

CHAPTER 6

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

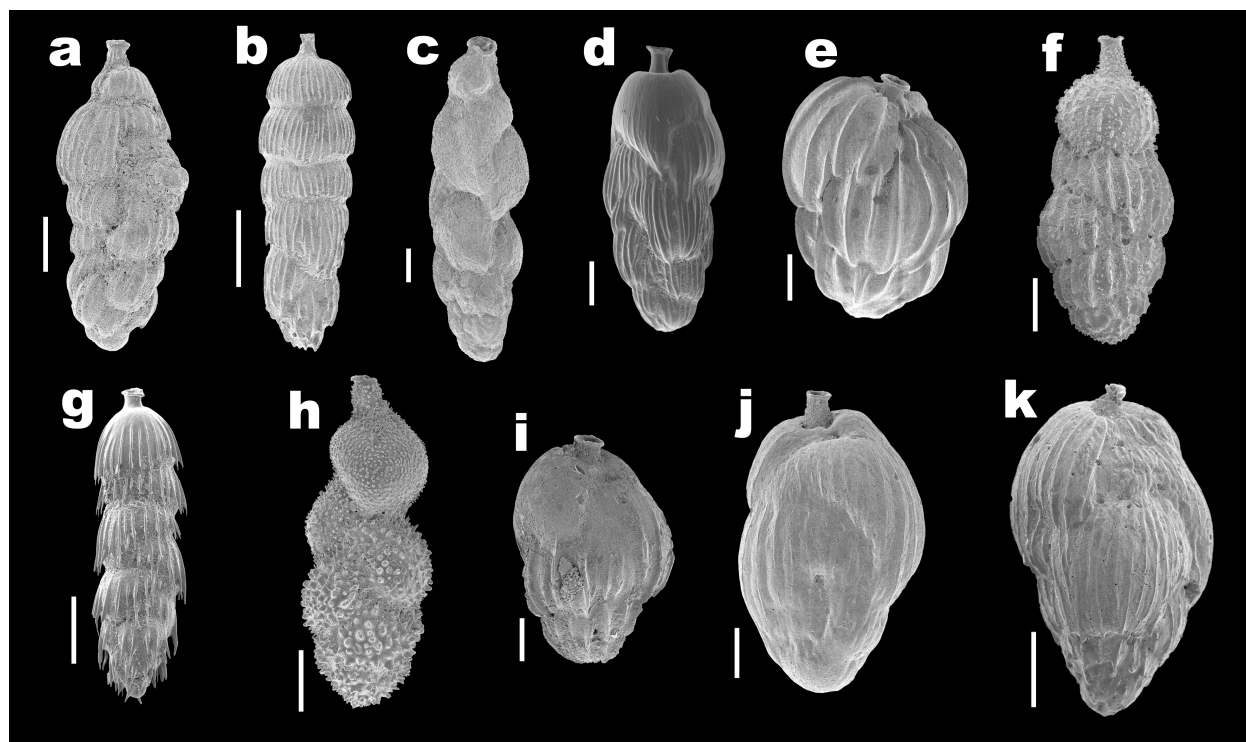


Figure 6.1.

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 boxcoreing 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 (Giblicemi, Punta Piccola, Vrica, Singa III, Punta di Maiata, Tremiti, Montalbani Ionico), Crete (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 foraminifera 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 125-595 μ m 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 Gibilscemi 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 Gibilscemi 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

