THE CLASSIFICATION OF THE FORAMINIFERA – A REVIEW OF HISTORICAL AND PHILOSOPHICAL PERSPECTIVES

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ABSTRACT. A historical review of the classification of Foraminifera reveals that the latest by Loeblich and Tappan is in the central tradition, leading from the work of the early English School, in which it is attempted to relate test composition and fine structure to physiology in formulating a sound basis for distinction of suprageneric rank. Although the early English School first distinguished homologous from analogous structures, their view that Foraminifera constituted a primitive, plastic group has inhibited biological and stratigraphical work, and distorted classification down to the present. The search for a single 'key' to turn the problem has also led to swings of fashion and, using Brady's metaphor, to 'cutting rather than untying the Gordian Knot'. Recent classifications are shown to retain considerable artificial elements. Attempts to substitute numerical taxonomy or cladistics for 'intuitive' taxonomy are misguided. Principles to assist the way forward are given.

THE Foraminifera are the most abundant marine invertebrates and play a major role in the economy of nature. The classification given in the *Treatise of invertebrate paleontology* (Loeblich and Tappan (1964) hereafter referred to as *Treatise* (1964)) has been treated as a standard for a quarter of a century, so the appearance of a comprehensive revision in book form (Loeblich and Tappan 1988*a*) is a considerable scientific event, not only for palaeontology but also for zoology. Its importance for geology is well expressed by the authors in their introduction: 'They are the most widely used fossil organisms for biostratigraphy, age dating and correlation of sediments, and paleoenvironmental interpretation, both as organisms whose living representatives provide ecologic data and as mineralized shells that are a geochemical record of paleotemperatures, extent of glaciation and other paleogeographic features' (p. 1). However, the very success of Foraminifera in applied palaeontology and palaeoecology has hindered advances in classification because workers have resisted changes, preferring the 'stability' created, at least in the West, by general acceptance of the *Treatise*. Indeed, suggested changes may provoke hostility. Symptomatic of the general attitude is this complaint in *Nature* about the alternative classifications put forward in *Comparative primate biology* (Martin 1988, p. 589): 'The Editors did not impose a uniform system... use of alternative schemes seen as a sign of healthy science better seen as an insidious ailment... a relatively stable classification is a prerequisite for other work... it is high time matters were put to rights... the present situation is comparable to a team of computer programmers arguing endlessly about whether they should use BASIC, FORTRAN or PASCAL, rather than getting on with the actual programming job in hand'.

Views of this kind mistake the fundamental purpose of classification which is to provide an orderly hierarchical array of taxa reflecting the genetic lines of descent, not simply to provide a convenient pigeon-holing, i.e. a natural classification is confused with an artificial identification key or retrieval system. A taxonomic scheme is useful for 'other work' in direct proportion to the extent it reflects the true lines of descent. An artificial scheme will probably be misleading in biostratigraphy and palaeoecology and certainly useless for studies of macro-evolution. It is the advances towards a genetic classification that are a prerequisite of greater precision in other work, especially in study of rates of evolution and diversity patterns. A good example is provided by the foraminiferal genera

[Palaeontology, Vol. 33, Part 3, 1990, pp. 503–528.]

Globigerina and *Globorotalia*, formerly included in one family and both considered to range back into the early Cretaceous. In Loeblich and Tappan's book they are now placed in different superfamilies and both are restricted to the Cenozoic, *Globorotalia* to the Neogene. The discovery that the globigerinids are near-surface plankton while the globorotaliids are deep-dwellers is in tune with this more discriminating approach. Similarly, the large orbitoidal foraminifera were originally placed in one family that straddled the Cretaceous-Tertiary boundary. Again, these genera are now recognized as belonging to distinct superfamilies with ranges which reveal and emphasize the marked break at that horizon. Changes of this kind are clearly a sign of scientific health and complaints about them reminiscent of the lamentations that arose because Copernicus destroyed the stability of the Ptolemaic system.

Another reason for the 'bad press' given to taxonomy is the common misconception that the important work on the major groups has been done, with the main goals achieved. Like the traditional comparative anatomy once taught at Oxford (as described by Sir Peter Medawar in his engaging autobiography, *Memoirs of a thinking radish*), it is seen as 'deadly dull' and no longer a 'live' issue, despite the 'grandeur' of the demonstration of evolution. Controversies in taxonomy are dismissed as mere squabbles about trivial matters, such as priority of names, and descriptive work on new species as a higher form of stamp collecting. However, there are very few groups in which the phylogeny is known with any certainty. In the Foraminifera it is a matter of continuing lively debate and a comparison between the classification set out by Loeblich and Tappan in their new book and those of earlier workers, including their own in the *Treatise* (1964), will silence criticism of this kind.

The general reader may be given a clearer picture of the problems faced in the attempt to produce a natural classification by a historical summary of past debates about the correct principles to be followed. The clash between the 'English School' and the 'Continental School' in the nineteenth century and between the English School and the 'American School' in the early twentieth century being particularly instructive, because the extreme positions taken up highlight the difficulties involved as well as differences in philosophy and attitude. This will also help to explain the paradox that late into this century the Foraminifera could be regarded as a simple, plastic group in which the shell composition reflected habitat, and differences in shape and ornament the impact of physico-chemical forces acting on the protoplasm (D'Arcy Thompson 1942), at the same time as they were being successfully used in biostratigraphy. No attempt is made to summarize all the classifications that have been proposed (for an exhaustive coverage see Loeblich and Tappan 1964, pp. 140–63). Instead, attention is directed to the most influential classifications in what may be called the central tradition; in particular, to the founder members of the English School because they were the first successfully to distinguish homologous from analogous structures and because the classification now produced by Loeblich and Tappan is, in many respects, 'the direct lineal descendant' of that of Carpenter (1861, 1862).

ATTEMPTS TO UNTIE THE GORDIAN KNOT

The clash between catastrophism and uniformitarianism

The dominant figures in the English School were largely biological in outlook and, appropriately for a maritime nation, were chiefly concerned with the study of the Recent and the dredge samples that became available as a result of the strong nineteenth century drive towards exploration of the oceans. The first work on foraminifera in England was on the Recent species of the south coast (Walker and Boys 1874). The dominant figures in the Continental School were largely palaeontological and geological in outlook, the first work in France being that on the Eocene of the Paris Basin (Lamarck 1804). There was also a deeper dichotomy in that Alcide d'Orbigny, the founding father of scientific foraminiferal studies and of the Continental School, was also a catastrophist (appropriate in post-revolutionary France), whereas, in contrast, the English School was strongly influenced by Lyellian uniformitarianism (see Heron-Allen 1917).

D'Orbigny (1826) was the first to recognize the Foraminifera as a separate group, considering them an order of the Cephalopoda distinguished by possession of a series of internal, basal chamber openings (foramina), rather than possessing a siphuncle. Concordant with his idea that the Foraminifera were cephalopods he divided them into families entirely on the basis of chamber arrangement or coiling mode, the simplest (and most severely parsimonious) solution.

After the discovery that Foraminifera were Protozoa by Dujardin (1835), d'Orbigny (1839) raised the group to Class status with six orders based on chamber arrangement, plus an extra one for single chambered forms. Despite the simplicity of his taxonomic scheme, d'Orbigny recognized a large number of genera and species. This was because he believed in the complete replacement of faunas at the end of each successive geological stage by special creation.

Although the discovery that the Foraminifera were Protozoa prompted d'Orbigny to give them class status, it had little other effect on his view of their classification. In contrast it had a profound influence on the whole philosophy of the English School, dominated by Williamson and Carpenter in the mid nineteenth century. Thus, Williamson (1858, p. ix) saw it as demonstrating the 'low organization' of 'diversified inferior creatures' with an 'anomalous and obscure' history. The external features of the shell, such as direction of growth and sculpture, considered important earlier when foraminifera were thought to be molluscs, were now seen as due to 'age and local circumstance' and possessing 'little value'. Carpenter (1862, p. vii) in classing them with the Rhizopoda commented on the soft parts as 'a little particle of homogeneous jelly', the 'protoplasm not yet differentiated into cell-wall and cell-contents' and more primitive than *Amoeba*, because, apparently, without nucleus. For this reason he concluded that variation in form of the shell aperture, which in higher animals with an alimentary canal would warrant generic or family distinction, was of 'comparatively little moment' and perhaps even a matter of 'individual difference'.

Both these key figures in the English School readily accepted the new doctrine of Darwinian evolution: Carpenter was close to the Darwin circle, wrote a supporting review (1860) and took a prominent part in debates on the subject as, 'one of the most active and respected interpreters of evolutionary theory' (Young 1985). Combined with their view of the low position of Foraminifera on the tree of life, this led them to reject outright d'Orbigny's classification based on geometrical plan. The 'extraordinary diversity' of Foraminifera and 'the gradational nature of these differences' which indicated 'community of descent more or less remote...from a small number of original types', also led them to dismiss not only his successive special creations but also his 'needlessly...multiplied...number of species'.

Williamson (1858, p. x) decided that 'real specific' features would only be shown by the soft parts, and that 'the hard shells of the Foraminifera do not constitute a sufficiently constant and important element in their organization to justify our trusting to them as guides in the discrimination of species'. While Carpenter (1862, p. vii) was forced to the conclusion that 'sharply defined divisions – whether between species, genera, families or orders do not exist' and that (p. x) the 'ordinary notion of species...was inapplicable', the term becoming one of convenience for intergrading assemblages grouped round a small number of family types, showing 'continuity through a vast succession of geological epochs'.

It would be anachronistic to complain that Carpenter and Williamson lacked an adequate species concept. The attempt to apply evolutionary ideas was premature. Adequate knowledge of the stratigraphical record, of true genetic diversity as distinct from dimorphism and polymorphism resulting from alternation of generations, and of the complications caused by changing apertural style during the growth of multiform species, lay in the future. But they were correct in their scathing attack on members of the Continental School, such as de Montfort (1808) who recognized individual variations as generic, e.g. nine genera based on '*Nautilus calcar*' – all synonymized with *Lenticulina* in Loeblich and Tappan's book. But in their extreme reaction to d'Orbigny on the side of Lyellian uniformitarianism they denied (Carpenter 1862, p. xi) there was 'any fundamental modification in the foraminiferous type from the Palaeozoic period to the present', and deduced (Williamson 1858, p. xii) that foraminifera have 'little value...in determining the relations between zoological provinces or in identifying stratified deposits'. These views cast a long shadow down the years, inhibiting stratigraphical work in Britain into the present century, despite their countervailing (and contradictory) remarks on the value of foraminifera as indicators of temperature and depth. They undoubtedly influenced Darwin, who otherwise might have found a paradigm in these 'intergrading forms' regarded as the 'direct lineal descendants' of remote ancestors. On this subject the first edition of the 'Origin' preserves a resounding silence, and, significantly, Carpenter does not mention foraminifera in his extended review of it (1860). In later editions (from the 4th, 1866, p. 402, see 1929 reprint of 6th edition, p. 293) Darwin notes 'Foraminifera have not, as insisted by Dr. Carpenter, progressed in organisation since even the Laurentian epoch'. Even a hundred years later it was concluded 'the morphological series... do not always seem to have very strong claims to being evolutionary series' (Challinor 1959, p. 79).

