

# MICROFOSSILS

## Microfossils – what are they?

Any dead organism that is vulnerable to the natural processes of sedimentation and erosion may be called a **fossil**, irrespective of the way it is preserved or of how recently it died. It is common to divide this fossil world into larger **macrofossils** and smaller **microfossils**, each kind with its own methods of collection, preparation and study. This distinction is rather arbitrary and we shall largely confine the term (**microfossil**) to those discrete remains whose study requires the use of a microscope throughout. Hence bivalve shells or dinosaur bones seen down a microscope do not constitute microfossils. The study of microfossils usually requires bulk collecting and processing to concentrate remains prior to study.

The study of microfossils is properly called micropaleontology. There has, however, been a tendency to restrict this term to studies of **mineral-walled microfossils** (such as **foraminifera** and **ostracods**), as distinct from **palynology** the study of organic-walled microfossils (such as pollen grains, dinoflagellates and acritarchs). It must be emphasized that micropaleontology, micropalaeontology and palynology share identical aims: to unravel the history of life and the external surface of the planet. These are achieved more speedily and with greater reward when they proceed together.

## Why study microfossils?

Most sediments contain microfossils, the kind depending largely on the original age, environment of deposition and burial history of the sediment. At their most abundant, as for example in back-reef sands, (10 cm<sup>3</sup>) of sediment can yield over (10,000) individual specimens and over (300) species. By implication, the number of ecological niches and biological generations represented can extend into the hundreds and the sample may represent thousands if not hundreds of thousands of years of accumulation of specimens.

By contrast, macrofossils from such a small sample are unlikely to exceed a few tens of specimens or generations. Because microfossils are so small and abundant (mostly less than 1 mm) they can be recovered from small samples. Hence when a geologist wishes to know the age of a rock or the salinity and depth of water under which it was laid down, it is to microfossils that they will turn for a quick and reliable answer. Geological surveys, deep sea drilling programmes (DSDP), oil and

mining companies working with the small samples available from borehole cores and drill cuttings have all therefore employed micropaleontologists to learn more about the rocks they are handling. This commercial side to micropaleontology has been a major stimulus to its growth. There are some philosophical and sociological sides to the subject, however. Our understanding of the development and stability of the present global ecosystem has much to learn from the microfossil record, especially since many microfossil groups have occupied a place at or near to the base of the food web. Studies into the nature of evolution cannot afford to overlook the microfossil record either, for it contains a wealth of examples. The importance of understanding microfossils is further augmented by discoveries in Precambrian rocks; microfossils now provide the main evidence for organic evolution through more than three-quarters of the history of life on Earth. It is also to microfossils that science will turn in the search for life on other planets such as Mars.

### **The stratigraphical column:**

**The succession of rocks exposed at the surface of the Earth** can be arranged into a stratigraphical column, with the oldest rocks at the base and the youngest ones at the top (Fig. 1). Although the absolute ages have been determined from studies of radioactive isotopes, it is customary to use the names of **stratigraphical units**, mostly distinguished on the basis of differences in their included fossils. These units are arranged into a number of hierarchies relating to rock-based stratigraphy (**lithostratigraphy**), fossil-based stratigraphy (**biostratigraphy**) and time-based stratigraphy (**chronostratigraphy**).

**Lithostratigraphical units**, such as **beds, members and formations**, are widely used in geological mapping but will not concern us further here. The **biozone** is the **fundamental biostratigraphical unit and comprises those rocks that are characterized by the occurrence of one or more specified kinds of fossil** known as zone fossils.

Formal chronostratigraphical time units are also important and include, in ascending order of importance, the age, epoch, period and era. For example we may cite the Messinian Age, of the Miocene Epoch, of the Neogene Period, of the Cenozoic Era. Rock units laid down during these times are properly referred to as stages, series, systems and erathems (i.e. the Messinian Stage, of the Miocene Series, etc.). Less formal divisions are also widely used so that we may talk of the lower Neogene rocks laid down during Early Neogene times. In the following text, these informal subdivisions are abbreviated as follows: lower (L.), middle (M.) and upper (U.) and their equivalents for chronostratigraphy early (E.), middle and late.

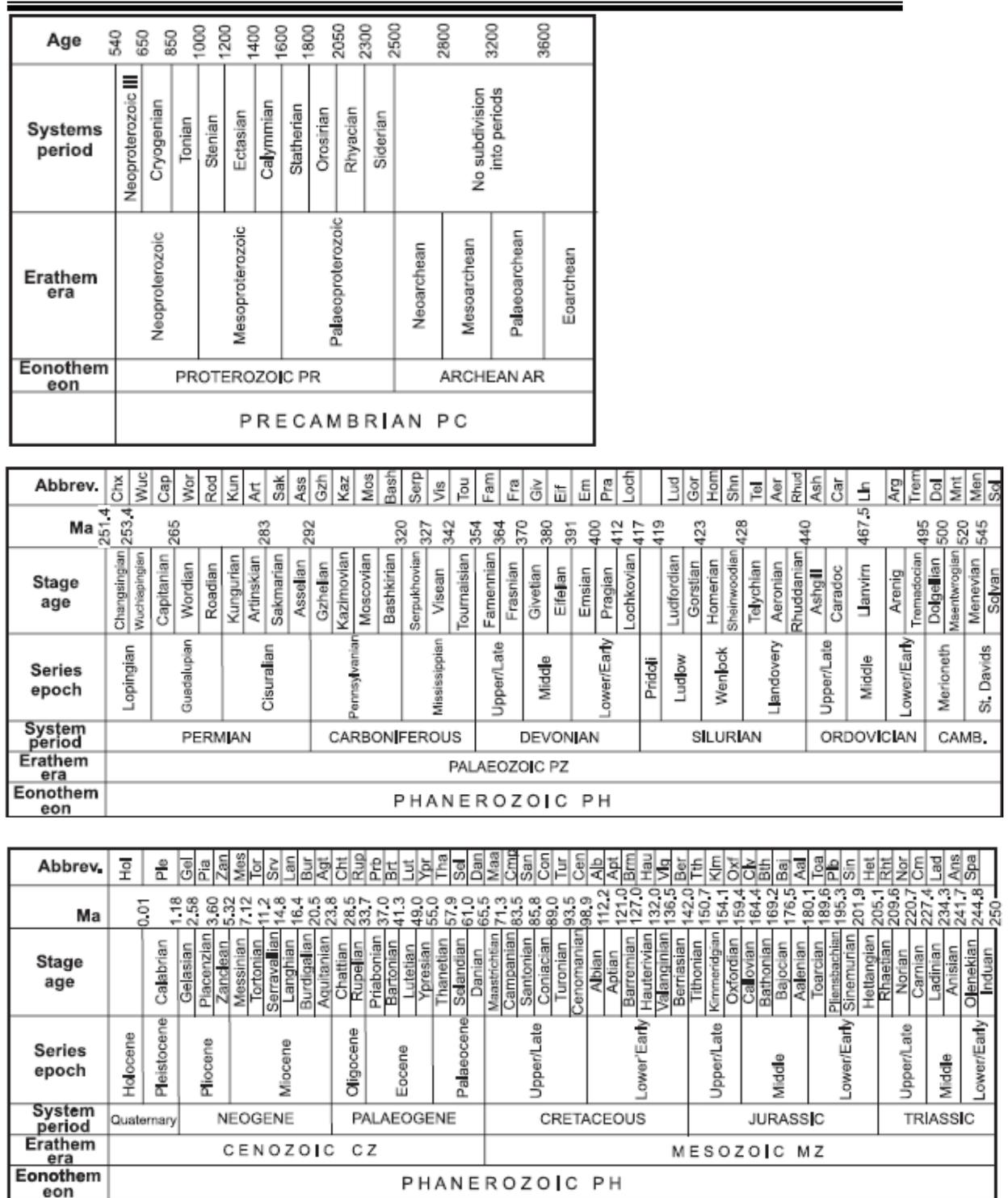


Figure (1) the stratigraphical column

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**Microfossils and biostratigraphy:**

**Biostratigraphy** is the **grouping of strata into units based on their fossil content with the aim of zonation and correlation**. As such biostratigraphy is concerned primarily with the identification of taxa, tracing their lateral and vertical extent and dividing the geological column into units defined on their fossil content.

Microfossils are among the best fossils for biostratigraphical analysis because they can be extremely abundant in rocks (a particular consideration when dealing with drill cuttings) and they can be extracted by relatively simple bulk processing methods. Many groups are geographically widespread and relatively free from facies control (e.g. plankton, airborne spores and pollen). Many of the groups evolved rapidly, allowing a high level of subdivision of the rock record and a high level of stratigraphical resolution. It should also be emphasized that spores, pollen, diatoms and ostracodes are indispensable for the biostratigraphy of terrestrial and lacustrine successions, where macrofossils can be scarce.

Detailed biostratigraphical zonations, using the groups mentioned here, have been developed for the entire Phanerozoic. Some areas of the column are better subdivided than others, for example the Cretaceous to Recent can be subdivided into approximately 70 biozones, based on calcareous nannoplankton and planktonic foraminifers, with an average duration of 2 million years per biozone. In comparison the Lower Palaeozoic has only been divided into 39 conodont biozones at an average duration of 3 million years.

The basic unit of biostratigraphy is the biozone and fossils that characterize and give their names to a particular biozone are called zone or index fossils, for example the *Orbulina universa* Biozone of the Miocene.

There are three basic types of biozone: the assemblage, abundance and interval biozones (Fig. 2). An assemblage biozone is based on the association between three or more species with little regard to the stratigraphical range of each. As species associations are strongly dependent upon local ecology, this type of biozone is most suitable for local or intra-basinal applications. The majority of defined biozones are interval biozones based upon the first appearance datum (FAD) and last appearance datum (LAD) of the named species. There are five types of interval biozone (Fig. 2); the most commonly used being the local range zone and the concurrent range zone. The latter comprises that interval which lies above the FAD of one species and below the LAD of a second species.

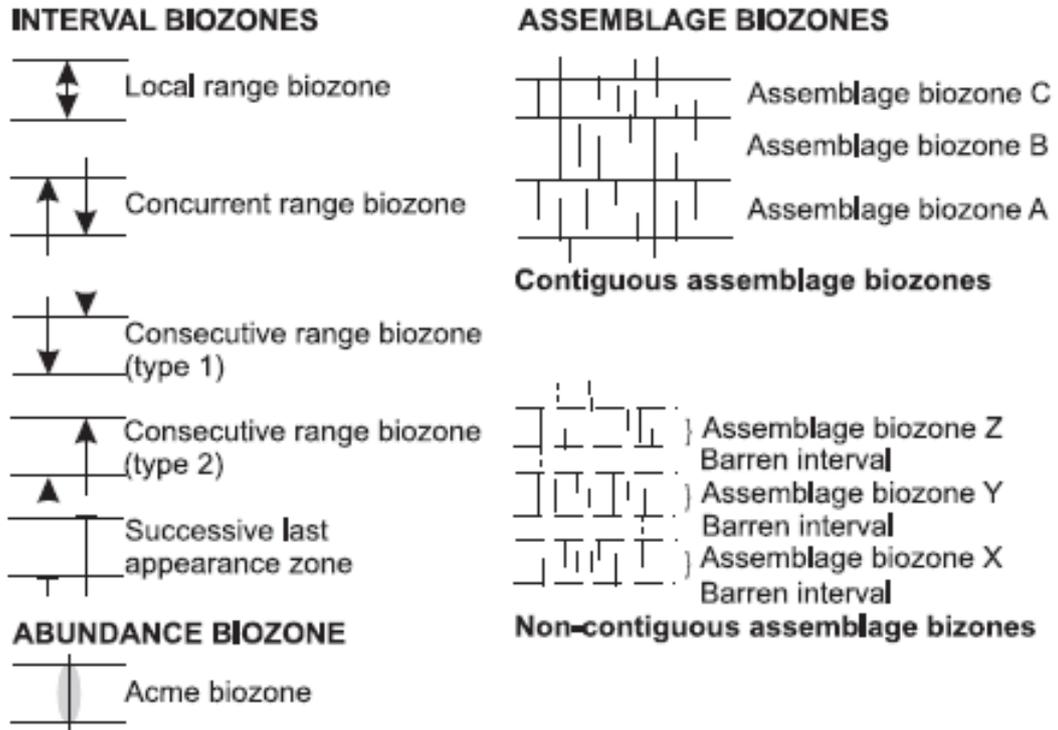


Figure (2) categories of biozones.

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## Foraminifera:

The foraminifera are an important order of single-celled protozoa that live either on the sea floor or amongst the marine plankton. The soft tissue (cytoplasm) of the foraminiferal cell is largely enclosed within a shell or test (Fig. 3A) variously composed of secreted organic matter (tectin), secreted minerals (calcite, aragonite or silica) or of agglutinated particles. This test consists of a single (unilocular) chamber or multiple (multilocular) chambers mostly less than 1 mm across and each interconnected by an opening, the foramen, or several openings (foramina). The group, which takes its name from these foramina, is known from Early Cambrian times through to recent times, and has reached its acme during the Cenozoic.

Foraminiferal tests can be very abundant; in the modern ocean they comprise over 55% of Arctic biomass and over 90% of deep sea biomass. In marine sediments, foraminiferal tests typically vary from a few individuals per kilogram to rock-forming *Globigerina* ooze and Nummulitic limestone.

Foraminifera are important as biostratigraphical indicators in marine rocks of Late Paleozoic, Mesozoic and Cenozoic age because they are **abundant, diverse and easy to study.**

Planktonic foraminifera are widespread and have had rapidly evolving lineages, factors which greatly aid the inter-regional correlation of strata in the Cretaceous (28 zones), Paleogene (22 zones) and Neogene (20 zones). Smaller benthic foraminifera are the most common and are widely used for regional stratigraphy.

Larger benthic foraminifera are typically larger than (2 mm) in diameter and (3 mm<sup>3</sup>) in volume and have complex internal structures which, when studied in thin section, are useful for the biostratigraphy of Tethyan and other tropical limestone.