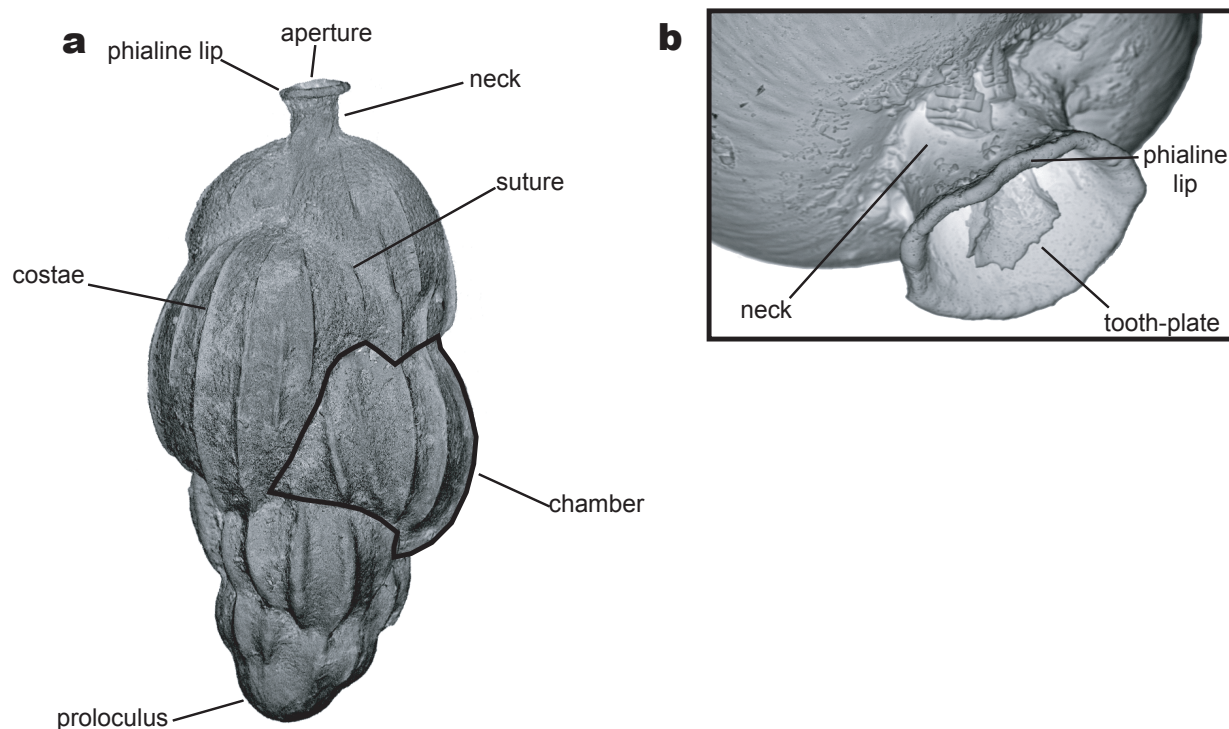


Figure 6.2. Terminology employed to name the different parts of the test (a) and the aperture (b) of *Uvigerina*.



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* group¹ – characterized by a triserial chamber arrangement, a short neck standing in a

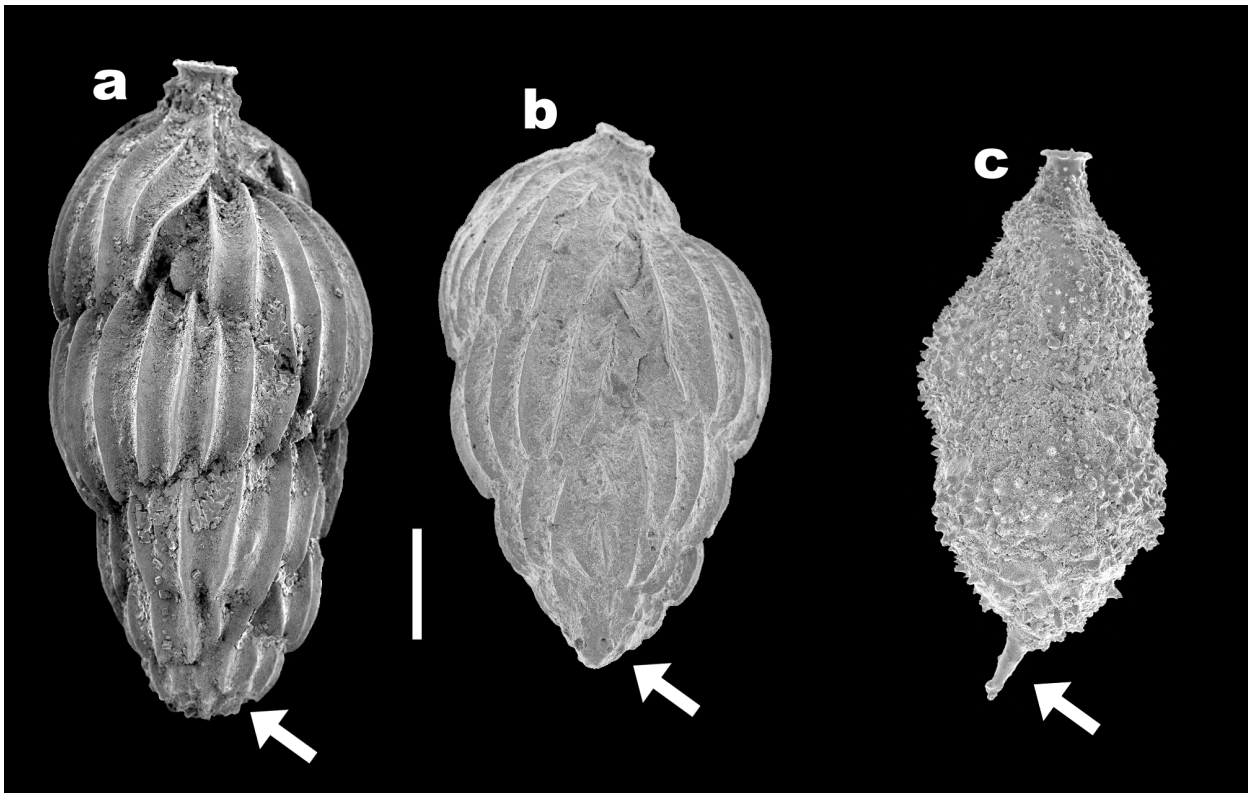


Figure 6.4. Difference in proloculus shape attributed to sexual/asexual generations dimorphism, with the megalospheric generation (a) and the microspheric one (b), which may bear a spine in some species (c). a) and b) *Uvigerina peregrina*; c) *U. proboscidea*. Scale= 100µm

