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Ecology of extant nummulitids and other larger benthic foraminifera: applications in palaeoenvironmental analysis

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Abstract

Larger benthic foraminifera (LBF) are important contributors to modern and ancient tropical, shallow-marine sediments. Over the past 30 years, a substantial body of literature has built up on the ecology of modern LBF, especially in terms of their environmentally sensitive depth distribution, reproductive strategy and morphology, and the symbiotic relationship between many larger foraminifera and photosynthetic algae. Over the same period, the extinct genus *Nummulites*, which is abundant in Eocene sediments of southern Europe, North Africa and the Arabian Peninsula, has increasingly been studied, principally because significant volumes of hydrocarbons have been discovered reservoired within nummulitic limestones offshore Tunisia and Libya. The modern ecological studies of LBF provide a powerful tool with which to develop palaeoecological models for fossil *Nummulites* (and other symbiont-bearing larger foraminifera in the rock record).

Keywords: larger benthic foraminifera; ecology; palaeoecology; *Nummulites*; nummulitic limestone; Early Tertiary

1. Introduction

Larger benthic foraminifera (LBF) are an informal group which occur as both fossil and extant forms. They have complex internal morphologies and commonly exceed 3 mm^3 in volume (Ross, 1974), although some fossil specimens have volumes in excess of 500 mm^3 and diameters approaching 150 mm (e.g., *Nummulites millecaput*). All living representatives occur within the Suborders Miliolina and Rotaliina of Loeblich and Tappan (1984) (= Orders Miliolida and Rotaliida of Haynes, 1981); ancient representatives also occur in the Orders Lituolida and Fusulinida of Haynes (1981). Hallock (1998) identifies seven families of free-living, extant LBF: the porcellaneous Archaiadae, Peneroplidae, Soritidae and Alveolinidae, and the hyaline Amphisteginidae, Calcarinidae and Nummulitidae. They occur most commonly in shallow, tropical carbonate environments, with many species hosting symbiotic algae within their tests, a feature also inferred for many extinct LBF (Cowen, 1983).

Our knowledge of the ecology of Recent LBF has made great progress in the last 30 years, especially in

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terms of understanding their environmentally sensitive depth distribution, reproductive strategy and morphology. However, the interactions between the various environmental factors are complex, as indicated in Fig. 1, which often makes it difficult to correlate the characteristics of LBF with specific external influences. This paper reviews current understanding about the effects of these external influences on test size, shape and distribution for some porcellaneous-walled (Suborder Miliolina) and hyaline-walled (Suborder Rotaliina) LBF, with particular emphasis placed on the nummulitids. The latter group has been selected because it contains several well-studied extant genera, as well as forms that were important sediment contributors in the Palaeogene. They also have economic importance because accumulations of Eocene *Nummulites* reservoir significant volumes of hydrocarbons (Racey, 2001).

Larger foraminifera have arisen many times in the geological record from ordinary-sized ancestors (Lee et al., 1979). They are biostratigraphically important zonal fossils because of these episodes of rapid diversification and abrupt extinction (Hallock, 1985). Their appearance is often related to periods of global warming, relative drought, raised sea levels, expansion of tropical and subtropical habitats, and reduced oceanic circulation (Hallock and Glenn, 1986). During such times, nutrient recycling to surface waters was dramatically reduced, and organic productivity in the oceans dropped by up to two orders of magnitude (Bralower and Thierstein, 1984). As will be shown, such oligotrophic conditions are highly advantageous for symbiont-bearing LBF. The early Tertiary is typical of such periods; following the demise of the rudist-coral assemblage at the end of the Cretaceous, nummulitid (*Nummulites*, *Assilina* and *Operculina*), orthophragminid (*Discocyclina*) and alveolinid (*Alveolina*) larger foraminifera thrived on shallow, oligotrophic, circum-Tethyan ramps, filling the role of inner- to midramp sediment producers (Buxton and Pedley, 1989).

Using the principle of taxonomic uniformitarianism, an understanding of the ecology of living species of LBF is an essential prerequisite to any interpretation of the forms which make up the accumulations observed in the geological record. Thus, the depth and habitat zonation exhibited by many living larger benthic foraminifera are potentially useful palaeoenvironmental indicators, and therefore, this review of the ecology of modern nummulitids (and selected other larger foraminifera) is partly intended for use as a tool to aid reconstruction of depositional environments for nummulitic limestones (and other rock-forming, symbiont-bearing larger foraminifera). However, because environmental factors exert such a strong control on LBF, a strictly uniformitarian approach to the interpretation of fossil forms that lived during the early Tertiary, under climatic conditions

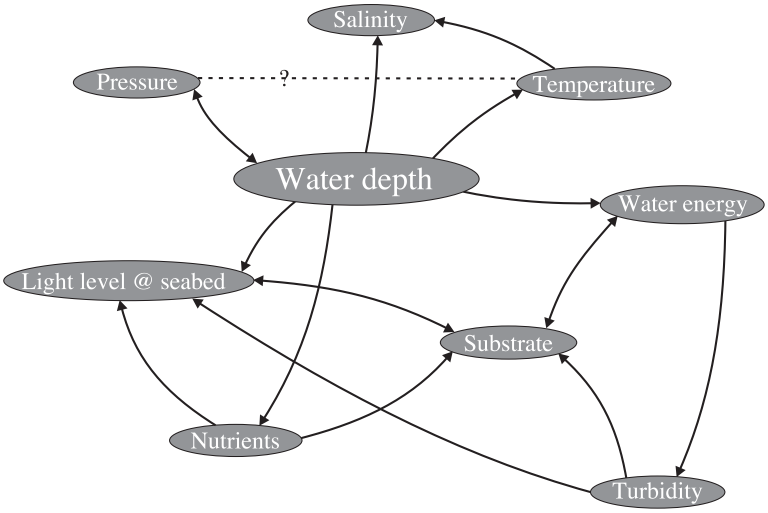

Fig. 1. Interaction of factors that affect morphology and distribution of LBF (modified from Racey, 1992).

very different to our own (see Berggren et al., 1998), is unwise. In addition, comparisons can only be made with confidence in extant species (and even then the possibility that the ecology of the organisms may have evolved through time needs to be considered); in the case of extinct species, comparisons must necessarily be reduced to generalisations at the family level. As Bosence and Allison (1995) point out, a holistic approach to palaeoenvironmental interpretation, drawing on palaeoecological, palaeontological and other methods, is essential if the potential pitfalls of a strictly uniformitarian approach are to be avoided.

The test composition and morphology of the foraminiferal groups that are the focus of this review (principally the nummulitids) are described below. The controls on the distribution and the test size and shape of these foraminifera are then reviewed, illustrating the significance of the environmentally influenced life cycle of LBF, and the symbiotic relationship between many larger foraminifera and photosynthetic algae. Other physical and chemical influences on LBF, including nutrient supply, substrate, water energy, salinity, temperature and taphonomic processes, are also discussed. Idealised models of the depth distribution of selected extant and Tertiary larger foraminifera are then presented, and the application of modern ecological studies to the interpretation of fossil foraminifera is discussed.

In contrast to studies of the ecology of modern larger foraminifera, comparatively little has been published on the palaeoecology of fossil LBF. Where pertinent within this review, published palaeoecological observations (particularly those relating to *Nummulites*) are discussed within the context of modern studies.

2. Test composition and morphology of the principal groups of extant larger benthic foraminifera

2.1. Suborder Miliolina Delage and Hérouard, 1896

The Miliolina have tests of porcellaneous calcite, constructed from tiny (1–2 μm size), irregularly orientated high magnesium calcite needles (Towe and Cifelli, 1967). Miliolid tests commonly have an organic lining and are generally imperforate in the postembryonic stage (Loeblich and Tappan, 1984). Of this group, this review is principally concerned with the superfamily Soritacea Ehrenberg 1839, which includes the Soritidae and Alveolinidae.

The Soritidae have a planispiral test (at least in the early stage; later stages may be uncoiled, flaring, fusiform or cylindrical) with numerous chambers that are commonly subdivided by interseptal pillars or septula and multiple apertures. The Alveolinidae commonly have a large test, which may be globular, fusiform or subcylindrical, and is coiled about the elongate axis. The numerous chambers are divided by secondary partitions or septulae into one or more layers of chamberlets, which are orientated parallel to the direction of coiling. Later, chambers may be quinqueloculine in arrangement in the microspheric juvenile stage. There are numerous apertures arranged in one or more rows, or rarely fused into a slit.

2.2. Suborder Rotaliina Delage and Hérouard, 1896

The rotaliids (which includes the nummulitids) build their test walls from regularly arranged, small, rhombohedral calcite crystals, with their optical axes orientated either perpendicular to, or at 45° to the surface, thus allowing incident light to pass through these 'hyaline' walls (see Fig. 2). Large genera appear within at least 12 families of this suborder. The two most important families are the Amphisteginidae and Nummulitidae, as detailed below.

The Amphisteginidae have tests with numerous chambers and complex chamberlets in the centre of the umbilical side. Their aperture is a narrow interiomarginal slit, and they may have interseptal pillars. The features considered important in the Nummulitidae are shown in Figs. 3–5. They are characterised by a flat planispiral coil which is bilaterally symmetrical about the equatorial plane, and which may be involute or evolute, or a combination of the two (Fig. 3). They all possess a marginal cord with an internal canal system and numerous equatorial chambers which may be simple (e.g., *Nummulites*, *Palaeonummulites*, *Planocamerinoides*, *Assilina*, *Ranikothalia*, *Numulitoides*, *Chordoperculinoides* and *Operculina*), or divided into chamberlets (e.g., *Heterostegina*, *Spiroclypeus* and *Cycloclypeus*). Lateral chamberlets (cubiculae) are present in *Spiroclypeus*, whilst annular chambers characterise *Cycloclypeus*. Genera with sim-

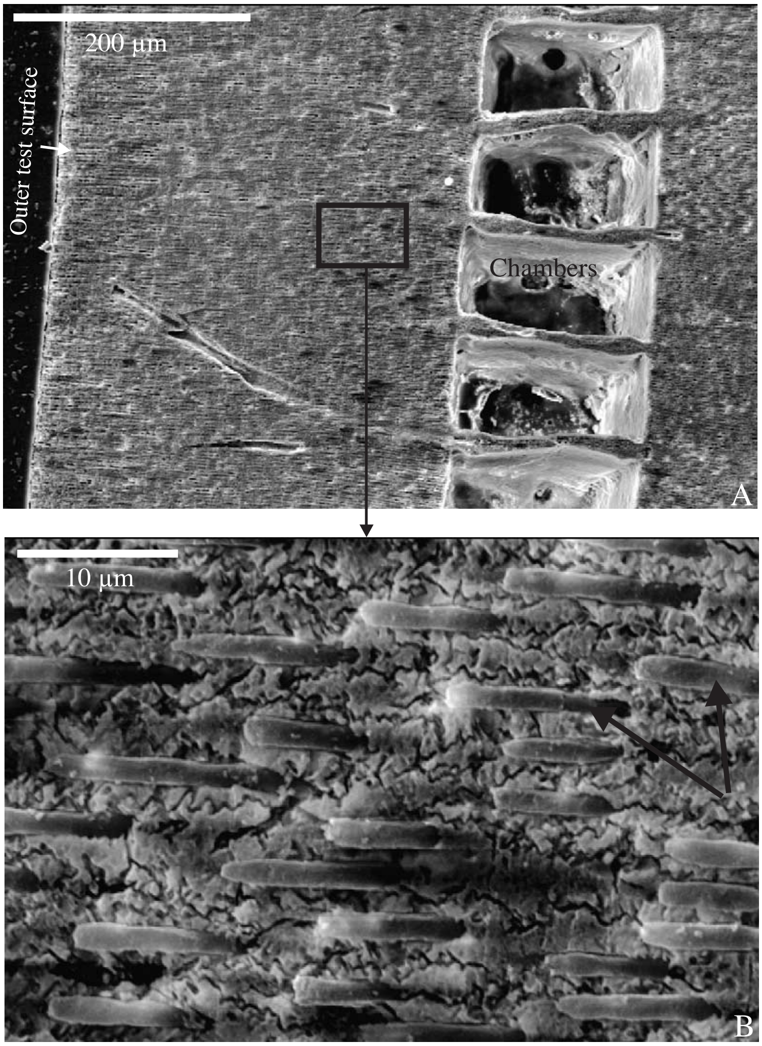

Fig. 2. Scanning electron microscope images showing the wall structure of the extant nummulitid *Cycloclypeus carpenteri*: (A) rhombohedral calcite crystals are arranged with their optical axes perpendicular to the test surface and the upper/lower chamber walls; (B) these crystals are irregularly sutured together; note organic lining to the pore network (arrowed).

ple chambers are distinguished on the basis of the involuteness/evoluteness of the chambers (presence/absence of alar prolongations; see below) and the spiral lamina, the rate of opening of the spire, the shape of the chambers and the presence/absence of a coarse canaliculate marginal cord. The marginal cord may be massively developed, permitting drastic thinning of the lateral walls, usually combined with pronounced lateral compression of the test. The genera *Nummulites* and *Palaeonummulites* include flattened to stoutly lenticular and even globular species with a periphery varying from sharp to rounded or somewhat undulose. The test is involute and, as in other planispiral involute genera, the chamber cavity (lumen) extends over previous whorls, referred to as the alar prolongation (see Figs. 4 and 5). The test comprises planispirally coiled chambers, separated by septa. The septa are usually curved and the portion overlying previous whorls (usually visible at the surface and in oblique thin sections) is called the septal filament (see Fig. 5). Septal filaments may be radial, sigmoidal or meandrine and may branch to give

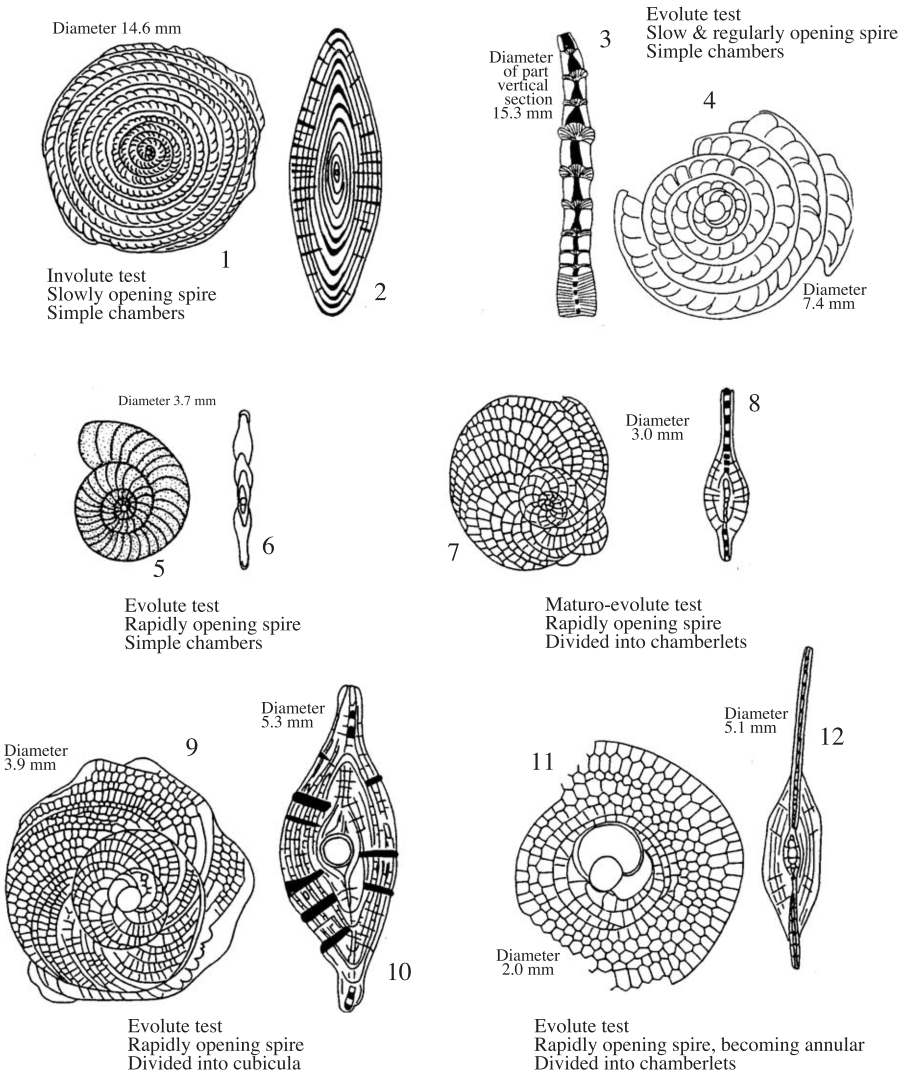

Fig. 3. Morphological characteristics of typical living and fossil nummulitid genera (modified from Haynes, 1981). (1, 2) *Nummulites laevigatus* (1: equatorial section; 2: vertical section); (3, 4) *Assilina spira* (3: part vertical section; 4: equatorial section); (5, 6) *Operculina ammonoides* (5: side view; 6: vertical section): (7, 8) *Heterostegina depressa* (7: equatorial section; 8: vertical section); (9, 10) *Spiroclypeus tidoenganensis* (9: equatorial section; 10: vertical section): (11, 12) *Cycloclypeus carpenteri* (11: equatorial section; 12: vertical section).

a reticulate pattern (incipient chamberlets). Successive whorls are bounded by a spiral sheet, which incorporates the peripheral marginal cord. The ratio of height to width of the chambers, which relates to the tightness of coiling, is considered specific and is measured in equatorial section, as is chamber number per whorl or quadrant. The initial chamber (proloculus) is often spherical, whilst the second (deuteroconch) is generally kidney-shaped. The chambers may be higher than long, longer than high, or isometric. The pattern of pillars may also be specific, often being arranged along septal filaments and/or along the spiral cord or over the poles (umbilical). The second chamber in nummulitids tends to be larger than the third. In well-preserved specimens, fine perforations can be seen over most of the test; only the septal filaments, septa, marginal cord and pillars are largely imperforate (see Fig. 4). In other genera such as *Assilina* and

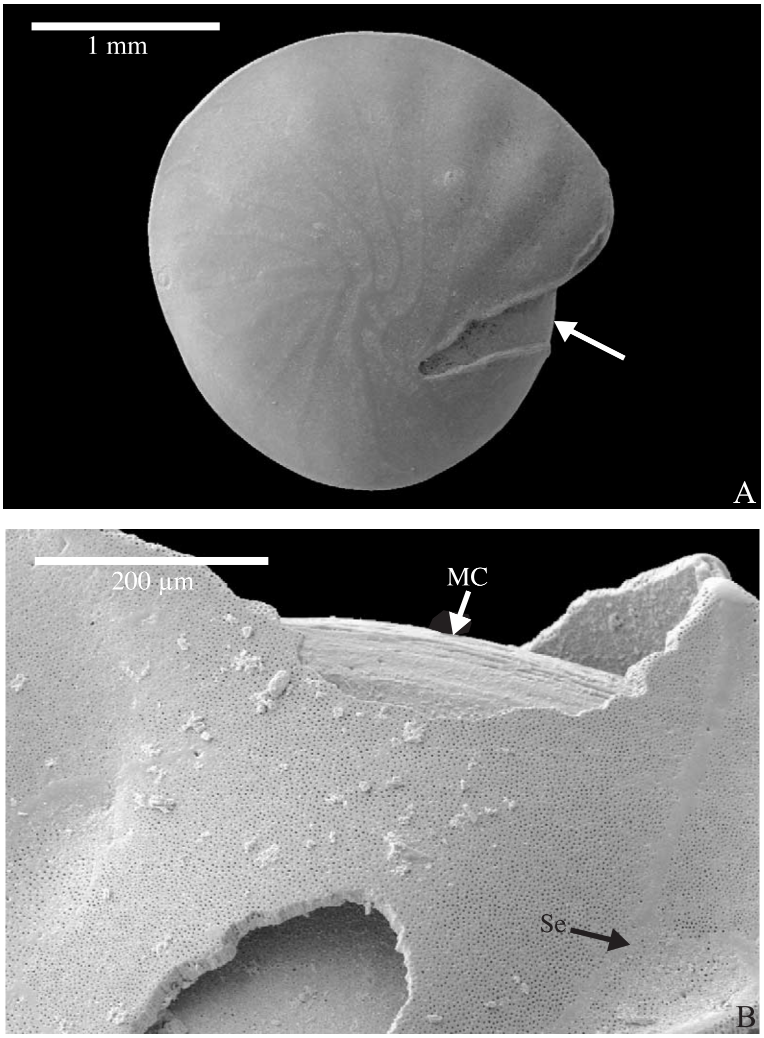

Fig. 4. Scanning electron microscope images of the extant nummulitid *Palaeonummulites venosus*, showing: (A) the involute test structure; damage to the terminal chamber reveals how the outer whorl extends over the previous whorl (arrowed); (B) with the exception of the marginal cord (MC) and the septal filaments and traces (Se), the test surface is finely perforated.

