South valley university

Faculty of science

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Micropaleontology

3rd year geology

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Chapter 1

The Scope of Foraminiferal Studies

> A palaeontologist, writing about their dead shells, would have no scruples in entitling them 'Famous Fossils'.
>
> (Sandon, 1957)

A possible title considered for this textbook was 'The Geological Uses of Foraminifera'. Certainly no other group of fossils is more important to the geologist, and the majority of palaeontologists employed in industry and oil exploration are specialists in Foraminifera. As a perusal of the 'Index and Bibliography of Micropalaeontology' will show, over 500 scientific articles are published each year on this group alone. This is a direct reflection of their importance in the economic field. But their fame rests equally on the attraction of their exquisite architecture to the artistic and scientific mind. Indeed, the early microscopists frankly disavowed any utilitarian intent and this attitude was strongly endorsed by Walker and Jacob (1798) in the earliest British study of Foraminifera with scientific (Linnean) nomenclature. This work includes the following quotation:

> Let not the minuteness of the objects here delineated call up the surly enquiries of those who have not been accustomed to live with their eyes open to the works of nature: they are not fit judges in this matter. If they will persist in asking 'Of what use is all this labour? What good can accrue to mankind from this knowledge, in point of food or other use?' We know of none at all, either present or likely to happen, as to the body, for use or ornament, or to the satisfying any appetite: nevertheless, a much nobler idea will take its rise in our opinion; one which, by displaying so momentously the power of the omniscient Creator, will thwart the infidel in his favourite ideas of escaping the eyes of the almighty, and force him as he descends the scale from the more immense objects to these minutissima, to confess, that the being which has formed these, can fully equal all that the tongue of man has yet declared of the possibility of his power. For what a train of wonders have we here to pursue? What must be the economy of animals so very diminutive, so weak, so exposed from their situation to the force of every rude wave, and who notwithstanding, so often escape unhurt? How do they rear their young? From whence collect their prey?

Two hundred years of research were to be devoted to these questions but, ironically, only a few years were to elapse before William Smith, early in the nineteenth century, demonstrated the stratigraphical usefulness of fossils and Foraminifera became prominent in classical palaeontology. But delight in their intricate beauty of form, so remarkable in a single-celled animal, has remained a mainspring of research into Foraminifera to our own day. This is shown by the signal contribution made by amateurs: Brady—a chemist, Flint—a surgeon, Wright—a grocer, and Earland—a post office official. Fortunately, despite the advent of expensive aids to research like the transmission electron microscope (TEM) and the scanning electron microscope (SEM), Foraminifera can still be effectively studied with quite simple equipment and amateurs can still play their part.

The complexity of shell structure in Foraminifera which attracted the early microscopists is also the basis of their geologic use. Simple forms appeared in the Cambrian and dominate the Lower Palaeozoic. The subclass became abundant with the evolutionary development of relatively large and complicated test architecture by the late Palaeozoic, and new families continued to appear through the Mesozoic and Cenozoic (figure 5.3). This long and well-marked evolutionary record makes Foraminifera of outstanding value in zonal stratigraphy.

An incident aptly illustrating this aspect of the geological utility of Foraminifera occurred during the drilling of the Mochras Borehole on the shore

of Northern Cardigan Bay (Wales), a joint venture between the Department of Geology, Aberystwyth and the Institute of Geological Sciences (plate 4). This borehole was sited west of the Mochras Fault by Professor A. Wood to investigate the previously unknown submarine stratigraphy of the bay by means of a continuously cored section. By March 1968 the drilling had penetrated over 300 m of red and green marls and sandstones of presumed Tertiary age, and the possible age of the next formation likely to be penetrated was debated with some excitement. Estimates ranged from as old as the nearby Lower Palaeozoic rocks of the Harlech Dome, east of the Mochras Fault, to as young as Upper Mesozoic, perhaps even as young as the Upper Cretaceous Chalk. Finally, the news was telephoned from the rig that the borehole had passed through an unconformity and penetrated a grey shale that resembled the Carboniferous shales in the Cheshire Basin. At this time Professor Wood and a number of members of the Department of Geology were away at sea, on the research vessel 'John Murray', carrying out marine, geological and geophysical researches. I therefore passed the news on to them by Radio Telegraph before visiting the rig to collect samples from the new cores for analysis.

Preparation of the core material was simple. The chips struck off the cores by the blows of a hammer were further broken down to pieces about 1 cm in diameter and boiled in water with washing soda. When the shale had broken down to mud the sample was poured through a fine mesh sieve so that the sand-sized material could be retained while the mud was washed away. The sample was then dried and shaken gently through a nest of sieves to separate it into different size fractions for ease of examination.

I first looked at the coarsest fraction under the lowest power ($\times 10$) of a stereoscopic, binocular microscope and after a little searching noticed a triangular shell flake. My first thought was that this could be a fragment of a bivalve or ammonite, but examination under a higher magnification soon revealed that it was a perfect specimen of the foraminifer, *Citharina* (plate 11, nos. 5, 8). This genus first appeared in the lower part of the Jurassic Period in the Liassic Epoch. Immediately it was clear that the shales penetrated by the cores were not Palaeozoic and were most probably early Mesozoic. This was confirmed by the microfauna in the finer fractions of the sample which included numerous other examples of Foraminifera belonging to the family Nodosariidae (chapter 9) and characteristic of the Lias.

Another message then crackled out from the radio station at Holyhead, North Wales to the Aberystwyth party in the storm-tossed research ship—'Forams indicate Lias'—a message no doubt thought to be in code by the operator but vital information for the geophysical investigation of the layers of rock beneath the sea floor.

The reason why Foraminifera are important in oil exploration and other subsurface work as *index fossils* (indicators of a particular geological age) lies not only in their abundance but equally in their range of size. This is generally between 0.10 mm and 1.00 mm and averages about 0.33 mm, equal to the fine sand grade of sediments, although some are macroscopic and exceed 5.00 mm in diameter, 'Larger Foraminifera', and some are smaller than 0.10 mm, 'Microforaminifera'.

The importance of the size of Foraminifera in subsurface work will become clear if we consider the basic technology of exploration drilling. The Mochras Borehole was drilled by a process of continuous coring with cores up to 6 in (150 mm) in diameter. This is very costly and is normally only indulged in by government or international agencies with the necessary financial backing and when a complete stratigraphical analysis is required of particular key sections. An up-to-date example is the United States programme of coring in the major oceans, JOIDES—Joint Oceanographic Institutions for Deep Earth Sampling, now replaced by IPOD—International Programme of Ocean Drilling, with participation by major European countries including Britain. The financial and scientific effort is on the scale of space exploration and radio astronomy and Foraminifera find their place in a general appraisal of the sediments which includes other, very small microfossils (nannoplankton) and the macrofauna such as Mollusca which is also preserved in large-diameter cores.

By contrast, in the hard-headed, cost-conscious world of the oil men the majority of boreholes are the result of rotary drilling with cores taken only at particularly important intervals. The basic technology is outlined in figure 1.1. The oil derrick (named after a notorious hangman of 'Tyburn Tree') supports a 'drill string' of hollow drill pipes with a drilling bit on the end which is rotated like an auger into the ground. The drill string which consists of round, 30 ft (9 m) pipes joined by collars turns freely on a 'swivel' and moves down on a 'travelling block', the weight of the string itself providing the necessary downward force. Rotation is transmitted by a diesel-powered winch ('draw works') via the 'rotary table' which grips a square 'kelly' at the top of the drill string. The bit which is of hardened or diamond-studded

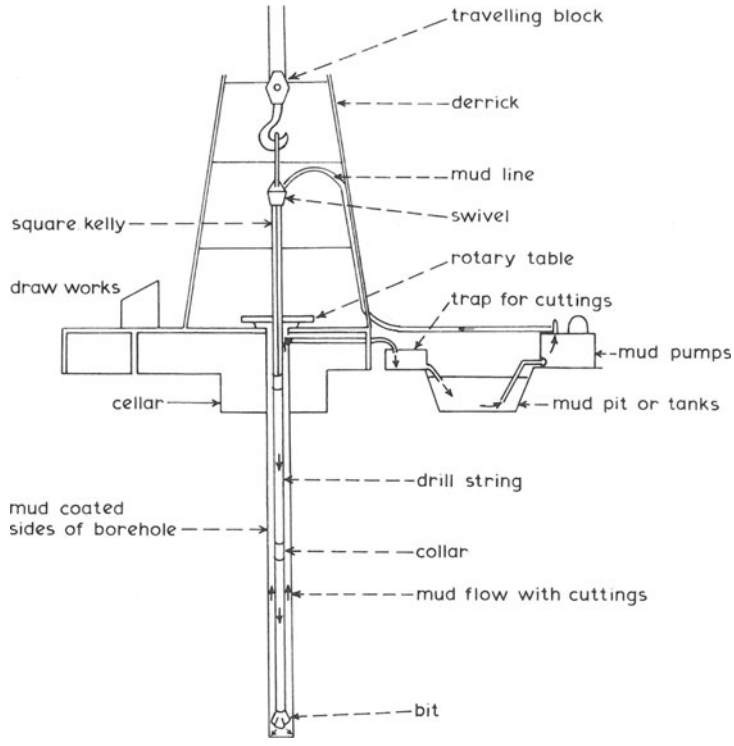

Figure 1.1 The basic technology of rotary drilling

steel is lubricated by a special drilling mud which is pumped down the drill pipe and through the bit to come back between the pipe and the borehole wall. The mud cools and lubricates the bit and provides a seal which helps to prevent the wall of the borehole caving or sloughing off with loss of fluids from the formations that have been penetrated. Not of least importance, the mud carries out the drill cuttings, sometimes called 'ditch cuttings' because in the old days they were simply run off into the ditch to the 'mud pit'. They are now caught in a box or mechanical sieve ('shale shaker') before the mud goes back into the mixing pit. Samples of the cuttings are usually taken to represent every 10 ft (3 m) interval drilled. The necessity for the mud to be of a quality to carry out these functions has called into existence a new tribe of specialists. These are the 'mud sniffers' who study mud chemistry and weight it with minerals such as barytes to counterbalance oil and water pressures. Nowadays this is done in special tanks.

Drilling can be continued until the top of the kelly is at the rotary table. It is then unscrewed and another pipe is winched up and attached before the kelly is replaced and drilling recommenced. Eventually, the drilling bit becomes ineffective through wear and the laborious process known as 'making a trip' supervenes. The whole drill stem has to be winched up and the pipes unscrewed one by one so that a new bit can be added. The pipes are then lowered again, one at a time, back into the hole.

It is an instructive and stirring experience to watch a well-trained and experienced drilling crew in action, whether stripped to the waist under the Saharan sun or padded up against the subzero winter temperatures of the Canadian Plains. The dangerous conditions of the rig floor, slippery with drilling mud, demand teamwork and skilful co-ordination as the 'rough-necks' grapple with the greasy pipes; a false move or inattention can result in a man being knocked down or sent spinning off the platform injured.

As the hole gets deeper, the time it takes to 'make a trip' takes longer. As depths over 10 000 ft (3 km) and even up to 20 000 ft (6 km) are commonly achieved it may eventually take several days and swallow up a considerable proportion (up to one-fifth) of the drilling time. It thus accounts for a considerable proportion of the costs. These can amount to £250 000 for a deep

hole on land, and may even reach £1 000 000 on the deeper parts of the continental shelf, as in the North Sea, where expensive drilling platforms or barges costing several million pounds are also required. On average, only one exploration borehole (wildcat) in ten is successful in finding oil, and in the case of the 'dry holes' the samples and various logs of the sections penetrated will be the only result of the expenditure of time, money and effort.

When a core is required it is necessary to fit a special drill pipe with diamond cutting wheels round the rim and a spring device for catching the core. Each time a core is taken it is necessary 'to make a trip'. It will thus be appreciated that both the driller and management will be keen to avoid coring unless absolutely necessary and to drill ahead as quickly as possible by the rotary method. In softer rocks such as shales it may be possible to drill several thousand feet of section before the bit wears out.

For this reason the majority of samples from oil company boreholes are finely crushed ditch cuttings in which only minute fossils such as Foraminifera stand a chance of escaping destruction. The economic application of the study of these fossils in the oil industry has led directly to the rise of 'micropalaeontology'—that is, the study of small fossils which because of their small size when adult require special methods of collection and examination, either by means of the light microscope or by the scanning electron microscope.

It is interesting to note that although the term was apparently coined for the microscopic study of bryozoans in 1875, micropalaeontology, for the oil industry during the early part of this century, became virtually synonymous with the study of Foraminifera and ostracods. This is because Foraminifera, like ostracods, are not only small enough to escape crushing during drilling but large enough to be identified by the same low magnification, wide-field binocular microscopes used by the well-site geologist when looking at ditch cuttings. The expensive methods of extraction, preparation and examination required by some other groups of smaller microfossils are not required. Despite certain difficulties attendant upon the use of ditch cuttings, quite adequate correlations can be made and the use of Foraminifera does not suffer from the disadvantage of requiring uncontaminated core as does the application of spores and pollen (palynology). The dramatic rise of Foraminifera as a major preoccupation of 'micropalaeontology' is therefore a reflection of the cost-effectiveness of their application in subsurface work dependent upon rotary drilling.

The chief difficulty that has to be faced in working with ditch cuttings is the strong possibility that the samples have been contaminated by geologically younger sediments caving off the side walls of the borehole during their ascent to the surface in the mud line. For this reason only the first appearances of index species can be relied on because there is no way of proving that further occurrences at lower depths are in place, rather than the result of caving. It is these 'tops', based on first appearance down the borehole (representing the last appearance in time), which are relied on for stratigraphical purposes in subsurface work. This procedure differs from that normal in surface work in which species can be traced from their first appearance in the strata through successively younger beds to their final extinction levels. Despite the disadvantage of this limitation to extinction levels (see further in chapter 14), effective correlation from well to well can be achieved by this means.

An example of the type of distribution chart usual in the oil industry is shown in figure 1.2. The species are plotted in order of appearance (with names of well-known index forms and numbers for local forms along the top). Only a semi-quantitative approach is possible with ditch cuttings, but it has been found useful to use symbols to distinguish relative frequencies in a unit sample, usually 100 g original weight.

The descending pattern of clustered symbols from left to right across the chart allows the tops to be selected on the basis of particular species and species groups. The intervals between important datum lines can then be distinguished as zones. The problem of caving is well brought out by the tendency of many species to recur at lower depths. In such cases, the complete absence of the species in question from cores taken at the same depth is very instructive. Fortunately, when conventional core is not available sufficient material for foram analysis can be obtained, in emergency, by the cheaper 'wire-line' method in which a small diameter, 1 in (25 mm), core tube is rotated on a line, or by 'side wall' coring in which a small tube is fired into the wall of the borehole by explosive.

Further difficulties include the possibility that samples may have taken longer than estimated from drilling times to reach the surface and that the tops are 'low'. This may be overcome by careful comparison of the results with the lithostratigraphy and especially with the geophysical logs which, as shown, may be conveniently included on the chart. The zonal

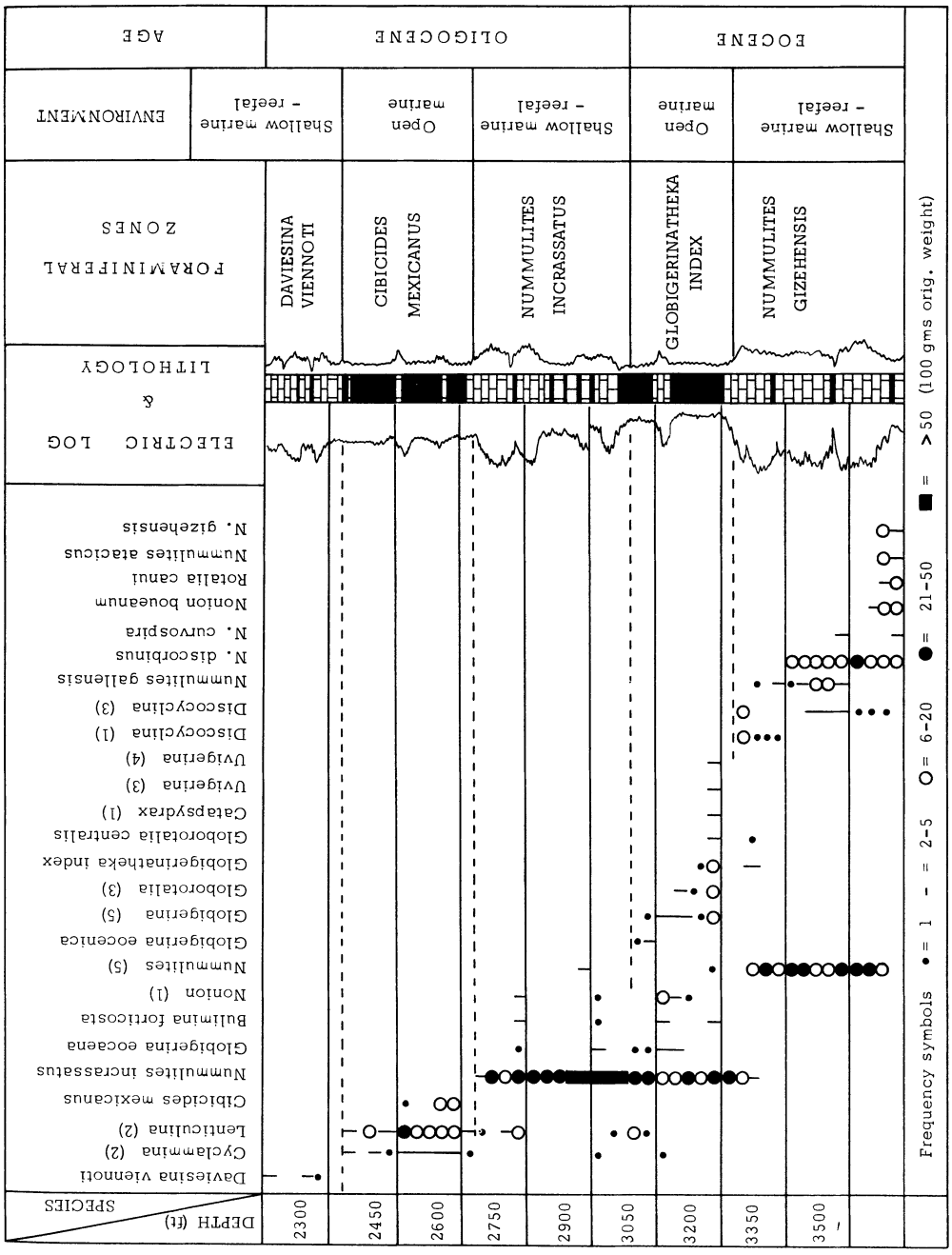

Figure 1.2 Distribution chart of Foraminifera in a subsurface borehole showing zones based on 'tops' in ditch cutting samples. Note that only a proportion of the index species are shown and the samples have been combined to represent 30 ft (9 m) intervals

stratigraphy and correlation with the standard stages, as well as the palaeo-ecological interpretation, is shown on the right-hand side. Evaluation of the oil prospects in a sedimentary basin generally requires study of several, strategically placed boreholes. The results can then be synthesised in a fence or panel diagram, as shown in figures 6.6 and 14.7.

It will be appreciated that as the deep sea drilling programme involves continuous coring, the problems of rotary drilling are not encountered and stratigraphical treatment of the samples is essentially the same as for surface samples.

In contrast to their position today, which is related to the economic imperatives of the twentieth century, the fame of forams in nineteenth century palaeontology was based largely upon the extraordinary abundance of Larger Foraminifera at certain stratigraphic levels (plates 1 and 3). On a number of occasions during the long evolutionary history of the group, relative giants of macroscopic size have arisen in a number of separate families widely separated in time. Some of these species were so successful, probably through exploiting the possibilities of a *symbiotic* mode of life in association with unicellular algae, that their dead shells built up massive limestones. This occurred particularly in the Upper Palaeozoic (fusulines), in the Upper Cretaceous (orbitoids), and in the Tertiary (nummulites, alveolines and lepidocyclines). Limestones consisting almost entirely of *Nummulites* are characteristic of the Eocene and Oligocene in the Mediterranean area of the former Tethyan seaway.

The Sphinx and the pyramids of Gizeh are all built from blocks of limestone from Mokattam in Egypt which consists almost entirely of one species, *Nummulites gizehensis* (plate 1). This genus was called *Nummulites* by Lamarck because of its resemblance to a coin (nummulus), while the trivial name indicates its provenance from the locality of Gizeh. This species was one of the largest foraminifers that ever existed and some specimens reach 7 cm in diameter. It was probably also the first known to man, as specimens were seen by the Greek historian Herodotus in his travels in the fifth century B.C. and were identified by Strabo as the petrified remains of lentils, provided by the Pharaohs as a food supply for the slaves employed in building their tombs.

Larger Foraminifera like *Nummulites* require the warm, sunlit waters of shallow, tropical and sub-tropical seas to live successfully. Similarly, most small, benthonic species (plate 2B) are acutely sensitive to facies control, including the factors of temperature, salinity, substrate and food supply. This means that the presence of extant species or related forms of fossils in stratified rocks is an extremely useful key to their environment of deposition.

A number of families of Foraminifera are abundant in the *plankton* of the pelagic realm in the open ocean. Many species are cosmopolitan and occur in broad latitudinal belts generally related to the temperature and the major ocean current systems.

Some species of *Globigerina* are so abundant that their dead shells make up a large proportion of the deep ocean 'ooze' (plate 2A). Almost a half of the abyssal plain beyond the continental shelves is covered with 'Globigerina ooze' which makes these Foraminifera the dominant rock-builders of recent time. In the North Atlantic the ooze is about 75 per cent Foraminifera and 25 per cent coccoliths (button-like plates of marine algae). To some extent it resembles the Chalk which represents a time in the geological past, at the height of the Cretaceous marine transgressions, when oceanic conditions of sedimentation invaded the continental shelves. However, the relative percentages of the two main groups are reversed in the Chalk and it is the coccoliths that dominate.

Planktonic Foraminifera show continuous evolutionary development from Cretaceous times. This, together with their wide distribution and independence of bottom conditions, makes them excellent index fossils. During the last two decades the attention of stratigraphers has increasingly turned to this group, especially after T. Grimsdale (former Chief Palaeontologist, Shell Oil Co.) outlined their possibilities for inter-regional correlation (Grimsdale, 1951). Eventually, W. Blow of British Petroleum Co. was able to erect 41 worldwide zones for the Cenozoic on the basis of these so-called 'ammonites of the Tertiary' (Blow, 1969). Figure 1.3 gives a version of this scheme taken from Saito, Burckle and Hays (1974). Incidentally, the history of the application of the planktonic Foraminifera in stratigraphy aptly illustrates the spur that economic use gives to foraminiferal studies.

SUMMARY OF THE REASONS FOR THE PARTICULAR VALUE OF FORAMINIFERA IN STRATIGRAPHY

(1) They are extremely abundant in most marine sediments, particularly in outer-shelf muds where several thousand specimens representing some fifty species frequently occur in a 10 ml volume

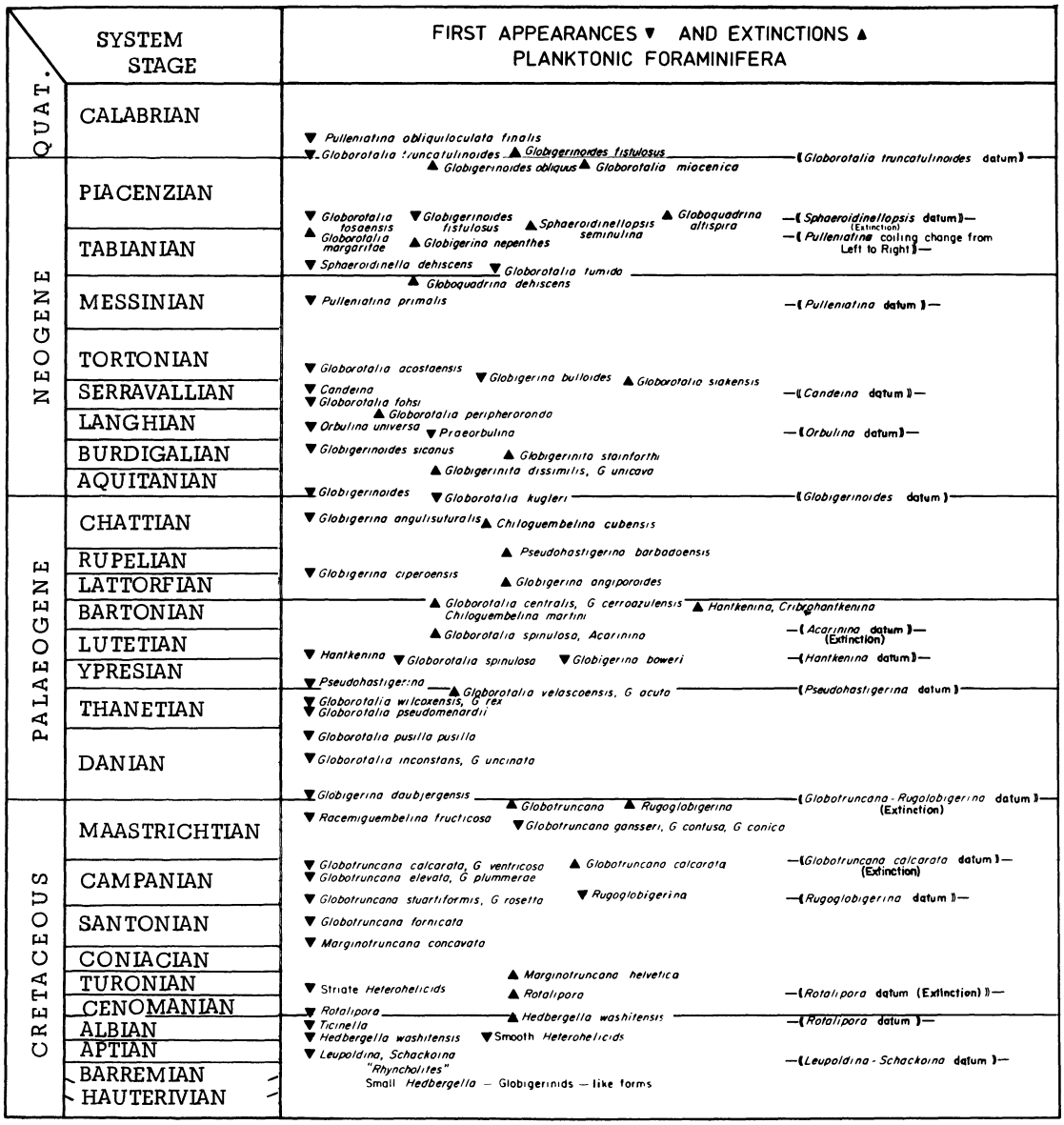

Figure 1.3 Datum levels in the Cretaceous and Cenozoic based on appearances (inverted triangles) and extinctions (upright triangles) of planktonic Foraminifera. From Saito, Burckle and Hays (1974)

sample. According to Levine (1962) they constitute 2½ per cent of the animal kingdom and more than half the known protozoa. A number of species belonging to different families also occur in brackish water but only members of the non-testate Allogromiida occur in freshwater, apart from the anomalous occurrence of *euryhaline* species in freshened areas of the River Plate (Boltovskoy and Lena, 1971). Normally, therefore, the occurrence of Foraminifera is an indication of marine (high marine to brackish) conditions.

