

Foraminifera

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Foraminifera are marine protozoans that play a major role in the ecology of the oceans.

Introduction

Foraminifera are amongst the most abundant marine invertebrates and play a major role in the economy of nature, both as benthic bottom dwellers and as free-floating members of the plankton in the surface waters of the open ocean. Benthic forms occur in most marine environments, particularly in deep-sea and outer shelf muds. Several thousand specimens representing some 50 species frequently occur in a 10-mL volume sample. Planktonic species may exceed 60% of the total zooplankton in certain areas in summer. Their dead shells rain down in a 'globigerine snowfall' to make a blanket of ooze on the deep-sea floor. This ooze is masked by terrigenous sediment on the shelves but is found in remarkably pure form on the abyssal plain. It covers almost half of the total deep-sea floor and is therefore the most extensive organic sediment on earth. Over 40 000 recent and fossil species of foraminifera have now been named.

Description and Characterization

Foraminifera are characterized by an organic and/or mineralized test (shell), usually with a number of compartments (chambers) which enlarge as they are added and thread-like extensions of the protoplasmic soft parts (pseudopodia) which anastomose to make a reticulate network. The chambers are connected with openings called foramina which give the name to the group.

Foraminifera average about 0.33 mm in diameter (fine sand size) with a general range from 0.10 mm to 1.00 mm, though some are smaller (microforaminifera) and some exceed 2 mm (larger foraminifera) with relative giants up to and even exceeding 1 cm diameter.

Soft part biology

Foraminifera are single celled (or rather acellular as there are multinucleate phases). The single cell has to carry out many of the functions carried out by specialized cells and by tissues in metazoa, including the construction of an architecturally complex test. This is reflected in the complexity of the cell with its range of organelles revealed by the scanning electron microscope (SEM) and the transmission electron microscope (TEM) even in the most primitive order, the Allogromiida, which includes naked

genera such as *Allogromia* and *Myxotheca* (Figure 1a). Here the test is an organic, gelatinous sac-like structure, 1–10 μm thick and composed of glycoprotein ('tectin'), a proteinaceous polysaccharide. It is an internal structure surrounded by a clear gel-like cytoplasm (ectoplasm) external to the primary cell membrane which contains the dense sol-like cytoplasm (endoplasm). In advanced foraminifera such as the globigerinids (Figure 1b) the organic layer becomes an inner lining to the calcareous test. The cytoplasm everywhere has the capacity for membrane formation and recombination.

Most structures, including the nucleus which controls the organization of the cell and contains the chromosomes, are within the endoplasm. There are seven chromosomes in *Myxotheca arenilega* and 24 in *Patellina corrugata*. There is

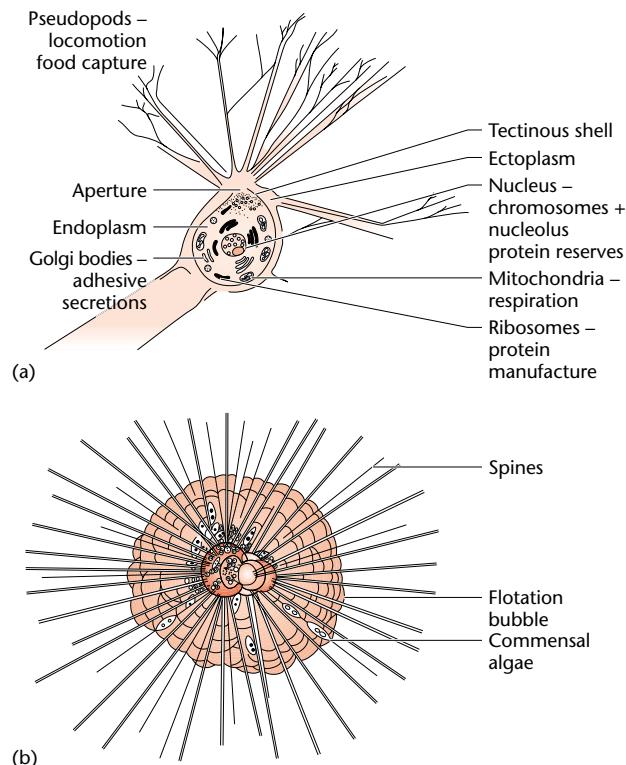


Figure 1 Soft part morphology of (a) an allogromiid, (b) a globigerinid.

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always one nucleus but there may be a multinucleate stage early in asexual reproduction. Other important structures are the endoplasmic reticulum – a network of membranous canals that transport the products of metabolism through the cell; ribosomes which synthesize proteins; Golgi complexes which produce polysaccharides and mucoid substances and mitochondria which store the energy of oxidation by synthesis of adenosine triphosphate (ATP).

