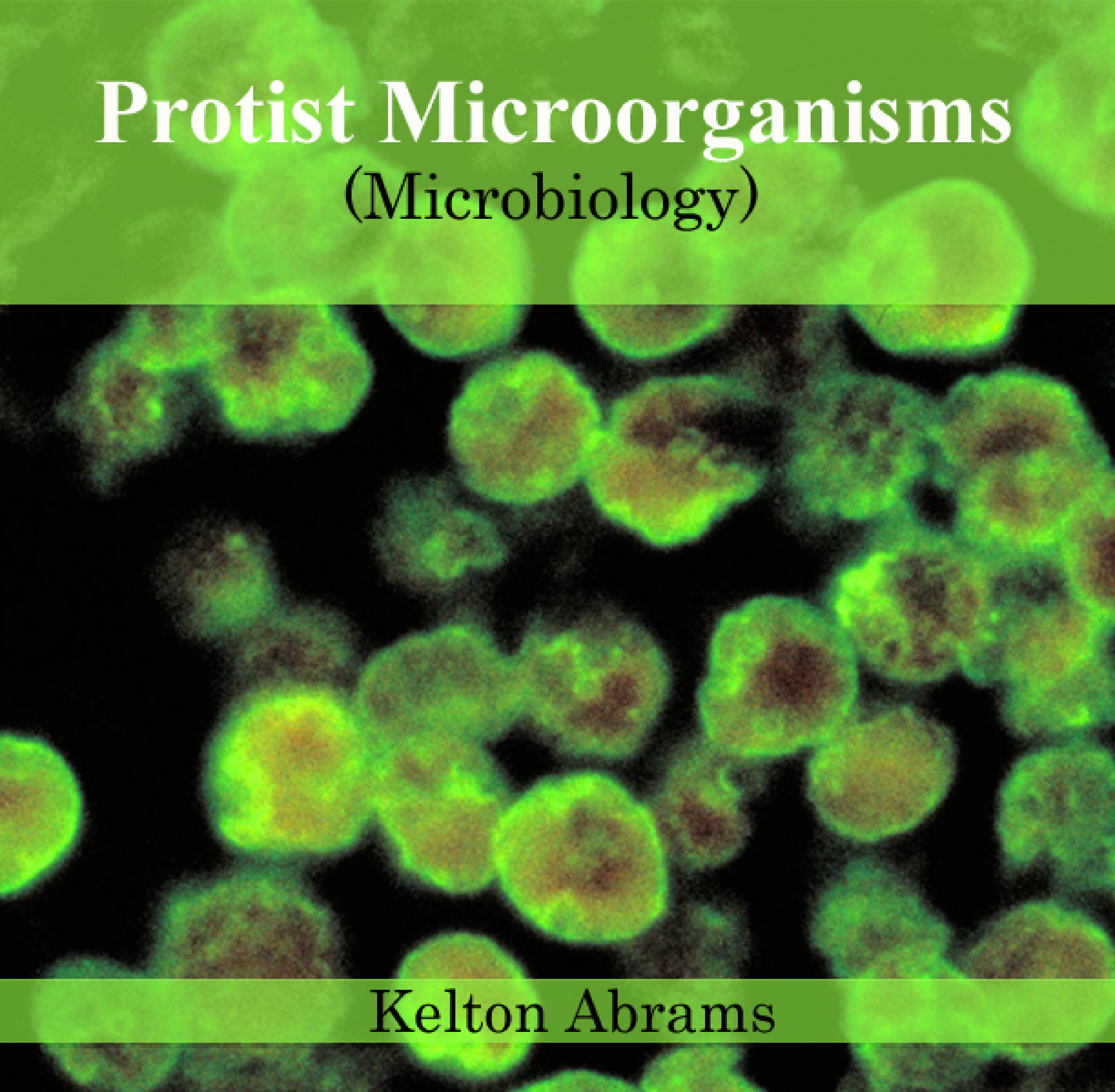

Protist Microorganisms

(Microbiology)

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Protist

Protist

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Kingdom:	**Protista*** Haeckel, 1866

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    - Haptophyta
    - Cryptophyta (cryptomonads)
    - **Alveolata**
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        - Apicomplexa
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- **Excavata**
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    - Metamonada

- **Rhizaria**
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    - Foraminifera
    - Cercozoa
- **Archaeplastida (in part)**
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    - Glaucophyta (basal archaeplastids)
- **Unikonta (in part)**
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Protists are a diverse group of eukaryotic microorganisms. Historically, protists were treated as the kingdom **Protista**, which includes mostly unicellular organisms that do not fit into the other kingdoms, but this group is contested in modern taxonomy. Instead, it is "better regarded as a loose grouping of 30 or 40 disparate phyla with diverse combinations of trophic modes, mechanisms of motility, cell coverings and life cycles."

The protists do not have much in common besides a relatively simple organization—either they are unicellular, or they are multicellular without specialized tissues. This simple cellular organization distinguishes the protists from other eukaryotes, such as fungi, animals and plants.

The term *protista* was first used by Ernst Haeckel in 1866. Protists were traditionally subdivided into several groups based on similarities to the "higher" kingdoms: the one-celled animal-like protozoa, the plant-like protophyta (mostly one-celled algae), and the fungus-like slime molds and water molds. Because these groups often overlap, they have been replaced by phylogenetic-based classifications. However, they are still useful as informal names for describing the morphology and ecology of protists.

Protists live in almost any environment that contains liquid water. Many protists, such as the algae, are photosynthetic and are vital primary producers in ecosystems, particularly in the ocean as part of the plankton. Other protists, such as the Kinetoplastids and Apicomplexa, are responsible for a range of serious human diseases, such as malaria and sleeping sickness.

Classification

Historical classifications

The first division of the protists from other organisms came in the 1830s, when the German biologist Georg A. Goldfuss introduced the word *protozoa* to refer to organisms such as ciliates and corals. This group was expanded in 1845 to include all "unicellular animals", such as Foraminifera and amoebae. The formal taxonomic category *Protoctista* was first proposed in the early 1860s by John Hogg, who argued that the protists should include what he saw as primitive unicellular forms of both plants and animals. He defined the Protoctista as a "fourth kingdom of nature", in addition to the then-traditional kingdoms of plants, animals and minerals. The kingdom of minerals was later removed from taxonomy by Ernst Haeckel, leaving plants, animals, and the protists as a “kingdom of primitive forms”.

Herbert Copeland resurrected Hogg's label almost a century later, arguing that "Protoctista" literally meant "first established beings", Copeland complained that Haeckel's term *protista* included anucleated microbes such as bacteria. Copeland's use of the term *protoctista* did not. In contrast, Copeland's term included nucleated eukaryotes such as diatoms, green algae and fungi. This classification was the basis for Whittaker's later definition of Fungi, Animalia, Plantae and Protista as the four kingdoms of life. The kingdom Protista was later modified to separate prokaryotes into the separate kingdom of Monera, leaving the protists as a group of eukaryotic microorganisms. These five kingdoms remained the accepted classification until the development of molecular phylogenetics in the late 20th century, when it became apparent that neither protists nor monera were single groups of related organisms (they were not monophyletic groups).

Modern classifications

Currently, the term *protist* is used to refer to unicellular eukaryotes that either exist as independent cells, or if they occur in colonies, do not show differentiation into tissues. The term *protozoa* is used to refer to heterotrophic species of protists that do not form filaments. These terms are not used in current taxonomy, and are retained only as convenient ways to refer to these organisms.

The taxonomy of protists is still changing. Newer classifications attempt to present monophyletic groups based on ultrastructure, biochemistry, and genetics. Because the protists as a whole are paraphyletic, such systems often split up or abandon the kingdom, instead treating the protist groups as separate lines of eukaryotes. The recent scheme by Adl *et al.* (2005) is an example that does not bother with formal ranks (phylum, class, etc.) and instead lists organisms in hierarchical lists. This is intended to make the classification more stable in the long term and easier to update. Some of the main groups of protists, which may be treated as phyla, are listed in the taxobox at right. Many are thought to be monophyletic, though there is still uncertainty. For instance, the excavates are probably not monophyletic and the chromalveolates are probably only monophyletic if the haptophytes and cryptomonads are excluded.

Metabolism

Nutrition in some different types of protists is variable. In flagellates, for example, filter feeding may sometimes occur where the flagella find the prey. Other protists can engulf bacteria and digest them internally, by extending their cell membrane around the food material to form a food vacuole. This is then taken into the cell via endocytosis (usually phagocytosis; sometimes pinocytosis).

Nutritional types in protist metabolism

Nutritional type	Source of energy	Source of carbon	Examples
Phototrophs	Sunlight	Organic compounds or carbon fixation	Algae, Dinoflagellates or Euglena
Organotrophs	Organic compounds	Organic compounds	Apicomplexa, Trypanosomes or Amoebae

Reproduction

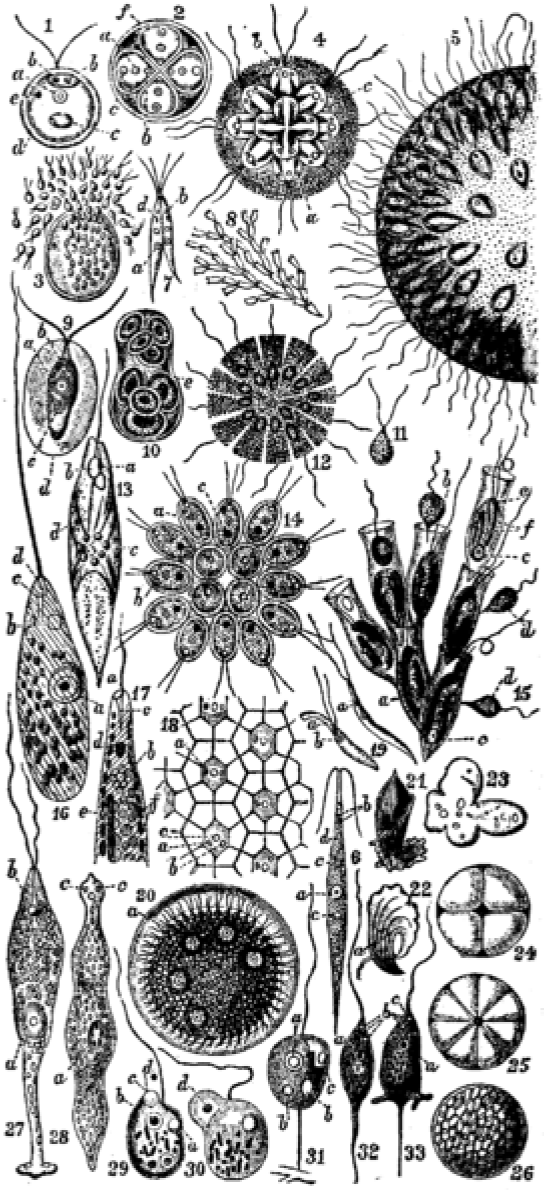
Some protists reproduce sexually (conjugation), while others reproduce asexually (binary fission).

Some species, for example *Plasmodium falciparum*, have extremely complex life cycles that involve multiple forms of the organism, some of which reproduce sexually and others asexually. However, it is unclear how frequently sexual reproduction causes genetic exchange between different strains of *Plasmodium* in nature and most populations of parasitic protists may be clonal lines that rarely exchange genes with other members of their species.

Role as pathogens

Some protists are significant pathogens of both animals and plants; for example *Plasmodium falciparum*, which causes malaria in humans, and *Phytophthora infestans*, which causes potato blight. A more thorough understanding of protist biology may allow these diseases to be treated more efficiently.

Researchers from the Agricultural Research Service are taking advantage of protists as pathogens in an effort to control red imported fire ant (*Solenopsis invicta*) populations in Argentina. With the help of spore-producing protists such as *Kneallhazia solenopsae* the red fire ant populations can be reduced by 53-100%. Researchers have also found a way to infect phorid flies with the protist without harming the flies. This is important because the flies act as a vector to infect the red fire ant population with the pathogenic protist.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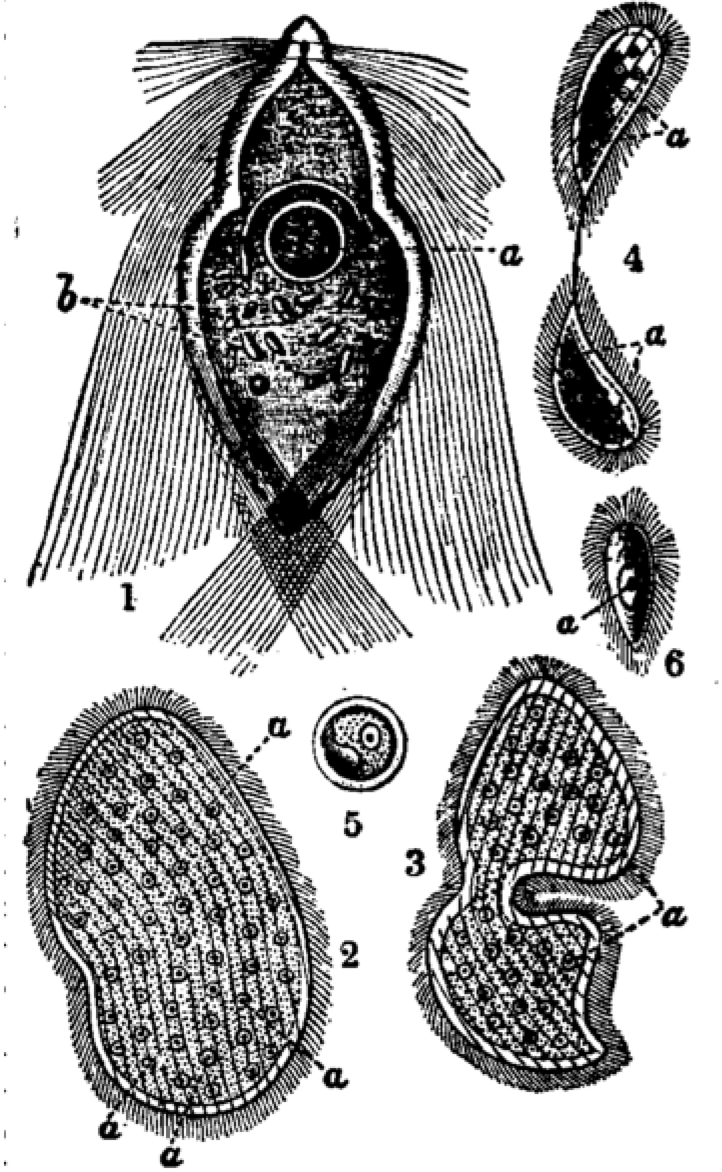
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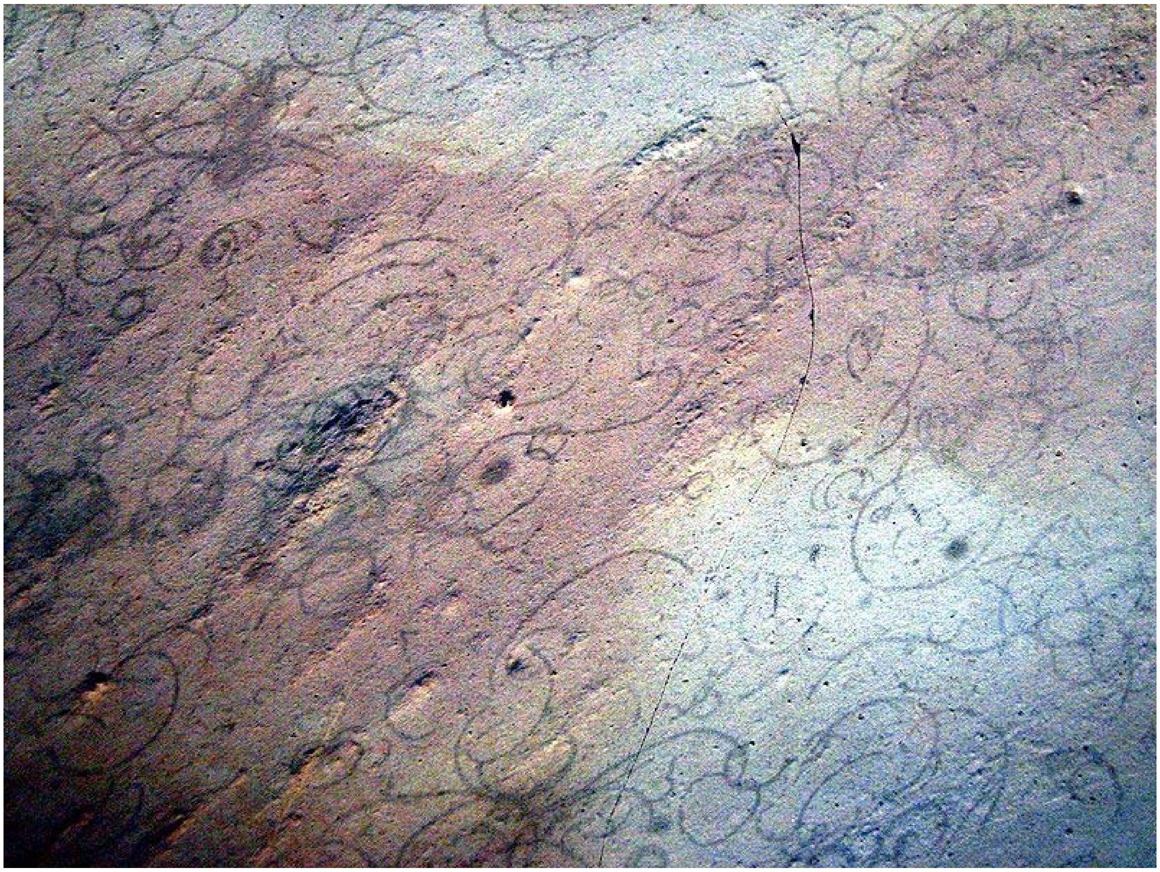

