Rhizaria RG

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Rhizaria Cavalier-Smith 2002
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The Rhizaria include five large clades that are the Cerocozoa, Imbricatea, Endomyxa, Foraminifera, and Radiolaria. The latter two are included in a larger group called Retaria. An additional Family, the Gymnosphaerida, is placed here as i*ncertae sedis* based on morphology as there are no phylogenies for the group. Two Genera included in Rhizaria may represent ancestral forms (*Aquavalon, Tremula*). In General, most species have mitochondria with tubular cristae. The main unifying morphology in the Rhizaria is the production of very fine pseudopodia, sometimes numerous, usually supported by microtubules called filopodia. Filopodia can be simple, branching, or anastomosing.

Two lone Genera are included in Rhizaria and they are significant in understanding the origin and diversity of the group. *Tremula* has a trailing long posterior cilium used for gliding, and a shorter anterior cilium pointing forward, also used for gliding. Cells are phagotrophic on bacteria and without cytostome, theca or scales. *Aquavalon* is cytotrophic by phagotrophy with a characteristic lateral depression. Cells are oval and slightly flexible. A pair of cilia emerge subapically and used for fast swimming, rarely gliding.

Table 9.1. Figure 9.1

9.1.Gymnosphaeridae Poche 1913 emend. Mikrjukov 2000

Cells are free-swimming and biciliated or amoeboid, sometimes forming a cytoplasmic pseudopodium as a simple stalk to hold-on to a substrate. There are no plastids, and mitochondria have tubular cristae. The filopodia are axopodial with microtubules arranged in irregular hexagonal arrays. Along the axopodia, there are diverse extrusomes, including kinetocysts. Cells can be multinucleate, often located in the stalk when present. There are five Genera (*Actinocoryne, Cienkowskya, Gymnosphaera, Hedraiophrys, Wagnerella*), but *Hedraiophrys* may be a junior synonym of *Cinekowskya*.

9.2.Cercozoa Cavalier-Smith 1998, emend. Adl et al. 2005; emend. Cavalier-Smith 2018

This diverse clade of heterotrophic small protists contains many poorly resolved clades (Families and higher ranks) due to poor taxon sampling. Species are common, often abundant in soil, but also occurring in sediments, with some marine Genera. The poor resolution of the Cercozoa, and Rhizaria in General is due to insufficient sampling of soil and terrestrial environments. Mitochondria are usually with microtubular cristae. Terrestrial Genera from cysts. Peroxisomes (or microbodies) and extrusomes are common. Cytoskeleton from the kinetosome extends to the nucleus. Sexual conjugation is unknown.

Five groups are placed as *incertae sedis* in the Cercozoa. Three are Discocellia Cavalier-Smith 2013, the Genera *Dictiomyxa, Katabia, Myxodictyium, Pontomyxa, Protomyxa, Protogenes, Pseudospora, Rhizoplasma,* and unrelated to these, *Kraken*. The other two are Families. Volutellidae Sudzuki 1979 are found in marine sediments. They have a test, half-coiled, of organic secretions, sometimes with embedded particles. The Psammonobiotidae Golemansky 1974, emend Meisterfeld 2002 are probably an adjacent clade to the Euglyphida or Silicofilosea, but they do not secrete silica scales. Cells form a vase-shaped test made or organic secretions. Genera are mostly marine, but specimen from freshwater or soil environments are also known. As the name indicates, species are found in soil or sediments.

Table 9.2.

9.2.1.Cercomonadida. Cercomonads are phagotrophic biciliated Genera found in soils and sometimes in freshwater. They are probably in freshwater from drainage, as species tend to be surface associated gliding on surfaces, occasionally detaching to swim a short distance. In cultures, some cells are swimming but most will be surface-associated and gliding. Cysts form when bacteria abundances are too high or too low, and in response to desiccation. The posterior trailing cilium contributes to gliding, while the anterior cilium pushes and beats asymmetrically on the left side. Both kinetosomes extend fibrillar cytoskeleton to the nucleus. Axoplast MTOC near kinetosomes. With the exception of *Cavernomonas*, other Genera have a spindle-shaped body during gliding. Cell posterior tends to trail into a pointy pseudopodial extension that can be long. On surfaces, cells spread out very thin and extend filopodia in different directions, searching for food inside particles and scour surfaces. Filopodia have been divided into seven categories to help distinguish Genera. Older cultures can display multiple mastigonts and have multinucleate or siphonous growth. 1-3 microtubules extend from kinetosomes. A small cone of singlet microtubules extends from one or both kinetosomes. Five Genera have been described: *Cercomonas, Eocercomonas, Filomonas, Neocercomonas, Cavernomonas*.

9.2.2.Paracercomonadida. These soil species are phagotrophic on bacteria and difficult to distinguish from cercomonads, although they tend to be smaller (3-18 µm). Ultrastructural morphology shows distinct difference in the details of the kinetid-associated cytoskeleton. Axoplast MTOC near kinetosomes. Single microtubules extend from the kinetosomes, two prominent ones posteriorly. Filopodia are finger-like, somewhat thicker than in cercomonads, and branching. Occasionally a transient lamellipodia may form.