The most striking structures of the ectoplasm are the pseudopods, which stream out in all directions reaching lengths many times the diameter of the test (**Figure 1a**) and exhibit a characteristic granular streaming. They may form a trunk-like mass issuing from the aperture (podostyle), particularly in species living within the sediment (infaunal), where the pseudopods are concentrated into bundles to push aside the grains. They can expand and contract and can be thrown out on one side and retracted on the other side in locomotion. In planktonic globigerinids a fine net of pseudopods is supported by the spines which arise from the calcareous test and radiate out in all directions. The ectoplasm is frothy and surrounds the test completely. In *Hastigerina*, a definite flotation bubble is developed up to 2 mm in diameter (**Figure 1b**). The strength of the pseudopodia is shown by the ease with which *Ammonia batava* can drag quartz grains along equal to its diameter in size.

Nutrition

The food of foraminifera includes unicellular algae, especially diatoms, other protozoa and small crustaceans such as copepods which are snared in the pseudopods. Many species appear to require a certain proportion of bacteria in their diet also. Commonly, particularly in globigerinids and in larger foraminifera, various algae occur in both the endoplasm and the ectoplasm, in a symbiotic relationship, both green algae (Zoochlorellae – mostly *Chlorella*) and golden/brown algae (Zooxanthellae – mostly dinoflagellates). Chloroplast symbiosis also occurs in which the sequestered chloroplasts obtained from algae continue to function in the host. Some genera, such as *Heterostegina*, can grow without ingesting other food and this relationship helps to explain the very high rates of carbonate shell production in larger foraminifera which is some 20–100 times as great as in the small calcareous benthic genera.

As well as ingesting live animals and plants and exploiting the possibilities of symbiosis, foraminifera feed on dead organisms, organic-rich grains including faecal pellets, particulate organic detritus and colloidal organic molecules, i.e. the six major classes of food resource available to benthic invertebrates. This reflects the versatility of the pseudopodial network and explains the abundance of the class across the broad spectrum of marine environments as well as the great variety of

adaptive test morphologies (and colour of protoplasm caused by pigments, food particles and symbionts).

Reproduction

Most species of foraminifera occur in two distinct size groups (dimorphism). This is the result of the alternation of two generations with different kinds of reproduction, involving an asexual generation (agamont or B-form) with a small initial chamber (proloculus or microsphere) and a sexual generation (gamont or A-form) with a large initial chamber (megalosphere). Adult B-forms are generally larger than the A-form with more chambers and also occur more rarely.

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 A-form (gamont). When the gamont has reached a certain size sexual reproduction takes place without further reduction of the chromosomes (mitosis) to give haploid gametes. These may be flagellate and free swimming or amoeboid. They leave the test and meet and fuse to produce the new, diploid, asexually reproducing agamont (B-form). It should be noted that different species show variations on this general theme. Conjugation may take place in a brood chamber and there may be successive A-forms (see Sleight, 1989, figure 4.6). Interestingly, this type of heterophasic alternation of generations with a diploid agamont is more typical of plants.

Special methods are employed to aid in the dispersal of gametes in *Tretomphalus bulloides* (see Haynes, 1985, figure 3.5), a multilocular, calcareous discorbid, with pairing of two A-forms (plastogomy) to ensure cross-fertilization. The B-form is attached and asexual reproduction takes place beneath a protective cyst of agglutinated debris. Some 200 embryos are produced which dissolve the test wall to escape. The A-form also lives attached until about 18 chambers are formed. It then encysts and grows a large, globular float chamber filled with gas. The foraminifer then bursts out of the cyst and floats to the surface of the sea, where sexual reproduction takes place in contact with another mature A-form, the flagellate gametes from the two individuals pairing to produce a zygote which sinks to the sea-bed to repeat the cycle.

Test morphology and composition

The foraminiferal test is either unilocular (nonseptate) or multilocular, being composed of more than one chamber and divided by septa.

Unilocular tests may possess simply 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. 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 arrangement are described in **Table 1** (see Haynes, 1985, figures 4.1 and 4.2):

Test composition and structure

There are three kinds of test wall. In the first the test is formed by an organic membrane of tectin. In the second this membrane becomes the foundation for an agglutinated wall (**Figure 2h**) and, in the third, the inner lining of a calcareous wall.

Membranous wall

In the membranous group (allogromiids) the test is unilocular, thin and flexible, allowing rapid changes of shape. A number of naked genera live inside dead shells of other foraminifera or worm tubes; others construct partial agglutinated coverings.

Agglutinated wall structure

There is a gradation from genera with adventitious material loosely attached to the organic membrane to strongly built genera where the grains are held firmly with calcareous and/or ferruginous cement (**Figures 2g** and **2j**). Many genera, such as *Astrorhiza*, are unselective and make use of material from the sea-bed indiscriminately,

including sand grains, sponge spicules, mica flakes, diatoms and heavy minerals. Others are highly selective and build their tests of particular kinds and sizes of material from sponge spicules to heavy minerals such as rutile (**Figures 2i** and **2k**). Most commonly however, especially in multilocular genera, the wall is of sand grains built flat on to the wall surface with the large grains characteristically packed in a matrix of smaller grains (**Figure 2l**).