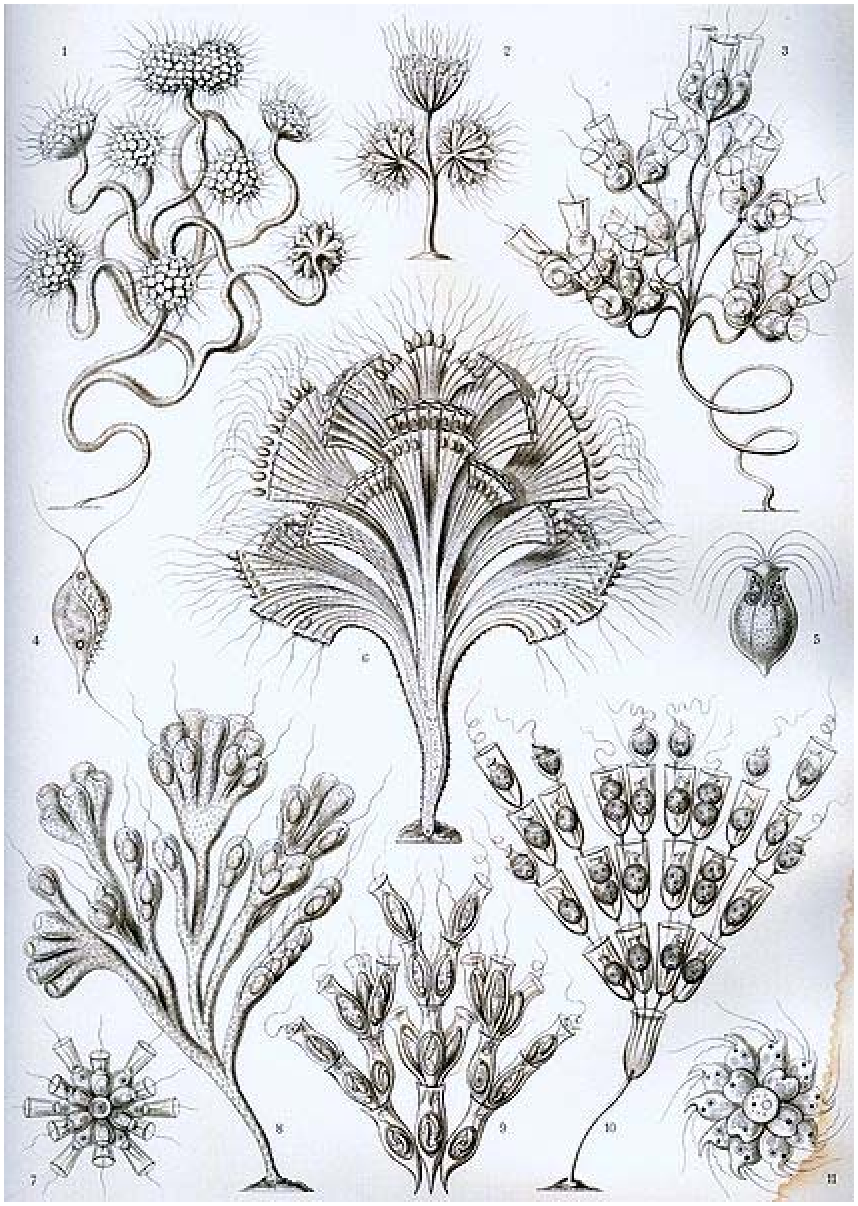
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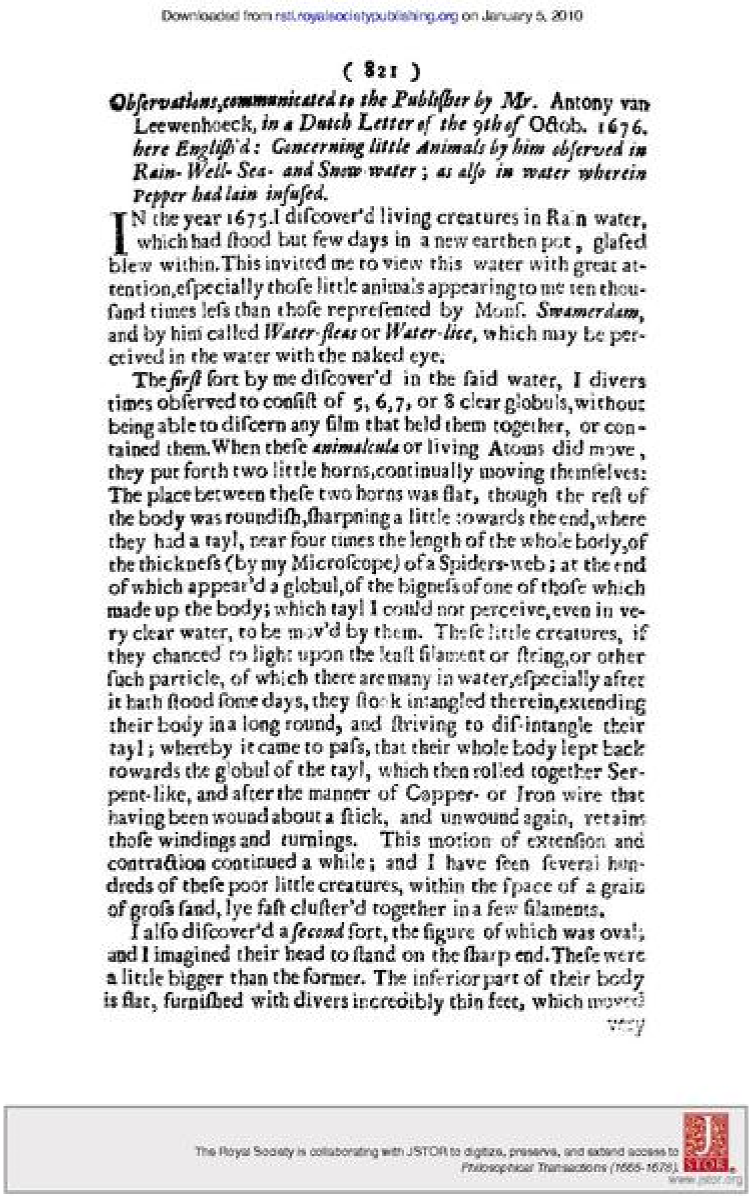


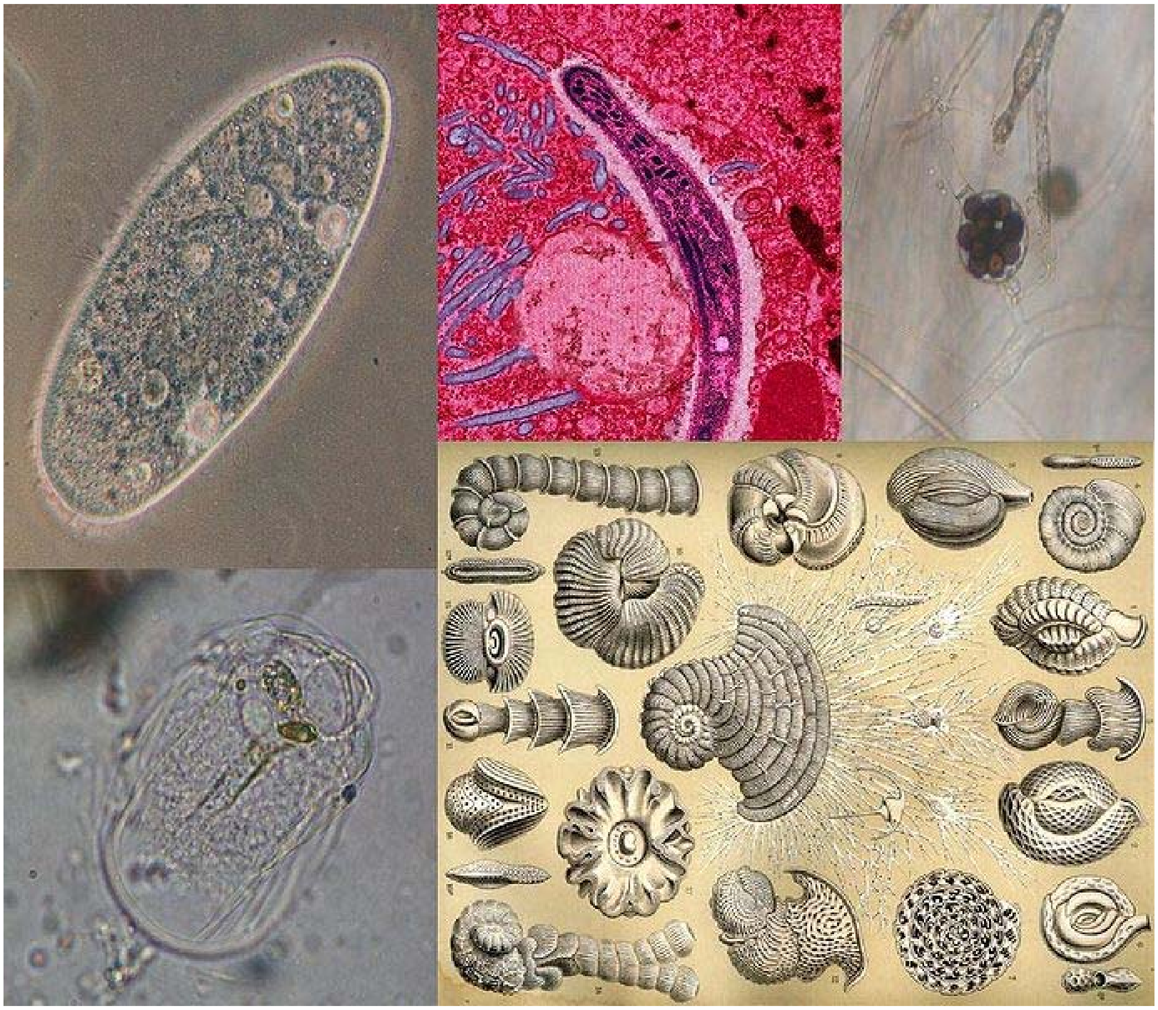
Obſervations, communicated to the Publiſher by Mr. Antony van Leewenhoeck, *in a Dutch Letter of the 9th of* Octob. 1676. *here Engliſh'd: Concerning little Animals by him obſerved in Rain- Well- Sea- and Snow water; as alſo in water wherein Pepper had lain infuſed.*

IN the year 1675. I diſcover'd living creatures in Rain water, which had ſtood but few days in a new earthen pot, glaſed blew within. This invited me to view this water with great attention, eſpecially thoſe little animals appearing to me ten thouſand times leſs than thoſe repreſented by Monſ. *Swamerdam*, and by him called *Water-fleas* or *Water-lice*, which may be perceived in the water with the naked eye.

The *firſt* ſort by me diſcover'd in the ſaid water, I divers times obſerved to conſiſt of 5, 6, 7, or 8 clear globuls, without being able to diſcern any film that held them together, or contained them. When theſe *animalcula* or living Atoms did move, they put forth two little horns, continually moving themſelves: The place between theſe two horns was flat, though the reſt of the body was roundiſh, ſharpning a little towards the end, where they had a tayl, near four times the length of the whole body, of the thickneſs (by my Microſcope) of a Spiders-web; at the end of which appear'd a globul, of the bigneſs of one of thoſe which made up the body; which tayl I could not perceive, even in very clear water, to be mov'd by them. Theſe little creatures, if they chanced to light upon the leaſt filament or ſtring, or other ſuch particle, of which there are many in water, eſpecially after it hath ſtood ſome days, they ſtook intangled therein, extending their body in a long round, and ſtriving to diſ-intangle their tayl; whereby it came to paſs, that their whole body lept back towards the globul of the tayl, which then rolled together Serpent-like, and after the manner of Copper- or Iron wire that having been wound about a ſtick, and unwound again, retains thoſe windings and turnings. This motion of extenſion and contraction continued a while; and I have ſeen ſeveral hundreds of theſe poor little creatures, within the ſpace of a grain of groſs ſand, lye faſt cluſter'd together in a few filaments.

I alſo diſcover'd a *ſecond* ſort, the figure of which was oval; and I imagined their head to ſtand on the ſharp end. Theſe were a little bigger than the former. The inferior part of their body is flat, furniſhed with divers incredibly thin feet, which moved

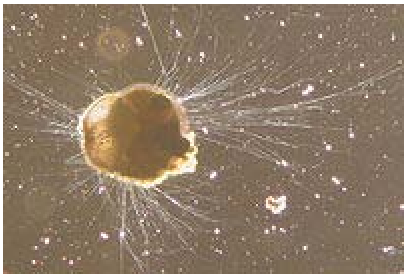
very



Chapter 2

Foraminifera

Foraminifera
Temporal range: Precambrian - Recent



Live *Ammonia tepida* (Rotaliida)

Scientific classification

Domain:	Eukaryota
Kingdom:	Rhizaria
Superphylum:	Retaria
Phylum:	**Foraminifera** d'Orbigny, 1826

Orders

Allogromiida
Carterinida
Fusulinida- *extinct*
Globigerinida
Involutinida - *extinct*
Lagenida
Miliolida
Rotaliida
Silicoloculinida
Spirillinida
Textulariida

incertae sedis
  Xenophyophorea
  Reticulomyxa

The **Foraminifera**, (**"hole bearers"**) or **forams** for short, are a large group of amoeboid protists with reticulating pseudopods, fine strands of cytoplasm that branch and merge to form a dynamic net. They typically produce a test, or shell, which can have either one or multiple chambers, some becoming quite elaborate in structure. These shells are made of calcium carbonate ($CaCO_3$) or agglutinated sediment particles. About 275,000 species are recognized, both living and fossil. They are usually less than 1 mm in size, but some are much larger, and the largest recorded specimen reached 19 cm.

