Acantharia

Secondary article

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

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

Acantharia are marine planktonic protozoa related to Radiolaria. Their main distinctive features are the mineral skeletons of strontium sulfate, the radial cytoplasmic extensions known as axopods, the extracellular fibrillar network or periplasmic cortex and the contractile filament bundles known as myonemes.

Introduction

Acantharia Haeckel, 1881 are marine solitary protozoa that live in warm oligotrophic waters from the equator to subtropical waters between 0 and 250 m depth. They are abundant in the Sargasso Sea, the Mediterranean, the Indian Ocean and the China Sea. They were discovered by Müller in plankton samples from the Mediterranean and were regarded by most zoologists of the nineteenth century as Radiolaria. On the basis of accurate descriptions of living specimens, Schewiakoff (1926) separated the Acantharia from the Radiolaria. Acantharia, Radiolaria and Heliozoa were then regrouped into the subphylum Actinopoda. Today, Acantharia and Radiolaria are placed in the phylum Radiozoa Cavalier-Smith, 1987. Acantharia are characterized by a skeleton of celestite with strictly defined architecture. Radial cytoplasmic processes or axopods project from the cell body into the surrounding water. The central body of cytoplasm is surrounded by two concentric fibrillar extracellular layers, an inner capsular wall and an outer periplasmic cortex. The cortex is anchored to the skeleton by contractile filament bundles, the myonemes. No fossils have been reported.

Description and Characteristics

Acantharia are delicate star-shaped solitary protozoa measuring 20–800 μm in diameter (**Figure 1**). The cytoplasm is organized around a large membrane-bound skeleton made of long radial spicules that cross or meet in the cell centre. The inner cytoplasm (endoplasm) contains conventional organelles, one large polyploid nucleus or several small nuclei, mitochondria with tubular cristae, pigment and mineral inclusions. This endoplasm is contained within a central capsule consisting of a thick extracellular, porous fibrillar meshwork. Rods of microtubules arise from tiny dense plaques or microtubule organizing centres (MTOCs). The peripheral 'ectoplasm' consists of cytoplasmic islets protruding through pores of the capsular wall. The ectoplasm is surrounded by an additional extracellular periplasmic cortex, a thin layer attached to the tips of the spicules by 2–80 contractile ribbons, the myonemes (**Figure 2**).

The skeleton

The mineral skeleton consists of 10 diametral or 20 radial spicules of rhombic monocrystals of strontium sulfate (celestite) contained within a perispicular vacuole. Their spatial organization is precisely defined according to Müller's law. Two quartets of 'polar' tips alternate with two quartets of 'tropical' tips and one quartet of 'equatorial' tips. Since the spicules are water-soluble after death, they are never found in sediments. In the subclass Holacanthia, the 10 spicules are needle-shaped, sometimes denticulated, and cross in the cell centre. In the subclass Euacanthia (orders Symphyacanthida, Chaunacanthida, Arthracanthida), the spicules are more or less tightly joined at their bases. In the Symphyacanthida, they are fused into a central tiny sphere which cannot be dissociated. In the Chaunacanthida, the 20 radial spicules are linked at their bases with contractile fibrils, allowing the spicules to move slowly. In the Arthracanthida, the 20 solid spicules, equal or unequal in length, have pyramidal bases, simply juxtaposed in the cell centre by their planar faces or leaf-shaped edges. Some have four lateral opposite spines, from which single or branched apophyses diverge, forming a

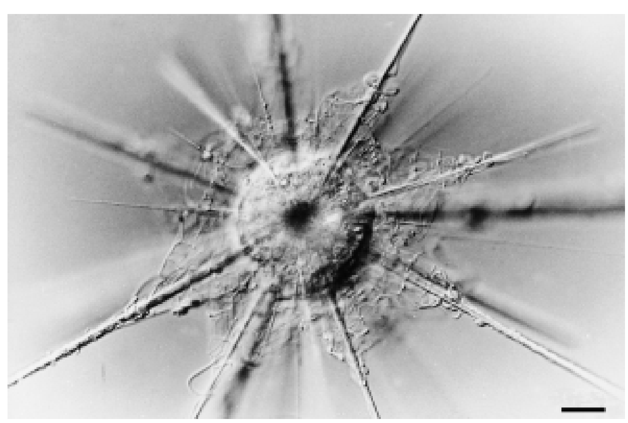

Figure 1 A living acantharian. Bar, 25 μm.