Calcareous wall structure

There are two major types of calcareous wall in post-Palaeozoic foraminifera, distinguished as porcelaneous or glassy (hyaline) according to their appearance in reflected light. In the porcelaneous group the wall resembles shiny white porcelain because the fine structure leads to maximum reflection of light. In contrast, the glassy group have a fine structure that readily allows light to pass through, so that many of these genera resemble clear soap bubbles or blown glass.

In the porcelaneous foraminifera the wall is generally composed of three layers: a thick median layer of calcite laths in random array with thin inner and outer veneers with preferred orientation (**Figures 2a** and **2b**). In smooth, shining species the laths in the surface veneer are arranged parallel to the surface, in a 'tile roof' or 'parquet floor' pattern. In rough-walled species 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 all cases. In transmitted light, porcelaneous walls show a characteristic rich brown coloration, apparently due to included organic matter.

Table 1 Major types of multilocular arrangements

Name	Description
Planispiral	Chambers coiled in a single plane
Fusifiform	Planispiral arrangement with the axis of coiling drawn out
Annular discoid	Initial chambers planispiral and the later ones added as annular rings
Annular complex	With annular discoid, middle (equatorial) layer and lateral layers (orbitoidal)
Biserial	Chambers arranged in two alternating rows
Trochospiral	Chambers coiled in a helicoid spiral as in the gastropod <i>Trochus</i>
High trochospiral	Trochoid with a high, elevated spire, often triserial
Uniserial	Chambers in a single series
Milioline	Winding growth with two chambers to the whorl with the aperture alternately at one end and then at the other
Polymorphic	Successive chambers spiralling about a vertical growth axis with apertures all pointing in the same direction
Other modes	Many Foraminifera show irregular growth, especially attached forms. A small number of attached forms are tree-like (arborescent) with many branches
Mixed growth	Change of style with growth is common with the adult different from the juvenile. In some cases three different modes may be shown, e.g. triserial to biserial to uniserial, typically curtailed in the A-form which may show only the uniserial stage

