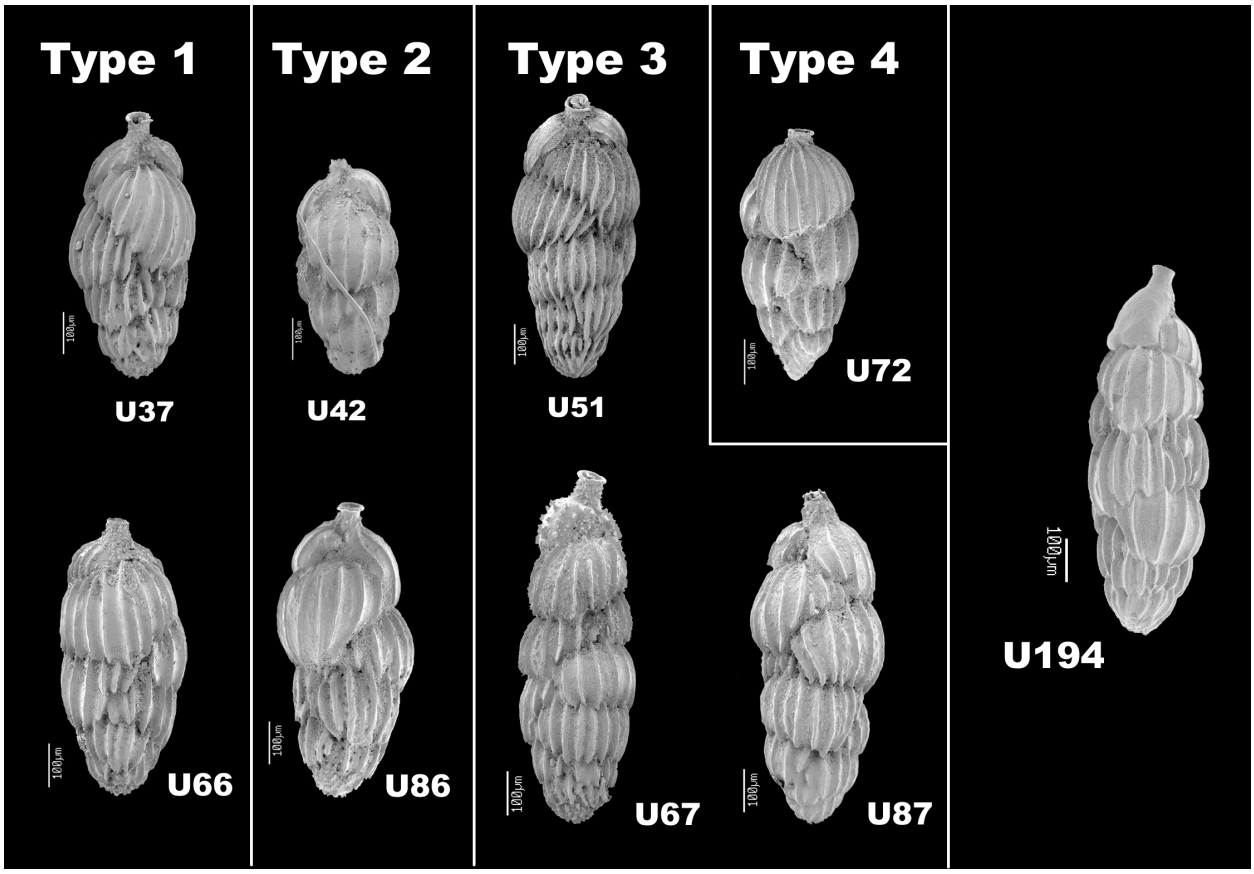

Figure 4.3. SEM pictures of the *U. peregrina* specimens used for the ITS. Morphologically, U37 and U66 belong to type 1, U42 and U86 to type 2, U51, U67 and U87 to type 3, and U72 to type 4. All these specimens were sampled in Oslo Fjord. U194 was collected on the Swedish coast of Skagerrak and was excluded from the morphometrical study.

unchanged. Positive PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics). PCR products obtained from DNA samples 170, 523, 1994, 2641, U32, and U67 were sequenced directly, while the remaining PCR products (see Tables 1 and 2) were ligated in the pGEM-T Vector (Promega) and cloned using ultracompetent cells XL2-Blue MRF' (Stratagene). Sequencing reactions were prepared using ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analysed with DNA sequencers ABI-377 or ABI-PRISM 3100 (Perkin-Elmer), all according to the manufacturer`s instructions.

4.2.4. Phylogenetic analysis

The new SSU and ITS sequences of rotaliids presented here have been deposited in the EMBL/GenBank data base, their accession numbers are reported in Tables 4.1 and 4.2. To extend our data set, we used rotaliid sequences deposited in the GenBank data base.
For the partial SSU, 52 sequences of Rotaliida and four sequences of Textulariida, used as outgroup, were analysed. We excluded from our analyses the sequences of *Ammonia*, *Elphidium*, *Haynesina* and the Glabratellidae available in the Genbank, because their very rapid rates of evolution reduce the number of unambiguously aligned sites and bias the analyses. Sequences were aligned manually employing Seaview (Galtier et al., 1996). Of the ~1,000 base-pair fragment of the SSU, 695 unambiguously aligned sites were used for the phylogenetic analysis of rotaliids and 781 for the analysis of uvigerinids. The maximum likelihood (ML) trees were obtained using the PhyML program (Guindon and Gascuel, 2003), with the HKY model (Hasegawa et al., 1985) allowing transitions and transversions to have potentially different rates and the General Time Reversible (GTR) model allowing all these rates to be different (Lanave et al., 1984; Rodriguez et

al., 1990). To correct the among-site rate variations, the proportion of invariable sites (I) and the α parameter of γ distribution (G), with eight rate categories, were estimated by the program and taken into account in all analyses. Non-parametric ML bootstraps (with 100 replicates) were calculated using PhyML. Bayesian inferences (BI) were obtained with MrBayes v.3.0 (Huelsenbeck and Ronquist, 2001), using the same models of DNA evolution as for the ML analyses. The program was run for 1,000,000 generations, sampled every 100 generations, with four simultaneous chains. 10,000 trees were sampled, of which the first 1,000 were discarded as burn-in.
For the constrained tree topology, we used TreeView (Page, 1996) to build the constrained tree and PAUP* version 4.0b10 (Swofford, 1998) for the K-H (Kishino and Hasegawa, 1989) and the S-H (Shimodaira and Hasegawa, 1999) tests.
In addition, the ITS region of 22 clones belonging to nine different specimens of *Uvigerina peregrina* was analysed with PhyML (871 unambiguously aligned sites).

4.3. Results

4.3.1. Morphometrical study

In the Oslo Fjord population of *Uvigerina peregrina*, four different morphological types can be distinguished with morphometrical analyses. The different morphotypes are shown in Figure 4.3. The type 1 (30 specimens) generally has a standard shape of the chambers, a large number of costae, spines between the costae or no spines, a small number of pores and the neck is positioned at the top. The type 2 (15 specimens) is characterized by inflated chambers and a low number of costae; it often has no spines or spines between the costae, a large number of pores and the neck is inclined and/or spinose. The type 3 (12 specimens) is characterized by an elongated shape; it usually has a standard shape of the chambers, a large number of costae, spines between the costae and a terminal neck. The type 4 (two specimens) is essentially defined by a marginate shape of the chambers, with no spines and a terminal neck. No relation was found between the morphotypes and the different sampling locations.
The type 3, with a more elongated shape, can be separated from the other specimens in a bivariate graph (Fig. 4.4a). Calculation of the ratio MTD/maxL*100 also allows to separate the type 3 (except 2 specimens), with values below 42, from the other types (Fig. 4.4b). DCA enables us to graphically link the criteria with the groups they characterize and the morphological variability of the specimens (Fig. 4.5). There is a good separation between types 2 and 3 on the first (horizontal) axis (except one specimen from type 3) and between type 4 and the other types on the second

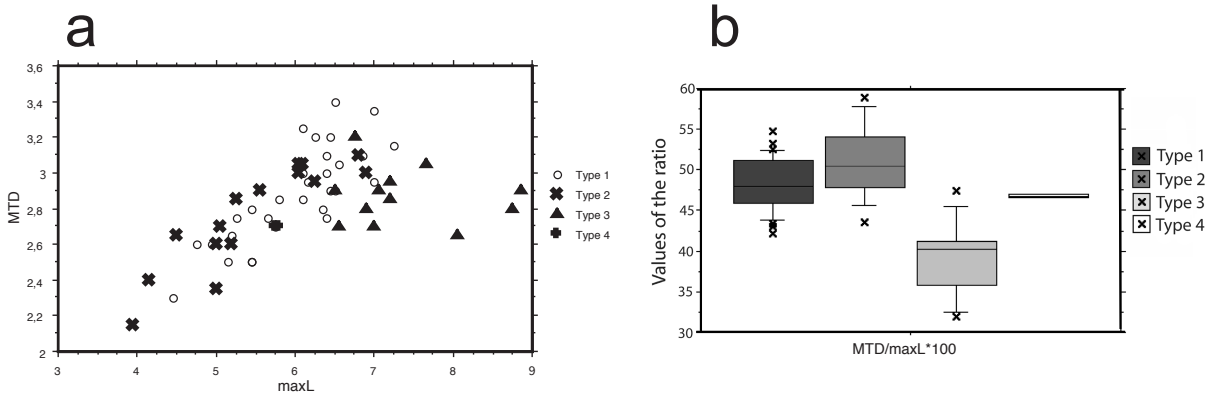

Figure 4.4.
a) Bivariate graph comparing the maximal length (maxL) and the maximum transversal diameter (MTD).
b) Box-plots of the ratio MTD/maxL*100 for each morphotype. The box and the vertical lines coming from it (the "whiskers") represent 100% of the values. The box is delimited by the first quartile (Q1, 25%) at the bottom and the third one (Q3, 75%) at the top. Inside the box, the horizontal line represents the median (50%). Crosses indicate values outside the limits of the "whiskers" (the "outliers").

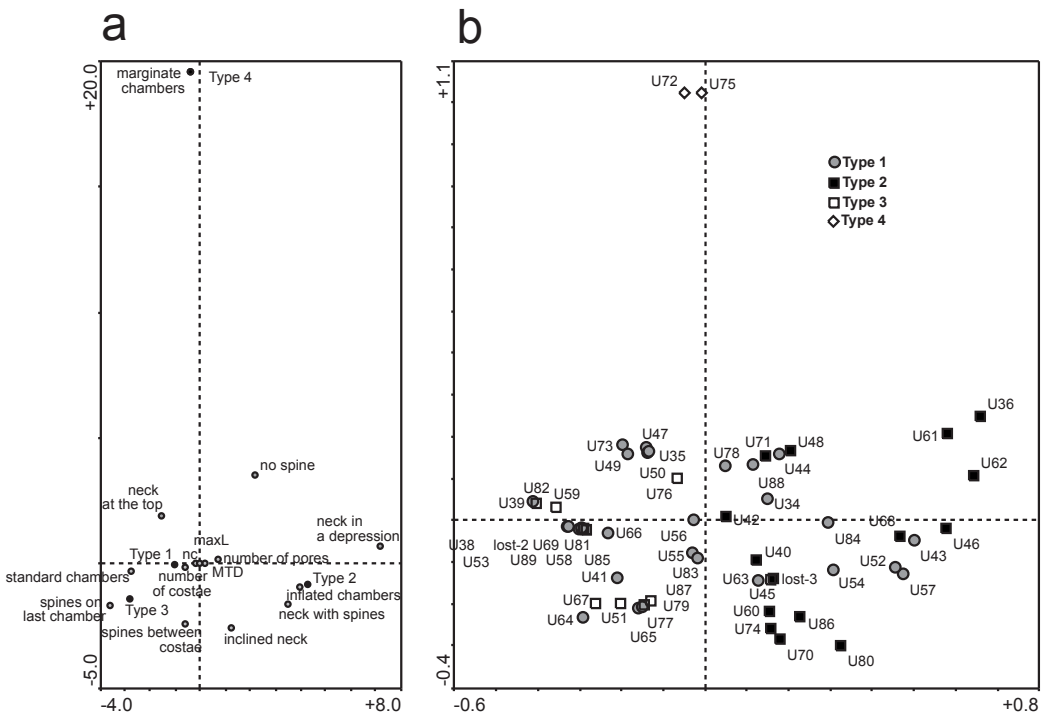

Figure 4.5. DCA graphs:
a) Position of the criteria and center of each group.
b) Position of the specimens, labelled after the analysis.
Eigenvalues of the 1st and 2nd axis were 0.194 and 0.143, respectively. The percentage of variance in the 'species' data accounted for by the 1st axis was 23.8%, and 41.4% for both axes together.

axis (vertical). Type 1 specimens form a cloud within the groups formed by types 2 and 3 (Fig. 4.5). Because type 4 specimens are strong outliers in the analyses, they were excluded from the CVA in order to improve the separation of the other three morphotypes. CVA maximizes the separation between the types based on the morphological characteristics on the first axis: type 2 is well separated from type 3; type 1, in the middle of the graph, overlaps on the left hand side with type 2 and with type 3 on the right hand side (Fig. 4.6). The second axis scores emphasize morphological differences between type 1 and the other two types.

4.3.2. Molecular phylogeny

The phylogeny of Rotaliida was inferred by using the ML method with the HKY model and an estimation of the parameters I and G (HKY+I+G model), and reveals three major groups of sequences, each one composed of several families (Fig. 4.7). The first group comprises the families Rosalinidae, Discorbidae, Planulinidae, Planorbulinidae, Calcarinidae and Nummulitidae. The second distinctive group includes the families Bolivinidae, Cassidulinidae, Uvigerinidae and Buliminidae (*Globobulimina*). The third group is composed of the families Nonionidae, Cibicididae, Pseudoparrellidae, Chilostomellidae, Virgulinellidae, Stainforthidae and Buliminidae (*Bulimina*). The first two groups appeared in all analyses, albeit without strong ML support (45% bootstrap (BS), 0.97 posterior probabilities (PP) and 41% BS, 0.98 PP, respectively). The third group is not stable and it appears only in ML analysis with HKY+I+G model, with very weak support (23% BS). In other analyses, the sequences forming this group appeared as a series of independent lineages branching at the base of other Rotaliida. This is probably due to the insufficient phylogenetic signal related to the slow rates of evolution of these sequences.
Despite the poor resolution of relationships at the base of the Rotaliida, there is a relatively good support for the majority of morphologically recognized families. Among eight families that are represented in our data by at least two genera, five (Nummulitidae, Calcarinidae, Cassidulinidae,

Bolivinidae and Uvigerinidae) are supported by more than 95% BS and 0.97 PP, and only three families appeared as polyphyletic (Planorbulinidae, Nonionidae and Buliminidae). The polyphyly of the three genera *Melonis*, *Pullenia* and *Nonionella*, representing Nonionidae in our analyses, can be an artefact given the fact that the relationships between their slowly evolving sequences are not well resolved. In the case of Buliminidae, the independent origin of *Bulimina* and *Globobulimina* seems more strongly supported. However, the Kishino-Hasegawa test used to compare our tree (Fig. 4.7) with a tree having a constrained topology imposing the monophyly of Buliminidae, show that the difference of likelihood between the forced (-lnL = 15,418.0) and non-forced (-lnL = 15,373.4) topologies is not significant.

The phylogenetic position of the genus *Uvigerina* among the Rotaliida is relatively stable. In all analyses, *Uvigerina* branches together with *Trifarina* and *Rectuvigerina* in the highly supported clade of Uvigerinidae (97% BS, 0.97 PP). This clade appears either as sister to the group Cassidulinidae + Bolivinidae (in ML analyses with HKY+I+G model, cf. Fig. 4.7) or more rarely as sister to the genus *Globobulimina* (in ML analysis with GTR+I+G model, supported by 33%). In the latter case, Bolivinidae and Cassidulinidae form a sister group to Rosalinidae and Planulinidae (data not shown).

Relationships within the clade of Uvigerinidae were analysed using the ML method with the HKY+I+G model, including 28 sequences of *Uvigerina*, *Rectuvigerina* and *Trifarina* as well as 4 sequences of *Globobulimina* used as outgroup. Our analyses (Fig. 4.8a) show the presence of two main clades: one containing *U. peregrina*, *R. phlegeri* and *T. earlandi* and the other comprising *U. elongatastriata* and *U. mediterranea*. There is a good support (95% BS, 1.0 PP) for the clade *elongatastriata* + *mediterranea*, but much weaker for the clade *peregrina* + *phlegeri* + *earlandi* (63% BS, 0.53 PP). Within this second clade, *R. phlegeri* branches as sister group to *T. earlandi* although their grouping is not strongly supported (81% BS, 0.94 PP). All five species form highly supported (91-100% BS, 0.95-1.0 PP) monophyletic clades. Two sequences obtained from GenBank database and identified as *U. akitaensis*, branch independently, one appears as sister

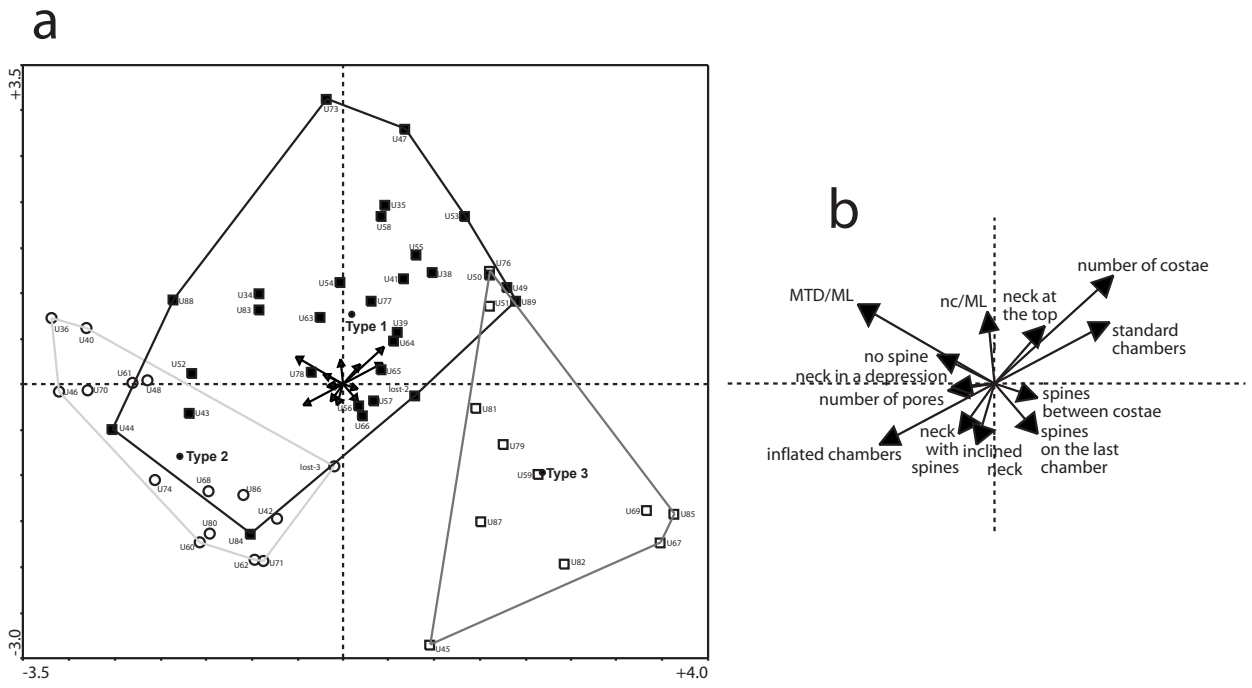

Figure 4.6. CVA triplot:
a) Complete triplot.
b) Detail of the morphological characteristics in the ordination.
CVA eigenvalues q were 1.817 and 0.667 for the 1st and 2nd axis, respectively. The percentage of variance in the 'species' data accounted for by the 1st axis was 32.2%, and 52.2% for both axes together. CVA did not include type 4.

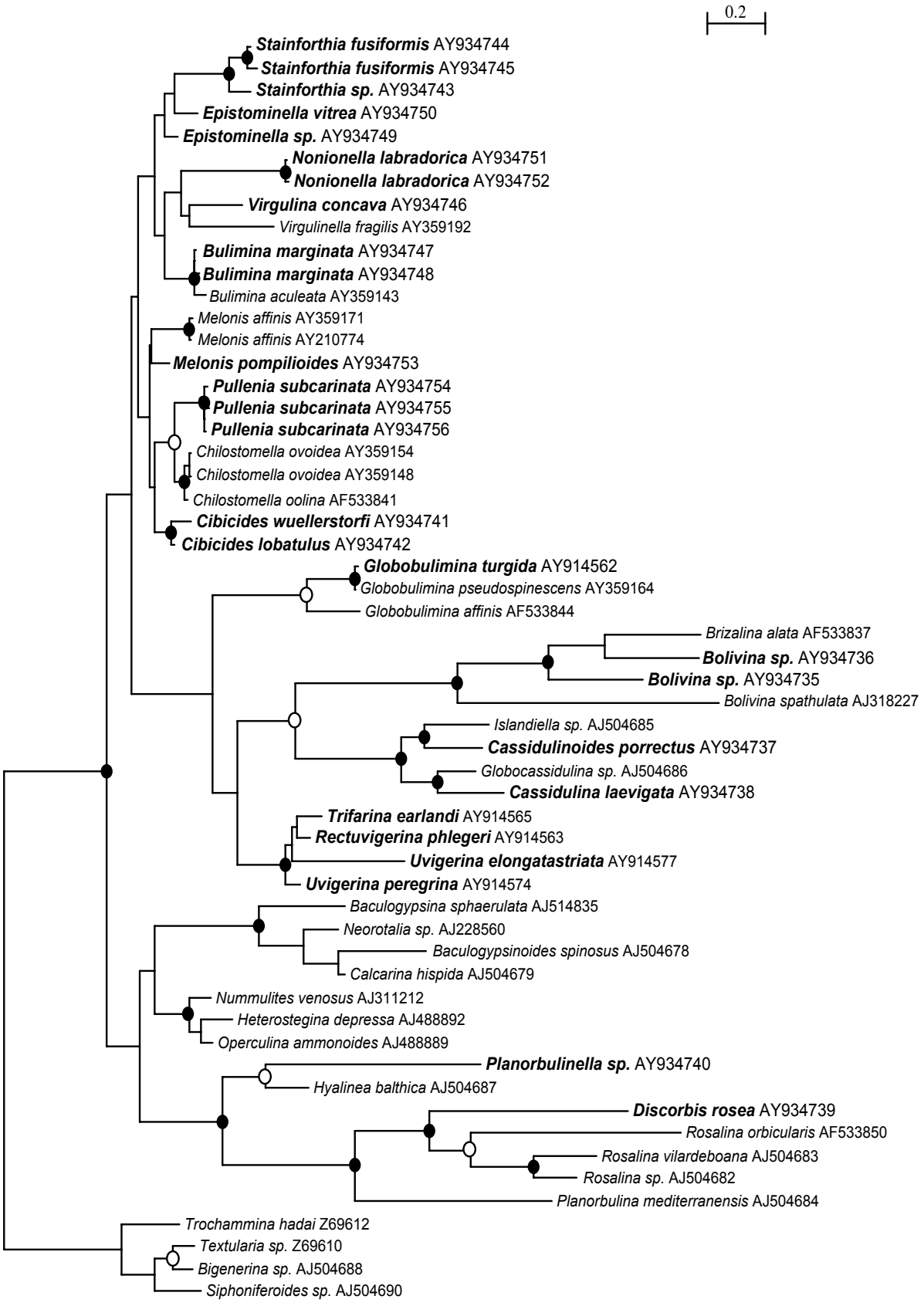

Figure 4.7. Phylogeny of Rotaliida inferred from partial SSU rDNA sequences (695 unambiguously aligned sites) using the ML (HKY+I+G) method. Tree rooted on textulariids. Black dots indicate the internal nodes supported by BS higher than 95% and PP higher than 0.95. White dots indicate the internal nodes supported by BS between 75% and 95%. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers are added).

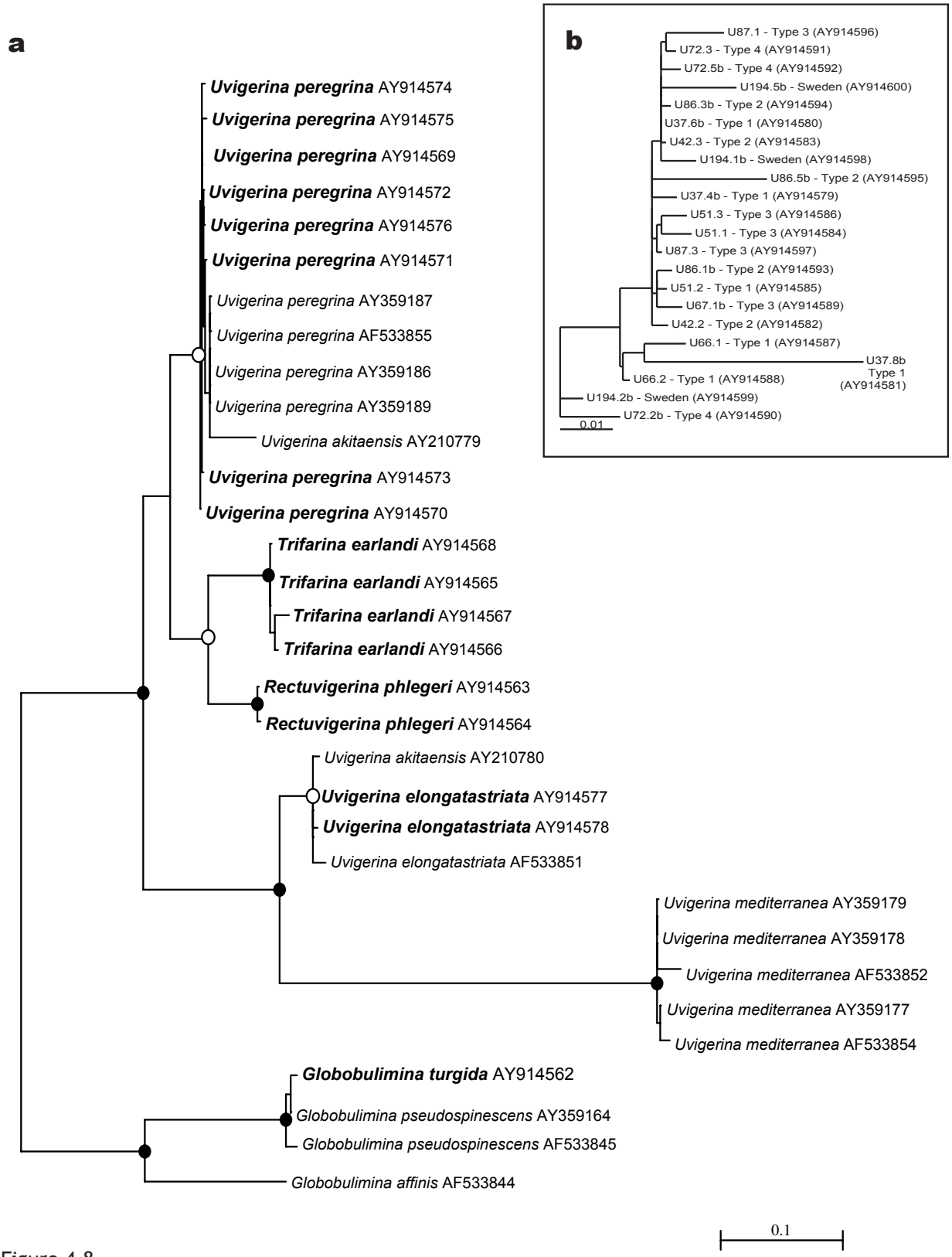

Figure 4.8.
a) Phylogeny of Uvigerinidae inferred from partial SSU rDNA sequences (781 unambiguously aligned sites) using the ML (HKY+I+G) method. Tree rooted on *Globobulimina*. Black dots indicate the internal nodes supported by BS higher than 95% and PP higher than 0.95. White dots indicate the internal nodes supported by BS between 75% and 95%. Species names written in bold designate new sequences, the other ones were taken from GenBank (accession numbers are added).
b) Phylogeny of *U. peregrina* inferred from the ITS sequences (871 unambiguously aligned sites). Accession numbers are added.

to *U. peregrina*, while the other is almost identical to the sequences of *U. elongatastriata*. This suggests that the determination of this species needs to be revised. It is interesting to note that D. B. Scott (Scott et al., 2000) considers *U. akitaensis* as a variant of *U. peregrina*, which seems to be confirmed by the molecular data.
Because a large morphological variation was observed within the population of *U. peregrina* sampled at Oslo Fjord (see previous section), we examined its genetic diversity by sequencing the ITS region, a part of the ribosomal DNA which is much more variable than the SSU. We analysed 22 sequences from 9 different specimens of which the PCR products were cloned. With the exception of a few rapidly evolving sequences (below 5% of divergence), the divergence of most of them is below 1%. The variations in ITS are mainly limited to single nucleotide substitutions and few differences in length of repetitive regions. The phylogenetic analysis of these sequences (Fig. 4.8b) does not reveal any particular grouping, neither according to the origin of the specimens (Oslo Fjord versus Swedish coast of Skagerrak) nor according to their morphology. The sequences of different clones originating from the same specimen often branch separately, suggesting that the range of intra- and interindividual ribosomal variation is about the same.

4.4. Discussion

4.4.1. Molecular phylogeny of Rotaliida

In the first attempt to establish the phylogeny of Rotaliida based on molecular data, Ertan et al. (2004, Fig. 7) distinguished two major groups: the buliminids and the rotaliids. The buliminids were composed of the genera *Bolivina*, *Globobulimina*, *Uvigerina*, *Bulimina* and *Virgulinella*, while the rotaliids included *Ammonia*, *Elphidium*, *Haynesina* and *Rosalina*, as well as an independent group comprising *Chilostomella* and *Melonis*. The distinction of these two rotaliid groups agrees with morphology-based classifications (cf. Haynes, 1981). However, the limited number of rotaliid species (11) used in the study of Ertan et al. (2004) and a very weak support for these two groups shed some doubts on the validity of such a distinction.
In our study we have examined the same fragment of the SSU rRNA gene, but we significantly increased the number of examined taxa by adding 21 new genera to our analyses. The general structure of our tree is similar to that obtained by Ertan et al. (2004). Although we did not include *Ammonia*, *Elphidium* and *Haynesina* in our dataset, independent analyses confirm their branching close to *Rosalina* (data not shown). The main difference between our results and those of Ertan et al. (2004) consists in the position of *Bulimina aculeata* and *Virgulinella fragilis*. These two species appeared at the base of buliminids in Ertan et al (2004), while they branch close to *Stainforthia*, *Epistominella* and *Nonionella* in all our trees.
The independent branching of *Bulimina* in our data is surprising given the fact that the position of this genus together with *Globobulimina* in the family Buliminidae, and the placement of this family together with Uvigerinidae in the superfamily Buliminacea, has never been questioned (Galloway, 1933; Cushman 1959; Loeblich & Tappan 1964, 1988). The characteristic features of Buliminacea are a high trochospiral coil and an internal toothplate which connects the aperture with the previous chamber foramen (Loeblich & Tappan, 1988). The internal toothplate is generally considered a very important taxonomic character and was used by some authors to group all foraminifera possessing this feature in higher rank categories, such as the orders Dentata (Hofker, 1956) and Buliminida (Haynes, 1981), or the superorder Buliminoida (Mikhalevich & Debenay, 2001). In view of our data the internal toothplates could have appeared independently several times in the evolution of foraminifera. However, we cannot exclude that the independent branching of *Bulimina* is an artefact of partial single gene phylogeny. Indeed, the support for the basic groups of Rotaliida is rather weak in all our analyses (Fig. 4.7). As shown by statistical tests, the relations between slowly evolving groups of sequences are not resolved and closer relationships between *Bulimina* and *Globobulimina* cannot be completely excluded. Moreover, an independent analysis of actin-coding gene sequences shows that although *Bulimina* and *Globobulimina* branch separately, both

genera lack an intron characteristic for rotaliids, which could suggest that they are not so distantly related (Flakowski et al., 2005). Clearly, additional sequence data on complete SSU rRNA and protein-coding genes are necessary to resolve this problem.

4.4.2. *Uvigerina*, *Rectuvigerina* and *Trifarina* are closely related

Phylogenetic analysis of our data suggests that besides the genus *Uvigerina*, the clade of Uvigerinidae also includes at least some members of the genera *Rectuvigerina* and *Trifarina* (Fig. 4.8a). In all analyses, both genera group with *U. peregrina* and although this grouping is not very well supported (63% BS, 0.53 PP), it is highly unlikely that the three *Uvigerina* species (*U. peregrina*, *U. elongatastriata* and *U. mediterranea*) form a monophyletic group. The morphological criteria used to separate the three genera are not very solid. For *Trifarina* the discriminating character is the triangular cross section: all other criteria are the same as for *Uvigerina* (Haynes, 1981; Loeblich & Tappan, 1988). *Rectuvigerina* differs from *Uvigerina* by one or more uniserial chambers and by an internal siphonlike toothplate (Mathews, 1945). However, a tendency to uniseriality is also observed in other species belonging to *Uvigerina.* Van der Zwaan et al. (1986a) argued that the tendency to reduced seriality is characteristic of more advanced, geologically younger morphologies. Moreover, toothplate morphology is extremely variable, even between populations. Separate classification of *Rectuvigerina* in the family Siphogenerinoididae Saidova, 1981 is not supported by our data. Indeed, *R. phlegeri* was included in the genus *Uvigerina*, as a member of the *U. bononiensis* group by Van der Zwaan et al. (1986a). Although we could not examine any other representatives of this group, the division of *Uvigerina* proposed by these authors is congruent with our molecular data, that show a separation between the *U. peregrina* and *U. elongatastriata* + *U. mediterranea* clades.

4.4.3. Skagerrak *U. peregrina* is genetically homogeneous

The statistical analyses of the morphology of the Oslo Fjord population of *Uvigerina* show a separation between four different morphological types (Figs. 4.4-4.6). Although overlaps were observed between type 1 and types 2 and 3, these different morphotypes could, in theory, be described as separate morphospecies.

Several recent studies revealed cryptic diversity of well established morphospecies in planktonic (Huber et al., 1997; de Vargas et al., 1999, 2001, 2002; Darling et al., 2000) and benthic (Pawlowski et al., 1995; Holzmann et al., 1996; Holzmann and Pawlowski, 1997, 2000; Tsuchiya et al., 2000, 2003; Hayward et al., 2004) foraminifera. Given the high morphological variability observed in *U. peregrina* from Oslo Fjord, we expected to find a high genetic divergence within this population.

The ITS sequences of nine specimens representing the different morphotypes of *U. peregrina* we examined did not confirm our expectations (Fig. 4.8b). The divergence observed in these sequences corresponds to the level of intraspecific variations, because the difference observed between sequences of distinct specimens is comparable to the one between clones from one individual. This confirms a certain homogeneity also detected in other North Sea foraminifera studied in our laboratory, especially *Ammonia* sp. and *Elphidium williamsoni* (unpublished data), although ITS sequencing was not carried out for these species. The morphological variability of *U. peregrina* noticed in our samples seems to be within the range of variability characteristic for a single species. To accurately define species in *Uvigerina* in terms of morphological and genetic variations, more precise studies on morphometry and genetic variations in other species of this genus would be necessary. The high morphological plasticity of *Uvigerina* species observed in this population could theoretically allow to distinguish separate morphospecies. However, the low genetic diversity obtained here shows that the origin of the variation could be ecological rather than genetic in nature and this should be taken into consideration when using this genus as a proxy in paleoecological reconstructions.

Chapter 5

Taxonomy, evolution over the past 15 Ma and micro-habitat occupation of 11 common species of *Cibicides*

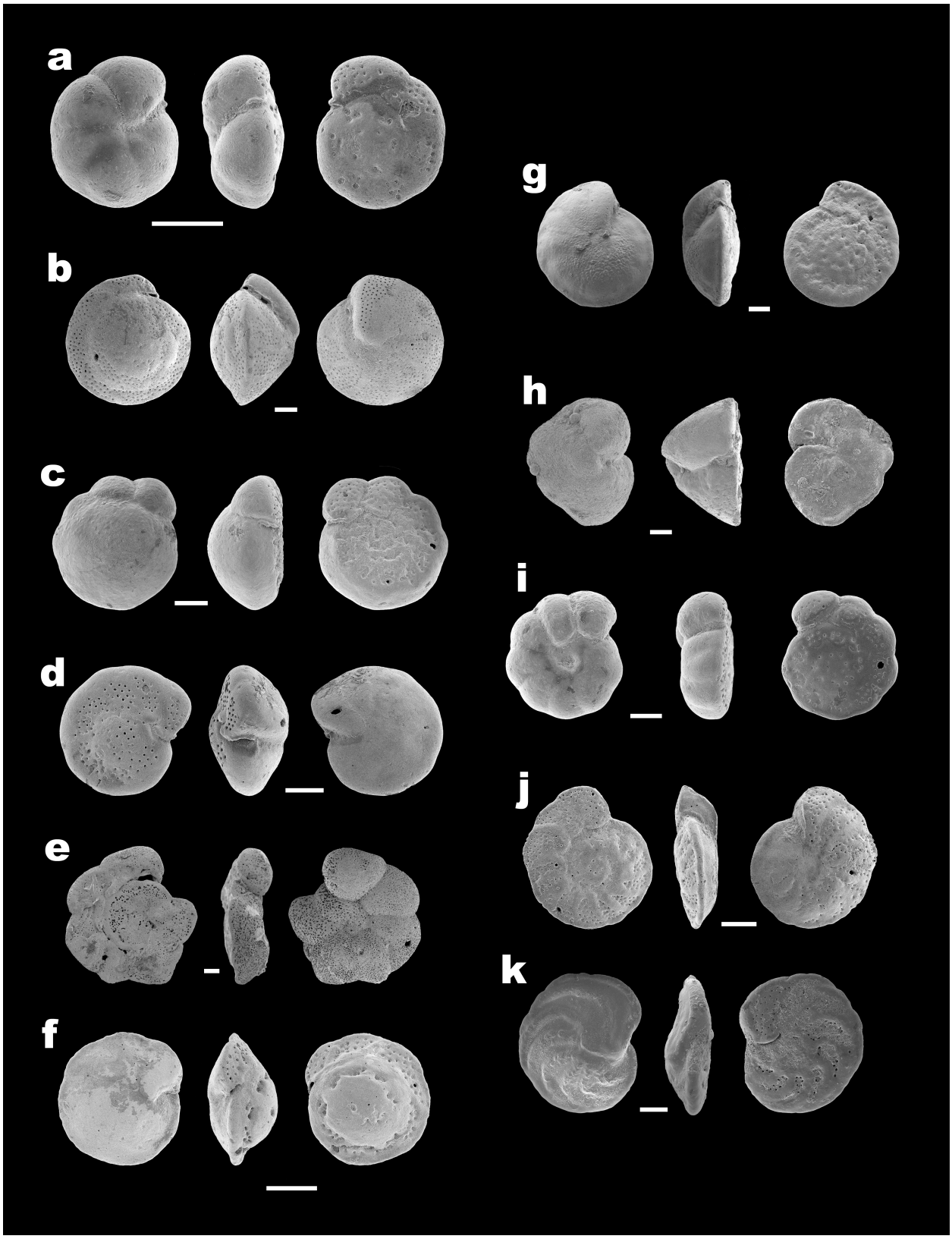

Figure 5.1.
a) *C. bradyi* (s, p, u), b) *C. dutemplei* (s, p, u), c) *C. italicus* (s, p, u), d) *C. kullenbergi* (s, p, u), e) *C. lobatulus* (s, p, u), f) *C. pachyderma* (u, p, s), g) *C. pseudoungerianus* (u, p, s), h) *C. refulgens* (u, p, s), i) *C. robertsonianus* (s, p, u), j) *C. ungerianus* (s, p, u), k) *C. wuellerstorfi* (u, p, s)
u= umbilical side, p= profile, s= spiral side. Scale= 100µm

The species studied here (Fig. 5.1) represent the most common cibicidids found in the Mediterranean and the North Atlantic Ocean during the Neogene (Miocene, Pliocene, Pleistocene, Holocene). They have been classified in various genera and superfamilies although they share common morphologies and ecological preferences. Molecular analyses involving the Small Subunit (SSU) of ribosomal RNA (rRNA) gene have shown that, contrary to the largely diffused habit of splitting the biconvex and planoconvex forms into two different genera (*Cibicidoides* and *Cibicides*), all these species should share the same genus name: *Cibicides* de Montfort, 1808 (see Chapter 3). The technical terms employed to describe the different parts of the test are shown in Figure 5.2. The words umbilical and spiral are preferred to ventral and dorsal to name the two different sides of the test, because they do refer to the real anatomy of foraminifers (with the presence of an umbo and a spiral) instead of the anatomy of animals, which have, in contrast with foraminifers a belly and a back.

5.1. Sample locations

5.1.1. Recent specimens

Extant *Cibicides* were collected in the Mediterranean, the North Atlantic, the North Sea and Antarctica (Fig. 5.3). Shallow water samples were collected on the coast and by SCUBA diving. Deep sea samples were collected during various cruises: in 2001 with the R/V Côtes de la Manche (Institut national des sciences de l'univers, France) in the Bay of Biscay (OXYBENT), with the R/V Jan Mayen (University of Tromsø, Norway) in Svalbard and with the R/V Bjarni Sæmundsson (Marine Research Institute, Reykjavik, Iceland) near Iceland (BIOICE); in 2002 with the R/V Trygve Braarud (University of Oslo, Norway) in the Oslo Fjord; in 2003 with the R/V Arne Tiselius (Kristineberg Marine Research Station, Fiskebäckskil, Sweden) in the Skagerrak and the Kattegat (Program för Miljökontroll, Statens Naturvårdsverk-PMK), with the R/V L'Atalante (IFREMER, France) in the Bay of Biscay, Cape Finisterre and the south-west coast of Portugal (FORAMPROX I), with the R/V Pelagia (Royal Netherlands Institute for Sea Research, Texel, The Netherlands) on the Portuguese coast of the Atlantic (Eurostrataform Canyons program).
Samples from the deep sea stations were collected by boxcoring and multicoring; the top first centimeters of the sediment were immediately sieved. After picking, the specimens were identified and stored on Chapman slides. Almost all the specimens used for molecular analyses were SEM pictured before their destruction for DNA extraction. Other morphologically interesting specimens were also SEM pictured and are presented in the plates (Pl. 1-12).

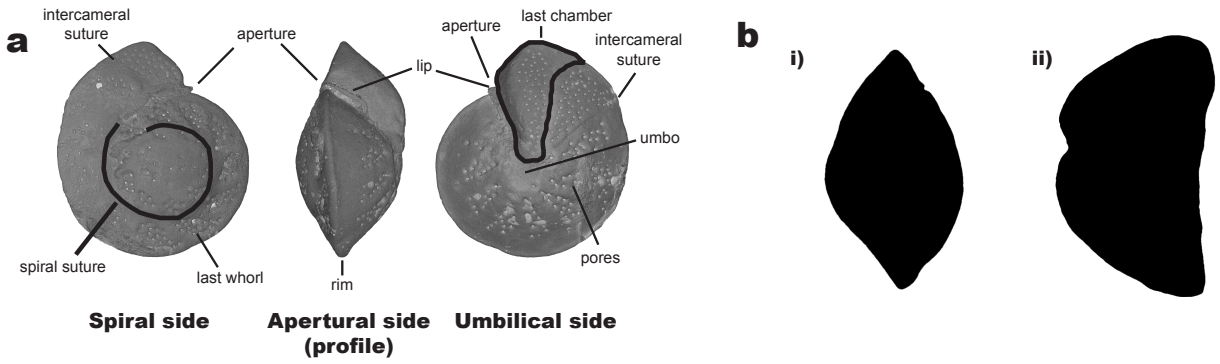

Figure 5.2.
a) Terminology used to describe the test of *Cibicides*.
b) Biconvex (i) and planoconvex (ii) profile outlines, umbilical side on the left.

Table 5.1. Number of specimens collected per species and sample. Samples in grey without *Cibicides*.

	Age (Ma)	sample number	*C. refulgens*	*C. refulgens-lobatulus*	*C. lobatulus*	*C. lobatulus-ungerianus*	*C. pachyderma-lobatulus-ungerianus*	*C. ungerianus*	*C. ungerianus-pseudoungerianus*	*C. pseudoungerianus*	*C. ungerianus-pachyderma*	*C. ungerianus-kullenbergi*	*C. pachyderma*	*C. pachyderma-kullenbergi*	*C. kullenbergi*	*C. dutemplei*	*C. dutemplei-pseudoungerianus*	*C. ungerianus-wuellerstorfi*	*C. wuellerstorfi*	*C. robertsonianus*	*C. bradyi*	*C. bradyi-ungerianus*	*C. italicus*	*C. grossorugosus ?*	*Cibicides sp. 1*	*Cibicides sp. 2 (C. cf. ungerianus)*	*Cibicides sp.*	*Total Cibicides*
Malta	15.0	1685	3		27	13		152			1		40		62	102											26	426
Malta	14.5	1776			13			113				1			38	84											2	251
Malta	14.0	1602			10	10		127		2			16		16	51												232
Tremiti	13.5	475	2		38	2		95	12				7	3	51	36			75						1			322
Tremiti	13.0	19'631			19	10		37	6					7	40	18		1	20	2	4	1			3			168
Tremiti	12.5	19'955	1		21			59		4				12	56	24			40		10	2			4			233
Gibliscemi	12.0	18'514						1											46							1	48
Gibliscemi	11.5	15'609			2			1							25					12	56	75						171
Gibliscemi	11.0	15'487			1			62							12					13	8	12				1		109
Gibliscemi	10.5	15'372			1										54				1	22	3	31	6					118
Gibliscemi	10.0	14'831						1							45					5	3	1						55
Gibliscemi	9.5	14'204													128					16	1	2						147
Gibliscemi	9.0	14'320						2							168					14	3							187
Gibliscemi	8.5	14'442			1										58					2	19	2	16					98
Gibliscemi	8.0	14'542						11							18					2								31
Faneromeni	7.5	5'725																										0
Faneromeni	7.0	5'857																										0
Faneromeni	6.5	5'912																										0
Ain El Beida	6.5	91.3			4			17					13		10	1									2			47
Ain El Beida	6.0	289.3			4	7		64		9		3	76		9	5									7			184
Loulia	5.5	674			11			66	24	4			170		10	7	1							16				309
Loulia	5.0	942	3		5	17	1	297	40	151	123	1			7	8												653
Punta di Maiata	4.5	12'168			3			19												1	5		17		3		3	51
Punta di Maiata	4.0	12'272			4			38							9	3				3	10		1		1			69
Punta Piccola	3.5	12'425			5			29		15			5		2					10	15	3	13		6			103
Punta Piccola	3.0	13'251a			11			53		3			7		5					3	14						1	97
Singa III	2.5	9334	7		41			41		6			28		90				6	3	32							254
Singa III	2.0	9484	6	2		53		46					85		31					1	44							268
Vrica	1.5	6326			37	1		12					2		61												7	120
Montalbano Ionico	1.0	H8214			38			143				4	79		194													458
Recent	0.0		4		282			26		54				8	146	1			89	4	5					189	808
Total number per species			26	2	578	113	1	1512	82	248	124	9	528	30	1345	340	1	1	277	113	232	129	53	16	19	8	230	6017

5.1.2. Fossil specimens

Fossil representatives of the genus *Cibicides* have been collected from sediments that cover the last 15 million years (Ma). A total of 27 samples, taken from time slices covering every 500,000 years from 1.0 to 15.0 Ma have been examined (Table 5.1). The samples were selected at intervals as regular as possible, but sapropels were avoided. Due to the decrease of oxygen during deposition, cibicidids and other common taxa are not present in these sediments (see e.g. Kouwenhoven et al., 1999, 2003; Schmiedl et al., 2003; Stefanelli et al., 2005). All the samples are from Mediterranean sites, located in Italy (Gibliscemi, Punta Piccola, Vrica, Singa III, Punta di Maiata, Tremiti, Montalbano Ionico) and Malta except four, which were collected on the Atlantic side of Morocco (Loulja and Ain El Beida) (Fig. 5.3). It was not possible to collect the samples corresponding to the interval from 5.0 to 6.5 Ma in the Mediterranean, because benthic foraminifers were scarce or absent prior to and during the Messinian salinity crisis (e.g. Krijgsman et al., 1999; Kouwenhoven et al., 1999, 2003; Schmiedl et al., 2003; Stefanelli et al., 2005).

