The relative taxonomic value of morphological characters in the genus *Nummulites* (Foraminiferida)

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ABSTRACT

The main evolutionary trends in the nummulites are briefly summarised and the value of certain morphological characters in species discrimination are summarised. The degree of interdependence of each morphological character on all other characters is assessed and the characters are weighted in order of importance. Environmental and ontogenetic effects on each character are then reviewed and the characters reweighted in order of importance. *J. Micropalaeontol.*, **11** (2): 197-209, December 1992.

INTRODUCTION

The main objectives of this paper are to assess the relative importance of the different taxonomic characters in the genus *Nummulites* (and related forms) and to summarise the ways in which environment may affect morphology in the Foraminifera, paying particular attention to the larger Foraminifera. The work comprises a review of published information, concentrating mainly on the family Nummulitidae, together with the authors own observations on the Late Palaeocene to Early Miocene nummulitid fauna of Oman. Of the seven principal nummulitid genera only *Operculina*, *Heterostegina* and *Cycloclypeus* have extant descendants, *Nummulites* having become extinct in the early Oligocene, *Assilina* in the late Middle Eocene, *Ranikothalia* in the Late Palaeocene and *Spiroclypeus* in the early Miocene.

GLOSSARY OF TERMS

Septal filament.: Extension of a septum over the lateral surface of the test between the spiral laminae.
Septal trace: The surface expression of septum on the outer surface of the test.
Septum : Partitions separating the chambers in each whorl.
Trabeculae : Narrow unperforated strip on the lateral wall of the chamber which represents the surface expression of the sutural canals which extend forwards and backwards from the septum.
Alar Prolongation : A lateral extension of the chamber cavity over the surface of the test.
Marginal Cord : A complex three-dimension meshwork of canals encased in shell material, but open to the outside, which forms the keel of the test and assumes the function of the aperture seen in other genera of foraminifera.
Tripartition : A threefold division of the spire into three distinctive styles of coiling usually "tight" in the early whorls, "loose" in the middle whorls, then "tight" again in the outer whorls.

MORPHOLOGY

Nummulitids are characterised by a flat planispiral coil which is bilaterally symmetrical about the equatorial plane. They all possess a marginal cord with an internal canal system, and numerous equatorial chambers which may be simple (*Nummulites, Assilina, Ranikothalia* and *Operculina*) or divided into chamberlets (*Heterostegina, Spiroclypeus, Cycloclypeus*). Lateral chamberlets are present in *Spiroclypeus*, whilst annular chambers characterise *Cycloclypeus*. Genera with simple chambers are distinguished on the basis of the involuteness/ evoluteness (presence/absence of alar prolongations) of the test, the rate of opening of the spire, the shape of the chambers, the presence/absence of trabeculae and the presence/absence of a coarse canaliculate marginal cord.

Morphological "gradation" has been observed between some of the these genera e.g. *Operculina* and *Heterostegina* (Papp and Kupper, 1954) and *Heterostegina* and *Cycloclypeus* (Tan Sin Hok, 1932) and is discussed at length by these authors and Racey (1988). However, for the purposes of this study it is suffice to note that the development /non-development of alar prolongations can occur without the introduction or loss of any of the small number of structural elements which make-up a nummulitid test, the difference between the genera being relatively "simple" e.g. the presence of annular chambers in a nummulitid implies that such a species belongs to the genus *Cycloclypeus* whilst lateral chambers indicate that a species belongs to the genus *Spiroclypeus*.

The morphology of *Nummulites* is illustrated in Fig. 1. The test shape varies from flat to subglobular, the periphery being sharp to rounded or somewhat undulose. The point most distant from the equatorial plane is described as polar. The test is composed of planispirally coiled chambers, separated by septa. Successive whorls are bounded by a spiral sheet which incorporates the peripheral marginal cord. In axial section, the chambers appear as chevron-shaped cavities separated by successive turns of the spiral sheet. The tapering lateral extensions of these cavities are known as alar prolongations. The initial chamber (proloculus) is spherical,

whilst the second chamber (deuteroconch) is generally kidney shaped, the following chambers may be higher than long, longer than high, or isometric. The spire may be lax (few whorls in a given radius) or tight (many whorls in a given radius). Septal filaments, formed by the extension of the septa over the lateral surfaces of the test between successive spiral sheets, are often visible on the test surface and in oblique thin sections. These may be radial, sigmoidal, meandrine or may branch to form a reticulum. The pattern of pillars/granules is often species diagnostic; they may be arranged on and/or between the septal filaments or over the poles to form polar plugs/pillars. 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. Nummulites possess a canaliculate marginal cord (Fig. 1). Röttger (1984), in a study of the Recent nummulitid *Heterostegina depressa*, demonstrated the importance of this canal system for growth, locomotion, reproduction, excretion and protection. Hottinger (1977a) noted that the nummulitids, unlike most multilocular Foraminifera, rarely have true primary or secondary apertures, a conclusion supported by Rottger (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.

EVOLUTIONARY TRENDS WITHIN THE NUMMULITES: CHANGE IN MORPHOLOGY WITH TIME

GENERAL

Before considering the relative importance of the different morphological characters in nummulite identification it is necessary to identify which evolutionary changes in morphology are currently used in phylogenetic studies.

Hottinger (1981) concluded that larger foraminiferal lineages could only be used to study evolution when :-
(1) Evolutionary trends are unidirectional with time, e.g. the gradual increase in test size of B-Forms and proloculus size in A-forms found within lineages of *Nummulites*.
(2) Trends can be interpreted as being genetically controlled. For example, broken tests of *Nummulites* and living nummulitids such as *Operculina* often regenerate shell material in the damaged area until the original test proportions are reached, i.e. test size/shape are genetically "fixed" time-dependant characters.
(3) Trends can be explained as having a positive selectional value in terms of functional morphology. The trend towards larger flatter test in *Nummulites*, for example, increases the surface area to volume ratio of the test, thus benefitting the algal symbionts, and may be regarded as an adaptation to oligotrophic or low light level conditions.

The most striking feature in the evolution of *Nummulites* is the increase in test size from their initial radiation in the Late Palaeocene to the major extinction of most really large species at the Middle-Upper Eocene boundary. This extinction coincides with the rapid decrease in numbers of many spinose planktonic foraminifera such as *Acarinina, Morozovella* and *Truncorotaloides* (Keller, 1983), and may possibly be related to the decrease in oceanic temperature noted by stable isotope workers (e.g. Shackleton & Kennet 1975). Few species of *Nummulites* survive into the Upper Eocene, and *Nummulites* finally became extinct in the mid-Oligocene. Evolution, from generally highly diversified assemblages of smaller forms in the Lower Eocene to less diverse assemblages of specialized large forms in the Middle Eocene is one of the most striking features in this genus.

