Chapter 4
Morphology, Taxonomy and Concepts of Species

4.1 Introduction

The living world displays an amazing range of variation in morphology. The variation is the result of ontogenetic differences (due to age), genetic differences (due to pressure of selection and mutation) and non-genetic differences (due to ecology) among organisms. Fossils show an even higher degree of morphologic variation due to the dimension of time through which the life evolved. The preservation potential of the organism, post-mortem transport, time averaging of assemblages and compaction of sediments are additional factors that introduce morphologic diversity into fossil populations. One cannot predict the amount of variation in a population, but a biologist or paleontologist specializing in a group of organisms gets accustomed to the amount of variation typical of populations within that group and can isolate the unusual variations. Morphology is an essential trait in the classification of the living world. The biological system of classification is referred to as *natural classification*, in which all features are considered for general resemblance rather than particular differences. A biologist or paleontologist classifies the organisms and names them (taxonomy), then determines their evolutionary relationships (phylogeny) and geographic relationships (biogeography). The sciences of taxonomy, phylogeny and biogeography together constitute Systematics. This chapter discusses the method for describing morphology, distinguishing microfossils and inferring phylogenetic relationships through cladistic analysis.

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4.2 Quantifying Morphology

Morphology is key to the identification and classification of fossils. Traditionally, morphologic description of fossils has been qualitative to semi-quantitative. Different dimensions of the skeletal elements are measured (as variables) and expressed as statistical parameters of range, mean and variance. Shape of the forms is often expressed as ratios of variables. Good progress has been made over the years in making morphology quantitative so that the taxonomy of fossils is practiced as a rigorous science. Microfossils are particularly amenable to statistical analysis of morphology due to the easy availability of a statistically significant number of well-preserved specimens, compared with fragmentary data in other groups of fossils. The application of quantitative morphology is established well beyond taxonomy to functional morphology and evolution. Due to enhanced computational facilities, quantitative analysis of morphology is becoming routine in taxonomy. The statistical techniques are based on certain assumptions and the users should know if the data to be analysed is suitable for a particular analysis. Some of the methods, for example, require normal distribution and multivariate normality of the data. In using these methods, data is tested for normality and the variables are suitably transformed prior to analysis. The textbooks listed at the end of the chapter discuss the basics of statistics, the assumptions involved and applications of multivariate statistical methods in paleontology.

There are several methods for quantifying morphology, and the choice of method depends on the purpose of the analysis. In most applications, the length, width and height of the shells and dimensions of the chambers are measured and the obtained data is analysed through univariate and multivariate procedures of statistics. Qualitative and multi-state characters can also be treated statistically. Shape is analysed by digitizing the outline of the shells and the coordinates of the equally spaced points are fitted to a Fourier series (see Boon et al. 1982, for stepwise computation, and Muthukrishnan and Saraswati 2001, for application in foraminiferal taxonomy). These two groups of methods are also referred to as conventional morphometrics to differentiate them from the later-developed geometric morphometrics. Geometric morphometrics has gained importance since Bookstein (1991) first presented the methodology and application of this new tool in morphometrics to compare biological shapes. It statistically analyses the coordinates of a set of homologous *landmarks* on the shell. A landmark is a diagnostic point on the shell, for example, an aperture or proloculus in foraminifera. The coordinates of the set of standardized landmarks constitute the Bookstein coordinates of the shape, and these are subjected to multivariate analysis to get information about the shape and shape change.

The measurement of microfossils can be carried out under a stereozoom binocular microscope by micrometre scale or by image analysis software. The preparation of specimens for measurement may be time-consuming. In larger foraminifera, for

example, oriented sections are carefully prepared to reveal the internal morphologic details for measurement. The effort, however, is worth taking, considering the quality of information achieved by morphometric analysis. Nowadays, X-ray tomography by micro-CT is enabling three-dimensional measurements of shell morphology without elaborate sample preparation or destruction of the shell (Briguglio et al. 2013).