(2) They average about 0.33 mm in diameter (fine sand on the Wentworth scale), with a general range from 0.10 mm to 1.00 mm. This means that they escape destruction during the ordinary process of rotary drilling. They are easily extracted, filed for future reference and readily identified by means of the cheap, wide-field, stereoscopic binocular microscope. Elaborate and expensive techniques are generally not required. (See chapter 2.)

(3) Stratigraphic markers, 'tops', based on the first appearance of species and assemblages in

ditch cuttings can be applied in correlation which can be carried out without expensive coring.

(4) The sub-class has existed in abundance since the Cambrian, showing well-marked evolutionary changes useful in stratigraphy. Different families mark the Eras and major time Periods. (See sections on stratigraphical use in chapters 6 – 14.)

(5) Many species are planktonic and of worldwide occurrence in the broad latitudinal temperature belts. When this wide geographical range is combined with a short vertical time range they make excellent *(empirical) index fossils.* (See chapter 14.)

(6) Many species are restricted in their habit and narrowly confined to a particular ecological niche. They are thus particularly useful in interpreting the character of ancient environments. (See sections on ecology, chapters 6 – 14. Oxygen and carbon isotope analysis is also covered in chapter 14.)

(7) Many species, especially amongst the Larger Foraminifera, are so prolific that they are important rock-builders. Foram-limestones are well developed in the Upper Palaeozoic, the Upper Cretaceous and in the Cenozoic. (See chapters 7, 8 and 13.)

(8) Classification is based upon characters shown by the fossilisable test and therefore avoids the difficulties faced in those groups where a knowledge of the soft parts is necessary, difficulties which become acute in the case of extinct families. (See chapter 5.)

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Chapter 2

Collection, Preparation and Examination

> Numerous samples collected without a clear idea of what is to be done with the data are commonly less useful than a moderate number of samples collected in accordance with a specific design.
>
> (Krumbein, 1965)

Foraminifera occur on a wide variety of substrates at all depths in the marine realm and because their tests are generally of sand size they are also commonly transported by currents before burial in the sediment. They are therefore found fossilised in most types of sedimentary rock, particularly in clays and marls. Foraminifera are usually scarce in coarse sands but they are often abundant in silts and fine sands, especially if glauconitic. Many limestones are built up of Foraminifera but are often too hard or altered, as in the case of dolomites, to yield them by ordinary disaggregation techniques. They can then only be studied in thin section. In some cases the foraminiferal tests are silicified and may occur in the 'flint meal' of hollow flints in limestone, as in the well-known flints from the Upper Cretaceous chalk of Sonning in Berkshire. Derived silicified Foraminifera also occur concentrated in the basal 'Bullhead Bed' of the Thanet Sands where it overlies the chalk of the Upper Cretaceous Campanian stage in Kent.

FIELD SAMPLING

Normally, smaller Foraminifera are only rarely seen in hand specimens of rock samples in the field, so the only guide to their presence will be the lithology and perhaps the presence of an abundant calcareous macrofauna which will indicate former environmental conditions favourable to abundant marine life. Larger Foraminifera can be collected in the field like other macroscopic invertebrate fossils. Where they make up most of the volume of the rock, as is often the case with fusulines, alveolinids and nummulites, then they are easily observed in fresh exposures of the rock. They may also be observed in relief on weathered surfaces as well as on bedding and joint planes. Large Foraminifera may also be picked up or sieved out of sediment on talus slopes, particularly from the down wash on sea cliffs or scarps in arid regions where there is little cover of vegetation. A good example in the UK is the abundant occurrence of *Nummulites laevigatus* (up to 1 cm diameter) in talus at the foot of exposures of the Bracklesham Beds in Whitecliff Bay on the Isle of Wight. *Nummulites gizehensis* is so abundant in the Middle Eocene of the Sahara that at some localities it can literally be collected with a shovel. These are unusual occurrences, however, and the micropalaeontologist usually has to make a careful appraisal of the terrain in order that outcrops can be sampled economically but with the maximum possibility of obtaining fruitful material.

The density of sample coverage depends on the purpose of the investigation. When an oil company begins exploration of a new, little known area, field mapping and section measuring is carried out together with palaeontological dating, in order to establish the stratigraphical sequence. The emphasis is on section measuring rather than routine outcrop mapping, because the chief interest is in the thickness and character of possible source and reservoir rocks. It is also necessary to establish criteria for the recognition and dating of the rocks likely to be encountered in the subsurface during the course of drilling the favourable structures indicated by geophysics.

The micropalaeontologist should consider himself part of the exploration team and make every effort to accompany the field parties as often as possible. In this way he not only becomes familiar with the stratigraphical sequence rather than learning about it from second hand, which makes all the difference in stratigraphical evaluation, but is able to personally supervise the collection of samples for dating. The field geologists, as might be expected, tend to confine their attention to the possible reservoir rocks and

as every commercial micropalaeontologist knows to his cost, will turn up at the micropalaeontological laboratory with requests for 'a date' on large, intractable lumps of crystalline limestone or even sucrosic dolomite! If the micropalaeontologist is a member of the field party, then as well as examining all rock types as far as practicable, special care can be taken to sample the finer clastics such as the clays and marls in which Foraminifera are often very abundant. A special effort should be made to search out clay partings between fossiliferous hard bands. In this connection, a former colleague developed a hooked device from a wire coat-hanger to pull out fragments of shale deeply recessed between limestone bands.

Commercial field work is usually severely limited by shortage of time and by the necessity to cover hundreds or even thousands of metres of vertical section in a season. So it may only be possible to sample each major lithological unit, say each member of a particular formation. But the effort should be made to take spot samples at approximately 10 ft (3 m) intervals, with combined or 'channel' samples through units considered important, with additional spot samples of shale-breaks and at particularly important horizons. This will give a coverage equal to the standard 10 ft intervals sampled in subsurface work and also enable the micropalaeontologist to go beyond simple dating to give some consideration to the palaeo-ecological relationships of the fauna and the environment of deposition. This will enable him to play his part in the full geological interpretation of the strata which is so important for the prediction of stratigraphical oil traps as well as for knowledge of the origin and time of migration of the oil. He may find that his colleagues need to be educated in the possibilities of micropalaeontology in this regard, and he should strongly resist any tendency to become stereotyped as merely the expert on biostratigraphical dating, which tends to happen as easily in large commercial concerns as in bureaucratic government research centres. There is no doubt that much of the potential of foraminiferal studies is lost in such an event.

Academic studies do not normally suffer the same constraints as commercial work and the strata can be more closely sampled. Attention may be confined to one formation only which can be fully covered, with channel samples taken bed by bed as well as spot samples taken at the bottom, middle and top of beds. Comparative samples can also be taken from equivalent sections down-dip or along the strike so that a full facies analysis can be undertaken. Where variation and evolutionary studies are being made it may be necessary to sample inch by inch or centimetre by centimetre depending on the degree of resolution required.

About 250 g weight of sample is usually considered sufficient for analysis, so about 500 g should be collected to give an adequate reserve.

While collecting, it is important to avoid contamination. Picks, shovels and trowels should be carefully cleaned and rock samples should be brushed over before bagging and later washed and scraped before preparation if necessary. Samples should be collected in thick-gauge plastic bags, or linen bags which are to be preferred for hand specimens of sharp-edged limestone and sandstone and have the advantage of attached labels and ties. Sample bags should be numbered on the outside and a duplicate label, with numbers in waterproof ink, placed inside. All 'float' samples collected from talus, etc., must be clearly indicated. Where the samples are collected as part of a field mapping survey, the numbers and localities are entered into a field notebook and plotted later on a base map. When collection proceeds together with detailed section measuring, a graphic lithological log should be drawn to accompany the detailed description with the position of the samples shown exactly. If possible, polaroid photographs should be taken of the section with sample bags (or marker flags) in position. Junctions can be drawn and explanations written on immediately in white ink. In many oil companies the field notebooks are company property and are eventually stored in the company library, while one base map records the sampling of all field parties. The notebook therefore has to be written up in a clear, explicit, logical manner so that it can be easily understood by other workers and leaving nothing to memory. The micropalaeontologist should adopt this approach as a matter of course.

Samples from Borings

As was explained in chapter 1, the majority of oil wells are drilled by the rotary drill and the cuttings are carried out by the drilling mud to be caught in a mechanical sieve, 'shale shaker'.

Samples representing each 10 ft (3 m) interval are usually taken, normally about half a kilo. The drilling mud is washed off and the material split into subsamples of approximately 100 g weight, and stored in plastic or linen bags marked with well name and sample interval. The subsamples

are needed not only for micropalaeontological and sedimentological research but because it is common practice for companies to swap runs of samples with competitors. The enormous number of bags that eventually come into the oil company warehouse from wells that may be over 10 000 ft (3 km) deep, together with boxes of core as well as field samples, make detailed accounting and documentation necessary. The micropalaeontologist is usually in charge of this material and a card file is kept to aid location and retrieval.

Cores, when properly cleaned of drilling mud, yield the best samples for foraminiferal analysis because the depth at which the sample is taken is accurately known and the material is uncontaminated. It is best to sample continuously through each lithological unit present in the core. Cores are usually boxed in 3 ft (1 m) or 5 ft (1.5 m) lengths, so a separate channel sample can be taken with a chisel along each length. In addition, spot samples can be taken at important horizons, as of shale breaks in sandstone or limestone. These samples are hammered or chiselled transversely off the core and slices about 1 cm thick are generally taken.

Samples taken at Sea

Cores of solid rock taken during marine geological surveys are treated in the same way as cores taken on shore, but cores and 'grab' samples of incoherent Recent sediments present a different problem. Cores taken by simple gravity corer, such as that of Phleger (1960), or by the Multiple Corer of Barnett and Watson (plate 4, no. 4) which is lowered to the sea bed to take an undisturbed sample, are recovered in a plastic tube. In this case subsamples are taken immediately on board the research vessel. The core is gently extruded by means of a cork on the end of a rod which allows 1 cm slices to be cut off in succession. These are placed for storage in plastic tubs with addition of 5 – 10 per cent formalin to prevent decay of the microfauna which are live at the time of collection. It is advisable to buffer the solution with borax at 10 g/l to counter undue acidity which could lead to dissolution of calcareous shells. Large cores taken by the Box Corer (Gage, 1977; cf. Hessler and Jumar, 1974) can be conveniently subsampled by inserting a small plastic tube which is then extruded for slicing.

Samples taken by a grab such as the 'Shipek', or from the bucket attached to the dredges used in macrofaunal surveys, are preserved in the same way. In this case the cut sediment is placed in a plastic tub, not more than half-filled, and left just covered with sea water which is then topped up with buffered formalin. Care should be taken to label the lid on the inside and the outside, as well as the tub, with the station number. When only cobbles and boulders are recovered by the grab these can be preserved intact if small enough, otherwise the epiflora and epifauna should be scraped off and preserved for later examination of the attached Foraminifera.

It is important to stress here that sampling should be carried out as part of a general marine survey, with side-scan sonar and subsea TV, so that samples can be taken of various substrates and material recovered representing as many micro-environmental niches as possible.

The location of the sample station and details of sediment character, associated macrofauna and flora, etc., are entered in a log book immediately upon sample recovery. The samples can be plotted on a base chart and the details transferred to reference cards on arrival of the samples at the shore-based laboratory.

SAMPLE PREPARATION

The different rocks containing Foraminifera require different methods of treatment, but as a rule the less rough treatment the samples receive the better; they will be less damaged and broken when recovered. The general procedure is as follows:

(1) *Crushing and boiling.* The sample is dried, either in the air or in an oven, and a subsample of a definite weight is soaked in water—if possible, not more than half the original sample so that ample material is left for future reference.

Some very soft, friable rocks including shales, marls and sands, particularly from the Cenozoic, may break down on soaking for an hour or two, but harder rocks first require crushing in a vice. Care must be taken that the rock is not broken into fragments smaller than the largest Foraminifera present, say 1 cm diameter, which is the average size of rotary cuttings. The sample from the Lower Lias of the Mochras Borehole, shown being weighed out in plate 5, no. 1, has been crushed to a smaller size because the Foraminifera are all very small at this horizon. The broken rock may then be soaked in water. This may be sufficient to bring about disaggregation, but normally slow boiling for an hour or more with washing soda (sodium

bicarbonate) at 50 g/l, or a spoonful of a sudsless detergent such as Alconox, is necessary to produce clean specimens. Plate 5, no. 2, shows the sample of crushed Liassic shale being boiled in a saucepan over a bunsen burner. Enamel saucepans are easier to handle than glass beakers and are used in preference to stainless steel or aluminium ones which tend to become pitted very rapidly. They are used until the enamel begins to crack off and are then thrown away.

(2) *Decanting*. As the mud goes into suspension during boiling it is poured off, half the volume of liquid at one time, the pans being topped up with fresh water until the residue is clean. To avoid loss of specimens this should be done through a fine mesh sieve (B.S. 240 mesh with openings of 63 μm will retain smaller Foraminifera and most of the juveniles) after cold water has been added to lower the temperature, as in plate 5, no. 3. The residue is finally poured into the sieve and the finer material flushed gently away with a spray nozzle.

(3) *Drying*. The residue can be dried, still in the sieve, under an infrared lamp or in a drying oven (plate 5, no. 2). Alternatively the residue can be flushed from the sieve into a filter paper in a glass funnel (plate 5, no. 3). The filter paper can be turned over and secured with a paperclip and the sample again oven dried or, as in the U.C.W. laboratories, dried over the bench radiator grilles at room temperature.

(4) *Storage*. If the sample is to be studied fairly soon it can be left in the filter paper, otherwise it must be transferred to a plastic or glass vial for safe storage.

It is important to adopt a clear system of labelling with numbers or letters that accompany the sample through the washing and drying process (plate 5, no. 3). The storage vial should be labelled outside and a paper label should also be placed inside.

ALTERNATIVE METHODS

Where the sediment proves difficult to disaggregate, all that may be necessary is to repeat the boiling procedure after the residue has been dried. In many cases the mud or shale pellets will then break down. Highly indurated shales may, however, require alternative methods. One technique that is often successful with bituminous or carbonaceous shales is the use of paraffin or white spirit as a solvent. The sample is dried and soaked in white spirit overnight. Excess white spirit is then poured off and hot water with Alconox or washing soda poured on, followed by the normal washing procedure. This method was discovered by one of the French oil companies drilling in the Sahara—it was noticed that hard dark shales outcropping near the drilling platform were breaking down after being soaked in waste petroleum.

Some shales will break down if first soaked in dilute hydrogen peroxide (15 per cent). The process is speeded up if the sample is hot, but the oxidation reaction is violent and care must also be taken with pyritous shales as the reaction may damage and even destroy the pyrite-filled tests as this mineral is converted to iron oxide.

It may be found that some sediments break down quite well initially but reduce to clay pellets that prove very difficult to disaggregate further. Such sediments often break down completely if transferred in a beaker of hot water to an ultrasonic vibrator for $1-2$ sec treatment. Only part of the residue should be treated at a time in case of breakage of the foraminiferal tests. The same treatment can be used for specimens such as planktonic species from ooze that have sediment adhering to the test and hiding important features.

Other methods which have been found successful in certain instances include:

(1) Use of a rolling mill. The sediment is rolled in screw-top glass jars, each with a rubber-covered lead slug inside, hot water and washing soda being added.

(2) Use of a kitchen mixer with hot sudsy water. The mixer bursts the shale fragments and the freed Foraminifera float up in the suds. The Foraminifera are often broken, but if the sample cannot be broken down by any other means this is still worth while.

(3) Pressure cooking.

(4) Freezing and thawing.

(5) By soaking in hypo with growth of crystals within the rock.

(6) By soaking in bromine.

Treatment of Recent Sediment Samples

Recent samples can be washed with cold water but require staining so that Foraminifera which are live at the time of collection can be detected. The procedure is as follows:

(1) A 10 ml cut is washed clean of mud and preservative under a fine spray of water over a fine mesh screen (B.S. 240 with openings of 63 μm). The volume of the cut can be measured in a graduated vial.

(2) The sieve containing the washed residue is

placed in a bowl of Rose Bengal stain (at 1 g/l) so that the solution well covers the sediment on the screen. Staining is allowed to proceed for 20 min with occasional shaking. In most cases this leads to pronounced red staining of contained protoplasm, although opaque species may have to be broken for this to be seen.

(3) The residue is washed under a fine spray of water to remove stain from the sediment and from the shell walls of the Foraminifera. It can then be examined wet in a petri dish (this is advisable in the case of material containing fragile membranous and agglutinating species), or alternatively flushed out of the sieve on to filter paper in a funnel where it is left to dry in the air. The filter paper can then be secured with a clip until examination or the sample stored in a standard 10 ml vial. An alternative staining method, using Sudan Black, which may give better results in certain circumstances but is more complicated to apply, is given by Walker, Linton and Schafer (1974).

Separation of Foraminifera from Limestones

Recovery of microfossils from limestones is more difficult than from the softer clastics. However, chalks and the softer marly and more crumbly limestones may be crushed and boiled with successful release of microfossils. This is particularly the case where the grain size is the same as that of the fossils, as in some fragmental limestones whole Foraminifera and ostracods will then break out. The Middle East Tertiary limestones are often highly foraminiferal and in most cases crushing and boiling release a good percentage of the fauna. Where fossils remain partly embedded in the limestone it is often possible to dig them out with a needle or break them out with a vibro-tool.

Membranous and arenaceous Foraminifera may be recovered from limestone by leaching with 10 per cent HCl or 5 – 50 per cent acetic acid. The rock specimen is immersed in the acid and when effervescence ceases more is added until no more effervescence occurs. The sample is then washed and dried very carefully, as the residue is usually very brittle. Results may be spectacular where the Foraminifera are silicified.

THIN SECTIONS

Foraminifera in hard dense limestones must be studied in thin sections made in the following way:

(1) By use of a diamond saw, cut a parallel-sided slice about 3 cm long by 2 cm wide by 5 mm thick.

(2) Surface the slice by grinding with 80 grade carborundum on an iron plate.

(3) Wash and transfer to a glass plate and grind with very fine carborundum.

(4) Cement the prepared surface to a glass slide with Canada balsam or Lakeside. The slide should be ground for better adherence. Heat the balsam to the necessary hardness on a hot plate—when a thread drawn out with forceps snaps at a touch. Mount specimen after slight reheating of the balsam, a drop of balsam being put on the slice as well as on the slide.

(5) Grind the other side of the slice in successive grades of carborundum until the required thinness is attained, and the fauna can be seen under the microscope.

(6) Warm the slide (when cleaned) to 100°C. Place a drop of balsam on a coverslip and place over the specimen.

Separating Foraminifera from Washed Residues

After the sample has been successfully washed down and dried, the residue of sand and mineral grains is sieved into fractions for ease of examination by reflected light under the binocular microscope. Brass sieves of a convenient size (100 mm diameter) are shown in plate 5, no. 5. Mesh sizes of B.S. 60 mesh, aperture 250 μm, and B.S. 100 mesh, aperture 150 μm are generally used and the finest fraction, +63 μm, is caught in a receiver. Most of the Foraminifera are generally found in the 60 and 100 mesh fractions but may on occasion, as in the case of the Liassic Foraminifera from Mochras, be concentrated in the fines which also tend to include the juveniles. Large Foraminifera will be retained on the 30 mesh sieve, aperture 500 μm. It is therefore necessary to look at all the fractions. Attention should not be solely confined to the 30 and 60 mesh, as was often the case in earlier times and is still sometimes practised by commercial concerns for 'economic reasons'.

The residue is tapped gently out of the sieve on to a small tray of metal or black card so that the grains are evenly spread and not on top of one another. Avoid the beginner's mistake of piling the material in heaps under the impression that this will speed up examination, as it makes it impossible to see and separate all the microfauna.

A useful tray of smooth, matt black 'scratch board' is shown in plate 5, no. 5. This has raised

sides of gummed card, to prevent specimens rolling off, with a small space at one corner for brushing the residue into a storage vial after examination. The tray is marked out in squares of approximately the area of the field of the binocular microscope and at a convenient magnification for general appraisal of the residue, about ×25. This allows all the residue on the tray to be looked over systematically.

The Foraminifera are picked up by means of a moistened artist's brush of 00 or 000 size and transferred to a cavity slide where they can be preserved loose for later examination. A 'three-hole' cavity slide of punched white card with a matt black scratch board base and coverglass held by gummed tape is shown in plate 5, no. 5. This type of slide allows the Foraminifera from the different fractions to be kept separate, which may be important for evidence of mechanical sorting in death assemblages. 'One-hole' slides are used for type and representative specimens, while rectangular cavity slides with a grid of white painted squares (5 to 100) are used to mount representative faunas, the individual specimens being stuck down with gum tragacanth or water-soluble plastic.

Most of these types of slide are manufactured commercially but often have fibrous black card as a base and plastic coverslips which become charged with static electricity and attract the specimens which may then be lost or crushed. They can easily be made in the laboratory with simple equipment including a punch to cut out circular holes, as in plate 5, no. 4.

The slide is made from a strip of white card 75 mm long by 25 mm wide and up to 3 mm thick. One to three holes of 14 mm diameter are punched out, or a rectangular cavity cut with a scalpel, and the slide is glued to a base of matt black scratch board. Up to ten can be made at a time and they can then be held all together in a vice to prevent warping while the glue sets. The sleeve is made from a thin glass microscope slide, to which strips of gummed tape are attached. These strips fold over to hold the base of the sleeve, which is made from thin white card with 'thumb holes' cut from each end to facilitate pushing out the cavity slide. The grid for the faunal slide can be made from the negative photograph of an indian ink drawing suitably reduced, which has the advantage that the emulsion will hold small Foraminifera when mounted with a wet brush. Care must be taken to cut the card precisely so that the slides will fit the trays in metal or wooden cabinets specially manufactured for their storage. The wooden slide cabinets illustrated in plate 5, no. 1 hold some 900 slides on trays, with three divisions each holding 12 slides (plate 5, no. 4). These cabinets have the advantage that they can be stacked as units on top of one another.

Use of Heavy Liquids

A liquid of high density such as carbon tetrachloride or bromoform can be poured on to the dried residue in order to float off the relatively light, air-filled Foraminifera which can then be caught on a filter paper in a glass funnel. This method has the disadvantage that infilled specimens and agglutinating forms may not float and the results are often quite variable. For quantitative work the residue must still be diligently searched, so two operations become necessary and time may not be saved. It is chiefly valuable as a way of concentrating specimens from large amounts of residue when strictly quantitative methods are not called for—see, however, Carlton (1933). When using heavy liquids the student must take care to carry out the operation under a fume-hood, as inhalation of the fumes is dangerous.

Sorting, Further Preparation and Identification

The experienced worker may recognise most of the genera and many of the species present in the residues, and be able to pick them out and mount them immediately on faunal grid slides. Otherwise, all the samples from the particular section under investigation should be picked and specimens compared before the species are identified and representative specimens are mounted for future reference on one-hole slides (for the principles of classification and description of new species, see chapter 5). These slides, unlike faunal grid slides, have the advantage that the name and full locality and samples details can be written on them. They *must* be used for new species so that after the publication of a formal description they can be safely deposited in a museum collection. A selection of specimens should be mounted, to show the full range of variation, on a separate slide from the 'type' in the case of new species.

