Radiolaria

Chapter · January 2016

DOI: 10.1002/9780470015902.a0001985.pub2

Yoshiyuki Ishitani
Japan Agency for Marine-Earth Science and Technology

Radiolaria

Yoshiyuki Ishitani, *Atmosphere and Ocean Research Institute, The University of Tokyo, Tokyo, Japan*

Colette Febvre-Chevalier, *Oceanological Observatory, Villefranche-sur-Mer, France*

Jean Febvre, *Oceanological Observatory, Villefranche-sur-Mer, France*

Advanced article

Article Contents

Online posting date: 15th January 2016

Based in part on the previous version of this eLS article 'Radiolaria' (2001) by Colette Febvre-Chevalier and Jean Febvre.

Radiolaria are marine unicellular zooplankton characterised by the presence of two types of pseudopodia called axopodia (pseudopodia having axial portion) and reticulopodia (pseudopodia make reticulated network). Class Phaeodarea, traditionally included in Radiolaria, were revised their taxonomic position (out of Radiolaria but in Cercozoa) on the basis of molecular studies. Also, a molecular perspective shows us that Radiolaria have five orders (Spumellaria, Nassellaria, Collodaria, Acantharia and Taxopodida) in two classes (former three in Polycystina, latter two in Spasmaria). Most of Radiolaria (excepting from some species of Collodaria) possess siliceous or celestite shells or spines, and both the fine structure and architectural diversity of the skeletons are used as taxonomic criteria. Good preservation of siliceous shells allows Radiolaria to be used as stratigraphic markers in Paleontology.

Introduction

The phylum Radiolaria were created by Haeckel, who described about 4000 species collected from plankton samples during the *R.V. Challenger* expedition. Radiolaria have a mineral skeleton which exhibits remarkable architectural diversity such as large hollow shells, long spines and parachute shape. Because of these mineral skeletons, Radiolaria have one of the best fossil records since their first appearance in the Cambrian era. Biologically, the cell has unique double structure; the central pigmented body of cytoplasm is surrounded by a thick perforated layer, the inner capsular wall. The outer cytoplasm gives rise to cytoplasmic projections known as axopods and reticulopods, and harbours symbiotic algae in some species. These skeletons and some biological functions (e.g. accumulation of lipids in the endoplasm and formation of bubbles at the cell surface) provide various buoyancy systems that control sinking and flotation in the water mass, resulting in their wide vertical distribution from the surface to bathypelagic zone. Moreover, Radiolaria are passively transported by ocean currents, facilitating their wide geographic distribution from equatorial to polar latitude. Their concentration is averaged around 400 individuals m^{-3}, and high in the polar and subpolar regions and below the chlorophyll maximum in vertical. **See also**: **Phytoplankton**; **Haeckel, Ernst Heinrich Philipp August**; **Protozoa**

eLS subject area: Microbiology

How to cite:
Ishitani, Yoshiyuki; Febvre-Chevalier, Colette; and Febvre, Jean (January 2016) Radiolaria. In: eLS. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0001985.pub2

Description and Characterisation

Radiolaria are marine unicellular holoplankton, with either a solitary or a colonial lifestyle. Solitary species are generally spherical, with tiny (20–30 µm) or large (3–5 mm in diameter) body size. They form a skeleton of silica or celestite with latticed shells and spines. The cell body is divided into a central dense endoplasm and a vacuolar ectoplasm by a mucoprotein membrane called as a capsular wall (**Figure 1**). The capsular wall is usually thick (up to 1 µm) and perforated by fusules. The cytoplasm is traversed by radial rods of microtubules (called as axopods) that project into long, slender and unramified processes. These axopods radiate from the axoplast in the capsular wall to the outer cell surface in all directions. On the other hand, the ectoplasm extrudes from cytoplasmic extensions through pores of the capsular wall and spreads superficial cytoplasm-forming thin pseudopodia (called as reticulopods), which are continuously remodelled. This cytoplasmic stream enables to provide a place for harbouring endosymbiotic algae.