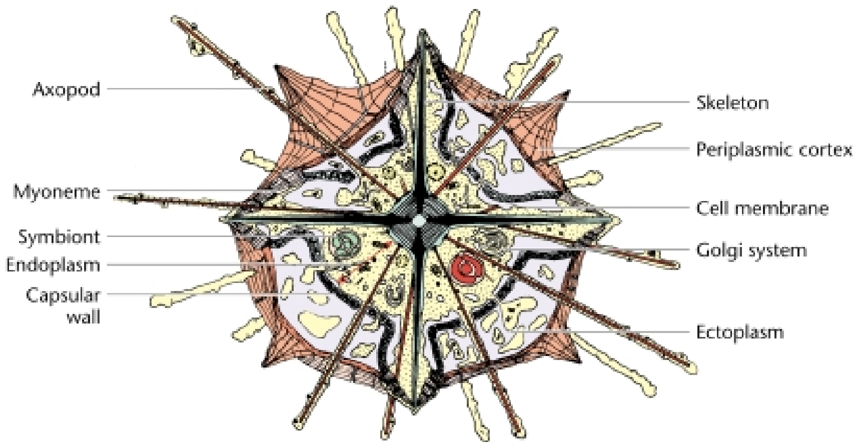

Figure 2 Structure of an acantharian showing the central spherical endoplasm, limited by the capsular wall, and the ectoplasm covered by the periplasmic cortex. The spicules, surrounded by a perispicular vacuole, radiate from the cell centre. Myonemes are linked proximally to the periplasmic cortex at the periphery of the cell and distally to the apex of the spicules. Thin radiating axopods project for a distance of several microns into the surrounding water. The cell membrane limits the endoplasm and the islets of ectoplasm; it surrounds the distal part of the spicules and the myonemes.

latticed or perforated plate. In some cases the plates are connected with one another laterally, forming a latticed shell around the endoplasm. In Euacanthia, where gametogenesis occurs in a cyst, the skeleton becomes completely remodelled during encystment. The spicules are released or broken, then adjacent plaques are secreted and joined to one another, forming an oval or round cyst wall.

The axopods

Acantharia, like other actinopods, are characterized by long, thin, slender and unramified processes called axopods, which radiate from the cell surface in all directions (Febvre-Chevalier and Febvre, 1993). Their number and position are species-specific. Axopods are strengthened by an axial rod of parallel microtubules crosslinked by bridges, making hexagonal or dodecagonal patterns in cross-section. The microtubular arrays arise from MTOCs, closely apposed to the perispicular membrane near the base of the spicules. Bidirectional transport of organelles and vesicles occurs along the axial rod. Although they are used for prey capture, the axopods of acantharians are not notably dynamic or sensitive.

The periplasmic cortex

The periplasmic cortex is an extracellular superficial thin fibrillar network which displays complex species-specific patterns in tangential sections. It consists of 20 large polygonal pieces, each centred on one spicule, and connected to each other by elastic junctions. Around each spicule, the periplasmic cortex turns down like a collar and links with the capsular wall. The cortex is suspended by the myonemes to the apex of the spicules. The cell membrane passes between the cortex and the myonemes so that the fibrils of the cortex are connected with its outer leaflet and the myoneme filaments with its inner leaflet.

The myonemes

The myonemes are contractile ribbon-like or cylindrical organelles, 8–60 μm long, that are connected proximally to the periplasmic cortex and distally with the apex of the spicules. There are 2–80 myonemes around each spicule. Each myoneme is a dense bundle of twisted, thin nonactin contractile filaments. These bundles show periodical cross-striations, the spacing depending on the extent of contraction. Acantharia may use myoneme contraction–relaxation for buoyancy regulation but not for locomotion: they are passively transported by currents. Myonemes can produce three kinds of movement: (1) rapid contraction, causing transient inflation of the cortex, which increases the volume of the protozoan and limits sinking; (2) relaxation, causing the cortex to return to its initial form; (3) slow undulating movement accompanied by progressive contraction without displacement of the attachment points. In living specimens, contraction is triggered by calcium influx through the cell membrane. Transitory increase in cytosolic calcium concentration induces coiling of the twisted filaments and myoneme shortening. Myonemes that have been isolated and had their membranes removed will contract in the presence of calcium or relax in calcium-free media (threshold concentration $10^{-7}\,\mathrm{mol\,L^{-1}}$). The major myoneme protein shares common molecular domains with the calcium-binding protein centrin.

