

MICROPALAEONTOLOGY

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. The microfossils, in general are the fossils that need microscopic techniques to study them.

The study of microfossils is properly called micropaleontology. It includes studies of **mineral-walled microfossils as well as the study of organic-walled 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 cm³ 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, 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. 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.

Micropalaeontology brings three unique perspectives to the study of evolution: the dimension of time, abundance of specimens (allowing statistical analysis of trends) and long complete fossil records, particularly in marine groups.

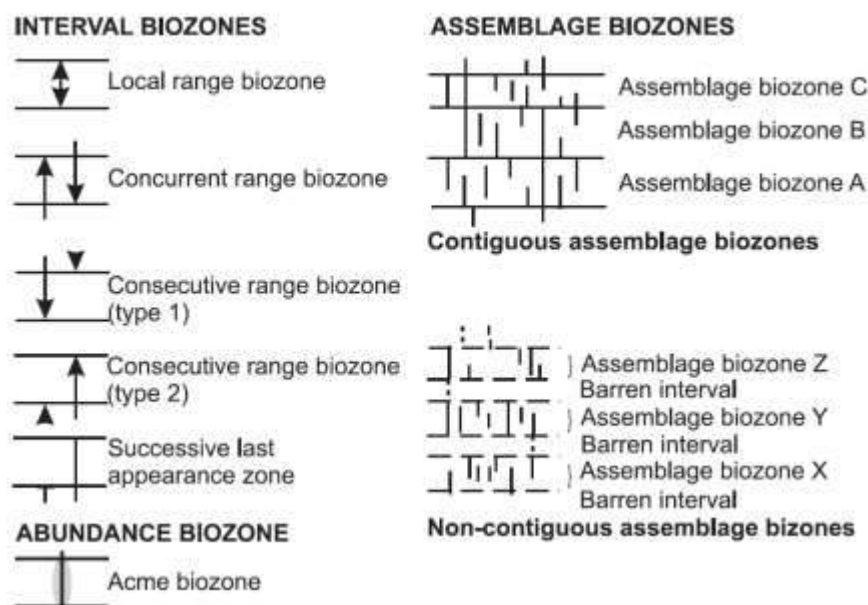
The succession of rocks exposed at the surface of the Earth can be arranged into a stratigraphical column, with the oldest rocks at the base and the youngest ones at the top. Although the absolute ages have been determined from studies of radioactive isotopes, it is customary to use the names of stratigraphical 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). 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.

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 ostracods are indispensable for the biostratigraphy of terrestrial and lacustrine successions, where macrofossils can be scarce. Detailed biostratigraphical zonations, using the groups mentioned in this book, 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 biozones: (i) assemblage, (ii) abundance and (iii) interval biozones



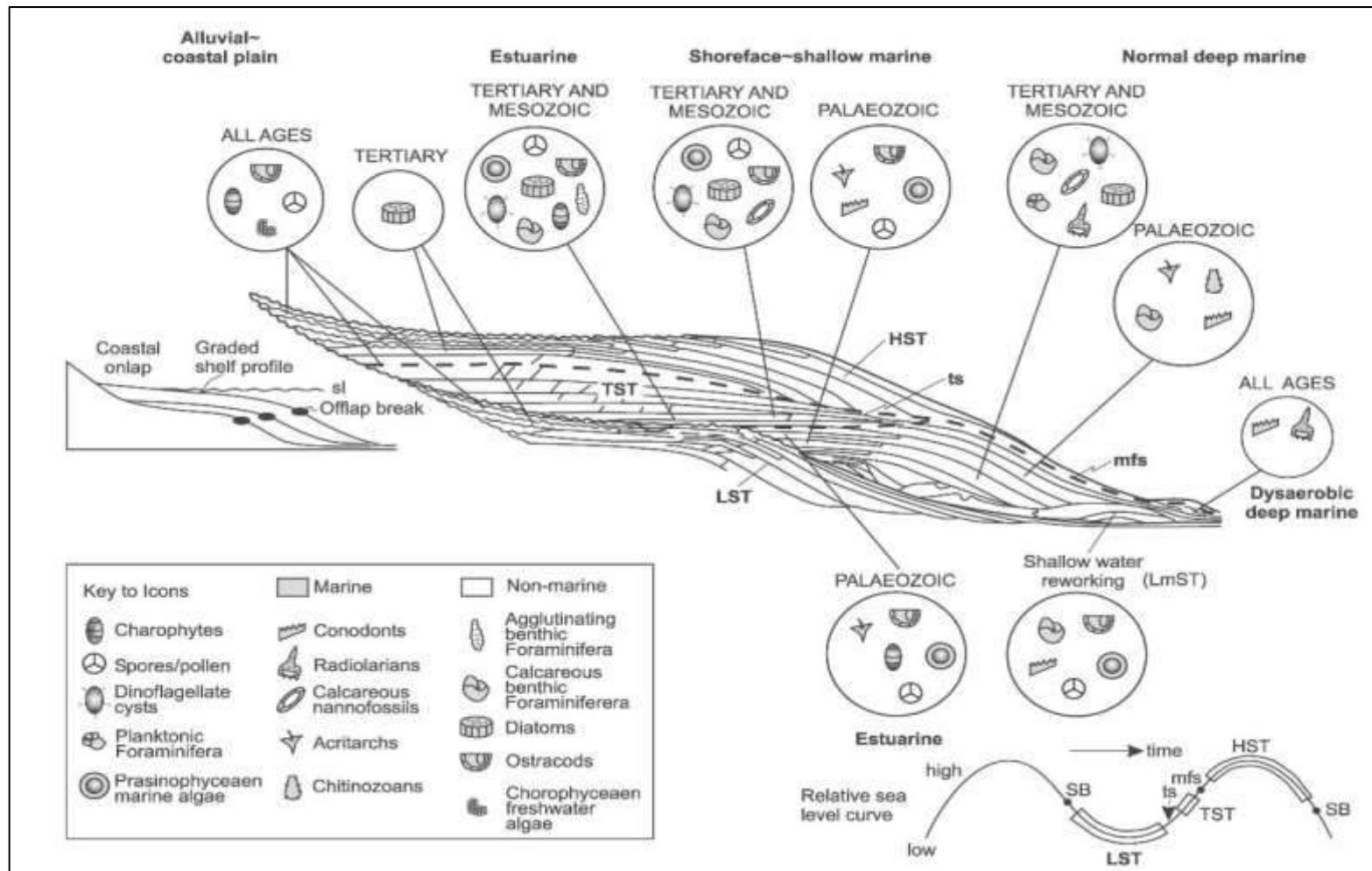
An assemblage biozone is based on the association between three or more species with little regard to the stratigraphical range of each. As species associations are strongly dependent upon local ecology, this type of biozone is most suitable for **local or intra-basinal** applications.

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, 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. The interval between two successive LADs is called a successive last appearance zone and is the most commonly used zone in commercial biostratigraphy where most of the samples are from borehole cores or cuttings and the FAD of a species cannot always be determined due to down-hole contamination ('caving').

Microfossils in Sequence Stratigraphy

Sequence stratigraphy is used for analysing familiar stratigraphical concepts such as transgression, regression and eustatic cycles and microfossils have a key role to play in sequence interpretation. The methods were largely developed as an extension of seismic stratigraphy and the need for correlation in the subsurface, but are equally applicable to outcrop geology where they have proved invaluable in understanding the influence of climate change on sedimentary successions. The basic philosophies of sequence stratigraphy are, firstly, that sediment accumulation occurs in discrete sequences, which are relatively conformable successions bounded by unconformities (or the correlative conformities in deep water). A sequence is considered to represent all the sediments deposited in an interval of time (0.5–5 Ma) and the sequence boundaries (**intervals of no or very slow deposition**) are considered effectively **synchronous** over large areas and can be used for matching sections. Secondly, the interaction of the rates of relative sea-level changes (eustasy), basin subsidence and sediment supply lead to variations in accommodation space, which is the space potentially available for sediment accumulation. The fundamental building blocks of sequences are **parasequences**, which generally represent shallowing or coarsening upwards cycles of short duration (10–100 kyr).

Every sequence comprises three systems tracts and potentially has a distinctive assemblage of microfossils: a lower one representing periods of rapid but decelerating sea-level fall (LST, lowstand systems tract); a middle one relating to increasing acceleration in sea-level rise (TST, transgressive systems tract); and an upper one relating to a decreasing rate of sea-level rise and initial sea-level fall (HST, highstand systems tract). **The base of each systems tract is defined as the sequence boundary, transgressive surface and maximum flooding surface respectively.**



Palaeoenvironmental distribution of some of the main microfossil groups through time. These are placed in a sequence stratigraphical framework. HST, highstand systems tract; LST, lowstand systems tract; mfs, maximum flooding surface; sl, sea level; ts, transgressive surface; TST, transgressive systems tract; SB, sequence boundary.

The interplay of environmental conditions, biological evolution, preservation potential of the microfossil group and cyclic changes in depositional style control the microfossil content of different sedimentary sequences. In a sequence stratigraphical analysis, it is the primary role of the micropalaeontologist to document changes in biofacies, and hence palaeoenvironment, and to provide a high-resolution biostratigraphical framework.

In the oil industry, benthic foraminifera are commonly used to define marine benthic paleoenvironments, although conodonts, ostracods and benthic algae have also been used. Palynofacies analysis is most useful in defining fluvio-deltaic subenvironment. Terrestrial microfossil assemblages can also provide a detailed record of climate changes around the margins of the sedimentary basin. With increasing knowledge of the ecological controls on microfossil groups, the relative abundances of different marine groups can be used to elucidate the changing paleoceanography. The transport or reworking of species into the marine environment by wind (e.g. bisaccate pollen) or rivers (e.g. miospores, charophytes, ostracods and woody material) or tides (e.g. foraminifera, dinoflagellates) can be problematic in biostratigraphy and palaeoenvironmental analysis. However the abundance gradients and size range of these derived fossils can be used to indicate the proximity of the source, location of palaeoshorelines and exposure and uplift histories of the hinterland.

TYPES OF MICROFOSSILS

The microfossils are the remains of the micro-fauna, and flora in the various environments, preserved by natural fossilization processes and are at least 10,000 years old. The classification of the microfossils has been done in several ways, which include the types of organism, composition of their shells/hard parts, living habits etc.

Classification of Microfossils

1. On the basis of type of organisms, the microfossils can be plant (phytos) microfossils or animal (zoos) microfossils.
2. On the basis of the mode of living, they can be classified as: floaters (planktons), sea-floor dwellers (benthic), burrowers (infaunal), surface dwellers (epifaunal).
3. On the basis of the chemical composition of the shells/hard parts, they can be classified as follows:

MICROFOSSILS		
ORGANIC WALLED	MINERAL WALLED	
1. POLLENS	1. CALCAREOUS	a. Foraminifera
2. SPORES		b. Pteropoda
3. DINOFLAGELLATE CYSTS		c. Ostracoda
		d. Calcareous nannofossils

	e. Calcareous algae
2. SILICEOUS	a. Radiolaria
	b. Diatoms
	c. Silicoflagellates
3. PHOSPHATIC	a. Conodonts

The organic walled microfossils are extremely resistant to weathering, and are useful in the correlation of terrestrial environment settings over a longer time scale. The mineral walled microfossils are quite prone to weathering.

CALCAREOUS NANNOPLANKTONS

Calcareous nannoplanktons are a heterogeneous group of calcareous forms, ranging in size from **0.25 to 30 μm** . In the fossil record they are found in fine-grained pelagic sediments and can be sufficiently abundant to become rock-forming, for example the Upper Cretaceous chalk.

Coccolithophores are unicellular planktonic protozoa with photosynthetic pigments, and are considered to be part of the algae group haptophyta. The group is an important constituent of the oceanic phytoplankton, providing a major source of food for herbivorous plankton.

Tiny calcareous scales called coccoliths (3–15 μm in diameter) form around these cells as a protective armour that eventually falls to the ocean floor to build deep sea ooze and fossil chinks. Being both abundant and relatively easy to recover from marine sediments, coccoliths are used for biostratigraphic correlation of **post-Triassic rocks** and in palaeoceanographic studies. The stellate calcareous nannofossils, the discoasters, are an extinct group that are exceedingly useful in the biostratigraphy of the Tertiary. Nannoconids are minute, cone-shaped microfossils (5–30 μm) that are useful in Cretaceous biostratigraphy in the absence of other groups.