All *Nummulites* have a characteristic set of generic characters which are broadly divided into two groups :-
(1) Those which do not change in form or function with time, e.g. the presence of a marginal cord and undivided planispirally arranged chambers.
(2) A set of characters which vary with time and which therefore have a biostratigraphic significance e.g. the increase in test diameter of B-Forms and proloculus diameter of A-Forms. Such quantitative characters are often of taxonomic value, and may change at different rates from one lineage to another (Schaub, 1981).

EVOLUTIONARY TRENDS IN *NUMMULITES*

(a) Test Size

(i) The overall size of B-forms increases with time in most lineages. Size increases in the A-generation are, however, less marked, and this leads to a progressive accentuation of dimorphism with time (Schaub, 1963, 1981; Blondeau, 1972; Herb & Heckel, 1973). *Nummulites* originated in the Late Palaeocene when they were represented by small species (<6mm in diameter), and reached their acme of development in the Middle Eocene, when they attained their maximum size. For example, *Nummulites millecaput* Boubée reached up to 160mm in diameter (Bieda, 1963, p. 191). The overall trend within many of these lineages in the Middle Eocene was towards larger and flatter tests, usually with a greater number of whorls.

This increase in size was accomplished, at least in part, by the introduction of intercalary whorls which produced multiple spires. In Oman this is commonly observed in Middle Eocene species such as *Nummulites perforatus, N. maculatus, N. somaliensis, and N. gizehensis*. Tripartition of the spire in *Nummulites* is often associated with the introduction of intercalary whorls and is best developed in species with thicker tests, such as those of the *N. perforatus* lineage. In some tripartite species the test walls of the outermost whorls are thinner and the marginal cord is lost, e.g. in *N. obtusus* (Racey, 1988, pl. 5.5, fig. 10) and *N. perforatus* (Racey, 1988, pl. 5.5, fig 3). Such thinning is usually accomplished by splitting of the spiral sheet and is best-developed in the most distal walls on either side of the equatorial plane. In *N. maculatus, N. gizehensis* and *N. somaliensis* the whorl laminae thin markedly away from the marginal cord towards the poles in axial section (Racey, 1988, pl. 5.4, fig. 17; pl. 5.5, fig. 21), forming a series of narrow, elongated, rectangular cavities between these thin walls. Samanta (1981b) suggests that such cavities in *N. maculatus* could have housed algal symbionts, as suggested by Haynes
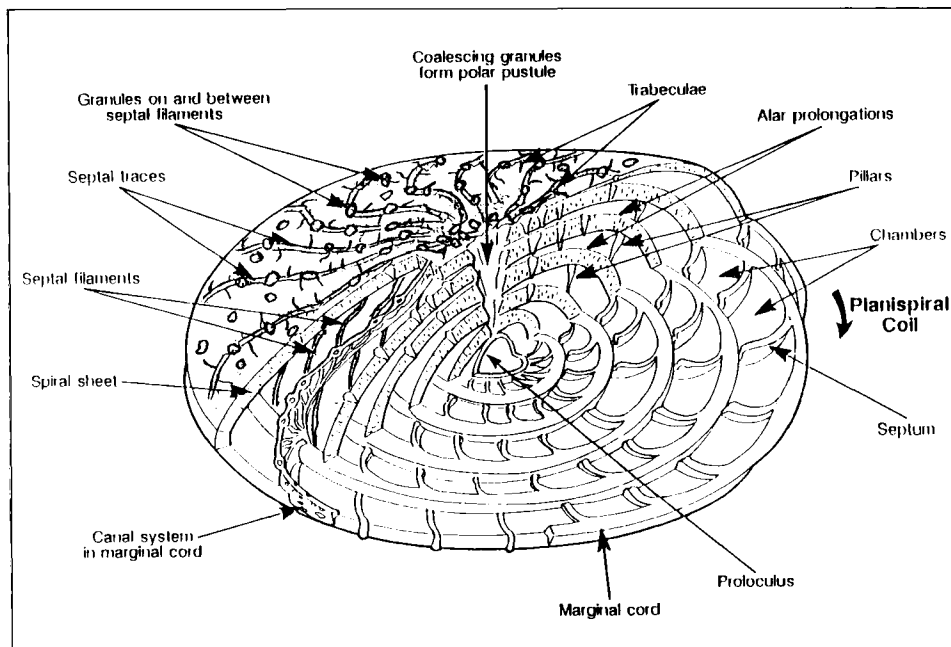
Fig. 1. Test structure of *Nummulites*, megalospheric form (modified from Carpenter 1850, Golev 1961 and Barrett 1974)

(1965) for other members of the Rotalidae. In large B-Forms such as *N. maculatus* and *N. gizehensis* the spiral laminae on each side of the test are modified to form long narrow, elongated cavities separated by thin walls (Racey, 1988, pl. 5.4, fig. 17; pl. 5.3, fig. 4). Such modifications also produce flatter tests. These "lateral chamberlets" are similar to those noted in *Lepidocyclina* which have been interpreted as "algal culture vessels" (Lee *et al.* 1979).

If the development of large complex tests was related to an increased need for algal symbionts, then the end-Middle Eocene extinction may have been due to the extinction of such symbionts (Samanta, 1981b). If large species were so highly specialized that most of their energy requirements had to be obtained through algal symbiosis, possibly under oligotrophic conditions (Hallock, 1985), they would have been poorly adapted to survive the extinction of their symbionts.

(ii) The increase in test size of A-Forms with time is much less marked, with test diameters rarely exceeding 8mm. The introduction of intercalary whorls is very rare and has not been noted in any of the Omani material. The author knows of only a single published record of intercalary whorls in an A-Form (*N. millecaput* figured by Bieda (1963; pl. 10, fig. 1). However, Bieda's plate shows no obvious thinning of the spiral laminae with the introduction of the intercalary whorl, nor does it show the complex meandriform septal filaments which are common in the B-Form.

(b) Proloculus Size in A-Forms
Many authors (e.g. Schaub, 1963, 1981; Blondeau, 1972 and Samanta, 1981a) have stated that one of the most noticeable evolutionary trends in *Nummulites* is the increase in proloculus size with time. Proloculus diameters increase from approximately 0.1mm in the Upper Palaeocene to a maximum of

about 1mm in the later part of the Middle Eocene, i.e. when the B-Forms reach their maximum test diameters. Dimorphism is therefore most marked in late Middle Eocene species making it difficult to pair A- and B- forms of the same species. Such trends only hold for species within a single lineage. Large proloculus sizes (>0.5mm in diameter) are, however, mostly restricted to Middle Eocene species. However, small proloculus sizes do not necessarily indicate the presence of primitive (older) species as was observed within the Seeb Limestone at Wadi Rusayl, Oman where unreworked, very small "primitive" *Nummulites minutus* (test diameter = 0.85 - 1.30mm; proloculus diameter = 0.075 - 0.090mm, see Racey 1988 and 1992 for description) were found with the larger, "more evolved" Middle Eocene species *N. obesus* (test diameter = 3.77 - 6.43mm; proloculus diameter = 0.36 - 0.80mm). If, however, only *N. minutus nov. sp.* were present, the sample would probably have been dated as Upper Palaeocene on the basis of test and proloculus size.