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	<i>U. bononiensis</i>	<i>U. cylindrica</i>	<i>U. elongatastriata</i>	<i>U. mediterranea</i>	<i>U. peregrina</i>	<i>U. phlegeri</i>	<i>U. proboscidea</i>	<i>U. semiornata + U. rutila + U. striatissima</i>	<i>Uvigerina</i> sp.	Total <i>Uvigerina</i> 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
Giblicsemi	12.0	18'514										0
Giblicsemi	11.5	15'609										0
Giblicsemi	11.0	15'487										0
Giblicsemi	10.5	15'372							3			3
Giblicsemi	10.0	14'831										0
Giblicsemi	9.5	14'204							1			1
Giblicsemi	9.0	14'320										0
Giblicsemi	8.5	14'442										0
Giblicsemi	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* group² – including smaller and slender species – could be recognized genetically (see Chapter 4). For the time being, the third group (*U. bononiensis* group³) 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 *Euvigerina*, subsequently validated by designation of type species (Thalman, 1952). Loeblich & Tappan considered *Aluvigerina* as a junior synonym of *Uvigerina* but did recognize *Euvigerina* (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 *Euvigerina*, *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 groups 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. elongatastriata* (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* d'Orbigny, 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*. Finally, *U. gracilis* is considered to be a synonym of *U. proboscidea* (Borsetti et al., 1986). According to Van Leeuwen (1986), *Uvigerina hispida* seems to intergrade⁴ 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.