Coccolith Morphology

Coccolith morphology is the basis for classification of both living and fossil members of the group. Two basic modes of construction are known from electron microscope studies:

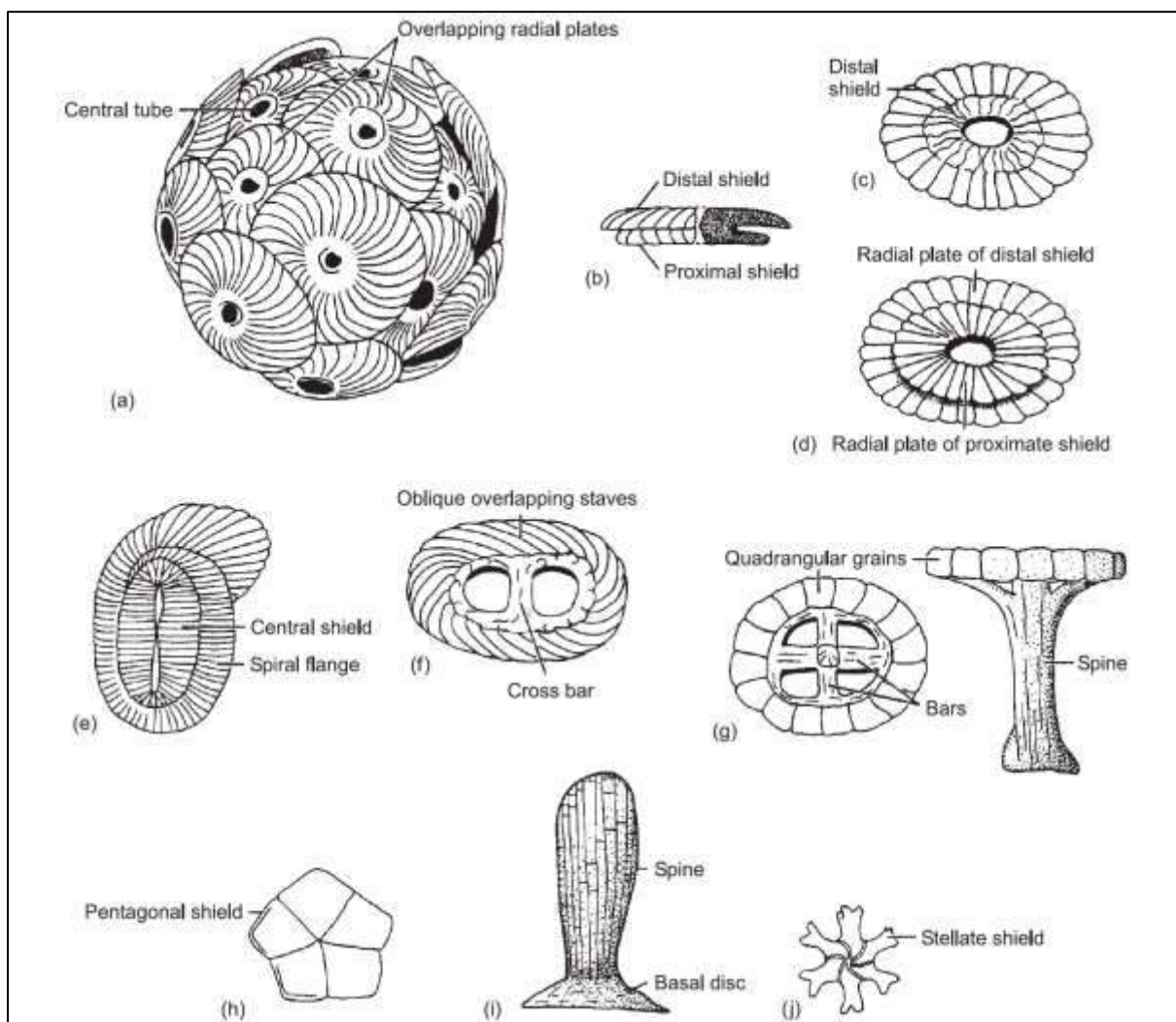
(i) **holococcoliths:** built entirely of submicroscopic calcite crystals, mostly rhombohedra, arranged in regular order;

(ii) **heterococcoliths:** usually larger and built of different submicroscopic elements such as plates, rods and grains, combined together into a relatively rigid structure.

As holococcoliths invariably disintegrate after they are shed, it is the heterococcoliths that provide the bulk of the microfossil record.

Heterococcoliths vary considerably in form and construction. The majority comprise discs of elliptical or circular outline (shields) constructed of radially arranged plates, enclosing a central area which may be empty, crossed by bars, filled with a lattice or produced into a long spine. The outward-facing (distal) side of the shield is often more convex with a prominent sculpture and may be provided with a spine, whilst the other proximal face is flat or concave and may have a separate architecture.

Coccolithophores have provided a major source for carbonate ooze since the Early Mesozoic and thus the biomineralization of coccoliths is a globally significant rock-forming process.



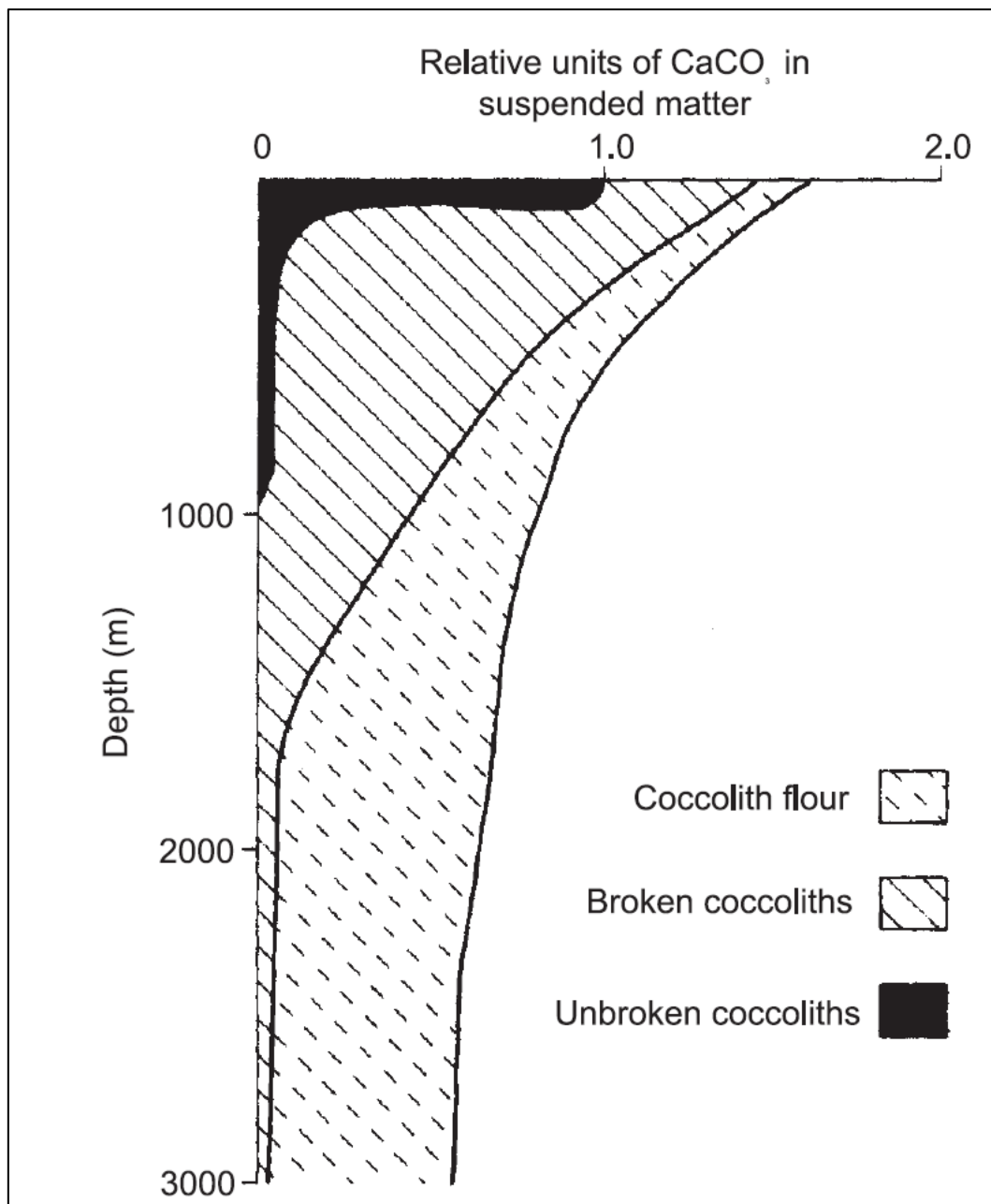
Various types of heterococcoliths

It is thought that coccoliths are formed for a number of reasons including protection from intense sunlight, to concentrate light, to provide a site for the disposal of toxic calcium ions or as supporting armour which stabilizes and acts as ballast for the cell.

Ecology of Coccolithophores

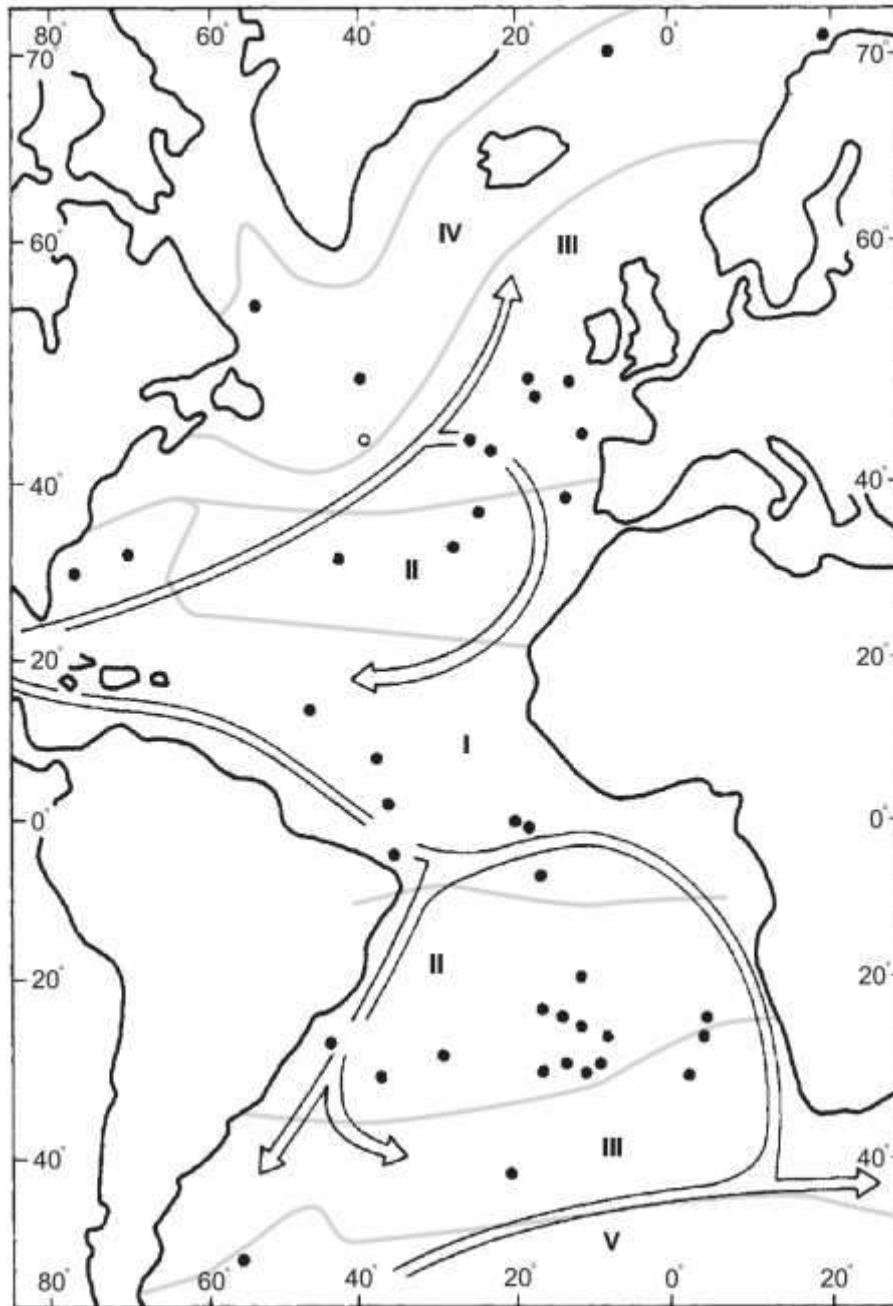
Coccolithophores are predominantly autotrophic nanoplankton, utilizing the energy from sunlight for photosynthesis. Living cells are therefore largely restricted to the photic zone of the water column (0–200 m depth) with the lighter, smaller cells living near the surface and heavier cells living lower down.

As such the distribution of coccolith species is under the direct control of climate. They thrive in **zones of oceanic upwelling** or of **pronounced vertical mixing**, as it is here that vital trace minerals are most readily available. Although a few species are adapted either to fresh or brackish waters, the majority of species are marine. The relative abundance of complete coccoliths to broken coccoliths and coccolith flour changes with depth.



