Centrohelida and Other Heliozoan-Like Protists

Rebecca J. Gast

Abstract

The Centrohelida has arisen through the dissolution of the Heliozoa and the gradual removal of morphologically similar, but ultrastructurally and genetically distinct taxa from the group. The taxonomy of these other heliozoan-like protists is still largely influx, as are the groups within the Centrohelida. Centrohelida and heliozoan-like protists are heterotrophic, free-living species that are found in most aquatic benthic environments where they feed on bacteria and other protists, including algae. Morphologically the cells are conspicuous, generally round in shape with eye-catching raylike axopodia. They can be found in habitats that represent a wide range of temperatures and salinities, including extreme environments. Most are free floating, but some attach to substrates by a stalk. Interest in the heliozoan-like protists ("sun animalcules") is largely in regard to cell biology. Their size (some can be 500 μm in diameter) and axopodial structure have made them useful subjects for biochemical and ultrastructural studies of microtubules.

Keywords

Axoplast • Axopodia • Centrohelids • Centroplast • Heliozoa

Contents

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Summary Classification

•Centrohelida
••Acanthocystidae (e.g., *Acanthocystis*, *Choanocystis*, *Pseudoraphidiocystis*, *Echinocystis*, *Pseudoraphidiphrys*, *Pterocystis*)
••Heterophryidae (e.g., *Sphaerastrum*, *Heterophrys*, *Oxnerella*, *Chlamydaster*)
••Raphidiophryidae (e.g., *Parasphaerastrum*, *Polyplacocystis*, *Raphidiophrys*, *Raphidiocystis*)
•Retaria
••Acantharia
•••Taxopodida *Sticholonche zanclea*
•Stramenopile
••Actinophryida (e.g., *Actinophrys*, *Actinosphaerium*)
•Rhizaria
••Cercozoa
•••Granofilosea
••••Clathrulinidae (e.g., *Clathrulina*, *Cienkowskya*, *Hedriocystis*, *Penardiophrys*)
•Rhizaria
••Incertae sedis Gymnosphaerida (e.g., *Hedraiophrys*, *Actinocoryne*, *Gymnosphaera*)
[**Incertae sedis Heliomonadida/Dimorphida** (e.g., *Heliomorpha*, *Tetradimorpha*, *Acinetactis*)]
[**Incertae sedis heliozoan-type genera** *Wagnerella*, *Actinolophus*, *Lithocolla*, *Actinosphaeridium*]

Introduction

General Characteristics and Occurrence

The phagotrophic spherical amoebae with microtubule-supported axopodia once called “sun animalcules” used to be grouped together into a formal class called Heliozoa. The cells range from 10 to 500 μm in size, either naked or coated with organic or siliceous scales, and radiating long axopodia (Fig. 1). Centrohelida and other heliozoan-like protists have been isolated from fresh and marine water; from polar, temperate, and subtropical regions; as well as from some extreme environments. They are generally found just above the sediment-water interface, but can be isolated from the pelagic environment as well.

Literature and History of Knowledge

The body of literature on heliozoan-like protists includes works from the end of the nineteenth century and the beginning of the twentieth century devoted to light microscopy and systematics and more recently papers focusing on ultrastructure (electron microscopy), life cycles and cell physiology (including motility and feeding processes), molecular systematics, and biogeochemistry. Articles that comprise the basis of this work include Penard’s monograph (Penard 1904); the descriptions of Valkanov (1940), Rainer (1968), and Tregouboff (1953); studies by Febvre-Chevalier (Febvre-Chevalier 1982; Febvre-Chevalier and Febvre 1984); and work by Mikrjukov, Patterson, and Cavalier-Smith (Mikrjukov 1998, 2000a, b; Mikrjukov and Patterson 2001; Cavalier-Smith and von der Heyden 2007).

Haeckel first described spherical protists with raylike pseudopodia as heliozoan in 1866 Haeckel 1866), and the name was eventually applied to many organisms with similar morphologies. Penard (1904) proposed the first classification of the group based largely upon morphological observations of their skeleton, resulting in the separation of the Heliozoa from the radiolarians. The Heliozoa included the groups Centrohelida, Actinophryida, Clathrulinidae, Dimorphida (or Heliomonadida), and Gymnosphaerida. *Sticholonche*, belonging to the Taxopodida, was also placed within the Heliozoa. Light and electron microscopy studies were next used to propose more comprehensive systematics (Hartmann 1913; Kühn 1926; Valkanov 1940; Rainer 1968; Febvre-Chevalier and Febvre 1984; Smith and Patterson 1986). Most recently, molecular phylogenetic methods have been used to help understand the evolutionary relationships between groups and species (Nikolaev et al. 2004; Cavalier-Smith and von der Heyden 2007; Bass et al. 2009; Yabuki et al. 2012). It is now generally recognized that the class Heliozoa was established based upon convergent morphological characteristics, and it has been dissolved in recent taxonomic revisions (Mikrjukov 1998, Mikrjukov and Patterson 2001; Adl et al. 2005, 2012). Currently many of the heliozoan-like protists are placed within the Centrohelida (see section “▶ Centrohelida and Heliozoan-Like Taxonomy” below).

