Biostratigraphic and Geological Significance of Planktonic Foraminifera

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Chapter 2

The biological and molecular characteristics of living planktonic foraminifera

2.1 The biological characteristics of modern planktonic foraminifera

Living planktonic foraminifera show a significant diversity and are highly adaptable, both in their morphology and biology. They exhibit characteristic cytoplasmic pseudopodal features that stream nutrients into, and waste out of the main body of the test. Many planktonic species harbour photosynthesizing symbionts in the pseudopodal structures, while others merely sequester chloroplasts on a temporary basis. In their open ocean habitat, planktonic species have developed a number of mechanisms for coping with the difficulties of reproduction. In this section, we briefly review the nature of the planktonic foraminiferal cytoplasm and their mechanism for test growth, the nature of their symbionts, and their reproductive strategy.

2.1.1 Cytoplasm and test growth

The vast bulk of the cytoplasm of the single cell of a living planktonic foraminifera is enclosed within a hard test, and fills the internal space to match its shape. Much of the inner space of the test is filled by vacuolated cytoplasm, and the nucleus is typically located in one of the inner chambers (Hemleben et al., 1989). The cytoplasm possesses organelles, known as fibrillar bodies (Lee et al., 1965), which in the deep evolutionary past may have originated as intracellular symbiotic bacteria (West, 1995). There are three zones of intergrading cytoplasm: the compact cytoplasm inside the test, the frothy or reticulate cytoplasm (usually observed in the final chamber or at the aperture), and the external cytoplasm (extrathalamous cytoplasm) comprising alveolate masses or reticulate to fibrose strands of pseudopodia emanating from it. Three types of pseudopodia may be observed, rhizopodia (bifurcating and anastomosing), filopodia (long, thin, and straight), and reticulopodia (net-like). The sticky rhizopodia (pseudopodia) stream outward into the surrounding environment forming a radial net that is used for feeding (Hemleben et al., 1989). They may radiate from the test to form an outer envelope or may extend along the spines in spinose species (see Plate 1.1).

Test (or shell) growth and the events leading to the formation and calcification of new chambers in foraminifera have been studied since 1854, when Schultze investigated chamber formation in Peneroplis. However, it is only since the pioneering work of Bé et al. (1977), that a more detailed understanding of the biomineralization process has become available. The formation of a new chamber is accompanied by the withdrawing of feeding rhizopodia, an increase of cytoplasmic streaming inside the test, and the development of a translucent bulge of cytoplasm from the aperture. This is followed by the radiation of thick fan-like rhizopodia from the bulge to define the margins of what will become the next chamber. The cytoplasmic bulge gradually extends out to fill the rhizopodal envelope, where upon it forms the outline of the new chamber. The establishment of the anlage, the organic structure that is primarily responsible for the calcification of the wall, then begins on the surface of the cytoplasmic bulge. Calcite crystallization and growth subsequently occurs, and the whole process is complete in approximately 6 hours (Hemleben et al., 1989). The wall of the chamber can be further thickened by lamellar accretion when subsequent chambers are added (Bé et al., 1979). Chamber formation is generally similar in spinose and nonspinose taxa; however, spines are developed in the spinose taxa after the chamber is largely complete (Hemleben et al., 1986). For a more detailed discussion of the complexities and details of biomineralization in nature as a whole, see Mann (2001).

The chemical and isotopic composition of planktonic foraminiferal tests are becoming increasingly important in the study of paleoclimatology and paleoceanography (e.g., Heuser et al., 2005; Shackleton and Opdyke, 1973; Wade et al., 2008). Thus, for example, the carbon and oxygen isotopic ratios, as well as the ratios of several trace elements to calcium content (e.g., Mg/Ca ratios), of the calcitic tests are being used as indicators of the following:

- environmental conditions during test growth (Pearson et al., 1993, 1997; Spezzaferri and Pearson, 2009);
- the temperature of the water column, seasonal effects, light intensity variations, and ocean water density stratification (Emelyanov, 2005; Haarmann et al., 2011); and
- the acquisition of photosymbionts in different phylogenetic lineages over time (Wade et al., 2008).