Vertical distribution of coccoliths and coccolith derived carbonates

In the Atlantic Ocean nannofloral provinces are delimited by temperature with different assemblages indicating **subglacial, temperate, transitional, subtropical and tropical** latitudes. It is in **tropical areas** where they are most abundant and their numbers may reach as many as 100,000 cells per litre of sea water. A similar latitudinal differentiation occurs in the Pacific Ocean but the greatest diversity occurs at 50°N. Depth stratification also occurs in the Pacific Ocean. Production of coccoliths is strongly but not completely controlled by light.



Coccolith concentrations in near-surface sediments of the Atlantic Ocean. Superimposed are major surface currents and calcareous nannoplankton provinces. Roman numerals in the figure correlate with the assemblages that follow. I – Tropical, II – Subtropical, III – Transitional, IV – Subarctic, V – Subantarctic

Coccoliths and Sedimentology

After death, coccolithophores sink through the water column at about **0.15 m per day** and the coccoliths fall away. With increasing depth these scales tend to dissolve or disaggregate into finely dispersed carbonate matter, this process operating first on holococcoliths or delicate

heterococcoliths. **Therefore coccolith assemblages from sediments deeper than 1000 m are not truly representative of the original nanoflora.**

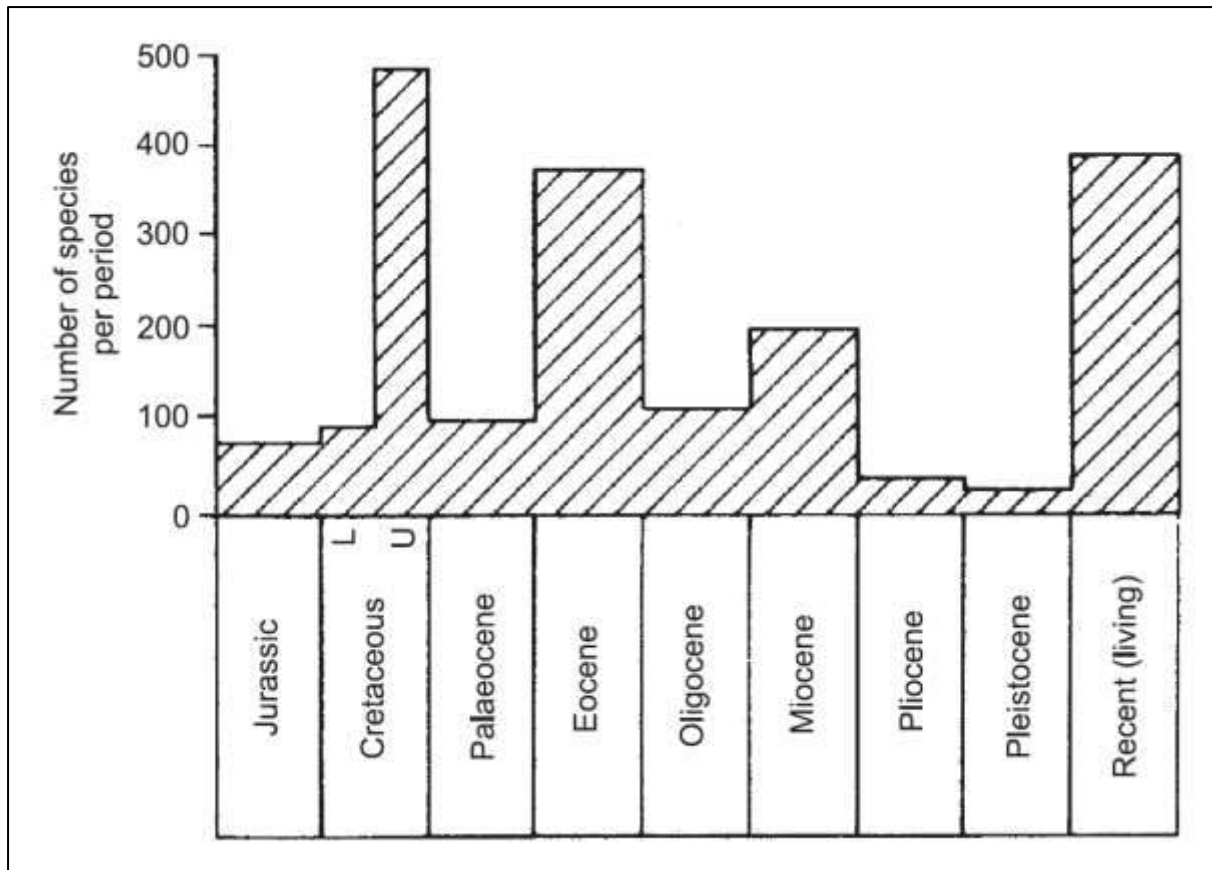
At depths of over 3000–4000 m, few coccoliths remain as most of the CaCO_3 has gone into solution due to CCD. At these depths, coccolith oozes are replaced by the diatom or radiolarian oozes, or by red clays.

Many factors may cause this dissolution, including high hydrostatic pressures, high CO_2 , low O_2 , low pH, low temperatures, low CaCO_3 precipitation by organisms, or sluggish recycling of CaCO_3 from the land. However, coccoliths (and even whole coccospheres) can reach ocean depths intact by settling rapidly within the faecal pellets of copepod crustaceans.

The proportion of coccolithic material in the Recent oceanic carbonates is greatest in **subtropical and tropical regions underlying waters with high organic productivity.** Coccoliths are likewise an important constituent of Cretaceous and Tertiary chalks. They are fewest in sediments from subglacial waters (about 1%) where both productivity and preservation conditions are unfavourable.

History of Coccolithophores

The coccolithophores are both, a primary source of food in the oceans and a significant producer of atmospheric oxygen. Paleozoic records are few and dubious. The first generally accepted fossil coccoliths are rare and reported from upper Triassic rocks. Their diversification in the Early Jurassic was a remarkable event that occurs along with the radiation of dinoflagellate cysts and both may be related to oceanographic changes connected with the opening of the Atlantic Ocean at this time. Their numbers and taxonomic diversity increased steadily until the Late Cretaceous period when there was a major marine transgression and a further, explosive radiation of many planktonic groups. These conditions led to the deposition of chalk over vast areas of the continental platforms. The vast majority of coccolithophores became extinct at the K-T boundary, many of their habitats being filled by the diatoms during the Early Cenozoic. Coccolithophores have since regained their dominance in tropical and temperate waters but are significantly less diverse than in the Mesozoic.



Species diversity of coccoliths through geological time.

Applications of Coccoliths

The biostratigraphic value of coccoliths is unrivalled in the Mesozoic and Cenozoic and they have become the standard biostratigraphic index fossils for the Cenozoic. Mesozoic and Cenozoic biostratigraphic zonation.

The increasingly large database relating coccolith assemblages to modern day water masses and latitudinal provincialism means coccoliths are extremely important in oceanographic studies. The distribution of coccolithophores has changed significantly over time. In the **Cretaceous** they were **cosmopolitan** and abundant in both coastal and oceanic waters and from the poles to the tropics. Now the highest diversity is found in the **subtropical gyres** or in areas of nutrient-rich upwelling. Most species live in stratified water and the degree of stratification affects abundance.

During the last glacial maximum, North Atlantic water masses and their constituent nanofloras shifted 15 degrees southwards of their present location. Vertical changes in nanofloras in sediment cores from cool- to warm-water assemblages reflect the glacial–interglacial cycling of the Pleistocene climate.

Coccolith morphology is also known to vary with temperature. The ratio between coccoliths of warm and cool water type (e.g. *Discoaster*, *Chiasmolithus*) is a useful tool for indicating the changing paleotemperature through Late Cenozoic time.

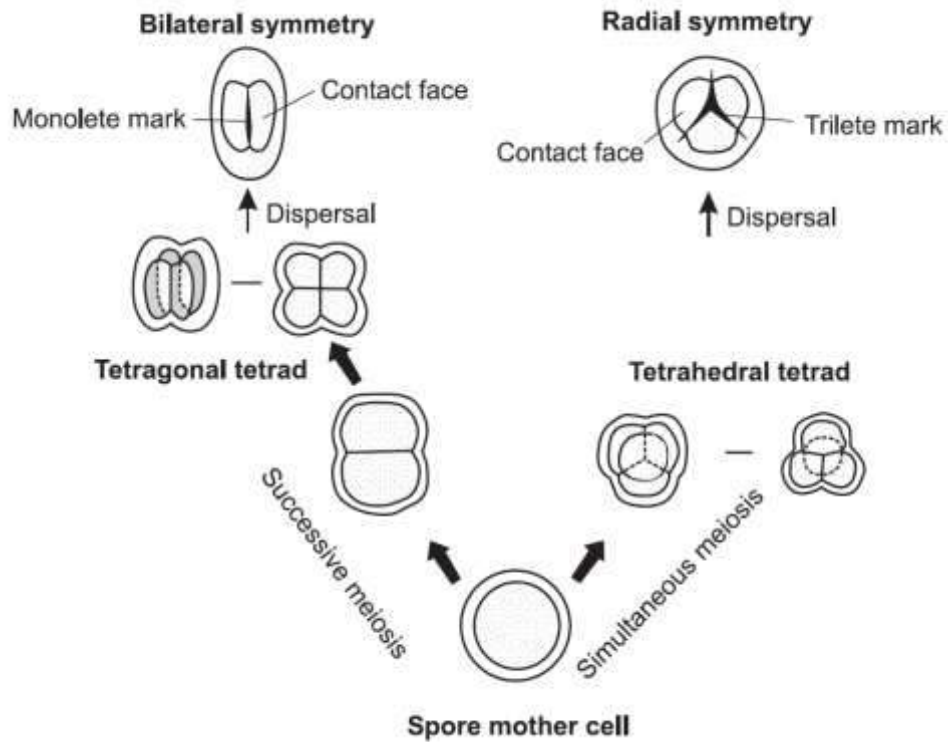
The analysis of stable isotopes from calcareous nannoplankton is hampered by their small size and problems caused by diagenetic overgrowths; typically bulk sediment samples are analysed. In general stable oxygen isotope values in the CaCO₃-living coccolithophores reflects the influence of temperature and vital effects. Despite these problems there is a strong correlation between the $\delta^{18}\text{O}$ values from planktonic foraminifera and coccolithophores through the Pleistocene. The progressive enrichment in $\delta^{18}\text{O}$ values from benthic to planktonic forams to coccolithophores probably reflects their depth of growth. The $\delta^{13}\text{C}$ data from coccolithophores are a better indicator of surface water chemistry and reflect surface productivity

SPORES AND POLLENS

Spores and pollen are produced during the life cycle of plants. Spores are produced by the bryophytes and ferns, and pollen by the gymnosperms and angiosperms. Both types of grain possess a wall that is remarkably resistant to microbial attack and to the effects of temperature and pressure after burial. Produced in vast numbers, these microscopic grains can travel widely and rapidly in wind or water, eventually settling on the bottom of ponds, lakes, rivers and oceans. Such features make them valuable to biostratigraphy, particularly when correlating continental and nearshore marine deposits of Silurian or younger age. Where the ecology of the parent plant is known, spores and pollen can be used for palaeoecological and palaeoenvironmental studies.

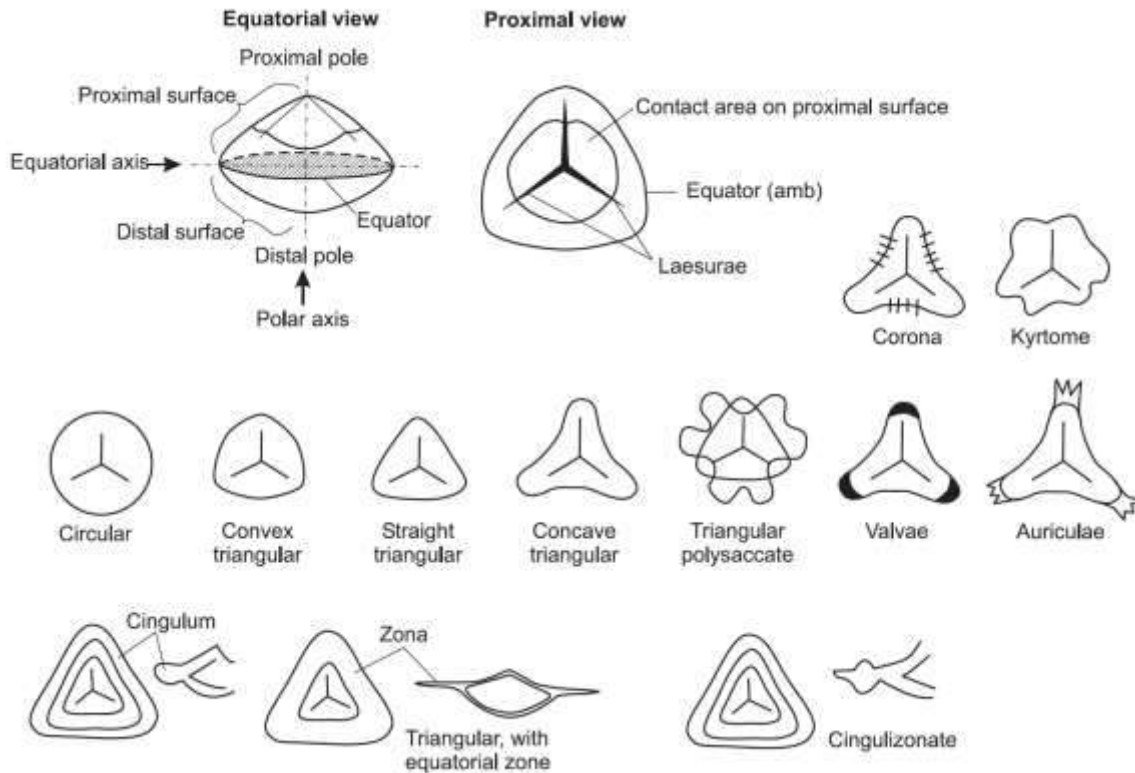
Spore morphology

The morphology of spores can be described according to their **shape, apertures, wall structure and size**. The shape of a spore owes much to the nature of the **meiotic divisions** of the spore mother cell. In simultaneous meiosis, the mother cell splits into a tetrad consisting of four smaller cells. In tetrahedral tetrads each of the four spores is in contact with all three of its neighbours on the proximal face.