Planocamerinoides, which are evolute, the alar prolongation is pinched off, although the spiral lamellae may continue over previous whorls. Both are tightly coiled with relatively low spires. Involute forms with loose (lax) coils and high spires, the diameter tending to double or more as each whorl is added, are often referred to *Operculinoides*, whilst evolute forms with a loose coil and high spire are assigned to *Operculina*.

The importance of the canaliculate marginal cord of the nummulitids for growth, locomotion, reproduction, excretion and protection has been demonstrated by Röttger (1984), in a study of the Recent nummulitid *Heterostegina depressa*. Nummulitids, unlike most multilocular foraminifera, rarely have primary or secondary apertures (Hottinger, 1977a; Röttger, 1984); instead, the canal system replaces the primary aperture seen in most other foraminifera and allows communication between the chamber cavities and the lateral surfaces of the test, and provides for removal of waste matter. It permits the extrusion of pseudopodia from any point on the marginal cord, even when protoplasm has been withdrawn from the peripheral

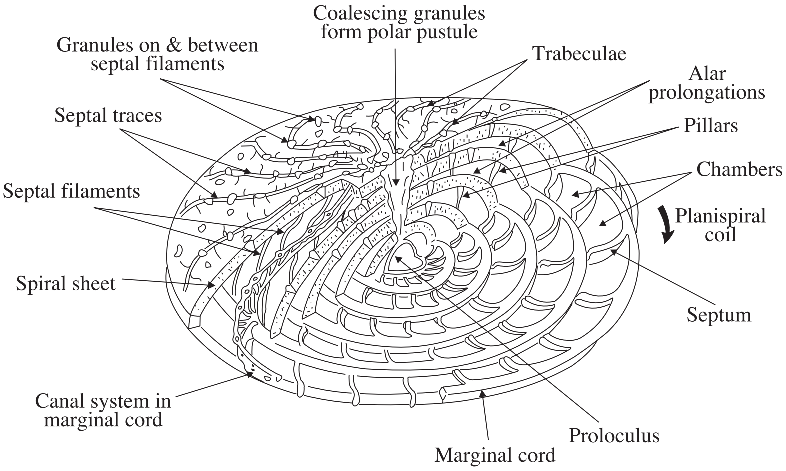

Fig. 5. Test structure of *Nummulites*, megalospheric form (modified from Carpenter, 1850; Golev, 1961; Barnett, 1974; after Racey, 1992).

chambers. In *H. depressa* the terminal openings of the canals in the marginal cord function as a multitude of small primary apertures and extrude protoplasm which forms the template for the new chamber. Röttger et al. (1984) suggest that nummulitids such as *H. depressa*, *Heterocyclina tuberculata* and *Operculina ammonoides* would probably be unable to construct large chambers if only a single exit for protoplasm was available.

Of the principal nummulitid genera, only *Operculina*, *Palaeonummulites*, *Heterostegina* and *Cycloclypeus* have extant descendants; *Nummulites* became extinct in the early Oligocene, *Assilina* in the late Middle Eocene, *Ranikothalia* in the late Palaeocene, and *Spiroclypeus* in the early Miocene. Some workers (e.g., Hohenegger, 2000) refer to one living species of *Nummulites* (*Nummulites venosus*) from the Pacific, although this has closer affinities with *Operculinella*, and following the more recent revised classification of Haynes et al. (in review) should be reassigned to *Palaeonummulites*.

3. Reproduction and its influence on test size, shape and distribution

3.1. Reproductive processes of larger foraminifera

Many groups of living and fossil foraminifera exhibit sexual dimorphism. Dimorphism involves an asexual generation (a diploid, multinucleate gamont) with a large proloculus (initial chamber) and small test diameter, generally referred to as the megalospheric form, or A-form, and a sexual generation (a haploid, uninucleate agamont) with a small proloculus and large test diameter, called the microspheric form, or B-form (see Fig. 6, top). Agamonts

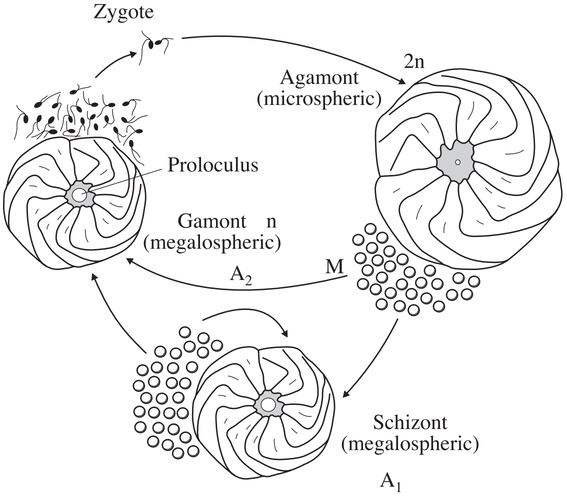

Fig. 6. Life cycle of the larger foraminifera *Amphistegina gibbosa* (modified from Dettmering et al., 1998). The upper part depicts the dimorphic life cycle of many foraminifera. The lower part represents the megalospheric schizont reproducing by cyclic schizogony. (M: meiosis; n: haploid; 2n: diploid; proloculus, gametes and offspring are enlarged relative to the tests).

reproduce by multiple fission, whereas gamonts reproduce by releasing gametes. These two modes of reproduction are associated with variations in test morphology.

A third generation, a megalospheric schizont, has been documented in 14 of the 40 extant species of foraminifera in which an alternation of generations has been observed (Dettmering et al., 1998). These include *Amphistegina radiata* (Chapman, 1895), *Marginopora vertebralis* (Lister, 1896; Ross, 1972), *Heterostegina depressa* (Röttger, 1974; Röttger et al., 1986), *Amphistegina papillosa* (unpublished comm. in Dettmering et al., 1998) and *Amphistegina gibbosa* (Dettmering et al., 1998; Harney et al., 1998). Rhumbler (1909) first suggested this trimorphic life cycle in which agamonts produce megalospheric schizonts rather than gamonts. The schizont, in turn, produces gamonts by multiple fission (Fig. 6, bottom). Le Calvez (1938) suggested that the type of nuclear division in the agamont determines whether schizonts or gamonts are formed. If meiosis occasionally failed during the multiple fission of the agamont then some diploid, megalospheric schizonts would occur together with a majority of haploid gamonts. In many extant foraminifera, such as *H. depressa* (Röttger, 1974; Röttger and Schmaljohann, 1976) and *M. vertebralis* (Ross, 1972), a succession of A1-generations dominates ("apogamic schizogony"). Dettmering et al. (1998) observed the production of four successive schizont generations in *A. gibbosa*, and they also suggest that their observations of *Planorbulina mediterranensis*, *H. depressa* and *A. gibbosa* confirm the supposition of Le Calvez (1938) that the formation of schizonts by agamonts, and of gamonts by schizonts, are rare and irregular events. They further suggest that such rare events are enough to explain the observed occurrence of flourishing schizont populations in natural habitats, and may, in part, explain the production of deposits such as nummulitic limestones. Röttger et al. (1990) noted that where an agamont of *H. depressa* produced solely schizonts (suggesting that no meiosis occurred in the parent), this could explain why most Recent and fossil assemblages are dominated by megalospheric (A-form) individuals.

During multiple fission, the entire protoplasm of the adult form is divided amongst its progeny. During asexual reproduction, symbiotic algae are passed from the parent to the megalospheric juveniles in *Amphistegina lessonii*, *Heterostegina depressa* and *Peneroplis pertusus* (Röttger, 1974, 1981). This transfer of symbionts to offspring is easily accomplished when schizonts reproduce, although algae being transferred from the agamont or schizont to the gamont are lost from the system when the gamont reproduces because the tiny gametes (2–3 μm in diameter) are too small to carry symbionts. Repeated asexual reproduction stabilises symbionts because they cannot be transmitted directly from parent to offspring during sexual reproduction. Thus, cyclic schizont production, not linked to sexual reproduction within the dimorphic cycle, is of particular advantage to species dependent on symbiotic algae.

The greater size of the mature tests of gamonts compared to schizonts has been demonstrated in *Heterostegina depressa* by Röttger et al. (1986). Dettmering et al. (1998) showed that in *Amphistegina gibbosa*, the mean size of mature tests from 108 gamonts was 1561 μm, and for 679 schizonts, it was 896 μm. The mean size of the six gamonts derived from schizonts was 1338 μm, and for the four schizonts from which they were derived, it was 975 μm. No difference was found in the size of the proloculus of gamonts and schizonts.

3.2. Environmental controls on life cycle and distribution

Under favourable environmental conditions, living foraminifera mature quickly and reproduce at relatively small sizes ('r-selection'; Hallock and Glenn, 1986). However, in populations stressed by low temperature, insufficient food or light (or other factors), individuals grow more slowly and mature at larger sizes ('K-selection'; Bradshaw, 1957). Where conditions are tolerable for growth, but outside the range of tolerance for reproduction, individuals continue to grow to giant size. This often happens when shallow-dwelling (< 20 m) species are washed into deeper (50–100 m) environments (Ross, 1972). Hallock (1985) and Drooger (1993) observed that, in many foraminiferal species, the size of the megalospheres and their embryos increases with increasing depth, and decreases again in the deepest part of the habitat range.

The relative and absolute numbers of microspheric forms increase with depth, and are highest over an optimum, intermediate interval of a specific depth range, e.g., 80–100 m for *Operculina ammonoides* and 60–70 m for *Heterostegina depressa* in the Gulf of Aqaba; in shallower water, B-forms are rare or even absent. This unequal distribution pattern indicates that sexual reproduction is limited to certain ecological (depth-related?) zones, possibly due to the difficulties associated with sexual reproduction in highly stressed environments (Hottinger, 1977a; Leutenegger, 1977b). Such zones may characterise the limits of the depth range, such as very shallow or very deep water where very high or very low light levels inhibit photosynthesis. Leutenegger (1977b) suggests that in such zones, a biphasic alternation of asexual and sexual reproducing generations (A–B–A...) predominates, whilst apogamic schizogony, i.e., asexual reproduction (A–A–A...), takes place in shallower water. Consequently, she suggests that megalospheric gamonts (A2-forms) should be found in deeper water, along with microspheric forms, and concludes that the life cycle of these foraminifera is controlled by their environment, although which factors cause the formation of gamonts is unclear. The major physical factor in the Gulf of Aqaba, which changes with depth, is light intensity. Because light intensity is related to vegetal growth, Leutenegger (1977b) suggests that factors inducing sexual reproduction are nutritional and/or dependent on a specific, physico–chemical and biological composition of the substrate and/or the water column. She also suggests that unequal distributions of A- and B-forms might be explained by sexual as well as asexual reproduction taking place preferentially at greater depths, with the megalospheric schizonts migrating into shallower waters. The distribution of megalospheric gamonts would then be similar to that of microspheric schizonts, whilst the high number of microspheric forms at greater depth could be due to downward migration or passive transport of the flagellate gametes; that is, megalospheric gamonts could be found at any water depth.

In extant *Heterostegina depressa* from Hawaii, Röttger et al. (1986) noted that agamonts were present only from 30–73 m depth, whilst Röttger and Schmaljohann (1976) collected gamonts from 100 m of water. In shallow-water habitats, only schizonts were found (Röttger, 1972), concurring with the observations of Krüger et al. (1996/1997), who found no schizonts of the deep-dwelling nummulitid *Cycloclypeus carpenteri* in Okinawa, and concluded that, as in *H. depressa*, schizonts of *C. carpenteri* were absent in deep water habitats. It is, however, unlikely that megalospheric gamonts and schizonts could be distinguished in the fossil record.

A trimorphic generation cycle may be the cause of a mean test size increase with depth in *Heterostegina depressa* of the west Pacific, from 1.4 mm at the surface to 3.5 mm at its lower distribution limit of approximately 90 m (Yordanova, 1998, quoted in Hohenegger et al., 2000). Whilst asexually reproducing schizonts dominate in shallow, high-energy water because the large juveniles are at lower risk (e.g., Leutenegger, 1977b; Röttger et al., 1990), small-sized zygotes that are less protected against turbulence prefer calm conditions below fair weather wave base. Gamonts and schizonts of *H. depressa* do not differ in proloculus size, but the tests of the former are significantly larger than those of the latter. The higher proportion of gamonts in the deeper water, combined with the presence of a small proportion of large agamonts, may explain the increase in mean test size. However, Hohenegger et al. (2000) observed that *Nummulites* (=*Palaeonummulites*) *venosus* from the same area showed no increase in test thickness with increasing depth.

Although, as shown above, the distribution of sexual and asexual forms throughout the photic zone is complex, it can be broadly concluded that the ratio of megalospheric to microspheric specimens may be used to distinguish marginal from intermediate parts of the depth range (Hottinger, 1982, 1997), although taphonomic factors also need to be considered.

Reiss and Hottinger (1984) studied the population dynamics of *Amphisorus hemprichii* by measuring the growth of living specimens collected from the plants and the seabed of a 4-m-deep *Halophila* meadow. During autumn and winter of the first year, the population consisted of 94% megalospheric and 6% microspheric individuals. Until the reproduction period, the mean standing crop (150 specimens per 225 cm^2 leaf surface) and the growth rate of the shell (100 μm growth of equatorial shell diameter per week) equal to about 14% weight increase, were stable. Immediately prior to reproduction, the growth rate declined. Asexual reproduction took place during April and May, apparently triggered by the rise of the surface water temperature. After reproduction, the standing crop rose by one or two orders of magnitude, although juvenile mortality reduced the population density back to normal levels within 2 months. However, the second generation comprised only megalospheric forms (with significantly larger megalospheres), with a standing crop stabilised at 350 specimens per 225 cm^2. These higher standing crop values can be related to a simultaneous, sharp decline in the population density of another associated LBF, *Sorites orbiculus*. However, for *A. hemprichii*, the larger proloculus size and the absence of microspheric individuals may indicate a trimorphic life cycle extending over 2 years. Zohary et al. (1980) noted that, in shallow water, the asexual reproduction cycles of *Amphisorus* and *Sorites* are synchronous and closely linked with the seasonal cycle. They also observed that *A. hemprichii* populations comprised high numbers of megalospheric forms with small embryos and few microspheric forms, whilst in the following year, the population comprised solely megalospheric forms with larger embryos.

Fujita et al. (2000) showed that populations of *Marginopora kudakajimensis* from a 1-m-deep lagoon in the Ryukyu Islands (subtropical Northwest Pacific) show seasonal variations in population density and size–frequency distribution which indicate that the population renews itself annually. Asexual reproduction occurs twice a year, in late spring and winter (Fig. 7), resulting in two "cohorts." The life span of the late spring cohort is up to 1 year, whilst that of the latter is up to 6 months. Megalospheric specimens comprise >99% of the population, with microspheric specimens (which were observed only in June, October and November) comprising just 1% of the total population. Population density reaches a maximum of $13 \times 10^5/m^{-2}$ in June. They observe that size-specific mortality rates are very low only in the smallest size classes, indicating low juvenile mortality with high mortality in later life, a pattern different from that previously reported for other LBF (e.g.,

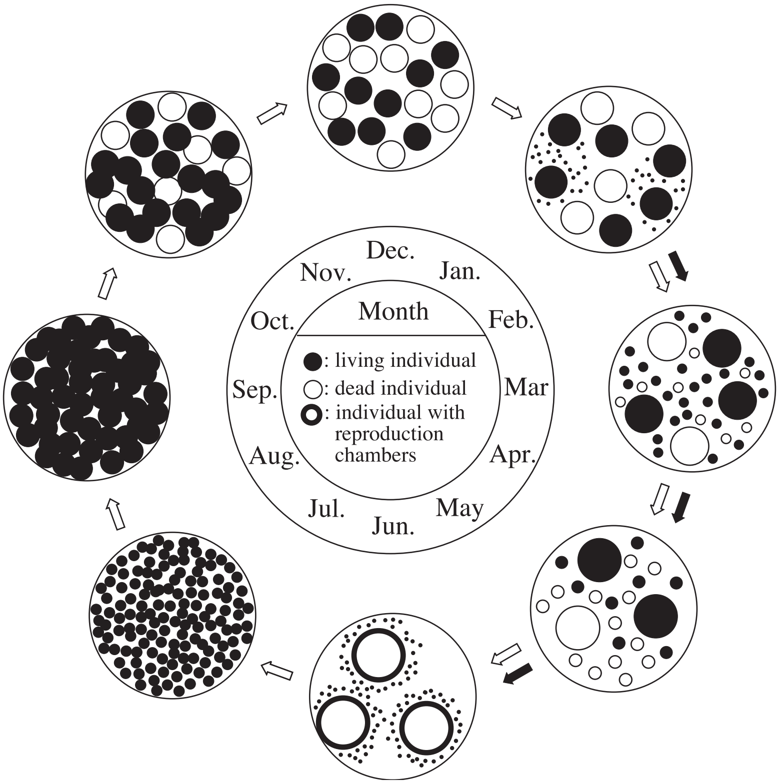

Fig. 7. Seasonal changes in megalospheric populations of *Marginopora kudakajimensis* from the Ryukyu Islands, Japan (modified from Fujita et al., 2000). (Open arrows represent the late spring cohort; filled arrows represent the winter cohort).