9.2.3.Glissomonadida. Glissomonads are represented by five clades, four of which have one described Genus, but this is due to under-sampling. They are phagotrophic on bacteria. Cells are more ovoid, less pseudopodial and make few filopodia, compared to cercomonads. Trailing cytoplasm along the posterior cilium is infrequent but occurs. The anterior cilium is shorter, in some species reduced to a stub without axoneme. The anterior cilium beats asymmetrically on the left side. The longer posterior cilium is ventral against the substrate and used for gliding. A peroxisome is found attached to the posterior of the nucleus, and the Golgi apparatus is associated with the nucleus. Species form cysts and are mostly terrestrial. The Sandonidae (*Sandona, Flectomonas, Neoheteromita, Mollimonas*) and Dujardinidae (*Dujardina*) are jerky gliders, while Bodomorphidae (*Bodomorpha*) and Allapsidae (*Allapsa, Allantoin, Teretomonas*) are smooth gliders. The derived *Proleptomonas* are primarily swimmers with elongated cells and have several cytoskeletal differences. The nucleus is posterior without the peroxisome attached to it. The posterior cilium nonetheless adheres to the cell and is trailing.

9.2.4.Viridiraptoridae. Cells are rigid biciliates when swimming, but amoeboid on surfaces with distinct attachment sites. The cytoplasm has various bodies, crystals and vesicles from digestion of food vacuoles. Only crystals remain in starving cells. The nucleus is anterior, with cytoskeletal attachment to the kinetosomes. Golgi apparati are found near the nucleus. The usually longer posterior cilium is trailing ventrally but unlike other Cercozoa, it is unattached to the cell membrane. The anterior cilium wags the cell body (rotation, jiggling, vibrating) when attached. Swimming involves both cilia. Species are cytotrophic, feed by perforating a small hole into protist cell walls (eg. green algal filaments) and extending pseudopodia to feed on the protoplasm. Samples are known from freshwater habitats. Two Genera are described, *Orciraptor* and *Viridiraptor*.

9.2.5.Pansomonadidae. Cells have two free heterodynamic cilia, alternating between swimming and attached to substrate with amoeboid locomotion. Species are phagotrophic on bacteria, and include *Agitata* and *Aurigamonas*.

9.2.6.Sainouroidea. Sainouroids are typically substrate-attached biciliates, gliding on the ventrally attached posterior cilium. Cells are phagotrophic on bacteria, and typically occur in habitats with elevated nitrogen content. Mitochondria cristae are tubular (as for most Cercozoa) but flat cristae occur in some species. Three clades are recognized.

The Sainouridae are biciliate or tetraciliate. One posterior cilium of each kinetosome pair is long, trailing, and acronematic. In species without four cilia, one or two stubs of cilia protrude like nipples, and with reduced cytoskeletal elements around the kinetosome, but instead a nine-fold membranous support. The nucleus is attached to the kinetosomes by one pair of striated rhizoplasts. The nuclear inner membrane has fine tubular invaginations. Peroxisomes occur attached to the nuclear envelope. Mitochondria cristae tend to be flat or peripheral vesicles. Genera include *Acantholus, Cholamonas, Homocognata*, and *Sainouron*. The Guttulinopsidae (*Guttulinopsis, Olivorum, Puppisaman, Rosculus*) and Helkesimastigidae (*Helkesimastix*) are distinct clades based on molecular phylogenies. The latter has a posterior trailing cilium but retains only a stump or very short anterior cilium. The nucleus is held to the kinetosomes by a pair of striated rhizoplasts. The MTOC is an anterior centrosomal plate from which single microtubules extend along the dorsal side like a cape. Fibres connect the kinetosome-bearing cilium to the centrosomal plate. There is a single ventral microtubule. Cells are typically swimming and phagotrophic on bacteria.

[Figure 9.2]

9.2.7.Thecofilosea. This large group includes includes the Phaeodaria (an Order) and 5-6 Families. Unlike other Cercozoa, the cell membrane is supported by a thick extracellular theca. Ancestrally surface-attached gliding biciliate, with several derived clades. The ventral surface has a groove (or clefts) from which filopodia emerge, thus technically a cytostome. Typically biciliated with divergent kinetosomes, and a posterior trailing cilium for gliding (except Ebriacea). The theca has perforations to allow passage of cilia and filopodia.

9.2.7.1. **Cryomonadida** have secondarily lost cilia and form three clades. Sexual conjugation is unknown. The Rhogostomidae (*Rhogostoma, Sacciforma, Capsellina*) have a rigid ventral cleft (or slit) from which filopodia emerge. Cells are phagotrophic on bacteria, and cytotrophic on small unicellular protists and yeasts. The theca is thin (width of cell membrane) and flexible. Pores in the theca expose extrusome aperture. Cells tend to be surface associated, adhering to the substrate. Cell division is longitudinal. The Protaspidae (*Cryothecomonas, Protaspa*) have subapical cilia, each separated by a short protrusion, with a distinct deep micropore. There is a ventral groove along the anterior half of the cell. The nucleus is located posteriorly and has permanently condensed chromosomes. The theca is thick, with seven layers, but with pores for extrusomes. Pseudopodia emerge from slits. The Ventricleftida (*Ventrifissura, Verrucomonas*) cells are flat ovals with rigid theca. Cilia emerge from an apical notch. The longer posterior cilium is ventral and used for gliding. There is a ventral cleft from which branching filopodia emerge, posterior to the ventral groove.

9.2.7.2. Tectofilosida. These species are unicellular, without cilia, sometimes forming aggregates of cells in a sarcinoid colony. Cells have an organic flexible theca (tectum) with a single basal opening for filopodia. The theca can include agglutinated mineral particles. Cells feed by phagotrophy on small protists. Mitochondria have tubular cristae. There are two clades; one includes *Pseudodifflugia, Rhizaspis*, and *Fisculla*, while the other contains *Chlamydophrys, Lecythium, Trachyrhizium, Diaphoropodon, Clypeolina,* and *Leptochlamydophrys* in the Chlamydophryidae.