Meiosis and the production of bilaterally or radially symmetrical spores.

The proximal face is characterized by three contact areas that are defined by a Y-mark or trilete mark centred on the proximal pole. The arms of the trilete mark may extend to the equator and can take the form of raised ridges or fissures in the surface, laesurae. The exterior surface of the spore in the tetrad is the distal polar face.

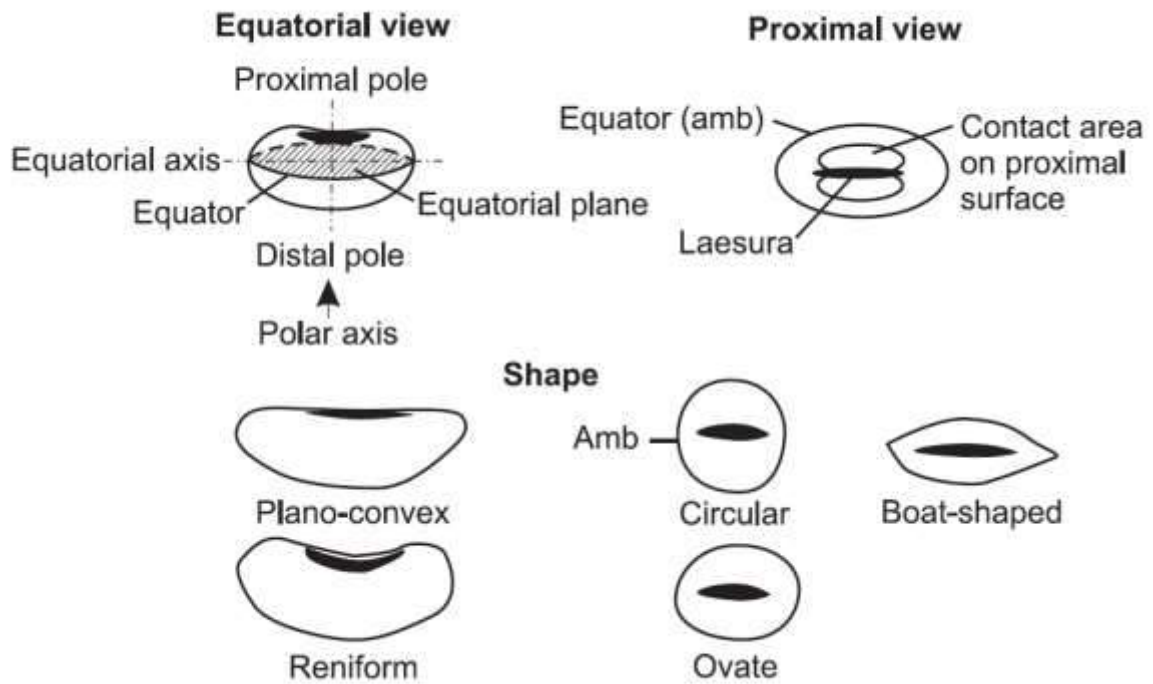


Morphology and terminology of trilete spores.

In successive stages of meiosis, the mother cell divides at first into two cells, these subdivide further along a single plane at right angles to the first division, or along two planes at right angles. The tetrads here are tetragonal and may resemble the segments of an orange in shape; each spore is only in contact with two of its neighbours and only has two contact areas and a single scar. These spores are often bean-shaped. Spores are most commonly compressed proximo-distally in fossil material. The equatorial contour is called the amb.

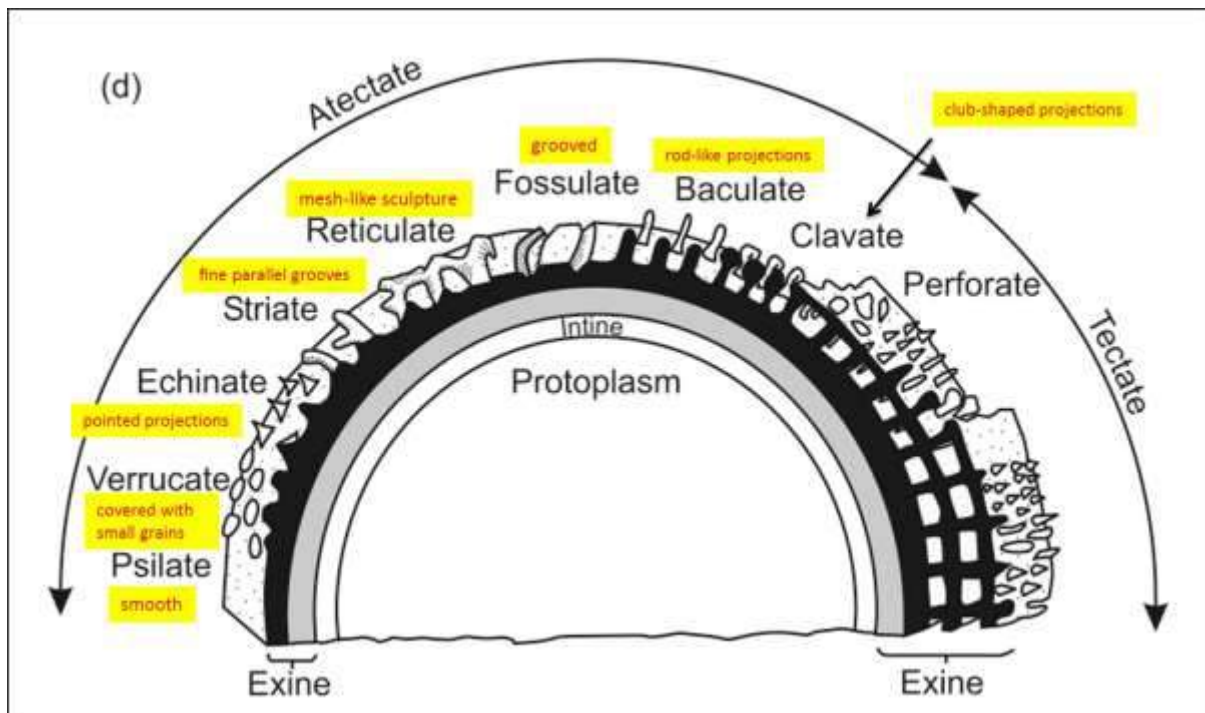
The spores of vascular plants are characterized by well-formed and consistently placed germinal apertures. These allow ready germination of the prothallus and accommodate size changes caused by fluctuations in humidity. The form and position of these apertures are important in describing and classifying fossil spores (and pollen). Trilete spores have three laesurae, which radiate 120 degrees from the proximal pole. The symmetry of trilete spores is therefore radial, but heteropolar, i.e. with differently formed polar faces.

Monolete spores tend to be less common, although they may be abundant in Palaeogene-Recent assemblages and only have one proximal laesura (the monolete mark) which separates the contact areas. The symmetry of monolete spores is therefore bilateral and heteropolar. Some spores that bear tetrad scars but lack laesurae possess a hilum. This can be developed on either the proximal or distal faces and functions as the germinal exit in many bryophytes. Spores lacking any apparent dehiscence structures are termed alete.



Morphology and terminology of monolete spores.

The development of a multilayered wall structure of spores and pollen is markedly different and the two may not be homologous.



Wall structure and surface ornament of angiosperm pollen

The inner cellulose layer, or the endospore, rarely survives fossilization, the exospore is either a single layer or multi-layered and consists largely of sporopollenin. The perispore is external to the exospore and is composed of sporopollenin material that is more electron dense than the exospore. The wall of many fossil spores (the sporoderm) has only one exine layer. Where two layers are present they can be in contact (acavate) or are separated to varying degrees (cavate). The cavum is most commonly developed in a distal or equatorial position. The layers may be homogeneous or finely lamellate. The layers can be uniform in thickness or variably thickened. A continuous equatorial thickening is known as a cingulum; a continuous equatorial flange is a zona. Spores with composite equatorial features are termed cingulizone. Discontinuous equatorial features usually developed in the radial areas are valvae (smooth) and auriculae (ear-like thickenings commonly fluted). The inter-radial areas can also develop flanges, coronae or kyrtoemes.

Pollen morphology

Gymnosperm pollen varies from small, simple, spherical and inaperturate to large bisaccate and ornamented grains and polyplicate forms. Saccate pollen is characteristic of the gymnosperms and grains can bear one (monosaccate), two (bisaccate) or rarely three sacs (trisaccate). The wall of the pollen grain comprises two layers, the outer, highly resistant exine and the inner intine that surrounds the cytoplasm.

Distribution and ecology

In a general way spores and pollen reflect the ecology of their parent plants. Because of size sorting in sediments, however, the leaves, wood, seeds and spores of a plant are rarely preserved together. The habitat and ecology of the spore- and pollen-producing plants can, none the less, be inferred, but an understanding of dispersal and sedimentation must precede this.

Dispersal and sedimentation

The distance travelled by air-borne pollen and spores depends greatly on their size, weight, sculpture and on atmospheric conditions. They are most frequently found about 350–650 m above the land surface during the day, but many sink to the surface at night or are brought down by rainfall. Under favourable conditions pollen grains have been known to drift for at least 1750 km, but about 99% tend to settle within 1 km of the source. Only a very small proportion ever reaches the oceans by aerial dispersal. Once the pollen grains or spores have settled, they stand a chance of entering the fossil record, either by falling directly into bogs, swamps or lakes, or by being washed into them and into rivers, estuaries and seas. By this stage the pollen record has already been filtered by differential dispersal in the air and may now undergo a similar filtering in water. For example, size sorting across the continental shelf can occur; large miospores, pollen grains and megaspores will tend to settle out in rivers, estuaries, deltas or shallow shelf areas, whereas small miospores and pollen grains may settle out in outer shelf and oceanic conditions. Those which are not buried in reducing sediments will tend to become oxidized and may ultimately be destroyed. Spores and pollen may suffer several cycles of reworking and redeposition, leading to some confusion in the

fossil record. Experienced palynologists detect these reworked forms by differences in preservation (e.g. colour, corrosion, abrasion and fragmentation), ecological or stratigraphical inconsistencies and associated evidence for reworking.

Geological history

Sediments from deltaic and lacustrine deposits of Mid-Ordovician to Early Silurian age yield cryptospore monads, dyads, triads and tetrads. Palynological preparations of this age can also contain tubes and sheets of cuticle that may represent debris from the first subaerial plants. The first macroplant remains of *Cooksonia* are found in deposits of Late Silurian age. From this time onwards the number of macroplant fossils and spore types found increases dramatically, reflecting a major diversification in primitive plants. The parent plants of these early spores appear to have had cosmopolitan distributions.

The Devonian probably marks the acme of pteridophytic plants. These were joined in the Early Devonian by the progymnosperms which produced true seeds and pollen grains by the Late Devonian. Initially these primitive pollen grains were indistinguishable from trilete miospores and as a result have been called pre-pollen. Increasing provinciality during the Devonian led to distinct equatorial-low latitude (North American-Eurasian), Australian and southern Gondwana floras. This increase in provincialism may have been a response to the greater latitudinal spread of the Devonian continents or global cooling associated with the onset of glacial conditions.

The importance of true megaspores seems to have declined after the Carboniferous, until the Jurassic and especially the Cretaceous when they may be common again in non-marine deposits. Carboniferous floras are extremely well known due largely to extensive coal deposits. Carboniferous coal swamps were characterized by lycopsids, seed-fern trees and shrubs, sphenopsid trees and shrubs, and shrub cordaitaleans such as cordaites which comprised primitive conifers. Tropical deltas have been used to provide analogues for Carboniferous coal swamps. Many spore-plant associations are known for the Carboniferous. Some plants produced more than one spore type in the same microsporangium.

