PROTOZOA, RADIOLARIANS

O. R. Anderson, Columbia University, Palisades, NY, USA

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Introduction

Radiolarians are exclusively open ocean, silica-secreting, zooplankton. They occur abundantly in major oceanic sites worldwide. However, some species are limited to certain regions and serve as indicators of water mass properties such as temperature, salinity, and total biological productivity. Abundances of total radiolarian species vary across geographic regions. For example, maximum densities reach 10 000 per m^3 in some regions such as the subtropical Pacific. By contrast, densities range about 3–5 per m^3 in the Sargasso Sea. Radiolarians are classified among the Protista, a large and eclectic group of eukaryotic microbiota including the algae and protozoa. Algae are photosynthetic, single-celled protists, while the protozoa obtain food by feeding on other organisms or absorbing dissolved organic matter from their environment. Radiolarians are single-celled or colonial protozoa. The single-celled species vary in size from $< 100\,\mu m$ to very large species with diameters of 1–2 mm. The larger species are taxonomically less numerous and include mainly gelatinous species found commonly in surface waters. The smaller species typically secrete siliceous skeletons of remarkably complex design (**Figure 1**). The skeletal morphology is species-specific and used in taxonomic identification. Larger, noncolonial species are either skeletonless, being enclosed only by a gelatinous coat, or produce scattered siliceous spicules within the peripheral cytoplasm and surrounding gelatinous layer. Colonial species contain numerous radiolarian cells interconnected by a network of cytoplasmic strands and enclosed within a clear, gelatinous envelope secreted by the radiolarian. The colonies vary in size from several centimeters to nearly a meter in length. The shape of the colonies is highly variable among species. Some are spherical, others ellipsoidal, and some are elongate ribbon-shaped or cylindrical forms. These larger species of radiolarians are arguably, the most diverse and largest of all known protozoa. Many of the surface-dwelling species contain algal symbionts in the peripheral cytoplasm that surrounds the central cell body. The algal symbionts provide some nutrition to the radiolarian

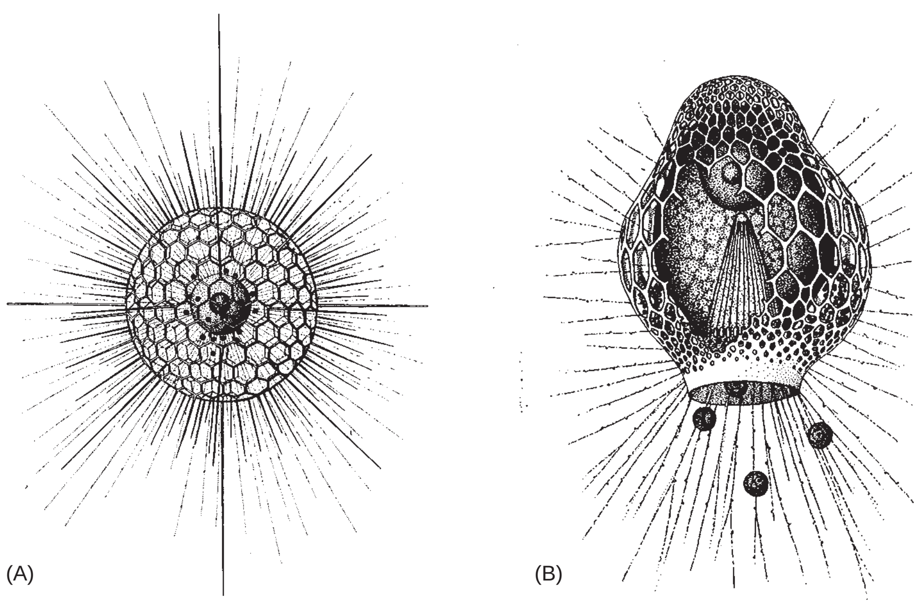

Figure 1 Morphology of polycystine radiolaria. (A) Spumellarian with spherical central capsule and halo of radiating axopodia emerging from the fusules in the capsular wall and surrounded by concentric, latticed, siliceous shells. (B) Nassellarian showing the ovate central capsule with conical array of microtubules that extend into the basally located fusules and external axopodia protruding from the opening of the helmet-shaped shell. Reproduced with permission from Grell K (1973) *Protozoology*. Berlin: Springer-Verlag.

