Heliozoa

Secondary article

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Heliozoa are typically spherical aquatic protozoa bearing thin, sensitive and dynamic cellular extensions known as axopods. The axopods are stiffened by bundles of unstable microtubules that radiate from the cell body in all directions. The skeleton, when present, consists of dispersed elements covering the cell surface. No fossils of Heliozoa have been reported.

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Introduction

Heliozoa (Gk *helios* sun, *zoon* animal) are unicellular phagotrophic animalcules with radiating axopods like the rays of the sun. These eukaryotes belong to the kingdom Protozoa and the supertaxon Actinopoda. They live at shallow depths in freshwater, brackish or marine environments. Most species are free-living, floating just above solid substrates or rolling among aquatic plants. They are never found in turbid water, which produces retraction of cytoplasmic extensions used for feeding. Reproduction is generally asexual but sexual processes with production of amoeboid or flagellate gametes have been described.

Description and Characteristics

Most species of Heliozoa are spherical, measuring 0.05–0.5 mm in diameter, although some are more complex, comprising a cytoplasmic base bearing a contractile stalk and an oval head. The cell membrane is covered with a mucous coat that can include dispersed mineral or organic scales and spicules. The cytoplasm of heliozoans is never enclosed in a central capsule as it is in radiolarians. Long, granule-studded processes known as axopods radiate from the cell body. Axopods (and the stalk when present) are strengthened by highly ordered bundles of unstable microtubules that radiate from one central mass of fibrillar-granular material in the cell body, or from multiple sites associated with the nuclear envelope. The cytoplasm includes microtubule organizing centres (MTOCs), Golgi elements and endoplasmic reticulum, mitochondria with tubular cristae, one or several nuclei and, in some species, endosymbiotic algae. Prey organisms, extrusive organelles involved in prey capture, food vacuoles, lysosomes and lipid droplets are present in the superficial cytoplasm (**Figure 1**).

Axopods

Axopods are slender extensions that project 0.04–0.8 mm from the cell body into the surrounding water. They are involved in many physiological functions, including recognition of environmental stimuli, cell contraction, locomotion and food capture. Axopods are stiffened by a rigid, though labile, axial rod which consists of a complex assembly of parallel microtubules and crosslinking bridges. The microtubule-based cytoskeleton is seen to be organized in specific and complex patterns when viewed in cross-section; for instance, including repeating motifs of double interlocking coils, elongated hexagons, regular hexagons and equilateral triangles, as well as other more complicated figures.

One of the distinctive features of the axopods is their sensitivity to a variety of physical stimuli, such as mechanical or electrical shocks, ultrasound, cold, high pressure and chemical agents. In some species, mechanical shocks induce slow membrane depolarization. In other species mechanical or electrical stimulation elicits a rapid, high-amplitude action potential; while in a few cases, the cell membrane is mechanically insensitive, stimulation up to 300 shakes per minute for 5 minutes producing no obvious effect. Chemotactic behaviour has been demonstrated using prey organisms or particles coated with specific proteins, suggesting chemosensitivity. Another distinctive feature of heliozoan axopods is their remarkable contractility. The highly ordered microtubular arrays responsible for maintaining the radial shape can dissociate almost completely within a few milliseconds in response to external stimuli. During rapid contraction, the microtubular rods first fragment, perhaps by the action of microtubule-associated severing proteins, then disassemble from the ends of fragments. Axopodial arrays then regrow from the MTOC. Certain chemicals, including microtubule inhibitors, urea and heavy and light metal ions, as well as mechanical and electrical stimuli can induce microtubule destabilization and axopodial retraction. Only agents that stabilize microtubules, such as heavy water, taxol (a drug isolated from the yew tree *Taxus brevifolia*) or calcium-free media are able to stabilize this highly unstable microtubule-based array under experimental stimulation.