The confusion about the value of the foraminifera in stratigraphy is a symptom of the confusion about species caused by the advent of Darwinism. When Carpenter (1862, p. x) states that the idea of the species as 'marked out from each other by definite characters... from original prototypes similarly distinguished', is quite inapplicable to this group, with the suggestion that this is unlike the case in the more advanced Cephalopoda, we see the persistence of the Linnaean idea of the species, i.e. separated by morphological gaps from their nearest relatives in the great chain of being. Underlined by his view (1860, p. 214) that the chief difficulties for Darwin's theory were those structures or habits 'difficult to imagine to have been acquired gradually by any process of consecutive modification'. Again echoed by Challinor (1959, p. 62), 'the apparent rarity of closely graded evolutionary series may express a real rarity and be due... to evolution usually proceeding in jumps rather than perfectly smooth gradation'. In this way, paradoxically, the profoundly anti-Darwinian, Linnaean species, the discrete 'particle' of Lyell, became incorporated into the philosophy of the English School as a justification of extreme lumping in the search for the 'morphological gap' between 'true' species. The pervasive influence of this idea, even today, is seen in ill-advised attempts to delineate this 'true' species by 'scientifically rigorous' methods, involving numerical taxonomy and cladistics (see p. 521).

Although the attempt to apply evolutionary ideas at the specific and generic level was a failure, the attempt to find a more natural basis for the higher divisions was much more successful. Both men (Williamson, a medical doctor and Professor of Natural History and Carpenter, one of the leading physiologists of his time) were highly skilled microscopists and their background and training prompted them to look for the possible connection between soft parts and fine structure and wall composition (texture) of the test, as a means of recognizing major groups. Carpenter (1850, 1856, 1862) made particular use of both natural and artificial casts as well as thin-sections in his studies of foraminifera from off Australia and the Philippines which included a number of larger calcareous genera. This led him to the discovery of canals and the distinction that could be drawn on the basis of the presence or absence of pores between annular discoid genera grouped together by d'Orbigny. By means of thin-sections and transmitted light, Williamson (1852, 1858) distinguished the three major wall structure groups of the post-Palaeozoic and the lamellar character of the hyaline group.

These observations led to a comprehensive reclassification by Carpenter (1861, 1862). Two suborders were recognized: Imperforata, to include membranous, 'porcellanous' (porcelaneous) and 'arenaceous' (agglutinated) families and the Perforata, taken to include three calcareous families – one finely perforate (Lagenida), one coarsely perforate (Globigerinida) and one finely perforated with canal system and supplementary skeleton (Nummulida). With its emphasis on fine structure and composition this classification is decidedly modern in outlook and it might be thought that simple elaboration of its main ideas would have taken place through the late nineteenth century. For a number of reasons this was not to be the case. In particular, although in outline the classification ostensibly presumes a necessary connection between wall structure and perforation, detailed perusal reveals a major contradiction. The tendency of some 'rough-cast' porcelaneous miliolids to acquire an outer agglutinated coat was considered 'a trifling variation', not justifying their separate treatment. Similarly, perforate agglutinated forms with calcareous cement were united with their calcareous homeomorphs and (1862, p. 48) separated from 'proper...purely arenaceous' forms with organic cement in which 'the absence of any pseudopodial pores...shows their affinity to be rather with the porcellanous than with the hyaline series'. In this way, Carpenter tried to rationalize a system based on the idea of the primacy of perforation as an indication of fundamental physiological distinction, but at the cost of considerably devaluing wall composition as well as chamber arrangement. It is interesting that in claiming that the porcelaneous and hyaline series are isomorphic in chamber arrangement he overlooked the distinctive milioline coiling of a major proportion of the porcelaneous group, including the 'rough cast' forms which could have assisted his argument. Quite apart from this contradiction at the heart of the classification, the very success of the rhetoric of the founder members of the English School regarding the impossibility of recognizing species on the basis of the hard parts (if at all) helped to undermine it from the start. Thus, ironically, despite its brilliant insights, it came to be seen as over-elaborate, like the parallel scheme of Reuss (1862), also based on the discoveries of the English School, but with twenty-eight families recognized.

The triumph of the English School

These changing ideas were well shown by the new classification proposed by Brady (1884), on the basis of comprehensive collections from all the major oceans, made during the voyage of the *Challenger* (1872–74).

Although during the intervening years there had been an attempt to solve the problem of the relationships of perforation and wall composition by putting composition at the higher hierarchical level (Rupert Jones 1875), Brady considered this 'cutting rather than untying the knot', and abandoned 'minute structure' as a means of subdividing the order as 'not uniformly applicable'. Carpenter's six families were refined and increased to ten (including twenty-nine subfamilies) with much more emphasis on chamber arrangement, particularly evident at subfamily level. Also, against the spirit of Carpenter's 'Principles', the unilocular family Astrorhizidae was set up to cover single chambered agglutinated genera from the Abyssal Plains and the Globigerinidae was restricted to planktonic genera. However, the family Textulariidae was still considered to include both agglutinated and hyaline, biserial and triserial genera. The Lyellian steady-state, uniformitarian dogma of the English School is also apparent in the idea that *Nummulites* ('*Nummulina*') ranged back to the Carboniferous, in the inclusion of *Fusulina* in the same family, and in the failure to separate *Endothyra* from the agglutinated group.

The continuing confusion about species was also still evident. On the one hand Brady quotes Carpenter's views with approval and states 'so-called species represent no more than terms of a series', but on the other hand he recognizes (p. vi) 'modifications...whether species or not which differ not merely in details of form and structure but in habit...with characters that afford means of easy identification'. The attempt to group varieties around a few primary types was abandoned and the treatment of species and genera is nearer to that of Reuss and the Continental School. Despite the continuing disagreement about stratigraphical ranges, it is possible to see here the beginning of a rapprochment, although Brady's species limits are extremely wide and he found the 'needless multiplication' of species by European workers 'a bar to progress'. In the event, reconciliation between the two schools lay well into the next century.

Brady's simple classification, backed by the beautiful lithographed plates in the Challenger Report (unsurpassed until the invention of the scanning electron microscope and still superior in some respects), was widely influential and remained in use, modified by Lister (1903), almost into our own day (Jepps 1956). This reflects the long dominance of the English School and the apparent confirmation of its views: first, by the detection of pores in the proloculus of the porcelaneous genus *Peneroplis* (Rhumbler 1895); second, by the discovery of calcareous genera, in supposed Cambrian limestone from Malvern, some specimens actually being put into three extant species by Chapman (1900). The issue of the 'Cambrian' calcareous foraminifera became the 'cause célèbre' of foraminiferal studies, not solved until Wood (1947) demonstrated that the fauna was derived from an erratic of early Mesozoic age. Meanwhile workers like Galloway (1933) and Chapman and Parr

(1936) who tried to take the occurrence into account in classification, were almost bound to decide that calcareous forms sprang from tectinous ancestors and that agglutinating forms arose later and were more advanced. The germ of this idea may be found in Carpenter (1862). Those that did not, like Cushman (1927), who on the basis of his stratigraphical work had good reason to find it suspect, were forced to try and explain it away as a result of post-mortem calcification. Inevitably, wall structure was further devalued to the point that Douvillé (1906) decided it was determined entirely by habitat.

Economic imperatives and the rise of the American School

It is interesting historically, that just as the philosophy of the English School apparently reached its apotheosis, developments elsewhere in the world, in particular, the successful application of larger foraminifera in the Far East and the Caribbean, and of smaller foraminifera in the oilfields of Texas, vindicated their use as biostratigraphical index fossils.

The name chiefly associated with the taxonomic work on the great number of new genera and species that now came to light was that of Joseph Cushman, the key figure in what came to be known as the American School (Galloway 1928). He began his career working mainly on Recent Foraminifera, indeed his interest in them continued until his death (Cushman 1932, 1933, 1942) and his knowledge was as extensive in this area as that of Brady. But he also became well known as a consultant for the U.S. Geological Survey and various oil companies. This allowed him to set up his own laboratory in 1924 and to begin the serial publication of the famous *Contributions from the Cushman Laboratory for Foraminiferal research* which attest to his unrivalled knowledge of foraminifera from both the subsurface and outcrop. With this background he was well suited to syncretize the philosophies of the English and Continental Schools and to mitigate their tendency towards excessive lumping on the one hand and excessive splitting on the other. This was not achieved immediately because the sheer volume of new material necessitated the creation of many new taxa and this was fiercely criticized by members of the English School, still labouring under the misapprehension that the fauna from the Malverns was Cambrian and clinging to Carpenter's central dogma: that the Foraminifera were a simple plastic group.

The initial reaction of the English School is well shown by Heron-Allen's review (1929) of Cushman's new classification (1927, 1928) which recognized some 600 genera (compared to the 141 of Brady), 'an overwhelming avalanche' causing the 'brain of the beginner to reel'. In particular, he deplored the splitting of many genera, with the revival of many of d'Orbigny's names, as well as previously abandoned names. Although admitting that the time had come for an 'exhaustive' reclassification, he was 'assailed by doubt' in his response to the argument for splitting based on stratigraphic utility and as well as pointing out the problem of facies, suggested that unconformities and faults could 'seriously embarrass' the petroleum geologist and that it was 'self-evident that the pelagic Foraminifera must be useless as stratigraphical indications'. That the battle was now between applied and academic workers rather than schools is revealed by later correspondence in *Nature* (Heron-Allen 1935) where he quotes Hans Thalmann's description of the creation of new genera and species in 1933 and 1934 (more than 300 per annum) as '*dementia nomenclatorica americana*'. It is interesting that, despite quoting Thalmann's remarks with apparent approval, he admits the responsibility of Earland (his co-worker on the *Discovery* material) for seventy-three of the new species for 1934. This contradiction is reminiscent of Brady who similarly found it necessary to legitimize his own taxonomic offspring by appealing for general adherence to the standards of rectitude set by the early Fathers of the English School.

Cushman not only increased the number of genera to some 600 but replaced earlier groupings by forty-five families (many based on the subfamilies of Brady) which were increased to fifty in the last edition of his book, *Foraminifera* (1948). These families were clearly distinguished on grounds of wall structure as far as it was then known, chamber arrangement and aperture form, with coiled genera regarded as leading to uncoiled genera. Unilocular agglutinating forms were considered the most primitive group and ancestral to most other families via coiled, unilocular genera already present in the Lower Palaeozoic. In his general acceptance of ontogeny and recapitulation as a key to unlock the phylogeny of multiform species, and of uncoiling as a dominant trend, he followed Lister (1903) and Schubert (1908, 1921) rather than Rhumbler (1895, 1911, 1923) and Douvillé (1906) who believed in proterogenesis and general coiling-up. There is an interesting correspondence here with the rejection by Spath (1933) of the idea of a general, coiling-up trend in the cephalopods as postulated by Hyatt (1900).

