Radiolaria

Secondary article

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Radiolaria are marine unicellular microorganisms characterized by skeletons of silica and the presence of cytoplasmic processes radiating from the cell body. Both the fine structure and architectural diversity of the skeletons are used as taxonomic criteria. They have been joined with Acantharia in the phylum Radiozoa Cavalier-Smith, 1987. Radiolaria are used as stratigraphy markers.

Article Contents

Introduction

The phylum Radiolaria was created by Haeckel, who described about 4000 species collected from plankton samples during the *R.V. Challenger* expedition. These protozoa live from the surface to the bathypelagic zone and from equatorial to polar latitude, with maximum abundance recorded in the tropical and subtropical regions. Although they have differentiated buoyancy systems that limit sinking and contribute to flotation in the water mass (large hollow shells, long spines, parachute shape, accumulation of lipids in the endoplasm, formation of bubbles at the cell surface), they are passively transported. The cell is sustained by a mineral skeleton which exhibits remarkable architectural diversity. The central pigmented body of cytoplasm is surrounded by a thick perforated layer, the inner capsular wall. The outer cytoplasm, which harbours symbiotic algae, gives rise to cytoplasmic projections known as axopods and filopods. Radiolaria appeared in the Precambrian era and have evolved little since this period.

Description and Characterization

Radiolaria are exclusively marine planktonic microorganisms, either solitary or colonial. Solitary species are generally spherical, with tiny (20–30 μm) or large (3–5 μm in diameter) body size. Their skeleton of silica forms 1–3 latticed shells. The cell body is divided into a central dense cytoplasm or endoplasm, and a vacuolar ectoplasm (**Figure 1**). The endoplasm is enclosed in a central capsule. The capsular wall is usually thick (up to 1 μm) and is made of several mucoprotein layers. The ectoplasm, extruding from cytoplasmic extensions passing through pores of the capsular wall, is vacuolar and can host endosymbiotic algae. The ectoplasm forms spreading superficial cytoplasm and thin filopods, which are continuously remodelled. The cytoplasm is traversed by radial rods of microtubules that project into long, slender and unramified processes, called axopods. These axopods radiate from the cell surface in all directions. Colonial species are among the largest planktonic protozoa. They consist of an assembly of several cellular bodies, with or without a skeleton.

Mineral skeleton diversity

Although some species lack a skeleton, many Radiolaria are remarkable and diverse examples of the architectural complexity of biological mineralization (**Figures 2** and **3**). Radiolarian skeletons are made of hydrated amorphous silica and consist of 1–3 concentric latticed shells, generally beautifully ornamented with curved spines, ramified apophyses or hollow tubes in species-specific patterns. The morphological characteristics of these skeletons represent the major taxonomic criteria. Almost nothing is known concerning physiology of silica deposition. The mechanism by which silica becomes concentrated in specific patterns, the rate of silica deposition, the extent to which environmental conditions influence these processes and the possible roles of specific ionic channels in allowing silica to pass across membranes all remain to be elucidated.

Structure of axopods

Axopods project several hundreds microns into the surrounding water and are capable of growing and shortening several micrometres in a few minutes. The axopodial cytoplasm includes membrane-bound organelles that move up and down the axopods in a saltatory motion. The axopods are strengthened by microtubule arrays forming the intraaxopodial cytoskeleton. Each array is made of six to several hundred microtubules crossconnected by bridges, seen in cross-section as a variety of open or closed patterns (branched, hexagonal, dodecagonal). Microtubules originate from a single or multiple dense mass of fibrogranular material forming the microtubule organizing centre (MTOC) or axoplast. Single MTOCs are either located in the cell centre within a caveola of the nucleus or are juxtanuclear. Multiple MTOCs are distributed on the outer surface of the capsular wall and are associated with perforated structures, known as fusules.