host by secretion of photosynthetically produced organic products. The food resources are absorbed by the radiolarian and, combined with food gathered from the environment, are used to support metabolism and growth. Radiolarians that dwell at great depths in the water column where light is limited or absent typically lack algal symbionts. The siliceous skeletons of radiolarians settle into the ocean sediments where they form a stable and substantial fossil record. These microfossils are an important source of data in biostratigraphic and paleoclimatic studies. Variations in the number and kind of radiolarian species (based on skeletal form) in relation to depth in the sediment provide information about climatic and environmental conditions in the overlying water mass at the time the radiolarian skeletons were deposited at that geographic location. The radiolarians are second only to diatoms as a major source of biogenic opal (silicate) deposited in the ocean sediments.

Cellular Morphology

The radiolarian cell body contains a dense mass of central cytoplasm known as the central capsule (**Figure 2**). Among the organelles included in the central capsule are the nucleus, or nuclei in species with more than one nucleus, most of the food reserves, major respiratory organelles, i.e., mitochondria, Golgi bodies for intracellular secretion, protein-synthesizing organelles, and vacuoles. The central capsule is surrounded by a nonliving capsular wall secreted by the radiolarian cytoplasm. The thickness of the capsular wall varies among species. It may be thin or in some species very reduced, consisting of only a sparse deposit of organic matter contained within the surrounding cytoplasmic envelope. In others, the wall is quite thick and opalescent with a pearl-like appearance. The capsular wall contains numerous pores through which cytoplasmic strands (fusules) connect to the extracapsular cytoplasm. The extracapsular cytoplasm usually forms a network of cytoplasmic strands attached to stiffened strands of cytoplasm known as axopodia that extend outward from the fusules in the capsular wall. The central capsular wall and axopodia are major defining taxonomic attributes of radiolarians. A frothy or gelatinous coat typically surrounds the central capsule and supports the extracapsular cytoplasm. Algal symbionts, when present, are enclosed within perialgal vacuoles produced by the extracapsulum. In most species, the algal symbionts are exclusively located in the extracapsulum. Thus far, symbionts have been observed within the central capsular cytoplasm in only a few species. Food particles, including small algae and protozoa or larger invertebrates such as copepods, larvacea, and crustacean larvae, are captured by the sticky rhizopodia of the extracapsulum. The cytoplasm moves by cytoplasmic streaming to coat and enclose the captured prey. Eventually, the prey is engulfed by the extracapsular cytoplasm and digested in digestive vacuoles (lysosomes). These typically accumulate in the extracapsulum near the capsular wall. Large prey such as copepods are invaded by flowing strands of cytoplasm and the more nutritious soft parts such as muscle and organ tissues are broken apart, engulfed within the flowing cytoplasm and carried back into the extracapsulum where digestion takes place. The siliceous skeleton, when present, is deposited within cytoplasmic spaces formed by extensions of the rhizopodia. This elaborate framework of skeletal-depositing cytoplasm is known as the cytokalymma. Thus, the form of the skeleton is dictated by the dynamic streaming and molding action of the cytokalymma during the silica deposition process. Consequently, the very elaborate