By the Permian the seed and pollen habit of the gymnosperms had become the dominant life cycles and pollen grains increasingly replace spores in Mesozoic palynological assemblages, particularly from mid-Cretaceous onwards, following the early evolution of the angiosperms. The pteridosperms or seed ferns were the first plants to produce pollen. They evolved from the pteridophytes, although the exact nature of this event is unclear; the heterosporous pteridophytes were probably an intermediate stage in their emergence. The oldest known pollen, termed pre-pollen, dates from the Late Devonian (Famennian). Gymnosperm pollen with distal germination is first found in Upper Carboniferous deposits. A large number of gymnosperm pollen types evolved in the later Palaeozoic. Saccate pollen grains are the most easily recognized of these and are common among many groups, including the extinct pteridosperms and conifers and cordaitaleans. Monosaccate grains were more common than bisaccates during the Carboniferous, Early Permian and Late Triassic.

Angiosperms evolved from a group of advanced gymnosperms, though the precise relationships are controversial. Angiosperm pollen characteristics include a non-laminate endoexine and a fully differentiated ectexine and many angiosperm pollen grains are triaperturate. The palynological record suggests the angiosperms arose during the Early Cretaceous. *Clavatipollenites hughesii* (Barremian, Lower Cretaceous) is one of the earliest angiosperm pollen grains; it is monosulcate and has a columellate, tectate exine. Either changes in palaeoclimate and palaeogeography may have controlled this geographical spread, or plants evolved rapidly and migrated into cooler latitudes. The appearance of tricolpate pollen was a major evolutionary innovation and this, plus a seed protected by carpels, was among the reasons for the success of the earliest angiosperms. All the structural features found in modern pollen grains had evolved by the end of the Cenomanian. As angiosperms diversified during the Late Cretaceous they became more provincial in their distribution. The modern flora emerged gradually from the Neogene onwards mainly by extinction of relict Cretaceous and Palaeogene species. Two new modern groups that became widespread in the mid-Tertiary are the Asteraceae (the composites) and the Poaceae (the grasses). They arose as a consequence of climate deterioration and have become the most successful of the modern groups, with a vast number of living species. The morphology of their pollen is very different because the grasses are anemophilous and the composites entomophilous. The pollen of the grasses is simple spheroidal and monoporate and is the major cause of hayfever. The structure of modern plant communities has developed since the last ice age and due to the influence of man some communities have only become established in the last 200 years.

Applications of fossil spores and pollen

Spores and pollen provide a continuous record of the evolutionary history of the vascular plants. Spores were first utilized economically in coal-seam correlation and biostratigraphy and now have wide-ranging uses in source rock provenance and palaeoenvironmental, palaeoecological and phytogeographical studies. Spores and pollen grains are widely utilized in hydrocarbon exploration through thermal maturity studies (Thermal Alteration Index (TAI) and equivalents) and palynofacies analysis. Spores and pollen in association with other palynomorphs have an application in delimiting palaeoshorelines.

Spores colour	SCI
Pale yellow	1
Pale yellow- lemon yellow	2
Lemon yellow	3
Golden yellow	4
Yellow orange	5
Orange	6
Orange brown	7
Dark brown	8
Dark brown- black	9
black	10

Spores and pollen colour	Thermal alteration index	Petroleum generation
Pale yellow- yellow	1	Immature kerogen
Yellow to light orange –medium orange	2	Oil window
Dark brown	3	Gas window
Brownish black to black colour	4	wet gas limit – dry gas preservation
Vitreous black- fossils brittle	5	Dry gas preservation limit

FORAMINIFERA

The Foraminiferida 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 foraminiferid cell is largely enclosed within a shell or test, variously composed of calcite, 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. Foraminiferid 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, foraminiferid tests typically vary from a few individuals per kilogram to rock-forming *Globigerina* ooze and Nummulitic limestone. Foraminifera are important as biostratigraphic indicators in marine rocks of Late Palaeozoic, Mesozoic and Cenozoic age because they are abundant, diverse and easy to study. Planktic foraminifera are widespread and have had rapidly evolving lineages, factors which greatly aid the inter-regional correlation of strata in the Cretaceous, Palaeogene and Neogene. 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 mm³ in volume and have complex internal structures which,

when studied in thin section, are useful for the biostratigraphy of Tethyan and other tropical limestone. These include the largest single-celled organisms known, reaching up to 180 mm across. Because the developmental stages and foraminiferid life history are preserved in the test, they are well suited to evolutionary studies. 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 because isotopes within their CaCO_3 tests record changes in temperature and ocean chemistry.

The test

The test is thought to reduce biological, physical and chemical stress. Biological pressures include the risk of accidental ingestion, predators or infections. 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_2 , O_2 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. CaCO_3 shells may also help to buffer the acidity of organic-rich, oxygen-deficient environments or digestive tracts.

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 planktic forms (e.g. spines and keels), improve adherence, strengthen the test against crushing and help to channel ectoplasmic flow to and from the apertures, pores and umbilicus.

Foraminiferal ecology

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 planktic 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*

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 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 (e.g. *Lagena*, Fig. 15.4b, 15.22e) and may lead a parasitic mode of life. It is thought to protect the cytoplasm from damage in shallow equatorial waters by scattering the short wavelength, ultraviolet light.

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 planktic forms. Although foraminifera have been found living up to 200 mm below the sediment surface, the majority are found within the top 10 mm or live at the surface. 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.

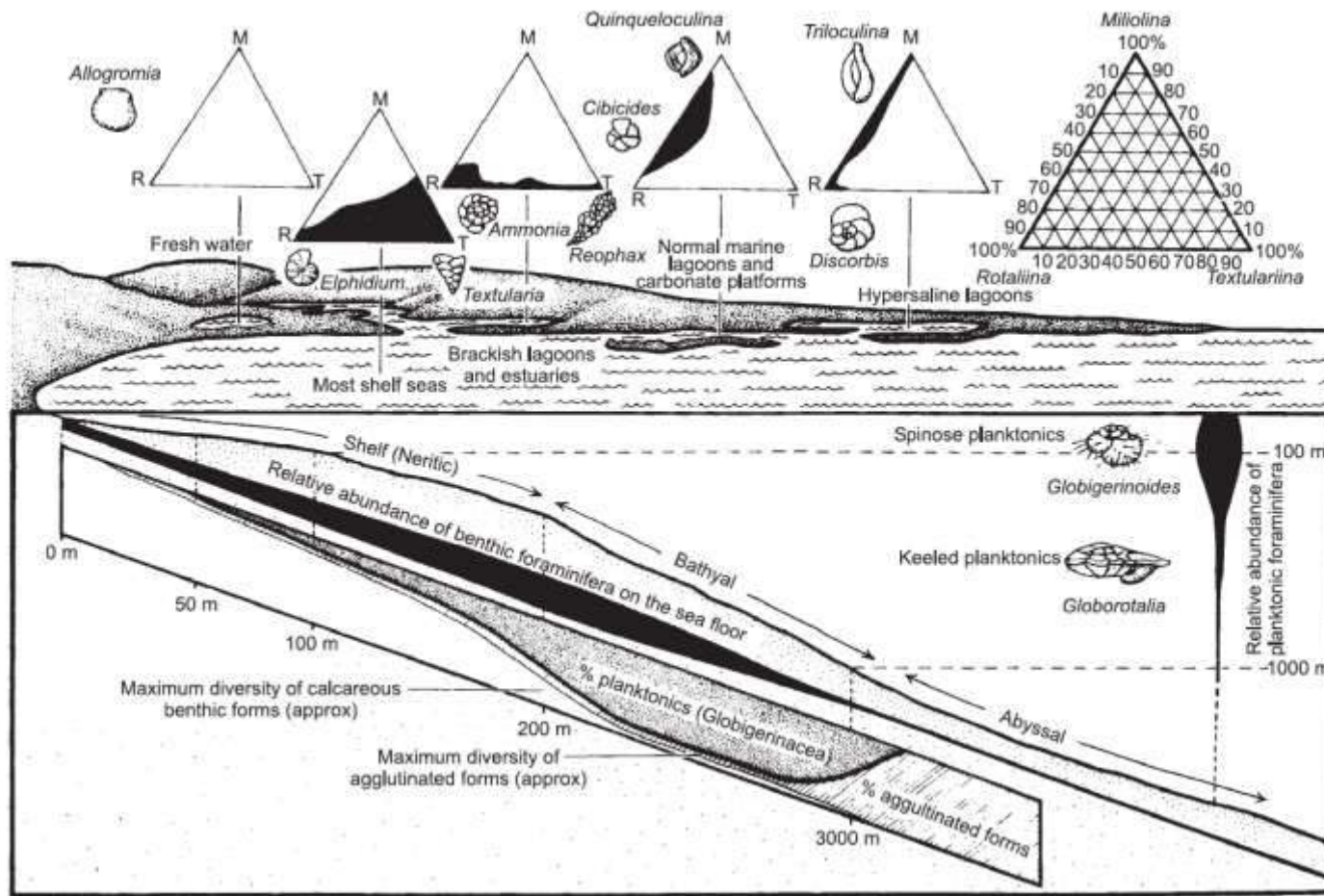
Salinity The majority of foraminifera are adapted to normal marine salinities (about 35‰) and the highest diversity assemblages are found here. The low salinity of brackish lagoons and marshes favours low-diversity assemblages of agglutinated foraminifera and certain hyaline forms. The high carbonate ion concentrations of hypersaline waters, where salinities are in excess of 40‰, appear to favour the porcelaneous *Miliolina* but deter most other groups. It seems that the imperforate tests of *Textulariina* and *Miliolina* are better at protecting the endoplasm from the stressful osmotic gradients of extreme salinity. Triangular plots of the relative proportions of *Textulariina*, *Miliolina* and hyaline forms have therefore proved useful as indices for palaeosalinity.

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 cm²) 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 planktic 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

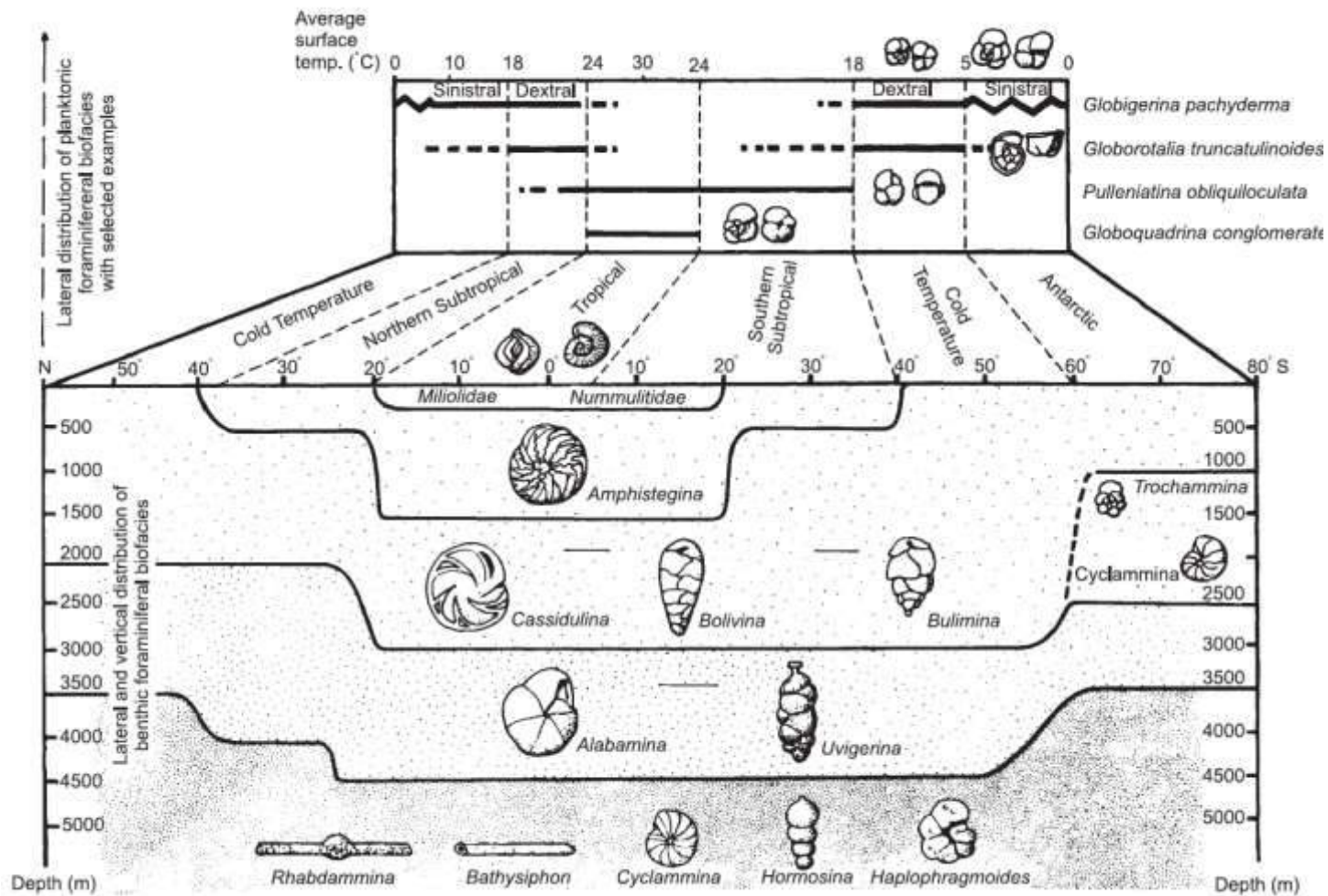
biota, with densities over 1000/10 cm². Oxygen deficiency does not entirely eliminate microscopic organisms such as foraminifera, presumably because of their low oxygen demand and the high diffusion rates associated with a high surface area–volume ratio.