All the samples were washed and sieved at Utrecht University where they are deposited. The 125-595µm fraction was screened to pick *Cibicides* specimens which were sorted by species and subsequently stored on Chapman slides.

The three youngest sampling sites – Montalbano Ionico, Vrica and Singa III – are located in Southern Italy (Fig. 5.3). The sections are described in detail by Verhallen (1991). On the basis of the P/B ratio (number of planktonic foraminifera over the number of benthic foraminifera; e.g. Wright, 1978; Van der Zwaan et al., 1990), the estimated paleodepths are 1000-1200m for Singa III, 800-1000m for Vrica and a shift from 500m to shallow water for Montalbano Ionico (Verhallen, 1991). Age control of the sections was initially based on biostratigraphy of planktonic foraminifers and magnetostratigraphy (Verhallen, 1991). Moreover, Hilgen (1991) and Lourens et al. (1996) established cyclostratigraphic age control for both Vrica and Singa sections. Other sites are

Punta Piccola (3.0 and 3.5 Ma) and Punta di Maiata (4.0 and 4.5 Ma), located on the south coast of Sicily (Fig. 5.3). The description of the sections can be found in Brolsma (1978). The paleobathymetric estimates, based on the preferential depths of the dominant species, show a value of 500-800m (Brolsma, 1978). This section was also dated biostratigraphically (Brolsma, 1978) and cyclostratigraphically (Hilgen, 1991; Lourens et al., 1996). Other samples sites are situated in Morocco (Fig. 5.3): Loulja (5.0 and 5.5 Ma) and Ain El Beida (6.0 and 6.5 Ma). An overview of the publications describing the Ain El Beida section is given in Krijgsman et al. (2004); these authors established cyclostratigraphic dating. The estimated paleodepth at Ain el Beida is 800 to 1000m (Kouwenhoven, unpublished data) For Loulja, the estimate of the paleodepth (2000-4000m), the description and the dating of the section can be found in Van der Laan et al. (in press). The Gibliscemi section, located in Sicily (Fig. 5.3), provided a long record with 11 samples between 8.0 and 12.0 Ma. The section is described by Hilgen et al. (2000b); the paleo-waterdepth is about 1000m or more (Kouwenhoven et al., 2003). Age control was established by integrated stratigraphy (Hilgen et al., 1995, 2000a). The Tremiti Islands (12.5-13.5 Ma) are situated in the Adriatic Sea (Fig. 5.3). The lithology of the sections sampled there was described by Lirer et al. (2002). The P/B ratio leads to a paleodepth estimate of about 700m (Verbruggen, 2004). The two sections used here have been astronomically tuned (Abels et al., 2005). The oldest sites sampled are located on Malta and Gozo. Sprong (2004) gave an overview of the sections. She also estimated the paleobathymetry for the three samples we used between 400 and 900m (Sprong, 2004). The age of the selected samples was obtained by Abels (unpublished data) by means of biostratigraphy and cyclostratigraphy.

Figure 5.3. Map of Europe indicating the sampling sites for fossil (white dots) and Recent (grey squares) material, with the names of the locations.

5.2. *Classification of cibicidids*

5.2.1. Definition of the genus *Cibicides*

The genus *Cibicides* has a calcareous wall, made of hyaline lamellar calcite and coarsely perforated. Contrary to the idea defended by Loeblich and Tappan (1964, 1988, 1992), who separated the species with optically radial or granular wall structures in different superfamilies, species having both optical structures are grouped here within the same genus. Indeed, as shown by Towe & Cifelli (1967, see Chapter 3 for the complete discussion), these structures are very similar and can easily give rise to each other. Bellemo (1976) has also demonstrated that intermediate structures can be found in the genus *Cibicides*. Following these authors, we conclude that the structure of the wall observed in polarized light is not a useful character in higher taxonomic ranks.

The main characteristics of *Cibicides* are the coiling and the aperture. The genus is characterized by a low trochospiral coil with an evolute spiral side (all the chambers visible) and an involute umbilical side (only the chambers of the last whorl visible). Both sides can be equally developed (biconvex forms) or one side can be flat and the other convex (planoconvex forms). In the majority of planoconvex specimens, the spiral side is flat and serves as an attachment surface; an exception is *C. italicus*, where the umbilical side is flat. Traditionally, the biconvex-planoconvex distinction was used to separate cibicidids in two genera: *Cibicides* de Montfort, 1808 and *Cibicidoides* Thalmann, 1939. However, this separation is based on ecological differences[1] which have no taxonomic basis. It was already observed that the distinction is not always clear within one species

1) The flattened side of the planoconvex specimens serves as a fixing surface for the attached specimens, whereas the vagile specimens usually are biconvex.

(Mead, 1985; Verhallen, 1991; Gupta, 1994) and molecular results confirm that this partition has no taxonomic value (see Chapter 3). The aperture is a simple slit, bordered by a lip and located near the peripheral margin on the umbilical side. Sometimes, it extends along the spiral suture on the spiral side; this was observed in several specimens belonging to different species, e.g. *C. kullenbergi*, *C. lobatulus*, *C. pseudoungerianus*, *C. robertsonianus*, *C. ungerianus*, *C. wuellerstorfi* (Cushman, 1931; Phleger et al., 1953; Jonkers, 1984; Hermelin, 1989; Van Leeuwen, 1989; Verhallen, 1991; Den Dulk, 2000; Holbourn & Henderson, 2002). This criterion was also used to separate *Cibicides* from *Cibicidoides* (Loeblich & Tappan, 1964, 1988; Boltovskoy, 1980; Mead, 1985).
Among the traits employed to distinguish the different species of *Cibicides*, the shape of the axial profile is important. Other criteria are the aspect and the shape of the sutures, the porosity and the thickness of the wall.

5.2.2. History of generic classification

Various genus names have been attributed to the species studied here (see the synonymy in the Appendix 1 for details). *Cibicides* de Montfort, 1808 is the first genus described, and is still valid. Other genus names like *Nautilus* and *Rotalina* were too widely defined and were no longer used at the end of the 19th century. During the 19th century (e.g. d'Orbigny, 1846; Brady, 1884; Rzehak, 1886; Flint, 1899) and the beginning of the 20th century (e.g. Cushman, 1918, 1922, 1929; Trauth, 1918), *Truncatulina* d'Orbigny, 1826 was widely in use for cibicidids. However, *Truncatulina* was put in synonymy with *Cibicides* by Galloway & Wissler, 1927. They did the same with *Lobatula* Fleming, 1828, *Heterolepa* Franzenau, 1884 and *Pseudotruncatulina* Andreae, 1884. Nevertheless, Loeblich & Tappan (1988) reinstalled *Heterolepa* and *Lobatula* as valid genus names for *H. dutemplei* and *L. lobatula*, respectively. During the 20th century, new genus names appeared. The first was *Cibicidoides*, described originally as a subgenus of *Cibicides* in 1936 by Brotzen and validated by Thalmann (1939) upon the designation of a subgenotype. This subgenus included the biconvex forms, whereas the planoconvex ones were kept in *Cibicides*. The distinction between both genera became widespread at the end of the 1970s. In 1956, Hofker created the genus *Parrelloides*, which was first put in synonymy with *Cibicidoides* (Loeblich & Tapan, 1964) and later separated again because of the nature of its wall (Loeblich and Tappan, 1988). Another new genus name, *Fontbotia*, was created by Gonzalez-Donoso & Linares (1970). This genus was recognized by Loeblich & Tappan (1988) but put in synonymy with *Cibicides* by Sen Gupta (1989). The species studied here were sometimes wrongly assigned to other genera like *Anomalina* d'Orbigny, 1826 (*A. wuellerstorfi,* Schwager, 1866), *Eponides* de Montfort, 1808 (*E. hyalinus* (= *C. bradyi),* Leroy, 1964; *E. haidingeri* (= *C. robertsonianus*), Gianotti, 1953), *Gyroidina* d'Orbigny, 1826 (*G.* cf*. gemma* (= *C. bradyi),* Corliss, 1979b; *G. jarvisi* (= *C. robertsonianus*)*,* Cushman & Stainforth, 1945), *Planorbulina* d'Orbigny, 1826 (*P. robertsoniana,* Brady, 1881; *P. wuellerstorfi*, Goës, 1894), *Rotalia* Lamarck, 1804 (*R. praecincta* (= *C. dutemplei*), Karrer, 1868). Finally, *Planulina* d'Orbigny, 1826 is very often used for *P. wuellerstorfi* (see synonymy list in the Appendix 1 for references), although this genus is defined as having a partially evolute umbilical side.
In the traditional classification (Loeblich & Tappan, 1964, 1988), cibicidids are considered to be closely related to genera like *Epistominella* (same superfamily as *Cibicidoides*) or *Hyalinea* and *Planorbulina* (same superfamily as *Cibicides*), whereas the genus *Heterolepa,* because of its different wall structure (granular instead of radial), is placed within the same superfamily as *Chilostomella*. Moreover, Nyholm (1961) supposed that *Planorbulina* could be a stage in the life cycle of *Cibicides*, although no *Cibicides* stage was observed in the life cycle of *Planorbulina* (Le Calvez, 1938). Molecular results (see Chapters 2 and 3) show that *Pullenia* and *Melonis* are the closest genera to *Cibicides*, although also *Epistominella* can be considered as a genus related to the cibicidids. These four genera form a group with *Bulimina* and *Stainforthia*, whereas *Planorbulina* and *Hyalinea*, grouping together with *Discorbis* and *Rosalina*, do not seem to be phylogenetically close to *Cibicides*.

5.2.3. Different species concepts in literature

Several species are rather homogenously perceived through the different taxonomic schools and scientists. *Cibicides wuellerstorfi* is well-defined and most people have the same notion of this species. The few authors mentioning *C. italicus* have the same concept (e.g. Verhoeve, 1971; Van der Zwaan, 1982; Hasegawa et al., 1990; Sprovieri & Hasegawa, 1990; Kouwenhoven, 2000). Both the species complexes *bradyi-robertsonianus* and *lobatulus-refulgens* are generally well identified. However, there are differences in the recognition inside these complexes. Some authors make a distinction between *C. bradyi* and *C. robertsonianus* (e.g. Van Morkhoven et al., 1986; Hermelin, 1989; Holbourn & Henderson, 2002), whereas others consider them as belonging to one single species (e.g. Brolsma, 1978; Belanger & Berggren, 1986; Van Leeuwen, 1989; Verhallen, 1991). The same happens to *C. lobatulus* and *C. refulgens*, usually separated, but sometimes merged together (e.g. Van der Zwaan, 1982; Verhallen, 1991). For *C. dutemplei*, the strong resemblance with *C. mexicanus* was observed by Van Morkhoven et al. (1986), although they are not put in synonymy. *Cibicides dutemplei* was identified as a synonym of *C. bradyi* by Schiebel (1992) and Timm (1992), but this is due to the attribution of the name *C. dutemplei* to a specimen of *C. bradyi* by Brady (1884) before the latter species was properly described.
The main taxonomic problems concern four species: *C. kullenbergi*, *C. pachyderma*, *C. pseudoungerianus* and *C. ungerianus*. *Cibicides kullenbergi* is considered as a synonym of *C. mundulus* Brady, Parker & Jones, 1888 by Van Morkhoven et al. (1986), followed by other authors (Hermelin, 1989; Holbourn & Henderson, 2002; Hess & Kuhnt, 2005). Elsewhere, *C. kullenbergi* is supposed to be a morphotype of *C. pseudoungerianus* (Verhallen, 1991). *Cibicides pseudoungerianus* itself is not a well-defined species; it is therefore put in synonymy with *C. pachyderma* by many workers (e.g. Van Morkhoven et al., 1986; Barbieri, 1998; Licari & Mackensen, 2005), and often used as a "garbage taxon" for the specimens difficult to attribute to better defined species. Finally, *C. ungerianus* is not always recognized as a distinct species and often included in *C. pachyderma* (Van Morkhoven et al., 1986) or subsumes *C. pachyderma* and *C. kullenbergi* (Jonkers, 1984). Sometimes, a putative synonym of *C. ungerianus* (Parker, 1958) or *C. pseudoungerianus* (Bremer et al., 1980), *C. floridanus,* is used for Mediterranean or Atlantic specimens.

5.2.4. Distinctions and relations between the different species in our material

Cibicides lobatulus and *C. refulgens* morphologically resemble each other, although they are quite well separated genetically (see Chapter 3). Until now, the main criterion to separate both species is the convexity of the umbilical side of the test. Similarly, *C. ungerianus* and *C. pseudoungerianus* are morphologically rather close; the distinction is mainly based on the degree of transparency (all the chambers are visible on the spiral side of *C. ungerianus*, whereas a thick supplement of calcite hides them in *C. pseudoungerianus*). Another couple of species, *C. pachyderma* and *C. kullenbergi*, morphologically shares many common traits; they can be distinguished by the shape of the profile (both sides are equally developed but the test is thicker in *C. kullenbergi*) and the porosity. Genetically rather close, they certainly belong to the same species (see Chapter 3).
Cibicides robertsonianus and *C. bradyi* are also close morphologically. For the time being, there is no molecular data available. Both species have a circular and slightly lobate test with a transparent spiral side where all the chambers are visible and the spiral suture is glassy. The distinction between *C. robertsonianus* and *C. bradyi* is mainly based on the size, the number of chambers in the last whorl, the axial profile and the umbo: *C. robertsonianus* is larger, has more chambers in the last whorl and an open umbo. In foraminifers, chambers are added during growth, and consequently, a specimen with more chambers will be older and bigger. All the differences mentioned could thus be only due to ontogenetic changes. If true, *C. robertsonianus* and *C. bradyi* could represent the same species at different ontogenetic stages as already suspected (Timm, 1992). Another hypothesis is that these morphospecies represent in fact the micro- and megalospheric generations of a single species (Belanger & Berggren, 1986). To test if *C. bradyi* and *C. robertsonianus* could be one single species, we counted the number of chambers in

the last whorl (NCLW) and the maximum diameter (MD) for the representatives of both species from our fossil material. The results show that the individuals recognized as *robertsonianus* have more chambers and are bigger than *bradyi* specimens but the ratio NCLW/MD*100 (number of chambers in the last whorl divides by the maximum diameter and multiplied by 100) of both species has the same value (Fig. 5.4). This suggests that the criteria used to distinguish the two species could be just variations during the ontogenetic development.

Within the assemblage concept of species (see Chapter 1), morphological intermediates are traditionally interpreted as links connecting two morphotypes, proving that these belong to a same species. From a morphological point of view, the species we study form a network, with *C. ungerianus* as a central form and morphological intermediates connecting it to the other studied species (Fig. 5.5). The observation of morphological intermediates has also been mentioned in the literature between *C. ungerianus* and *C. lobatulus* (Batjes, 1958; Van der Zwaan, 1982), *C. lobatulus* and *C. refulgens* (Verhoeve, 1971; Hageman, 1979; Van der Zwaan, 1982; Verhallen, 1991; Jonkers et al., 2002), *C. robertsonianus* and *C. bradyi* (Phleger & Parker, 1951; Pflum & Frerichs, 1976; Brolsma, 1978; van Morkhoven et al., 1986; Van Leeuwen, 1989; Verhallen, 1991), *C. ungerianus* and *C. pachyderma* (Jonkers, 1984), *C. ungerianus* and *C. pseudoungerianus* (Van der Zwaan, 1982). Intermediates between *C. kullenbergi* and *C. wuellerstorfi* (Lohmann, 1978; Corliss, 1979b; Mead, 1985), *C. ungerianus* and *C. dutemplei* (Batjes, 1958; Van der Zwaan, 1982) or *C. dutemplei* and *C. lobatulus* (Batjes, 1958) have not been observed in our material.

Molecular studies showed that these morphological intermediates did not always have the same meaning (see Chapter 3). For *C. pachyderma* and *C. kullenbergi*, the intermediates could indeed represent links between two morphotypes of the same species. On the other hand, *C. lobatulus* and *C. refulgens* appeared as truly separated species in the molecular analyses. Therefore, the concept of morphological intermediates should be considered with care if it is taken as measure to define one species. Further studies are needed to search for morphological detectable differences between both molecular defined groups. Furthermore, the presence of cryptic species was detected inside the *refulgens* clade (Mediterranean and Antarctic populations can be seen as distinct species according to their genetic divergence, see Chapter 3), and this also needs supplementary morphological investigations.

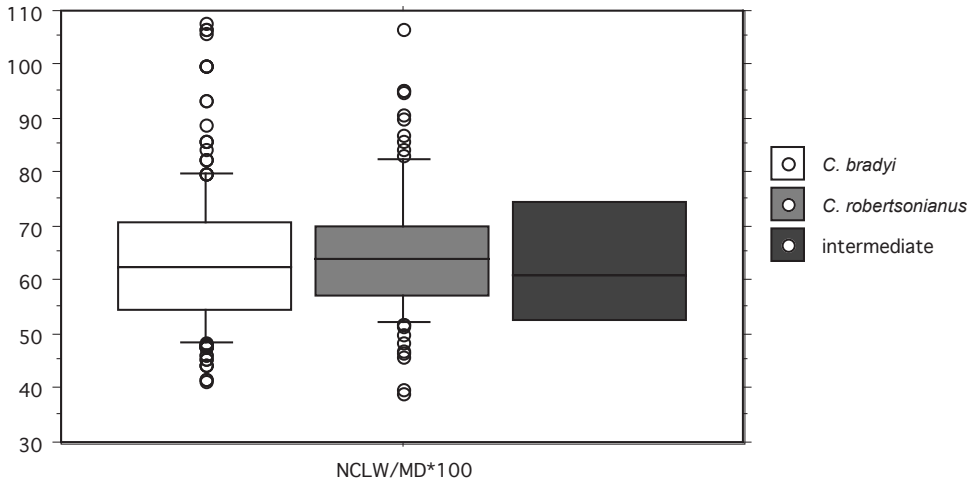

Figure 5.4. Box-plots of the ratio NCLW/MD*100 for *C. bradyi* and *C. robertsonianus*. The box and the vertical lines coming from it (the "whiskers") represent 100% of the values. The box is delimited by the first quartile (Q1, 25%) at the bottom and the third one (Q3, 75%) at the top. Inside the box, the horizontal line represents the median (50%). Crosses indicate values outside the limits of the "whiskers" (the "outliers").
NCLW= number of chambers in the last whorl; MD= maximal diameter

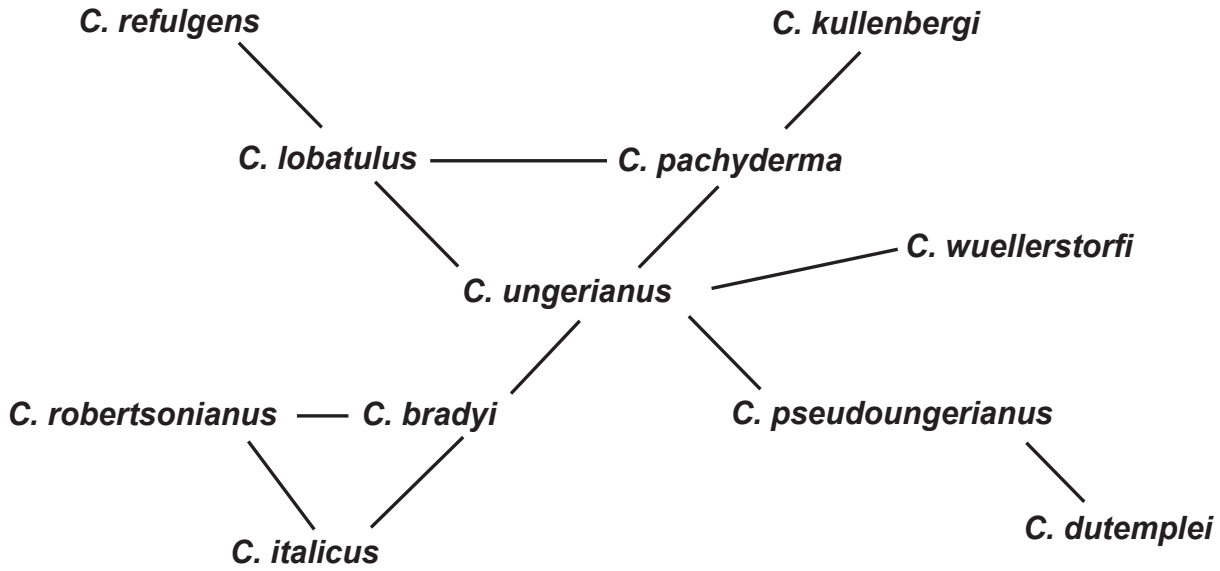

Figure 5.5. Network representing the studied species of *Cibicides*, connected through intermediate morphologies observed in our material.

5.3. Ecology and paleoecology of *Cibicides*

5.3.1. Proxy value of *Cibicides*

Due to their epifaunal mode of life, species like *C. wuellerstorfi* or *C. kullenbergi* are considered to build their shells in equilibrium with bottom water chemistry. Consequently, they are widely used in, for instance, stable oxygen and carbon isotopic analyses (e.g. Rathburn et al., 1996; McCorkle et al., 1997; Schmiedl et al., 2004) and Mg/Ca paleothermometry (e.g Rathburn & De Deckker, 1997; Lear et al., 2000, 2002, 2003, 2004; Billups & Schrag, 2002, 2003; Martin et al., 2002). *Cibicides* species are also employed as proxies of trophic state (Altenbach & Sarnthein, 1989), oxygen (Kaiho, 1994, 1999), water masses (Lohmann, 1978; Corliss, 1979b, 1983; Schnitker, 1979; Miller and Katz, 1987; Woodruff and Savin, 1989; Woodruff, 1992; Mackensen, 1992; Smart and Ramsay, 1995; Yasuda, 1997; Schmiedl et al., 1997) and (paleo-)water depth (Pflum & Frerichs, 1976; Wright, 1978; Van der Zwaan et al., 1999; Van Hinsbergen et al., 2005).

5.3.2. Bathymetry and paleobathymetry

The bathymetric distribution of benthic foraminifera is not a static concept, although it is sometimes used in a rather rigid sense (e.g. Spencer, 1992, 1996). Already in 1966 Bandy and Chierici described certain species occupying different water depths in different basins. It was also demonstrated that the bathymetric preferences of a species can change through time (Douglas & Woodruff, 1981; Van Morkhoven et al., 1986; Berggren & Miller, 1989; Mackensen & Berggren, 1992). Finally, the bathymetrical distribution of benthic foraminifers is more consistent in shallow water depths than in deeper areas (Morigi et al., 2005). Van der Zwaan et al. (1999) speculated on the reasons behind the bathymetrical control on foraminiferal taxa and concluded that amongst others, oxygen and food played a role. In spite of the uncertainties, foraminifera are often applied in reconstructions of basin configurations and vertical movements and seem to provide more accurate control on paleo-water depth than other proxies. Also cibicidids have often been used as indicators of (paleo)bathymetry (e.g. Pflum & Frerichs, 1976; Van der Zwaan et al., 1999; Van Hinsbergen et al., 2005). The bathymetric preferences of the 11 species studied here cover the neritic, bathyal and abyssal zones (Fig. 5.6).

Cibicides lobatulus and *C. refulgens* are typical neritic species, found chiefly from the beach to about 200m depth. However, living *C. lobatulus* are regularly found in upper and middle bathyal zones down to 1000m (Sejrup et al., 1981; Jorissen, 1988; Galluzzo et al., 1990; McCorkle

et al., 1997; Altenbach et al., 1999; Schönfeld & Zahn, 2000; Holbourn & Henderson, 2002) and *C. refulgens* is common between 345 and 950m in Antarctica (Murray, 1991). Moreover, a specimen of *C. refulgens* alive at 1000m in the Mediterranean was collected for DNA studies (see Chapter 3 and Appendix 2). Both species seem to live deeper in oligotrophic polar oceans: a few individuals were recorded down to 1800m for *C. refulgens* (Osterman & Kellogg, 1979) and more than 2000m for *C. lobatulus* (Bergsten, 1994; Wollenburg & Mackensen, 1998a). The presence of specimens from both species in fossil bathyal assemblages has been explained by sediment displacement (e.g. Phleger et al., 1953) or rafting of plant material to which cibicidids lived attached into pelagic environments after storms (Sprovieri & Hasegawa, 1990). However, the presence of living specimens at least down to 1000m depth indicates that *C. lobatulus* and *C. refulgens can* also live in bathyal environments. *Cibicides ungerianus* is another neritic species (Murray, 1971; Pujos, 1972; Blanc-Vernet et al., 1984) although it seems always occurring on muddy substrates in the sub-littoral zone. *Cibicides pseudoungerianus* (Frerichs, 1970; Hermelin, 1989; Lutze & Thiel, 1989; Altenbach et al., 2003) and *C. dutemplei* (van Morkhoven et al., 1986*)* seem to live somewhat deeper (from neritic to bathyal) although reliable observations lack.

Cibicides pachyderma is typically found in the upper bathyal zone (200-1000m) but occurs occasionally on the shelf (Van Morkhoven et al., 1986; Galluzzo et al., 1990). Some authors found it deeper, down to 2000m (Fontanier et al., 2002) or even 3000m-4000m (Lutze & Coulbourn, 1984; Miao & Thunell, 1993; Licari & Mackensen, 2005).

Cibicides kullenbergi is considered to be a deep sea species, mainly found from 2000 to 4000m. Nevertheless, this species also occurs shallower, at least up to 1200m (Jorissen et al., 1998; Morigi et al., 2001). *Cibicides bradyi*, *C. robertsonianus* and *C. italicus*[2] are all considered inhabitants of deeper waters. The observations and estimates vary from 1000 to 4000m. Sometimes, *C. bradyi* and *C. robertsonianus* are observed in shallower water (Phleger & Parker, 1951; Bandy &

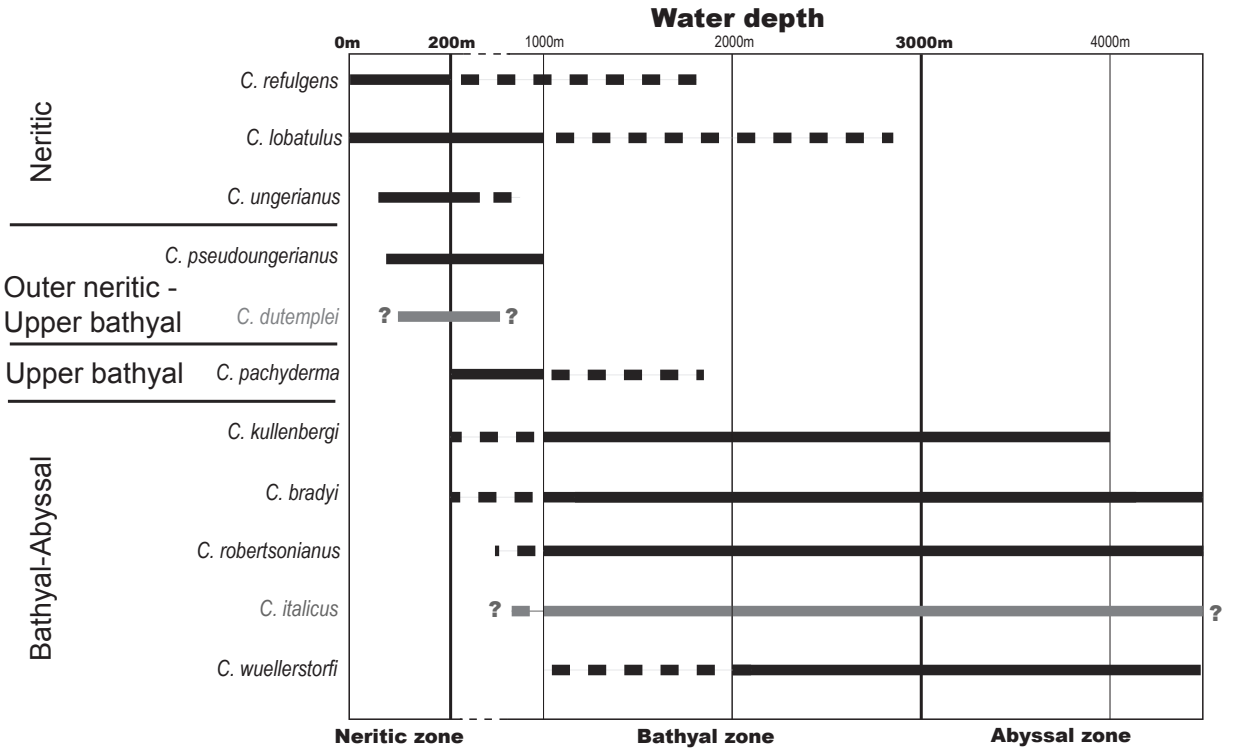

Figure 5.6. Representation of the water depth at which live the 11 studied cibicidids, from the neritic zone (0-200m), the bathyal zone (200-3000m) and the abyssal zone (>3000m). Dashing lines represent depths were the species are less abundant and less typical, grey lines with question marks represent paleoreconstructions deduced for extinct species.

2) This taxon is extinct and estimates are based on their surrounding sediments and co-occurring foraminiferal associations.

Chierci, 1966; Frerichs, 1970; Berggren et al., 1976; Brolsma, 1978; Van Morkhoven et al., 1986; Hermelin, 1989).
Finally, *C. wuellerstorfi*, is a well known deep sea inhabitant, usually found below 2000-3000m water depth, and more rarely up to 1000m (Sejrup et al., 1981; Burke, 1981; Miao & Thunell, 1993; Rathburn & Corliss, 1994; Mackensen et al., 1995; Wollenburg & Mackensen, 1998a, 1988b; Jorissen et al., 1998; Altenbach et al., 1999; Holbourn & Henderson, 2002). Sometimes, this species was observed at shallower depths than 1000m (Phleger & Parker, 1951; Frerichs, 1970; Berggren et al., 1976; Van Morkhoven et al., 1986).

5.3.3. Microhabitat

A microhabitat is defined as "a microenvironment characterized by a combination of physical, chemical and biological conditions" (Jorissen, 2002). Representatives of the genus *Cibicides* generally live in well oxygenated environments with stable physico-chemical conditions (Van der Zwaan, 1982; Kaiho, 1994, 1999; Kouwenhoven, 2000). Most cibicidids have an epibenthic or shallow infaunal habitat (Fig. 5.7). According to Buzas et al. (1993), the term epifaunal has to be reserved for species living on hard substrate or grazing at the sediment-water interface and is not suitable for a species living in the top 1cm of the sediment. Here, the distinction between both microhabitats becomes difficult since most substrates are soft and the species is always at least partially living as infauna (Murray, 2003). "Epifaunal" taxa like *C. lobatulus* (Blanc-Vernet, 1969; Wollenburg & Mackensen, 1998b), *C. pachyderma* (Schmiedl et al., 2000) *C. refulgens* (Mullineaux & DeLaca, 1984) or *C. wuellerstorfi* (Jorissen, 2002) have been sometimes observed living in the topmost sediment, although most of these cibicidids have an epibenthic habitat (Lutze & Thiel, 1989) when observed on a solid substrate. *Cibicides lobatulus*, *C. refulgens* and *C. wuellerstorfi* are well known as inhabiting elevated microhabitats: they live preferably fixed to animals, plants or hard substrates like pebbles. They are thought to be suspension feeders because they are found in areas with strong currents (Murray, 1971, 1991; Lutze & Thiel, 1989; Schönfeld, 2002) and oligotrophic conditions such as deep-sea and polar oceans (Altenbach & Sarnthein, 1989; Wollenburg & Mackensen, 1998a, 1998b). However, *C. refulgens* also feeds on diatoms (Langer, 1988; Alexander & DeLaca, 1987) and on the extrapallial cavity fluids of its host, a pecten, for Antarctic specimens (Alexander & DeLaca, 1987). *Cibicides lobatulus* and *C. refulgens* seem strongly fixed to their substrate[3] and they adopt its shape during their growth, whereas *C. wuellerstorfi* is freely moving at its surface. Sometimes, however, specimens of *C. lobatulus* and *C. wuellerstorfi* were found as epifaunal sediment dwellers (Wollenburg & Mackensen, 1998b; Jorissen, 2002; Jennings et al., 2004). Additionally, *C. refulgens* from the Mediterranean was classified as a motile predator by Langer (1993).
Other species – *C. ungerianus, C. pseudoungerianus, C. dutemplei, C. pachyderma, C. kullenbergi* – live at the sediment-water interface and are mud-dwellers if one judges the reported occurrences. The same microhabitat was assumed for the extinct species *C. italicus* (Di Napoli Alliata, 1952; Van der Zwaan, 1982; Kouwenhoven, 2000, Kouwenhoven et al., 2003). *Cibicides kullenbergi* and *C. pseudoungerianus* were sometimes described as attached epifauna (Brasier, 1975; Lutze & Thiel, 1989). Schmiedl et al. (2000) supposed that *C. pachyderma* might also be a suspension feeder because of its partly epifaunal microhabitat. On the other hand, *C. pachyderma* and *C. mundulus* (=*C. kullenbergi* here) were found at different depths inside the sediment depending on their ontogenetic stage by Rathburn & Corliss (1994), the young specimens were found deeper (1.5-6.0cm) than the adults (0-1.0cm). *Cibicides kullenbergi* is an oligotrophic species (Woodruff et al., 1980, 1992; Fariduddin & Loubere, 1997; Morigi et al., 2001) as well as *C. pachyderma* (Miao & Thunell, 1993; Schmiedl et al., 2000; Almogi-Labin et al., 2000), although other authors reported differently (Fontanier et al., 2002; Licari & Mackensen, 2005; Murgese & De Deckker, 2005). *Cibicides pseudoungerianus* seems to need more food (Altenbach et al., 1999, 2003; Licari & Mackensen, 2005).

3) Nevertheless, they were also observed moving on the substrate (Beaulieu, 2001; Sgarella & Montcharmont-Zei, 1993).

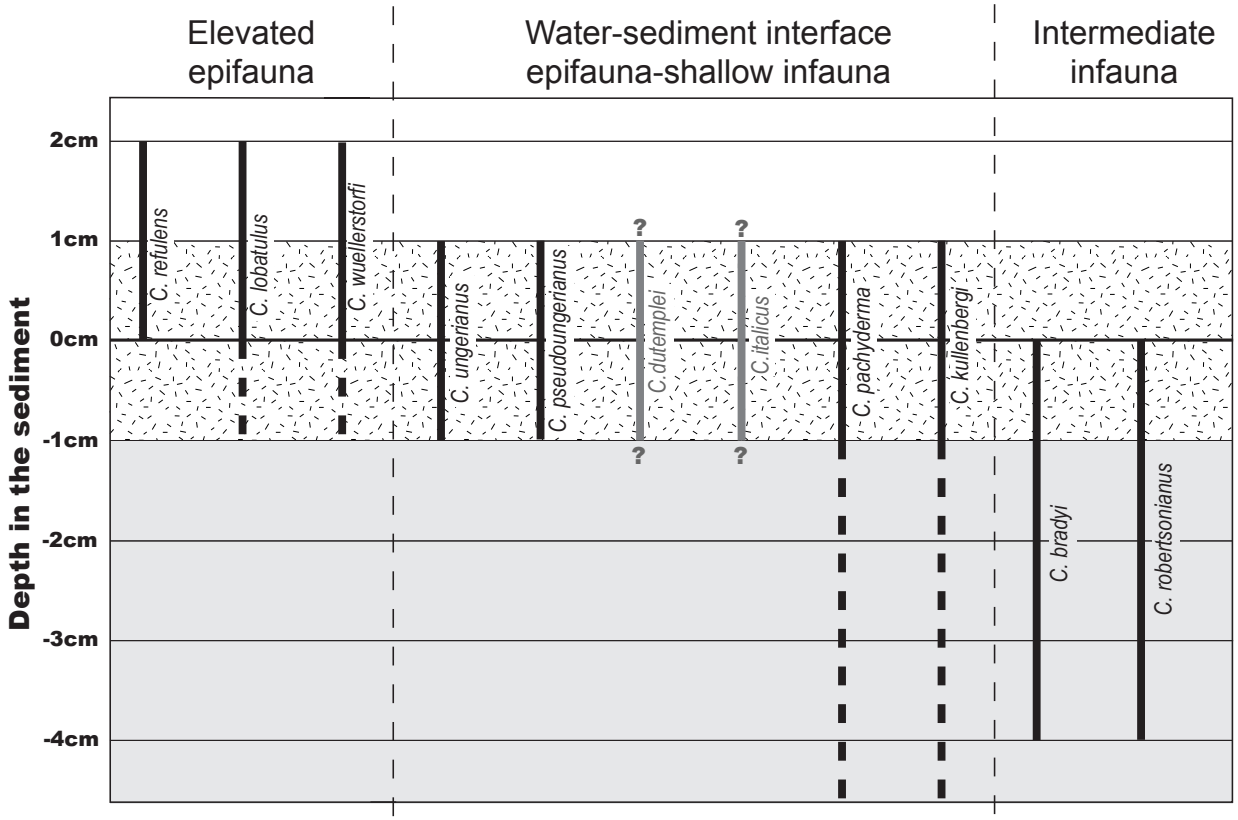

Figure 5.7. Representation of the sediment depth at which are living the 11studied species. Between +1 and –1cm, the sediment layer interface is not clear ("fluffy" layer represented by confetti). Dashing lines represent depths were the species are rarely found; question marks mean that the microhabitat is not well known. Grey lines represent paleoreconstructions deduced for extinct species.

It appears that *C. bradyi* and *C. robertsonianus* live deeper in the sediment (down to 4.0cm) than most cibicidids, and they are described as intermediate infauna by some authors (Corliss, 1991; Rathburn et al., 1996; Fontanier et al., 2002), whereas others keep them in the shallow infaunal group (Jorissen et al., 1998; Tachikawa & Elderfield, 2002). According to Corliss (1985, 1991; Rathburn & Corliss, 1994), the rounded periphery and the distribution of pores all around the surface of these two species could be interpreted as an adaptation to lower oxygen conditions.

5.4. Phylogeny of *Cibicides*

5.4.1. The fossil record of *Cibicides*

The combination of data from our own material for the Mediterranean, that covers records dating back to 15.0 Ma, and literature permitted to estimate more or less accurately the occurrences of the 11 studied species (Fig. 5.8). Establishing ranges of taxa from literature may be hampered by the accessibility of data and the inconsistent use of names by different researchers (e.g. Boltovskoy, 1978 versus Thomas, 1990). The ranges are indicated in million years (Ma) and with the planktonic foram zones (P1-P22 for the Paleogene, and N1-N23 for the Neogene) as shown in Van Morkhoven et al. (1986).

The oldest of the studied species seems to be *C. bradyi*. It is recognized from the beginning of the middle Eocene (P9) by Van Morkhoven et al. (1986). Another Eocene species is *C. dutemplei*, present in the late Eocene (Corliss, 1981; Setiawan, 1983).

During the Oligocene, *C. pseudoungerianus* (Agip, 1982; Schröder-Adams, 1991), *C. pachyderma* (Van Morkhoven et al., 1986; Mackensen & Berggren, 1992) and *C. kullenbergi* (Boltovskoy, 1978, 1980, 1983; Van Morkhoven et al., 1986 (as *C. mundulus);* Hermelin, 1989; Boersma,

1990; Schröder-Adams, 1991 (as *C. mundulus*); Katz & Miller, 1993 (as *C. mundulus*); Holbourn & Henderson, 2002 (as *C. mundulus*)) appear. According to one author (Nomura, 1991b), *C. kullenbergi* occurs already in the early Eocene.

It seems likely that *C. lobatulus* originates during the Langhian (Holbourn & Henderson, 2002), although other authors place it as early as late Oligocene (Butt, 1966; Boersma, 1990) and even late (Setiawan, 1983) and middle (Agip, 1982) Eocene. *C. refulgens* is morphologically close to *C. lobatulus* and many authors do not distinguish it. It is recorded from the Tortonian (Agip, 1982). However, we found older specimens in our own material; it is present in the oldest sample, from Malta, at 14.8 Ma. Also the time of origination of *C. ungerianus* is fuzzy. It is recorded from the Serravallian (Agip, 1982) but was observed as early as the middle (Miller, 1983; Schröder-Adams, 1991) or late (Boersma, 1990) Eocene. In our material, *C. ungerianus* is present throughout the record down to 14.8 Ma, the oldest sample from Malta.

Due to the many available observations and the more typical morphology, the reports on *C. wuellerstorfi* seem more solid. It is well established at the beginning of the middle Miocene (Wright, 1980; Woodruff, 1980; Boltovskoy, 1984; Van Morkhoven et al., 1986; Hermelin, 1989; Katz & Miller, 1993; Holbourn & Henderson, 2002) and rarely observed in early Miocene assemblages (Boltovskoy, 1978, 1980; Sen Gupta, 1989; Boersma, 1990). According to Van Morkhoven et al. (1986), *C. robertsonianus* appears during the middle Miocene (N12); the specimens found earlier (e.g. Agip, 1982) have to be classified as *C. bradyi*. *Cibicides italicus* is a short-ranged species, which appears during the Serravallian and disappears during the Pliocene (Agip, 1982; Sprovieri & Hasegawa, 1990).

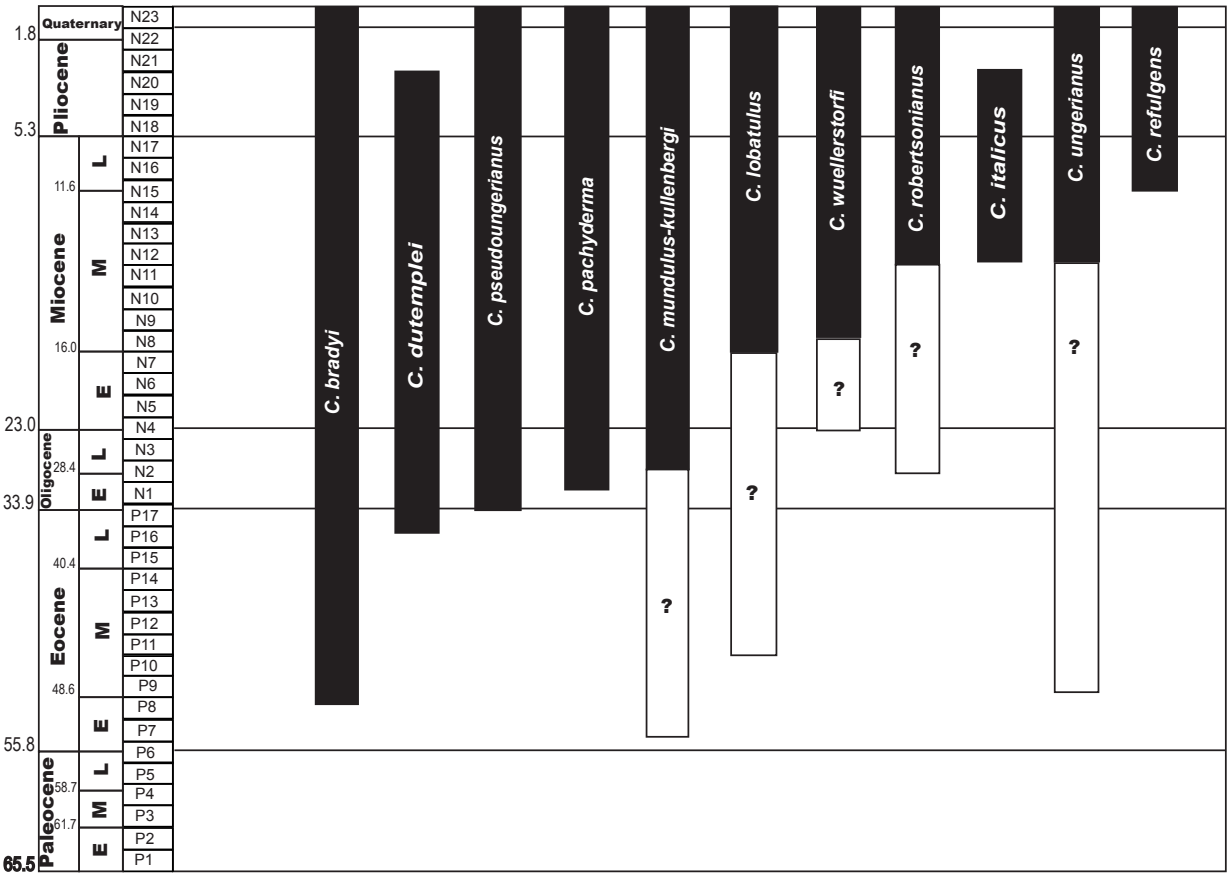

Figure 5.8. Fossil record of the 11 studied cibicidids. Black rectangles represent well established observations, whereas white ones with question marks are less sure.

5.4.2. Inferred phylogeny of *Cibicides*

In Chapter 3 we used molecular evidence to investigate the monophyly of *Cibicides*, its position among rotaliids and the relationships within the genus (Figs. 3.4-3.6). The results showed that, among the six species we studied, *C. refulgens* with populations from Antarctica and the Mediterranean has the most basal position, i.e. is least related to the other species. *Cibicides pachyderma* and *C. pachyderma-kullenbergi* have an intermediate position, whereas *C. wuellerstorfi*, *C. ungerianus* and *C. lobatulus* are closely related.

Comparing the fossil record and the molecular results, it is possible to synthesize a most likley phylogeny of *Cibicides* (Fig. 5.9). The black branches represent the species for which DNA was analysed and the topology obtained by molecular analyses. According to the DNA results, *C. refulgens* is much older than fossil evidence suggests. It could have appeared well before the Miocene, i.e. the Oligocene or even the Eocene. The reverse happens for *C. lobatulus*: the species was sometimes recorded in the Oligocene or the Eocene whereas the DNA results suggest that it is a young species. The difficulty to distinguish both species morphologically could explain this discrepancy. In the case of *C. ungerianus*, the fossil record suggests an older date of origination than the molecular data; also here the disagreement could be due to a problem of species identification or a morphologic convergence between two separated species. On the other hand, the molecular results of the remaining species fit well with the fossil record: a first occurrence in the Oligocene for *C. pachyderma* and *C. kullenbergi* and during the early or middle Miocene for *C. wuellerstorfi*.

To this backbone based on the DNA analyses, we added the five other taxa for which we had no such data. Morphologically, *C. pseudoungerianus* is thought to be close to *C. pachyderma* (Fig. 5.9a) or *C. ungerianus* (Fig. 5.9b). The second hypothesis does not fit with the fossil records, but this might be due to the chaotic taxonomic status of both taxa. Because *C. dutemplei* appears as the oldest species of the group of keeled cibicidids, it was placed at the origin of the clade represented by the six DNA studied species (Fig. 5.9a). Alternatively, *C. dutemplei* could originate from *C. refulgens* (Fig. 5.9b). Because the representatives of the group with a rounded periphery are rather different morphologically, they were probably separated from the keeled-clade a long time ago. *Cibicides bradyi* appeared during the early Eocene and according to our data gave rise to *C. robertsonianus* and *C. italicus* during the middle Miocene (Fig. 5.9a). However, *C. italicus* could be related to another cibicidid, *C. velascoensis*, a late Crecaeous-Paleocene species (Van Morkhoven et al., 1986) which also has a flat umbilical side and a convex spiral side. In this case, *C. italicus* belongs to another lineage since the end of the Mesozoic era (Fig. 5.9b).

The fact that *C. pachyderma* and *C. kullenbergi* on the one hand, and *C. bradyi* and *C. robertsonianus* on the other hand perhaps are one single species was also represented in the phylogeny (Fig. 5.9b).