For a detailed discussion on the use of stable isotopes in the reconstruction of the evolutionary history of planktonic foraminifera, see Pearson (1998), and for a summary of the information that can now be inferred from the chemical signature of planktonic foraminiferal tests, see Rohling and Cooke (1999).
Figure 2.1. Examples of symbiotic and nonsymbiotic planktonic foraminifera. All images from the UCL Collection,
2.1.2 Symbionts

Symbiosis is particularly prevalent in tropical larger benthic foraminifera and in the planktonic foraminifera. However, unlike the larger benthic foraminifera, which harbour different types of symbionts (including diatoms, dinoflagellates, red algae, and chlorophytes; see BouDagher-Fadel, 2008), planktonic foraminifera have a symbiotic relationship only with two types of algal symbiont, either (but not both) dinoflagellates or chrysophytes (Bé, 1982; Hemleben et al., 1989). These symbionts play an important role in foraminiferal reproduction, calcification, and growth (Bé, 1982; Bé et al., 1982; Caron et al., 1981; Duguay, 1983; ter Kuile, 1991). The symbionts benefit the foraminiferal hosts by providing a source of energy via photosynthesis (Falkowski et al., 1993; Hallock, 1981) and by possibly removing host metabolites (Hallock, 1999). The endosymbionts (e.g., dinoflagellates) are advantageous for planktonic foraminifera, as they allow them to thrive in environments that are oligotrophic (low in nutrients) but which have abundant sunlight (Hallock, 1981). Photosymbiosis may have contributed to species diversification (Norris, 1991), and its development in the geological past was a key innovation in the evolutionary development of the planktonic foraminifera (Margulis and Fester, 1991).

Foraminifera do not inherit their photosymbionts but acquire them throughout their life cycle from the ambient sea water (Bijma et al., 1990; Hemleben et al., 1989). About one-quarter of extant tropical to subtropical surface-dwelling, spinose planktonic foraminifera (such as Globigerinoides ruber, G. conglobatus, G. sacculifer, and Orbulina universa) harbour dinoflagellate symbionts (Faber et al., 1985; Hemleben et al., 1989; Fig. 2.1), all of which possibly belong to a single species, Gymnodinium béii (Gast and Caron, 1996; Lee and Anderson, 1991). The spines of spinose planktonic foraminifera may aid Bation but certainly allow them to capture prey items (e.g., zooplankton and phytoplankton) and to carry symbionts (in Plate 1.1, the algal symbionts can be clearly seen among the radially arranged spines). In some species (e.g., Globigerinoides sacculifer), dinoflagellate symbionts are transported out to the distal parts of the test in the morning and are returned back into the test at night. For symbiotic spinose forms, the symbiosis is thought to be obligative (i.e., survival outside the relationship is impossible; Hemleben et al., 1989). However, a few spinose foraminifera (e.g., Globigerina bulloides and Hastigerina pelagica) are unusual in being symbiont barren, though the latter houses commensals (Spindler and Hemleben, 1980). The planispiral spinose Globigerinella possesses two different photosymbionts, both of them chrysophytes.

In contrast to the carnivorous spinose forms, the nonspinose planktonic foraminifera are herbivorous, like benthic forms. Many nonspinose planktonic foraminifera (e.g., Globigerinita glutinata, Neogloboquadrina dutertrei, Pulletiatina obliquiloculata, Globorotalia inflata, and Gt. menardii) harbours facultative chrysophytes (see Fig. 2.1). These nonobligative symbionts are housed either on a nonpermanent basis, photosynthesizing within perialgal vacuoles, or they are sometimes digested (Hemleben et al., 1988). Other nonspinose taxa (e.g., Neogloboquadrina pachyderma, Truncorotalia truncatulinoides, Gt. hirsuta) are symbiont barren (Hemleben et al., 1989; Fig. 2.1).