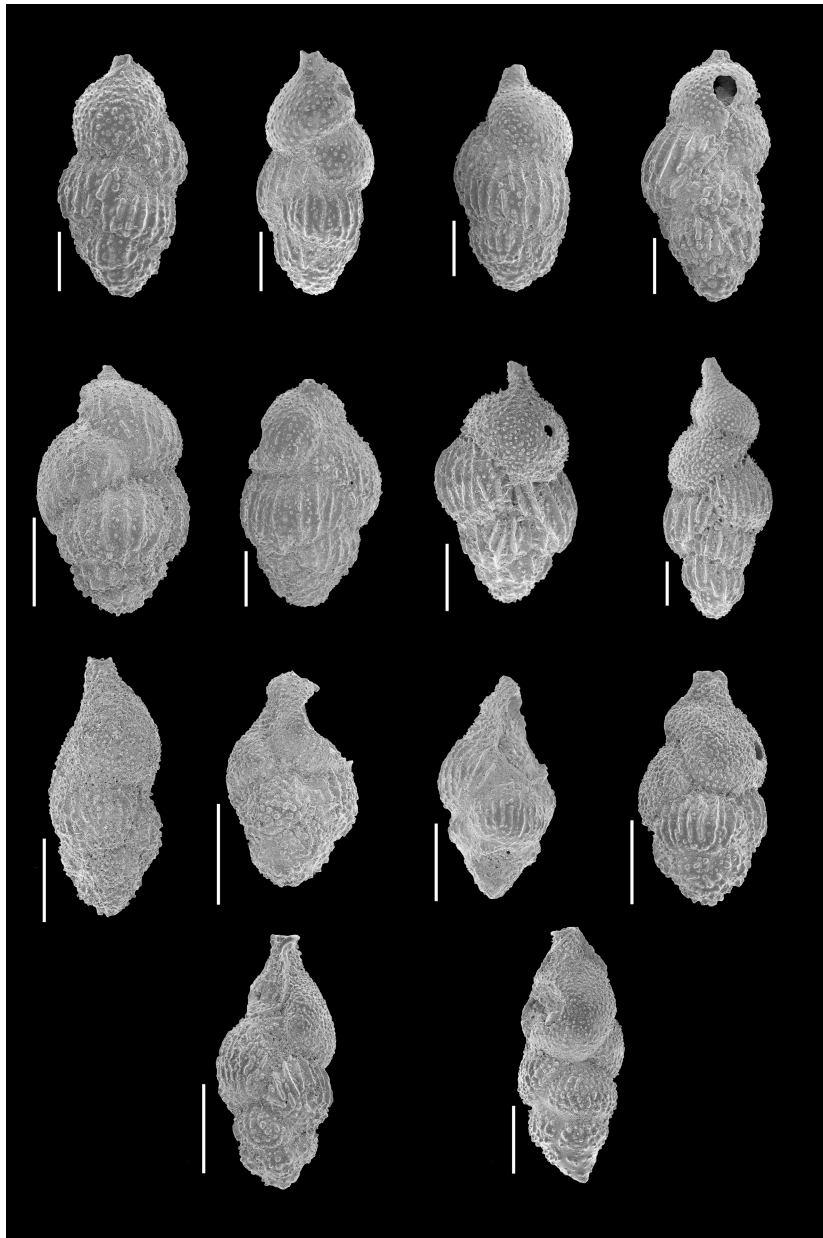


Figure 6.5. Morphological intermediates between *Uvigerina peregrina* and *U. proboscidea* from Faneromeni (7.0 Ma). Scale= 100 μ m

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,

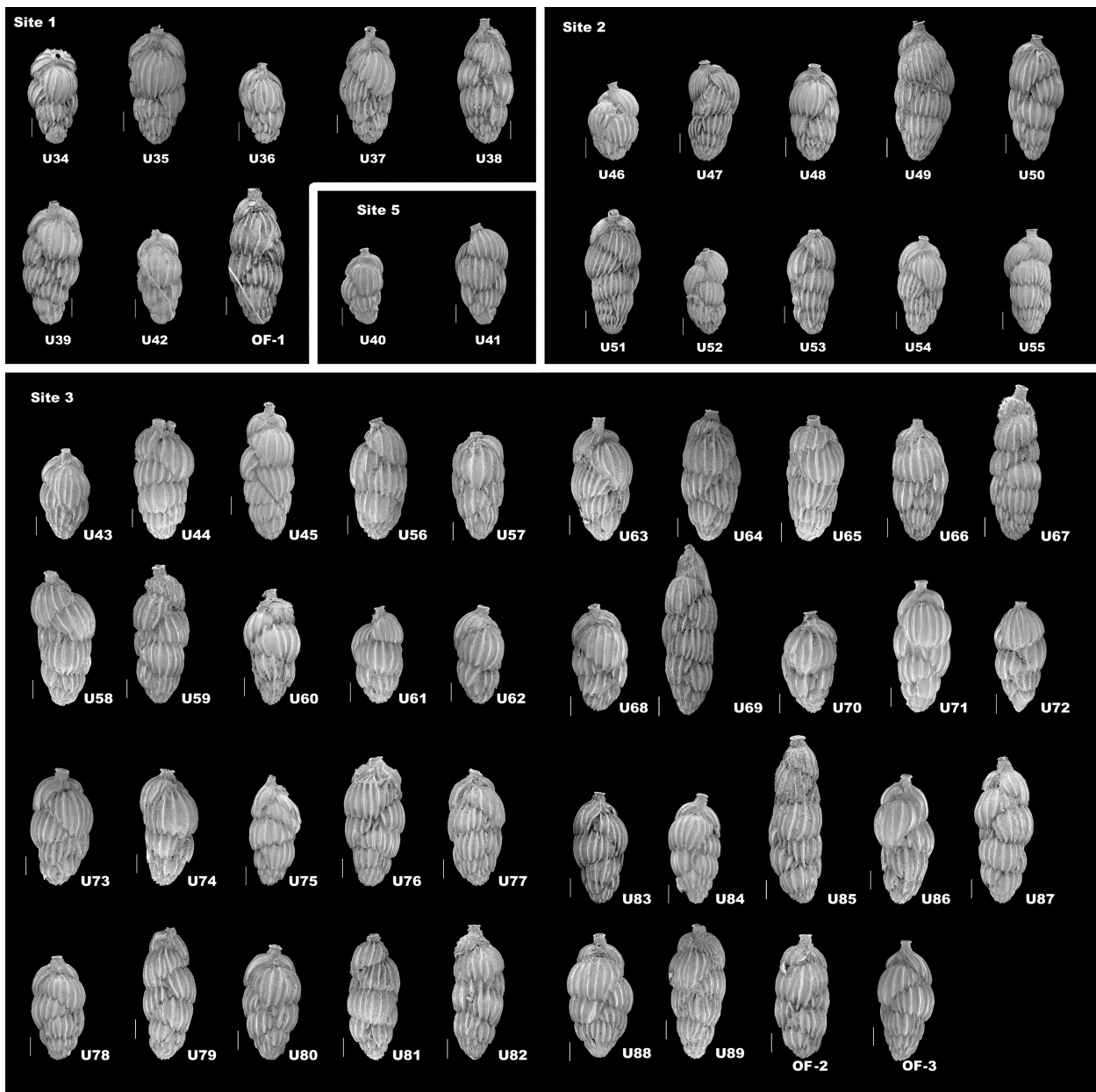


Figure 6.6. Representatives of the Oslo Fjord population of *U. peregrina*, sorted by sampling site (coordinates and depths of the sites are placed in Appendix 2). Scale= 100µm