Foraminifera have a wide environmental range, from terrestrial to deep sea and from polar to tropical. Ecological sensitivity renders the group particularly useful in studies of recent and ancient environmental conditions. Changes in the composition of foraminiferal assemblages may be used to track changes in the circulation of water masses and in sea-water depth. They are especially important in studies of Mesozoic to Quaternary climate history.

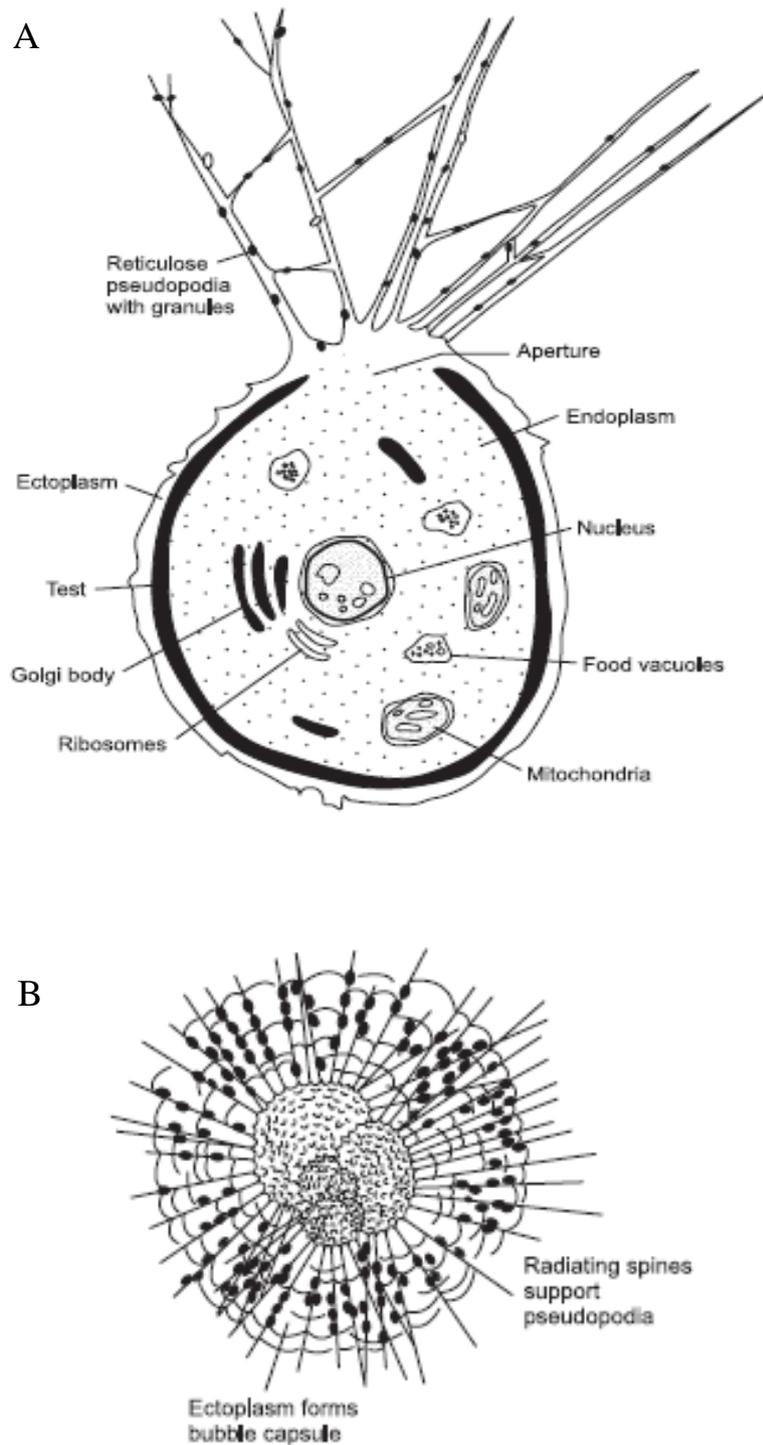


Figure (3) (A) A living, single-chambered benthic foraminifera, as seen in cross-section with transmitted light. (B) A living multichambered planktonic foraminifera surrounded by radiating spines and pseudopodia (not all drawn) which support photosymbionts and frothy ectoplasm of the bubble capsule as seen in transmitted light.

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## Living foraminifera:

### The cell

The cytoplasm of foraminifera comprises a single-cell differentiated into an outer layer of clear ectoplasm and an inner layer of darker endoplasm (Fig. 3A). The ectoplasm forms a thin and extremely mobile film around the test which gives rise to fans of numerous, finely branching granular and reticulate pseudopodia whose form is ever changing. Foraminifera feed by trapping and engulfing small organisms and organic particles with these sticky pseudopodia, which are used to draw in the food material towards the test and later to expel it. Food requirements vary between species but include bacteria, diatoms and other protozoa, small crustaceans, mollusks and invertebrate larvae.

A few foraminifera are thought to be parasitic. Pseudopodia are further employed, in benthic forms, as a means of pulling the test along and for anchorage. The ectoplasm is connected with the inside of the test by means of an aperture, which acts as the 'front door' for the passage of cytoplasm, food, excretory products and reproductive cells.

### The test

The test is thought to reduce biological, physical and chemical stress. Biological pressures include, for example, the risk of accidental ingestion by worms, crustaceans, gastropods, echinoderms and fish that deposit feed or browse on detritus on the sea floor.

Others, such as gastropods, actually prey upon benthic foraminifera, while the tests may also risk being infested by parasitic nematode worms. Physical stresses include harmful radiation (including ultraviolet light) from the Sun, water turbulence and abrasion. Test strength is therefore likely to be important. Chemical stresses encompass fluxes in salinity, pH, CO<sub>2</sub>, O<sub>2</sub> and toxins in the water. In all these cases, the cytoplasm can withdraw into the inner chambers leaving the outer ones as protective 'lobbies', or a detrital plug may close the aperture.

Additional advantages of the test include the negative buoyancy it gives to a group of organisms especially adapted to a benthic way of life. Surface sculpture may variously assist positive buoyancy in planktonic forms (e.g. spines and keels), improve adherence, and strengthen the test against crushing.

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## Wall structure and composition

The structure and composition of the test wall is important to the classification of the group. **Organic-walled** forms belong to the **suborder Allogromiina**. These have a thin, non-rigid test of proteinaceous or pseudochitinous matter generally termed tectin (Fig. 4). Similar material is also present as a thin lining to the chambers of most hard tested foraminifera, where it may act as a template for mineralization. The **suborder Textulariina** encompasses forms with **agglutinated** tests. In these, organic and mineral matter from the sea floor is bound together by an organic, calcareous or ferric oxide cement (Fig. 4). The grains are commonly selected for size, texture or composition (e.g. coccoliths, sponge spicules and heavy minerals). Tests of the **suborder Fusulinina** are **microgranular** and appear dark in thin section when viewed with transmitted light and opaque (usually brown or grey) when viewed in reflected light. The micro granules may be packed randomly or aligned normal to the surface of the test and interspersed with mural pores, thereby giving the wall a fibrous appearance (Fig. 4), especially in more advanced forms. These granular and fibrous layers of microgranular calcite are often combined in the structure of a single, multilayered wall. **Calcareous** tests are by far the most abundant and occur in all the remaining suborders. There are three main types of calcareous wall:

- 1- **Porcelaneous Imperforate.**
- 2- **Microgranular.**
- 3- **Hyaline perforate.**

Porcelaneous imperforate tests are characteristic of the **suborder Miliolina**. These lack mural pores and are a distinctive milky white in reflected light and an amber colour in transmitted light. They are constructed of tiny needles of high magnesium calcite randomly arranged for the most part, but the outer and inner surfaces are coated with a layer of horizontally arranged needles (Fig. 4). A single taxon of the Miliolina, *Miliammellus*, has a comparable wall constructed of needles of opaline silica. In the Miliolina, the test is built by the secretion of biomineral needles within tiny vesicles in the cytoplasm, which are then exported to the outer margin of the cell. In the remaining suborders, a tectinous template is laid down first, upon which carbonate is then precipitated.

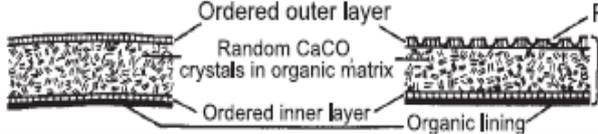
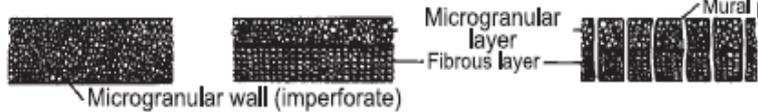
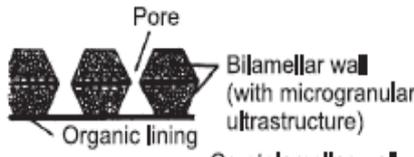
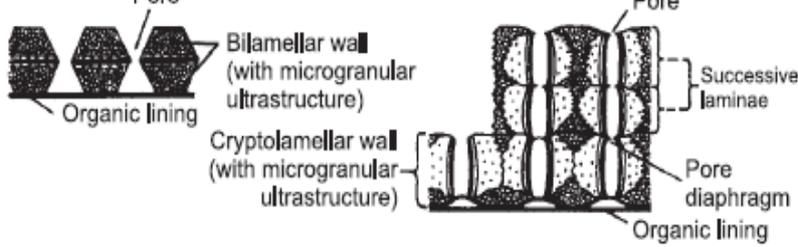
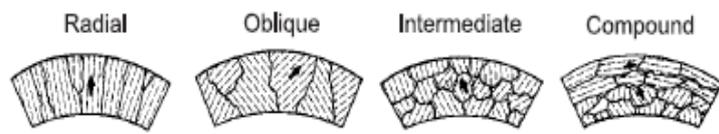
	Wall Structure	Suborder
Tectinous	 Loosely attached grains Flexible, thin and tectinous	Allogromiina
Agglutinated	 Agglutinated wall Organic lining Alveoli (labyrinthic wall)	Textulariina
Porcelaneous	 Ordered outer layer Random CaCO <sub>3</sub> crystals in organic matrix Ordered inner layer Organic lining Pseudopunctae	Miliolina
Microgranular + Microgranular compound	 Microgranular wall (imperforate) Microgranular layer Fibrous layer Mural pore	Fusulinina
	 Pore Organic lining Bilamellar wall (with microgranular ultrastructure)	Globigerinina Spirillinina
	 Pore Organic lining Cryptolamellar wall (with microgranular ultrastructure) Pore diaphragm Successive laminae	Involutinina (arag) Robertinina (arag)
Hyaline	 Radial Oblique Intermediate Compound	Rotallina

Figure (4) examples of wall structures in the foraminifera (diagrammatic, mainly based on studies using scanning electron microscopy).

### Test growth

Feeding adds continually to the bulk of the cytoplasm. In related testate amoebae, which live for only 2–4 days, the test is not enlarged and consists of a single chamber (unilocular).

In foraminifera, which generally live for between 1 month and several years, several strategies for test enlargement have arisen. The tests of many primitive foraminifera are unilocular, although test form varies greatly (Fig. 5 a, c). Such tests may be said to show contained growth because there is little or no capacity for enlargement. The foraminifera must therefore expend energy in rebuilding the wall, vacate the test and grow a new one. These limitations of contained growth have been overcome in some primitive lineages by the addition of a second tubular chamber, which shows continuous growth (Fig. 5 d–j). Such simple forms

predominated in the lower Paleozoic but can still be found today, especially in marginal marine and abyssal habitats. Unilocular tests are also found in modern parasitic forms.

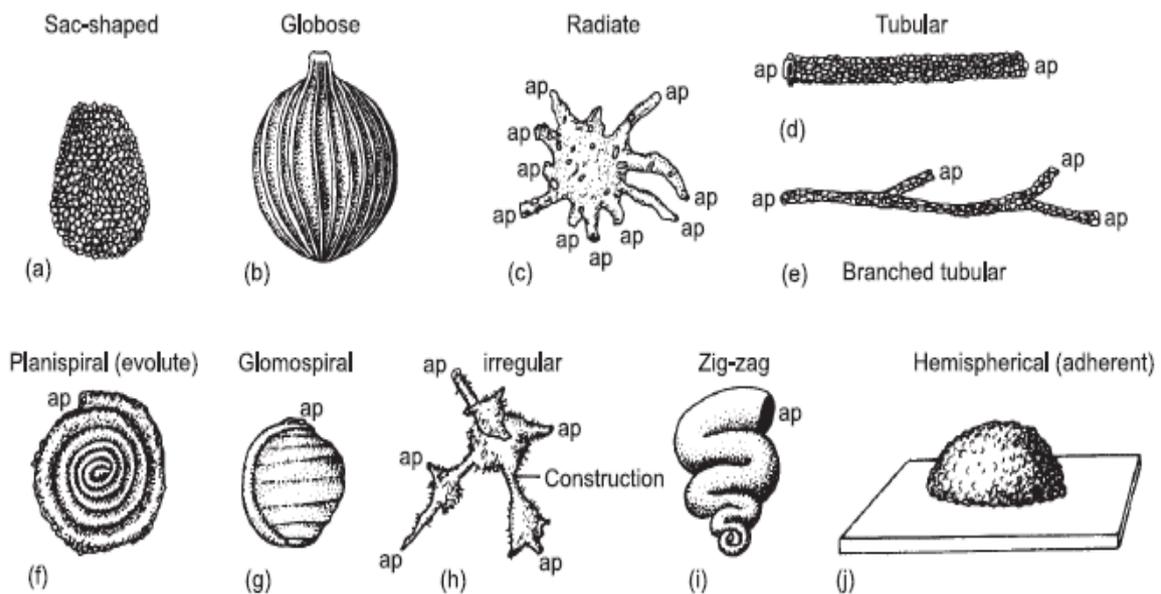


Figure (5) unilocular and bilocular tests. (a) Pleurophrys  $\times 200$ . (b) Lagena  $\times 53$ . (c) Astrorhiza  $\times 49$ . (d) Bathysiphon  $\times 7$ . (e) Rhizammina  $\times 12$ . (f) Ammodiscus  $\times 17$ . (g) Usbekistania  $\times 66$ . (h) Aschemonella  $\times 3$ . (i) Ammovertella about  $\times 2$ . (j) Hemisphaerammina about  $\times 16$ ; ap. = aperture.