If we combine the various lines of evidence, we might assume that the *C. bradyi* group was separated from the *dutemplei* clade already in the Eocene. The modern ecology suggests that the first was mostly living as infauna. Within the cibicidids it is the group with the highest tolerance to oxygen deficiency and at the same time the group with a consistent deep sea occurrence. However, it could well be that in early Tertiary times the group also occupied shallow water habitats although the evidence in that respect is weak. If they did, they were certainly replaced in shallow waters by representatives of the *dutemplei* clade, mostly well keeled taxa with a sharp periphery. It seems likely that *C. refulgens* or *C. dutemplei* were the first living representatives of the clade. Certainly for *C. dutemplei* all evidence suggest that this is a shallow water species living as epifauna and with a low tolerance to oxygen deficiency. From these shallow water populations gradually the deeper waters were invaded with successive occurrences of *C. pachyderma* and *C. kullenbergi*. This would fit very well a model of speciation where the oldest species originate on the biologically productive shelf and successively more specialist and k-selected descending taxa invade the deeper ocean zones. If true, the middle Miocene events form a remarkable contrast with that pattern. The molecular data indicate that *C. ungerianus*/*(pseudoungerianus)* is the closest relative of *C. wuellerstorfi* and that *C. lobatulus* belongs to the same clade (Figs. 3.5-3.6). The entry of these taxa coincides with a number of ecological changes in the tropical-

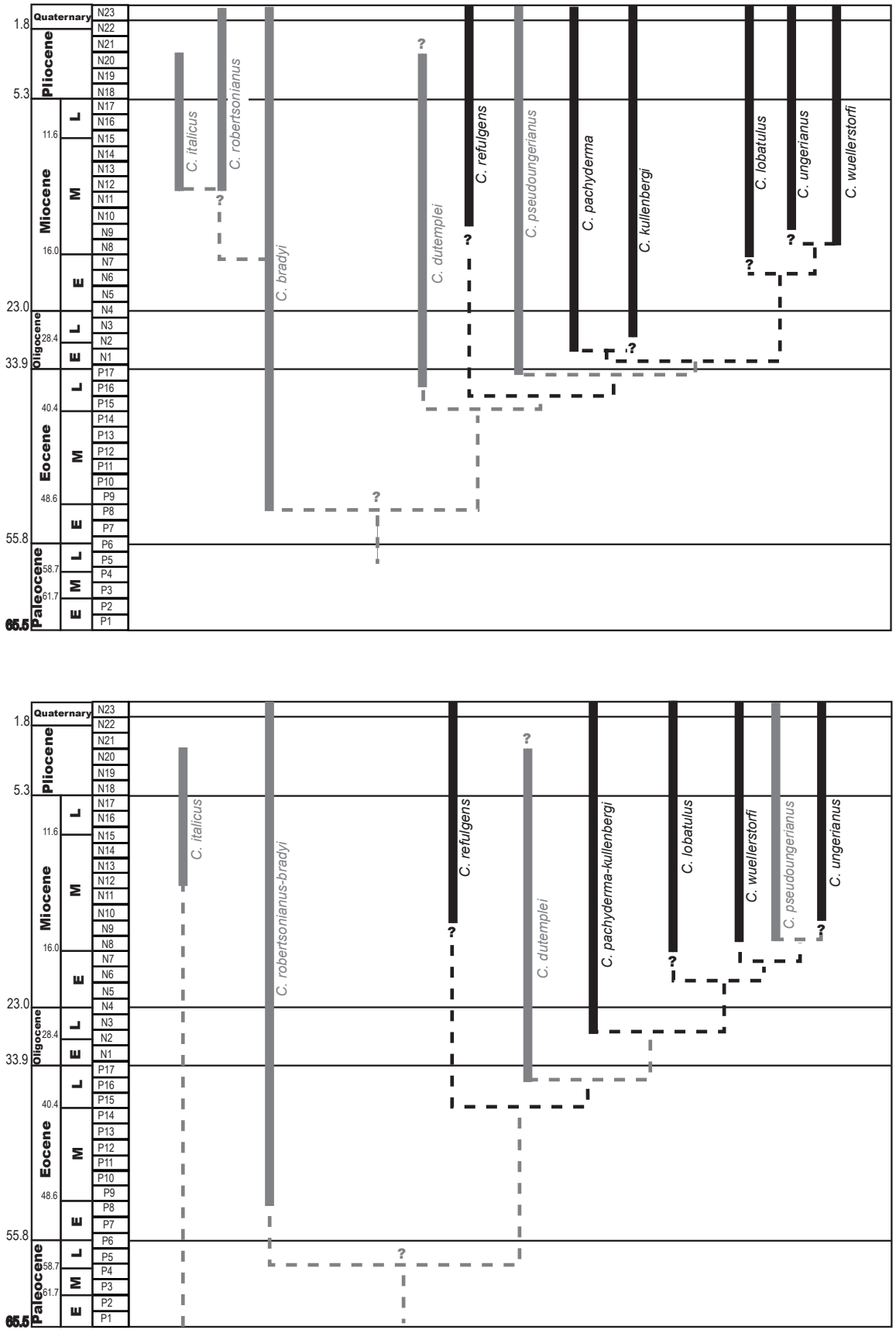

Figure 5.9. Supposed phylogeny of the 11 studied cibicidids inferred from the molecular analyses and the fossil record. Black lines represent species which gave DNA results, whereas grey lines represent species with no DNA data.

subtropical zone in which the Mediterranean was at that time. The stepwise cooling that is well established might explain the gradual disappearance of *C. dutemplei* from Miocene to Pliocene from the Mediterranean record. This coincides with the disappearance of larger foraminifera (Meulenkamp and Van der Zwaan, 1989; Adams et al., 1983). The climate change and ensuing ecological conditions might also be the driving factor behind the origination, or immigration in shallow water communities of many new taxa belonging to the genera *Ammonia* and *Elphidium* in the same period. The molecular data seem to suggest that from the shallowest living populations of *C. pachyderma* descendants populated the shallow marine zone and took over the role of *C. dutemplei*. The first taxon would be *C. lobatulus* which specialized to live attached to vegetation. From *C. lobatulus* again evolutionary invasion of the deeper marine domain took place leading to the mud dwelling *ungerianus-pseudoungerianus* stock and *C. wuellerstorfi*. This origination is characteristically related to the middle Miocene cooling. With the gradual disappearance of *C. dutemplei, C. ungerianus* took over its niche and its role as mud dweller in the shallow zone.

5.8. Summary

The cibicidids include species which were classified within various genera although they share common morphological and ecological characteristics. The monophyly of the group was shown by DNA analyses, confirming the doubts expressed about the taxonomic value of the wall structure as a good criterion to separate the cibicidids between different superfamilies. These results also disclaimed the validity of the partition plano-/biconvex in the recognition of two different genera.
The distinction of the different species within the genus is difficult considering the presence of numerous morphological intermediates and the various taxonomic concepts. In spite of the taxonomical problems, cibicidids were regularly used as bathymetric indicators. Many *Cibicides* species are epibenthic – living on an elevated substrate or at the sediment-water interface – whereas *C. bradyi* and *C. robertsonianus* live deeper in the sediment.
The resulting phylogeny presented here is based on the molecular data and data on the fossil distribution. The first phylogeny proposed (Fig. 5.9a) agrees better with the known fossil record, because *C. pseudoungerianus* is supposed to appear much earlier than stated in the second phylogeny (Fig. 5.9b). However, the second phylogeny fits more with morphological and molecular results (*C. robertsonianus* and *C. bradyi*, *C. pachyderma* and *C. kullenbergi* are merged together and *C. pseudoungerianus* is closer to *C. ungerianus*). The data suggests that two main events of speciation, the first speciation pattern being from shallow to deeper waters. The first event, at the end of the Eocene and during the Oligocene, can be explained by the opening of new spaces in the deep-sea due to the appearance of a psychrosphere (Douglas & Woodruff, 1981). During the middle Miocene, when the second radiation occurred (*C. lobatulus, C. wuellerstorfi*, *C. pseudoungerianus* (?), *C. ungerianus*), the physico-chemical conditions changed again to lead to those present in the modern oceans (Douglas & Woodruff, 1981). In that case, invasion of shallower habitats could be explained by the extinction of other taxa (e.g. *C. dutemplei*), which left empty ecospace. The second group, represented by the cibicidids with rounded periphery, is less well known yet. DNA data would help to know if *C. bradyi* and *C. robertsonianus* belong to the same species and how they are linked to the other cibicidids. For *C. italicus*, an extinct species, the origin and links can only be inferred from the fossil record. We assume that it is a *Cibicides*, closer to *C. bradyi* and *C. robertsonianus* than to the other cibicidids, because of its morphology. However, a close relation to *C. velascoensis* cannot be excluded in which case it would constitute a separate evolutionary branch.

Chapter 6

Taxonomy, evolution over the past 15 Ma and micro-habitat occupation of 13 common species of *Uvigerina*

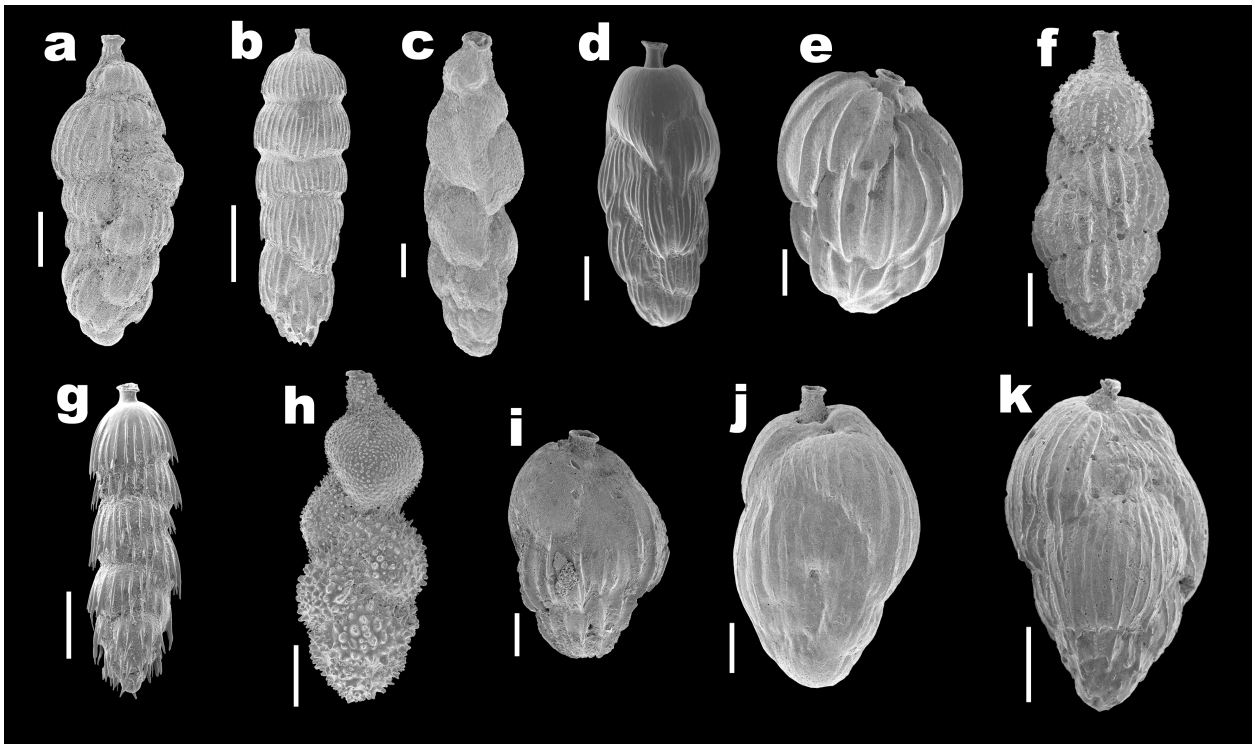

Figure 6.1.
a) *Uvigerina bononiensis*, b) *U. cylindrica*, c) *U. earlandi*, d) *U. elongatastriata*, e) *U. mediterranea*, f) *U. peregrina*, g) *U. phlegeri*, h) *U. proboscidea*, i) *U. semiornata*, j) *U. rutila*, k) *U. striatissima*.
Scale= 100μm

The genus *Uvigerina* d'Orbigny, 1826, evolved during the Cenozoic (early Eocene of the southern Tethyan, R. P. Speijer, pers. comm.), and became important in marine environments during the late Eocene (Douglas & Woodruff, 1981). The species studied here (Fig. 6.1) belong to the most common Neogene uvigerinids from the Mediterranean, and the North Atlantic Ocean: *Uvigerina bononiensis* Fornasini, 1888; *U. cylindrica* (d'Orbigny, 1826); *U. elongatastriata* (Colom, 1952); *U. mediterranea* Hofker, 1932; *U. peregrina* Cushman, 1923; *U. phlegeri* (Le Calvez, 1959); *U. proboscidea* Schwager, 1866; *U. rutila* Cushman & Todd, 1941; *U. semiornata* d'Orbigny, 1846; *U. striatissima* Perconig, 1955. A common species from Antarctica was also added to the study: *U. earlandi* (Parr, 1950). Additionally, two hispid species related to *U. peregrina* and *U. proboscidea* are discussed here, although they were not found in our material: *U. auberiana* d'Orbigny, 1839 and *U. hispida* Schwager, 1866.
Terminology used to describe the morphology of the test is shown in Fig. 6.2.

6.1. Sample locations

Extant *Uvigerina* were collected by boxcoring and multicoring in the Mediterranean, the North Atlantic and the North Sea (Fig. 6.3), during different cruises (see Chapter 5.1.1 for details). After picking, the specimens were identified and stored on Chapman slides. Nearly all specimens used for molecular analyses were pictured before their destruction for DNA extraction. Other interesting specimens were also pictured (see Pl. 13-19).
To get an overall impression, fossil representatives of the genus *Uvigerina* were collected from Mediterranean material corresponding to the last 15 million years (Ma). A total of 23 samples, taken every 500,000 years have been examined (Table 6.1); they were selected from fully marine records, and as close as possible to the required age. Aberrant sediments like sapropels were avoided. The samples come from Mediterranean sites located in Italy (Gibliscemi, Punta Piccola, Vrica, Singa III, Punta di Maiata, Tremiti, Montalbani Ionico), Creta (Faneromeni) and Malta except four, which were collected on the Atlantic side of Morocco (Loulja and Ain El Beida) (Fig. 6.3). It

was not possible to cover the time slice between 5.0 and 6.5 Ma in the Mediterranean because benthic foraminifers were scarce or absent prior to and during the Messinian salinity crisis (e.g. Krijgsman et al., 1999; Kouwenhoven et al., 1999, 2003; Schmiedl et al., 2003; Stefanelli et al., 2005). All samples were washed and sieved at Utrecht University where they are deposited. Uvigerinids were picked from the 125-595µm fraction and subsequently stored on Chapman slides, sorted by species.
The sampling sites have been described in the previous chapter (section 5.1.2.), with the exception of the Faneromeni section. This section, located in the north-east of Crete, gave supplementary samples for the time slice 6.5-7.5 Ma to complete the fossil record. The section was described in Nijenhuis et al. (1996), and the age established by integrated stratigraphy (Krijgsman et al., 1994). Paleodepth was estimated between 200 and 700m (Kouwenhoven, 2000, p. 95).
There is a gap in the *Uvigerina*-record between 8.0 and 12.0 Ma (Table 6.1). The absence is perhaps due to the deeper water origin of the Gibliscemi samples, since this period is mainly documented with samples from that section. Depth as a factor is supported by the occurrence of cibicidids from the bathyal-abyssal group (see Table 5.1 and Fig. 5.7). However, no *Cibicides wuellerstorfi* (a deep-sea indicator, see 5.3.2.) has been recorded, and only a few hispid uvigerinids occurred (indicative of deeper environments, see 6.3.2. and Table 6.1). Since uvigerinids prefer carbon rich environments (see 6.3.1. and 6.3.3.) their absence in Gibliscemi could also be due to the existence of oligotrophic conditions.

6.2. Classification of *Uvigerina*

6.2.1. Definition of the genus *Uvigerina*

The genus *Uvigerina* is characterized by an elongate test with a round, flattened or triangular cross-section. The chamber arrangement is usually triserial, but can become bi- or uniserial throughout ontogeny (Cushman, 1923). The wall is calcareous and perforate. The surface of the test often bears ornamentations (costae and/or spines). The most typical feature is the

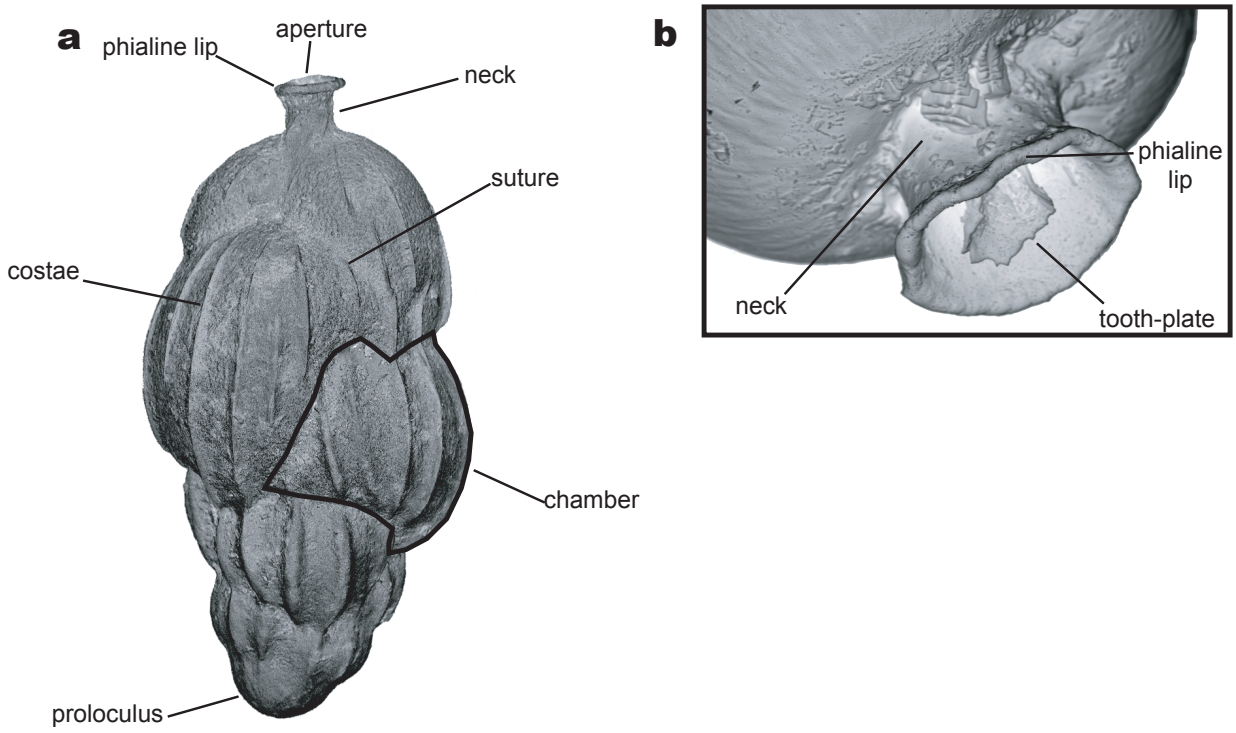

Figure 6.2. Terminology employed to name the different parts of the test (a) and the aperture (b) of *Uvigerina*.

Figure 6. 3. Map of Europe indicating the sampling sites for fossil (white dots) and Recent (grey squares) material, with the names of the locations.

location of the aperture on a tubular neck, often with a phialine lip. According to Lamb (1964), the tests from the sexual (megalospheric) and the asexual (microspheric) generations possess a differently shaped proloculus (Fig. 6.4). Moreover, the microspheric form of *U. hispida* and *U. proboscidea* may have a basal spine (Van Morkhoven et al., 1986). The main criteria distinguishing the different species are the arrangement of the chambers, their shape, the position of the neck, and the ornamentation. The ornamentation is the most obvious feature, but its taxonomic importance is rather weak because it seems to be dependent on ecological conditions (e.g. Cicha et al., 1986). The triangular cross-section was formerly attributed specifically to the genus *Trifarina*, but DNA results showed it is not taxonomically relevant for the generic separation (see Chapters 4 and 6.2.2.). Moreover, *U. elongatastriata* has a rounded-triangular section and a tendency to become bi- or uniserial (Lutze, 1986), which shows that seriality (uni-, bi-, or triseriality) is not a stable diagnostic feature.

On the basis of the chamber arrangement, the position of the neck and the shape of the pores, *Uvigerina* was separated into three different groups (Van der Zwaan et al., 1986). The *U. semiornata* group[1] – characterized by a triserial chamber arrangement, a short neck standing in a

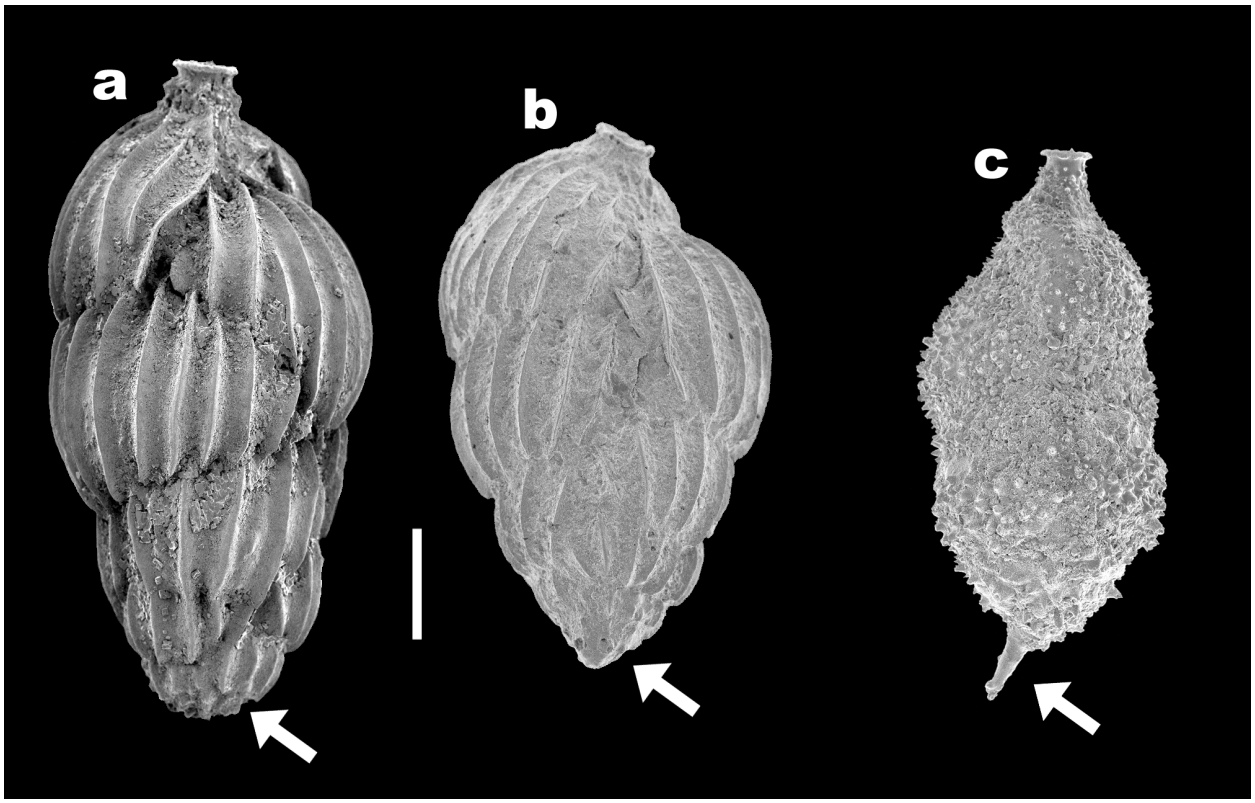

Figure 6.4. Difference in proloculus shape attributed to sexual/asexual generations dimorphism, with the megalospheric generation (a) and the microspheric one (b), which may bear a spine in some species (c). a) and b) *Uvigerina peregrina*; c) *U. proboscidea*. Scale= 100μm

1) Represented here by *U. semiornata, U. rutila, U. striatissima, U. elongatastriata* and *U. mediterranea*.

Table 6.1. Number of specimens collected per species and sample.

Site	Age (Ma)	Sample number	*U. bononiensis*	*U. cylidrinca*	*U. elongatastriata*	*U. mediterranea*	*U. peregrina*	*U. phlegeri*	*U. proboscidea*	*U. semiornata + U. rutila +U. striatissima*	*Uvigerina sp.*	*Total Uvigerina* per sample
Malta	15.0	1685	1				55			40	7	102
Malta	14.5	1776	1				1			83	6	90
Malta	14.0	1602	2				17		1	33		51
Tremiti	13.5	475							224	11		235
Tremiti	13.0	19'631					6		53	20		79
Tremiti	12.5	19'955					40		146	21		207
Gibliscemi	12.0	18'514										0
Gibliscemi	11.5	15'609										0
Gibliscemi	11.0	15'487										0
Gibliscemi	10.5	15'372							3			3
Gibliscemi	10.0	14'831										0
Gibliscemi	9.5	14'204							1			1
Gibliscemi	9.0	14'320										0
Gibliscemi	8.5	14'442										0
Gibliscemi	8.0	14'542										0
Faneromeni	7.5	5'725					5		74	13		92
Faneromeni	7.0	5'857		10			94		14	10	1	119
Faneromeni	6.5	5'912		18					2			2
Ain El Beida	6.5	91.3					183			37		220
Ain El Beida	6.0	289.3					180		20	60		260
Loulia	5.5	674					118			11	1	130
Loulia	5.0	942		8			151			60		211
Punta di Maiata	4.5	12'168							2			2
Punta di Maiata	4.0	12'272					10		10		1	21
Punta Piccola	3.5	12'425					5		73	23		101
Punta Piccola	3.0	13'251a					40		79			119
Singa III	2.5	9334					76		13			89
Singa III	2.0	9484					16		12			28
Vrica	1.5	6326					179					179
Montalbano Ionico	1.0	H8214					94					94
Recent	0.0				27	730	699	43	6		2	750
Total number per species			4	36	27	730	1969	43	733	422	18	3185

depression, and broad and high chambers strongly overlapping the previous ones – and the *U. peregrina* group[2] – including smaller and slender species – could be recognized genetically (see Chapter 4). For the time being, the third group (*U. bononiensis* group[3]) appears to belong to the *U. peregrina* group. Additional DNA samples from other members of these different groups are needed to confirm these first results.

6.2.2. History of generic classification

Contrary to cibicidids (see Chapter 5), the generic attribution of uvigerinids is relatively simple: they are mainly grouped under the genus *Uvigerina*. However, some authors have divided *Uvigerina*

2) Represented here by *U. peregrina, U. auberiana, U. hispida* and *U. proboscidea.*
3) Represented here by *U. bononiensis, U. cylindrica* and *U. phlegeri.*

into several genera. On the basis of the tooth-plate morphology, Hofker (1951) subdivided *Uvigerina* into three genera: *Aluvigerina*, *Neouvigerina* and *Euuvigerina*, subsequently validated by designation of type species (Thalmann, 1952). Loeblich & Tappan considered *Aluvigerina* as a junior synonym of *Uvigerina* but did recognize *Euuvigerina* (1964, 1988). Revets, however, considered this last genus a junior synonym of *Uvigerina* (cited by Jones, 1994). *Neouvigerina* was first synonymized with *Siphouvigerina* Parr, 1950 (Loeblich & Tappan 1964; Jones, 1994), and later validated as a separate genus (Loeblich & Tappan, 1988). Vella (1961) described supplementary genera for New Zealand uvigerinids mainly on the basis of the ornamentation: *Hofkeruva*, *Norcottia*, *Miniuva*, *Ruatoria* and *Ciperozoa*. These names were first put in synonymy with existing genera (respectively *Euuvigerina*, *Trifarina*, *Uvigerina* and *Rectuvigerina* for the latter two) by Loeblich & Tappan (1964) and later reestablished as valid names inside the Uvigerinidae (Loeblich & Tappan, 1988). Despite the validation of many of them by Loeblich & Tappan in their reference classification (1988), these generic names have never been used regularly to name uvigerinids (see synonymy in the Appendix 1).

Other generic names were attributed to specific goups of uvigerinids. *Rectuvigerina* is often used for species with a uniserial part (mainly *R. phlegeri* Le Calvez, 1959 among the studied species), but also *R. bononiensis* (e.g. Souaya, 1965; Schiebel, 1992)*, R. cylindrica* (e.g. Christodoulou, 1960; Souaya, 1965; Schiebel, 1992) or *R. elongatastriata* (e.g. Cimerman & Langer, 1991). This genus was established by Matthews (1945) for separating members of the genus *Siphogenerina* with an early triserial stage from the ones with an early biserial one. *Rectuvigerina* was first classified in the family Uvigerinidae (e.g. Mathews, 1945; Cushman, 1959; Loeblich & Tappan, 1964) and subsequently moved to the family Siphogenerinoididae (Loeblich & Tappan, 1988). The distinction between *Rectuvigerina* and *Uvigerina* is based on the presence of one or more uniserial chambers and an internal siphon in the former genus (Mathews, 1945). However, the homogeneity of *Rectuvigerina* seems questionable regarding the various morphologies of its members. Some species appear close to *Uvigerina* (e. g. *R. phlegeri* or *R. multicostata* (Cushman & Jarvis, 1929)), whereas others look rather different (the costae run throughout the test and/or the section is more angular, e.g. *R. transversa* (Cushman, 1918), *R. senni* (Cushman & Renz, 1941)). Molecular results indicated a close relation between *R. phlegeri* and *U. peregrina* (see 4.4.2. and Fig. 4.8a), and thus, the inclusion of this species inside *Uvigerina*. This suggests that a shift from a triserial to a uniserial coiling is thus not taxonomically significant for generic attribution, which confirms the statements of Hofker (1956) and Thomas (1980). The other feature distinguishing *Rectuvigerina* from *Uvigerina* – the presence of an internal siphon – can be explained by the fixed position of the neck in the subsequent uniserial chambers, and is as such a consequence of the uniserial coil. Due to important morphological differences inside *Rectuvigerina*, polyphyly of this genus is suspected and further investigations are needed to identify which members can be attributed to *Uvigerina, Siphogenerina* or other genera.

Trifarina Cushman, 1923 and *Angulogerina* Cushman, 1927 are employed for species with a triangular section (e.g. *A.* or *T. earlandi* (Parr, 1950; Osterman & Kellogg, 1979)*, A. or T. elongata-striata* (Colom, 1952, 1974; Haake, 1980)). They are placed in the subfamily Angulogerininae Galloway, 1933, whereas *Uvigerina* is in the subfamily Uvigerininae Haeckel, 1894. Both subfamilies are classified inside the family Uvigerinidae Haeckel, 1894, and are separated on the basis of the section shape (respectively triangular or rounded). According to our molecular analyses (see Fig. 4.8a), *T. earlandi* groups with *R. phlegeri* and *U. peregrina*, while *U. elongatastriata* and *U. mediterranea* form another clade. This result indicates that the section shape is taxonomically no more significant than the shift to uniseriality, as already stated by Jonkers (1984). Because the chamber arrangement of certain species (e.g. *T. angulosa* or *T. bradyi*) looks rather different from that of *T. earlandi,* DNA sequencing of other members of *Trifarina* and *Angulogerina* is also needed to check whether all the members of these genera group with *T. earlandi* inside *Uvigerina* or if these genera are polyphyletic.

Besides these established and possible synonyms of *Uvigerina*, other generic names sometimes used for the studied species are *Hopkinsina* Howe & Wallace, 1932 for *H. bononiensis* (Marks, 1951; Dieci, 1959; Verdenius, 1970; Verhoeve, 1971; Brolsma, 1978), *Siphouvigerina* Parr,

1950 for *S. ampullacea* (Jones, 1994) and *S. auberiana* (Kohl, 1985), and finally *Eouvigerina* Cushman, 1926 for *E. mediterranea* (Hofker, 1960). *Uvigerina cylindrica* was first described under the generic name *Clavulina* dOrbigny, 1826, but this genus was subsequently attributed to agglutinated foraminifers.

6.2.3. Different species concepts in literature

Uvigerina semiornata has been divided in several subspecies (see e.g. Boersma, 1984; Borsetti et al., 1986; Cicha et al., 1986; Von Daniels, 1986). *Uvigerina striatissima* and *U. longistriata*, both described by Perconig (1955) in the same article, are considered to be synonyms (Jonkers, 1984). Among the modern species, *U. finisterrensis* is regarded a synonym of *U. mediterranea* (Van Morkhoven et al., 1986). Sometimes, *U. mediterranea* is considered to be a junior synonym of *U. peregrina* (Höglund, 1947; Barker, 1960; Pflum & Frerichs, 1976; Haake, 1977; Lutze & Coulbourn, 1984 (as *U. finisterrensis*); Hermelin, 1989), but molecular analyses have shown that they are truly different species (see Chapter 4).

Due to the wide morphological variation of *U. peregrina*, many other species were put in synonymy with this species and considered as varieties or subspecies, e.g. *U. asperula* (Belanger & Berggren, 1986), *U. bifurcata* (Borsetti et al., 1986; Verhallen, 1991), *U. hollicki* (Belanger & Berggren, 1986; Borsetti et al., 1986; Van Leeuwen, 1986; Lutze, 1986; Hermelin, 1989). Moreover, some authors included all deep sea uvigerinids under the names *U. peregrina* s. l. or *Uvigerina* spp. (e.g. Lohmann, 1978; Corliss, 1979a, 1983; Peterson, 1984; Mead, 1985; Hermelin, 1989; Miao & Thunell, 1993; Rathburn & Corliss, 1994). On the other hand, close species or subspecies such as *U. hollicki, U. peregrina, U. peregrina parva* or *U. pygmaea* are still distinguished by other authors (Lutze, 1986; Schiebel, 1992; Timm, 1992; Schönfeld & Altenbach, 2005). *Uvigerina pygmaea* and *U. peregrina* may be synonyms (Boersma, 1984; Lutze & Coulbourn, 1984; Jonkers, 1984; Borsetti et al., 1986; Verhallen, 1991). If true, *U. pygmaea* is the senior synonym, but because it is an extreme variant of the species, Borsetti et al. (1986) prefer the much better established name *peregrina* for this species. *U. akitaensis*, sampled outside the study area, was suspected to be a synonym of *U. peregrina* by Scott (Scott et al., 2000). Molecular analyses confirmed that suspicion (see Chapter 4).

The taxonomy of the spinose species remains unclear; moreover, the descriptions of these hispid species do not always seem to apply to the same species concept. *Uvigerina proboscidea* is alternatively considered as a junior synonym of *U. auberiana* (Berggren et al., 1976; Hermelin, 1989; Timm, 1992) or of *U. hispida* (Verhoeve, 1971). The characteristic *U. ampullacea* is put in synonymy with *U. auberiana* (Phleger et al., 1953) or considered a variety of *U. hispida* (Cushman, 1933; Van Leeuwen, 1986) or *U. proboscidea* (Belanger & Berggren, 1986). *Uvigerina asperula, U. interrupta* and *U. senticosa* are thought to be synonyms of *U. auberiana* (Berggren et al., 1976; Hermelin, 1989) or *U. proboscidea* for the latter one (Van Morkhoven et al., 1986). In addition, *U. aculeata* (Van der Zwaan et al., 1986), *U. rustica* (Van Morkhoven et al., 1986) and *U. asperula* var. *auberiana* (Belanger & Berggren, 1986) are supposed to be synonyms of *U. hispida*. Finallly, *U. gracilis* is considered to be a synonym of *U. proboscidea* (Borsetti et al., 1986). According to Van Leeuwen (1986), *Uvigerina hispida* seems to intergrade[4] with *U. peregrina* (through the *dirupta* type). Borsetti et al. (1986), however, found no transition between *U. hispida* and other species. Belanger & Berggren (1986) interpreted a morphological series with *U. peregrina, U. hollicki, U. senticosta, U. asperula, U. ampullacea* and *U. proboscidea* as ecophenotypes, and Loubere & Banonis (1987) observed morphological intermediates between *U. auberiana* and *U. peregrina*. The tests with a bottle-like last chamber were alternatively attributed to *U. auberiana* (Cushman, 1923; Phleger et al., 1953; Berggren et al., 1976; Boersma, 1984; Hermelin, 1989) or *U. proboscidea* (Boltovskoy, 1978; Boersma, 1984; Jonkers, 1984; Van Morkhoven et al., 1986; Belanger & Berggren, 1986; Borsetti et al., 1986; Van Marle, 1988; Boersma, 1990; Verhallen, 1991; Kaiho & Nishimura, 1992; Wells et al., 1994; Den Dulk, 2000; Murgese & De Deckker,

4) The general shape is the same, and sometimes the spines are aligned in rows.

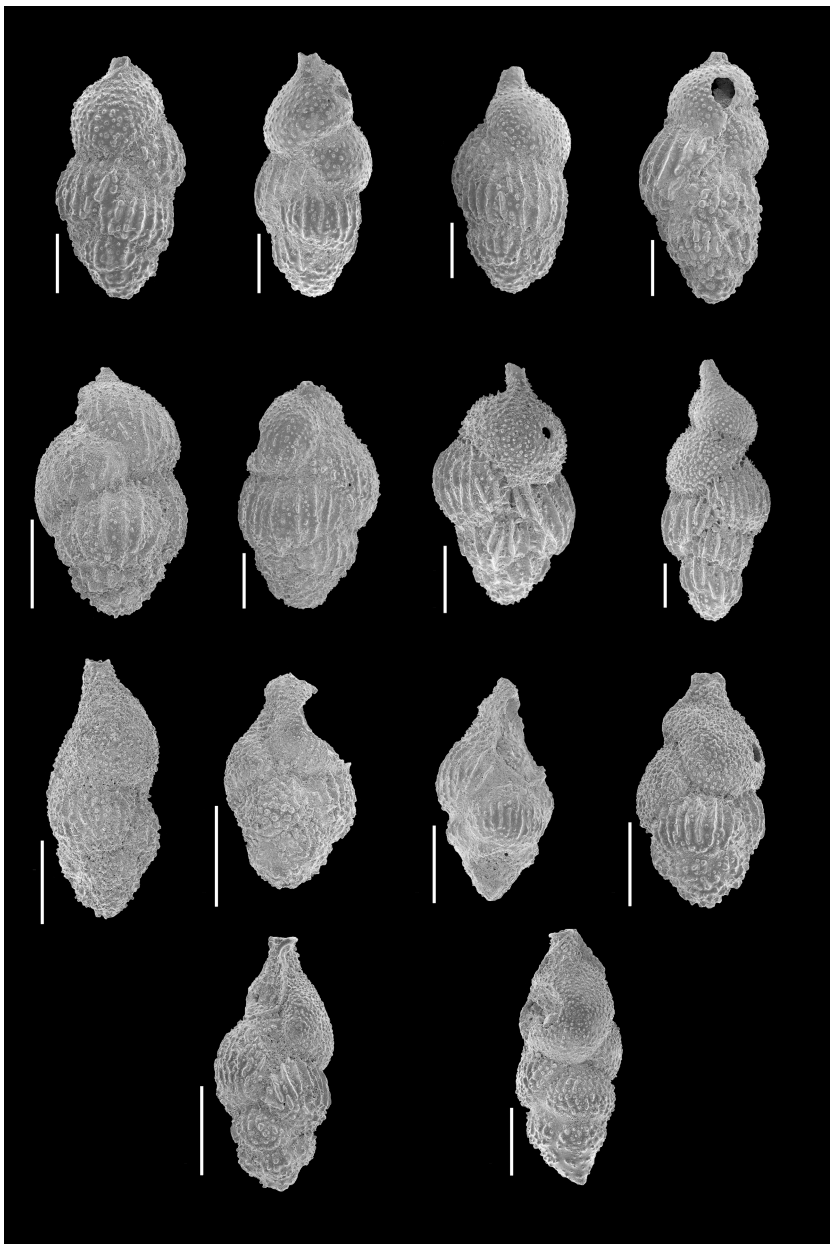

Figure 6.5. Morphological intermediates between *Uvigerina peregrina* and *U. proboscidea* from Faneromeni (7.0 Ma). Scale= 100μm

2005). A biserial part is sometimes described in *U. auberiana* (Boltovskoy, 1978; Boersma, 1984; Van Leeuwen, 1986). *Uvigerina hispida* is considered to be a robust and tall species (Boersma, 1984; Belanger & Berggren, 1986; Borsetti et al., 1986; Van Leeuwen, 1986; Van Morkhoven et al., 1986), or a small one (Verhoeve, 1971). Usually the spines are described as not aligned in *U. hispida* (Borsetti et al., 1986; Hermelin, 1989), but according to Van Leeuwen (1986), this is the case for *U. auberiana*.

Of the uniserial uvigerinids, *Uvigerina compressa* is a junior synonym of *U. bononiensis* (Meulenkamp, 1969; Jonkers, 1984; Cicha et al., 1986). According to Lutze (1986), *U. phlegeri* intergrades with *U. bononiensis* and is therefore interpreted as an ecophenotype. The uniserial uvigerinids belonging to the species *U. cylindrica* have been described under various names (see Meulenkamp, 1969 and Thomas 1980 for the synonymy).

According to Quilty (2003), *Uvigerina earlandi* is synonymous with *Trifarina pauperata*, *U. bassensis* and *T. angulosa* and comprises the non-hispid ribbed forms with carinate chambers found in the Neogene of Antarctica. This species is called *T. angulosa* by Mackensen (1992).

6.2.4. Distinctions and relations between the different species in our material

Among the members of the *U. semiornata* group, *U. semiornata*, *U. striatissima* and *U. rutila* are rather difficult to distinguish, especially when preservation is not good. The distinction is mainly based on the number of costae per chamber: specimens with a few low costae or striae and a smooth last chamber are attributed to *U. rutila*, while more densely or more heavily costate individuals belong respectively to *U.striatissima* or *U. semiornata*. The recognition of *U. elongatastriata* poses no problem, because this species has a rather typical shape and ornamentation. *Uvigerina mediterranea* is well separated from *U. peregrina* in morphological and molecular phylogenies. The difference, however, is sometimes difficult to see under a dissection microscope, particularly for young specimens of *U. mediterranea* and fully costate *U. peregrina* (e.g. *U. peregrina bifurcata* of Borsetti et al., 1986). Criteria used for the separation are the larger size, the more inflated chambers, the absence of spines, and the presence of a depression at the basis of the neck for *U. mediterranea* (see Fontanier et al., 2002 for detailed description of the distinctive features). Furthermore, *U. peregrina* specimens usually look more yellowish and sandy at low magnifications. This granular aspect is caused by the costae, which are basically interconnected spines in *U. peregrina*.

Inside the *U. peregrina* group, the small hispid species (*U. auberiana, U. proboscidea*) are difficult to separate. The general shape of *U. auberiana* resembles the one of *U. peregrina* with a diamond-shaped form. Spines may be arranged in lines in *U. proboscidea*, but it is never the case for *U. auberiana*. The last chamber of *U. proboscidea* has a typical "bottle-like" shape with a long neck, which gives a decreasing width to the test from a broader beginning. These hispid species are classified in the *peregrina* group because they are thought to be evolutionary close to *U. peregrina* (Van der Zwaan et al., 1986a). In our fossil material, the discrimination between *U. peregrina* and *U. proboscidea* was sometimes difficult, particularly in the 7.0 Ma sample from Faneromeni because there was an intergradation between both taxa (Fig. 6.5).

The wide morphological variability of *U. peregrina* has often been noticed and was usually interpreted as ecophenotypical (Boltovskoy, 1978, 1980; Lohmann, 1978; Mead, 1985; Lutze, 1986; Van Leeuwen, 1986; Borsetti et al., 1986; Belanger & Berggren, 1986; Williams et al., 1988; Hermelin, 1989). Specimens with costae are named *peregrina*, whereas the more spinose variants are called *dirupta* or *hollicki*, and replace the type *peregrina* in deeper waters (e.g. Phleger et al., 1953; Lutze, 1986; Van Leeuwen, 1986). Specimens of *U. peregrina* from the Skagerrak provide a good example of the morphological variation found within this species (Fig. 6.6). Molecular analyses of rDNA (the SSU and a more variable part, the ITS, see Chapter 4) showed virtually no genetic variation, whereas the morphological variation was wide and included more or less inflated and elongated specimens (see morphometrical analysis in Chapter 4 and Fig. 6.6). In the Skagerrak population, all individuals have well developed costae, but Atlantic deeper specimens are more spinose (Fig. 6.7).

Lutze (1986) observed morphological transitions between *U. bononiensis* and *U. phlegeri*. In our material, *U. bononiensis* was only recognized in the fossil material from Malta (see Table 6.1), while *U. phlegeri* was identified in the Recent material from the Portuguese coast. The small partly uniserial *U. cylindrica* was separated into two subspecies (*U. cylindrica cylindrica* and *U. cylindrica gaudryinoides*) by Thomas (1980). The test is more slender, the uniserial part longer, and uniserial chambers are arranged more regularly in adult specimens of *U. cylindrica cylindrica* (Borsetti et al., 1986).

6.3. Ecology and paleoecology of *Uvigerina*

6.3.1. Proxy value of *Uvigerina*

Uvigerinids were initially used as indicators of bathymetry (Bandy, 1960; Sliter, 1970; Pflum & Frerichs, 1976; Wright, 1978; Van der Zwaan et al., 1999; Van Hinsbergen et al., 2005) and water masses (Streeter, 1973; Lohmann, 1978; Corliss, 1979b; Schnitker, 1979; Streeter & Shackleton,

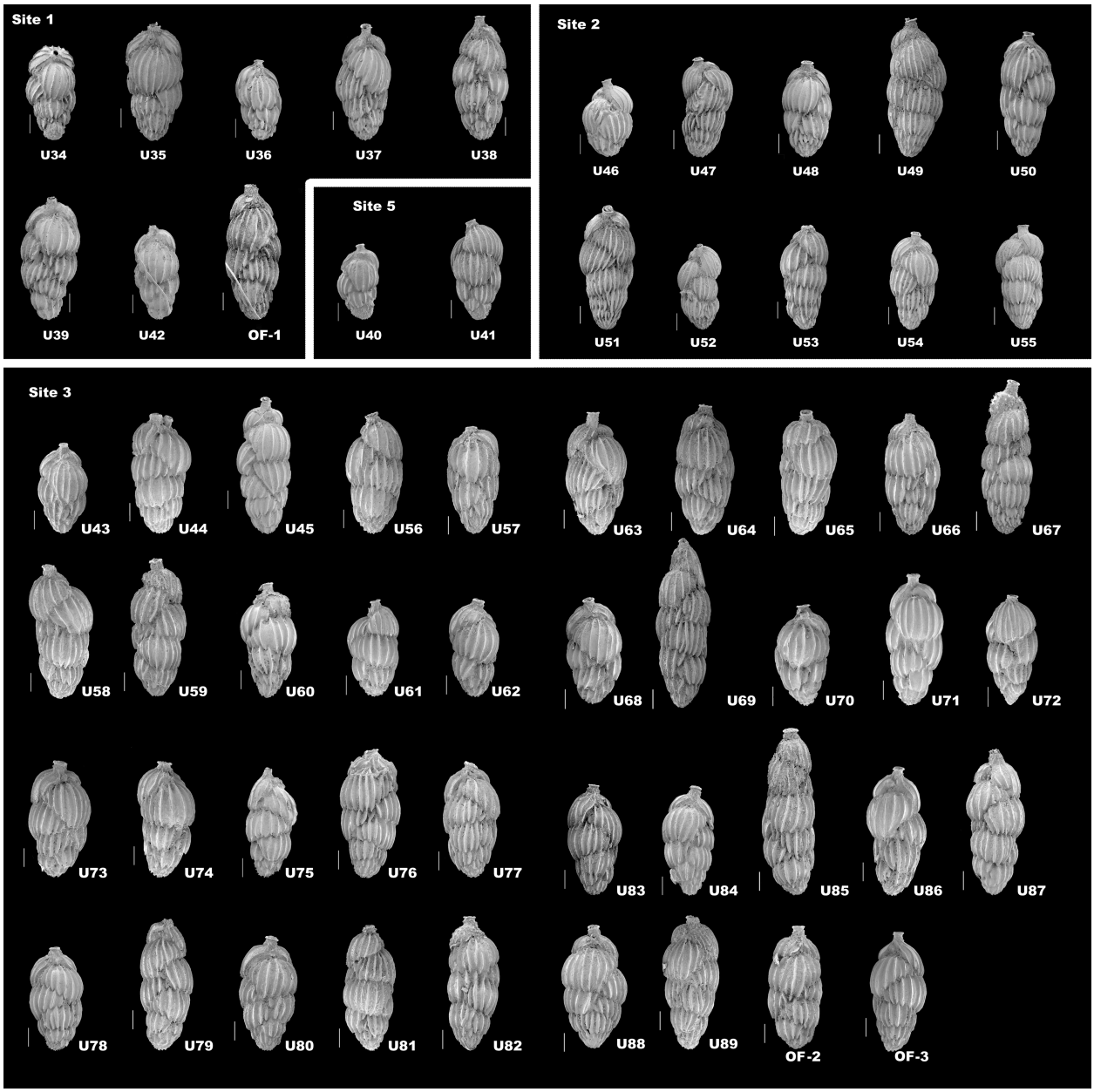

Figure 6.6. Representatives of the Oslo Fjord population of *U. peregrina*, sorted by sampling site (coordinates and depths of the sites are placed in Appendix 2). Scale= 100μm

1979; Douglas & Woodruff, 1981; Rytter et al., 2002). Later, the question arose whether they were favored by low oxygen conditions or organic carbon enrichment. Because both parameters are closely interrelated (e.g. Altenbach & Sarnthein, 1989; Van der Zwaan et al., 1999))[5], divergent opinions occurred (Schnitker, 1974; Lohmann, 1978; Streeter & Shackleton, 1979; Lutze, 1980; Douglas & Woodruff, 1981; Miller & Lohmann, 1982; Van der Zwaan, 1982; Corliss, 1983; Lutze & Coulbourn, 1984; Ross & Kennett, 1984; Van der Zwaan et al., 1986b; Altenbach & Sarnthein, 1989; Boersma, 1990; Gupta & Srinivasan, 1992b; Ishman, 1996). However, the notion that carbon content is the driving factor is now dominant (Gooday, 1994; Rathburn & Corliss, 1994; Mackensen et al, 1995; Schmiedl, 1995; Fariduddin & Loubere, 1997; Gupta, 1999; Altenbach et al., 2003). Because both factors are interrelated, *Uvigerina* species are used as indicators of carbon rich and oxygen poor conditions (Sen Gupta & Machain-Castillo, 1993; Kaiho, 1994; Thomas & Gooday, 1996; Schmiedl & Mackensen, 1997; De Rijk et al., 2000; Van der Zwaan et al., 1999; Hess & Kuhnt, 2005; Kawagata et al., 2006). Another useful role is played by *U.*

5) This phenomenon is described through the TROX model (Jorissen et al., 1995).

peregrina in stable isotope studies (Rathburn et al., 1996; Tachikawa & Elderfield, 2002; Schmiedl et al., 2004; Fontanier et al., 2006). The assumption is that the species precipitates its test close to equilibrium with sea water (Shackleton, 1974, Woodruff et al., 1980; Hendy & Kennett, 2000; but see Dunbar & Wefer, 1984; Wilson-Finelli et al., 1998), and that it reflects the local pore water $\delta^{13}C$ (McCorkle et al., 1990, 1997; Schmiedl et al., 2004).