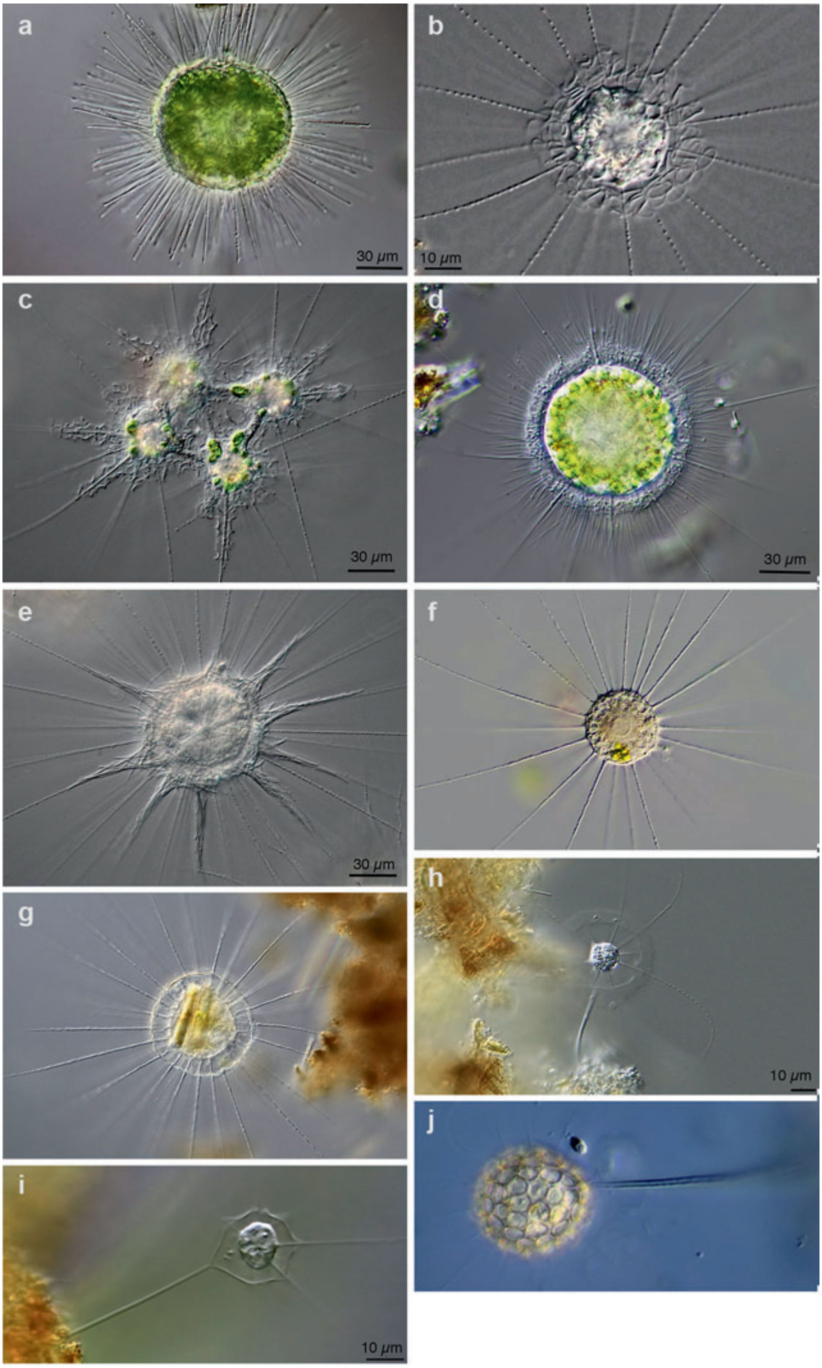

Fig. 1 Light microscope images of centrohelid and heliozoan-like protists. (**a**) *Acanthocystis turfacea*, (**b**) *Raphidophrys intermedia*, (**c**) *Raphidiophrys elegans*, (**d**) *Heterophrys myriopoda*,