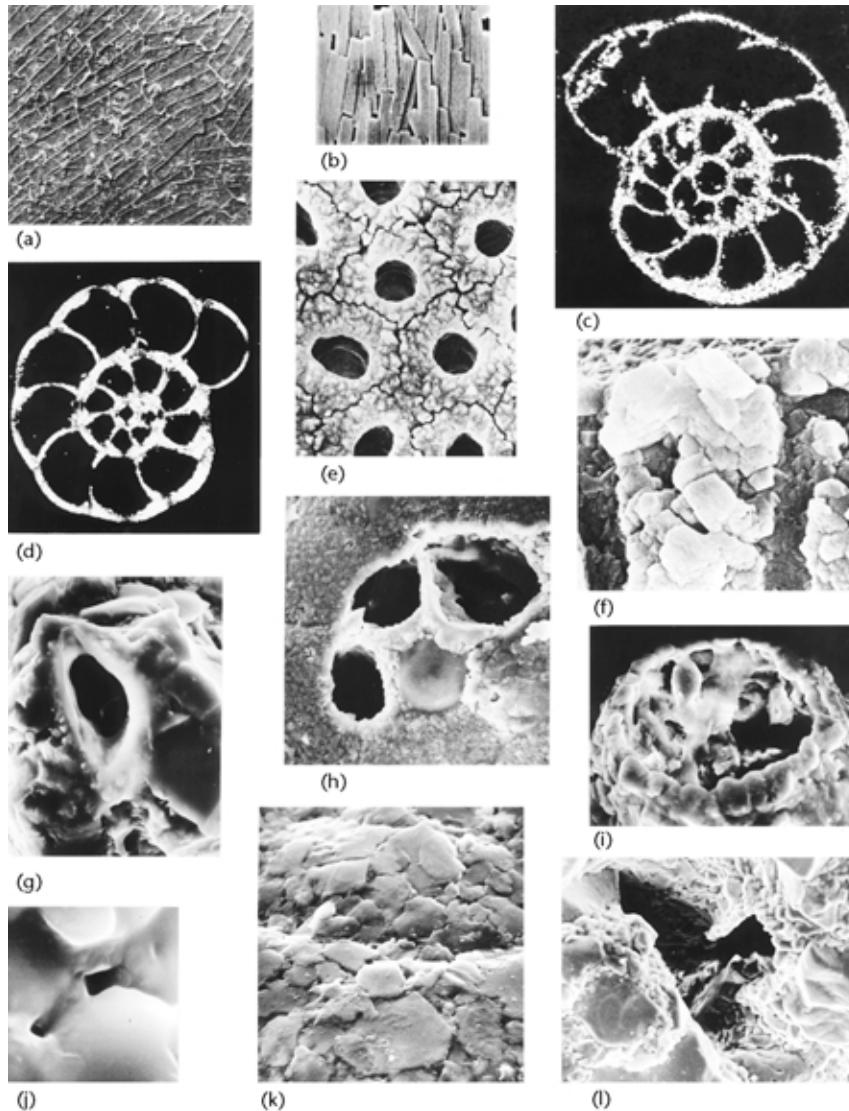


Figure 2 Wall structures. (a) Mosaic of calcite laths in the external layer of the porcelaneous species, *Quinqueloculina seminulum*. $\times 5250$, by TEM. (b) Calcite laths in the external layer of *Triloculina tricarinata*. $\times 5250$, by SEM. (c) Oblique hyaline structure in *Elphidium exoticum*. $\times 158$, under crossed nicols. Note 'granular' appearance. (d) Radial hyaline structure in *Elphidium selseyense*. $\times 84$, under crossed nicols. Note extinction cross in proloculus and shadows across other chambers. (e) Pores piercing sutured units of microcrystals in the radial hyaline species *Ammonia batava*. $\times 5250$, by SEM after etching. (f) Stacks of rhomboid microcrystals in *Ammonia batava*, with pores seen in section. $\times 5250$, by SEM after etching. (g) Aperture in *Clavulina arctica* showing abundant cement. $\times 788$, by SEM. (h) Detail of breached dorsal side of *Trochammina inflata* showing minute agglutinated grains and tectin lining. $\times 366$, by SEM. (i) Fine structure of the apertural lip in the agglutinating species *Lagenammina arenulata* showing size selection. $\times 550$, by SEM. (j) Small, rectangular pores in the agglutinated species, *Clavulina arctica*. $\times 3675$, by SEM. (k) Irregular grains laid flat-on in the agglutinated species *Trochammina intermedia?* $\times 788$, by SEM. (l) Detail of the apertural tooth in the agglutinating species *Eggerelloides scaber*, showing size selection. Note how the large grains in the wall are packed in a matrix of smaller grains. $\times 263$, by SEM. Reproduced from Haynes (1985) plate 7. a) from Towe and Cifelli, 1967, *Journal of Paleontology*, 41(3). b) from Haake, 1971, *Journal of Foraminiferal Research*, 1(4). e) and f) from Belleo, 1974, *Bulletin of the Geological Institutions of the University of Uppsala*, New Series 4.

In the hyaline or glassy group two kinds of wall can be distinguished on the basis of optical characters observed in thin sections or fragments under crossed nicols of the polarizing microscope. Walls with a hyaline radial structure are characterized by a black cross with concentric rings of colour closely mimicking a typical (negative)

uniaxial interference figure (Figure 2d). The test is built of crystals of calcite with their *c*-axes normal to the surface. In walls with a hyaline oblique structure there is no extinction pattern, only a multitude of tiny flecks of colour (Figure 2c). Electron microscopy reveals that in both cases the test is built of units composed of numerous plate-like or

rhomboidal crystals about 1 μm in diameter. These units are enclosed in an organic membrane and irregularly sutured together (Figures 2e and 2f). The difference in optical characteristics of the hyaline oblique type is caused by the microcrystals being stacked obliquely across the wall with the *c*-axes inclined at about 5° and never perpendicular to the surface. For this reason none are seen to extinguish when pieces of test wall are examined under crossed nicols; the wall then appears to be built of randomly oriented grains. Note that mixed and intermediate structures can occur in some genera.

The truly 'microgranular' wall structure appears to be confined to the Palaeozoic Fusulinida, in which the wall is built of layers of subhedral microcrystals, partly stacked in columns but without optical orientation.

Thin sections of glassy foraminifera show that not only are many tests layered but that generally they are lamellar with the walls of later chambers being carried back over the previously formed test, unlike agglutinating, porcelaneous and microgranular groups, where new chambers simply abut previously formed ones. This lamellar structure allows the development of continuous ornamentation of ribs, ridges and peripheral keels, so characteristic of the calcareous groups.

The walls of hyaline foraminifera are usually perforated (Figures 2e and 2f). Pores also occur in the microgranular group and more rarely in agglutinating genera with calcareous cement (Figure 2j) but are absent in the porcelaneous group (apart from the juvenile stages of some forms). In perforate genera the walls between the chambers (septa) and the 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 may be of different sizes in the same individual. The organic membrane is imperforate but is thickened at the base of each pore, this pore plug being microporous. The pore is also lined with an organic membrane and calcified sieve plates may occur where the pore passes through the layers of a lamellar test.

Other important structures

Modifications of the aperture such as coverplates and toothplates connecting the aperture with the previous foramen (often becoming quite elaborate) occur in all the main wall structure groups, as do passageways in the walls (canals). These last are of particular importance in the larger foraminifera where their complexity relates to the requirements of metabolism involving symbiosis and the difficulties in communication caused by greatly increased size (see Haynes, 1985, plate 12).