In commercial work, study of rotary cuttings begins from the top downwards (see chapter 1), and there is usually pressure for information before the worker has looked at all the samples, but here too selection of representative specimens

of new species and species occurring for the first time in the area should be delayed until a range of samples from the particular zone has been examined. It is common practice to give numbers provisionally to species which cannot be readily identified, but identification should be carried out as soon as possible so that the full stratigraphical and ecological value of each species is realised.

Details of the external structure may be shown more clearly if the specimen is stained with malachite green, methylene blue or even green ink. Normally, careful examination under the optical microscope is sufficient to establish specific distinctions and the results are quite adequate for application in stratigraphical research and commercial work. But, the description of new species and redescription of old-established ones may require examination of the very fine details (ultrastructure) of the wall, ornament, perforation and apertural form and recourse to the scanning electron microscope. The Cambridge Instruments model S600 is shown in operation in plate 6, no. 1. In this microscope the specimen is scanned by a narrow beam of electrons (width about 100 Å) focused through a series of magnets, and the differential return of secondary electrons and reflected primary electrons builds up a picture on a screen. Advantages are the high resolution down to 200 Å, considerable depth of field, hundreds of times greater than the optical microscope, and possible magnifications to over $\times 20\,000$. A further advantage is the working distance of about 3 cm between the specimen and the electron collector (Oatley, 1966; Paterson, 1965).

Preparation of specimens for examination by SEM is fairly simple compared to the replication process required for examination of specimens by transmission electron microscope (TEM):

(1) Carefully clean specimen, particularly of gum tragacanth, and dry off with 80 per cent alchohol mixed with methanol.

(2) Mount on aluminium stub with wax, 'dag' (a suspension of silver in alchohol), double-sided transparent adhesive tape, or Kodaflat.

(3) Plate with gold or aluminium evaporated under vacuum.

An even and complete metal coating is required together with secure mounting to prevent build-up of electrons in the specimen and charging effects.

A disadvantage of examination by SEM is that, although it allows the mapping of surface features in beautiful detail, internal features are obscured and smooth opaque specimens show less detail than by optical microscope.

The examination of opaque specimens by optical microscope is made easier if the specimen is wetted or removed to a hollow glass slide and immersed in a drop of xylene which acts as a clarifier, cutting down the reflected light. Fine details, including the arrangement of the chambers in the initial part, may now be seen, especially if the specimen is looked at in transmitted light. The advantage of the use of xylene is that it evaporates from the specimen after a short while, leaving it clean. For more prolonged study of internal characters, the specimen can be mounted in glycerine or castor oil (Hofker, 1951) or embedded permanently in Canada balsam or Lakeside 70.

Where internal details cannot be seen by these methods it may be possible to breach the external surface by use of dilute acid applied with a fine brush. Otherwise it will be necessary to make thin sections; these are obligatory in the case of the annular complex and fusiform Larger Foraminifera which generally require both equatorial (or median) and axial sections for identification.

Thin Sectioning of Individual Foraminiferal Tests

Sometimes only a half-section is required and a large specimen of a nummulite or orbitoid may be rubbed down on a fine hone with a slightly hollowed cork or even with the fingers until one-half of the specimen is worn away. Both axial and equatorial sections can be made in this way.

For the sectioning of Larger Foraminifera:

(1) Cement the specimen with balsam to a glass slide.

(2) Grind to the middle line or desired point with a ground glass slide.

(3) Warm the slide and turn the specimen over with a needle.

(4) Grind to the required thinness.

(5) Warm the slide. Place a drop of balsam on a coverslip and place over the specimen.

For the sectioning of Smaller Foraminifera, following the method of Wood (1948):

(1) Immerse the specimen in xylene with a little added Canada balsam in a hollow glass slide.

(2) Allow the xylene to evaporate naturally so that the balsam penetrates into the interior chambers of the test.

(3) Cement a celluloid or mica coverslip (2 cm square) to a glass slide.

(4) Place specimen on top of the slip in balsam and heat to the correct hardness.
(5) Grind down the specimen to the desired plane with the finest laevigated carborundum or with a ground glass slide.
(6) Wash and flake off the coverslip with the specimen attached.
(7) Remount the coverslip in clean balsam on a new glass slide, with the specimen now on the underside.
(8) When cold, flake off the coverslip leaving the specimen on the slide, 'upside down'.
(9) Grind the specimen to the required thinness.
(10) Wash then warm the slide. Place a drop of balsam on a coverslip and place over the specimen.

Use of the celluloid or mica slip ensures that the two sides of the section are parallel.

A method which avoids the problem of contamination by carborundum particles by the use of small grinding stones is given by Hofker (pers. comm.):

(1) Suspend the carborundum in dentist's cement.
(2) Harden in small boxes.
(3) Grind to a flat surface on a carborundum stone.
(4) Grind the embedded specimens on the prepared stone using *Rhicinus* oil.
(5) On completion, remove any extraneous grains by adding a drop of oil and lightly rubbing the surface.
(6) Remove the oil with paper tissue.

Special Techniques for Examining Internal Structures

Casts

Natural casts formed by infilling of the test with minerals such as pyrite sometimes reveal details of internal structure not seen externally. The making of artificial casts goes back to Carpenter, Parker and Jones (1862) and a method is described by Hofker (1927) who produced beautiful casts of Nummulitidae showing the internal canal system:

(1) Soak test in xylene.
(2) Cook in Canada balsam.
(3) Slightly grind and immerse in 5 per cent acetic acid for 24 h until decalcified.

Satisfactory impregnation of specimens to fill all the chambers and canals is difficult and to overcome this Hansen and Lykke-Anderson (1976) suggest the making of half-sections:

(1) Grind down the specimen which is embedded horizontally in Lakeside 70 on a glass slide to plane of proloculus.
(2) Reheat and turn over the specimen with a hot needle so that the section is in contact with the slide.
(3) Cool and remove excess cement with a pointed scalpel under the microscope. A thick layer of cement is required so that brittle splinters can be removed to expose the shell surface.
(4) Immerse in 10 per cent HCl for some minutes to decalcify.
(5) Wash in water and dry.

X-ray Microscopy

Sectioning and the making of casts leads to partial or complete destruction of the test. A method of revealing internal structures without damaging the specimen is by microradiography—either contact microradiography, where the specimen is placed in the path of the beam very close to the photographic plate, or by point projection microradiography, where the beam is focused on a metal target which emits the X-rays which then penetrate the specimen to produce an enlargement on a photographic plate (Hedley, 1957; Hooper, 1959).

The mineralogical constitution of the test is also best studied by the techniques of X-ray microscopy, employing X-ray diffraction equipment (Switzer and Boucot, 1955). Using the powder technique the X-ray beam is diffracted from the planes of the atoms in a crystal in patterns that reveal its form according to Bragg's law. This allows the recognition of the two main groups of calcareous Foraminifera—those composed of calcite, the hexagonal crystal form, and those composed of aragonite, the orthorhombic crystal form, to be distinguished. Using this technique a specimen can be X-rayed uncrushed, held at the end of a glass fibre.

A further development is the electron probe microanalyser (EPM) which focuses down to a spot about 1 μm in diameter and allows study of the variation in elements in different parts of the test (Hooper, 1964). For this technique the specimen must be embedded in epoxy resin or polystyrene and sectioned as for examination by SEM. The sections are then polished on rotating

wet velvet discs with chromium oxide powder before being placed under the probe.

Special Techniques for Examining Wall Structure

Whole specimens can be examined as advised by Wood (1963):

(1) Clean the specimen and immerse it in absolute alchohol.
(2) Place in xylene in a hollow glass slide.
(3) Examine under the crossed nicols of a petrological microscope at $\times 100$ with the condenser out, brightly lit and with the plane side of the mirror in use.

Alternatively the specimen may be crushed under a coverslip and the fragments examined or sections cut at right angles to the wall and septa.

Freshly broken surfaces and transverse sections made by the normal methods require special preparation for examination by the scanning electron microscope. To follow the method of Hansen and Lykke-Anderson (1976):

(1) Prepare the transverse section on a glass slide in Lakeside cement.
(2) Polish on a wet, velvet-covered disc with MgO powder or Al_2O_3 paste.
(3) Wash with oil-free detergent.
(4) Etch with aqueous EDTA solution buffered to pH 7.0 by NaOH for 15 – 60 sec according to wall thickness.
(5) Cut out the specimen from the slide with a glass cutting pencil to give an area small enough to mount with double-sided transparent adhesive tape on aluminium specimen stub.
(6) Plate with 250 – 500 Å gold under vacuum with two tungsten filaments rotating at 5° and 45° angles of evaporation.

For studying the surfaces of fractured specimens, Bellemo (1974a) has used the following method:

(1) Remove organic membranes with concentrated sodium hypochlorite.
(2) Etch crystalline elements with 25 per cent solution of glutaraldehyde buffered to pH 3.5 for 5 – 20 min.

The specimen is then mounted on an aluminium stub and plated with evaporated gold as above. If it is desired to examine the organic lamellae then the test can be demineralised with chromium sulphate solution, with immersion for 8 – 30 min.

The student must take great care in the interpretation of the results of these etching processes in order not to confuse artefacts of the technique with natural structures.

LITERATURE SEARCH

Identification of species requires careful comparison with published figures and descriptions in literature dealing with the area under investigation, or on strata of the same age in adjacent regions, and use of catalogues such as the McLean Card Catalogues and the Ellis and Messina Catalogue of Foraminifera, listed in the literature to chapter 1. In plate 5, no. 6 the Ellis and Messina Catalogue is shown arranged alphabetically by genus in suspension files which makes both consultation and addition of new species descriptions easy. Other catalogues such as the McLean series are stored in small cabinets above.

The vast literature on Foraminifera now makes the Ellis and Messina Catalogue practically obligatory for serious foraminiferal work. The problem is made more difficult because most descriptions and discussions of faunas are published in papers widely scattered in various learned journals. These papers are most easily dealt with as 'separates' or xerox copies. Some 6000 are stored in the Micropalaeontological Library of the University College of Wales under authors' names, in alphabetical order. As shown in plate 5, no. 6 they are kept in cardboard pamphlet boxes and retrieval is aided by a cross-reference system on small cards arranged by topic, stratigraphic system, family group, etc.

Consultation of the literature and comparison with specimens in museum collections is required not only to identify each species but to check all records in order to establish its full stratigraphical and geographical range. This information is entered on separate data sheets, together with details of the occurrence of the species in the sections and samples under investigation. Separate data sheets are also kept on each sample. These record:

(1) Sample number, location and collector.
(2) Horizon or depth in borehole.
(3) General character and lithology.
(4) Preparation techniques and amount treated.
(5) Residues examined.
(6) Associated fauna.
(7) Foram species and frequency.
(8) Age.
(9) Ecology.

This information can conveniently be entered on prepared form sheets with columns for the species names, frequencies in different fractions and, if necessary, an indication of whether the specimens were live or dead on collection. In ecological work, where the expected species are well known, the names can also be written into the form sheet in advance.

ILLUSTRATION

The literature search and comparison with descriptions and actual specimens of other species is made easier if figures have already been prepared to illustrate the characteristic features of the species under investigation. Care should also be taken to show variations that may be confined to the local population. A convenient way to do this is by a camera lucida attachment to the binocular microscope, as shown in plate 6, no. 4. Here the equipment is attached to the right-hand ocular of the microscope and consists essentially of a prism and a mirror which allow the image of the specimen seen through the microscope and that of the paper on the drawing board to be brought together. The outline of the specimen and other features may then be accurately traced out. As shown in the plate, the drawing board needs to be fixed at the angle of inclination of the oculars. Also, the lighting of specimen and drawing board has to be balanced so that the point of the pencil used can be clearly seen against the image of the specimen, achieved in this case by use of a fluorescent tube attached to the drawing board.

In the case of new species and redescription of established species, where the illustrations are intended for publication, the drawings should be done on good quality white card, such as Bristol board. They can be carried to completion with indian ink stipple shading or pencil shaded and cut out for mounting on matt black card, which gives the realistic effect of viewing the specimen down the microscope. The drawings should be prepared at a size which will allow reduction to half-size in the final publication.

In the recent past, illustration of Foraminifera by photomicrography, apart from thin sections, was beset by considerable difficulties caused by the limited resolution and depth of field of the optical microscope. The appearance of the SEM with its great range of magnification, high resolution and depth of field has made photomicrography of external details relatively easy, including the making of stereopairs. This method has now become standard. In plate 6, no. 1, a 35 mm camera can be seen mounted to the right of the display unit of the SEM; this allows a photograph to be taken of the image and simultaneously shown on the screen as well as the TV monitor. Photographs made by this means can be cut out and mounted on black card in the same way as pencil drawings (plate 6, no. 2). In this case there is no advantage to be gained by reduction so the plate can, with economy, be prepared at publication size. The individual figures can be labelled with stick-on letters.

Despite the success of photomicrography by means of the SEM, the student should not be led to the belief that light photomicrography is now quite redundant. There are a number of groups, particularly smooth, lamellar forms, which show little detail under the SEM. Better results may be achieved by light photomicrography if advantage is taken of the methods introduced by Fournier (1954, 1956), including the use of the pinhole diaphragm to increase the depth of field. The student should also note the excellent results of Albani (1964) using Zeiss Luminar lenses and bellows and universal stage for orientating the specimen. A modification of this system, developed by Dr D. Bates of the University College of Wales, is shown in plate 6, no. 3. Here, a polaroid film holder is attached to the bellows and the specimen, a foraminifer fixed to a scallop shell, is mounted on a simple microscope substage and lit from three sides by a flexible glass fibre intensity lamp. With the film holder removed and a ground glass screen in place on the bellows, the specimen can be brought into focus by movement of the stage. Photographs can be taken one at a time and the results examined immediately when using this equipment.

Photographs of the internal structures of opaque specimens and specimens with involute and embracing chambers can be made by X-ray microradiography. Results obtained by this means and details of apparatus can be found in Bé, Jongebloed and McIntyre (1969).

SUMMARY

Foraminifera occur in most sedimentary rocks but particularly in the finer clastics. Few can be observed in hand specimens, so collection must be systematic and planned according to the purpose of the investigation. Normally, the range of different rock types present should be sampled to allow a full stratigraphical appraisal. Sufficient

material must be obtained to allow a reserve for future research and exchange. Great care must be taken to avoid contamination, to bag the samples securely and to provide full documentation. In particular, talus must never be included with *in situ* material. Detailed filing is necessary for retrieval of cuttings and core stored in company warehouses, and special care must be taken to preserve submarine cores and grab samples containing Foraminifera which are live at the time of collection.

Samples should be disaggregated in a manner that will maximise faunal recovery with least breakage of the tests. Simple washing should be tried before more elaborate methods are resorted to. Decanting should be done through a sieve with a mesh opening of 63 μm and the residue picked after sieving into fractions on mesh openings of 500, 250 and 125 μm. A clear, foolproof system of labelling should be followed throughout the whole washing, drying and picking process. Recent material requires staining with Rose Bengal or Sudan Black, and picking and counting should be done wet if fragile agglutinating species are present.

Highly indurated limestone and sandstone must be examined in sections cut by the normal petrological methods, while special techniques are required for sections of individual foraminiferal tests and for preparation of sections for examination by TEM or SEM.

Picked material can be sorted on simple cavity slides made in the laboratory, and 'three-hole' slides are especially useful for the study of size sorting. Selection of type specimens of new species should be delayed until a range of material has been sorted.

The recognition of new species and proving the range of those already known requires a thorough literature search and reference to catalogues such as that of Ellis and Messina (1940 – date). This information, together with the results of evaluation of the samples, should be systematically entered up on formal data sheets.

Fine details of the test surface and ultrastructures are best observed and photographed by SEM. Smooth, lamellar forms give better results by light photomicrography and can be drawn by camera lucida. Internal structures can be revealed by moulds or observed and photographed by the 'non-destructive' method of X-ray microradiography.

ANNOTATED LITERATURE ON TECHNICAL METHODS

General

Brotzen, F. (1950). Method and techniques in routine work. *Micropaleontologist,* **4**(2): 18 – 20

Douglass, R. C. (1965). General procedures and techniques applicable to major fossil groups—Larger Foraminifers: pp. 20 – 25 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco
Importance of collecting from outcrop. Preparation of fusulines and sectioning techniques. Peel technique of Honjo and ground glass technique. Correct labelling after frosting and use of diamond scriber

Horsfield, Brenda and Stone, P. B. (1972). *The Great Ocean Business.* Hodder and Stoughton, London
Includes description of Glomar Challenger and techniques employed in the JOIDES programme

Ku, T. and Oba, T. L. (1978). A method for quantitative evaluation of carbonate dissolution in deep-sea sediments and its application to paleoceanographic reconstruction. *Quat. Res.,* **10**(1):112 – 129
Degree of attrition of species such as *G. menardii* and *G. tumida* used to scale the amount of $CaCO_3$ dissolved from the sediment

Kummel, B. and Raup, D., Eds. (1965). *Handbook of Paleontological Techniques.* W. H. Freeman, San Francisco

Leroy, L. W. (1949). *Subsurface Geologic Methods.* Colo. Sch. Mines, Golden, Colarado

Lipps, J. H. (1973). Microfossils: pp. 308 – 312 in *Encyclopaedia of Microscopy and Microtechnique* (Gray, P., Ed.). Van Nostrand Reinhold, New York
Gives three procedures to free calcareous microfossils: (1) sodium pyrophosphate and dilute hydrogen peroxide (15 per cent); (2) quaternary O; (3) kerosene – sodium bicarbonate at 50 – 100 g/qt. Also deals with magnetic separation where microfossils are few, as well as sectioning and peels and preparation of oriented sections

McLean, J. D. Jr., Ed. (1959 – 72). *Manual of Micropaleontological Techniques,* vols. 1 – 12. McLean Paleont. Lab. Alexandria, Va., USA
Collected reprints of significant articles

Field Work, Sampling and Boreholes

Benson, R. H. and Kaesler, R. L. (1965). The Benson – Kaesler bolapipe dredge. *Micropaleontology,* **11**(3):369 – 372

Berger, W. H. (1969). Ecologic patterns of living planktonic Foraminifera. *Deep-Sea Res.*, **16**(1):1 – 24
Considers factors affecting number of tests per cubic metre (FNp/m³) and plankton nets of mesh size No. 10 (0.158 mm) are recommended

Boltovskoy, E. and Wright, R. (1976). *Recent Foraminifera.* Dr W. Junk, The Hague
Description of various samplers and coring devices including Phleger corer, Kullenberg piston corer and Ewing piston corer. Sampling of planktonic Foraminifera with nets of various designs.

Cochran, W. G. (1963) *Sampling Techniques,* 2nd edn. John Wiley, New York
Standard reference

Hills, J. M. (1949). Sampling and examination of well cuttings. *Bull. Am. Ass. Petrol. Geol.*, **33**(1):73 – 91

Hottinger, L. (1977). Distribution of larger Peneroplidae, *Borelis* and Nummulitidae in the Gulf of Elat, Red Sea. *Utrecht. Micropaleont. Bull.*, **15**:35 – 109
Methods of collecting and mapping distribution of larger Foraminifera by divers

Hulme, S. G. (1964). Recent foraminifera from Manakau Harbour, Auckland, New Zealand. *N.Z. Jl Sci.*, **7**(3):305 – 340
Description of simple pipe dredge

Krumbein, W. C. (1965). Collecting techniques —sampling in paleontology: pp. 137 – 150 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco
Covers search sampling to locate fossil horizons, purposive selection for stratigraphic correlation, statistical sampling with an element of randomisation for making inferences about populations, systematic grids for mapping

Kullenburg, B. (1947). The piston core sampler. *Svenska hydrogr.-biol. Komm. Skr. (3, Hydr.),* **1**(2):1 – 46

Ladd, H. S. (1965). Collecting fossils in tropical islands: pp. 163 – 168 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco
'In Palau the Eocene is known only from larger foraminifera recovered from pieces of limestone in a volcanic agglomerate.'

Rouvillois, Armelle and Rosset-Moulinier, Marie (1969). Mise au point d'un petit carottier pour le prélèvement sans perturbation de la partie superficielle des sediments marin. *Cah. océanogr.*, **21**(10):1 – 9
Device for collecting small undisturbed samples in water up to 40 m depth

Schafer, C. T. (1971). Sampling and spatial distribution of benthonic foraminifera. *Limnol. Oceanogr.*, **16**(6):944 – 951

Schenck, H. G. and White, R. T. (1942). Collecting microfossils. *Am. Midl. Nat.*, **28**:424 – 450

Smith, W. and McIntyre, A. D. (1954). A spring loaded bottom sampler. *J. mar. biol. Ass. U.K.*, **33**:257 – 264

Vlerk, I. M. Van Der. (1933). The task of the oil paleontologist. *Geologie Mijnb.*, No. 2:15 – 19

Collection and Culture of Live Foraminifera

Adshead, P. C. (1967). Collection and laboratory maintenance of living planktonic foraminifera. *Micropaleontology,* **13**(1):32 – 40
Simple techniques of culture-floating in containers

Arnold, Z. M. (1974). Techniques for the study of living foraminifera: pp. 153 – 206 in *Foraminifera,* vol. 1 (Hedley, R. H. and Adams, C. G., Eds.). Academic Press, London
Complete guide to collecting and culture maintenance

Bé, A. W. H., Hemleben, C. and Anderson, O. R. *et al.* (1977). Laboratory and field observations of living planktonic foraminifera. *Micropaleontology,* **23**(2):155 – 179
Collection by diving and methods of maintenance in the laboratory

Boltovskoy, E. and Wright, R. (1976). Foraminiferal cultures: chap. 15, pp. 391 – 400 in *Recent Foraminifera.* Dr W. Junk, The Hague

Buzas, M. A. (1978). Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments. *J. mar. Res.*, **36**(4): 617 – 625
Methods of caging Foraminifera

Freudenthal, H. D., Lee, J. J. and Pierce, S. (1963). Growth and physiology of foraminifera in the laboratory, Part 2—a tidal system for laboratory studies on eulittoral foraminifera. *Micropaleontology,* **9**(4): 443 – 448

Lee, J. J., Pierce, S., Tentchoff, Marilyn and McLaughlin, J. J. A. (1961).
Growth and physiology of foraminifera in the laboratory, Part 1—collection and maintenance. *Micropaleontology,* **7**(4):461 – 466

Muller, Pamela H.(1974). Sediment production and population biology of the benthic foraminifer *Amphistegina madagascariensis. Limnol. Oceanogr.*, **19**(5):802 – 809
Basic laboratory culture methods

Murray, J. W. (1979). British nearshore foraminiferids: pp. 1 – 68 in *Synopses of the British Fauna (n.s.),* vol. 16 (Kermack, Doris, M. and Barnes R. S. K., Eds.), Academic Press, London
Includes methods of collection of live specimens, staining with Rose Bengal, flotation with heavy liquids, picking, sorting and recognition of wall structure and staining for aragonite

Rouvillois, Armelle (1977). Milioux d'élevage de Foraminifères en aquarium à Paris. *Rev. de Micropaleont.*, **20**(1):53 – 58

UNESCO (1968). *Zooplankton Sampling*. Unesco, Geneva

Disintegration and Concentration

Bolli, H. (1952). Note on the disintegration of indurated rocks. *Micropaleontologist,* **6**(1):46 – 48

Boltovskoy, E. (1966). Methods for sorting of foraminifera from plankton samples. *J. Paleont.*, **40**(5):1244 – 1246
Simple filtration method, most rapid and convenient, followed by classical method of picking out from a petri dish

Carlton, C. M. (1933). A method of concentrating foraminifera. *J. Paleont.* **7**(4):439
Describes bromoform technique in which air-filled Foraminifera are separated from sand by throwing the dried residue on bromoform and sinking the quartz by adding absolute alcohol. Pyritised Foraminifera in shale can be sunk in full-strength bromoform and the shale flakes floated off

Craig, G. Y. and Hogg, J. (1962). A rapid sorting device for microfossils.
Micropaleontology, **8**(1):107 – 108

Gibson, T. G. and Walker, W. M. (1967). Flotation methods for obtaining foraminifera from sediment samples. *J. Paleont.*, **41**(5):1294 – 1297

Hanna, G. D. and Church, C. (1928). Freezing and thawing to disintegrate shales. *J. Paleont.*, **2**:131
See Glaessner (1945, p.37; see 1963 reprint, detailed in main reference list under Glaessner, 1963a) for similar technique using sodium sulphate

Howe, H. V. (1941). Use of soap in the preparation of samples for micropaleontological study. *J. Paleont.* **15**(6):691
Method found useful for sands. Samples washed on 200-mesh screen in warm sudsy water and suspension decanted through another 200-mesh sieve

Kennard, M. C. and Smith, A. J. (1961). A simple micro-sample splitter. *J. Paleont.*, **25**(2):396 – 397
Ingenious device made entirely from glass slides

Laboratory, N. V. De Bataafsche Petroleum Maatschappi (1935).
Recovery of foraminifera by means of flotation. *J. Paleont.*,**9**(8):745 – 746
Describes washing, floating, use of soap as foam and technique of bubbling air through the mixture

Parker, Frances L. (1948). Foraminifera of the Continental Shelf from Gulf of Maine to Maryland. *Bull. Mus. comp. Zool. Harv.*, **100**(2):213 – 241
Includes description of a simple sample splitter

Redmond, C. D. (1953). Further notes on the disintegration of shale samples. *Micropaleontologist,* **7**(2):47 – 48

Stevens, C. H., Jones, D. H. and Todd, R. G. (1960). Ultrasonic vibration as a cleaning agent for fossils. *J. Paleont.*, **34**:727 – 730

Stinemeyer, E. H. (1965). Microfossil vacuum-needle segregating pick: pp.276 – 283 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Thiel, T., Thistle, D. and Wilson, G. D. (1975). Ultrasonic treatment of sediment samples for more efficient sorting of meiofauna. *Limnol. Oceanogr.*, **20**(3):472 – 473

Todd, Ruth, Low, Doris and Mello, J. F. (1965). General procedures and techniques applicable to major fossil groups—Smaller Foraminifera: pp.14 – 20 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco
Dangers of contamination and difficulties of sampling. Use of hydrogen peroxide technique, cinnamon oil in gum tragacanth, water soluble vegetable stains, removal of plant debris by carbon tetrachloride

Triebel, E. (1938). Ueber das Auslesen von Mikrofossilien. *Senckenbergiana,***20**(314):292 – 296
Improved 'Franke's picking tray' with holes at all grid intersections—less movement of tray but tendency of Smaller Foraminifera to stick on edge of holes

Sectioning

Akpati, B. N. (1969). A new technique for serial sectioning of foraminifera. *J. Paleont.*, **43**(4):1046 – 1048

Arnold, Z. M. (1965). An improved instrument for sectioning microfossils: pp. 232 – 238 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Cole, W. S. (1952). Eocene and Oligocene larger Foraminifera from the Panama Canal Zone and vicinity. *Prof. Pap. U.S. geol. Surv.*, **244**:1 – 41
Illustrates half-vertical sections made after the specimen is cut to the equatorial layer and photographed—to give paired thin sections from the same specimen

Croft, W. N. (1950). A parallel grinding instrument for the investigation of fossils by serial sections. *J. Paleont.*, **24**(6):693 – 698

Cummings, R. H. (1950). Oriented thin-sectioning of microfossils. *Contr. Cushman Fdn. foramin. Res.*, **1**(3 – 4):66 – 67

Cummings, R. H. (1952). Developments in micropaleontological technique. *J. Paleont.*, **26**(1):123
Further development of Wood's method of tracing off camera bellows. Bromide paper used on microprojector screen to produce 'trace' photographs for routine measurements. Use of plastic resins for mounting specimens for serial sections—series of cellulose peels taken after etching with dilute hydrochloric acid, care and practice required, difficulties arise through excessive or

insufficient etching or incorrect viscosity of the cellulose

Emiliani, C. (1951). Notes on the thin sectioning of smaller foraminifera. *J. Paleont.*, **25**(4):531 – 532

Hagn, H. (1953). A new method of preparing oriented thin sections of foraminifera and other small paleontologic specimens. *Micropaleontologist,* **7**(1):34

Hansen, H. J. and Lykke-Anderson, Anne-Lise (1976). Wall structure and classification of fossil and Recent elphidiid and nonionid Foraminifera. *Fossils and Strata,* **10**:1 – 37

Hofker, J. (1951). The Foraminifera of the Siboga Expedition. Part III—Ordo Dentata, Subordines Protoforaminata, Biforaminata, Deuteroforaminata. *Uitk. Zool. Bot. Oceanogr. Geol. Geb.*, monogr. IVc, 1 – 513
Castor oil *(Rhicinus)* as clarifier (does not evaporate). Describes sectioning small Foraminifera with Solenhofen chalk and castor oil

Honjo, S. (1960). A study of some primitive *Neoschwagerina* by a new serial section technique. *J. Fac. Sci. Hokkaido Univ.*, ser. 4, *Geol. and Min.* **10**(3):457 – 470
Ground surface etched with an inorganic salt solution (this gives more control than an acid solution) and peels taken with Bioden plastic. They show more detail than is generally visible on thin sections and can be taken every 10 μm.