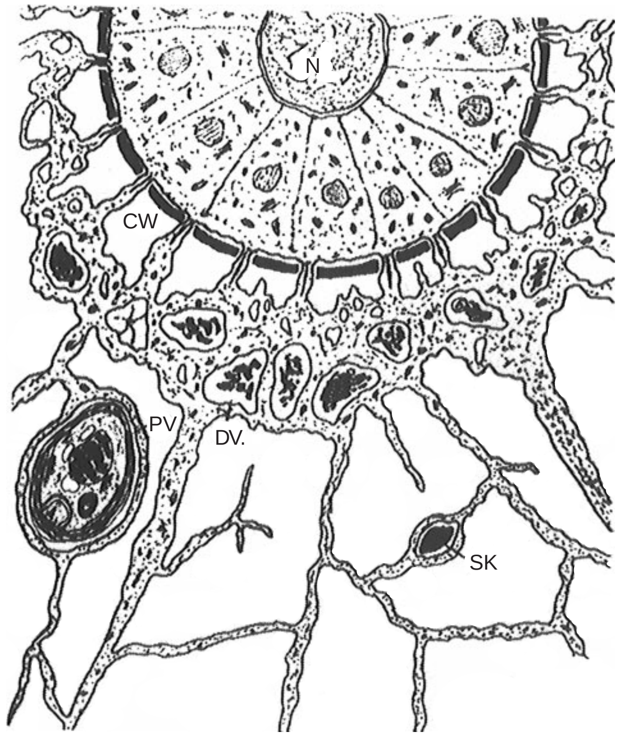

Figure 2 Cytoplasmic organization of a spumellarian radiolarian showing the central capsule with nucleus (N), capsular wall (CW) and peripheral extracapsulum containing digestive vacuoles (DV) and algal symbionts in perialgal vacuoles (PV). The skeletal matter (SK) is enclosed within the cytokalymma, an extension of the cytoplasm, that acts as a living mold to dictate the shape of the siliceous skeleton deposited within it. Reproduced with permission from Anderson OR (1983) *Radiolaria*. New York: Springer-Verlag.

and species-specific form of the skeleton is determined by the dynamic activity of the radiolarian and is not simply a consequence of passive physical chemical processes taking place at interfaces among the frothy components of the cytoplasm as was previously proposed by some researchers.

Taxonomy

Radiolarians are included in some modern classification schemes in the kingdom Protista. However, the category of radiolaria as such is considered an artificial grouping. Instead of the group 'Radiolaria', two major subgroups previously included in 'Radiolaria' are placed in the kingdom Protista. These are the Polycystina and the Phaeodaria. Polycystina are radiolarians that contain a central capsule with pores that are rather uniform in shape and either uniformly distributed across the surface of capsular wall, or grouped at one location. The Phaeodaria have capsular walls with two distinctive types of openings. One is much larger and is known as the astropyle with an elaborately organized mass of cytoplasm extending into the extracapsulum. The other type is composed of smaller pores known as parapylae with thin strands of emergent cytoplasm. Some Phaeodaria also have skeletons that are enriched in organic matter compared with the skeletons of the Polycystina. Among the Polycystina, there are two major taxonomic groups, the Spumellaria and Nassellaria, assigned as orders in some taxonomic schemes. Spumellaria have central capsules that are usually spherical or nearly so at some stage of development and have pores distributed uniformly over the entire surface of the capsular wall. All known colonial species are members of the Spumellaria. Although expert opinion varies, there are two families and about 10 genera of colonial radiolarians. There are seven widely recognized families of solitary Spumellaria with scores of genera. Nassellaria have central capsules that are more ovate or elongated and the fusules are located only at one pole of the elongated capsular wall. This pore field is called a porochora and the fusules tend to be robust with axopodia that emerge through outward-directed collar-like thickenings surrounding the pore rim. Moreover, the skeleton of the Nassellaria, when present, tends to be elongated and forms a helmet-shaped structure, often with an internal set of rods forming a tripod to which the external skeleton is attached. Current systematics include seven major families with numerous genera. Spumellarian skeletons are typically more spherical, or based on a form that is not derived from a basic tripodal or helmet-like architectural plan. The shells of the Phaeodaria are varied in shape. Some species have ornately decorated open lattices resembling geodesic structures composed of interconnected, hollow tubes of silica. Other species have thickened skeletons resembling small clam shells with closely spaced pores on the surface. There are 17 major families with scores of genera. Since many species of radiolarians were first identified from sediments based solely on their mineralized skeletons, much of the key taxonomic characteristics include skeletal morphology. Increasingly, evidence of cytoplasmic fine structure obtained by electron microscopy and molecular genetic analyses is being used to augment skeletal morphology in making species discriminations and constructing more natural evolutionary relationships. It is estimated that there are several hundred valid living species of radiolarians.