The dominant factors controlling the size and distribution of both symbiotic and asymbiotic planktonic foraminiferan species are light and nutrient density. Nutrient flux decreases offshore, while light, needed for symbiont photosynthesis, increases offshore as water turbidity lessens, but naturally decreases with increasing water depth. Asymbiotic foraminifera, which survive by grazing, dominate coastal fauna. Species that benefit from symbiont photosynthesis dominate the offshore fauna (Ortiz et al., 1995). They tend to have relatively large size tests, which facilitate the support of the symbionts and which benefit from enhanced photosynthetic activity (Norris, 1996; Spero and DeNiro, 1987). They have a more cosmopolitan distribution than asymbiotic foraminifera and a greater ability to withstand periods of nutrient stress (Norris, 1996).

Isotopic methods have been used to determine possible symbiotic associations in fossil planktonic foraminifera (e.g., D’Hondt and Zachos, 1993; D’Hondt et al., 1994; Norris, 1996), as the vital processes often leave a characteristic isotopic signature. Correlation between test size and characteristic stable isotopic ratios indicated that photosymbiosis existed in some Late Maastrichtian planktonic foraminifera (Bornemann and Norris, 2007; D’Hondt and Zachos, 1998). It has been suggested that photosymbiosis as a life strategy was given a competitive advantage by the development at this time of oligotrophic conditions associated with increased water-mass stratification (Abramovich and Keller, 2003). All photosymbiotic forms, however, went extinct at the End Cretaceous catastrophe. In the fossil record, however, photosymbiosis reappeared in the acarinins and morozovellids in the Paleogene. D’Hondt et al. (1994) hypothesized that their reappearance was closely linked to habitat and not to test morphology; Acarinina and Morozovella occupied the same habitat as modern photosymbiotic taxa, but they differ greatly in morphology from living forms.

2.1.3 Reproduction

In contrast to the variety of reproductive strategies seen in the benthic foraminifera (BouDagher-Fadel, 2008), sexual reproduction is the only strategy that has ever been recorded for the planktonic foraminifera (Goldstein, 1999; Hemleben et al., 1989). It is not possible to make detailed observations of the physiological and morphological changes during the entire life cycle of planktonic foraminifera, as they have not as yet not produced viable offspring in the laboratory (Lee and Anderson, 1991). However, test size distributions, coupled with abundance changes and more general laboratory observations, have been used by Hemleben et al. (1989) and Lee and Anderson (1991) to infer the life cycle of Globigerinoides sacculifer (Plate 6.3, Figs. 9–10) and Hastigerina pelagica (Plate 6.8, Fig. 11).
Hemleben et al. (1988) recorded that the planktonic foraminifera have developed a number of mechanisms for coping with the difficulties of reproduction in an open ocean environment, in order to maximize the chances that compatible gametes of the correct species will meet. Throughout the year, most species will migrate throughout the water column, a strategy that is thought to maximize the access to available food sources. Approximately a day preceding gamete release, mature individuals of spinose planktonic foraminifera (e.g., *Globigerinoides sacculifer*) start to sink down below the photic zone, while digesting their symbionts, and accumulate in the thermocline to release their gametes. During this time, they produce additional calcification of final chambers just before shedding their spines. Then nuclear division occurs, filling the cytoplasm with daughter nuclei, and the gametes are released from an expanding bulge of the cytoplasm (Lee and Anderson, 1991); at least $10^7$ gametes are released from each parent cell (Bé and Anderson, 1976). Several days later, juvenile individuals appear again in the productive surface waters and the cycle repeats itself (Erez et al., 1991; Taniguchi and Bé, 1985). The sinking of planktonic foraminifera into deeper water in their reproductive cycles may have many advantages, such as accessing a stable breeding environment where food source for juveniles is available, and enhancing the survival of the gametes and resulting juveniles by placing them where they can avoid predators.

Gamete release in planktonic foraminifera is mainly synchronized by a lunar, semilunar, or diurnal cycle (Hemleben et al., 1989), although food availability may also play some role in the timing of reproduction (Hemleben et al., 1989). Gametes are released in their hundreds of thousands and though not proven conclusively, evidence suggests that the primary reproductive strategy may be dioecious (i.e., each individual has reproductive units that are either simply male or simply female), with gametes from different parents fusing to form the new juvenile (Hemleben et al., 1989). The general reproductive strategies and habitat-horizons of some modern planktonic foraminifera, as recorded by Hemleben et al. (1989), are shown in Fig. 2.2.
2.2 Biogeography and ecology of the modern planktonic foraminifera