Like Brady, Cushman did not group his families in phylogenetic lines (probably because of the difficulties caused by the confused stratigraphical evidence) but fifteen of the calcareous perforate families were regarded as having common descent from a rotaliid ancestor. As was shown by Wood (1949), apart from *Peneroplis* and its allies which Cushman separates from other porcelaneous forms on the groups of their postulated perforate ancestry, his families can be grouped into distinct higher categories based on wall structure. That this was not done reflects the continuing doubts about the importance of wall structure and the persistence of the idea of the primary importance of perforation. Cushman also followed Brady in including the Palaeozoic endothyrids with the agglutinating lituolids.

The families were grouped into higher categories by Glaessner (1945) who recognized seven superfamilies based on wall structure, chamber arrangement and apertural form. The endothyrids were placed in a separate superfamily with the fusulines on the grounds of their microgranular wall structure (Henbest 1937) and the porcelaneous families were also regarded as a natural group originating from a coiled unilocular ancestor. Glaessner laid particular stress upon the value of biological studies in interpreting the fossil record and pointed out how the work of Myers (1935, 1936), Le Calvez (1938) and Jepps (1942) not only clarified problems of dimorphism and reproduction, but proved the stability of species and of wall structure, perforation and chamber form under different ecological conditions. However, although the superfamilies were considered to have a common origin in coiled, unilocular, agglutinated ancestors, the continuing existence of the 'stumbling block' to confident phylogenetic work, created by the supposed Cambrian fauna of the Malverns, meant that no attempt was made to recognize suborders on the basis of wall structure.

The return to wall structure as the primary basis of subdivision

Wood (1947, 1949) not only removed the 'stumbling block' in the way of recognition of the stratigraphical succession of the major groups of Foraminifera but greatly clarified knowledge of wall structure. The optical characteristics of the main types were clearly defined and the hyaline group was shown to include both radial and oblique ('optically granular') genera. It also encouraged other work on fine structure which with the help of TEM now proceeded apace, leading to the suggestion there were three types of lamellar wall, monolamellar, monolamellar with septal flap and bilamellar (Smout 1954; Reiss 1958, 1965). This microscopical work on fine structure is reminiscent of that of the early English School and in the same way came to underpin a new classification, that of Loeblich and Tappan (1964), the most important and widely followed of those proposed in the wake of the great expansion of foraminiferal studies during and immediately after the Second World War. Compared with Cushman's scheme the number of genera and families was practically doubled, to 1194 and 95, grouped in seventeen superfamilies and five suborders. The outcry that greeted the appearance of Cushman's classification was not repeated in the case of that of Loeblich and Tappan. Although Berggren in his review (1965), remarked that few could have been prepared for the appearance of such a 'two volume tome' he went on to say that comparison of the numbers of taxa recognized with those in other invertebrate groups, revealed it was actually conservative. It is also significant that the main criticism made by Lee (1966) in his review of the biological section, is of the assertion that 'the simpler genera' with a single-chambered test of pseudochitin or pseudochitin combined with agglutinated particles also have simpler histories, remarking that the life cycle in *Allogromia* is complicated and indicates the opposite. This general change in attitudes was largely due to the influence of Cushman's book, which went through four editions, to the impact of biological work, and to the successful stratigraphical application of larger, smaller and planktonic foraminifera in the subsurface (in which British micropalaeontologists fully participated, particularly in the Middle East and Caribbean). Although problems of definition remained, the 'new synthesis' between population genetics and Darwinism in the 1930s and 1940s established the modern species concept and thereafter the debate was between individuals rather than schools. The idea that foraminifera were a simple, plastic group in which true species did not exist largely disappeared.

Wall composition and fine structure were now regarded as most important and the basis for recognition of the suborders and superfamilies, with apertural characters and chamber arrangement second and third. Thus we find that, after just over a hundred years, wall composition and fine structure have returned to favour, on the lines of Rupert Jones's attempted revision of Carpenter's scheme with perforation made subordinate:

Allogromiina – membraneous
Textulariina – agglutinated
Fusulinina – microgranular
Miliolina – porcelaneous (imperforate in post-embryonic stage)
Rotaliina – calcareous perforate

Apart from the microgranular group, the major subdivisions are based on the wall structure categories of Williamson, and reliance on wall composition and layering is carried to great lengths in the recognition of the superfamilies. In particular, aragonitic, calcitic spicular, calcitic single crystal and hyaline-oblique ('optically granular') structures were given superfamily status. However, the attempt to use wall structure as a key led to inherent difficulties like those in Carpenter's scheme. Although the Rotaliina were defined as calcareous perforate and the Miliolina as imperforate in the post-embryonic stage, separate status was not given to the perforate families in the calcareous microgranular group or to those in the agglutinated group (also discounted by Carpenter). Again, although aperture form is stated to be more important than chamber arrangement, in practice, the lower divisions were recognized on a combination of characters, and where wall structure and apertural changes with ontogeny were ill-understood, chamber arrangement inevitably took precedence.

History also repeated itself in that opinion swiftly swung away from the extremes of this mid-twentieth century cutting of the Gordian Knot. Towe and Cifelli (1967) showed that although radial and hyaline-oblique structure are distinct optically they are close crystallographically, and one may easily give rise to the other. Indeed, intermediate forms have been shown to exist (Bellemo 1974). This confirmed the variation noted at the specific and generic level in many families by Haynes (1956) and Wood and Haynes (1957). It thus became clear that the Cassidulinacea was an artificial grouping and that wall structure shows progressive changes in many groups, e.g. in the Elphidiidae and Cibicididae (Anomalinidae) where chamber arrangement remains stable, in contrast to the Nodosariidae in which wall structure is stable while chamber arrangement shows rapid progressive change along many lines. Similarly, the attempt to subdivide the hyaline group on the basis of layering ran into problems of conflicting observations until it was decided that all the Rotaliina, apart from the monolamellar Nodosariacea were bilamellar (Hansen and Reiss 1972; Grønlund and Hansen 1976). Some of these problems were taken into account by Loeblich and Tappan in various modifications of their scheme (1974, 1984). In particular, in 1974, they abandoned the attempt to make hyaline-oblique and bilamellar structure the basis of separate superfamilies, although wall composition was retained as the basis of the overall grouping.

The *Treatise* classification became the dominant influence on foraminiferal studies for more than two decades. Of other classifications proposed, the most interesting was that of Hofker (1951) in which the hyaline foraminifera, considered to be derived from agglutinated forms with a toothplate, are divided into three suborders:

Protoforaminata – single aperture, finely perforate (protopores)
Biforaminata – two apertures, finely perforate
Deuteroforaminata – secondary aperture dominant, coarsely perforate (deuteropores)

Unfortunately, although this arrangement emphasizes the aperture and internal characters and brings perforation back into consideration as a major factor, it largely ignores wall structure and stratigraphical relationships and although modified by Reiss (1958) has not been followed.

The classification of Haynes (1981) retained wall structure as the major consideration at the higher level but with recognition of nine orders and a return to class distinction. The hyaline group was considered polyphyletic and broken into five orders, e.g. the Buliminida were considered to have been derived from high trochospiral agglutinated forms (following Hofker in echoing Carpenter) and the 'vitreous' Palaeozoic genera were separated as a suborder within the microgranular group. The superfamilies were recognized on a combination of coiling mode and apertural form and emphasis was placed on umbilical characters. A major weakness is that perforation is ignored and the presence of pores in the megalosphere of *Peneroplis* is dismissed (along with the much more doubtful 'pores' in the walls of adult peneroplids and miliolids). This leads to the contradiction that although the hyaline group is regarded as polyphyletic, porcelaneous genera are considered to constitute a natural group. Further contradictions are that milioline agglutinating genera are left within the Miliolida (as by Brady) and that the single crystal Spirillinacea are considered the possible rootstock for the microcrystalline Rotaliida, although the genome is apparently more complex in genera such as *Patellina* than in simple discorbaceans.

Summary

This review of the most influential of past classifications reveals: the baneful influence of the idea that the Foraminifera are a very simple, plastic group; the strong influence of ideas about species on classification and biostratigraphical use; the uncertainty about the value of wall composition and fine structure until biological studies showed modern species to be stable and the stratigraphical relationships of the major groups were clarified. It is also clear that use of a single factor at the higher hierarchical levels, cuts rather than unties the Gordian Knot, as Brady remarked, i.e. a solution likely to be as short-lived as Alexander's empire. In this respect, it is interesting to see how well the new classification of Loeblich and Tappan avoids the pitfalls of the past.

THE NEW CLASSIFICATION OF LOEBLICH AND TAPPAN (1988)

The period since the publication of the classification in the *Treatise* of 1964 has been a time of unprecedented growth in foraminiferal studies, especially as applied to subsurface stratigraphy by the oil companies and to the core material made available since the initiation, in 1968, of the Deep Sea Drilling Project which has triggered an explosive outburst of activity on planktonic groups. The providential, commercial appearance of the Scanning Electron Microscope, at almost the same time, has also allowed more accurate discrimination of taxa on the basis of internal, apertural and external features, leading to the recognition of large numbers of new genera. In addition, many of those synonymized in 1964 are now regarded as distinct. This has brought the total number of genera considered acceptable by Loeblich and Tappan in 1964 (1,192) to more than double that figure in 1988 (2,446). These have not just been added to existing suprageneric taxa, as might be expected in a 'relatively stable' classification, because these categories have also more than doubled: suborders (5 to 12); superfamilies (17 to 65); families (95 to 296); subfamilies (129 to 300). This is not only because of the discovery of new supra-generic taxa but also because of the higher weighting now given to certain criteria as compared to their approach in 1964. This explains why the number of families has trebled and the number of superfamilies almost quadrupled, although the number of genera has little more than doubled. A possible cause for concern is that fifty-six of the subfamilies, forty-four of the families, three of the superfamilies (two in open nomenclature) and two of the suborders are represented by one genus only (105 taxa in all). A simple explanation is that many genera cannot be placed close to existing taxa because of the incomplete (as well as incompletely known) stratigraphic record. Alternatively, it may be argued that the group is being oversplit. Probably both tendencies are at work. The large number of families recognized is clearly important for macro-evolution, presuming that 'the taxonomic family is the conventional unit for studies of large scale extinction and rates of change of diversity' (Newell 1982, p. 260). It may also be considered encouraging that the average number of genera per family is 8·26 which falls between the 5 to 10 considered the general average by Van Valen (1973) presuming these numbers are not artifacts and are telling us something about niche partitioning. This may also suggest that the families and subfamilies with very high numbers are probable candidates for further splitting, if we consider that ideally a subfamily should represent a single evolutionary lineage, e.g. thirty-seven genera are included in the subfamily Miliolinellinae. However, there will clearly be differences according to whether evolution in the family is dominantly allopatric and branching, or sympatric and phyletic.