In multilocular forms (Fig. 6) protoplasmic growth is gradual but test growth is periodic, with a new and larger chamber being added at regular intervals. Each chamber is provided with a distinct apertural face (septum) that confines the aperture and improves protection of the endoplasm. Chamber addition begins with the construction of a loosely bound growth cyst, composed largely of food debris.

The pseudopodia are then withdrawn to occupy the space of the new chamber, building first a thin organic wall and then an agglutinated or calcareous one on the outer side, or on both sides. This simple septate growth condition is predominant today, being found in planktonic foraminifera and many smaller benthic foraminifera.

In complex septate growth, the chambers' shape is greatly modified and the chambers may be subdivided by partitions into chamberlets which have multiple apertures. This condition is typically found in larger benthic foraminifera which have photosymbionts.

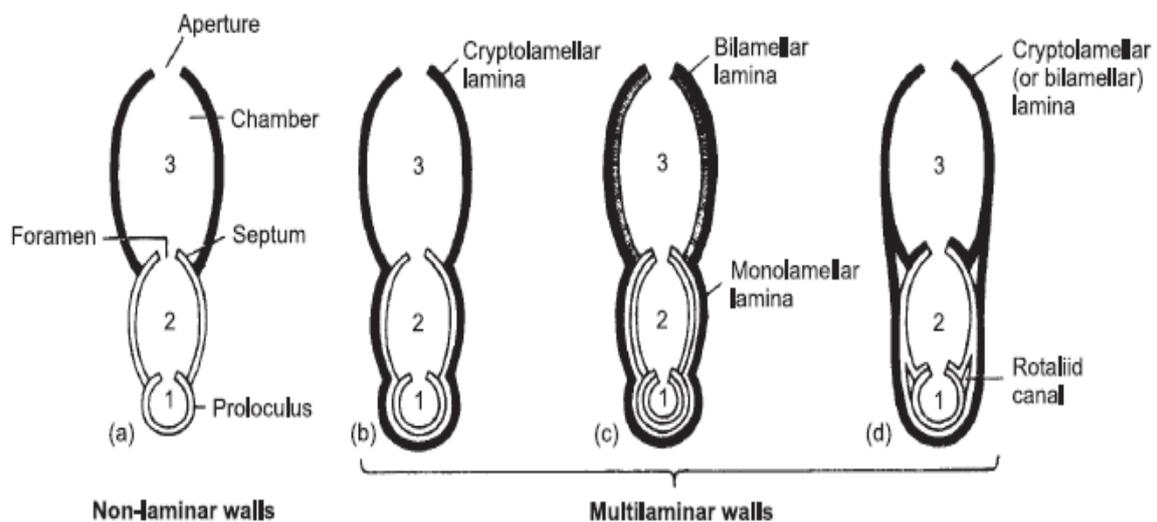


Figure (6) diagrammatic axial sections illustrating different modes of chamber addition. (a) Non-laminar. (b) Multilaminar cryptolamellar. (c) Multilaminar, monolamellar-bilamellar. (d) Multilaminar, cryptolamellar, with septal flaps and canals. The uniserial growth is shown here for simplicity.

### Wall ultrastructure

Foraminifera can have either lamellar (Fig. 6 a) or multilamellar ultrastructure (Fig. 6 b–d). In hyaline perforate forms, septate growth can bring about changes in the fine structure of the test when seen in thin section. Where there is no overlap of previous chamber walls by the new wall, the arrangement is termed **non-laminar** (Fig. 6 a). This is the typical arrangement in non-hyaline, imperforate foraminifera.

**Monolamellar** structure occurs where each chamber is composed of a single layer which also overlaps previous chambers (Fig. 6 b), as in the finely perforate suborder Lagenina. In the majority of hyaline forms, multilamellar ultrastructure (Fig. 6 b–d) is seen.

Each chamber wall is here composed of two distinct lamellae of calcite (i.e. **bilamellar**, Fig. 6 c) on either side of a tectin membrane, of which only the outer lamella coats previous chambers. Multilamellar ultrastructure has the advantage of increasing the strength of the test with growth. It also allows the development of complex architecture not seen in non-hyaline groups, such as the spines of planktonic foraminifera. In the suborder Rotaliina, the inner lamella also coats the previous apertural face and forms a septal flap together with a space called a rovaliid canal (Fig. 6 d). Such canal systems provide for the rapid extrusion of cytoplasm during chamber construction and reproduction.

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## Chamber architecture

Foraminiferid tests may appear to represent a bewildering array of modes of growth. Although the variation is remarkable, it is possible to impose a degree of order by recognizing that most multilocular test types arise as the result of interaction among three variables during growth: **the rate of translation** (i.e. the net rate of movement along the growth axis to the net movement away from the growth axis), **the rate of chamber expansion** and **the chamber shape** (Fig. 7).

Different rates of translation produce the four common growth plans of the foraminiferid test: **planispiral**, **trochospiral**, **biserial** and **uniserial**. In **planispiral tests** the rate of translation is zero, the chamber or chambers being arranged more or less symmetrically in a plane coil about the growth axis. This growth plan may be further modified by different rates of chamber overlap towards the coiling axis (e.g. evolute to involute form) and in involute forms by an extension of growth along the coiling axis (e.g. discoidal to fusiform; Fig. 7).

Where material is added in a helical coil the test is called **trochospiral**. Such tests have a spiral side and an umbilical side, which are more evolute and more involute respectively (Fig. 8 a). In multilocular tests, a successive decrease in the spiral angle may ultimately bring about a reduction in the number of chambers per whorl to three (triserial), although triserial and biserial forms with wide spiral angles are known. Further reduction may obscure or eliminate the spiral component resulting generally in biserial and uniserial growth plans (i.e. two and one chamber per whorl respectively, Fig. 7). Some of these arrangements may be found together in one test, with developmental changes from planispiral or triserial to uniserial.

## Chamber shape

The rate of chamber expansion may be defined as the rate of increase in volume (or of width, length or depth) from one chamber to the next. In most foraminifera this remains a fairly constant logarithmic trend, at least through early ontogeny. However, the number of chambers per whorl in a species can change through life or between localities and is therefore an unreliable taxonomic character.

Chamber shape varies widely. Unilocular tests may be flask-shaped, globose, tubular, branched, radiate or irregular (Fig. 5). Although the chambers of multilocular forms generally remain of constant shape through ontogeny, their arrangement and ornament can vary. Common shapes include globular, tubular and wedge-shaped.

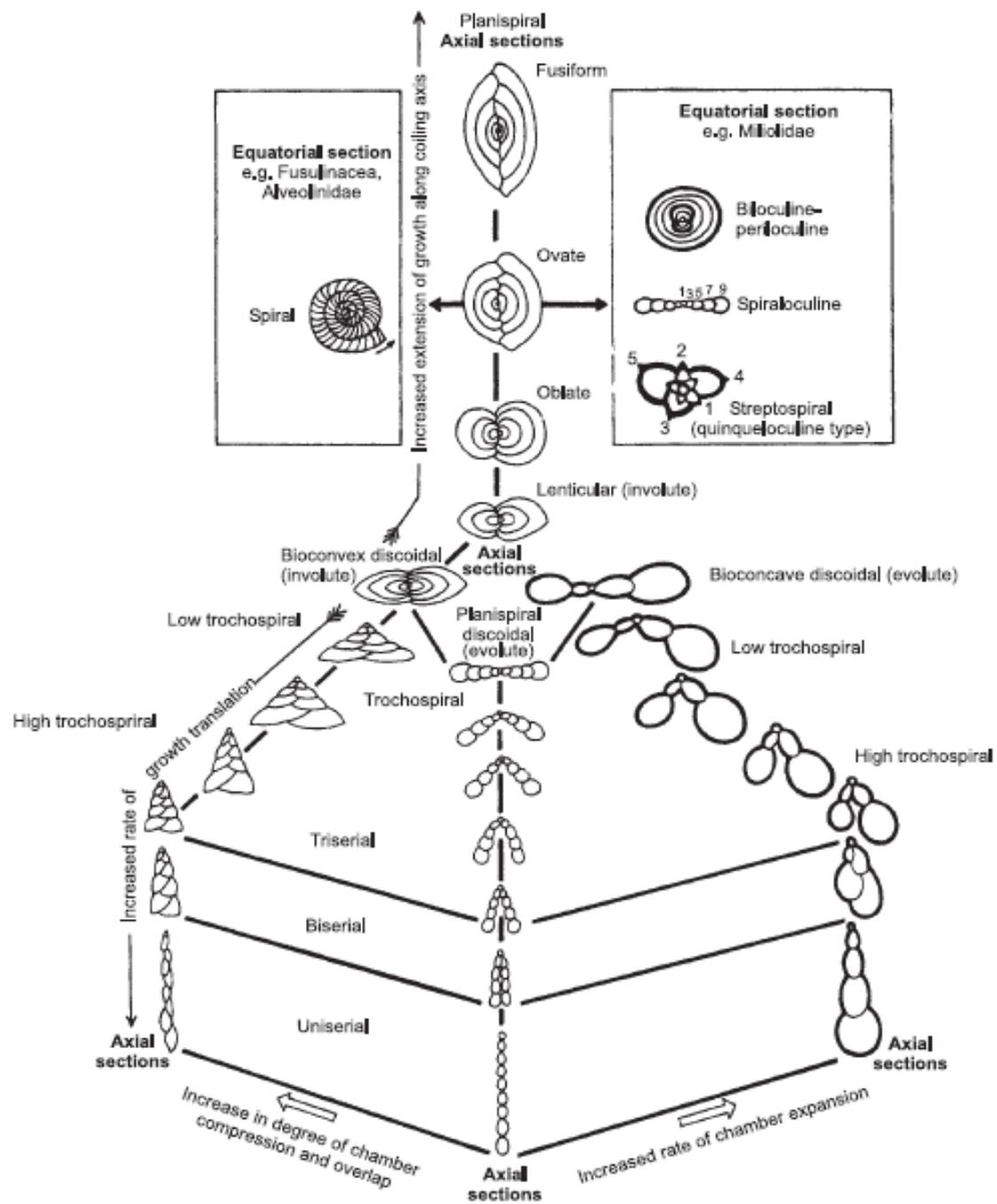


Figure (7) the main growth forms in multilocular tests of foraminifera. Axial sections are those cut parallel to and including the main axis of symmetry and growth. Equatorial sections are cut at right angles to this axis, at the widest point on the test.

**Apertures and foramina**

The aperture is found in the wall of the final chamber and serves to connect the external pseudopodia with the internal endoplasm, allowing passage of food and contractile vacuoles, nuclei and the release of the daughter cells. Its position remains more or less constant through ontogeny so that each chamber is linked to the next by a foramen or several foramina (Fig. 6). In forms that lack apertures, foramina may be secondarily developed by resorption of the chamber wall.

The primary aperture(s) may be single or multiple in number and terminal, areal, basal, extraumbilical or umbilical or in position (Fig. 8). Their shape varies widely, for example rounded, bottle-necked (phialine), radiate, dendritic, sieve-like (cribrate), cruciform, slit- or loop-shaped. Apertures can be further modified by the presence of an apertural lip or flap (termed a labiate aperture, Fig. 8 c), teeth (dentate aperture, Fig. 8 e), a cover plate (bullate aperture, Fig. 8 f ) or an umbilical boss (Fig. 8 g). Secondary apertures may also be added, for example along the sutures or the periphery of the test (Fig. 8 d). Such apertural and foraminal structures are used for classification, especially below the subordinal level.

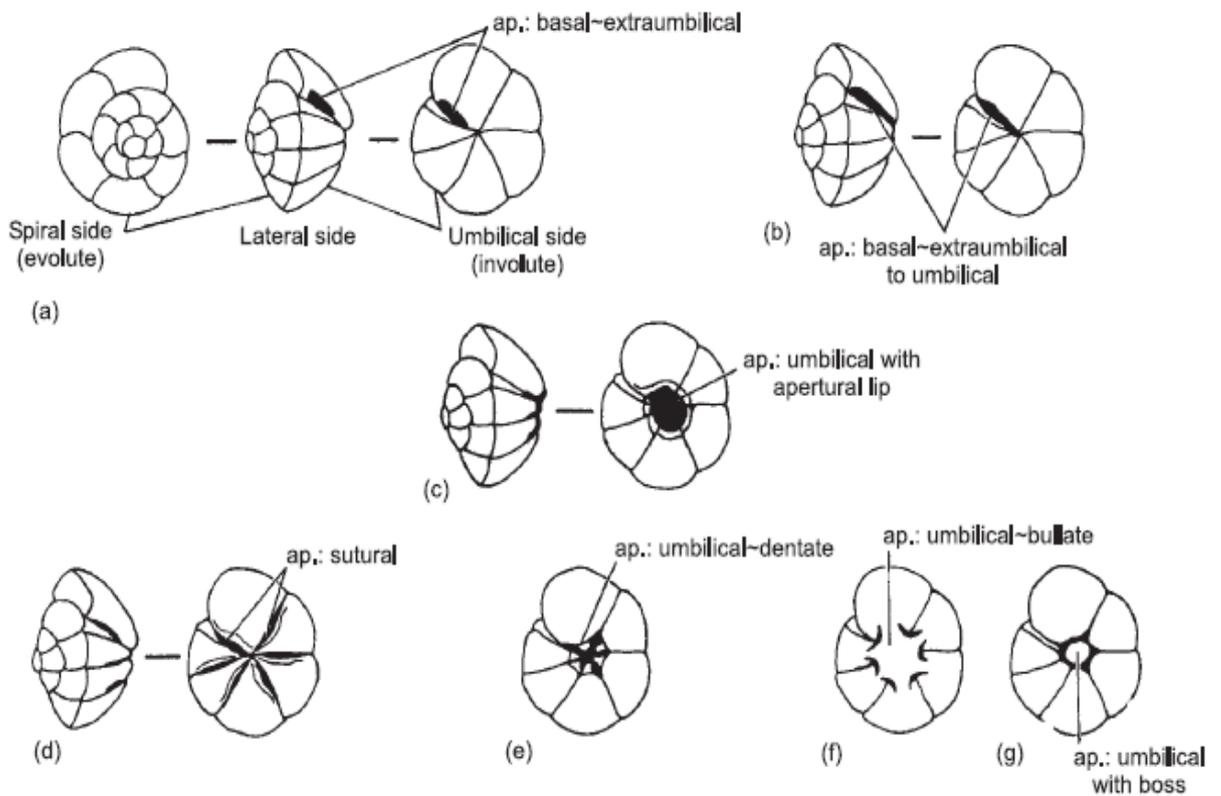


Figure (8) (a) – (g) Trochospiral tests with different kinds of aperture (ap).