9.2.7.3. The **Ebriacea** have two subapical cilia, and are cytotrophic on phytoplankton, including filaments of diatoms which become folded into the cell. There is no cytostome, and feeding is assumed to be by pseudopodial phagotrophy. They have an internal mineral skeleton of hollow silica tubes. The nucleus has permanently condensed chromosomes as in *Protaspis* (Cryomonadida). Species are cosmopolitan in marine coastal waters but never abundant.

9.2.7.4. Phaeodarea. There are about 400-500 describes species but many more are undescribed, as evidenced by sequences in environmental samples. Cell organization in the phaeodarians is peculiar and shows adaptations to a planktonic existence. Specimens occur mostly in deeper waters, 100 m down and even some beyond 300 m depths, with a peak abundance around 200 m. However, specimens occur as far as in the abyssal depth of 2-8,000 m. These depths are below the photic zone; thus, phaeodarians do not hold phytoplankton symbionts. The central capsule consists of a double layer of wall material. The main opening is a cytostome allowing cytoplasm to come out and called the astropyle. There are typically two smaller openings in the capsule called parapylae that allow thinner cytoplasm strands to emerge, supported by microtubles. The cytoplasm inside the capsule is called the endoplasm, and that outside the capsule called the ectoplasm. The filopodia are branched and anastomosing into a network. In the cytoplasm outside of the capsule astropyle, there are undigested remains in a mass called the phaeodium. The phaeodium has been speculated to have a role in silicon metabolism. The mineral skeleton is composed of hollow silica tubes and spicules in the ectoplasm held together by organic material into a cage. (For more on mineral cage growth see the Polycystinea.) The mineral elements tend not to fossilize. Shapes of the cage of mineral skeleton vary showing geodesic patterns, polyhedral shapes, or clam-shaped bivalve tests. Mitochondria have tubular cristae. Although motile biciliate tomites are common, it is unclear if they are associated with sexual conjugation, as sex is unknown in the group, as for the rest of the cercomonads. In *Coelodendrum ramosissimum,* at reproduction, the phaeodium and the capsule disappear, and spheres form in the cytoplasm, which contains hundreds of polynucleated amoeboid cells. These are released as cells that become biciliated tomites with one nucleus. Phaeodaria have low endemicity with most known species found in all parts of oceans except near the coast, where salinity is lower. Although common, they are never abundant in samples. Species are omnivorous and phagotrophic on prey of appropriate size, including protists, small invertebrates or bacteria and detritus.

Four subgroups are recognized based on skeleton morphology. The **Phaeoconchia** (2 Families) form a bivalve shaped mineral cage (*Coelodendrum, Coelographis, Conchellium, Conchopsis*). The **Phaeocystina** (4 Families) have an incomplete mineral skeleton with dispersed unconnected spicules, or it is missing altogether, with a centrally located central capsule and endoplasm (*Aulacantha, Aulographis, Cannoraphis*). The **Phaeogromia** (*Castanella, Challengeron, Haeckeliana, Medusetta, Tuscarora*) have a central capsule not located centrally, and an astropyle with characteristic tooth-like structures or elongated structures called feet. The cage is simple, with a larger opening above the astropyle axis. There are 8 Families. The **Phaeosphaeria** (*Aulosphaera, Cannosphaera, Sagosphaera*) have a centrally located capsule, with a simple or double mineral cage (two halves), and a simple opening. There are 3 Families.

9.2.8. The **Granofilosea** have very fine branching or unbranched granular filopodia, with regular extrusomes. Filopodia in some species are axopodial also with extrusome granules. The filopodia are supported by microtubules. Cells adhere to substrates and use filopodia to search for food, similar to cercomonads. Filopodia are typically not anastomosing. Some species have biciliate swimming or gliding stages. The group includes *Massisteria*, and *Minimassisteria*, and about a dozen other Genera. The group also includes the **Clathrulinidae**, which have an extracellular capsule (lorica) attached to the substrate or found free-floating. Often cells have a mucus cover. Mitochondria have tubular cristae. Filopodia are anastomosing and supported by microtubules, bearing kinetocyst extrusomes. There are both biciliate and amoeboid stages. Some species can be colonial. Cysts are common.

9.2.9. The **Chlorarachnea** are marine amoeboid cells with a biciliate dispersal stage. Filopodia with extrusomes are used to capture prey. Any prey particle of small size (bacteria, protists) can be obtained by phagotrophy; thus, species are omnivorous (bacteritrophic and cytotrophic) or microbivores. Food vacuole digestion occurs in the filopodia. Anastomosing filopodia occur in some species. Cells have secondarily acquired plastids from a photosynthetic eukaryote that retained a nucleomorph. The plastid is most related to a Bryopsidales (Chlorophyta) siphonous green algae. The plastid is surrounded by four membranes with two external membranes not connected to the ER, which represent the relic cell membrane of the ancient eukaryotic symbiont. Plastids have chlorophyll *a* and *b*. Some species are plasmodial linked with reticulopodia. Mitochondria have tubular cristae. Golgi apparati are found close to the pyrenoid. A pyrenoid capping vesicle holds the main storage compound β-1-3-glucans and cells do not make starch. The plastids have 1-3 lamellae. The nucleomorph retains a nuclear membrane with three small linear chromosomes and about 300 genes with more than 800 short (18-21 bp) introns. There are ribosomes in the periplastid space (the relic cytoplasm of the symbiont). The mechanisms for targeting proteins to the correct compartment, through the various membranes, are only partially elucidated. Amoeboid stages are benthic small cells (8-20 μm). Coccoid cells (5-15 μm) with a cell wall occur in older cultures and could function as cysts. However in some species, the walled coccoid cells are partially amoeboid and can extend short pseudopodia. Division of coccoid cells can give rise to amoeboid or dispersal tomites. The tomites are 4-24 μm with a granular cytoplasm at the anterior, and a single cilium (one kinetosome, except a vestigial second kinetosome occurs in *Bigelowiella natans*). The cilium wraps around the body in a cavity. The anterior can form short pseudopodia in some species. Tomites divide into amoeboid or coccoid cells, depending on the species. Nuclear division is open, but part of the nuclear membrane remains. Nucleomorph division is by amitosis without condensation of the chromosomes. The nucleomorph is diploid and the nucleus is haploid. Sexual conjugation was reported in tomites of *Chloroarachnion reptans* and in amoebae of *Cryptochlora perforans*. There are eight Genera and the closest sister clade appears to be *Minorisa*, a picoplankton bacteritroph.