Criteria employed at generic level

As the title suggests, the work was conceived as a handbook of genera. There is a prodigious number of excellent plates and most genera considered synonymous are also illustrated. The success of the authors in carrying out this massively daunting task, is attested by the comments of reviewers: thus Banner (1988) considered it 'virtually miraculous' that not only had they managed to complete the task but had 'done it very well'; and Haman (1988), although he regretted that 'rigorous criteria were not used', considered the work a 'scholarly endeavour', and a 'useful, well-illustrated catalogue'. The reaction to the decision not to recognize subgenera was more mixed. Although approved by Haman, Banner considered recognition would have helped to diminish the rigidity of the generic diagnoses and Jenkins (1989) that they are essential to show iterative, evolutionary lines. Adams (pers. comm.) has also pointed out that subgenera have been raised to full genera without discussion, as in the case of the Lepidocyclinidae (see Adams 1987*a*).

Although it is not made explicit, the genera are recognized on the basis of test architecture and coiling mode, aperture form and accessory structures and internal structures. The authors also carry through the presence/absence of keels, umbilical bosses and supplementary apertures as generic criteria much more consistently than in the *Treatise*. An important innovation is the use of ornament at generic level, following its successful use recently in the planktonic forms. The well known *Lingulina tenera* plexus of the Lias is thus transferred to *Paralingulina*. Although this may cause raised eyebrows, the re-instatement of many genera previously put in synonomy is to be generally welcomed. A good example is that of *Ornatanomalina* from the Palaeocene of Pakistan, formerly put in synonomy with *Thalmannita*, described from the Palaeocene of Cuba. This led to widespread records of *Thalmannita madrugaensis* in Africa and Europe which on inspection are found to refer to species of *Ornatanomalina* (Haynes and Nwabufo-Ene 1988). This perfectly illustrates the palaeogeographical importance of refinements in taxonomy. A common fault in palaeontology (which also tends to bring taxonomy into disrepute) is the confusion of a diagnosis with a full palaeontological description. As pointed out by Banner (1988), this is not avoided here. In fairness to the authors, they have obviously tried to include all the features that may be relevant, including in some cases long accounts of reproduction. But this means that the reader has to search, often vainly, for the distinguishing features of the genus amongst specific details and repeated suprageneric characters sometimes, but all too rarely, finding what is required only under the Remarks. A minor point, but a possible source of confusion, is the continued use of spiral and umbilical as descriptive terms for the dorsal and ventral sides of the test. As both sides in a trochoid test are spiral (and may be umbilicate) the older terms are much to be preferred.

Criteria employed at the suprageneric level

Predictably, the reaction to the changes at suprageneric level have been more adverse. Thus Haman (1988) who provides a synopsis of the main taxonomic changes, considered the 'rationale not easily determined', and some of the family distinctions only generic. He clearly felt the new scheme inferior to the 'incisive and decisive' classification of the *Treatise* and that 'desired stability had not been achieved'. Banner (1988) was also 'unhappy about some of the concepts... and the suprageneric importance... given to some morphocharacters'. How far can these criticisms be sustained?

Loeblich and Tappan have had the problem of revising their suprageneric arrangement at the same time as incorporating a large number of new genera. They have made their task somewhat harder by continuing to cramp the Foraminifera within one Order, following Levine *et al.* (1980), a procedure that looks increasingly outdated in the light of the statement by Sleigh (1989) that the amoeboid protists comprise a number of evolutionary lines and are 'almost certainly polyphyletic'. Margulis (1974) has even suggested the Foraminifera should be considered a phylum. Upgrading them at least to class or subclass status would seem to be warranted by their position as the largest and most varied group of invertebrates and unique style of reproduction, with, like plants, a diploid asexual generation.

The five suborders of the *Treatise* are now increased to twelve:

Allogromiina	organic wall, unilocular (may tend to multilocular)
Textulariina	agglutinated
Fusulinina	homogeneously microgranular
Involutinina	aragonitic, non-septate
Spirillinina	calcitic, single crystal, non-septate (may have few chambers)
Carterinina	spicular, secreted calcite crystals
Miliolina	porcelaneous imperforate, true pores in protoconch of some
Silicoloculinina	opaline silica, imperforate
Lagenina	calcitic, hyaline-radial, monolamellar
Robertinina	aragonitic, hyaline-radial, septate, internal partitions, finely perforate
Globigerinina	calcitic, hyaline-radial, perforate, bilamellar, planktonic.
Rotaliina	calcitic, hyaline-radial or oblique, perforate, bilamellar, benthonic.

This breakdown reveals the authors continued reliance on wall structure at this level, though there are inconsistencies. Two, the Globigerinina (planktonic habit) and the Lagenina (fine structure of lamellae), are recognized on other criteria which leaves the Rotaliina inadequately diagnosed. On this basis the buliminids also merit equal recognition and separation from the rotaliids. The Fusulinina are defined as microgranular but include the Archaediscacea and Colaniellacea, described as having radial layers, and included in the Archaediscina by Haynes (1981). Other difficulties include separation of the non-septate, aragonitic group, as the Involutinina, from the septate Robertinina, whereas in the Allogromiina, Spirillinina and the Textulariina, non-septate and septate forms are included together. Agglutinated genera with milioline coiling (Rzehakinacea) are included in the Textulariina but their relationships with miliolids in the Recent (Haynes 1973) and first appearance in the Lower Cretaceous associated with acidic and low oxygen environments suggests a separate origin from within the Miliolida, dentate forms via the Miliolacea, edentate forms via the Ophthalmidiacea. The single species, *Miliammelus legis*, included in the supposedly siliceous Silicoloculinina may represent a similar response, in this case to life below the Calcite Compensation Depth (CCD) by agglutination of siliceous rods. The Carterinina is also based on a single genus in which the test is composed of calcareous spicules. However, these were regarded as agglutinated by Brönniman and Whittaker (1983). Perhaps *Carterina* should have been placed under 'Genera of Uncertain Status' pending the necessary tank studies.

The features now considered important at superfamily level are the unilocular, bilocular or multilocular character of the test, presence or absence of perforation, canals and major apertural features. Bilocular is not defined in the glossary and generally includes non-septate forms in which the initial end is expanded to form a cavity, considered homologous with a proloculus in septate forms. Non-septate multilocular forms, where the chambers are connected by stolons, are not separately considered. Family features now include free or attached habit, presence of internal subdivisions and surface texture as well as coiling mode. Because they regard wall structure as more fundamental than number and arrangement of chambers, both of which may change during ontogeny and therefore being more indicative of evolutionary relationships, they (paradoxically) tend to discount ontogeny as a key to phylogeny at the highest levels so that coiled, uncoiled, uniserial and unilocular genera tend to be put in separate groups. For instance, fully uniserial agglutinating genera are separated from those which become uniserial in the adult and regardless of apertural style are included in a single superfamily, the Hormosinacea.

They may have been unduly influenced here by the current, fashionable revival of the idea of a general coiling up trend involving proterogenesis, as against uncoiling involving recapitulation; exemplified by Brasier's attempt (1982) to show that the overriding imperative in the evolution of test architecture is towards minimum lines of communication between proloculus and aperture ('MINLOC'). This idea is somewhat weakened by the observation that the soft parts are generally confined, or retract into, the penultimate chamber. Their approach makes particular coiling modes 'stable' by default and produces a horizontal arrangement. On the whole, forams show new features in the adult and the stratigraphic record provides evidence of repeated uncoiling trends with connected serial changes in aperture form and position. The ideal shape for rapid movement through sediment by retraction of the podostyle directed forwards from a terminal aperture is apparently reached in many unrelated lines of smaller deep-sea forams. Recognition of these lines would have simplified the classification at family and superfamily level, especially if the difficulties encountered by the authors at the subordinal level were eased by the recognition of orders (as by Haynes 1981). It would also have helped to remove some of the inconsistency inevitable in horizontal groupings of a class that exhibits rapid evolution with serial development of all features of the test at some time, usually in combination. The only 'key' to these developments is the stratigraphic and evolutionary record and it cannot be predetermined. To be fair to the authors much of the inconsistency arises because of the different levels reached by research into different families. The Nummulitidae, probably the most famous fossil forams, are a good case. In the *Treatise* (1964), Cole lumped most of the genera previously recognized under *Nummulites* because they grade into each other. This extreme lumping, neo-linnaean in its search for morphological gaps, pleased no-one, except perhaps, punctuationists convinced that evolution proceeds by genuine saltations ('hopeful monsters'). Most of the genera remained in use and are reinstated in the present work. However, genera with subdivided chambers, even the sub-annular complex form *Spiroclypeus*, are included in the same family, rather than being separated as Cycloclypeidae (Haynes 1981) though this would be consistent with their own criteria. Already since publication, the wave of research has undermined this systematic sand castle. Adams (1988) has shown that the type species of *Nummulites* has secondary chamberlets and Haynes (1988) has redefined *Ranikothalia* with revival of *Nummulitoides*. This illustrates how the numbers of taxa recognized (diversity) varies not only with the data available but also according to the current philosophical paradigm and underlines the futility of pious prayers for 'stability'. As Knoll and Butterfield (1989, p. 602) wrote recently, 'Taxonomic changes both reflect and influence the way we think about evolutionary pattern and process'.

A review of the treatment of major suborders will indicate some of the difficulties to be overcome, especially necessary considering the use already made of the taxa recognized (in the evolutionary and diversity study published by Loeblich and Tappan 1988*b*).

Problems in the treatment of the suborders by Loeblich and Tappan (1988a)

Allogromiina. Although the naked Allogromiina are defined as membranous or proteinaceous, the included families Lagynidae and Allogromiidae are defined as being both, the Allogromiidae as proteinaceous on a plasma membrane. Within the Allogromiidae the only difference between the subfamilies Shepheardellinae and Argillotubinae appears to be that the Argillotubinae are wrinkled and may be fixed.

Textulariina. Within the non-septate, agglutinating superfamily Astrorhizacea the only difference between the family Astrorhizidae and the Rhabdamminidae, as defined, appears to be the greater selectivity shown by the latter, because *Rhabdammina* also has branches leading off a 'globular central area'. The Rhabdamminidae also includes both free and fixed forms, in contradiction to the stated criteria. In the remarks on the sub-family Halyphyseminae the comparison is presumably being made with the Dendrophyrinae, not Rhabdammininae. The family Psammosphaeridae is defined as coarsely agglutinated but the subfamily Psammosphaerinae as finely to coarsely agglutinated. *Technitella* is figured upside down and on the basis of the spicular wall and the broken attachment end (Haman 1967) mistaken formerly as the aperture, should be transferred from the family Saccamminidae to the Rhabdamminidae, subfamily Halyphyseminae. No clear distinction is made between the family Hemisphaeramminidae and the Saccamminidae and Psammosphaeridae. The Diffusilinidae is defined as being distinguished by an irregular mass of branching tubes but this does not agree with the diagnosis of the two genera included. There is no mention of tubes in *Diffusilina*.

The superfamily Hippocrepinacea is defined as possessing a proloculus and tubular or flaring second chamber. However, the subfamily Hippocrepininae does not show a prolocular initial end and the Notodendrodidae (one genus) actually has a bulbous central region leading to tubular arms. Within the planispiral to uncoiled superfamily Lituolacea, the family Lituolidae is defined by possession of simple interiors and terminal apertures which is taken to differentiate them from the Discamminidae which is diagnosed as having internal partitions, i.e. secondary septa. However, the figures given of *Discammina* and *Ammoscalaria* seem to show primary septa (organic without agglutination) only, with no subdivision of the chambers. There seems little reason to separate them from *Eratidus* and other genera included in the Lituolidae, subfamily Ammomarginulininae. Also, it is not clear why a simple wall is considered important in the definition of most of the families and subfamilies when it is not mentioned in the superfamily definition and no cases of complicated walls are included. No reason is given for including the Adhaerentiinae which lack an initial coil and are biserial, in the superfamily.