Practical Importance

The Centrohelida and heliozoan-like protists have been useful for investigating aspects of cell biology. Studies of fibrillar proteins and microtubules involved in cell shape and movement (Cachon et al. 1977; Cachon and Cachon 1984; Febvre-Chevalier and Febvre 1980), the role of the cell membrane in detection and response to stimuli and control of contraction (Febvre-Chevalier et al. 1983, 1986), and the influence of the environment on the cell (Febvre-Chevalier 1981) were conducted using *Sticholonche* and *Actinocoryne*. Morphogenesis (Tilney and Byers 1969; Roth and Shigenaka 1970; Edds 1975), feeding (Suzaki et al. 1980; Patterson and Hausmann 1981; Hausmann and Patterson 1982; Linnenbach et al. 1983), and the biochemistry of tubulin and associated proteins within the axoneme (Little et al. 1983) were all studied using isolates of *Actinosphaerium*. $Ca2^{+}$-dependent axopodial contraction (Arikawa et al. 2006; Kakuta and Suzaki 2008) and feeding behavior (Pierce and Coats 1999; Sakaguchi et al. 1998) have been studied using *Actinophrys sol*.

Habitats and Ecology

Centrohelida and other heliozoan-like protists are widely distributed in aquatic environments, and while they have been isolated primarily from freshwater, they have also been observed in brackish or marine water in the euphotic zone. Primarily sub-benthic or benthic, they can be sampled with plankton net tows and can be abundant when conditions are favorable. The only exclusively pelagic marine form is *Sticholonche zanclea*. Freshwater centrohelid-like organisms have been collected from diverse sources of relatively still water, including lakes, regions of rivers, stagnant water, artificial ponds, marshes, and temporary pools (Penard 1904; Rainer 1968). Marine and brackish species are found in the coastal zone, again in waters that are not energetic, like harbors, coves, and brackish channels. Most species are free living and float or roll in the water, but *Sticholonche* is unique and moves by using an axopodial rowing motion (Cachon and Cachon 1978). Some species may secrete a long proteinaceous peduncle or stalk that temporarily attaches them to surfaces in the environment (e.g., *Clathrulina*, *Wagnerella*, *Actinocoryne*).

Centrohelida and heliozoan-like cells seem to prefer oxygenated water with plenty of organic matter to support the growth of other protists that serve as prey organisms. They also appear to be able to tolerate a wide range of temperatures and salinities. For example, *Cienkowskya mereschkovskyi* was found by Villeneuve

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Fig. 1 (continued) (**e**) *Polyplacocystis pallida*, (**f**) *Actinophrys sol* (cell body is approximately 43 μm in diameter), (**g**) *Actinosphaerium eichornii*, (**h**) *Actinosphaeridium* sp., (**i**) *Hedriocystis pellucida*, and (**j**) *Clathrulina elegans* (the shell is 35 μm and the stalk 112 μm) (All images are courtesy of Ferry Siemensma. Additional images of amoeboid protists may be viewed at Microworld (http://www.arcella.nl))

(1937) in salt-marsh channels near Sete, France, that experience highly variable salinities, and Febvre-Chevalier reported collecting it in Villefranche in water of salinities between $37^0/_{00}$ and $38^0/_{00}$ (Febvre-Chevalier 1990). *Cienkowskya* also illustrates the wide temperature range that some isolates can tolerate; it has been isolated from the White Sea (mean temperature of 2 °C), from Villefranche (temperatures between 13 °C and 27 °C), and from salt-marshes near Sete (temperatures up to 30 °C).

pH also likely plays a role in the distribution of these species with different habitats varying from pH 4.6–8.5, (Rainer 1968). *Actinophrys sol* and *A. eichorni* tolerate very wide ranges in pH (4.6–8.5), while species like *Raphidophrys elegans* and *Acanthocystis echinata* are observed at more limited ranges (between 6.0 and 8.2 for the former and 4.5–5.4 for the latter). *Polyplacocystis symmetrica*, *Raphidophrys intermedia*, *R. ovalis*, *R. echinata*, *Clathrulina elegans*, and *Pompholyxophrys punicea* were isolated from acidic bogs (pH 4.3–5.1) in Russia (Leonov 2010). Recently, the acidic limits of pH tolerance have been lowered further with reports of *Actinophrys* species in Spain's Rio Tinto (pH approximately 2.0; Amaral Zettler et al. 2000) and of *Actinophrys sol* in lower Lusatia, Germany, at pH 2.3 and 2.6 (Packroff 2000).

Centrohelida and heliozoan-like protists feed by phagocytosis of bacteria, other protists (including algae), and larvae of invertebrates. They are generally considered passive predators that capture prey as it comes along. Despite the occurrence of free-floating forms, their ecological niche is considered to be the benthic environment where they inhabit the superficial layer of detritus and interstitial spaces. Swimming prey is thought to impact and stick to the mucous coat of the axopodia, stimulating contraction and movement of the prey toward the cell where a food vacuole is formed (Febvre-Chevalier and Febvre 1980; Patterson and Hausmann 1981; Suzaki et al. 1980).