Mineral skeleton diversity

Although some species lack a skeleton, many radiolarians are remarkable and diverse examples of the architectural complexity of biological mineralisation (**Figures 2**, **3**, and **4**). Radiolarian skeletons are made of two kinds of biominerals: hydrated amorphous silica consisting of 1–3 latticed shells and spines, and celestite-formed 10 diametral (or 20 radial) spicules arranged according to the geometric Müller's law (Müller, 1859). The morphological characteristics of these skeletons represent the major

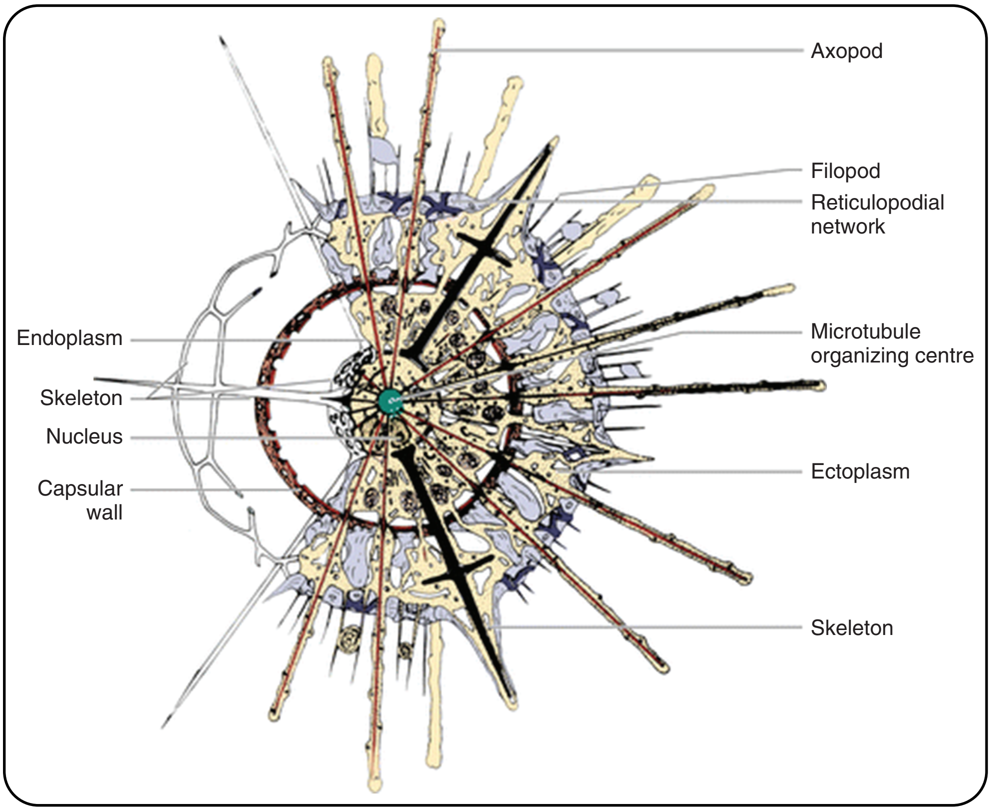

Figure 1 Structure of a polycystid radiolarian. Skeleton (black), microtubule-organising centre and axis of the axopodia (green), capsular wall (red), surface of the cross section through the cytoplasm (yellow), surface of the cell membrane outside the section plane (blue).

taxonomic criteria. Their siliceous skeletons secrete in the cytoplasmic sheath called a cytokalymma. Granular silica (ca. 80 nm diameter) deposits inside the cytokalymma aggregate to a mature silica product, which has a more electron-opaque and smooth surface. The physiology of silica and celestite deposition has been poor so far. The mechanisms: which biominerals become concentrated in specific patterns, the rate of biomineral deposition, the effective environmental conditions for biomineral deposition and the roles of specific ionic channels across membranes as biomineral pathway remain to be elucidated. **See also**: **Silica**; **Acantharia**