Muller, 1974; Hallock et al., 1986a). This could be explained by Hallock's (1985) suggestion that *Marginopora* avoids high mortality typical of megalospheric individuals by producing relatively large embryos and reproducing asexually within reproduction chambers. They attribute the seasonality of the population, especially the population density, to changes in the physical and biotic conditions, and suggest that the late spring reproduction may be due to a rise in water temperature, although this would not explain the winter reproduction.

Lipps (1982) suggested that asexual reproduction becomes the dominant mode of increasing population size when environmental conditions, usually associated with increased nutrient supply, are favourable. Thus, stable environments will have a predominance of megalospheric (A-) forms. However, Harney et al. (1998) suggested that repeated asexual reproduction may be an effective method of increasing population densities following mortality events, and also during occupation of marginal habitats and colonisation of new areas, whilst alternation of asexual and sexual generations is more common under favourable environmental conditions.

Bradshaw (1961) observed that reproduction of smaller benthic foraminifera only occurs within a narrow temperature range, which is different for each species. Growth proceeds in a broader depth range but stops close to the minimum limits which cause death.

Buzas (1968, 1970) showed that smaller benthic foraminifera typically display a patchiness on a scale of a few metres, which he related to asexual reproduction. Murray (1991) suggested that this patchiness may be a consequence of variations in the nature of the habitat. However, Buzas et al. (2002) observed metre-scale spatial patchiness within "single" habitats and concluded that such distribution patterns are a consequence of asynchronous reproduction, which results in "pulsating patches" of foraminifera that vary in space and time. These studies are based on foraminifera living in very shallow water; the limited data from deeper waters suggests that the common species are more regularly distributed or have very large clusters (in excess of 2000 m^2), but the rare species show small-scale patchiness (Murray, 1991).

Little data has been published on the ratio of A- to B-forms for fossil *Nummulites* populations. Bombita (1973) observed that microspheric forms are very rare in the Eocene of the east Carpathians. A similar scarcity of B-forms was noted by Brasier and Green (1993) for populations of the Eocene *Nummulites prestwichianus* from the Barton Clay of the Isle of Wight, which have an A- to B-form ratio of 49:1. Other studies, however, have shown that microspheric forms can occur in larger proportions. For example, Aigner (1983) noted that *Nummulites* from the Middle Eocene Mokattam Formation (Egypt) have an average A- to B-form ratio of 7:1, whilst Abdulsamad and Barbieri (1999) recorded an average ratio of 15:1 from the Eocene of Al Jabal al Akhdar (Libya). Buxton (pers. comm. in Brasier and Green, 1993) had observed Lutetian nummulitic limestones containing *Nummulites laevigatus* with an A- to B-form ratio of 1:1. However, because studies of nummulitic limestones often define A- and B-form *Nummulites* only on the basis of size, generally referring to them as "small" or "large" (e.g., Bernasconi et al., 1987; Anketell and Mriheel, 2000; Vennin et al., 2003), or identify A- and B-forms during examination of outcrops or hand specimens (e.g., Aigner, 1983; Kondo, 1995), some of this published data on proportions of megalospheric and microspheric forms, and environmental interpretations based on the data, may be incorrect. As Racey (2001) points out, identification of A- and B-forms based only on size, without observation of the nature of the proloculus, can lead to the calculation of incorrect ratios because interspecific variation in test size may result in A-forms of one species being mistaken for B-forms of another, and juvenile B-forms may be confused with A-forms of the same species.

Following the suggestion of Blondeau (1972) that an A- to B-form ratio of 10:1 typified a 'normal' *Nummulites* population, several authors used deviations from this value to define autochthonous and allochthonous populations (e.g., Aigner, 1983; Moody, 1987; Moody and Grant, 1989; Kondo, 1995). Clearly, evidence from extant nummulitids and other LBF described earlier suggests that the 10:1 ratio is incorrect. It appears to be impossible to define a 'normal' population because the ratio of A- to B-forms can vary with different environmental conditions. The variability of A- to B-form ratios in many *Nummulites* populations is demonstrated by Beavington-Penney (2002), in a study of the early Eocene El Garia Fm. (Tunisia). *Nummulites* communities identified on the

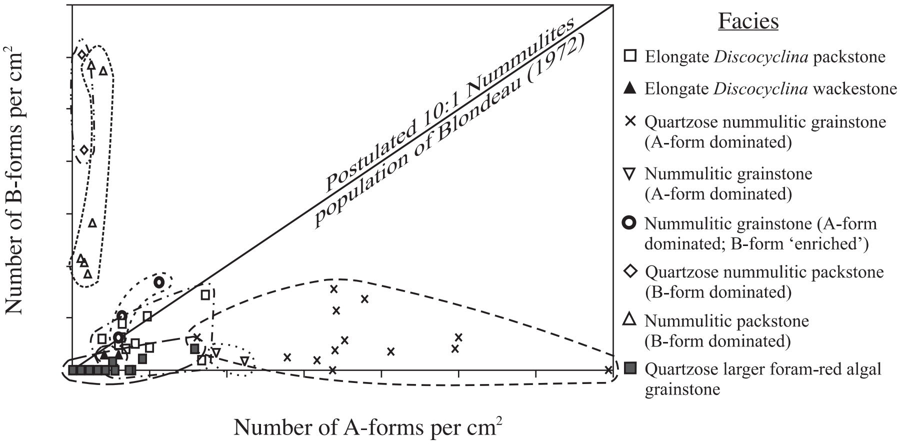

Fig. 8. Variability in A- to B-form ratios from El Garia Formation *Nummulites* palaeocommunities (i.e., *Nummulites* populations identified as autochthonous or parautochthonous on the basis of detailed sedimentological, taphonomic and biofabric study). The A- to B-form ratio of these palaeocommunities varies from the 10:1 ratio hypothesised by Blondeau (1972) for a 'normal' *Nummulites* community, deviations from which were subsequently used by several workers to define in situ and transported assemblages. Counts of *Nummulites* were made from thin sections and acetate peels, and have been normalised to number/cm^{-2} to aid comparison.

basis of detailed sedimentological, taphonomic and biofabric analysis as autochthonous or parautochthonous (i.e., palaeocommunities cf. Brenchley and Harper, 1998) exhibit a wide range of A- to B-form ratios (Fig. 8). Similar, largely facies-dependent A- to B-form ratios were also noted by Kondo (1995) from the Lutetian sediments of the Ogasawara Islands, Japan (Fig. 9). However, in the latter study, biofabrics suggesting post mortem modification, combined with field-based identification of megalospheric and microspheric forms (see objection of Racey, 2001, above) means that the data should be treated with a degree of caution.

3.3. Fecundity and longevity

There is an obvious correlation between the accumulation rates of foraminifera-bearing sediments and

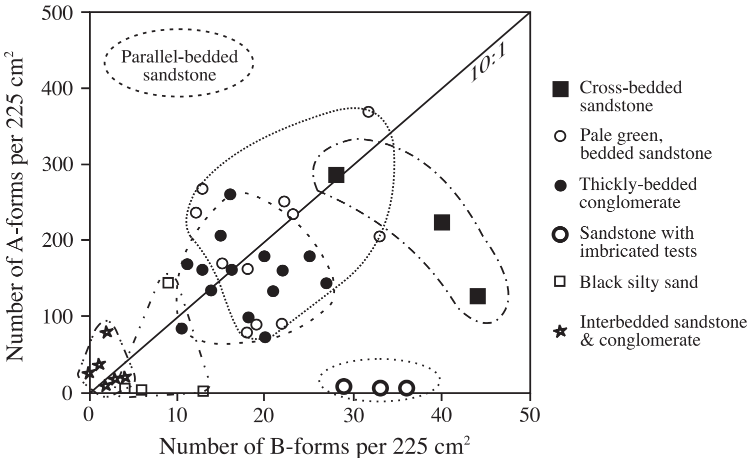

Fig. 9. Density and relative abundance of A- and B-form *Nummulites* sp. (showing relation to 'normal' 10:1 ratio) for various facies from Nankinhama (modified from Kondo, 1995).

the life span, frequency of reproduction and the number of young produced during reproduction of those foraminifera. The birthrate in a foraminiferal species has two components: sexual and asexual reproduction. Virtually nothing is known about the former (Hallock, 1985). Data on the asexual longevity (the typical life span of the asexual generation) and fecundity (the number of young produced by a parent individual during asexual multiple fission) for four species of larger foraminifera are presented in Table 1. LBF fecundity has been shown to be a function of test size (Hallock, 1985; Hallock et al., 1986a). Studies of living, larger benthic foraminifera (Muller, 1974, 1977; Zohary et al., 1980; Hallock et al., 1986a) have shown that mortality can be high among small juveniles. As individuals attain diameters of approximately 0.5 mm, mortality rates drop until reproduction occurs. Because the parent test is usually vacated, reproduction is a major cause of mortality among adults (Muller, 1974, 1977; Hallock, 1981a). Thus, the size at reproductive maturity is reflected by the size of empty adult tests common in unsorted sediments. Size-specific mortality data from field studies have been published for two genera of larger foraminifera. In both, as discussed above, mortality rates for juveniles in their first month were high: about 95–97% for *Amphisorus hemprichii* (Zohary et al., 1980) and more than 99% for *Amphistegina* spp. (Muller, 1974, 1977). Subsequently, monthly mortality declines to 30–50% of the individuals that reached a size exceeding approximately 0.5 mm in diameter. Nonreproductive mortality of individuals larger than 1 mm is, according to Hallock (1985), difficult to estimate but appears to be less than 10% per month in *Amphisorus*.

Muller (1974, 1977) also reported that, in Hawaii, *Amphistegina lessonii* took about 4 months to reach reproductive maturity and produced several hundred young with fecundity proportional to parent size. In the same environment, *Amphistegina lobifera* grew for approximately 1 year before producing 1000–2000 young, again with fecundity proportional to parent size.

Hallock (1979) showed that size, longevity and fecundity are related to the probability of reproductive success in some foraminifera. *Amphistegina lobifera*, which lives in shallow (< 10 m), turbulent waters, grows relatively large (up to 2 mm in diameter) with thickness to diameter ratios of 0.6–0.7, and produces up to 2000 young per reproduction. *Amphistegina lessonii*, which has a shorter life span and lives in slightly deeper water (5–30 m on Indo–Pacific reefs) than *A. lobifera*, reproduces at approximately 1 mm in diameter, has a thickness to diameter ratio of 0.35–0.5 and usually produces several hundred young. *Heterostegina depressa* usually grows to a much larger diameter (up to several mm) but is much flatter (Röttger and Hallock, 1982) and commonly produces less than 200 young per adult (Röttger, 1972). All three species produce similarly sized megalospheric young. *Amphistegina lobifera* lives in the most physically rigorous environment and produces the most young; *H. depressa* lives in the least rigorous environment and produces the fewest young. Hallock (1981b) also suggested that asexual multiple fission external to the test may be fairly hazardous, for *A. lobifera* individuals produce 5–10 times as many young as *Marginopora vertebralis* which lives in a similar environment but produces its young in brood chambers. *Amphistegina lobifera* must grow large enough to accumulate sufficient protoplasm and algal symbionts for 1000–2000 young, whilst *M. vertebralis* must secrete a large brood chamber in which 100–200 young can develop. Both strategies result in relatively long lives and large adult sizes.

Some foraminifera have the intraspecific capability of responding to environmental stress in such a way as to increase fecundity. As noted earlier, when conditions are unfavourable for reproduction but tolerable for

Table 1
Fecundity, longevity and adult size data on four species of foraminifera (modified from Hallock, 1985)

Species	Adult diameter (mm)	Fecundity	Longevity	Source
Amphistegina lessonii	1–2	200–900	4–12 months	Muller (1977)
Amphistegina lobifera	1.5–3	900–2400	6–12 months	Muller (1977)
Heterostegina depressa	3–5	60–400	4–12 months	Röttger (1974)
Marginopora vertebralis	5–12	60–150	1–2 years	Ross (1972)

growth, some foraminifera continue to grow until conditions improve and they reproduce, or until they eventually die. Because the number of young produced is directly proportional to the size of the parent (Röttger, 1974; Muller, 1974, 1977), by delaying reproduction and continuing to accumulate more mass, more young are produced when reproduction finally occurs. This increased fecundity can increase the likelihood that some offspring will survive.

When growth rate is reduced (due to environmental factors such as decreased light levels, increased water motion, increased nutrient levels, etc.; see later discussion), more time is spent at smaller sizes, increasing the chance that the individual will be eaten or swept away by currents. During times of low growth rate, juvenile survival rates also drop, and natural selection for increased longevity and fecundity should occur. When growth rates do not vary greatly, the probability of survival is also age specific (Hallock, 1985).

Published estimates of the life span of Eocene *Nummulites* are generally consistent with the data for extant forms documented above (i.e., several months to a few years; see Table 1). Based on oxygen isotope analysis, Brasier and Green (1993) suggested a life span of 1 year for Eocene A-forms of *Nummulites prestwichianus* (with test diameters of approximately 1.5 mm) from the Isle of Wight (U.K.), with larger specimens (up to 3.8 mm in diameter) having possibly lived for at least an additional season. Purton and Brasier (1999) concluded that variations in stable isotopes of Middle Eocene B-forms of *Nummulites laevigatus* from Bracklesham Bay, Hampshire, represent seasonal changes in growth rate, with growth beginning in the early spring and continuing at a slow rate for 5 years, with a decrease in growth rate after 2 years. They also used this growth rate to calculate that B-forms of *Nummulites millecaput*, a giant form from the Mediterranean region, may have lived for 107 years. However, the extrapolation of conclusions based on *N. laevigatus* from the Hampshire basin to the presumed warmer water habitat of *N. millecaput* is questionable. Purton and Brasier's seasonal interpretation of isotope fluctuations is also questionable, in that, as demonstrated by Reiss and Hottinger (1984), oxygen (and, to a lesser extent, carbon) isotope values for the living nummulitids *Operculina ammonoides* and *Heterostegina depressa* vary significantly with increasing water depths. In addition, the growth rates for *N. laevigatus* and *N. millecaput* were completely different (based on a comparison of winding diagrams from Schaub, 1981), thus throwing into doubt the conclusions of Purton and Brasier (1999) concerning the longevity of *N. millecaput*.

Sarangi et al. (2001) also contradict the findings of Purton and Brasier (1999). In an assessment of Sr/Ca ratios of *Nummulites* tests, they concluded that the large test size characteristic of many specimens of that genus was the result of rapid growth over relatively short periods of time.

Said (1950) considered that 'tightening' of the spire in Middle Eocene B-forms of *Nummulites gizehensis* from Egypt was a seasonal effect. This led him to conclude that this species had a life span of 1 year and could add a new whorl every 10 days (much faster than that documented for living nummulitids: megalospheric *Heterostegina depressa* grown in the laboratory added a new whorl in 5 months (Röttger and Berger, 1972)).

An absence of modern analogues for the giant, symbiont-bearing foraminifera of the early Tertiary, which presumably lived for several years at least, makes it hard to reach convincing conclusions about their longevity, although life spans of 1 to 5 years are most likely based on the current data available.

3.4. Variation in proloculus size

A trend which appears commonly, but not consistently, in the history of larger foraminifera is that of increased proloculus or embryon size along with overall increase in test size (e.g., Van Gorsel, 1978). Hallock (1985) suggests that increased proloculus size can increase the probability of juvenile survival by decreasing the time the individual protists spend at small sizes. For example, *Marginopora vertebralis* produces embryons that are approximately 800 μm in diameter (Ross, 1972), whilst *Amphistegina* juveniles require about 50 days to attain a similar size. If the former's mortality sources are similar to those of *Amphistegina lobifera* and *Amphistegina lessonii*, with which it occurs, *Marginopora* apparently avoids the kinds of mortality that eliminate over 99% of the young *Amphistegina* by producing larger young and by reproducing within large reproductive chambers in which the protoplasm is enclosed (i.e., protected) during multiple fission. Hallock (1985) suggested a possible mechanism for this variation based upon dependence on algal symbionts. She suggested that if juveniles received more protoplasm and symbionts from the parent, they would remain small for only a short period, thus increasing their chances of survival. She also argued that relatively high fecundity would produce young with a small proloculus size, thus increasing their chances of survival under variable conditions that can influence survival of both adults and juveniles, whilst production of young with larger embryos is more useful in stable, low-light conditions.

Fermont (1977) noted an increase in proloculus size with depth in Recent *Operculina ammonoides* from the Red Sea and also in the Eocene *Discocyclina varians* group from Ein Advat, Israel. However, Röttger et al. (1980) suggested that the apparent increase in size of the proloculus was in fact a result of the presence of two megalospheric forms, based on their studies of Recent *Heterostegina depressa* from Hawaii. The asexually reproducing form was dominant in shallow water, its numbers decreasing with increasing water depth. The sexually reproducing form increased in numbers with increasing water depth. This mixture of two megalospheric types could explain the depth-related change in mean proloculus size observed by Fermont.

Pecheux (1995) noted that specimens of *Operculina ammonoides* from hard substrates in the Gulf of Aqaba, Red Sea, possessed a distinctly smaller proloculus than those collected from soft substrates. However, this was observed only at depths less than 60 m; at greater depths, no significant difference was observed.

4. Symbiosis and its influence on test size, shape and distribution

4.1. Symbiotic processes in larger benthic foraminifera

In addition to their size, larger foraminifera are characterised by complex internal morphologies. Haynes (1965) related this complexity to the presence of photosynthetic, symbiotic algae within the tests of many species. This host–symbiont relationship means that most living larger foraminifera are restricted to shallow, well-lit sea floors, and, if untransported, their presence is generally indicative of water depths less than 130 m, i.e., within the euphotic zone (Hottinger, 1983; Hallock, 1984).

Ross (1972) suggested that algal symbiosis in larger foraminifera is comparable in terms of growth stimulation and calcium carbonate fixation to that found in hermatypic corals. Subsequently, growth and calcification in several species of larger foraminifera have been shown to be dependent on algal symbiont activity (Leutenegger, 1984), although different taxa may derive different benefits from the relationship. For example, rotaliids, which are typical of oligotrophic environments, may be more reliant on their symbionts as a food source than miliolids, which are common in mesotrophic to eutrophic environments (i.e., symbiosis may be obligatory in the former and facultative in the latter; Jones, 1999). Furthermore, Röttger et al. (1980) found that *Amphistegina* and *Heterostegina*, which harbour diatom symbionts, fix CO_2 at significantly higher rates than rhodophyte-bearing peneroplids, whilst Ter Kuile et al. (1987) reported that symbiosis is a more important source of energy for *Amphistegina* than for soritids.