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## Sculpture

The external surface of the test may bear spines (termed spinose), keels (carinate), rugae (rugose), fine striae (striate), coarser costae (costate), granules (granulate) or a reticulate sculpture. These features should be used with caution in distinguishing certain genera and species for they vary through ontogeny and with environment.

## Foraminiferal ecology

### 1- Smaller benthics

About 5000 species of living smaller benthic foraminifera are known. They are especially important as environmental indicators because they have colonized marine habitats from the most extreme tidal marshes to the deepest trenches of the oceans. Exploitation of resources across this wide range of habitats is reflected in adaptations of test morphology.

#### Light:

The zone of light penetration in the oceans (the photic zone) is affected by water clarity and the incident angle of the Sun's rays. Hence the photic zone is deeper in tropical waters (<200 m) and decreases in depth towards the poles where it also varies with marked seasonality. Primary production by planktonic and benthic protozoa, and the protection and substrates provided by algae and sea grasses, render this zone attractive to foraminifera, especially the Miliolina. The porcelaneous wall of miliolines such as *Quinqueloculina* is thought to protect the cytoplasm from damage in shallow equatorial waters by scattering the short wavelength, ultraviolet light.

#### Food:

Foraminifera play a prominent role in marine ecosystems as micro-omnivores, i.e. they feed on small bacteria, protozoa and invertebrates. Epifaunal forms living in the photic zone feed especially upon diatoms so that their numbers may fluctuate in relation to the seasonal cycle. These often have tests that are flattened on one or both sides. Some smaller benthic forms are known to culture photosymbionts. Others live infaunally within the sediment or below the Photic zone and feed on dead organic particles or graze upon bacteria. The tests of active forms tend to be lenticular or elongate. Those living on the abyssal plains, such as *Bathysiphon* may extend their pseudopodia into the water column to capture the seasonal rain of phytodetritus. Such forms tend to have erect,

tubular, often branched, tests that are fixed to the substrate. Some hyaline foraminifera have degenerate unilocular tests and may lead a parasitic mode of life.

**Substrate:**

Those foraminifera which prefer hard substrates (i.e. rock, shell, sea grasses and algae) are normally attached, either temporarily or permanently, by a flat or concave lower surface. Typical growth forms are hydrodynamically stable and include discoidal, plano-convex, concavo-convex, dendritic and irregular shapes. Adherent forms often develop a relatively thin test and will tend to exhibit greater morphological variability than seen in sediment-dwelling and planktonic forms.

Although foraminifera have been found living up to 200 mm below the sediment surface, the majority is found within the top 10 mm or lives at the surface. The larger pore spaces of higher-energy sands and gravel of the inner shelf may only support sparse populations. Foraminifera from these coarser substrates tend to be either adherent forms or free-living and thick-shelled, heavily ornamented forms of lenticular or globular shape.

Low-energy habitats with silty and muddy substrates typical of lagoons, and the mid-shelf to bathyal slope, are often rich in organic debris and the small pore spaces tend to encourage bacterial blooms. Such substrates are therefore attractive to free-living foraminifera and can support large but patchy populations.

Many of the infaunal species are thin-shelled, delicate and elongate; their activities can produce minute burrow systems.

**Salinity:**

The majority of foraminifera are adapted to normal marine salinities (about 35‰) and the highest diversity assemblages are found here. The low salinity of brackish lagoons and marshes favors low-diversity assemblages of agglutinated foraminifera, and certain hyaline forms. The tectinous imperforate *Allogromiina* are also found in fresh and brackish waters, but their delicate tests are rarely encountered as fossils. The high carbonate ion concentrations of hypersaline waters, where salinities are in excess of (40‰), appear to favor the porcelaneous *Miliolina* but deter most other groups.

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**Nutrients and oxygen:**

The biolimiting nutrients of phosphate and nitrate exert considerable control over the rates of primary productivity in seas and oceans.

Where the rates of food supply are low, as in the deep sea, foraminiferal densities tend to be low ( $<10/10 \text{ cm}^2$ ) but diversity can be high. In upwelling zones where rates of nutrient supply to the surface are high, foraminiferal diversities tend to be reduced for several reasons. High rates of nutrient flux tend to discourage photosymbiosis, so that planktonic and larger benthic foraminifera which culture symbionts and other oligotrophic species are discouraged. High rates of primary production at the surface also lead to anaerobic bacterial blooms in the oxygen minimum zone of mid-waters and on the sea floor beneath. In anaerobic conditions, foraminifera may be scarce but in dysaerobic conditions eutrophic benthic foraminifera may dominate the biota, with densities over ( $1000/10 \text{ cm}^2$ ). Such assemblages are typified by small, thin-shelled, unornamented calcareous buliminaceans or primitive agglutinated forms. Oxygen deficiency does not entirely eliminate microscopic organisms such as foraminifera, presumably because of their low oxygen demand and the high diffusion rates associated with a high surface area–volume ratio.

**Temperature:**

Each species is adapted to a certain range of temperature conditions, the most critical being that range over which successful reproduction can take place. Generally, this range is narrowest for low latitude faunas adapted to stable, tropical climates. However, stratification of the oceans results in the lower layers of water being progressively cooler, as for example in tropical waters where the surface may average  $28^\circ\text{C}$  but the bottom waters of the abyssal plains may average less than  $4^\circ\text{C}$ . These cooler, deeper waters are characterized by cool-water benthic assemblages that otherwise are found at shallower depths nearer the Poles (Fig. 9).

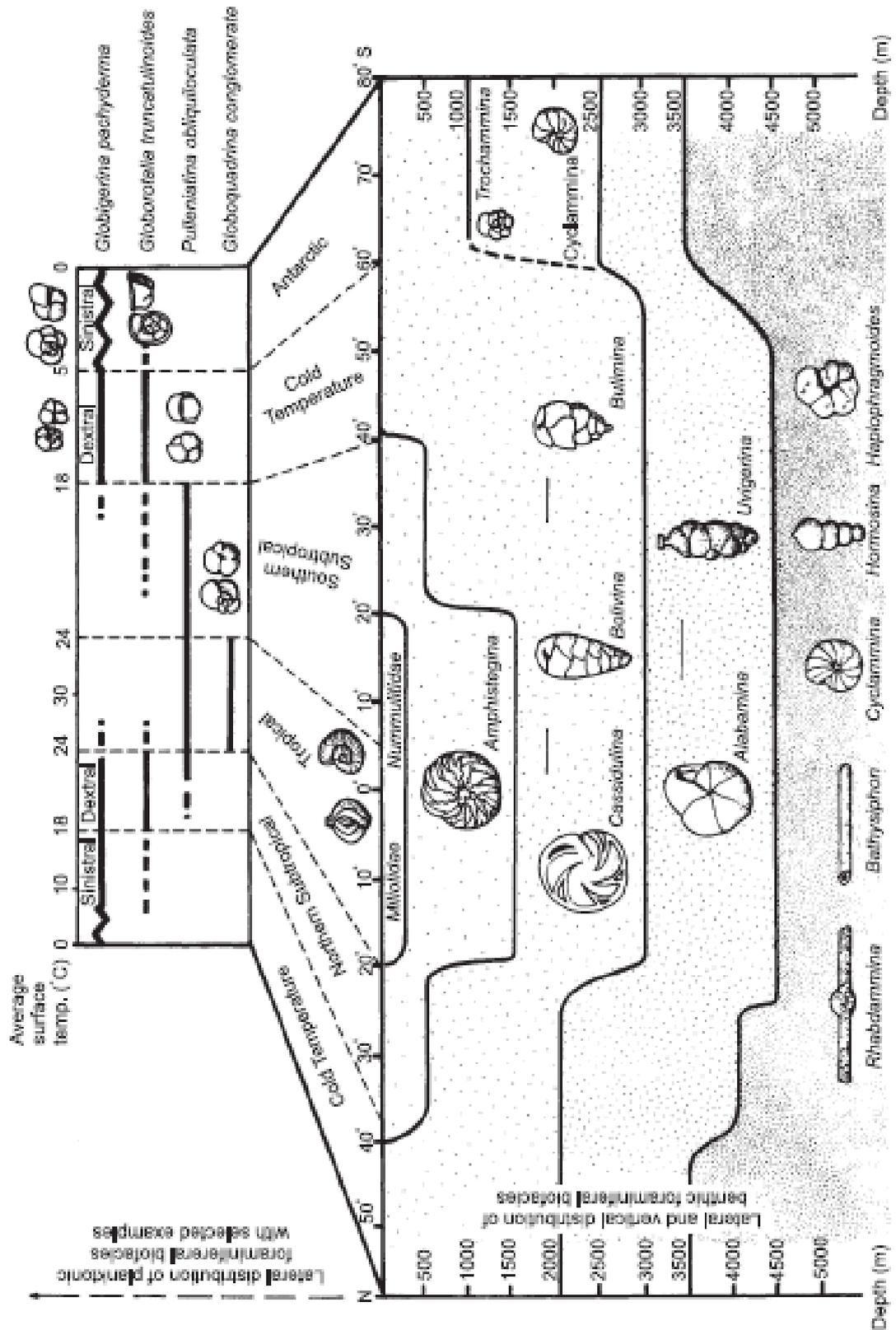


Figure (9) how benthic and planktonic assemblages (and some typical taxa) change with depth and latitude in the Pacific Ocean, especially in relation to temperature.

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## 2- Larger benthics

Larger benthic foraminifera are living largely in oligotrophic reef and carbonate shoal environments where terrestrial and seasonal influences are slight. They culture endosymbiotic diatoms, dinoflagellates, rhodophytes or chlorophytes, in much the same way as do the hermatypic corals. These endosymbionts release photosynthates to their hosts and also take up respiratory CO<sub>2</sub> during photosynthesis, which allows for high rates of CaCO<sub>3</sub> precipitation during test growth. It follows that larger foraminifera are very sensitive to light levels. Many have their chambers partitioned into small chamberlets with translucent outer walls, which allow for more efficient culturing of the symbionts.

Some, such as *Amphistegina*, are known to increase their surface area–volume ratio (i.e. become flatter) and thin their outer walls with increasing water depth and decreasing light intensity.

Pillars of calcite that radiate through the test may even have functioned as fiber-optic lenses in fossil *Nummulites*. The depth distribution of living larger benthic foraminiferal taxa is also closely related to the light wave lengths required by their symbionts, from shallowest to deepest: *Archaias* (0–20 m, chlorophytes, red light); *Peneropolis* (0–70 m, rhodophytes, yellow light), *Amphistegina* (0–130 m, diatoms, blue light). It therefore appears that fossil larger benthic foraminifera, which have evolved repeatedly since the Carboniferous, have achieved their great size (up to 180 mm in Oligocene *Lepidocyclina*) and skeletal complexity through co-evolution with endosymbionts. Many larger foraminifera have adapted to a life in mobile carbonate sands and their tests are therefore robust and fusiform, conical or biconvex. Those reclining on sediments in the deeper part of the photic zone tend to be large and discoidal in shape. Forms adapted for adherence to sea grass or algal fronds tend to be small and flat or have robust spines for anchorage.

Large test size and rapid rates of growth mean that larger benthic foraminifera are major contributors to modern carbonate sedimentation, producing as much as 2800 g CaCO<sub>3</sub>/m<sup>2</sup> every year in modern tropical oligotrophic settings. Vast areas of carbonate ramp environments have also been colonized, and at times built up, by larger fossil foraminifera, especially during the Carboniferous and the Tertiary. Nummulitic sands, in particular, are important as hydrocarbon reservoirs in the Middle East, where they may host as much as 60% of the petroleum reserves of the planet.

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## Planktonic foram ecology

The environmental controls on planktonic foraminifera are much better understood than those for benthics, because the only major ecological factors here are temperature and salinity. Species are distributed in large latitudinal provinces showing some bipolar distribution with temperature as the dominant control. This characteristic has been of great value in estimating Quaternary sea-surface temperatures, from the fossil record of extant species.

### Depth and food

There are about 100 species of living planktonic foraminifera. They tend to be small (mostly <100  $\mu\text{m}$ ) and short lived (about 1 month) with tests that are adapted to retard sinking. Most modern species reproduce in the surface layers of the ocean. Towards the end of adult life, they sink slowly through the water column. Each species tends to end up in an oceanic layer of a particular temperature and density range.

Shallow species live mainly in the upper 50 m of the photic zone. Those forms that live in oligotrophic, central oceanic water masses feed on zooplankton, especially copepods. They supplement their diet by culturing dinoflagellate or chrysophyte photosymbionts. Long spines and globular chambers with high porosity (and hence low relative mass) may help to improve buoyancy, while secondary apertures may allow increased mobility of the symbionts. Intermediate species live mainly at 50–100 m (except as juveniles) and include spinose forms with symbionts adapted to oligotrophic waters and non-spinose forms without symbionts that are adapted to more eutrophic waters.

Deeper species living mainly below 100 m (except as juveniles) include forms with club-shaped (clavate) chambers or lack spines but bear keels that may help to retard the settling velocity.