Hottinger (1977b) has suggested that proloculus size increases with time because it reflects the volume of a young specimen's protoplasm. This in turn affects the size of its pseudopods and therefore determines the growth rate (Hottinger, 1977b, fig. 23). The largest proloculus sizes are therefore almost invariably found in species which have large B-Forms. However, Hallock (1985) has demonstrated that for such semiperalous organisms with life spans limited to one year, e.g. Recent *Amphistegina*, the disadvantages of reduced fecundity outweigh the advantages of slightly increased embryon sizes. Consequently only very large megalospheres are advantageous. This may explain why an increase in proloculus size is not consistently observed in all larger foraminiferal lineages.

(c) Septal Filaments
Septal filaments show an increase in complexity with time and can broadly be divided into three groups; simple, meandriform and reticulate. Simple radiating (striate), falciform, or curved septal filaments predominate in Upper Palaeocene to Lower Eocene species (though they are also present in later species); meandriform and complex branching septal filaments are most common in Middle Eocene species and reticulate septal filaments are common in the Upper Eocene *N. fabianii* and attain their acme of development in the Oligocene *N. fichteli* group.

(d) Ornament (pillars and granules)
Schaub (1981) suggests that within certain lineages the amount of ornamentation increases with time, for example, in the *N.*
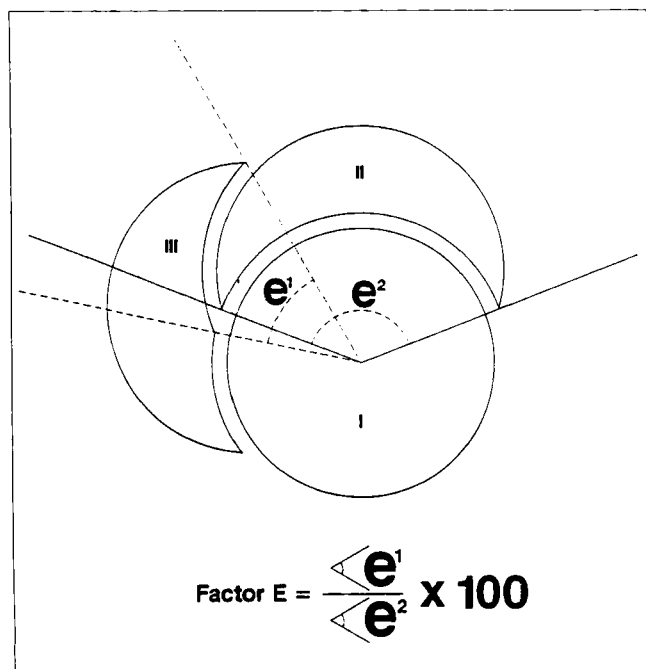
$$\text{Factor E} = \frac{\widehat{e^1}}{\widehat{e^2}} \times 100$$

Fig. 2. Method of calculation of Factor E (after Van der Vlerk & Bannink 1969)

burdigalensis and *N. partschi* groups. However, although early species within these two groups have few pillars, younger species often exhibit a wide range of variation in ornament within single assemblages.

(e) Embryonic Chambers
Various biometric methods for studying the embryonic development of larger foraminifera have been proposed of which one, the Factor E method of Van der Vlerk & Bannink (1969) is herein applied for the first time to *Nummulites* (see Fig. 2 for method of calculation). Van der Vlerk & Bannink (1969) tried to determine the age of *Operculina* - bearing rocks by measuring the degree of enclosure of the second chamber by the third and quantifying this as "Factor E". They studied a number of Eocene to Recent species of *Operculina* from Indonesia and noted a marked increase in the value of Factor E with time. However, they did not mention which species were measured and it is unlikely that the specimens studied were from the same lineage, though this is known to be important. Whittaker & Hodgkinson (1979) tested this method using *Operculina ammonoides* and *O. bartschi* from the Togopi Formation (Pliocene to Pleistocene), Sabah, Malaysia. They demonstrated that *O. ammonoides* yielded Factor E values indicative of an Late Pliocene age, whilst *O. bartschi* gave an Early Miocene age. They also examined *Operculina heberti* from the Palaeocene of France which gave an "Oligocene" date; *Operculinella* from the Middle Miocene gave a fairly accurate result whilst Recent *Operculina ammonoides* gave values slightly higher than those of Van der Vlerk & Bannink's Recent species. The species studied did not, however, belong to the same lineage.

In the writer's opinion, the value of Factor E as an indicator of age has not yet been assessed properly, since none of the studies mentioned above involved successive species from well-known and well-dated lineages. However, any change in Factor E with time, should be more easily recognisable, and therefore of greater stratigraphic value, if measured within a single lineage, since such changes would, theoretically at least, be more uniform. Recent work on the genus *Nummulites*, especially that of Schaub (1981), has led to a better understanding of nummulite phylogeny and to the improved definition and dating of several nummulite lineages. Consequently, it was decided to test the Factor E hypothesis by using two well-known nummulite lineages (*N. fichteli* and *N. perforatus*) from Oman. Additional data were obtained by measuring some of Schaub's (1981) figures and plates in order to give a broader data-base and wider geographical coverage. Trends in Factor E values are notably different for these two lineages and the results are outlined briefly below:-

N. fichteli **lineage**
(i) *N. ptukhiani* from the Upper Lutetian. Factor E=16.42-25.76. Mean =18.4. Nine measured specimens.
(ii) *N. fabianii* from the Upper Eocene. Factor E=17.21-28.3.3 Mean=23.22. Fifteen measured specimens.
(iii)*N. fichteli* from the Lower Oligocene. Factor E=31.06-42.31. Mean=37.14. Fifteen measured specimens.

N. perforatus **lineage**
(i) *N. campesinus* from the Upper Ypresian. Factor E=17-29.61. Mean=22.69. Ten measured specimens.
(ii) *N. obesus* from the Lower Lutetian. Factor E=24.47-48.75. Mean=36.34. Fifteen measured specimens.
(iii)*N. beneharnensis* from the lower part of the Middle Lutetian. Factor E=10.7-23.8. Mean=22.6. Eight measured specimens.
(iv)*N. deshayesi* from the upper part of the Middle Lutetian to Upper Lutetian. Factor E=18.17-37.12. Mean=31. Eight measured specimens.
(v) *N. perforatus* from the Upper Lutetian. Factor E=27.66-41.71. Mean=33.71. Fifteen measured specimens.
The *N. fichteli* lineage showed an increase in Factor E from 18.4 for Biarritzian species (*N. ptukhiani*), to 23.2 for the Upper Eocene *N. fabianii* to 37.4 for *N. fichteli* in the Lower Oligocene. However, the *N. perforatus* lineage showed an initial increase from 22.7 for Upper Ypresian-basal Lutetian *N. campesinus* to 36.3 for basal to Lower Lutetian *N. obesus*. Thereafter values for Middle and Upper Lutetian forms show a slight drop for *N. beneharnensis* (22.6), and followed by an increase from 31-34 for *N. deshayesi* and *N. perforatus*.