The algal symbionts may be distributed throughout the cytoplasm of the foraminifera, as in *Amphistegina hemprichii*, or they may be restricted to certain parts of the test interior, as in *Amphistegina lessonii*, where they only occur in the upper portions of the cytoplasm (McEnery and Lee, 1981). In *Palaeonummulites*, *Operculina* and *Amphistegina* sp., most algae are arranged below the lateral, perforate chamber walls of the last one or two whorls (Leutenegger, 1977a). The symbionts in *Heterostegina* are concentrated below the lateral walls of the planispiral-evolute to annular chambers.

Symbionts lack cell envelopes; in contrast, ingested food organisms and nonsymbiotic algae possess a cell wall and occur in very small numbers, usually near test openings, and in association with pseudopodial cytoplasm (Leutenegger, 1977a). Algal chloroplasts present in certain species of foraminifera are interpreted to be symbiotic if they are intact, isolated from other algal cell organelles, and occur in high numbers in the endoplasm. Photosynthesis of isolated algal chloroplasts in foraminifera was demonstrated by Lopez (1979). All members of a foraminiferal species are associated with the same type of symbionts, independent of locality, or of ecological factors such as water depth or season (Leutenegger, 1984). Hohenegger et al. (2000) state that all living nummulitids house diatoms exclusively, but each species harbours a different mixture of different diatom species (e.g., Lee and Anderson, 1991; Lee, 1994).

Although possible symbionts have been identified in well-preserved late Palaeozoic fusulinid tests (Lee and Hallock, 1987), no incontrovertible evidence of symbiosis in fossil larger foraminifera has been found. However, numerous authors have suggested that the phylogenetic history of several, if not all groups of LBF can be interpreted in the light of algal symbiosis (e.g., Van Gorsel, 1978; Lee et al., 1979; Hallock, 1982, 1985). Ross (1974) suggested that the symbiotic relationship between algae and foraminifera may have evolved independently during the Carboniferous in the Fusulina and later in the Cretaceous and Cenozoic in the Miliolina, Textulariina and Rotalina, and Leutenegger (1984) concluded that the relationships seen today between foraminifera and symbionts were probably established in Palaeogene to Neogene times.

Similarities between the test structure of fossil forms and symbiont-bearing Recent LBF have commonly been cited as evidence of symbiosis in the former, e.g., in late Palaeozoic fusulinids (Ross, 1974) and Palaeocene–Eocene *Discocyclina* (Ferràndez-Cañadell and Serra-Kiel, 1992). Generally, however, such features cannot be conclusively attributed to symbiosis. For example, the "cup" at the base of pores in the tests of many perforate rotaliines appears to function as a receptacle for algal symbionts, although such pore cups also occur in symbiont-free Bolivinidae and Acervulinidae, and are virtually absent in some symbiont-bearing species (Hansen and Buchardt, 1977; Leutenegger, 1977a,b, 1984).

Symbiosis in fossil forms has also been suggested on the basis of stable isotopes. Carbon and oxygen isotopes are fractionated during photosynthesis in algae, and the fractionation may be preserved in the carbonate skeleton of the host. Such disequilibrium isotopic fractionation has been identified in many Recent LBF (e.g., Erez, 1978; Wefer and Berger, 1980, 1991; Williams et al., 1981; Brasier and Green, 1993; Langer, 1995); the presence of biogeochemical markers specific to dinophytes has been identified in the tests of fossil soritids (De Leeuw et al., 1995; Fensome et al., 1996), suggesting that these taxa housed dinophyte endosymbionts. The probable presence of dinophyte endosymbionts within fossil soritids has also been suggested on the basis of cladistics in a study of the extinct forms *Orbitolites complanata* and *Amphisorus americanus* (Richardson, 2001).

4.2. Morphological adaptations for housing symbionts

The presence of symbionts may be due to modifications in the calcareous test of the foraminifera (Haynes, 1965, 1981). These include small spaces within the test walls that harbour algae (Hansen and Dalberg, 1979), pits on the interior of the chamber walls in which the algal cells reside (Hansen and Reiss, 1972; McEnery and Lee, 1981), plus chamberlets and other similar test complexities (Ross and Ross, 1978). Hallock (1982) suggested that chamberlets and other partitions strengthen the test whilst allowing it to remain transparent for algal symbiosis. The thin walls beneath the pits in *Amphisorus hemprichii* also permit the passage of CO_2 for use by the symbiotic algae (Hansen and Dalberg, 1979), whilst the thin walls in *Sorites* and *Marginopora*, the pitted walls of *Spirolina* and *Cyclorbiculina*, and the furrowed walls of *Peneroplis* may serve a similar function. The walls of foraminifera include various crystal arrangements, such as rods, stacks and platelets, and a radial crystal orientation. These arrangements, and a reduction in the amount of organic matter in the test wall, may aid light transmission to the symbionts (Ross and Ross, 1978). The three nummulitid species (*Operculina ammonoides*, *Heterostegina depressa* and *Heterocyclina tuberculata*) living below 60 m water depth in the Gulf of Aqaba are characterised by their single or multiple interseptal pillars, which form semispherical "humps" on the lateral shell surface. Reiss and Hottinger (1984) interpret these as lenses designed to collect the dwindling light to the profit of the symbionts.

Many living larger foraminifera shelter their symbionts in separate chamber compartments, moving their cytoplasm via canal and stolon systems (Hottinger, 1978; Hottinger and Leutenegger, 1980). This helps to stabilise the symbionts' preferred position directly below the chamber walls and avoids the larger cytoplasmic currents which would otherwise carry the algal symbionts away. The canal system of the Nummulitidae consists of relatively narrow channels (Hottinger and Dreher, 1974; Hottinger, 1977b), which may permit algal symbiont reproduction inside the host, whilst at the same time avoiding algal symbionts being taken up from the surrounding environment.

4.3. Advantages of algal symbiosis

Foraminifera may obtain all or part of their nutritional requirements from their endosymbionts (McEnery and Lee, 1981). The extrametabolites of the symbionts may be utilised by the foraminiferal host, and in some foraminiferal species, the symbionts themselves may be digested. Müller-Merz and Lee (1976) observed that most healthy symbionts in *Sorites marginalis* occur in the intermediate chambers, whilst food vacuoles were concentrated in the outer chamber. They suggest that *S. marginalis* may optimise its benefit from the symbiotic relationship by harvesting those symbionts crowded out of the interior chambers into the outer chambers; that is, the symbionts multiply faster than the foraminifera can provide space, and the excess are eaten. These nutrient sources may provide an energetic advantage to the foraminifera living in low-nutrient (oligotrophic) tropical waters (Hallock, 1981a). Not all symbiont-bearing foraminifera depend entirely on their symbionts for food; for example, *Archaias angulatus* and *S. marginalis* actively feed as well (Lee and Bock, 1976).

The probability of being eaten or swept away decreases as the foraminifera become larger and more heavily calcified (Hallock, 1982). Consequently, algal symbiont-bearing species with the genetic capability to use some of their energetic advantage to secrete thicker walls would appear to be less at risk from predation in oligotrophic environments. However, such thicker walls could prevent light from reaching the symbionts within the test; forms with thinner walls over the chambers and thick partitions between the chambers would be relatively heavily armoured, yet light could penetrate into the interior, whilst subdivision of the chambers into chamberlets would increase the strength of a shell whilst still permitting very thin lateral chamber walls. Symbiont-bearing species with a genetic tendency towards thin, transparent chamber walls, thick septal walls and/or subdivision of chambers would therefore seem to be favoured.

Duguay and Taylor (1978) showed that test calcification rate is directly affected by symbiont photosynthesis over certain ranges of light intensity. They examined the relationship between calcification in the soritid foraminifer *Archaius angulatus* and photosynthesis of its symbiont *Chlamydomonas hedleyi* and observed that both are directly proportional to light intensity in the range 0–200 μEinsteins m^{-2} s^{-1}. Calcification in the light is directly proportional to photosynthesis and proceeds at a rate 2–3 times greater than that observed in the dark.

4.4. Foraminifera and light tolerance: implications for distribution and test shape

Haynes (1965) proposed that test shape is a compromise between the metabolic requirements associated with algal symbiosis, hydrodynamic factors and light. Many studies have documented systematic morphology changes with variation in habitat depth in living, symbiont-bearing species (e.g., Haynes, 1965; Hottinger and Dreher, 1974; Larsen, 1976; Hansen and Buchardt, 1977; Hottinger, 1977a; Larsen and Drooger, 1977; Hallock, 1979; Hallock and Hansen, 1979). These authors have related such morphological trends to decreasing photosynthetic activity of the algal symbionts with increasing water depth. Within the same species, and between different species of the same genus, the test form varies depending on the amount of light received (Hallock, 1979; Hallock and Hansen, 1979). More oblate and thicker tests are found in species inhabiting shallow water, suggesting that light availability controls test morphology through symbiotic interactions (Hallock, 1979), as illustrated in Fig. 10. This dependence of larger foraminifera on their algal symbionts, and the influence of the symbionts on the shape of the foraminiferal test provides a powerful tool in palaeoenvironmental interpretation (Hallock, 1980, 1983; Leutenegger, 1984).

Larsen (1976), in a study of Recent amphisteginids from the Gulf of Aqaba, suggested that interspecific changes in the diameter to thickness ratio (*D*/*T* ratio) of four species can be related to the level of incoming light. He identified three groupings (see Fig. 11): the *Amphistegina lobifera* group, the *Amphistegina lessonii* group and the *Amphistegina papillosa–Amphistegina bicirculata* group. A general tendency towards increasing *D*/*T* ratio with depth was observed, which is not only an interspecific tendency but also applies to intraspecific variation. This was seen most clearly in *A. lessonii*, where shallow-, medium- and deep-dwelling groups were identified. He suggests that the grouping of shallow populations sampled in dense *Halophila* vegetation (giving a shallow, shadowed biotope), to-

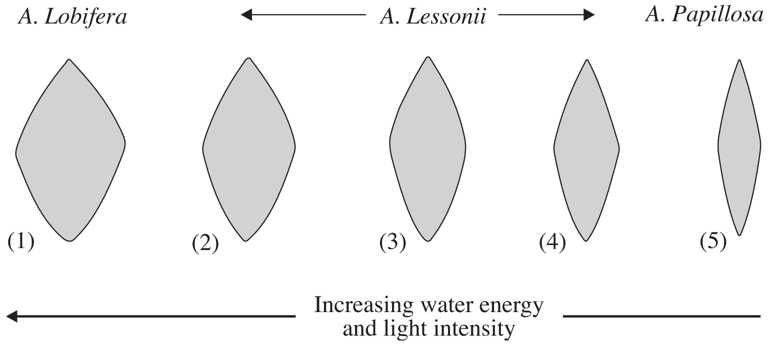

Fig. 10. Silhouettes illustrating the range of shapes in three Indo–Pacific species of *Amphistegina*: (1) *A. lobifera*, high-energy, high-light environment; (2) *A. lessonii*, moderate-energy, high-light environment; (3) *A. lessonii*, low-energy, moderate-light environment; (4) *A. lessonii*, low-energy, low-light environment; and (5) *A. papillosa*, low-energy, very low light environment (modified from Hallock and Glenn, 1986).

gether with medium depth populations, indicates that light is the determining factor for the shape index.

A correlation exists between foraminiferal depth distribution, symbiont type and light spectrum, i.e., wavelength and intensity (Leutenegger, 1984). There is a progressive increase in the lower end of the depth zonation from chlorophycean-bearing species (at approximately 15 m), including *Peneroplis proteus* and several species of Archaiasinae, through to species hosting rhodophyceans or dinophyceans (60–70 m), including several species of soritids, to the species harbouring diatoms (0–130 m), including nummulitids, calcarinids, amphisteginids and alveolinids. Whilst the members of the latter group all have distinct depth ranges, their overall distribution indicates that, of these four algal classes, the diatoms have the greatest adaptive potential for utilising varying light quality. Leutenegger (1984) showed that red and violet light favours chlorophyte symbionts in shallow water (<20 m); yellow, green and blue light favours rhodophytes or dinoflagellates at intermediate depths (<70 m); and green and blue light favours chrysophyte diatom symbionts in deeper waters (<130 m).

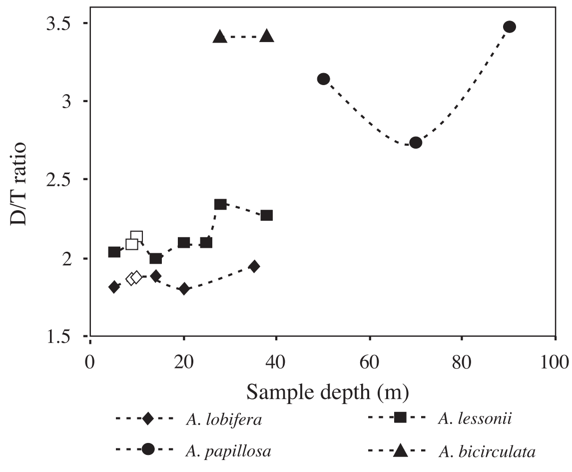

Fig. 11. Variation in mean diameter to thickness ratio with depth in recent amphisteginids from the Gulf of Aqaba (modified from Larsen, 1976). Open symbols indicate samples from dense vegetation of *Halophila*.

In *Amphistegina*, decreasing test sphericity with increasing water depth is paralleled by a thinning of the secondary lamellae and by a reduction in ^{18}O of shell carbonate, indicating decreasing symbiont activity with increasing depth (Buchardt and Hansen, 1977; Hallock and Hansen, 1979). Symbiont-bearing soritid species tend to have more depressed tests than rotaliine species (Hallock, 1979). Soritids also have lateral walls which are markedly thinner than those of most symbiont-bearing rotaliine foraminifers. Only rotaliid species inhabiting deep water, such as *Amphistegina papillosa* and *Heterocyclina tuberculata*, show comparably thin walls (approximately 10 μm) (Hallock and Hansen, 1979; Hottinger, 1977b). Diatom symbionts associated with rotaliine species can therefore tolerate a wider variation in light intensity and wavelength than chlorophycean, dinophycean and rhodophycean symbionts which are associated with the soritidae.

Sustenance and growth of symbiont-bearing foraminifera depends on the intensity of the available light and the exposure time (Hallock, 1981a). Laboratory studies of Hawaiian *Amphistegina* demonstrate a niche separation of two very similar species because of photoinhibition. *Amphistegina lobifera* prefers very shallow (<3 m) waters and requires higher light intensities for reproduction, whilst *Amphistegina lessonii* inhabits deeper waters, has thinner test walls and does not reproduce in well-lit near-surface waters. *Heterostegina depressa* from the same region is also adapted to low-light intensities (Röttger, 1976). Röttger (1972) observed that *H. depressa* obtained its nutrients from photosynthesising symbiotic algae, and that he could regulate the rate of growth in the foraminifera by regulating the duration and intensity of light that the specimens received. Röttger and Berger (1972) showed in the laboratory that the optimum light intensity is approximately 300 lx. Above and below this value, rates of growth declined. Röttger et al. (1980) noted that growth in *H. depressa* and *A. lessonii* depended on light intensity; optimum growth in *A. lessonii* occurred at 800 lx, whilst in *H. depressa*, it occurred between 400 and 600 lx. In both species, there was no growth in darkness. They also observed that $^{14}CO_2$ fixation in *H. depressa*, *A. lessonii* and *A. lobifera* increased with increasing light intensity.

Hottinger (1983) observed that, in the presence of very intensive irradiation by sunlight, the behaviour of symbionts and their host may avoid or reduce photoinhibition. In *Sorites*, *Amphisorus* and *Marginopora* (associated with dinoflagellates), the symbionts are motile and move to the shaded side of the shell (Leutenegger, 1977b). In addition, the substrate selected by the host is dark so that the light regulation mechanism is unhampered by reflection from the substrate. Amphisteginids show negative phototaxis, hiding in the shade of boulders, plants or corals (Zmiri et al., 1974), and *Heterostegina depressa* lives in shaded pools or reef front overhangs at very shallow depths (Röttger, 1976; Hottinger, 1981).

In the Gulf of Aqaba, Red Sea, the overall foraminiferal zonation is strongly influenced by the degree of light penetration. The Gulf has no significant vertical variation in temperature or salinity. The upper zone (0–50 m) is dominated by porcellaneous forms. Rotaliids, such as *Amphistegina* and *Operculina*, are common to a depth of 130 m, i.e., around the base of the photic zone (at which depth the illumination corresponds to 0.5% of the surface light intensity; Hottinger, 1983), whilst, below this depth, smaller benthic foraminifera dominate. Except for some soritid and nummulitid larger foraminifera studied by Hottinger (1977a), the distribution is little influenced by the nature of the substrate. Reiss (1977) noted that algal symbionts are present in all porcellaneous and larger rotaliid forms of the Gulf, but not in all smaller rotaliid forms. The distribution of light therefore affects the depth-zonation of the benthic foraminifera in some unknown way, apart from controlling the photosynthetic symbionts.

As shown above, the morphology and distribution of living LBF is controlled by a complex interaction of environmental factors. Similar environmentally controlled variations in test morphology and distribution have also been documented for *Nummulites*. Trevisani and Papazzoni (1996) noted an environmental control on the distribution and shape of late Priabonian *N. fabianii* of the Venetian Alps (northern Italy). They identified two subspecies which occur in the upper and lower facies of shallowing-upwards cycles, with the flatter form (*N. fabianii retiatus*; *D*/*T* ratio average 2.8) occurring in base–cycle marls, and the more ‘robust’ form (*N. fabianiii fabianii*; *D*/*T* ratio average 2.1) being restricted to shallower, cycle-top limestones. These differences were attributed to the effects of water energy, light intensity and substrate, which agrees with the work of Herb and Hekel (1973), who noted that *N. fabianii fabianii* in the upper Eocene of Possagno, northern Italy, are restricted to limestones, whilst *N. fabianii retiatus* from the same area are only found in “silty–argillaceous” sediments.

4.5. Variations in colour of symbiont-bearing larger foraminifera

Whilst colouration of some LBF may be due to symbiotic algae, Leutenegger (1984) suggests it is not a reliable indicator of the presence of symbionts because it can be due to ingested food, storage products or pigmented shell components. The colour of the dinophycean- and diatom-bearing foraminifera may also vary widely depending on the thickness of the host shell, the abundance and distribution pattern of the symbionts within the host (which changes when foraminifera retract their endoplasm into inner parts of the shell) and on the symbiont’s own colouration (which may change with varying light conditions). Alternatively, colour may be indicative of the nature of the symbionts if closely related hosts with similar shell morphology and structure are compared, and the above are considered.