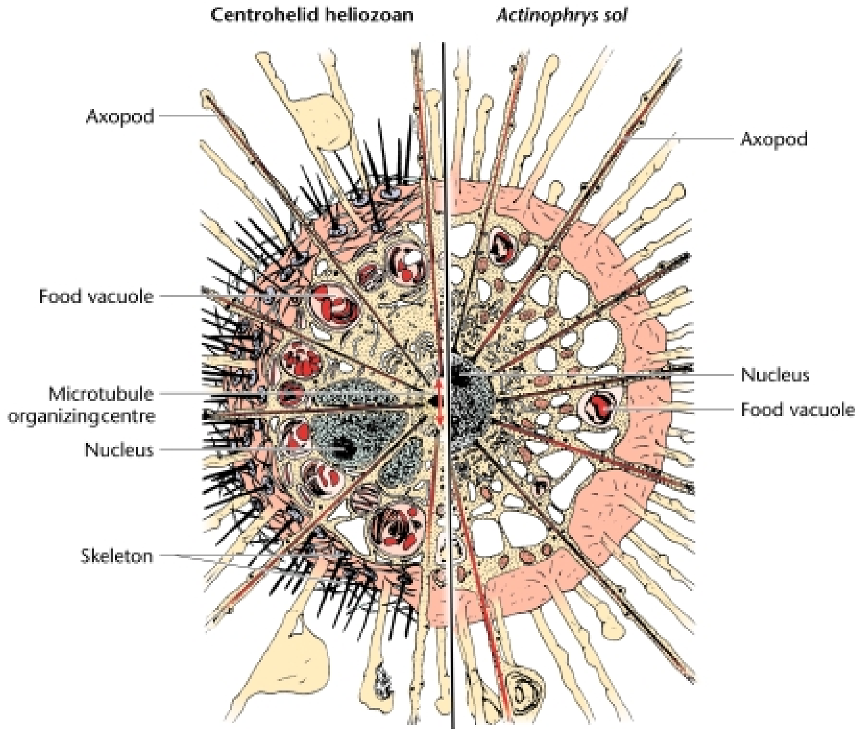

Figure 1 Structure of two heliozoa: a centrohelid heliozoon (left) and the actinophryid species *Actinophrys sol* (right).

Microtubule organizing centres

In Heliozoa of the class Centrohelidea, rods of microtubules radiate from a single large MTOC located in the cell centre (**Figure 1**, left), while in the class Actinophryidea they arise from numerous tiny sites closely fitted to the nuclear envelope (**Figure 1**, right). The central MTOC may include an inner trilamellar disc or consists of a fibrillar bulk without discernible inner differentiation. In some Heliozoa, the surface of the nuclear envelope is connected to the end of a large rod of microtubules involved in formation of a hollow mucous stalk. In the pelagic taxopodid *Sticholonche zanclea*, axopodial rods terminate at numerous dense MTOCs lying in caveolae of a stratified sheet covering the nuclear envelope. Recent data indicate that the MTOCs seen in Heliozoa share common structural, behavioural and molecular characteristics with the centrosomes of lower and higher organisms. Although they lack a pair of centrioles, they are likewise not membrane bound, exist in only one copy during the vegetative stage and are duplicated once during each cell cycle before nuclear division. In addition, heliozoan MTOCs serve as sites for growth of interphase microtubules and form the poles of the mitotic apparatus. They contain a variety of structural and functional proteins involved in microtubule nucleation and the regulation of microtubule dynamics.

Extrusive organelles

Heliozoa contain membrane-bound extrusive organelles (0.2–0.8 μm in diameter), including mucocysts and kinetocysts involved in cell coat formation and prey capture. These organelles arise from the Golgi apparatus. Mucocysts contain a homogeneous, mottled or flocculent matrix. Kinetocysts include a dense pointed missile-like core embedded in a fuzzy material. Mature organelles are found in the superficial cytoplasm and axopods, and are linked to the cell membrane by proteinaceous particles. In the presence of prey organisms, they move in both directions along the axopodial axis at a velocity of about $0.5\,\mu m\,s^{-1}$. They stop moving in the absence of stimulation.

Skeleton diversity

Except for a dozen naked species, Heliozoa have skeletons consisting of single or multiple tangential sheets of dispersed organic or siliceous elements. Three types of structure have been described: tiny spheres, elliptic or lens-shaped scales and thin hollowed or compact radial spines or spicules resembling spatulae, needles, cups, tubes or funnels. Scales and spicules are produced by the Golgi system and released at the cell surface, where they become embedded in the mucous coat overlying the cell surface.

This composite layer is periodically cast off and replaced by a new one.

Behaviour

Food capture and ingestion

Heliozoa are passive predators. Prey organisms colliding with the axopods are liable to stick to the cell membrane as the result of exocytosis of adhesive substances by mucocysts. The prey becomes entangled and progressively paralysed. It is then translocated towards the cell body. Membrane recognition of the prey by the predator is crucial. Some prey organisms are never captured, while others are killed, then rejected without having been ingested. Some heliozoan species have a strict diet, but most feed on a variety of prey organisms, such as bacteria and blue-green algae, coloured flagellates, and ciliates. Both the size and the swimming velocity of prey are crucial. Tiny algae are immediately captured by single axopodia, while quick-swimming larvae trigger simultaneous contraction of several axopodia.