Taxonomic relations

Foraminifera are typically included in the Kingdom Protozoa, although some taxonomies put them in the equivalent Protoctista or Protista. There is also compelling evidence, based primarily on molecular evidence, for their belonging to a major group within the Protozoa known as the Rhizaria. Prior to the recognition of the Rhizaria as a taxon, Foraminifera were generally place in the Class Granuloreticulosa, Phylum Rhizopodea (or Sarcodina). This morphology based perspective remains in use today.

Rhizaria is somewhat problematical as it is often referred to simply as a "supergroup", which may account for its sometimes over-elevated status, although Cavalier-Smith does define it as an infrakingdom within the Kingdom Protozoa. Otherwise Rhizaria could easily be recognized as a phylum, equivalent to the Rhizopodea which it replaces.

The taxonomic position of Foraminifera has varied since their recognition as protozoa (protists) by Schultze in 1854, most often being referred to as an order, but sometimes a class. Leoblich and Tappan (1992) redefined Foraminifera as a class from its previous ordinal rank (as Foraminiferida) in the Treatise, where it now sits. Some taxonomies go so far as to put foraminifera in phylum of their own, putting them on par with the amoeboid Sarcodina in which they had been placed.

Although as yet unsupported by morphological correlates, molecular data strongly suggest that Foraminifera are closely related to the Cercozoa and Radiolaria, both of which also include amoeboids with complex shells; these three groups make up the Rhizaria. However, the exact relationships of the forams to the other groups and to one another are still not entirely clear.

Living forams

Modern forams are primarily marine, although some can survive in brackish conditions. They are most commonly benthic, and about 40 morphospecies are planktonic. This count may however represent only a fraction of actual diversity, since many genetically discrepant species may be morphologically indistinguishable.

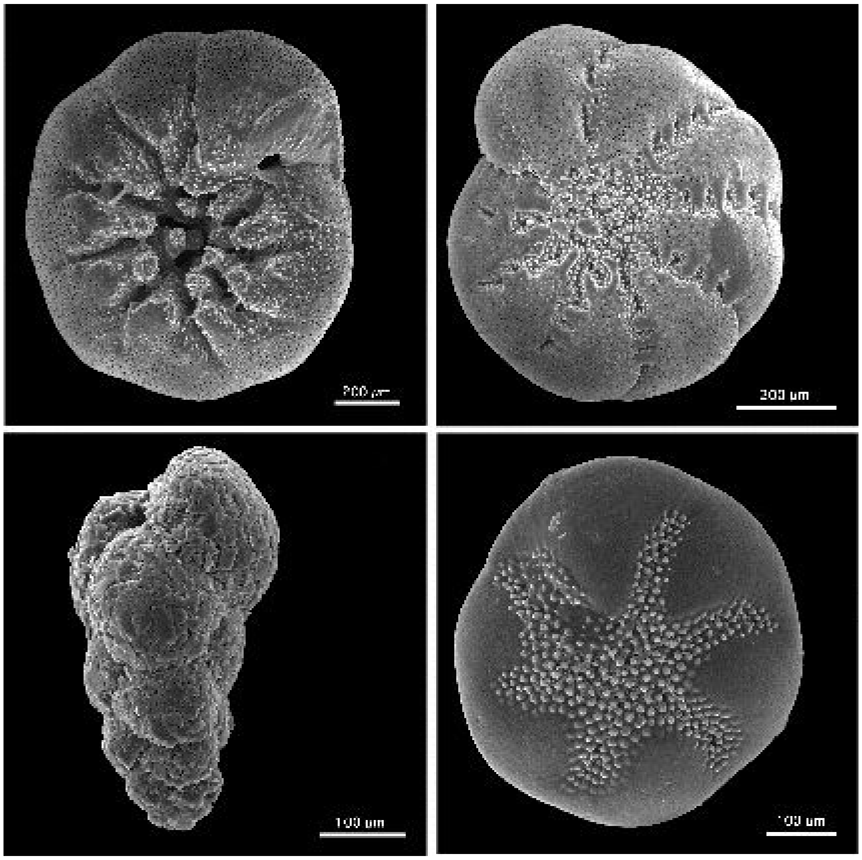
A number of forms have unicellular algae as endosymbionts, from diverse lineages such as the green algae, red algae, golden algae, diatoms, and dinoflagellates. Some forams are kleptoplastic, retaining chloroplasts from ingested algae to conduct photosynthesis.

Biology

The foraminiferal cell is divided into granular endoplasm and transparent ectoplasm from which a pseudopodial net may emerge through a single opening or through many perforations in the test. Individual pseudopods characteristically have small granules streaming in both directions. The pseudopods are used for locomotion, anchoring, and in capturing food, which consists of small organisms such as diatoms or bacteria.

The foraminiferal life-cycle involves an alternation between haploid and diploid generations, although they are mostly similar in form. The haploid or gamont initially has a single nucleus, and divides to produce numerous gametes, which typically have two flagella. The diploid or schizont is multinucleate, and after meiosis fragments to produce new gamonts. Multiple rounds of asexual reproduction between sexual generations is not uncommon in benthic forms.

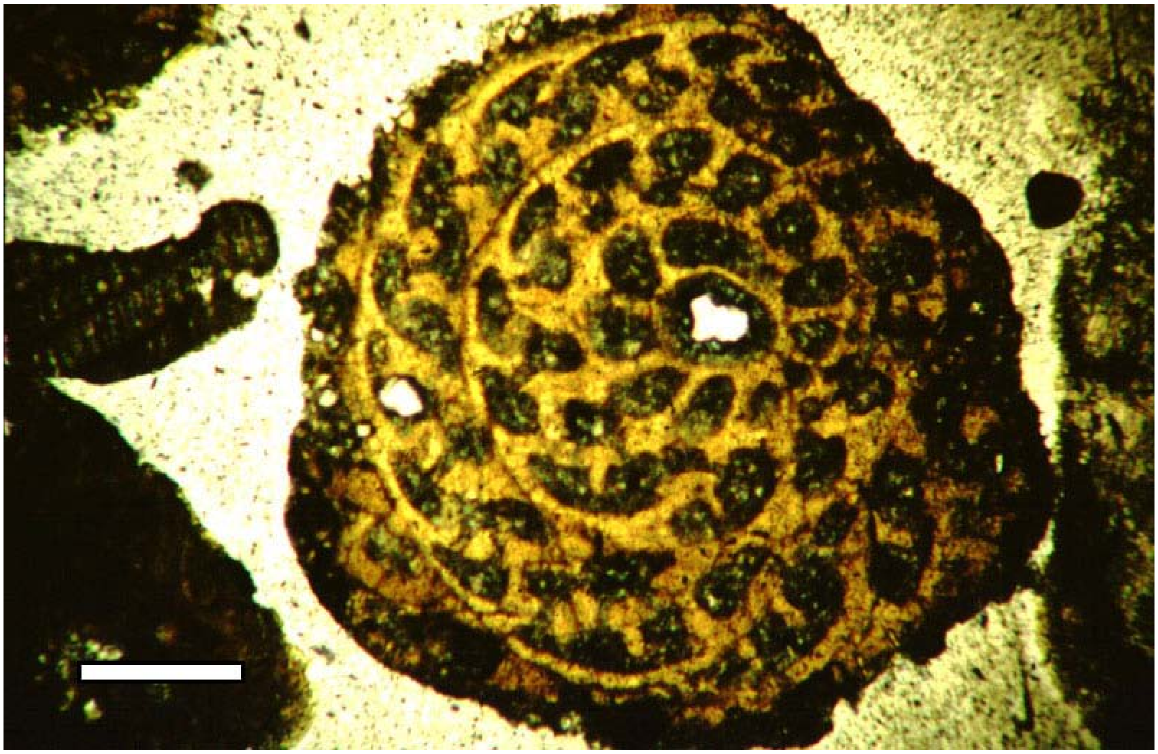
Tests



Foraminiferan tests (ventral view)

Fossil nummulitid foraminiferans showing microspheric and megalospheric individuals; Eocene of the United Arab Emirates; scale in mm.

The miliolid foraminiferan *Quinqueloculina* from Donegal Bay, Ireland.



Thin section of a peneroplid foraminiferan from Holocene lagoonal sediment in Rice Bay, San Salvador Island, Bahamas. Scale bar 100 micrometres.

The form and composition of the test is the primary means by which forams are identified and classified. Most have calcareous tests, composed of calcium carbonate. In other forams the test may be composed of organic material, made from small pieces of sediment cemented together (agglutinated), and in one genus of silica. Openings in the test, including those that allow cytoplasm to flow between chambers, are called apertures. The test contains an organic matrix, which can sometimes be recovered from fossil samples.

Tests are known as fossils as far back as the Cambrian period, and many marine sediments are composed primarily of them. For instance, the limestone that makes up the pyramids of Egypt is composed almost entirely of nummulitic benthic foraminifera. Production estimates indicate that reef foraminifera annually generate approximately 43 million tons of calcium carbonate and thus play an essential role in the production of reef carbonates.

Genetic studies have identified the naked amoeba "Reticulomyxa" and the peculiar xenophyophores as foraminiferans without tests. A few other amoeboids produce reticulose pseudopods, and were formerly classified with the forams as the Granuloreticulosa, but this is no longer considered a natural group, and most are now placed among the Cercozoa.

Deep sea species

Foraminifera are found in the deepest parts of the ocean such as the Mariana Trench, including the Challenger Deep, the deepest part known. At these depths, below the carbonate compensation depth, the calcium carbonate of the tests is soluble in water due to the extreme pressure. The foraminifera found in the Challenger Deep thus have no carbonate test, but instead have one of organic material.

Four species have been found in the Challenger Deep that are unknown from any other place in the ocean, one of which is representative of an endemic genus unique to the region. They are *Resigella laevis* and *R. bilocularis*, *Nodellum aculeata*, and *Conicotheca nigrans* (the unique genus). All have tests that are mainly of transparent organic material which have small (~ 100 nm) plates that appears to be clay

Evolutionary significance

Dying planktonic foraminifera continuously rain down on the sea floor in vast numbers, their mineralized tests preserved as fossils in the accumulating sediment. Beginning in the 1960s, and largely under the auspices of the Deep Sea Drilling, Ocean Drilling, and International Ocean Drilling Programmes, as well as for the purposes of oil exploration, advanced deep-sea drilling techniques have been bringing up sediment cores bearing foraminifera fossils by the millions. The effectively unlimited supply of these fossil tests and the relatively high-precision age-control models available for cores has produced an exceptionally high-quality planktonic foraminifera fossil record dating back to the mid-Jurassic, and presents an unparalleled record for scientists testing and documenting the evolutionary process. The exceptional quality of the fossil record has allowed an impressively detailed picture of species inter-relationships to be developed on the basis of fossils, in many cases subsequently validated independently through molecular genetic studies on extant specimens. Larger benthic foraminifera with complex shell structure react in a highly specific manner to the different benthic environments and, therefore, the composition of the assemblages and the distribution patterns of particular species reflect simultaneously bottom types and the light gradient. In the course of Earth history, larger foraminifera are replaced frequently. In particular, associations of foraminifera characterizing particular shallow water facies types are dying out and are replaced after a certain time interval by new associations with the same structure of shell morphology, emerging from a new evolutionary process of adaptation. These evolutionary processes make the larger foraminifera prone to be fossil index for the Permian, Jurassic, Cretaceous and Cenozoic (e.g. Lukas Hottinger).

Uses of forams

Because of their diversity, abundance, and complex morphology, fossil foraminiferal assemblages are useful for biostratigraphy, and can accurately give relative dates to rocks. The oil industry relies heavily on microfossils such as forams to find potential oil deposits.

Calcareous fossil foraminifera are formed from elements found in the ancient seas they lived in. Thus they are very useful in paleoclimatology and paleoceanography. They can be used to reconstruct past climate by examining the stable isotope ratios of oxygen, and the history of the carbon cycle and oceanic productivity by examining the stable isotope ratios of carbon. Geographic patterns seen in the fossil records of planktonic forams are also used to reconstruct ancient ocean currents. Because certain types of foraminifera are found only in certain environments, they can be used to figure out the kind of environment under which ancient marine sediments were deposited.

For the same reasons they make useful biostratigraphic markers, living foraminiferal assemblages have been used as bioindicators in coastal environments, including indicators of coral reef health. Because calcium carbonate is susceptible to dissolution in acidic conditions, foraminifera may be particularly affected by changing climate and ocean acidification.

Foraminifera can also be utilised in archaeology in the provenancing of some stone raw material types. Some stone types, such as chert, are commonly found to contain fossilised foraminifera. The types and concentrations of these fossils within a sample of stone can be used to match that sample to a source known to contain the same "fossil signature".

Chapter 3

Cercozoa and Alveolate

Cercozoa

Cercozoa

Cercomonas

Scientific classification

Domain:	Eukaryota
Kingdom:	Rhizaria
Phylum:	**Cercozoa** Cavalier-Smith 1998

The **Cercozoa** are a group of protists. They are sometimes described as a kingdom.

Characteristics

The group includes most amoeboids and flagellates that feed by means of filose pseudopods. These may be restricted to part of the cell surface, but there is never a true cytostome or mouth as found in many other protozoa. They show a variety of forms and have proven difficult to define in terms of structural characteristics, although their unity is strongly supported by genetic studies. Cercozoa are closely related to Foraminifera and Radiolaria, amoeboids that usually have complex shells, and together with them form a supergroup called the Rhizaria.

Types

They are sometimes grouped by whether they are "filose" or "reticulose".

Filose (subphylum Filosa)

The best-known Cercozoa are the euglyphids, filose amoebae with shells of siliceous scales or plates, which are commonly found in soils, nutrient-rich waters, and on aquatic plants. Some other filose amoebae produce organic shells, including the tectofilosids and *Gromia*. They were formerly classified with the euglyphids as the Testaceafilosia. This group is not monophyletic, but nearly all studied members fall in or near the Cercozoa, related to similarly shelled flagellates.

Reticulose (subphylum Endomyxa)

Another important group placed here are the chlorarachniophytes, strange amoebae that form a reticulating net. They are set apart by the presence of chloroplasts, which apparently developed from an ingested green alga. They are bound by four membranes and still possess a vestigial nucleus, called a nucleomorph. As such, they have been of great interest to researchers studying the endosymbiotic origins of organelles.

Chlorarachniophytes are sometimes considered Filosa, rather than Endomyxa, while groups such as *Gromia* are considered Endomyxa.

Ungrouped

Other notable cercozoans include the cercomonads, which are common soil flagellates, and the Phaeodarea, marine protozoa that were previously considered radiolarians. In addition, three groups that are traditionally considered heliozoans belong here: the dimorphids, desmothoracids, and gymnosphaerids.

Classification

The exact composition and classification of the Cercozoa are still being worked out. A general scheme is:

Class Chlorarachnea	chlorarachniophytes
Class Proteomyxidea	gymnophryids, dimorphids, desmothoracids, gymnosphaerids, etc.
Class Sarcomonadea	cercomonads
Class Imbricatea /	euglyphids and thaumatomonads

Silicofilosea	
Class Thecofilosea	tectofilosids and cryomonads
Class Phaeodarea	
Class Ebridea	ebriids

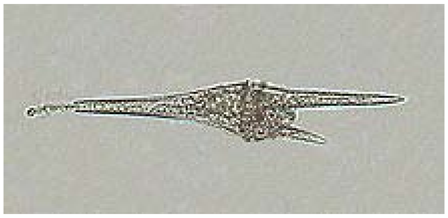
In addition two groups of parasites, the Phytomyxea and Ascetosporea, and the shelled amoeba *Gromia* may be basal Cercozoa, although some trees place them closer to the Foraminifera.