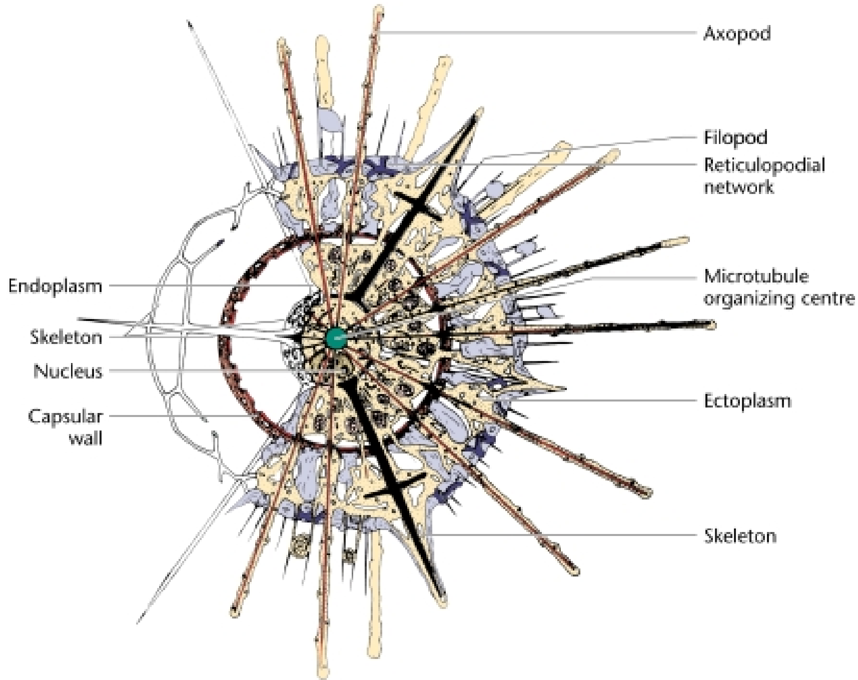

Figure 1 Structure of a polycystid radiolarian. Skeleton (black), microtubule organizing centre and axis of the axopodia (green), capsular wall (red), surface of the cross-section through the cytoplasm (yellow), surface of the cell membrane outside the section plane (blue).

Behaviour and Physiology

Food capture and ingestion

Relatively little is known about food capture and nutrition. Attempts at maintenance and culture of a few species have allowed the analysis of types of prey organisms and how they are digested. Radiolaria use both axopods and filopods and a reticulopodial network for predatory activity. Many species are omnivorous, injesting other protozoans, coloured flagellates and even small crustaceans such as brine shrimp larvae. Prey organisms become entangled in the superficial cytoplasm, then enclosed in a food vacuole, and finally transferred into deeper ectoplasm near the capsular wall, where they are digested.

Symbiosis

Radiolaria harbour endosymbiotic unicellular green or yellow-green algae and zooxanthellae that live in the extracapsular cytoplasm. Colonial species always bear symbiontic algae, while solitary species may or may not have symbionts. The number of symbionts associated with Radiolaria varies among species. Colonial forms, consisting of small cell units, contain 30–50 symbionts per cell, while some large solitary species contain up to 5000. In some cases radiolarian endosymbionts live diurnally in the reticulopodial network and the axopods, migrating inwards around the capsular wall at sunset. Experiments using ^{14}C have indicated a significant accumulation of photosynthetically derived carbohydrates in the intracapsular cytoplasm, suggesting that diurnally synthesized nutrients are assimilated at night by the host. It has often been suggested that Radiolaria feed on their symbionts, a combination of auto- and heterotrophic diets, called 'symbiotrophy'. Light and electron microscopical observations of colonies cultivated under illumination or in the dark have suggested that a dynamic equilibrium exists between the ingestion rate of degenerating zooxanthellae and the division rhythm of the photosynthesizing symbionts (Anderson, 1980).

Life cycle and reproduction

Since continuous culture of Radiolaria has not proven possible, few data on life cycle and reproduction are available. Asexual reproduction occurs via binary fission, multiple fission or budding, whereas the occurrence of sexual reproduction remains controversial. Division is a 'closed pleuromitosis' without breakdown of nuclear envelope. Microtubules are generated by large dense plaques or 'spindle pole bodies' inserted in the nuclear envelope.

In the class Polycystina, the single nucleus becomes polyploid after several cycles of endomitosis and contains

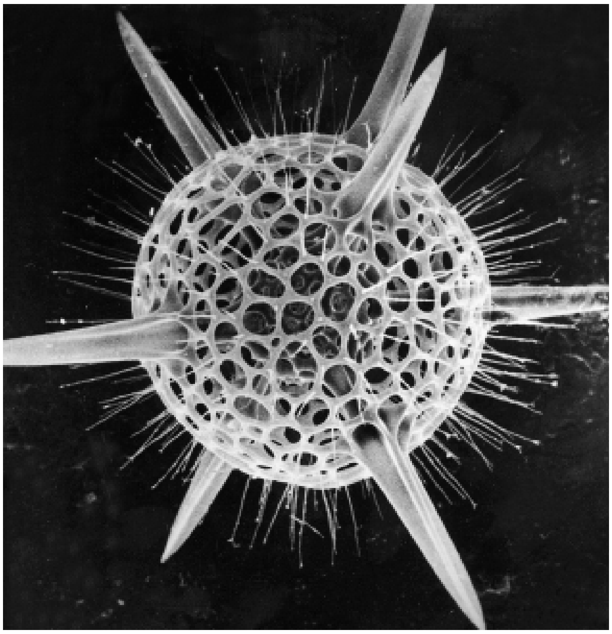

Figure 2 Scanning electron micrograph of a radiolarian skeleton: Polycystina Spumellarida, *Hexacontium* sp. The original resolution of this image is × 2000; it is reproduced here at ×1380. Courtesy of M Cachon.

several nucleoli. Multiple division gives rise to secondary nuclei through a rapid process of 'depolyploidization', in turn giving rise to uninucleated swarmers or 'spores' that include a crystal of strontium sulfate. Shedding of swarmers takes place immediately after 'sporogenesis' (Cachon and Cachon, 1985, 1990).