Characterization and Recognition

General Appearance and Ultrastructure

Centrohelida and heliozoan-like protists are spherical, 10–500 μm in diameter, with long slender axopodia and short pseudopods, or branched filopods (Fig. 1). The genera *Heliomorpha*, *Tetradimorpha*, and *Acinetactis* have one or more flagella in addition to axopodia. In general, Centrohelida lack a central capsule and are either naked or covered with a mucoid cell coat. Some members of the heliozoan-like protists belonging to the Clathrulinidae have latticed organic capsules. The mucous coat, ranging in thickness from 0.05 to 5 μm depending upon the species and physiology, is secreted at the cell surface. Most cell surfaces also contain external skeletal spicules, scales, or small spheres. These can be composed of silica or organic material, and the morphology of the spheres, spicules (spatula, needles, tubes, cups, funnels, clubs), and scales (elliptic, lens shaped) is a key element of species identification and systematics.

Various kinds of extrusomes (organelles involved in prey capture) are scattered in the axopodial and cortical cytoplasm. Their contents are ejected after excitation by an outside stimulus by rupture of the cell membrane. The different types of extrusomes that have been described include dense and mottled granules (Actinophryidae), mucocysts, and kinetocysts (Centrohelida and Clathrulinidae) (Febvre-Chevalier 1985; Mikrjukov 1998; Davidson 1976).

Vegetative cells can be either mono- or multinucleated, and some genera alternate between spherical free-living and stalked sessile forms (members of the Gymnosphaerida and Clathrulinidae). Some stalks are inert, while others are cytoplasmic and may be capable of contraction (*Actinocoryne* and *Wagnerella*). The formation of resting cysts when growth conditions become unfavorable has been observed. Some heliozoan-like protists have also been reported to contain symbiotic algae (*Hedraiophrys* Febvre-Chevalier 1973a), or to retain functional chloroplasts from their algal food (*Acanthocystis*, *Raphidiocystis*, and *Chlamydaster*; Patterson and Dürrschmidt 1987).

A key feature of heliozoan-like protists is the axopodia, although this is now considered to be a trait acquired independently in the different lineages rather than an indication of shared evolutionary history. These are long, thin projections supported by arrays of microtubules called axonemes. Axopodia are able to contract rapidly, at a velocity of 50–300 lengths of the cell per second (Davidson 1975; Febvre-Chevalier and Febvre 1980). Filopods, long supple projections of the cell body, and pseudopods, temporary extensions of the cell surface, lack microtubular structure. All three structures are involved in feeding.

The axopodia are made up of bundles of microtubules (Little et al. 1983) connected to one another by cross-bridges resulting in distinct patterns (see Dustin 1978). There are five basic patterns that are generally recognized. There are the slightly irregular hexagons and equilateral triangles found in the Centrohelida (Fig. 2, panel 1b and 2b, e.g., *Heterophrys*, *Raphidiophrys*, *Acanthocystis*; Tilney 1971; Bardele 1975). Two interlocking coils in a spiral pattern are present in the Actinophryidae (Tilney and Porter 1965; Roth et al. 1970; Ockleford and Tucker 1973). Irregular adjacent hexagons that form a "parquet" pattern are present in the Gymnosphaerida (Febvre-Chevalier 1973a, 1975, 1982). A square microtubule arrangement is found in the Heliomonadida (Fig. 2, panel 3b; Brugerolle and Mignot 1983, 1984), while the Clathrulinidae exhibit an irregular pattern (Fig. 2, panel 4b; Bardele 1972).

Microtubules are generated by microtubule-organizing centers or microtubule-nucleating centers (MTOC or MNC: Pickett-Heaps 1969). These are located in the center of the cell or on the outer nuclear membrane (Actinophryidae and Clathrulinidae). The central MTOC, called a centroplast, may possess a central disc sandwiched between two dense caps about 0.1–1.5 μm in diameter (Centrohelida; Fig. 2, panel 1a, 2a). In other instances it may lack this inner differentiation and is then sometimes called an axoplast (Anderson 1988; Febvre-Chevalier 1973b; Gymnosphaerida and Heliomonadida; Fig. 2, panel 3a, 4a).