Kennedy, Clarice M. A. (1978). An improved technique for revealing the internal structure of microfossils by scanning electron microscopy. *J. Paleontol.*, **52**(2):506 – 508
Specimens embedded in polyvinyl acetate which can be dissolved by soaking in acetone (30 – 60 min) after the section is cut. Section then washed in water and dried before mounting for scanning

Kennedy, C. and Zeidler, W. (1976). The preparation of oriented thin sections in micropaleontology: an improved method for revealing the internal morphology of foraminifera and other microfossils. *Micropaleontology,* **22**(1):104 – 107

Kremp, G. (1953). Preparation of oriented sections of microfossils. *Micropaleontologist,* **7**(1):29

Morkhoven, F. P. C. M. Van. (1958). A simplified method of grinding foraminifera. *Micropaleontology,* **4**(2):209 – 210

Pohl, E. R. and Browne, R. G. (1973). A thin section method for ultrasmall paleontologic specimens. *J. Paleont.*, **47**(2):221 – 225

Wood, A. (1948). Sectioning small foraminifera. *J. Paleont.*, **22**(4):530

Microscopy (including Methods of Preparation, including Sectioning for TEM and SEM)

Bellemo, S. (1974). Ultrastructures in Recent radial and granular calcareous foraminifera. *Bull. geol. Instn Univ. Uppsala, N.S.,* **4**:117 – 122
Preparation of sections for SEM examination of wall structures. Etching with sodium hypochlorite to remove organic matrix and glutaraldehyde which fixes protein and dissolves calcite

Deutsch Conger, Susan and Green, H. W. (1976). Preparation of thin-foil specimens for transmission electron microscopy of microorganism tests. *J. Paleontol.*, **50**(5):795 – 798

Grønlund, H. and Hansen, H. J. (1976). Scanning electron microscopy of some Recent and fossil nodosariid foraminifera. *Bull. geol. Soc. Denmark,* **25**:121 – 134

Hansen, H. J. (1968). X-ray diffractometer investigations of a radiate and a granulate foraminifera. *Meddr. dansk geol. Foren.,* **18**(3 – 4):346 – 348

Hansen, H. J. (1970). Electron-microscopical studies on the ultrastructures of some perforate calcitic radiate and granulate foraminifera. *K. danske Vidensk. Selsk. Skr.,* **17**(2):1 – 16
TEM techniques: To obtain replicas of inner surfaces the specimen was embedded with the chambers air-filled and aperture sealed with gum tragacanth. After hardening of Araldite, the specimen was ground to midpoint with frosted glass. Before etching with ethylenediamine tetra-acetate it was replicated 2 – 3 times to remove dust and inner organic membrane and after etching to remove the free etched membrane. Replication with collodion was found to be the most convenient. Describes technique whereby several replicas can be made without losing the specimen

Hansen, H. J. and Reiss, Z. (1972). Scanning electron microscopy of wall structures in some benthonic and planktonic Foraminiferida. *Revta est. Micropaleont.,* **4**(2):169 – 179

Hansen, H. J., Reiss, Z. and Schneidermann, N. (1969). Ultramicrostructure of bilamellar walls in Foraminiferida. *Revta esp. Micropaleont.,* **1**(3):293 – 316
TEM: Specimen ground in Araldite with carborundum paper 600 and polished with MgO powder 0.8 μm; cleaned in ultrasonic vibrator for 5 sec, etched EDTA 3 – 4 min, washed in demineralised water. Dried specimen replicated with collodion or platinum – carbon shadowed peels made; transferred to cut-off grids and replicas dissolved
SEM: Dry specimen embedded in Lakeside 70 on stubs and broken with needle to show septa

Hay, W. W. and Sandberg, P. A. (1967). The scanning electron microscope, a major break-through for micropaleontology. *Micropaleontology,* **13**(4): 407 – 418

Hay, W. W., Towe, K. M. and Wright, R. C. (1963). Ultrastructure of some selected foraminiferal tests. *Micropaleontology,* **9**(2):171 – 195
TEM: Specimen washed in acetone then carbon replicas made under vacuum, calcium carbonate tests then dissolved in HCl; replicas washed in distilled water and picked up on Formvar. A coated electron microscope specimen screen is used for viewing

Hyde, P. and Krinsley, D. (1964). An improved technique for electron microscopic examination of foraminifera. *Micropaleontology,* **10**(4):491 – 493

Jahn, Brigette (1953). Elektronenmikroskopische Untersuchungen an Foraminiferenschalen. *Z. wiss. Mikrosk.,* **61**:294 – 297
Pioneer TEM study on Foraminifera

Jones, D. J. (1956). Use and care of the microscope: appendix A, pp. 337 – 341 in *Introduction to Microfossils.* Harper, New York

Kimoto, S. and Honjo, S. (1968). The SEM as a tool in geology and biology: in *Manual of Micropaleontological Techniques.* McLean Paleont. Lab. Alexandria, Va., USA *(J. Fac. Sci., Hokkaido Univ.,* ser. IV, **14**(1):57 – 59)

Kimoto, S. and Russ, J. C. (1969). The characteristics and applications of the scanning electron microscope. *American Scientist,* **57**(1):112 – 133

Krinsley, D. and Bé, A. W. H. (1965). Electron microscopy of internal structures of foraminifera: pp.335 – 344 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.), W. H. Freeman, San Francisco
TEM: Acetate peel replicas obtained after etching with EDTA for 1 – 2 min, shadowed with platinum – palladium alloy. Replica dissolved in acetone before TEM photography

McGee-Russel, S. M. and Orville, R. E. (1974). Aspects of image analysis of high voltage electron micrographs of air-dried whole mounts of pseudopodial networks of the marine protozoan *Allogromia* (Foraminifera); hand methods and electronic methods: pp.155 – 162 in *High Voltage Electron Microscopy; Image Recording and Resolution.* Academic Press, London

Neumann, Madeleine (1974). Aperçu sur l'apport du microscope electronique à balayage à la connaissance des Foraminifères. *Trav. Lab. Micropal. Univ. Paris,* **6**(3):27 – 70

Oatley, C. W. (1966). The scanning electron microscope. *Science Progress,* **54**(216):483 – 495.
The original description

Paterson, D. (1965). Microscopy in the round. *New Scientist,* **28**:737 – 739.
How the SEM works.

Sylvester-Bradley, P. C. (1969). Aluminium coating in scanning electron microscopy. *Micropaleontology,* **15**(3):366

Walker, D. A. (1978). Preparation of geological samples for scanning electron microscopy: pp. 185 – 192 in *Scanning Electron Microscopy,* vol. I. SEM Inc., A.M.F. O'Hare, Illinois

Wood, A. (1963). Wall structure of foraminifera in polarised light. *Micropaleontology,* **9**(4):432

Special Methods of Preparation and Examination

Anderson, O. R. and Bé, A. W. H. (1978). Recent advances in foraminifera fine structure research: pp. 121 – 202 in *Foraminifera,* vol. 3 (Hedley, R. H. and Adams, C. G., Eds.). Academic Press, London and New York
Chemical fixatives, techniques, fixation procedure for electron analysis, use of glutaraldehyde and anaesthetic ($MgCl_2$)

Arnold, Z. M. (1965). The vacuum oven for impregnating microfossils: pp. 262 – 263 in *Handbook of Paleontological techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

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Chapter 3

The Living Foraminifer

Unique animals.

(Hedley, 1964)

The micropalaeontologist is concerned with the abandoned, dead shells of Foraminifera and classification of fossil species proceeds entirely upon the basis of the morphology of the hard parts or test. However, he requires a knowledge of the live animal because the morphology and the evolutionary changes so important in stratigraphy can only be understood when the adaptive function of the test in the living animal is known. Also, as will be seen, study of the soft parts and of life history has revealed a number of remarkable features and helped to solve some long-standing problems in the palaeontology of the group.

Foraminifera are single-celled animals (phylum Protozoa) and belong to the same class (Rhizopoda or 'root feet') as *Amoeba*, distinguished by temporary extrusions of the protoplasm or pseudopodia. Foraminifera differ from *Amoeba* in that the pseudopods are fine and hair-like and anastomose together to form a spreading, reticulate network, as well as in the possession of either a gelatinous or a hard, agglutinated or calcareous test.

It must not be thought that because Foraminifera are single celled they are necessarily simple animals. The single cell of the protozoan has to carry out many functions that may be carried out by a range of specialised cells and tissues in the Metazoa including, in Foraminifera, the construction of an architecturally complicated test. This is reflected in the complexity of the protozoan cell with its numerous organelles, as revealed by the electron microscope (figure 3.1).

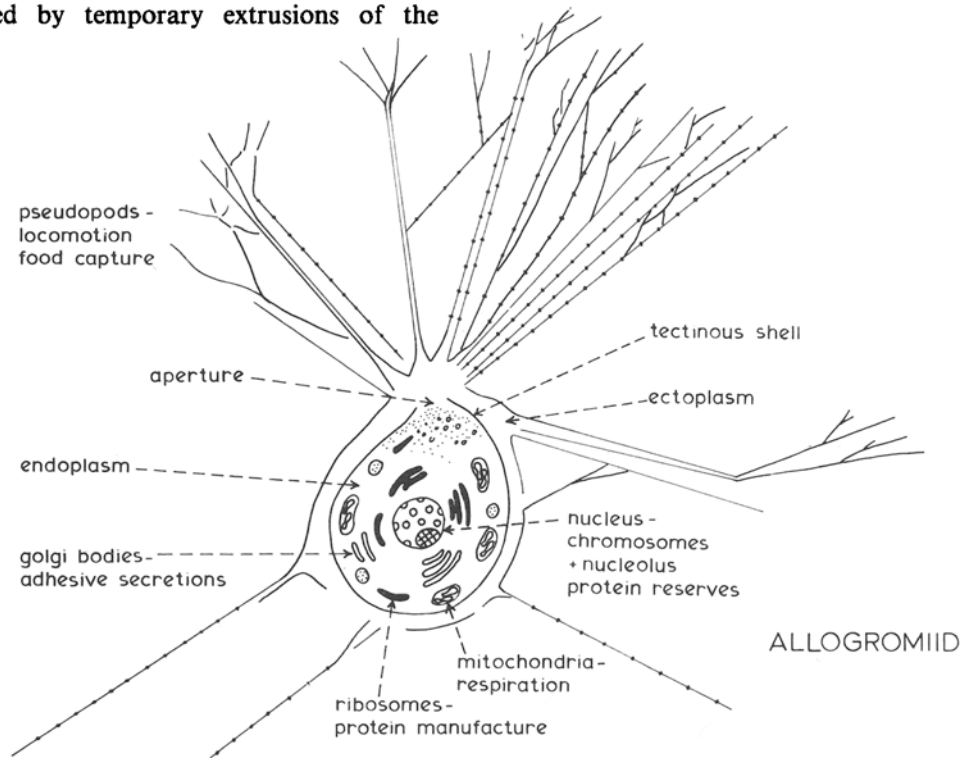

Figure 3.1 Basic soft part morphology, allogromiid

THE STRUCTURES OF THE CELL

The most primitive order, the Allogromiida, includes naked genera such as *Allogromia, Myxotheca* and *Shepheardella*. Here, the test is an organic, gelatinous sac-like structure, $1-10$ μm thick, composed of glycoprotein (proteinaceous mucopolysaccharide, according to Hedley, 1964) and referred to as tectin. It is an internal structure (figure 3.1) surrounded by ectoplasm (a clear gel-like cytoplasm) immediately external to the primary cell membrane (pellicle or plasmalemma) which contains the dense sol-like endoplasm. In advanced Foraminifera such as the globigerinids (figure 3.2), the organic layer becomes an inner lining to the calcareous test. It should be noted that the cytoplasm everywhere has the capacity for membrane formation and recombination.

Most structures occur in the endoplasm. The overall organisation of the cell is controlled by the nucleus. This is confirmed by the consequences of its removal which leads to disorganisation, failure to digest and eventual death. It has a porous envelope for communication with the rest of the cell and contains the chromosomes which bear the genetic codes needed to produce new cells and are the only structures capable of identical reduplication. There are 7 in *Myxotheca arenilega,* 18 in *Rotaliella heterocaryotica* (9 in *R. roscoffensis* but twice as large) and 24 in *Patellina corrugata* (Grell, 1973). These numbers are constant, which indicates that the chromosomes are regularly distributed to daughter cells on reproduction. The nucleolus is probably responsible for protein reserves.

There is always one nucleus but there are multinucleate development phases. The nuclei may be all alike (homokaryotic) as in *Spirillina* or there may be two kinds (heterokaryotic) — generative nuclei which take part in reproduction and somatic nuclei which take part in some processes and then die, as in *Rotaliella* (Grell, 1973).

The products of metabolic processes are transported through the cell via a continuous network of membranous canals—the endoplasmic reticulum. Granules may coat the outside; these are the ribosomes which synthesise proteins. Also, the ribosomes commonly occur free in the ground cytoplasm. Membranous sacs free of granules also occur; these are the Golgi complexes which function in the production of polysaccharides as

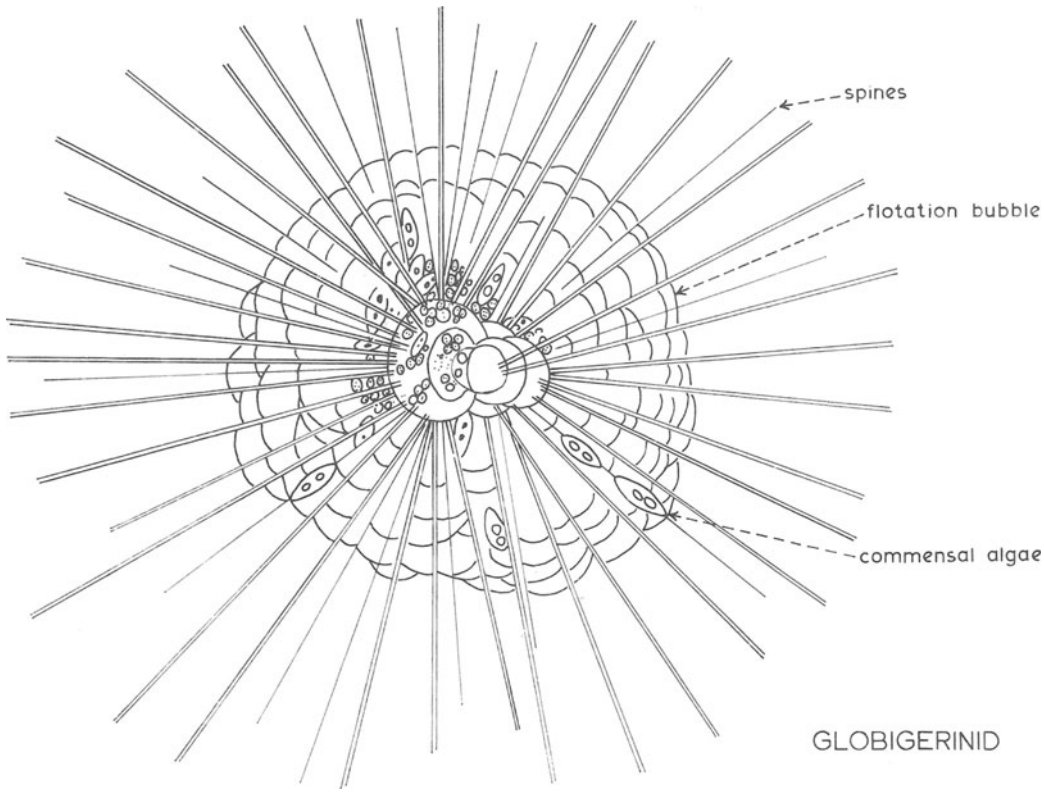

Figure 3.2 Basic soft part morphology, globigerinid

well as mucoid substances and may also be concerned with the packaging of enzymes into the lysosomes. The lysosomes are small vesicles that surround the food vacuoles and deliver their contents during digestion (see further discussion below).

The 'power stations' of the cell are the mitochondria. These are sausage shaped with two membranes, the inner forming invaginations in the outer. The large surface area reflects the function of this organelle, which is to store the energy of oxidation by synthesis of adenosine triphosphate (ATP) until required for energy-consuming reactions.

The most striking structures of the ectoplasm are the pseudopods. These are granular threads that stream out in all directions, reaching lengths of up to three times the diameter of the test (figure 3.1). They may follow a 'guide rhizopodium' and form a distinct trunk-like mass issuing from the aperture (podostyle) with linear elements that fuse and divide to form a broadly ramifying network. Frankel (1975) has shown that a distinct podostyle is formed by the multichambered, agglutinated species *Miliammina fusca* when it is living within the sediment. Under these confined conditions the pseudopods are concentrated into bundles rather than spread out, perhaps in order to push aside and probe through the sedimentary grains. In those species which live within the sediments (infaunal) or live on it (epilithic), the net of pseudopodia developed below the surface becomes an important binding agent (Nyholm, 1957), strong enough to bind reefal sands into an aggregate that can withstand wave action, as has been observed by Ross (1972c) on the Great Barrier Reef.

The tectin wall may be thickened near the aperture in Allogromiids and this oral structure (stomostyle) is turned out (everted) when the pseudopods which can be traced into the endoplasm are extruded (Hedley, 1964).

An oscillatory two-way movement is detectable in the pseudopods. This has been explained as due to two semi-cylindrical units moving in opposite directions as a result of shearing forces (Jahn and Rinaldi, 1959) or by a relatively solid axis moving inwards while a more fluid outer layer moves outwards (Kavanau, 1962). The granules may be mitochondria, and opaque particles which have been observed may be waste particles concentrated as 'stercomata'. The pseudopods can expand and contract and are thrown out on one side—'shot out' in the graphic phrase of Jepps (1942)—and retracted on the other side in locomotion. Proceeding in this way, hauling itself along by its pseudopodia, speeds of a few millimetres an hour may be achieved.

Sheehan and Banner (1972) and Banner and Williams (1973) have shown that very similar pseudopodial networks are a feature of calcareous genera such as *Elphidium* and *Ammonia*. Here the pseudopods arise from ectoplasm which appears to be largely concentrated in the apertural and umbilical regions and covers the last chamber. Speeds of movement of up to 2 mm/h were noted for *Ammonia*.

In Globigerinids a fine net of pseudopods, 'resembling a cobweb of very fine dimensions' (Anderson and Bé, 1976) is supported by the spines which rise from the calcareous test and radiate out in all directions. The Globigerinids are free-floating members of the plankton in the surface waters of the open ocean. Here, the ectoplasm which is frothy and highly vacuolated surrounds the test completely. A vesicular 'fibrillar system' developed in the vacuoles may aid in flotation and control vertical diurnal movements in the water column (Zucker, 1973). In *Hastigerina*, a definite flotation bubble is developed up to 2 mm in diameter (figure 3.2). However, even these pelagic forms can creep along various substrates and oar themselves along just below the surface film of sea water by means of their pseudopods.

The strength and adhesiveness of the pseudopods and their effectiveness in food gathering and test construction is indicated by the ability of *Ammonia* to drag quartz grains along, equal to the test diameter, for several millimetres.

NUTRITION

The food of Foraminifera includes unicellular algae, especially diatoms, other protozoans and small metazoans including crustaceans such as copepods. In addition, according to Muller and Lee (1969), a proportion of bacteria is also an indispensable element in their diet. The pseudopods which are able to become sticky, possibly as a result of secretions produced by the Golgi apparatus (Anderson and Bé, 1976), may also be able to attract algae such as dinoflagellates (Christiansen, 1971) and even paralyse small animals.

Solid food may be carried through the aperture and digested with the help of enzymes secreted by the lysosomes or partly digested in place (phagocytosis). Liquids and macromolecules are taken up by invagination of the cell wall and pinching off of the vesicles so formed—usually at

the tips of the pseudopods (pinnocytosis), as described by Sheehan and Banner (1972).

The capture of a crustacean and its digestion have been graphically described by Bé *et al.* (1977):

> When a crustacean comes into contact with *Hastigerina pelagica*'s spines, the prey is immediately and inextricably snared by the rhizopodia. The great mechanical stress to which the foraminifer is subjected and the extraordinary ability of the rhizopodia to adhere to several actively pulling crustaceans at the same time are worthy of closer observation. Despite strong efforts to escape, the prey is gradually drawn into the bubble capsule, displacing some bubbles in the process. An adhesive substance is released from vacuoles within the rhizopodia which cover the surface of the prey. The rhizopodia penetrate into crevices in the cuticle of the prey, invade the underlying soft tissue and engulf liquid droplets and small particles of tissue that are released by the dying cells. Engulfed particles of food are carried by rhizopodial streaming into the foraminiferal cytoplasm, where food vacuoles containing the engulfed prey tissue become converted into digestive vacuoles.

In many species of Foraminifera, particularly in Globigerinids and Larger Foraminifera, various algae occur in the endoplasm as well as in the ectoplasm in an association which strongly suggests a symbiotic relationship (living together for mutual benefit). Both green algae (Zoochlorellae—mostly *Chlorella*) and golden/brown algae (Zooxanthellae—mostly dinoflagellates) occur. The symbionts may be attracted to their hosts, as Ross (1972c) noticed that several actively swimming dinoflagellates commonly congregated near *Marginopora*. Their density throughout the protoplasm in this species imparted a distinct yellow-brownish green colour to the foraminifer and was found to be strongly controlled by light. Specimens which had lain on one side for some time became much darker on the upper side with up to 16 symbionts per chamber compared with 2–4 on the poorly lighted side. The symbionts are evidently strongly phototropic. In *Sorites* and *Archaias* they are concentrated beneath the test wall and move actively through the host cytoplasm and through the stolons between the chamberlets (Leutenegger, 1977).