Although the superfamily Haplophragmiacea is defined as streptospiral to uncoiled, it includes the streptospiral to planispiral Recurvoidinae (as a subfamily of the streptospiral Ammosphaeroidinidae). It also includes the calcareous trochospiral and planispiral families Nezzazatidae and Barkerinidae. (Note that although the Nezzazatidae are defined as trochospiral *to* planispiral, the subfamily Nezzazatinae is defined as trochospiral *or* planispiral.) These families, with their digitate internal partitions and areal apertures, may represent diagenetically altered robertinids. They are certainly not close to *Ammosphaeroidina*.

The family relationships within the superfamily Cyclolinacea are not made clear and the diagnosis given for the family Orbitopsellidae does not adequately distinguish it from the Cyclolinidae. The terminology used here, as in the case of the Loftusiacea (inherited from previous workers it must be said) is not helpful and the fog-index is high. The family Cyclamminidae is defined as involute and rarely uncoiling, yet it includes the subfamilies Pseudochoffatellinae (evolute) and the Choffatellinae (only one out of eight genera with no tendency to uncoil). Neither the subfamilies Alveophragmiinae nor the Hemicyclamminae seem to be adequately diagnosed on the criteria given.

The superfamily Spiroplectamminacea is defined as planispiral to biserial and uniserial development is not mentioned (nor is streptospiral coiling) although the family Spiroplectamminidae is defined as planispiral or streptospiral to biserial, rarely becoming uniserial. In fact, two of the eight members of the Spiroplectamminae become uniserial and both the genera placed in the Vulvulininae. Three of the seven genera placed in the family Textulariopsidae become uniserial and one of the three placed in the Pseudobolivinidae. It is not possible to distinguish between these two families on the criteria given.

The subfamily and family distinctions are not clear in the diagnoses given for the superfamily Pavonitinacea. This group may be of polyphyletic origin.

Within the superfamily Trochamminacea the sub-family Trochammininae are diagnosed as 'trochospiral or may tend to uncoil'. None of the ten genera included and illustrated shows uncoiling.

All the canaliculate, high trochospiral agglutinating genera are included, with the biserial Textulariidae, in the superfamily Textulariacea and the non-canaliculate genera are accommodated in three other superfamilies. Because this emphasis on perforation tends to cut across groupings made on other features the superfamilies show a mixture of coiling modes and apertural styles. The Verneuilinacea and Ataxophragmiacea are not actually distinguishable as defined and it must be pointed out that the family Prolixoplectidae are included in the Verneuilinacea on the assumption they are non-canaliculate but the fine structure is only known in three of the nine genera. A number of families in the Ataxophragmiacea are defined as possessing a two-layered wall but the terminology is confusing. In the family Textulariellidae 'beams and rafters' are said to produce an 'alveolar wall'. In the Dicyclinidae there are 'transverse or radial partitions'. The Dictyopsellidae have a 'subepidermal network', and partitions are not mentioned, but in the Pfenderinidae, 'vertical or horizontal partitions' result in a 'reticulate subepidermal layer'. However the wall structure is defined, these families do not appear to be close to the Ataxophragmiidae and the family Cuneolinidae (which includes *Sabaudia*, characterized by a double-walled embyron with microgranular inner and radial outer layer) probably does not belong here either. The Coskinolinidae appear more closely related to the superfamily Orbitolinacea. They have been excluded because they lack marginal exoskeleton (marginal subepidermal partitions). They are also stated to lack the embyron of protoconch and deuteroconch diagnostic for the subfamily Dictyoconinae but that feature has only been found in eight of the twenty six genera included.

Within the superfamily Textulariacea the subfamily Minouxiinae in the family Eggerellidae is defined as cribrate which conflicts with the definition of the Dorothiinae as also developing multiple apertures and which includes *Arenodosaria* in which the aperture is described as sometimes becoming cribrate. The definition of the family Pseudogaudryinidae is incomplete, the aperture being described as an interiomarginal arch with the trend to multiple apertures not included.

Fusulinina. Within the Fusulinina, defined as 'homogeneously microgranular', the unilocular Parathuramminacea is divided into families mainly on the number of layers and character of the wall. However, the Parathuramminidae appears to be distinguished from the Chrysothuramminidae by wall thickness alone.

The superfamily Moravamminacea which includes genera with proloculus and tubular second chamber is distinguished from the Earlandiacea simply on the basis of the appearance of incipient septa and otherwise shows a very similar range of morphology. The distinctions as defined between the families in the two groups are not clear. The Earlandiidae are not distinguished as straight but defined as free, although *Warnantella*, put in the Pseudoammodiscidae, may be free. Both the Pseudoammodiscidae and Pseudolituotubidae include streptospiral forms. The Caligellidae, defined as curved to straight, includes genera showing initial coiling and therefore cannot be distinguished from the Moravamminidae.

As defined, the Tourneyellacea cannot be distinguished from the Moravamminacea and the definition actually should exclude the subfamily Palaeospiroplectamminae which would be better placed within the family Palaeotextulariidae.

The definition of the superfamily Archaediscacea does not make a clear distinction from these two superfamilies either, because the appearance of a 'radially built' outer wall layer in this group is only introduced in the family diagnoses. Inclusion of this superfamily in the Fusulinina clearly offends the stated criteria as does the inclusion of the Nodosinellacea 'fibrous inner layer', the Geinitzinacea 'radially fibrous' outer layer and the Colaniellacea outer 'vitreous' layer. The imprecision of this terminology and the description of the Nodosinellidae as 'fibrous or perforate', suggests that more detailed research is required into this whole group and that perpendicularly arranged granules without optical alignment (fibrous structure as in *Palaeotextularia*) is being confused with radial hyaline structure.

The superfamily Endothyracea is not defined as multilocular or septate, although they follow the Tourneyellacea, and although most of the genera show streptospiral to planispiral coiling with growth the superfamily and the family Endothyridae and the subfamily Endothyrinae are defined as 'planispiral to streptospiral'.

The coiling mode in the superfamily Fusulinacea is not given in the superfamily definition. In the definition given for the family Ozawainellidae it is stated that geological early taxa are planispiral and evolute but three of the four Carboniferous genera are involute and only *Pseudonovella* is evolute with the final whorl enveloping. This genus should probably be removed to the Loeblichiidae. This weakens the supposed distinction between the Ozawainellinae and the Pseudostaffellinae and between the Ozawainellidae and Staffellidae. The presence of early streptospiral coiling is inadvertently left out of the definition of *Pseudostaffella*. Within the Fusulinidae the distinction between the subfamilies Fusulinellinae and Wedekindellininae is not clear. Within the Schwagerinidae the subfamily Chusenellinae is defined as possessing plane or weakly folded septa in the early stage but both the genera described have plane septa initially. The definition of the Verbeekinidae does not include the vital information that the septa are plane (only given in the case of the subfamily Pseudodoliolininae). The subfamily Kahlerininae, defined as small with single tunnel, does not fit the family definition.

Miliolina. Within the superfamily Cornuspiracea the distinction between the family Cornuspiridae (planispiral *to* streptospiral) and the Hemigordiopsidae (streptospiral *to* planispiral) is not clear. This is because the subfamily Meandrospirinae (planispiral *or* streptospiral) is included in the Cornuspiridae. Also, as defined, the Meandrospirinae do not appear to be separable from the Calcivertellinae. Genera in which incipient chambers and definite septation appear in the adult whorls are included in the Baisalinidae and those with a few chambers throughout, and definite flexostyle, in the Fischerinidae. However, *Dolosella* in which the holotype has several undivided whorls, is included in the Fischerinidae. The subfamily Spiriamphorellinae is defined as like *Ophthalmidium* in the early stage. If so (the type figures are obscure) it cannot be included in the Nubeculariidae, as defined.

The definition of the superfamily Miliolacea which rests entirely on coiling mode does not exclude the Ophthalmidiidae and other forms with chambers of half-coil length included in the Cornuspiracea. This also applies to that given for the family Hauerinidae because genera with simple apertures without teeth are not excluded. Because the authors have now defined the family Miliolidae on the basis of its pseudoporous wall, simple wall structure should have been included in the diagnosis of the Hauerinidae. Quinqueloculine genera are included in the Miliolinellinae, so the distinction with the Hauerininae is not clear. The Riveroinidae are defined as planispiral but only *Riveroina* is planispiral throughout. *Pseudohauerinella* is quinqueloculine and may become planispiral in the final whorl.

The definition given for the superfamily Alveolinacea does not make a clear distinction with the Miliolacea. This is largely because of the inclusion of the Fabulariidae which are milioline. They are defined as, 'with milioline early stage' but the coiling mode in *Fabularia* and its allies is milioline throughout, the biloculine adult chambers still being added end to end. *Pseudofabularia* and *Pseudolacazina* show a fundamentally different coiling mode. The Mesozoic and Tertiary alveolines form two stratigraphically distinct groups. This is not recognized at subfamily level.

The inclusion of the family Milioporidae within the Soritacea distorts the definition of that superfamily so that it is described as 'early stage pitted or perforate and less commonly may be perforate throughout growth' which disagrees with the suborder diagnosis. However, although the Milioporidae are defined as perforate throughout ontogeny, in three of the six subfamilies it is said to occur in the outer chambers or adult and in *Kamurana*, the single genus in the Kamuraninae, it is also described as an adult character. In the other two superfamily diagnoses it is not mentioned. Although the Milioporidae are defined as being coiled in various planes (not in the superfamily diagnosis) the subfamilies show a variety of styles, even uncoiled rectilinear. *Kamurana* is described as consisting of a globular proloculus followed by an individual tube, so may have strayed in from the Cornuspiracea. The best place for this 'family' would seem to be amongst the genera of uncertain status.

Lagenina. The Lagenina are defined as radiate (as is the genus *Cryptoseptida*) rather than radial, and genera within the family Syzraniidae are confusingly described as 'radial fibrous' and 'hyaline pseudofibrous' without explanation. The family Robuloididae is inadvertently described as uniserial instead of planispiral. The diagnoses given do not make a clear distinction between the Nodosariidae and Vaginulinidae because both can include arcuate to uncoiled genera. The subfamily Marginulininae cannot be distinguished from the Vaginulininae on the diagnoses given. The inclusion of *Rimalina* with apertural slit in the Glandulininae means that this subfamily cannot be distinguished from the Entolingulininae on the criteria given.

Robertinina. The Robertinina are defined as planispiral to trochospiral and with internal partitions. However, genera which becomes uniserial or uncoiled biserial are included in three of the four superfamilies recognized. Only one of the three families within the Duostominacea is known to have partitions. The family Epistominidae within the Ceratobuliminacea is defined as having peripheral apertural slits but the subfamily Garantellinae is defined on the basis of its umbilical, ovate and areal apertures.