Hansen and Buchardt (1977) noted that the colour of symbiont-bearing *Amphistegina* from the Gulf of Aqaba varied from green to olive green to "brownish." Some brown forms were also observed to have a reddish tint. Their studies of the ultrastructure of the cytoplasm of the red-tinted forms indicated that these were dead specimens in the process of decomposition, the red colouration possibly being due to the breakdown of chlorophyll.

5. Other external physical and chemical influences on larger benthic foraminifera

5.1. Nutrient supply

Larger benthic foraminifera are highly adapted to stable, oligotrophic, nutrient-deficient conditions, but they cannot respond competitively when nutrient resources become plentiful (Hallock, 1985). Inorganic, "biolimiting" nutrients enter shallow-water communities principally by turnover or upwelling of deeper waters, by run-off from land or by advection from areas of upwelling or runoff (Hallock and Schlager, 1986). An input of nitrates and phosphates into the shallow-marine environment stimulates the growth of plankton, which reduces water transparency, limiting the depth ranges of the foraminifera, and thus also reducing carbonate production.

Hallock (1981a) showed the tremendous energetic advantage of algal symbiosis to both host and symbiotic algae under oligotrophic conditions. However, this specialisation may have been the cause of the numerous extinctions of probable algal symbiont-bearing forms seen in the rock record. When nutrients are readily available, free-living algae can rapidly reproduce themselves. Abundant algae provide an abundant food supply for other animals which are then able to grow rapidly and reproduce. Consequently, slow-maturing, highly specialised, algal symbiont-bearing foraminifera cannot compete. Miliolids and smaller rotaliines therefore commonly replace symbiont-bearing, larger rotaliines and soritids when food supplies increase (Hirschfield et al., 1968; Hallock, 1985).

Diversity appears to be favoured by prolonged, stable, oligotrophic conditions (Hallock and Schlager, 1986), implying that an increase in nutrient levels could bring about the decline and extinction of oligotrophs for a variety of reasons, as outlined below (after Hallock and Schlager, 1986; Hallock, 1988; modified from Brasier, 1995):

1. *Plankton blooms* reduce water transparency, or bring about toxicity, slowing the growth of larger foraminifera and lowering the rate of carbonate production.
2. *Freely available nutrients* encourage symbiotic protists to escape and lead a free planktonic life.
3. *Phosphates* may act directly as crystal poisons to calcification.
4. *Oxygen depletion or sulphide poisoning* on the seafloor (from decomposing plankton or mucus) kills larger foraminifera.
5. *Genetic variation* of forms largely produced by asexual reproduction is low, reducing the potential range of response to changing conditions.
6. *Competitors*, such as coralline algae, fleshy algae, homotrematids, barnacles and bryozoans, the crown-of-thorns starfish, etc., may be favoured by higher nutrients and plankton production.
7. *Bioeroders*, such as endolithic algae and fungi, clionid sponges, boring bivalves and echinoids, may flourish.

Nutrient availability is often linked to temperature and salinity; upwelling adds nutrients whilst reducing temperature, runoff adds nutrients whilst reducing salinity, and evaporation concentrates nutrients whilst raising salinity (Hallock and Schlager, 1986).

Brasier (1972) showed that, in the mesotrophic, hypersaline lagoons of Barbuda, Lesser Antilles, the percentage of microbored and micritised foraminiferid tests increases dramatically near the landward margin close to Codrington, the only settlement. However, Brasier (1995) cautions the use of bioerosion as an index of nutrient availability in the fossil record because the potential effects of slower sedimentation rates, temperature-related oxygen deficiency, depth and light limitation must also be considered.

5.2. Substrate

Substrate (which is related to water turbulence; Hallock and Glenn, 1986) may exert a significant influence on the distribution of some larger foraminiferal species. Substrate comprises inorganic particles (including shell debris) and organic particles (e.g., plant material, faecal pellets and detritus) plus interstitial water and air. The quantity of available nutrients often depends on the substrate (Gerlach, 1972). Silty and muddy substrates are often rich in organic debris, and the small pore spaces may contain bacterial blooms, which can support large populations of foraminifera. Many of these foraminiferal species are delicate, often elongate forms. However, the large pore spaces of sand and gravel contain fewer nutrients, and therefore support sparser populations. Foraminifera from these coarser substrates may be thicker-shelled, heavily ornamented and of biconvex or fusiform shape (Brasier, 1980). Hottinger (1983) noted that the soft or solid nature of the substrate produces, at comparable depths, two fundamentally different biosystems, inhabited by different genera or species of larger foraminifera. There is a bias towards explaining such changes in the fossil record as being solely depth related, whilst on Recent sea floors, the distribution according to depth and substrate is equally well documented. A systematic distinction of hard bottom (high-energy) and soft bottom (low-energy) depth sequences based on the shell morphology in larger foraminifera would, as suggested by Hottinger (1983), considerably enhance palaeobathymetric interpretations.

Foraminifera may be encrusters, epiphytes, or live in or on the sediment. In higher energy environments, encrusters and epiphytes are most common. In lower energy environments, algal film and sediment dwellers predominate. Foraminifera which prefer hard substrates (i.e., rock, shell, etc.) are normally attached, either temporarily or permanently, by a flat or concave lower surface. They often develop a relatively thin test and exhibit greater morphological variablity than observed in sediment-dwelling and planktonic forms (Brasier, 1975c). The combined effect of depth and substrate on the distribution of certain soritids and nummulitids has been reported for the Gulf of Aqaba, Red Sea (Hottinger, 1977a). The epiphytic *Amphisorus hemprichii* and *Sorites orbiculus* occur in water depths of 0–20 m, with *S. orbiculus* more frequent in very shallow *Diplanthera* meadows, and *A. hemprichii* occuring mainly on *Halophila* leaves or occasionally on loose boulders. *Sorites variabilis* occurs both as a free and an attached form. Free specimens have regular discoidal tests, whilst attached specimens follow the surface relief of their substrate during growth, often producing contorted tests. Of the nummulitids, *Heterostegina compressa* prefers hard bottoms between 20 and 70 m, whilst *Operculina ammonoides* and *Heterocyclina tuberculata* live on soft bottoms between 30 and 150, and 70 and 150 m, respectively. Reiss and Hottinger (1984) also recorded the distribution of nummulitids in the Gulf of Aqaba, noting that *O. ammonoides* and *Heterostegina depressa* share roughly the same depth zone, between 20 and 130 m, but are separated by the characteristics of their preferred substrate. The former lives on a soft substrate between *Halophila* plants, where water energy is low, whereas the latter lives on hard bottoms at the base of corals, on boulders or coarse coral debris. Near boundaries of ecosystems corresponding to hard- or soft-bottom communities, the distribution of the two species overlaps, especially in the deeper part of their depth range, where sedimentation rates are low. Below the growth of dense coral carpets on hard substrates, or of permanent vegetation covers on soft substrate (limited to a depth of 70 m), the nummulitid *H. tuberculata* is found in densities one to three orders of magnitude lower than those of *O. ammonoides*. Only 1% of these are microspheric. *H. tuberculata* is found on both soft substrates with low sedimentation rates and hard bottoms down to the limit of the euphotic zone.

Reiss and Hottinger (1984) also noted that *Amphistegina lessonii* and *Amphistegina lobifera* from shallow waters are gradually replaced by the comparatively thin-walled, lenticular *Amphistegina papillosa* and *Amphistegina bicirculata* at depths of between 40 and 80 m. *Amphistegina lobifera* occurs in high energy environments (e.g., below fringing reef fronts), whilst *A. lessonii* dominates the faunas of quieter lagoons or channels. The shallow-water species live as epiphytes on *Halophila* or other plants and also share the hard bottom substrate of *Heterostegina depressa*. On boulder-covered and current-exposed slopes, large numbers of *A. lobifera* and *A. lessonii* live at depths of 10 to 20 m, on the lower, shaded surface of the boulders. The deep-water species *A. bicirculata* and *A. papillosa* live on both soft (sand) and hard substrates on the open shelf, between 80 and 130 m depths.

Hohenegger et al. (2000) noted that *Nummulites* (=*Palaeonummulites*) *venosus* from the west Pacific prefers coarse sand substrates below fair weather wave base, whilst the deep-dwelling *Planoperculina heterosteginoides* is restricted to poorly illuminated areas of 0.3% to 2.5% surface light intensity and preferred medium- to fine-grained sand substrates and calm water. *Planoperculina heterosteginoides* has mean test sizes of 2.8 mm at 90 m and 3.7 mm at 100 m water depth.

In St. Lucia, West Indies, patch reef faunas comprise abundant *Amphistegina gibbosa*, *Rotorbinella rosea*, *Sorites marginalis* and *Rosalina floridensis*, whereas the adjacent fine substrate is dominated by the smaller benthic foraminifera *Ammonia beccarii* and *Buliminella elegantissma* (Sen Gupta and Schafer, 1973).

Seagrasses, which are found between mean water level and approximately 30 m water depth (Brasier, 1975d; C. Perry, pers. comm., 2001) are the preferred substrate of many large, discoid foraminifera such as *Sorites*, *Amphisorus*, *Marginopora*, *Archaias* and *Peneroplis*, although no foraminifera have yet been shown to be restricted to them. Various studies (e.g., Taylor, 1971; Brasier, 1975a,c) have shown that diversity, biomass, standing crop and productivity are greater in seagrass communities than in those of surrounding waters, thus ancient seagrass assemblages might also be expected to show an increase in diversity compared with neighbouring facies. Brasier (1975d) states that, because the distributions of Recent and fossil seagrasses are similar to the distribution of Recent and fossil seagrass-dwelling foraminifera, the latter may be used as indices of probable geographic dispersal of seagrass communities through time. He suggests that seagrass communities were probably present in the shallow sublittoral waters of the Tethys in the Late Cretaceous, and almost certainly in Eocene times.

Several authors have attributed variations in test size of fossil *Nummulites* to changes in substrate (often related to changes in water depth). Pomerol (1981) noted that the size of *Nummulites laevigatus* was inversely proportional to the clay content of the surrounding sediment, whilst Nemkov (1962) concluded that *Nummulites* were larger in shallow-water calcareous and sandy deposits than in deeper water clay-rich sediments. However, Racey (1992) pointed out that none of these studies indicated whether the work was based on specimens at a similar ontogenetic stage (because test shape may vary with the stage of ontogenetic development).

Beavington-Penney (2002) identified two A-form-dominated *Nummulites* populations associated with seagrass-vegetated environments in the Middle Eocene Seeb Formation of Oman. Both contained a highly diverse biota typical of shallow marine, protected environments (including micritic peloids, the soritid foraminifera *Orbitolites*, alveolinids, miliolids, peneroplids, textulariids, probable encrusting foraminifera and dasycladacean green algae), many of which are common in (although not restricted to) seagrass environments. However, several lines of evidence more conclusively suggest deposition under the influence of seagrasses. Tests from one population display occasionally well-developed "constructive micrite envelopes" (Fig. 12A), features identified in modern seagrass communities and considered by Perry (1999) to be a diagnostic tool for the recognition of ancient seagrass environments and other marine vegetation-stabilised substrates. However, the common presence of infaunal spatangoid echinoid burrows suggests that the vegetation cover would have been relatively sparse because living relatives of these forms cannot cope with extensive seagrass roots or green algal holdfast filaments (Kier and Grant, 1965; A. Smith, pers. comm., 2001). The second population comprises a monospecific community of A-form *Nummulites* ex. gp. *discorbinus*, and is commonly associated with crustose coralline red algae, which occur as both foliose 'crusts' up to several millimetres long and several hundreds of microns thick (Fig. 12B), and also as tubular forms several millimetres in length and with internal diameters up to 1.3 mm. Both morphologies are highly suggestive of encrusting habits, and there are obvious similarities with encrusting coralline red algae (and also bryozoans) from modern seagrass beds of western Australia (Davies, 1970), the northern Belize Shelf (Pusey, 1975), the south Florida Shelf (Enos, 1977) and Mozambique (Beavington-Penney et al., 2004). The presence of abundant *Nummulites* (which have never previously been described as seagrass dwellers) within this facies argues against deposition under dense seagrass cover, and suggests either

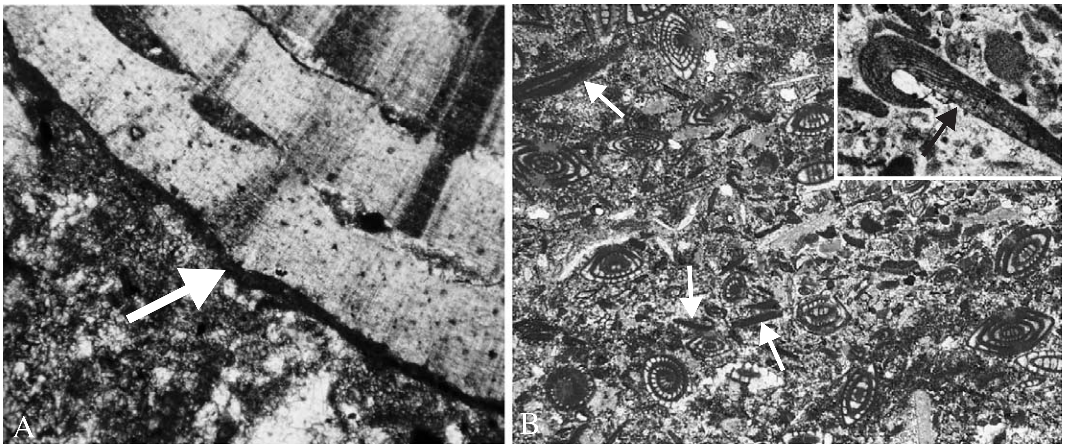

Fig. 12. Indicators of deposition within a seagrass-influenced environment from the middle Eocene Seeb Fm. (Oman), including: (A) constructive micrite envelope (arrowed) on a *Nummulites* test (field of view: 1.3 mm); (B) A-form *Nummulites*-dominated peloidal-red algal packstone, with foliose crustose coralline red algae (arrowed; field of view: 14 mm). Insert shows the flat, encrusting(?) surface on a degraded fragment of crustose coralline red algae. This example also shows the 'shepherd's crook'-shaped termination typical of many of the grains, which, it may perhaps be speculated, resulted from growth of the algae over the seagrass leaf margin. Field of view of insert: 1.3 mm.

deposition in a sparsely/seasonally(?) vegegated area, or in close proximity to seagrasses.

5.3. Water motion

Hallock (1979) indicated that water motion can influence test shape, and Ter Kuile and Erez (1984) confirmed that *Amphistegina lobifera* produces thicker tests when subjected to water motion during growth. Hallock et al. (1986b) observed that test shape in *Amphistegina gibbosa* and *Amphistegina lessonii* grown in culture was affected by light flux and water motion. These factors influenced the deposition of secondary lamellae in the test wall; increased light saturation and water motion produced a thicker wall, and therefore a thicker test. However, they also noticed that, although water motion increased the test thickness (through increased calcification), it retarded the overall growth rate. Slower growth rates were also noted by Röttger (1976) in *Heterostegina depressa* under conditions of increased water motion.

5.4. Salinity

Salinity variations are generally too minor to be ecologically significant in offshore settings, although in nearshore areas with high runoff salinity, variations are marked and may be of considerable importance in controlling foraminiferal distribution (Phleger, 1960).

The rotaliine larger foraminifera are typically stenohaline, with tolerance limits in the range of 30–45‰(Hallock and Glenn, 1986), between which the highest diversity assemblages are found. Some near-shore benthic foraminifera are euryhaline. Salinity tolerances decline as other significant factors (i.e., temperature or concentration of dissolved gasses) increase or decrease beyond optimal values. They are protected to some extent from drastic salinity changes by the "dampening" effects of the substrate (Kinne, 1971), partly a consequence of the fact that salinity variations may be less extreme in the substrate than in the free water above. Hottinger (1983) noted that at extreme values, temperature and salinity are limiting factors for all larger foraminifera, whilst at intermediate values, they have a negligible selective effect. Short-lived extreme values, as observed in tidal pools, often produce contorted tests, such as the supplementary half disc perpendicular to the original observed in some discoid porcellaneous forms.

Reiss and Hottinger (1984) report that LBF are abundant and diverse in the Gulf of Aqaba at salinities of 40–41‰(i.e., at the upper end of their typical salinity tolerance).

5.5. Temperature

Temperature strongly affects many physical and chemical properties and biological processes within the marine environment. Foraminifera are poikilothermic; that is, their body temperature is very close to that of the surrounding water. Their small mass responds very quickly to even small changes in the ambient water temperature, although these changes are partially dependent on changes that may take place simultaneously in other properties of the environment, such as light, salinity, pressure and dissolved gases (Kinne, 1970). The relative effects of these different factors on benthic foraminifera are hard to evaluate. However, temperature is generally considered to be the single most important physical factor influencing the distribution of species or assemblages (Lee, 1974).

The large-scale distribution of benthic foraminifera can be clearly related to temperature ranges, particularly the seasonal ranges that affect reproduction. The distribution of symbiont-bearing LBF broadly parallels that of tropical and subtropical organisms, such as corals and mangroves, and falls within a global climatic belt defined by the 25 °C summer isotherm (Murray, 1973; Adams et al., 1990; Plaziat and Perrin, 1992). Langer and Hottinger (2000) observed that, in most instances, the general distribution of LBF is limited by winter minimum isotherms of between 15 and 20 °C, although they state that one exception is the southwestern tip of Australia, where LBF (including nummulitids) exist in temperatures that fall below 15 °C in winter. They suggest that this is due to the Leeuwin current, which transports warm, nutrient-poor equatorial waters from the tropics of the Indian Ocean southwards to western Australia. Hollaus and Hottinger (1997) suggest that an LBF distribution limit of 16–18 °C is related to the minimum temperature required for the growth of their endosymbionts. Interestingly, and conversely, Hallock et al. (1991) showed how, in theory, lower water temperatures may actually promote the growth of LBF because, physiologically, it takes twice as much energy for a foraminifera to live at 11 °C as at 1 °C, four times as much to live at 21 °C, and eight times as much energy to live at 31 °C; as a consequence, they suggest, a rate of nutrient flux that might support a tropical oligotrophic community is effectively doubled in the subtropics and quadrupled in temperate waters. Of the LBF, amphisteginids and soritids display the widest latitudinal distribution, related to their tolerance of a relatively wide temperate range (Murray, 1991; Langer and Hottinger, 2000), as shown in Fig. 13.