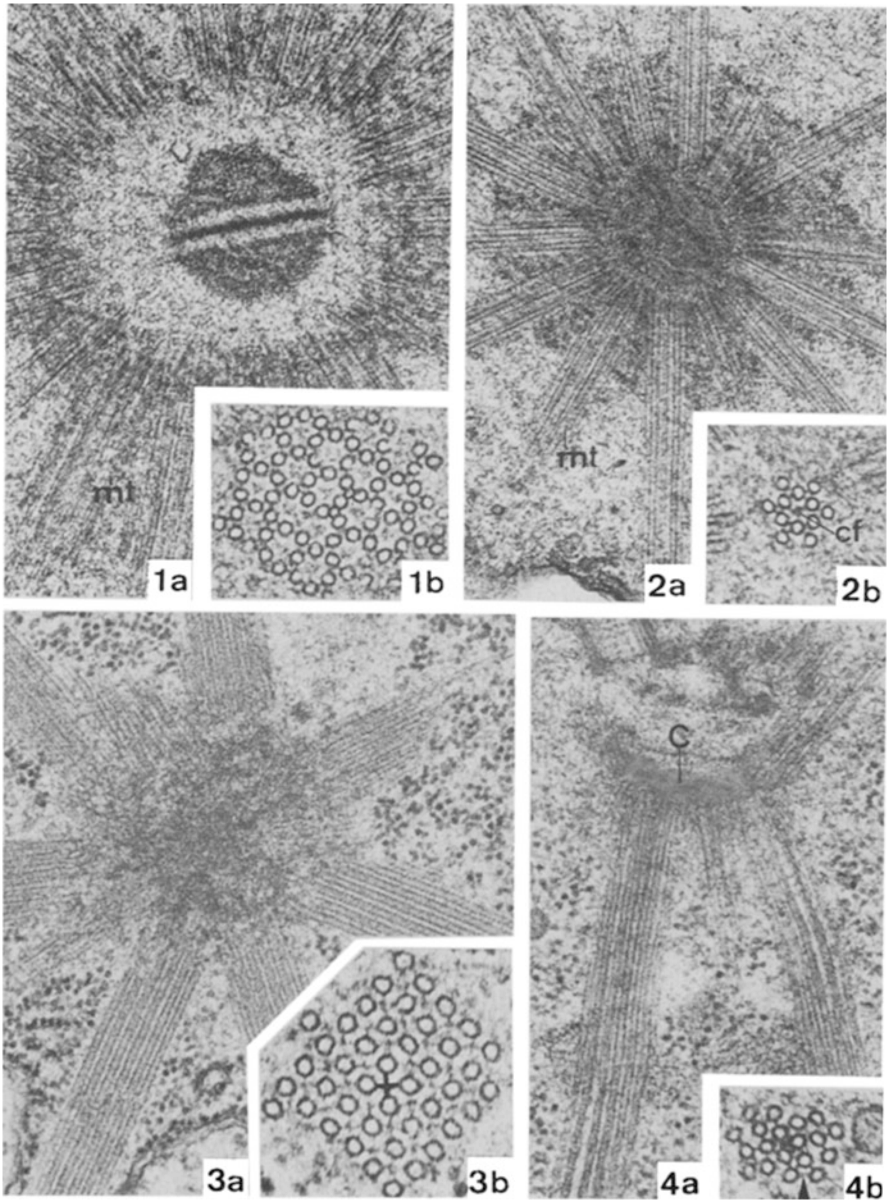

Fig. 2 Transmission electron micrographs of *Raphidiophrys elegans*, *Acanthocystis turfacea*, *Dimorpha mutans*, and *Tetradimorpha radiata*. Panel **1a** The centroplast of *Raphidiophrys elegans* has a tripartite central disc with an electron dense equatorial plate. Axopodial MTs arise from a shell around the centroplast. ×60,000. **1b** Axopodial MTs are triangles grouped in x-shapes, resulting in hexagonal or irregular hexagon patterns. ×90,000. Panel **2a** In the centroplast of *Acanthocystis turfacea*, the dense plate at the equator of the central disc is less obvious, and the axopodial MTs originate directly from the dense material around the disc. ×60,000. **2b** Axopodial MTs are

Life Cycle

Reproduction is usually asexual, with binary cell division most commonly observed. Division can give rise to equal- or unequal-sized offspring cells, with the smaller cell in the unequal division called a bud. Multiple fission, where multiplication of nuclei is followed by rapid synchronous division, can result in a large number of offspring cells produced at the same time. Division in stalked, sessile species takes place in the head, or in the base after withdrawal of both stalk and head (Zuelzer 1909; Febvre-Chevalier 1982). The offspring cells become free and fall onto the substratum where they undergo morphogenesis to give rise to a stalked cell.

Sexual reproduction occurs through autogamy in the cysts of *Actinophrys* and *Actinosphaerium* (Mignot 1979; Bělař 1923). First, the parent cell encysts and forms the gamontocyst, followed by progamic fission, resulting in two gamonts. Each gamont goes through meiotic division, after which one offspring nucleus degenerates. The remaining two cells differentiate into male and female gametes, and they fuse to form a zygote.