Uvigerinids are usually found in fine grained sediments (Van der Zwaan et al., 1986a). Because the high carbon level is correlated with lower oxygen concentrations, uvigerinids tolerate oxygen depletion better than cibicidids (Van der Zwaan et al., 1999). Some species are opportunistic and can adapt to quick changes as algal blooms: e.g. *U. peregrina* and *U. mediterranea* (Verhallen, 1991; De Stigter et al., 1998; Jorissen, 2002; Fontanier et al., 2003a, 2006). Abundance of *Uvigerina* species has also been correlated with glacial periods in the late Cenozoic (Schnitker, 1974; Lutze, 1977; Streeter & Shackleton, 1979; Gupta & Srinivasan, 1990). The hispid taxa,

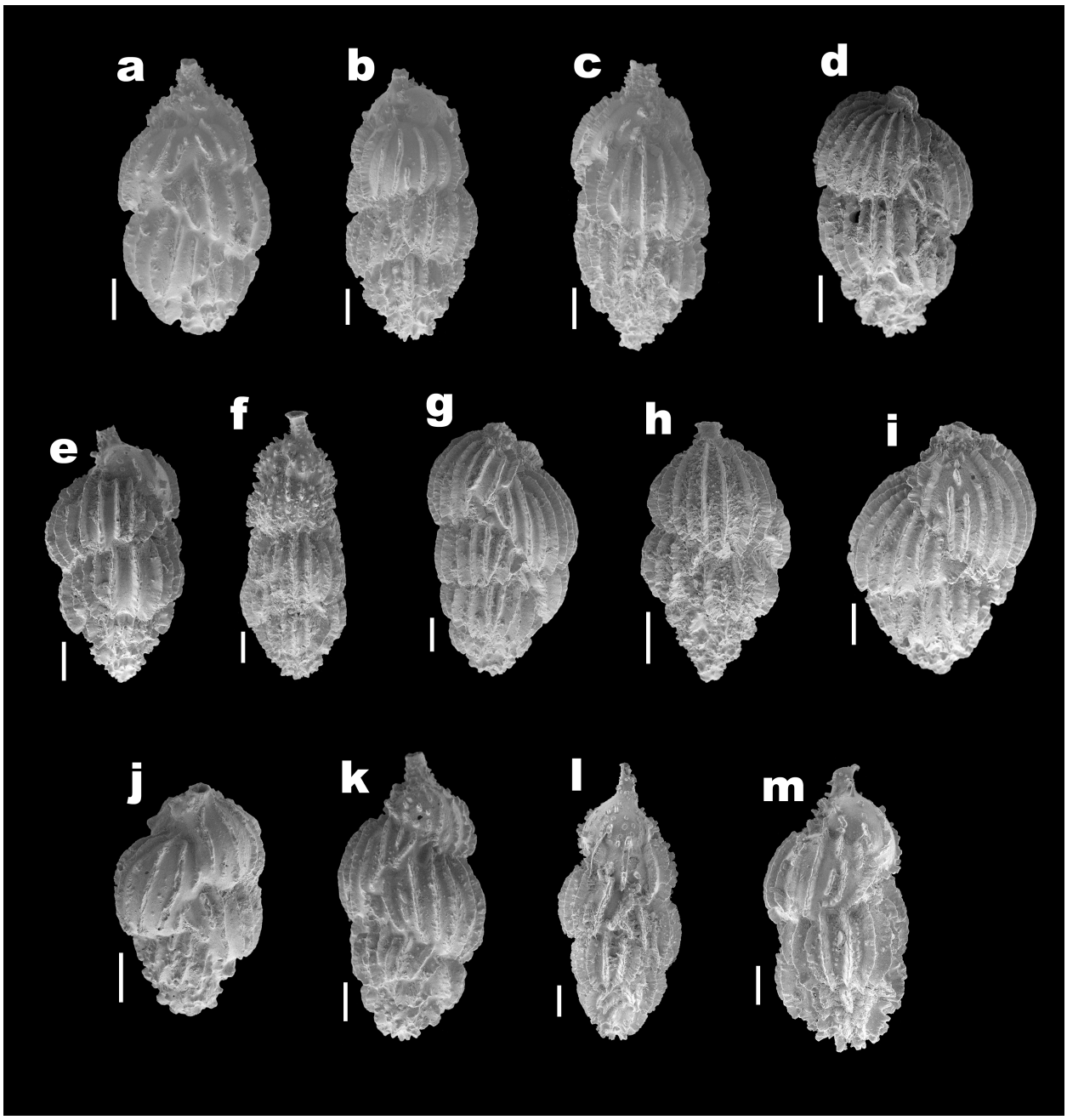

Figure 6.7. Hispid *U. peregrina* coming from deep sites in the Atlantic: (a-d) Bay of Biscay, 3000m, (e-m) Finisterre (Spain), 2122m. Scale= 100μm

however, are restricted to subtropical and tropical associations (Van der Zwaan et al., 1986a); therefore *U. proboscidea*, for instance, is less common during the glacial maxima (Almogi-Labin et al., 2000).

6.3.2. Bathymetry and paleobathymetry

As discussed previously (see 5.3.2.), the bathymetric distribution of benthic foraminifers is not static: species may have shifted their bathymetric range through time and this range may differ between different regions.

Besides *U. peregrina*, which has a wide bathymetric range, three different bathymetric groups were recognized in the studied species (Fig. 6.8).

Typical neritic species include *U. bononiensis* (Colom, 1952; Lutze, 1980; Lutze, 1986; Schiebel, 1992) and *U. phlegeri* (Pujos, 1972; Haake, 1980; Lutze, 1980; Blanc-Vernet et al., 1984; Lutze, 1986; Schiebel, 1992; Sgarrella & Moncharmont Zei, 1993; De Rijk et al., 2000; Fontanier et al., 2002; Altenbach et al., 2003).

Other species occupy the outer neritic to middle bathyal range: *U. cylindrica* (Haake, 1980; Lutze, 1980; Lutze, 1986; Schiebel, 1992; Altenbach et al., 2003), *U. earlandi* (Mackensen, 1992), *U. elongatastriata* (Blanc-Vernet et al., 1984; Fontanier et al., 2002; Schönfeld, 2002; Altenbach et al., 2003), *U. mediterranea* (Van Morkhoven et al., 1986; Hasegawa, 1990; Sgarrella & Moncharmont Zei, 1993; De Stigter et al., 1998; De Rijk et al., 2000; Morigi et al., 2001; Fontanier et al. 2002).

The bathyal and abyssal zones are colonized by the spinose species. *Uvigerina auberiana* lives below 200m (Bandy & Chierici, 1966; Blanc-Vernet et al., 1984; Schiebel, 1992; Sgarrella & Moncharmont Zei, 1993) and above 2500m (Resig & Cheong, 1997) or 4500m (Harloff & Mackensen, 1997). *Uvigerina proboscidea* was recorded between 300 and 3300m (Van Marle, 1988; Rathburn & Corliss, 1994; Rathburn et al., 1996; Harloff & Makcensen, 1997; Fontanier et

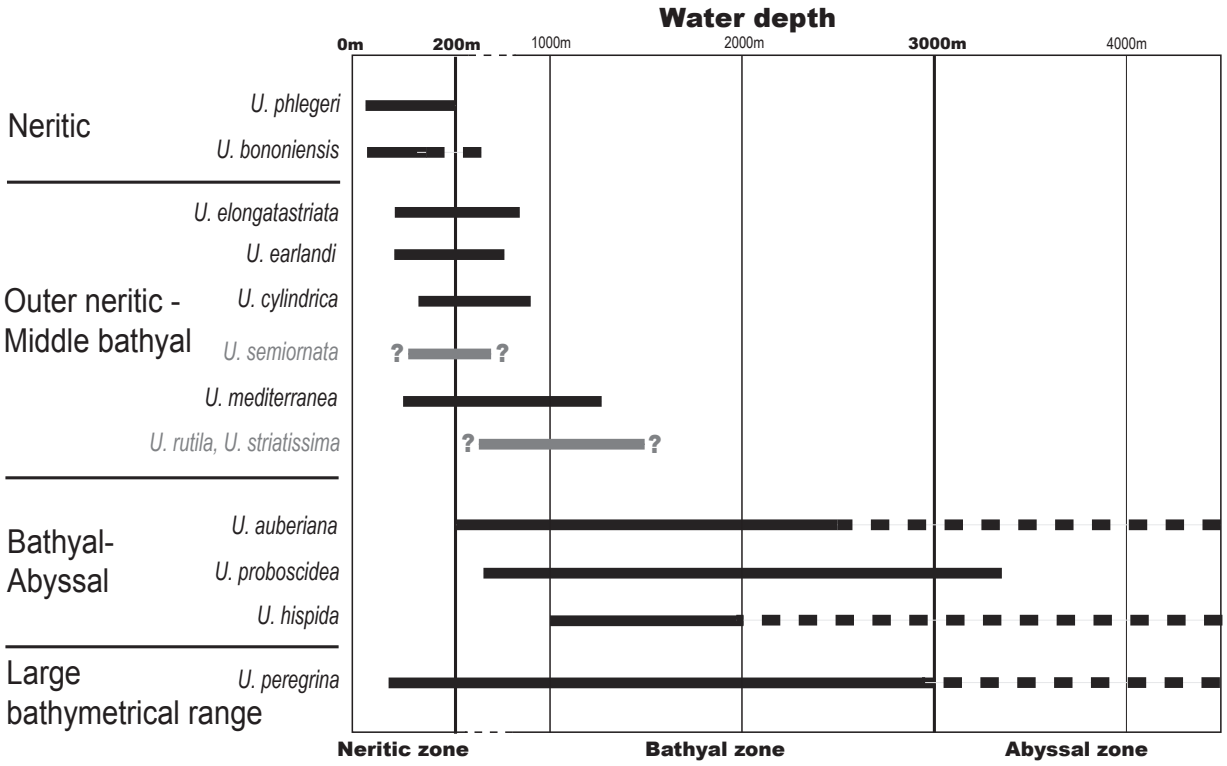

Figure 6.8. Indication of the water depth at which live the 13 studied uvigerinids, from the neritic zone (0-200m), the bathyal zone (200-3000m) and the abyssal zone (>3000m). Dashing lines represent depths were the species are less abundant and less typical, grey lines and question marks represent paleoreconstructions deduced for extinct species.

al., 2002). *Uvigerina hispida* usually has an upper depth limit of 1000m (Bandy & Chierci, 1966; Van Marle, 1988; Sen Gupta & Machain-Castillo, 1993) and was observed up to 4800m (Harloff & Mackensen, 1997).
Finally, *U. peregrina* (with the broad species concept discussed previously) shows a wide depth range from the neritic to the abyssal zone (Bandy & Chierici, 1966; Lutze & Coulbourn, 1984; Lutze, 1986; Van Leeuwen, 1986; Van Marle, 1988; Timm, 1992; Harloff & Mackensen, 1997; Altenbach et al., 1999, 2003; Morigi et al., 2001; Fontanier et al., 2002; Hayward et al., 2002; Schönfeld & Altenbach, 2005).
Bandy (1960) first observed that *Uvigerina* tends to increase its size and its ornamentation with increasing water depth. A shift from costate to spinose ornamentations was often noticed (Smith, 1964; Frerichs, 1970; Grünig, 1977; Boersma, 1984, 1990) and interpreted as a morphocline within *U. peregrina* (Theyer, 1971; Pflum & Frerichs, 1976; Lutze, 1986; Van Leeuwen, 1986). However, the depth succession observed with *U. peregrina parva*, *U. peregrina* and *U. pygmaea*, is rather interpreted as a succession of subspecies or species than a morphocline by Schönfeld & Altenbach (2005). In our material, *U. peregrina* from the Skagerrak are costate (Fig. 6.6), while specimens from deeper locations are more spinose (Fig. 6.7). Other species such as *U. mediterranea* (Borsetti et al., 1986) or *U. eocaena* (Grünig, 1984), a fossil species, present a reduction of the number or the height of the costae with increasing water depth. A series with *U. asperula*, *U. auberiana* and *U. ampullacea* was also interpreted as a bathymetrically controlled morphocline (Berggren et al., 1976).
Paleoenvironmental reconstructions indicate a shelf to upper bathyal habitat for *U. semiornata* and a upper to middle bathyal one for *U. rutila* and *U. striatissima* (Boersma, 1984; Cicha et al., 1986; Kouwenhoven, 2000). Bathymetrical preferences of species are not fixed through time: *U. hispida* has expanded its depth range through late Neogene (Boersma 1984) and a change in depth preference has also been observed for *U. peregrina* (Van der Zwaan, 1982).

6.3.3. Microhabitat

Uvigerinids are usually considered to be infaunal species (Fig. 6.9). Many species are shallow infaunal or even live close to the sediment-water interface: *U. proboscidea, U. auberiana, U. hispida, U. phlegeri, U. mediterranea* and *U. peregrina* (Corliss & Emerson, 1990; Nishi, 1992; Rathburn & Corliss, 1994; Rathburn et al., 1996; Schmiedl et al., 2000; Morigi et al., 2001; Tachikawa & Elderfield, 2002; Fontanier et al., 2002, 2003a, 2006; Licari et al., 2003). These shallow infaunal taxa are sometimes found deeper in the sediment in connection with burrows (McCorkle et al., 1997; Schmiedl et al., 2004). Detailed studies of the microhabitat have shown that *U. mediterranea* and *U. peregrina*, roughly living at the same sediment depth, developed in fact slightly differentiated niches: *U. peregrina* lives usually deeper in the sediment (Fontanier et al., 2002). Gary & Healy-Williams (1988) noticed that the chamber lobateness is reduced in *U. mediterranea* individuals from the lower boundary of the oxygen minimum zone. Morphological differences between *U. peregrina* living at different depths were also observed (Loubere et al., 1995); moreover, smaller specimens were found at greater sediment depths than larger ones. The same was observed for *C. pachyderma* and *C. kullenbergi* (Rathburn & Corliss, 1994, see 5.3.3.), indicating that juveniles are living deeper, perhaps to avoid predation. Shallow infaunal uvigerinids are usually found in high productivity areas and can tolerate low oxygen conditions generated by elevated carbon concentrations (Van der Zwaan et al., 1999). However, they do not live in anoxic environments (Loubere et al., 1995; Gupta & Srinivasan, 1992a; Schmiedl et al., 2000; Fontanier et al., 2002; Casford et al., 2003). Under particular conditions, such as coarse sediment, uvigerinids are able to live in elevated habitats; for instance, *U. vadescens* was observed climbing on top of a polychaete tube and extruding its pseudopodia in water (Kitazato, 1994).
Uvigerina elongatastriata lives deeper in the sediment and is considered as intermediate infauna (Fontanier et al., 2002, 2003a, 2006). Consequently, this species is also more tolerant to oxygen

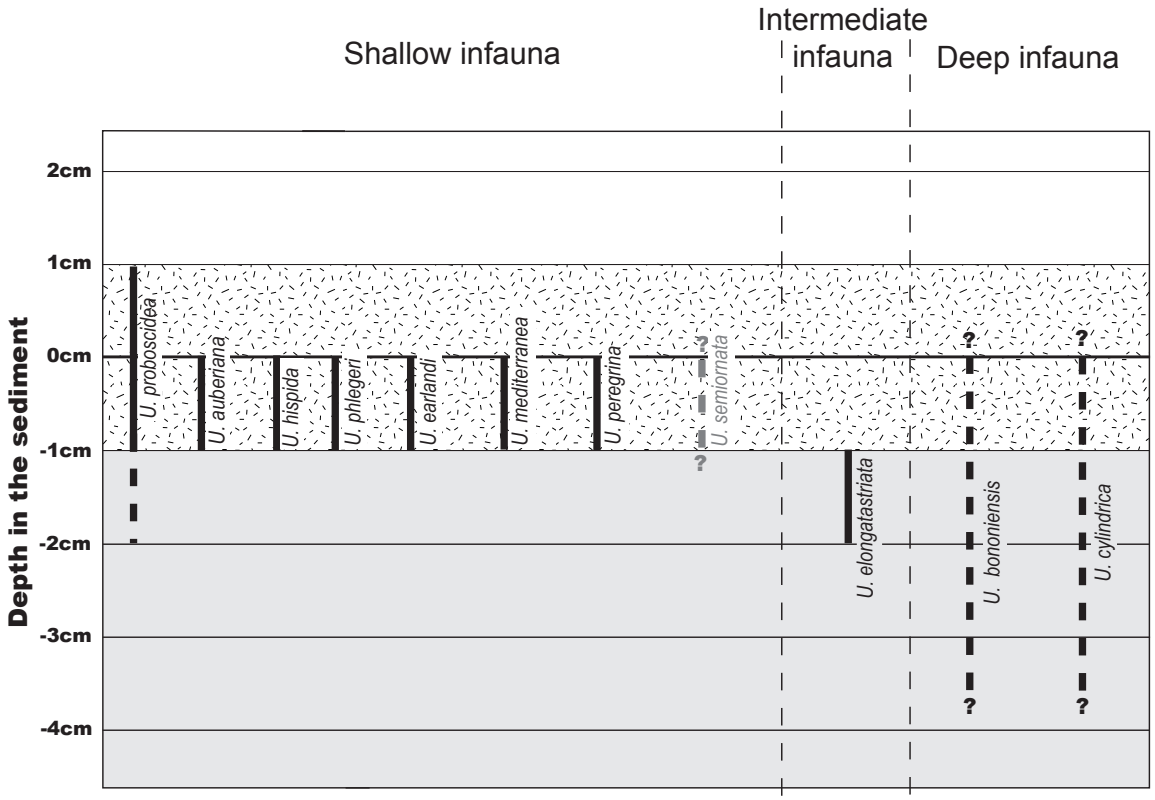

Figure 6.9. Indication of the sediment depth at which are living the 13 different species. Between +1 and -1cm, the sediment layer interface is not clear ("fluffy" layer represented by confetti). Dashing lines represent depths were the species are rarely found or are supposed to live; question marks mean that the microhabitat is not well known. Grey lines represent paleoreconstructions deduced for extinct species.

depletion than the shallow infaunal taxa[6] and replaces *U. peregrina* below 500m in high productivity areas, for instance dominated by river discharge (Lutze, 1986). Fossil reconstructions deduced a sediment-water interface habitat for *U. semiornata* (Van der Zwaan et al., 1999).
Another species found in high productivity areas and tolerant to extremely low oxygen content is *U. cylindrica* (Van der Zwaan, 1982; Lutze, 1986; Altenbach et al., 2003). In paleoenvironmental reconstructions, *U. bononiensis* is also associated with high environmental stress and decreasing oxygen (Jonkers, 1984; Seidenkrantz et al., 2000). These stress tolerant species are supposed to live deeper in the sediment under normal conditions (Van der Zwaan et al., 1999). The slender shape caused by the uniserial coiling could be interpreted as an adaptation to deeper burrowing, because smooth and slender tests are supposed to be more functional for infaunal taxa (Corliss, 1985, 1991; Corliss & Chen, 1988), but it has never been confirmed by ecological studies (Van der Zwaan et al., 1999). Moreover, *U. phlegeri* is shallow infaunal in spite of its uniserial coil.

6.4. Phylogeny of *Uvigerina*

6.4.1. The fossil record of *Uvigerina*

Uvigerinids have been used as biostratigraphic markers (e.g. Lamb, 1964; Hornibrook, 1968; Papp & Schmid, 1971) and several works focusing exclusively on uvigerinids have been published (e.g. Vella, 1961; Meulenkamp, 1969; Thomas, 1980; Boersma, 1984; Lamb & Miller, 1984; Van der Zwaan et al., 1986b). For these reasons, much more information is available on the fossil record of uvigerinids than cibicidids. The abundance of data, however, tends to create rather than solve confusion, particularly with the profusion of species names used to label slightly different

6) This species is a good indicator of the present oxygen minimum off northwest Africa (Lutze & Coulbourn, 1984).

forms. Some work has already been done to synonymize redundant names (e.g. Boersma, 1984; Jonkers, 1984; Belanger & Berggren, 1986; Van der Zwaan et al., 1986; Van Morkhoven et al., 1986; Verhallen, 1991), and the fossil pattern inferred from the literature is rather consistent (Fig. 6.10).

Depending on taxonomic concept, *U. peregrina* is inferred to be a fairly recent species when a narrow definition is used (middle Miocene (Agip, 1982; Borsetti et al., 1986) or Pliocene (Boersma, 1984)), whereas broader taxonomic concepts place it in the late (Boltovsoky, 1978) or early (Mackensen & Berggren, 1992; Miller et al., 1992) Oligocene, and even the late Eocene (Schröder-Adams, 1991). The early Oligocene seems the most likely, because this period also records the first occurrence of *U. pygmaea* (Boersma, 1984), which is sometimes considered as a synonym of *U. peregrina* (see above). The hispid species *U. proboscidea* appeared during the early (Nomura, 1991a) or more probably late (Boltovskoy, 1978; 1980; Boersma, 1990; Katz & Miller, 1993) Oligocene; however, the lineage may be tracked back to the Eocene with *U. gracilis*,

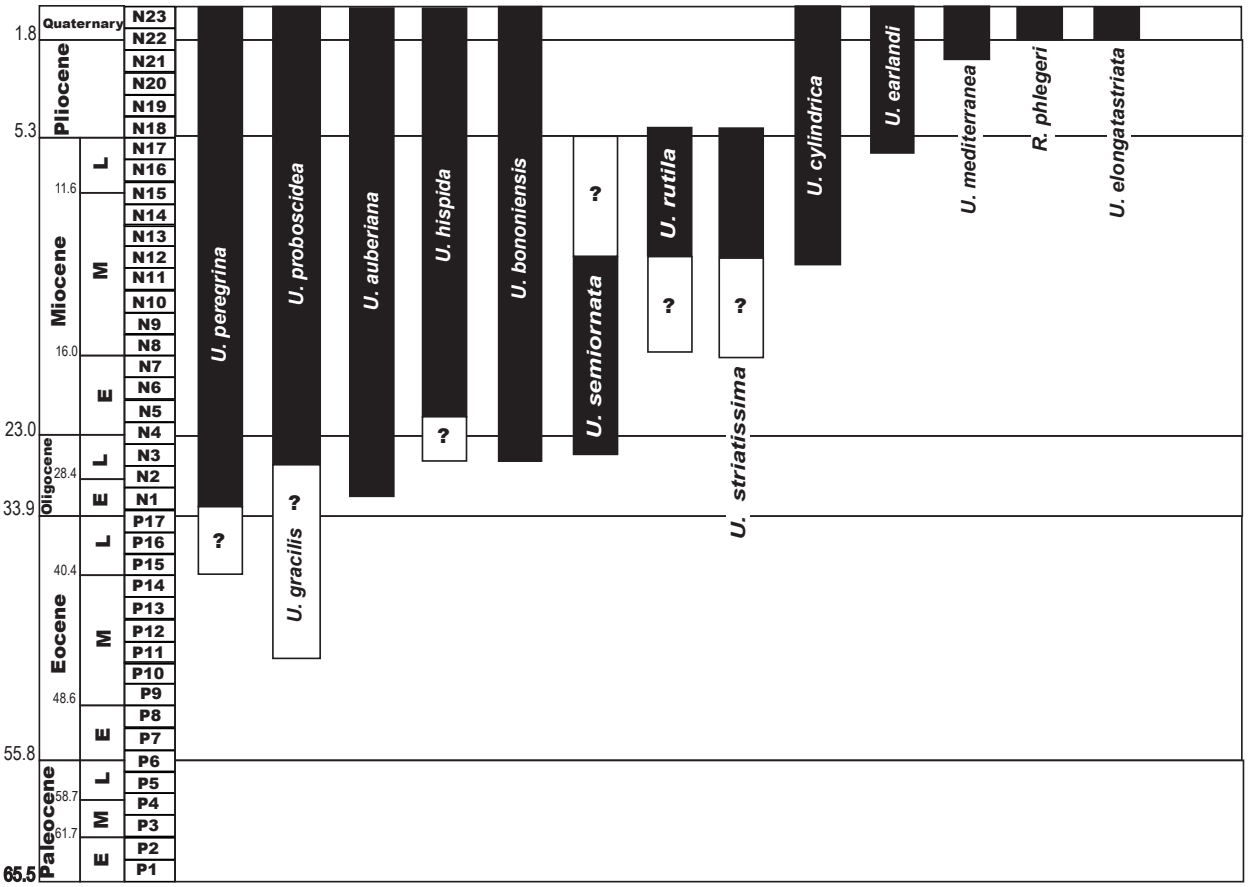

Figure 6.10. Fossil record of the 13 studied uvigerinids. Black rectangles represent well established observations, whereas white ones with question marks are less sure.

a possible ancestor (Borsetti et al., 1986). *Uvigerina auberiana* first occurred in the early (Agip, 1982) or middle (Boersma, 1984; Hermelin, 1989; Boersma, 1990) Oligocene.

Uvigerina hispida possibly appeared in the late Oligocene (Katz & Miller, 1993), or during the early (Lutze, 1977; Van Morkhoven et al., 1986) or middle (Boersma, 1984; Borsetti et al., 1986) Miocene. *Uvigerina bononiensis* first occurred in the late Oligocene (Cicha et al., 1986) or the early Miocene (Agip, 1982). The Oligocene-Miocene boundary is the time of appearance of *U. semiornata* (Boersma, 1984; Borsetti et al., 1986). This species disappeared during the Late Miocene (Boersma, 1984) or gave rise to *U. rutila* in the Serravallian (Borsetti et al., 1986). *Uvigerina striatissima* originated at the same time as *U. rutila*: Langhian (Agip, 1982; Boersma, 1984) or Serravallian (Borsetti et al., 1986). Both disappeared in the early Pliocene (Boersma,

1984; Borsetti et al., 1986).
During the Miocene, *U. cylindrica* (Serravallian: Meulenkamp, 1969; Thomas, 1980; Borsetti et al., 1986) and *U. earlandi* (latest Miocene: Mackensen, 1992) appeared.
The three last species have a really recent record: from the Late Pliocene for *U. mediterranea* (Agip, 1982; Boersma, 1984; Van Morkhoven et al., 1986) and the Quaternary for *U. phlegeri* (Borsetti et al., 1986) and certainly *U. elongatastriata*.

6.4.2. Inferred phylogeny of *Uvigerina*

The three morphological groups defined previously (Van der Zwaan et al., 1986a) were supposed to reflect the natural classification of uvigerinids. Molecular results confirmed the existence of the *semiornata* and *peregrina* groups (see Chapter 4). The only representative of the *bononiensis* group (*U. phlegeri*) clustered close to the *peregrina* group (Fig. 4.8). This would mean that the tendency to uniseriality, which is one of the criteria to distinguish the *bononiensis* group, is not taxonomically discriminating. This statement is confirmed by the fact that *U. auberiana* and *U. proboscidea* show a tendency to biserial or uniserial coiling (e.g. Cushman, 1923, 1933; Borsetti et al., 1986; Van Morkhoven et al., 1986; Van Leeuwen, 1986). However, *U. phlegeri* is morphologically rather close to *U. bononiensis* (Lutze, 1986) and *U. cylindrica* (Borsetti et al., 1986). An alternative solution could be that *U. phlegeri* is in fact belonging to the *peregrina* group, and therefore, no member of the third group was represented in the molecular analyses. Both hypotheses are represented in the supposed phylogeny (Fig. 6.11).
Inside the *semiornata* group, *Uvigerina semiornata* is the oldest taxon (Fig. 6.10). *U. rutila* and *U. striatissima* probably originated from this species during the middle Miocene, considering the fossil record and the morphological proximity of the three species (Fig. 6.11a). Alternatively, these morphospecies are sufficiently close to suppose they belong to the same clade (Fig. 6.11b). The two recent taxa *U. elongatastriata* and *U. mediterranea* group together in the molecular analyses (Fig. 4.8). Lutze (1986) assumed that *U. semiornata* was the ancestor of *U. elongatastriata*. Therefore, the clade *semiornata-rutila-striatissima* certainly belongs to the same lineage as *elongatastriata-mediterranea*, in spite of the gap observed in the record during the Pliocene (Fig. 6.10).
Inside the *peregrina* group, *U. peregrina* is the oldest species, except if the succession *U. gracilis-U. proboscidea* is accepted (Borsetti et al., 1986). If *U. proboscidea* is the oldest species, *U. auberiana*, *U. hispida* could have originated from it, whereas *U. peregrina, U. earlandi* and *U. phlegeri* could belong to a sister-group (Fig. 6.11a). In the other case (Fig. 6.11b), *U. peregrina* would have appeared at the end of the Eocene or the early Oligocene and given rise to the hispid species: *U. auberiana*, *U. proboscidea* and *U. hispida*. This order reflects the fossil record and the bathymetry (Figs. 6.7 and 6.9). These species share some morphological characteristics, among which a spinose ornamentation[7]. Moreover, morphological intermediates were observed between *U. peregrina* and *U. proboscidea* (Belanger & Berggren, 1986; Verhallen, 1991) or *U. hispida* (Van Leeuwen, 1986). Nevertheless, *U. hispida* could belong to the *semiornata* group (Van der Zwaan, pers. comm.).
The *bononiensis* group either separated early from the *peregrina* group (Fig. 6.11a) or is a sister-group of *U. earlandi* and includes *U. phlegeri* (Fig. 6.11b). *Uvigerina bononiensis*, the older species of this group, was designated as the ancestor of *U. cylindrica* (Meulenkamp, 1969; Thomas, 1980). *Uvigerina phlegeri* is supposed to be closer to *U. bononiensis* (Lutze, 1986) or to *U. cylindrica*, because the test is not compressed as in *U. bononiensis* (Borsetti et al., 1986; Barbieri, 1998). A morphological link between *Rectuvigerina multicostata* and *U. phlegeri* is also observed (Barbieri, 1998).

7) Even the costae of *U. peregrina* are built of spines (Fontanier et al., 2002), as can be observed with hispido–costate forms (Fig. 6.7 for instance).

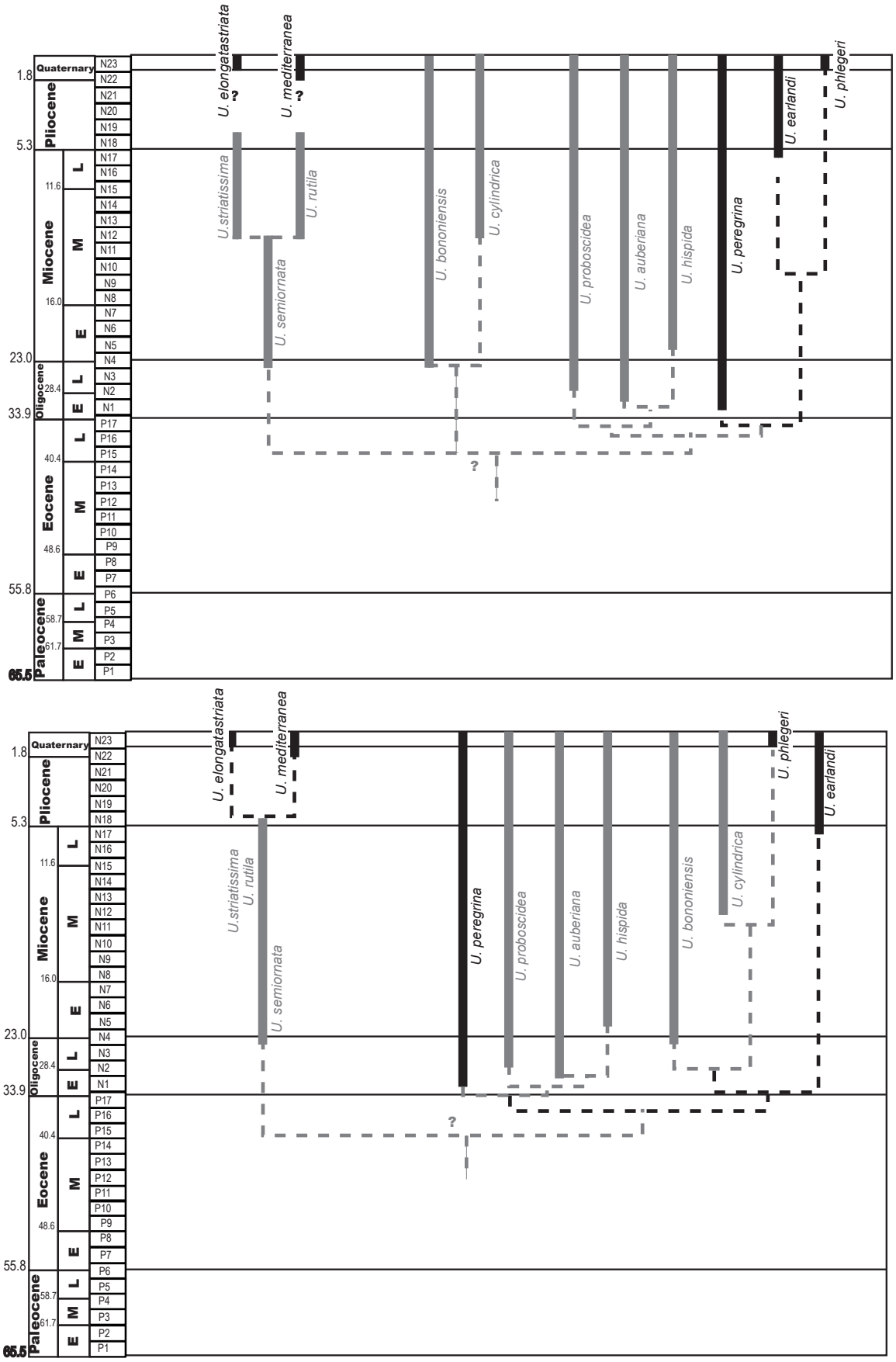

Figure 6.11. Supposed phylogeny of the 13 studied uvigerinids inferred from the molecular analyses and the fossil record. Black lines represent species which gave DNA results, whereas grey lines represent species with no DNA data.

6.5. Summary

In spite of some attempts to split the genus up (see 6.2.2.), uvigerinids are mainly classified in *Uvigerina*. The uniserial species have often been grouped under the name *Rectuvigerina*, whereas the ones with a triangular cross-section were included in *Trifarina*. However, molecular analyses have shown that these criteria were not adequate for the attribution to different genera. Further investigations are needed to check if all the representatives of *Rectuvigerina* and *Trifarina* belong in fact to *Uvigerina* or if these genera are monophyletic.

A more natural classification of uvigerinids was proposed (Van der Zwaan et al., 1986a), which grouped the different species in three different units: the *semiornata* group, the *peregrina* group and the *bononiensis* group (6.2.1.). Molecular results have confirmed the existence of the two first groups, while one representative of the third clade was included in the second one. Therefore, two possibilities exist: the *bononiensis* group is either closer to the *peregrina* than to the *semiornata* group, or *U. phlegeri* belongs in fact to the *peregrina* group, and no member of the third group was represented in the molecular analyses. DNA analyses of *U. bononiensis* or *U. cylindrica* would allow deciding.

Among the studied uvigerinids, several species are rather typical and easy to recognize (*U. bononiensis, U. cylindrica, U. elongatastriata, U. phlegeri*). The others form well distinguished (possibly taxonomical) units where the members are difficult to recognize (*U. semiornata-U. rutila-U. striatissima* and *U. auberiana-U. proboscidea-U. hispida*) or belong to two distinct groups (*U. peregrina* and *U. mediterranea*).

The literature reflects these problems. Additionally, many names were attributed to different morphotypes, which actually belong to *U. peregrina*. Successive monographs (Thomas, 1980; Boersma, 1984; Van der Zwaan et al., 1986b) allowed reducing the number of names by synonymizing many of them, and synthesized the knowledge about this genus.

The uvigerinids colonized a wide range of environments; they are present from the neritic to the abyssal zone. Most of them are shallow infaunal, but some species can be found deeper in the sediment, and are, therefore, more tolerant to oxygen depletion (e.g. *U. bononiensis, U. cylindrica* or *U. elongatastriata*).

The fossil record of the studied species starts in the Eocene. Other radiations apparently occur during the middle Miocene and at the end of the Pliocene. By the end of the Eocene *Uvigerina* became important in bathyal environments (Douglas & Woodruff, 1981). Uvigerinids probably invaded the deep sea from a neritic habitat (Miller et al., 1992). Among them, the *semiornata* group – with neritic-bathyal and shallow infaunal representatives – is the less specialized and perhaps the most primitive group. *Uvigerina peregrina* is the oldest and the less specialized member of the second group. It could have given rise to taxa preferring to live in deeper waters during the Oligocene (the hispid group), after new ecological niches have opened in the deep ocean with the appearance of the psychrosphere at the end of the Eocene (Schnitker, 1980; Douglas & Woodruff, 1981). Inside the *bononiensis* group, species stayed in the neritic-upper bathyal zone, but explored extreme environments deeper in the sediment. *Uvigerina bononiensis* appeared at the end of the Oligocene, and *U. cylindrica* during the middle Miocene, when new stressful conditions arose at the time of establishment of the modern ocean water circulation, decrease of temperature (Douglas & Woodruff, 1981) and possibly subsequent increase of ocean bioproduction. A last wave of radiations occurred at the end of the Pliocene with the appearance of *U. phlegeri*, *U. mediterranea* and *U. elongatastriata* at the time of onset of northern hemisphere glaciations (Douglas & Woodruff, 1981).

Chapter 7
General conclusions

7.1. Introduction and summary

The aim of this thesis was to study the evolution and molecular phylogeny of two benthic foraminiferal genera: *Cibicides* and *Uvigerina*. In order to assess their position among the Rotaliida, sequences of other rotaliid taxa were also considered. Important results obtained concern the molecular phylogeny of the rotaliids and the position of *Cibides* and *Uvigerina* in the phylogenetic tree. Based on SSU rDNA sequences a partition of Rotaliida in three groups was found. Furthermore, based on our results, the subdivision Buliminida-Rotaliida, proposed earlier by several authors within the group of hyaline foraminifers seems highly unlikely. Cryptic speciation, earlier established for planktonic foraminifers and shallow-water benthic foraminifers, is suspected to occur also in the group of foraminifers studied here.

As expected, many generic names appeared to be redundant. There are strong indications that the cibicidids are monophyletic; among the cibicidids, it was shown that *Cibicidoides*, *Fontbotia* and *Lobatula* are synonymous with *Cibicides*. On the other hand, *Cibicides lobatulus* and *C. refulgens* are distinct species. Within the uvigerinids, *Trifarina* and *Rectuvigerina* are at least partly subsumed in *Uvigerina*. *Uvigerina mediterranea* and *U. peregrina* are distinct species, whereas *U. akitaensis* is synonymous with *U. peregrina*.

Links were investigated between morphospecies and genetic species, and the validity of morphology-based taxonomy was partially checked against molecular data. These new results allowed better insight in the molecular phylogeny, the diversity and evolutionary rates of deeper water foraminifers.

There are many points which still need further investigation before they can be solved. For instance, the presence of ecophenotypes was suspected for *Uvigerina peregrina* from the Oslo Fjord, but the precise influence of ecological parameters has yet to be established. A reverse problem occurred with cryptic species, for which we failed to identify means for morphological distinction. A second area where we need much more information concerns the paleontological background. We need more detailed descriptions including proper pictures for species of which the species concept was not clear (as *Cibicides kullenbergi* or *C. pseudoungerianus*). The same confusion in the literature concerning species-concept often leads to a diffuse picture of the geological ranges of the taxa involved. Also for this we need more, and more precise, data to unravel the detailed phylogenies and rates of evolution.

7.2. Classification of the rotaliids

The molecular phylogeny of the SSU rDNA indicates a partition of the Rotaliida in three clades (see Chapter 2). The first group represents all the sampled uvigerinids and cassidulinids, *Bolivina* and possibly *Globobulimina* (a sequence of the complete SSU is needed to confirm its position). The second group includes *Discorbis, Rosalina*, all the Planorbulinacea except the cibicidids, the Nummulitidae, the Calcarinidae and the Rotaliidae. The third group represents the Nonionacea, *Chilostomella, Epistominella, Cibicides* and a part of the Buliminida (*Bulimina, Stainforthia, Virgulina, Virgulinella*). This polyphyly (some Buliminida in the first group and others in the third group) contradicts the separation of Buliminida and Rotaliida (Haynes, 1981; Loeblich & Tappan, 1992; Sen Gupta, 2002). Some of the morphologically defined taxa (mainly families) are supported by the SSU phylogeny, such as the Rotaliacea, the Uvigerinidae, the Cassidulinidae, the Glabratellidae, the Cibicididae, the Nummulitidae or the Calcarinidae. Moreover, all the sampled genera appeared monophyletic, usually on the basis of the 3' end fragment (see Chapter 2) and with the addition of the 5' end fragment for *Cibicides* (see Chapter 3), except *Epistominella*. On the other hand, some morphology-based orders and families are polyphyletic: the Nonionidae, the Planorbulinacea, the Discorbacea, the Buliminacea and the Buliminidae. These latter polyphylies (Buliminacea and Buliminidae) are surprising because the placement of *Bulimina* together with *Globobulimina* (in the Buliminidae) and *Uvigerina* (in the Buliminacea) has been constant through many morphology-based classifications (Galloway, 1933; Cushman, 1959; Loeblich & Tappan, 1964, 1988). Moreover, *Bulimina* was supposed to be the ancestor of *Uvigerina* because its

loop-shaped aperture is found in young stages of uvigerinids (e.g. Galloway, 1933; Cushman, 1959; Haynes, 1981). To check to what extent the molecular phylogeny is really in contradiction with the morphological one, analyses of other genes which are less subject to evolutionary rate heterogeneity are indispensable.

7.3. Taxonomic status of *Cibicides* and *Uvigerina*

Molecular analyses showed that cibicidids and uvigerinids – which are classified under several names in traditional classifications (e.g. Loeblich & Tappan, 1964, 1988) – are monophyletic and that some other generic names can be put in synonymy with them or suspected to be synonyms. Due to the (unjustified) separation on the basis of the wall structure and taxonomical splitting, too many generic names have been introduced for rotaliids. Besides the synonyms of *Cibicides* (see Chapter 5) or *Uvigerina* (see Chapter 6), for instance some redundancy can be suspected within *Brizalina-Bolivina* and *Stainforthia-Fursenkoina*. Further molecular studies and a better knowledge of ecology will help to recognize these redundant genera.

7.3.1. *Cibicides*

The cibicidids have been classified under many different generic names (see Chapters 3 and 5). However, molecular analyses of the small subunit of ribosomal DNA (SSU rDNA) have shown that this group is monophyletic and that *Fontbotia*, *Lobatula* and *Cibicidoides* can be therefore considered junior synonyms of *Cibicides*, as already stated by several authors (Galloway & Wissler, 1927; Sen Gupta, 1989). Molecular results and earlier studies based on morphology have demonstrated that the crystallographic structure of the wall is not taxonomically relevant. Therefore, and in agreement with Galloway & Wissler (1927), the genus *Heterolepa* can be also considered as a junior synonym of *Cibicides*. The six cibicidids for which we could obtain DNA form three different groups in the molecular analyses (Figs. 3.4-3.5). However, we think it is premature to separate them into three different genera; additional samples and taxa are needed to investigate this. Given the preliminary evidence, the 11 species of cibicidids studied were kept under the generic name *Cibicides.* Candidates for a separate taxonomic status are certainly *C. robertsonianus* and *C. bradyi*, distinguished by their rounded periphery and their more infaunal microhabitat, and the extinct *C. italicus*, which also has a distinctive rounded periphery. The first species have been sometimes classified under the name *Parrelloides* (e.g. Belford, 1966; Sprovieri & Hasegawa, 1990; Loeblich & Tappan, 1994; Barbieri, 1998), whereas *C. italicus* resembles *C. velascoensis*, a Campanian-Paleocene species sometimes attributed to *Anomalina* or *Gavellina* (Van Morkhoven et al., 1986).

A clear distinction between *C. lobatulus* and *C. refulgens* was observed with the SSU rDNA, although these species are morphologically close. Within *C. refulgens*, important differences observed between populations from Antarctica and the Mediterranean lead us to consider them as cryptic species. Sampled populations of *C. lobatulus* were geographically less separated (Mediterranean and North Atlantic-Skagerrak), and showed smaller genetic divergence. However, in general these shallow water taxa seem to show a larger genetic variability than deep-sea taxa, such as *C. wuellerstorfi* (Pawlowski et al., in prep.).

On the other hand, DNA samples from Portugal showed that *C. pachyderma* and *C. kullenbergi* possibly are the same species. A similar morphology and the presence of morphological intermediates corroborated that result. However, DNA samples from typical *C. kullenbergi* are needed to confirm this inference, because the taxonomy of this species is not uniform and the species concept varies between authors. Similarly, the morphology of *C. bradyi* and *C. robertsonianus* made us suspect that they also belong to the same species (Chapter 5). Finally, relations between *C. ungerianus* and *C. pseudoungerianus* have to be investigated morphologically and molecularly to check if they are synonymous.