The spongomonads have been included here, but more recently have been considered Amoebozoa.

Some other small groups of protozoans are considered Cercozoa but are of uncertain placement, and it is likely many obscure genera will turn out to be cercozoans with further study.

Alveolate

Alveolata
Temporal range: Ediacaran - Recent



Ceratium furca

Scientific classification

Domain:	Eukarya
Kingdom:	Chromalveolata
Superphylum:	**Alveolata**

Phyla

Ciliophora
Apicomplexa
Dinoflagellata

The **alveolates** ("with cavities") are a major line of protists.

Phyla

There are three phyla, which are very divergent in form, but are now known to be close relatives based on various ultrastructural and genetic similarities:

- Ciliates, very common protozoa, with many short cilia arranged in rows
- Apicomplexa, parasitic protozoa that lack axonemal locomotive structures except in gametes
- Dinoflagellates, mostly marine flagellates, many of which have chloroplasts

Characteristics

The most notable shared characteristic is the presence of cortical alveoli, flattened vesicles packed into a continuous layer supporting the membrane, typically forming a flexible pellicle. In dinoflagellates they often form armor plates. Alveolates have mitochondria with tubular cristae, and their flagella or cilia have a distinct structure.

Classification

The Apicomplexa and dinoflagellates may be more closely related to each other than to the ciliates. Both have plastids, and most share a bundle or cone of microtubules at the top of the cell. In apicomplexans this forms part of a complex used to enter host cells, while in some colorless dinoflagellates it forms a peduncle used to ingest prey. Various other genera are closely related to these two groups, mostly flagellates with a similar apical structure. These include free-living members in *Oxyrrhis* and *Colponema*, and parasites in *Perkinsus*, *Parvilucifera*, *Rastrimonas*, and the ellobiopsids. In 2001, direct amplification of the rRNA gene in marine picoplankton samples revealed the presence of two novel alveolate linages, called group I and II. Group I has no cultivated relatives, while group II is related to the dinoflagellate parasite *Amoebophrya*, which was classified until now in the Syndiniales dinoflagellate order.

Relationships between some of these the major groups were suggested during the 1980s, and a specific relationship between all three was confirmed in the early 1990s by genetic studies, most notably by Gajadhar *et al.*. Cavalier-Smith, introduced the formal name Alveolata in 1991, although at the time he actually considered the grouping to be a paraphyletic assemblage, rather than a monophyletic group.

Some studies suggested the haplosporids, mostly parasites of marine invertebrates, might belong here but they lack alveoli and are now placed among the Cercozoa.

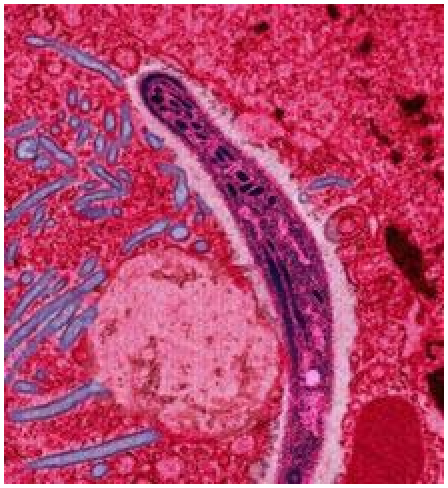
Development

The development of plastids among the alveolates is uncertain. Cavalier-Smith proposed the alveolates developed from a chloroplast-containing ancestor, which also gave rise to the Chromista (the chromalveolate hypothesis). However, as plastids only appear in relatively derived (as opposed to ancestral) groups, others argue the alveolates originally lacked them and possibly the dinoflagellates and Apicomplexa acquired them separately.

Chapter 4

Apicomplexa

Apicomplexa



Plasmodium

Scientific classification

Domain:	Eukaryota
Kingdom:	Chromalveolata
Superphylum:	Alveolata
Phylum:	**Apicomplexa**

Classes & Subclasses

Aconoidasida

- Haemosporasina
- Piroplasmasina

Conoidasida

- Coccidiasina
- Gregarinasina

The **Apicomplexa** (also referred to as **Apicomplexia**) are a large group of protists, most of which possess a unique organelle called apicoplast and an *apical complex* structure involved in penetrating a host's cell. They are unicellular, spore-forming, and exclusively parasites of animals. Motile structures such as flagella or pseudopods are present only in certain gamete stages. This is a diverse group including organisms such as coccidia, gregarines, piroplasms, haemogregarines, and plasmodia. Diseases caused by apicomplexan organisms include, but are not limited to:

- Babesiosis (*Babesia*)
- Malaria (*Plasmodium*)
- Coccidian diseases including:
    - Cryptosporidiosis (*Cryptosporidium parvum*)
    - Cyclosporiasis (*Cyclospora cayetanensis*)
    - Isosporiasis (*Isospora belli*)
    - Toxoplasmosis (*Toxoplasma gondii*)

The name of the taxon *Apicomplexa* is derived from two Latin words - *apex* (top) and *complexus* (infolds) - and refers to a set of organelles at the in the sporozoite. The older taxon *Sporozoa* grouped the *Apicomplexa* together with the *Microsporidia* and *Myxosporida*. This grouping is no longer regarded as biologically valid and its use is discouraged.

History

The first apicomplexan protozoan was seen by Antony van Leeuwenhoek who in 1674 saw oocysts of *Eimeria stiedae* in the gall bladder of a rabbit. The first member of the phylum to be named (by Dufour in 1828) was *Gregarina ovata* in earwigs. Since then many more have been identified and named. During the quarter century 1826-1850, 41 species and 6 genera of Apicomplexa were named. In the quarter century 1951-1975, 1873 new species and 83 new genera were added.

By 1987 a comprehensive survey of the phylum was completed: in all, 4516 species and 339 genera had been named. They consisted of:

- the gregarines (subclass *Gregarinasida*) with 1624 named species and 231 named genera
- the hemogregarines (family *Haemogregarinidae*) with 399 species and 4 genera
- the eimeriorins (order *Eimeriorida*) with 1771 species and 43 genera
- the hemospororids (order *Haemospororida* with 444 species and 9 genera
- the piroplasmids (order *Piroplasmorida*) with 173 species and 20 genera

- and a few others (105 species and 32 genera)

Although there has been considerable revision of this phylum (the order Haemosporidia now has 17 genera rather than 9) it seems likely these numbers are still approximately correct.

General morphological features

All members of this phylum have an infectious stage - the sporozoite - which possess an apical complex. This complex consists of a set of spirally arranged microtubules (the conoid), a secretory body (the rhoptry) and one or more polar rings. Additional slender electron dense secretory bodies (micronemes) may also be present. It is this structure that gives the phylum its name.

Other morphological findings that are common to all members of this phylum include:

- The nucleus is haploid.
- Flagellae are found only in the motile gamete. These are posteriorly directed and vary in number (usually one to three).
- Basal bodies are present. Although hemosporidians and piroplasmids have normal triplets of microtubules in their basal bodies and coccidians and gregarines have 9 singlets.
- The mitochondria have tubular cristae.
- A Golgi apparatus is present.
- Chloroplasts and centrioles are absent.
- Colourless plastids are present in some species.
- The cell is surrounded by a pellicle of three membrane layers (the alveolar structure) penetrated by micropores.
- Other inclusions and ejectile organelles are absent.

General features

Within this phylum there are four groups - *Perkinsus*, coccidians, gregarines and haemosporidians. The coccidians and gregarines appear to be relatively closely related and *Perkinsus* appears to be basal within this phylum.

Perkinsus is a parasite of bivalve mollusks and is currently the only known species in this class. It displayes a number of features characteristic of the dinoflagellates including laterally inserted heterodynamic flagella. It is likely there are additional species in this class that have yet to be described.

The gregarines are generally parasites of annelids, arthropods and mollusks. They are often found in the guts of their hosts but may invade the other tissues. In the typical gregarine life cycle a trophozoite develops within a host cell into a plasmodium. This then divides into a number of merozoites by schizogony. The merozoites are released by lysing the host cell which in turn invade other cells. At some point in the life cycle gamonts are formed. These are released by lysis of the host cells and group together by syzygy. Each gamont forms multiple gametes. The gametes fuse with another to form oocysts. The oocysts leave the host to be taken up by a new host.

Coccidians are generally parasites of vertebrates. Like gregarines they are commonly parasites of the epithelial cells of the gut but may infect other tissues. The typical coccidial life cycle while similar to that of the gregarines differs in zygote formation. Some trophozoites enlage and become macrogamete while others divide repeatedly to form microgametes. The microgametes are motile and must reach the macrogamete to fertilize it. The fertilized macrogamete forms a zygote which in its turn forms an oocyst which is normally released from the body.

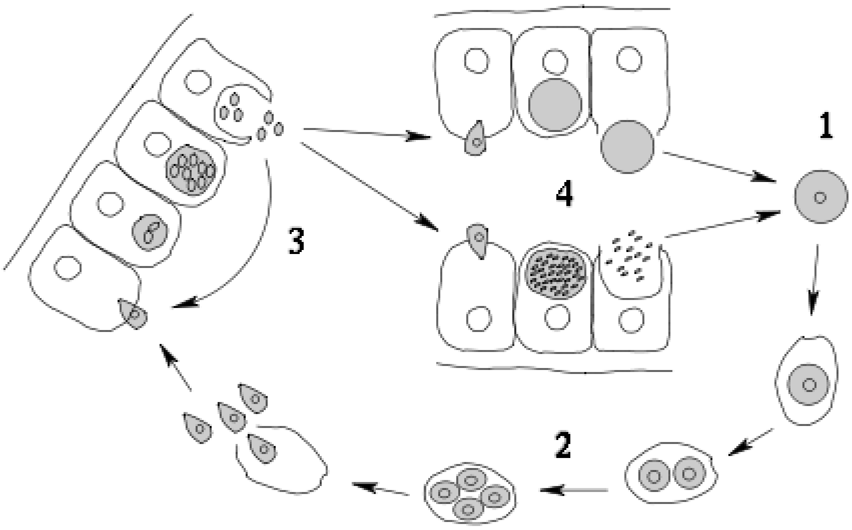
The Haemosporidians have more complex life cycles that alternate between an arthropod and a vertebrate host. The trophozoite parasitises erythrocytes or other tissues in the vertebrate host. Microgametes and macrogametes are always found in the blood. The gametes are taken up by the insect vector during a blood meal. The microgametes migrate within the gut of the insect vector and fuse with the macrogametes. The fertilized macrogamete now becomes an ookinete which penetrates the body of the vector. The ookinete then transforms into an oocyte and divides initially by meiosis and then by mitosis to give rise to the sporozoites. The sporozoites escape from the oocyst and migrate within the body of the vector to the salivary glands where they are injected into the new vertebrate host when the insect vector feeds again.

Evolution

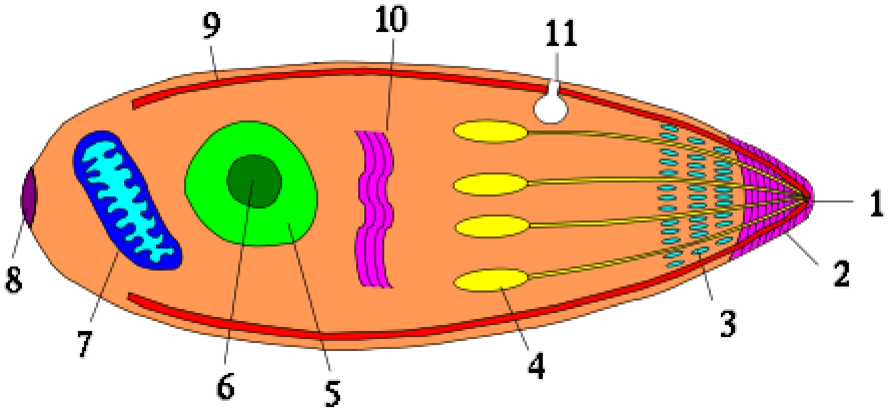
Many *Coccidiomorpha* have an intermediate host as well as a primary host, and the evolution of hosts proceeded in different ways and at different times in these groups. For some coccidiomorphs, the original host has become the intermediate host while in others it has become the definitive host. In the genera *Aggregata*, *Atoxoplasma*, *Cystoisospora*, *Schellackia* and *Toxoplasma* the original is now definitive while in *Akiba*, *Babesiosoma*, *Babesia*, *Haemogregarina*, *Haemoproteus*, *Hepatozoon*, *Karyolysus*, *Leucocytozoon*, *Plasmodium*, *Sarcocystis* and *Theileria*, the original hosts are now intermediate.

Similar strategies to increase the likelihood of transmission have evolved in multiple genera. Polyenergid oocysts and tissue cysts are found in representatives of the orders Protococcidiida and Eimeriida. Hypnozoites are found in *Karyolysus lacerate* and most species of *Plasmodium*; transovarial transmission of parasites occurs in life cycles of *Karyolysus* and *Babesia*.

Life cycle



Generic life cycle of an apicomplexa: 1-zygote (cyst), 2-sporozoites, 3-merozoites, 4-gametocytes.



Apicomplexan structure: 1-polar ring, 2-conoid, 3-micronemes, 4-rhoptries, 5-nucleus, 6-nucleolus, 7-mitochondria, 8-posterior ring, 9-alveoli, 10-golgi apparatus, 11-micropore.

Most members have a complex life-cycle, involving both asexual and sexual reproduction. Typically, a host is infected via an active invasion by the parasites (similar to entosis), which divide to produce *sporozoites* that enter its cells. Eventually, the cells burst, releasing *merozoites* which infect new cells. This may occur several times, until *gamonts* are produced, forming gametes that fuse to create new cysts. There are many variations on this basic pattern, however, and many Apicomplexa have more than one host.

The apical complex includes vesicles called rhoptries and micronemes, which open at the anterior of the cell. These secrete enzymes that allow the parasite to enter other cells. The tip is surrounded by a band of microtubules, called the *polar ring*, and among the Conoidasida there is also a funnel of rods called the *conoid*. Over the rest of the cell, except for a diminished mouth called the micropore, the membrane is supported by vesicles called alveoli, forming a semi-rigid pellicle.

The presence of alveoli and other traits place the Apicomplexa among a group called the alveolates. Several related flagellates, such as *Perkinsus* and *Colpodella* have structures similar to the polar ring and were formerly included here, but most appear to be closer relatives of the dinoflagellates. They are probably similar to the common ancestor of the two groups.

Another similarity is that apicomplexan cells contain a single plastid, called the apicoplast, surrounded by either 3 or four membranes. Its functions are thought to include tasks such as lipid synthesis, and it appears to be necessary for survival. Plastids are generally considered to share a common origin with the chloroplasts of dinoflagellates, and evidence generally points to an origin from red algae rather than green.

The Apicomplexa comprise the bulk of what used to be called the Sporozoa, a group for parasitic protozoans without flagella, pseudopods, or cilia. Most of the Apicomplexa are motile however. The other main lines were the Ascetosporea, the Myxozoa (now known to be derived from animals), and the Microsporidia (now known to be derived from fungi). Sometimes the name Sporozoa is taken as a synonym for the Apicomplexa, or occasionally as a subset.

Blood-borne genera

Within the Apicomplexa there are three suborders of parasites.

- suborder Adeleorina - 8 genera
- suborder Haemosporina - all genera in this suborder
- suborder Eimeriorina - 2 genera (*Lankesterella* and *Schellackia*)

Within the *Adelorina* are species that infect invertebrates and others that infect vertebrates.

The *Haemosporina* includes the malaria parasites and their relatives.