These species are adapted to cooler, denser, more eutrophic water masses and hence have fewer buoyancy problems and consequently lower test porosity than those from warmer or shallower waters. Deep-water planktonic forms have to cope, however, with the effects of  $\text{CaCO}_3$  solution (due to higher pressure, lower pH and other factors) which may account for the extra crust of radial, hyaline calcite seen in some forms. Species that live below the photic zone are thought to scavenge the sinking phytodetritus.

## Temperature and latitude

Modern assemblages can be arranged into biogeographic provinces: Arctic; Subarctic; Transitional; Tropical; Subtropical; Transitional; Subantarctic; Antarctic (Fig. 10). A number of trends should be noted here. The distributions are bipolar, so that *Globorotalia truncatulinoides*, for example, is characteristic of both northern and southern subtropical waters. The number of endemic forms, and hence diversity, increases towards the tropics. Keeled forms (*Globorotalia* spp.), for example, are not found at higher latitudes in waters cooler than 5°C. Test porosity of shallow and intermediate species (e.g. *Orbulina universa*) also increases towards the equator, presumably in relation to the lower density of warmer water. In *Globigerina pachyderma*, subpolar and polar populations can be distinguished by a predominance of left- (sinistral) or right-handed (dextral) coiling (Fig. 9). Sinistral coiling tests have the aperture on the left when the spire is uppermost. The distribution of these assemblages shows a strong correlation with surface circulation pattern. The history of Quaternary oceanic and temperature fluctuations can therefore be determined from the distribution of planktonic foraminifera preserved in deep sea cores.

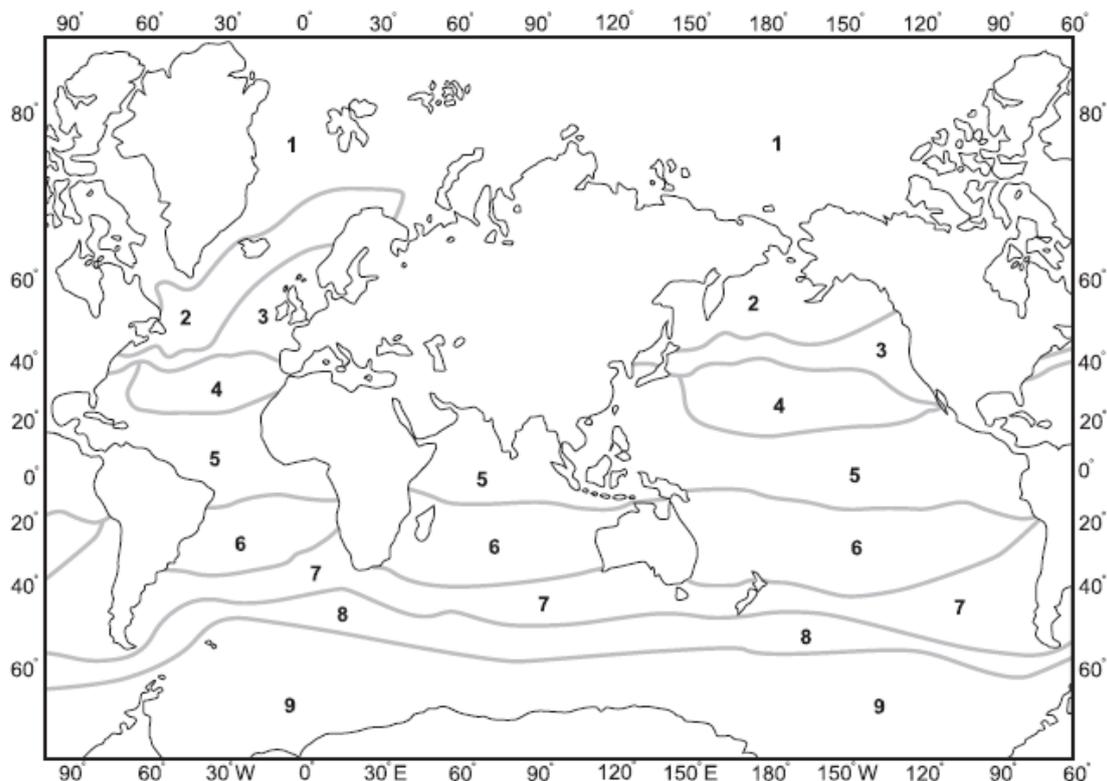


Figure (10) modern planktic foraminiferal provinces. 1, Arctic; 2, subarctic; 3, transitional; 4, subtropical; 5, tropical; 6, subtropical; 7, transitional; 8, subantarctic; 9, antarctic.

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## Calcite compensation depth (CCD)

The solubility of  $\text{CaCO}_3$  is less in warm than in cool waters. This in part favors the thicker tests and the occurrence of foraminiferal limestones and oozes at low latitudes. More important, however, is the vertical change in  $\text{CaCO}_3$  solubility, which also increases with greater pressure, and hence with greater depth in the ocean. The partial pressure of  $\text{CO}_2$  also increases with depth because there is no photosynthesis below the photic zone, although animals and bacteria continue to respire. These factors led to a decrease in pH with depth, from about 8.2 to as low as 7.0. **The level in the water column at which  $\text{CaCO}_3$  solution equals  $\text{CaCO}_3$  supply is called the calcium carbonate compensation depth (or CCD).** As this is impractical to locate in the geological record, the concept of the lysocline (i.e. the level of maximum change in the rate of solution of foraminiferal test calcite) is widely used.

The net result, of course, is a drop in the number of calcareous organisms with depth, there being few below 3000 m. For this reason, benthic agglutinated foraminifera dominate populations from abyssal depths.

### Classification

Kingdom PROTOZA  
Phylum SARCODINA  
Class RHIZOPODA  
Order FORAMINIFERIDA

### Suborder Allogromiina

These foraminifera have an entirely organic test with only one chamber. They are rarely encountered as fossils, being found largely in Recent, fresh or brackish water sediments. They are known in marine sediments since Late Cambrian times. *Allogromia* (Fig. 11a) has an ovate test with a rounded terminal aperture. *Shepherdella* (Fig. 11b) has a long tubular test with an aperture at each end. Both larger and planktonic types are unknown in this suborder.

### Suborder Textulariina

The Textulariina are characterized by non-laminar, agglutinated tests. The Ammodiscacea range from Early Cambrian to Recent times and all would be considered smaller benthic foraminifera and are mostly unilocular; *Saccamina* (Figs 11 f) is a simple globular form with a terminal aperture. Irregularly arranged chambers of similar type are found in the

multilocular *Sorosphaera* (Fig. 11 e). In *Technitella* (Fig. 11 d) the test is fusiform and built of carefully selected sponge spicules. Tubular tests generally have several apertures and may be simple and unbranched as in *Bathysiphon* (Fig. 5 d), branched as in *Rhizammina* (Fig. 5 e) or radiating from a central point as in *Astrorhiza* (Fig. 5 c), *Aschemonella* (Fig. 5 h) and *Rhabdammina* (Fig. 11 c).

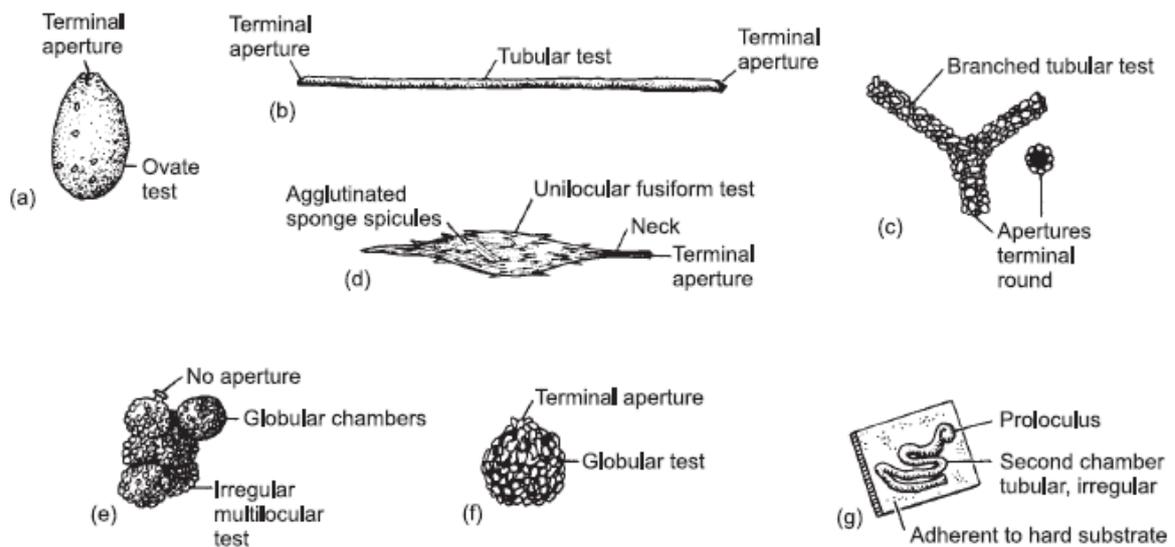


Figure (11) Suborder Allogromiina. (a) *Allogromia*  $\times 23$ . (b) *Shepherdella*  $\times 8$ . Suborder Textulariina, superfamily Ammodiscacea. (c) *Rhabdammina*  $\times 10$ . (d) *Technitella*  $\times 17$ . (e) *Sorosphaera*  $\times 7.5$ . (f) *Saccamina*  $\times 10.5$ . (g) *Tolypamma*  $\times 12.5$ ; ((e) After Loeblich & Tappan 1964 (from the Treatise on Invertebrate Paleontology).

Planispiral coiling is seen in *Ammodiscus* (Fig. 5 f) and glomospiral coiling (like a skein of wool) in *Usbekistania* (Fig. 5 g).

Adherent forms are irregularly branched or may meander and zig-zag across the substrate (e.g. *Ammoverrella* (Fig. 5 i); *Tolypamma* (Fig. 11 g). The tests of the Lituolacea are more complex than those of the Ammodiscacea. The simplest of the smaller benthic forms are commonly straight uniserial (e.g. *Reophax* (Fig. 12 a), *Hormosina* (Fig. 12 b) or the biserial *Textularia* (Fig. 13 b). Both kinds of growth are combined in different stages of *Bigenerina* (Fig. 13c).

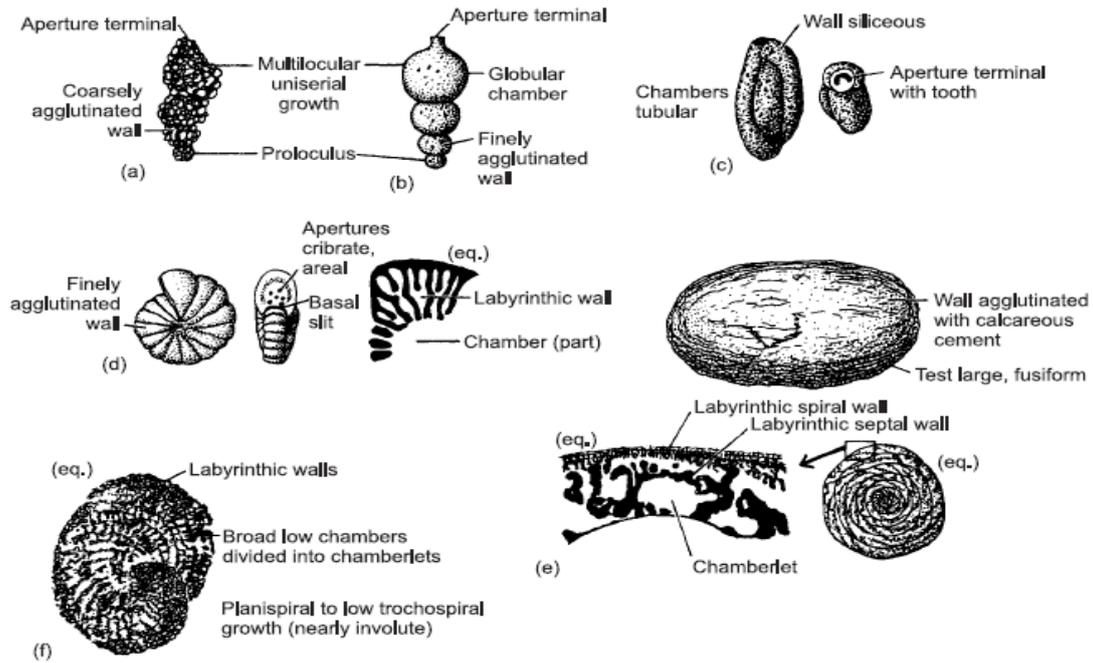


Figure (12) Suborder Textulariina, superfamily Lituolacea. (a) *Reophax*  $\times 18$ . (b) *Hormosina*  $\times 6$ . (c) *Miliammina*  $\times 33$ . (d) *Cyclammina*  $\times 4$ . (e) *Loftusia* above  $\times 0.7$ , lower left  $\times 92$ , upper right  $\times 3.5$ . (f) *Spirocyclina*  $\times 9.5$ . (eq), equatorial section; (ax), axial section.