In the Class Phaeodaria, reproduction occurs through a series of binary fissions. In the species *Aulacantha scolymantha*, the vegetative stage includes a single large polyploid nucleus (up to 2000 chromosomes) which occupies almost the whole volume of the central capsule. During division, the chromosomes are in the midregion of the nucleus, forming the mother plate. Two daughter plates move towards the opposite poles of the nucleus. Connecting structures resembling synaptonemal complexes (structures uniting homologous chromosomes during meiotic prophase in most eukaryotes) are visible in the axis of chromosomes, suggesting either a 'particular sharing of chromosomes' or meiotic division (Raikov, 1982).

Place in Overall Taxonomic Scheme

At present, Radiolaria Haeckel, 1887 and Acantharia J. Müller, 1858 are included in the phylum Radiozoa itself comprising two classes: Polycystinea Ehrenberg 1838, and Phaeodarea Haeckel, 1879

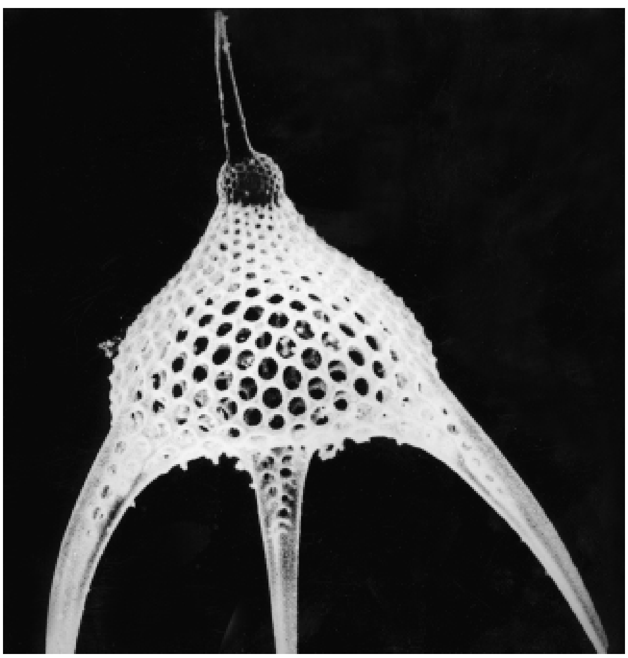

Figure 3 Scanning electron micrograph of a radiolarian skeleton: Polycystina Nassellarida, *Pterocanium trilobum*. The original resolution of this image is × 2000; it is reproduced here at ×1460. Courtesy of M Cachon.

Historical view

Haeckel's classification of the Radiolaria was based on the architecture of their mineral skeletons and included the classes Radiolaria and Acantharia. This system remained unchanged for over 70 years. But Grassé (1953), considering the axopods as the major taxonomic criterion, grouped the three related classes Radiolaria, Acantharia and Heliozoa into the supertaxon Actinopoda Calkins, 1902. In the 1960s electron microscopy provided new insights into ultrastructure, allowing more accurate characterization of Actinopoda. Particular attention was paid to the patterned arrays of microtubules strengthening the axopods and the MTOCs from which they are nucleated. A new classification based on the fine cellular organization was proposed (Cachon and Cachon, 1985) in which Actinopoda were divided into four classes, Polycystina (= Radiolaria), Phaeodaria, Acantharia and Heliozoa. Finally, Radiolaria and Acantharia were regrouped in a 'conservative approach' in the same phylum Radiozoa, while the Heliozoa were separated into a distinct phylum. Although recent molecular analysis suggested that the Polycystinea are monophyletic, Corliss' (1994) classification has been chosen in this current work as it adopts recent cellular and molecular data and is 'familiar and acceptable to the larger number of users'.

Class 1: Polycystinea Ehrenberg, 1838

The mineral skeleton generally consists of a single piece of amorphous silica deposited in an organic matrix. The structure of the axopodial system (MTOCs and microtubule patterns forming the axial rods) is representative of the families. An axial rod passes through the capsular wall via fusules. Fusules are scattered on the whole surface of the capsule or clustered at one pole. The thick capsular wall is made of polygonal plaques with 'fissures', allowing communication between endoplasm and ectoplasm. The ectoplasm contains symbiotic xanthellae.