Theoretical morphology is another way of looking at the shape of the biological forms. It models biological shape to relate form with function. Raup (1966) pioneered this study and constructed a cubic morphospace to represent morphologic variations in mollusks and brachiopods. Theoretical morphology models the existent forms with minimal mathematical complexity by taking a minimum number of parameters. It tries to explain why, in a range of forms produced theoretically, some forms exist in nature while others do not and have never been produced. The analysis is a three-step process:

1. The construction of a theoretical morphospace of hypothetical yet potentially existent morphologies.
2. The examination of the distribution of existent forms in the morphospace to determine which forms are common, rare or non-existent in nature.
3. The functional analysis of both existent and non-existent forms to determine whether the distribution of existent forms is, indeed, of adaptive significance.

Berger (1969) was the first to create a two-dimensional morphospace for planispiral and trochospiral foraminifera, although he did not elaborate the adaptive significance of the generated shapes. Since then, theoretical morphology has received much attention in explaining the functional significance of the gross morphology of foraminiferal shells. Signes et al. (1993) mathematically modelled the growth of planktic foraminifera by establishing four parameters (Box 4.1). They investigated how surface area and shell volume change with growth. Among the four parameters considered in the model, only the proportionality between the consecutive chamber volumes (Kt) is found to influence the values of surface area and volume. It is also noted that both surface area and shell volume change exponentially with size. These observations have important consequences for physiology and the functional requirement of foraminifera because:

1. The increase in outer surface area and consequent increase in porosity may govern the maximal rate of gas exchange, and thus relate to rate of respiration.
2. Shell volume is related to biomass and, therefore, to the amount of oxygen and prey (nutrition) needed.
3. The ratio of total surface area to shell volume is related to the total calcification effort per unit of biomass (energy required for calcification).

The mathematical modelling of shell morphology has given new insights into the growth of shells modulated by the physiological requirements of foraminifera (see Brasier 1982, Renzi 1988 for more examples).

Box 4.1: Mathematical Modelling of Growth of Planktic Foraminifera

Signes et al. (1993) modelled the growth of planktic foraminifera by way of the following four parameters (see Fig. 4.1 for explanation). A number of growth pattern and possible shapes of the shells can be generated through various combinations of these parameters. The functional significance of the generated shapes is discussed in the text.

1. Kt = ratio of chamber volume to the volume of the pre-existing shell ($CVn + 1/SVn$).
2. φ = angle between consecutive chambers (2π/no. of chambers per whorl).
3. Ky = displacement of the chambers along the axis of coiling [$(Yn+1 - Yn)/(Xn+1-Xn)$].
4. D = distance of the centre of the chamber to the axis of coiling divided by the radius of the chamber (Xn/Rn).

Shapes generated at different values of Ky are shown in Fig. 4.1. The side views are shown on the left and the frontal views are on the right. The shell is planispiral at $Ky = 0$ (A); trochospiral at $Ky = 1$ (B); and high trochospiral at $Ky = 2$ (C).

The opening of the umbilicus is achieved by changing the parameter D (Fig. 4.1). The upper row shows spiral views and the lower row shows umbilical views generated at D = 0.8 (A, D), D = 1 (B, E) and D = 1.2 (C, F).

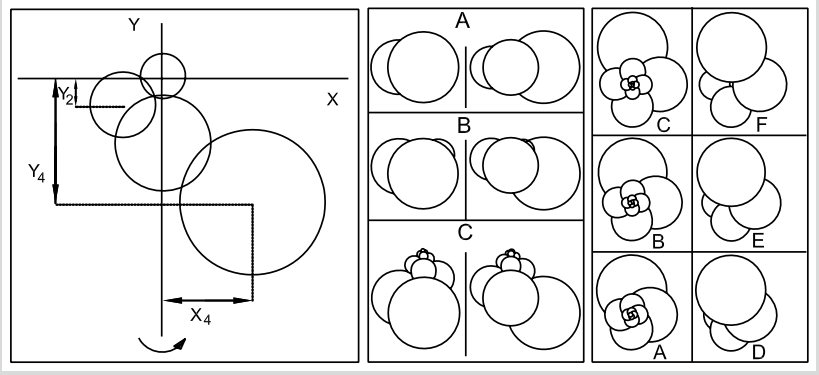

Fig. 4.1 Theoretically simulated growth of planktic foraminifera: the parameters used to generate the shapes (*left*) and shapes generated at different values of *Ky* (*middle*) and *D* (*right*) (redrawn after Signes et al. 1993, with permission © the Paleontological Society)