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°C but the bottom waters of the abyssal plains may average less than 4°C. These cooler, deeper waters are characterized by cool-water benthic assemblages that otherwise are found at shallower depths nearer the Poles.

Water mass history Until the 1970s it was widely thought that certain smaller, hyaline, benthic foraminiferal species were adapted to specific water depths, largely controlled by temperature, and could therefore be used to estimate ancient water depth (palaeobathymetry). Research has since shown that these species are closely tied to specific water masses. For example, *Epistominella* is typical of North East Atlantic Deep Water, *Fontbotia* of North Atlantic Deep Water and *Nutallides* of Antarctic Bottom Water. This means that the ancient distribution of such benthic species can be used to reconstruct the history of a specific water mass in relation to changes in global climate or in basin geometry.



How benthic and planktic foraminiferid assemblages (and some typical taxa) change with depth and latitude in the Pacific Ocean, especially in relation to temperature



How benthic and planktic foraminiferid abundance and general composition change with depth and salinity. Some typical genera are shown.

Diversity This refers to the number of taxa in an assemblage. In living assemblages one species is normally found to be more abundant than any other and is said to be dominant. Species dominance is commonly expressed as a percentage of the population, and lower dominance tends to be found with higher diversity. The diversity of modern benthic foraminiferal assemblages from marginal marine habitats is less than that of normal marine and deep sea habitats. Higher diversity of the latter may be taken to suggest greater partitioning of resources among species. Conversely, oscillations in environmental stability, such as found in marshes and lagoons, result in foraminiferid blooms of great abundance but lower diversity.

Larger benthics

Larger benthic foraminifera live largely in oligotrophic reef and carbonate shoal environments where terrestrial and seasonal influences are slight. They culture endosymbiotic diatoms, dinoflagellates, rhodophytes or chlorophytes. These endosymbionts release photosynthates to their hosts and also take up respiratory CO₂ during photosynthesis, which allows for high rates of CaCO₃ precipitation during test growth. It follows that larger foraminifera are very sensitive to light levels. The depth distribution of living larger benthic foraminiferal taxa is also closely related to the light wave lengths required by their symbionts. It therefore appears that fossil larger benthic foraminifera, which have evolved repeatedly since the Carboniferous, have achieved their great size (up to 180 μm in Oligocene) 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 seagrass 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 CaCO₃/m² 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 Permian 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.

Planktic foram ecology

The environmental controls on plankticforaminifera 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.

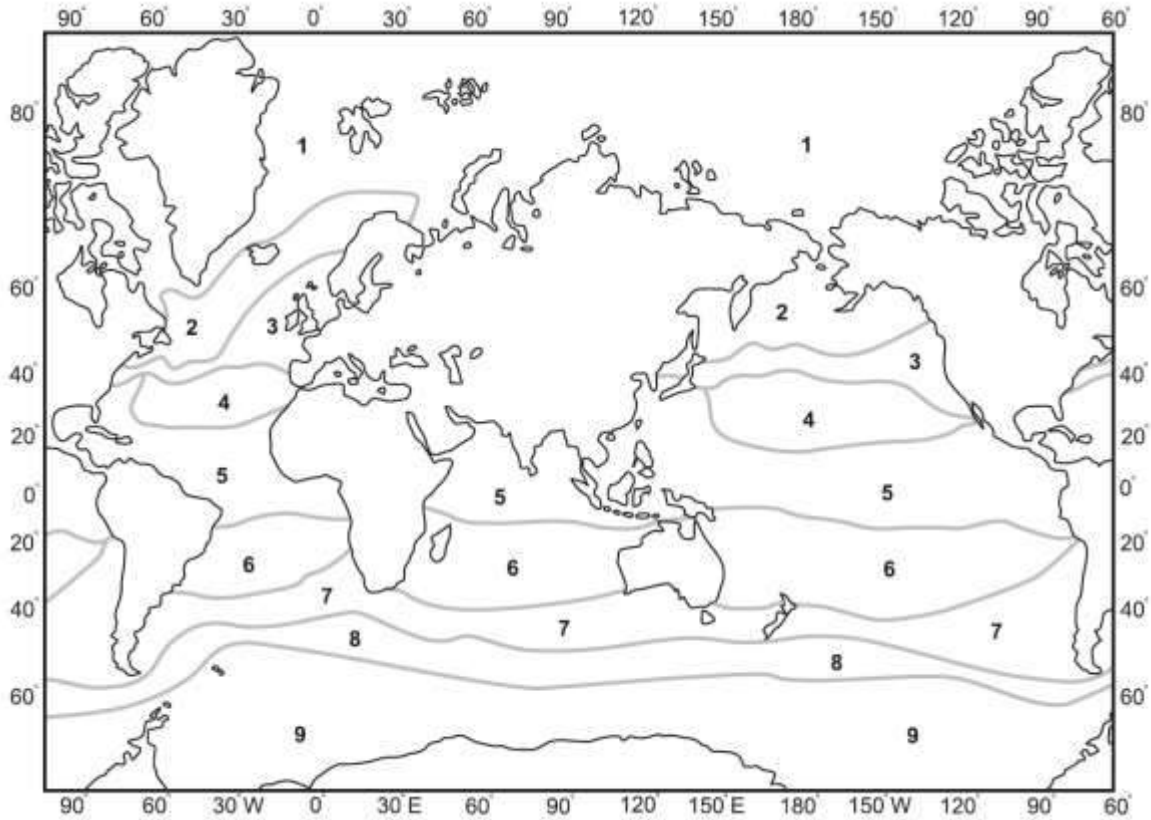
Depth and food

There are about 100 species of living planktic foraminifera. They tend to be small (mostly <100 µm) 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 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 planktic forms have to cope, however, with the effects of CaCO₃ 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

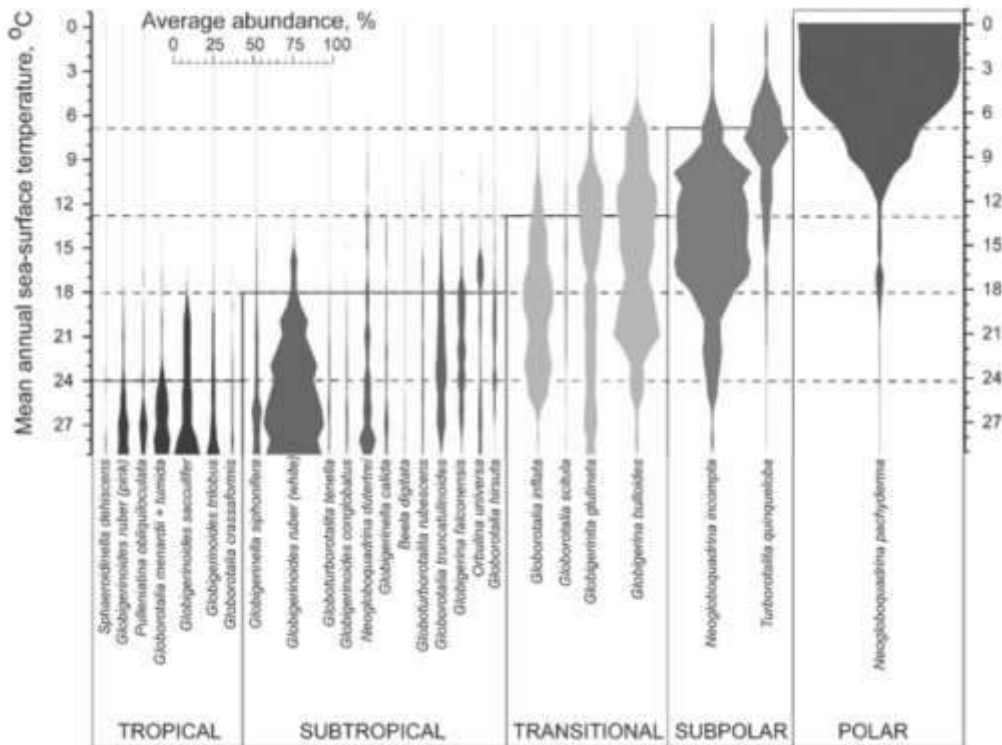
Temperature and latitude

Modern assemblages can be arranged into five biogeographic provinces: 1. Polar (includes Arctic and Antarctic); 2. Subpolar (includes Subarctic and Subantarctic); 3. Transitional; 4. Subtropical and 5. Tropical. It is called the latitudinal provincialism in planktic foraminifera. A number of trends should be noted here. The distributions are bipolar, so that a few species are characteristic of both northern and southern subtropical waters. The number of endemic forms, and hence diversity, increases towards the tropics. Keeled forms are not found at higher latitudes in waters cooler than 5°C. Test porosity of shallow and intermediate species also increases towards the equator, presumably in relation to the lower density of warmer water. In *Neogloboquadrina pachyderma*, subpolar and polar populations can be distinguished by a predominance of left- (sinistral) or right-handed (dextral) coiling. 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 planktic foraminifera preserved in deep sea cores.

Almost two-thirds of the world oceans are covered by the warm-water provinces. The boundary between the warm subtropical and colder transitional province is marked by the annual isotherm of 18⁰C, which corresponds approximately to the latitude of balanced radiative heat budget. Most extant species are cosmopolitan within their preferred bioprovince, although three Indo-Pacific (*Globigerinella adamsi*, *Globoquadrina conglomerata*, *Globorotaloides hexagona*) and one Atlantic tropical species (*G. ruber* pink) are endemic.



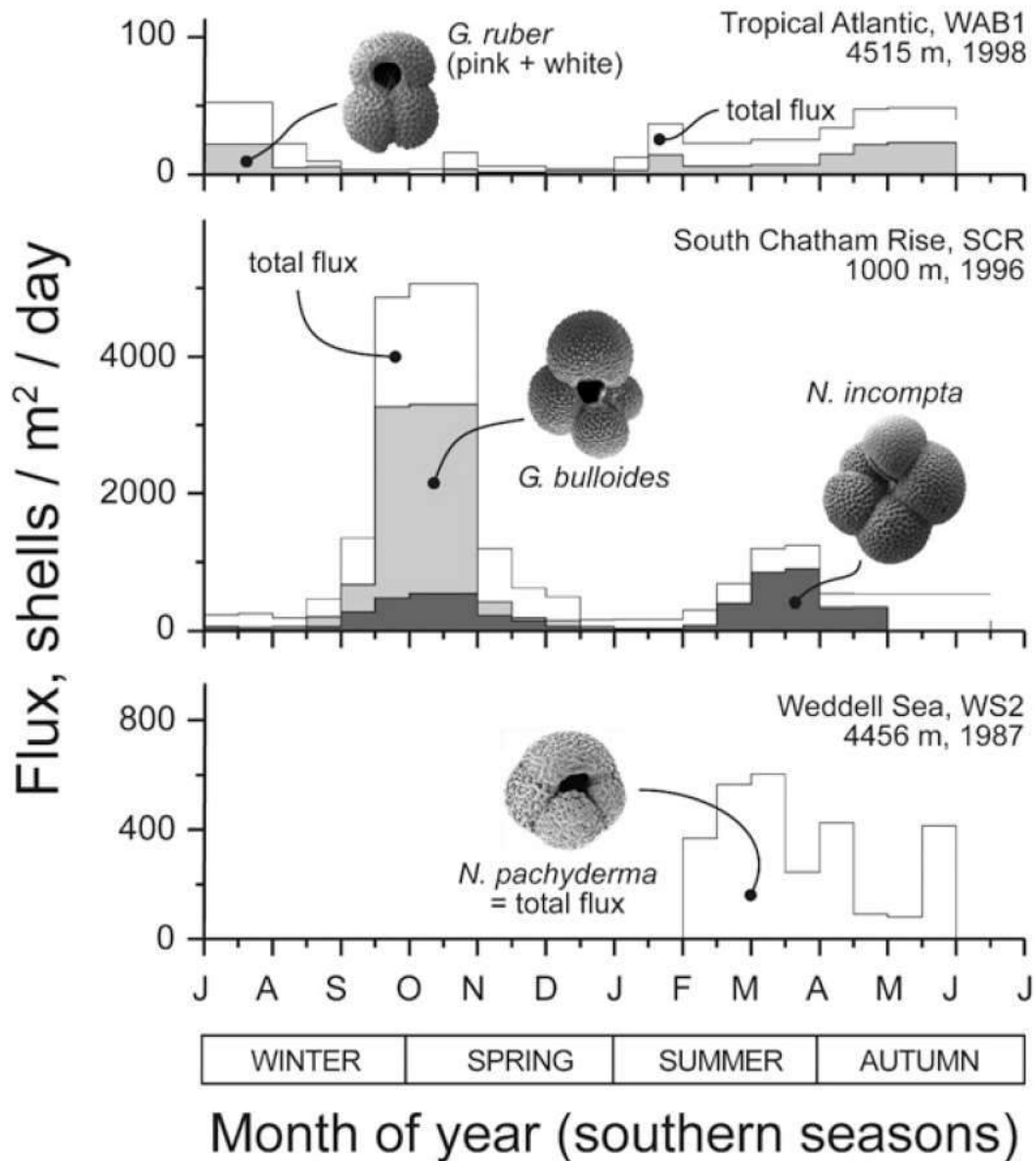
Modern planktic foraminiferal provinces. 1, Arctic; 2, subarctic; 3, transitional; 4, subtropical; 5, tropical; 6, subtropical; 7, transitional; 8, Subantarctic; 9, Antarctic.