Globigerinina. The Globigerinina are defined as 'radiate' rather than radial hyaline and within the superfamily Heterohelicacea, the family Guembelitriidae is defined as having trochospiral, triserial or biserial early stage although the superfamily is defined as biserial or triserial which would appear to rule this family out. The family Heterohelicidae is defined entirely on aperture form and the distinction with the Guembelitriidae is therefore not clear.

The superfamily Rotaliporacea is defined as having extra-umbilical-umbilical aperture but the family Globuligerinidae have umbilical apertures as well as imperforate pustules and should probably be transferred to the Guembelitriidae. Within the family Hedbergellidae the subfamily Helvetoglobotruncaninae is defined as possessing portici extending to the umbilicus. *Whiteinella*, included in the Hedbergellinae is also described as having this feature so that distinction between the subfamilies breaks down.

The superfamily Globotruncanacea is defined as having umbilical aperture and tegilla covering the umbilical area. However, in many genera the aperture is described as extra-umbilical-umbilical, e.g. *Marginotruncana*, and many are described as possessing portici rather than tegilla. The subfamily Abathomphalinae is defined as having narrow umbilicus with 'tegilla, that of final chamber covering the umbilical area'. This is inadequate considering the superfamily definition. What is presumably meant is that the tegillum of the final chamber becomes a single umbilical cover or 'techo'. Within the family Globotruncanidae, the subfamily Globotruncanellinae is defined as single keeled but genera with single keel are included in the Globotruncaninae, e.g. *Globotruncanita*, and a number become single keeled with growth.

The superfamily Globorotaliacea cannot be distinguished from the Globigerinacea as defined. The Globorotaliacea are defined as 'non-spinose, but may be pustulose or pitted', whereas the Globigerinacea 'May be covered with narrow spines'. The additional character of 'numerous small pores or fewer large ones' given for the Globigerinacea does not overcome the lack of a clear distinction. Within the Globorotaliacea smooth genera are included within the family Eoglobigerinidae, also defined as having extra-umbilical aperture without lip. However, of the four genera included only *Parvularugoglobigerina* fits this diagnosis. I agree with Brinkhuis and Zachariasse (1988) that names of this length should be excluded under the rules of the ICZN, and in this case, *Planconusa* be substituted. The other three genera including *Eoglobigerina*, should be transferred to the Guembelitriidae. As both the Globorotaliidae and Truncorotaliidae can be pustulose the distinction between these family groups is not clear. The family Pulleniatinidae is described as streptospiral. This character is not included in the superfamily diagnosis.

Within the Hantkeninacea the family Globanomalinidae includes *Globanomalina* which is low trochospiral to planispiral. This is not included in the family or superfamily definitions.

The diagnosis of the superfamily Globigerinacea does not include the trochospiral to streptospiral coiling of the included family Hastigerinidae or the areal apertures of the subfamily Orbulininae. The distinction between the Porticulasphaerinae and the Orbulininae is not clear because both can have a later enveloping or enclosing chamber.

Rotaliina. The authors subsume the Buliminida *sensu* Haynes (1981) within their Rotaliina. This leads to a very unwieldly subordinal diagnosis and attempted recognition of twenty-four superfamilies but the criteria used are inconsistent. The Bolivinitacea is reduced to two genera only. These can be distinguished from the others, removed to the new superfamily Bolivinacea only by possession of truncate and carinate periphery. Genera without toothplate are removed to the Loxostomatacea. Neither of these superfamilies would appear to warrant recognition on the authors' own stated criteria. Within the Bolivinitacea, the family Bolivinoididae is set up to accommodate one genus, *Bolivinoides*, characterized by heavy costae, and a well known lineage in the Upper Cretaceous. However, a number of Tertiary species within the Bolivinidae show a similar type of ornament. Unless they are all to be given separate names, family distinction is hardly warranted.

The superfamily Cassidulinacea is much reduced, compared with the 1964 *Treatise*, when it accommodated all hyaline-oblique rotaliids. Indeed, both radial and hyaline forms are now included in the family Cassidulinidae, as are genera with and without toothplates. But although *Orthoplecta* is given separate subfamily status because of possession of toothplates which make a 'spiral column', *Islandiella*, with its cornet shaped toothplate is included with *Cassidulina* in the Cassidulininae. I consider these genera, both, incidentally, radial, should be removed to the Bolivinitacea (Islandiellidae). The one trochoid, enrolled biserial genus known is placed in a family of its own, Cassidulinitidae but the superfamily definition does not accommodate it.

As defined, the Eouvigerinacea cannot be satisfactorily separated from the Bolivinacea. The Lacosteinidae includes some disparate forms probably of separate origin although initially planispiral. *Lacosteina* has a drawn out 'buliminelline' adult spiral with loop-shaped aperture, while *Elhasaella* is twisted biserial with terminal aperture. Interestingly, the surface textures are quite different.

The diagnoses given do not clearly separate the Turrilinacea and the Buliminacea. Although defined as possessing simple aperture and toothplate the Turrilinacea include the Stainforthiidae with loop-shaped aperture and well developed toothplate. A triserial genus without toothplate is also given family status.

Within the Buliminacea the family Reussellidae is not well defined because the angular chambers are not mentioned. The distinction with the family Trimosinidae is not clear and this group probably deserves subfamily status only. Despite the difficulties experienced earlier with the Cassidulinacea the authors exclude hyaline-oblique forms from the Buliminacea and Turrilinacea and place them in the Fursenkoinacea. The family Fursenkoinidae can only be distinguished from the Stainforthiidae on this basis. I consider that the superfamilies Fursenkoinacea and Turrilinacea should be reunited in the Buliminacea, which should probably include the Delosinacea as well which shows development of septal pits and bridges like the Virgulinellidae. Similarly, I would include the Stilostomellacea (five genera only) in the Bolivinitacea on the grounds that they represent uniserial end forms. Note that Revets (1989), considers that *Buliminella* lacks a toothplate and should be excluded from the Buliminacea.

The superfamily Discorbacea is defined as low trochospiral but the first family within it, the Conorbinidae is defined as low to high trochospiral and it also includes, within the Eponididae, the subfamily Rectoeponidinae which becomes uncoiled and uniserial in the adult. The superfamily includes fifteen disparate families. No clear distinction is made between families such as the Discorbidae and Rosalinidae which have open umbilicus tending to become secondarily closed by umbilical flaps or bosses and those such as the Eponididae in which the umbilicus is primarily closed. I consider these features should carry more weight than the presence of the poreless patch used to bring together *Baggina* and *Cancris* which have very different umbilical characters. Poreless areas are common in genera of diverse groups and like ornament and surface texture should not be used at family level in isolation from other features. Incidentally, *Baggina* is defined as possessing closed umbilicus but on pl. 591, fig. 6, the umbilicus is shown to be open. The Discorbidae are described as having the chambers subdivided by a 'paries proximus' defined (Glossary) as a septal flap. This confuses the toothplate (umbilical flap) with the septal flap attached to the previous apertural face.

The superfamily Glabratellacea is distinguished from the Discorbacea by the presence of radial striae around the umbilicus on the ventral side which are presumed to facilitate and indicate plastogamic reproduction. The mode of reproduction in most foraminifera is unknown and it is difficult to accept that plastogamy and radial umbilical ornament is necessarily confined to one superfamily (largely to one family) considering the range of the morphologies (including the high trochoid *Buliminoides* considered *incertae familiae* by Revets (1989)) that are brought together by this approach. A case in point is that of *Rosalina parisiensis*. Specimens in the British Museum (Natural History) collections, ascribed to this species on grounds of prominent ventral ornament, include forms that otherwise clearly belong to *Discorbis*, *Rosalina*, *Discorbitura*, *Discorbinella*, *Neoglabratella*, *Neoconorbina*, etc. (Haynes and Whittaker in prep.). This suggests that ornament should be allowed little more than specific weight in this group.

The superfamily Siphoninacea is not adequately defined. The development of planispiral and streptospiral growth is only introduced in the definition of the family Siphoninidae. Uniserial should have been added to the description of the subfamily Siphonininae to distinguish them from the trochospiral to uncoiled, biserial Siphonidinae. However, there are only five genera in all.

The superfamily Discorbinellacea is distinguished from the Discorbacea on the basis of possession of an arched or slit-like equatorial, basal aperture but this superfamily definition is inadequate because genera with areal apertures such as *Discorbitura* are also included. This approach also brings together the Pseudoparrellidae, with closed ventral umbilicus and the Discorbinellidae with umbilical open or secondarily closed with umbilical flaps and/or bosses. It is also inaccurate in that four of the nine genera included in the family Discorbinellidae do not possess equatorial apertures. One of these genera, *Carlfranklinoides* is clearly shown to have radiating striae around the ventral umbilical aperture in pl. 631, fig. 14, although it is stated that 'none is present on the holotype'. On the authors' own criteria this genus should have been transferred to the Glabratellacea. The genus *Cibicidoides* is transferred to the family Parrelloididae although the aperture appears to extend around the dorsal spiral suture as in other members of the *Cibicides* group. *Woodella* does not show the differentiation into a relatively poreless ventral side and coarsely perforate dorsal side given as a family characteristic, so all three genera placed here probably belong in different groups elsewhere.

As defined, the superfamily Planorbulinacea is stated to be distinguished by extra-umbilical to nearly equatorial aperture and coarse perforations while planispiral coiling is not mentioned. This would exclude the Planulinidae, trochospiral to planispiral and finely perforate with equatorial aperture, and the Cibicididae, aperture equatorial and possibly extending over the periphery and with a number of finely perforate genera. The Bisacciidae are irregularly planispiral with sutural canals so probably should, indeed, be excluded. Within the Cibicididae the genera are finely split but the distinctions are not clear, especially between *Cibicides* and *Lobatula*. *Discorbia* with umbilical flaps round an open ventral umbilicus would be better placed in the Discorbinellacea. The Planorbulinidae clearly derive from the Cibicididae but the Cymbaloporidae included here with them show no such relationship. The presence of umbilical apertures and cover plates, and lack of dorsal attachment surface indicates a closer relationship with the Discorbacea. *Montfortella*, included in the Cibicididae, should probably be transferred to the Victoriellidae which show the development of a pseudumbilicus with secondary umbilical openings on the spiral, ventral side. The range of the Planorbulinacea is given as Early Cretaceous to Recent on the basis of one genus only, *Epithemella*. Its ventral, umbilical aperture and attachment surface suggest removal to the Discorbacea. This would make the range of the superfamily, Late Cretaceous to Recent.

Spreading, irregular and branching forms are included in the superfamily Acervulinacea, described as lacking an aperture apart from mural pores. In *Acervulina* the aperture is stated to consist only of coarse perforations. However, the figures of *A. inhaerens* given on plate 659 clearly show peripheral and dorsal, sutural apertures resembling those of *Planorbulina*. This seems to indicate that *Acervulina* probably represents an extreme, irregular variant of *Planorbulina* and cannot be used as the type of a new superfamily.