Work on the ultrastructure of *Globigerinoides sacculifer* by Anderson and Bé (1976) reveals at least three species of symbionts. During the day these occur mainly in the outer net of fine pseudopodia. In the evening they become surrounded by pseudopods and sequestered in the vacuoles of the ectoplasm and are finally carried through the aperture into the endoplasm. During the night it appears that dense deposits, occasionally seen in the membranous folds of the symbionts when they are in the ectoplasm, may be transferred to the host cytoplasm. In the morning the symbionts are carried out again and transferred along the spines to the net of pseudopods, where they can carry out photosynthesis under the most favourable conditions. No evidence of digestion of the algae was found, so the symbionts were not being used directly as food particles.

As well as symbiosis with algae, the phenomenon of 'chloroplast symbiosis' has also been discovered in the calcareous, brackish water and marsh species, *Elphidium williamsoni* and *Haynesina germanica* (=*Nonion germanicum*), Christensen (1977). In these small, benthonic species, chloroplasts obtained by ingestion of algae, probably diatoms, continue to function as transplants in the endoplasm of the foraminifers. As the chloroplasts are small, 2–3 μm in diameter, they can easily be passed through the small, multiple apertures and foramina of these species. Up to 100 000 occur sequestered in the endoplasm of one individual of *E. williamsoni*, and the products of their photosynthetic activity provide a considerable energy source.

It is difficult to tell at this stage of research to what extent the algae or sequestered chloroplasts are necessary to different foraminifer species. However, vigour and $CaCO_3$ productivity have been related to the presence of symbionts (Röttger, 1972; Muller, 1978), and it is tempting to ascribe the restricted range of *E. williamsoni* to its symbiotic habit and relation to particular littoral diatoms. The algae supply oxygen which may be of benefit when the foraminifer draws calcium from sea water to build its test (as in the analogous case of the Corals in association with Zooxanthellae). Such a partnership probably accounts for the rate of carbonate shell production in calcareous Larger Foraminifera, which is 20–100 times as great as in smaller benthonics (Ross, 1974). They may also bind carbonic acid and take up nitrate and phosphates. Röttger (1973) has described the remarkable case of *Heterostegina depressa* which can grow without ingesting food other than that provided by its symbionts. It is apparently able to lead a sessile mode of life inside a hyaline sheath secreted by the

ectoplasm. The sheath is fixed to the substrate by branched processes and the foraminifer can move about inside by means of its pseudopodia.

According to Hedley (1964) the various colours of protoplasm that have been reported are largely a reflection of the contained symbiotic algae and accumulated wastes as well as cytoplasm pigments and may therefore be changeable. The colours include: vivid sky blue, *Alveolinella;* pale grey-green, *Operculina*; green, *Heterostegina, Elphidium (crispum), Amphistegina* (also with red flecks); lavender, *Peneroplis;* red to dark brown, *Discorbis* (Myers, 1942). Ross (1972c) notes that *Marginopora* can be distinguished from *Amphisorus* by its yellowish – brownish green protoplasm. Distinctions can also be made at the species level in *Elphidium*. In the Dovey estuary (Wales), *Elphidium williamsoni* is generally green, while *E. waddensis* is golden-brown when recovered from the same samples. However, *Allogromia laticollaris* is orange when grown in cultures containing abundant algae, but white or grey when cultured on bacteria or corn starch (Arnold, 1955).

In summary it appears that, as well as exploiting the possibilities of symbiosis in both the benthonic and planktonic realms, Foraminifera also exploit all the six major classes of food resource available to benthonic invertebrates according to Walker and Bambach (1974). These are: dissolved and colloidal organic molecules; organic rich grains (fungal and algal coated and including faecal pellets); particulate organic detritus; live plants; live animals; dead organisms. This success is due to the versatility of the pseudopodial network and explains the abundance of the subclass across the broad spectrum of marine environments. It also helps to explain the great variety of test shapes, coiling modes and apertural modifications in the group, discussed in chapter 4.

REPRODUCTION

During the nineteenth century it gradually became clear that many species of Foraminifera constantly occur in two distinct size groups (dimorphism). It is particularly well marked in Larger Foraminifera such as *Nummulites,* in which it was first pointed out by De La Harpe (1879a) (plate 1). The biological explanation of dimorphism was discovered by Lister (1895), when working on *Elphidium crispum,* to be the result of the alternation of two generations with different kinds of reproduction. Further studies (Jepps, 1942, 1956; Lister, 1903) have shown that this involves an asexual generation (agamont) with a small proloculus (microsphere) and a sexual generation (gamont) with a large proloculus (megalosphere). As this cycle has been found to occur generally in all the main groups of Foraminifera it is appropriate to look at it in detail in the closely studied species, *Elphidium crispum*.

In asexual reproduction, reduction division of the nucleus takes place (meiosis) to give daughter cells with half the number of chromosomes (haploid). These haploid 'agametes' grow to give the haploid, sexually reproducing, gamont generation (A form). When the gamont has reached a certain size sexual reproduction takes place without further reduction of the chromosomes to give haploid gametes (mitosis). These are flagellate and free swimming. They leave the test, meet and fuse to produce a resting stage (zygote) which gives rise to the new, diploid, asexually reproducing, agamont generation (B form). This process with one generation diploid and one haploid is 'heterophasic alternation of generations' and is general in the Protozoa. However, the possession of a diploid, asexual generation in all foraminiferal species studied (Hedley, 1964), as in plants, is unique among Protozoans and, indeed, among animals.

The haploid gamont has a single nucleus only, but in the B form nuclear multiplication takes place before the zygote hatches, so it is multinucleate throughout life. The B form is also larger and develops more chambers than the A form.

The complete cycle for *E. crispum* takes two years in the shallower parts of the English Channel, although it may be delayed at deeper stations. Asexual reproduction reaches a peak in April. All the protoplasm leaves the test and within the protection of a 'halo' of pseudopods separates into the daughter cells which secrete a calcareous megalosphere before dispersal. Chambers are added at the rate of about two per day. Most are full grown by the end of the summer and pass the winter in a state of inactivity. Sexual reproduction begins early in the second spring as temperatures begin to rise. The biflagellate gametes are produced inside the test and escape via the aperture and septal pores, leaving it undamaged. The gametes conjugate outside in the open sea to produce zygotes and the B form then develops and matures during the second summer. They always appear to be less abundant than the A

forms and Jepps found that megalospheric forms outnumber microspheric forms by about 30 to 1 throughout the winter months.

That the same cycle occurs in other major groups of forams, including primitive allogromiids, is shown by figure 3.3 which illustrates the reproduction phases in *Myxotheca arenilega*. Again, thousands of flagellate gametes, each with a full complement of organelles, are produced at mitosis (Angell, 1971) to give a diploid zygote and, although unilocular, the B form can be seen to be distinctly larger.

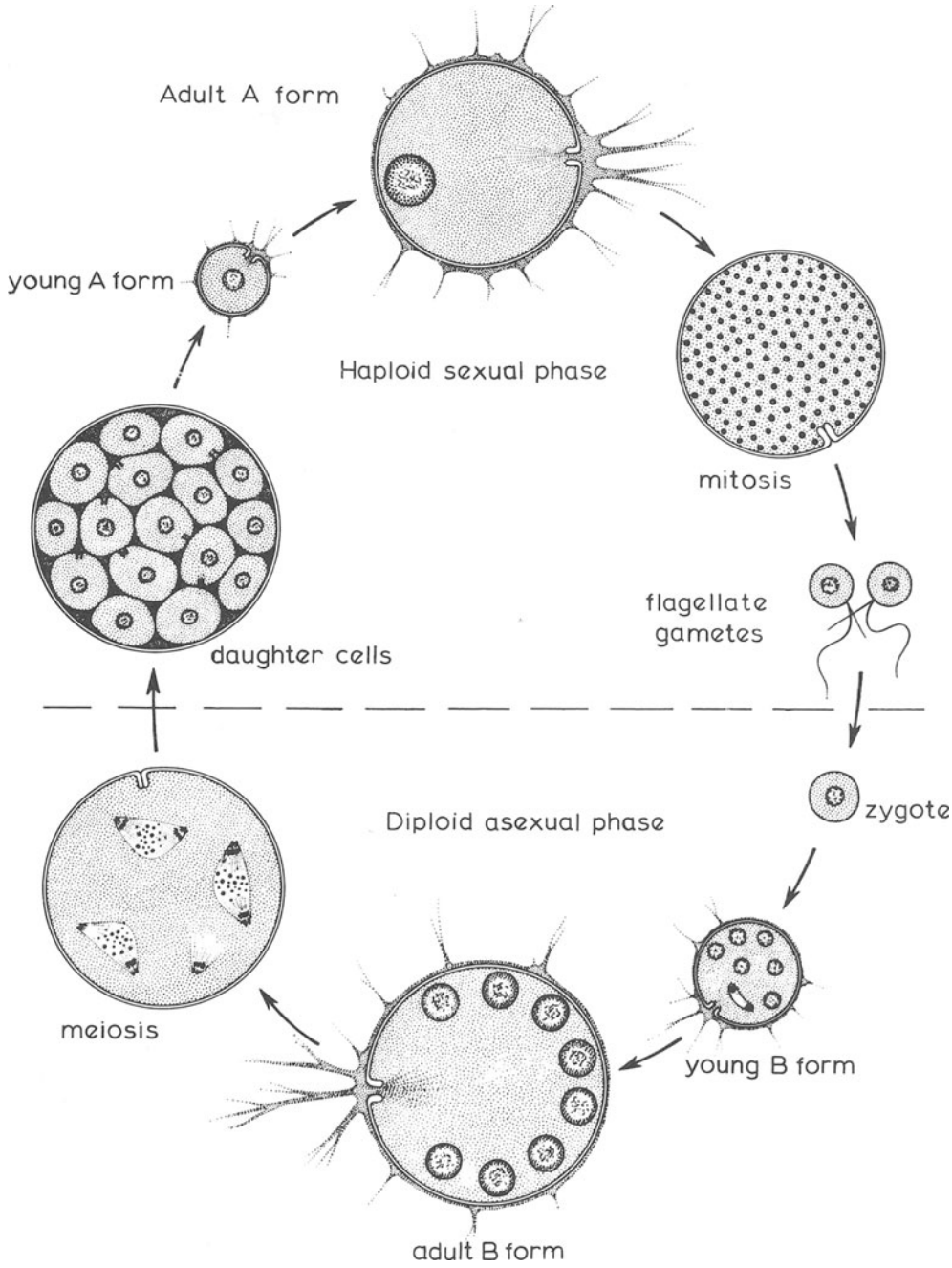

Figure 3.3 Alternation of generations in *Myxotheca arenilega*. After Grell (1973)

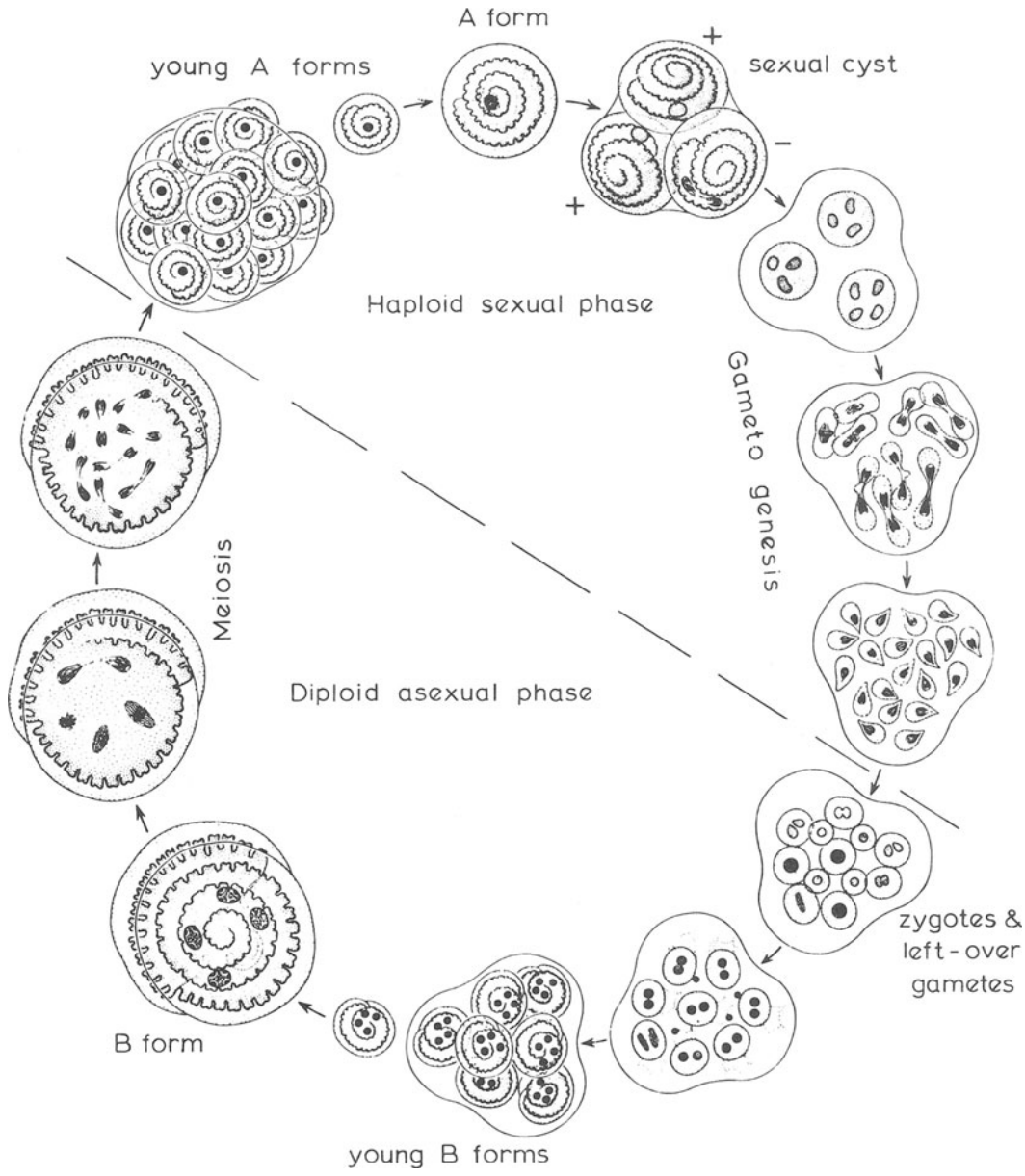

Figure 3.4 Alternation of generations in *Patellina corrugata*. After Grell (1973)

Interesting variations on the general theme are shown by other allogromiids and the Spirillinidae (including the possibly related *Rotaliella*). In these groups the gametes are amoeboid rather than flagellate, although otherwise the ultrastructure appears to be the same (Schwab, 1976). The life cycle of the multichambered, calcareous spirillinid, *Patellina corrugata* was first worked out by Myers (1935), supplemented by Grell (1959). The phases are shown in figure 3.4. The adult B form builds a protective cyst for asexual reproduction and the daughter cells secrete the initial, undivided spiral part of their tests (juvenarium) using the parent as a source of calcium before breaking free. At maturity the A forms congregate in groups of up to nine individuals inside sexual reproduction cysts. According to Grell the A form is sexually differentiated and the gametes only fuse with those from a parent of the opposite 'sex'. As shown in figure 3.4 both sexes are normally present in the aggregates. In a case where two plus

individuals (with 3 nuclei) are associated with one minus individual (with 4 nuclei) only 8 zygotes will be produced, the spare nuclei being consumed as food. Although this species has an undivided juvenarium, and no true proloculus is distinguishable, pronounced dimorphism is exhibited and the B form is clearly larger.

The low numbers of gametes produced in *P. corrugata* is doubtless connected with the development of the protective cyst around the multiple aggregates of the adult sexual generation. In those genera like *Elphidium* where the gametes are flagellate and released into the open sea, vast numbers are produced—described by Jepps (1956) as, 'a dancing multitude of biflagellate swarm spores. They usually leave the shell in the middle of the night, in a milky stream as if the parent were smoking hot'. An attempt to estimate the actual numbers involved has been made by Bé and Anderson (1976) in their study of gametogenesis in the planktonic globigerinid, *Globigerinoides sacculifer*. Counts made from thin sections of fixed and stained specimens indicate that the number produced may exceed three million, each about 5 μm in diameter. As Bé and Anderson point out, although planktonic Foraminifera are abundant in the water column, they are so widely spaced that only the production of myriads of gametes can ensure cross-fertilisation. Even so, it appears that A forms always greatly outnumber the B forms.

Special methods are employed to aid the disposal of gametes in the multilocular, calcareous discorbid, *Tretomphalus bulloides* (figure 3.5) with pairing (plastogamy) to ensure cross-fertilisation. The B form is attached and asexual reproduction takes place beneath a protective cover of agglutinated debris (cyst). Some 200 embryos are produced which dissolve the test wall to escape. The A form also lives as an attached form until it has developed up to 18 chambers, when it again forms a cyst. This is followed by the formation of a large, spherical float chamber filled with gas. The foraminifer then bursts out of the cyst and floats to the surface. Sexual reproduction with formation of flagellate gametes takes place after pairing with another individual that has reached the planktonic stage. The float chambers are brought together by movements of the pseudopodia and the gametes are discharged through special pores. This process is probably made easier if the coiling directions are the same. The fused gametes, which are the product of two different parents, then sink to the bottom and form a zygote which gives rise to the attached benthonic, microspheric phase.

In *Marginopora* a number of cyclic 'reproduction chambers', without partitions, are produced at maturity by the asexual form. Up to 150 embryos are nurtured in these special chambers and are released by breakdown of the peripheral margin. The rest of the reproduction chambers also rapidly disintegrate under reefal conditions, so that quite soon only a jagged remnant of the first reproduction chamber is observable (Ross, 1972c). The life cycle in this large, tropical genus also appears to be longer than that of genera such as *Elphidium* and *Ammonia* in the temperate zone, and asexual reproduction may not occur until growth has proceeded for two years or more. The largest individuals, up to 3 cm diameter, showed no reproduction chambers and may have lived, still growing, below the depth limit for reproduction. Jepps (1942) showed that *Elphidium crispum* took longer to mature at greater depths, and tank experiments (Bradshaw, 1955; Murray, 1963) confirm that reproduction occurs earlier under optimum conditions whereas at low temperatures and with decreased food growth may continue longer, resulting in larger individuals.

The alternation of generations is not strict in all species and asexual reproduction may be repeated giving an intermediate A form (trimorphism of Hofker, 1925) or even a series of A forms with different sized megalospheres (polymorphism). Under tank conditions, only asexual reproduction has been observed in some species (Lecalvez, 1950; Ross, 1972c). McEnery and Lee (1976) report the interesting case of *Allogromia laticollaris*, in which three different strains all show different styles of this apogamic reproduction, differing from the 'classical' mode.

GENERAL HABIT

The majority of Foraminifera live on the sea bed (benthonic), while a small number of genera and species, often represented by a very large number of individuals, float freely in the water column of the open ocean. A relatively small number of benthonic genera live permanently attached with their tests firmly cemented to various objects on the sea floor. Different species are adapted to the full range of temperatures and salinities that occur in the oceans as well as marginal marine environments, and some groups can withstand low levels of oxygen and alkalinity and flourish below the depth of calcium carbonate dissolution (CCD) on the abyssal plain.

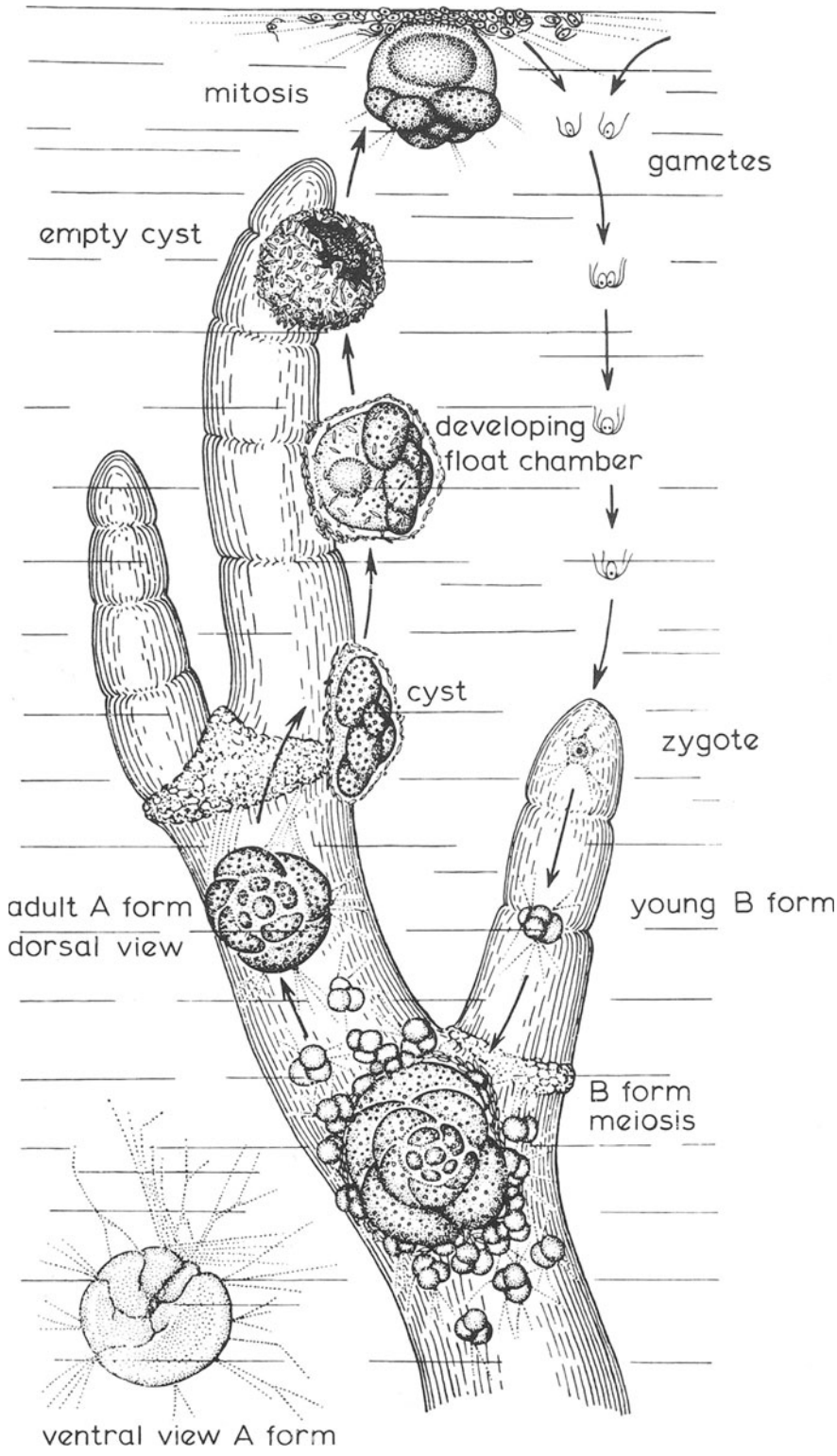

Figure 3.5 Alternation of generations in *Tretomphalus bulloides*. After Grell (1973)

The free benthonic forms occur on most sediments (epilithic) and also live within them infaunally to depths controlled largely by the onset of anaerobic conditions. Ross (1972c) has described how even large discoid species such as *Marginopora vertebralis* can work to the top of a layer of coarse, shell sand 1 – 2 cm thick within 12 h. However, under conditions of extreme turbulence and continual sediment movement such as occur on the exposed, shallow shelf areas around the British Isles, the vagrant Foraminifera, like the attached forms, are limited to sheltered niches on hard substrates and in particular to the shelter afforded by 'seaweed'. In the shallow, sunlit (photic) zone the vagrant Foraminifera cling by means of their pseudopods and congregate in the 'holdfasts', especially of *Laminaria*. They similarly occur as epiphytes on *Zostera,* the eel grass, as they do on its tropical counterpart *Thalassia,* the turtle grass (Brasier, 1973, 1975a). Below the zone of macroscopic algae the Foraminifera cling to animal substrates, particularly hydroids (Dobson and Haynes, 1973) and bryozoans such as *Flustra*. They even occur on large mobile, invertebrates such as molluscs, including swimmers like scallops (Haward and Haynes, 1976).

Foraminifera living symbiotically with algae, particularly the Larger Foraminifera, are restricted to the photic zone. This may extend to only some 20 m or less in the temperate zone, but to 120 m in the tropics, before the point is reached where the products of photosynthesis can no longer balance respiration, at the respiration compensation depth (RCD). Conditions favourable for symbiosis probably disappear well before these depths; also, light penetrates only a few millimetres into the sediments.

When epiphytic and epizoic Foraminifera die they fall from their 'hosts' and accumulate in the sediments on the sea floor. Carried along by currents they become size sorted, together with the dead tests of species that live in or on the sediments. Fragile species may break down completely and robust species build up preferentially in number. Light species may be winnowed away and carried in suspension to be deposited with fine muds in quiet areas many miles from their point of origin. Even live species can be put into suspension by extreme turbulence and taken in plankton nets (Loose, 1970). It is clear that in cases like this there is no similarity between the life assemblage (biocoenosis) and the death assemblage (thanatocoenosis). The work of Atkinson (1971) shows how the numbers of dead Foraminifera in southern Cardigan Bay relate closely to the pattern of sediments. Predation may also alter the number and sizes of tests being contributed to the sediment and lower abundance by removal of individuals prior to reproduction. Worms and sponges make irregular tunnels into the test wall, gastropods make neat holes and longitudinal scrapes, while echinoderms make round holes with radiating grooves, caused by the Aristotles' Lantern (Earland, 1956; Sliter, 1971). These attacks probably contribute to the rapid breakdown of fragile tests. Further changes as a result of diagenesis would attend the transformation of the incoherent sediment into a lithified stratum in the geological column.