Structure of axopods

Axopods project several hundred microns into the surrounding water, and are quickly 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 intra-axopodial cytoskeleton. Each array is made of more than 600 microtubules cross-connected by bridges, seen in cross section as a variety of open or closed patterns (branched, hexagonal and dodecagonal). Microtubules originate from a single or multiple dense mass of fibrogranular material forming the microtubule-organising centre (MTOC) or axoplast (**Figure 1**). Single MTOCs are either located in the cell centre within a caveola of the nucleus or juxtanuclear. Multiple MTOCs are distributed on the outer surface of the capsular wall associating with perforated structures, known as fusules. **See also**: **Heliozoa**

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 their digestions. Radiolaria use both axopods and reticulopods for predatory activity. Many species are omnivorous, injesting other protozoans (e.g. diatoms), even small tintinnids and crustaceans such as copepods. Prey organisms become entangled in the superficial cytoplasm, then enclosed in a food vacuole and finally transferred into the deeper ectoplasm near the capsular wall for digestion. **See also**: **Protozoan Nutrition and Metabolism**

Symbiosis

Radiolaria harbour endosymbiotic unicellular green or yellow-green algae (e.g. dinoflagellates, prasinophytes and

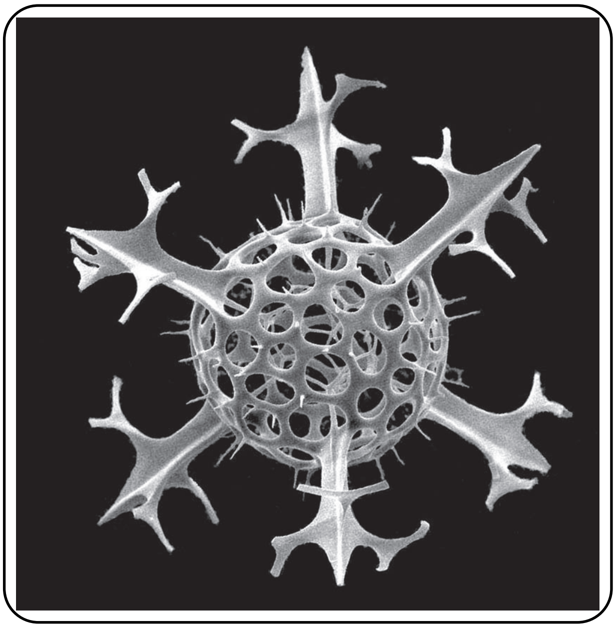

Figure 2 Scanning electron micrograph of a radiolarian skeleton: Polycystina Spumellarida, *Hexacontium* sp. The original resolution of this image is × 1000; it is reproduced here at × 1260.

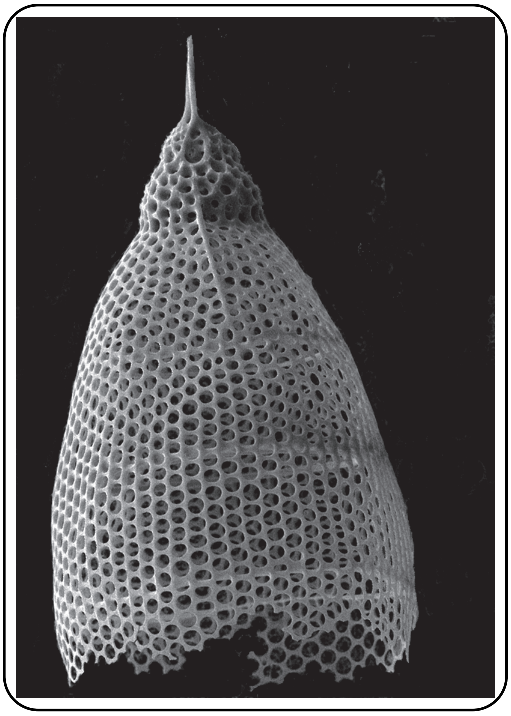

Figure 3 Scanning electron micrograph of a radiolarian skeleton: Polycystina Nassellarida, *Eucyrtidium hexagonatum*. The original resolution of this image is × 1100; it is reproduced here at × 620.