The definition of the superfamily Asterigerinacea is inadequate in that it does not cover the orbitoidal Lepidocyclinidae which are included. It is also defective in that it includes the formation of supplementary chambers as a key feature which excludes the Epistomariidae, subfamily Nuttallidinae, on the authors' own criteria. Further, the families, Alfredinidae, Asterigerinatidae, Asterigerinidae (one genus only) and Amphisteginidae (one genus only) cannot be distinguished on the criteria given. The authors synonymize the Anomalinacea with the Asterigerinacea following the suggestion of Hansen and Rögl (1980) that *Anomalina* (Anomalinidae) is identical with *Epistomaroides* (Alfredinidae). Here the authors have acted hastily. The type of *Anomalina* has certainly been lost but the International Committee on Zoological Nomenclature has not yet suppressed the name. Although Hansen and Rögl recovered *Epistomaroides* from Mauritius but failed to recover the type species of *Anomalina* (*A. punctulata* d'Orbigny), in what is its type locality, this does not (and cannot) prove that d'Orbigny actually described what we now call *Epistomaroides* as *Anomalina*. This is unlikely because although there is a general similarity in coiling mode (shared by many genera) the apertural and sutural details are quite different. The case of *Anomalina* should remain open.

The superfamily Nonionacea is defined as 'planispiral to slightly asymmetrical' but a number of the genera included are described as low trochoid, such as *Spirotectina* and in the case of *Queraltina*, described as 'distinctly trochoid'. The *Pullenia* group is included in the family Nonionidae although they have primarily closed umbilicus and lack the distinct perforation of *Nonion* and its allies. *Melonis*, although it is described as having ten to twelve chambers in the final whorl, is included in the subfamily Pulleniinae, defined as possessing 'few chambers per whorl'. The Almaenidae are also included in this superfamily although the general form, peripheral apertures and coarse perforation suggest closer links with the Planorbulinacea.

The definition of the superfamily Chilostomellacea as trochoid and hyaline-oblique ('granular') is defective because the family Chilostomellidae is then defined as trochospiral to planispiral and hyaline-radial genera are included in the family Trichohyalidae. It also fails to cover the families included with the deep folds in the apertural face (Alabaminidae), supplementary apertures (Oridorsalidae) and toothplate (Coleitidae). Although the superfamily is defined as with ventral ('umbilical') aperture, the family Heterolepidae in which the aperture runs on to the dorsal side, as in *Cibicides*, is also included. This is largely because of wall structure, revealed by the authors' statement that 'optically granular' species of *Cibicidoides* should be transferred to *Gemellides*, a hang-over from their attempted splitting of the Anomalinidae on these grounds in 1964, shown to be unsound (Wood and Haynes 1957; Bellemo 1974; Haynes 1981). This family is better included in the Planorbulinacea. The family Gavelinellidae differs from the Chilostomellidae in that the ventral aperture runs into the umbilicus which tends to become closed with umbilical flaps and is nearer to the Discorbacea. Genera with primarily closed umbilicus such as *Hollandina* and *Paralabamina* belong elsewhere. *Hanzawaia*, with flaps (lappets) on the dorsal side, is another anomalinid. *Discanomalina* as illustrated appears to include disparate forms and requires restudy; the inclusion of Irene McCullock's figures of *Pseudorosalinoides chatamensis* being possibly a *lapsus calami*. Unrelated forms also appear to be included in the family Trichohyalidae. *Trichohyalus* appears to be a highly ornamented discorbid, near to *Neoglabratella*, whereas *Aubignya* lacks radial costae and has umbilical lobes. The type of *Aubignya*, *A. mariei*, is closely similar to *Ammonia perlucida* and should probably be transferred to the Rotaliacea.

The treatment of the superfamily Orbitoidacea is confused. The family Orbitoididae is split into two subfamilies according to whether lateral chamberlets are differentiated or not but *Schlumbergeria* is synonymized with *Orbitoides*, although it is without lateral chamberlets and appears to be its undifferentiated ancestor. The superfamily is diagnosed as without canals and this is repeated in the definition of the family Lepidorbitoididae. However, the subfamily Lepidorbitoidinae is taken to include *Arnaudiella* which has radial canals. The subfamily is also taken to include the non-orbitoidal, canaliculate *Daviesina*, *Praesiderolites*, *Pseudosiderolites* and *Sulcoperculina*. These genera belong elsewhere but this treatment supports the idea of Van Gorsel that the Lepidorbitoididae originated from *Pseudosiderolites* (see Haynes 1981) and its inclusion in the Rotaliacea.

The superfamily Rotaliacea is inadequately defined because it does not cover the orbitoidal families. Pseudorbitoididae and Miogypsinidae which are included, or the conical Chapmaninidae. The Rotaliidae are defined as trochoid but include the subfamily Cuvillierininae defined as trochospiral to nearly planispiral. On examination this subfamily is found to include both trochoid forms, *Pseudowoodella* and fully planispiral forms, *Fissoelphidium*. These should be excluded, with the *Cuvillierina* group recognized as a full family. It is not clear what is meant by the distinction drawn between the subfamilies Rotaliinae and the Ammoniinae on the basis that the umbilical area is 'primarily closed' by an umbilical flap in *Rotalia*, while it is 'secondarily closed' by a foraminal plate in *Ammonia*. A scroll-like toothplate is attached below the areal foramen in *Ammonia*, whereas a partial umbilical partition is formed in *Rotalia* and the foramen remains a basal opening, like the primary aperture. Both appear to be built at the same time as the chamber. In both genera communication into the umbilical area below the umbilical ends of the chambers is initially open. In *Ammonia* the umbilical area tends to be filled with a plug or plugs. In *Rotalia*, the umbilical (astral) lobes coalesce and fuse as an umbilical coverplate similar to that in *Discorbis*. Together with the presence of the umbilical partitions ('toothplate') this prompted the suggestion by Lévy *et al.* (1984, 1986), that the Rotaliidae should be subsumed within the Discorbidae. However, in the adult this coverplate is broken up by growth of pillars and development of open sutural canals by resorption (Haynes and Whittaker, in press) which clearly distinguish the genus from *Discorbis*. The authors also include the Elphidiidae, a primarily planispiral group in this superfamily. However, I believe a more natural place for this group is within the Nonionacea, as early forms grade with the Nonionidae both in wall structure and gross morphology. The appearance of the septal flap seems to have been an independent development in this superfamily (Haynes 1973).

The Nummulitacea are defined as planispiral but include the family Pellatispiridae described as planispiral to low trochoid. This family, without marginal cord and showing development of fissures, would more naturally find a place in the Rotaliacea. Incidentally, although the authors state 'vertical canals or fissures may be well developed', in the Pellatispiridae, they are not mentioned in any of the genera described, e.g. *Miscellanea*. The orbitoidal nummulitaceans are split into two families according to whether the annular chambers of the equatorial layer are divided or not. However, *Asterophragmina* is included in the Discocyclinidae, defined as subdivided, although the adult annular rings of this genus are clearly undivided (pl. 819), and in the genera included in the Asterocycylinidae, defined as undivided, the annular rings are clearly divided (Pls. 824 and 825). The reason for this apparent anomaly, is that the authors regard the annular rings of the Asterocyclinidae as consisting of cycles of small, spatulate to rectangular, primary chambers, whereas in the Discocyclinidae each adult equatorial chamber is a ring, that may or may not be subdivided into small secondary chamberlets. This should have been made clear. If it is actually the case, it indicates that these two families are of quite separate origin and probably belong to different superfamilies, other superfamilies in the scheme have been separated on features of rather less weight.

DISCUSSION AND CONCLUSIONS

Understandably, considering the complexity of the problem and the present state of knowledge, the authors have only been partially successful in producing a more natural (genetic) classification. Despite a brave attempt to 'untie the knot', they would almost certainly be the first to admit that large elements remain clearly artificial. Also, as pointed out by the reviewers, in many cases the diagnoses are vague and even contradictory and they have not been able to push through a thorough-going, logical, hierarchical scheme. As might be expected, the large amount of new material and information that has become available (and is still in full flood) has produced more problems than it has solved. It has forced them to abandon their 1964 attempt to make a clearcut division on the basis of wall structure, aperture form and coiling mode and to raise other characters to suborder and superfamily rank. In so far as this is a measure of the real complexity of relationships it is to be welcomed, because there can be no return to past simplicities, however beguiling.

A positive attempt is made to solve the problem of Carpenter's perforate 'arenaceous' group by recognizing them as a separate superfamily. Although it is still not clear whether the diverse canaliculi, passages, pseudopores and tubuli in other agglutinated genera all represent separate lines, this move is supported by work on wall structure by Brönniman and Whittaker (1988) and by Bender (1989). Other changes, such as the use of surface texture at superfamily rank, are likely to be more controversial. Certain weaknesses also persist from their former classification. Despite the demonstration that hyaline-radial and hyaline-oblique ('granular') wall structure are close to each other, so that one is easily derived from the other, and the consequent abandonment of hyaline-oblique structure as a basis for recognition of the Cassidulinacea, this distinction is still a major factor in regrouping of genera in other superfamilies. The tendency to discount ontogeny as an indication of evolution is also inherited from the *Treatise* and also leads, I believe, to horizontal groupings, particularly in the case of the Textulariina and the Lagenina.

It is evident from this historical account, down to the latest and most ambitious attempt, that a stable, i.e. natural, classification of the Foraminifera is still a distant goal. The lesson for stratigraphers and, particularly, macro-evolutionists, is that they must treat suprageneric taxa and even genera with great caution. In the circumstances, workers not primarily interested in classification and evolution can be forgiven for thinking they should be abandoned. For instance, Culver *et al.* (1987, p. 169) suggest that, ideally, species-level data should be employed, because they doubt 'the significance of evolutionary generalisations based on the entirely human constructs of higher taxonomic categories'. But the horizontal limits we draw between species are also artificial, and as viewed in time, species are human artifacts, whether recognized as part of a phyletic line or as an allopatric branch (in both space and time) where the connecting cline is known. The objective biological reality of living species viewed as interbreeding population groups, separated from their closest relatives by morphological discontinuities, must not be confused with the subjective limits we are bound to draw between these species and their ancestors. For instance, even where we know the ancestry in a clear cut case of allopatric speciation, we still have the problem of deciding the limits between parent species (type subspecies), the peripheral subspecies (possible founder populations) and the new species (type subspecies). Most species are cryptogenes (the ancestry is not known) and we can only estimate the possible number of ancestral taxa and intermediate forms lost in the stratigraphical gaps or not preserved. We have to be careful not to confuse the species, as preserved, with the 'natural species' and appearance in the stratigraphical record with 'origination'.

It is precisely these confusions which vitiate recent attempts to replace 'traditional intuitive' taxonomy, by the methods of numerical taxonomy, or those of cladistics, with which it is hoped to draw hard and fast lines between species. In the case of numerical taxonomy, there will be no quarrel with the introduction of more refined measurements. It is the attempt to place reliance entirely upon numerical values, given equal weight, that cannot be sustained. Of course, if weighting is applied, the supposed 'objective' nature of the enterprise is destroyed. Numerical methodology cannot be more than the handmaid of taxonomy and in this role provides a very useful adjunct, as is shown by the work of Barnett (1974), Malmgren (1974) and Scott (1974).