Temperature also appears to control the diversity of LBF assemblages: tropical to subtropical, shallow-water assemblages are generally characterised by more than 10 species, whilst very warm (greater than approximately 31 °C) and warm–temperate (less than

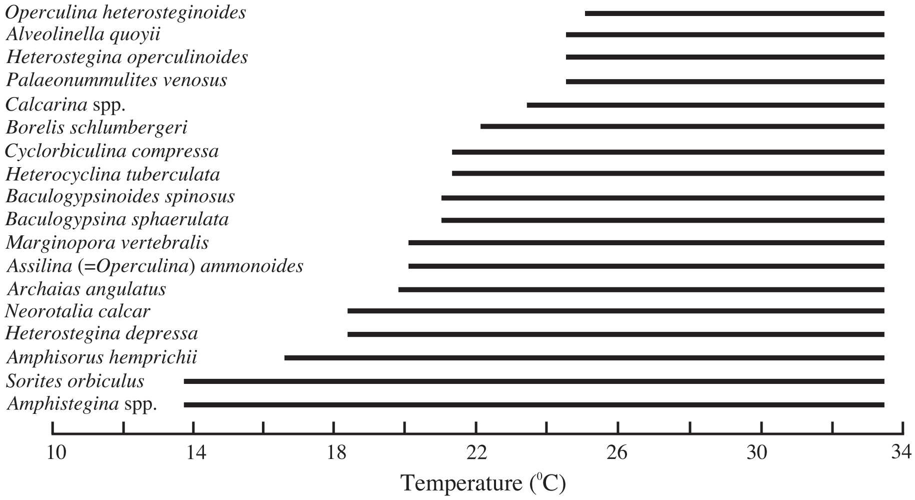

Fig. 13. Sea surface temperature ranges of selected larger benthic foraminifera (modified from Langer and Hottinger, 2000).

approximately 20 °C) shallow-water environments generally contain far fewer species (Murray, 1987; Adams et al., 1990; Jones, 1999). However, it should be noted that diversity also appears to be a function of trophic regime (being highest in oligotrophic environments), evolution (being highest at times or in areas of intense evolutionary activity), position relative to migration routes (with the highest diversity found along the routes) and also sampling or taxonomic artefacts (Jones, 1999).

5.6. Taphonomic processes

Transportation of both living and dead tests by storm and tidal currents could have a significant impact upon the distribution of many LBF. However, very few studies of the distribution of modern larger foraminifera have considered the importance of such modifications (e.g., Coulbourn and Resig, 1975; Debenay, 1988). Hohenegger and Yordanova (2001) observed that the transport of LBF tests living offshore Okinawa (Japan) disguises the clear depth dependence shown by living species and concluded that transport into deeper water was controlled by offshore-directed sea floor and storm-induced currents, submarine slope steepness and differences in test buoyancy, although susceptibility to transportation generally decreases with increasing water depth. They noted that, of the shallowest-dwelling species, the buoyant porcellaneous forms *Alveolinella quoyi* and *Amphisorus hemprichii* are commonly transported down slope, whilst the less buoyant, hyaline form *Heterostegina depressa* shows less displacement.

Beavington-Penney (2004) observed the mechanical abrasion of the extant nummulitid *Palaeonummulites venosus* during experimental transportation equivalent to approximately 71 km within simulated tide- and storm-driven currents. He showed that such transport cannot reproduce the degree of test breakage observed in many Eocene, allochthonous *Nummulites* accumulations, and concluded that likely candidates responsible for the additional damage include transport within turbidity currents and predation by large bioeroders such as fish and echinoids.

Dissolution of calcareous tests in waters undersaturated with respect to $CaCO_3$ causes postmortem changes to assemblages of modern benthic foraminifera (Murray, 1989). These changes include a progression from etching, making the test wall appear dull and opaque, to breakage of the final chamber, followed by extensive chamber breakage and, finally, total destruction of the test. Assemblages unaffected by dissolution exhibit well-preserved, shiny tests, whilst those that have undergone total dissolution have no calcareous foraminifera. Murray suggests that partial dissolution can be quantified by a comparison of the percentage of agglutinated tests in the living and dead assemblages from the same sample. Failure to recognise partial dissolution can, he suggests, leads to misinterpretations of modern assemblages, and therefore has consequences for palaeoecological comparisons.

Bioerosion of LBF, by both microboring organisms and larger predators, may destroy tests completely or may weaken tests, making them more susceptible to dissolution and/or abrasion. Predation by grazers and detrital feeders (“foraminiferivory”) may seriously affect the distribution and standing crop of benthic foraminifera. The effects of predation on living populations are, at present, poorly understood. Smaller foraminifera are ingested by numerous organisms, including fish, crabs, shrimps, gastropods, bivalves and polychaete worms (Buzas, 1978; Hickman and Lipps, 1983). Lipps (1988) observed the common consumption of foraminifera by fish on Enewetak Atoll; they are ingested by omnivores and herbivores feeding on the substrate that the foraminifera are inhabiting. Damage inflicted on the tests ranges from punctured and broken chambers, scratches and gouges on the test surface and broken test peripheries, to complete destruction by dissolution or crushing, although he suggests that the large, flat tests of many rotaliines may provide protection against such predation. This “foraminiferivory” results in the transportation of tests away from their life habitat and may also explain the patchy distribution of populations of living foraminifera. However, Lee (1974) suggested that such patchiness may be an ecological strategy, leading to diversification of habitats and limitation of competition (see also earlier note on asexual reproduction as a possible cause of the patchiness of LBF communities). Magean and Walker (in Schafer and Pelletier, 1976) suggested that the fossil record may be distorted by the selective destruction of tests in the gut of many deposit feeders.

Microboring of LBF tests has often been observed. However, although such bioerosion is common in shallow tropical environments, with the infestation of skeletal grains by microendolithic organisms occurring within a few days (Perry, 1998), LBF tests show variable susceptibility to this predation. For example, Peebles and Lewis (1988) observed that rotaliine foraminifera appear to be more resistant to microboring organisms than milioline foraminifera; the rotaliines *Amphistegina* and *Discorbis* from reefs around San Salvador consistently showed no evidence of microboring, whilst associated miliolines were heavily infested. They attributed this in part to wall microstructure and suggested that test mineralogy may also be important. Other larger foraminifera have demonstrated a remarkable degree of resistance to microboring; dead *Alveolinella quoyi* tests from the lagoon around Motupore Island, Papua New Guinea, are not predated but rather undergo very slow dissolution (J. Lipps, pers. comm., 2001). Such resistance may be the result of the protection offered by the organic layer that surrounds the test, which, after death, appears to retain its ability to prevent boring (P. Hallock, pers. comm., 2000). Water energy may also explain differences in the degree of infestation exhibited by LBF; rates of grain infestation are highest in shallow, low-energy, Back-reef environments, whilst assemblages from high-energy environments are largely unaltered (Swinchatt, 1965; Budd and Perkins, 1980; Perry, 1998).

Rapid burial of LBF tests may also protect them against microboring. Perry (1998) observed that coarse-grained skeletal material from sites bioturbated by the shrimp *Callianassa* in Discovery Bay, Jamaica, is often well preserved, with few, if any, borings. He suggests that this is due to rapid burial in the shrimp burrows, and thus short residence times in the "taphonomically active zone" (TAZ). This effect was also noted by Tudhope and Scoffin (1984) and Bradshaw and Scoffin (2001). Short residence times in the TAZ may also explain the very limited bioerosion (mostly unfilled microborings) of tests of dead amphisteginids and nummulitids from the temperate southwestern Australia shelf (James et al., 1999). Suchanek and Colin (1986) report that carnivorous fish around Enewetak and Bikini Atolls bioturbate the sediment to a depth of 8–10 cm, which also results in the removal of foraminiferal tests from the TAZ.

Significant variations have been observed in the degree of bioerosion exhibited by LBF tests within Eocene nummulitic limestones. Bioerosion traces are common in *Nummulites* tests from Spain and Italy (Serra-Kiel, 1982; Serra-Kiel and Reguant, 1984; Mateucci and Pignatti, 1988), whilst no micro- or macroboring of *Nummulites* tests was observed in the El Garia Fm. of Tunisia by Beavington-Penney (2002), and he noted only very rare examples in the Seeb Fm. of Oman.

Intense bioturbation is evident in many Eocene nummulitic limestones, e.g., in the Tatra Mountains of Poland (Roniewicz, 1969) and in the Kirthar Mountains of Pakistan (Wells, 1986). *Thalassinoides*-type bioturbation is very common in the El Garia and Seeb Formations, as are horizontal echinoid burrows, both often back-filled with pristine *Nummulites* tests (Beavington-Penney, 2002). In the light of the modern studies (mentioned above) into the taphonomic effect of rapid burial of skeletal carbonate grains, this bioturbation appears to offer a good explanation for the general lack of bioerosion in these (and other) formations.

Differences in test structure may also help explain variation in resistance to boring observed in different species of Eocene nummulitids. Beavington-Penney (2002) noted that specimens of *Nummulites* and *Assilina* (in the same sample) from parautochthonous nummulitid shoals of the Seeb Fm. of Oman often show marked variations in the degree of infestation (although such borings are relatively rare).

5.7. Other factors

Oxygen depletion may lead to a reduction in species diversity and to an increase in population size for selected smaller benthic species. On the continental slope and deep ocean floor, sharp changes in both have been correlated with the presence of O_2-minimum layers (Golik and Phleger, 1977; Ingle et al., 1980). Other abiotic factors, which influence the distribution of benthic foraminifera, include the pH of the seawater. The effect of low pH is seen mainly in the stress produced on calcareous species in the secretion of $CaCO_3$; the effect of high pH is unknown (Sen Gupta, 1982).

The quantity and type of food available can have a large impact on the distribution, rate of production and rate of growth of many species. High-diversity assemblages suggest a wide range of available food resources. Conversely, seasonal fluctuations in food supply may result in foraminiferal blooms of great abundance but low diversity. These opportunistic species must reach maturity quickly; hence, they are relatively small in size (Phleger, 1960).

6. Habitat and distribution of modern and ancient larger benthic foraminifera

6.1. Idealised distribution model (after Hallock and Glenn, 1986)

Hallock and Glenn (1986) presented an idealised distribution model for modern reef-associated foraminifera (Fig. 14), summarised from the work of Brazier (1975a, 1975b), Hallock (1980, 1983, 1984), Montaggioni (1981), Glenn et al. (1981), Gabie and Montaggioni (1982), Hottinger (1983) and Reiss and Hottinger (1984). They used the "Standard Carbonate Facies Belts" of Wilson (1974) as reference categories for facies analysis. A summary of the foraminifera found within each environment is given below. It should be noted that, whilst these associations of foraminifera relate to oceanic settings, most Palaeogene foraminifera lived in epicontinental seas. On continental shelves openly connected to the open ocean (as illustrated in Fig. 14), both the ratio of planktonic to benthic foraminifera and the diversity of the planktonic assemblage decrease away from the open ocean. These trends show a general correlation with decreasing water depth and distance from the ocean (Murray, 1976). However, in modern epicontinental seas, such as the Persian Gulf, the decline in the abundance of planktonic tests is more related to distance from the ocean than to shallowing water depths.

6.1.1. Standard facies 1

Basin (above CCD)—Predominantly planktonic forms with deep benthic species comprising 25% or less of the population.

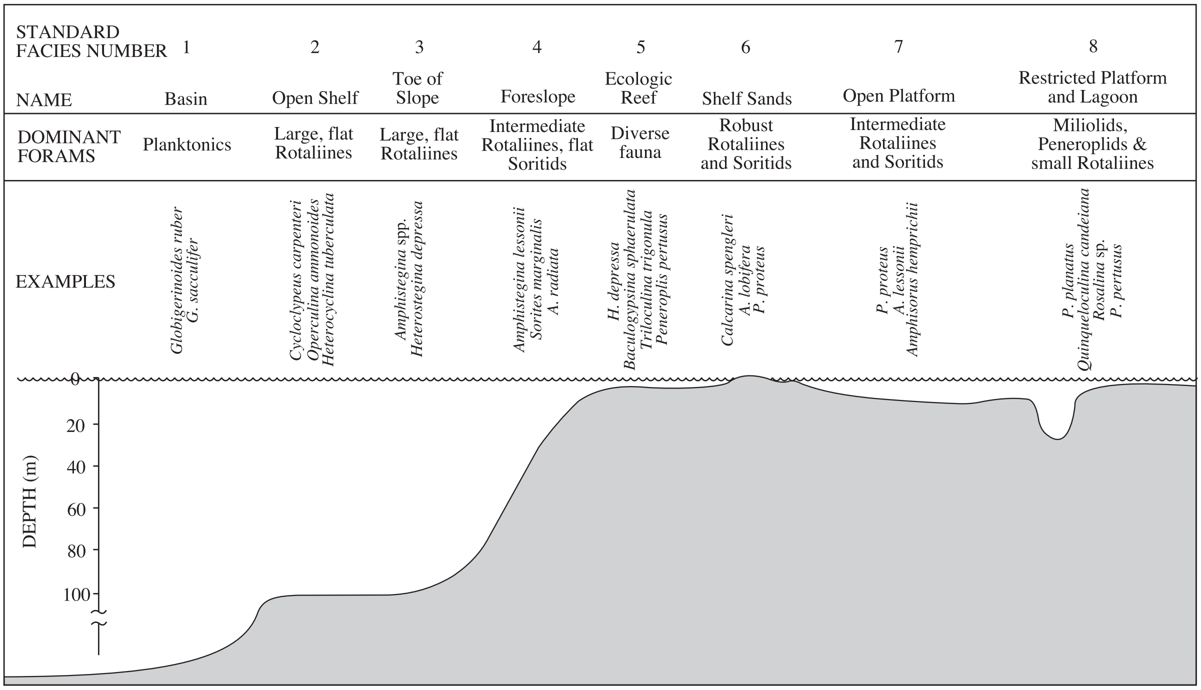

Fig. 14. Idealised distribution of major foraminiferal groups in reef-associated environments (modified from Hallock and Glenn, 1986).

6.1.2. Standard facies 2

Open Shelf—At subeuphotic (>120–200 m) depths, planktonics and outer shelf benthics dominate in situ faunas. Open carbonate shelves within the euphotic zone (approximately 40–120 m) are characterised by diverse foraminiferal faunas including planktonics, typical shelf benthics and large (up to several centimetres), very flat, discoid foraminifera. Sediment grain sizes are often highly bimodal, with large foraminiferal tests lying in a matrix of fine carbonate sands or muds, forming wackestones and packstones. Modern Indo–Pacific faunas are characterised by *Heterostegina*, *Cycloclypeus*, *Operculina* and the flatter species of *Amphistegina*; *Heterocyclina* replaces *Cycloclypeus* in these deeper environments of the Red Sea–East African faunal province (Reiss and Hottinger, 1984).

6.1.3. Standard facies 3

Toe of Slope—Packstones and wackestones tend to dominate, although grainstones are found. Modern faunas of larger foraminifera are similar to those of the euphotic open shelf.

6.1.4. Standard facies 4

Reef Foreslope—Subfacies here can be extremely diverse, including planktonic foraminifera, diverse in situ biota and allochthonous shallow-water forms. In the Indo–Pacific, modern faunas of larger foraminifera from deeper foreslopes are characterised by *Amphistegina* spp., *Heterostegina*, *Operculina* and *Heterocyclina* or *Cycloclypeus*. Shallower foreslopes are dominated by intermediate forms such as *A. lessonii* in the Indo–Pacific and *A. gibbosa* in the Caribbean, and by alveolinids in both regions. Smaller foraminifera include miliolids and some of the more robust discorbids.

6.1.5. Standard facies 5

Reef—The foraminiferal fauna is often diverse, representing forms that lived among the reef frame builders, as well as foraminiferal tests carried by currents or wave turbulence and deposited in sheltered places within the reef. Practically all types of low-latitude, shallow-water, benthic foraminifera are encountered, as well as a few planktonics. Encrusting foraminifera also occur. Foraminifera in coarser sands between corals or in other high-energy zones are chiefly robust, ovoid forms. Miliolids, peneroplids and small rotaliines are also common, especially in finer-grained sediments. In modern Indo–Pacific reefs, *Calcarina*, *Baculogypsina* (both distinct spinose, globular forms) and *Amphistegina lobifera* are the dominant robust larger foraminifera.

6.1.6. Standard facies 6

Platform Margin Sands—Modern Indo–Pacific sandy shoals and beaches can be almost entirely dominated by *Calcarina*, *Baculogypsina* or *Amphistegina* tests. Analogous sediments in the Caribbean are characterised by robust peneroplids and soritids, and by thick-shelled or agglutinating miliolids (Brasier, 1975b).

6.1.7. Standard facies 7

Shallow Open Platform—These shallow (<20 m) zones have a diverse foraminiferal fauna. Smaller rotaliine and milioline species can be quite diverse where hydraulic sorting has not removed them. Larger, rotaliine foraminifera are prolific, sand-sized sediment producers in these environments. In very shallow (<5 m), high-energy environments where coral rubble or coralline algae provide substrate, ovoid to subspheroid forms like *Calcarina* dominate. *Amphistegina*, alveolinids (*Alveolinella* and *Borelis*), or larger soritids dominate quieter environments, dwelling on algal film substrates, sand, dead coral or on macroalgae or seagrass.

6.1.8. Standard facies 8

Restricted Platform and Lagoon—Finer-grained sediments winnowed from the reef flats of Standard Facies 6 or 7 are deposited here. These sediments typically contain relatively high percentages of milioline foraminifera, including larger soritids and peneroplids that live on algae, sea grasses or sand-binding algal films. Alveolinids may be present, and tests of smaller rotaliines and juveniles of larger species may be present.