4.3 Taxonomy

The classification and nomenclature of lifeforms constitute taxonomy. Until the 1970s, most paleontologists were *evolutionary taxonomists*. These classical taxonomists used a traditional and flexible combination of criteria to erect a hierarchical classification. Morphological resemblance and phylogenetic relationships were the basis of classification. The order of succession in the rock record and geographical distribution played important parts in establishing phylogenetic relationships. Some taxonomists criticized this method for its uncertainties and subjectivity. A school of *numerical taxonomists* tried to avoid subjectivity by following a quantified phenetic similarity for natural groupings. The basic premises of numerical taxonomy are as follows (Sneath and Sokal 1973):

1. The greater the content of information in the taxa of a classification and the more characters on which it is based, the better a given classification will be.
2. A priori, every character is of equal weight in creating natural taxa.
3. Overall similarity between any two entities is a function of their individual similarities in each of the many characters through which they are being compared.
4. Taxonomy is viewed and practiced as an empirical science.
5. Classifications are based on phenetic similarity.

A large number of characters are chosen in numerical taxonomic classification. The data may be both qualitative and quantitative. The first step in the classification is to estimate similarity among the taxonomic units by calculating the similarity coefficient or distance coefficient. In the next step, the similarity (or distance) matrix is subjected to cluster analysis for hierarchical arrangement of the taxa in the form of a phenogram (Box 4.2). The numerical taxonomy has proven useful in many cases, but subjectivity could not be eliminated because there are a number of algorithms for computing resemblance and there are a number of procedures of cluster analysis. The hierarchical structure of the resulting phenogram can change markedly by altering the procedure.

The biological classification is hierarchic in nature and all natural groups of about the same status are given rank names. Linnaeus was the first to provide a comprehensive scheme, and the rank names used in biological taxonomy derive mainly from him. Linnaeus recognized five ranks, but many additional ranks have come into use over the years. The following example shows the classification of a benthic foraminifer *Nummulites acutus*:

Phylum: Protista Haeckel, 1866.
Class: Rhizopodea von Siebold, 1845.
Order: Foraminiferida Eichwald, 1830.
Suborder: Rotaliina Delage and Herouard, 1896.
Super-family: Nummulitacea de Blainville, 1827.
Family: Nummulitidae de Blainville, 1827.
Genus: *Nummulites* Lamarck, 1801.
Species: *Nummulites acutus* (Sowerby), 1840.

Box 4.2: Numerical Taxonomy

There have been differences of opinion on the validity of two subgenera of *Lepidocyclina*, *L.* (*Eulepidina*) and *L.* (*Nephrolepidina*). Numerical taxonomic analysis was carried out on the population of *Lepidocyclina* to see if the two taxa are statistically valid. A number of variables were measured on the embryonic apparatus of the genus in equatorial sections (Fig. 4.2). Based on this, several parameters were calculated (refer to Saraswati 1995 for details on the calculation of these parameters). In all, seven parameters were used in analysis; their statistical summary is given in Table 4.1. For numerical taxonomic analysis, taxonomic resemblance is estimated by the Euclidean distance coefficient as follows:

$$d_{ij} = \sqrt{\frac{\sum_{k=1}^{m}\left(X_{ik} - X_{jk}\right)^2}{m}}.$$

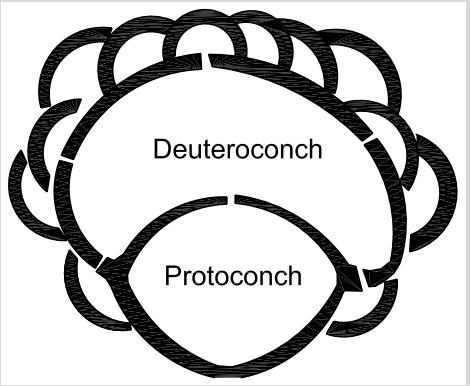

Fig. 4.2 Embryonic apparatus of *Lepidocyclina*

Table 4.1 Morphometric parameters of two subgenera of *Lepidocyclina* used for statistical analysis