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 $\delta^{13}\text{C}$ (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,

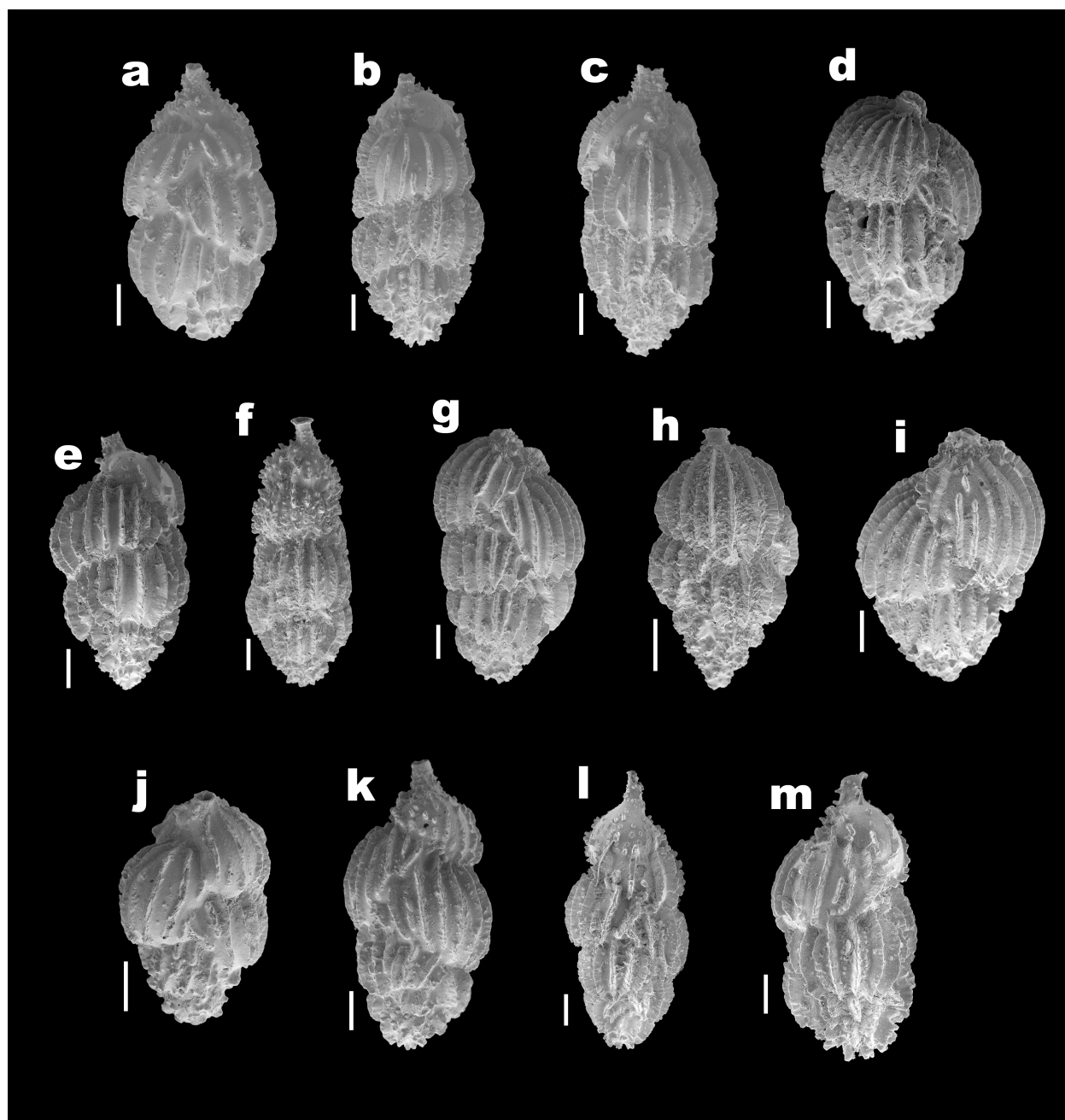


Figure 6.7. Hispid *U. peregrina* coming from deep sites in the Atlantic: (a-d) Bay of Biscay, 3000m, (e-m) Finisterre (Spain), 2122m. Scale= 100 μm