6.2. Depth distribution of selected extant and Tertiary LBF

Fig. 15 shows a depth distribution chart of some extant LBF, summarised from data quoted above, and also from Table 2 (which is a summary of published

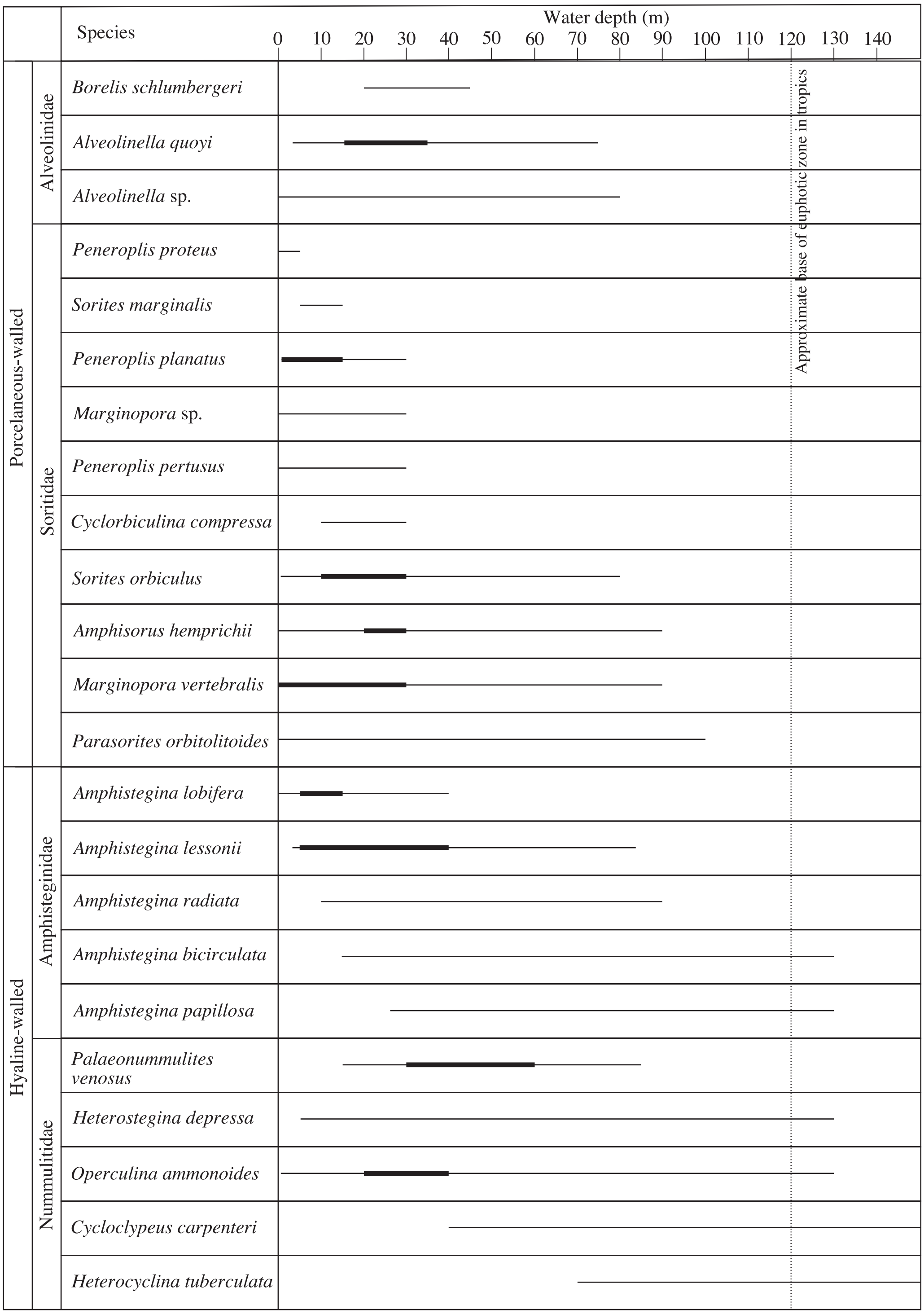

Fig. 15. Depth distribution of selected extant LBF. Thicker lines indicate ‘ideal’ distribution.

Table 2
Distribution data for selected extant larger benthic foraminifera

Species	Depth (m)/environment	Substrate	Location	Reference
Alveolinidae				
Alveolinella quoyi	3–5 m; 'protected' waters	Epibiont on algal-covered rubble	Papua New Guinea	Severin and Lipps (1989)
	20–30 m	Epibiont on stable substrates covered with in organic detritus		
	12–65			Murray (1987)[a]
	Fore-reef		Tropical seas	Ghose (1977)[a]
	Back-reef			Henson (1950), Maiklem (1968), Ghose (1977)[a]
	Shallow shelf		Great Barrier Reef	Maiklem (1968)
	5–75 (MA at 16–33)		West Pacific	Hohenegger (2000)
	3–50	Hard substrates; occasionally on sand	Sesoko Island, Japan	Hohenegger et al. (1999)
	Reef base	Coarse sand	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
Alveolinella sp.	10–80; fore and back-reef		Tropical seas	Hottinger (1973)
	10–80		Tropical seas	Reichel (1964)
	20–80		Sulu Sea	Bandy (1964)
	0–6			Davies (1971)[a]
	Lagoon;< 30		Raroia Atoll	Newell (1956)
	Reefal bars			Hottinger (1973)
	Back-reef shoals	Low/no clastic input		Henson (1950)
	Reef-flat channels		Great Barrier Reef	Maxwell et al. (1961)
		Sand, laterally adjacent to seagrass		Eva (1980), and refs therein
	Upper 40 m of reef slope		Sesoko-Jima, Japan	Hohenegger (1994)
Borelis schlumbergeri	25–35		Gulf of Aqaba, Red Sea	Reiss and Hottinger (1984)
	20–45		Gulf of Aqaba, Israel	Hottinger (1977a)
Soritidae				
Amphisorus hemprichii	Lagoon; also down to 40 seaward of reef		Chagos Archipelago	Murray (1994)
	0–90 (MA at 25–29)		West Pacific	Hohenegger (2000)
	Reef; 10–60	Dark substrates; also on seagrass	R.Sea; E.Africa;S.Pacific	Langer and Hottinger (2000)[a]
		Seagrass	Barbuda, West Indies	Brasier (1975a)
	Reef edge–50 (MA at 20–30)	Not correlated with specific substrate	Sesoko Island, Japan	Hohenegger et al. (1999)
	Front and central reef moat		Sesoko-Jima, Japan	Hohenegger (1994)
	< 35	On *Halophila* leaves and boulders	Gulf of Aqaba, Israel	Hottinger (1977a)
	4	*Halophila* meadow	Gulf of Aqaba, Red Sea	Reiss and Hottinger (1984)
	0–20; high and low energy	Coral rubble	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
Cyclorbiculina compressa	Reef margins; 10–30	Also in shallow seagrass beds	Caribbean	Langer and Hottinger (2000)[a]

Table 2 (*continued*)

Species	Depth (m)/environment	Substrate	Location	Reference
Marginopora spp.		Seagrass	Barbuda, West Indies	Brasier (1975a)
	Common to 30		Sesoko-Jima, Japan	Hohenegger (1994)
	< 90	Gravel to sand-sized substrate	Miyako Islands, Japan	Tsuji (1993)
Marginopora vertebralis	< 30		Oahu, Hawaiian Is.	Hallock (1984)
	Frontal/central reef 'moat'		Sesoko-Jima, Japan	Hohenegger (1994)
Parasorites orbitolitoides	0–100		West Pacific	Hohenegger (2000)
	20–80	Sandy substrates	Sesoko Island, Japan	Hohenegger et al. (1999)
	Reef base; 6–24	Sand	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
Peneroplis pertusus	< 30		Oahu, Hawaiian Is.	Hallock (1984)
Peneroplis planatus	1–5;< 30		Palau, W. Caroline Is.	Hallock (1984)
Peneroplis proteus	< 5		Palau, W. Caroline Is.	Hallock (1984)
Peneroplis spp.		Seagrass	Barbuda, West Indies	Brasier (1975a)
Sorites marginalis	>30		Oahu, Hawaiian Is.	Hallock (1984)
Sorites orbiculus	Lagoon		Chagos Archipelago	Murray (1994)
	1–80 (MA at 16–21)		West Pacific	Hohenegger (2000)
	Upper half of photic zone		Circumtropical	Langer and Hottinger (2000)[a]
	Reef edge–50 (MA at 10–30)	Firm substrate	Sesoko Island, Japan	Hohenegger et al. (1999)
	< 35	Seagrass meadows	Gulf of Aqaba, Israel	Hottinger (1977a)
Sorites spp.		Seagrass	Barbuda, West Indies	Brasier (1975a)
Soritids	Subtidal environments		Sesoko-Jima, Japan	Hohenegger (1994)
Amphisteginidae				
Amphistegina bicirculata	>40		Gulf of Aqaba, Israel	Hansen and Buchardt (1977)
	>15		Oahu, Hawaiian Islands	Hallock (1984)
	$38–100^+$(MA at 75–84)		West Pacific	Hohenegger (2000)
	Open shelf; 80–130	Soft and hard substrates	Gulf of Aqaba, Israel	Hottinger (1977a)
Amphistegina gibbosa	>20	Coarse-grained carbonate sand	Serranilla Bank, Nicaraguan Rise	Triffleman et al. (1991)
Amphistegina lessonii	< 80 (MA< 40)		Gulf of Aqaba, Isreal	Hansen and Buchardt (1977)
	5–20	Algal veneer over rubble	Palau, W. Caroline Is.	Hallock (1984)
	5–15		Oahu, Hawaiian Islands	Hallock (1984)
	3–83 (MA at 15–20)		West Pacific	Hohenegger (2000)
	Reef edge–50 (MA at 20)	Sandy substrate	Sesoko Island, Okinawa, Japan	Hohenegger et al. (1999)
	0–40	No preference	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
	10–20	On lower, shaded side of boulders	Gulf of Aqaba, Israel	Hottinger (1977a)
Amphistegina lobifera	< 40		Gulf of Aqaba, Israel	Hansen and Buchardt (1977)
	1–5	Algal veneer over rubble	Palau, W. Caroline Is.	Hallock (1984)
	0–35 (MA at 0–12)		West Pacific	Hohenegger (2000)
	10–20	On lower, shaded side of boulders	Gulf of Aqaba, Israel	Hottinger (1977a)
	0–12	No preference	SW Sulawesi, Indonesia	Renema and Troelstra (2001)

(*continued on next page*)

Table 2 (*continued*)

Species	Depth (m)/environment	Substrate	Location	Reference
Amphisteginidae				
Amphistegina papillosa	>30; dominant species 60–120		Gulf of Aqaba, Israel	Hansen and Buchardt (1977)
	27–100^{+}(MA at 80–92)		West Pacific	Hohenegger (2000)
	Open shelf; 80–130	Soft and hard substrates	Gulf of Aqaba, Israel	Hottinger (1977a)
Amphistegina radiata	MA at 20–30	Algal veneer over rubble	Palau, W. Caroline Is.	Hallock (1984)
	10–90 (MA at 20–40)	Firm substrates; occasionally on sand	Sesoko Island, Okinawa, Japan	Hohenegger et al. (1999)
	0–33	"Solid", including coral rubble	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
Amphistegina spp.	Open shelf; 60–150	Gravel substrate (< 5% mud)	Miyako Islands, Japan	Tsuji (1993)
	1–120	Soft and hard substrates	Cosmopolitan	Langer and Hottinger (2000)[a]
		Prefers hardgrounds	Sesoko Island, Japan	Hohenegger et al. (1999)
	< 130 (equal to 0.5% SLI)		Gulf of Aqaba, Israel	Hottinger (1983)[a]
Nummulitidae				
Cycloclypeus carpenteri	40–95 (MA at 63–68)		Okinawa, Japan	Hohenegger (2000)
	Below SWB (~ 50); lower limit at ~ 0.4% SLI	Hard substrates	Central Indo–Pacific	Langer and Hottinger (2000)[a]
Cycloclypeus sp.	Open shelf; 60–150	Gravel substrate (5% mud)	Miyako Island, Japan	Tsuji (1993)
	Fore-reef; 50–base of photic zone		Sesoko-Jima, Japan	Hohenegger (1994)
Heterocyclina tuberculata	70–150	Soft substrates with low sedimentation rates	Gulf of Aqaba, Israel	Hottinger (1977a)
	70 to base of photic zone	Soft substrates with low sedimentation rates and hard substrates	Gulf of Aqaba, Israel	Reiss and Hottinger (1984)
Heterostegina depressa	MA at 20–30		Palau, W. Caroline Is.	Hallock (1984)
	< 110; dominant 5–15		Oahu, Hawaiian Islands	Hallock (1984)
	Only nummulitid that inhabits high energy zones			Hallock (1984)
	1–100^{+}; MA at 21–29		Okinawa, Japan	Hohenegger (2000)
	Shallow reef slope to lower photic zone (>90)	Hard substrates; well-shaded shallow water to avoid photoinhibition	Circumtropical	Langer and Hottinger (2000)[a]
	>80	Hard substrates (occasionally sandy)	Sesoko Island, Japan	Hohenegger et al. (1999)
	Reef slope	Hard substrates	Sesoko-Jima, Japan	Hohenegger (1994)
	Within the range 2–70% of SLI; MA at 27 (= 31% SLI)	Firmly attached to hard substrates	Sesoko Island, Japan	Hohenegger et al. (2000)
	0–33; exposed reef slopes	"Solid"	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
	MA at 60–70		Gulf of Aqaba, Israel	Leutenegger (1977b)
	20–130	Hard substrates (base of corals, on boulders or on coarse coral debris)	Gulf of Aqaba, Israel	Hottinger (1977a)

Table 2 (*continued*)

Species	Depth (m)/environment	Substrate	Location	Reference
Nummulitidae				
Operculina ammonoides	>26		Chagos Archipelago	Murray (1994)
	Below wave base	Sandy (occasionally firm) substrates	Okinawa, Japan	Hohenegger (2000)
	< 1 to lower limit of photosynthetic activity (MA at 15–40)	Soft substrates	Indian/Pacific Oceans	Langer and Hottinger (2000)[a]
	20–60 (MA at 30–40)	Prefers sandy substrates; occasionally on coral rubble	Sesoko Island, Japan	Hohenegger et al. (1999)
	Lagoon	Fine-grained substrate	Sesoko Island, Japan	Hohenegger et al. (1999)
	Within 1.5–68% SLI; MA at 14% SLI (45 m in clear water)	Prefers coarse substrate (occasionally on hard substrate)	Sesoko Island, Japan	Hohenegger et al. (2000)
	0–80 (MA at 41)		Okinawa, Japan	Hohenegger (2000)
	20–130	Soft sed., between *Halophila* plants	Gulf of Aqaba, Israel	Hottinger (1977a)
	MA at 80–100		Gulf of Aqaba, Israel	Leutenegger (1977b)
	9–45; reef base	Coarse sand	SW Sulawesi, Indonesia	Renema and Troelstra (2001)
Operculina complata	Deepest photic zone	Sandy substrates	Okinawa, Japan	Hohenegger (2000)
	Within 0.2–12% SLI; MA at 3% SLI (80 m in clear water)	Coarse sands	West Pacific	Hohenegger et al. (2000)
Operculina discoidalis	Medium light conditions–10% SLI		West Pacific	Hohenegger et al. (2000)
Operculina sp.	Low energy areas between islands and reefs	Fine carbonate sand and mud	Miyako Island, Japan	Tsuji (1993)
	Deep water below reef slope	Independent of substrate	Sesoko-Jima, Japan	Hohenegger (1994)
	To 130 (= 0.5% SLI)		Gulf of Aqaba, Israel	Hottinger (1983)[a]
Palaeonummulites venosus		Sandy substrates	Okinawa, Japan	Hohenegger (2000)
	15–85 (MA at 32–52)		Okinawa, Japan	Hohenegger (2000)
	Avoids high energy areas; common in quiet Back- and Fore-reef areas< 85 (MA at 35–40)	Sandy substrates	West Pacific	Langer and Hottinger (2000)[a]
	MA at 50–60		Minna Island, Japan	Hohenegger, pers. comm.
	20–90 (MA at 50)	Sandy substrates	Sesoko Island, Japan	Hohenegger et al. (1999)
	30–60	Sandy substrates	Sesoko-Jima, Japan	Hohenegger (1994)
	Avoids areas of highly mobile sediment; below FWWB; within 2.5–80% SLI	Coarse sand	West Pacific	Hohenegger et al. (2000)
	15–40; reef base	Sandy substrates	SW Sulawesi, Indonesia	Renema and Troelstra (2001)

MA: maximum abundance; SLI: surface light intensity; FWWB: fair weather wave base; SWB: storm wave base.

[a] Not primary data.

water depth, habitat and substrate preferences of selected living larger foraminifera). These depth distributions cannot be used for strictly uniformitarian palaeobathymetric interpretation of Tertiary larger foraminifera because the distribution and faunal associations of LBF have varied with palaeobiogeography and with time. Throughout Tertiary time, three main LBF faunal provinces are recognised within the circumtropical region (Caribbean, Tethyan and Indo–Pacific), each of which included a number of endemic taxa (for details, see Adams, 1967, 1973; Adams et al., 1990). It is difficult to compile a general model for the distribution of LBF along the environmental gradient (coenocline) of Tertiary carbonate platforms due to the complexity of this relationship, and also the possibility, as noted by Buxton and Pedley (1989), that during the Cenozoic, there has been a progressive down-ramp shift of LBF over time, with "novel" genera occupying shallow-water environments. Similarly, Chaproniere (1975) suggested that some nummulitids, such as *Cycloclypeus*, have gradually been forced to occupy deeper water niches with time. Such habitat changes may reflect competitive exclusion by more advanced forms.

Racey (2001) summarised the complex relationships between LBF typical of early Tertiary carbonate platforms, concluding that *Nummulites* occupied a broad range of open-marine environments on both ramps and shelves, and were generally absent from more restricted waters. Large flat *Nummulites* tend to be associated with similarly shaped *Assilina* and *Discocyclina* in relatively deep water environments, whilst smaller, lenticular *Nummulites* occur in shallower, inner ramp/shelf settings, often coexisting with *Alveolina*; "banks" of medium- to large-sized, lenticular- to globular-shaped *Nummulites* tend to occupy intermediate environments.

This broad pattern is also reflected (with minor modifications) in several recent studies of ancient ramps (e.g., Luterbacher, 1998; Sinclair et al., 1998; for details, see Table 3, which summarises published palaeoenvironmental interpretations of *Nummulites* and selected other early Tertiary LBF). The key Eocene and Oligo–Miocene foraminiferal associations identified by these models are summarised for idealised ramp successions in Fig. 16. Variations in the water depth, habitat and substrate preferences of individual species of living LBF described from different localities (see Table 2) indicates that the distribution and associations of larger foraminifera also depend on local factors such as the availability of suitable habitats. As noted by Renema (2002), the absence of a habitat considered typical for a species of LBF causes it to either occupy another habitat, or results in its absence. Similarly, Beavington-Penney (2002) identified local variations in depth distributions of larger foraminifera from the Eocene Seeb Fm. of Oman, where deposition in relatively protected environments resulted in a 'compression' of the coenocline, when compared to more open marine settings. Although the foraminiferal associations remained essentially the same across the ramp, foraminifera from protected marine environments were living in shallower water than those from open-marine, higher-energy settings. For example, whilst large, elongate *Assilina* and *Discocylina* were living in relatively deep water (50–80 m) on more open parts of the ramp (Racey, 1994), biofabrics and association with fauna such as dasycladacean green algae indicate that the same species in more sheltered environments were living in water no deeper than 30 m. Such observations indicate that associations of larger foraminifera from the rock record can only be used as relative palaoebathymetric indicators, rather than as a guide to absolute water depth during deposition.