Although Factor E for *Nummulites* has not been used previously to date sequences it seems to show distinct changes within individual nummulite lineages. However, the nummulite lineages studied above did not show the same trend, and at present it is not possible to suggest why this should be the case.

Mechanism of Evolutionary Change
The geographic dispersal of a new species is usually too rapid for detection with the resolution currently provided by the biostratigraphic time scale. The limitation of this resolving power may explain why punctuated evolution appears within a lineage showing continuous, gradual changes. Within

the nummulitids phyletic gradualism predominates, whilst "punctuations" may be due to imperfections of the geological record. The gradualistic trends are often due to gradual modifications of existing characters such as the increase in test size of B-Forms and proloculus size of A-Forms in successive species of the *N. perforatus* lineage. Punctuations occur at the beginning of lineages and are due to the introduction of characters which show no gradation between ancestor and descendant, i.e. the species does or does not have a new character.

For the genus *Nummulites* the principal evolutionary changes are therefore an increase in test size of B-forms, (with an associated increase in the number of whorls) an increase in proloculus size of A-forms and an increase in complexity of septal filaments in both A & B forms. In general it has been these gradual changes that have been used to subdivide the genus.

RELATIVE TAXONOMIC VALUE OF MORPHOLOGICAL CHARACTERS

Gradual morphological changes have often been used to delineate evolutionary lineages within the genus *Nummulites*, and have enabled workers to recognise more nominal species than in any other larger foraminiferal genus. This has occurred because authors have failed to assess the relative values of characters used to distinguish species. Neither Blondeau (1972) nor Schaub (1981) in their monographic works on *Nummulites* (and *Assilina*) sought to rank characters in order of taxonomic importance, possibly because they did not think it necessary but more probably because morphological characters used for species discrimination are to some extent interdependent, and most characters may be influenced by environmental factors.

INTERDEPENDENCE OF MORPHOLOGICAL CHARACTERS

It has become apparent to the writer that many characters (e.g. spire regularity and chamber shape) mentioned in species descriptions are to a greater or lesser extent interdependent. This fact may possibly be generally understood, but is usually ignored. It is also known, for example, that test size is influenced by environmental factors such as temperature, water depth and substrate (see below). The principal characters used for species discrimination in *Nummulites* are weighted (Fig. 3) in order of taxonomic importance according to the degree of interdependence. The taxonomic value of a character is thought to be inversely proportional to the number of characters affecting its development. Test shape, being influenced by six other factors, is thus considered less important than regularity of spiral growth which is affected by only two. The presence or absence of characters such as pillars and granules, tripartition and doubling of the spire, are recorded and are especially valuable because they are not present in all species. If environmental influences are set aside, the morphological characters of specific value can be arranged in the following theoretical order of importance:-

(1) Proloculus size and proloculus shape in the megalospheric generation.

(2) Marginal cord and canal system, trabeculae.
(3) Regularity/irregularity of spire, tripartition of spire, pillars/granules.
(4) Alar prolongations, septa, chambers, tightness/looseness of spire.
(5) Septal filaments/traces, doubling of spire, reversals.
(6) Test shape.
(7) Test size.

The environmental and genetic factors affecting this ranking are outlined below and briefly summarised in Fig. 4, and in the light of these considerations, the characters are reweighted.

ENVIRONMENTAL AND ONTOGENETIC EFFECTS ON MORPHOLOGICAL CHARACTERS
(1) Test Size

Ross (1972, 1975) has observed that *Marginopora vertebralis* on the Great Barrier Reef reaches reproductive maturity after about two years in shallow water (8-10m), where it attains diameters of 13-15mm. In deeper water (25-30m) it grows more slowly, reaching a larger size (22mm) before reproduction, suggesting a less optimal environment. Consequently, it may be concluded that for this larger foraminifer test size is related to water depth and temperature. Reiss & Hottinger (1984) have noted that *Heterostegina depressa* and *Operculina ammonoides* in the Red Sea (see (2) below) vary in shape but not in size with increasing water depth. Water temperature within the depth range of these foraminifera was observed to be relatively constant in the area studied. Their results suggest that the variation observed in the test shape of these two species is unlikely to be temperature controlled. Hallock & Glenn (1986) noted that under favourable conditions, larger foraminifera mature rapidly and reproduce at relatively small adult sizes, whereas under unfavourable conditions (low light, low temperature) they grow more slowly thus maturing and reproducing at larger sizes. This phenomenon was also observed by Bradshaw (1957) in his study of the smaller benthic species *Streblus beccarii tepida*. Hallock & Glenn (1986) also conclude that if conditions are marginal for growth, but outside the range of tolerance for reproduction, growth continues until giant individuals are produced. This often occurs when living shallow-dwelling (<20m) individuals are washed into deeper (50-100m) environments (Ross, 1972; Hallock, 1986).

Changes in substrate, often related to changes in water depth, have also been thought to cause variation in the size of fossil forms. Pomerol (1961) noted that the size of *N.laevigatus* was inversely proportional to the clay content of the surrounding sediment. Similarly, Nemkov (1962) concluded that nummulites were larger in shallow water calcareous and sandy deposits than in deeper water clayey sediments. Herb and Heckel (1973), in a study of *N. fabiani* (A-forms), concluded that they were usually larger in marly silts than in other sediments. However, none of these authors indicated whether their studies were based on specimens at a similar ontogenetic stage, and none considered the possible effects of winnowing and sorting.