Centrohelida and Heliozoan-Like Taxonomy

The revised taxonomy of the Centrohelida and other heliozoan-like protists presented here is based upon Adl et al. (2005, 2012). The taxonomy of these protists is actively under revision, and other versions can be found in Cavalier-Smith and von der Heyden 2007; Mikrjukov et al. 2000; Mikrjukov 2000a, b; Mikrjukov and Patterson 2001; Yabuki et al. 2012; and on the web at *Microworld, world of amoeboid organisms* Siemensma, F. J. 2015 http://www.arcella.nl.

Eukaryota; Centrohelida (Kühn 1926)

Members of the Centrohelida have axonemes arising from a centroplast that has a tripartite disc flanked by two regions of electron-dense material. Axonemes have

Fig. 2 (continued) arranged in a single hexagon containing a central filament (cf) which is linked to the six neighboring MTs. ×90,000. Panel **3a** The centroplast of *Dimorpha mutans* is composed of microfibrillar material from which the axopodial axonemes arise. ×54,000. **3b** Axopodial MTs are arranged in a “quincunx” pattern that makes a squared packed array. ×150,000. Panel **4a** In *Tetradimorpha radiata* the lens-shaped centroplast (C) is composed of unstructured dense material, with the axopodial MTs arising from its periphery. ×93,000. **4b** The MTs are arranged irregularly with some having more than four links and others having triangular figures (*arrow*). ×102,000 (Used with kind permission from Springer Science+Business Media: Origins of Life, *The cell characters of two Helioflagellates related to the Centrohelidian lineage: Dimorpha and Tetradimorpha*, volume 13, 1984, 305–314, Guy Brugerolle and Jean-Pierre Mignot, Figs. 1, 2, 3, 4; original (first) copyright by D. Reidel Publishing Company) hexagonal and triangular patterns of microtubules, and the mitochondrial cristae are lamellate (flat) in shape. The kinetocysts are complex ball-and-cone-shaped structures. Some members have mucous stalks, and cell body coverings include naked, mucous, organic spicules, and siliceous rods, platelike scales, and spicules (tubelike, trumpetlike, and spine-like).

Heterophryidae (Poche 1913). Members of this group are naked or with a mucous coat. Some have tangential or radial organic spicules (revised in Mikrjukov 1996a).

Genera *Sphaerastrum*, *Heterophrys*, *Oxnerella*, *Chlamydaster.*

Acanthocystidae (Claus 1874). The surface of these protists is composed of two to three types of siliceous scales. The basal layer is usually composed of oval scales, the outer layer is composed of funnel-like structures or radial spicules (may have branched tips and/or flat, centrally attached basal disc).

Genera *Acanthocystis*, *Choanocystis*, *Pseudoraphidiocystis*, *Echinocystis*, *Pseudoraphidiphrys*, *Pterocystis.*

Raphidoiophryidae (Mikrjukov 1996b). This group of centrohelid protists has siliceous scales or spicules (trumpetlike, tubelike, or funnel-like) (revised in Mikrjukov 1996b).

Genera *Parasphaerastrum*, *Polyplacocystis*, *Raphidiophrys*, *Raphidiocystis.*

Rhizaria; Cercozoa; Granofilosea; Clathrulinidae (Claus 1874; Desmothoracida Hertwig and Lesser 1874)

The most distinctive characteristic of this group is the presence of a perforated or latticed capsule. Some have a non-cytoplasmic stalk, while others do not. There is a single, central nucleus, and the mitochondrial cristae are tubular. Axopodia tend to be long and are sometimes branched or forked, with the axonemes terminating on the nuclear envelope. The axonemes have unorganized microtubular arrays. Extrusomes are present, but resemble ones of cercomonads more than those of centrohelids. Reproduction occurs by binary fission, with one of the daughter cells forming a uni- or biflagellated cell that transforms into an amoeba after settling. The stalk and capsule are then secreted. Most isolates are freshwater organisms.

Genera *Clathrulina*, *Cienkowskya*, *Hedriocystis*, *Penardiophrys.*

Incertae sedis Clathrulinidae Servetia – A marine genus with a naked spherical head and hollow, non-cytoplasmic stalk with a broad base.

SAR; Stramenopile; Actinophryidae (Claus 1874; Emend Hartmann 1926)

Members of the actinophryid group are round bodied with stiff axopodia that taper from the base out to the tip. Microtubule organization within the axopodia is a striking double hexagonal spiral array, and the MTOCs are present on electron-dense material at the surface of the nucleus or near a nucleus. Cells have either a single central nucleus or multiple nuclei located centrally in the cell, and mitochondrial cristae are tubular. The extrusomes are of two types – large and osmiophilic and small and granular. The cell surface is naked and cysts with multiple walls can form. Binary fission is the primary mode of reproduction, but autogamy within the cyst occurs through the formation and fusion of amoeboid gametes. Actinophryids are the heliozoan-type most commonly recovered from freshwater, but are also found in marine and soil environments. The flagellated genus *Ciliophrys* (Cienkowsky 1876) was originally included among the actinophryids, but is now considered a member of the pedinellids.