Locomotion

Most Heliozoa roll slowly along solid substrata or aquatic plants on their axopods. An unusual locomotory system is observed in the marine planktonic species *S. zanclea*, which uses rows of rigid axopods as oars to swim slowly through water. This rowing motion takes place via contraction–relaxation of thin bundles of filaments that link bases of axopods to the edges of the caveolae of the nuclear envelope. This unique swimming behaviour has been compared to the propelling mode of a trireme.

Reproduction

Binary and multiple fissions are very common processes of asexual reproduction. Binary fission gives rise to two daughter heliozoans. Multiple fission occurs through repeated divisions of the parent nucleus and formation of many daughter cells, each with one nucleus. Sexual reproduction has been observed in a few heliozoans. In *Actinophrys sol*, two amoeboid gametes are generated from a single parental cell and then fuse together via a characteristic sexual process called autogamy. This entire process takes place in a cyst (gamontocyst) after axopodial retraction. Mitosis gives rise to two equal daughter cells having the same diploid genome. The nucleus of each cell then undergoes meiosis. However, during each of the two successive divisions, one nucleus per cell degenerates so that only two gametes are formed. These then fuse within the cyst, forming a diploid zygote. When decystment takes place, axopods grow again, restoring the sun-like appearence. In the stalked species, *A. contractilis*, the life cycle comprises two phases, asexual multiplication through binary or multiple fission and sexual reproduction, the whole heliozoan giving rise to thousands of biflagellated gametes that are shed synchronously. Gametes swim actively, then are likely to fuse.

Place in Overall Taxonomic Scheme

As Heliozoa, Radiolaria and Acantharia all have radiating axopods, they were originally classified in the phylum Actinopoda Calkins, 1902. In current classifications, Actinopoda has been retained as a supertaxon, with its members having been divided into two distinct phyla, the Radiozoa and the Heliozoa. Radiozoa exhibit a central capsule and accumulate strontium sulfate as crystals in swarmers, while Heliozoa are devoid of these distinctive features. Until recently, Heliozoa included the previously named helioflagellates *Dimorpha*, *Tetradimorpha*, now placed in the phyla Opalozoa. The third genus *Ciliophrys* has been placed in the phylum Chromista because it is closely related to pedinellid algae.

In a recent classification (Corliss, 1994), Heliozoa are divided into four classes.

Class Actinophryidea Hartmann, 1913

There are one or several nuclei; MTOCs are scattered over the nuclear envelope. The cross-sectional pattern of the axonemal microtubules is 'double helix coiled'. Extrusive organelles appear as dense mottled granules. The cell body is naked. The genera are *Actinosphaerium*, *Echinosphaerium*, *Actinophrys*, *Camptonema*.

Class Desmothoracidea Hertwig and Lesser, 1874

There is one nucleus; MTOCs are fitted on to the outer surface of the nuclear envelope. There are imprecise microtubule patterns, and missile-like kinetocysts. An organic latticed shell encloses the cell body. The genera are *Clathrulina*, *Hedriocystis*, *Orbulinella*.

Class Centrohelidea Kühn, 1926

There are one or several nuclei, a single central large MTOC and hexagonal patterned arrays of axonemal microtubules.

Order 1: Centroplasthelida

The MTOC includes a central trilamellar disc; the nucleus is crossed by 1–4 axopods passing through nuclear channels; extrusive organelles are missile-like kinetocysts and mucocysts. There are three families: Heterophryidae

(*Heterophrys*, *Oxnerella*), Acanthocystidae (*Acanthocystis*) and Raphidiophryidae (*Raphidiophrys*).

Order 2: Axoplasthelida

The MTOC has no central trilamellar disc; axopodial microtubules are patterned as lengthened hexagons in cross-section; extrusive organelles are mucocysts and dense granules. There are two families: Gymnidae (*Gymnosphaera*, *Actinocoryne*) and Hedraiophryidae (*Hedraiophrys*).

Class Taxopodea Fol, 1883

There is one nucleus; MTOCs are stratified, articulated in caveolae of the nuclear envelope. There is a rowing motion of axonemes, a hexagonal microtubule pattern and hollowed spatula-like siliceous spicules forming bouquets. There is one species, *Sticholonche zanclea*.

Phylogenetic Evolutionary Considerations

Heliozoa are likely to be polyphyletic rather than monophyletic. It is unclear whether microanatomical diversity of MTOCs, axopodial microtubule patterns and the substructure of extrusive organelles diverge from a common origin or not. Close similarities in the organization of the MTOC and the microtubular architecture of certain Heliozoa, Acantharia and Radiolaria suggest that a common ancestor may have existed. Molecular data which could bring useful phylogenetic clues are still lacking.

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