Variation in size has been found to be greater in

MORPHOLOGICAL CHARACTER		A DEPENDENT UPON	B PRESENCE OR ABSENCE	C WEIGHTING
1. TEST SIZE		5, 6, 7, 9, 10, 11 & 12		7
2. TEST SHAPE		4, 5, 6, 7, 10 & 11		6
3. SEPTAL FILAMENTS/TRACES		4, 5, 6, 10(f) & 12		5
4. PILLARS/GRANULES		3 & 7	YES	2
5. CHAMBERS	(a) SHAPE	2, 6, & 10		3
	(b) SIZE	2, 6 & 10		3
	(c) NUMBER	2, 6 & 10		3
6. SEPTA	(a) SHAPE	2, 5 & 10		3
	(b) NUMBER	2, 5 &10		3
7. MARGINAL CORD		4		1
8. PROLOCULUS SIZE				0
9. PROLOCULUS SHAPE				0
10. SPIRE	(a) REGULAR	5 & 6		2
	(b) IRREGULAR	5 & 6		2
	(c) TIGHT	1, 5 & 6		3
	(d) LOOSE	1, 5 & 6		3
	(e) TRIPARTITION	5 & 6	YES	2
	(f) DOUBLING	1, 2, 5, 6 & 7	YES	5
	(g) REVERSALS	1, 2, 5, 6 & 7	YES	5
11. ALAR PROLONGATIONS		2, 5 & 7		3
12. TRABECULAE		3		1

Fig.3. Relative taxonomic importance of characters according to their degree of interdependence. Column A lists those characters upon which each character is dependent, for example the alar prolongations (character 11) are dependent on test shape (character 2), Chambers (character 5) and the marginal cord (character 7). Column B lists those characters which can be present or absent. Column C weights the morphological characters on the basis of their degree of interdependence with respect to all other characters. For example test size is dependent on 7 other characters (Column A) and hence has a weighting of 7 whilst proloculus size is not dependent on any of the other morphological characters and thus has a weighting of zero. Theoretically the lower the weighting the more potentially useful the character in species discrimination.

megalospheric than microspheric forms. For example, in *N. gizehensis* A-forms from a single bed in Oman, test diameters varied from 3.67mm to 6.41mm and thicknesses from 1.6mm to 3.75mm (Racey, 1988). Such ranges encompass those of a number of species of similar age and test size and is not, therefore, considered to be a generally reliable character for species discrimination, at least not for species of similar age. It is, however, sufficiently variable within the genus to be of value for the discrimination of some species, for example, a small primitive Upper Palaeocene species e.g. *N. deserti* could readily be distinguished from a much larger, more evolved, Middle Eocene species e.g. *N. gizehensis* on size alone. Lanterno & Roveda (1957) examined variation in diameter to thickness ratio in three groups of nummulites; *N. ramondiformis*, *N. boucheri* and *N. vascus*. They concluded that the diameter to thickness ratio showed distinct clusters for the three B-forms. However, the values for the A-forms showed complete intergradation.

It is concluded that test size is affected by temperature, water depth and substrate. Variation in megalospheric

forms is greater than in microspheric forms. Test size is, therefore, not considered a reliable character for species discrimination.

(2) Test Shape

Reiss *et al.* (1977) have shown that in *Operculina ammonoides* and *Heterostegina depressa* (extant nummulitids) from the Red Sea, involute, thick tests are commonest in shallow waters, and evolute, thin tests in deeper waters. Larsen (1976) noted a similar trend for Recent *Amphistegina* from the Gulf of Elat, Red Sea. Furthermore, Hallock (1986) observed that test shape in *Amphistegina gibbosa* and *A. lessoni* grown in culture was affected by light flux and water motion. She demonstrated that these factors influenced the deposition of secondary lamellae in the test wall, noting that increased light saturation and water motion produced a thicker wall and therefore a thicker test. However, she also noticed that although water motion increased the test thickness (through increased calcification) it retarded the overall growth rate. Slower growth was also observed by Röttger (1976) in *Heterostegina depressa* under

MORPHOLOGICAL CHARACTER	INTERDEPENDENCE RATING	PRESENCE/ABSENCE IMPORTANT	ONTOGENIC VARIATION	ENVIRONMENTAL INFLUENCE Recent	INFLUENCE Fossil	OTHER
TEST SIZE	7		YES	Depth, Temp, Nutrients, Substrate	Substrate, ? Depth	Increases with time
TEST SHAPE	6		YES	Water energy, Depth, Light	Substrate, Water Energy, ? Depth	
PILLARS AND GRANULES	3	YES	YES	Depth, Substrate, ? Light		
SEPTAL FILAMENTS/TRACES	5		YES		? Substrate	More complicated with time
CHAMBERS	4		YES	Food, Temp.		
SEPTA	4		YES	Food, Temp., Depth		
MARGINAL CORD	2		YES		Substrate	
PROLOCULUS SIZE	1		NO	Depth, Food, Temp, Salinity ?Water, Energy		Increases with time
PROLOCULUS SHAPE	1		NO			
SPIRE REGULARITY	3		YES		? Substrate	
SPIRE LAXITY	5		YES	Depth	Substrate, Food	Possibly related to reproduction
DOUBLING	5	YES	YES		Food	
SPIRE REVERSALS	5	YES	YES		Food	
TRIPARTITION	3	YES	YES		Food	
ALAR PROLONGATIONS	4		YES			
TRABECULAE	2		NO			

Fig. 4. Environmental and ontogenic influences on morphological characters. For the method of derivation of the interdependence rating see Fig. 3 caption.

conditions of increased water motion. Hallock & Hansen (1986) concluded that thin tests represented quiet, low light saturation environments whereas thick tests were indicative of higher energy, higher light saturation, shallower environments. Other studies (Hansen & Buchardt, 1977; Larsen & Drooger 1977; Hallock & Hansen 1979) of Recent symbiont-bearing species have also indicated that test morphology changes with habitat depth.

Environmentally controlled variation in test shape has also been reported for fossil species. Flatter nummulites were observed by Veillon & Vigneux (1960) in calcareous-sandy sediments, while lenticular forms were most commonly found in marly-calcareous strata and globular forms in marly-sandy deposits. However, the definitions of the these sediment types and test shapes were poor. Nemkov (1962) concluded that nummulites in more calcareous deposits were larger and flatter than those found in sandy sediments, a conclusion not in agreement with that of Veillon & Vigneux (1960). In a study of *N. fabiani* (A-forms), Herb & Heckel (1973) recorded a three-fold division of test shapes, possibly related to substrate, noting that thin, flat forms occurred in siltstones, thick lenticular forms in limestones and intermediate forms in marly siltstones. In the Gulf of Aqaba, Red Sea, Reiss & Hottinger (1984) observed that although the extant nummulitids, *Operculina ammonoides* and *Heterostegina depressa*, occupy the same depth zone (20-130m) they are separated by the characters of their preferred substrate. The former lives on soft sediment between *Halophila* plants where water energy is low, whereas the latter lives on a firm substrate at the base of corals, on boulders or on coarse coral debris where water energy is higher. Gary & Healy-Williams (1986), in a study of morphological variability in Recent *Bolivina albatrossi* from the Gulf of Mexico, noted distinct changes in test form (spindle-shaped to triangular), and related this to dissolved oxygen content.