Growth of the test

Test construction appears to take place within a protective cyst and observation is restricted to a few species. The pseudopods are active in the formation of new chambers, flowing out and coalescing to form an internal mould of the new chamber with a membrane which acts as a surface for nucleation of calcite crystals or for assembly of agglutinated grains gathered by the pseudopods. In the hyaline group calcification is initially patchy, the sutured units being laid down like the pieces of a jigsaw puzzle. In the porcelaneous group, growth seems to be different, with mineralization of a thick organic 'mouillage' gradually spreading from the centre to reach the apertural and aboral ends of the chamber.

Function of the test

The organic wall of the allogromiids and the inner lining and external tectin membranes of the calcareous genera control exchange with the exterior by osmosis and act as a protective shield against external physical and chemical changes, particularly in waters of low pH or undersaturated in carbonate.

In perforate genera the pores are lined and plugged with organic material. Cytoplasm occurs within the pores and small particles can enter and leave after filtering through the perforated plugs and sieve plates, but these openings are too fine to allow the pseudopods to pass through.

The low domes and tent-like structures that occur in the simplest agglutinated forms probably arose as protective covers and perhaps to control buoyancy. Tubular and branched fixed forms are adapted to suspension feeding while enrolled forms demonstrate the advantage of a compact test for free wandering forms. Some 90% of the hard-shelled genera are multilocular, an indication of the extra protection afforded by the constricted chain of apertures and internal foramina which checks density currents and allows time for osmoregulatory adjustment.

Coiling mode and test shape relate to feeding habits (and the deployment of pseudopods) as well as environmental and especially hydrodynamic effects and the repeated appearance of the same coiling modes in the different wall structure groups indicates adaptive convergence.

Low trochoid coiling is well adapted to fixed or temporary attachment and for herbivorous browsing on hard substrates in current-swept areas, planispiral coiling for an active vagrant life, scavenging detritus on soft sediments or in weed, and the development of an extended series of uniserial chambers with terminal aperture for an infaunal habit. Active and passive carnivores have diverse morphologies: *Astrorhiza*, which is a passive carnivore, has a symmetrical star-shaped test and drops a net of pseudopods into the sediment to trap minute animals.

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. The appearance of a glassy wall structure was a factor in the rise of the symbiotic groups ('algal greenhouse') while a porcelaneous wall structure affords protection from ultraviolet light in very shallow water.

It should be noted that simple correlations between morphology and habit are not possible because a particular coiling mode may allow more than one feeding strategy and many species are opportunistic, omnivorous feeders.

Ecology

Foraminifera are almost exclusively marine with only a few known cases of adaptation to freshwater. The majority are benthic with a small number of planktonic species (some 30 at the present time—but represented by countless individuals). A relatively small number of benthic genera live permanently attached with their tests firmly cemented to various objects on the sea floor.

The chief factors controlling distribution of species are temperature, salinity, substrate, turbidity and current energy, and light penetration in the case of symbiotic species. Particular species occur adapted to the whole range of different environments from the deep sea to the marginal marine zone. Some groups can withstand low levels of oxygen and alkalinity, such as the organic walled agglutinating forms which can flourish below the depth of carbonate dissolution (CCD = calcite compensation depth) on the abyssal plain and in the ocean trenches, as well as being prominent in transitional marine environments of lowered salinity.

Free benthic forms (**Figure 3b**) occur on most sediments (epilithic) and within them infaunally to depths controlled largely by the onset of anaerobic conditions. Under conditions of extreme turbulence and continuous movement in shallow water, vagrant species as well as attached forms are limited to sheltered niches on hard substrates and, in particular, to the shelter given by seaweed. In the sunlit photic zone they cling by their pseudopods and congregate in holdfasts, especially of *Laminaria* and other algae. They also occur as epiphytes in eel grass (*Zostera*) and in its tropical counterpart, turtle grass (*Thalassia*). Below the photic zone the foraminifera cling to animal substrates, particularly hydroids and bryozoans, such as *Flustra*, and even molluscs like scallops.

Symbiotic species are restricted to the photic zone which extends to some 20 m in the temperate regions but down to 120 m in the tropics. The symbiotic larger foraminifera are further restricted largely to the tropics because of the high temperatures required for reproduction. The importance of temperature in the case of the planktonic species is indicated by their occurrence in global latitudinal belts

with a gradual decrease from between 20 and 30 species in the tropics to one or two in cold, polar waters (**Figure 3a**). The sharp distinction that can be drawn between warm- and cold-water globigerinid faunas has proved extremely useful in the analysis of long cores of deep-sea ooze, allowing the recognition of the successive phases of the Ice Age. Direct temperature measurements are also made from oxygen isotope measurements of the tests of species such as *Globigerinoides sacculifer*.

Taxonomic Position

Foraminifera are a class within the kingdom Protista (Protoctista of some authors) which covers eukaryote organisms formerly classed as algae, protozoa and flagellate fungi (protozoa is now used informally to cover animal-like protists). However, it should be noted that Sleigh (1989) considers the Protista a level of evolutionary development rather than a true kingdom as it contains several, separate evolutionary branches. It has even been suggested by Margulis (1974) that the level and range of complexity in the Foraminifera alone is sufficient for recognition as a phylum.