9.3.Imbricatea Cavalier-Smith 2011

This group displays secreted silica scales, except where secondarily lost, or in some basal clades where the character has not evolved. Mitochondria have tubular cristae. Cells have a ventral groove and a pair of cilia unless secondarily lost (as in Euglyphida).

Table 9.3.

Several basal clades are without secreted siliceous scales. **Spongomonadida** are simple biciliated cells with asymmetrical projections at the anterior (*Rhipidodendron, Spongomonas*). An additional Genus, *Discomonas* is placed as *incertae sedis* in the Imbicatea. The **Marimonadida** (*Auranticordis, Pseudopirsonia,* *Rhabdamoeba, Abollifer, Cyranomonas*) are marine biciliated species without scales or theca. They occur in marine sediments as surface associated gliding cells. Cells have a semi-rigid flexible pellicle with mucocysts docked at the cell membrane. Four posterior cilia are associated with a ventral cleft in *Auranticordis,* or amoeboid biciliates with two posterior cilia used for gliding. *Rhabdamoeba* has lost the cilia and has an amoeboid cell with a broad fan-shaped pseudopodia. One Genus (*Pseudopirsonia*) is a free-swimming parasite of diatoms. The **Variglissida** group three Genera *Clautriavia, Nudifila*, and *Quadricilia*. The **Metromonadea** (*Metromonas, Metopion, Micrometopion, Kiitoksia*) are gliding biciliated cells, without pseudopodia or filopodia. They are marine cytrophic predators. Cells are covered with dense single or double layered coat, which can continue up the cilia. Elongated extrusomes are docked at the cell membrane.

9.3.1. The **Silicofilosea** have secreted silica scales, or they were secondarily lost, depending on the taxon. Thaumatomonadida and the Euglyphida are the two principal subgroups.

Thaumatomonadida. Cells are flattened and biciliated (except *Penardeugenia),* usually surface-attached and gliding on posterior cilium located ventrally. Cilia emerge from a subapical micropore. Occasionally cells detach to swim for a short time. Some species have only one cilium. Filopodia emerge from the ventral groove or subapically. Cells have extrusomes. Some species have multinucleate stages with several cilia. They can form cysts. There are three subgroups. Most Genera form one clade, the Thaumatomonadidae (*Allas, Hyaloselene, Reckertia, Thaumatomonas, Thaumatomastix, Ovaloplaca, Scutellomonas, Thaumatospina, Penardeugenia*). The long posterior cilium is used for gliding, while the short anterior cilium can be naked (*Allas, Thaumatomonas*) or covered with small siliceous scales (*Reckertia, Thaumatomastix*). The oval and triangular scales are produced in vesicles that are adjacent to the mitochondria. Scales cover the cell membrane except at the ventral groove (a cytostome) where filopodia emerge. The scales have an upper plate with species-specific patterns. The other two small clades include Peregriniidae (*Gyromitus, Peregrinia*) which are devoid of scales on cilia, do not glide, and only have oval scales. The micropore is apical. Some species are very amoeboid and without definite shape, whereas others are swimmers. The last clade is known only from *Esquamula* which are gliding cells on the posterior cilium. Cells have a rigid surface, but without scales or theca. There are filose, sometimes lobose, pseudopodia. Both cilia emerge from the same micropore. There are slim extrusomes.

Euglyphida. Most Genera form one clade, with five Families that are common in surface soils (in the litter) and mosses. Euglyphids are testate amoebae with secreted siliceous scales. They make beautiful apparitions at the microscope as a clear transparent vase made with glass scales. Scales are formed in Golgi vesicles and cemented together on the cell surface with an organic matrix. Mitochondria have tubular cristae. Filopodia emerge from the aperture of a vase shaped test. Scales and test shape help in species identification and vary in traits between Families. Sex has been documented in the group. There are two other Families, the Cyphoderiidae, which are found in freshwater sediments, on plants, and in sublittoral sands, and the Paulinellidae, which have sometimes secondarily lost siliceous scales (*Micropyxidiella, Ovulinata*), are found in marine sediments, plankton, on freshwater plants, and in soil litter and mosses. *Paulinella* (9 species) have three species with a cyanobacteria derived photosynthetic plastid called a cyanelle. It is a recent primary endosymbiosis event with a cyanobactreia related to the *Prochlorococcus* and *Synechococcus* (a related but different clade than the plastid in Archaeplastida). The cyanelle genome has lost about 2/3 of its genes, with some found in the nuclear genome.

9.4.Endomyxa. There are two free-living groups and two parasitic groups in this clade that has been controversial because the node was unresolved. Recent phylogenies form a convincing clade. There are many undescribed species known from environmental sequences.

Table 9.4.