The *Eimeriorina* - the largest suborder in this phylum - the life cycle involves both sexual and asexual stages. The asexual stages reproduce by schizogony. The male gametocyte produces a large number of gametes and the zygote gives rise to an oocyst which is the infective stage. The majority are monoxenous (infect one host only) but a few are heteroxenous (life cycle involves two or more hosts).

Both the number of families in this later suborder is debated with the number of families being between one and twenty depending on the authority and the number of genera being between nineteen and twenty five. This somewhat unsatisfactory state of affairs awaits resolution with DNA based methods.

Disease genomics

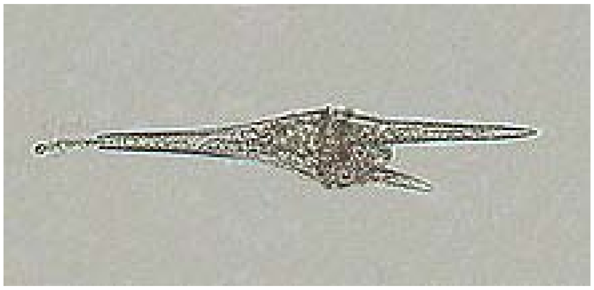
As noted above, many of the apicomplexan parasites are important pathogens of human and domestic animals. In contrast to bacterial pathogens, these apicomplexan parasites are eukaryotes and share many metabolic pathways with their animal hosts. This fact makes therapeutic target development extremely difficult – a drug that harms an apicomplexan parasite is also likely to harm its human host. Currently there are no effective vaccines or treatments available for most diseases caused by these parasites. Biomedical research on these parasites is challenging because it is often difficult, if not impossible, to maintain live parasite cultures in the laboratory and to genetically manipulate these organisms. In the recent years, several of the apicomplexan species have been selected for genome sequencing. The availability of genome sequences provides a new opportunity for scientists to learn more about the evolution and biochemical capacity of these parasite. A NIH-funded database, ApiDB.org, provides public access to currently available genomic data sets. One possible target for drugs is the plastid, and in fact existing drugs such as tetracyclines which are effective against apicomplexans seem to operate against the plastid.

Most apicomplexans have plastid genomes as well as nuclear ones, although *Cryptosporidium* spp. and possibly gregarines are exceptions as they are thought to have lost plastids after the diverging last common ancestor of apicomplexans.

Chapter 5

Dinoflagellate

Dinoflagellates **Temporal range: 440–0 Ma** **Silurian - Present**	



Ceratium furca

Scientific classification	
Domain:	Eukarya
Kingdom:	Chromalveolata
Superphylum:	Alveolata
Phylum:	**Dinoflagellata** Bütschli 1885

Classes

Dinophyceae
Noctiluciphyceae
Syndiniophyceae

The **dinoflagellates** (Greek δῖνος *dinos* "whirling" and Latin *flagellum* "whip, scourge") are a large group of flagellate protists. Most are marine plankton, but they are common in fresh water habitats as well. Their populations are distributed depending on temperature, salinity, or depth. About half of all dinoflagellates are photosynthetic, and these make up the largest group of marine eukaryotic algae aside from the diatoms. Being primary producers makes them an important part of the aquatic food chain. Some species, called zooxanthellae, are endosymbionts of marine animals and protozoa, and play an important part in the biology of coral reefs. Other dinoflagellates are colorless predators on other protozoa, and a few forms are parasitic.

This group is also known as the order **Dinoflagellata** or the class **Dinophyceae**.

An algal bloom of dinoflagellates can result in a visible coloration of the water colloquially known as red tide.

Classification

In 1753 the first modern dinoflagellates were described by Baker and named by Muller in 1773. The term derives from the Greek word δῖνος (dinos), meaning 'whirling,' and Latin flagellum, a diminutive term for a whip or scourge.

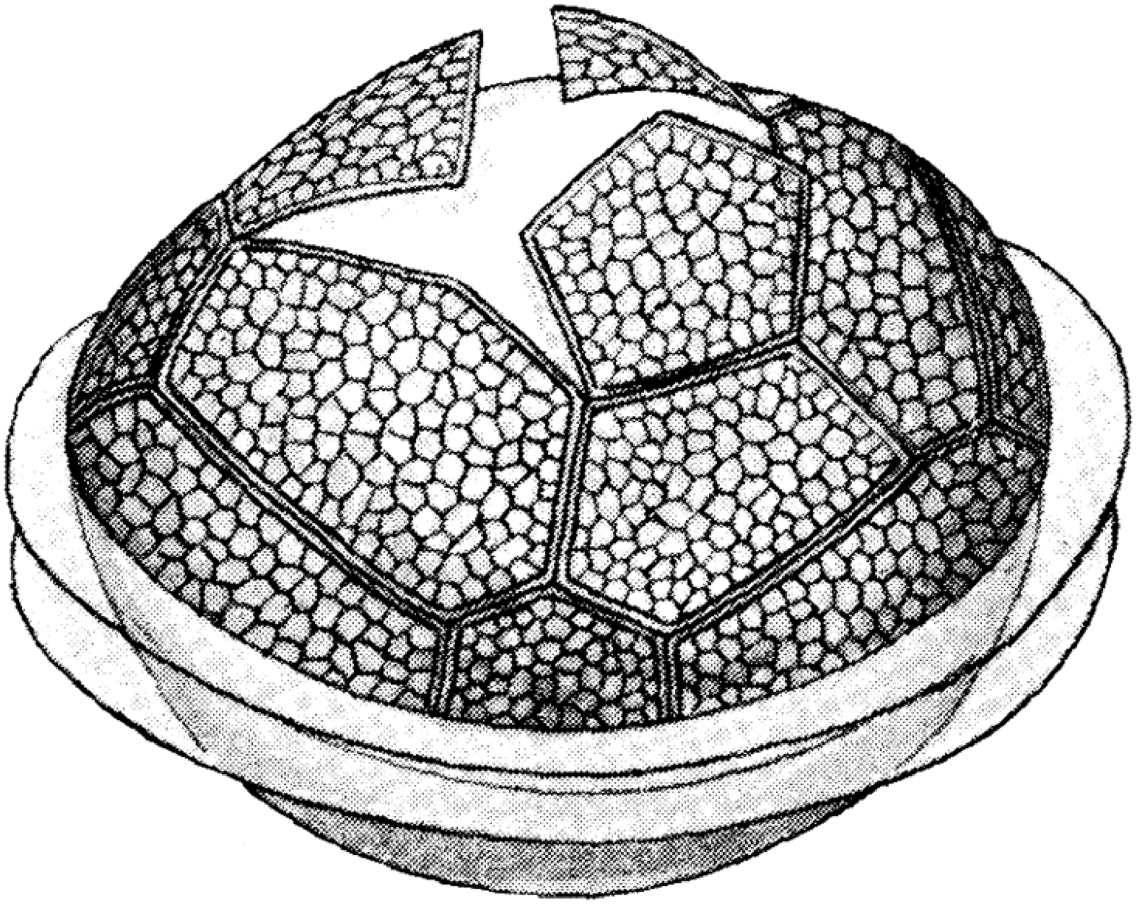
These same dinoflagellates were first defined by Otto Bütschli in 1885 as the flagellate order dinoflagellida. Botanists treated them as a division of algae, named **Pyrrophyta** or **Pyrrhophyta** ("fire algae"; Greek *pyrr(h)os*, fire) after the bioluminescent forms, or **Dinophyta**. At various times the cryptomonads, ebriids, and ellobiopsids have been included here, but only the last are now considered close relatives. Dinoflagellates have a known ability to transform from non-cyst to cyst-forming strategies which makes it extremely difficult to recreate their evolutionary history.

Part of the challenge in dinoflagellate taxonomy and nomenclature is that they have been independently classified by the rules of zoology and botany, and only recently have the disciplines converged.

Most (but not all) dinoflagellates have a dinokaryon, described below (see: Life-cycle, below.). Dinoflagellates with a dinokaryon are classified under Dinokaryota, while dinoflagellates without a dinokaryon are classified under Syndiniales.

Although classified as eukaryotes, the dinoflagellate nuclei are not characteristically eukaryotic, as they lack histones, nucleosomes and maintain continually condensed chromosomes during mitosis. In fact, Dodge (1966) termed the dinoflagellate nucleus as ‘mesokaryotic’, due to its possession of intermediate characteristics between the coiled DNA areas of prokaryotic bacteria and the well-defined eukaryotic nucleus. This group, however, does contain typically eukaryotic organelles, such as golgi bodies, mitochondria and chloroplasts

Morphology



The cyst of *Peridinium_ovatum*, showing the excystment opening.

Most dinoflagellates are unicellular forms with two *flagella*. One of these extends towards the posterior, called the *longitudinal* flagellum, while the other forms a lateral circle, called the *transverse* flagellum. In many forms these are set into grooves, called the *sulcus* and *cingulum*. The transverse flagellum, which is coiled, provides most of the force propelling the cell, and often imparts to it a distinctive whirling motion, which is what gives them their name. The longitudinal flagellum acts mainly as a rudder, but provides a small amount of propulsive force as well.

Dinoflagellates have a complex cell covering called an *amphiesma*, composed of flattened vesicles, called *alveoli*. In some forms, these support overlapping cellulose plates that make up a sort of armor called the *theca*. These come in various shapes and arrangements, depending on the species and sometimes on the stage of the dinoflagellate. Fibrous extrusomes are also found in many forms. Together with various other structural and genetic details, this organization indicates a close relationship between the dinoflagellates, Apicomplexa, and ciliates, collectively referred to as the alveolates.

The chloroplasts in most photosynthetic dinoflagellates are bound by three membranes, suggesting they were probably derived from some ingested algae, and contain chlorophylls *a* and *c* and either peridinin or fucoxanthin, as well as various other accessory pigments. However, a few such as zooxanthellae, which are endosymbionts of corals and other marine animals, have chloroplasts with different pigmentation, sexuality, and structure, some of which retain a nucleus. This suggests their chloroplasts were incorporated by several endosymbiotic events involving already colored or secondarily colorless forms. The discovery of plastids in Apicomplexa have led some to suggest they were inherited from an ancestor common to the two groups, but none of the more basal lines have them. All the same, the dinoflagellate cell consists of the more common organelles such as rough and smooth endoplasmic reticulum, Golgi apparatus, mitochondria, lipid and starch grains, and food vacuoles. Some have even been found with light sensitive organelle, the eyespot or stigma, or a larger nucleus containing a prominent nucleolus. The dinoflagellate *Erythropsidium* has the smallest known eye.

Life cycle

Most dinoflagellates have a peculiar form of nucleus, called a *dinokaryon*, in which the chromosomes are attached to the nuclear membrane. These lack histones and remain condensed throughout interphase rather than just during mitosis, which is closed and involves a unique external spindle. This sort of nucleus was once considered to be an intermediate between the nucleoid region of prokaryotes and the true nuclei of eukaryotes, and so were termed *mesokaryotic*, but now are considered advanced rather than primitive traits.

In most dinoflagellates, the nucleus is dikaryotic throughout the entire life cycle. They are usually haploid, and reproduce primarily through fission, but sexual reproduction also occurs. This takes place by fusion of two individuals to form a zygote, which may remain mobile in typical dinoflagellate fashion or may form a resting dinocyst, which later undergoes meiosis to produce new haploid cells.

When conditions become unfavourable, usually when nutrients become depleted or there is insufficient light, some dinoflagellate species alter their life cycle dramatically. Two vegetative cells will fuse together forming a planozygote. Next is a stage not much different from hibernation called hypnozygote, when the organism takes in excess fat and oil. At the same time its body enlarges and the shell gets harder. Sometimes even spikes are formed. When the weather allows it, these dinoflagellates break out of their shell and are in a temporary stage, planomeiocyte, when they quickly reform their individual thecae and return to the dinoflagellates at the beginning of the process.

Dinoflagellates sometimes bloom in concentrations of more than a million cells per millilitre. Some species produce neurotoxins, which in such quantities kill fish and accumulate in filter feeders such as shellfish, which in turn may pass them on to people who eat them. This phenomenon is called a red tide, from the color the bloom imparts to the water. Some colorless dinoflagellates may also form toxic blooms, such as *Pfiesteria*. Some dinoflagellate blooms are not dangerous. Bluish flickers visible in ocean water at night often come from blooms of bioluminescent dinoflagellates, which emit short flashes of light when disturbed.

The same red tide mentioned above is more specifically produced when dinoflagellates are able to reproduce rapidly and copiously on account of the abundant nutrients in the water. Although the resulting red waves are an unusual sight, they contain toxins that not only affect all marine life in the ocean but the people who consume them as well. A specific carrier is shellfish. This can introduce both non-fatal and fatal illnesses. One such poison is saxitoxin, a powerful paralytic. Human inputs of phosphate further encourage these red tides, and consequently there is a strong interest in learning more about dinoflagellates, from both medical and economic perspectives.

Evolutionary history

Dinoflagellate cysts are found as microfossils from the Triassic period, and form a major part of the organic-walled marine microflora from the middle Jurassic, through the Cretaceous and Cenozoic to the present day. Because some species are adapted to different surface water conditions, these fossils from sediments can be used to reconstruct past surface ocean conditions. *Arpylorus*, from the Silurian of North Africa was at one time considered to be a dinoflagellate cyst, but this palynomorph is now considered to be part of the microfauna (Arthropoda). It is possible that some of the Paleozoic acritarchs also represent dinoflagellates.

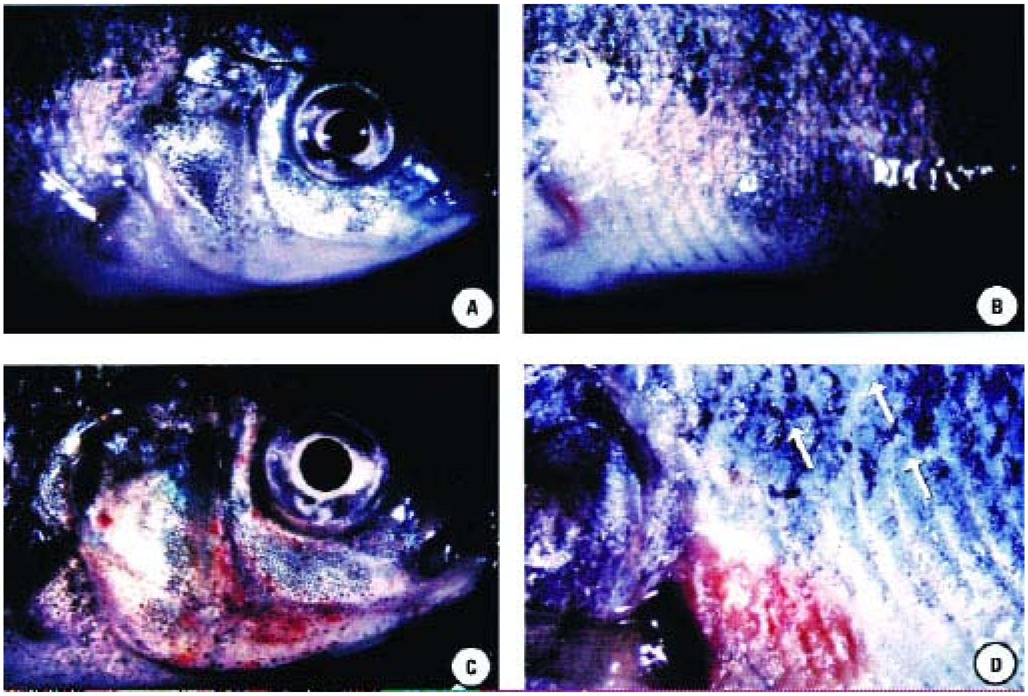
Examples

- *Noctiluca* (Sea Ghost or "Fire of sea" : Origin of Bioluminescence.
- *Ceratium*
- *Gonyaulax*
- *Gymnodinium*
- *Symbiodinium* (Zooxanthella, a coral endosymbiont)

Chapter 6

Carnivorous Protist and Centrohelid

Carnivorous protist



Acute pfiesteriosis in tilapia: top = unaffected fish; bottom = fish preyed upon by the carnivorous alga *Pfiesteria shumwayae*

Predatory dinoflagellates are predatory heterotrophic or mixotrophic alveolate protists that derive some or most of their nutrients from digesting other organisms. About one half of dinoflagellates lack photosynthetic pigments and specialize in consuming other eukaryotic cells, and even photosynthetic forms are often predatory.