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

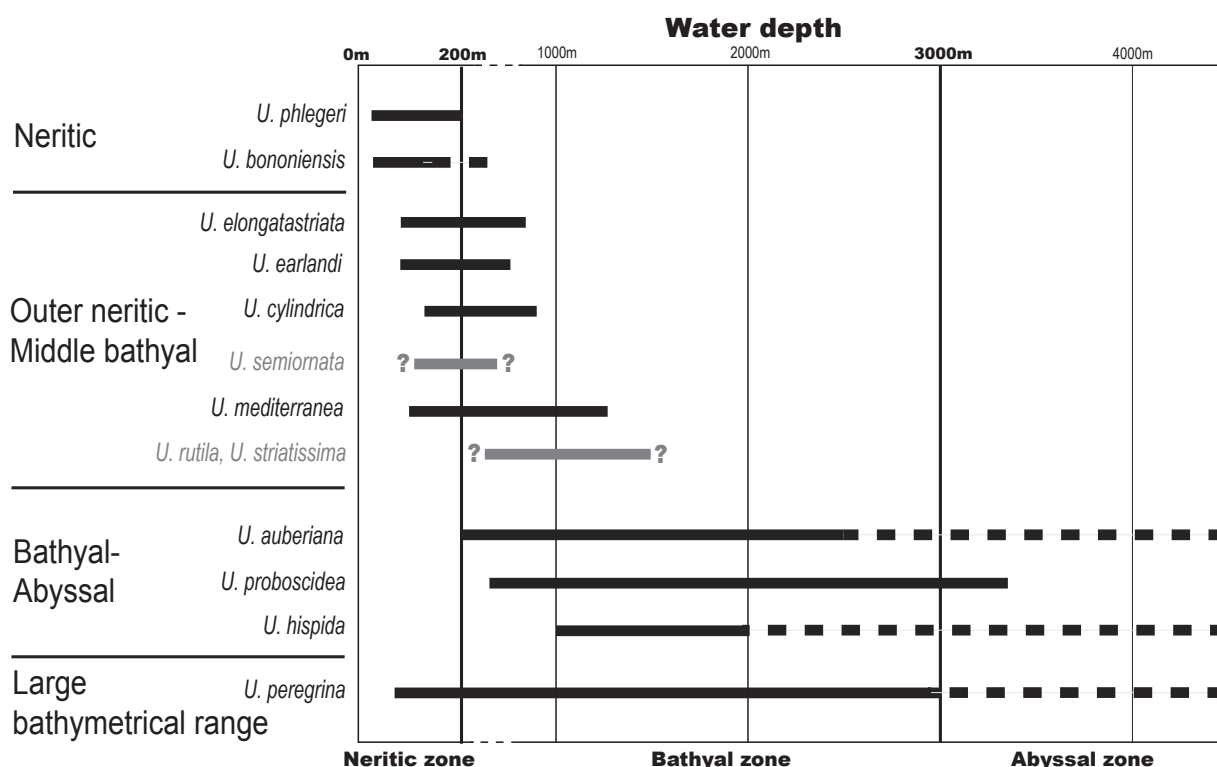


Figure 6.8. Indication of the water depth at which live the 13 studied uvigerinids, from the neritic zone (0-200m), the bathyal zone (200-3000m) and the abyssal zone (>3000m). Dashing lines represent depths where the species are less abundant and less typical, grey lines and question marks represent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

al., 2002). *Uvigerina hispida* usually has an upper depth limit of 1000m (Bandy & Chierici, 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