SUMMARY OF IMPLICATIONS FOR STRATIGRAPHY

As pointed out by Hedley (1964), the life histories of only a few species representing but a few families are known in detail. This is still true and we must recognise the force of his argument that generalisations based on this evidence may be misleading for the Foraminifera as a whole. There is also the problem that tank experiments cannot duplicate natural conditions and results so obtained must be treated with reserve. However, bearing this in mind some generalisations do appear to be possible and there are some clear implications for the stratigraphical application of the group:

(1) The ultrastructure of the soft parts and the life histories prove to be complex, matching the complication of shell structure. On the whole the distinctions that can be made support the taxonomic categories made on the basis of hard parts alone. This is important for the confident recognition of species only found as fossils. Differences in the fine structure of the pseudopods and colour of the protoplasm do not appear to be specific, but symbiotic species may associate with particular algae.

(2) The well-known dimorphism exhibited by many foraminifer species is the result of an alternation of generations. The reproductive cycle involves a diploid (B form), which after asexual meiosis produces the haploid (A form), sexual generation, as in plants. Generally the B form is larger than the A form, is microspheric and develops more chambers in multilocular species. There are variations at the specific level but the species regarded as more primitive on grounds of test structure appear to have the lowest chromosome numbers and the simplest reproduction cycles. In groups which do not

possess a true proloculus but develop a juvenarium this, like the adult test overall, is larger in the B form.

(3) Where the daughter cells and gametes are released into the open sea, as in *Elphidium,* the dead tests are vacated and left in good condition in the death assemblage, with the A forms generally much outnumbering the B forms. In species where the final chamber or chambers of the B forms are modified as brood chambers, these may be damaged or destroyed during growth and release of the embryos. The last chamber in the A form may also be modified and bear special pores for the release of the sexual gametes. These modifications must be taken into account in classification. In some cases the B forms are completely destroyed and are therefore not found in the death assemblage or as fossils at all.

(4) Under optimum conditions Foraminifera complete their reproduction cycles as soon as they reach maturity. This may be delayed, although growth continues, under adverse conditions. As the test is usually vacated after reproduction this means, paradoxically, that a large, well-grown fauna may indicate slow growth with reproduction inhibited or delayed, while a fauna of relatively small individuals may indicate favourable conditions. It is clear that faunas of small individuals occurring in the stratigraphic column should not be confused with dwarfed or 'depauperate' faunas.

(5) In life many species cling firmly to various substrates by means of their pseudopods. On death their tests accumulate in the sediment and, particularly on the turbulent, shallow shelf become current sorted along with the shells of species that live in the sediment and, perhaps, also the dead shells of planktonic species. When such faunas are encountered in the stratigraphic column they must not be confused with life assemblages. It is also possible for considerable mixing of species from different habitats to take place without marked size sorting. Apparent lack of size sorting should therefore not be taken as necessarily indicating a biocoenosis. Plainly, the use of fossil Foraminifera as indicators of past environments requires patient detective work and a thorough knowledge of their 'natural history'.

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Chapter 4

Test Morphology and Composition

> The case of the three species of protozoan ... which apparently select differently sized grains of sand, etc., is almost the most wonderful fact I ever heard of.
>
> (Darwin to Carpenter)

CHAMBER ARRANGEMENT

We have seen how the soft part biology of the Foraminifera presents certain unique features. The group is also unique among the invertebrates in the variety of test shapes and styles of chamber arrangement developed, in some cases achieving an architectural complexity that has anticipated the geodesic domes of Buckmaster Fuller. The main types are illustrated in figures 4.1 and 4.2.

The Foraminifera test is either unilocular (non-septate) or multilocular, being composed of more than one chamber and divided by septa.

Unilocular tests may simply possess an open end (or ends in branched forms) which serves as an aperture; there may be no apparent opening in some globular and hemispherical attached forms, while in others there is a definite, restricted, consistently placed opening. In the multilocular group the aperture is usually restricted and when a new chamber is added it becomes an internal foramen (plural: foramina). The foramen is often modified and different from the aperture. A tooth or teeth may be present in the aperture and in some genera the tooth is developed as a plate or tube which extends back to the previous foramen.

The chief kinds of multilocular test arrangement are as follows:

Planispiral (figure 4.2)

In this type of arrangement the series of chambers is coiled in a single plane. The chambers of each turn (whorl) may embrace former whorls (involute) or may only touch the periphery of the preceding whorl (evolute). The central area where the septal traces (sutures) meet is called an umbilicus.

Fusiform (figure 4.2)

Planispiral arrangement with the axis of coiling drawn out so that the chambers are long and low and the test is fusiform or spindle shaped.

Annular discoidal (figure 4.2)

With initial chambers planispiral and the later ones added as annular rings (concentric). The ring-like later chambers are commonly subdivided by secondary septa into chamberlets.

Annular complex (figure 4.2)

With annular discoidal 'equatorial' layer and layers of lateral chamberlets on each side, giving a generally flattened spheroidal shape.

Biserial (figure 4.1)

Chambers arranged in two alternating rows. The initial part may be trochospiral or planispiral. Planispirally wound biserial arrangement also occurs (enrolled biserial).

Trochospiral (figure 4.1)

Here the chambers are coiled in a helicoid spiral as in the gasteropod *Trochus*. The figures show the typical case where the aperture is at the basal suture on the involute underside (ventral) and the evolute upperside (dorsal) is equally raised (test biconvex).

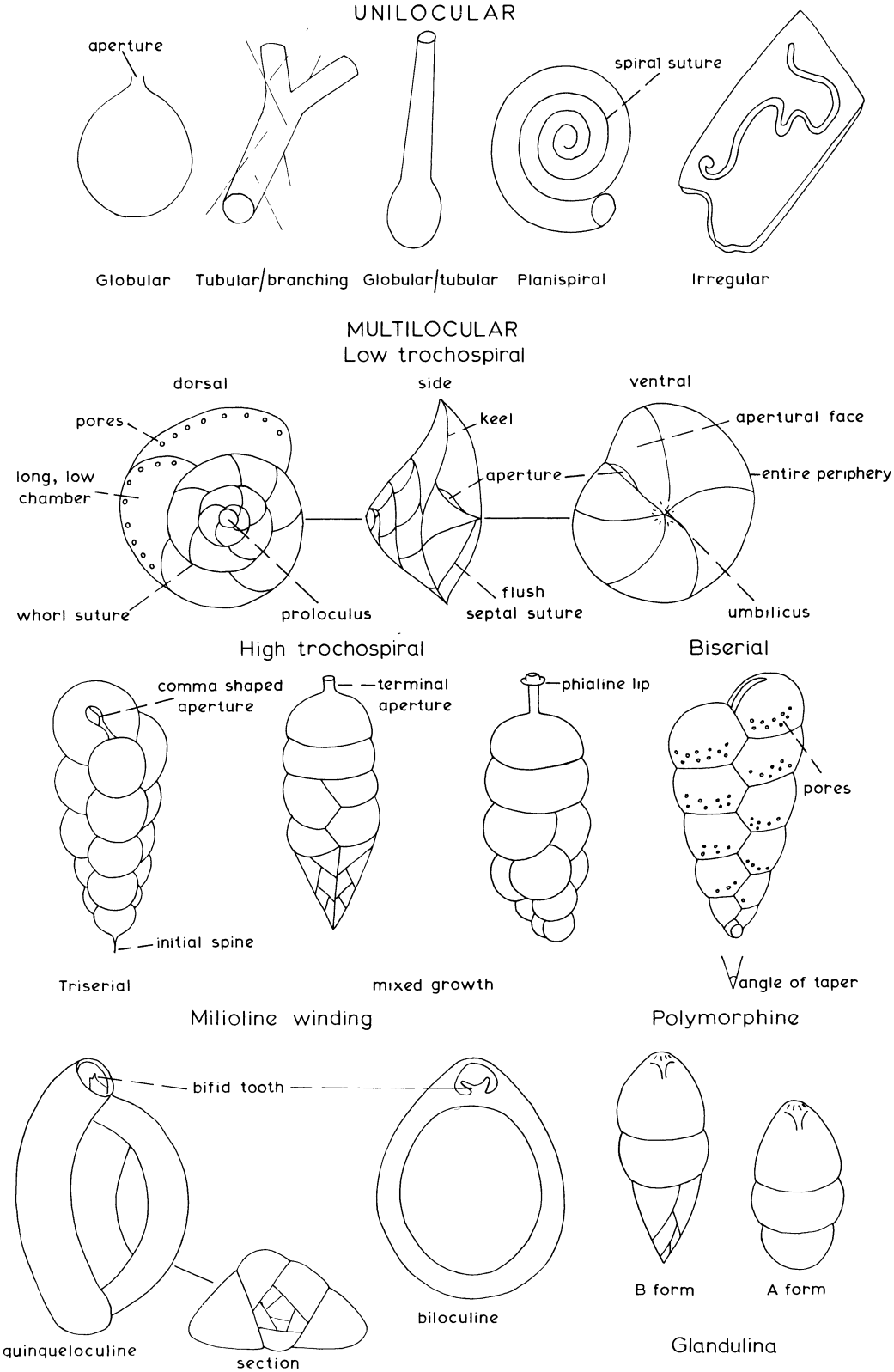

Figure 4.1 Coiling modes in Foraminifera: unilocular, trochospiral, milioline and polymorphine

High trochospiral (figure 4.1)

Trochoid genera with a very high spire exist and triserial arrangement with three chambers to the turn is particularly common. High, conical forms with annular chambers and chamberlets also occur.

Uniserial (figure 4.2)

Here the chambers are arranged in a single series, straight (rectilinear) or curved (curvilinear), the simplest form of multilocular arrangement.

Milioline (figure 4.1)

Winding growth with two chambers to the whorl with the aperture alternately at one end and then at the other. The successive chambers are added at 144° to each other (quinqueloculine), 120° (triloculine) or 180° (biloculine).

Polymorphine (figure 4.1)

Alternating growth with five chambers in each whorl added at 144° to each other, or three chambers at 120° or two at 180°. The successive chambers spiral about the growth axis of the test, all the apertures pointing in the same direction.

Other modes

Many Foraminifera also show irregular growth. This applies especially to attached forms. A small number are attached and arborescent with many branches.

Mixed chamber arrangement

Mixed or multiform growth, where the juvenile is different in arrangement from the adult chambers, is common and in some cases three different modes may be shown. Examples which appear to involve simplification include:

Planispiral to uncoiled uniserial, *Astacolus*.
Planispiral to biserial, *Spiroplectammina*.
Biserial to uniserial, *Rectobolivina*.
Trochospiral to triserial, *Eggerella*.
Triserial to biserial, *Gaudryina*.
Triserial to uniserial, *Clavulina*.

Examples which involve complication and subdivision of later chambers include:

Trochospiral to annular conical, *Patellina*.
Planispiral to annular discoid, *Archaias*.
Trochospiral or planispiral to annular complex, *Orbitoides* s.l.

These stages are normally shown more completely in the larger B form and only the final stage may be shown by the A form. For instance, in *Glandulina laevigata* (figure 4.1) the microspheric form has more chambers and is polymorphine (biloculine) in the initial part, whereas the A form is uniserial throughout and may be reduced to two or three chambers only.

It has been assumed that in multiform genera the juvenile recapitulates an ancestral adult growth stage. Phylogeny (race history) can thus be worked out from ontogenetic (individual growth) stages, shown most completely in the B form (Schubert, 1907).

According to Lecalvez (1938) the acceleration of development and lower total chamber number shown by the A form is because chamber volume is dependent on the volume of protoplasm. If the amount of protoplasm brought by the asexual daughter cell is equal to the amount carried by the first 10 chambers of the B form, then the megalosphere formed will be equal in diameter to the tenth chamber of the B form. If the B form normally develops 25 chambers then the A form will go on to develop 15. The A form then simply shows the last part of the developmental series shown by the microspheric generation which Lecalvez considered the more stable form, showing the full ontogeny. He regarded the microspheric stages as specific characters rather than a recapitulation of ancestral modes of coiling.

Support for this idea is given by details of the life cycle in *Patellina corrugata* (figure 3.4). Here, where only a few relatively large amoeboid sexual gametes are produced, the non-septate juvenarium is larger than in the A form. Nevertheless, beautiful morphological trends can be distinguished in many different groups of Foraminifera in which coiling modes first shown in both generations gradually become restricted to the B form and finally lost altogether. The microspheric generation then clearly repeats in the juvenile characters once shown more fully in the adult. In this sense many foraminiferal genera can be regarded as showing recapitulation, without this being taken to imply that the juvenile repeats

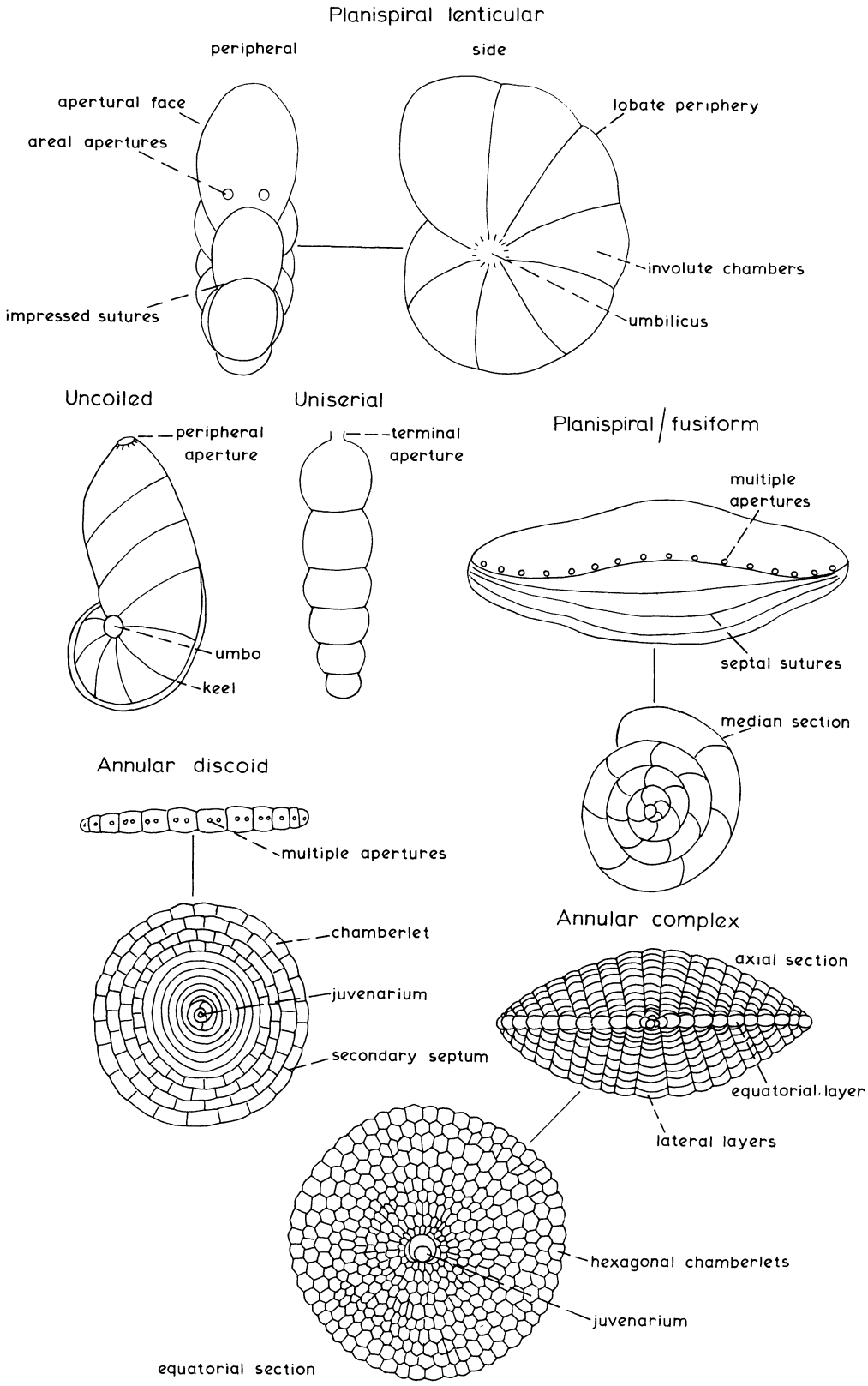

Figure 4.2 Coiling modes in Foraminifera: planispiral, uniserial, annular discoid and annular complex

all the characters shown by the ancestral forms or repeats a coiling mode regardless of its developmental and adaptive value. The stratigraphic evidence (Wood and Barnard, 1946; Cifelli and Glaçon, 1978) strongly supports recapitulation, and reversals, such as uniserial to planispiral which could be taken to support proterogenesis (evolutionary appearance of new characters in the juvenile), apparently do not occur. Nevertheless, this idea put forward by Rhumbler (1895, 1911, 1923) has been revived by Brotzen (1963) and Sellier de Civrieux (1969).

The table in figure 4.3 shows the percentages of each kind of chamber arrangement obtained from an analysis of the total fossil and recent genera of Foraminifera included in the *Treatise on Invertebrate Paleontology* by Loeblich and Tappan (1964). There are a number of difficulties in the way of accurate counts, so these are crude figures. In the case of intermediate forms and mixed growth an arbitrary decision has to be made on the grouping. No distinction is made between high and low trochospiral and regularly conical, unilocular forms. Note also that the orders recognised do not follow the 'Treatise'. It has also been thought advisable to leave out taxonomically doubtful genera. Allogromiids with partial test covering are also omitted. The imperfect nature of the fossil record must also be kept in mind. However, despite these difficulties figure 4.3 does bring out some striking statistics.

Only just over 10 per cent of the total 1110 genera are unilocular. Most of these are globular, or are spiral (dominantly planispiral) tubular forms. There are relatively small numbers of straight, tubular branching forms with open ends (apertures); tubular forms with globular initial end; and irregular forms.

Almost 90 per cent of the total genera are multilocular. Trochospiral chamber arrangement is clearly the dominant mode and low trochoid (20 per cent) and high trochoid (16 per cent) genera together make up more than one-third of all foraminiferal genera. Next in abundance are planispiral forms (15 per cent) which together with planispiral fusiform genera (8 per cent) make up

CHAMBER FORM / ORDERS	Numbers	Percent	Agglutinating	Microgranular	Porcelaneous	Hyaline	Unilocular	Multilocular	Free	Attached	Benthonic	Planktonic	UNILOCULAR: Tubular Branching	Globular-tubular	Globular (inc. hemispher).	Planispiral	Conical	Irregular	MULTILOCULAR: Planispiral-uncoiled	Fusiform & globular	Low trochoid	High trochoid	Conical	Discoidal	Annular complex	Biserial-uniserial	Enrolled biserial	Uniserial	Milioline	Polymorphine	Irregular (inc. spreading)	Arborescent
Total Genera	1110						11	89	93	7	95	5	1	<1	4	4		1	15	8	20	16		5	2	6	1	4	5	2	4	<1
Astrorhizida	81	7	25				100	0	67	33	100	0	18	9	51	13	2	9														
Lituolida	215	19					0	100	95	5	100	0							19	<1	7	35	5	8		10		6	4		5	
Fusulinida	138	13		13			6	94	95	5	100	0				6			21	49	2		3			5	2	5			5	
Miliolida	144	13			13		11	89	92	8	100	0			<1	8	1	3	27	9	2		3	7					33		5	
Nodosariida	84	8					7	93	90	10	100	0			7				17							7		29		30	10	
Buliminida	97	9					0	100	100	0	99	?1									2	70				17	10	1				
Robertinida	36	3				49	0	100	100	0	100	0							7		86	7										
Rotaliida	256	23					5	95	91	9	100	0				2	2		18	1	40	1	5	8	14	2					4	2
Globigerinida	59	6					1	99	100	0	0	100			2				21	7	50	7				8					5	

Figure 4.3 Coiling modes in the main groups of Foraminifera analysed by genera. Numbers based on the 'Treatise' (Loeblich and Tappan, 1964). Note that there have been subsequent increases in all groups

one-quarter of all foraminiferal genera. Biserial (to uniserial) arrangement (6 per cent), annular discoidal (5 per cent) and milioline winding (5 per cent) are less abundant and the other modes including uniserial, enrolled biserial, annular complex, polymorphine and irregular are less than 5 per cent, with the arborescent mode less than 1 per cent. Of course, these figures give no idea of the relative abundance of the different genera and species. For instance, it is largely the fusiform, annular discoidal and annular complex, Larger Foraminifera that are responsible for the foraminiferal limestones. However, the figures do give a good idea of the preferred coiling arrangements at the generic level which, we can assume, must relate to the different life 'strategies' of the Foraminifera (see below).

COMPOSITION AND STRUCTURE OF THE TEST WALL

There are three basic kinds of test wall. In the first, the test is formed by an organic membrane composed of tectin (a proteinaceous mucopolysaccharide—that is to say a complex carbohydrate plus protein) in the form of a soft film (Hedley, 1964). In the second group, this membrane becomes the foundation for an agglutinated wall and, in the third, the inner lining for a calcareous wall (Banner and Williams, 1973; Poignant and Rouvillois, 1978).

The test in the membranous group (Allogromiids) is unilocular, thin and flexible. Hedley (1964) has shown how *Shepheardella* and *Allogromia* can change their shape very rapidly. A number of these naked genera, such as *Neogullmia*, live inside the dead shells of other Foraminifera and in worm tubes, while others like *Myxotheca* develop a partial agglutinated covering or a ferruginous encrustation, as in *Kibisidytes*.

In detail, the structure of the membrane appears to be quite complex, consisting of a spongy, possibly fibrous, network in *Shepheardella* (Hedley, Parry and Wakefield, 1967) and laminated in *Myotheca* with the fibres of one layer laid down at right angles to those of adjacent layers (Angell, 1971). Different species of *Allogromia* have also been shown to have differences in the fine detail of the wall (Hedley, Ogden and Wakefield, 1972).

Agglutinated Wall Structure

There is a gradation from genera with adventitious material loosely attached to the organic membrane, such as *Rhizammina*, to strongly built genera where the grains are held firmly with calcareous or ferruginous cement such as *Eggerellina*. Many genera such as *Astrorhiza* are not selective and make use of the available material of the sea bed indiscriminately, including sand grains, sponge spicules, mica flakes, coccoliths, diatoms and heavy minerals.

Others are selective of particular kinds and sizes of materials, in particular: sponge spicules in *Technitella legumen*, arranged in a two-layered warp and weft pattern, echinoderm plates in *T. thompsoni*, the dead tests of other Foraminifera in *Reophax testacea*, mica flakes and needles of rutile in *Bathysiphon argenteus* (Dick, 1928). A possible example of selection of extra-terrestrial microtectites has been reported by Baker and Glass (1974) in *Rhabdammina* and *Gaudryina* from deep sea sediments of Eocene age in the Caribbean. Although abundant in the sediment the microtectites selected are generally larger than the rest of the agglutinated material and usually centrally placed on the test. More commonly calcareous or arenaceous grains are built flat on to the wall surface with the large grains characteristically packed in a matrix of smaller grains (Haynes *et al.*, 1973; Murray, 1973a; Towe, 1967).

Although larger grains may be used as growth proceeds, the size range may be specific. Thus Lipps (1973) found that *Trochammina pacifica* consistently incorporates finer sized material than *Miliammina fusca*, although these species live together on marshes at Bodega Bay, Northern California. Similarly, on the Dovey marshes, Wales, *Miliammina fusca* consistently builds its test of relatively large silt grains, while *Trochammina inflata* is constructed of very minute grains averaging about 3 μm in diameter (plate 7, no. 8). Many species show selection of material of a particular size and shape for a particular purpose (Haynes *et al.*, 1973). Thus *Lagenammina* cf. *hancocki* shows selection of small-sized grains for the apertural rim (plate 7, no. 9) and *Ammobaculites balkwilli* has sharp silt grains set up on end around the aperture. *Halyphysema tumanowiczii* has sponge spicules jutting out at an angle from the head and apertural end. *Saccammina spherica* var *anglica* builds its test on a tripod of spicules.

As pointed out by Lipps (1973): 'the biochemistry of the organic linings or cements of agglutinated foraminifera remains largely unknown', and what is thought to be known is surrounded by controversy. Hedley (1964) considered that the organic linings were equivalent to the tectin membrane of the allogromiids but the variation that probably exists is indicated by the discovery of a collagenous, fibrous sheath in *Halyphysema* (Hedley and Wakefield, 1967) together with an acid, mucopolysaccharide cement.

In the majority of agglutinating forms (perhaps all genera) the cement is mixed with organically bound iron (Hedley, 1963; Towe, 1967; Murray, 1973a) which on oxidation hardens the test and gives it a red-brown colour. The last-formed chamber may be white but Hedley found that the cement in this part and in white shells contains equal amounts of iron. In a number of genera from normal marine environments the cement is also mixed with considerable amounts of calcium.

Although ferric granules appear in the cytoplasm of both *Haplophragmoides* and *Rhabdammina*, Hedley still considers that the ability of Foraminifera to secrete iron is unproven. Lipps considers that there is no direct evidence that the agglutinating forms secrete calcium either and that both iron and calcium may become bound in the organic cement by inorganic processes.