Subgenera		D_I (μm)	D_{II} (μm)	A (%)	X	E (%)	Y	Dc (%)
Eulepidina	Max	1330	1760	86	2.0	100	1.1	127
	Min	480	830	53	1.3	25	0.8	20
	Av	773	1204	73	1.6	82	1.0	78
	SD	181	226	11	0.2	26	0.1	28
Nephrolepidina	Max	400	660	57	2.3	90	1.5	60
	Min	120	200	32	1.2	19	0.8	15
	Av	235	347	42	1.5	34	1.0	27
	SD	72	102	07	0.2	16	0.2	11

(continued)

Box 4.2 (continued)

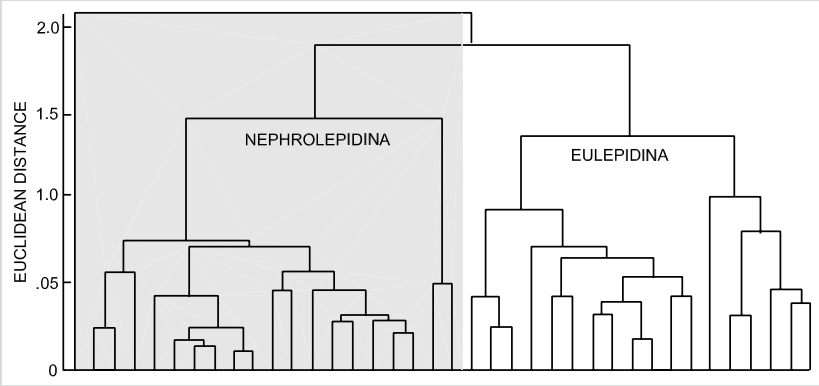

Fig. 4.3 Phenogram illustrating two clusters of taxa corresponding to *Eulepidina* and *Nephrolepidina*

The data matrix of the Euclidean distance coefficient is subjected to cluster analysis. The resulting phenogram (Fig. 4.3) clearly distinguishes two groups. Except for one specimen, all the specimens clustered in two groups correspond to the conventionally identified subgenera.

A classification not only provides information about the morphological attributes of the organism but also reflects its evolutionary relationship with other organisms. There are procedures and rules for the naming of species and the formation of taxonomic categories recommended by the International Code of Zoological Nomenclature (ICZN). While reporting a new species, the researcher should follow the guidelines of the ICZN. In recent years, an important initiative in the field of taxonomy has been taken to prepare global databases of fossil occurrences. The database serves two important purposes. It brings consistency to taxonomy by making the morphological and stratigraphic details of species easily accessible to all and it provides data for addressing large-scale processes in the evolution of life. Some of the databases of particular interest to micropaleontology are discussed later (Sect. 4.6).

4.4 Cladistic Analysis

Both biologists and paleontologists aim to establish the evolutionary or genealogical relationship (phylogeny) of organisms. Biologists use DNA and other molecular data to reconstruct phylogeny. Paleontologists use morphology and the temporal position of the taxa in the geological record to infer ancestral descendant relationships and visually represent them through an *evolutionary tree*. In 1966, a German

entomologist, Willi Hennig, proposed cladistic analysis to reconstruct phylogeny based on "shared evolutionary novelties" (or "shared derived characters") and portrayed it through a branching tree called a *cladogram*. Conceptually, cladistics is different from phenetics (or numerical taxonomy). It postulates that classification should only reflect evolutionary history and ignore overall phenetic similarity. Cladistic analysis soon found wide application in paleontology. The central concept of cladistic analysis is that, in any group of organisms, characters are either primitive (plesiomorphy) or derived (apomorphy). Closely related groups have "shared derived characters", called synapomorphies (see Box. 4.3 for terminology).