The class Polycystinea is divided into two orders: Spumellarida (**Figure 2**) and Nassellarida (**Figure 3**).

Spumellarida are large solitary or colonial forms having a single nucleus located in a spherical central capsule. The capsule is surrounded by a latticed shell and the capsular wall is traversed by numerous, regularly distributed fusules. MTOCs are at the level of the fusules. Swarmers include a crystal of strontium sulfate. The most common genera are *Thalassophysa*, *Thalassicolla*, *Thalassolampe*, *Centrocolla*, *Spongosphaera*, *Rhizophaera*, *Sphaerozoum*, *Collozoum*.

Nassellarida are tiny Radiolaria with bilaterally symmetrical or cone-shaped skeletons. The oval central capsule contains a single nucleus and central MTOC. Bundles of microtubules are distributed on a cone leading to a single pore field. Fusules are formed from outward projections of the capsular wall.

Class 2: Phaeodaria

The mineral skeleton consists of hollow tubes of silica and organic substances with traces of magnesium, calcium and copper. The endoplasm contains a single large nucleus, surrounded by a layer of endoplasmic reticulum and a superficial trophic cytoplasm covered with the capsular wall. The ectoplasm contains mucus, food vacuoles, black pigments, mitochondria and phaeodarium forming waste products. The endoplasm communicates with the ectoplasm through three pores. The largest, the astropyle, is involved in food capture. The two smallest pores, the parapylae, are located at the opposite pole. Two large axopodial rods project from the parapylae. The microtubules grow from a cup-shaped MTOC located at the base of each parapyla.

The class Phaeodaria comprises seven orders (only some genera are cited): Phaeogymnocellida (genera *Phaeosphaera*, *Phaeodina*, *Planktonetta*), Phaeocystida (*Aulacantha*, the most widely distributed and extensively studied genus), Phaeosphaerida (*Aulosphaera*), Phaeocalpida (*Castanidium*), Phaeogromida (*Challengeria*, *Medusetta*), Phaeoconchia and Phaeodendrida (*Coelodendron*).

Phylogenetic Evolutionary Considerations

Radiolaria are the most significant source of planktonic protozoan fossils deposited in marine sediments as far back as the late Precambrian era. They are major components of radiolarites and 'radiolarian oozes' in the Pacific ocean. Since they are well preserved, they are used as stratigraphy markers allowing phylogenetic relationships between taxa. Molecular analysis offers new tools towards phylogeny. To reach a natural phylogeny, both approaches must be convergent. Although members of the Actinopoda share several common features, it was recently suggested that they represent a polyphyletic assemblage and that the Polycystine Radiolaria diverged independently before the Acantharia.

References

Anderson OG (1980) Radiolaria. In: Levandowsky M and Hutner SH (eds) *Biochemistry and Physiology of Protozoa*, pp. 1–42. New York: Academic Press.

Corliss JO (1994) An interim utilitarian ('user-friendly') hierarchical classification and characterization of the protists. *Acta Protozoologica* **33**: 1–51.

Cachon J and Cachon M (1985) Superclass Actinopodea Calkins, 1902. In: Lee JJ, Hutner SH and Bovee EC (eds) *Illustrated Guide to the Protozoa*, pp. 274–302. Lawrence, KS: Allen Press.

Cachon J and Cachon M (1990) Phylum Actinopoda, Classes Polycystina (= Radiolaria) and Phaeodaria. In: Margulis L, Corliss JO, Melkonian M and Chapman D (eds) *Handbook of Protoctista*, pp. 334–346. Boston: Jones and Bartlett.

Grassé PP (1953) *Traité de Zoologie*. Paris: Masson.

Raikov IB (1982) *The Protozoan Nucleus: Morphology and Evolution*. Vienna: Springer.

Further Reading

Abelmann A and Gowing MM (1997) Spatial distribution pattern of living polycystine radiolarian taxa – baseline study for paleoenvironmental reconstructions in the Southern Ocean (Atlantic sector). *Marine Micropaleontology* **30**: 3–28.

Anderson OR (1996) The physiological ecology of planktonic sarcodines with applications to paleoecology: Patterns in space and time. *Journal of Eukaryotic Microbiology* **43**: 261–274.

Caron DA, Michaels AF, Swanberg NR and Howse FA (1995) Primary productivity by symbiont-bearing planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda. *Journal of Plankton Research* **17**: 103–129.

Chen M and Tan Z (1997) Radiolarian distribution in surface sediments of the northern and central South China Sea. *Marine Micropaleontology* **32**: 173–194.

Welling LA and Pisias NG (1998) Radiolarian fluxes, stocks and population residence times in surface waters of the central equatorial Pacific. *Deep-Sea Research* **45**: 639–671.