Living planktonic foraminifera have expanded to fill a wide variety of niches within the global ocean, including tropical waters as well as subtropical and polar water masses. They live mostly in the photic zone but descend to waters as deep as several thousand meters. In comparison with their highly diverse benthic counterparts, there are only about 90 extant species of planktonic foraminifera (see Charts 6.1–6.3 online). Their species diversity peaks in the sub-tropics and decreases steeply toward the poles (see Fig. 2.3). They are most abundant in euphotic, near-surface waters, in water depths between 10 and 50 m. The surface waters of the sea are usually saturated or supersaturated in oxygen, which is dissolved from the air...
that is mixed into the oceans by wave action. It is in these most superficial layers of seawaters that symbiotic or asymbiotic planktonic foraminifera with subglobular chambers are found (e.g., Globigerina and Hastigerina). At greater depths, the oceanic oxygen levels drop, and forms with a greater surface area to volume ratio have an advantage (as they enable oxygen to diffuse into the cell more effectively than the more spherical forms, e.g., Beella and Hastigerinopsis, see Chapter 6).

The distribution of each species is controlled by various factors, such as temperature, light intensity, and prey or nutrient availability, and this can be used as a proxy for the reconstruction of paleoenvironments. For example, the geographic distribution of Neogloboquadrina pachyderma (Fig. 2.4) is mainly controlled by seawater temperature. However, two morphotypes of Globigerinoides ruber (Gdes ruber s.s. and Gdes ruber s.l.) collected from the South China Sea showed different vertical distributions, with Gdes ruber s.s. predominant in surface waters and Gdes ruber s.l. in a deeper ones. This difference in habitat can be attributed to a difference in light intensity and food availability, with the shallower-living morphotype being more dependent upon symbionts (Kuroyanagi and Kawahata, 2004).

The direction of coiling (dextral or sinistral) of some planktonic foraminifera has been used for some time as a proxy for paleoclimate. For example, variants of Neogloboquadrina pachyderma have long been used as tools to infer changes in polar ocean temperatures over geological time (Peck et al., 2008). It had been thought that the sense of coiling within N. pachyderma was temperature dependent, such that during periods of relatively colder oceanic temperatures, its test coils sinisterly (Fig. 2.4), while during periods of relative warmth, assemblages with more than 50% dextral coiling are found. However, more recent research (see the following section) now shows that these two coiling variants are in fact genetically distinct species (Darling and Wade, 2008; Darling et al., 2006; de Vargas et al., 2001), with N. pachyderma having the sinistral coiling (Fig. 2.4) and Paragloborotalia incompta being dextral. Similar behavior is exhibited by Truncorotalia (Fig. 2.5; Fig. 6.13). Truncorotalia species have always been deep dwelling, with left coiling groups found in subpolar regions, and right coiling forms (Fig. 2.5) found in relatively warmer waters. These changes in coiling direction correlate with isotopic shifts associated with temperature changes (Feldman, 2003). However, the coiling variants of T. truncatulinoides have also now been shown to be genetically different (de Vargas et al., 2001) and may even be distinct species.

2.3 The molecular biological studies of the planktonic foraminifera

Relatively recent molecular biological studies based on the analysis of DNA sequences have led to an extensive increase in our understanding of the evolutionary relationships between the species of planktonic foraminifera living in the oceans today, the origin of major phylogenetic lineages, and the likelihood that stable morphospecies are in fact species clusters. Furthermore, as seen above, genetic studies have also given new insights into their biogeography and ecological diversity.