That environmental factors affect test morphology is evident from the material collected in Oman. The microspheric forms of *N. gizehensis* and *N.perforatus* develop more rounded peripheries in high energy grainstones, but are thinner and possess more angular peripheries in low energy wackestones. Serra-Kiel & Reguant (1983) stated that B-forms of *N. perforatus* have more whorls and become more spherical in higher energy environments and Haynes (1965) commented that shape should be a useful indicator of environments if, in symbiont-bearing taxa, it is controlled by hydrodynamic factors and the metabolic needs of the symbiotic relationship. This possibility is discussed again below. Test shape is not, however, controlled solely by environmental factors since it may also vary with the stage of ontogenetic development. Juvenile B-forms of *N. obtusus* and *N. perforatus* form Oman have biconvex tests with angular peripheries, whereas adults have plano-convex to concavo-convex tests with well-rounded peripheries.

It is concluded that test shape is affected by water movement, light intensity, temperature, water depth and substrate. It is not therefore considered a reliable species-diagnostic character.

(3) Ornament
(a) Septal Filaments/Filament Traces
Little has been published on variation in septal filaments with respect to environmental changes. Herb & Heckel (1973) in

their study of *N. fabiani* A-forms, concluded that forms from silty sediments exhibited a greater degree of reticulation than those from limestones. Septal filaments are known to vary during ontogeny. For example, in *N. gizehensis* they are initially simple and radiate, but in later whorls they become more complex, i.e. meandriform. In *N. fichteli* they are initially simple, radiating around a single polar pustule, developing later into a complex reticulate network. It is concluded that septal filaments may be affected by substrate (carbonate content) and that they reflect stages of ontogenetic development.

(b) Granules/Pillars
External characters have often been used for the discrimination of new species and varieties. Some authors, for example Schaub (1963, 1981), have used the arrangement of pillars/granules to define groups of nummulites. Ornament can, however, vary in strength, position, and number of granules/pillars within a single population, especially among A-forms, though it cannot at present be positively correlated with changes in environment. Freudenthal (1969), in a study of Neogene *Heterostegina* from Crete, noted that external ornament and test shape could often be correlated with substrate type and were therefore unreliable for the discrimination of species within this genus. He observed that specimens collected from limestones and sandy limestones were thick and had smooth or very lightly granulated surfaces whereas those from sandstones were distinctly granulated. Individuals from argillaceous sediments were the thinnest and most strongly granulated.

Reiss & Hottinger (1984) noted that the evolute, flat *Operculina ammonoides* (living below 60m depth in the Gulf of Aqaba) is characterised by single or multiple interseptal "pillars" which reach the shell surface to form "bumps", whereas involute forms from shallower water coral and sand substrates are smooth. They interpreted these pillars as "lenses" for collecting the reduced light at these depths, thus allowing the algal symbionts to continue photosynthesising. However, pillars in species which live in shallower water could equally well be simple strengthening devices for adaptation to higher energy environments. Moreover, pillars and granules may change in strength and number during ontogeny. For example, in the A-form of *N.obtusus*, juveniles have well-developed pustules whereas adults are non-granulate (see Samanta 1981a). Reiss (1963) stated that the continuity of inflational pillars over chamber sutures, often emphasised by various authors, is due simply to lamellar superposition and represent no special feature. He further notes that the same is true of inflational pillars which are "weaker" on ontogenetically later chambers, an observation made previously by others (e.g. Pokorny, 1958) and believed to represent a gerontic character. Such pillars may have acted as light-collecting lenses for juvenile forms living in deeper water, which later migrated into shallower water where the light flux was sufficient to sustain algal symbiosis without the need for "lenses" (Hottinger, 1977b). There is, however, no direct evidence for such migrations nor is there any evidence from the pillar composition and structure to suggest that such pillars could function as lenses. In *Nummulites discorbinus*, for example, the polar pillar visible on

the test surface of some juvenile B-forms may be obscured by the later spiral laminae of the adults, in others it is absent altogether. This feature is therefore not always species-diagnostic. Studies of ornament in other genera have also revealed changes associated with environment. For example, Lutze (1964), in a study of Recent *Bolivina argentea*, noted that the length of the basal spine, length of the costae and the width/length ratio of the test increased gradually from basin to slope environments. He concluded that no new species should be erected unless material from more than one locality ("environment") was available, and attempts had been made to find transitional forms from different biotopes Gary & Healy-Williams (1986) noted a gradual reduction in the coarseness of surface sculpture, and an increase in spine density with increasing water depth, for Recent *Bolivina subspinescens* and *Uvigerina peregrina*.

It is concluded that pillars/granules are affected by water depth, substrate, light intensity and stage of ontogenetic development. They are therefore not considered to be reliable species-diagnostic characters.

(4) Spire

Veillon and Vigneux (1960) concluded that nummulites with looser spires (and flatter tests) were commonest in calcareous sands, whereas those with compact spires (and globular tests) are most common in marly sands. Said (1950) suggested that the tightening of the outer whorls to form a tripartite spire in *N. gizehensis* may be a seasonal feature caused by a limited food supply during winter months. This hypothesis was based on the work of Myers (1943) who observed that Recent Pacific larger foraminifera (including *Operculina*) added lower and longer chambers during seasons of limited food supply, thus forming a tighter spire compared with those added when food was abundant. Hottinger (1977b), in a study of Recent *Operculina ammonoides* from the Red Sea, observed that involute, thick forms with a narrow growth spiral occupied shallower water than evolute thin forms with a broader growth spiral which tend to occur in deeper water.

Roveda (1970) noted that some species of *Nummulites* have been erected mainly on the character of the spire. Arni (1967) based several new varieties on the basis of differences in the spiral diagram. Arni observed that the adult coiling curves often formed an elongated "s", and interpreted the moderately curved end portion as representing a declining growth rate. The steep middle portion was considered to represent the main phase of shell growth. He (Arni) argued that growth in this middle portion of the test may have been accelerated by the introduction of intercalary whorls, often causing variation in chamber shape and number of chambers per whorl. Arni postulated that agamont multiplication occurred during the growth of this middle portion of the spire when the nummulite was at its "strongest" (suggested by the occurrence of intercalary whorls) the implication being that intercalary whorls allow a rapid increase in size, and in conjunction with the tightness/looseness of coiling may control the size required for reproduction. He suggested that the moderate curvature of the end portion of the spire (declining growth rate) may be due to the loss of protoplasm and nutrients during reproduction. However, Röttger's laboratory experiments have shown that once reproduction begins, growth of the individual ceases, and that afterwards "death" occurs. Roveda (1970) has suggested that spiral growth may be controlled by ecological factors, citing Myers' (1943) observations (outlined previously) for Recent *Operculina* in support of this conclusion. He also suggested that "oversplitting" of *Nummulites* may be caused by over-emphasis of the species-diagnostic value of chamber size, shape and number, all of which affect the form of the spire. Herb & Heckel (1973), in a study of the megalospheric generation of *N. fabianii*, concluded that the spire was looser than normal in siltstones, tighter in limestones and normal (i.e. relatively loose) in marly siltstones. However, in the associated B-forms they observed no significant changes in the spire from one lithology to another, though they did record a wide range of variation. In a study of Upper Eocene and Lower Oligocene nummulites from north-west Europe, Drooger *et. al* (1971) noted that A-forms increased the diameter of the first two whorls and the number of chambers in them with time, and concluded that this permitted the recognition of species within an evolutionary series.