7.3.2. *Uvigerina*

Our molecular analyses have shown that species belonging to the genera *Trifarina* (*T. earlandi*) and *Rectuvigerina* (*R. phlegeri*) branch inside *Uvigerina* and are closer to *Uvigerina peregrina* than to *U. mediterranea* and *U. elongatastriata* (Chapter 4). One possibility would be to keep the name *Uvigerina* for the small species (*U. peregrina*, *T. earlandi* and *R. phlegeri*), because the type species of the genus is *U. pygmea*, a putative synonym of *U. peregrina*, and give another generic name to the large species (*U. mediterranea* and *U. elongatastriata*). Nevertheless, due to the morphological homogeneity of these species, it seems logical to keep all of them under the same generic name for the time being. Therefore, the description of the genus *Uvigerina* should be adapted such that it also includes species with a triangular section (*Trifarina*) and with a uniserial part (*Rectuvigerina*).

Three morphological groups have been defined within *Uvigerina* (Chapter 6). In the *semiornata* group, the connections between the modern species (*U. mediterranea* and *U. elongatastriata*) and the fossil ones (*U. semiornata*, *U. rutila* and *U. striatissima*) need to be further explored with the help of the fossil record. The status of the different fossil species is also questionable (one or more species?).

Uvigerina peregrina is thought to have a broad morphological variation. Therefore, many names were attributed to the different varieties at the specific (e.g. *akitaensis*, *bifurcata, hollicki, pygmea*) or subspecific level (e.g. *dirupta, parva*). DNA samples from the Skagerrak, the Bay of Biscay and the Pacific (*U. akitaensis*) demonstrated that the species is genetically really homogenous. On the other hand, *U. mediterranea* – which is sometimes considered a synonym of *U. peregrina* – is a truly different species as it is confirmed by molecular analyses. The small hispid species (*U. auberiana and U. proboscidea*[1]) are probably close to *U. peregrina* and *U. proboscidea* is perhaps a junior synonym of *U. auberiana*. For the moment, there are no molecular data available to confirm or reject these hypotheses.

Finally, the existence of the third morphological group needs to be confirmed. Our data show that one member of this group (*U. phlegeri*) should be included in the *peregrina* group. Further molecular data are needed, such as the sequencing of a *U. bononiensis* or other extant species of this group, to check if the complete group is subsumed in the *peregrina* group or if this only concerns *U. phlegeri*.

7.4. Presence of cryptic species

Until now, the most interesting molecular results for the community of micropaleontologists concern the discovery of cryptic molecular species inside the allogromiids (Pawlowski et al. 2002b, 2005), planktic foraminiferal morphospecies (Huber et al, 1997; Darling et al., 1999; de Vargas, 1999; 2001; 2002; Stewart et al., 2001), and shallow water benthic foraminifers such as *Ammonia* (Pawlowski et al., 1995; Holzmann & Pawlowski, 1997; 2000; Hayward et al., 2004) and *Planoglabratella* (Tsuchiya et al., 2000; 2003).

In the case of allogromiids, the lack of morphological criteria for the test explains the underestimation of morphospecies compared to genetic species (Pawlowski et al., 2002b). For *Ammonia* the status of morphospecies was not clear; to avoid taxonomical problems many authors decided to use one species name only (see Hayward et al., 2004 for a review). Within the hyaline benthic foraminifers studied here, the molecular results showed that several species could include cryptic species, but also that some morphospecies should be merged (*Melonis affinis* and *M. barleeanum*, and possibly *C. kullenbergi* and *C. pachyderma*). This last result can be explained by the huge amount of rotaliid species described. The exact number of described species is not known, but the rotaliids comprise 627 of the 3620 genera recognized by Loeblich & Tappan (1988), whereas the planktonic foraminifers include 129 genera. Estimates of the number of extant foraminiferal species give a total of 10,000 (Sen Gupta 2002 citing Vickman, 1992), of which an important amount belongs to rotaliids, whereas the number of extant planktonic foraminifers does not exceed 40-50 species (Sen Gupta, 2002).

1) The true *U. hispida* is more robust and thought to be related to the *semiornata* group (Van der Zwaan, pers. comm.).

7.5. Cosmopolitan species and geographical distribution

Among benthic foraminifers some species are widely distributed. An interesting question is to know whether these species are truly (morphologically and genetically) cosmopolitan. *Uvigerina peregrina* is one of these cosmopolitan benthic taxa for which DNA from distant locations was available. We have already seen that, in contrast to a wide morphological variation, the genetic variation was really low in the Skagerrak population. Sequences from the Bay of Biscay and the East and West Pacific (the latter identified as *U. akitaensis*, Ertan et al., 2004) take a position within the genetic variation of the Skagerrak population (Fig. 7.1). These results indicate that *U. peregrina* is a true cosmopolitan species. On a smaller geographical scale, *U. mediterranea* also shows close relationships between populations from the Mediterranean (Aegean Sea and Gulf of Lions) and the Atlantic (Bay of Biscay and Portugal) (Fig. 7.1). However, a more extensive geographical sampling is needed to check the homogeneity of *U. mediterranea*. Indeed, the Mediterranean and the Bay of Biscay samples belong genetically to the same populations for all the species we could obtain (Fig. 2.5: *Bolivina variabilis*, Fig. 2.7: *Chilostomella ovoidea*). Another genetically rather homogeneous species is *Chilostomella ovoidea* collected from different locations in the Pacific (Costa Rica, Oregon, Japan) (Fig. 2.7).

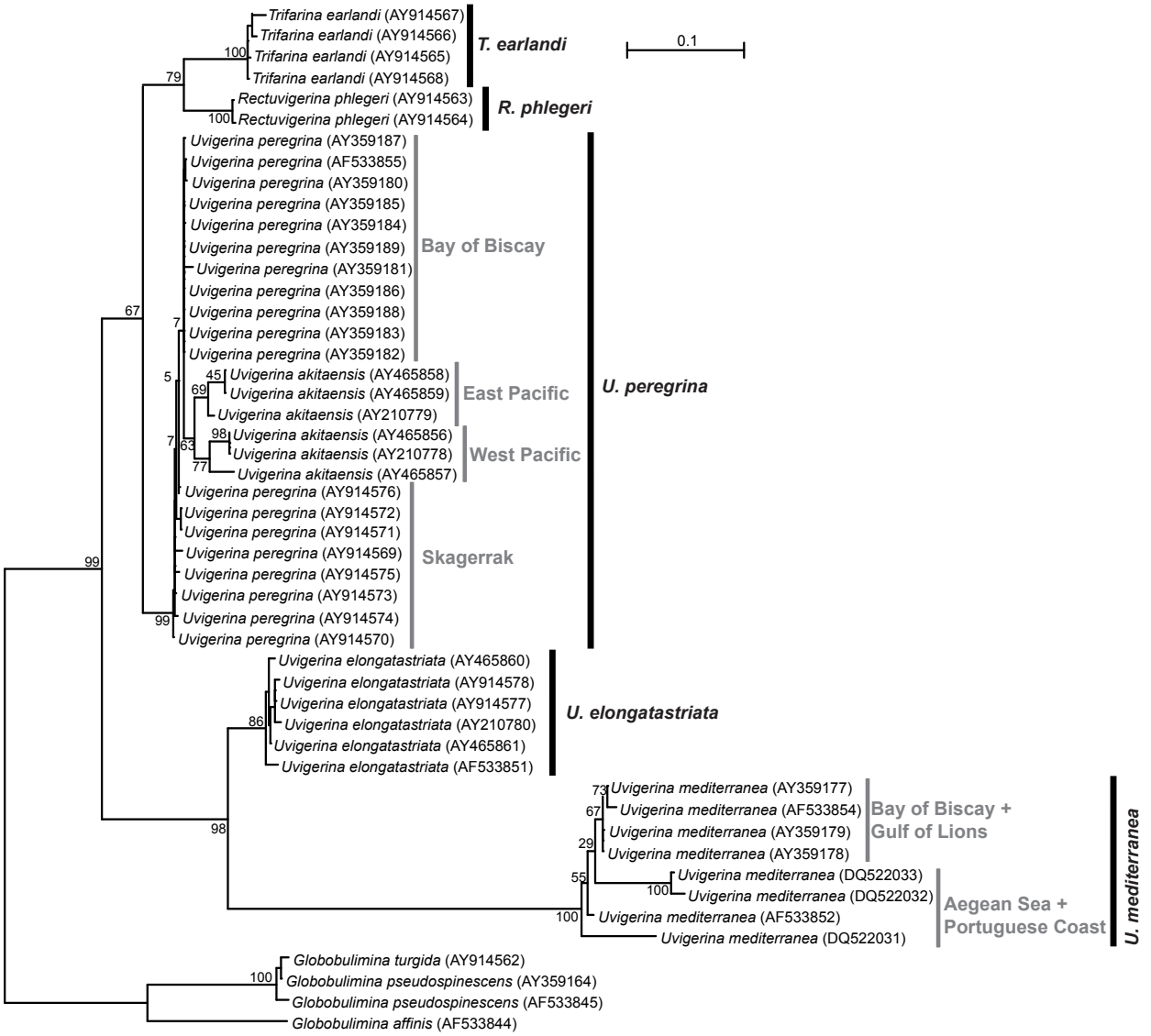

Figure 7.1. Phylogenetic tree of uvigerinids inferred from partial SSU sequences (3' end fragment) using the ML (HKY+I+G) method. Values of the bootstrap (100 replicates) are given at the nodes. DQ522031= U283, DQ522032= U285, DQ522033= U286.

Other morphospecies considered as cosmopolitan include cryptic molecular species. The case of *C. refulgens* is rather clear: two populations, which are morphologically close are well separated genetically. These species live in different locations (Mediterranean and Antarctica) and could have ecological differences such as feeding strategies. The same situation probably applies to *C. lobatulus* from the Mediterranean and the North Atlantic, although the genetic differences are smaller, certainly when correlated with the geographical distances. Molecular phylogenies also allowed identifying cryptic species occurring in assemblages sampled at the same site, such as *Bolivina variabilis* from Kenya and *Globobulimina pseudospinescens* from the Sea of Marmara (Fig. 2.5.), *Rosalina orbicularis* from the Red Sea (Fig. 2.6) and *Chilostomella ovoidea* from Costa Rica (Fig. 2.7). Therefore, the notion that polymorphism is common in species with broad biogeographical ranges (Douglas & Woodruff, 1981) does not always prove correct.

7.6. Evolution in relation to large scale geography

Although evolutionary theory contains many divergent views, a rather widely accepted assumption is that evolution proceeds most rapidly in variable environments. In this sense, the shallow marine zone would be the place where rapid evolution is likely to occur, as opposed to the deep sea where due to stable conditions evolution is supposed to proceed much slower (Parker 1964). Molecular data obtained from deep-sea species showed a great homogeneity between samples from different locations, e.g. *Cibicides wuellerstorfi* (Pawlowski et al., in prep.). By comparison *Cibicides* from shallow water depths (*C. refulgens* and *C. lobatulus*) present well separated populations, certainly cryptic species in the case of *C. refulgens* from Antarctica and the Mediterranean, and probably for *C. lobatulus* from the Mediterranean and North Atlantic-Skagerrak. On the other hand, *C. lobatulus* from the Skagerrak and the North Atlantic belong to the same population, which was also observed for *Haynesina germanica* (Langer, 2000).

Sampled specimens of *Uvigerina mediterranea*, *Bolivina variabilis* and *Chilostomella ovoidea* from the Bay of Biscay, the Portuguese coast and the Mediterranean could be considered as belonging to the same population genetically. This means that regular exchanges occur between the East Atlantic and the Mediterranean, maintaining the gene flow; this genetic proximity certainly originates from the repopulation of the Mediterranean from the near Atlantic after the Messinian salinity crisis (Wright, 1980) or the glaciations. The fact that *U. peregrina* from the Bay of Biscay and the Skagerrak are also rather close genetically shows that exchanges could expand beyond the Atlantic-Mediterranean bioprovince. However, *Cibicides lobatulus* from the Skagerrak and the Mediterranean show marked genetic differences. This can be explained either by the presence of cryptic species cohabiting in the same area, as already observed with *Bolivina variabilis, Globobulimina pseudospinescens, Rosalina orbicularis, Chilostomella ovoidea*, or/and by different rates and mechanisms of evolution between species.

The molecular phylogeny of the SSU showed marked differences in rates of evolution between the studied taxa. Within the analysis made with the 3' fragment, *Cibicides* and other members of group 3 were the slowest ones with short branches (Fig. 4.7). Nevertheless, this difference of evolutionary rates between *Cibicides* and *Uvigerina* decreased in further analyses of the 3' end and the 5' end fragments (Fig. 3.4) and the complete SSU (Fig. 2.3). Data from the fossil record, however, would support that the observed difference is real: all studied cibicidids appeared a long time ago (at least in the middle Miocene or before, see Figs. 5.8-5.10), whereas some uvigerinids first occurred in the Quaternary (see Figs. 6.9-6.10).

7.7. Recognizing living foraminifers

Obtaining DNA from deeper water specimens proved to be time consuming. The samples never contained a large number of live foraminifers and it was often hard to determine which specimens were alive. Because deep-sea foraminifers do not show pseudopodial activity, recognition of live specimens depends on other factors, such as the colour of the protoplasm.

Because no staining[2] was used during collection, the live foraminifers showed their natural color which is mainly depending on the food they eat. The *Uvigerina peregrina* and the *Bulimina marginata* we have observed in the Skagerrak were green. The same was noticed for *U. phlegeri* from the Portuguese canyons, whereas *U. elongatastriata* from the same location were orange. *Globobulimina turgida* from Portugal and Skagerrak were orange too. *Cibicides* from Skagerrak, Iceland, Portugal and Mediterranean were usually more pinkish or red. It is classically thought that the green comes from chlorophyll of algae but orange and pink colors have a more mysterious origin (A. Gooday, pers. comm.).
Goldstein & Corliss (1994) observed that *U. peregrina* from the San Pedro Basin (California, USA) ate diatoms whereas this was not the case for *Globobulimina pacifica* from the same locality, showing that foraminifers were food-selective. We got a confirmation that *U. peregrina* also eats diatoms in the Skagerrak thanks to a mistake. The first time we amplified the ITS region, we did not use any foraminiferal-specific primer. When the eukaryotic DNA which was in the biggest quantity in our *Uvigerina* was amplified, two strips of different lengths appeared on the electrophoretic gel. The BLAST showed that the DNA from the shortest fragment belonged to a diatom genetically close to *Chaetoceros*[3]. It is interesting to note that the same species of diatom was found in five clones we got from four *U. peregrina*. Because the *Uvigerina* were carefully cleaned before DNA extraction, the diatom DNA certainly comes from ingested algae. The fact that DNA could be amplified means that the molecule was not degraded and that the diatoms were probably alive or very recently dead (see 1.6. for life time of DNA) upon ingestion by the foraminifers.
Cibicides refulgens from the Mediterranean and Antarctica are also feeding on diatoms (Langer, 1988; Alexander & DeLaca, 1987) The first ones were red, whereas we could not observe the color of living Antarctic specimens because we had only dried material. Nevertheless, some SEM pictures of Antarctic material showed diatoms[4] near the *Cibicides*, as well as the agglutinated tubes covering the pseudopodia[5] (Fig. 7.2).

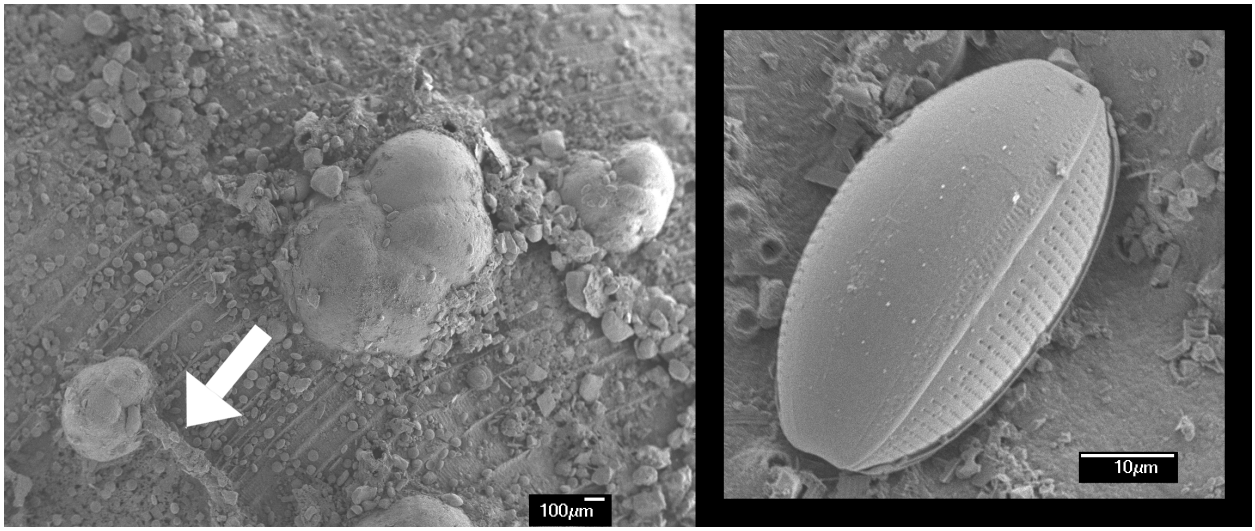

Figure 7.2. SEM picture of *Cibicides refulgens* fixed on the scallop shell (left) and enlargement of a diatom found on the foraminifer shell (right). The arrow shows one of the agglutinated tubes covering the pseudopodia.

2) Rose Bengal is routinely employed to recognize the live specimens and the resulting pinkish color impedes the observation of the natural color of the foraminifer.
3) *Chaetoceros* sp. can be really abundant in Oslo Fjord, (e.g. Kristiansen et al. 2001).
4) Mullineaux & DeLaca (1984) observed a diatom film covering the pecten shells.
5) These tubes are thought to help feeding on suspended material (Mullineaux & DeLaca, 1984).

7.8. Unsolved questions and further research

To further investigate the phylogeny of the Rotaliida, it is inevitable to use the complete SSU instead of partial sequences. In addition to the common species we already sampled, more taxa are needed to have a complete overview of the order phylogeny using the SSU rDNA. Furthermore, analyses with other genes are needed to verify this phylogeny and elaborate a new classification of the rotaliids, not based only on the test morphology but also taking the molecular results into account.

Among *Cibicides*, the monophyly needs to be tested with the addition of close genera such as *Hanzawaia, Planulina, Cibicidina* or other species attributed to *Cibicides* or *Parrelloides* such as *C. bradyi* and *C. robertsonianus*. The addition of DNA from the extant species studied in Chapter 5 (*C. bradyi*, *C. dutemplei*?, *C. kullenbergi*, *C. pseudoungerianus*, *C. robertsonianus*) will allow to check the phylogeny elaborated with our first results (Fig. 5.9). In particular, the sampling of a "true" *C. kullenbergi* (the deep-sea modern species as defined by Corliss (1979a) or Lohmann (1978) for instance) would permit to determine whether the taxonomic concept of this species is homogeneous between different schools[6]. More specimens of all the extant species sampled in different locations are also needed to define the geographical, morphological and genetic variation of these species and to check the presence of cryptic species. Moreover, a detailed study coupling morphometrics and genetics would allow investigating the existence of morphological differences between *C. lobatulus* and *C. refulgens* from the Mediterranean.

Within the uvigerinids, the sampling of other members of *Trifarina* and *Rectuvigerina* would show whether these genera are subsumed in *Uvigerina* or polyphyletic. Among the extant studied species, DNA is still lacking for the spinose species. Molecular studies would allow checking whether *U. auberiana* and *U. proboscidea* are synonyms and the true *U. hispida* really belongs to a completely different group. Another interesting field concerns the study of the morphological and genetic variations within *U. peregrina*. DNA samples of related species (*U. hollicki , U. pygmea*) or subspecies (*U. peregrina parva, U. peregrina dirupta*) could indicate if these taxa belong all to *U. peregrina* and are therefore ecophenotypes or if they are separated populations or species.

To summarize, more samples are needed for the DNA studies, but also a better knowledge of the fossil record is required in order to be able to date the nodes of the molecular phylogenies and tune the molecular clocks. Finally, besides the taxonomic field, molecular tools also allow to investigate the ecology of foraminifers. The use of universal 18S primers will permit to obtain the total eukaryotic DNA present inside a foraminifer, including the cells ingested for feeding.

6) The species concept of *C. kullenbergi* as defined in the Utrecht school is closer to *C. pachyderma* and perhaps even included in that species according to others (J. Schönfeld, pers. comm.).

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Appendix 1

Taxonomic notes and comments on the studied species

Genus *Cibicides* de Montfort, 1808

Type species: *Cibicides refulgens* de Montfort, 1808
Range and occurrence: Paleocene to Recent, cosmopolitan

Nomenclature

Because many cibicidids were alternatively put in different genera, the grammatical form taken by the name of the species sometimes had to change its gender. The International Code of Zoological Nomenclature (ICZN, 2000) gives clear indications to apply these changes. The main points concerning the cibicidids are described below.
When the species name is an adjective, the nominative singular is used (ICZN, 2000, 11.9.1.1.) and the adjective must agree in gender with the generic name (ICZN, 2000, 31.2.). For this reason, certain species which were described or put under a female genus name (*Truncatulina* or *Rotalina*, for example), have a species name ending with an a (e.g. *T. lobatula*, *T. mundula*, *T. ungeriana*, *T. pseudoungeriana*, *T. robertsoniana*). When the species are moved or belong to a male genus name like *Cibicides* (see Stainforth (1949) for the discussion on the gender of this genus), the ending of the species name becomes us (e.g. *C. italicus*, *C. lobatulus*, *C. mundulus*, *C. pseudoungerianus*, *C. robertsonianus*, *C. ungerianus*). For *refulgens*, the nominative form is the same whatever the gender is.
When the species name is a noun in the nominative singular standing in apposition to the generic name (ICZN, 2000, 11.9.1.2.), it does not need to agree in gender with the generic name (ICZN, 2000, 31.2.1.) and must not be changed to agree in gender with the generic name (ICZN, 2000, 34.2.1.). According to Stainforth (1949), this situation applies to the species *pachyderma* coming from the greek adjective παχυς (thick) and name το δερμα (the skin). For this reason, whether it is described under a female genus name (e.g. *Truncatulina*) or a male one (e.g. *Cibicides*), the species name *pachyderma* remains unchanged.
The last case encountered here is a noun (proper nouns in our case) in the genitive case (ICZN, 2000, 11.9.1.3.). In that situation, the genitive remains the same, whatever is the gender of the genus name. The species names *bradyi*, *dutemplei*, *kullenbergi*, *wuellerstorfi* are in the genitive case.

Cibicides bradyi (Trauth), 1918

1884 *Truncatulina dutemplei* (d'Orbigny) – Brady, p. 665, pl. 95, fig. 5 (not *Rotalina dutemplei* d'Orbigny, 1846).
1918 *Truncatulina bradyi* – Trauth, p. 235.
1951 *Cibicides hyalinea* – Hofker, p. 359, text figs. 244-245.
1953 *Cibicides robertsonianus* (Brady) – Phleger et al., pl. 11, figs. 15-16 (not 17) (not *Truncatulina robertsoniana* Brady, 1881)
1960 *Cibicides bradyi* (Trauth) – Barker, p. 196, pl. 95, fig. 5a-c.
1964 *Cibicidoides bradyi* (Trauth) – Parker, p. 624, pl. 100, figs. 19, 21-23.
1964 *Eponides hyalinus* (Hofker) – Leroy, p. F37, pl. 7, figs. 24-26.
1966 *Parrelloides bradyi* (Trauth) – Belford, pp. 100-102, pl. 11, figs. 10-19.
1976 *Cibicides bradyi* (Trauth) – Pflum & Frerichs, pl. 3, figs. 6-7.
1978 *Cibicides bradyi* (Trauth) – Boltovskoy, pl. 3, figs. 6-8.
1978 *Cibicides bradyi* (Trauth) – Brolsma, p. 129, pl. 4, figs 1a-2c.
1979 *Cibicidoides bradyi* (Trauth) – Corliss, pp. 9-10, pl. 3, figs. 1-3.
1979 *Gyroidina* cf. *gemma* Bandy– Corliss, p. 9, pl. 4, figs. 7-9 (not *Gyroidina gemma* Bandy, 1953).
1982 *Cibicides bradyi* (Trauth) – Van der Zwaan, p. 145, pl. 4, figs. 2a-b.
1983 *Cibicidoides haitiensis* (Coryell & Rivero) – Miller, p. 433, pl. 2, fig. 5.
1984 *Cibicides bradyi* (Trauth) – Jonkers, pl. 4, figs. 1a-c.
1985 *Cibicidoides bradyi* (Trauth) – Mead, p. 242, pl. 7, figs. 1a-b, 2, 4.
1986 *Cibicidoides bradyi* (Trauth) – Van Morkhoven et al., pp. 100-101, pl. 30, figs 1a-2c.
1987 *Cibicidoides bradyi* (Trauth) – Miller & Katz, p. 126, pl. 7, fig. 2.
1988 *Parrelloides hyalinus* (Hofker) – Loeblich & Tappan, p. 573, pl. 625, figs. 1-7.
1989 *Cibicidoides bradyi* (Trauth) – Hermelin, pp. 85-86, pl. 17, figs. 2-4.
1990 *Cibicidoides bradyi* (Trauth) – Galluzzo et al., pl. 3, fig. 5.
1994 *Cibicides bradyi* (Trauth) – Gupta, pl. 5, figs. 3-4.
1994 *Gyroidina bradyi* (Trauth) – Jones, p. 99, pl. 95, fig. 5.
1994 *Parrelloides bradyi* (Trauth) – Loeblich & Tappan, p. 144, pl. 301, figs. 1-9.
1994 *Parrelloides hyalinus* (Hofker) – Loeblich & Tappan, p. 145, pl. 301, figs. 10-12; pl. 302, figs 1-7.
2000 *Cibicides bradyi* (Trauth) – Den Dulk, pl. 6, fig. 2a-b.
2000 *Cibicides bradyi* (Trauth) – Kouwenhoven, pl. 3, fig. 1a-c.

Original designation: *Truncatulina bradyi* Trauth, 1918
Stratigraphic range: Eocene (Ypresian)-Recent

(Holbourn & Henderson, 2002)
Geographical occurrence: cosmopolitan
Bathymetry: bathyal to abyssal
Cibicides bradyi is a relatively small species having a biconvex test with a rounded periphery (Pl. 1). The low convex umbilical side possesses a closed umbo whereas the flatter spiral side shows clearly the spiral suture and all the chambers. The sutures on the spiral side are straight and depressed, the ones on the umbilical side are flush. Five to seven slightly lobate chambers are present in the last whorl. The porosity is coarse on the spiral side.
In our material, morphological intermediates between *C. bradyi* and *C. ungerianus* or *C. robertsonianus* were observed.
Cibicides bradyi is a mud-dweller, living usually deeper in the sediment than other *Cibicides* (Corliss, 1991; Rathburn et al., 1996; Tachikawa & Elderfield, 2002). This species has no tolerance to increased salinity or oxygen deficiency (Van der Zwaan, 1982).

<u>*Cibicides dutemplei* (d'Orbigny), 1846</u>

1846 *Rotalina dutemplei* – d'Orbigny, p. 157, pl. 8, figs. 19-21.
1848 *Rotalina conoidea* – Czjzek, Haid. Nat. Abhandl. 2, p. 145, pl. 13, figs. 4-6.
1855 *Rotalina bruckneri* – Reuss, Zeitschr. deutsche geol. Gesell. 7, p. 273, pl. 12, fig. 7.
1857 *Rotalina dutemplei* d'Orbigny – Egger, Neues Jahrb., p. 274, pl. 7, fig. 8.
1868 *Rotalia praecincta* – Karrer, p. 189, pl. 5, fig. 7.
1884 *Truncatulina praecincta* (Karrer) – Brady, p. 667, pl. 95, figs. 1-3.
1884 *Heterolepa simplex* – Franzenau, Természetrajzi Füzetek, Budapest 8, p. 215, pl. 5, figs. 1a-c.
1884 *Heterolepa costata* – Franzenau, Természetrajzi Füzetek, Budapest 8, p. 216, pl. 5, figs 2a-c.
1953 *Cibicides dutemplei* (d'Orbigny) – Giannotti, p. 287.
1958 *Cibicides dutemplei* (d'Orbigny) – Batjes, pp. 150-151, pl. 9, figs. 9-11.
1960 *Cibicides dutemplei* (d'Orbigny) – Christodoulou, p. 92, pl. 13, fig. 8a-c.
1962 *Heterolepa dutemplei* (d'Orbigny) – Loeblich & Tappan, p. 72.
1964 *Heterolepa dutemplei* (d'Orbigny) – Loeblich & Tappan, p. C758, pl. 623, fig. 3a-c.
1966 *Cibicides dutemplei* (d'Orbigny) – Butt, p. 68, pl. 4, fig. 9a-c.
1970 *Cibicides dutemplei* (d'Orbigny) *praecinctus* (Karrer) – Verdenius, pl. 6, figs. 4a-c, 5.
1971 *Heterolepa dutemplei* (d'Orbigny) – Verhoeve, p. 109, pl. 5, fig. 18a-c; pl. 10, fig. 7.
1979 *Cibicides dutemplei* (d'Orbigny) – Hageman, p. 91, pl. 3, fig. 5a-b.
1982 *Cibicides dutemplei* (d'Orbigny) – Van der Zwaan, pp. 145-146, pl. 5, figs. 1a-c and 2a-c.
1983 *Cibicides dutemplei* (d'Orbigny) – Setiawan, p. 126, pl. 11, fig. 4a-c.
1984 *Cibicides dutemplei* (d'Orbigny) – Jonkers, pl. 4, figs. 2 and 3a-b.
1986 *Cibicidoides dutemplei* (d'Orbigny) – Van Morkhoven et al., pp. 112-113, pl. 35, figs. 1-2.
1994 *Cibicides mexicanus* (Nuttall) – Gupta, pl. 5, fig. 6.
2000 *Cibicides dutemplei* (d'Orbigny) – Den Dulk, pl. 7, fig. 2a-b.
2000 *Cibicides dutemplei* (d'Orbigny) – Kouwenhoven, pl. 2, fig. 2a-c.

Original designation: *Rotalina dutemplei* d'Orbigny, 1846
Stratigraphic range: early Miocene to Pliocene, up to Recent in Indian Ocean?
Geographical occurrence: cosmopolitan
Bathymetry: outer neritic to upper bathyal (Van Morkhoven et al., 1986)
Cibicides dutemplei specimens are thick walled and often large. The umbilical side is highly convex, with a plug and triangular chambers. The spiral side is flat to slightly convex; the chambers are only visible in the last whorl. The sutures are flush, straight and imperforate. The porosity is coarse on the spiral side and draws triangles on the umbilical side due to the imperforate sutures bording the chambers (Pl. 2). Intermediates between *C. dutemplei* and *C. pseudoungerianus* were observed in our material (Pl. 12).
Cibicides dutemplei is a mud-dweller from shallow water with low tolerance to increased salinity or oxygen deficiency (Hageman, 1979; Van der Zwaan, 1982).

<u>*Cibicides italicus* Di Napoli Alliata, 1952</u>

1952 *Cibicides italicus* – Di Napoli Alliata, pp. 1-3. pl. 1, figs. 1-7.
1963 *Cibicides bellincionii* Giannini & Tavani – Christodoulou, p. 106, pl. 3, fig. 2a-b.
1971 *Cibicides italicus* Di Napoli – Verhoeve, p. 61, pl. 3, fig. 2a-c.
1978 *Cibicides italicus* Di Napoli – Brolsma, pl. 4, fig. 4a-b.
2000 *Cibicides italicus* Di Napoli Alliata – Kouwenhoven, pl. 3, fig. 2a-c.

Original designation: *Cibicides italicus* Di Napoli Alliata, 1952
Stratigraphic range: late Miocene to early Pliocene
Geographical occurrence: Mediterranean
Bathymetry: bathyal-abyssal
Cibicides italicus has a thick walled and glassy test (Pl. 3). The umbilical side is flat and the spiral side highly convex and hemispheric; it often

has many chambers. The periphery is rounded. The sutures are flush and glassy imperforate. The porosity is coarse on the spiral side.
This species is a mud dweller preferring deep stable water and has a low tolerance to deviation in salinity and oxygen values (Van der Zwaan, 1982).

Cibicides kullenbergi Parker, 1953

1953 *Cibicides kullenbergi* – Parker, in Phleger et al., p. 49, pl. 11, figs. 7-8.
1976 *Cibicides kullenbergi* Parker – Pflum and Frerichs, pl. 2, figs. 6-8.
1978 *Cibicidoides kullenbergi* (Parker) – Lohmann, p. 29, pl. 2, figs. 5-7.
1979 *Cibicidoides kullenbergi* (Parker) – Corliss, p. 10, pl. 3, figs. 4-6.
1982 *Cibicides kullenbergi* Parker – Van der Zwaan, p. 146, pl. 4, fig. 4a-c.
1984 *Cibicides ungerianus* Parker – Jonkers, pl. 3, fig. 4a-c.
1985 *Cibicidoides* cf. *kullenbergi (*Parker) – Mead, p. 242, pl. 6, fig. 6a-b.
1991 *Cibicidoides kullenbergi (*Parker) – Corliss, pl. 1, figs. 6, 8-9.
1994 *Cibicides kullenbergi* Parker – Gupta, pl. 5, fig. 5.
2000 *Cibicides kullenbergi* Parker – Den Dulk, pl. 6, fig. 4a-c (non 5a-b).
2000 *Cibicides kullenbergi* Parker – Kouwenhoven, pl. 1, fig. 4a-c.

Original designation: *Cibicides kullenbergi* Parker, 1953
Stratigraphic range: late Oligocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: bathyal-abyssal
Specimens of *C. kullenbergi* are often large with a thick walled, milky white test (Pl. 4). The umbilical side shows a plug and the spiral side is covered by extra-calcite, hiding the sutures and the chambers. The test is biconvex with both sides equally developed and bluntly keeled. The sutures are flush and, on the umbilical side, sigmoidal around the plug. The porosity is coarse on the spiral side. Morphological intermediates were observed in our material between this species and *C. ungerianus* and *C. pachyderma* (Pl. 12).
This species prefers deep water with normal marine salinity and oxygen conditions (Van der Zwaan, 1982).

Cibicides lobatulus (Walker and Jacob), 1798

1798 *Nautilus lobatulus* – Walker and Jacob, In: Kanmacher, Adams' essays on the microscope, p. 642, pl. 14, fig. 36.
1884 *Truncatulina lobatula* (Walker and Jacob) – Brady, p. 660, pl. 92, fig. 10; pl. 93, fig.1.
1931 *Cibicides lobatula* (Walker & Jacob) – Cushman, pp. 118-119, pl. 21, fig. 3.
1953 *Cibicides lobatulus* (Walker & Jacob) – Phleger et al., p. 49, pl. 11, figs. 9, 14.
1960 *Cibicides lobatulus* (Walker & Jacob) – Barker, p. 190, pl. 92, fig. 10; p. 192, pl. 93, figs. 1, 4, 5.
1966 *Cibicides lobatulus* (Walker & Jacob) – Butt, pl. 4, figs. 5-7.
1971 *Cibicides lobatulus* (Walker and Jacob) – Murray, pl. 2, figs. 13-14.
1978 *Cibicides lobatulus* (Walker & Jacob) – Brolsma, pl. 4, fig. 6a-c.
1978 *Cibicidoides sp.* – Lohmann, pl. 3, figs. 13-14.
1979 *Cibicides lobatulus* (Walker & Jacob) - Hageman, pp. 91-92, pl. 3, fig. 6a-b, pl. 4, fig. 1a-b.
1980 *Cibicides lobatulus* (Walker & Jacob) – Boltovskoy et al., p. 24, pl. 9, figs. 1-4.
1980 *Cibicides lobatulus* (Walker & Jacob) – Bremer et al., pl. 3, figs. 9-11.
1981 *Cibicides lobatulus* (Walker & Jacob) – Sejrup et al., p. 290, pl. 1, fig. 4.
1982 *Cibicides lobatulus* (Walker & Jacob) – Agip, pl. 51, fig. 6.
1982 *Cibicides lobatulus* (Walker and Jacob) – Van der Zwaan, p. 146, pl. 7, figs. 1-2.
1983 *Cibicides lobatulus* (Walker & Jacob) – Setiawan, pl. 11, fig. 2a-c.
1984 *Cibicides lobatulus* (Walker & Jacob) – Jonkers, pl. 12, fig. 1a-c.
1988 *Lobatulua lobatula* (Walker and Jacob) – Loeblich & Tappan, pl. 637, figs. 10-13.
1991 *Lobatula lobatula* (Walker & Jacob) – Cimerman & Langer, p. 71, pl. 75, figs. 1-4.
1991 *Cibicides lobatulus* (Walker & Jacob) – Verhallen, pp. 128-129, pl. 15, figs. 1-2.
1994 *Cibicides lobatulus* (Walker & Jacob) – Jones, p. 97, pl. 92, fig. 10; pl. 93, figs. 1, 4-5.
1994 *Lobatula lobatula* (Walker & Jacob) – Loeblich & Tappan, p. 150, pl. 316, figs. 8-11; pl. 319, figs. 1-7.
2000 *Cibicides asanoi* Matsunaga – Scott et al., p.12, fig. 3, 56-57.
2000 *Cibicides cushmani* Ujiie & Kusukawa – Scott et al., p.12, fig. 3, 58-60.
2000 *Cibicides lobatulus* (Walker & Jacob) – Den Dulk, pl. 6, fig. 5a-b (non 4a-c).
2000 *Cibicides lobatulus* (Walker & Jacob) – Kouwenhoven, pl. 1, fig. 1a-c.
2002 *Cibicides lobatulus* (Walker & Jacob) – Schönfeld, pl. 1, figs. 2-3.
2003 *Cibicides lobatulus* (Walker & Jacob) – Murray, p. 21, fig. 6, 13-15.

Original designation: *Nautilus lobatulus* Walker & Jacob, 1798
Stratigraphic range: Miocene (Langhian)-Recent (Holbourn & Henderson, 2002)
Geographical occurrence: cosmopolitan
Bathymetry: relatively shallow water (<1000m)
Cibicides lobatulus can become really large and may adopt a wide range of strange shapes depending on the substrate on which it is fixed (Pl.

5). The outline is irregular and lobate, the last chambers are often inflated. The umbilical side is high convex, whereas the spiral side is flat to concave. The sutures are flush to depressed, and the porosity is very coarse, especially on the spiral side. Beside the fixed specimens, often irregularly shaped, regular specimens, thought to be vagile, are also found (Pl. 5). Molecular studies showed that both morphotypes belong to the same species (see Chapter 3). Specimens showing intermediate morphology between *C. lobatulus* and *C. refulgens* have been observed in our material, as well as between *C. lobatulus*, *C. pachyderma* and *C. ungerianus* (Pl. 12).

This species lives mainly fixed on a wide variety on substrates (rocks, mollusk shells, polychaetes, *Posidonia* leaves, …), but can also have a vagile way of life on the sediment (Wollenburg & Mackensen, 1998b). This species is much more tolerant to increased salinities than other *Cibicide* species (Van der Zwaan, 1982). It was reported living at depths shallower than 1000m; however the species was sometimes found deeper (Phleger et al., 1953, p.86; Wollenburg & Mackensen, 1998a, 1998b).

Cibicides pachyderma (Rzehak), 1886

1884 *Truncatulina ungeriana* (d'Orbigny) – Brady (non d'Orbigny), p. 664, pl. 94, fig. 9a-c.
1886 *Truncatulina pachyderma* – Rzehak, p. 87, pl. 1, fig. 5a-c.
1959 *Cibicides pachydermus (*Rzehak) – d'Onofrio, Giorn. Geol., ser. 2a, 27 (1956-1957), p. 180, pl. 11, fig. 12a-c.
1978 *Cibicides pachydermis (*Rzehak) – Wright, p. 713, pl. 3, figs. 19-20.
1986 *Cibicidoides pachyderma* (Rzehak) – Van Morkhoven et al., pp. 68-70, pl. 22, fig. 1a-c.
1990 *Cibicidoides pachyderma* (Rzehak) – Galluzzo et al., pl. 3, figs. 8-9.
1992 *Cibicidoides pachyderma* (Rzehak) – Spencer, pl. 1, figs. 5-6.
1993 *Cibicides pachyderma* (Rzehak) – Katz and Miller, pl. 2, fig. 4a-c.
1994 *Cibicidoides pachyderma* (Rzehak) – Jones, p. 98, pl. 94, fig. 9.
2000 *Cibicides pachyderma* (Rzehak) – Kouwenhoven, pl. 2, fig. 1a-c.

Original designation: *Truncatulina pachyderma* Rzhehak, 1896
Stratigraphic range: early Oligocene to Recent
Geographical occurrence: cosmopolitan?
Bathymetry: upper bathyal

Cibicides pachyderma is a relatively small species (Pl. 6). The spiral side is convex, with some additional calcite, and more developed than the umbilical side, convex to flat. The test is white and opaque; only the last whorl is visible on the spiral side. The profile shows a very angular subacute periphery. The sutures are flush on the spiral side, depressed and imperforate glassy on the umbilical side. The porosity is coarse on the spiral side. Morphological intermediates were observed in our material between this species and *C. ungerianus* and *C. kullenbergi* (Pl. 12).

This species has been sometimes observed living in the topmost sediment (Schmiedl et al., 2000), although it is supposed to live in an epibenthic habitat when observe on a solid substrate.

Cibicides pseudoungerianus (Cushman), 1922

1884 *Truncatulina ungeriana* (not d'Orbigny), Brady, p. 664, pl. 94, fig. 9.
1899 *Truncatulina ungeriana* (not d'Orbigny) – Flint, p. 333, pl. 77, fig. 2.
1918 *Truncatulina ungeriana* (not d'Orbigny – Cushman, p. 69, pl. 24, fig. 1.
1922 *Truncatulina pseudoungeriana* - Cushman, Prof. Pap. US Geol. Surv., 129, p. 97, pl. 20, fig. 9.
1931 *Cibicides pseudoungeriana* (Cushman) – Cushman, pp. 123-124, pl. 22, figs. 3-7.
1951 *Cibicides ungerianus* (d'Orbigny) – Marks, p. 73, pl. 8, figs. 2a-b.
1953 *Cibicides pseudoungerianus* (Cushman) – Giannotti, p. 288.
1959 *Cibicides pseudoungerianus* (Cushman) – Dieci, pp. 100-101, pl. 8, fig. 1.
1960 *Cibicides pseudoungerianus* (Cushman) – Barker, p. 194, pl. 94, figs. 9a-c.
1960 *Cibicides pseudoungerianus* (Cushman) – Christodoulou, p. 94, pl. 14, fig. 7a-b.
1970 *Cibicides pseudoungerianus* (Cushman) – Verdenius, pl. 6, fig. 3.
1971 *Cibicides pseudoungerianus* (Cushman) – Verhoeve, p. 63, pl. 3, fig. 5a-c.
1976 *Cibicides* cf. *pseudoungerianus* (Cushman) – Pflum & Frerichs, pl. 2, fig. 9, pl. 3, figs. 1-2.
1978 *Cibicides pseudoungerianus* (Cushman) – Brolsma, pl. 3, fig. 7a-c.
1979 *Cibicides ungerianus* (d'Orbigny) – Hageman, p. 92, pl. 4, figs. 2a-c, non fig. 3a-b.
1980 *Cibicidoides floridanus* (Cushman) – Bremer et al., p. 24, pl. 3, figs. 12-14.
1982 *Cibicidoides pseudoungerianus* (Cushman) – Agip, pl. 52, fig. 1.
1991 *Cibicidoides pseudoungerianus* (Cushman) – Cimerman & Langer, p. 69, pl. 74, figs. 2-3.
1991 *Cibicides pseudoungerianus* (Cushman) – Verhallen, pp. 129, 136, pl. 16, figs. 1-4.
2000 *Cibicides pseudoungerianus* (Cushman) – Den Dulk, pl. 6, fig. 3a-c.
2000 *Cibicides pseudoungerianus* (Cushman) – Kouwenhoven, pl. 1, fig. 3a-c.

Original designation: *Truncatulina pseudoungeriana* Cushman, 1922
Stratigraphic range: early Oligocene-Recent
Geographical occurrence: cosmopolitan?
Bathymetry: neritic-upper bathyal
Cibicides pseudoungerianus has a medium size. The test is biconvex with a more developed umbilical side; supplementary calcite on the spiral side designs a belly (Pl. 7). There is a sharp angle at the periphery separating the umbilical from the spiral side. The wall is thicker than in *C. ungerianus*, and only the last whorl is visible on the spiral side. The sutures are flush to slightly depressed, and relatively straight on the umbilical side. The porosity is coarse on the spiral side. This species is morphologically close to *C. ungerianus* and morphological intermediates have been observed in our material between both species and between *C. pseudoungerianus* and *C. dutemplei* (Pl.12)

Cibicides refulgens de Montfort, 1808

1808 *Cibicides refulgens* – de Montfort, Conchyliologie syst., p. 123, pl. on p. 122.
1884 *Truncatulina refulgens* (de Montfort) – Brady, p. 659, pl. 92, figs. 7-9.
1931 *Cibicides refulgens* de Montfort – Cushman, pp. 116-117, pl. 21, figs. 2a-c.
1951 *Cibicides refulgens* de Montfort – Hofker, p. 346, figs. 233-234.
1953 *Cibicides* cf. *refulgens* de Montfort – Phleger, Parker & Peirson, pp. 49-50, pl. 11, figs. 10-11.
1960 *Cibicides refulgens* de Montfort – Barker, p. 190, pl. 92, figs. 7-9.
1960 *Cibicides refulgens* de Montfort – Christodoulou, p. 94, pl. 14, figs. 15-16.
1964 *Cibicides refulgens* de Montfort – Loeblich & Tappan, p. C688, pl. 554, fig. 1a-c.
1971 *Cibicides lobatulus* (Walker and Jacob) *refulgens* type – Verhoeve, p. 62, pl. 3, fig. 4.
1982 *Cibicides lobatulus* type *refulgens* de Montfort – Van der Zwaan, pl. 7, fig. 4.
1991 *Cibicides refulgens* de Montfort – Cimerman & Langer, pp. 70-71, pl. 75, figs. 5-9.
1994 *Cibicides refulgens* de Montfort – Jones, p. 97, pl. 92, figs. 7-9.
1994 *Cibicides refulgens* de Montfort – Loeblich & Tappan, p. 149, pl. 318, figs. 7-9.
2002 *Cibicides lobatulus* (Walker & Jacob) – Jonkers et al., fig. 12d-f.
2002 *Cibicides refulgens* de Montfort – Schönfeld, pl. 1, figs. 11-12.
2003 *Cibicides refulgens* de Montfort – Murray, p. 21, fig. 7, 1-2.
2003 *Cibicides refulgens* de Montfort – Javaux & Scott, Paleont. Electronica, 6(4): fig. 2, 16-17.

Original designation: *Cibicides refulgens* de Montfort, 1808
Stratigraphic range: probably older than middle Miocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: neritic zone
Cibicides refulgens is morphologically really close to *C. lobatulus* (Pl. 8). Its shape, also depending of the substrate to which it is fixed, can be rather irregular. The spiral side is flat and the umbilical side highly convex (higher than for *C. lobatulus*, which is the main criterion to distinguish between both species) with an angular periphery. The sutures are flush to depressed. The porosity is coarse. A molecular study of *C. refulgens* from Mediterranean and Antarctic populations showed that at least two cryptic species cohabited under a same morphotype identity (see chapter 3).
This species is epifaunal and lives fixed on various substrates. Specimens from the Mediterranean were found attached to algae, whereas Antarctic populations lived attached to scallop shell (*Adamussium colbecki*). These Antarctic *C. refulgens* are thought to occasionally feed on the mantle of their host, and can therefore be considered as parasites or predators (Alexander & DeLaca, 1987).