The focus of research in this field has been on the ribosomal ribonucleic acid (rRNA) of the planktonic foraminifera. rRNA is the RNA component of the ribosome, which is the enzyme that is the location of protein synthesis in all living cells. The rRNA forms two subunits, the large subunit (LSU) and small subunit (SSU). Planktonic foraminifera show an unusually high level of genetic diversity in their SSU rRNA (Aurahs et al., 2009; Darling et al., 1996; Pawlowski et al., 1996; Wade et al., 1996), and many contain more than one genetically distinct unit that can be used to differentiate between different species. These sequences of protein-coding genes provide an important alternative source of phylogenetic information to the morphological data upon which fossil analysis depends (Flakowski et al., 2005). It has been found that some different types of “morphospecies” can indeed be highly divergent genotypes, having slight morphological differences and displaying distinct ecological adaptations. They can, therefore, be separated taxonomically into clusters of cryptic or sibling species, which may have diverged many millions of years ago (Darling et al., 1999, 2007; de Vargas et al., 2002; Huber et al., 1997; Wade and Darling, 2002). Not only do data on rRNA give us insight into the genetics of modern planktonic foraminifera, but they can also be used to confirm the validity (or otherwise) of the phylogeny of these forms inferred from the fossil, morphological record.

2.3.1 Molecular and genetic insights into the origin of planktonic foraminifera

As introduced above, recent studies on planktonic foraminifera have focused on partial sequences of the SSU rRNA gene (Aurahs et al., 2009; Darling et al., 1996; Pawlowski et al., 1996; Wade et al., 1996) and the LSU rRNA gene (Pawlowski et al., 1994). Both units can easily be obtained from single cells captured in environmental samples (Flakowski et al., 2005). SSU rRNA sequences can be amplified using the “universal” eukaryote primers of White et al. (1990), originally designed for use on fungi. As noted in Chapter 1, molecular analyses have shown that the Order Foraminifera are a mono-phyletic group within the eukaryotic phylogeny (Archibald et al., 2003; Berney and Pawlowski, 2003; Darling et al., 1996; Flakowski et al., 2005; Keeling, 2001; Longet et al., 2003; Pawlowski et al., 1996; Wade et al., 1996), and they seem to form one of the earliest diverging eukaryote lineages in the “tree of life.”

Molecular studies have provided information about subtle features of the evolutionary history of planktonic forms (Aze et al., 2011). For example, as referred to above, prior to genetic studies, it had been thought that the morphologically similar Neogloboquadrina pachyderma and “N.” incompta were a single species, but with coiling direction being an ecophenotypic response to temperature (Ericson, 1959; Ottens, 1992). Genetic studies, however, have revealed substantial divergence
between the two forms, and the coiling direction in *N. pachyderma* is a consistent genetic trait, heritable through time (Darling et al., 2004, 2006). Indeed, detailed morphological study reveals them even to belong to different genera. The species *incompta* belongs to the genus *Paraglobaloritulia*, because of its wall structure (pustules on surface, with no ridge growth) and the shape of its aperture (umbilical–extraumbilical throughout adult growth), while *Neogloboquadridina pachyderma* has an antero-intraumbilical aperture and a build-up of a calcitic crust on its test (see Fig. 2.4 and Chapter 6).

Molecular systematics and genetic analyses have also been used to determine the phylogenetic evolutionary lineages of the planktonic forms and their relationship to benthic form. Fossil evidence suggested that the earliest planktonic foraminifera evolved from benthic lineages, originating in the Late Triassic and the Jurassic (see Chapter 3). Their evolution occurred initially by adopting a meroplanktonic mode of life, in which benthic forms (living mainly attached to the sediment) adopted the planktonic mode for a part of their life cycle (perhaps the reproductive stage). Such transitions from the benthic to the planktonic mode of life are well documented (Banner et al., 1985; BouDagher-Fadel et al., 1997) in many modern benthic rotaline foraminifera, which are usually resident on firm substrates (stones or algae, etc.) during which time the adherent side of their tests become flattened. When the planktonic mode of life is adopted, the chambers lose their adherence and become more fully globular (see Fig. 2.6). The development of a planktonic state, before reproduction, enables a species to disperse its gametes more freely throughout the seawater and so to spread its progeny more widely. The holoplanktonic (fully planktonic) mode of life did not appear in the fossil record before the Middle Jurassic, with the development of *Globuligerina*. A second development of holoplanktonism occurred later in the Cretaceous, giving rise to the triserial guembelitriid lineage. Genetic studies of the only living representative of this guembelitriid lineage (*Gallitellia vivans*) show that this lineage is quite distinct from the globigerinid planktonic foraminifera and that genetically the guembelitriids are more closely related to the benthic rotaliids than they are to the globigerinids (see Chapter 6). The genetically inferred divergence time of *Gallitellia vivans* (Ujié et al., 2008) is, however, estimated as being no older than 18 Ma (i.e., the Early Miocene). This suggests, therefore, that the origin of this living guembelitrid is in fact independent from the other Cretaceous and Paleogene *Heterohelicida* (see Fig. 1.6), and that *Gallitellia vivans* might have acquired the planktonic mode of life by a relatively recent transition from the benthos to the planktonic mode somewhere between the Miocene and the Pliocene.