The distribution and abundance of plankticforaminifera species is strongly linked to surface-water properties. Sea-surface temperature (SST) appears to be the single most important factor controlling assemblage composition, diversity, and shell size. Planktic foraminifera species survive under a considerable range of SST, but that their optimum ranges, defined by highest relative and absolute abundances, are typically narrow and distinct. At present, the polar waters of both hemispheres are dominated by a single small species (*N. pachyderma*), while the highest diversity and largest sizes are found in the oligotrophic subtropical gyres. The increase in SST toward the equator is accompanied by a proportional increase in surface-water stratification. The strength of vertical gradients in the ocean determines the number of physical niches available for passively floating plankton, and may thus control their diversity and morphological disparity.

The general trend toward higher diversity and larger sizes with increasing SST is reversed in equatorial and coastal upwelling zones, which are characterized by higher population densities of smaller species. Large, symbiont-bearing carnivorous specialists are adapted to oligotrophic conditions, and in high-productivity regimes they are easily outnumbered by omnivorous and herbivorous species such as *Globigerina. bulloides* and *Globigerinita glutinata*.

These opportunists can rapidly react to organic particle redistribution and phytoplankton blooms following nutrient entrainment. Episodic pulses of primary productivity, coupled with the seasonal SST cycle result in predictable successions of plankticforaminifera species, which react to the changing environmental conditions according to their ecological preferences. Such successions have been documented in numerous sediment-trap studies and their understanding is of great importance for geochemical proxies. In general, the flux rate of plankticforaminiferal shells follows primary productivity cycles with a lag of several weeks. In polar oceans, the flux peak is observed during the summer, whereas in temperate oceans the spring flux maximum is often followed by a smaller autumn peak. Tropical and subtropical oceans are characterized by a steady rain of foraminiferal shells throughout the year.



Typical patterns of annual cycle of planktic foraminifera shell flux in polar, temperate, and tropical oceans. The flux in the polar ocean is limited to ice-free conditions; in temperate oceans it is typically focused into two seasonal peaks, each dominated by different species, and the oligotrophic tropical waters are characterized by extremely low and even fluxes throughout the year.

Within the range of normal marine conditions (33–36‰), salinity does not appear to exert any significant influence on planktic foraminifera. Laboratory experiments indicate that some species can tolerate a remarkable range of salinities (*G. ruber*: 22–49‰) and that salinity tolerances differ among species. In nature, no planktic foraminifera are known to live under hyposaline conditions. *N. pachyderma* is known to avoid low salinity (<32‰) surface layers. Low salinity waters are also inhabited by a distinct assemblage dominated by *G. ruber* pink and *Neogloboquadrina dutertrei*. At the other end of the spectrum, planktic foraminifera inhabiting the Red Sea live at salinities in excess of 40‰ and the Antarctic *N. pachyderma*

live in sea-ice where brine salinities exceed 80‰. The influence of ecological factors other than temperature, salinity, and fertility is difficult to disentangle, because most surface-water properties are strongly inter-correlated.

Planktic foraminiferal densities can be very high around the margins of oceanic gyres, where upwelling and mixing take place and nutrient levels are high. Where seasonal perturbations take place at lower latitudes (e.g. with monsoonal upwelling), then an ecological succession of species is found. In a transect across the inner shelf to bathyal slope, there is typically an increase in the ratio of planktic to benthic tests within the total foraminiferal assemblage. This takes place in part because an increase in water depth increases the biomass of plankton above a given area of sea floor and in part because the food supply reaching the sea floor tends to diminish as water depth increases. The ratio is only a crude index of palaeobathymetry, however, because local conditions can vary the test production rate of either planktic or benthic foraminifera.

***Globigerina* ooze**

Planktic foraminifera are important contributors to deep sea sedimentation and, with coccoliths, account for more than 80% of modern carbonate deposition in seas and oceans. At present the foraminifera contribute more than the coccolithophores, although this was not the case during Mesozoic.

Three factors are important in controlling the deposition of *Globigerina* ooze (i.e. ooze in which over 30% of sediment comprises of the shells of *Globigerina* planktic foraminifera): (i) climate, (ii) depth of the lysocline and (iii) terrigenous sediment supply.

The position and strength of currents, especially diverging and upwelling currents, are greatly affected by climate and hence affect the plankton productivity. The empty foraminiferal tests settle quite rapidly and are less susceptible to dissolution than coccoliths (which lack organic outer layers), except when they approach the lysocline which usually lies between 3000 and 5000 m depth. Fluctuations in the depth of the calcite compensation depth during the Mesozoic and Cenozoic are now known to have caused cycles of deposition and dissolution, selectively removing some of the smaller or more delicate forms and rendering the fossil record of the deep sea incomplete. Even where the conditions are otherwise favourable, *Globigerina* oozes cannot accumulate where there is an influx of terrigenous clastics, hence they are rarely found on continental shelves. At present such oozes are mainly accumulating between 50°N and 50°S at depths between about 200 and 5000 m, especially along the mid-oceanic ridges. In many cases, though, they are diluted with the siliceous remains of diatoms and radiolarians.

Calcite compensation depth (CCD)

The solubility of CaCO₃ is less in warm than in cool waters. This in part favours the thicker tests and the occurrence of foraminiferid limestones and oozes at low latitudes. More important, however, is the vertical change in CaCO₃ solubility, which also increases with greater pressure, and hence with greater depth in the ocean. The partial pressure of CO₂ also

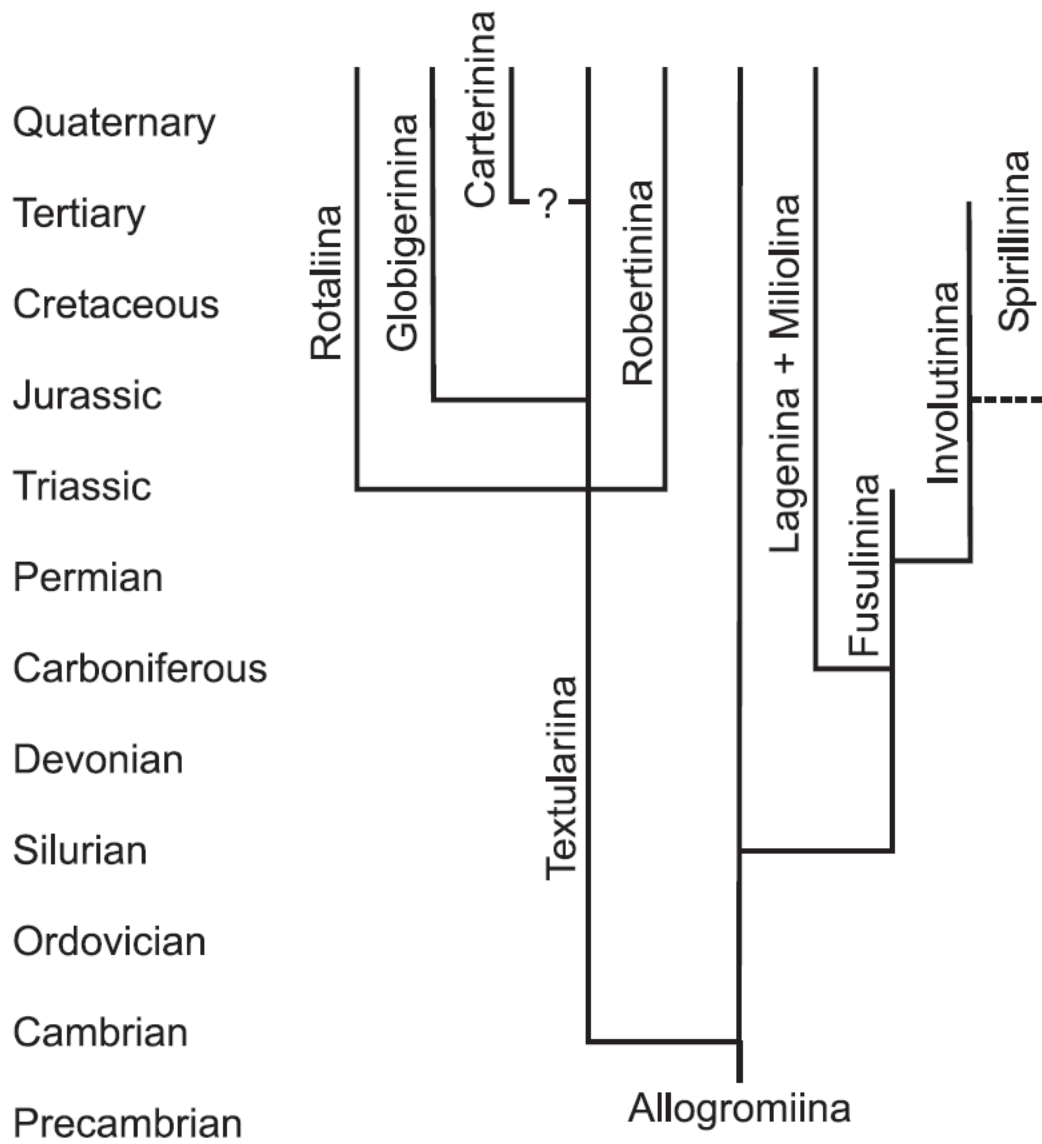
increases with depth because there is no photosynthesis below the photic zone, although animals and bacteria continue to respire. These factors led to a decrease in pH with depth, from about 8.2 to as low as 7.0. The level in the water column at which CaCO_3 solution equals CaCO_3 supply is called the 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.

Geological history of foraminifera

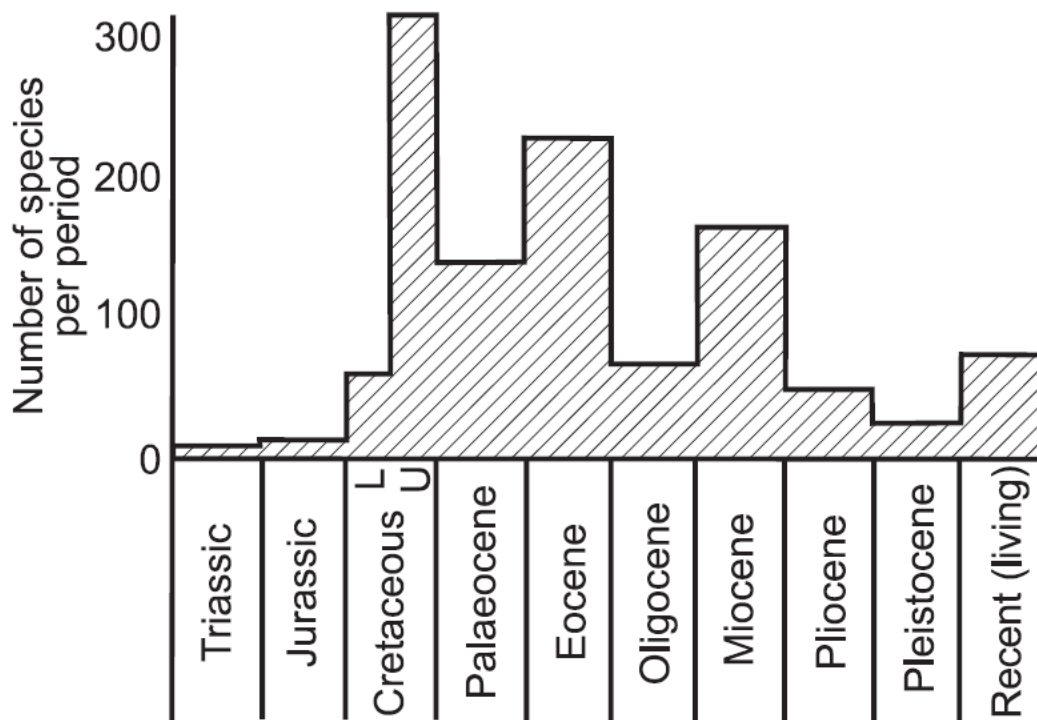
The oldest fossil foraminifera are simple, agglutinated tubes in the earliest Cambrian resembling the modern genus *Bathysiphon* indicating shelled protozoa appeared at the same time as shelled invertebrates. Agglutinated foraminifera became more abundant in the Ordovician but true multichambered forms did not appear until the Devonian, during which period the Fusulinina began to flourish, culminating in the complexly constructed tests of the Fusulinacea in Late Carboniferous and Permian times. This super-family died out at the end of the Palaeozoic. Miliolina and Lagenina first appeared in the Early Carboniferous. Important Mesozoic events include the appearance and radiation of the Rotaliina, Miliolina and complex Textulariina in the Jurassic, soon followed by the appearance of the first unquestionably planktic foraminifera. Cretaceous tropical regions witnessed a flowering of larger miliolines and rotaliines while the widespread chalk seas and newly opened Atlantic Ocean favoured a thriving planktic population.