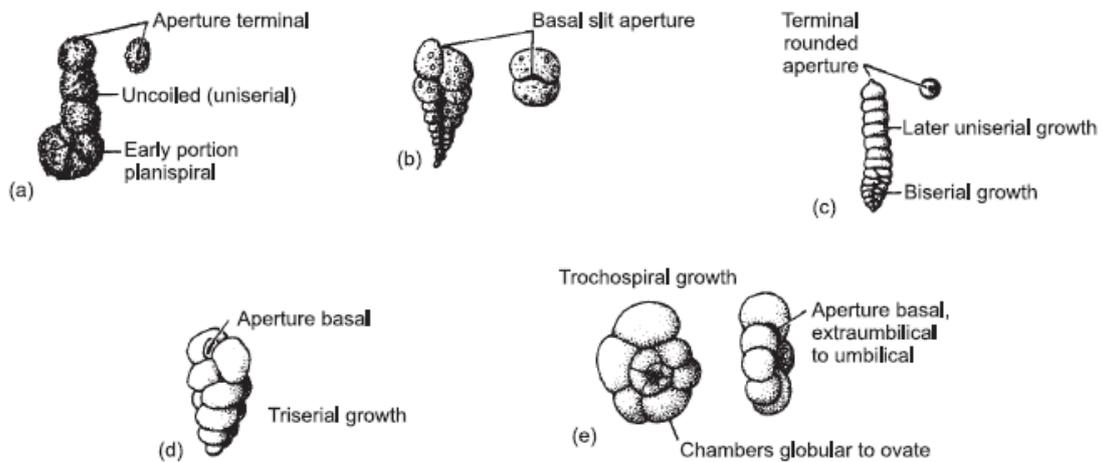


Figure (13) Suborder Textulariina, superfamily Lituolacea. (a) *Ammobaculites*  $\times 20$ . (b) *Textularia*  $\times 12.5$ . (c) *Bigenerina*  $\times 11.5$ . (d) *Verneuilina*  $\times 13.5$ . (e) *Trochammina*  $\times 29$ .

## Suborder Fusulinina

The Fusulinina contains those foraminifera with calcareous, microgranular walls; advanced forms may have two or more layers. The group was largely Palaeozoic in age, becoming extinct in the Triassic.

The Parathuramminacea were small benthic forms with simple microgranular walls. The architecture was also simple, ranging from unilocular to straight uniserial (e.g. *Saccaminopsis*, Fig. 14 a; *Earlandinita*, Fig. 14 b). This group is known with certainty from Ordovician through to Carboniferous times.

The Endothyracea (U. Sil.-Trias.) were small, multilocular foraminifera with walls generally differentiated into an outer granular layer and an inner fibrous layer, also microgranular but of fibrous appearance owing to the perforations. The architecture was variable and included uniserial forms (e.g. *Nodosinella*, Fig. 15 c), biserial (e.g. *Palaeotextularia*, Fig 15 d), high trochospiral (e.g. *Tetrataxis*, Fig. 15 e).

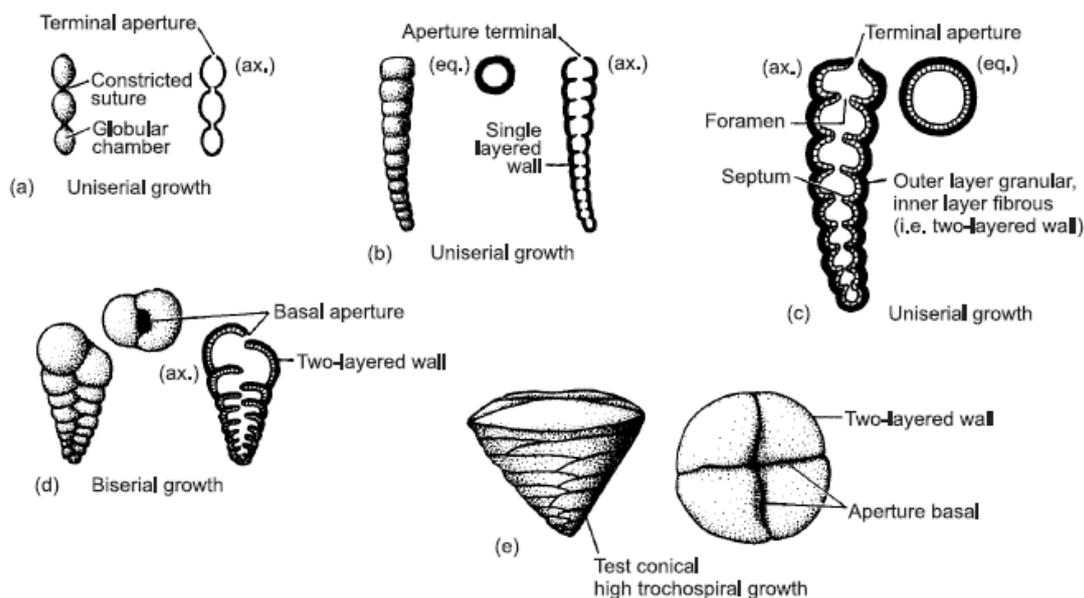


Figure (15) Suborder Fusulinina, superfamily Parathuramminacea. (a) *Saccaminopsis*  $\times 1.5$ . (b) *Earlandinita*  $\times 40$ . Superfamily Endothyracea. (c) *Nodosinella*  $\times 16.5$ . (d) *Palaeotextularia*  $\times 23$ . (e) *Tetrataxis*  $\times 34$ .

## Suborder Miliolina

The Miliolina have imperforate calcareous tests of porcelaneous appearance with a planispirally coiled proloculus. Subsequent growth may continue planispirally (e.g. *Cyclogyra*, Fig. 16 a), uncoil and develop uniserially (e.g. *Nubeculinella*, Fig. 16 b) or coil streptospirally. Streptospiral coiling here involves the addition of tubular chambers (generally half a whorl in length) arranged lengthwise about a growth axis. When added in the same plane (i.e. at 180 degrees to one another) the arrangement is called spiroloculine if the chambers are evolute and biloculine if they are involute (Fig. 7).

More commonly, however, chambers are added at angles of 144 degrees leaving five chambers visible from the outside (quinqueloculine e.g. *Quinqueloculina*, Fig. 16 e).

Such streptospiral growth forms may later unroll to uniserial as in *Articulina* (Fig. 16 d).

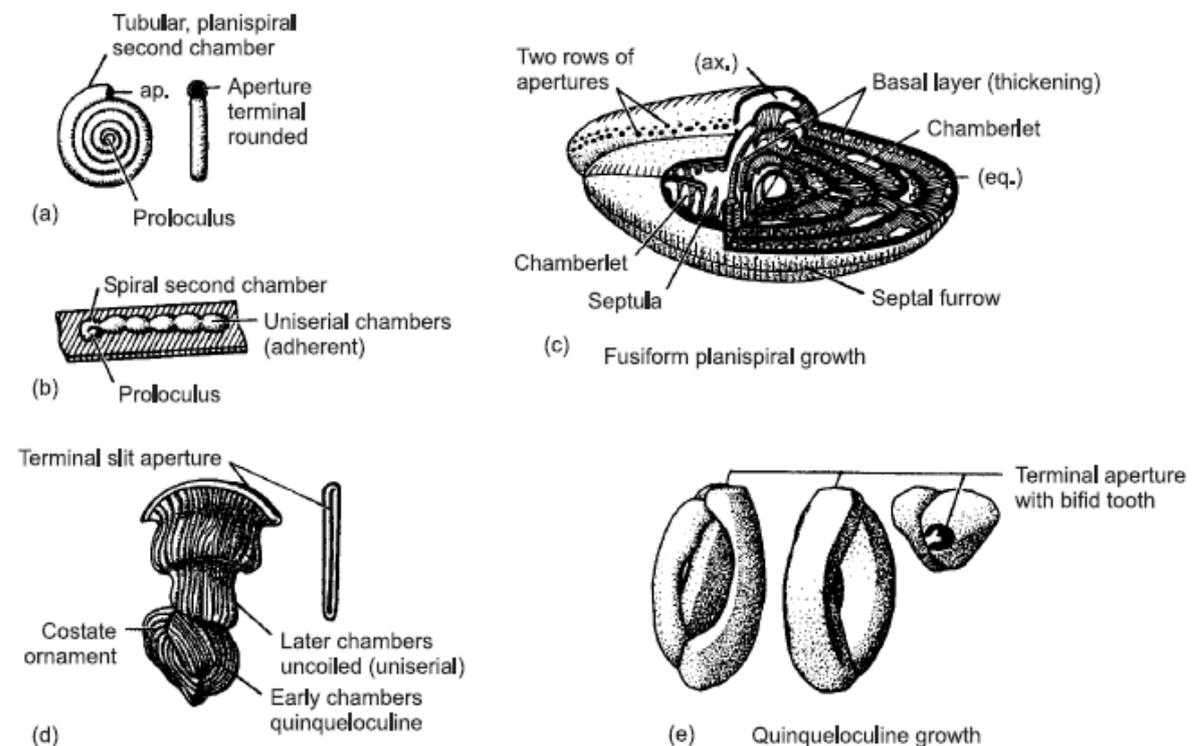


Figure (16) Suborder *Miliolina*. (a) *Cyclogyra*  $\times 40$ . (b) *Nubeculinella*  $\times 37$ . (c) Schematic diagram of the alveolinid *Fasciolites*  $\times 21.5$ . (d) *Articulina*  $\times 33$ . (e) *Quinqueloculina*  $\times 23$ .

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## Ostracods

Ostracods (Class) are one of the most diverse groups of living crustaceans; they are the most abundant of fossil arthropods and are represented by some 33,000 living and fossil species. Ostracods are small, bivalved Crustacea, with two chitinous or calcareous valves that hinge above the dorsal region of the body form their carapace. Ostracods were originally marine and probably benthic, but by the Silurian had expanded into reduced salinity and pelagic environments. Some Ostracods are adapted to a semi-terrestrial life living in damp soil and leaf litter. The class is subdivided into two subclasses, the weakly calcified, marine **Myodocopa** and the **Podocopa**. The **podocopans** include a high diversity of ecologically widespread forms and have the better fossil record. The vast majority of living forms are **podocopans**.

Ostracods are widely used in biostratigraphy, in determining palaeoenvironments and palaeoclimates and are indispensable as indicators of ancient shorelines and plate distributions. Ostracods have a long and well-documented fossil record from the Ordovician to the present day.

### Soft body structure

The soft parts are rarely preserved in fossils, as in other arthropods the soft parts are covered by a rigid, jointed exoskeleton of chitin. The head is large and bears a centrally placed mouth and a dorsal, usually single, eye. The anus is at the posterior end of the body. The head and the thorax are fused to form a **cephalothorax** and it is difficult to homologize the segments and appendages with other crustaceans (Fig. 17 a). On either side of the head/thorax junction arise large, flap-like outgrowths, the duplicatures, which totally enclose the rest of the animal and form the **carapace** (Fig. 17 b).

Ostracods have commonly seven, but up to eight pairs of jointed limbs in the adult stage, borne on the ventral side of the body (Fig. 17 c). In addition they have a furca (a pair of **caudal rami**) near the posterior end of the body, not generally considered as limbs. As in other Crustacea, the limbs are basically biramous, comprising two distinct branches: an outer **exopodite** and an inner **endopodite**. In many instances, however, the exopodite has become reduced or lost during evolution, resulting in a uniramous limb. These ostracod appendages bear fine chitinous bristles called setae (which usually arise from just below the joints) and terminate in claws.

In the Myodocopa, five pairs of limbs arise from the head, whilst the Podocopa may only have four pairs.

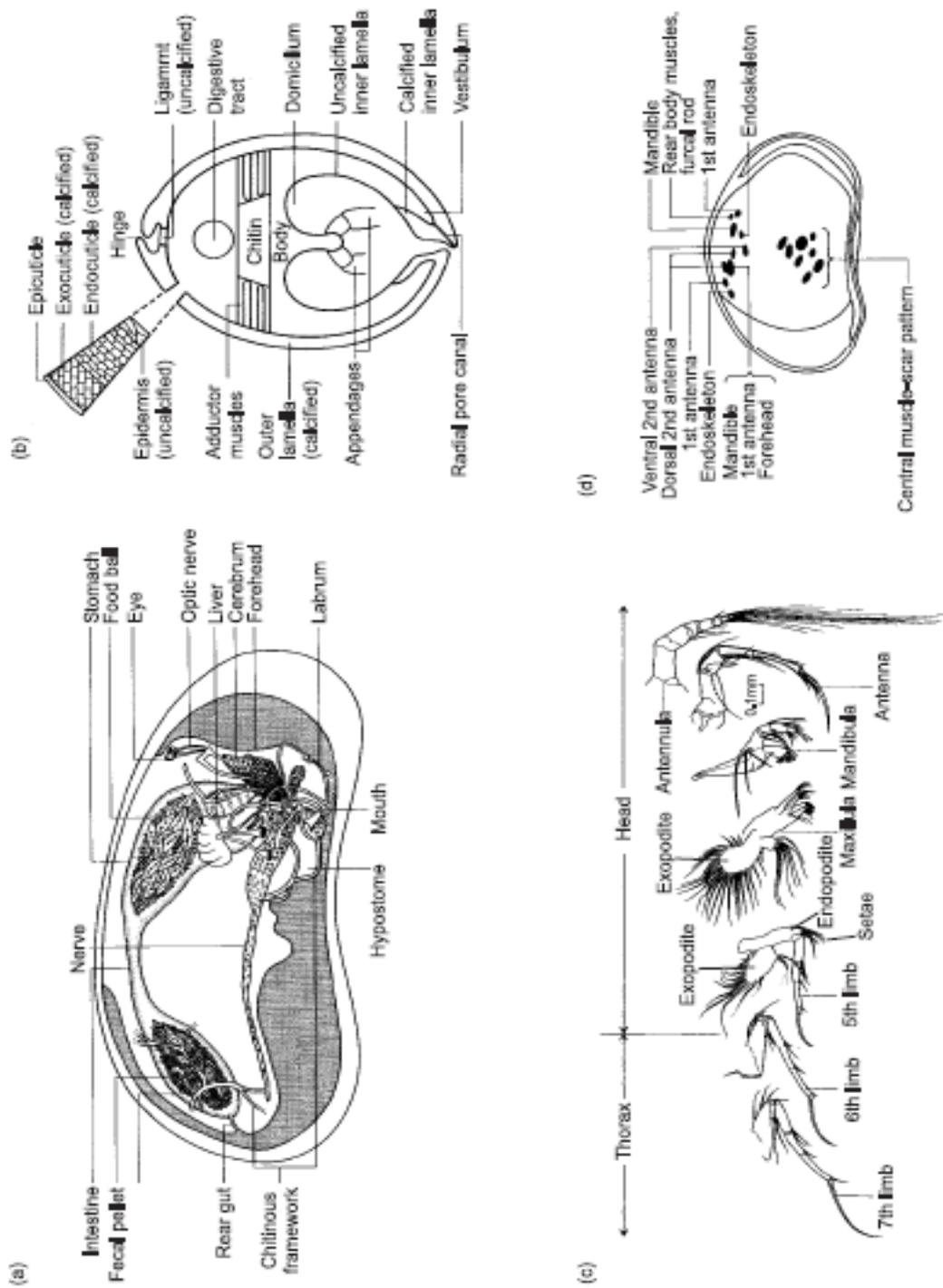


Figure 17 (a) Soft-part anatomy of an ostracoda. (b) Diagrammatic transverse section through an ostracoda. (c) Appendage morphology of *Bairdia* (order Podocopida). (d) Details of muscle scars.