Biomineralization

Biomineralization is a biological process of secreting mineral matter as a skeleton or other hardened product. The skeleton of radiolaria is composed of hydrated opal, an oxidized compound of silicon (nominally $SiO_2 \cdot nH_2O$) highly polymerized to form a space-filling, glassy mass incorporating a variable number (n) of water molecules within the molecular structure of the solid. Electron microscopic evidence indicates that some organic matter is incorporated in the skeleton during early stages of deposition, but on the whole, the skeleton is composed mostly of pure silica. Electron microscopic, X-ray dispersive analysis shows that a small amount of divalent cations such as Ca^{2+} may be incorporated in the final veneer deposited on the surface to enhance the hardness of the skeleton. During deposition of the skeleton, the cytoplasm forms the living cytokalymma, i.e., the cytoplasmic silica-depositing mold, by extension of the surface of the rhizopodia. The cytokalymma enlarges as silica is deposited within it, gradually assuming a final form that dictates the morphology of the internally secreted skeleton. Small vesicles are observed streaming outward from the cell body into the cytoplasm of the cytokalymma and these may bring silica to be deposited within the skeletal spaces inside the cytokalymma. The cytoplasmic membrane surrounding the developing skeleton appears to act as a silicalemma or active membrane that deposits the molecular silica into the skeletal space. During deposition, the dynamic molding process is clearly evident as the living cytoplasm continuously undergoes transformations in form, gradually approximating the ultimate geometry of the species-specific skeleton being deposited by the radiolarian cell. In general, species with multiple, concentric, lattice shells surrounding the central capsule appear to lay down the lattices successively, progressing outward from the innermost shell.

The process of skeletal construction has been documented in fair detail for a few species, most notably among the colonial radiolaria. Two forms of growth have been identified. Bar growth is a process of depositing silica as rodlets within a thin tubular network of cytoplasm formed by the cytokalymma. The rodlets become connected during silicogenesis and further augmented with silica to form a porous lattice with typically large polygonal pores. The pores, once formed, may be further subdivided into smaller pores by additional bar growth that spans the opening of the pore. Rim growth occurs by deposition of silica as curved plates that are differentially deposited at places to form rounded pores. At maturity, these are typically spherical skeletons with rather regular, rounded pores scattered across the surface. For both types of skeletons, in some species, the ratio of the bar width between the pores to the pore diameter is a taxonomic diagnostic feature.

The rate of silica biomineralization in some species has been determined by daily observation of growth of individuals in laboratory culture using light microscopy. The amount of silica in the skeleton of a living radiolarian is mathematically related to the size of the skeleton. For example, in the spumellarian species *Spongaster tetras* with a rectangular, spongiose skeleton, the amount of silica (W) in micrograms (μg) as related to the length of the major diagonal axis of the quadrangular shell (L) in micrometers (μm) is approximated as follows:

$$W = (3.338 \times 10^{-6}) \cdot L^{2.205} \qquad [1]$$

The average daily growth in cultures of an *S. tetras* is 3 μm with an average daily gain in weight of *c.* 8 ng. The total weight gain for one individual radiolarian during maturation is about 0.1 μg. Silica deposition during maturation appears to be sporadic and irregular, varying from one individual to another, with periods of rapid deposition followed by plateaus in growth. The amount of skeletal opal produced by *S. tetras* alone in the Caribbean Sea, for example, is *c.* 42 μg per m^3 of sea water, with a range of 8–61 μg per m^3. Peak production occurred in mid-summer (June to July). The rate of total radiolarian-produced biogenic opal settling into the ocean sediments at varying oceanic locations has been estimated in the range of 1–10 mg per m^2 per day.

Reproduction

Protozoa reproduce by either asexual or sexual reproduction. Asexual reproduction occurs by cell division during mitosis to produce two or more genetically identical offspring. Sexual reproduction occurs by the release of haploid gametes (e.g., sperm and egg cells) that fuse to produce a zygote with genetic characteristics contributed by both of the parent organisms. Thus, sexual reproduction permits new combinations of genetic material and the offspring are usually genetically different from the parents. There is evidence that some colonial radiolaria have asexual reproduction. The central capsules within the colony have been observed to divide by fission. This increases the number of central capsules and allows the colony to grow in size. The colony may also break into parts, thus increasing the total numbers of colonies at a given location. In most species of radiolaria, reproduction occurs by release of numerous flagellated swarmer cells that are believed to be gametes. The nucleus of the parent radiolarian undergoes multiple division and the entire mass of the parent cell is converted into uninucleated flagellated swarmers. These are released nearly simultaneously in a burst of activity, and presumably after dispersal fuse to form a zygote. The details of gamete fusion and the early ontogenetic development of radiolaria are poorly understood and require additional investigation. Ontogenetic development of individuals from very early stages to maturity has been documented in laboratory cultures and the stages of skeletal deposition are well understood for several species, as explained above in the section on biomineralization.