The Foraminifera were first separated from the Cephalopoda, as a distinct order, by d'Orbigny (the 'Father of foraminiferal studies') and when it was discovered that they were protozoa he gave them class status (1839). This was not generally accepted, especially by the 'English school', deterred by their presumed, low organization, apparently without a nucleus and more primitive than amoeba. They were returned to ordinal level and this has been followed in the most influential classifications of both the nineteenth and twentieth centuries, including the treatment by Loeblich and Tappan, in 1964, where they were considered an order within the subclass Granuloreticulosa (with delicate reticulate pseudopods and granular cytoplasm) and the class Reticularia (with filose, reticulate or microtubular pseudopods).

In 1985, Haynes treated the Foraminifera as a subclass but they were not formally designated as such. This step was finally taken by Lee (1990) who brought them back to full class status within the phylum Granuloreticulosa; an approach accepted by Loeblich and Tappan (1992).

According to Sleigh (1989), the common occurrence of heterodynamic biflagellate gametes and the presence of tubular cristae in the mitochondria suggest a relationship to the heterokont flagellates such as xanthophytes.

Classification and Major Subtaxa

Species are distinguished largely on chamber shape and quantitative differences in number and volume per whorl. Genera are distinguished largely on qualitative differences

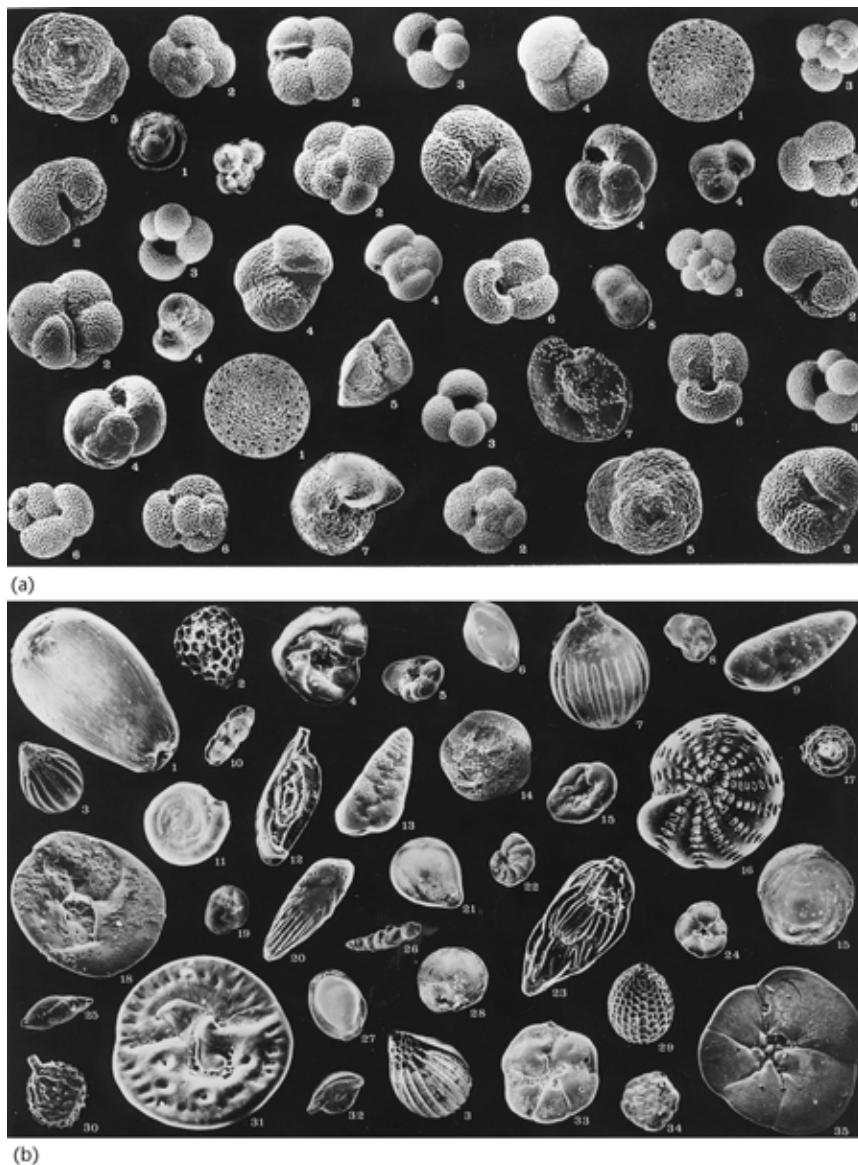


Figure 3 Foraminiferal faunas of the Northeast Atlantic. (a) Temperate latitude, 'transitional province', planktonic foraminifera, NE Atlantic. $\times 19\text{--}38$ (actual size range between 0.25 and 0.50 mm maximum diameter), by SEM. 1, *Orbulina universa*; 2, *Turborotalia pachyderma*; 3, *Globigerina bulloides*; 4, *Turborotalia inflata*; 5, *Globobulimina crassaformis*; 6, *Globobulimina ruber*; 7, *Globobulimina truncatulinoides*; 8, *Borbulina bilobata*. (b) Some typical, temperate latitude, benthic foraminifera, NE Atlantic. $\times 15\text{--}75$ (actual size range between 0.20 and 0.65 mm diameter and length), by SEM. 1, *Oolina lineata*; 2, *Oolina hexagona*; 3, *Oolina williamsoni*; 4, *Rosalina anomala*; 5, *Trochammina inflata*; 6, *Pyrgo* sp.; 7, *Oolina borealis*; 8, *Elphidium magellanicum*; 9, *Bolivina* sp.; 10, *Bulimina elongata*; 11, *Cornuspira selseyense*; 12, *Spirophthalmidium acuta*; 13, *Bolivina variabilis*; 14, *Rosalina* cf. *bradyi*; 15, *Asterigerinata mamilla*; 16, *Elphidium williamsoni*; 17, *Turrispirillina* sp.; 18, *Rosalina neopolitana*; 19, *Rosalina* sp.; 20, *Bolivina striatula*; 21, *Oolina laevigata*; 22, *Haynesina depressula*; 23, *Trifarina angulosa fluens*; 24, *Trochammina astrifica*; 25, '*Stainforthia*' *fusififormis*; 26, *Clavulina arctica*; 27, *Pyrgo constricta*; 28, *Siphonina georgiana*; 29, *Oolina squamosa*; 30, *Lagena hibernica*; 31, *Patellina corrugata*; 32, *Quinqueloculina mediterranea*; 33, *Gavelinopsis preageri*; 34, *Planorbulina distoma*; 35, *Rosalina williamsoni*.