Formerly, a number of agglutinating forms were considered to possess siliceous cement (Rzehakinidae) because their tests did not dissolve in acids. However, Lipps (1971) has shown that the tests of this group disaggregate in hydrogen peroxide, indicating that the siliceous grains of the tests are held in an organic cement. These results have been confirmed by Hansen and Hanzlikova (1974) by electron microscopy, electron microprobe and X-ray diffraction studies. Again, no evidence of siliceous cement was found, although sutured areas indicating diagenetic welding of the siliceous grains in fossil species was observed.

Calcareous Wall Structure

Very early in foraminiferal studies the major groups of calcareous genera were distinguished as porcelaneous or glassy according to their appearance in reflected light. Thus in the porcelaneous group the wall may resemble porcelain with a shiny white surface that results from a fine structure that leads to maximum reflection of light. On the other hand the glassy group have a fine structure that readily allows light to pass through, so that some of these genera resemble clear soap bubbles or blown glass. Crystallographic investigations were started by Sorby (1879), continued by Sollas (1921) and taken up with such affect by Wood (1949a) that for three decades they have been a major area of research and the results the basis of modern classification of the Foraminifera.

Porcelaneous

The white, porcelain-like group of calcareous genera studied in thin section and in isolated fragments by Wood were found to be built of a random array of calcite laths exhibiting first-order grey, interference colours under crossed nicols. Some areas of the wall showed preferred orientation, and further studies by TEM (Lynts and Pfister, 1967) and SEM (Haake, 1971; Cherif and Flick, 1974) have shown that generally the wall is composed of three layers: a thick median layer of laths in random array with thin inner and outer veneers (figure 4.4). In smooth, shining species the laths in the surface veneer are arranged parallel to the surface, in a 'tile-roof' 'or parquet-floor' pattern (plate 7, nos. 1, 2). In rough-walled species such as *Quinqueloculina berthelotiana* the laths of the external veneer are arranged perpendicularly to the surface to give a cobble pattern. The laths of the inner veneer appear to be parallel to the surface in both cases.

In transmitted light, porcelaneous walls show a characteristic rich brown coloration. This appears to be due to included organic matter, the organic 'moulage' of Arnold (see below).

Microgranular

An important group of calcareous Foraminifera occur in the Upper Palaeozoic and as they have a dark wall which sometimes includes agglutinated grains they were considered by the early workers to belong to the agglutinated group. This view was followed by Cushman (1948) who considered the wall was composed of adventitious material bound by a calcareous cement. On the other hand, Plummer (1930), Galloway (1933) and Rauzer-Chernousova (1936) considered the wall could have been secreted by the animal itself.

In large part the difficulty workers have had in interpreting the structure is because the wall is commonly recrystallised. However, detailed work by Wood (1949a) and Cummings (1955, 1956)

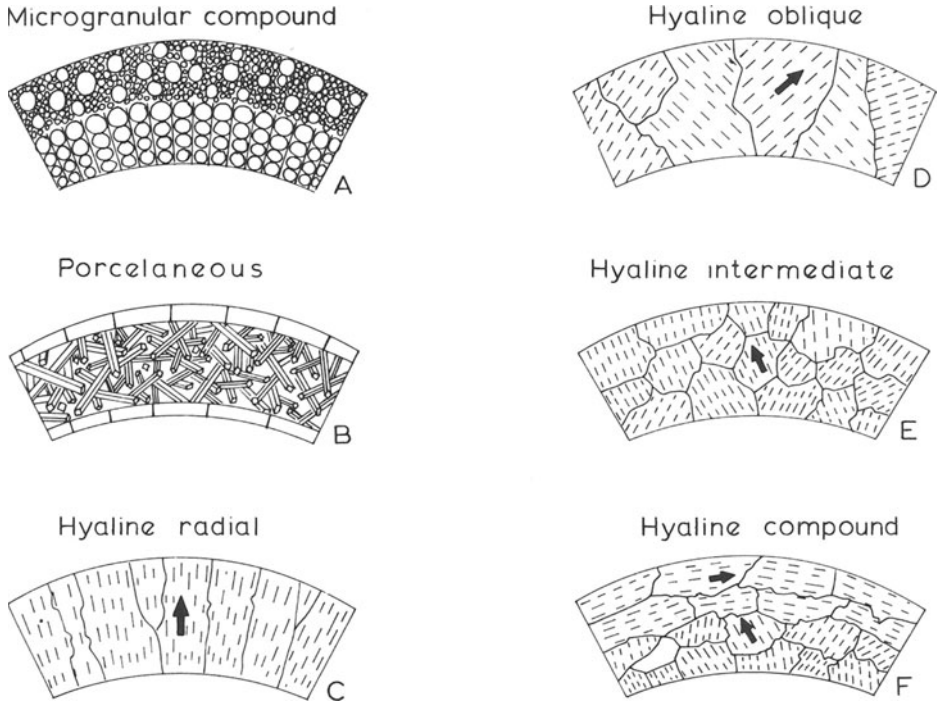

Figure 4.4 The main types of secreted, calcareous walls

showed that the wall is formed of equidimensional, subspherical granules of calcite closely packed together but without detectable cement. It is commonly compound with an outer layer of irregularly packed grains and an inner layer of granules arranged in orderly rows perpendicular to the test surface, as in *Palaeotextularia* (figure 4.4A). As pointed out by Cummings, this linear arrangement of grains produces a light and dark 'fibrous' appearance as seen in thin section. There is apparently no preferred orientation of the c-axes and the structure is quite distinct from that of the hyaline group.

Hyaline or glassy

Two major types of hyaline wall were distinguished by Wood (1949a, 1963) on the basis of optical characters observed in thin sections or fragments under crossed nicols of the polarising microscope. These are first, radial structure, characterised by, 'a black cross with concentric rings of colour closely mimicking a typical (negative) uniaxial interference figure. The test is built of crystals of calcite with their c-axes normal to the spherical surface'. The second structure showed no extinction pattern but, 'a multitude of tiny flecks of colour, and in section their structure is seen to be minutely granular'.

Further work by TEM (Towe and Cifelli, 1967; Hansen, 1970a; Stapleton, 1973), X-ray diffraction (Hansen, 1968) and SEM (Hansen and Reiss, 1971; Bellemo, 1974a, 1974b, 1976) has shown that in both cases the test is built of units composed of numerous platelike or rhomboidol crystals each about 1 μm in diameter. These units are enclosed in an organic membrane and irregularly sutured together. The difference in optical characteristics is caused by growth of the crystals preferentially on the basal pinacoid (0001) crystal face in the radial type, whereas in the type considered 'granular' by Wood growth is preferentially on one of the rhombohedral faces (1011). In the radial type the rhomboidal microcrystals are stacked in columns which extend fully across the wall (figure 4.4C) and the c-axes are perpendicular to the surface with only minor deviations. In the 'granular' type the stacks of microcrystals extend obliquely across the wall (figure 4.4D) and the c-axes incline at 5° (Stapleton, 1973). Adjacent units may incline in different directions because of rotation of the stacks of crystals (Bellemo, 1974b), but the c-axis is never perpendicular to the test wall. For this reason none is seen to extinguish when pieces of

test wall are examined under crossed nicols which then appears to be built of randomly orientated grains.

The difference between radial and oblique microstructure is dramatic when seen through the polarising microscope (plate 7, nos. 3,4), but as Towe and Cifelli (1967) point out they are crystallographically very similar and one could easily give rise to the other. Mixed types do occur and Bellemo (1974b) has shown that the wall in species such as *Cibicides refulgens* and *Cibicidella variabilis* which has been found difficult to interpret (Wood and Haynes, 1957) and described as indistinctly radial by Towe and Cifelli, is actually of intermediate type (figure 4.4E). The crystal units are small and do not extend fully across the wall. In the inner and outer zones the c-axes are almost perpendicular to the test surface, while in the middle they are more oblique, about 60°. Compound structures also occur in *Cibicides lobatulus* and *C. floridanus*, where the inner layer of the two-layered wall is of intermediate structure while the outer is composed of units of crystals with the c-axes parallel and the a-axes perpendicular to the test surface, as in figure 4.4F (Bellemo, 1976; Towe, Berthold and Appleman, 1977). Similar mixed structures occur in *Lepidocyclina* and *Miogypsina* (Ouda and Sharara, 1978).

An interesting and unusual structure occurs in the Spirillinidae, considered by Wood (1949a) to have tests constructed of a single crystal. This observation has been confirmed by X-ray diffraction and crystal overgrowth techniques as well as polarised light microscopy (Towe, Berthold and Appleman, 1977), which show that *Patellina corrugata* behaves as a single crystal of calcite with the c-axis parallel to the base of the conical test and the a-axis parallel to the axis of the cone. Individual plates and spines of echinoderms are single crystals but this group of Foraminifera are the only organisms known in which the entire skeleton is a single crystal.

A small but important group of hyaline Foraminifera are built of aragonite rather than calcite (Troelsen, 1955; Todd and Blackmon, 1956; Vénec-Peyré and Jaeschke-Boyer, 1978). A recent example is *Hoeglundina* which is common in cool, deep water and possesses a beautifully glassy wall seen in reflected light. *Epistomina*, an allied form abundant in the Mesozoic, is often found as a cast with the test partially dissolved away. This is because aragonite goes into solution more readily than calcite on fossilisation.

Aragonite crystallises in the orthorhombic system but pseudohexagonal twins are commonly formed. These have been shown to occur in the wall of *Hoeglundina*, arranged with the basal pinacoids parallel to the test surface. The crystals are optically biaxial but the angle is so small that extinction under crossed nicols resembles that of the radial, calcitic forms (Reiss and Schneidermann, 1969).

Fine Structure of the Wall in Hyaline Foraminifera

Thin sections of glassy Foraminifera studied both by light and electron microscopy show that not only are many tests layered with compound wall structures but that generally they are lamellar, as originally discovered by Williamson (1852). This means that when a new chamber is added a layer (or layers) of calcite extends back to cover the previously formed test (Smout, 1954; Hansen and Reiss, 1971, 1972a; Grønlund and Hansen, 1976). The main kinds that have been distinguished are shown in Figure 4.5A – F.

In the agglutinating, porcelaneous and microgranular groups, when a new chamber is added to the test it simply abuts the previous chamber, as in A. Although nonlamellar structure also occurs in the hyaline group, lamellar investment is a general feature. Monolamellar structure, where each chamber is composed of one layer, either fully developed as in B, or partial as in C, is characteristic of the nodosariids. Multilamellar structure, where each chamber has several primary layers, also occurs, as in D.

In the other groups of hyaline Foraminifera, including the aragonitic genera, bilamellar structure appears to be general. The chamber wall has a basic construction of two layers separated by a membranous 'median layer' or 'primary organic membrane' (POM of Hemleben *et al.*, 1977), and it is the outer layer that extends back over the previously formed test, as in E.

A number of genera show a further complication in that the inner layer coats the apertural face of the previous chamber to a greater or lesser extent, as a septal flap, shown in F, often modifying the internal foramen and giving rise to a tooth plate.

The outer lamella gives rise to ornament of spines and ribs by localised thickening, and the presence of an external layer of protoplasm capable of laying down a complete lamella of calcite over the previously formed test explains how ribs and keels can be formed running its entire length.

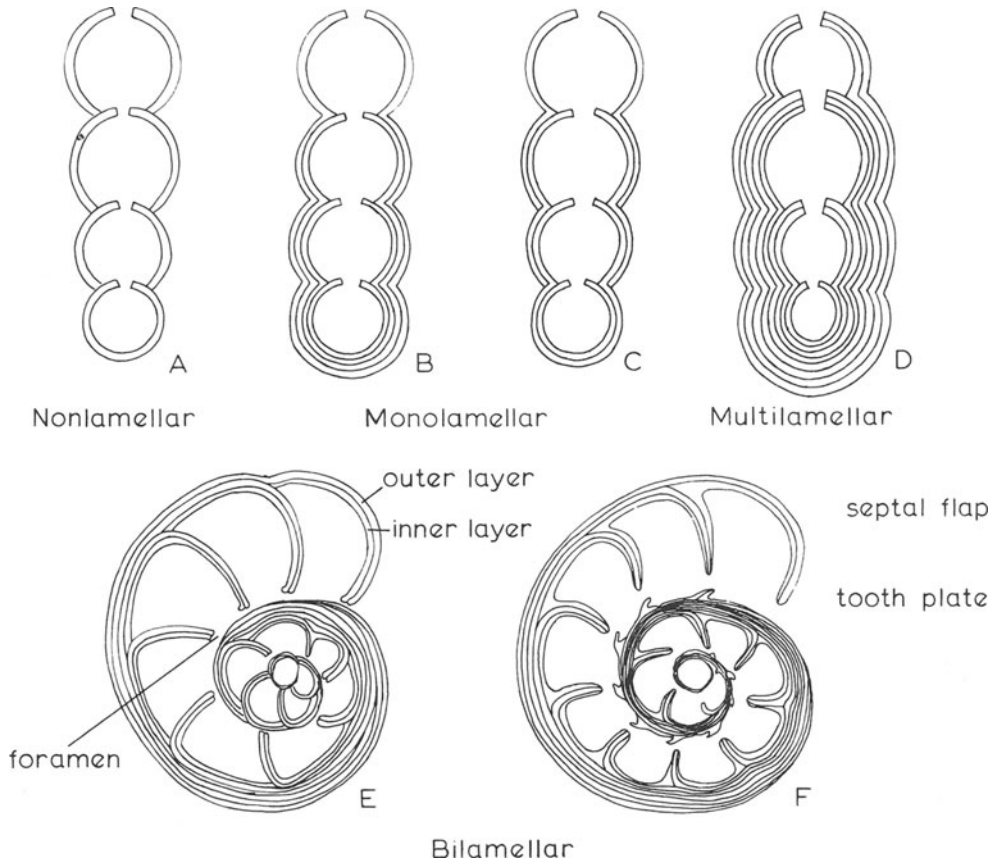

Figure 4.5 Sections showing various types of lamellar wall structure in the hyaline Foraminifera (idealised). A – D uniserial nodosariids: A nonlamellar, B lamellar and fully investing, C partially lamellar, D multilamellar. After Grønlund and Hansen (1976). E and F equatorial sections of low trochospiral or planispiral rotaliids: E bilamellar, F bilamellar with septal flap

Perforations

The walls of hyaline Foraminifera are usually perforated (plate 7, no. 5). Pores also occur in the microgranular group and more rarely in certain agglutinating genera, but are absent in the porcelaneous Foraminifera. In perforate genera, the walls between the chambers (septa) and external ridges and keels remain imperforate. Externally the pores appear round to oval or slit-like and the opening on the inside of the test is usually larger and funnel shaped. They may be restricted to particular zones and be of different sizes in the same individual, although the range may be constant for the species. Large ones may occur only on one side in trochospiral species.

The organic membrane is imperforate but Arnold (1954a, 1954b) and Angell (1967) have shown how it is thickened at the base of each pore, this 'pore plug' being microporous. The pore is also lined with a membrane that appears as an elongate tubule in etched specimens (Jahn, 1953; Banner and Williams, 1973). Although occasionally interrupted, the pores normally continue through the successive lamellae giving a 'fibrous' appearance to hyaline tests. Calcareous plates which are also perforated (sieve plates) may be present at the junctions or 'nodes' representing calcification of the organic membranes. The pore plug may also be calcified.

GROWTH OF THE TEST

Test construction in Foraminifera appears to take place within a protective cyst, so observation is difficult and is limited to a few species. The pseudopodia are active both in the construction of

the cyst and in the building of the test which begins with the formation of the tectin lining. The process was well described by Jepps (1942), and it is worth while quoting in full her description of the growth of a new chamber in *Elphidium crispum*:

> An unusually dense fan-shaped mass of closely-set anastomosing pseudopodia make their appearance, radiating out from the terminal apertures of the last chamber of the shell. Beyond them bundles of ordinary pseudopodia may reach out farther to collect any material that may be available (diatoms, excretory granules, sand, etc.) to make into a 'face-mask', inside which the new chamber will be formed. But the process can go without this cover.... Activity usually begins in the late afternoon or early evening, the protoplasm, which may be withdrawn at the time from the last chamber, passing out in the form of pseudopodia which flow through the successive sets of foramina, and also emerge at the fossettes and pores at the sides of the last chamber which will be partly covered by the new one. Some of the special pseudopodia after a time begin to arch over in a reticulum which outlines the cavity of the future chamber, usually about 10 p.m. to midnight, the 'face-mask', when present, being pushed away to the outside. They gradually swell at their bases and merge into one another there, whilst a fluid wells out amongst them and comes to fill up the space they enclose under their extremities with a uniformly granular mass of colourless protoplasm in which the pseudopodial streams fade out and ultimately disappear into the general circulation of the mass. This comes to have a clear-cut surface, fashioned in the shape of the new cavity even to the retral processes and the projections at the future foramina.... The longer and more active pseudopodia which normally collect the 'face-mask' material have disappeared, and the short pseudopodia remaining at the surface of the protoplasmic mass now appear stiff, with very sluggish movements. They may come and go, as the shell is deposited on the mass; it is impossible to know how much of their variation under observation is due to unnatural illumination, etc., but in any case the shell seems to be porous from the beginning, and therefore, bathed in protoplasm which lays it down initially and may continue to add to it (and at times to reabsorb it) throughout life. As soon as the surface is available a collection of shining granules may be seen there which gradually form a thin layer of shell. This seems to be laid down in patches like the pieces of a jigsaw puzzle, which unite, losing their separate outlines more or less completely as the shell thickens. After a time the characteristic tubercles are formed on the outside and the keel is laid down at the periphery. During the next day the *Polystomella* remains immobile, while the shell is deposited. There is a flow of brown protoplasm into the now penultimate chamber and sometimes into the base of the new one. Then the colourless mass there becomes vacuolated and may be withdrawn altogether, leaving the new chamber empty for a time, as is usual during the greater part of the life of a *Polystomella*. Pseudopodia emerge, the 'face-mask' is cast off, and the *Polystomella* moves away to begin feeding again some 24 hours after the emergence of the protoplasmic mass.

This process was observed to take about 8 h for completion. Of particular interest is the observation that the pseudopods appear to be responsible for the secretion of calcite and that calcification is patchy and resembles the pieces of a jig-saw puzzle. It is noteworthy that Towe and Cifelli (1967) use this same simile when describing the sutured units of microcrystals observed by TEM in *Lenticulina calcar*.

The process appears to be rather different in the porcelaneous group. The growth of a new chamber in *Spiroloculina hyalina*, as described by Arnold (1964), involves mineralisation of a thick organic 'moulage' with an internal wall of 6 μm. Mineralisation begins in the central area with formation of crystals on the internal wall which build up into hummocks and ridges that gradually coalesce and spread over the test wall, eventually reaching the aboral and oral areas. There may be several waves of mineralisation before the organic matrix is completely calcified.

Further observations of growth in the hyaline Foraminifera have been made by Angell (1967). During chamber formation in *Rosalina floridana* the organic lining of the new chamber was seen to be secreted by the pseudopodia. It is a two-layered structure composed of a thick mat of fibres with a fine outer layer of beaded fibrils. The thick inner layer also coats the inside of the chambers of the previously formed test each time a new chamber is added. The inner lining of the test is therefore laminated and thickens towards the proloculus.

Towe and Cifelli (1967) have suggested that the organic membrane serves as a template that determines the orientation of crystal growth

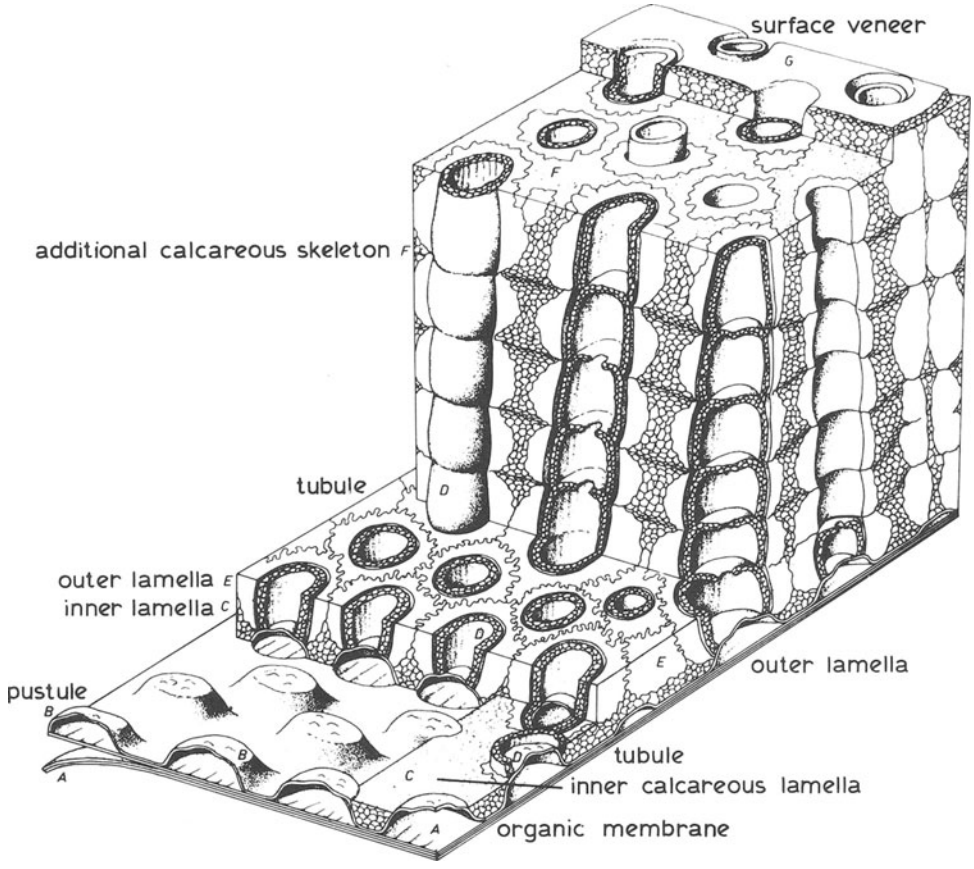

Figure 4.6 Detailed structure of the wall in *Ammonia*. After Banner and Williams (1973)

(epitaxy) or that calcification takes place in organic compartments. However, they admit there are a number of weighty objections to either hypothesis, including failure to explain the preferred orientations in the hyaline group.

Although Angell was unable to observe calcification in *Rosalina floridana* the new chamber, prior to this process, is filled with a gel-like, vesicular protoplasm. This flows out on to the outer surface as dense cytoplasm flows in from the penultimate chamber to replace it. Lipps (1973) suggests that nucleation of crystals may take place on the organic membrane and that their three-dimensional growth is supported by the gel-like ectoplasm.

In an attempt to explain the structures found in several species of *Ammonia*, Banner and Williams (1973) postulate the following sequence in wall construction (see figure 4.6):

(1) Formation of 'chitinoid' organic membrane with pustular outer lamina, A and B.

(2) Deposition of calcareous granules (rhomboid microcrystals of Bellemo) around the pustulae to form the inner lamella, C.

(3) Formation of tubules with calcareous granules incorporated in cylindrical tectin sheets, D.

(4) Tectin secreted around tubules and over inner lamella (median layer of Hansen, Reiss and Schneiderman, 1969).

(5) Deposition of sutured units of 'blocky grains of calcite' around the tubules as the framework of the outer lamella, E, with additional granular 'calcareous skeleton' between, F.

(6) Deposition of thin surface veneer of smaller granules protected by a tectin outer coat which also covers the tubules, G.

Subsequently, as new chambers are added, extra outer lamellae build up on this essentially bilamellar structure. The tubules are added to lengthwise, each new section being built on the perforate roof of the previous section and marked by a constriction. Again, as each new chamber is added an extra lamina is added to the 'chitinoid' inner lining.

In contrast to this idea that the inner lining is the first to be formed, Hemleben *et al.* (1977) on

the basis of their studies of *Globorotalia cultrata* regard the median layer as the 'primary organic membrane'. They believe that calcification starts with the simultaneous secretion of the inner and outer calcite lamellae on either side of the POM. These calcite layers are in turn bounded by inner and outer tectin membranes formed by the inner and outer cytoplasm. Their observations also indicate that the incipient wall is calcified before the pores appear. Micropores appear first, on the site where the pores are eventually formed by resorption. The wall apparently remains flexible during the early stages of calcification. Individual crystallites appear surrounded by organic material. These are granules at first, but later become euhedral.

The view that the inner lining does not act as a template for subsequent calcification is supported by the work of Spindler (1978b). In *Heterostegina* it develops some days after chamber formation is complete, starting beneath the pores. It also appears to be missing in the youngest chamber.

It will be seen that in the multilocular Foraminifera, growth is episodic. This led Smout (1954) to consider each episode of chamber growth as a separate 'instar'. In tubular, unilocular genera growth may be more or less continuous. Growth in spherical, unilocular genera is believed to involve continuous rebuilding of small sections of the wall (Glaessner, 1945; see reprint, 1963a), but as both *Iridia* and *Saccammina* are known to vacate their tests and build completely new ones (Hedley, 1962) it may be that both agglutinating and calcareous genera produce a series of true instars during growth.

FUNCTION OF THE TEST

The Organic Membrane

In the 'naked' allogromiids the test is restricted to a membranous envelope which is all that stands between the foraminifer and the external environment. Transport through the membrane appears to be only by osmosis and as well as controlling exchange with the exterior it acts as a protective shield against external physical and chemical changes.