Box 4.3: The Terminology of Cladistics

Plesiomorphy: a primitive character.
Apomorphy: an advanced or derived character.
Autapomorphy: a derived character shared by a single group.
Synapomorphy: a derived character that is shared by two groups.
Symplesiomorphy: a shared primitive character.
Monophyletic groups contain the common ancestor and all of its descendants (D, C, B and A in Fig. 4.4).
Paraphyletic groups are descended from a common ancestor but do not include all descendants (B and C, Fig. 4.4).
Polyphyletic groups are the result of convergent evolution. Their representatives are descended from different ancestors, and hence, although they may look superficially similar, any polyphyletic group comprising them is artificial (Fig. 4.4).

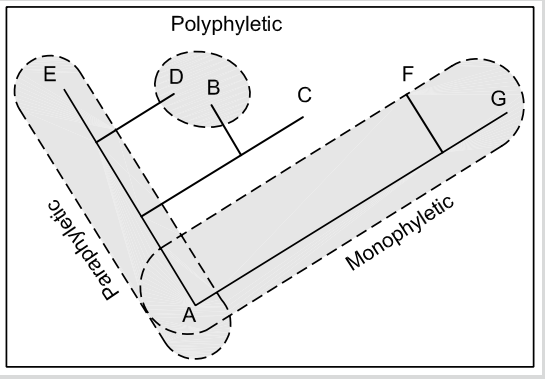

Fig. 4.4 A cladogram illustrating the different groups of taxa in cladistic analysis

Cladistic analysis begins with construction of a "character matrix", in which rows consist of taxa and columns of characters. The character states in the matrix are generally represented by 0 (for absence) and 1 (for presence), although there are ways to represent multistate characters as well. The next step involves identifying the *polarity* of characters, whether they are primitive or derived. A cladogram is constructed based on shared derived characters. Phylogeny can be complicated and

there may be several possible cladograms based on the given data set. The principle of parsimony helps in choosing the best tree. According to this principle, the theory of nature should be the simplest explanation. The cladogram having the fewest steps of character transition for the given data is the most parsimonious tree. A simplified example of cladistic analysis of recent foraminifera belonging to the Soritacea group is discussed in Box 4.4. In practice, however, a much larger data set of species

Box 4.4: Cladistic Analysis of Soritacea

The data matrix showing presence (1) and absence (0) of nine characters in five species of Soritacea is given below. *Peneroplis planatus* is taken as the outgroup.

Character/species	1	2	3	4	5	6	7	8	9
Marginopora kudakajimaensis	1	1	1	1	1	1	1	1	1
Amphisorus hemprichii	1	1	1	1	1	1	1	0	1
Sorites orbiculus	0	1	1	1	0	1	0	0	1
Sorites orbitoides	0	1	1	1	0	1	0	0	0
Sorites bradyi	0	1	0	0	0	1	0	0	0
Peneroplis planatus	0	0	0	0	0	0	0	0	0

The characters are as follows: (1) median apertures between marginal apertural rows; (2) multiple apertural rows of circular or crescentic form; (3) flabelliform chambers; (4) cyclic chambers; (5) A-form embryo possesses a vorhof; (6) internal skeleton consists of septula; (7) duplex skeleton; (8) median skeleton; (9) outer wall with evenly dispersed pits (data after Gudmundsson 1994).

In the following sequence of cladograms (Fig. 4.5), shared derived character (apomorph) determines the classification at each step. The ticked characters on the branches are the apomorphs that define the sister taxa. In step 1, for example, characters 2 and 6 are derived characters that separate the five species from the outgroup. Similarly, other characters are involved in subsequent steps. The final cladogram is highlighted.