Genera *Actinophrys*, *Actinosphaerium.*

Retaria; Acantharia; Taxopodida

The single member of this pelagic marine group is *Sticholonche zanclea* Hertwig, 1877. It is about 200 μm in size and has a bilateral symmetry rather than the radial symmetry seen in other members of the heliozoan-like protists. Its oar-shaped axopodia are arranged in 50–60 rows that terminate on the surface of the large central nucleus. Axopodia are used for buoyancy and movement. The microtubules are arranged in irregular hexagonal arrays. There has been debate regarding the taxonomic placement of *Sticholonche*, but molecular evidence indicates this organism is related to the Polycystinea and Acantharea (Nikolaev et al. 2004).

Incertae Sedis Rhizaria; Gymnosphaerida (Poche 1913; Emend Mikrjukov 2000b)

Most of the gymnosphaerid protists are found in marine environments. Cells can be uni- or multinucleate, and the nuclei can be present in the amoeboid base of the cytoplasmic stalk. The cell body with radiating axopodia is present at the top of the stalk, and the surface of the cell may be naked or covered by mucous or siliceous spicules. Mitochondria have tubular cristae. The life cycles appear to be complex and are not fully resolved. The original description of *Hedraiophrys hovassei* reported the presence of algal and bacterial symbionts (Febvre-Chevalier 1973a).

Genera *Hedraiophry*s, *Actinocoryne*, *Gymnosphaera.*

Incertae Sedis Eukaryota; Heliomonadida (Formerly Dimorphida); Heliomorphidae/Acinetactidae/Tetradimorphidae (Helioflagellates or Heliomonads; Siemensma 1991)

Axopodial microtubules arise from MTOCs near the flagellar bases. The cells are mononuclear and have tubular mitochondrial cristae, and kinetocysts are present. Members of the genus *Heliomorpha (Dimorpha)* and *Acinetactis* have two flagella, while members of the genus *Tetradimorpha* have four. Molecular studies suggest placement of these organisms as relatives of the Cercozoa, and *Acinetactis* was added to this group by Bass et al. (2009).

Genera *Heliomorpha (Dimorpha)*, *Tetradimorpha*, *Acinetactis.*

"Other" Heliozoan-Type Genera

Wagnerella incertae sedis Rhizaria – This marine genus has a noncontractile cytoplasmic stalk with an enlarged base and a spherical head. The axoplast is located centrally within the head, and the head is covered by mucilaginous material and siliceous spicules. Amoeboid cells are produced during reproduction, from both the head and from the base.

Actinolophus incertae sedis Rhizaria – A marine genus with a noncontractile cytoplasmic stalk and a pyriform head that is covered by a gelatinous layer. The single nucleus is located eccentrically within the head, and the axoplast is pear shaped.

Actinosphaeridium incertae sedis Granofilosea – A space is present between the mucous layer and the cell body of this organism, and the stalk ends at the mucous coat rather than on the cell body. The species was previously called *Nuclearia caulescens*.

Lithocolla incertae sedis Eukaryota – Found in both marine and freshwater, this organism is covered in a dense coating of sand grains. Movement is accomplished by rodlike filopods, and the nucleus is located centrally. The sand coat has made ultrastructure studies difficult, and its taxonomic position remains largely uncertain.

Maintenance and Cultivation

Benthic cells are collected by direct sampling of the sediment surface at the water-sediment interface. *Sticholonche zanclea* and other pelagic forms can be collected using a plankton net (mesh size of 40 μm). The organisms can be cultivated from collected sediments using serial dilution into a culture medium (e.g., SES medium for freshwater or Plymouth Erdschreiber medium for marine, Catalogue of the UK National Culture Collection). They can be enriched from water samples by adding Cerophyll or a grain of rice or barley to the collected sample. Algae, such as *Chlorogonium elongatum* (freshwater) or *Dunaliella* (marine; Davidson 1975), can be added as a food source, but enrichments generally support the growth of bacteria and small flagellated protists that serve as prey. Although enrichment cultures are usually successful in initially recovering heliozoan-like cells, it can be difficult to maintain them for long periods and to isolate the organisms into clonal culture. Some species may be available from culture collections like the Culture Collection of Algae and Protozoa, but this is rare.