Organisms that derive their nutrition in this manner include *Oxyrrhis marina*, which feeds phagocytically on phytoplankton, *Polykrikos kofoidii*, which feeds on several species of red-tide and/or toxic dinoflagellates, *Ceratium furca*, which is primarily photosynthetic but also capable of ingesting other protists such as ciliates, *Cochlodinium polykrikoides*, which feeds on phytoplankton, *Gambierdiscus toxicus*, which feeds on algae and produces a toxin that causes ciguatera fish poisoning when ingested, and *Pfiesteria* and related species such as *Luciella masanensis*, which feed on diverse prey including fish skin and human blood cells. Predatory dinoflagellates can kill their prey by releasing toxins or phagocytize small prey directly.

Some predatory algae have evolved extreme survival strategies. For example, *Oxyrrhis marina* can turn cannibalistic on its own species when no suitable non-self prey is available, and *Pfiesteria* and related species have been discovered to kill and feed on fish, and since have been (mistakenly) referred to as carnivorous "algae" by the media.

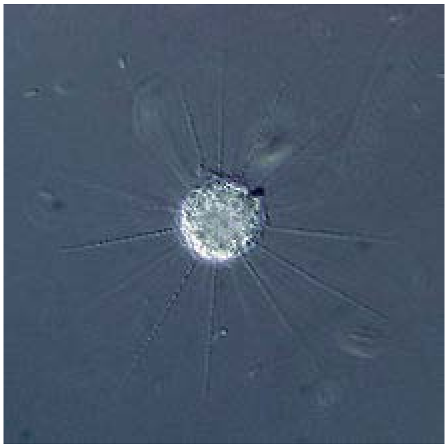
Usage in the popular media

The media has applied the term carnivorous or predatory algae mainly to *Pfiesteria piscicida*, *Pfiesteria shumwayae* and other *Pfiesteria*-like dinoflagellates implicated in harmful algal blooms and fish kills. *Pfiesteria* as an "ambush predator" utilizes a "hit and run" feeding strategy by releasing a toxin that paralyzes the respiratory systems of susceptible fish, such as menhaden, thus causing death by suffocation. It then consumes the tissue sloughed off its dead prey. *Pfiesteria piscicida* (Latin: *fish killer*) has been blamed for killing more than one billion fish in the Neuse and Pamlico river estuaries in North Carolina and causing skin lesions in humans in the 1990s. It has been described as "skinning fish alive to feed on their flesh" or chemically sensing fish and producing lethal toxins to kill their prey and feed off the decaying remains. Its deadly nature has led to *Pfiesteria* being referred to as "killer algae" and has earned the organism the reputation as the "*T. rex* of the dinoflagellate world" or "the Cell from Hell."

"*Pfiesteria* hysteria"

The prominent and exaggerating media coverage of *Pfiesteria* as carnivorous algae attacking fish and humans has been implicated in causing "*Pfiesteria* hysteria" in the Chesapeake Bay in 1997 resulting in an apparent outbreak of human illness in the Pocomoke region in Maryland. However, a study published the following year concluded the symptoms were unlikely to be caused by mass hysteria.

Centrohelid

Centrohelids	
	
Raphidiophrys contractilis	
Scientific classification	
Domain:	Eukaryota
Order:	**Centrohelida** Kühn 1926
Families	
Raphidiophryidae Acanthocystidae Heterophryidae	

The **centrohelids** or **centroheliozoa** are a large group of heliozoan protists. They include both mobile and sessile forms, found in freshwater and marine environments, especially at some depth.

Characteristics

Individuals are unicellular and spherical, usually around 30-80 µm in diameter, and covered with long radial axopods, narrow cellular projections that capture food and allow mobile forms to move about.

A few genera have no cell covering, but most have a gelatinous coat holding scales and spines, produced in special deposition vesicles. These may be organic or siliceous and come in various shapes and sizes. For instance, in *Raphidiophrys* the coat extends along the bases of the axopods, covering them with curved spicules that give them a pine-treeish look, and in *Raphidiocystis* there are both short cup-shaped spicules and long tubular spicules that are only a little shorter than the axopods. Some other common genera include *Heterophrys*, *Actinocystis*, and *Oxnerella*.

The axopods of centrohelids are supported by microtubules in a triangular-hexagonal array, which arise from a tripartite granule called the *centroplast* at the center of the cell. Axopods with a similar array occur in gymnosphaerids, which have traditionally been considered centrohelids (though sometimes in a separate order from the others). This was questioned when it was found they have mitochondria with tubular cristae, as do other heliozoa, while in centrohelids the cristae are flat. Although this is no longer considered a very reliable character, on balance gymnosphaerids seem to be a separate group.

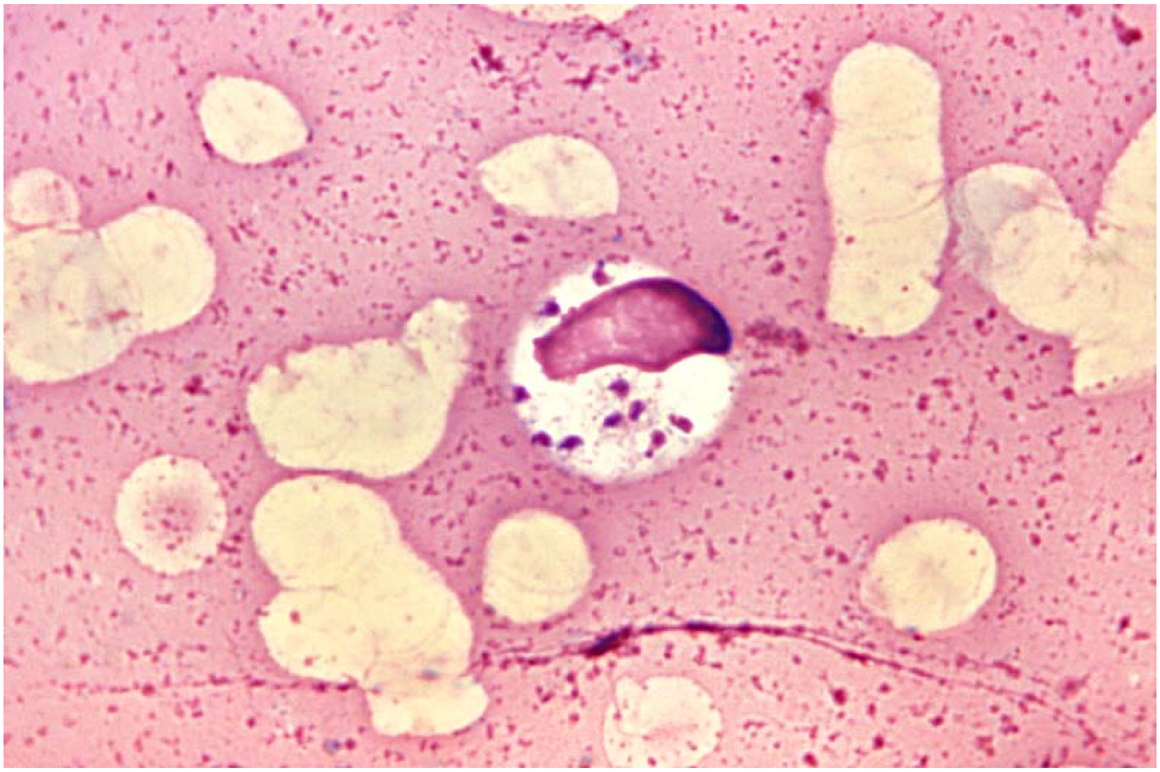
Classification

The evolutionary position of the centrohelids is not clear. Structural comparisons with other groups are difficult, in part because no flagella occur among centrohelids, and genetic studies have been more or less inconclusive. Cavalier-Smith has suggested they may be related to the Rhizaria, but for the most part they are left with uncertain relations to other groups. A 2009 paper suggests that they may be related to the cryptophytes and haptophytes. They are currently classified as Hacrobia, under the Plants+HC clade.

Chapter 7

Protozoa and Sarcocystis

Protozoa



Leishmania donovani, (a species of protozoa) in a bone marrow cell

Protozoa (from the Greek words *proto*, meaning "first", and *zoa*, meaning "animals") are a diverse group of single cell eukaryotic organisms, many of which are motile. Historically protozoa were defined as single cell protists with animal-like behaviour, e.g.

movement. Protozoa were regarded as the partner group of protists to protophyta which have plant-like behaviour, e.g. photosynthesis. The term protozoa is generally not used in modern scientific contexts.

Terminology

The word *protozoan* was originally an adjective but can also be used as a noun.

Protozoans are referred to generally as animal-like protists because of movement (motile). However, both protozoa and protists are paraphyletic groups (not including all genetic relatives of the group). For example, *Entamoeba* is more closely related to humans than to *Euglena*. "Protozoa" is considered an outdated classification in more formal contexts. However, the term is still used in children's education.

While there is no exact definition for the term *protozoan*, it often refers to a unicellular heterotrophic protist, such as the amoeba and ciliates. The term *algae* is used for microorganisms that photosynthesize. However, the distinction between protozoa and algae is often vague. For example, the algae *Dinobryon* has chloroplasts for photosynthesis, but it can also feed on organic matter and is motile.

- Protozoa are their own "kingdom" by the Integrated Taxonomic Information System 2009 classification.
- It is sometimes considered a subkingdom.
- It was traditionally considered a phylum under Animalia.

Characteristics

The most important protozoans range usually from 10 to 52 micrometers, but can grow as large as 1 mm, and are seen easily by microscope.

They were considered formerly to be part of the protista family. Protozoa exist throughout aqueous environments and soil, occupying a range of trophic levels.

Motility and digestion

Tulodens are one of the slow-moving form of protozoans. They move around with whip-like tails called flagella, hair-like structures called cilia, or foot-like structures called pseudopodia. Others do not move at all.

Protozoa may absorb food via their cell membranes, some, e.g. amoebas, surround food and engulf it, and yet others have openings or "mouth pores" into which they sweep food. All protozoa digest their food in stomach-like compartments called vacuoles.

Ecological role

As components of the micro- and meiofauna, protozoa are an important food source for microinvertebrates. Thus, the ecological role of protozoa in the transfer of bacterial and algal production to successive trophic levels is important. As predators, they prey upon unicellular or filamentous algae, bacteria, and microfungi. Protozoa are both herbivores and consumers in the decomposer link of the food chain. They also control bacteria populations and biomass to some extent. Protozoa such as the malaria parasites (*Plasmodium* spp.), trypanosomes and leishmania are also important as parasites and symbionts of multicellular animals.

Life cycle

Some protozoa have life stages alternating between proliferative stages (e.g. trophozoites) and dormant cysts. As cysts, protozoa can survive harsh conditions, such as exposure to extreme temperatures or harmful chemicals, or long periods without access to nutrients, water, or oxygen for a period of time. Being a cyst enables parasitic species to survive outside of a host, and allows their transmission from one host to another. When protozoa are in the form of trophozoites (Greek, *tropho* = to nourish), they actively feed. The conversion of a trophozoite to cyst form is known as encystation, while the process of transforming back into a trophozoite is known as excystation.

Protozoa can reproduce by binary fission or multiple fission. Some protozoa reproduce sexually, some asexually, while some use a combination, (e.g. Coccidia). An individual protozoon is hermaphroditic.

Classification

Protozoa were previously often grouped in the kingdom of Protista, together with the plant-like algae and fungus-like slime molds. As a result of 21st-century systematics, protozoa, along with ciliates, mastigophorans, and apicomplexans, are arranged as animal-like protists. With the possible exception of Myxozoa, protozoa are not categorized as Metazoa. Protozoans are unicellular organisms and are often called the animal-like protists because they subsist entirely on other organisms for food. Most protozoans can move about on their own. Amoebas, Paramecia, and Trypanosomes are all examples of animal-like Protists.

Sub-groups

Protozoa have been divided traditionally on the basis of their means of locomotion, although this character is no longer believed to represent genuine relationships:

- Flagellates (e.g. *Giardia lamblia*)
- Amoeboids (e.g. *Entamoeba histolytica*)
- Sporozoans (e.g. *Plasmodium knowlesi*)
    - Apicomplexa

    - Myxozoa
    - Microsporidia
- Ciliates (e.g. *Balantidium coli*)

Human disease

Some protozoa are human parasites, causing diseases.

Examples of human diseases caused by protozoa:

- Malaria
- Amoebiasis
- Giardiasis
- Toxoplasmosis
- Cryptosporidiosis
- Trichomoniasis
- Leishmaniasis
- Sleeping Sickness
- Dysentery

Sarcocystis

Sarcocystis

Sarcocystis cyst in a sheep oesophagus. The cyst is approximately 4mm across.

Scientific classification

Kingdom:	Protista
Phylum:	Apicomplexa

Class:	Conoidasida
Order:	Eucoccidiorida
Family:	Sarcocystidae
Genus:	***Sarcocystis***

Species

Sarcocystis accipitris
Sarcocystis alces
Sarcocystis alceslatrans
Sarcocystis ameivamastigodryasi
Sarcocystis americana
Sarcocystis arieticanis
Sarcocystis asinus
Sarcocystis atheridis
Sarcocystis aucheniae
Sarcocystis bertrami
Sarcocystis bigemina
Sarcocystis booliati
Sarcocystis bovicanis
Sarcocystis bovifelis
Sarcocystis bovihominis
Sarcocystis buffalonis
Sarcocystis cameli
Sarcocystis camelopardalis
Sarcocystis campestris
Sarcocystis chamaleonis
Sarcocystis cernae
Sarcocystis cervi
Sarcocystis cervicanis
Sarcocystis canis
Sarcocystis capracanis
Sarcocystis cornixi
Sarcocystis crotali
Sarcocystis cruzi
Sarcocystis cuniculi
Sarcocystis cymruensis
Sarcocystis danzani
Sarcocystis dasypi
Sarcocystis debonei
Sarcocystis diminuta
Sarcocystis dirumpens
Sarcocystis dispersa
Sarcocystis dubeyella
Sarcocystis dubeyi
Sarcocystis equicanis
Sarcocystis falcatula

Sarcocystis fayeri
Sarcocystis felis
Sarcocystis fusiformis
Sarcocystis gallotiae
Sarcocystis garnhami
Sarcocystis gracilis
Sarcocystis grueneri
Sarcocystis hoarensis
Sarcocystis fusiformis
Sarcocystis gallotiae
Sarcocystis gerbilliechis
Sarcocystis gigantea
Sarcocystis giraffae
Sarcocystis gongyli
Sarcocystis gracilis
Sarcocystis greineri
Sarcocystis grueneri
Sarcocystis hardangeri
Sarcocystis hemioni
Sarcocystis hemionilatrantis
Sarcocystis hericanis
Sarcocystis hircicanis
Sarcocystis hirsuta
Sarcocystis hofmanni
Sarcocystis hominis
Sarcocystis horvathi
Sarcocystis idahoensis
Sarcocystis inghami
Sarcocystis jorrini
Sarcocystis kinosterni
Sarcocystis kirkpatricki
Sarcocystis kirmsei
Sarcocystis klaseriensis
Sarcocystis kortei
Sarcocystis lacertae
Sarcocystis lamacanis
Sarcocystis leporum
Sarcocystis levinei
Sarcocystis lindemanni
Sarcocystis lindsayi
Sarcocystis medusiformis
Sarcocystis melis
Sarcocystis mephitisi
Sarcocystis miescheriana
Sarcocystis mihoensis
Sarcocystis mitrani

Sarcocystis mongolica
Sarcocystis montanaensis
Sarcocystis mucosa
Sarcocystis moulei
Sarcocystis murinotechis
Sarcocystis muris
Sarcocystis muriviperae
Sarcocystis neotomafelis
Sarcocystis nesbitti
Sarcocystis neurona
Sarcocystis odoi
Sarcocystis odocoileocanis
Sarcocystis ovicanis
Sarcocystis ovifelis
Sarcocystis oviformis
Sarcocystis ovalis
Sarcocystis phacochoeri
Sarcocystis phoeniconaii
Sarcocystis podarcicolubris
Sarcocystis poephagi
Sarcocystis poephagicanis
Sarcocystis porcifelis
Sarcocystis porcihominis
Sarcocystis rangi
Sarcocystis rangiferi
Sarcocystis rauschorum
Sarcocystis rileyi
Sarcocystis rodentifelis
Sarcocystis roudabushi
Sarcocystis scandinavica
Sarcocystis sebeki
Sarcocystis sibirica
Sarcocystis sigmodontis
Sarcocystis singaporensis
Sarcocystis speeri
Sarcocystis stehlinii
Sarcocystis stenodactylicolubris
Sarcocystis suicanis
Sarcocystis suihominis
Sarcocystis sulawesiensis
Sarcocystis sybillensis
Sarcocystis tarandi
Sarcocystis tarandivulpes
Sarcocystis tenella
Sarcocystis tilopodi
Sarcocystis turcicii

Sarcocystis turdi
Sarcocystis ursusi
Sarcocystis villivilliso
Sarcocystis wapiti
Sarcocystis zamani

Sarcocystis is a genus of protozoa. Species in this genus infect reptiles, birds and mammals. The name is dervived from Greek: *sarx* = flesh and *kystis* = bladder.