Cibicides robertsonianus (Brady), 1881

1881 *Planorbulina robertsoniana* Brady, p. 65.
1884 *Truncatulina robertsoniana* Brady, p. 664, pl. 95, fig. 4.
1899 *Truncatulina robertsoniana* Brady - Flint, p. 333, pl. 77, fig. 3.
1931 *Cibicides robertsoniana* (Brady) – Cushman, pp. 121-122, pl. 23, fig. 6a-c.
1945 *Gyroidina jarvisi* – Cushman & Stainforth, p. 62, pl. 11, fig. 3.
1951 *Cibicides robertsonianus* (Brady) – Phleger & Parker, p. 31, pl. 16, figs. 10-13.
1953 *Cibicides robertsonianus* (Brady) – Phleger et al., p. 50, pl. 11, figs. 15-17.
1953 *Eponides haidingeri* (d'Orbigny) – Gianotti, p. 278, pl. 17, fig. 3.
1960 *Cibicides robertsonianus* (Brady) – Barker, p. 196, pl. 95, fig. 4a-c.
1976 *Cibicidoides robertsonianus* (Brady) – Berggren et al., pp. 219-220, pl. 5, figs. 3-5.
1976 *Cibicides robertsonianus* (Brady) – Pflum & Frerichs, pl. 3, figs. 3-5.
1978 *Cibicides bradyi* (Trauth) type *robertsonianus* (Brady) - Brolsma, p. 129, pl. 4, figs. 3a-c.
1982 *Cibicides robertsonianus* (Brady) - Agip, pl. 52, fig. 4.
1982 *Cibicides robertsonianus* (Brady) – Van der Zwaan, p. 147, pl. 4, figs. 3a-c.
1986 *Cibicidoides robertsonianus* (Brady) – Van Morkhoven et al., pp. 41, 43, pl. 11, fig. 1a-c.
1987 *Cibicidoides robertsonianus* (Brady) – Miller & Katz,

p. 132, pl. 7, fig. 1.
1989 *Cibicidoides robertsonianus* (Brady) – Hermelin, p. 86-87.
1990 *Cibicidoides robertsonianus* (Brady) – Galluzzo et al., pl. 3, fig. 10.
1992 *Cibicidoides robertsonianus* (Brady) – Spencer, pl. 1, figs. 7-8.
1994 *Cibicidoides robertsonianus* (Brady) – Jones, p. 99, pl. 95, fig. 4.
1997 *Cibicidoides robertsonianus* (Brady) – Resig & Cheong, pl. 2, figs. 7, 11, 15.
2000 *Cibicides robertsonianus* (Brady) – Kouwenhoven, pl. 3, fig. 3a-c.

Original designation: *Planorbulina robertsoniana* Brady, 1881 and *Truncatulina robertsoniana* Brady, 1884
Stratigraphic range: middle Miocene (Serravallian) to Recent
Geographical occurrence: cosmopolitan
Bathymetry: bathyal-abyssal
Cibicides robertsonianus is larger than *C. bradyi* and has also a biconvex test with a rounded periphery (Pl. 9). The low convex umbilical side possesses an open umbo whereas the flatter spiral side shows clearly the spiral suture and all the chambers. The sutures on the spiral side are straight and depressed, the ones on the umbilical side are flush. More than six slightly lobate chambers are present in the last whorl. The porosity is coarse on the spiral side.
In our material, morphological intermediates between *C. robertsonianus* and *C. bradyi* were observed.

Cibicides ungerianus (d'Orbigny), 1846

1846 *Rotalina ungeriana* – d'Orbigny, p. 157, pl. 8, figs. 16-18.
1884 *Truncatulina ungeriana* (d'Orbigny) – Brady, p. 644, pl. 94, fig. 9.
1951 *Cibicides ungeriana* (d'Orbigny) – Hofker, p. 357, fig. 242.
1951 *Cibicides ungerianus* (d'Orbigny) - Marks, p. 73, pl. 8, fig. 2a-b.
1958 *Cibicides ungerianus* (d'Orbigny) – Batjes, pp. 152-153, pl. 9, fig. 6.
1959 *Cibicides ungerianus* (d'Orbigny) – Dieci, p. 102, pl. 8, fig. 17.
1960 *Cibicides ungerianus* (d'Orbigny) – Christodoulou, p. 95, pl. 14, figs. 8-9.
1970 *Cibicides ungerianus* (d'Orbigny) – Verdenius, pl. 6, fig. 1.
1971 *Cibicides ungerianus* (d'Orbigny) – Verhoeve, p. 65, pl. 3, fig. 6a-c.
1979 *Cibicides ungerianus* (d'Orbigny) – Hageman, p. 92, pl. 4, figs. 2a-c, 3a-b.
1982 *Cibicidoides ungerianus* (d'Orbigny) – Agip, pl. 52, fig. 4.
1982 *Cibicides ungerianus* (d'Orbigny) – Van der Zwaan, p. 147, pl. 6, fig. 2a-b.
1984 *Cibicides ungerianus* (d'Orbigny) – Jonkers, pp. 128-129, pl. 3, figs. 1-4 (rem. figs. 2-4 not typical).
1991 *Cibicides ungerianus* (d'Orbigny) – Verhallen, p. 129, pl. 16, figs. 5-9.
2000 *Cibicides ungerianus* (d'Orbigny) – Den Dulk, pl. 6, fig. 1a-c.
2000 *Cibicides ungerianus* (d'Orbigny) – Kouwenhoven, pl. 1, fig. 2a-c.

Original designation: *Rotalina ungeriana* d'Orbigny, 1846
Stratigraphic range: middle Miocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: neritic-upper bathyal
Cibicides ungerianus can reach a large size. The outline is often oval but can be circular (Pl. 10). The umbilical side is always better developed than the spiral side, that is flat to slightly convex, and the periphery is angular. The test is rather thin and transparent; all the whorls and the spiral suture are visible on the spiral side. The sutures are flush to slightly depressed and bent backwards on the umbilical side, whereas they are simply flush on the spiral side. The porosity is coarse on the spiral side and coarser towards the last chamber on the umbilical side. This species has a "central" morphological position in *Cibicides* group and shares morphological intermediates with many other species: *C. bradyi*, *C. kullenbergi*, *C. lobatulus*, *C. pachyderma*, *C. pseudoungerianus* and *C. wuellerstorfi* (Pl. 12).
This species is thought to be an open-marine mud-dweller, with no tolerance to oxygen deficiency or to increased salinities (Van der Zwaan, 1982).

Cibicides wuellerstorfi (Schwager), 1866

1866 *Anomalina wuellerstorfi* – Schwager, p. 258, pl. 7, figs. 105, 107.
1884 *Truncatulina wuellerstorfi* (Schwager) – Brady, p. 662, pl. 93, fig. 9.
1894 *Planorbulina wuellerstorfi* (Schwager) – Goës, p. 89, pl. 15, fig. 777.
1929 *Truncatulina wuellerstorfi* (Schwager) – Cushman, p. 104, pl. 15, figs. 1-2.
1931 *Planulina wuellerstorfi* (Schwager) – Cushman, p. 110-111, pl. 19, figs. 5-6.
1951 *Cibicides wuellerstorfi* (Schwager) – Hofker, p. 350, text fig. 237.
1951 *Planulina wuellerstorfi* (Schwager) – Phleger & Parker, p. 33, pl. 18, fig. 11, pl. 19, fig. 1 (non 2, 3).
1953 *Planulina wuellerstorfi* (Schwager) – Phleger, Parker & Peirson, p. 49, pl. 11, figs. 1-2.
1958 *Cibicides wuellerstorfi* (Schwager) – Parker, p. 275, pl. 4, figs. 41-42
1959 *Planulina wuellerstorfi* Schwager – Dieci, p. 97, pl.

8, figs. 6a-b.
1960 *Planulina bradii* Tolmachoff – Barker, p. 192, pl. 93, fig. 8a-c.
1960 *Planulina wuellerstorfi* (Schwager) – Barker, p. 192, pl. 93, fig. 9a-c.
1960 *Planulina wuellerstorfi* (Schwager) – Christodoulou, p. 96, pl. 8, figs. 3-4.
1964 *Cibicides wuellerstorfi* (Schwager) – Leroy, p. F45, pl. 8, figs. 25-26.
1964 *Cibicidoides wuellerstorfi* (Schwager) – Parker, pp. 624-625, pl. 100, fig. 29.
1966 *Planulina wuellerstorfi* (Schwager) – Belford, p. 120, pl. 20, figs. 1-6.
1970 *Fontbotia wuellerstorfi* (Schwager) – Gonzalez-Donoso & Linares, p. 238, pl. 1, fig. 4a-c.
1976 *Cibicides wuellerstorfi* (Schwager) – Pflum & Frerichs, pl. 4, figs. 2-4.
1976 *Planulina wuellerstorfi* (Schwager) – Berggren et al., p. 215, pl. 4, figs. 9-10.
1978 *Cibicides wuellerstorfi* (Schwager) – Boltovskoy, pl. 3, figs. 19-21.
1978 *Planulina wuellerstorfi* (Schwager) – Lohmann, p. 26, pl. 2, figs. 1-4.
1979 *Planulina wuellerstorfi* (Schwager) – Corliss, pp. 7-8, pl. 2, figs. 13-16.
1980 *Cibicides wuellerstorfi* (Schwager) – Srinivasan & Sharma, p. 56, pl. 8, figs. 11-13.
1985 *Cibicidoides wuellerstorfi* (Schwager) – Mead, p. 240, pl. 6, figs. 1a-b, 2.
1986 *Planulina wuellerstorfi* (Schwager) – Van Morkhoven et al., pp. 48, 50, pl. 14, figs. 1-2.
1987 *Planulina wuellerstorfi* (Schwager) – Miller & Katz, p. 136, pl. 6, fig. 2.
1988 *Fontbotia wuellerstorfi* (Schwager) – Loeblich & Tappan, p. 583, pl. 634, figs. 10-12; pl. 635, figs. 1-3.
1989 *Cibicides wuellerstorfi* (Schwager) – Sen Gupta, p. 706, figs. 1-3.
1989 *Cibicidoides* sp. 1 – Hermelin, pp. 87-88, pl. 17, figs. 6-8.
1990 *Cibicides wuellerstorfi* (Schwager) – Galluzzo et al., pl. 3, figs. 18-19.
1991 *Planulina wuellerstorfi* (Schwager) – Corliss, pl. 1, figs. 1-2, 5.
1994 *Cibicides wuellerstorfi* (Schwager) – Gupta, pl. 5, figs. 8-9.
1994 *Cibicidoides wuellerstorfi* (Schwager) – Jones, p. 98, pl. 93, figs. 8-9.
1994 *Fontbotia wuellerstorfi* (Schwager) – Loeblich & Tappan, p. 150, pl. 319, figs. 7-12.
1997 *Fontbotia* cf. *wuellerstorfi* (Schwager) – Resig & Cheong, pl. 1, figs. 16-18.
2000 *Cibicides wuellerstorfi* (Schwager) – Den Dulk, pl. 6, fig. 6a-c.
2000 *Cibicides wuellerstorfi* (Schwager) – Kouwenhoven, pl. 2, fig. 3a-c.

Original designation: *Anomalina wuellerstorfi* Schwager, 1866
Stratigraphic range: middle Miocene (Langhian) to Recent
Geographical occurrence: cosmopolitan
Bathymetry: over 1000m
Cibicides wuellerstorfi can reach quite large sizes (Pl. 11). The outline is circular in juveniles and tends to become oval in adults. This species has a rather low axial profile with a flat spiral side, with which the organism might be attached to the substrate where it lives fixed, and a low convex umbilical side. The sutures are flush to slightly depressed, very glassy (imperforate) and sigmoidal on the umbilical side and flush on the spiral side. The porosity is coarse on the spiral side. In our material one intermediate with *C. ungerianus* has been observed.
It is a bathymetric indicator for deep sea (below 1000m) and low intermediate carbon flux (Holbourn & Henderson, 2002). This species generally has a epiphytic mode of life (Lutze & Thiel, 1989) and is used as an indicator of bottom water stable isotopes.

Genus *Uvigerina* d'Orbigny, 1826

Type species: *Uvigerina pygmea* d'Orbigny, 1826
Range and occurrence: early Eocene to Recent, cosmopolitan

Uvigerina auberiana d'Orbigny, 1839

1839 *Uvigerina auberiana* – d'Orbigny, Cuba, p. 106, pl. 2, figs. 23-24.
1884 *Uvigerina asperula* var. *auberiana* d'Orbigny – Brady, pl. 74, figs. 6-9.
1923 *Uvigerina auberiana* d'Orbigny – Cushman, p. 163, pl. 42, figs. 3-4.
1927 *Uvigerina auberiana* d'Orbigny – Galloway & Wissler, p. 75, pl. 11, fig. 22.
1953 *Uvigerina auberiana* d'Orbigny – Phleger et al., pp. 37-38, pl. 7, figs. 30-35.
1953 *Uvigerina senticosa* Cushman – Phleger et al., p. 38, pl. 8, figs. 4-5.
1958 *Uvigerina auberiana* d'Orbigny –Parker, pl. 2, figs. 35-36.
1959 *Uvigerina auberiana* d'Orbigny – Dieci, p. 70, pl. 6, fig. 3
1973 *Uvigerina vadescens* (Cushman) – Douglas, p.8, fig. 7.
1976 *Uvigerina auberiana* d'Orbigny – Berggren et al., p. 211, pl. 3, figs. 1-7.
1978 *Uvigerina auberiana* d'Orbigny – Lohmann, pl. 4, fig. 16.
1980 *Uvigerina auberiana* d'Orbigny – Bremer et al., pl. 2, fig. 1.
1981 *Siphouvigerina interrupta* (Brady) – Burke, pl. 1, fig. 16.
1985 *Siphouvigerina auberiana* (d'Orbigny) – Kohl, pp. 70-71, pl. 22, figs. 7-8, pl. 23, fig. 1.
1989 *Uvigerina auberiana* d'Orbigny – Hermelin, pp. 64-65, pl. 12, figs. 4-5.
1990 *Uvigerina auberiana* d'Orbigny – Galluzzo et al., pl. 2, fig.16.

1993 *Uvigerina auberiana* d'Orbigny – Sgarella & Montcharmont Zei, p. 214, pl. 15, fig. 13.
1994 *Uvigerina auberiana* d'Orbigny – Jones, p. 86, pl. 75, figs. 6-9.
1997 *Uvigerina pseudoampullacea* Asano – Resig & Cheong, pl. 1, figs. 11-12.
1999 *Uvigerina auberiana* d'Orbigny – Villanueva Guimerans & Cervera Currado, Bol. Inst. Esp. Oceanogr. 15, pp. 195-196, fig. 2.3a-c.
2005 *Uvigerina auberiana* d'Orbigny – Licari & Mackensen, pl. 2, figs. 4-5

Original designation: *Uvigerina auberiana* d'Orbigny, 1839
Stratigraphic range: middle Oligocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: bathyal (abyssal)
Uvigerina auberiana is a small spinose species which tends to become biserial. Its general shape resembles the one of *U. peregrina* which distinguishes it from *U. proboscidea* as well as a finer ornamentation and its smaller size (Boersma, 1984). The distinction between *U. auberiana* and *U. proboscidea* is subtle (see Pl. 13) and many authors put them in synonymy (e.g. Berggren et al., 1976; Hermelin, 1989).

Uvigerina bononiensis Fornasini, 1888

1888 *Uvigerina bononiensis* - Fornasini, Boll. Soc. Geol. Ital., 7, p. 48, pl. 3, fig. 12, 12a.
1898 *Uvigerina bononiensis* Fornasini – Fornasini, Riv. Ital. Pal., p. 27, pl. 1, figs. 1-8.
1925 *Uvigerina compressa* - Cushman, p. 10, pl. 4, fig. 2.
1951 *Hopkinsina bononiensis* (Fornasini) – Marks, pp. 62-63, pl. 7, fig. 8.
1959 *Hopkinsina bononiensis* (Fornasini) – Dieci, p. 73, pl. 6, fig. 10.
1960 *Uvigerina cushmani* Todd – Barker, p. 154, pl. 74, figs. 4-7.
1965 *Rectuvigerina bononiensis* (Fornasini) – Souaya, p. 319, no fig.
1969 *Uvigerina bononiensis* Fornasini subsp. *compressa* Cushman – Meulenkamp, p. 156, pl. 2, figs. 1-2.
1969 *Uvigerina pappi* – Meulenkamp, p. 135, pl. 1-2, figs. 3-11.
1970 *Hopkinsina bononiensis* (Fornasini) – Verdenius, pl. 5, fig. 3.
1971 *Hopkinsina bononiensis* (Fornasini) – Verhoeve, p. 112, pl. 5, fig. 20a-b; pl. 10, fig. 8.
1978 *Hopkinsina bononiensis* (Fornasini) – Brolsma, pl. 1, fig. 16.
1980 *Uvigerina bononiensis* Fornasini – Lutze, p. 72.
1980 *Uvigerina bononiensis* Fornasini - Thomas, pl. 2, figs. 1-7.
1982 *Uvigerina bononiensis* Fornasini – Van der Zwaan, p. 193, pl. 11, figs. 2-3.
1984 *Uvigerina bononiensis* Fornasini – Jonkers, p. 134, pl. 10, figs. 1-12.
1986 *Uvigerina bononiensis* Fornasini - Borsetti et al., pl. 19, figs. 3-7.
1991 *Uvigerina bononiensis* Fornasini – Verhallen, p. 152, pl. 12, figs. 4-8.
1992 *Rectuvigerina bononiensis* (Fornasini) – Schiebel, p. 54, pl. 3, fig. 8a-d.

Original designation: *Uvigerina bononiensis* Fornasini, 1888
Stratigraphic range: late Oligocene-Recent
Geographical occurrence: at least Mediterranean and Atlantic domains
Bathymetry: neritic
Uvigerina bononiensis is a small species with an often laterally compressed test and becoming quickly biserial (Pl. 14). The sutures have a characteristic "en crochet" shape. The ornamentation is made up of fine costae which stop at the sutures between the chambers.

Uvigerina cylindrica (d'Orbigny, 1826)

1826 *Clavulina cylindrica* – d'Orbigny, p. 268.
1852 *Clavulina cylindrica* – d'Orbigny, Prodrome, p. 194.
1932 *Uvigerina tenuistriata* Reuss var. *gaudryinoides* - Lipparini, Giorn. Geol., ser. 2, 7, p. 65, pl. 6, figs. 7-8.
1932 *Uvigerina tenuistriata* Reuss var. *siphogenerinoides* – Lipparini, Giorn. Geol., ser. 2, 7, p. 64, pl. 6, figs. 2-6.
1945 *Rectuvigerina nicoli* – Mathews, p. 593, pl. 81, fig. 2
1959 *Uvigerina tenuistriata* Reuss, subsp. *gaudryinoides* Lipparini – Dieci, p. 72, pl. 6, fig. 8.
1959 *Uvigerina tenuistriata* Reuss var. *siphogenerinoides* Lipparini – Dieci, p. 72, pl. 6, fig. 9.
1960 *Rectuvigerina tenuistriata gaudryinoides* (Lipparini) – Christodoulou, p. 46, pl. 16, fig. 45.
1960 *Rectuvigerina tenuistriata siphogenerinoides* (Lipparini) – Christodoulou, p. 46, pl. 16, fig. 43.
1960 *Uvigerina* cf. *cylindrica* (d'Orbigny) – Christodoulou, p. 45, pl. 6, fig. 36.
1961 *Rectuvigerina cylindroides* – Moncharmont Zei, Boll. Soc. Nat. Napoli, 69, p. 149, pl. 4, figs. 14-17.
1965 *Rectuvigerina tenuistriata* Reuss *gaudryinoides* – Souaya, p. 319, pl. 2, fig. 3.
1969 *Uvigerina arquatensis* Papp – Meulenkamp, pp. 143-144, pl. 4, figs. 21-24, pl. 5, fig. 25, pl. 6 figs. 11-15.
1969 *Uvigerina cretensis* – Meulenkamp, p. 141, pl. 3, figs. 16-21, pl. 5, figs. 5-19.
1969 *Uvigerina gaulensis* – Meulenkamp, p. 137, pl. 2, fig. 18.
1969 *Uvigerina lucasi* – Meulenkamp, p. 142, pl. 4, figs. 1-20.
1969 *Uvigerina selliana* – Meulenkamp, p. 138, pl. 3, figs 3-15; pl. 5, figs. 1-4.
1971 *Uvigerina gaudryinoides* Lipparini – Verhoeve, p. 199, pl. 9, fig. 14.
1980 *Rectuvigerina arquatensis* Papp – Lutze, p. 72.
1980 *Uvigerina cylindrica cylindrica* (d'Orbigny) – Thomas, p. 150, pl. 1, figs. 1a-c, pl. 5, figs. 3, 5.
1980 *Uvigerina cylindrica* (d'Orbigny) *gaudryinoides* Lipparini – Thomas, p. 159, pl. 1, fig. 2a-c; pl. 4, figs 5-6; p. 167, pl. 5, figs. 2, 4, 7.
1982 *Uvigerina cylindrica cylindrica* (d'Orbigny) – Van der Zwaan, p. 193, pl. 11, figs. 5-6.

1982 *Uvigerina cylindrica* (d'Orbigny) *gaudryinoides* Lipparini – Van der Zwaan, pp. 153-154, pl. 11, fig. 4.
1984 *Uvigerina cylindrica cylindrica* (d'Orbigny) – Jonkers, pl. 9, fig. 1.
1984 *Uvigerina cylindrica* (d'Orbigny) *gaudryinoides* Lipparini – Jonkers, p. 135, pl. 9, fig. 3.
1992 *Rectuvigerina cylindrica* (d'Orbigny) – Schiebel, pp. 54-55, pl. 3, fig. 9a-d.
2000 *Uvigerina cylindrica cylindrica* (d'Orbigny) – Kouwenhoven, pl. 11, fig. 9.
2000 *Uvigerina cylindrica gaudryinoides* Lipparini – Kouwenhoven, pl. 11, fig. 10.

Original designation: *Clavulina cylindrica* d'Orbigny, 1826
Stratigraphic range: middle Miocene-Recent
Geographical occurrence: at least Mediterranean and Atlantic domains
Bathymetry:outer neritic-middle bathyal
Uvigerina cylindrica is a small species (Pl. 14). The early stages of growth are triserial but the test becomes rapidly bi- and uniserial. The ornamentation is composed of fine costae. This species was separated in two subspecies (*U. cylindrica cylindrica* and *U. cylindrica gaudryinoides*) by Thomas (1980). The test is more slender, the uniserial part longer, and uniserial chambers are arranged more regularly in adult specimens of *U. cylindrica cylindrica* (Borsetti et al., 1986).

Uvigerina earlandi (Parr, 1950)

1858 *Uvigerina angulosa* – Williamson, p. 67, pl. 15, fig. 140.
1932 *Uvigerina angulosa* Williamson – Heron-Allen & Earland, Discovery Repts., 4, p. 397, pl. 12, figs. 32-39.
1937 *Angulogerina angulosa* (Williamson) – Chapman & Parr, Australasian Antarctic Exped. 1911-1914, Sci. Repts., ser. C, 1, pt. 2, p. 97 (part).
1950 *Angulogerina earlandi* – Parr, p. 341, pl. 12, fig. 21.
1979 *Trifarina earlandi* (Parr) – Osterman & Kellogg, p. 266, pl. 2, figs. 6-7.
1988 *Angulogerina angulosa* (Williamson) – Loeblich & Tappan, p. 525, pl. 574, figs. 5-9.
1993 *Angulogerina angulosa* (Williamson) – Mackensen et al., p. 55, pl. 1, figs. 1, 2.

Original designation: *Angulogerina earlandi* Parr, 1950
Stratigraphic range: late Miocene-Recent
Geographical occurrence: Southern Ocean
Bathymetry: outer neritic-middle bathyal
Uvigerina earlandi is a relatively small species (Pl. 14). Its test presents a triangular section which laid caused the species to be first classified in *Angulogerina* or *Trifarina*. The surface of the test is smooth with fine and low costae.

Uvigerina elongatastriata (Colom, 1952)

1941 *Uvigerina* cf. *U. tenuistriata* Reuss – Colom, Notas y Res. Inst. Esp. Oceanogr., ser. 2, 96, p. 17, pl. 3, figs. 57-58.
1952 *Angulogerina elongatastriata* – Colom, p. 29, pl. 4/6-9, fig. 5.
1975 *Trifarina elongatastriata* (Colom) – Seiler, Meteor Forsch. Ergebn., C, 23, p. 68, pl. 2, figs. 5-6.
1980 *Trifarina elongatastriata* (Colom) – Haake, p. 13, pl. 2, fig. 35.
1986 *Uvigerina elongatastriata* (Colom) – Lutze, p. 43, pl. 6, figs. 1-8.
1991 *Rectuvigerina elongatastriata* (Colom) – Cimerman & Langer, p. 61, pl. 63, figs. 7-9.
1992 *Uvigerina elongatastriata* (Colom) – Schiebel, p. 59, pl. 3, fig. 5.
1999 *Uvigerina elongatastriata* (Colom) – Villanueva Guimerans & Cervera Currado, Bol. Inst. Esp. Oceanogr. 15, p. 196-197, fig. 5.1a-c.
2002 *Uvigerina elongatastriata* (Colom) – Ernst, Geol. Ultraiectina, 220, p. 87, pl. 1, fig. O (non M).
2003 *Uvigerina elongatastriata* (Colom) – Fontanier, PhD thesis, pl. 10, figs. J-L.

Original designation: *Angulogerina elongatastriata* Colom, 1952
Stratigraphic range: Quaternary
Geographical occurrence: Mediterranean, East Atlantic (Gulf of Guinea-Bay of Biscay)
Bathymetry: outer neritic-middle bathyal
Uvigerina elongatastriata is a large species (Pl. 15). Because of the angular cross section of the test, this species has been sometimes assigned to *Angulogerina* or *Trifarina.* The neck stands in a depression as in other members of the *semiornata*-group. The test is ornamented with fine and numerous costae; the last chamber is more or less smooth.

Uvigerina hispida Schwager, 1866

1866 *Uvigerina hispida* – Schwager, p. 249, pl. 7, fig. 95.
1884 *Uvigerina asperula* Czjzek var. *auberiana* d'Orbigny – Brady, pl. 75, fig. 9.
1953 *Uvigerina hispida* Schwager – Gianotti, p. 263.
1964 *Uvigerina hispida* Schwager – Leroy, p. 34, pl. 4, figs. 2-3.
1966 *Euuvigerina hispida* (Schwager) – Belford, p. 78, pl. 7, figs. 14-16.
1971 *Uvigerina hispida* Schwager – Verhoeve, p. 200, pl. 9, fig. 15.
1976 *Uvigerina hispida* Schwager – Pflum & Frerichs, pl. 8, figs. 8-10.
1978 *Uvigerina hispida* Schwager – Boltovskoy, 1978, pl. 8, figs. 12-16.
1984 *Uvigerina hispida* Schwager – Boersma, pl. 5, fig. 3
1986 *Uvigerina hispida* Schwager – Boersma, pl. 20, figs. 5-6.
1986 *Uvigerina hispida* Schwager – Van Morkhoven et al., pp. 62, 64, pl. 20, figs. 1-4.
1993 *Uvigerina hispida* Schwager – Katz & Miller, pl. 4,

fig. 7a-b.
2000 *Uvigerina hispida* Schwager – Den Dulk, pl. 2, fig. 12.

Original designation: *Uvigerina hispida* Schwager, 1866
Stratigraphic range: late Oligocene or early Miocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: middle bathyal-abyssal
Despite some discrepancies (see 6.2.3), this species is usually described as a robust and fully hispid form. Its spines are never aligned (Srinivasan & Sharma, 1980; Hermelin, 1989). The microspheric form can have a spine extending from the proloculus (Van Morkohven et al., 1986).

Uvigerina mediterranea Hofker, 1932

1932 *Uvigerina mediterranea* – Hofker, Publ. Staz. Zool. Napoli, 12, p. 118, fig. 32a-g.
1952 *Uvigerina finisterrensis* – Colom, 51, fig. 4.
1958 *Uvigerina mediterranea* Hofker – Parker, pl. 2, figs. 39-40.
1960 *Eouvigerina mediterranea* (Hofker) – Hofker, p. 251, fig. 107c-d.
1974 *Uvigerina mediterranea* Hofker – Colom, p. 122, fig. 19h-n.
1977 *Uvigerina peregrina* Cushman – Haake, pl. 3, fig. 9.
1980 *Uvigerina finisterrensis* Colom - Haake, pl. 2, fig. 29.
1980 *Uvigerina mediterranea* Hofker – Van der Zwaan, Proc. Kon. Ned. Akad. Wet., ser. B, 83, pl. 2, fig. 1.
1981 *Uvigerina peregrina* Cushman – Sjerup et al., pl. 2, fig. 12.
1984 *Uvigerina finisterrensis* Colom – Lutze & Coulbourn, p. 390.
1986 *Uvigerina mediterranea* Hofker – Borsetti et al., p. 213, pl. 9, figs. 1-5.
1986 *Uvigerina mediterranea* Hofker – Lutze, p. 41, pl. 5, figs. 1-7.
1986 *Uvigerina mediterranea* Hofker – Van Morkhoven et al., pp. 16, 18, pl. 1, figs. 1-2.
1991 *Uvigerina mediterranea* Hofker – Cimerman & Langer, p. 63, pl. 65, figs. 7-9.
1992 *Uvigerina mediterranea* Hofker – Schiebel, p. 59, pl. 3, fig.7.
1993 *Uvigerina mediterranea* Hofker – Sgarrella & Moncharmont Zei, pp. 214-215, pl. 16, figs. 1-2.
1999 *Uvigerina mediterranea* Hofker – Villanueva Guimerans & Cervera Currado, Bol. Inst. Esp. Oceanogr. 15, p. 195, fig. 2.2a-c.
2001 *Uvigerina mediterranea* Hofker – Jannink, Geol. Ultraiectina, 203, pl. 3, fig. 3.
2002 *Uvigerina mediterranea* Hofker – Ernst, Geol. Ultraiectina, 220, p. 87, pl. 1, figs. P-Q.
2003 *Uvigerina mediterranea* Hofker – Fontanier, PhD thesis, pl. 10, figs. M, N, Q, R.

Original designation: *Uvigerina mediterranea* Hofker, 1932
Stratigraphic range: late Pliocene-Recent
Geographical occurrence: Mediterranean, east(?) Atlantic
Bathymetry: outer neritic-middle bathyal
This large and stout species has inflated chambers and a neck standing in a depression (Pl. 16). It is ornamented with smooth costae; no spines are present, although the neck bears sometimes pustules. The distinction from *U. peregrina* is sometimes difficult, particularly with juvenile *U. mediterranea* and/or completely costate *U. peregrina*.

Uvigerina peregrina Cushman, 1923

1923 *Uvigerina peregrina* – Cushman, p. 166, pl. 42, figs. 7-10.
1927 *Uvigerina peregrina* Cushman – Galloway & Wissler, p. 76, pl. 12, figs. 1, 2a-b.
1947 *Uvigerina peregrina* Cushman – Höglund, pp. 279-283, pl. 23, fig. 9, text-figs. 191-304.
1951 *Euuvigerina peregrina* (Cushman) – Hofker, pp. 219-226.
1951 *Uvigerina peregrina* Cushman – Phleger & Parker, p. 18, pl. 8, figs. 22, 24-26.
1956 *Euuvigerina peregrina* (Cushman) – Hofker, pp. 82-84, pl. 9, figs. 14-19.
1958 *Uvigerina peregrina* Cushman – Parker, p. 263, pl. 2, figs. 37-38.
1959 *Uvigerina peregrina* Cushman – Dieci, p. 70, pl. 6, fig. 2.
1960 *Euuvigerina peregrina* (Cushman) – Barker, p. 154, pl. 74, figs. 11-12.
1960 *Uvigerina bifurcata* (d'Orbigny) – Barker, p. 154, pl. 74, figs. 13-14.
1960 *Uvigerina bradyana* Fornasini – Barker, p. 156, pl. 74, figs. 24-26.
1960 *Uvigerina peregrina* Cushman – Christodoulou, p. 50, pl. 16, fig. 31.
1964 *Uvigerina hispido-costata* Cushman & Todd – Leroy, p. 35, pl. 16, fig. 7.
1964 *Uvigerina peregrina* Cushman var. *dirupta* Todd – Leroy, p. 34, pl. 4, fig. 4.
1969 *Uvigerina peregrina* Cushman – Blanc-Vernet, p. 203.
1971 *Uvigerina peregrina* Cushman – Murray, p. 121, pl. 50, fig. 1-7.
1971 *Uvigerina peregrina* Cushman – Verhoeve, p. 202, pl. 9, fig. 16.
1973 *Uvigerina peregrina* Cushman – Douglas, pl. 8, figs. 4-6, 9.
1976 *Uvigerina peregrina mediterranea* Hofker – Pflum and Frerichs, pl. 8, fig. 1.
1976 *Uvigerina peregrina* Cushman var. *dirupta* Todd – Pflum & Frerichs, pl. 8, figs. 4-5.
1976 *Uvigerina peregrina* Cushman var. *peregrina* Cushman – Pflum & Frerich, pl. 8, figs. 2-3.
1978 *Uvigerina peregrina* Cushman – Brolsma, pl. 1, fig. 13.
1978 *Uvigerina peregrina* Cushman – Lohmann, p. 26, pl. 4, figs. 14-15.

1979 *Uvigerina peregrina* Cushman – Hageman, pp. 107-108, pl. 10, fig. 5.
1980 *Uvigerina peregrina* Cushman – Boltovskoy et al., p. 53, pl. 34, figs. 15-16.
1980 *Uvigerina peregrina* Cushman – Bremer et al., pl. 2, figs. 2-3.
1981 *Uvigerina peregrina* Cushman – Sejrup et al., pl. 2, fig. 12.
1982 *Uvigerina peregrina* Cushman – Agip, p. 34, fig. 1.
1982 *Uvigerina peregrina* Cushman – Van der Zwaan, p. 154, pl. 11, fig. 9.
1982 *Uvigerina peregrina* Cushman – Miller & Lohmann, pl. 1, figs.11-12.
1984 *Uvigerina peregrina* Cushman – Boersma, pl. 7, fig. 6.
1985 *Uvigerina peregrina* Cushman – Kohl, pp. 73-74, pl. 24, fig. 7.
1985 *Uvigerina peregrina* Cushman – Mead, p. 229, pl. 1, figs. 7-10.
1986 *Uvigerina peregrina* Cushman – Lutze, p. 33, pl. 1, figs. 1-6.
1986 *Uvigerina peregrina* Cushman – Van Leeuwen, p. 59, pl. 1, figs. 1-5.
1989 *Uvigerina peregrina* Cushman – Hermelin, pp. 66-67, pl. 12, figs. 6-8.
1990 *Uvigerina peregrina* Cushman – Galluzzo et al., pl 2, fig. 17.
1991 *Uvigerina peregrina* Cushman – Corliss, pl. 1, fig. 17.
1991 *Uvigerina peregrina* Cushman – Verhallen, p. 153, pl. 8, figs. 1-5, pl. 9.
1992 *Uvigerina peregrina* Cushman – Spencer, pl. 1, figs. 19-21.
1992 *Uvigerina peregrina* Cushman – Timm, pp. 67-68, pl. 6, fig. 2.
1993 *Uvigerina peregrina* Cushman – Katz & Miller, pl. 4, fig. 9a-b.
1993 *Uvigerina peregrina* Cushman – Sgarella & Moncharmont Zei, p. 215, pl. 16, fig. 5.
1994 *Uvigerina bifurcata* d'Orbigny – Jones, p. 86, pl. 74, figs. 13-14.
1994 *Uvigerina bradyana* Fornasini – Jones, p. 86, pl. 74, figs. 24-26.
1994 *Uvigerina mediterranea* Hofker – Jones, p. 86, pl. 74, figs. 11-12.
1994 *Uvigerina hispido-costata* Cushman & Todd – Gupta, pl. 3, figs. 11-13.
1994 *Uvigerina peregrina* Cushman – Gupta, pl. 3, figs. 14-15.
1999 *Uvigerina peregrina* Cushman – Villanueva Guimerans & Cervera Currado, Bol. Inst. Esp. Oceanogr. 15, p. 195, fig. 2.1a-c.
2000 *Uvigerina peregrina* Cushman – Den Dulk, pl. 2, figs. 10-11.
2000 *Uvigerina peregrina* Cushman – Kouwenhoven, p. 197, pl. 11, figs. 1-2.
2001 *Uvigerina peregrina* Cushman – Jannink, Geol. Ultraiectina, 203, pl. p. 159, fig. 6.
2002 *Uvigerina peregrina* Cushman – Ernst, Geol. Ultraiectina, 220, pl. 1, figs. R-S (non P-Q).
2003 *Uvigerina peregrina* Cushman – Langezaal, Geol. Ultraiectina, 229, pl. 7.5, figs. 1-2.
2003 *Uvigerina peregrina* Cushman – Murray, fig. 10, 6.
2005 *Uvigerina peregrina* Cushman – Licari & Mackensen, pl. 1, figs. 1-2.

Original designation: *Uvigerina peregrina* Cushman, 1923
Stratigraphic range: early Oligocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: neritic-abyssal
This relatively small species possesses a test which is widest in the middle (Pl. 17). The neck stays at the top of the last chamber. The proloculus and the last chamber are often spinose, but completely costate specimens also occur (see Fig. 6.6). The ornamentation presents a wide variability, from costae to spines with specimens at both extremes. Costate specimens can be hard to distinguish from *U. mediterranea*.

Uvigerina phlegeri (Le Calvez, 1959)

1953 *Rectuvigerina* sp. – Phleger et al., p. 38, pl. 8, fig. 8.
1959 *Rectuvigerina phlegeri* – Le Calvez, Rec. Trav. Inst. Pêches Maritimes, 23, p. 263, pl. 1, fig. 11.
1961 *Rectuvigerina raricosta* – Moncharmont Zei, Boll. Soc. Nat. Napoli, 69, pp. 149-150, pl. 4, figs. 18-20.
1980 *Rectuvigerina phlegeri* Le Calvez – Haake, p. 13, pl. 2, fig. 32.
1980 *Rectuvigerina phlegeri* Le Calvez – Lutze, p. 42.
1988 *Rectuvigerina phlegeri* Le Calvez – Alavi, Mar. Micropal., 13, pl. 1, fig. 4.
1992 *Rectuvigerina phlegeri* Le Calvez – Schiebel, pl. 3, figs 10a-d.
1993 *Rectuvigerina phlegeri* Le Calvez – Sgarrella & Moncharmont Zei, p. 215, pl. 16, figs. 3-4.
1999 *Rectuvigerina phlegeri* Le Calvez – Villanueva Guimerans & Cervera Currado, Bol. Inst. Esp. Oceanogr. 15, p. 198-199, fig. 5.5a-c.
2003 *Rectuvigerina phlegeri* Le Calvez – Fontanier, PhD thesis, pl. 10, fig. A.
2003 *Rectuvigerina phlegeri* Le Calvez – Langezaal, Geol. Ultraiectina, 229, p. 207, pl. 7-5, figs. 3-4.

Original designation: *Rectuvigerina phlegeri* Le Calvez, 1959
Stratigraphic range: Quaternary
Geographical occurrence: Mediterranean, east Atlantic (Gulf of Guinea-Bay of Biscay)
Bathymetry: neritic
Uvigerina phlegeri is a small species with an early triserial stage becoming rapidly uniserial (Pl. 18). It is ornamented with costae that continue as spines at the limit between chambers.

Uvigerina proboscidea Schwager, 1866

1866 *Uvigerina proboscidea* - Schwager, p. 250, pl. 7, fig. 96.
1884 *Uvigerina asperula* var. *ampullacea* – Brady, pl. 74, figs. 10-11.
1923 *Uvigerina ampullacea* (Brady) – Cushman, p. 162, pl. 42, figs. 5-6.

1933 *Uvigerina proboscidea* Schwager var. *vadescens* – Cushman, p.85 pl. 8, figs. 14-15.
1959 *Uvigerina proboscidea* Schwager – Dieci, p. 70, pl. 6, fig. 3.
1960 *Neouvigerina ampullacea* (Brady) – Barker, p. 156, pl. 75, figs. 10-11
1960 *Uvigerina asperula* Czjzek – Barker, p. 156, pl. 75, figs. 6-9.
1960 *Uvigerina proboscidea* Schwager – Christodoulou, p. 51, pl. 16, figs. 17-18.
1964 *Uvigerina proboscidea* Schwager – Leroy, p. 35, pl. 16, fig. 8.
1964 *Uvigerina proboscidea* Schwager va.r *vadescens* Cushman – Leroy, p. 35, pl. 3, fig. 38.
1973 *Uvigerina proboscidea* Schwager – Douglas, pl. 8, fig. 8.
1978 *Uvigerina auberiana* d'Orbigny – Lohmann, pl. 4, fig. 16.
1978 *Uvigerina proboscidea* Schwager – Boltovskoy, pl. 8, figs. 22-23.
1978 *Uvigerina proboscidea* Schwager – Brolsma, pl. 1, fig. 14.
1980 *Uvigerina proboscidea* Schwager – Thomas, p. 163, pl. 3, fig. 2a.
1982 *Uvigerina proboscidea* Schwager – Agip, pl. 34, fig. 2.
1984 *Uvigerina proboscidea* Schwager – Boersma, pl. 8, fig. 3.
1984 *Uvigerina proboscidea* Schwager – Jonkers, pl. 4, fig. 7.
1986 *Uvigerina proboscidea* Schwager – Boersma, pl. 20, fig. 2.
1986 *Uvigerina proboscidea* Schwager – Van Morkhoven et al., pp. 28, 30, pl. 6, figs. 1-4.
1986 *Uvigerina proboscidea* Schwager - Borsetti et al., p. 218, pl. 12, figs. 1-4.
1991 *Uvigerina proboscidea* Schwager – Verhallen, p. 156, pl. 23, fig. 6.
1993 *Uvigerina proboscidea* Schwager – Katz & Miller, pl. 4, fig. 8a-b.
1994 *Neouvigerina ampullacea* (Brady) – Loeblich & Tappan, p. 126, pl. 246, figs. 9-19.
1994 *Siphouvigerina ampullacea* (Brady) – Jones, pp. 86-87, pl. 75, figs. 10-11.
1997 *Uvigerina proboscidea* Schwager – Resig & Cheong, p. 439, pl. 1, fig. 10.
2000 *Uvigerina proboscidea* Schwager – Den Dulk, pl. 2, fig. 9.
2000 *Uvigerina proboscidea* Schwager – Kouwenhoven, pl. 11, fig. 4.

Original designation: *Uvigerina proboscidea* Schwager, 1866
Stratigraphic range: late Oligocene-Recent
Geographical occurrence: cosmopolitan
Bathymetry: bathyal-abyssal
This small species is completely hispid (Pl. 13). The earlier part is usually broader and the test becomes more slender during growth. The last chamber has often a particular bottle-like shape, with a long neck extending from a narrow chamber.

Uvigerina rutila Cushman & Todd, 1941

1941 *Uvigerina rutila* – Cushman & Todd, Contr. Cushm. Lab. Foram. Res., 17 (2), p. 78, pl. 20, figs. 16-22.
1953 *Uvigerina rutila* Cushman & Todd – Gianotti, p. 264, pl. 13, fig. 5.
1957 *Uvigerina rutila* Cushman & Todd – Agip, Foram. Padani, pl. 34, fig. 5.
1959 *Uvigerina rutila* Cushman & Todd – Dieci, p. 71, pl. 6, fig. 6.
1960 *Uvigerina flintii* (not Cushman) – Christodoulou, p. 50, pl. 16, fig. 27.
1965 *Uvigerina rutila* Cushman & Todd – Souaya, p. 331, pl. 2, fig. 18
1970 *Uvigerina rutila* Cushman & Todd – Verdenius, pl. 5, fig. 2.
1971 *Uvigerina rutila* Cushman & Todd – Verhoeve, p. 203, pl. 9, fig. 17.
1980 *Uvigerina rutila* Cushman & Todd – Thomas, pl. 3, fig. 1.
1982 *Uvigerina rutila* Cushman & Todd – Agip, pl. 34, fig. 5.
1984 *Uvigerina rutila* Cushman & Todd – Jonkers, pl. 4, fig. 4.
2000 *Uvigerina rutila* Cushman & Todd – Kouwenhoven, pl. 11, fig. 8.

Original designation: *Uvigerina rutila* Cushman & Todd, 1941
Stratigraphic range: middle Miocene-early Pliocene
Geographical occurrence: Mediterranean, east Atlantic (?), Indian Ocean (?)
Bathymetry: upper-middle bathyal
Uvigerina rutila is a large and inflated species (Pl. 19). The neck is set in a depression. The ornamentation is composed of low and scarce costae and the last chamber is often smooth.

Uvigerina semiornata d'Orbigny, 1846

1846 *Uvigerina semiornata* – d'Orbigny, p. 189, pl. 11, figs. 23-24.
1846 *Uvigerina urnula* – d'Orbigny, p. 189, pl. 11, figs. 21-22.
1884 *Uvigerina canariensis* not d'Orbigny – Brady, pl. 74, figs. 1-3.
1978 *Uvigerina semiornata* d'Orbigny – Papp & Schmid, Chronostrat. Neostrat., Baden., p. 281, pl. 10, figs. 4-7.

Original designation: *Uvigerina semiornata* d'Orbigny, 1846
Stratigraphic range: early-late Miocene
Geographical occurrence: Mediterranean, east Atlantic (?), Indian Ocean (?)
Bathymetry: neritic-upper bathyal
This is also a large species with the neck placed in a depression (Pl. 19). The distinction with *U. rutila* and *U. striatissima* is mainly based on the

stratigraphical position and the number of costae per chamber. *Uvigerina semiornata* has a medium number of costae and the costae are often heavier than in the other two species.

Uvigerina striatissima Perconig, 1955

1955 *Uvigerina longistriata* – Perconig, p. 182, pl. 2, figs. 1-4.
1955 *Uvigerina striatissima* – Perconig, p. 187, pl. 3, figs. 1-4.
1984 *Uvigerina longistriata* Perconig – Jonkers, p. 136, pl. 4, fig. 8.
2000 *Uvigerina striatissima* Perconig – Kouwenhoven, pl. 11, fig. 7.

Original designation: *Uvigerina striatissima* Perconig, 1955
Stratigraphic range: middle Miocene-early Pliocene
Geographical occurrence: Mediterranean, east Atlantic (?), Indian Ocean (?)
Bathymetry: upper-middle bathyal
Uvigerina striatissima is a large and stout species with the neck placed in a depression (Pl. 19). The distinction with *U. rutila* and *U. semiornata* is mainly based on the stratigraphical position and the number of costae per chamber. This is the species with the highest number of costae per chamber.