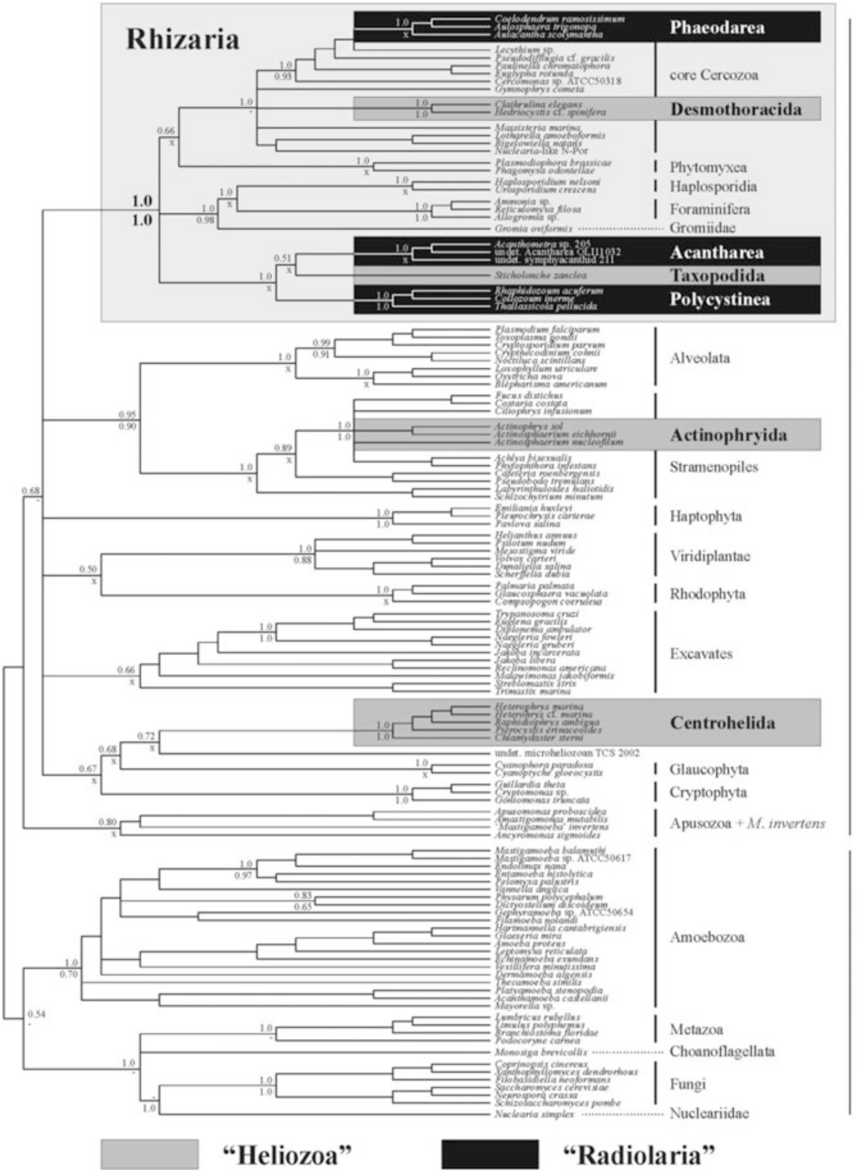

Fig. 3 Molecular phylogeny of Centrohelida and heliozoan-like protists (Used with kind permission from National Academy of Sciences. *The twilight of Heliozoa and rise of Rhizaria, an emerging supergroup of amoeboid eukaryotes*, volume 101, issue 21, 2004, 8066-8071, Sergey I. Nikolaev, Cedric Berney, Jose F. Fahrni, Ignacio Bolivar, Stephane Polet, Alexander P. Mylnikov, Vladimir V. Aleshin, Nikilai B. Petrov and Jan Pawlowski, Fig. 1. Copyright (2004) National Academy of Sciences, U.S.A.)

Evolutionary History

Over the past 15 years, it has become accepted that the heliozoan-like protists are a polyphyletic group based upon both morphological (Smith and Patterson 1986; Mikrjukov 1998, 1999, 2000a, b; Mikrjukov et al. 2000) and largely 18S rDNA-based molecular studies (e.g., Nikolaev et al. 2004; Cavalier-Smith and von der Heyden 2007; Cavalier-Smith and Chao 2003). The centrohelids are proposed to share a molecular evolutionary history with the haptophytes and cryptomonads and more broadly with the stramenopile/alveolate/Rhizaria (SAR; Cavalier-Smith and von der Heyden 2007; Burki et al. 2009). The Heliomorphids (Dimorphids) and Clathrulinids (Desmothracids) are considered to share an evolutionary history with the Cercozoa, and actinophryids are proposed to share common ancestry with the Stramenopiles (Fig. 3; Nikolaev et al. 2004; Bass et al. 2009). Due to a lack of molecular data, the history of the gymnosphaerids remains unresolved, with their placement limited to incertae sedis within the Rhizaria.

Acknowledgments Revised from the original chapter of Colette Febvre-Chevalier

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