In the case of cladistics we have to separate the extraordinary claims made for it as 'scientifically rigorous and operational' compared with traditional taxonomy, and its results in practice. Like numerical taxonomy, it pretends to objectivity in replying on morphological characters given equal weight to establish the degree of genetic difference. It is supposed that 'real' species, as distinct from 'hypothetical' species, can be defined on the basis of 'splitting events', i.e. 'discontinuities', and further, that these 'speciation events' are the only objective ('non-intuitive') boundaries, apart from terminal extinction, available for definition of species taxa. Genera are taken to include daughter species and ancestral species back to the next available name.

The most ambitious attempt to apply cladistics to foraminifera is that by Fordham (1986), on the Cenozoic planktonic fauna of the Pacific, reviewed by Banner (1987), Chaproniere (1987) and Adams (1987). These authors are as one in dismissing it as neither objective, nor operational or practical. The discontinuities between species-clusters are distinguished by the first and last appearances of constituent subspecies (phena), some by only one, although it is admitted they are arbitrary. The fossil record is presumed to be complete and no account is taken of discontinuities caused by variations in sedimentation rate, sedimentary breaks, oceanographical changes and inclusion in the death assemblage of species and subspecies adapted to different levels of the stratified water column. A further serious objection is that the method relies on a severely restricted model of allopatric speciation in which the dichotomous appearance of two daughter species leads to elimination of the ancestral species. As Adams points out, most biostratigraphical work proceeds on the 'well-justified' assumption that ancestral species do not necessarily die out as a consequence of speciation. Not only are geological events confused with originations of palaeontological species but also with biological 'speciation events'. Clearly, cladistics is a metaphysical system imposed upon the facts rather than arising from them. It is unlikely to lead to more soundly based species or supraspecific categories. The bold claim that 'Histories, terminations and the reproductive nexus are easy' (Kitcher 1989) will, therefore, ring hollowly in the ear of the practising taxonomist.

The central place occupied in cladistics by an extreme model of allopatric speciation reflects recent fashion, particularly in America (one does not have to be a marxist to see the connection). However, although Haldane (1959) prophesied that allopatric speciation would come to be accepted as the norm, and Ruse (1982) decided that 'totally sympatric speciation is rare', the stratigraphical record of the Foraminifera suggests that both rapid allopatric branching and relatively slower, sympatric transformation take place. Well known evolutionary trends in larger foraminifera interpreted as examples of phyletic evolution are shown by *Lepidolina* (Ozawa 1975), the *Orbitoides* lineage (Gorsel 1978), *Cycloclypeus* (MacGillavry 1978) and in planktonics by the *Globorotalia menardii/tumida* lineage (Malmgren *et al.* 1983). The gradual trend in *Lepidolina* was dismissed as 'pseudogradualism' by Gould and Eldredge (1977) and a possible result of 'clone selection'. However, these larger foraminifera show both sexual and asexual generations.

One of the reasons for the popularity of exclusively, allopatric solutions may be that formerly, average selection pressure was thought to be quite low; Fisher (1930) considered 1% selection for advantageous qualities was a reasonable average throughout geological time. As a consequence, emphasis was put on the isolation of small populations (even reduction to a biblical pair) with only a fraction of the parental gene-pool, to account for rapid change. However, it is now known (Ford in Huxley 1974) that selective forces are up to thirty times greater in nature than had been realized, and therefore more effective on larger populations than previously admitted. After all, although the Galapogos finches are a remarkable example of rapid differentiation from small, immigrant, founder populations, the case of the medium ground finch (*Geospiza fortis*), which was permanently reduced to the large beaked form by a major drought (Boag and Grant 1981), represents rapid sympatric evolution through operation of an environmental 'bottleneck' on a relatively large population.

The many convergent lines of evolution towards complex orbitoidal structure in the large rotaliids appear to be related to the development of low fertility, reefal environments, perhaps with initial 'bottleneck' reduction to the most effective symbiotic species, amongst small rotaliids, followed by gradual acquisition of a more efficient algal-greenhouse structure. All the stages can be seen particularly well in the Miogypsinidae, Orbitoididae and Lepidocyclinidae. There is, of course, no occasion for the use of the 'morphological gap', but genera can be distinguished on the basis of important structural changes and innovations ('novelties' of Adams 1983), e.g. the appearance of lateral chamberlets which distinguish *Miogypsina* from *Miogypsinoides*, and *Orbitoides* from *Schlumbergeria*.

Generic and suprageneric categories are natural as far as they represent clusters of species that have evolved from ancestral groups by changes at the species (subspecies) level. Again, as far as they are natural, they will be 'real entities' that reflect major evolutionary responses to the challenge of global physiographic change and the opportunities provided by extinction of groups that formerly dominated a particular environmental range. Loeblich and Tappan's new classification, despite its imperfections, reveals even more dramatically than formerly how replacement has been a constant theme in the evolution of the Foraminifera (for ranges of the suprageneric groups see Ross and Haman 1989). Generic ranges are given by Danielle Decrouez (1989). However, it is sobering to realize that in no case is there direct proof of the evolutionary origin of any of the twelve suborders recognized and the ancestral groups remain speculative.

PRINCIPLES OF CLASSIFICATION

After the historical study it will be helpful to provide a brief statement of what appear to be the prerequisites of a more natural classification.

1. Foraminifera are the largest and most varied invertebrate group, have the most complex shells and include some of the largest protozoans. Although acellular, life histories are complex, there may be multinucleate phases and chromosome numbers are high. Even Class status may provide too narrow a framework for the complexity of relationships to be expressed.

2. A simple ordinal/subordinal scheme based on wall structure is not possible. There are at least two calcitic Palaeozoic groups, one microgranular, one largely 'vitreous'; both perforate and imperforate groups of agglutinated forms, plus a group secondarily derived from the miliolids; two groups of porcelaneous forms, one with perforate ancestry; four groups of microcrystalline calcitic, hyaline forms, the buliminids possibly derived from perforate agglutinated forms, the nodosariids from 'vitreous' ancestors, and the globigerinids and rotaliids of unknown origin. The relationship of the calcitic groups to the poorly known aragonitic group is obscure.

3. Coiling modes are not 'isomorphous' in the different wall structure groups but adaptive radiation at different times into broadly similar environments and ecological niches has led to heterochronous homoeomorphy with the constant repetition of certain styles. There are trends in test architecture towards both increased complexity and simplification and both coiling-up and uncoiling (even recoiling and uncoiling) occur. In general, groups adapted to vagrant surface feeding in high energy environments remain close-coiled; groups secondarily adapted to infaunal environments often show uncoiling and simplification with growth and attendant serial, apertural modifications; groups adapted to symbiotic life show increased size and complication of structure. Contrasting modes within the larger Foraminifera illustrate the 'developmental constraints' of the non-lamellar test, i.e. only the *Somalina* line in the porcelaneous group achieves 'orbitoidal' structure. New features tend to occur in the adult and proterogenesis is less common, but especially in symbiotic forms there is often striking differentiation of the juvenile (possibly connected with dispersal). Multiform genera probably adopt different life habits at different stages. Neotony may be a factor in the rise of certain groups, such as the planktonics. Ontogeny, therefore, has to be used with great care as a guide to phylogeny.

4. Only detailed stratigraphical and evolutionary studies can solve the problems of iterative evolution, parallel development and convergence peculiar to Foraminifera. In these circumstances, numerical taxonomy and cladistics (which in its 'transformed' manifestation excludes these problems from consideration) cannot be substituted for traditional taxonomy, i.e. the careful comparison of test architecture and wall structure, apertural and internal features, taking gross similarities and differences into account, with the evidence of ontogeny and the stratigraphical record, to establish phylogeny.

5. Although it is not true that traditional taxonomy relies exclusively on unique rather than shared characters, as supposed by Fortey (1989), care must be taken not to employ any one feature as a single 'key'. As Carpenter put it, 'a natural system depends on the whole aggregate of ascertainable characters'. In this aggregate we must include coiling-mode; banished by Carpenter but continuing to haunt classification like Banquo's ghost. The supposition that features established

at one level in one order can be applied with equal weight in another order, with a different evolutionary history, must also be avoided.

6. 'Species are made by isolation,' as Darwin put it, but populations can be 'islanded' in time as well as space and evolutionary patterns are complex in Foraminifera, suggesting that both allopatric branching and sympatric phylogenesis have taken place. As is to be expected, rates are variable, though sympatric phylogenesis appears generally to be relatively slow, perhaps because selection is working on larger populations. Attempts to arrive at an 'objective', supraspecific classification by application of a stereotyped model of dichotomous allopatric speciation should be avoided. Darwin's famous model of the irregularly branching tree of life (the only diagram in the *Origin*) is more appropriate. Also, as pointed out by Adams (1983) the relatively rapid appearance of 'novelties' which then become stable, together with the slower modification of existing characters can give the appearance of punctuated equilibrium and gradualistic evolution in the same family.

7. The contribution of biological studies, although important, is so far limited. Paradoxically, despite their stratigraphical importance, less is known about living Foraminifera than about the living representatives of any other major group. Further studies of life history, functional morphology, genetics and cytology are a *sine qua non* of an improved classification. The study of living, naked forms (Allogromiida) is also a particular need.

Acknowledgements. I am indebted to the two referees who commented on the original draft of this paper, intended as an essay review of Loeblich and Tappan's book, and who encouraged me to examine it in historical context, especially in regard to problems that can be traced back to the work of the English School. In particular, Dr C. G. Adams and Dr J. E. Whittaker provided references and copies of reviews of earlier classifications, including the attempt to use cladistics by Fordham. Unfortunately, I was unable to borrow a copy of the doctoral thesis on foraminiferal classification by Martin Janal for copyright reasons. The paper was typed by Mrs Janice Evans.

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Typescript received 5 April 1989
Revised typescript received 4 December 1989

NOTE ADDED IN PROOF

Since the publication of Loeblich and Tappan's book in 1988 the following modifications have been made to their subordinal scheme. First, Loeblich and Tappan (1989) have recognized the new suborder Trochamminina of Brönniman and Whittaker (1988) and in addition they have reinstated the suborders Haplophragmiina and Astrorhizina. This gives the following four-fold breakdown for the agglutinated group:

Astrorhizina – unilocular with organic cement
Trochamminina – multilocular, cement organic, wall simple
Haplophragmiina – multilocular, cement organic wall simple to alveolar
Textulariina – multilocular, cement calcareous, typically canaliculate

Secondly, Revets (1989) has erected the new suborder Delosinina to accommodate the genus *Delosina*, considered to have a unique monolamellar, irregular microgranular, calcitic wall. The addition of this last would bring the number of suborders in Loeblich and Tappan's scheme to sixteen.

Further to the above it can now also be stated that the International Committee on Zoological Nomenclature has decided to take no action in the case of *Anomalina* and the Anomalinidae and their status therefore remains unchanged (Whittaker, pers. comm.).

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