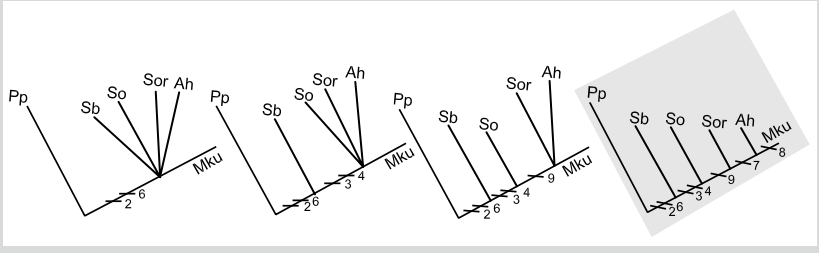

Fig. 4.5 Cladogram illustrating the relationship between the selected species of recent Soritacea

and characters is involved and manual construction may not be possible. Software (Sect. 4.6) is run to generate the most parsimonious or all possible equally parsimonious trees. Cladistic hypotheses have made major advancements since development of the method and readers should refer to the literature for detailed discussions on tree construction (e.g. Eldredge and Cracraft 1980).

4.5 Species Concepts

Species are taxa of the lowest rank in the Linnaean hierarchy of life. It is the smallest unit that a taxonomist identifies in his/her study. Essentially, there are two concepts of species: biological and morphological. Biologists define species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". The application of the above definition relies on the identification of the actual or inferred reproductive potential (interbreeding) between populations. This definition is inappropriate for fossils, because interbreeding in a population cannot be demonstrated and genetic and ecological information other than by inference are lacking. All paleontological species are, therefore, necessarily morphological species, though we can gain some insight into the scales of morphologic variation between species from modern biological species. The paleontological species concept is derived from the "evolutionary species" definition of G. G. Simpson, according to which "species are groups of individuals which exchange genetic information primarily with other members of the group and which share a common evolutionary history". How do species originate? There are several models of speciation (the process by which species are formed). The geographically based models consider physical isolation of populations to be the mechanism of species formation. The ecological models stress the role of differential ecological adaptation and genetic models consider internal genetic mechanism as the cause of species divergence (Lazarus 2003).

How do we identify species? The Linnean system of drawing boundaries between species is based on discontinuities in the range of morphologic variation. At times, it may be arbitrary in the fossil populations that gradually change from one form to another. The difference between the beginning and the end of the gradually evolving population, however, is so great that paleontologists tend to subdivide the lineage, even if it is arbitrary. Taxonomists are often categorized as "splitters" and "lumpers" (Hornibrook 1968). Due to the usefulness of fossils in stratigraphic zonation, micropaleontologists give new names to separable morphological groups even if variation is slight but consistent. On the other side of these splitters are the lumpers, who accept wider variations in species and genera. There are criticisms of excessive splitting of species, but the observation of molecular systematics is interesting in this context. The molecular study of a living foraminifer, *Ammonia*, has shown that there are as many molecular types of the genus as the morphologically distinguished species recorded globally (Hayward et al. 2004). The morphologically separable species are, thus, also distinguishable by molecular type. The identification of a group of specimens as a new species is largely a subjective one, based on the specialist's long experience

with the range of variation commonly found in the group of fossils studied and the range found in modern species of related organisms. It is a common understanding that many fish at first glance may look similar, but a fisherman knows how to separate them (for more on species identification and nomenclature, read Prothero 1998).

The skill of a taxonomist to link morphospecies phylogenetically and biochronologically to develop an evolutionary tree is fundamental to the science of biostratigraphy. A recent planktic foraminifer *Neogloboquadrina dutertrei* occurs as two distinct morphogroups in tropical and subtropical areas, respectively. The scanning electron microscopy revealed that the ultrastructures in the two groups are distinctly different. The two groups, however, are linked by intermediate ultrastructures and, thus, represent phenotypic variants within a cline extending from tropical to cool subtropical areas (Srinivasan and Kennett 1976). It required an intensive study of these forms across the latitude and through the Neogene to recognize two evolutionary bioseries in *Neogloboquadrina*, both having been derived from *Globorotalia* (*Turborotalia*) *continuosa* (Fig. 4.6). Whether the two morphogroups of *Neogloboquadrina dutertrei* are two distinct "species" or "phenotypic variants" was subject to in-depth observation of evolutionary changes in several morphological traits of the foraminifer.