There are two free-living Genera, the *Filoreta* and the *Gromia. Filoreta* are reticulate large amoeboid cells with anastomosing filopodia. *Gromia* are multinucleate and resemble monothalamic foraminifera with which they were confused. Found in regularly wet soils and riparian habitats, in freshwater and marine deep-sea sediments, branching filopodia emerge from a single roundish organic test with a single aperture. Although anastomosing, the filopodia do not form a reticulated net as in *Filoreta*. The cytoplasm is non-granular. There is a biciliated dispersal stage.

9.4.1.Vampyrellida. One common free-living group is the curious vampyrellids which spread over filaments of algae or fungal hyphae. A small hole is perforated by digestive enzymes in the cell wall (chitin or cellulosic) and filopodia penetrate the filament to ingest cytoplasm by phagocytosis. Cells can enter the filament and feed from inside. Fungal spores are also perforated. Cells are amoeboid with numerous thin branching but relatively short filopodia. The cell periphery and filopodia are hyaline. Digestive cysts form after feeding. Species are known from soils, sediments and marine habitats. One attempt at combatting plant pathogenic fungi in the soil with vampyrellids against wheat take-all disease has been successful.

9.4.2.Phytomyxea. These are parasites or parasitoids of plants and Stramenopiles. There are 42 species in 12 Genera. Cells are amoeboid and can become plasmodial in the trophont stage. Feeding is by phagotrophy of host cytoplasm. Dispersal cells are either biciliated or tetraciliated. Some species (maybe all) have an extrusome (called a dagger) for host cell penetration. A nucleolus persists during mitosis, as an elongated form across the mitotic spindle. Thick-walled resistant spores form that persist and remain viable in the soil for years. Dispersal tomites emerge to find hosts by chemotaxis. On contact cilia are resorbed, encystment begins and a penetration organelle forms. The penetration organelle (dagger, *Stachel* in German) is forced through the host cell membrane by contraction of the membrane surrounding it. The protoplasm is also expulsed into the host cell by rapid expansion of a large vacuole that forms in the tomite. Inside the host cell, the parasite cell grows until it undergoes several synchronous mitotic divisions forming a plasmodium. The plasmodium from time to time separates into two multinuclear plasmodia. Nuclei in the plasmodium can form tomites which reinfect host cells and can find their way outside of the host through wounds. Sexual conjugation occurs in the resting spore by meiosis, leading to a haploid nucleus in each germinating tomite. The nucleolus disappears during meiosis. Fusion of nuclei to form a zygote likely happens in the plasmodial trophont stage.

Two subgroups exist. The **Plasmodiophorida** are soil species that infect plants, and the **Phagomyxida** are parasites of Stramenopiles in marine habitats such as diatoms and brown algae. The better studied Phytomyxea are the Plasmodiophorida and known species have been studied extensively because they are parasites of crops. These include the clubroot disease of Brassicae (cabbage and mustard Family, including *Arabidopsis*) and the powdery scab of potatoes amongst many others. Host range is uncertain because infections occur in diverse plants but the entire life cycle with dispersal tomites is completed in fewer hosts. Some plasmodiophorids infect the Stramenopiles *Pythium* and *Phytophthora* (both Peronomomycetes), themselves plant pathogens. Others are parasites of freshwater vascular plants. About 20 plant viruses are dispersed through Phytomyxea, 19 of which are non-enveloped positive-polarity single-stranded RNA viruses.

[Figure 9.3]

9.4.3.Ascetosporea. This group are parasites of invertebrates. A common feature is the complex spore that consists of one or more cells, with one or more sporoplasm. Mitochondria have tubular cristae. The **Paradiniida** are parasites of marine crustaceans. They have a biciliated dispersal tomite with two cilia of unequal lengths. They form a plasmodial (multinucleate) trophont. The **Haplosporida** are plasmodial endoparasites of marine animals but sometimes (some species) occur in freshwater animals. There is an intranuclear mitotic spindle at division, but a rudiment persists after mitosis (the *kernstab* in German). The spore has a distinctive hinged lid called operculum. The *Claustrosporidium* are not intracellular but endoparasites. They form a sporoplasm with a single nucleus and haplosporosome. The haplosporosome is a vesicle bound by a membrane with an additional membrane centrally, separating the core from the periphery. Shapes and details of membrane arrangement vary, even within one cell. It is present in plasmodial stages prior to spore formation, it disappears at spore formation, then reappears in the sporoplasm. Spore wall is extracellular and without operculum or aperture. **Mikrocytida** are parasites of aquatic invertebrates. Unusually spores are unknown. *Paramikrocytos* form a plasmodial stage; otherwise, infective cells are very small and are called microcells. The **Paramyxida** form unusual bicellular spores without aperture. One cell is the sporoplasm and forms inside the other called parietal cell or primary cell. The sporoplasm (secondary cell) can divide into several more sporoplasms (tertiary cells) that form a spore wall and are shed for spore dispersal. The pattern of divisions and number of cells is taxonomically relevant. The primary cell is amoeboid and feeds with short branching filopodia. As in Haplosporida, haplosporosomes disappear at spore formation and reappear after. All are parasites of marine crustaceans, mollusks, and polychaetes. Cells are intracellular and tissue parasites with sporulation in reproductive tissues or digestive tract epithelium. They can be devastating to shellfish aquaculture and oysters especially.

The next two groups, the Radiolaria and the Foraminifera, are adjacent-groups in a clade called the **Retaria**. These are principally marine heterotrophs, usually with a mineral skeleton and axopodia or reticulopodia.