7. Application of modern ecological studies to the interpretation of fossil foraminifera

Hallock and Glenn (1986) have already demonstrated the successful application of studies of the ecology of living species of LBF to the interpretation of Neogene fossil assemblages, using a Miocene example. Although a strictly uniformitarian approach to the interpretation of older Tertiary populations is inadvisable, broad ecologically controlled trends identified in this review can be selectively used to refine palaeoenvironmental models for Palaeogene rocks containing symbiont-bearing larger foraminifera. The most important of these trends are briefly summarised below, focusing on Eocene *Nummulites*. Whilst, as noted above, the depth distributions of the major groups of living LBF given in Fig. 15 cannot be used as an indicator of actual water depth in the early Tertiary, they can be used as a relative palaeobathymetric guide, allowing water depth and energy

Table 3
Distribution data for *Nummulites* and selected other early Tertiary larger benthic foraminifera

Foraminifera	Age	Location	Interpreted environment	Additional comments	Reference
Nummulites	Early Eocene	Tunisia (El Garia Fm)	Mid ramp, sheet-like, low relief accumulation	Transported *Nummulites*, comprised of two species	Racey (2001)
	Lower Oligocene	Slovenia (Gornji Grad Beds)	Nearshore, high energy environment	Small *Nummulites*, associated with coarse terrigenous material and bioturbation	Nebelsick et al. (2000)
	Eocene	Offshore Libya (Jdeir Fm)	Bank on shelf margin; FWWB to low tide (max. 30 m)		Anketell and Mriheel (2000)
	Palaeogene	Southern Pyrenean foreland basin	Mid ramp	Associated with *Operculina* in bioturbated mudstones	Luterbacher (1998)
	Early Eocene	Tunisia (El Garia Fm)	Low relief bank on ramps between FWWB and SWB (30–60 m); inner ramp shoals		Loucks et al. (1998)
	Eocene	French Alps	Inner ramp shoals (< 5 m water depth); more robust forms in fore–shoal area (< 35 m)		Sinclair et al. (1998)
	Early Eocene	Sierra del Cadí platform, southeastern Pyrenean foreland basin	Inner ramp shoreface and back-barrier environments; mid ramp grainstone shoals and fore-barrier		Gilham and Bristow (1998)
	Late Eocene	Northern Italy	Mid ramp and uppermost outer ramp	Associated with *Assilina*, *Spiroclypeus* and small orthophragminids	Bassi (1998)
	Middle Eocene	Oman (Seeb Fm)	Low amplitude banks; mid ramp	Diverse *Nummulites* assemblage associated with *Assilina*, *Discocyclina* and *Alveolina*	Racey (1994)
	Lower–Middle Eocene	Nafoora oilfield (Sirte Basin, Libya.)	Bank on structurally controlled Amal–Nafoora high	Very shallow supra- to intertidal/ open marine	Belazi (1989)
	Early–Middle Eocene	Southern Tethys	Platform margin		Sartorio and Venturini (1988)
	Middle Eocene			*N. perforatus* group common in sandy, nearshore environments	Herb (1988)

(*continued on next page*)

Table 3 (*continued*)

Foraminifera	Age	Location	Interpreted environment	Additional comments	Reference
Nummulites	Early Eocene	Central Tunisia	Elongate bank in shallow water (mid- to outer-shelf)	Banks resulted from hydrodynamic processes	Moody (1987)
	Ypresian	Offshore Libya (Jdeir Fm)	Bank on structural high		Bernasconi et al. (1987)
	Eocene (Colbàs Fm)	Igualada Basin, Barcelona	Shallow (monospecific) bank to deep shelf	Deep shelf flat *Nummulites* associated with *Discocyclina* and *Operculina*	Serra-Kiel and Reguant (1984)
	Middle Eocene	Egypt (Mokkatam Fm)	Bank on palaeohigh; initiated below SWB, but subsequently built up into much shallower water	Largely monospecific (*N. gizehensis*) para-autochthonous coquinas	Aigner (1983)
	Upper Eocene	Northern Italy	Shoals	Dominated by robust forms	Setiawan (1983)
	Palaeocene	Ras al Hamra, Oman	Reef and Fore-reef; 8–40 m		Rácz (1979)
	Palaeogene	Northeast India	Fore- and Back-reef; shallow water	*Nummulites* from high energy areas are 'stouter' and larger than those from less turbulent water	Ghose (1977)
	Middle Eocene	Verona, Northern Italy	Allochthonous shelf edge banks; shallow (tidal) water	Associated with discocyclinids and red algae (*Lithothamnium*)	Arni and Lanterno (1972)
	Lower Eocene	Sirte Basin, Libya	Shelf margin bank	Largely composed of two species: *N. gizehensis* and *N. perforatus*. More diverse bank-bank assemblage	Arni (1965)
			Back-reef		Phleger (1960)
			Fore-reef shoals		Henson (1950)
Assilina	Late Palaeocene–middle Eocene		Indicative of open marine conditions down to 80 m		Geel (2000)
	Early Eocene	Sierra del Cadí platform, southeastern Pyrenean foreland basin	Back barrier to outer ramp environments		Gilham and Bristow (1998)
	Palaeogene	Southern Pyrenean foreland basin	Outer ramp	Associated with *Discocyclina*	Luterbacher (1998)
	Middle Eocene	Oman (Seeb Fm.)	Outer ramp		Racey (1994)
		Helvetic Nappe, Switzerland		Specimens of *A. exponens* lived in slightly deeper water than *A. spira*	Herb (1988)
	Palaeogene	Northeast India	Fore- and back-reef	Turbid water	Ghose (1977)

Table 3 (*continued*)

Foraminifera	Age	Location	Interpreted environment	Additional comments	Reference
Operculina	Eocene	French Alps	Lower mid ramp; below FWWB		Sinclair et al. (1998)
	Early Eocene	Sierra del Cadí platform, southeastern Pyrenean foreland basin	Back-barrier to outer ramp environments		Gilham and Bristow (1998)
	Lower Eocene	Sirte Basin, Libya	Basin-ward of fore-bank	Soft substrates	Arni (1965)
Rotaliids (undifferentiated)	Late Cretaceous to Recent		Shallow, turbulent water (0–40 m) in the "shorezone" on carbonate sands; also reef and interreef areas	Relates to robust, highly ornamented forms. Symbiont-bearing	Geel (2000)
Discocyclina	Late Palaeocene to late Eocene		Normal marine conditions; occurred in deeper water than *Assilina*, but shallower than *Operculina*	Small specimens also found in near-reef back-reef environments, associated with *Alveolina* and miliolids	Geel (2000)
	Eocene	Offshore Libya (Jdeir Fm)	Forebank	Broken discocyclinids associated with *Assilina* and *Nummulites* fragments	Anketell and Mriheel (2000)
	Early Eocene	Tunisia (El Garia Fm)	Ovate forms found in inner ramp above FWWB; flattened forms occur in mid to outer ramp		Loucks et al. (1998)
	Eocene	French Alps	Generally mid ramp; 'robust' forms in "fore shoal" above FWWB; flattened forms in back-shoal lagoons (5–20 m) and below FWWB		Sinclair et al. (1998)
	Early Eocene	Sierra del Cadí platform, southeastern Pyrenean foreland basin	Outer ramp		Gilham and Bristow (1998)
	Late Eocene	Northern Italy	Largest forms occur in inner and mid ramp		Bassi (1998)
	Middle Eocene	Oman (Seeb Fm.)	Outer ramp		Racey (1994)
	Palaeocene	Ras al Hamra, Oman	Fore-reef; 10–32 m		Rácz (1979)
	Palaeogene	Northeast India	Middle to outer bank; also fore- and back-bank areas near the reef-core	Fore-reef forms are 'stout' and large	Ghose (1977)
			fore-reef		Henson (1950)

(*continued on next page*)

Table 3 (*continued*)

Foraminifera	Age	Location	Interpreted environment	Additional comments	Reference
Orbitolites	Late Palaeocene to late Eocene		"Well-flushed" back-reefs and other carbonate facies free of mud	Closely related to the Recent LBF *Marginopora*	Geel (2000)
	Middle Eocene	Oman (Seeb Fm.)	Shallow inner ramp		Racey (1994)
	Eocene	Catalan Basin	Restricted environments between *Nummulites* banks and the shoreline	Associated with *Alveolina*	Serra-Kiel and Reguant (1984)
	Eocene		Protected areas e.g., back-reef and algal and coral pools on reef flats	Structure/distribution similar to that of modern *Marginopora*	Ghose (1977)
	Eocene			Possibly seagrass-dwelling form	Brasier (1975d)
			Back-reef		Henson (1950)
Alveolina	Mid Cretaceous to Recent		On all substrate types in relatively shallow water (0–75 m)	Symbiont-bearing	Geel (2000)
	Eocene	Offshore Libya (Jdeir Fm)	Back-bank	Associated with *Orbitolites*	Anketell and Mriheel (2000)
	Early Eocene	Sierra del Cadí platform, southeastern Pyrenean foreland basin	Inner ramp, comprised of protected open lagoon, skeletal beach barrier and shoreface	Associated with miliolids and *Orbitolites* (the latter restricted to open, 'clean' water)	Gilham and Bristow (1998)
	Palaeogene	S. Pyrenean foreland basin	Inner ramp	Associated with *Orbitolites*	Luterbacher (1998)
	Middle Eocene	Oman (Seeb Fm.)	Shallow inner ramp		Racey (1994)
	Palaeocene	N.E. Sirte Basin, Libya	Partly restricted inner ramp; land-ward of *Nummulites* accumulation	Associated with miliolids. ?Leeward ramp	Mresah (1993)
	Early–Middle Eocene	Southern Tethys	Inner shallow platform	Landward of *Nummulites* along platform margin	Sartorio and Venturini (1988)
	Palaeocene	Ras al Hamra, Oman	Reef and fore-reef; 8–38 m		Rácz (1979)
	Lower Eocene	Sirte Basin, Libya	Shallow water	Landward of back-bank facies	Arni (1965)
Miliolids	Mesozoic to Recent		Very shallow water, from saline to hypersaline, and also on Fore-reef slopes	Prefers low turbulence and soft substrates. When abundant indicates restricted/lagoonal and /or nutrient-rich back-reefs	Geel (2000) and references therein
			When abundant indicates a connection to the open ocean		Chassefiere et al. (1969)
			Shallow lagoons and Fore-reefs		Schlanger (1963)

FWWB: fair weather wave base; SWB: storm wave base.

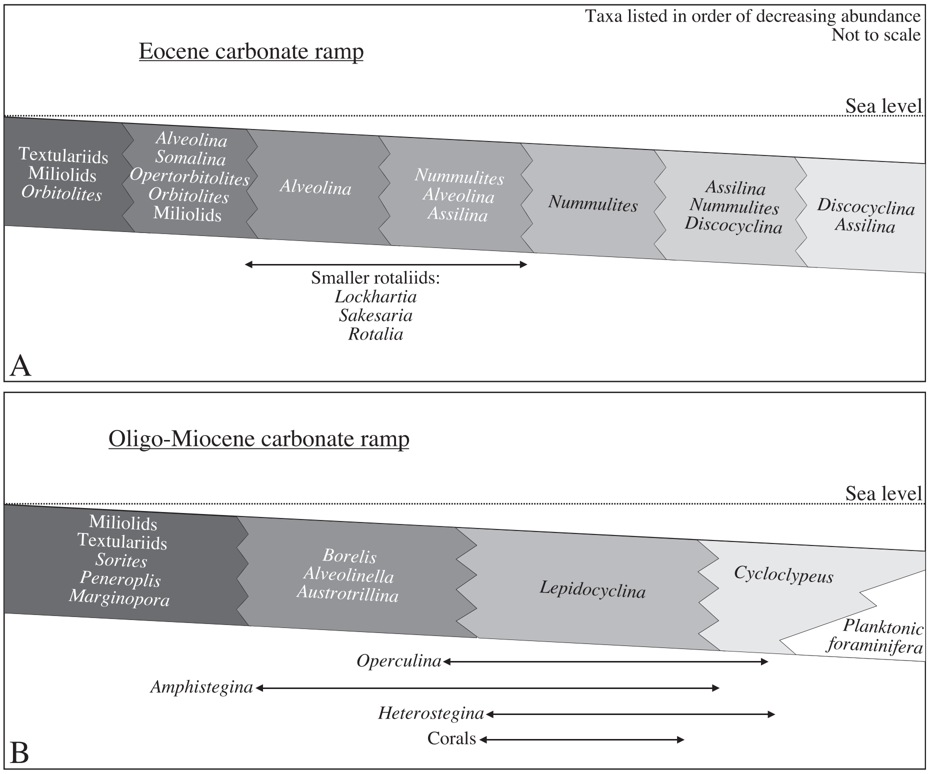

Fig. 16. Summary of the key faunal associations on idealised carbonate ramps during: (A) the Eocene (after Racey, 1994); and (B) the Oligo–Miocene.

comparisons to be made between facies on the basis of LBF content.

7.1. A:B ratio

A-form dominated fossil communities (the result of repeated asexual reproduction) are likely to have formed in the shallowest or deepest parts of the depth range of a particular species (see 'A' and 'C' on Fig. 17). These two environments can be distinguished on the basis of test shape, as discussed below, and analysis of associated biota, matrix and sedimentary structures. The production of solely A-forms can be explained by two conflicting theories: Lipps (1982) suggested that asexual reproduction becomes the dominant method of reproduction when environmental conditions become favourable (usually due to slightly elevated nutrient levels), although Harney et al. (1998) suggest that asexual reproduction is probably used to rapidly increase population density, either after mortality events, or during occupation of marginal habitats or colonisation of new areas.

Sexually produced B-forms are most common in intermediate intervals of a specific depth range (see 'B' on Fig. 17), partly because sexual reproduction is less likely to be successful in shallow, turbulent water, and zygotes are restricted to deeper environments, below fair weather wave base.

It is suggested that identification of A- and B-forms should not be made in the field but should only be based on observation of test structure in thin section, or equatorial section of isolated tests. The ratio of megalospheric to microspheric tests cannot on its own be used to define autochthonous and allochthonous populations of *Nummulites*.

7.2. Test shape

Foraminifera that live in shallow water produce 'robust', ovate tests with thick walls to prevent

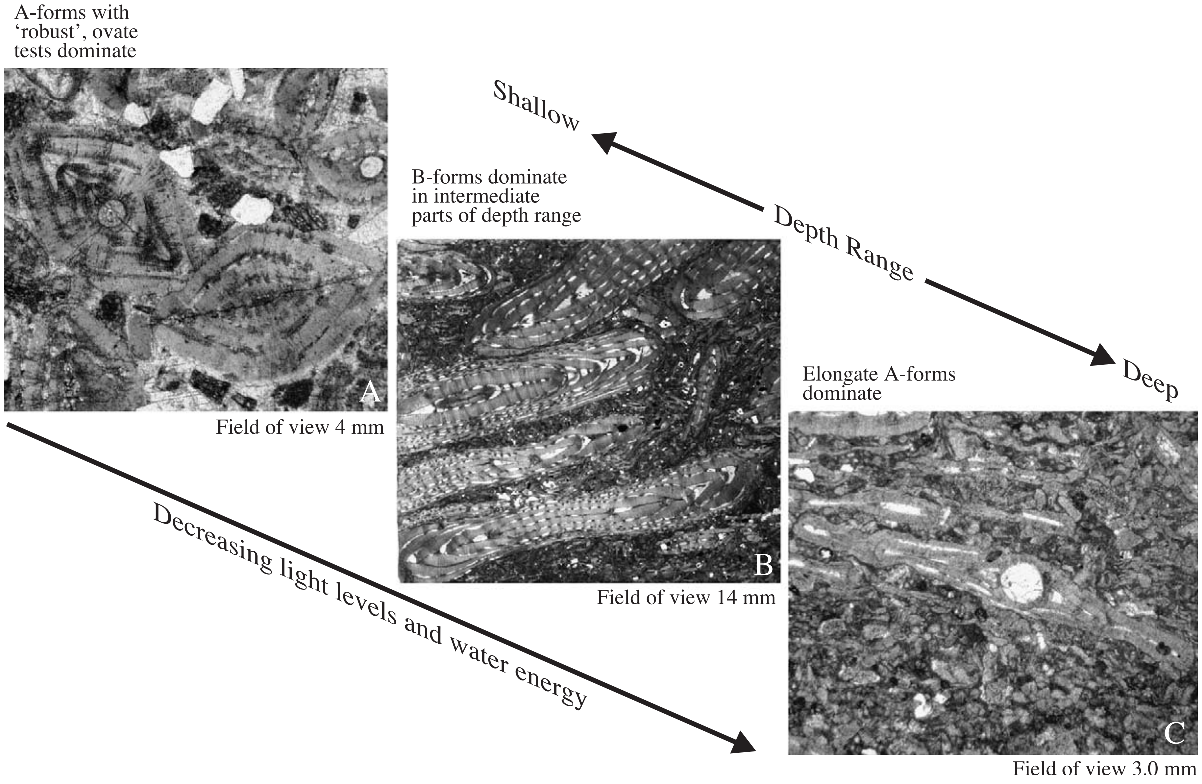

Fig. 17. *Nummulites* from the Eocene El Garia Formation (Tunisia), showing variation in test shape and A:B ratio along the palaeo-environmental gradient. Autochthonous and parautochthonous A-form *Nummulites* deposited in the shallowest and deepest environments show marked variations in average diameter to thickness (*D*/*T*) ratio between different facies. Facies are generally dominated by one species (or two, similarly shaped species), although the dominant species varies between facies. Facies deposited in shallow, wave-influenced environments exhibit A-form *D*/*T* values ranging from 2.44 to 2.84, whilst tests from a facies deposited in much deeper, oligophotic water, have an average *D*/*T* ratio of 7.42 (Beavington-Penney, 2002).

photoinhibition of symbiotic algae within the test in bright sunlight, and/or test damage in turbulent water. Inter- and intraspecific tendency is towards increasing *D*/*T* ratio (i.e., flatter tests) and thinner test walls with increasing water depth (contrast 'A' and 'C' on Fig. 17), reflecting decreased light levels at greater depths (or perhaps poor water transparency in shallow water).

7.3. Test size

An abundance of individuals with small tests may represent a population of 'r-selection' strategists living under favourable environmental conditions, maturing and reproducing early. In environments stressed by low temperatures and light levels, and/or a poor food supply (and other factors), individuals grow more slowly and mature at larger sizes (K-selection). However, unfavourable conditions may also cause 'stunting' of foraminiferal tests and early death, features which may be confused with those typical of more ideal habitats.

An increase in mean test size with depth has been reported in the literature. This may actually reflect the presence of two megalospheric forms: mature gamonts (which should occur in deep water) have larger test sizes than similarly aged, shallow-dwelling schizonts.

As can be seen, palaeoecological analysis of LBF assemblages based solely on modern ecological studies can sometimes produce several possible, often contradictory, interpretations. Rather, such studies should be performed as part of a standard lithofacies analysis, including assessment of foraminiferal taphonomy and biofabric.

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