The first and second, the antennula (which is uniramous) and the antenna (biramous), are long, tapering, limbs attached to the forehead and are employed variously in walking, swimming and feeding. The upper lip (or labrum) forms the front and the hypostome the back of the mouth. A Pair of biramous mandibula and maxillula is attached to the hypostome and aid mastication of the food. In the Podocopa, but not the Mydocopa, the exopodites of mandibula and first maxillula are modified into a large brancial plate, which stirs up the water to provide feeding currents, improve water circulation around the animal or to take up oxygen.

A pair of lateral eyes rather than the single dorsal eye typical of many benthic forms can further distinguish some of this group. Many deeper water genera are blind. Muscles that operate the appendages are attached to the chitinous endoskeleton or the central or dorsal part of the carapace where they form the dorsal muscle-scar pattern. The adductor muscles (Fig. 17 b) close the valves and form the central muscle-scar pattern on the valves (Figs 17 d, 18), their position is marked on the outside of the valve by a subcentral tubercle or an infold of the valve known as the sulcus. The number and arrangement of muscle scars is diagnostic for many of the higher ostracod taxa but they are rarely seen in Archaeocopida and Palaeocopida. In the latter, the position of the muscles is marked by a prominent median sulcus, running from dorsum to venter.

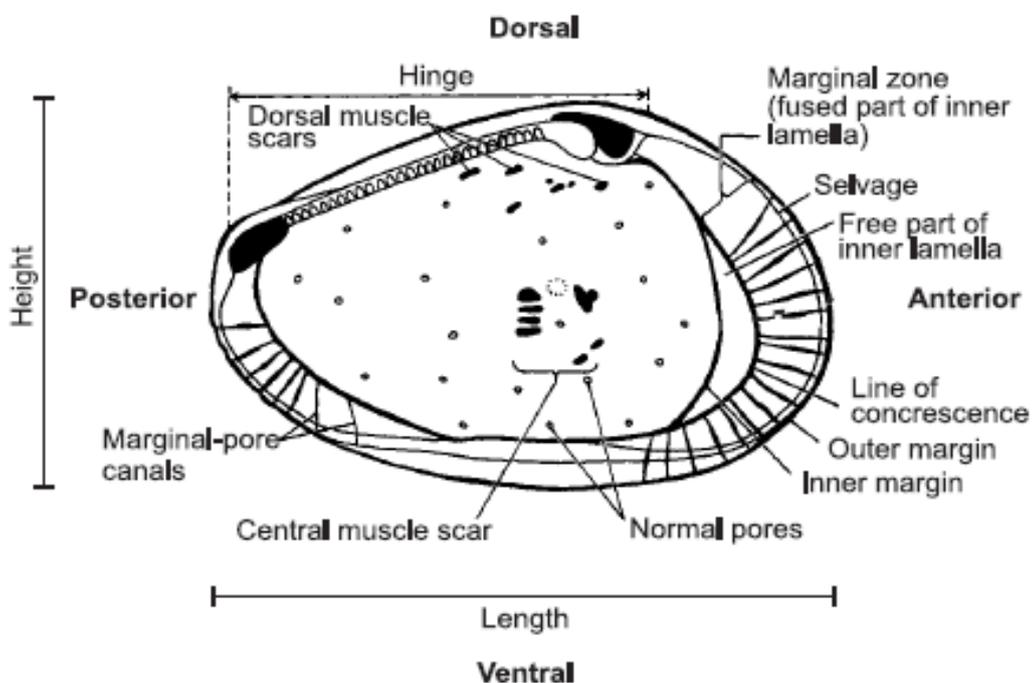


Figure (18) the internal features of a podocopid left valve.

## The Ostracoda carapace

The ostracoda carapace is usually ovate, kidney-shaped or bean-shaped with a hinge along the dorsal margin.

Most adult carapaces measure only 0.5–3 mm long though some species can reach up to 30 mm long. The bivalved carapace is secreted by the epidermis and forms a continuous sheet covering the whole body and limbs. The carapace is formed by two lateral folds of epidermis, the duplicatures, which originate in the head region and extend forwards, backwards and downwards to enclose the body and limbs. The duplicatures have an outer and inner lamella. The inner lamella that may either be fused or free from the outer lamella (Fig. 18) and can have calcified and uncalcified parts (Fig. 19). In the latter case a space between these lamellae, a vestibulum, is an extension of the body, which in some taxa can house digestive and reproductive organs (Fig. 17 b). Ridges on the duplicature called selvages may aid closure of the valves along the ventral margin. The innermost line of contact between the fused lamellae is called the line of concrescence, and the area between this and the outer margin is known as the marginal zone (Fig. 18).

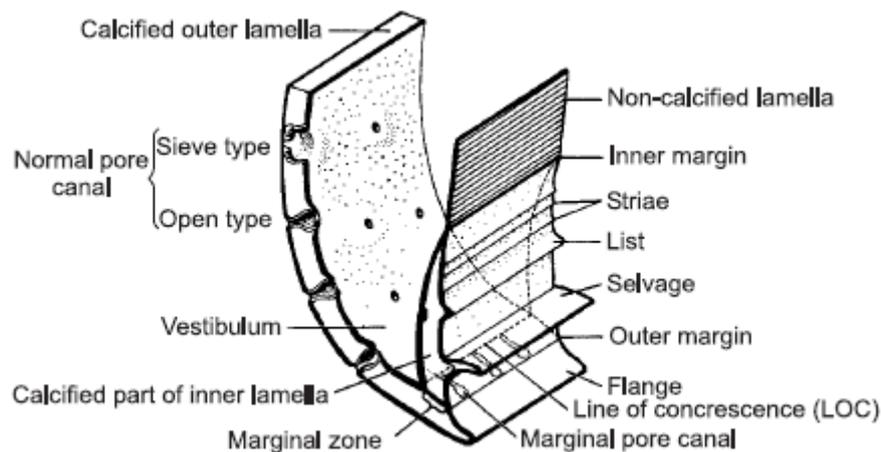


Figure (19) diagrammatic section of the peripheral part of the podocopid ostracod valve, with the outer lamella and duplicature.

In the Podocopa one valve is usually larger than the other and overlaps the smaller valve along all or part of the margin. In the Myodocopa this overlap is usually less obvious. The external surfaces of the inner and outer lamellae are covered with a thin layer of cuticle which is continuous across the dorsal margin and connects the valves as a ligament (Fig. 17b). The valves are closed by the adductor muscles running through the body and fixed to the inner surface of the calcified outer lamellae, where distinctive and diagnostic muscle scars are formed (Fig. 17 b, d).

There may also be frontal scars associated with the mandibular muscles and pair of mandibular scars which are not muscle scars but an area for the attachment of chitinous rods that help support the mandibulae.

The ostracod is kept in touch with its surroundings by tactile bristles (sensilla) which penetrate the outer lamella through normal pore canals. Sensilla that penetrate the marginal zone are called marginal pore canals whilst those traversing the rest of the shell are termed normal pore canals (Fig. 19). Their form (e.g. branched or unbranched) and arrangement can be useful to taxonomy. Sieve pores (Fig. 19), also with sensilla, are found in some podocopans and can also be useful taxonomically but their shape has also been linked to changes in salinity. Clear eye spots or raised eye tubercles may also be developed adjacent to the eyes especially in shallow-water species.

In some taxa the valves have a dorsal hinge structure of interlocking grooves and teeth and sockets. Three basic kinds of dorsal hinge structure are considered here but they may be subdivided (Fig. 20). Most Palaeozoic and freshwater ostracods have an **adont** hinge (Fig. 20a), this is the simplest, lacking teeth and sockets but often provided with a single groove along the margin of the larger valve and a corresponding ridge on the smaller valve. The **merodont** hinge (Fig. 20b, c) has elongate and strongly crenulated terminal elements on the right valve; the median elements may be smooth or crenulated. The **amphidont** hinge (Fig. 20d) has short terminal elements that consist of well-developed teeth on the right valve that may be crenulated, divided or smooth. The median element comprises an anterior socket (can be smooth or divided) and a median groove that is usually smooth.

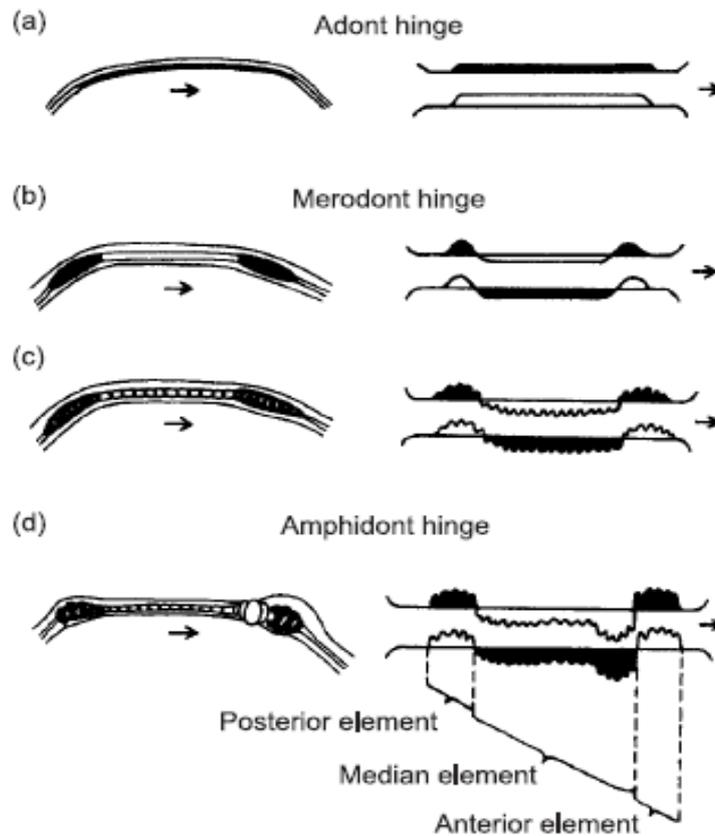


Figure (20) some ostracod hinge types, seen in lateral view of the left valve and from above.

## Ostracoda distribution and ecology

### Substrate and food

Living Ostracods are predominantly benthic or pelagic throughout their life cycle. Benthic ostracods occupy freshwater and marine habitats (Fig. 21). Members of the Terrestriocytheroidea (e.g. *Mesocypris*) are adapted to living in damp soils and leaf litter. Freshwater ostracods tend to have smooth, thin, weakly calcified carapaces of a simple bean shape. Many of these consume detritus or living organisms (e.g. diatoms, protists, bacteria) stirred up by the antennae or mandibulae. *Cypridopsis* is a scavenger that holds dead plant and animal particles with its mandibulae or antennae and tears at these with its maxillulae. One species is known to predate the gastropod vector of the sickness 'Bilharzia' and hence has some medical interest.

Whereas the freshwater ostracods may spend much time swimming several centimeters above the substrate, marine benthic forms are heavier

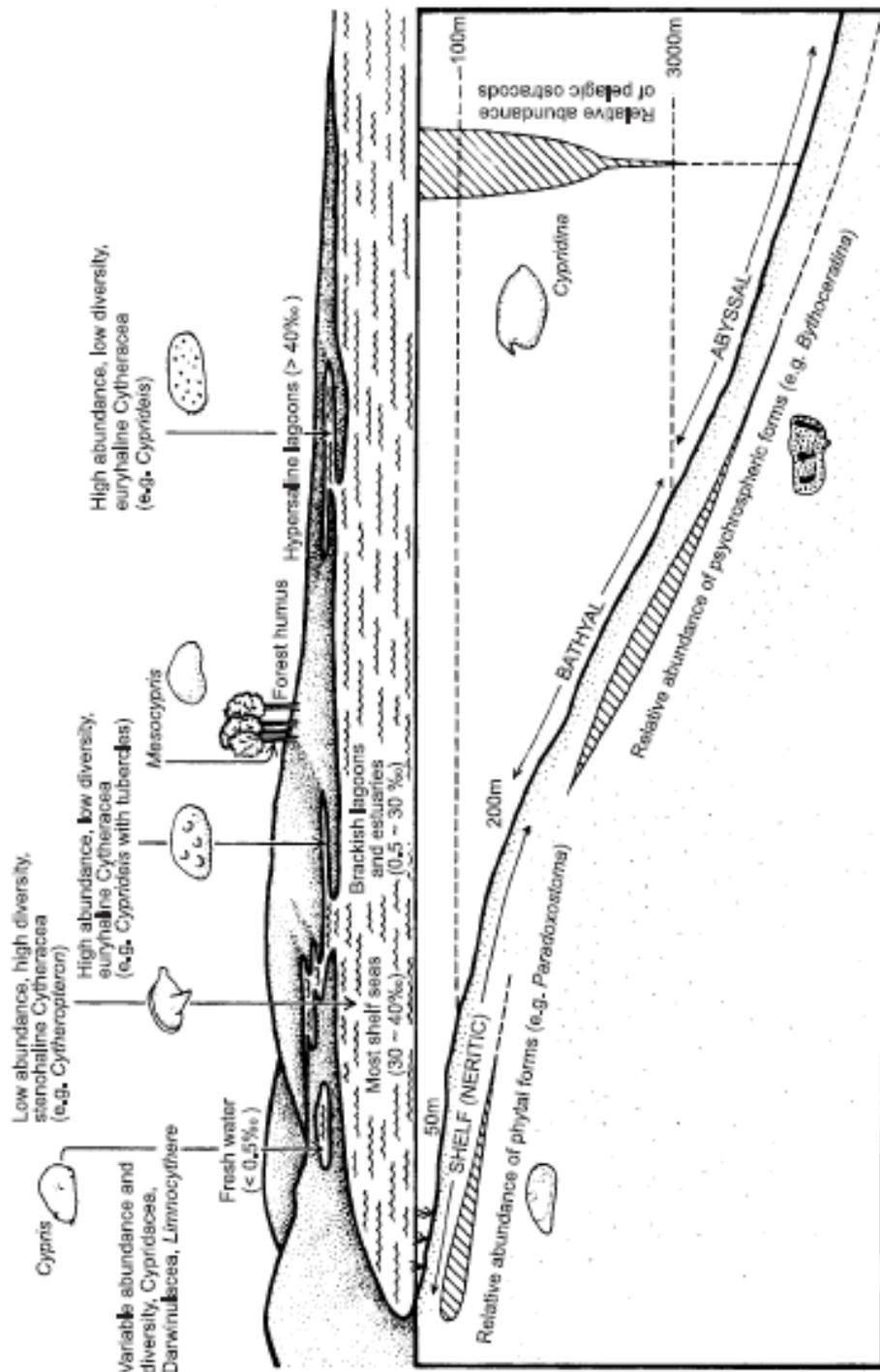


Figure (21) distribution of living Ostracoda with some typical forms represented.

and tend to be either crawlers, burrowers or interstitial, feeding on detritus or predate diatoms, foraminifera.