Behaviour

Food capture, symbiosis and involvement in nutrition

Although quantitative data on feeding behaviour and nutritional physiology are presently lacking, Acantharia are known to be microphagic protozoa that use axopods for feeding on tiny protozoa and miscellaneous particles. Many species of Acantharia host endosymbionts, such as Haptophyta and Dinoflagellata, in their endoplasm. Nutrients from photosynthesis may be accumulated during the day during exposure to light, then released at night and used by the host, as has been documented in Radiolaria.

Life cycle and reproduction

The life cycle of Acantharia has not been fully elucidated. All Acantharia except for the order Arthracanthida undergo pregametogenetic encystment. Nuclear division occurs without breakdown of the nuclear envelope. The mitotic apparatus consists of spindle pole bodies (dense plaques included in the nuclear envelope), from which spindle microtubules arise. Chromosomes are connected to spindle microtubules via trilamellar kinetochores. In some species, the nucleus can become progressively polyploid during vegetative growth. After a series of synchronous divisions within the cyst, biflagellate swarmers or gametes are shed.

Place in Overall Taxonomic Scheme

The class Acantharea is divided into two subclasses, Holacanthia and Euacanthia.

Comparison between Radiolaria and Acantharia

Since Acantharia and Radiolaria are now united in the phylum Radiozoa, their common features should be noted.

- The basic symmetry of the body plan is radial, due to axopod and skeleton organization.
- Endoplasm lies in a central capsule.
- Axopodial microtubule arrays share pattern identity in many species.
- Mitochondria bear tubular cristae.
- Nuclear division is a closed mitosis with spindle microtubules arising from spindle pole bodies.
- Biflagellate swarmers include a crystal of strontium sulfate.

Acantharia can be distinguished from Radiolaria by the following features.

- In Acantharia the skeleton is composed of spicules of strontium sulfate, arranged according to Müller's law, while in the Radiolaria the skeleton forms a single or multiple latticed shell or hollow tubes of silica.
- The entire capsular wall is a thin fibrillar meshwork lacking complex apertures, whereas in Radiolaria it forms a dense, thick wall with porous plaques or fusules.
- Acantharia microtubular arrays arise from dense plaques at the surface of the spicular vacuole, rather than from a single (central) or multiple (peripheral) MTOC.
- Radiolaria have neither periplasmic cortex nor myonemes.
- Endosymbiotic algae, when present, lie in the endoplasm, but in the ectoplasm in Radiolaria.
- The biflagellate swarmers are thought to be gametes issuing from meiotic divisions in the Acantharia, but to be spores issuing from an asexual reproduction in the Radiolaria. Recent molecular-based trees suggest that both taxa evolved independently and that Acantharia are monophyletic.

Classification of the subphylum Acantharia (phylum Radiozoa)

Subclass Holacanthia

There are two orders, Holacanthida and Plegmacanthida, both having 10 diametral spicules which cross in the cell centre. The endoplasm includes symbiotic algae and brown-red pigments; the ectoplasm is lacunar. The capsular wall and cortex are very thin. Ribbon-like myonemes are not obvious in living specimens. Gametogenesis occurs in a cyst. There are four genera of Holacanthida: *Acanthochiasma*, *Acanthocyrtha*, *Acanthospira*, *Acanthocolla*; and one genus of Plegmacanthida: *Acanthoplegma*.

Subclass Euacanthia

There are three orders, Symphiacanthida, Chaunacanthida, Arthracanthida, all bearing 20 radial spicules united in the cell centre. The capsular wall is thick. The periplasmic cortex exihibits highly organized fibrillar patterns. Endosymbiotic algae belong to Haptophyta. The axopods are stiffened by hexagonal microtubule patterns. Reproduction occurs via biflagellated swarmers without cyst formation in the Athracanthida. Gametes are formed in a cyst in the Symphiacanthida and Chaunacanthida. The order Symphiacanthida comprises four families: Astrolithidae (*Astrolonche*, *Heliolithium*, *Astrolithium*, *Acantholithium*), Amphilithidae (*Amphilithium*, *Amphibelone*), Pseudolithidae (*Pseudolithium*, *Dipelicophora*) and

Haliommatidae (*Haliommatidium*). The order Chaunacanthida includes three families: Gigartaconidae (*Gigartacon*, *Stauracon*, *Heteracon*), Conaconidae (*Conacon*) and Stauraconidae (*Stauracon*). The order Arthracantha is divided into two suborders: Sphaenacantha with seven families, and Phyllacantha with three families. Some representative genera are: *Icosaspis*, *Dorataspis*, *Acanthometra*, *Lithoptera*, *Phyllostaurus* and *Acanthostaurus*.

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