This multiple occurrence of the evolutionary transition from benthic to planktonic is further corroborated by an increasing amount of evidence from molecular studies, which suggest that even living globigerinid foraminifera are polyphyletic in origin. Most analyses of living globigerinid planktonic foraminifera show three separate clusters in the molecular tree (Fig. 2.7), which equate to the morphologically defined microperforate, nonspinose forms (e.g., *Globigerinida uvula*; Plate 6.1, Fig. 15); macroperforate, nonspinose forms (e.g., *Globoratulina menardii, Neogloboquadridina dutertrei*; Plate 6.7, Figs. 14–15); and spinose forms (e.g., Globigerinoides ruber; Plate 6.3, Figs. 7–8). Such distinct genetic clustering may indicate that the planktonic way of life of these living Globigerinida evolved from three (or more) independent preexisting benthic lines (de Vargas et al., 1997).

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**Figure 2.6.** The gamonts of some species of the normally benthic Discorbidae and Cymbaloporidae have a planktonic stage just before and during reproduction. They independently evolved flotation structures in subglobular chambers at the last stage of growth. (A) *Neoconorbina concina* Brady, Holocene, Kenya, spiral view, x55; (B) *Cymbaloporetta* sp., Holocene, Kenya, x60; (C) *Cymbaloporetta cifelli* Banner, Pereira, and Desai, Holocene, Kenya, x40; (D) *Cymbaloporetta* sp. Holocene, offshore Lebanon, x40. All images from the UCL Collection.
The placement in Fig. 2.7 of the spinose Globigerinidae and the nonspinose Globorotaliidae in separate lineages contrasts with the traditional paleontological view of their common origin. Evidence that the globorotaliids diverged from a globigerinid ancestor in the Eocene (Fig. 1.6) is well documented in the fossil record (see Chapter 5). However, the molecular data suggest that some living globorotaliids are far more closely related to some benthic taxa than they are to living globigerinids (Aurahs et al., 2009; Darling et al., 1997, 1999, 2000, 2006; de Vargas et al., 1997; Stewart et al., 2001). However, this differentiation between planktonic and benthic affiliations may be a false dichotomy. In laboratory experiments, Hilbrecht and Thierstein (1996) were able to observe forms with compressed tests, conventionally classified as planktonic forms, Globigerinella siphonifera and Globorotalia menardii undertaking benthic activities through their life cycle. *G. siphonifera* was able to create well-organized burrows and to excavate sediment in a circular pile. *G. menardii* and *G. siphonifera* have specific crawling and burrowing orientations. This behavior is in contrast to that of planktonic foraminifera with globular chambers and buoyant tests, such as Globigerinoides ruber, Globigerinoides sacculifer, Hastigerina pelagica, and Orbulina universa, which when observed did not exhibit any benthic activity and in fact died if placed on a sediment substrate (Hilbrecht and Thierstein, 1996).

The monophylogeny of the Neogloboquadrina and its relationships to *Globorotalia* is strongly supported in the fossil record (see Chapter 6). However, Darling et al. (1999) found that the only two globorotaliids in their sample of analyzed species, *N. dutertrei* and *Gt. menardii*, do not cluster together, but rather branch off deeply within the benthic group and are genetically widely separated from each other (Fig. 2.7). According to Darling et al., the nonspinose *Neogloboquadrina dutertrei* (Plate 6.7, Figs. 14–15) is genetically more closely related to benthic species, from which they infer either that it has only recently evolved from a benthic habitat or that it exhibits a much slower rate of genetic evolution than other planktonic species. Similarly, the origin of the extant family Hastigerinidae (which possesses monolamellar shells) remains genetically ill-defined (Aurahs et al., 2009), while the microperforate *Tinophodella glutinata*, the only representative of the Globigerinidae so far studied, appears to be genetically closer to the globorotaliids and the benthic rotaliids than it is to the globorotaliids (Aurahs et al., 2009). In contrast to the inconclusive genetic data in the nonspinose species, the relationships between the globular spinose forms (with globular buoyant tests), such as Globigerina bulloides–Globigerina falconensis, Globigerinoides ruber–Globigerinoides conglobatus, and Globigerinoides sacculifer–*Orbulina universa*, are in agreement with the fossil record (see Fig. 2.7; Aurahs et al., 2009).