[Table 9.5]

9.5.Radiolaria. A secreted central capsule of organic material surrounds the cell membrane. Through apertures of the capsule, axopodia extend out, supported by microtubules, and a mass of pseudopodial cytoplasm outside of the cell forms the ectoplasm. The ectoplasm contains food vacuoles and symbionts (when present), and lipid globules. The mineral skeleton is strontium sulfate in Acantharia and of amorphous silica in Polycystinea. The shapes of these mineral scaffolds are complicated, and the group was made famous partly due to the beautiful drawing of their appearance at the microcope by Ernst Haeckel.Mitochondria have tubular cristae. All are marine planktonic, and their biogeography follows water temperature in oceanic currents. Their skeletons accumulate in marine sediments and are used for dating rocks and identifying petroleum deposits; they have also been useful in tracking past climate changes.

[Figure 9.4]

9.5.1.Taxopodida are known from few specimens of *Sticholonche,* but there are more uncharacterized environmental sequences. Microtubules originating from depressions in the nuclear membrane (MTOC sites) extend radially outwards to support axopodial filopodia. The axopodia microtubules are arranged in characteristic irregular hexagonal arrays. Axopodia are devoid of extrusomes and used as oars for locomotion. The cell is covered with siliceous spicules that tend to occur at about 100-500 m depths.

9.5.2.Acantharea. Cells are surrounded by a thick capsule (outside the cell membrane) traversed by axopodia, a network of anastomosing pseudopodia and spines. The cytoplasm inside the capsule is called endoplasm and contains the organelles. The pseudopodia network outside the capsule is called ectoplasm. The ectoplasm is also surrounded by a fibrillar cortex. The axopodia, with kinetocyst extrusomes, are supported by microtubules arrays from a centrally located MTOC, called the centroplast. There is a centroplast near the base of each spine. Twenty spines of strontium sulfate point radially outwards and join together at the cell center. The spines are mobile with each tip connected to contractile myonemes from the ectoplasm cortex. The ectoplasm contains captured prey and the endoplasm often includes algal symbionts. Reproduction is sexual, with meiosis followed by mitotic divisions to produce a swarm of biciliated isogametic tomites. A strontium sulfate crystal in each tomite is the starting point for new mineral skeleton synthesis. Complementary tomites fuse to produce a diploid cell which becomes the trophont. Unusually, asexual reproduction is unknown. The **Chaunocanthida** hold many nuclei in the pigmented endoplasm and have a clear ectoplasm. Sexual conjugation takes place inside gamontocysts. The gamontocyst wall is formed from lithosomes from the Golgi apparatus. The axopodia are supported by hexagonal arrays of microtubules. The spines have a contractile matrix at their base. The **Holocanthida** have a pigmented endoplasm with several nuclei and sexual conjugation involves a gamontocyst with wall formed from lithosomes. The axopodia are supported by dodecagonal microtubule arrays. The **Symphyacanthida** have a pigmented endoplasm with just one nucleus and a clear ectoplasm. The outer endoplasm is clearer and holds anastomosing pseudopodia, as in the ectoplasm. Sexual conjugation involves a gamontocyst with wall formed from lithosomes. Both the capsule and ectoplasm cortex are visible by light microscopy. The **Arthracanthida** have a thick capsule separating the pigmented endoplasm with several nuclei from the ectoplasm. The axopodia are supported by hexagonal microtubule arrays. Algal symbionts occur in all known species but are lost at sexual conjugation. Sexual conjugation is without the gamontocyst stage.

9.5.3.Polycystinea. There are about 400-800 described species and thousands in the fossil record from deposited mineral skeletons. Most specialists of this group are paleontologists. Most extant species occur in the top 100 m of marine waters. The same morphological species can be found around the planet’s oceans. The central capsule has round apertures (fusules) distributed evenly across the capsule or aggregated near one pole. In addition to axopodia, filopodia radiate outwards. A mineral siliceous skeleton is either absent, or composed of spines or a cage-like shell. The mineral skeleton is shaped inside vesicles called cytokalymma. The shape of the mineral cage is species-specific. Growth of the mineral cage is by rim growth of existing apertures that become narrower, or by depositing rod projections that bridge gaps to form additional new lattice material. Sexual conjugation is unknown. Symbionts are common in the ectoplasm. The diversity of symbionts found includes cyanobacteria, dinoflagellates, prasinophytes and prymnesiophytes. Cells are best described as omnivorous, and those with algal symbionts are mixotrophic and omnivorous. Prey of suitable size (bacteria, protists, small invertebrates) can be ingested by phagotrophy once held by axopodia; invertebrate prey includes copepods and their larvae. Ingestion of protists is by phagocytosis into a food vacuole after being trapped in the axopodia array. Ingestion of micro-invertebrates is more elaborate. Filopodia and axopodia adhere to the animal and elongate to wrap the prey, and to penetrate into tissues through weaker parts of the prey exoskeleton. Prey tissues are obtained by phagocytosis and vesicle transported towards the endoplasm. In the **Spumellaria** (37 Families, 8 with extant species) the capsule apertures are evenly (radial symmetry) distributed, and the mineral cage is covered by the ectoplasm. One Family (Collosphaeridae) is colonial. Subdivisions within the clade are still unresolved. A mineral skeleton is either absent, or composed of spines or a cage-like shell. In the **Nassellaria** (54 Families, 7 with extant Families) the central capsule apertures are localized at one pole (monoaxial symmetry). The mineral skeleton, when present, is composed of a tripod, a sagittal ring without tripod, or a porous helmet-shaped cage (it can be quite ornate) around the central capsule. The axopodia microtubules emerge from a centroplast in the endoplasm. The **Collodaria** (four Families) are unicells but sometimes in colonies, with reduced or absent mineral skeleton. When the mineral skeleton is present, it consists of scattered spines in the ectoplasm. The fossil species are placed into four subgroups containing 37 Families in all, called the Archaeospicularia, Albaillelaria, Latenfistularia, and Entactiniaria.