Appendix 2

Localization of sampled specimens

N° ADN	Species	ADN	Region	Station	Depth	Latitude	Longitude
C1	*C. lobatulus*	no	Iceland	Sandgerdi	shallow water		
C2	*C. lobatulus*	yes	Iceland	Sandgerdi	shallow water		
C10	*C. pachyderma*	no	Bay of Biscay	IIP			
C12	*C. pachyderma*	no	Bay of Biscay	IIP			
C14	*C. pachyderma*	no	Bay of Biscay	IIQ (2 core)			
C15	*C. pachyderma*	no	Bay of Biscay	IIQ (1 core)			
C16	*C. kullenbergi*	no	Bay of Biscay	IIQ (1 core)			
C18	*C. ungerianus*	no	Bay of Biscay	IIQ (1 core)			
C19	*C. pseudoungerianus*	no	Bay of Biscay	IIQ (1 core)			
C22	*C. lungerianus*	no	Bay of Biscay	IIQ (1 core)			
C24	*C. lobatulus*	yes	Norway	2	54m	59º 39.1`N	10º 37.0`E
C29	*C. ungerianus*	yes	Norway	1	195m	59º 38.2`N	10º 37.3`E
C31	*C. ungerianus*	no	Norway	4	350m	59º 14.9`N	10º 37.1`E
C34	*C. lobatulus*	no	Norway	2	54m	59º 39.1`N	10º 37.0`E
C35	*C. lobatulus*	yes	Norway	2	54m	59º 39.1`N	10º 37.0`E
C37	*C. lobatulus*	yes	Norway	2	54m	59º 39.1`N	10º 37.0`E
C38	*C. refulgens*	no	Norway	2	54m	59º 39.1`N	10º 37.0`E
C39	*C. lobatulus*	yes	Norway	2	54m	59º 39.1`N	10º 37.0`E
C40	*C. lobatulus*	yes	Norway	2	54m	59º 39.1`N	10º 37.0`E
C78	*C. refulgens*	yes	Gulf of Lions	Canyon du Planier	1000m		
C86	*C. kullenbergi-pachyderma*	yes	Nazaré Canyon	station 56	338m	39°38.91'N	09°14.71'W
C87	*C. kullenbergi-pachyderma*	yes	Nazaré Canyon	station 56	338m	39°38.91'N	09°14.71'W
C106	*C. kullenbergi-pachyderma*	no	Gulf of Lions	Canyon du Marti	1000m		
C107	*C. kullenbergi-pachyderma*	no	Gulf of Lions	Canyon du Planier	1000m		
C108	*C. kullenbergi-pachyderma*	no	Gulf of Lions	Canyon du Planier	1000m		
C110	*C. lobatulus*	no	Gulf of Lions	Canyon du Planier	1000m		
C114	*C. pachyderma*	no	Gulf of Lions	Canyon du Planier	1000m		
C120	*C. lobatulus*	yes	Skagerrak-Kattegat	SK23	32m	58°20.8N	11°24.1E
C131	*C. ungerianus*	no	Skagerrak-Kattegat	SK17	42-43m	58°42.05N	11°10.82E
C137	*C. wuellerstorfi*	no	Bay of Biscay	FP 1a	3000m		
C140	*C. wuellerstorfi*	no	Finisterre (Spain)	FP 4a(1)	2122m	42°55'N	90°52'30W
C142	*C. pseudoungerianus*	no	Bay of Biscay	FP 1b	3000m		
C143	*C. wuellerstorfi*	no	Bay of Biscay	FP 2b	4800m		
C147	*C. wuellerstorfi*	no	Finisterre (Spain)	FP 3c	1002m		
C159	*C. pseudoungerianus*	no	Finisterre (Spain)	FP 6-2	1750m		
C163	*C. wuellerstorfi*	no	Finisterre (Spain)	FP 7a	2600m		
C170	*C. lobatulus*	yes	Gulf of Lions	Marseille	shallow water		
C171	*C. refulgens*	yes	Gulf of Lions	Marseille	shallow water		
C172	*C. refulgens*	yes	Gulf of Lions	Marseille	shallow water		
C173	*C. refulgens*	yes	Gulf of Lions	Marseille	shallow water		

C176	*C. refulgens*	yes	Gulf of Lions	Marseille	shallow water		
C183	*C. wuellerstorfi*	no	Setubal Canyon	station 20	2774m	38°12.02'N	09°31.71'W
C184	*C. wuellerstorfi*	yes	Setubal Canyon	station 20	2774m	38°12.02'N	09°31.71'W
C186	*C. kullenbergi*	no	Setubal Canyon	station 16	430m	38°16.00'N	08°56.00'W
C187	*C. kullenbergi*	no	Setubal Canyon	station 18	1605m	38°16.44'N	09°12.00'W
C195	*C. kullenbergi*	no	Portuguese coast	?			
C196	*C. pachyderma*	yes	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
C198	*C. pseudoungerianus*	no	Setubal Canyon	station 18	1605m	38°16.44'N	09°12.00'W
C199	*C. pseudoungerianus*	no	Setubal Canyon	station 18	1605m	38°16.44'N	09°12.00'W
C208	*C. kullenbergi?*	yes	Gulf of Lions	Marseille	shallow water		

N° ADN	Species	ADN	Region	Station	Depth	Latitude	Longitude
U3	*U. mediterranea*	no	Iceland	3257			
U4	*U. mediterranea*	no	Iceland	3257			
U9	*U. mediterranea*	no	Bay of Biscay	IIP			
U13	*U. elongatastriata*	no	Bay of Biscay	IIP			
U14	*U. mediterranea*	no	Bay of Biscay	IIQ			
U26	*U. peregrina*	yes	Norway	1	195m	59º 38.2'N	10º 37.3'E
U27	*U. peregrina*	yes	Norway	1	195m	59º 38.2'N	10º 37.3'E
U32	*U. peregrina*	yes	Norway	1	195m	59º 38.2'N	10º 37.3'E
U34	*U. peregrina*	no	Norway	1	195m	59º 38.2'N	10º 37.3'E
U35	*U. peregrina*	no	Norway	1	195m	59º 38.2'N	10º 37.3'E
U36	*U. peregrina*	no	Norway	1	195m	59º 38.2'N	10º 37.3'E
U37	*U. peregrina*	yes	Norway	1	195m	59º 38.2'N	10º 37.3'E
U38	*U. peregrina*	no	Norway	1	195m	59º 38.2'N	10º 37.3'E
U39	*U. peregrina*	no	Norway	1	195m	59º 38.2'N	10º 37.3'E
U40	*U. peregrina*	no	Norway	5	140m	59°43.0'N	10° 35.0'E
U41	*U. peregrina*	no	Norway	5	140m	59°43.0'N	10° 35.0'E
U42	*U. peregrina*	yes	Norway	1	195m	59º 38.2'N	10º 37.3'E
U43	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U44	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U45	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U46	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U47	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U48	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U49	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U50	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U51	*U. peregrina*	yes	Norway	2	54m	59º 39.1'N	10º 37.0'E
U52	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U53	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U54	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U55	*U. peregrina*	no	Norway	2	54m	59º 39.1'N	10º 37.0'E
U56	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U57	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U58	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U59	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U60	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U61	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U62	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U63	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U64	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U65	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U66	*U. peregrina*	yes	Norway	3	87m	59° 17.9'N	10° 32.7'E
U67	*U. peregrina*	yes	Norway	3	87m	59° 17.9'N	10° 32.7'E
U68	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U69	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U70	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U71	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E

U72	*U. peregrina*	yes	Norway	3	87m	59° 17.9'N	10° 32.7'E
U73	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U74	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U75	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U76	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U77	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U78	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U79	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U80	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U81	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U82	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U83	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U84	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U85	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U86	*U. peregrina*	yes	Norway	3	87m	59° 17.9'N	10° 32.7'E
U87	*U. peregrina*	yes	Norway	3	87m	59° 17.9'N	10° 32.7'E
U88	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U89	*U. peregrina*	no	Norway	3	87m	59° 17.9'N	10° 32.7'E
U154	*U. mediterranea*	no	Gulf of Lions	Canyon du Marti	1000m		
U155	*U. mediterranea*	no	Gulf of Lions	Canyon du Planier	1000m		
U156	*U. mediterranea*	no	Gulf of Lions	Canyon du Marti	1000m		
U157	*U. mediterranea*	no	Gulf of Lions	Canyon du Marti	1000m		
U169	*U. peregrina*	yes	Skagerrak-Kattegat	SK13	91-92m	58°52,08'N	11°06.75'E
U184	*U. peregrina*	yes	Skagerrak-Kattegat	SK11	59-60m	58°58.15'N	11°05.43'E
U194	*U. peregrina*	yes	Skagerrak-Kattegat	SK11	59-60m	58°58.15'N	11°05.43'E
U195	*U. peregrina*	yes	Skagerrak-Kattegat	SK11	59-60m	58°58.15'N	11°05.43'E
U218	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U219	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U220	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U224	*U. mediterranea*	no	Setubal Canyon	station 16	430m	38°16.00'N	08°56.00'W
U225	*U. elongatastriata*	no	Setubal Canyon	station 16	430m	38°16.00'N	08°56.00'W
U234	*R. phlegeri*	no	Setubal Canyon	station 21	498m	38°29.99'N	09°16.03'W
U235	*U. mediterranea*	no	Setubal Canyon	station 18	1605m	38°16.44'N	09°12.00'W
U236	*U. elongatastriata*	no	Setubal Canyon	station 18	1605m	38°16.44'N	09°12.00'W
U237	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U238	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U239	*R. phlegeri*	yes	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U240	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U241	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U242	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U243	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U244	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U245	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U246	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U247	*U. elongatastriata*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U248	*U. elongatastriata*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U254	*U. elongatastriata*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W

U255	*U. elongatastriata*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U256	*R. phlegeri*	no	Nazaré Canyon	station 5	321m	39°38.80'N	09°15.00'W
U264	*U. mediterranea*	no	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
U269	*U. elongatastriata*	no	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
U270	*U. elongatastriata*	no	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
U271	*U. elongatastriata*	no	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
U272	*U. elongatastriata*	no	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W
U273	*U. elongatastriata*	yes	Nazaré Canyon	station 57	151m	39°38.50'N	09°16.99'W

Plates

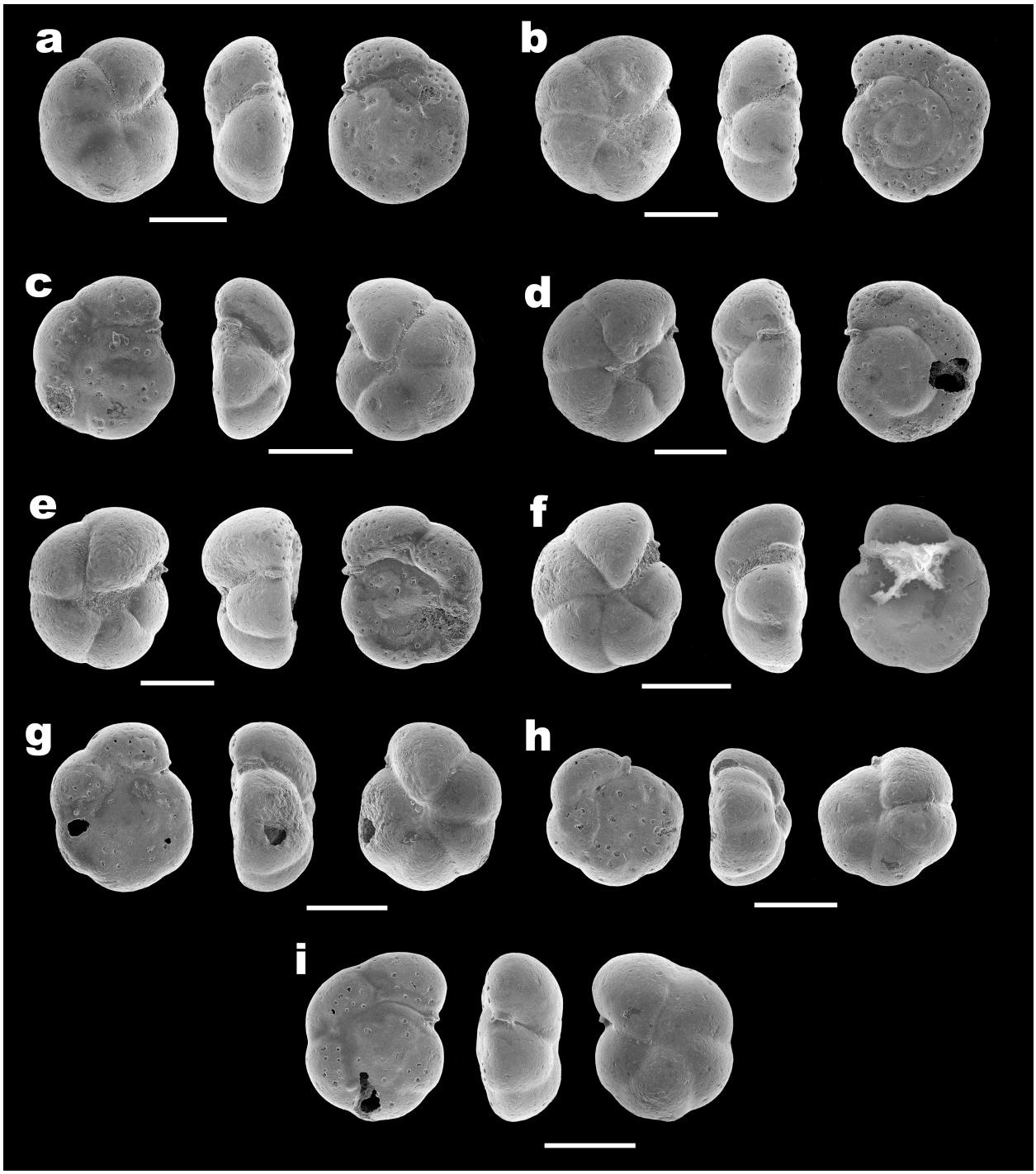

Plate 1. SEM pictures of *Cibicides bradyi* (umbilical/spiral sides and axial profile).
a-f) 7.5Ma, g-i) 7.0Ma.
Scale= 100µm

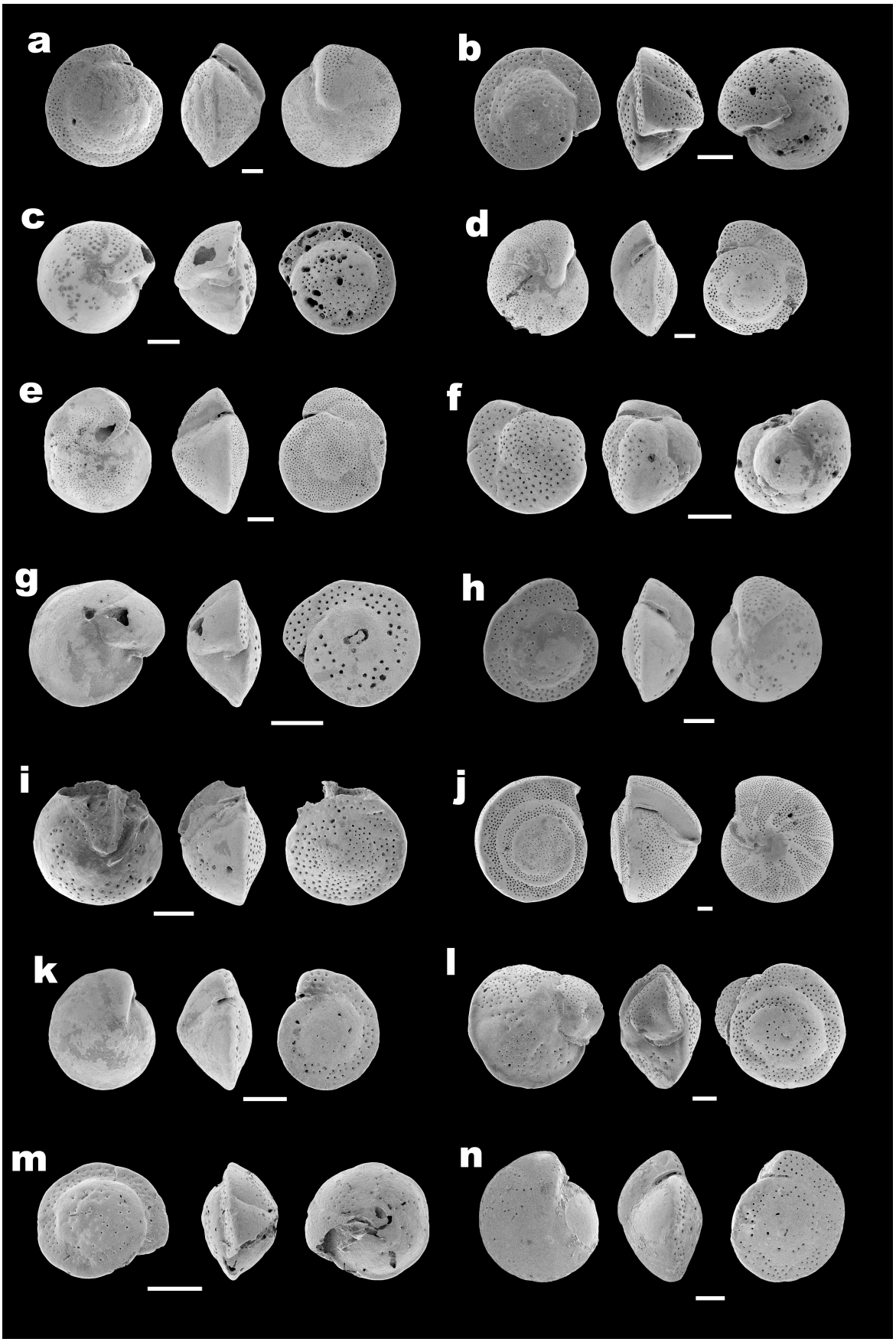

Plate 2. SEM pictures of *Cibicides dutemplei* (umbilical/spiral sides and axial profile).
a-b) 14.5Ma, c-k) 13.5Ma, l-n) 5.0Ma.
Scale= 100µm

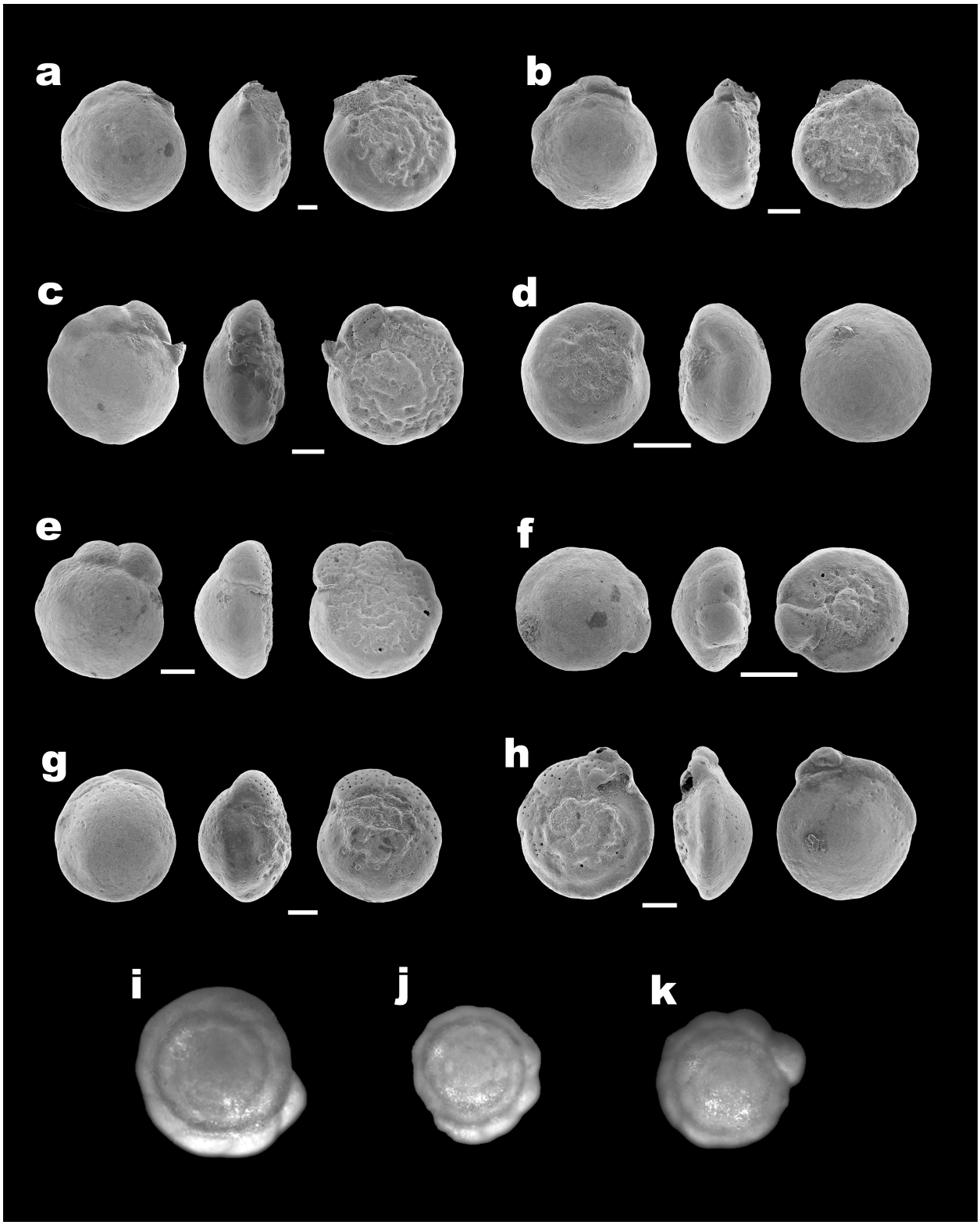

Plate 3. SEM pictures of *Cibicides italicus* (umbilical/spiral sides and axial profile).
a-f) 8.5Ma, g-h) 7.0Ma.
Light photomicrographs of the spiral side, i-k) 8.5Ma.
Scale= 100μm

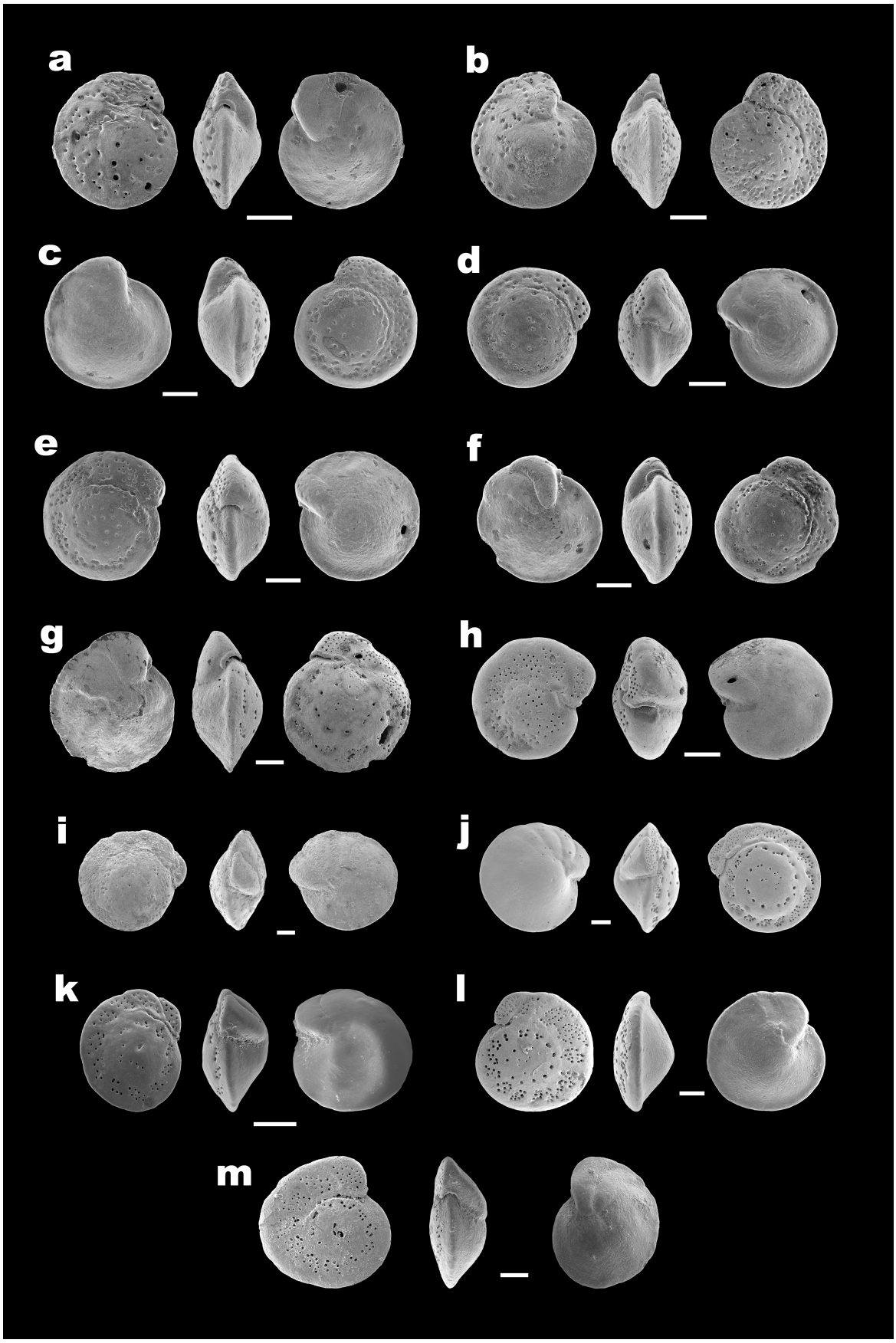

Plate 4. SEM pictures of *Cibicides kullenbergi* (umbilical/spiral sides and axial profile).
a-b) 14.5Ma, c-f) 7.0Ma, g-h) 5.5Ma, i-m) Recent, i) C16, j) C107, k) C186, l) C187, m) C195.
Scale= 100μm

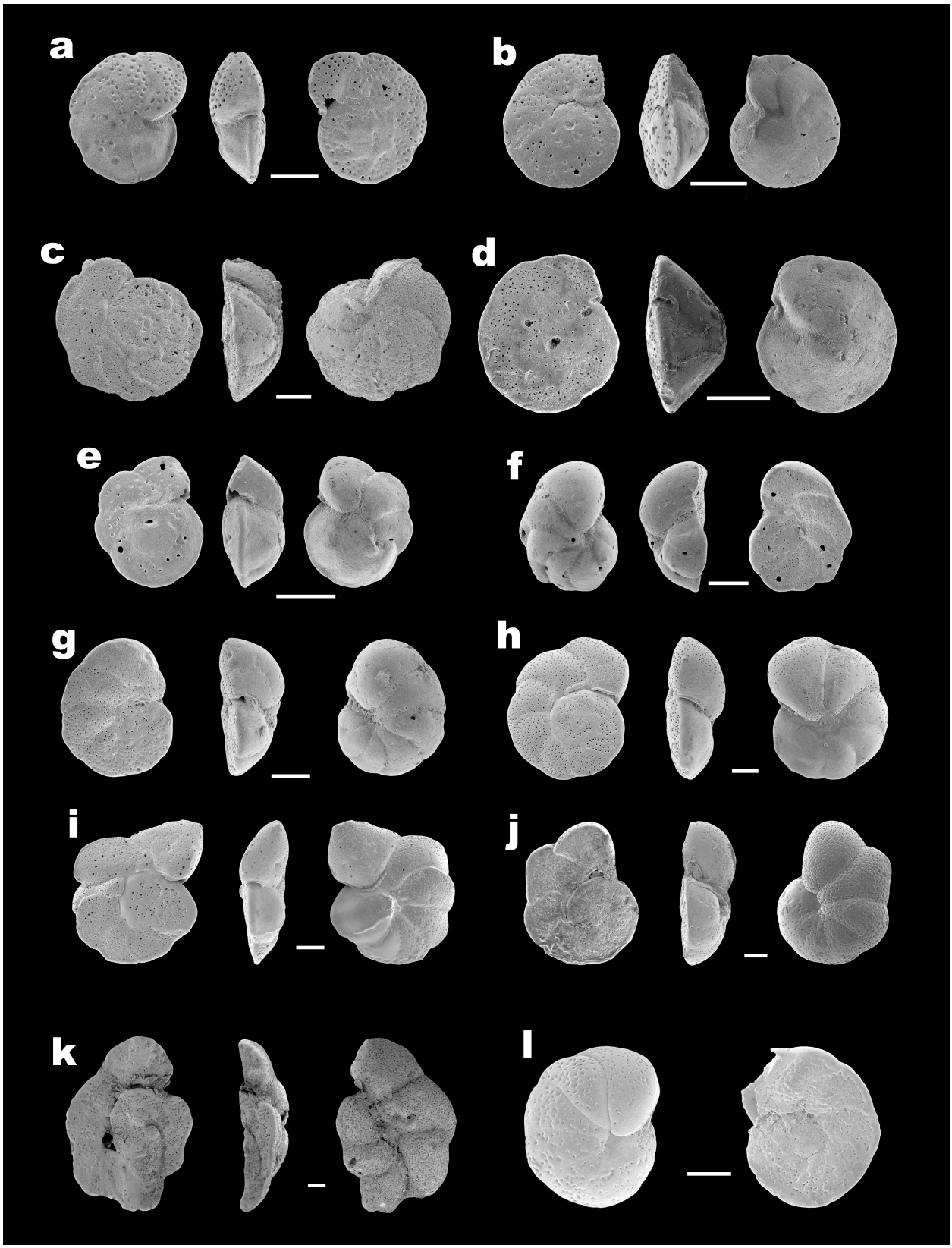

Plate 5. SEM pictures of *Cibicides lobatulus* (umbilical/spiral sides and axial profile).
a-b) 14.5Ma, c-d) 14.0Ma, e-g) 5.0Ma, h) 1.0Ma, i-l) Recent, i) C110, j) C1, k) C34, l) C120.
Scale= 100μm

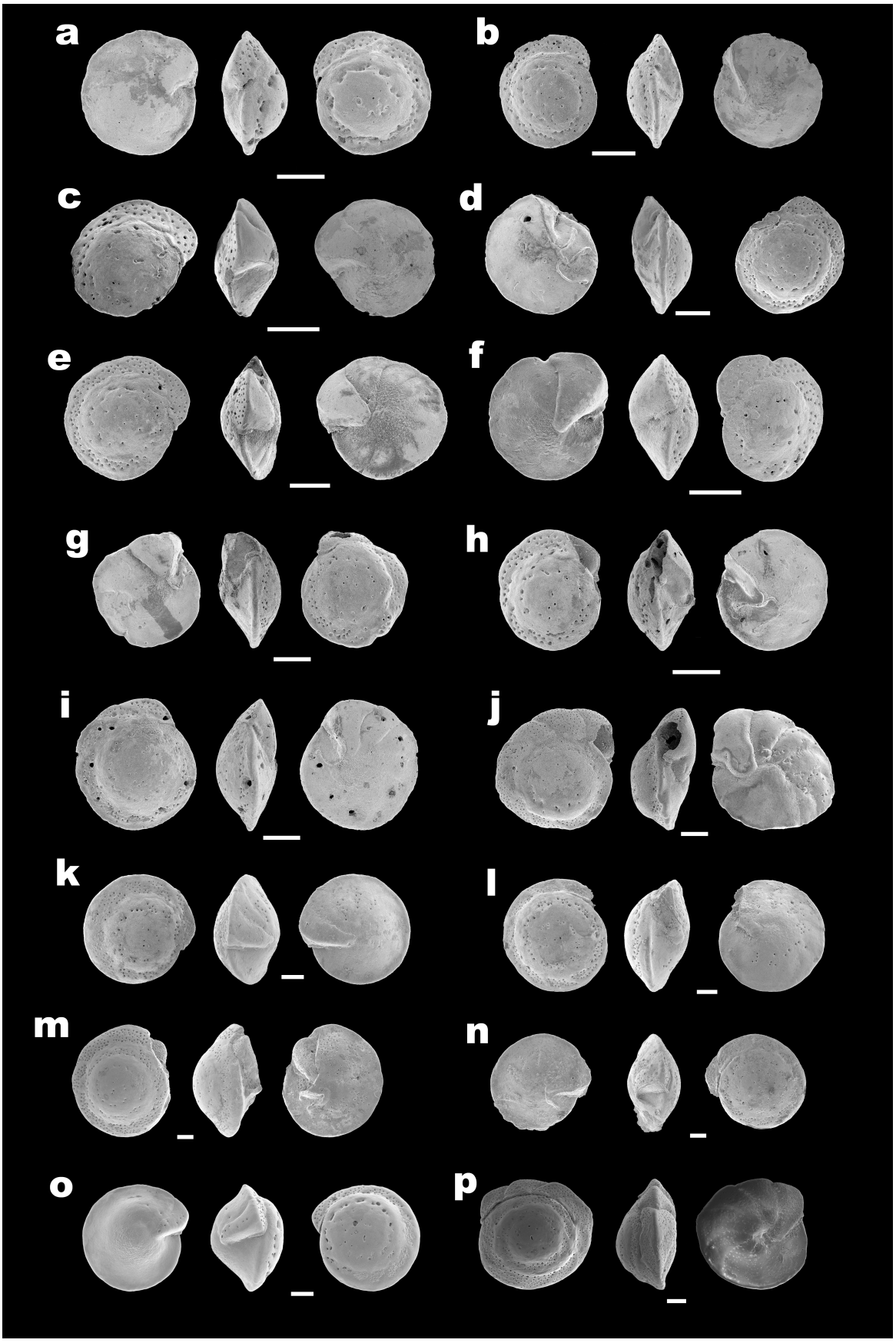

Plate 6. SEM pictures of *Cibicides pachyderma* (umbilical/spiral sides and axial profile). a-i) 6.0Ma, j) 1.0Ma, k-p) Recent, k) C10, l) C12, m) C14, n) C15, o) C114, p) C196. Scale= 100μm

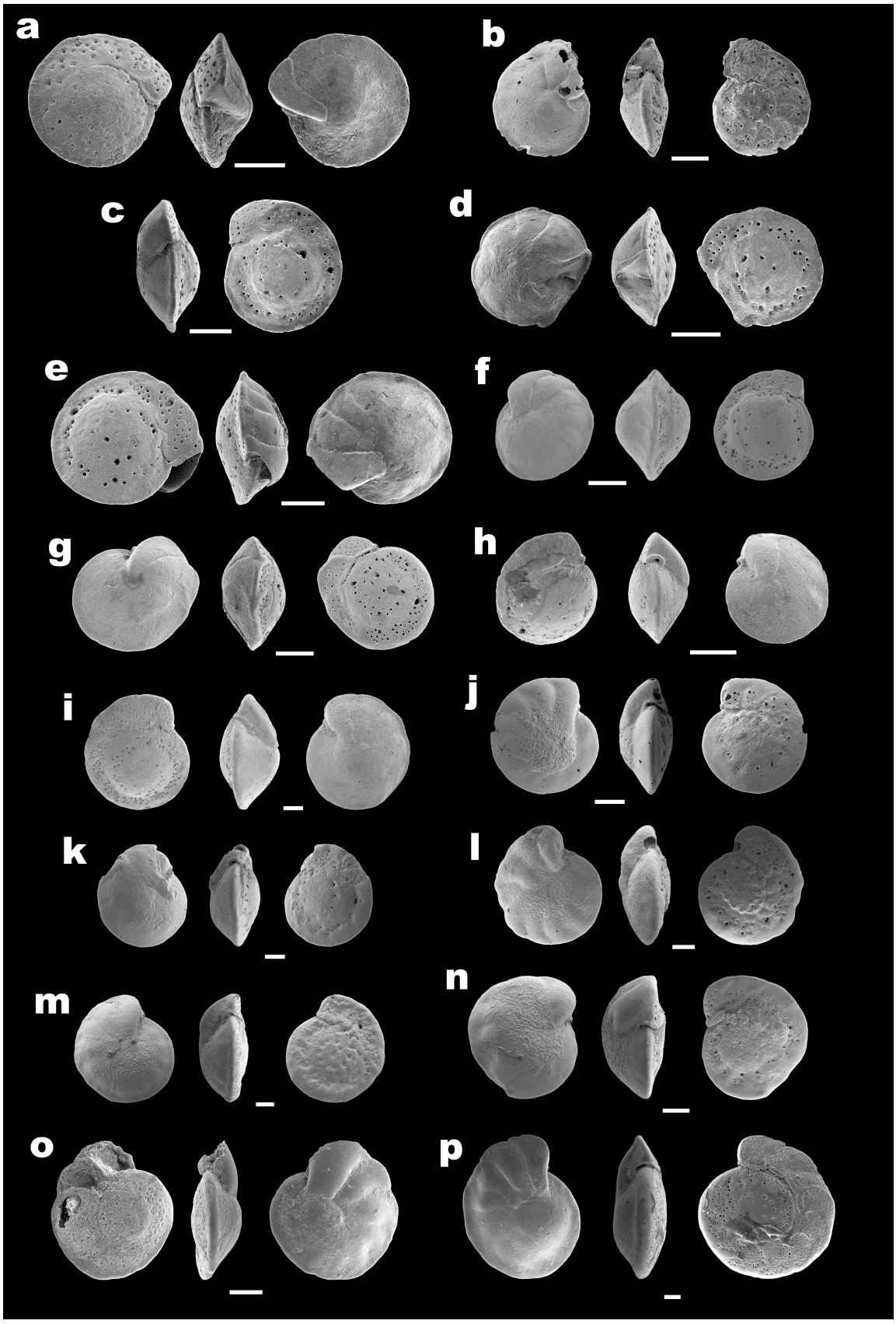

Plate 7. SEM pictures of *Cibicides pseudoungerianus* (umbilical/spiral sides and axial profile).
a-b) 14.0Ma, c-e) 5.5Ma, f-h) 5.0Ma, i-p) Recent, i) C19, j) C142, k) C159b, l) C159c, m) C159i, n) C159j, o) C198, p) C199.
Scale= 100μm

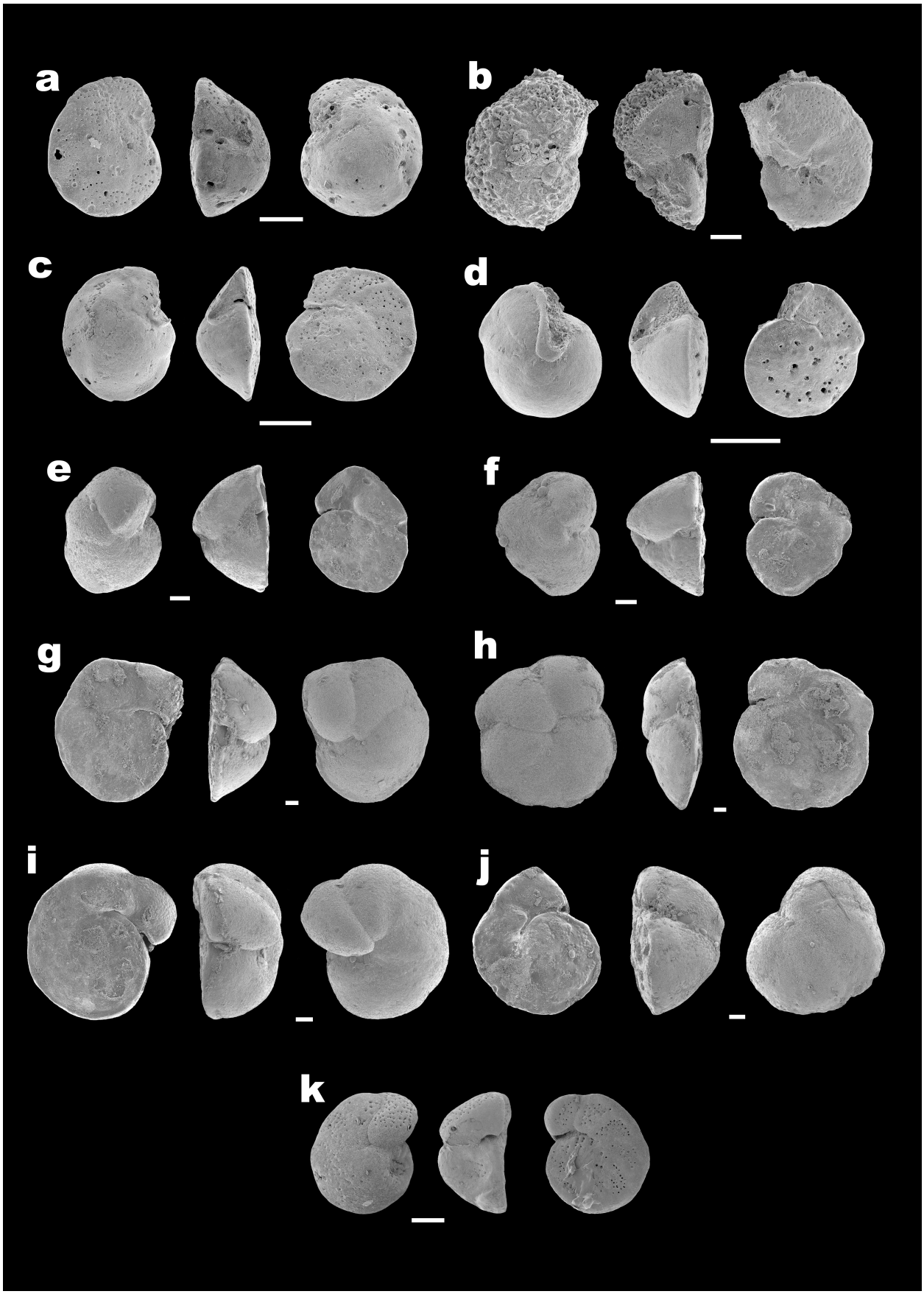

Plate 8. SEM pictures of *Cibicides refulgens* (umbilical/spiral sides and axial profile).
a-c) 15.0Ma, d) 5.0Ma, e-l) Recent, e-j) Mc Murdo Sound, Antarctica, k) C38.

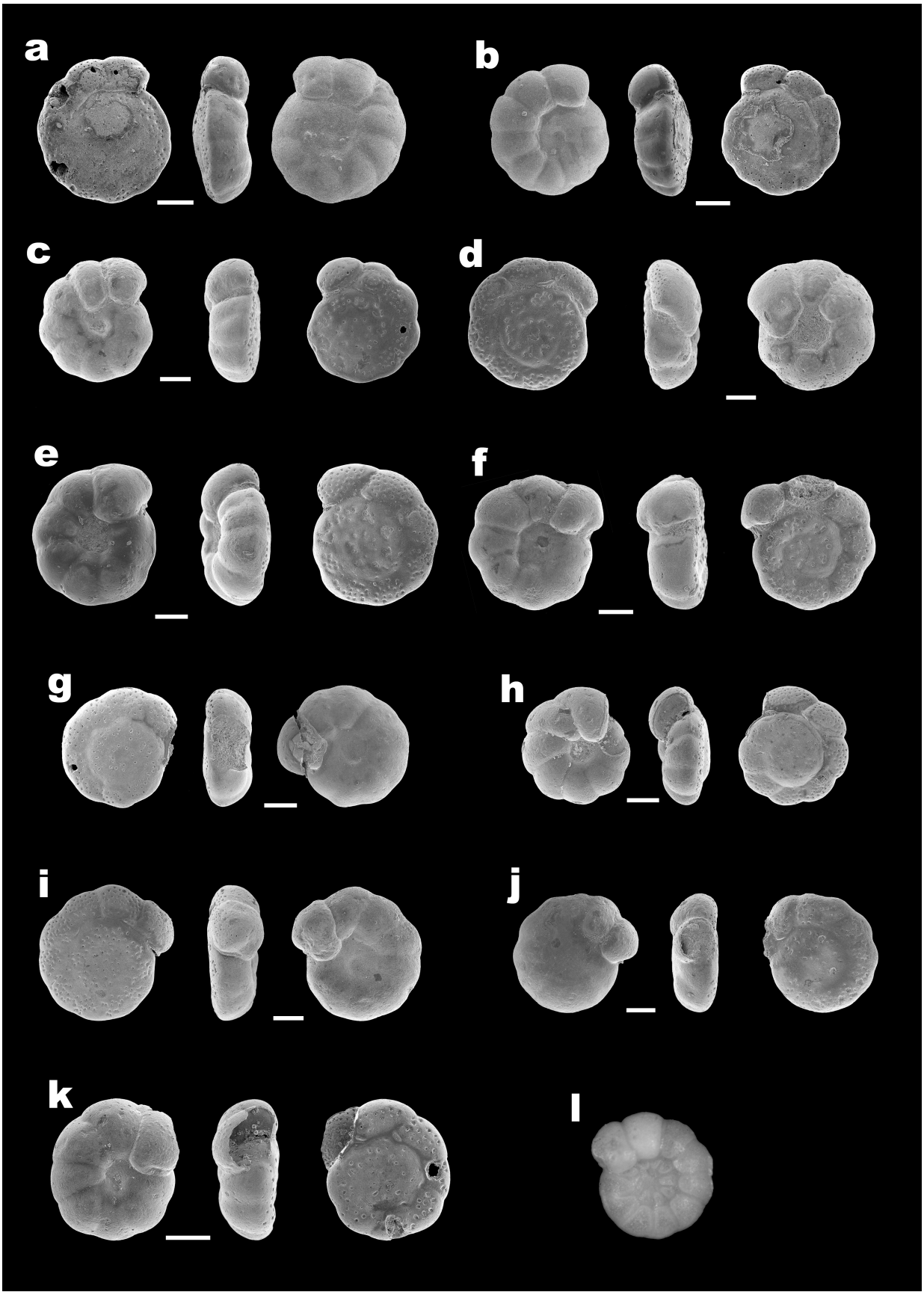

Plate 9. SEM pictures of *Cibicides robertsonianus* (umbilical/spiral sides and axial profile).
a-b) 9.0Ma, c-f) 7.5Ma, g-k) 7.0Ma.
Light photomicrograph of the umbilical side, i) 9.0Ma.
Scale= 100μm

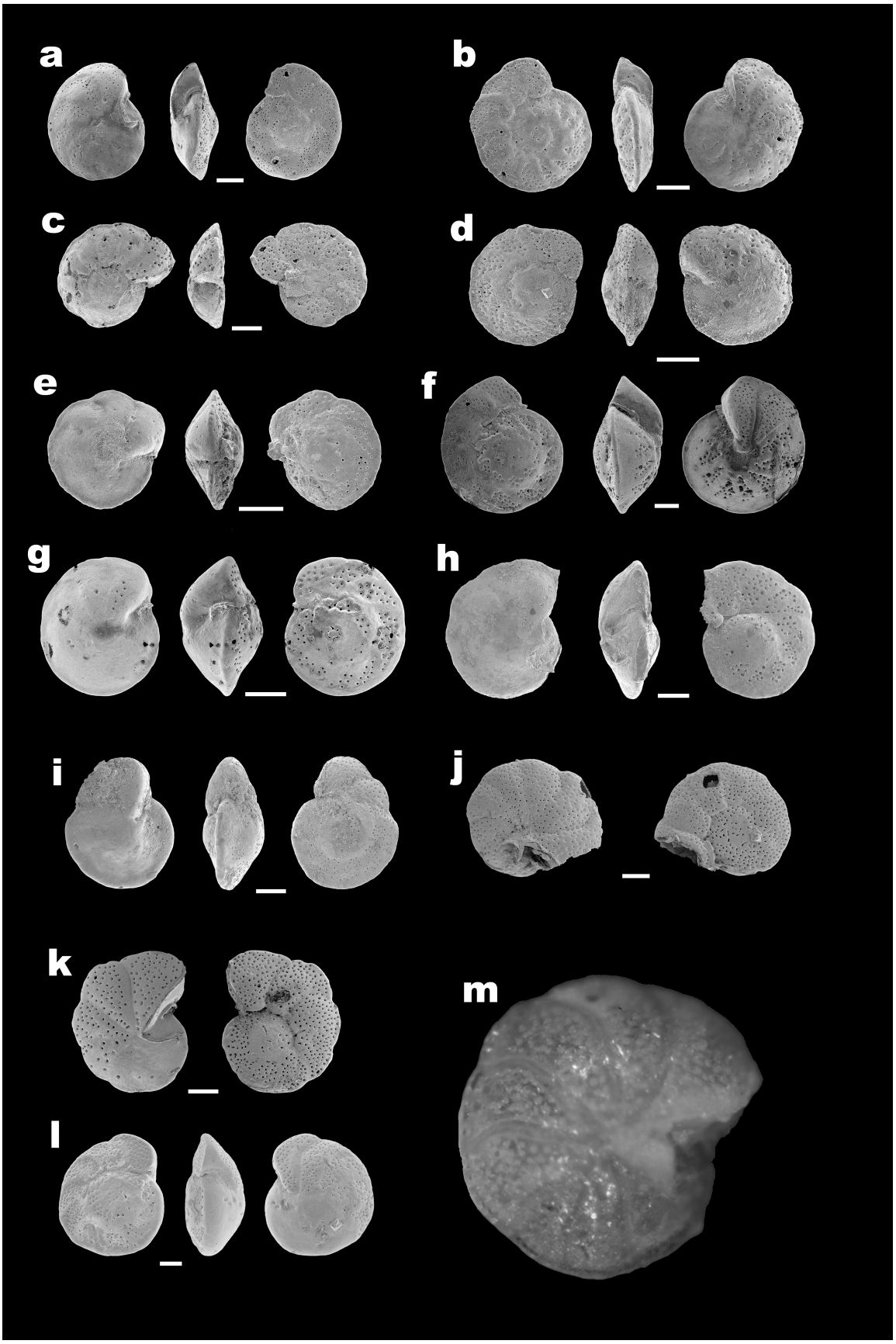

Plate 10. SEM pictures of *Cibicides ungerianus* (umbilical/spiral sides and axial profile).
a-b) 14.5Ma, c-d) 14.0Ma, e) 5.0Ma, f-g) 1.0Ma, h-l) Recent, h) C18, i) C22, j) C29, k) C31, l) C131
Light photomicrograph of the umbilical side, m) 5.5Ma.
Scale= 100μm