In the fossil record, the relationship between the microperforate, the spinose macroperforate, and the nonspinose macroperforate foraminifera is inferred from their morphology (overviewed in Chapter 1 and discussed further in Chapter 6). Figure 1.6 shows continuous evolutionary lineages of planktonic forms over the past...
200 Ma. However, the recent genetic and observational evidence discussed above suggests a more complex picture in which the interchange between the planktonic and benthic realms may be partially reversible when, for example, compressed planktonic forms that are specialized in the exploitation of deeper water columns (e.g., *Globorotalia* and *Globigerinella*) can also exploit the benthic realm. This might explain the observed molecular branching of *Globorotalia* deeply within the benthic group and separately from the spinose globular planktonic foraminifera, and hence provides evidence of a polyphyletic origin for the planktonic foraminifera. Similarly, the multiserial planktonic foraminifera have almost certainly experienced repeated transitions between the benthic and the planktonic realms, suggesting that they too can exploit both niches. Indeed, recently, Darling *et al.* (2009) demonstrated that the extant biserial planktonic *Streptochilus globigerus* is genetically identical (and so belongs to the same biological species) as the benthic form *Bolivina variabilis*. This “benthic” or “pseudobenthic” behaviour in planktonic foraminifera, especially in the compressed or uncoiled species, may have been widespread among fossil planktonic foraminifera; however, no direct evidence of such behavioural complexity is or can be retained in the fossil record. As a result, a simple and apparently continuous phylogenetic tree (e.g., Fig. 1.6) is the inevitable consequence of morphologically based analyses; however, the interpretation of such trees must always be tempered by the suspicion that the behaviour of many now extinct species may have been more complex when they were alive than is evident from their fossilized forms.

### 2.3.2 Biogeography, cryptic speciation, and molecular biology

The global open ocean is not a uniform ecosystem, but one comprised of regionally distinct climate zones. Global circulation patterns and climate zones define basic physical boundaries for the planktonic foraminifera that inhabit the ocean. The ocean environment is also a complex ecosystem, and within the faunal provinces, other factors such as salinity, prey abundance or nutrient levels, turbidity, illumination, chemistry, and thermocline gradient may also affect diversity, abundance, and distribution of the planktonic foraminifera. In studying the global distributions of modern planktonic foraminifera, broad planktonic provinces can be designated as tropical, subtropical, temperate, and polar (see Fig. 2.3). Specific assemblages of morphologically adapted species are associated with each of these regions. The fact that planktonic foraminiferal species adhere to these faunal provinces, coupled with their widespread global latitudinal distribution, has made them extremely useful in the study of both modern and ancient marine ecosystems (Hemleben *et al.*, 1989). Discrete assemblages are also found in transitory provinces associated with regional upwelling (Hemleben *et al.*, 1989; Lipp, 1979). Indeed, individual species may be found across several zones, such as tropical–subtropical, subtropical–temperate, and even across all zones, as cosmopolitan forms (see Charts 6.1–6.3 online), suggesting that gene flow is common globally, with genetic intermixing between populations occupying several climatic zones.