in chamber arrangement, aperture position, tooth structure and other internal characters. However, in both cases the boundaries between related forms may be gradational. Ornament and presence or absence of a keel may also be considered generic.

The main diagnostic suprageneric characters are: at ordinal level – wall composition and structure (with three bilamellar, calcitic orders recognized on grounds of habit and internal structures); and at superfamily/family level – whether unilocular, bilocular or multilocular, coiling

Table 2 Major orders and superfamilies of the Foraminifera

Wall composition and structure	Orders	Coiling mode	Aperture form	Superfamilies	Stratigraphical range
Agglutinated, commonly layered	Astrorhizida	Nonseptate, globular, tubular or branching	Simple terminal	Ammodiscacea	Cambrian–Recent
	Lituolida	Planispiral to uniserial or annular Trochospiral	Basal median to terminal and multiple Basal ventral to terminal and multiple (may be dentate)	Lituolacea Ataxophragmiacea	Carboniferous–Recent Carboniferous–Recent
Calcitic microgranular Nonlamellar, simple to layered	Fusulinida	Nonseptate, globular or tubular	Simple to multiple	Parathurammina- cea	Upper Palaeozoic
	Fusulinina	Planispiral to uniserial Trochospiral	Basal median to terminal and multiple Basal ventral to multiple	Endothyracea	Upper Palaeozoic
				Tetrataxacea	Carboniferous–Permian
Outer hyaline radial layer	Archaeodiscina	Nonseptate, tubular, planispiral, conical or winding	Simple terminal to stellate	Fusulinacea Archaeodiscacea	Carboniferous–Permian Carboniferous–Permian
		Uniserial and overlapping	Terminal, simple or ‘radiate’	Colaniellacea	Upper Palaeozoic
Porcelaneous, layered, nonlamellar	Miliolida	Bilocular or bilocular to irregular	Simple terminal	Nubeculariacea	Carboniferous–Recent
		Winding with elongate chambers	Simple terminal	Ophthalmidiacea	Carboniferous–Recent
		Planispiral to uniserial or annular	Median and multiple	Soritacea	Jurassic–Recent
		Winding to uncoiled cylindrical or compressed, or fusiform	Dentate terminal to multiple	Miliolacea	Jurassic–Recent
Calcitic, hyaline radical, monolamellar or multilamellar	Nodosariida	Planispiral to uniserial, unilocular	Peripheral to terminal, ‘radiate’	Nodosariacea	Permian–Recent
		Alternating to unilocular	Terminal, ‘radiate’	Polymorphinacea	Triassic–Recent
Aragonitic, hyaline radial, bilamellar	Robertinida	Planispiral to trochospiral	Double or umbilical with distal arch and proximal notch	Duostominacea	Triassic–Jurassic
		Trochospiral	Umbilical to marginal or peripheral, narrow toothplate, secondary foramen	Ceratobuliminacea	Jurassic–Recent
		Trochospiral to planispiral	Umbilical to areal, broad partition, primary foramen	Robertinacea	Eocene–Recent
Calcitic, hyaline radial or oblique, bilamellar	Buliminida	High trochospiral to biserial, uniserial and unilocular	Basal and comma-shaped to terminal with toothplate	Buliminacea	Jurassic–Recent
		Compressed or enrolled biserial to uniserial	Basal median, marginal or terminal slit, with toothplate	Bolivitinaea	Jurassic–Recent
		Triserial to biserial (or enrolled biserial) to uniserial	Marginal, subterminal or terminal slit with internal tube (may be lost)	Cassidulinacea	Cretaceous–Recent