There are about 130 recognised species in this genus. Revision of the taxonomy of this genus is ongoing, and it is possible that all the currently recognised species may in fact be a single species or much smaller number of species that can infect multiple hosts.

While the majority of the species in this genus infect mammals, about a dozen are known to infect snakes.

History

The organism was first recognised in a mouse by Miescher in 1843. His findings were not recognised as a protist initially and the literature referred to the structures he described as "Miescher's Tubules". Incidentally Miescher's son — Johann Friedrich Miescher — discovered DNA. Similar structures were found in pig muscle in 1865 but these remained unnamed until 1899 when the name *Sarcocystis meischeriana* was proposed to identify them.

Initially it was unclear whether these organisms were fungi or protozoa. This uncertainty was resolved in 1967 when electron microscopic studies showed that these organism were protozoa related to *Toxoplasma* and *Eimeria*. The life cycle remained unknown until 1970 when bradyzoites from sarcocysts in bird muscles were inoculated into cultured mammalian cells and underwent development into sexual stages and oocysts. Transmission studies with the three morphotypes found in cattle then considered a single species - *Sarcoplasma fusiformis* - in dogs, cats and humans revealed that these were three different species now named *Sarcoplasma bovicanis*, *Sarcoplasma bovifelis* and *Sarcoplasma bovihominis*.

Life cycle

The heteroxenous (more than one obligatory host in its life cycle) life cycle of these apicomplexan parasites remained obscure until 1972 when the prey-predator relationship of its' definitive and intermediate hosts was recognised. The life cycles of about 60 of these species is now known.

In outline gametogony and sporogony occur in the intestine of the definitive host while both schizogony which occurs in various tissues and the formation of sarcocysts (containing bradyzoites and metrocytes) occurs prinicpally in the muscles of the intermediate host. In some cases a single species may act as both the definitive and intermediate host.

Oocysts are passed in the feces of an infected definitive host. The oocyst undergoes sporogony creating two sporocysts. Once this is complete oocyst itself undergoes lysis releasing the sporocysts into the environment. Sporocysts typically contain 4 sporozoites and measure 15-19 by 8-10 micrometres.

An intermediate host such as a cow or pig then ingests a sporocyst. Sporozoites are then released in the body and migrate to vessels where they undergo the first two generation of asexual reproduction. These rounds result in the development of meronts. This stage lasts about 15 to 16 days after ingestion of sporocysts. Merozoites emerge from the second generation meronts and enter the mononucleate cells where they develop by endodyogeny. Subsequent generations of merozoites develop downstream in the direction of blood flow to arterioles, capillaries, venules, and veins throughout the body subsequently developing into the final asexual generation in muscles.

Merozoites entering muscle cells round up to form metrocytes and initiate sarcocyst formation. Sarcocysts begin as unicellular bodies containing a single metrocyte and through asexual multiplication numerous metrocytes accumulate and the sarcocyst increases in size. As the sarcocyst matures, the small, rounded, noninfectious metrocytes give rise to crescent-shaped bodies called bradyzoites that are infections for the definitive host. Time required for maturation varies with the species and may take 2 months or more.

In species in which symptoms develop these typically occur 20–40 days after ingestion of sporocysts and during the subsequent migration of sporozoites through the body vessels. Acute lesions (oedema, hemorrhages and necrosis) develop in the affected tissues. The parasite has a predilection for skeletal muscle (myositis), cardiac muscle (petechial hemorrhages of cardiac muscle and serosae), and lymph nodes (oedema, necrosis and hemorrhage). These lesions are associated with maturation of second generation of meronts within the endothelial and subendothelials cells. Occasionally mononuclear infiltration or hyperemia has been observed in the lamina propria of the small intestine. After the acute phase cysts may be found in various muscular tissues, generally without pathology.

Once the intermediate host is eaten by the definitive host such as a dog or human, the parasite undergoes sexual reproduction within the gut to create macrogamonts and microgamonts. Most definitive hosts do not show any clinical sign or symptoms. Fusion of a macrogamont and a microgamont creates a zygote which develops into an oocyst. The oocyst is passed through the faeces completing the life cycle.

A second life cycle has more recently been described whereby carnivores and omnivores pass the infectious stages in their faeces. Ingestion of this material may lead to successful infection of the ingesting animal.

Birds

Although sarcocysts were first reported in the muscles of birds by Kuhn in 1865 not until 1977 was the first life cycle involving a bird (*Gallus gallus*) and a carnivore (*Canis familiaris*) described by Munday et al. In 1986 the first life cycle involving birds as both the definitive (*Northern Goshawk*) and intermediate (*Serinus canaria*) hosts was described by Cern and Kvasnovsk.

Taxonomy

The taxonomy of this genus and its relationship to other protozoal genera is currently under investigation.

Related genera include: *Besnoitia*, *Caryospora*, *Cystoisospora*, *Frenkelia*, *Isospora*, *Hammondia*, *Hyaloklossia*, *Lankesterella*, *Neospora* and *Toxoplasma*.

Sarcocystis is the largest genus within the family *Sarcocystidae* and consists of species which infecting a range of animals including mammals, birds and reptiles. *Frenkelia*, another genus within this family, consists of parasites that use rodents as intermediate hosts and birds of prey as definitive hosts.

It appears that *Besnoitia*, *Hammondia*, *Neospora* and *Toxoplasma* form a single clade. Within this clade *Toxoplasma* and *Neospora* appear to be sister clades. *Isospora* also appear to belong to this clade and this clade is a sister to *Sarcocystis*. *Frenkelia* appears to be very closely related to *Sarcocystis*.

Several molecular studies have suggested that *Frenkelia* is actually a species of *Sarcocystis*. This genus was distinguished from *Sarcocystis* on the basis of its tendency to encyst within the brain rather than within muscle. This distinction may not be taxonomically valid.

Within the genus a number of clades have been identified. These include one that contains *S. dispersa*, *S. lacertae*, *S. mucosa*, *S. muris*, *S. neurona* and *S. rodentifelis*. *Frenkelia* also groups with this clade.

Evolution

These protozoa are mostly found in mammals. They do not appear to infect mammals of the superorder Afrotheria and infect only two species of the Xenarthra. Because of this pattern the genus may have evolved in the Northern hemisphere from a preexisting protozoan species that infected mammals.

Alternatively because a number of Australian marsupials are also infected by this genus, marsupials may have been the original hosts of this genus and the parasites were spread to the Northern hemisphere by birds.

A third possibility is that the genus originally infected birds and was spread world wide by these hosts.

A final possibility because of the existence of life cycles where both the intermediate and final hosts are reptiles, the genus may have originated in reptiles and spread from there to other genera.

The resolution of this question awaits the outcome of further molecular studies.

Clinical notes: Human

Infection with this parasite is known as sarcosporidiosis. Because of initial confusion over the taxonomy of this parasite it was originally referred to as *Isospora hominis*. The older literature may refer to this organism.

Epidemiology

Human infection is considered rare with less than one hundred published cases of invasive disease (approximately 46 cases reported by 1990). These figure represent a gross understimate of the human burden of disease.

The extremes of age reported to date are a 26-day-old infant and a 75-year-old man. Infectons have been reported from Africa, Europe (Germany, Spain and Poland), the United States (California), Central and South America, China, India, Tibet, Malaysia and Southeast Asia.

Stool examinations in Thai laborers showed that sarcocystis infection had a prevalence of ~23%. Virtually all cases appeared to be asymptomatic which probably explains the lack of recognition. A study of 100 human tongues obtained at post mortum in Malaya revealed an infection rate of 21%. There was no sex difference and the age range was 16 to 57 years (mean 37.7 years).

Historical details

The first report of human infection was by Lindemannl in 1868. Although several additional reports were subsequently published, these early descriptions were not considered definitive. The first generally agreed definitive description of this disease was published in 1894 by Baraban and Saint-Remy. This species was named by Rivolta after Lindemannl in 1898.

The invasive forms were considered to belong to a single species - *S. lindemanni* - and the intestinal form due to *S. hominis* (from undercooked beef) or *S. suihominis* (from undercooked pork). The description of *S. lindemanni* has since been considered to be unsatisfactory and has been declared a *nomem nudum* (a name without a recognised species). Two species currently considered to be capable of causing human infection: *S. bovihominis* (*S. hominis*) and *S. suihominis*.

Route of infection

Infection occurs when undercooked meat is ingested. The incubation period is 9–39 days. Human outbreaks have occurred in Europe. Rats are a known carrier.

It has been suggested that contaminated water may be able to cause infection but this presently remains a theoretical possibility.

Pathology

The pathology is of two types: a rare invasive form with vasculitis and myositis and an intestinal form that presents with nausea, abdominal pain, and diarrhea. While normally mild and lasting under 48 hours, the intestinal form may occasionally be severe or even life threatening. The invasive form may involve a wide variety of tissues including lymph nodes, muscles and the larynx.

Clinical features

In volunteer studies with infected beef symptoms appeared 3–6 hours after eating. These included anorexia, nausea, abdominal pain, distension, diarrhea, vomiting, dyspnoea and tachycardia. All symptoms were transient and lasted about 36 hours. In a second series symptoms - abdominal pain, distension, watery diarrhea and eosinophilia - appeared at 1 week and resolved after 3 weeks.

Clinical cases have been associated with acute fever, myalgias, bronchospasm, pruritic rashes, lymphadenopathy, subcutaneous nodules associated with eosinophilia, elevated erythrocyte sedimentation rate and elevated creatinine kinase levels. Symptoms may last as long as five years. Segmental necrotizing enteritis has been reported on one occasion.

Diagnosis

Definitive diagnosis by biopsy of an infected muscle. Sarcocysts are identifiable with hematoxylin and eosin. The PAS stain may be helpful but variable uptake of stain is common. Along with the sarcocysts inflammatory cells may be found. Other findings include myositis, myonecrosis, perivascular and interstitial inflammation, vasculitis and eosinophilic myositis.

Treatment

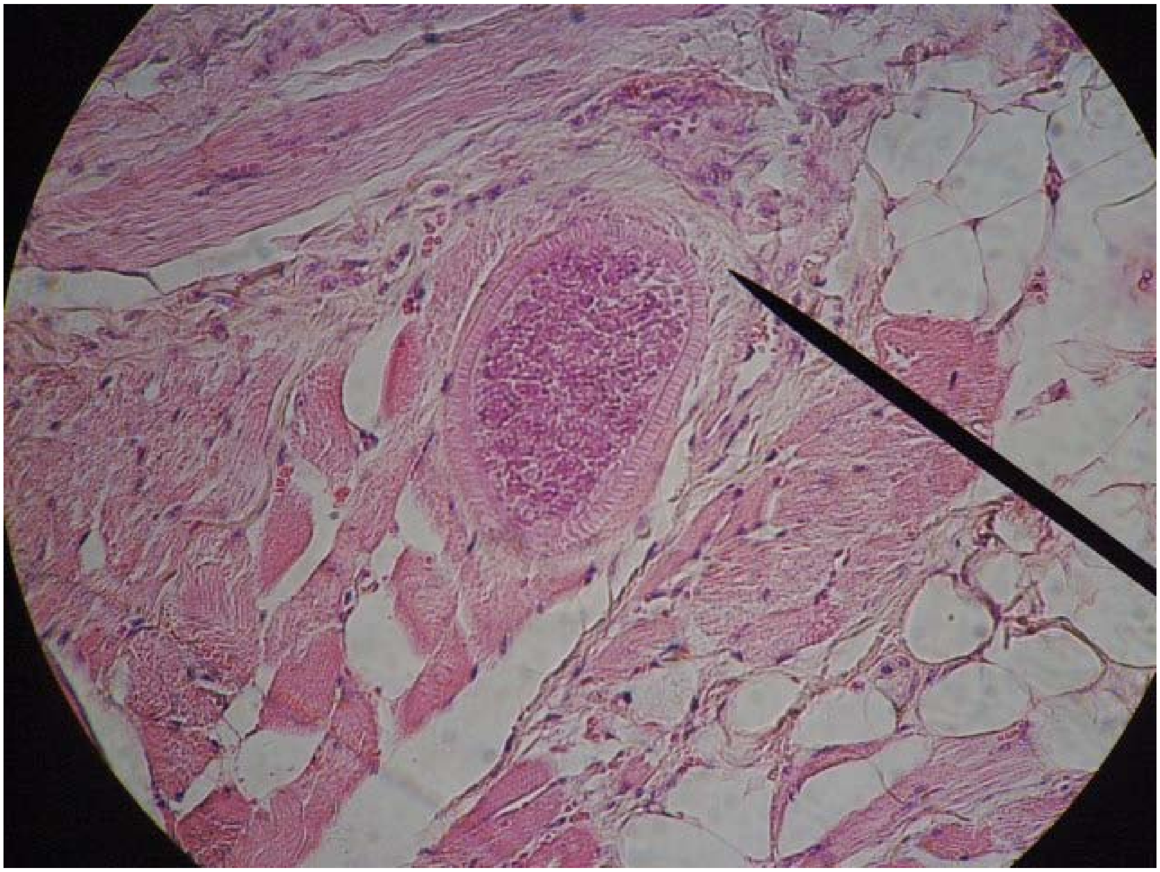
Because infection is rarely symptomatic, treatment is rarely required. There have been no published trials so treatment remains empirical. Agents that have been used include albendazole, metronidazole and cotrimoxazole for myositis. Corticosteroids have also been used for symptomatic relief.

Amprolium and salinomycin was effective in preventing severe illness and death in experimentally infected calves and lambs. These agents have not been tried in humans to date.

Prevention

Infection can be prevented by cooking the meat before eating. Alternatively freezing the meat at -5C for several days before ingestion will kill the sporocysts.