Superficially, land-mass barriers and water-mass fronts do not generally seem to form insuperable divisions. Morphologically, identical assemblages of warm-water species, such as *Orbulina universa*, are found in geographically distinct bioprovinces, such as the Caribbean, the Coral Seas, and the Mediterranean. Furthermore, data from the SSU rRNA genes of specimens of *Globigerina bulloides*, *Turborotalita quinqueloba*, and *Paragloborotalia incompata*, collected from the Arctic and Antarctic regions, show that species from these two isolated regions possess identical rRNA genotypes (Darling and Wade, 2008). Thus, although these species are only found in the high latitudes and are absent from tropical regions, it appears that either the water-mass that separates them is not a major barrier to gene flow or that these assemblages have been separated for too short a period of time for them to develop distinct genetic identities. In contrast, however, genetically distinct forms of *Neogloboquadrina pachyderma* are found in the Arctic and Antarctic waters, while *Globorotalioide sens hexagona* is found only in the tropics of the Indo-Pacific suggesting that for this form at least the Southern Africa Cape currently presents a barrier to their passage into the Atlantic (Darling and Wade, 2008).

However, increasingly more detailed studies that combine molecular, ecological, and morphological evidence are now revealing multiple cases of “cryptic speciation” among planktonic foraminifera (Darling and Wade, 2008; Ujiie and Lipp, 2009), which challenge the morphospecies concept and the paleoceanographic interpretations based up on them. So, for example, *Truncorotalia truncatulinoides* has been found to be a complex of four genetic species adapted to particular oceanic conditions, two occurring in the subtropics, one in the sub-Antarctic convergence zone, and one in Antarctic waters (de Vargas *et al.*, 2001). Likewise, it seems that *Orbulina universa* comprises three cryptic species (Darling and Wade, 2008; de Vargas *et al.*, 1999), also distributed according to oceanic provinces and particularly to chlorophyll concentration at the sea surface. *Globigerinella siphonifera* comprises over five types, which can be divided into at least two sibling species that can be distinguished by isotopic variations, shell porosity, and the species of their photosymbionts (Darling and Wade, 2008; Darling *et al.*, 1997, 1999; Huber *et al.*, 1997). Within the realm of planktonic foraminifera, therefore, there indeed seems to be an abundance of cryptic species. Seears *et al.* (2012) proposed that sea surface, primary productivity is the main factor driving the segregation of planktonic foraminifera, with variations in symbiotic associations possibly playing a role in the specific ecological adaptations observed. They suggested that ecological partitioning could be contributing to the high levels of cryptic genetic diversity observed within the planktonic foraminifera and support the view that ecological processes may play a key role in the diversification of marine pelagic organisms. The newly discovered genotypes show non-random distributions, suggestive of distinct ecology ecotypes (Darling and Wade, 2008; de...
Vargas et al., 2002). This widespread development of cryptic speciation among the planktonic foraminifera hints, therefore, at the processes that underpin Darwinian evolution, namely, that genetic divergence and eventual speciation is driven when communities become isolated, colonize different niches, or adopt different strategies for survival. This process has been exemplified par excellence by the planktonic foraminifera as they evolved over geological time to produce the wide diversity of species seen today and in the fossil record.

In conclusion, therefore, in this chapter, we have reviewed evidence linking molecular biology to species diversification and shown how molecular studies help constrain the phylogenetic evolution of recent forms. When studying fossil forms, however, genetic data are not available and only information drawn from test morphology can be used to develop phylogenetic relationships. We have explained, however, that such fossil-based studies may miss some of the true complexity of the modes of life that the foraminifera exploited when extant. So bearing this caveat in mind, we use in the following chapters the morphological approach to the definition of the taxonomy and the phylogenetic evolution of the fossil record to define the biostratigraphic and environmental significance of the Mesozoic and Cenozoic planktonic foraminifera. In Chapter 3, we review the earliest planktonic radiation, which possibly occurred in the Late Triassic, but which certainly was established in the Jurassic. In Chapters 4 and 5, we extend the analysis of the development of the planktonic foraminifera through the Cretaceous and the Paleogene, and finally in Chapter 6, we show how the morphologically based studies of the Neogene forms relate to the developing genetic understanding that has been described in this chapter. We will see that more molecular data, covering all known planktonic species, are needed to resolve the many issues that remain outstanding, and only then will it be possible to combine the insights from genetics with morphological and fossil data to provide a complete (or as complete as will ever be possible) understanding of the evolutionary unfolding of planktonic foraminifera over geological time.