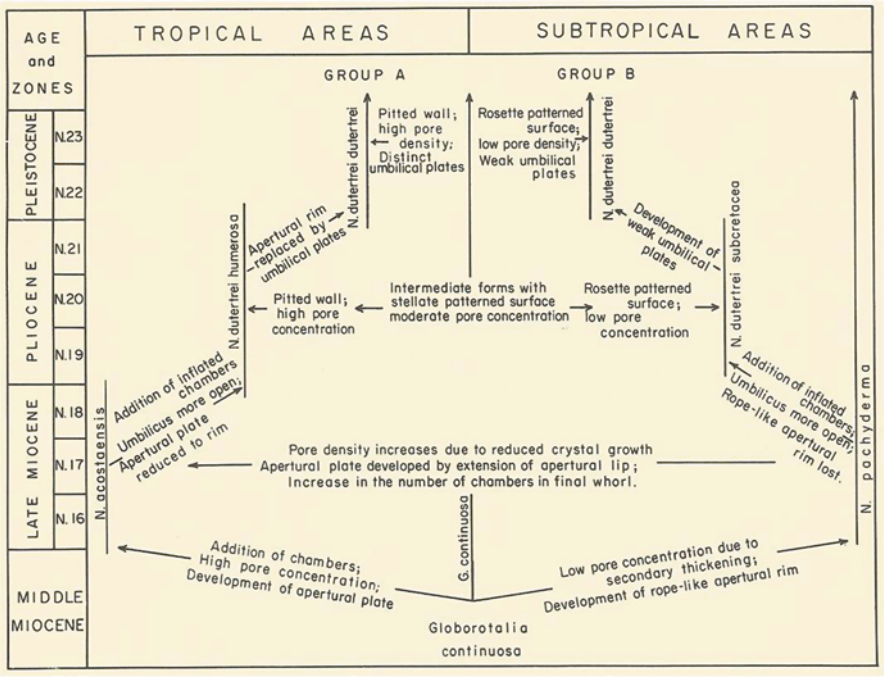

Fig. 4.6 Phenotypic and evolutionary relationships established through comparative morphologic and ultrastructural studies of planktic foraminifera (reproduced after Srinivasan and Kennett 1976)

4.6 Database and Software Program

Database: The taxonomic information, illustrations and stratigraphic distribution of microfossils are available online through several databases. Some of them are listed below.

CHRONOS: Many databases of micropaleontologic interest are available through this portal. Of specific interest in regard to microfossils reported in DSDP and ODP samples are the databases *Neptune* and *Janus*. The *Paleobiology Database* and *PaleoStrat* hosted on this site, despite being of wider use for marine and terrestrial animals and plants, provide taxonomic and stratigraphic information on microfossils.

WoRMS: This is the World Register of Marine Species, a part of which is the World Foraminifera Database cataloguing foraminiferal species.

Palydisk: This is the palynological database of the American Association of Stratigraphic Palynologists.

Nannoware/BugCam: This is managed by the International Nannoplankton Association and has a digital image catalogue of Cenozoic calcareous nannofossils.

Software Programs: The most widely used software for statistical analysis includes SPSS, SAS and Systat. A number of freely downloadable software programs are also available for statistical analysis and morphometric analysis. PAST (Paleontological Statistics) contains a number of statistical methods generally used for paleontological data analysis. Some individual efforts are making computations easily accessible for morphometric analysis. These include *Morphometrics at SUNY Stony Brook* and *Morpho-tools.net*. The latter contains tools for Eigen-shape and landmark analysis and statistical analysis of morphometric data, including linear regression, principal component analysis and canonical variety analysis. Software named Phylogenetic Analysis Using Parsimony (PAUP) and MacClade are used to run cladistic analysis to generate cladograms.

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