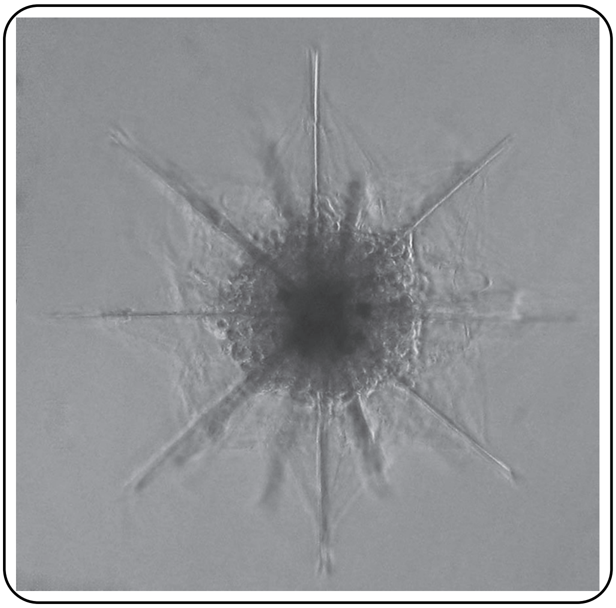

Figure 4 Light micrograph of a living radiolarian: Spasmaria Acarharia. The original resolution of this image is × 200; it is reproduced here at × 630.

haptophytes) that live in the extracapsular cytoplasm (ectoplasm). 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 significant accumulation of photosynthetically derived carbohydrates in the intracapsular cytoplasm, suggesting that diurnally synthesised nutrients are assimilated at night by the host. It has often been reported 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 hosts and the division rhythm of the photosynthesising symbionts (Anderson, 1980). **See also**: **Protozoan Symbioses**

Life cycle and reproduction

Few data on life cycle and reproduction are available, because of technical difficulties of breeding in captivity. Radiolarians have two reproductive systems: asexual reproduction occurs via binary and multiple fissions and sexual reproduction by flagellated swarmers (ca. 5 μm). Division is a ‘closed pleuromitosis’ without breakdown of the nuclear envelope. Microtubules are generated by large, dense plaques or ‘spindle pole bodies’ inserted in the nuclear envelope. **See also**: **Protozoan Asexuality**; **Protozoan Sexuality**

In the class Polycystina, the single nucleus becomes polyploid after several cycles of endomitosis and contains several nucleoli. Multiple division gives rise to secondary nuclei through a rapid process of ‘depolyploidisation’, 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).

Some of the order Acantharia release flagellated swarmers after the cyst-forming and the others directly through the vegetative stage. Although indirect evidence shows a distribution pattern of acantharians along the water column by using a gene marker, their swarmers are released in deeper waters and float to the sea surface (Decelle *et al*., 2012).

Place in Overall Taxonomic Scheme

To date, Polycystina Ehremberg, 1838, Acantharia J. Müller, 1858 and Taxopodida H. Fol, 1883 are included in the phylum Radiolaria, but Phaeodarea Haeckel, 1879 are out of the phylum Radiolaria. **See also**: **Protozoan Taxonomy and Systematics**; **Protist Evolution and Phylogeny**

Historical view

Haeckel’s classification of the Radiolaria was based on the architecture of their mineral skeletons and included the classes Polycystina, Acantharia and Phaeodarea. This system had been used 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 characterisation 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 organisation was proposed (Cachon and Cachon, 1985) in which Actinopoda were divided into four classes, Polycystina (= Radiolaria), Phaeodarea, Acantharia and Heliozoa.

Molecular phylogenetic analyses regrouped Polycystina and Acantharia in phylum Radiolaria, and *Sticholonche zanclea*, which is in order Taxopodida, were membered in the same phylum Radiolaria. Cavalier-Smith (1993) grouped Acantharia with Taxopodida on the basis of the common morphological feature of myoneme, and named this group as class Spasmaria. This phylogeny is also supported by later studies of molecular phylogeny of Radiolaria, and Radiolaria are composed of Polycystina and Spasmaria (Krabberød *et al*., 2011). Moreover, the recent molecular perspective unveiled the phylogenetic position of Radiolaria themselves among the Eukayote. Radiolaria are sister to Foraminifera as Retaria, which is an ingroup of the eukaryotic supergroup Rhizaria together with members of Cercozoa and Endomyxa (Ishitani *et al*., 2011).