Calcium carbonate is normally soluble in oceanic water, so calcareous forms require the protection of the inner lining and the external tectin membranes that coat each lamella (Banner and Williams, 1973), particularly in waters of low pH or undersaturated in carbonate. The efficiency of the membranes as a protective device is revealed by Bradshaw's experiments on *Ammonia tepida* (Bradshaw, 1961), which show that even if the calcareous outer wall is dissolved by acid the foraminifer can survive, protected by its membranes, and build a new calcareous shell. The aperture and foramina may also be closed off by membranous partitions in unfavourable environments (Arnold, 1967).

In perforate genera the pores are lined and plugged with organic material. Cytoplasm has been noted within the pores and it is thought that small particles can enter and leave after filtering through the perforated plugs and sieve plates (Arnold, 1954a; Towe, 1971; Sheehan and Banner, 1972). However, Berthold (1976) considers their function to be osmoregulation, gas exchange or the intake or excretion of dissolved organic substances. It now seems certain that the sieve plates are too fine to allow pseudopods to pass through the pores. In many cases, when live Foraminifera are treated with reagents such as rose Bengal only the protoplasm in the ultimate and penultimate chambers stains which suggests that the pores in the earlier chambers may be permanently closed off. That the foraminifer exerts control over this process is shown in *Tretomphalus* where the pores, in the free-floating planktonic stage, are sealed by a pigmented membrane, apparently to prevent escape of the gametes (Myers, 1943b).

As well as protecting the foraminifer against chemical changes in the sea water the organic membranes, particularly the 'chitinoid' inner lining of many genera, may act as a light filter, excluding the oxidising and metagenic shorter wave lengths while transmitting the range suitable for photosynthesis by algal symbionts (Banner and Williams, 1973; cf. Haynes, 1965).

The importance of the organic membranes is underlined when in addition to their primary protective function we consider that, as has been seen, they are the foundation for the construction of the agglutinated test and of the secreted calcareous test.

The Hard Shell

The simplest type of agglutinated test is a low dome or tent-like structure, as in *Iridia*, or a subspherical mass of agglutinated grains, as in *Psammosphaera*. These probably developed from the partial, agglutinated coverings which occur in genera such as *Myxotheca* which may have arisen as an attempt to control buoyancy (cf. Marszalek, Wright and Hay, 1969). As shown by figure 4.3,

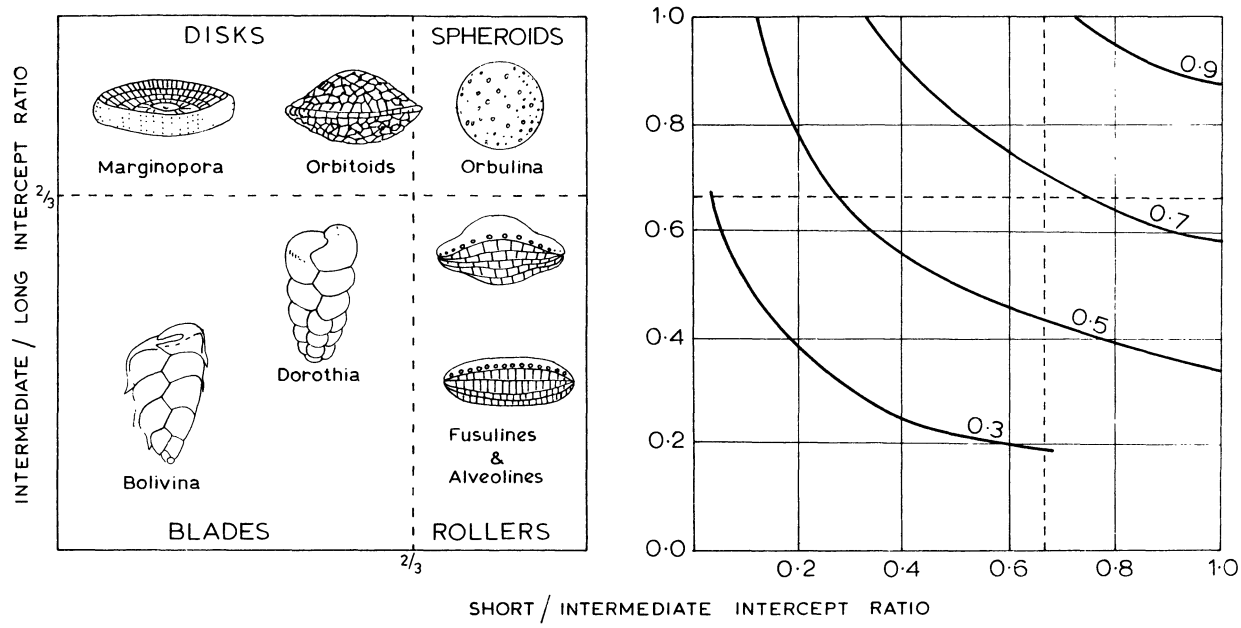

Figure 4.7 Shape classification of Foraminifera based on ratios of intercepts, the ratio of intermediate to long intercept plotted against the ratio of the shortest to the intermediate intercept. This gives the four shape classes shown on left. On the right, lines of equal sphericity are plotted as curves on the same diagram. These are derived from the equation for measuring sphericity which considers the object relative to an enclosing sphere. The sphericity of the object increases as it occupies more of the circumscribing sphere. When the two volumes coincide the sphericity is 1.0. Krumbein and Sloss (1953)

slightly more than half of the unilocular agglutinating genera are globular or hemispherical forms, with almost equal numbers of these being attached or free. A general tendency towards restriction of the aperture indicates the protective function of the complete, agglutinated covering. Approximately 13 per cent are enrolled, demonstrating the advantage of a compact test for free, wandering forms. The adoption of a hard test meant the inevitable loss of flexibility so well shown by many allogromiids. However, it is possible that some simple agglutinated forms could build a range of test shapes (Hedley, 1964).

As noted, some 90 per cent of the hard-shelled Foraminifera are multilocular. The peculiar advantage of the multichambered form indicated by this high percentage has been explained by Marszalek *et al.* (1969) as due to the extra protection afforded by the constricted chain of apertures and internal foramina which checks density currents and diffusion processes and allows time for osmoregulatory adjustment. When the pores of perforated genera are sealed by organic plugs and membranes, the test is then an effective barrier against changes in osmotic pressure and water chemistry. It is noteworthy in this regard that the endoplasm is commonly restricted to the penultimate chamber.

The strikingly different modes of coiling in the multilocular Foraminifera are considered by Lipps (1975) to be related to different feeding strategies. This is because feeding habits affect the deployment of the pseudopods and may dictate test structure. Lipps distinguished four main groups:

Suspension feeders. Erect tubular, often branched forms fixed to the sea bed or embedded in sediment and spreading their pseudopods in the water column. Common in quiet conditions, as on the abyssal plain.

Detrital scavengers. Active lenticular forms on soft substrates or in weed and elongate forms passively feeding near the sediment/water interface.

Herbivores. Largely trochoid or flattened forms browsing on algae on various substrates as active vagrants or fixed temporarily with the pseudopods streaming in all directions.

Carnivores. Active or passive forms with diverse morphologies like *Astrorhiza,* which is a passive carnivore that extends its pseudopods into the sediment to prey on minute, interstitial animals (see Buchanan and Hedley, 1960).

Lipps emphasises that the different strategies are not adapted to particular food types and that most species are opportunistic, omnivorous, feeders. Also, as we have seen in chapter 3, many Foraminifera appear to require a mixed diet. This means that a particular coiling mode may allow exploitation of more than one feeding strategy. However, the 'striking correlation' recognised by Bandy (1960a) between test structure and composition of Foraminifera with environment (broadly with temperature and depth) strongly supports the idea that the different coiling modes are adaptive and that their repetition in the major groups is the result of evolutionary convergence.

Although research is only at the beginning in this field, and is still largely speculative, it is worth while to examine the frequency of the different coiling modes (figure 4.3) and relate them to feeding strategies as well as environmental and hydrodynamic factors (figure 4.7).

Tubular branching and arborescent forms make up about 2 per cent of the whole and are practically confined to the Astrorhizida (27 per cent) and Rotaliida (71 per cent). The majority of the tubular astrorhizids, including numerous fragile genera, occur in the deep sea in soft ooze, a sediment that is largely built up from fine organic material dropped from suspension. The arborescent rotaliids are more strongly built and attached to hard substrates in current swept conditions, as in the wave zone and in reefs. In both cases these forms are well adapted to live as suspension feeders although a stellate, branching, tubular form is also consistent with carnivorous feeding in *Astrorhiza* and possibly also with detrital feeding in other cases.

Lenticular, planispiral genera, which Lipps supposes are adapted to active detrital feeding and bacterial scavenging, are much more abundant and make up some 18 per cent of all genera. In particular they make up a high proportion of miliolids (27 per cent), fusulinids (21 per cent), lituolids (19 per cent) and nodosariids (17 per cent). This coiling mode is consistent with an active life both as a browser in weed and as a deposit feeder on soft substrates. It is exemplified by *Elphidium macellum* which is abundant in the littoral algal zone. The compressed test is hauled along by the pseudopods in a semi-upright position and the juveniles have a spinose keel which helps them to lodge in the algal fronds. The peripheral keel commonly developed in these lenticular forms, especially in the nodosariids such as *Lenticulina*, may help to stabilise the test on soft substrates.

Elongate genera, which Lipps supposes are adapted to passive deposit feeding near the sediment/water interface, are equally abundant and if high trochospiral/uniserial, biserial/uniserial and uniserial are grouped together make up some 25 per cent of all genera. These modes are dominant in the lituolids (56 per cent), buliminids (87 per cent) and in the nodosariids (36 per cent). This figure reaches 66 per cent in the nodosariids if polymorphine coiling (30 per cent) is also included.

Elongate, quinqueloculine coiling is also associated with an infaunal feeding strategy in *Miliammina*, allowing it to move easily below the surface. Here the terminal aperture directs a podostyle of pseudopods into the sediment (Frankel, 1975). It may be that the remarkable tendency for chamber reduction and development of uniserial chambers with terminal apertures (often produced and with tooth plates) seen in so many lines of Foraminifera is the result of convergent adaptation to this feeding strategy. The observation that benthonic food resources are concentrated at the sediment/water interface and in the top 5 cm of sediment is very significant in this context (Walker and Bambach, 1974). The flattened, shovel shape of many species of *Biloculinella* may also have originated in the same way. However, chamber reduction with a return to a unilocular adult form occurs in *Fissurina* and *Lagena* which are parasitic upon other Foraminifera (Lecalvez, 1947; Haward, 1977). But whereas the aperture appears to be developed as a probe in *Lagena*, in *Fissurina* the aperture is a compressed slit and the tube is internal only. In part then the trends towards chamber reduction and development of uniserial chambers in both buliminids and nodosariids may also relate to parasitic feeding strategies.

Highly compressed biserial genera like *Bolivina* and *Textularia* which are very unstable hydrodynamically (figure 4.7), and the more stable triserial, *Bulimina*, also occur on firm substrates and Haward (1977) has shown how *T. truncata* apparently orientates its rudder-shaped test parallel to the currents when living between the ornamental ridges of a bivalve shell. Hydrodynamically unstable, elongate, forms (blades) are therefore not necessarily restricted to quiet habitats and an infaunal strategy.

Low trochoid genera, which Lipps supposes adapted to an active or temporarily fixed life as herbivores, are the most abundant group and make up 20 per cent of all genera, largely because of the dominance of this coiling mode among the

rotaliids (52 per cent). To this total can be added the hemispherical, fixed, agglutinating forms (some 2 per cent of the whole) which have the same, hydrodynamically stable, limpet shape ideally suited to life on the shallow shelf and attachment to various substrates. The percentage of low trochoid genera is even higher among the planktonic rotaliids, but here the test tends to become globular with strong trends towards the perfect sphericity (attained in *Orbulina*) appropriate to a floating life. Significantly, 20 per cent of the planktonic rotaliids are planispiral, often with extended chambers. This lateral flattening appears to be an adaptation which lowers the sinking rate, as do the long, flexible spines present in many of the planktonic genera until reproduction. The spines also help to spread the net of pseudopods.

Among the Larger Foraminifera the most common coiling modes are planispiral fusiform, almost 50 per cent of the Fusulinida and 10 per cent of the Miliolida, flattened planispiral, annular discoidal, particularly well developed in the lituolids (8 per cent) and in the miliolids (7 per cent) and annular complex, 8 per cent of the rotaliids. As noted above the frequency of the individuals of the species among the Larger Foraminifera and thus the success of the life strategies these modes represent is much greater than those figures seem to suggest. Recent Larger Foraminifera appear to be confined to shallow shelf environments in the tropics and the extinct fusulines and orbitoids probably occupied similar habitats. Bandy (1960a) notes how simple discoid genera occupy extremely shallow depths, 0 – 30 m, while discoid forms with chamberlets, fusiform genera and annular complex genera occupy the 20 – 80 m depth range. It seems clear that these modes and the characteristic external shapes can again be related to hydrodynamic factors and in particular to the exigencies of a symbiotic life in association with algae (Haynes, 1965; Ross, 1974).

It was pointed out by Smout (1954) that the shapes in Larger Foraminifera tend to those that give maximum surface to volume ratio. He also noted that the effect of the main morphological trends in the larger rotaliids, involving the introduction of chamberlets as well as annular and cyclical growth, is to reduce the tendency for the successive lamellae to build up into a thick mass. Thus in *Nummulites*, although the successive 'instars' build up a massive marginal cord, the lamellae thin out on the side walls with the introduction of meandrine filaments. In annular complex genera such as *Miogypsina* the lamellae become buckled to form the lateral chamberlets.

Figure 4.7 shows the major types of Larger Foraminifera grouped according to Zingg's classification of pebble shapes. Maximum sphericity and perfect adaptation to current swept reefal conditions is seen in *Gypsina* and *Baculogypsina* which also possesses strong spines to assist lodgement. In these genera, as in *Orbulina* which is equally well adapted to a planktonic life, the ratio of surface to volume is low. As noticed by Smout, the majority of Larger Foraminifera show much lower sphericities and it is very striking how they are found to fall mainly between the 0.5 and 0.7 lines of intercept sphericity with discs, flattened spheres and rollers. Although very different to the eye these shapes are of equal hydrodynamic stability. Thus disc-shaped *Marginopora* and roller-shaped alveolines would have equal stability in the same environment. The miliolids are largely epiphytic and the discoid shape allows firm attachment to algal fronds and sea grasses as well as to sedimentary substrates. The milioline coiling of many of the smaller genera such as *Quinqueloculina* also produces a globular to fusiform shape which together with the very smooth surface allows the foraminifer to move freely in weed with least danger of being swept away by currents.

The apparent tendency for Larger Foraminifera to sacrifice hydrodynamic stability to achieve a greater surface to volume ratio as well as keeping the outer walls thin is probably connected with the storage of symbiotic algae which depend upon adequate light penetration. These are known in the annular discoid genera *Marginopora* and *Cycloclypeus* as well as in the fusiform *Alveolinella*. Ross (1972c) has recorded how the algal symbionts in *Marginopora* which attaches itself to the substrate by the pseudopods migrate to the well-lit side, and he has also observed (Ross, 1974) that the outer walls remain highly transparent during life. Flattening to achieve a maximum surface to volume ratio is also seen in *Heterostegina* which, as already discussed in chapter 3, can subsist entirely by symbiosis, living attached within a hyaline sheath (Röttger, 1972). It seems logical to assume that the extinct allies of *Heterostegina* and *Cycloclypeus* within the Nummulitidae, in particular *Nummulites* (planispiral lenticular to globular) and *Spiroclypeus* (subannular complex), followed similar life strategies and that the very large species of *Nummulites* were also sessile. Complex canal systems are found in this group and are probably connected with the metabolic

requirements of this type of nutrition. (See further in chapter 13.)

Increased stability and strength without changing the shape is achieved in these genera by adding to the mass. This explains the remarkable tendency of the large rotaliids and orbitoids to deposit secondary calcite in the form of pillars at the corners of the lateral chambers and within the septa, or as umbilical bosses, while keeping the outer walls thin.

The roller-shaped fusulines and alveolines show similar trends. Dunbar (1963) finds that the largest schwagerinids show the 'surprising' tendency to both thinning of the outer wall by honeycombing and to deposition of axial deposits. Similar internal deposition of secondary calcite (flosculinisation) takes place in the alveolines while, again, the outer walls remain thin.

The Adaptive Significance of Wall Structure

Agglutinated tests of adventitious material appear to have been the first hard shells to appear in Foraminifera, and the adaptive success of this type of wall structure is shown by the abundance of the agglutinating group at all depths. Significantly, non-calcareous members of this group dominate in extreme environments, as on the abyssal plain below the CCD, in silled basins and in marginal marine conditions of lowered oxygen and salinity. Most genera in marginal marine and shallow water environments are simple, whereas forms with complex interiors, such as *Cyclammina*, are more common in deeper water (Bandy, 1960a).

In 'normal' marine environments a secreted calcareous test frees the foraminifer from dependence on bottom material and allows the construction of a lighter, architecturally more complex shell. The evolution of this type of wall was clearly a factor in the development of floating brood chambers and the invasion of the pelagic realm by the planktonic families. The appearance of lamellar structure was also a considerable evolutionary step, as it allowed adaptive radiation along a number of different lines and, in particular, the development of annular complex structure. It also allowed the development of spines, costae and keels by localised thickening which are such a feature of the planktonic families and also of benthonic groups like the buliminids, especially in deep water on soft substrates.

The occurrence of several, sharply different, types of calcareous wall structure, characteristic of different major groups, strongly suggests adaptive radiation. It is possible that this variation, like the trend towards a test shape with a high surface to volume ratio and thin outer wall, also relates in part to a symbiotic feeding strategy. This is because the dependence of algae (or sequestered chloroplasts) upon adequate light means that symbiotic Foraminifera are restricted to the photic zone.

The maximum depth of the photic zone is taken to be where green plus blue light is reduced to 1 per cent. This appears to be at about 120 m depth in the very transparent centres of the ocean gyres in the tropics, such as the Sargasso Sea (Steemann-Nielson, 1975). The water is always less transparent at higher latitudes and in coastal areas with corresponding restriction of the photic zone.

The compensation point, where respiration begins to exceed photosynthesis in diatoms, is at about 50 m in the English Channel on a sunny day in midsummer (Harvey, 1963) when the light energy equals that in the tropics. Photosynthesis is at a maximum between about 15 m and 5 m and falls off markedly from 5 m to the surface due to the inhibiting effect of ultraviolet light. In very bright light it is arrested due to contraction of the chloroplasts. Effective symbiosis can therefore only take place in a narrow range of water depths. In these circumstances it would seem likely that any advantage that might accrue from wall structure, especially the appearance of semi-translucent or glassy shells, would be of great adaptive significance. Also, it may be that different wall structures allow symbiotic genera to exploit different depths within the phototropic zone.

In the simple, agglutinated *Iridia* the algae are carried outside when the pseudopodia are active (Cushman, 1922). This process, which apparently ensures effective photosynthesis, has also been observed in the planktonic Foraminifera (Hemleben *et al.*, 1977; Bé *et al.*, 1977). However, it seems very probable that a wall structure that allows the algae to photosynthesise within the test, as appears to be the case in the Larger Foraminifera in particular, confers a positive advantage. The hyaline wall, especially radial structure, possibly has an adaptive advantage towards the deep limit of the phototropic zone and it is significant that the large rotaliids and the planktonic Foraminifera are all radial. Again, although at the present day the major types of hyaline wall occur at all depths, it is also significant that families with oblique structure such as the Cassidulinidae, Chilostomellidae, Nonionidae and Pleurostomellidae are a particular feature of cool, deep water. In contrast,

the porcelaneous group are particularly abundant in shallow waters, especially in the tropics on the inner shelf in open bays and lagoons (Bandy, 1960a; Murray, 1973b). This distribution suggests that porcelaneous structure may bestow a protective advantage, the crystal arrangement helping to scatter short wavelength, ultraviolet light. The fact that *Marginopora* has been found to have clear windows in the outer chamberlets where the symbionts are concentrated, created by the alignment of the calcite laths perpendicular to the surface (Ross and Ross, 1978), can be taken as evidence of an exception that proves the rule. The thick brown organic membranes characteristic of miliolids and peneroplids may also absorb the short metagenic wavelengths. Agglutinated structure may also be an advantage at these shallow, extremely well-lit depths, the layer of grains embedded in the organic membrane performing the same protective function. This may explain the success of the large, fusiform, arenaceous genus *Loftusia* during the Maastrichtian stage. Similar considerations may help to explain the variations in the number and thickness of the layers in the microgranular fusulinids.

It must be emphasized to the student that these ideas on form and function are largely speculative and require much more research on living Foraminifera for their confirmation or rejection. As Morley Davies (1939) said in another context:

> Here I must end. I have shown you some of the problems and puzzles that confront palaeontologists as soon as they attempt something more than empirical treatment of the fossils they collect. Such feeble attempts as I have made at explanations are only gropings in the dark; but I hope some of you who are concerned with living molluscs may be able to throw some light on the secrets of the dead. Even if you can only show that my own suggestions are absurd and impossible, that will be better than nothing.

SUMMARY

The Foraminifera present a unique variety of test shapes and coiling modes. The majority are multilocular and characteristically the test has a restricted aperture and internal foramina and a toothplate is often present. The main kinds in order of abundance (total genera) are low trochospiral, high trochospiral/uniserial, planispiral lenticular, fusiform, biserial/uniserial, discoid, milioline, uniserial, polymorphine and annular complex. Mixed growth is common and it has been assumed that ontogeny reflects phylogeny with the stages shown most completely in the B form. This is supported by the stratigraphical evidence.

The test wall which is either of agglutinated grains or of secreted calcite is built up on a tectin membrane. The agglutinated grains may be carefully selected for size, shape and composition and are bound with organic cement. This is usually ferruginous, and under normal marine conditions, often highly calcareous. In the calcareous Foraminifera the wall is either microgranular (fusulines) or composed of randomly arranged calcite laths (porcelaneous—miliolids) or of rhomboid microcrystals (hyaline group) showing the complete range of orientations possible for calcite—on the a-axis, on the c-axis and on the rhomb face. Compound structures and tests composed of a single crystal also occur.

Hyaline Foraminifera are generally lamellar: either monolamellar, where each chamber is composed of one layer which invests the previously formed test, or multilamellar. In this latter group the wall is usually bilamellar, with two layers of calcite on either side of an organic membrane. The inner calcite lamella may coat the previous apertural face as a 'septal flap'.

The walls of hyaline Foraminifera are perforated and pores also occur in many genera of the microgranular and the agglutinating groups.

Growth of a new chamber in the hyaline group involves the active participation of the pseudopods and begins with the formation of the tectin membrane and by the secretion of calcite in patches which gradually coalesce to form the wall-like pieces of a jig-saw puzzle. The units are first granules but later become euhedral. In the porcelaneous group the process is rather different and involves the gradual mineralisation of a thick organic 'moulage'.

Two views prevail regarding the sequence of events in the formation of the bilamellar wall which is believed either to be built up step by step on the basis of the tectinous or 'chitinoid' inner lining or to result from simultaneous secretion of inner and outer calcite lamellae on either side of the organic 'median layer'. In the first case the wall is considered to be built around the organic tubules which become the pore linings; in the second the pores are considered to arise later by resorption.

As well as providing a foundation for the construction of the hard shell the organic

membranes act as a shield against physical and chemical changes. The organic pore plugs are minutely perforated and probably act as a fine filter. When necessary, the aperture and foramina as well as the pores can be completely closed off.

The hard test may have arisen to control buoyancy as well as being a protective device and the multichambered form affords extra protection against external physical and chemical effects and extends the time available for osmoregulatory adjustment.

The different coiling modes appear to relate to feeding strategies as well as to environmental, especially hydrodynamic, effects. Their repeated appearance in the different wall structure groups indicates adaptive convergence, with low trochoid forms occurring mainly as active herbivores in shallow water, high trochospiral/uniserial forms as deposit feeders at the sediment/water interface and infaunally and planispiral genera as active deposit feeders in weed and on soft substrates. The Larger Foraminifera occur in weed and are attached by their pseudopods to the sedimentary substrate in shallow water in the high energy zone, and their disc and roller shapes appear to represent a compromise between the requirements of a symbiotic life involving a high surface to volume ratio and hydrodynamic stability. Simple correlations between morphology and habit are not possible because a particular coiling mode may allow more than one feeding strategy and many genera are opportunistic, omnivorous feeders. The occurrence of mixed growth may indicate changing requirements during ontogeny.

The plastic response of Foraminifera to environmental pressures, together with convergent evolution in the major groups which often appears to have 'followed curiously devious paths', makes it difficult to assess the adaptive significance of wall structure. In general, the agglutinating group dominates below the CCD and in marginal marine environments, while the calcareous groups dominate 'normal marine environments'. The appearance of the calcareous wall and, in particular, lamellar bonding has allowed the construction of lighter, stronger tests and led to adaptive radiation along a number of different lines, including the rise of annular complex genera and forms with complex canal systems. Foraminifera are unique in exploiting all the preferred orientations of calcite as well as producing a random array of calcite laths. This may in part relate to the symbiotic feeding strategy which is restricted to a narrow range of depths in the phototropic zone. Radial structure may have an advantage towards the deep limit, 50 m plus, while porcelaneous structure may have a protective advantage at very shallow depths near the surface.

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