9.6.Foraminifera. Anastomosing branched filopodia forming an extensive network outside a chamber is a main character of the group. The filopodia are granular and display a bidirectional flow of cytoplasm and vesicles at about 10 μm s^{-1}. The network of external filopodia is called the reticulopodium. Foraminifers feed by capturing passing prey and particles of appropriate size with the reticulopodium network. Filopodia emerge from countless small apertures in the test wall. Captured prey are enveloped and cells or tissues are ingested as described for the Polycystinea. Microtubules occur in loose clusters or singly in the filopodia for support and helping with locomotion. Mitochondria contain tubular cristae. Cells accumulate nuclei in a plasmodial growth form inside the test, so that older specimen can have thousands of nuclei. The test consists of an organic matrix, sometimes calcareous, and sometimes with additional mineral elements, in a clade-specific manner. Older individuals can reach several cm in diameter, and up to 20 cm, representing years of growth. Tests accumulate in the fossil record, stratified in geological formations. These fossilized tests have been important to recognize geological ages of strata in petroleum exploration. There are about 36,000 extinct species described from the fossil record, with about 4,000 extant species. Test growth is characteristic in multichambered froms, where new chambers are larger than the previous ones in succession. The test wall, as it thickens, is penetrated by a labyrinth of channels which contain protoplasm. The successive chambers can form in spirals, in an elongating tubular form, or a combination of both. They are used to identify Genera or species. Most extant species are marine and benthic, with about 50 freshwater species. Shallow water benthic forms have endosymbionts. The endosymbionts are red algae, green algae, dinoflagellate or diatoms, and can number in the thousands. Some marine forms are planktonic also with photosynthetic endosymbionts. These endosymbionts may also include chrysophytes, *Symbiodinium* and *Gymnodinium beii*. There are cases of plastid retention (kleptoplasty) from ingested protists. Species are assumed to be sexual as sex is common, with alternation of generations. Sex by autogamy instead of conjugation is also known in the Foraminifera, and best studied in *Allogromia* (Monothalamea). Haploid cells are typically biciliate but in some species they are amoeboid without cilia. After conjugation, diploid cells settle and become vegetative cells with the formaniferan test and morphology. With growth, nuclei become larger and ribosomoal gene copy number increases, as do some other genes. The ribosomal copy number is about 30,000 copies for a 100-200 μm cell. Prior to gamete formation, much of this DNA is digested.

[Table 9.6.]

9.6.1.Monothalamea include Genera that form a single chamber of organic material, and those previously called **Xenophyophorea**. Although mostly marine, there are 4-5 freshwater clades. The intriguing Xenophyophorea form an agglutinated clump composed of the organic matrix with embedded mineral sand particles from the surrounding. The clump of reticulopodia and minerals appears like a porous small rock of agglutinated sand about the size of your head. A mucoid amorphous material contributes to the agglutination. Examples of Monathalamea Genera are *Allogromia, Astrammina, Crithionina, Notodendrodes, Psammophaga, Bathysiphon* and *Reticulomyxa*.

9.6.2. The **Tubothalamea** form tubular chambers when young and can grow into bicameral or multichambered tests. The cell wall is an organic matrix with agglutinated mineral particles, or alternatively, it is calcified. The basal clades are those with agglutinated tests and simple chambers. Three subgroups exist: the **Miliolida**, the **Spirillinda** and the **Ammodiscidae**. The Miliolida with calcareous test have a porcelainous appearance due to randomly oriented crystals of high-magnesium calcite. Test wall is Generally without pores. The test is tubular or elongated with a spiral twist that continues as new chambers form with growth. Some species host algal endosymbionts in adapted organelles, and some species with simple agglutinated test only. The **Spirillinida** form a wall of low-magnesium calcite that appears as a single homogeneous crystalline test. The chamber growth forms whorls that are undivided or separated into chambers by mineral wall deposition. The **Ammodiscidae** have a test of a coiled tubular chamber with agglutinated mineral material that is undivided with a terminal aperture.

[Figure 9.5]

9.6.3.Globothalamea have multichambered tests with globular or crescent-shaped chambers at least in young specimen. The test wall can be agglutinated or calcareous. The Globothlamea are divided into five groups. The **Rotaliidae,** with 32 Families, contains most of the extant foraminifera. The test wall in Rotaliidae is made of low-magnesium calcite, and it grows into trochospirally coiled chambers. The others are **Carterina** with wall of rod-like spicules held in an organic layer with many trochospirally coiled chambers; **Textulariida** with an agglutinated wall composed of foreign and mineral particles held together by an organic layer or cemented with low-magnesium calcite; **Robertinida** with a perforated (with numerous apertures) hyaline wall of aragonite forming divided chambers; and **Globerinida** that form a wall of low-magnesium calcite perforated with apertures, that can be covered with spines. All are benthic species, except for the planktonic Globerinida.

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Figure legends

Figure 9.1 Rhizaria, showing filopodia, posterior gliding cilium, microtubular rib from MTOC adjacent to kinetid, with micropore in a depression in some, silica scales present in some. Foraminifera zoospores (with two anterior and one posterior cilium), where present retain this morphology including the micropore and sub-apical depression. (Thecofilosea have a thick theca instead of scales. Filopodia anastomosing in some. Cilia numbers can be doubled to four, or each cilium reduced to short stubs).
Figure 9.2. Images of Cercozoa.
Figure 9.3. Images of Endomyxa.
Figure 9.4 Images of Radiolaria.
Figure 9.5. Images of Foraminifera.

Table 9.1. Sub-groups within the Rhizaria (Phylum), as indicated.