In a recent study of *Heterostegina depressa* from Ontong, Java, Hughes (1985) showed that the diameter of the first whorl appeared to decrease slightly from 275-450 microns at 31m, to 277-400 microns at 38m depth. A similar trend has been recorded for the same species in the Gulf of Aqaba, Red Sea (Reiss & Hottinger, 1984). Schaub (1962, 1963, 1966, 1981) has demonstrated a gradual differentiation of the microspheric spire of *Nummulites* into three well-defined sections (tripartition) in several lineages, within the Eocene. He considers this to be one of the most important evolutionary trends within *Nummulites*, and concludes that the middle portion of the spire shows features characteristic of the species, whereas the inner part is more conservative and shows ancestral characters of value for determining phylogeny. He also observes that the outer portion of the spire increases in width, at the expense of the middle part, during evolution, and attains its maximum in the youngest representative of the lineage. This phenomenon has been observed in B-forms of the *N. perforatus* and *N. gizehensis* lineages (Racey, 1988) in Oman. Associated A-forms often show a wider range of spiral variation (Racey, 1988). Hottinger (1977b) commented that intraspecific variation in nummulitid growth is greatest in the outermost whorls.

It is concluded that the spire is affected by substrate and food supply, though such affects have been demonstrated only for microspheric forms. Test thickening through the production of many closely appressed whorls, (seen in B-forms of the *N. perforatus* group from Oman (Racey, 1988) and Spain (Serra-Kiel & Reguant, 1984), may be related to increased water energy. Abnormalities in the spire (possibly caused by environmental influences) are common and can therefore be eliminated as species-diagnostic. The character of the spire (especially in the early and middle whorls) is usually constant and is considered to be a feature of diagnostic importance.

(5) Septa and Chambers

Myers (1943), in his study of Recent *Operculina* from the Pacific and *Elphidium crispum* from the English Channel, noted that

short, narrow chambers were added during periods of limited food supply. Bradshaw (1957), whilst experimenting on growth rates in the extant smaller benthic foraminifer, *Streblus beccarii tepida*, observed that specimens living at higher temperatures (>30° C) tended to add smaller chambers than those kept at lower temperatures and to produce misshapen tests with chambers of different sizes. He noticed that reproduction in specimens kept under unfavourable conditions produced larger individuals with a greater number of chambers than those which reproduced under favourable conditions. However, his specimens were collected initially from temperate waters around the U.K. The behaviour of such a temperate water species when kept at high temperature may not be a guide to the behaviour of warm-water species normally adapted to temperatures of 25-30°C. Gary & Healy-Williams (1986) noted changes in chamber shape in Recent *Uvigerina peregrina* and *Bolivia subspinescens* which showed a strong correlation with the dissolved oxygen depth profile. They also observed a linear reduction in chamber lobation in *Bolivina albatrossi* with increasing water depth. In a study of *Heterostegina depressa* from the Gulf of Aqaba, Red Sea, Fermont (1977) showed that the average number of operculine chambers is inversely proportional to depth (14-15 at 28m, 12-13 at 38m and 10-11 at 68m). Specimens grown in laboratory cultures tended to have 10-20 operculine chambers. In the Oman material, chamber shape and size were found to be relatively constant and although variation was seen, e.g. in *N. perforatus*, this tended to occur at specific points in the spire and could often be related to ontogeny. For example, in B-forms of *N. beneharnensis* the initial chambers are isometric, representing the shape seen in adult forms of the ancestral nummulite, but becoming two to three times longer than high in the outer whorls. Variation in chamber shape and size often occurs in the middle part of the spire where it is related, especially in the larger species, to the introduction of intercalary whorls, e.g. *N. gizehensis* and *N. perforatus*.

It is concluded that septa and chambers are affected by food availability and temperature. They are, however, reliable taxonomic features, variations from the norm (usually associated with abnormalities of the spire) being easily recognised.

(6) Proloculus

Although often regarded as an essential character for species discrimination, variation in proloculus size in single assemblages has rarely been studied. Khan & Drooger (1970 in a study of various nummulites A-forms only) from the Lower Eocene of Gan, northern Pyrenees, noted that the diameters given by Schaub (1966) did not truly reflect the range of variation. They concluded that either many unnamed species were present or that proloculus size was variable. Later work on Upper Eocene to Lower Oligocene radiate nummulites from northwest Europe led Drooger *et al.* (1971) to conclude that megalosphere size was highly variable (30-250 microns). Since an increase in megalosphere size with time is considered to be an important evolutionary trend, such a wide range of values may be thought to be surprising; indeed *N. fraasi* had already attained megalosphere diameters of 100-120 microns by the Late Palaeocene. However, *N. minutus*, a new Middle Eocene species from Oman (Racey, 1988; 1992) has a far smaller proloculus (0.05-0.07) than any previously recorded, i.e. approximately half the size of any published species description. Adams (pers. comm.) has observed a new species of *Nummulites* with similar proloculus dimensions to *N. minutus* from an Early Palaeogene sequence in India.

Studies of the proloculus size in *N. gizehensis* (A-forms) from a single Oman sample show a marked size variation (0.66 - 1.25mm), a phenomenon also noted by Schaub (1981) in an Egyptian population of the same species. Mean values in successive assemblages do, however, show a general increase in size with time, as noted by Drooger *et al.* (1971) and inferred by Schaub (1981). Drooger *et al.* (1971) showed that the diameter of the megalosphere was independent of the diameter of the microspheric form. Serra-Keil & Reguant (1984) concluded that megalosphere size does not vary significantly between populations of the same species from different lithologies, a conclusion partially supported by studies of species from Oman. However, in the Oman material, megalosphere size was found to be fairly variable in some populations and more uniform in others, irrespective of lithology.

Studies of the Recent nummulitid *Operculina ammonoides* from the Red Sea (Reiss & Hottinger, 1984) have shown a wide variation in megalosphere size (25-125 microns), and these authors have concluded that the frequency distribution of megalosphere diameter from all depths is bimodal for evolute and unimodal for involute forms. Hughes (1985), in a study of Recent *Heterostegina depressa* from Ontong, Java, noted proloculus diameters of 37-75 microns at 31m depth and 30-75 microns at 38m depth. However, specimens of the same species from the Red Sea have far larger proloculi at similar depths, 79.9 - 169.9 microns at 28m depth and 79.9-199.9 microns at 68m depth. In a study of Recent *Elphidium crispum* from the English Channel, Myers (1943) reported that the diameter of the megalosphere from tidal pools varied from 28-73 mircons. Reiss & Hottinger (1984) have suggested that variations in megalosphere size reflect different initial volumes of protoplasm in juveniles and that this depends on the ratio of the total volume of protoplasm in the parent shell to the number of offspring produced during asexual reproduction. They concluded that the final volume of the protoplasmic mass in the parent generation may be related to the rate of food uptake which, in turn, is dependent on food production and population density (=food availability) and to metabolic rates. Nigam and Rao (1987) have shown that in *Cavarotalia annectens* from the west coast of India, proloculus size is inversely proportional to temperature (range studied = 27.5-29.25°C) and to salinity (range studied = 37.7-36 p.p.t.). Fermont (1977) noted a tendency towards increased proloculus size with depth in Recent *Operculina ammonoides* from the Red Sea, and also in the Eocene *Discocyclina varians* group from Ein Advat, Israel; a similar depth related morphocline has been suggested for *Miogypsina* species (Drooger and Raju, 1973).