continued

Table 2 – *continued*

Wall composition and structure	Orders	Coiling mode	Aperture form	Superfamilies	Stratigraphical range
Calcitic, hyaline radical, oblique, compound or single crystal, bilamellar or with septal flap	Rotaliida	Nonseptate, or multilocular with 2 or 3 chambers per whorl ^a	Simple terminal or umbilical	Spirillinacea	Triassic–Recent
		Trochospiral, umbilicus open or secondarily closed	Umbilical to extraumbilical	Discorbacea	Cretaceous–Recent
		Trochospiral to planispiral and uncoiled or annular, umbilicus closed	Extraumbilical to multiple	Asterigerinacea	Cretaceous–Recent
		Trochospiral to annular or arborescent	Ventro-median to medio-dorsal or multiple	Orbitoidacea	Cretaceous–Recent
		Trochospiral to involute planispiral with retral processes and canals	Basal ventral to multiple	Nonionacea	Cretaceous–Recent
		Trochospiral to planispiral septal fissures or canals ^b	Basal ventral to multiple	Rotaliacea	Cretaceous–Recent
		Planispiral with marginal cord and canals or annular ^b	Basal median to multiple	Nummulitacea	Cretaceous–Recent
Calcitic, hyaline radial, bilamellar	Globigerinida	Trochospiral	Umbilical to extraumbilical with asymmetric flaps	Hedbergellacea	Cretaceous
		Planispiral to biserial	Median with flaps or lip	Heterohelicacea	Cretaceous–Miocene
		Trochospiral or streptospiral	Umbilical to extraumbilical with lip, teeth or bullae	Globigerinacea	? Jurassic–Recent
		Trochospiral to planispiral	Ventro–median to median with extensions or areal	Hantkeninacea	Upper Palaeocene–Recent

^a Foraminifera consisting of a calcitic, hyaline radical, oblique compound or single crystal.

^b Foraminifera consisting of a bilamellar or with septal flap.

mode, apertural form, internal characters, including canals, and perforation (Table 2). At the present time the soft parts are not a major consideration but details of reproduction (e.g. plastogomy) have been used to establish relationships at the family level.

Phylogeny

There is a general succession of wall structure groups through time providing good evidence of evolutionary development and replacement. The unilocular agglutinating astrorhizids are the sole Foraminifera of the Early Palaeozoic. They gave rise to the microgranular fusulinids in the Devonian which rapidly became the dominant group with species as large and complicated as in any other group since (one of the reasons that early workers thought foraminifera showed no evolutionary, 'progressive', development through time). Before dying out at the end of the Permian the microgranular group gave rise to both the porcelaneous miliolids and the calcitic, monolamellar nodosariids via unilocular forms. Also in the Late Palaeozoic the unilocular astrorhizids gave rise to the multilocular, agglutinating lituolids.

The ancestry of the aragonitic robertinids which appear in the Triassic is unknown. The spirillinids, in which the test is a single calcite crystal, appear at the same time. It has been supposed that the bilamellar, calcitic, hyaline rotaliids (with the wall built of sutured units of rhomboid microcrystals) sprang from unilocular members of this group in the Cretaceous but the crystallographic differences make this doubtful. The calcitic, bilamellar buliminids, with their characteristic tooth structures and high trochospiral tests, appear in the Jurassic, probably descended from perforate, high trochospiral agglutinating forms with calcareous cement. Primitive planktonic species also appear in the Jurassic but their origin is unknown. A marked expansion of these Mesozoic groups took place in the Cretaceous and genera of relatively giant size appear in both the Miliolida (alveolines) and Rotaliida (orbitoids) in rock-forming abundance in shallow water, while the globigerinids began to build up extensive deposits of deep-sea ooze. Many genera, including all the larger foraminifera, and most of the planktonic species, became extinct at the end of the Cretaceous period, whereas smaller benthic species were relatively little affected.

Although only a few, simple, planktonic species survived the massive extinction at the Mesozoic/Tertiary boundary,

they rapidly evolved to fill vacant ecological niches and build up deposits of deep-sea ooze during the Palaeocene and their continued development through the Cenozoic has been used to such effect in stratigraphy that they are known as the 'ammonites of the Tertiary'. The Tertiary is also characterized by the adaptive radiation of the rotaliids which become the dominant group with a number of lines of rock-forming, larger foraminifera prominent at times of global warming, particularly during the Eocene (nummulites) and early Miocene (miogypsinids). Another family of giant alveolines also appeared in the Eocene. Apart from the microgranular fusulinids, all the major wall structure groups have survived to the present day. However, there are no annular complex genera (orbitoids) and the dominant larger foraminifera are discoid and fusiform porcelaneous genera.

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