Gymnosphaerida Poche 1913, emend. Mikrjukov 2000 (F)	
Cercozoa Cavalier-Smith 1998, emend. Adl et al. 2005; emend. Cavalier-Smith 2018 (C)	
Endomyxa Cavalier-Smith 2002, emend. Bass & Berney in Adl et al. 2019 (C)	
Retaria Cavalier-Smith 2002 (SC)	Radiolaria Müller 1858, sensu Adl et al. 2005 (C)
	Foraminifera d'Orbigny 1826 (C)
Aquavolonida Bass & Berney 2018 (F)	*Aquavolon*
Tremula Howe et al. 2011	

Table 9.2. Sub-groups within the Class Cercozoa, as indicated.

Cercomonadida Poche 1913, emend. Cavalier-Smith 2012 (O)	*Cercomonas, Filomonas, Neocercomonas*
Paracercomonadida Cavalier-Smith 2018 (F)	*Brevimastigomonas, Pracercomonas*
Glissomonadida Howe & Cavalier-Smith 2009 (O/SF)	*Sandona, Neoheteromita, Dujardina, Bodomorpha, Proleptomonas, Allapsa, Allantion*
Viridiraptoridae Hess & Melkonian 2013 (F)	*Viridiraptor,Orciraptor*
Pansomonadidae Vickerman in Vickerman et al. 2005 (F)	*Agitata, Aurigamonas*
Sainouroidea Schuler et al. 2018 (SF)	Sainouridae Cavalier-Smith 2008 (Family)
	Helkesimastigidae Cavalier-Smith 2008 (Family)
	Guttulinopsidae Olive 1970 (Family)
Thecofilosea Cavalier-Smith 2003, emend. Cavalier-Smith 2011 (SO)	Phaeodarea Haeckel 1879 (Order)
	Cryomonadida Cavalier-Smith 1993 (super-Family)
	Ventricleftida Cavalier-Smith 2011 (Family)
	Tectofilosida Cavalier-Smith 2003 (super-Family)
	Ebriacea Lemmermann 1901 (Order)
Granofilosea Cavalier-Smith & Bass 2009 (SF)	Clathrulinidae Claus 1874 (F)
	Incertae sedis ~20 genera
Chlorarachnea Hibberd & Norris 1984 (SF)	*Bigelowiella, Chlorarachnion, Lotharella*
Incertae sedis Genera and Families	Psammonobiotidae Golemansky 1974, emend Meisterfeld 2002
	Volutellidae Sudzuki 1979
	At least 12 other genera

Table 9.3. Subgroups within the Class Imbricatea (with example genera or subgroups indicated).

Spongomonadida Hibberd 1983 (F/SF)	*Rhipidodendron, Spongomonas*
Marimonadida Cavalier-Smith & Bass 2011 (SF)	*Abollifer, Cyranomonas, Rhabdamoeba*
Variglissida Cavalier-Smith 2014 (SF)	*Clautriavia, Nudifila, Quadricilia*
Silicofilosea Adl et al. 2005, emend. Adl et al. 2012 (SO)	Thaumatomonadida Shirkina 1987 (O)
	Euglyphida Copeland 1956, emend. Cavalier-Smith 1997 (O)
Metromonadea Cavalier-Smith 2007, emend. Cavalier-Smith 2011 (SF)	*Metromonas, Metopion, Kiitoksia*

Table 9.4. Subgroups within the Class Endomyxa (can be considered Orders with sub-groups as indicated).

Vampyrellida West 1901, emend. Hess et al. 2012	*Arachnula, Hyalodiscus, Vampyrella, Penardia*
Phytomyxea Engler & Prantl 1897	Plasmodiophorida Cook 1928 (SF)
	Phagomyxa
Ascetosporea Sprague 1979, emend. Cavalier-Smith 2009	Haplosporida Caullery & Mesnil 1899 (SF)
	Mikrocytidae Hartikainen et al. 2013 (F)
	Paramyxida Chatton 1911(SF)
	Paradiniidae Schiller 1935 (F)
	Claustrosporidium
Incertae sedis	*Filoreta, Gromia*

Table 9.5. Subgroups within the Class Radiolaria (can be considered super-Orders with Orders, except Taxopodida is Family)

Acantharea Haeckel 1881, emend. Mikrjukov 2000 (SO)	Chaunocanthida Schewiakoff 1926
	Holocanthida Schewiakoff 1926
	Symphyacanthida Schewiakoff 1926
	Arthracanthida Schewiakoff 1926
Taxopodida Fol 1883 (F)	*Sticholonche*, several environmental clades
Polycystinea Ehrenberg 1838, emend. Haeckel 1887 (SO)	Spumellaria Ehrenberg 1875, Haeckel 1887, emend. Riedel 1967
	Nassellaria Ehrenberg 1875, emend. Haeckel 1887
	Collodaria Haeckel 1887

Table 9.6. Subgroups within the Class Foraminifera d'Orbigny 1826 (can be considered super-Orders, with sub-groups as Orders, super-Families, Families, or with example genera)

Monothalamea Pawlowski et al. 2013 (SO)	*Allogromia, Bathysiphon, Reticulomyxa*
Tubothalamea Pawlowski et al. 2012 (SO)	Ammodiscidae Reuss 1862
	Spirillinida Hohenegger & Piller 1975
	Miliolida Delage & Hérouard 1896
Globothalamea Pawlowski et al. 2012 (SO)	Rotaliida Delage & Hérouard 1896
	Globigerinida Delage & Hérouard 1896
	Robertinida Loeblich & Tappan 1984
	Textulariida Delage & Hérouard 1896
	Carterina Brady 1884