Hallock (1985) has suggested a possible mechanism for variation in proloculus size based upon dependence on algal symbionts. She argued that if juveniles receive more protoplasm and symbionts from the parent, they will remain

small for only a short period, thus increasing their chances of survival. However, she does not explain why species with small proluculi do not become extinct. Water motion and light decrease with depth; and although water motion is highly variable (changing daily, seasonally etc.) light levels are relatively constant and are therefore predictable, providing that water clarity does not change. She further argued that relatively higher fecundity would produce young with a small proloculus size, thus increasing their chances of survival under highly variable conditions. The production of young with larger embryons would be more likely in stable, low-light conditions. However, Röttger *et al.* (1987) have proposed an alternative hypothesis based on observations of Recent *Heterostegina depressa* from Hawaii. Their laboratory observations suggest that two megalospheric forms are distinguishable; one reproducing asexually and the other sexually. They noted that the asexually reproducing form was reproductively isolated from that reproducing sexually and that it therefore constituted a separate apogamic species. The asexually reproducing form was observed to be predominant in shallow water and to decrease in numbers with increasing depth. The sexually reproducing form increased in numbers with depth. This mixture of two megalospheric types could explain the depth-related cline in mean proloculus size noted by Fermont (1977).

Zohary *et al.* (1980) noted that asexual reproduction cycles for Recent shallow-dwelling *Amphisorus* and *Sorites* were synchronous and closely linked with the seasonal cycle. They observed that a population of *Amphisorus hemprichii* would consist one year of large numbers of megalospheric individuals with comparatively small proloculi and few microspheric forms; the following year the population would comprise only megalospheric forms with large proloculi. As there was no evidence for the migration of microspheric forms out of the system, Leutenegger (1977) suggested that this cycle should be interpreted as being paratrimorphic and co-ordinated with the seasonal cycle over two successive years. If the co-ordination with the seasonally cycle becomes weaker or lost in deeper water (a conclusion supported by Leutenegger's (1977) in-situ observations) then the mixture of megalospheric schizonts and gamonts in a population will change. Consequently changes in proloculus size observed along the depth gradient (Fermont, 1977) may reflect changes in the co-ordination of reproduction cycles with the seasonal cycle. Such a model can however, only be tested by sampling populations over a long time interval, using techniques which avoid the effects of mixing by bioturbation and take into account the patchy distribution of living populations. However, in fossil larger foraminifera it is not possible to find evidence of depth-related intraspecific morphoclines attributable to different types of reproduction, as postulated above.

It is concluded that proloculus size can be affected by temperature, water depth and food supply. Variation is marked and this character is therefore considered to be unreliable, when used in isolation, for species differentiation.

(7) Marginal Cord
Few data are available concerning the relationship (if any) between marginal cord development and environmental fac-

tors. Herb & Heckel (1973), in a study of *N. fabiani* (B-forms), concluded that individuals from carbonate-rich environments had relatively thick marginal cords. Serra-Keil & Reguant (1984) correlated marginal cord development in *N. perforatus* with changes in lithology. However, other nummulitids such as *R. nuttalli* and *O. canalifera* have thick marginal cords, yet occur in limestones with perfectly ordinary species of *Nummulites* in Oman. Marginal cord development cannot, therefore, be easily correlated with carbonate content.

SUMMARY
All morphological characters, save proloculus size and shape, can vary during the course of ontogeny. Such changes are often well-documented (Schaub, 1981) and should not pose major problems for species discrimination. Environmental influences on morphological characters appear, however, to be complex, while genetic controls are insufficiently known (save for variation in proloculus size) to be considered further here, although they are undoubtably important. Although test size, test shape, ornament and proloculus size show marked intraspecific variation they help to identify the groups to which species belong.

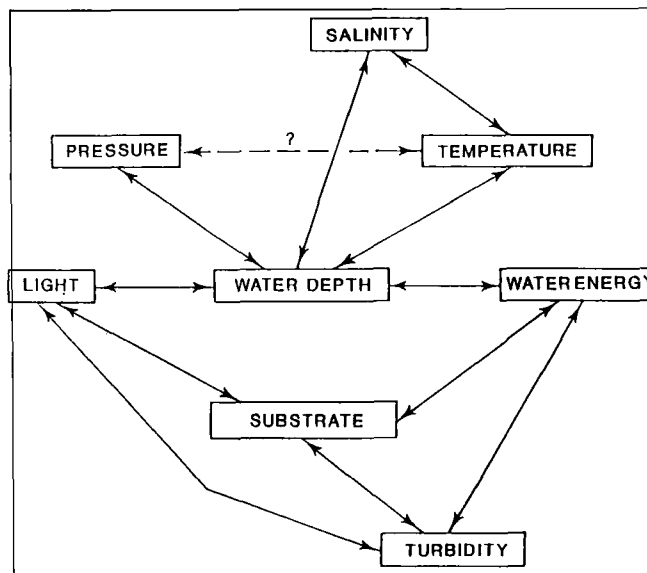From the above conclusions it is evident that morphological

Fig. 5. Interaction of environmental influences

characters are affected to varying degrees by environmental factors. The main problem for the palaeontologist is, however, to assess the relative effects of the various environmental factors on different morphological characters, i.e. in quantifying changes in morphology and determining which environmental influences are most important. Such assessments are difficult because of the interactions between the environmental controls outlined in Fig. 5. Thus, for example, if we conclude that substrate affects a certain morphological character, then we must also consider factors such as water depth, water energy, light intensity and water turbidity which all affect the substrate type.

Having discussed how morphological characters may be affected by environmental and ontogenic factors (summarised in Fig. 3 & 4) - they are reweighted in order of importance below :-

(a) Shape and form of the septa and chambers

(b) Form of the spire (including presence/absences of doubling, tripartition and or reversals in coiling direction).

(c) Thickness of the marginal cord (including the spiral sheet).

(d) Proloculus size in the megalospheric generation.

(e) Test size and shape.

(f) Septal filaments/filament traces.

(g) Presence/absence and position of pillars/granules.

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