The planktic Globotruncanidae became extinct at the end of the Cretaceous. In the low latitude Tethys Ocean about 75% of species disappeared at or near the K-T boundary. Extinction was highly selective and only ecological generalists survived. This mass extinction pattern coincides with dramatic changes in temperature, salinity, oxygen and nutrients across the boundary, the result of both long-term environmental changes (e.g. climate, sea level, and volcanism) and short term effects such as the proposed bolide impact.

A relatively rapid radiation followed in the Palaeocene with the appearance of the planktic Globigerinidae and Globorotalidae and in the Eocene with the development of Nummulites and soritids in the Old World and orbitoids in the New World, although they eventually became almost worldwide. Orbitoids died out in the Miocene, since which time larger foraminiferal stocks have progressively dwindled in distribution and diversity, mostly because of climatic deterioration. Planktics have also diminished in diversity since Late Cretaceous times.



Phylogeny of the Foraminifera



Changes in the specific diversity of planktic foraminifera through time. Because of the complex evolutionary history, the likely existence of many cryptic taxa and the varied life habits and habitats measures of standing diversity in the foraminifera are probably less meaningful than in other groups.

Applications of foraminifera

Foraminifera are in many respects ideal index fossils for marine rocks, being small, abundant, widely distributed and often extremely diverse. Many also have an intricate morphology in which evolutionary changes can be readily traced. Planktic foraminifera provide the basis of important schemes for intercontinental correlation of Mesozoic (especially upper Cretaceous) and Cenozoic rocks. Benthic foraminifera tend to be more restricted in distribution but provide useful schemes for local correlation. Environmental interpretations that use fossil foraminifera are founded mainly on comparisons with the numerous studies of modern ecology. For example, dramatic changes in depth, salinity and climate can be traced in late glacial and postglacial raised beaches and beach deposits from studies of their foraminifera (e.g. Bates et al. 2000; Roe et al. 2002). The value of benthic foraminifera as indicators of the depth of deposition has been based on the known depth distribution of modern foraminifera. Trends in species diversity, planktic–benthic ratios, shell type ratios and morphology have been utilized to plot changes in depth. In general terms, species diversity increases offshore to the continental slope, as does the planktic–benthic ratio. Planktic life assemblages are depth stratified and so give rise to higher-diversity death assemblages in deeper waters than in shallower waters. Benthic depth-related assemblages can also be recognized in Cretaceous sediments.

The planktic–benthic ratio can be used for the interpretation of Jurassic and younger rocks. Test types, the agglutinated–porcelaneous–haline proportions, vary with habitat and this appears to hold into the Palaeogene. Modern marginal marine species are strongly influenced by changes in salinity. In water of normal marine salinity numerous workers have recognized distinctive foraminiferal assemblages in the inner and outer continental shelves, upper slope and deep sea. Recognition of patterns and distribution of deep sea benthic foraminifera are beginning to emerge from the many studies of the upper parts of DSDP and ODP cores. The biogeography of modern foraminifera is related to the distribution of water masses and ocean currents. The palaeobiogeographical patterns of benthic and planktic foraminifera are therefore indispensable in inferring palaeoceanography. At bathyal depths there is a strong correlation between the oxygen minimum zone and the foraminiferal assemblage. Benthic foraminifera are also indicators of productivity in areas of upwelling. The relative abundances of *Cibicides wuellerstorfi* and *Bulimina alazanensis* are related to changes in the advection of North Atlantic Deep Water during the Quaternary. Cretaceous current patterns and ocean stratification have also been reconstructed from the distribution and stable isotope chemistry of foraminifera. Price & Hart (2002) used both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in benthic and planktic foraminifera to document changing oceanic temperature gradients in the Early-Middle Albian of the Pacific Ocean. An increase in ocean temperature (and/or decrease in salinity) in the Cenomanian suggests a reduction of the poleward heat flux, promoting the build up of limited polar ice. Stable isotopes in planktic and benthic foraminifera also indicate a 100–500 kyr long period of instability in oceanic bottom-water temperature and sea level prior to the K-T boundary transition at Stevns Klint, Denmark. During the latest Maastrichtian, bottom water temperatures gradually cooled by about 1.5°C as surface water temperatures remained constant, perhaps consistent with the initiation of a thermohaline circulation and the formation of some polar ice. The narrow temperature ranges of living planktic species have become useful tools in palaeoclimatology especially of Quaternary sediments. *Neogloboquadrina pachyderma* and *Globigerina bulloides* have been extensively used as a paleotemperature proxy from the Late Miocene through the Quaternary, exploiting the modern polar affinity of the sinistrally coiled forms. However, the relationship between sea surface temperature and coiling direction is not a simple one. Pliocene and Pleistocene sinistral forms of *N. pachyderma* are morphologically and ecologically different and the modern sinistral form only appeared ~1 Myr. This suggests that *N. pachyderma* (sinistral) should not be used for calibrated paleoceanographical reconstructions prior to the Middle Pleistocene. *N. pachyderma* (sinistral) may have evolved in response to the onset of the 100 kyr climate regime in the Middle Pleistocene. The proportions of sinistral and dextral forms of *N. pachyderma* and *G. bulloides* have also been shown to change in response to the vigour of oceanic upwelling.

Studies on the oxygen isotope ratios of calcareous foraminiferid shells have become one of the primary tools in palaeoceanographic and palaeoclimatic studies.

Paired Mg/Ca and $^{18}\text{O}/^{16}\text{O}$ measurements are being made on both benthic foraminifera to separate global temperature and ice volume changes during the Cenozoic and even to challenge those hypotheses that relate to ice advance to orbital forcing. Differences in the

$\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ between shallow- and deep-living planktic foraminifera are proxies for the stratification of surface waters.

Foraminifera are particularly useful in palaeoecology and palaeo-oceanography when used in association with other palaeoceanographic proxies. Many case studies are available from the Cenozoic or document global cooling events at the Eocene–Oligocene boundary, Miocene and during the Quaternary with the most studied events. The onset and orbital forcing of the Messinian Salinity Crisis has been documented with the help of foraminifera and even changes in solar irradiance have been inferred from the $\delta^{13}\text{C}$ profile in *Globigerinoides ruber* over the last 2000 years. The tectonic history of opening and closing of ocean gateways have been reconstructed with the help of planktic foraminifera.

Foraminifera have been extensively used in hydrocarbon exploration. They are important tools for biostratigraphy, paleoenvironment analysis and biosteering.

PTEROPODS

Pteropods, also known as sea butterflies, are marine gastropods adapted to pelagic life. Some species possess delicate external calcareous shells while others are devoid of it. Pteropods are widespread in the world oceans and after the animals' death their empty shells, together with the skeletal remains of other calcareous planktonic organisms, settle to the sea floor. In certain regions sediments are composed in large part of the remains of calcareous organisms; these sea-floor deposits are termed calcareous oozes. When pteropods constitute a high percentage of the ooze the deposit is called pteropod ooze.

The aragonitic shell of pteropods is much more susceptible to solution than the calcitic skeletal remains of coccoliths and foraminifers. For this reason the depth range of pteropod oozes is considerably more limited than that of coccolith and foraminiferal oozes. They are preserved between about 700 and 3000 m, but depths differ in the various marine basins and depend in part on bottom-water temperatures, circulation, and rates of sedimentation of biogenic and clastic materials. Pteropods are better preserved in basins having high bottom temperatures, sluggish circulation, and rapid rates of sedimentation such as the Mediterranean and the Red seas.

ECOLOGY

Pteropods are exclusively marine and generally live in the open ocean, swimming in the uppermost 500 m; however, some forms are known to live at great depths. The present-day distributional patterns of pteropods are fairly well known. They are ubiquitous and abundant and about eighty species and subspecies inhabit the world's oceans. Their distribution is controlled by various physical and chemical parameters of the environment, such as temperature, salinity, food, oxygen and water depth.

Temperature

Temperature is the main factor governing the distribution of pteropods. At present, well-defined latitudinal temperature gradients exist; from the cold polar regions, temperatures increase progressively toward the equator. This gradual water temperature change is reflected in pteropod population composition.

Salinity

Marine holoplanktonic invertebrates are cold-blooded and have body fluids isotonic with the surrounding water. For this reason they are limited to the narrow salinity ranges of oceanic water. The average sea-water salinity varies between 35‰ and 36‰. The warm regions of

the three major oceans, Atlantic, Indian and Pacific, support a diversified pteropodal fauna. However, in land-locked warm seas where evaporation exceeds precipitation and runoff from land, salinities are much higher than in the open ocean. In the Red Sea with surface-water salinities greater than 40‰ but with temperatures similar to those of the oceans, only about 50% of the oceanic species are known to occur. In the Mediterranean where salinities are intermediate between the Red Sea and the open ocean and temperatures are similar to the oceans at comparable latitudes, about 75% of the open-ocean species have been recorded. Their number decreases from the western Mediterranean basins, where conditions are milder, towards the eastern sector of the sea where salinities are higher, suggesting that salinity rather than temperature controls the distribution of certain species. A small number of pteropods have adapted to low salinities. Occasionally, a few hardy forms survive in deltaic or estuarine regions where large volumes of fresh water drain into the sea and lower salinities considerably. Pteropods apparently cannot survive in the Black Sea where salinities are much lower than those of open ocean waters.

EVOLUTIONARY TRENDS

Phylogenetic relationships among pteropods have been a matter of debate and the precise ancestry and interrelationships within this group are still unknown. It is probable that pteropods evolved from bottom-dwelling littoral gastropods and then adapted to a pelagic mode of life. The coiled *Limacina* and *Peraclis* are thought to be primitive genera. Changes that have occurred within each group may have been adaptive to changing environments and/or adaptation to cope better with the existing environment.

FOSSIL RECORD AND BIOSTRATIGRAPHY

Two living families with known fossil representatives are the Limacinidae, ranging from Eocene to Recent, and the Cavoliniidae. *Clio*, which belongs to the Cavoliniidae, has been found in Upper Cretaceous rocks. *Vaginella*, one of the earliest pteropods, resembling the living *Cuvierina*, ranges from Upper Cretaceous through Miocene. Although many fossil pteropods have been described, their identification and geologic range is still disputed. The rare preservation of pteropods in the geologic record, particularly in pre-Pleistocene sediments, is mainly due to their thin and fragile aragonitic tests which are more susceptible to solution than are those of other marine calcitic microfossils. Therefore stratigraphic divisions as well as correlations over widely separated geographic regions have not been attempted. On the other hand, the usefulness of pteropods in local correlations is well established, particularly in the Mediterranean and Red Sea basins where Quaternary deep sea sediments are composed of pteropodal, calcareous oozes.

PALEOECOLOGY

The Pleistocene was marked by repeated world-wide temperature fluctuations; cold episodes (glacials) were interrupted by mild periods (interglacials) with climates similar to or warmer than those of today. During glacials, air and sea temperatures dropped and continental ice sheets grew as water was extracted from oceans and precipitated on land covering large portions of continental areas on both hemispheres. The repeated waxing of glaciers during cold periods brought about world-wide lowering of sea level by more than 100 m, whereas waning of glaciers during interglacials resulted in sea-level rise.

The distributional patterns of living pteropods indicate that many species have a limited tolerance to changes in temperature and salinity. Accordingly, variations in faunal composition in consecutive sediment layers should reflect changes in climatic and hydrologic conditions at the time of their burial. In addition, other variables determine the composition of faunal remains in sediments. Important among these are variations in production rates, redistribution by currents and burrowing animals, accumulation rates of detrital sediments and solution of calcareous tests.

Recent studies of pteropodal distribution in time and space indicate their usefulness in paleoecology, paleohydrology and paleobathymetry.