Class 1: Polycystina 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 photosynthesising symbionts.

The class Polycystina is divided into three orders: Spumellarida (**Figure 2**), Nassellarida (**Figure 3**) and colonial Collodaria.

Spumellarida are large solitary cells (ca. 0.1–1 mm) 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 (**Figure 5a**). The most common genera are *Centrocolla*, *Spongosphaera* and *Rhizosphaera*.

Nassellarida are tiny Radiolaria (ca. 0.1–0.5 mm) 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 (**Figure 5b**). The most common genera are *Cladoscenium*, *Pterocorys* and *Eucyrtidium*.

Collodaria are large solitary (ca. 1 mm) or colonial forms (some colony exceed the 1 m size). Each cell having a single nucleus is located in a spherical central capsule. The capsule is surrounded by a latticed shell or spicules. The capsular wall is traversed by numerous, regularly distributed fusules formed by a cylindrical pore outward the central capsule. MTOCs are at the level of the fusules (**Figure 5c**). Swarmers include a crystal of strontium sulfate. The most common genera are *Thalassophysa*, *Thalassicolla* and *Thalassolampe*.

Class 2: Spasmaria Cavalier-Smith, 1993

Acantharia are large solitary radiolarians (ca. 0.05–5 mm) with a spherical central capsule and strontium sulfate skeletons or spines arranged in a sophisticated symmetrical row called Müller’s rule. The capsular wall is traversed by numerous simple fusules, and MTOCs arise from the perispicular membrane near the centre part of the central capsule (**Figure 5d**).The most common genera is *Acanthometra*, *Astrolonche* and *Amphiacon*. **See also**: **Acantharia**

Taxopodida comprise a single species *S. zanclea* having siliceous spines and oarlike axopods. This species can propel through the seawater by rowing its oarlike axopods. It does not have central capsule as per the other radiolarians. Its MTOCs arise from a dorsal groove of nuclear membrane, and its microfilaments connecting between the MTOCs on the basis of axopod and socket-like MTOCs on the nuclear membrane, move their axopods to row oarlike axopods (**Figure 5e**).

Phylogenetic Evolutionary Considerations

Radiolaria are the most significant source of planktonic protozoan fossils deposited in marine sediments as far back as the Cambrian