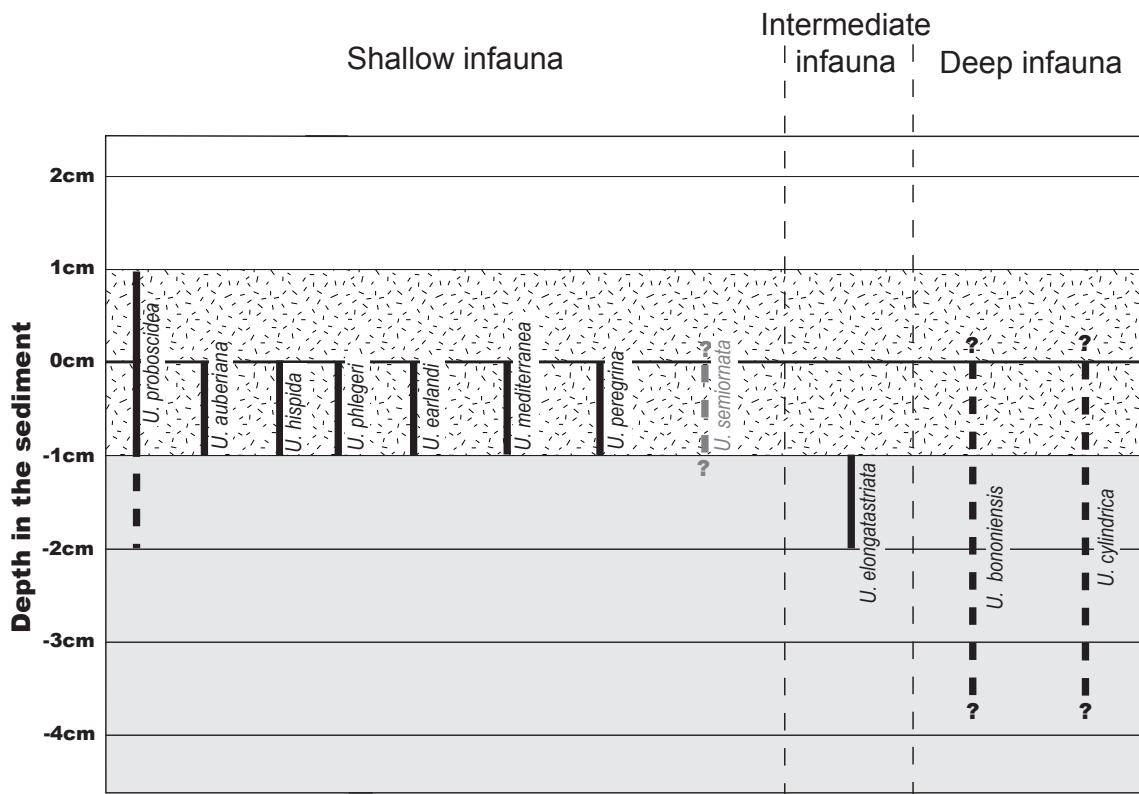


Figure 6.9. Indication of the sediment depth at which are living the 13 different species. Between +1 and -1cm, the sediment layer interface is not clear ("fluffy" layer represented by confetti). Dashing lines represent depths where the species are rarely found or are supposed to live; question marks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

depletion than the shallow infaunal taxa⁶ 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 (Boltovsoky, 1978; 1980; Boersma, 1990; Katz & Miller, 1993) Oligocene; however, the lineage may be tracked back to the Eocene with *U. gracilis*,

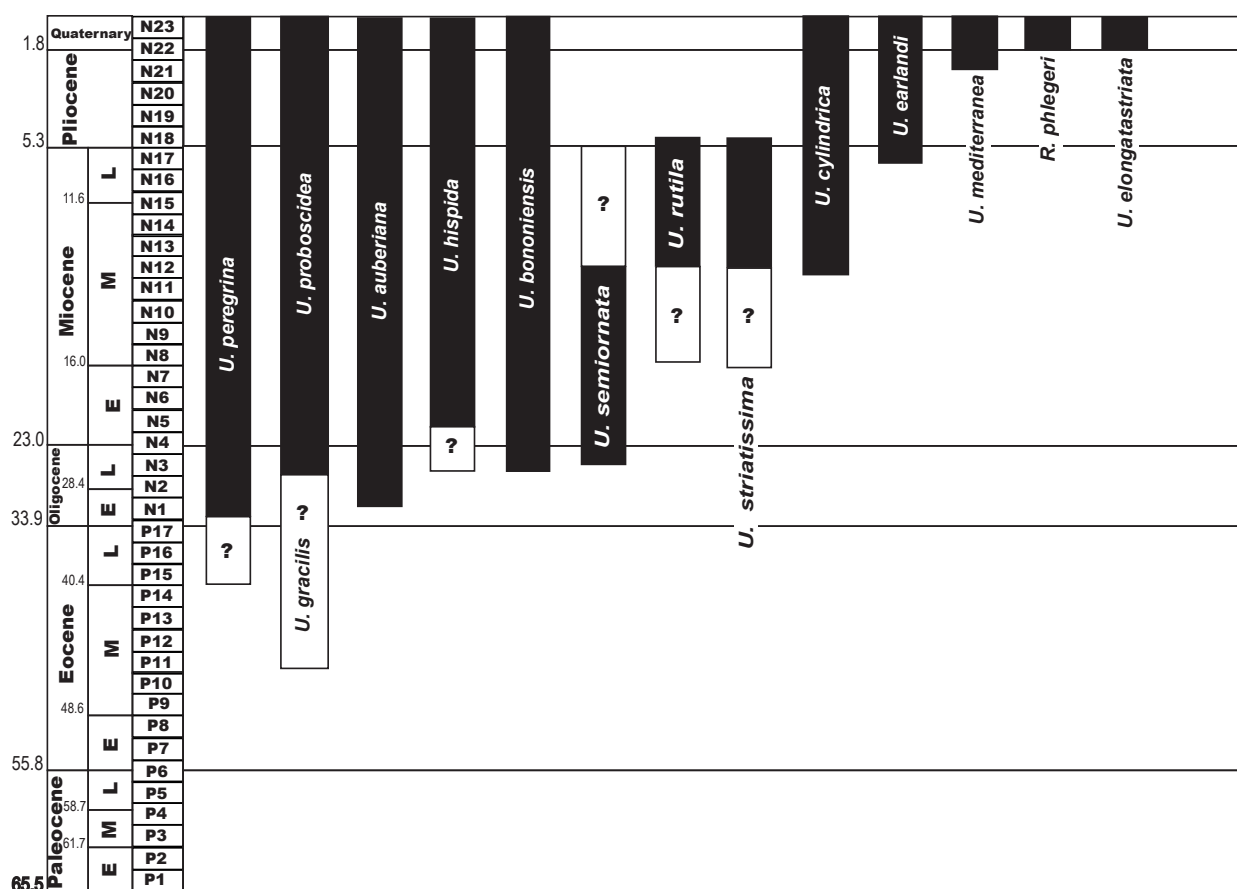


Figure 6.10. Fossil record of the 13 studied uvigerinids. Black rectangles represent well established observations, whereas white ones with question marks are less sure.