Physiological Ecology and Zoogeography

The physiological ecology of radiolaria has been studied by collecting samples of radiolaria and other biota at varying geographical locations in the world oceans to determine what abiotic and biotic factors are correlated with and predict their abundances, and by experimental studies of the physical and biological factors that promote reproduction, growth, and survival of different species under carefully controlled laboratory conditions. Temperature appears to be a major variable in determining abundances of some species of radiolaria. For example, high latitude species that occur abundantly at the North or South Poles are also found at increasing depths in the oceans toward the equator.

Since the water temperature in general decreases with depth, these organisms populate broad depth regions within the water column that match their physiological requirements. Species that occur in subtropical locations, where the water is intermediate in temperature based on a global range, are found at the equator at intermediate water depths that are cooler than the warm surface water. Some species are characteristically most abundant in only warm, highly productive water masses. For example, some species of colonial radiolaria occur typically in surface water near the equator in the Atlantic Ocean, while others are most abundant at higher latitudes in the Sargasso Sea where usually the water is also less productive. Upwelling regions where deep, nutrient-enriched sea water is brought to the surface are typically highly productive regions for radiolaria, as occurs for example along the Arabian, Chilean, and California coast lines. Shallow-water dwelling species have been categorized into seven zoogeographic zones based on water mass properties: (1) SubArctic at high northern latitudes; (2) transition region as occurs in the North Pacific drift waters; (3) north central region, typical of waters within the large anticyclonic circulation of the North Pacific; (4) equatorial region in locations occupied by the North and South Equatorial Current systems; (5) south central water mass, as in the South Pacific anticyclonic circulation pattern; (6) subAntarctic, a water regime bounded on the north by the Subtropical Convergence and on the south by the Polar Convergence; and (7) Antarctic, bounded by the Polar Convergence on the north and the Antarctic Continent on the south.

The growth requirements of some species have been studied extensively in laboratory cultures. For example, the following three surface- to near-surface-dwelling species exhibit a range of optimal growth conditions. *Didymocyrtis tetrathalamus*, with a somewhat hourglass-shaped skeleton (150 μm), prefers cooler water (21–27°C) and salinities in the range of 30–35 ppm. *Dictyocoryne truncatum*, a spongiose triangular-shaped species (300 μm), is more intermediate in habitat requirements with optimal temperature of 28°C and salinity of 35 ppm. *Spongaster tetras*, a quadrangular, spongiose species (300 μm), prefers warmer, more saline water (*c*. 28°C and 35–40 ppm). The temperature tolerance ranges (in °C) for the three species also show a similar pattern of increasing preference for warmer water, i.e., 10–34, 15–28, and 21–31, respectively.

The prey consumed by radiolarians varies substantially among species, but many of the polycystine species appear to be omnivorous, consuming both phytoplankton and zooplankton prey. The smaller species consume microplankton and bacteria. Larger species are capable of capturing copepods and small invertebrates. Phaeodaria, especially those species dwelling at great depths in the water column, appear to consume detrital matter in addition to preying on plankton in the water column. The broad range of prey accepted by many of the radiolarians studied thus far suggests that they are opportunistic feeders and are capable of adapting to a broad range of trophic conditions.

The role of algal symbionts, when present, has been debated for some time – beginning with their discovery in the mid-nineteenth century. At first, it was supposed that the green symbionts may largely provide oxygen to the host. However, most radiolaria dwell in fairly well-oxygenated habitats and it is unlikely that photosynthetically derived oxygen is necessary. The other competing hypothesis was that the symbionts provide organic nourishment to the host. Modern physiological studies have confirmed that the algal symbionts provide photosynthetically produced nutrition for the host. Biochemical analyses combined with ^{14}C isotopic tracer studies have shown that stores of lipids (fats) and carbohydrates in the host cytoplasm contain carbon derived from algal photosynthetic activity. Well-illuminated, laboratory cultures of symbiont-bearing radiolaria survive for weeks without addition of prey organisms. Some of the algal symbionts are digested as food and can be replaced by asexual reproduction of the algae, but it appears that much of the nutrition of the host comes from organic nutrients secreted into the host cytoplasm by the algal symbionts. This readily available, 'internal' supply of autotrophic nutrition makes symbiont-bearing radiolaria much less dependent on external food sources and may account in part for their widespread geographic distribution, including some oligotrophic water masses such as the Sargasso Sea.

See also

Marine Silica Cycle.

Further Reading

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