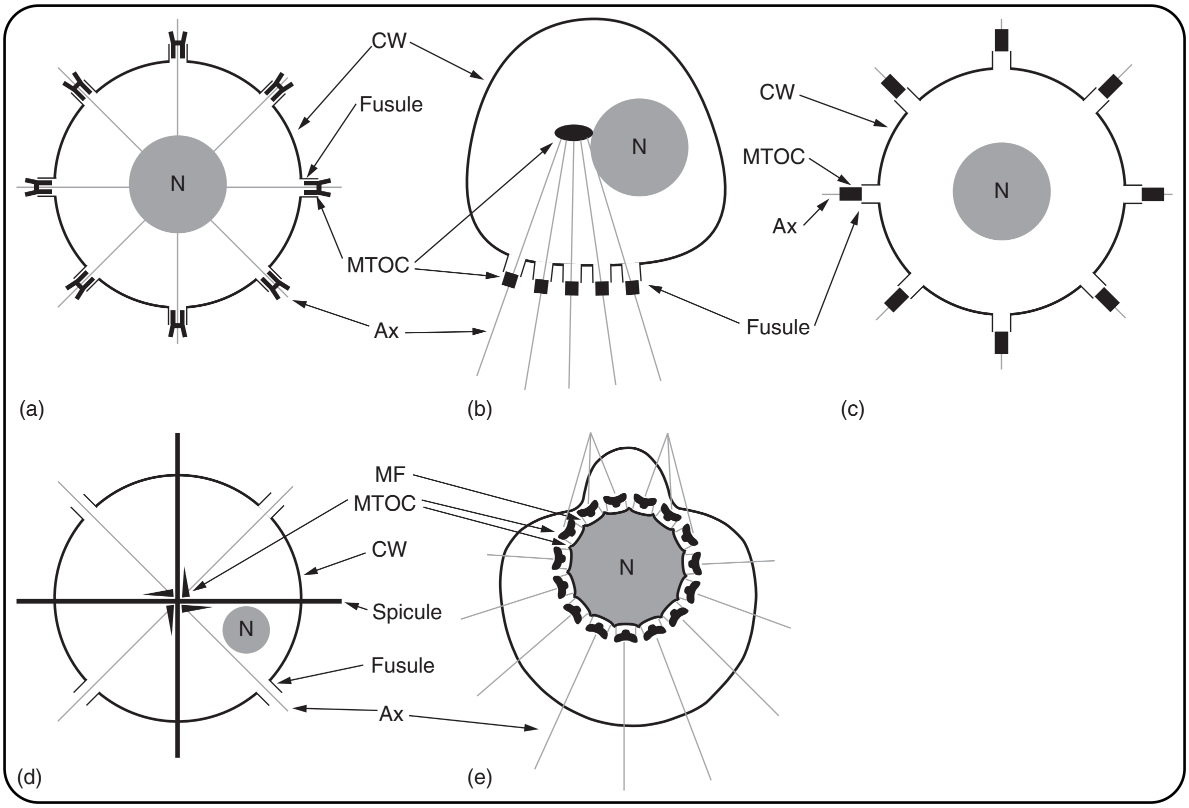

Figure 5 Schematics of cell structure of (a) Spumellaria, (b) Nassellaria, (c) Collodaria, (d) Acantharia and (e) Taxopodida. Nucleus (N) and microtubule-organising centre (MTOC) are shown as grey and black, respectively. Axopod (Ax) and microfilament (MF) are shown as grey line. Capsular wall (CW) is shown as black line.

era. They are major components of radiolarites and 'radiolarian oozes' in the Ocean. As 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. Also, sharing a common ancestor between Radiolaria and one of the important microfossil organisms, Foraminifera, will help understand the nature of ancestral radiolarians. **See also**: **Protist Evolution and Phylogeny**

References

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

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.

Cavalier-Smith T (1993) Kingdom protozoa and its 18 phyla. *Microbiology and Molecular Biology Reviews* **57**: 953–994.

Decelle J, Martin P, Paborstava K, *et al.* (2012) Diversity, ecology, and biogeochemistry of cyst-forming Acantharia (Radiolaria) in the oceans. *PLoS One* **8**: e53598.

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

Ishitani Y, Ishikawa SA, Inagaki Y, *et al.* (2011) Multigene phylogenetic analyses including diverse radiolarian species support the "Retaria" hypothesis – the sister relationship of Radiolaria and Foraminifera. *Marine Micropaleontology* **81**: 32–42.

Krabberød AK, Bråte J, Dolven JK, *et al.* (2011) Radiolaria divided into Polycystina and Spasmaria in combined 18S and 28S rDNA phylogeny. *PLoS One* **6** (8): e23526.

Müller J (1859) Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, **1858**: 1–62.

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.

Balzano S, Corre E, Decelle J, *et al.* (2015) Transcriptome analyses to investigate symbiotic relationships between marine protists. *Frontiers in Microbiology* **6**: 98.

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.

Gilg IC, Amaral-Zettler LA, Countway PD, *et al.* (2010) Phylogenetic affiliations of mesopelagic Acantharia and acantharian-like environmental 18S rRNA genes off the Southern California Coast. *Protist* **161**: 197–211.

Ishitani Y, Ujiié Y, de Vargas C, Not F and Takishita K (2012) Phylogenetic relationships and evolutionary patterns of the order Collodaria (Radiolaria). *PLoS One* **7**: e35775.

Ishitani Y, Ujiié Y and Takishita K (2014) Uncovering sibling species in Radiolaria: evidence for ecological partitioning in a marine planktonic protist. *Molecular Phylogenetics and Evolution* **78**: 215–222.

Lazarus DB, Kotrc B, Wulf G and Schmidt DN (2009) Radiolarians decreased silicification as an evolutionary response to reduced Cenozoic ocean silica availability. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 9333–9338.

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.