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 ornamentation⁷. 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).

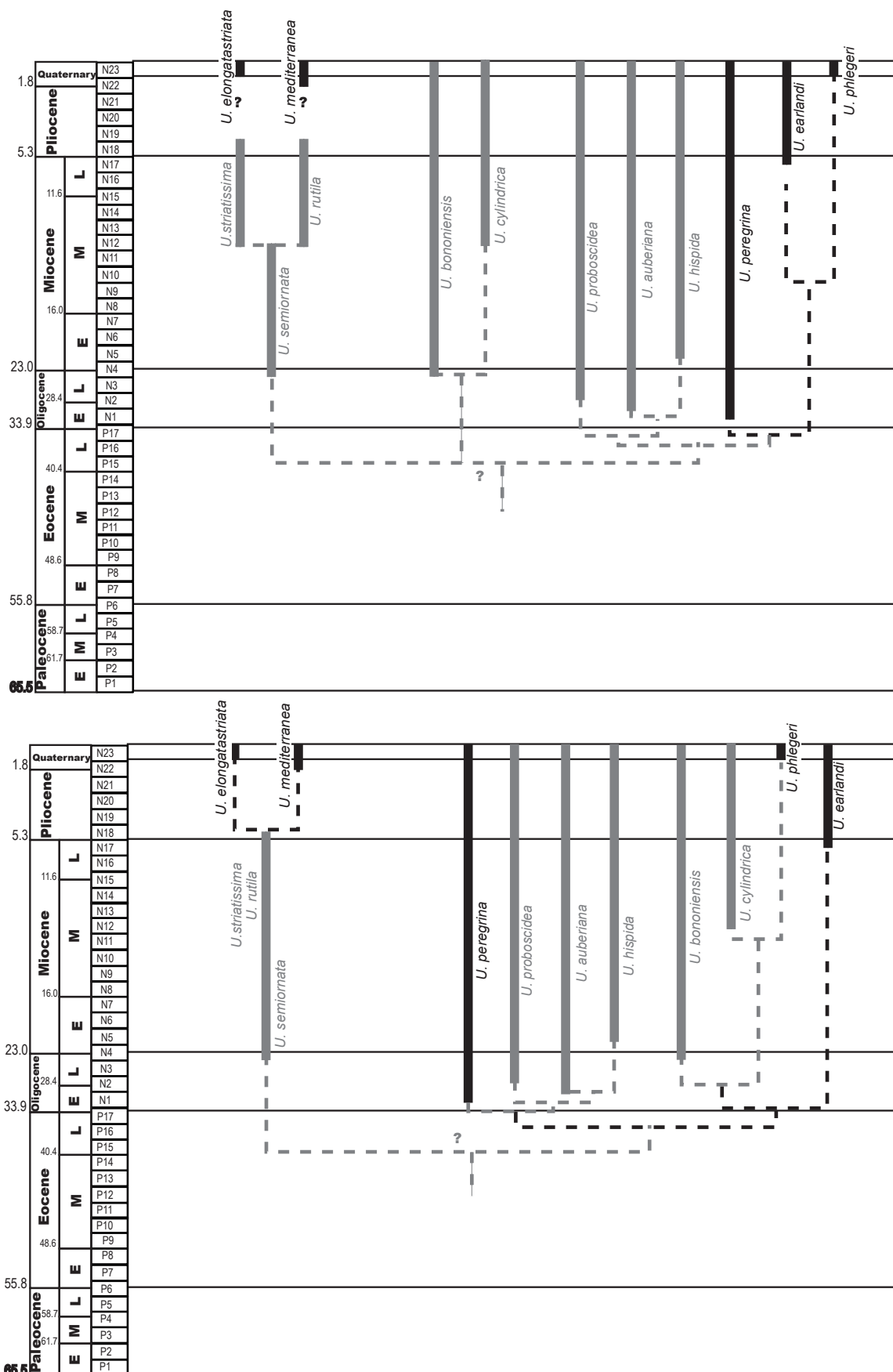


Figure 6.11. Supposed phylogeny of the 13 studied uvigerinids inferred from the molecular analyses and the fossil record. Black lines represent species which gave DNA results, whereas grey lines represent species with no DNA data.

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).