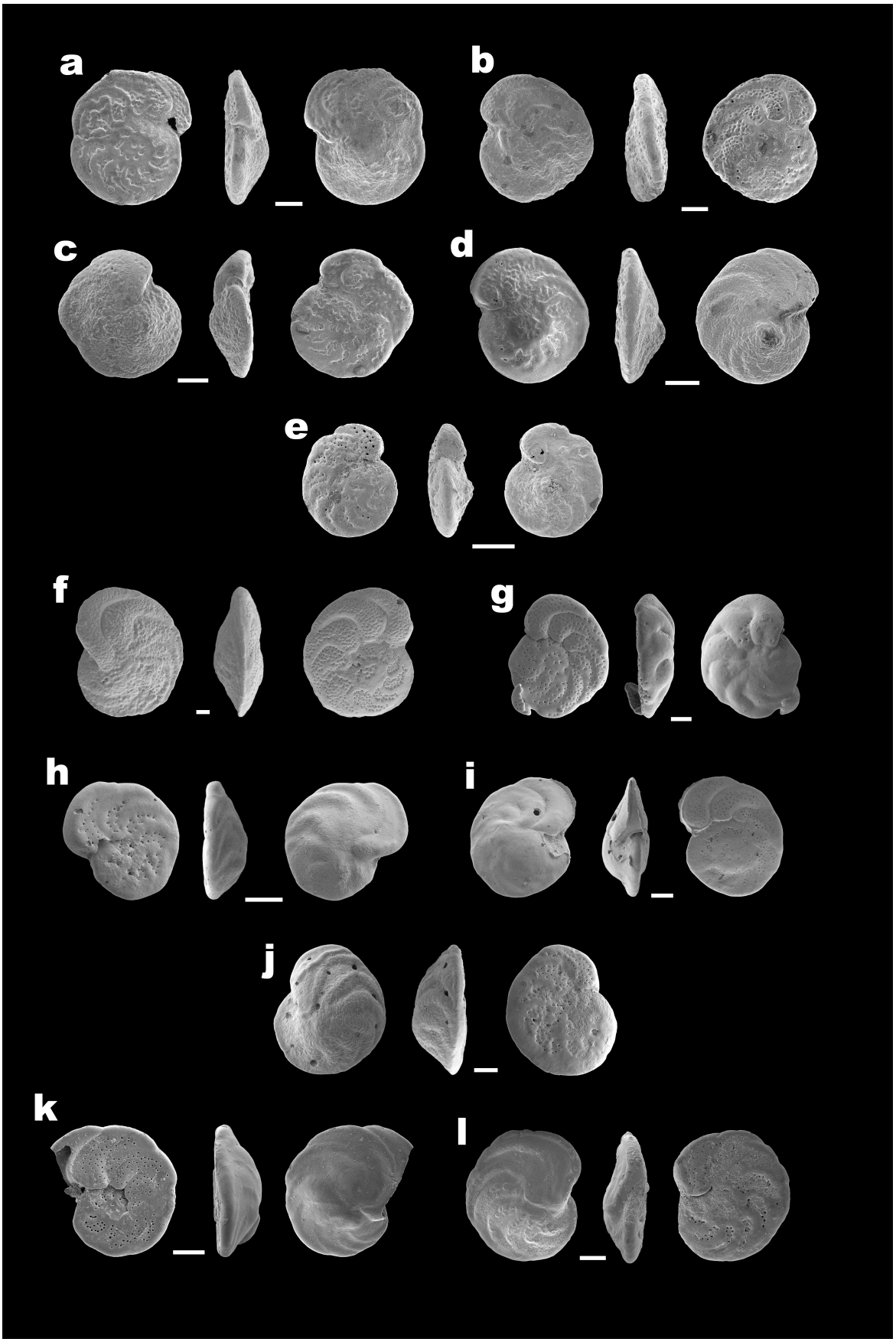

Plate 11. SEM pictures of *Cibicides wuellerstorfi* (umbilical/spiral sides and axial profile). a-e) 10.0Ma, f-l) Recent, f) C137, g) C143, h) C140b, i) C147, j) C163, k) C183, l) C184. Scale= 100μm

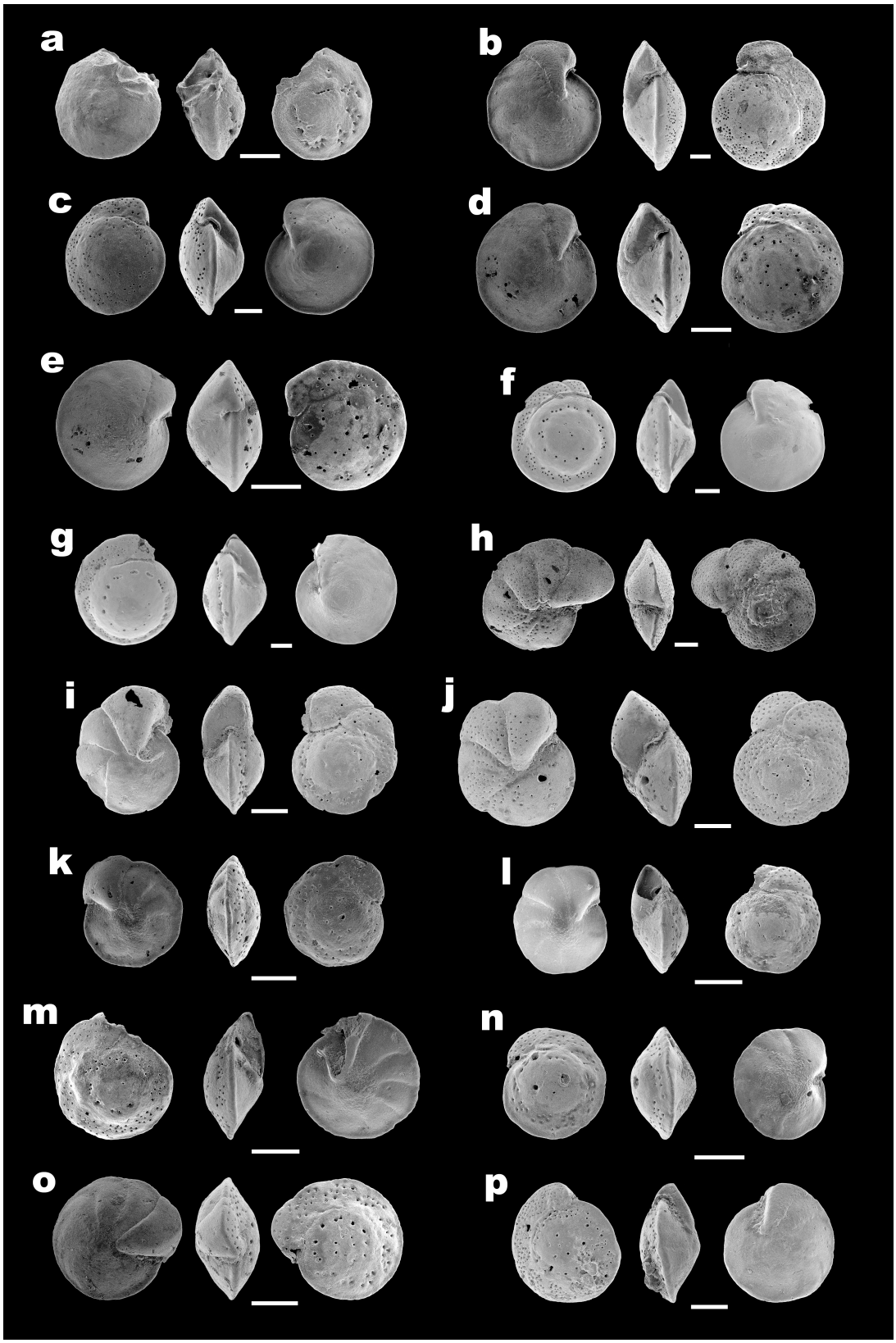

Plate 12. SEM pictures of intermediate forms between the studied cibicidids(umbilical/spiral sides and axial profile).
a-b) *C. dutemplei-pseudoungerianus*, 5.5Ma, c) *C. ungerianus-kullenbergi*, 1.0Ma,
f-g) *C. kullenbergi-pachyderma*, Recent, f) C106, g) C108, h-j) *C.lobatulus-ungerianus,* 5.0Ma,
k-l) *C. lobatulus-pachyderma-ungerianus,* 5.0Ma, m-n) *C. pachyderma-ungerianus*, 5.0Ma,
o-p) *C. ungerianus-pseudoungerianus*, 5.0Ma.
Scale= 100μm

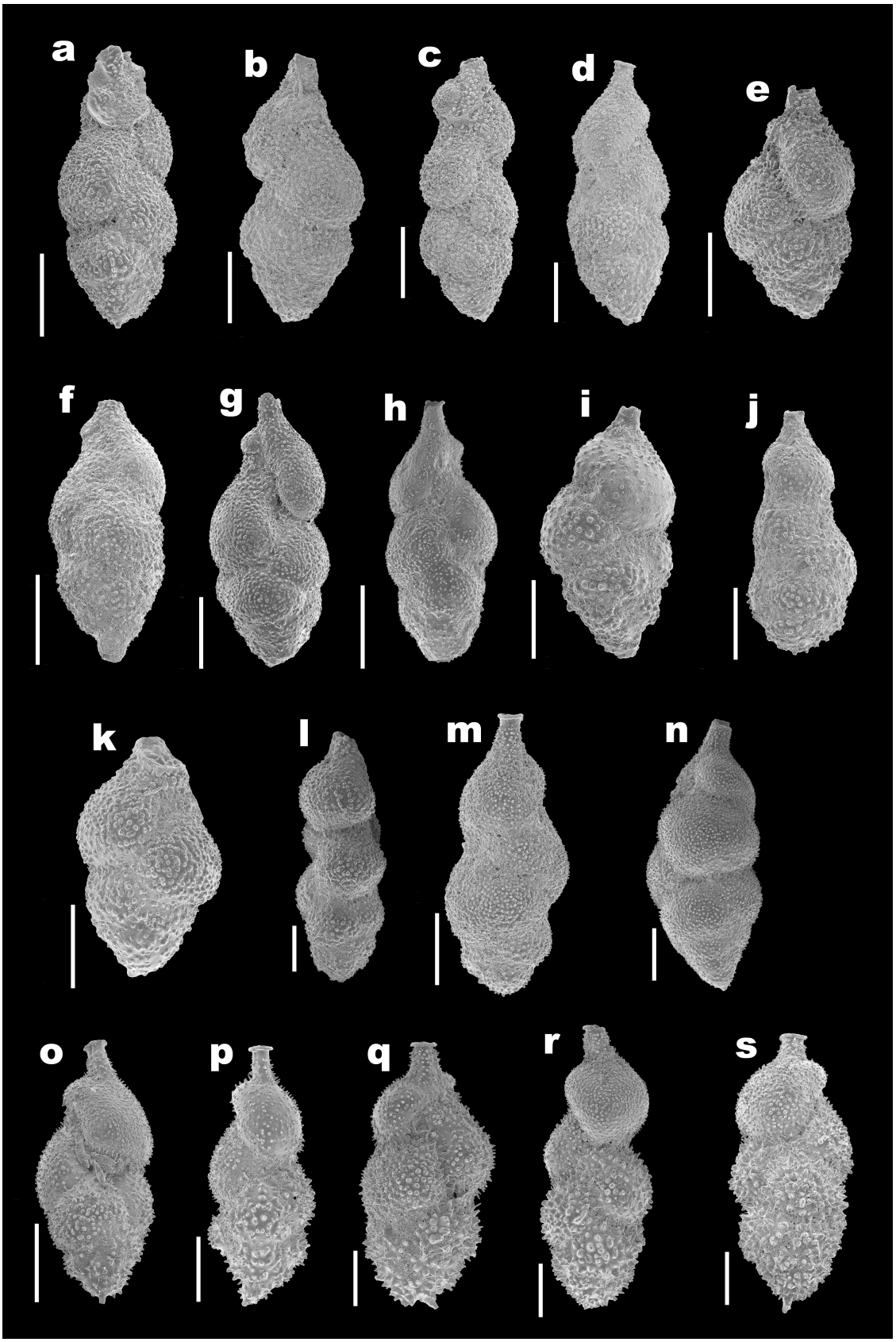

Plate 13. SEM pictures of *Uvigerina proboscidea*.
a) 13.5Ma, b-c) 13.0Ma, d-e) 12.5Ma, f) 8.0Ma, g-h) 6.0Ma, i-j) 4.0Ma, k-l) 3.5Ma, m-n) 3.0Ma, o-p) 2.5Ma, q-s) 2Ma.
e, i, k, n, q, s resemble *U. auberiana*.
Scale= 100μm

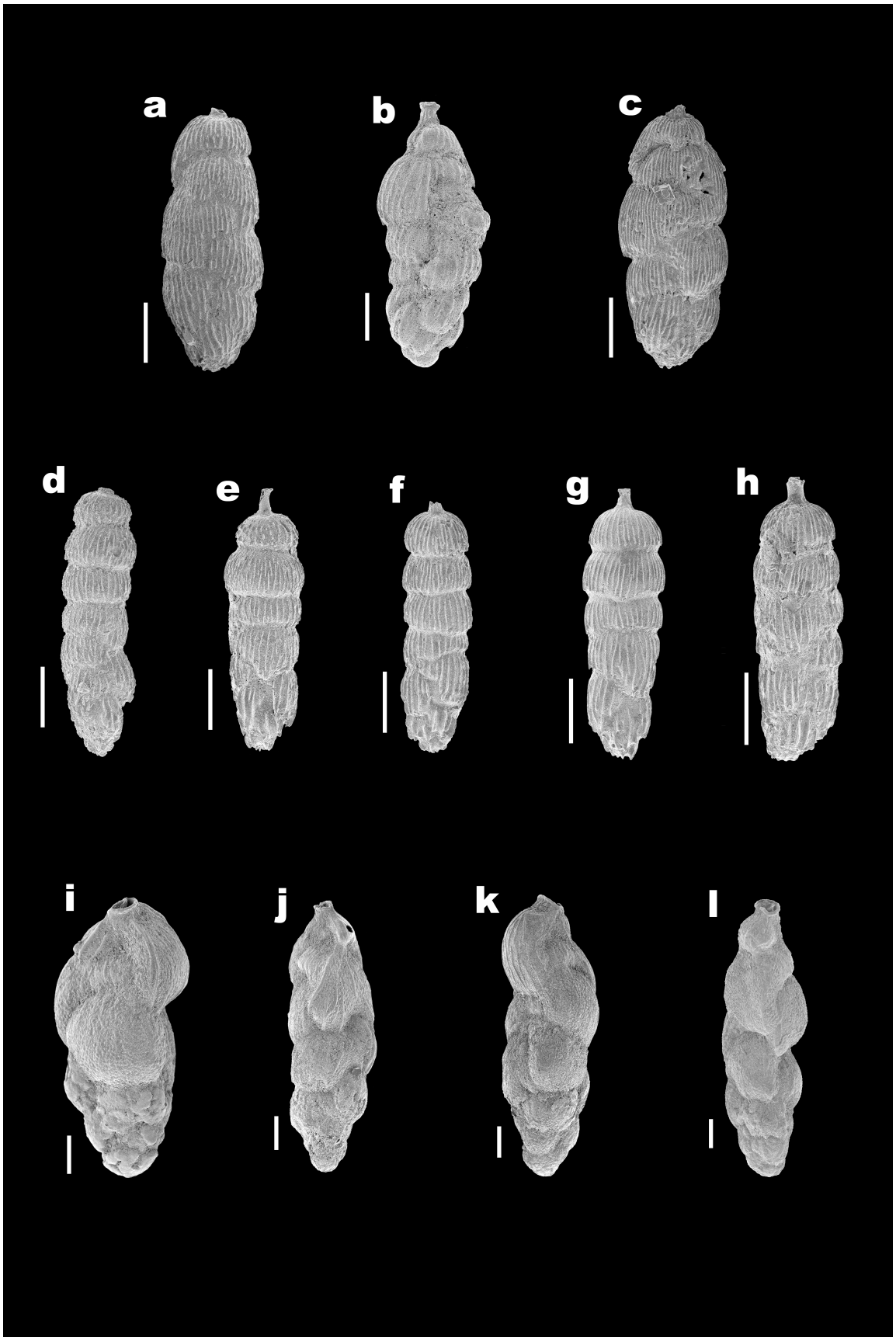

Plate 14. SEM pictures of *Uvigerina bononiensis*, a) 14.5Ma, b) 6.0Ma, c) 14.0Ma;
U. cylindrica, d-h) 5.0Ma;
U. earlandi, i-l) Recent, Mc Murdo Sound, Antarctica.
Scale= 100μm

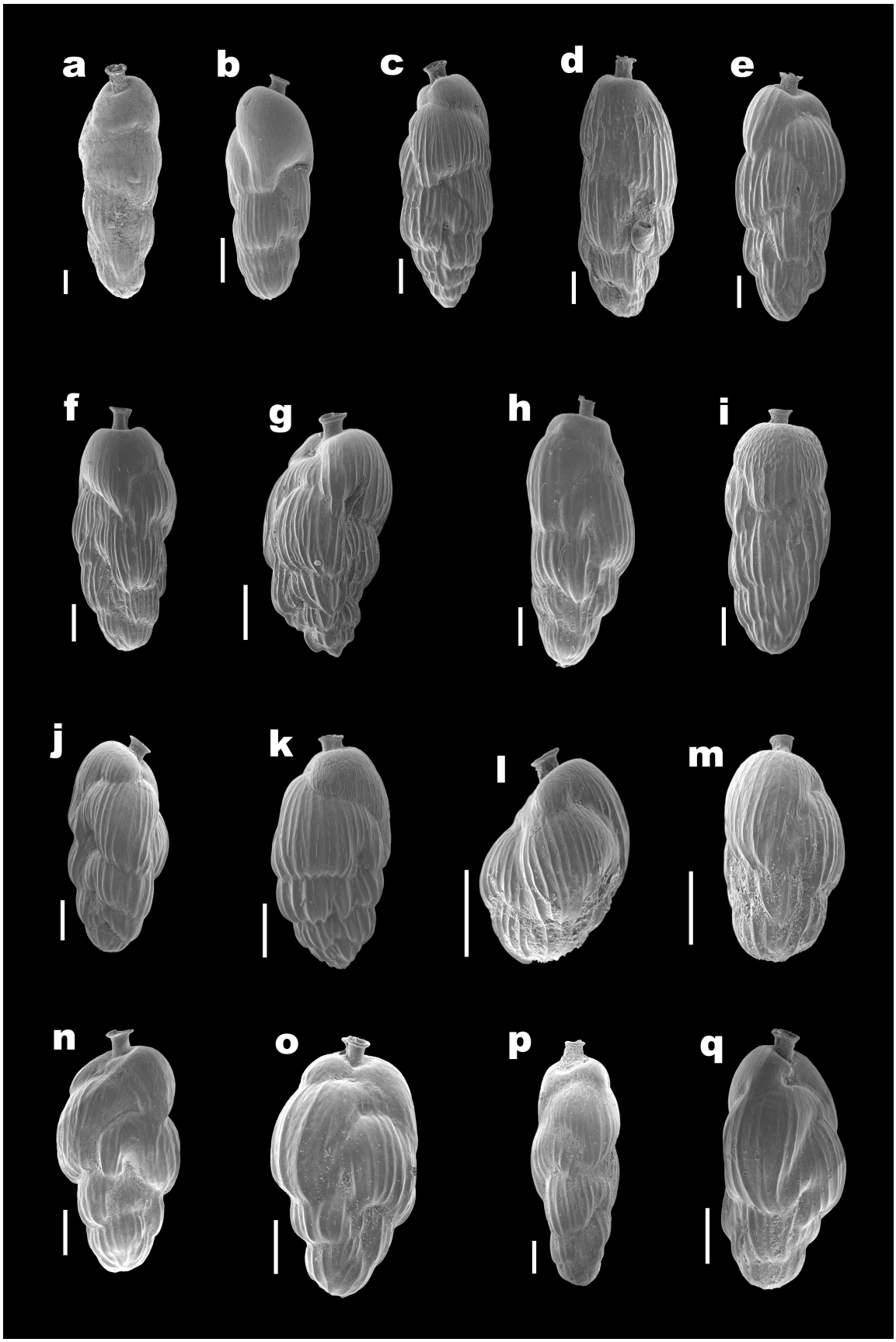

Plate 15. SEM pictures of *Uvigerina elongatastriata*, Recent.
a) U13, b) U225, c) U236, d) U247, e) U248a, f) U248b, g) U248c, h) U248d, i) U248e, j) U248f, k) U248g, l) U254, m) U255, n) U269, o) U270, p) U271, q) U272.
Scale= 100µm

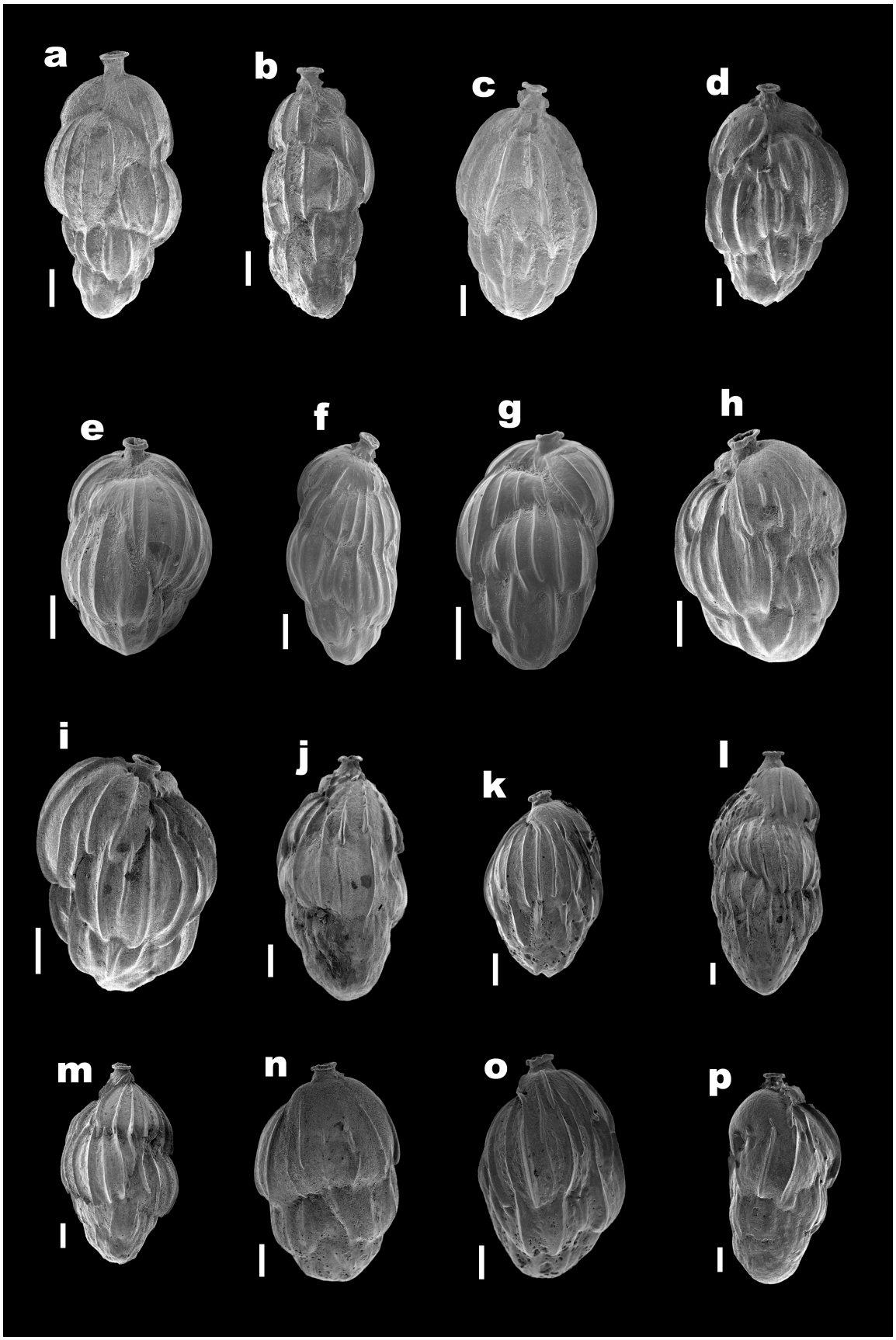

Plate 16. SEM pictures of *Uvigerina mediterranea*, Recent.
a) U3, b) U4, c) U9, d) U14, e) U224b, f) U224c, g) U235a, h) U264, i) U286, j) U154, k) U155, l) U156, m) U157a, n) U157b, o) U157c, p) U157e.
Scale= 100µm

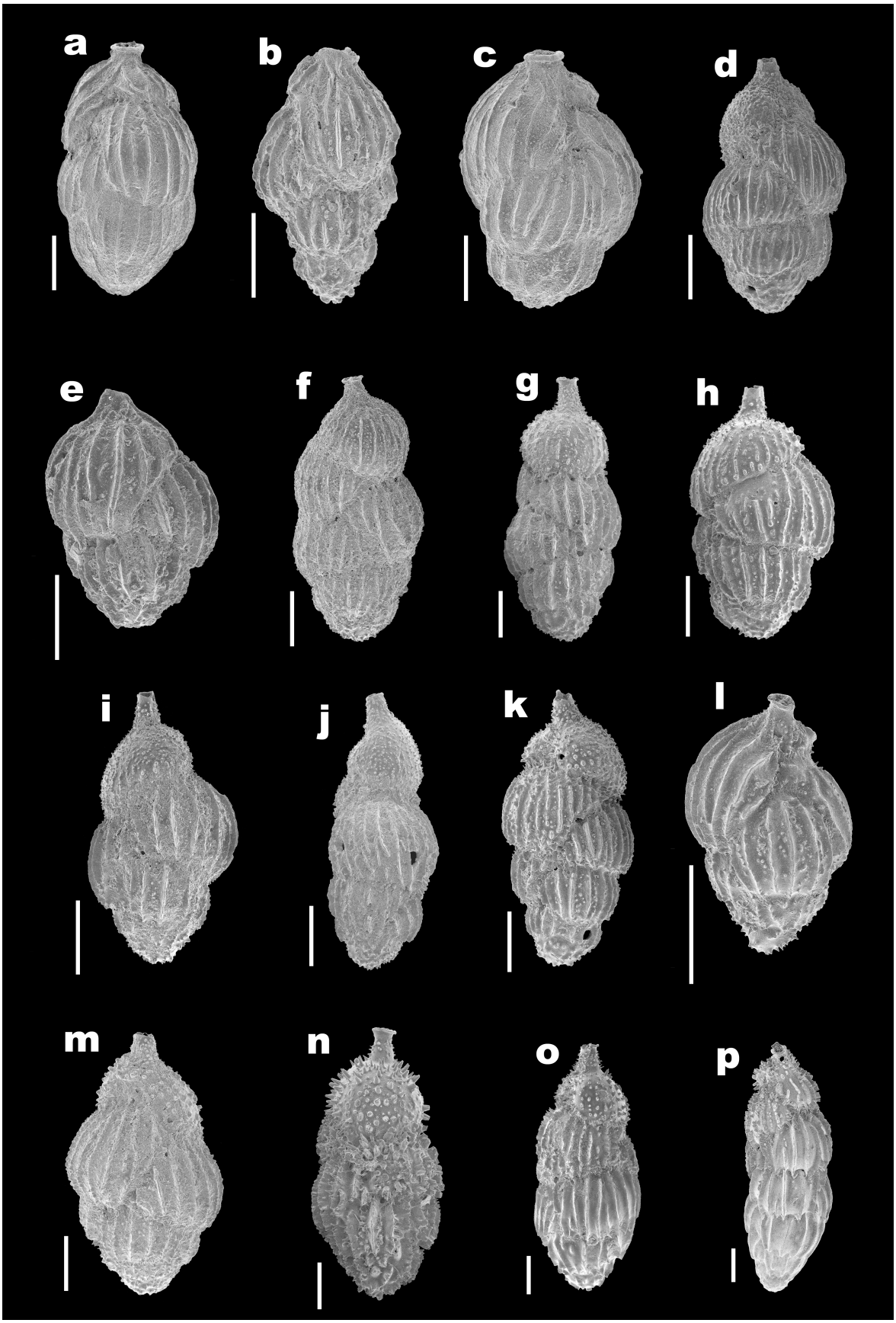

Plate 17. SEM pictures of *Uvigerina peregrina*,
a-c) 15.0Ma, d) 12.5Ma, e-f) 13.0Ma, g-h) 6.5Ma, i-j) 6.0Ma, k-l) 5.0Ma, m) 3.0Ma, n) 2.5Ma, o) 1.5Ma, p) 1.0Ma.
Scale= 100μm

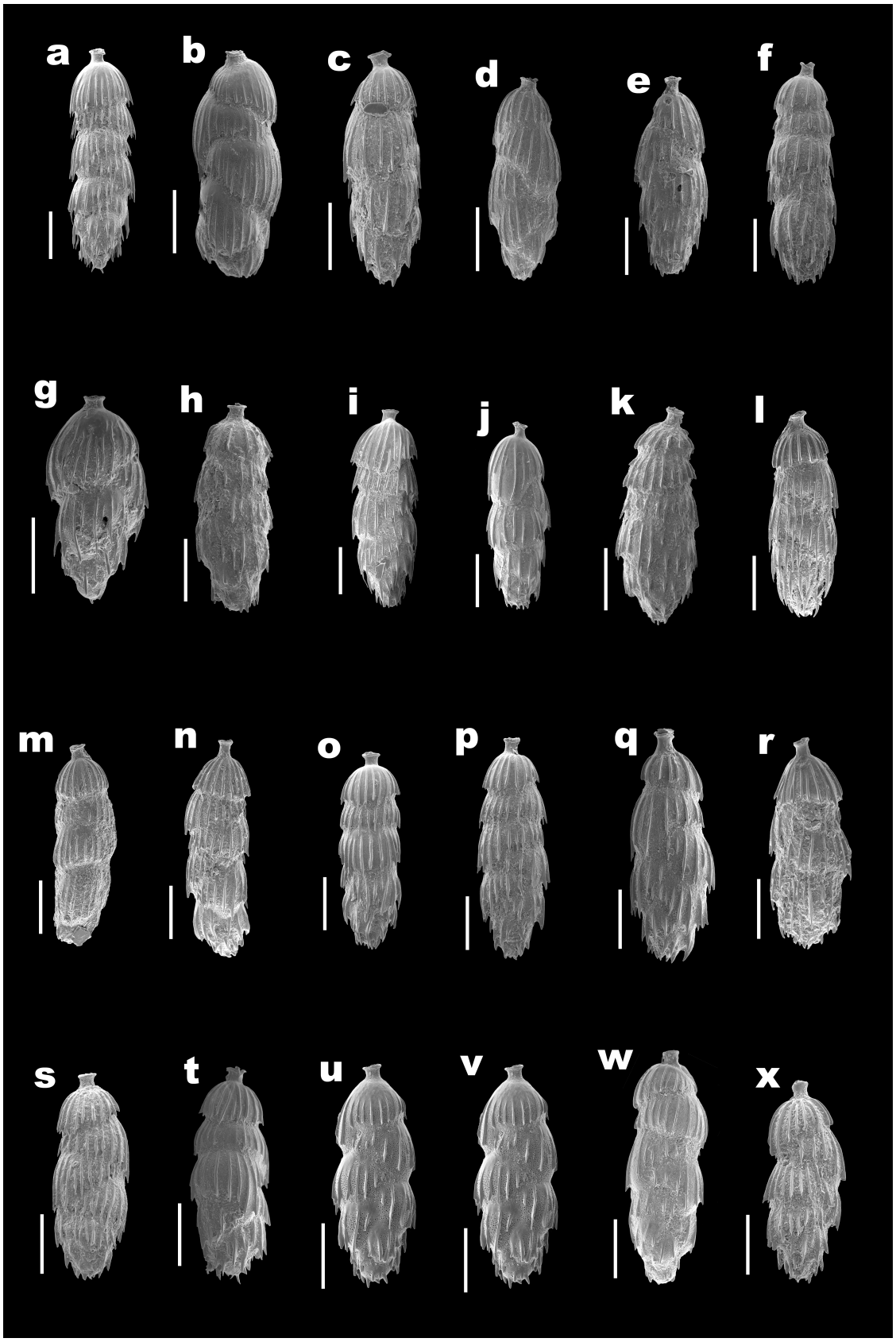

Plate 18. SEM pictures of *Uvigerina phlegeri*, Recent.
a) Por1, b) Por7, c) U218a, d) U218b, e) U218c, f) U218d, g) U218e, h) U218f, i) U219, j) U220, k) U234, l) U237, m) U238, n) U240, o) U241, p) U242, q) U243, r) U244, s) U245, t) U246, u) U256, v) U256a, w) U256b, x) U256c.
Scale= 100µm

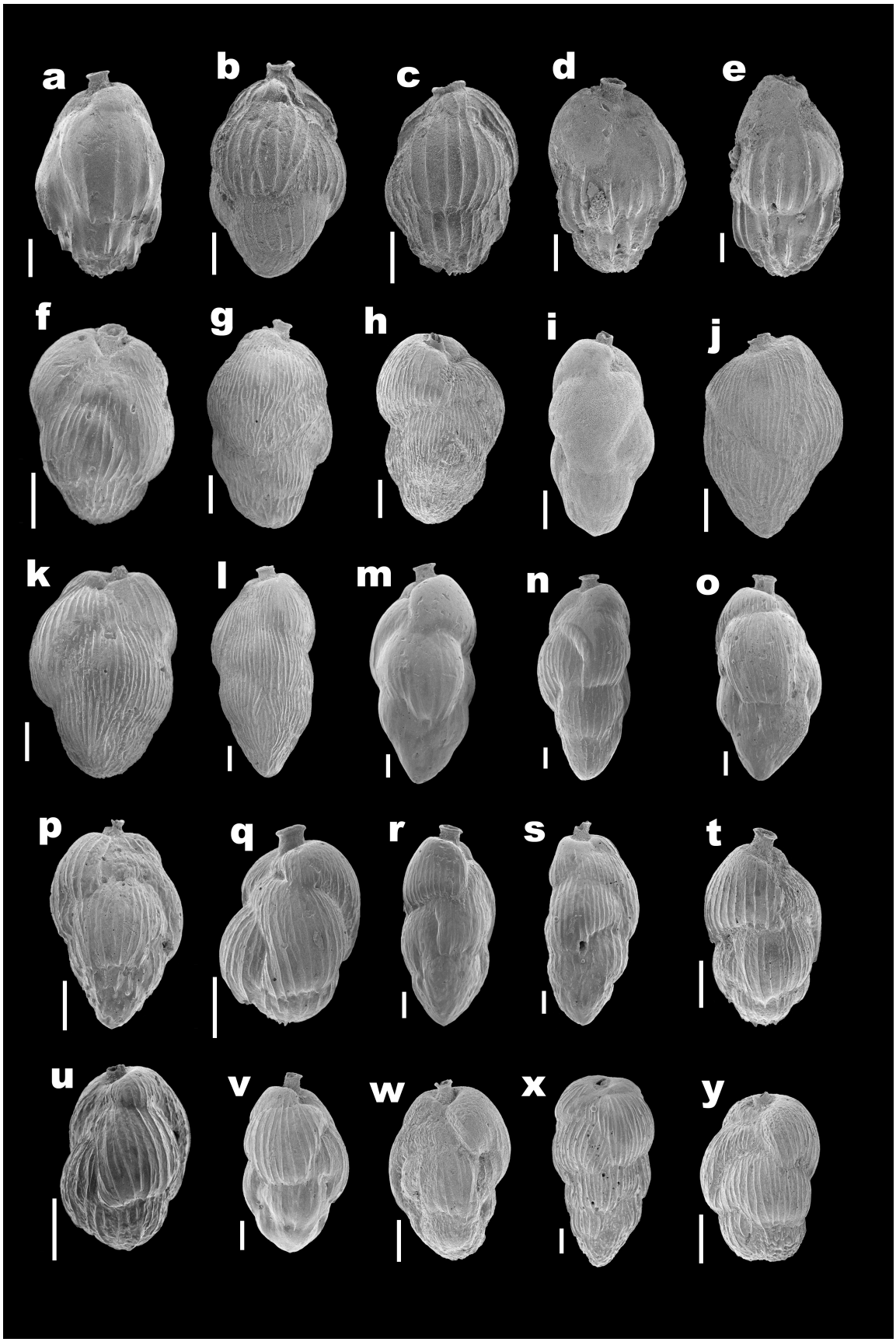

Plate 19. SEM pictures of *Uvigerina semiornata*, a-c) 14.5Ma;
U. rutila, d-e) 14.0Ma, u) 5.5Ma, v-w) 5.0Ma, x-y) 3.5Ma;
U. striatissima, f-h) 13.5Ma, i-j) 13.0Ma, k-l) 12.5Ma, m-o) 6.5Ma, p-q) 6.5Ma, r-t) 6.0Ma.
Scale= 100μm

Summary

English summary

Foraminifers are a widely distributed group of unicellular organisms present in all the oceans and seas and even in fresh water and soil. Among the foraminifers bearing a shell, the Rotaliida represent the main part of hyaline calcareous ones. Molecular studies based on the complete SSU (small subunit) rDNA (ribosomal DNA) have shown a partition of rotaliids in three main groups. *Uvigerina* belongs to the first group (including also *Bolivina* and the Cassidulinidae), whereas *Cibicides* belongs to the third group (with *Bulimina, Stainforthia, Epistominella, Pullenia* and *Melonis*).

Phylogenetic analyses based on partial SSU showed the monophyly of *Cibicides* and the existence of cryptic species within two shallow species: *C. lobatulus* and *C. refulgens*. On the other hand, the existence of five species (*C. lobatulus, C. pachyderma, C. refulgens, C. ungerianus, C. wuellerstorfi*) out of six was molecularly confirmed.

From the numerous generic names used for cibicidids, many appear to be synonymous with *Cibicides* in view of the molecular results (e.g. *Cibicidoides, Fontbotia, Heterolepa, Lobatula*). Cibicidids occur from the shelf to the deep sea and the different species can be used as indicators of (paleo)bathymetry in spite of the fact that the controlling parameters are not known. Among *Cibicides* species, certain are preferentially elevated epifauna, whereas others live at the sediment water interface or deeper in the sediment. Inferring the phylogeny of cibicidids from molecular and fossil data, the species seemed to evolve first from the shelf to the deep sea. In the middle Miocene, new species originated possibly from the shelf again and evolved to deeper species, perhaps because of the climatic changes occurring at that time.

Molecular studies of *Uvigerina* based on partial SSU indicated the inclusion of *Rectuvigerina* and *Trifarina* species inside the genus *Uvigerina*. Moreover, two out of three previously morphologically defined groups (*peregrina* and *semiornata* groups) were also recognized in molecular phylogenies.

Among the generic names used for uvigerinids, many have already been put in synonymy with *Uvigerina*, *Trifarina* or *Rectuvigerina* (*Aluvigerina, Neouvigerina, Euuvigerina, Hofkeruva, Norcottia, Miniuva, Ruatoria, Ciperozoa*). It seems also likely that *Trifarina* and *Rectuvigerina* are synonyms with *Uvigerina*. Uvigerinids are preferentially deep sea species, but some are found in neritic environments or at the top of the slope. The ornamentation is widely used for the specific distinction but it seems strongly influenced by ecological and/or depth factors; *Uvigerina peregrina* is a good example with a wide morphological variability and a weak genetic diversity. The phylogenetic reconstruction based on molecular and fossil data shows that studied uvigerinids either appeared a long time ago or really recently. This contrasts with the cibicidids phylogeny where all studied species originated a long time ago (middle Miocene at the minimum) and perhaps confirms a difference in the evolutionary rates already suspected with the partial SSU phylogenies.

Nederlandse samenvatting

Foraminiferen zijn een wijd verspreide groep van ééncellige organismen die voorkomen in alle mariene milieus, in zoetwatermilieus en eveneens in bodems. Onder foraminiferen die een uitwendig mineraal skelet dragen (een schaaltje of een 'test') zijn de Rotaliida de belangrijkste groep mariene foraminiferen met een schaaltje dat uit kalk gevormd is. Moleculaire studies gebaseerd op de complete SSU (Small Sub Unit) van het rDNA (ribosomaal DNA) laten een onderverdeling zien van de Rotaliida in drie belangrijke groepen. *Uvigerina* behoort tot de eerste groep (die ook *Bolivina* en de Cassidulinidae omvat), terwijl *Cibicides* behoort tot de derde groep (samen met *Bulimina, Stainforthia, Epistominella, Pullenia* en *Melonis*).
Moleculair-fylogenetische analyses gebaseerd op een deel van de SSU wijzen op monofylie van *Cibicides* en het bestaan van cryptische speciatie binnen twee ondiepe soorten: *C. lobatulus* en *C. refulgens*. Daarnaast kon het bestaan van vijf uit de groep van zes bestudeerde soorten, namelijk van *C. lobatulus, C. pachyderma, C. refulgens, C. ungerianus* en *C. wuellerstorfi* moleculair bevestigd worden.
Van de talrijke generieke namen die in gebruik zijn voor cibicidae lijken er, in het licht van de moleculaire bevindingen, vele synoniem te zijn met *Cibicides* (o.a. *Cibicidoides, Fontbotia, Heterolepa, Lobatula*).
Cibicidae komen voor van het continentaal plat tot in de diepzee en de verschillende soorten worden door micropaleontologen gebruikt als indicatoren voor (paleo-)bathymetrie, in weerwil van het feit dat de factoren die de dieptedistributie bepalen nog niet goed bekend zijn. Van de verschillende *Cibicides* soorten leven zeker een aantal bij voorkeur als epifauna op harde substraten boven het sediment, terwijl andere op het interface tussen sediment en water leven of zelfs tot centimeters diep in het sediment. Wanneer de fylogenie van de cibicidae wordt beschouwd in het licht van zowel moleculaire als fossiele data, lijkt het dat soorten oorspronkelijk evolueerden op het continentaal plat en en daarna in het diepere mariene bereik. In het midden Mioceen zijn waarschijnlijk wederom nieuwe soorten geëvolueerd op het continentaal plat en vervolgens opnieuw naar het dieper mariene bereik gemigreerd, mogelijk als reactie op klimaatsveranderingen die in die periode plaatsvonden.
Moleculaire studies van *Uvigerina* gebaseerd op gedeeltelijke sequenties van de SSU indiceren de inclusie van *Rectuvigerina* en *Trifarina* binnen het genus *Uvigerina*. Bovendien worden twee van drie voorheen morfologisch gedefinieerde groepen, *peregrina* en *semiornata*, ook in de moleculaire fylogenie herkend.
Onder de generieke namen de gebruikt worden voor uvigerinidae zijn vele in het verleden al in synoniemie geplaatst met *Uvigerina*, *Trifarina* of *Rectuvigerina* (zoals *Aluvigerina, Neouvigerina, Euuvigerina, Hofkeruva, Norcottia, Miniuva, Ruatoria* en *Ciperozoa*). Het is waarschijnlijk dat ook *Trifarina* en *Rectuvigerina* synoniemen zijn van *Uvigerina*. Uvigerinidae komen voornamelijk voor in de diepzee, maar sommige soorten worden gevonden vanaf het neritisch bereik tot boven aan de continentale helling. De ornamentatie van uvigerinidae wordt algemeen gebruikt voor het onderscheiden van soorten, maar lijkt duidelijk beïnvloed te worden door factoren als ecologie en/of waterdiepte; *Uvigerina peregrina* is een goed voorbeeld en koppelt een grote morfologische variabiliteit aan een zwakke genetische diversiteit.
De fylogenetische reconstructies zoals gebaseerd op moleculaire en fossiele data laten zien dat de uvigerinidae ofwel lang geleden evolueerden, ofwel geologisch vrij recent. Dit contrasteert met de fylogenie van de cibicidae, waarvan alle bestudeerde soorten lang geleden evolueerden (minimaal in het midden Mioceen) en bevestigt wellicht een verschil in de tempi van evolutie dat al vermoed werd op grond van de SSU fylogenieën.

Résumé en français

Les foraminifères forment un groupe d'organismes unicellulaires marins largement répartis dans tous les océans et mers du globe, certaines espèces peuvent même vivre en eau douce ou dans le sol. Parmi les foraminifères possédant un test (une coquille), les rotaliides représentent la majeure partie du groupe avec un test calcaire hyalin. Les études moléculaires basées sur la séquence complète de l'ADN ribosomique de la petite sous-unité (SSU rDNA) ont montré une séparation des rotaliides en trois groupes principaux. *Uvigerina* appartient au premier groupe (qui comprend aussi *Bolivina* et les cassidulinidés), tandis que *Cibicides* fait partie du troisième groupe (avec *Bulimina, Stainforthia, Epistominella, Pullenia* et *Melonis*).

Les études phylogénétiques basées sur des séquences partielles de la petite sous-unité ont démontré la monophylie de *Cibicides* et l'existence d'espèces cryptiques au sein de deux taxons vivant en eau peu profonde : *C. lobatulus* et *C. refulgens*. D'autre part, l'existence de cinq (*C. lobatulus, C. pachyderma, C. refulgens, C. ungerianus, C. wuellerstorfi*) des six espèces étudiées a été confirmée par les résultats moléculaires.

Parmi la pléthore de noms génériques utilisés pour les cibicides, nombreux sont les synonymes de *Cibicides* d'après les résultats moléculaires (p. ex. *Cibicidoides, Fontbotia, Heterolepa, Lobatula*). Les cibicides vivent à des profondeurs très variées, du bord de mer jusqu'aux profondeurs abyssales, suivant les espèces qui peuvent dès lors être utilisées comme indicateurs (paléo)bathymétriques malgré la méconnaissance des facteurs agissant sur cette répartition. Parmi les différentes espèces appartenant au genre *Cibicides*, certaines préfèrent les habitats élevés tandis que d'autres vivent à l'interface entre eau et sédiment ou plus profondément dans le sédiment. La phylogénie des cibicides basée sur les données moléculaires et fossiles indique une première évolution des nouvelles espèces de la zone néritique vers les zones bathyale puis abyssale. Lors du Miocène moyen, il est possible que de nouvelles espèces soient d'abord apparues dans la zone néritique et aient à nouveau évolué vers des espèces plus profondes, peut-être à cause des changements climatiques survenant à cette époque.

Concernant les uvigerinides, les études phylogénétiques basées sur des séquences partielles de la petite sous-unité ont démontré l'inclusion d'espèces appartenant aux genres *Rectuvigerina* et *Trifarina* dans le genre *Uvigerina*. En outre, deux des trois groupes morphologiques décrits précédemment (groupes *semiornata* et *peregrina*) ont également été reconnus dans les phylogénies moléculaires. De nombreux noms génériques décrits pour les uvigerinides avaient déjà été placés en synonymie avec *Uvigerina*, *Trifarina* ou *Rectuvigerina* (p. ex. *Aluvigerina, Neouvigerina, Euuvigerina, Hofkeruva, Norcottia, Miniuva, Ruatoria, Ciperozoa*). *Trifarina* et *Rectuvigerina* sont vraisemblablement aussi des synonymes d'*Uvigerina*. Les uvigerinides sont surtout représentées par des espèces d'eau profonde mais certaines vivent dans la zone néritique et au sommet du talus continental. L'ornementation du test est fréquemment utilisée pour la distinction spécifique mais semble fortement influencée par des facteurs environnementaux ; un bon exemple est fourni par *Uvigerina peregrina*, une espèce présentant une large variabilité morphologique couplée à une très faible diversité génétique. La reconstruction phylogénétique déduite des données fossiles et moléculaires indique que les uvigerines étudiées sont apparues il y a très longtemps ou très récemment. Ces résultats contrastent fortement avec ceux trouvés pour *Cibicides*, car toutes les espèces de cibicides étudiées sont apparues il y a longtemps (au moins durant le Miocene moyen). Ces observations peuvent être mise en relation avec les différences observées dans les vitesses d'évolution des séquences partielles de la petite sous-unité des deux genres.

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