It has often been observed that the size, shape and sculpture of benthic ostracods broadly reflects the stability, grain size and pore size of the substrate on, or in which, they live. For example, crawling forms dwelling on soft, relatively fine-grained substrates tend to have a flattened ventral surface perhaps with weight distributing projections called alae or frills, keels and lateral spines. Ostracods dwelling on coarser substrates from the more turbulent, nearshore habitats are commonly thicker shelled with a coarse sculpture of ribs, reticulations or robust spines housing sensory setae. Infaunal ostracods, which live within or burrow through the pore spaces of sandy substrates, tend to be small, smooth and robust (e.g. *Polycope*), those that burrow through silts and muds need more streamlined carapaces and are usually smooth and elongated (e.g. *Krithe*). Nektonic ostracods (particularly in the order Myocopida) spend their lives swimming in the oceans.

They do this primarily by means of pairs of the hairy exopodites on the antenna. Food particles in the water are moved towards the maxillulae and thoracic limbs by water currents produced from the beating of epipodites on the modified first thoracic legs.

## Salinity

Ostracods are ubiquitous in aquatic environments with species and genera living under well-defined salinity ranges within the freshwater to hypersaline range.

Chlorinity is a good measure of salinity in the marine realm, but in inland saline lakes other solutes contribute more to the salinity, in these settings athalassic is used instead of brackish.

Three main salinity assemblages are distinguishable: **freshwater (<0.5‰)**, **brackish-water (0.5–30‰)** and **marine (30–40‰)**. Hypersaline assemblages (>40‰) mainly contain euryhaline marine and brackish-water forms. The majority of living species are adapted to a normal marine salinity of around 35‰ (i.e. stenohaline). Ostracod assemblages and species abundance can be used to plot rapid or cyclic changes in environment.

## Depth

Depth in itself does not affect Ostracod distributions. However, a number of important ecological factors including hydrostatic pressure, temperature, salinity and dissolved oxygen change with depth and are paralleled by changes in ostracod faunas and diversity. Ostracods are

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therefore sensitive indicators of bottom-water conditions and the geographical distribution of Ostracod assemblages are effective tracers of different benthic environments and distinct water masses.

Benthic marine ostracod depth assemblages may be categorized broadly as **inner-shelf, outer-shelf and bathyal-abyssal**. The shelf (or neritic) assemblages live between 0 and 200 m depth, and include many of the marginal marine forms mentioned above. Whereas the densest populations are found in the marginal areas, the highest diversities tend to occur in shallow-shelf seas. The presence of thick valves with eye spots, strong sculpture, amphidont hinges and conspicuously branched pore canals are features common in extant shallow-water ostracods from coarse-grained substrates.

Deeper-water neritic substrates, which tend also to be finer grained, support forms with smooth, thin, often translucent carapaces with relatively weak hinges and no eyes or eye spots.

### **Temperature**

Latitudinal temperature control of shallow-water species has given rise to numerous localized (endemic) assemblages ranging from high latitudes (at temperatures below 0°C) to the subtropics and tropics (where they may live in waters up to 51°C). This endemism is enhanced in benthic ostracods by the lack of a planktonic larval stage for dispersal. As with most groups, tropical assemblages tend to be more diverse than those in higher latitudes. Some of the latter are, however, of relatively large body size, explained by their slower metabolism and the longer time it takes them to reach maturity.

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## Classification

Kingdom ANIMALIA  
Phylum CRUSTACEA  
Class OSTRACODA

The following carapace features are of value in the classification of fossil taxa:

- 1- Basic carapace shape.
- 2- Muscle scar position and arrangement.
- 3- Degree of development and fusion of the duplicature with the outer lamella.
- 4- Structure, shape, size and arrangement of normal and marginal pore canals.
- 5- Nature, location and degree of valve overlap.
- 6- Hinge elements.
- 7- Nature of surface sculpture, and presence of eye spots.
- 8- Nature of marginal zone.
- 9- Form of selvages and flanges.

## Class Ostracoda

**Order Podocopida** The Podocopida comprise the bulk of the Mesozoic and Cenozoic fossil ostracods, although they have a longer history (L. Ord.-Rec.). Living forms are largely diagnosed from their soft parts. The antenna exopodite is greatly reduced, the maxillula has a large branchial plate and the eighth limb is usually absent. Fossil taxa have been erected on carapace morphology. Podocopid valves are well calcified, of unequal size and have a convex dorsal margin and a weakly convex, straight or concave ventral margin. (Fig. 22).

**Order Palaeocopida** The Palaeocopida had their acme in the Palaeozoic and can be recognized by their long straight hinge line, lobate and sulcate sculpture. The valves do not overlap and muscle scar patterns are poorly known. The inner lamella is not calcified. (Fig. 23).

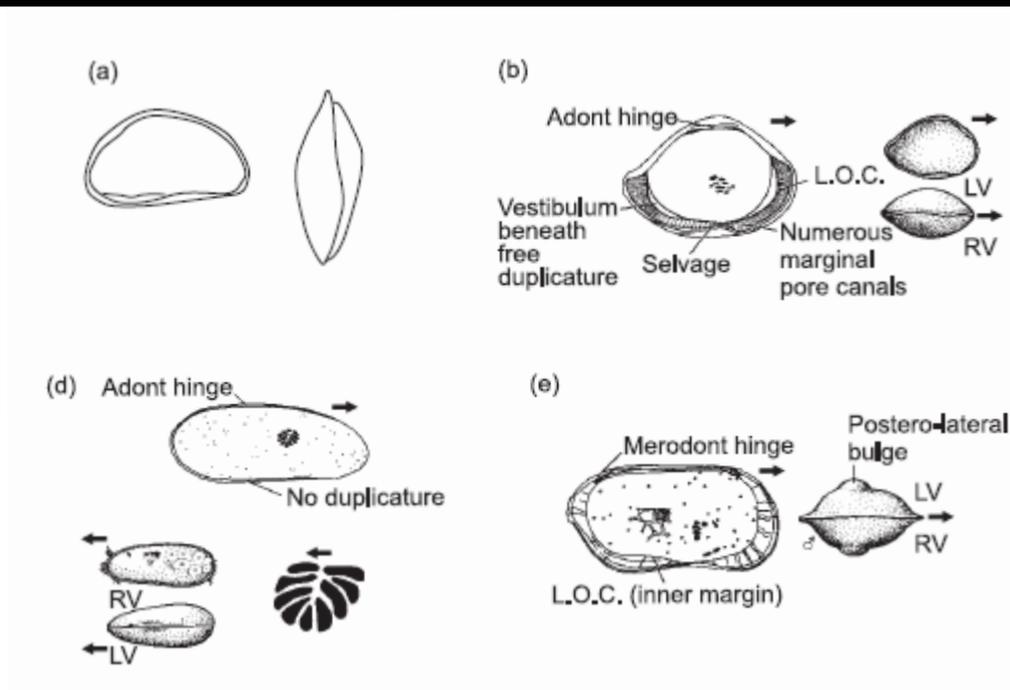


Figure (22)

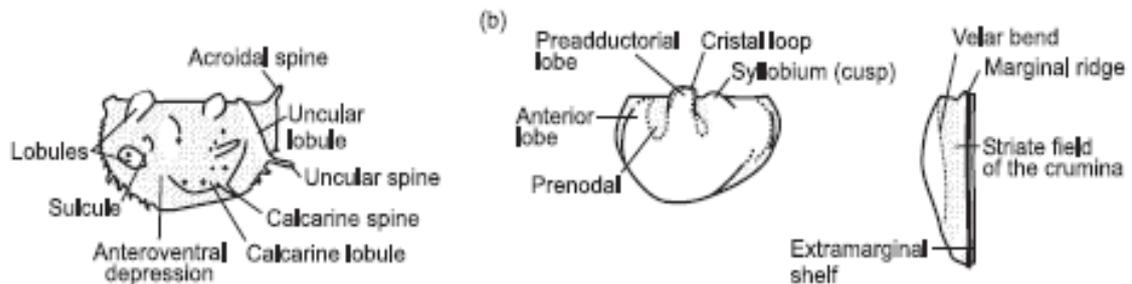


Figure (23)

**Order Leiocopida** (Ord.-Perm.) Members of this order are superficially similar to palaeocopids but generally lack lobes and sulci. The carapace is inequivalved and an adductor muscle-scar is rarely visible. A velar structure can be developed as a low ridge. Dimorphism is not observed. *Aparchites* (L.-M. Ord., Fig. 24 a) has an ovate, non-sulcate carapace in which the hinge line is shorter than the length of the carapace. Cardinal angles are obtuse and the velar ridge is smooth or tuberculate or often with small spines. Dimorphism is not known here. *Paraparchites* (Dev.-Perm., Fig. 24 b) is ovate and smooth except for a postero-dorsal spine in a few species. The left valve usually overlaps the right along the free margin. The carapace has its greatest height medial or forward and the greatest width medial in males and posterior in females. (Fig. 24).

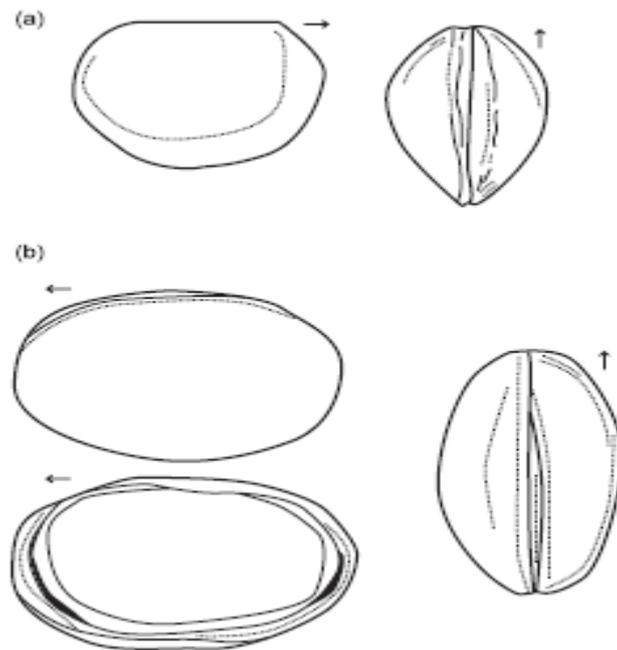


Figure (24)

**Order Myodocopida** The Myodocopida (Ord.-Rec.) include a large number of the pelagic ostracods. They have weakly calcified carapaces with equal to unequal valves and no valve overlap; the dorsal and ventral margin may be convex and the inner lamella is only partially calcified. The muscle-scar pattern consists of numerous elongate scars. (Fig. 25).

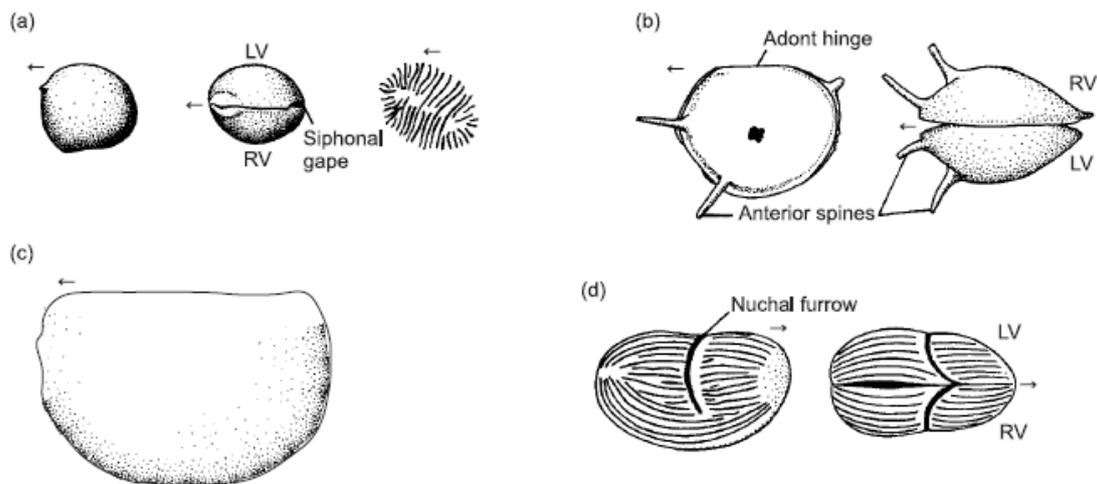


Figure (25)