Clinical notes: Other



Sarcocysts within pig skeletal muscle. Note the readily visible striated border.

Four recognised species infect cattle: *S. bovifelis*, *S. bovihominis* (*S. hominis*) *S. cruzi* (*S. bovicanis*) and *S. hirsuta*. *S. cruzi* is the only species known to be pathogenic in cattle. A number of clinical syndromes have been reported in connection with this parasite: eosinophilic myositis; abortions, stillbirths and deaths in pregnant cows; two cases of necrotic encephalitis in heifers have also been reported. Typical clinical signs of acute bovine sarcocystosis are: anorexia, pyrexia (42C or more), anemia, cachexia, enlarged palpable lymph nodes, excessive salivation and loss of hair at the tip of the tail.

Sheep may be infected by four recognised species of *Sarcocystis*: *S. arieticanis* and *S. tenella* (*S. ovicanis*) are pathogenic; *S. gigantea* (*S. ovifelis*) and *S. medusiformis* are non-pathogenic. Infection with these parasites is common in the US with over 80% of sheep examined showing evidence of infection. *S. arieticanis* and *S. tenella* both produce extra intestinal disease. Anemia, anorexia, ataxia, and abortions are the chief clinical signs. Myositis with flaccid paralysis has been reported as a consequence of infection. Ovine protozoan myeloencephalitis is a recognised syndrome that may occur in outbreaks. The usual pathological findings in such cases are multifocal spinal cord white matter oedema and necrosis, glial nodules and mild to moderate nonsuppurative encephalomyelitis. The diagnosis may be established finding protozoan bodies (12.7-23.0 micrometres) that stain immunocytochemically for *Sarcocystis* epitopes.

Four recognised species infect pigs: *S. medusiformis*, *S. meischeriana* (*S. suicanis*), *S. porcifelis* and *S. suihominis*. *S. porcifelis* is pathogenic for pigs causing diarrhea, myositis and lameness.

Five species infect horses: *S. asinus*, *S. bertrami*, *S. equicanis*, *S. fayeri* and *S. neurona* (*S. falcatula*). All utilize canids as definitive hosts: transplacental infection has also been reported. *S. neurona* causes equine protozoal myeloencephalitis. Exposure to this parasite appears to be common in the United States with serological surveys indicating that 50-60% percent of all horses in the Midwest United States have been exposed to it. Clinical signs include gait abnormalities including ataxia, knuckling and crossing over. Muscle atrophy, usually unilateral, may occur. The lesions are typically focal. Brain-stem involvement is common. Depression, weakness, head tilt and dysphagia also occur.

S. fayeri may cause myositis in horses.

Fatal infection of an alpaca (*Lama pacos*) with an unnamed species has been reported. Findings included disseminated eosinophilic myositis, abortion and haemoabdomen. The myositis was associated with hameorrhage, necrosis and degeration. Infection by *S. tilopodi* of muscle tissue in the Guanaco has been reported.

S. hemionilatrantis infects mule deer. Death from experimental inoculation have been reported.

These parasites can also infect birds producing three different clinical forms: an acute pulmonary disease, muscular disease and neurological disease. Symptoms include lethargy, shortness of breath, tail bobbing, yellow tinted droppings and sudden death.

The presence of the cysts in the muscle of wild birds is known as "rice breast".

Incidence in animals

Infection with *Sarcocystis* is common. Rates in pigs vary: 18% in Iowa,, 27% in the Philippines , 43% in Spain , 57% in Uruguay , and 68% in India The infection rate in sheep is commonly above 90%. Camels have a similarly high incidence of infection.

Rates above 80% are known in cattle and goats. The incidence in water buffaloes, yak and hainag exceeds 80% while the incidence in horses, donkeys and chickens is lower.

Diagnosis

There are several other genera of heteroxenous and cyst-forming coccidia including *Besnoitia*, *Cystoisospora*, *Frenkelia*, *Hammondia*, *Neospora* and *Toxoplasma*. Related but monoxenous spore forming genera include *Isospora*. Differentiating these genera from *Sarcocystis* in diagnostic material may be difficult without immunochemical stains.

The diagnosis is usually made *post mortum* by examination of the skeletal muscle. In some species the cysts may be visible to the naked eye (ducks, mice, rabbits and sheep) but in most microscopic examination is required. *Ante mortum* diagnosis may be made with the use of dermal sensitivity testing or complement fixation tests. Muscle biopsy is also diagnostic but this is much less commonly used.

Oocysts with two sporocysts or individual sporocysts in human feces are diagnostic of intestinal infection. These first appear 14 to 18 days after ingesting beef (*S. hominis*), and 11 to 13 days after ingesting pork (*S. suihominis*). Flotation based on high-density solutions incorporating sodium chloride, cesium chloride, zinc sulfate, sucrose, Percoll, Ficoll-Hypaque or other such density gradient media is preferred to formalin-ethyl acetate or other sedimentation methods. Sporocysts of *S. hominis* average 9.3 by 14.7 micrometres and those of *S. suihominis* average 10.5 by 13.5 micrometres. Because of the overlap in size, size alone is not reliable as a diagnostic criterion of the species. Confirmatory staining with the periodic acid-Schiff (PAS) can be performed as the walls stain positively. PCR amplification of the rRNA may also be used.

The walls of the sarcocyst may be helpful in species diagnosis with 24 wall types identified in 62 species. *S. hominis* and *S. suihominis* both have walls of type 10. The wall of *S. hominis* is up to 6 micrometres thick and appears radially striated from villar protrusions up to 7 micrometres long. Its bradyzoites are 7 to 9 micrometres long. The wall of *S. suihominis* is 4 to 9 micrometres thick, with villar protrusions up to 13 micrometres long. Its bradyzoites are 15 micrometres long.

Treatment

Current treatments are not entirely satisfactory. Amprolium (100 mg/kg, sid for 30 days), fed prophylactically, reduced illness in cattle inoculated with *S. cruzi*. Prophylactic administration of amprolium or salinomycin also protected experimentally infected sheep.

In horses treatment has been confined to dihydrofolate reductase inhibitors such as the sulfonamides and pyrimethamine. Sulfadiazine (20 mg/kg orally) once or twice a day is a commonly used. Infected horses should also be placed on pyrimethamine at the dose of 1.0 mg/kg given once a day orally for 120 days or longer. Diclazuril and Toltrazuril and other coccidiostats are being evaluated to treat EPM.

Vaccination

No vaccines are currently known. Experimentally inoculated pigs appear to develop a persistent immunity so a vaccine may be possible.

Host-parasite relations

The parasite's life cycle typically involves a predator and a prey animal. A single species may infect multiple prey or predator animals. In at least 56 species definitive and intermediate hosts are known. Many species are named after their recognised hosts.

A listing of the known host-parasite relations can be found on the page Sarcocystis: Host-parasite relations.

Notes

Hoareosporidium is now considered a synonym of *Sarcocystis*.

The original type species was *Sarcocystis miescheriana*. Its description has since been considered less than satisfactory and *S. muris* has been proposed as the type species.

S. turdi may not be a valid species.

Isospora bigemina has been reclassified as *Sarcocystis bigemina*.

Isospora hominis has been reclassified as *Sarcocystis hominis*.

Synonoms

S. bertrami is a synonym of *S. equicanis*.

S. bovihominis is a synonym of *S. hominis*.

S. cruzi is a synonym of *S. bovicanis*.

S. gigantea is a synonym of *S. ovifelis*.

S. hirsuta is a synonym of *S. bovifelis*.

S. idahoensis and *S. roudabushi* may be the same species.

S. miescheriana is a synonym of *S. suicanis*

S. neurona is a junior synonym of *S. falcatula*. *S. neuroma* is the more commonly used name for this species.

S. poephagi may be the same species as *S. hirsuta*.

S. poephagicanis may be the same species as *S. cruzi*.

S. tenella is a synonym of *S. ovicanis*.

Chapter 8

Red Algae

Red algae

Temporal range: Mesoproterozoic–present

Had'n

Archean

Proterozoic

Pha.

Scientific classification

Domain:	Eukarya
(unranked):	Archaeplastida
Division:	**Rhodophyta** Wettstein, 1922 Classification is currently disputed.

The **red algae** are one of the oldest groups of eukaryotic algae, and also one of the largest, with about 5,000–6,000 species of mostly multicellular, marine algae, including many notable seaweeds. Other references indicate as many as 10,000 species; more detailed counts indicate ~4000 in ~600 genera (3738 marine spp in 546 genera and 10 orders (plus the unclassifiable); 164 freshwater spp in 30 genera in 8 orders).

The red algae form a distinct group characterized by the following attributes: eukaryotic cells without flagella and centrioles, using floridean starch as food reserve, with phycobiliproteins as accessory pigments (giving them their red color), and with chloroplasts lacking external endoplasmic reticulum and containing unstacked thylakoids. Most red algae are also multicellular, macroscopic, marine, and have sexual reproduction.

Many of the coralline algae, which secrete calcium carbonate and play a major role in building coral reefs, belong here. Red algae such as dulse *(Palmaria palmata)* and laver (nori/gim) are a traditional part of European and Asian cuisine and are used to make other products like agar, carrageenans and other food additives.

Habitat

Most rhodophytes are marine, although there are freshwater species; these generally prefer clean, running water, although there are some exceptions.

Fossil record

The oldest fossil identified as a red alga is also the oldest fossil eukaryote that belongs to a specific modern taxon. *Bangiomorpha pubescens*, a multicellular fossil from arctic Canada, strongly resembles the modern red alga *Bangia* despite occurring in rocks dating to 1200 million years ago.

Red algae are important builders of limestone reefs. The earliest such coralline algae, the solenopores, are known from the Cambrian Period. Other algae of different origins filled a similar role in the late Paleozoic, and in more recent reefs.

There are also calcite crusts, which have been interpreted as the remains of coralline red algae dating to the terminal Proterozoic. Thallophytes resembling coralline red algae are known from the late Proterozoic Doushantuo formation.

Taxonomy

In the system of Adl et al. 2005, the red algae are classified in the Archaeplastida, along with the glaucophytes and green algae plus land plants (Viridiplantae or Chloroplastida). The authors use a hierarchical arrangement where the clade names do not signify rank; the class name Rhodophyceae is used for the red algae. No sub-divisions are given; the authors say "Traditional subgroups are artificial constructs, and no longer valid."

The system reflected the consensus in 2005. Many studies published since this date have provided evidence which is in agreement. However, other studies have suggested that Archaeplastida is paraphyletic. As of January 2011, the situation appears unresolved.

Below are other published taxonomies of the red algae, although none necessarily has to be used, as the taxonomy of the algae is still in a state of flux (with classification above the level of order having received little scientific attention for most of the 20th century).

- If one defines the kingdom Plantae to mean the Archaeplastida, the red algae will be part of that kingdom
- If Plantae are defined more narrowly, to be the Viridiplantae, then the red algae might be considered their own kingdom, or part of the kingdom Protista.

A major research initiative to reconstruct the Red Algal Tree of Life (RedToL) using phylogenetic and genomic approaches is funded by the National Science Foundation as part of the Assembling the Tree of Life Program.

Species of red algae

There are around 6,500 to 10,000 known species, nearly all of which are marine, with about 200 that only live in fresh water. However, estimates of the number of real species vary by 100%.

Some examples of species and genera of red algae are:

- *Atractophora hypnoides*
- *Gelidiella calcicola*
- *Lemanea*, a freshwater genus
- *Palmaria palmata*, dulse
- *Schmitzia hiscockiana*
- *Chondrus crispus*, Irish moss
- *Mastocarpus stellatus*
- *Vanvoorstia bennettiana*, became recently extinct

Chemistry

Algal group	$\delta^{13}C$ range
HCO_3-using **red algae**	−22.5‰ – −9.6‰
CO_2-using red algae	−34.5‰ – −29.9‰
Brown algae	−20.8‰ – −10.5‰
Green algae	−20.3‰ – −8.8‰

The $\delta^{13}C$ values of red algae reflect their lifestyles. The largest difference results from their photosynthetic metabolic pathway: algae that use HCO_3 as a carbon source have far more negative $\delta^{13}C$ values than those that only use CO_2. An additional difference of about 1.71‰ separates groups intertidal from those below the lowest tide line, which are never exposed to atmospheric carbon. The latter group use the more ^{13}C negative CO_2 dissolved in sea water, whereas those with access to atmospheric carbon reflect the more positive signature of this reserve.

Morphology

Red algae have a double cell wall. The outer layer are usually composed of "pectic substances", from which agar can be manufactured. The internal wall is mostly cellulose.

Pit connections and pit plugs

Pit connections

Pit connections and pit plugs are unique and distinctive features of red algae that form during the process of cytokinesis following mitosis. In red algae, cytokinesis is incomplete. Typically, a small pore is left in the middle of the newly formed partition. The pit connection is formed where the daughter cells remain in contact.

Shortly after the pit connection is formed cytoplasmic continuity is blocked by the generation of a pit plug, which is deposited in the wall gap that connects the cells.

Connections between cells having a common parent cell are called primary pit connections. Because apical growth is the norm in red algae, most cells have two primary pit connections, one to each adjacent cell.

Connections that exist between cells not sharing a common parent cells are labeled secondary pit connections. These connections are formed when an unequal cell division produced a nucleated daughter cell that then fuses to an adjacent cell. Patterns of secondary pit connections can be seen in the order Ceramiales.

Pit plugs

After a pit connection is formed, tubular membranes appear. A granular protein, called the plug core, then forms around the membranes. The tubular membranes eventually disappear. While some orders of red algae simply have a plug core, others have an associated membrane at each side of the protein mass, called cap membranes. The pit plug continues to exist between the cells until one of the cells dies. When this happens, the living cell produce a layer of wall material that seals off the plug.

Function

It is thought that the pit connections function as structural reinforcement, and as an avenue for cell to cell communication and/or symplastic transport in red algae. While the presence of the cap membrane could inhibit this transport between cells, it has been hypothesized that the tubular plug cores serve as a means of transport.

Reproduction

The reproductive cycle of red algae may be triggered by factors such as day length.

Fertilization

Red algae lack motile sperm. Hence they rely on water currents to transport their gametes to the female organs – although their sperm are capable of "gliding" to a carpogonium's trichogyne.

The trichogyne will continue to grow until it encounters a spermatium; once it has been fertilized, the cell wall at its base progressively thickens, separating it from the rest of the carpogonium at its base.

Upon their collision, the walls of the spermatium and carpogonium dissolve. The male nucleus divides and moves into the carpogonium; one half of the nucleus merges with the carpogonium's nucleus.

The polyamine, *spermine* is produced, which triggers carpospore production.

Spermatangia may have long delicate appendages, which increase their chances of "hooking up".

Life cycle

They display alternation of generations; as well as a gametophyte generation, many have two sporophyte generations, the carposporophyte producing carpospores, which germinate into a tetrasporophyte – this produces spore tetrads, which dissociate and germinate into gametophytes. The gametophyte is typically (but not always) identical to the tetrasporophyte.

Carpospores may also germinate directly into thalloid gametophytes, or the carposporophytes may produce a tetraspore without going through a (free living) tetrasporophyte phase. Tetrasporangia may be arranged in a row (Zonate), in a cross (cruciate), or in a tetrad.

The carposporophyte may be enclosed within the gametophyte, which may cover it with branches to form a cystocarp.

A couple of case studies may be helpful to understand some of the life histories algae may display.

In a simple case, such as *Rhodochorton investiens*:

In the Carposporophyte: a spermatium merges with a trichogyne (a long hair on the female sexual organ), which then divides to form carposporangia – which produce carpospores.

Carpospores germinate into gametophytes, which produce sporophytes. Both of these are very similar; they produce monospores from monosporangia "just below a cross wall in a filament" and their spores are "liberated through apex of sporangial cell."

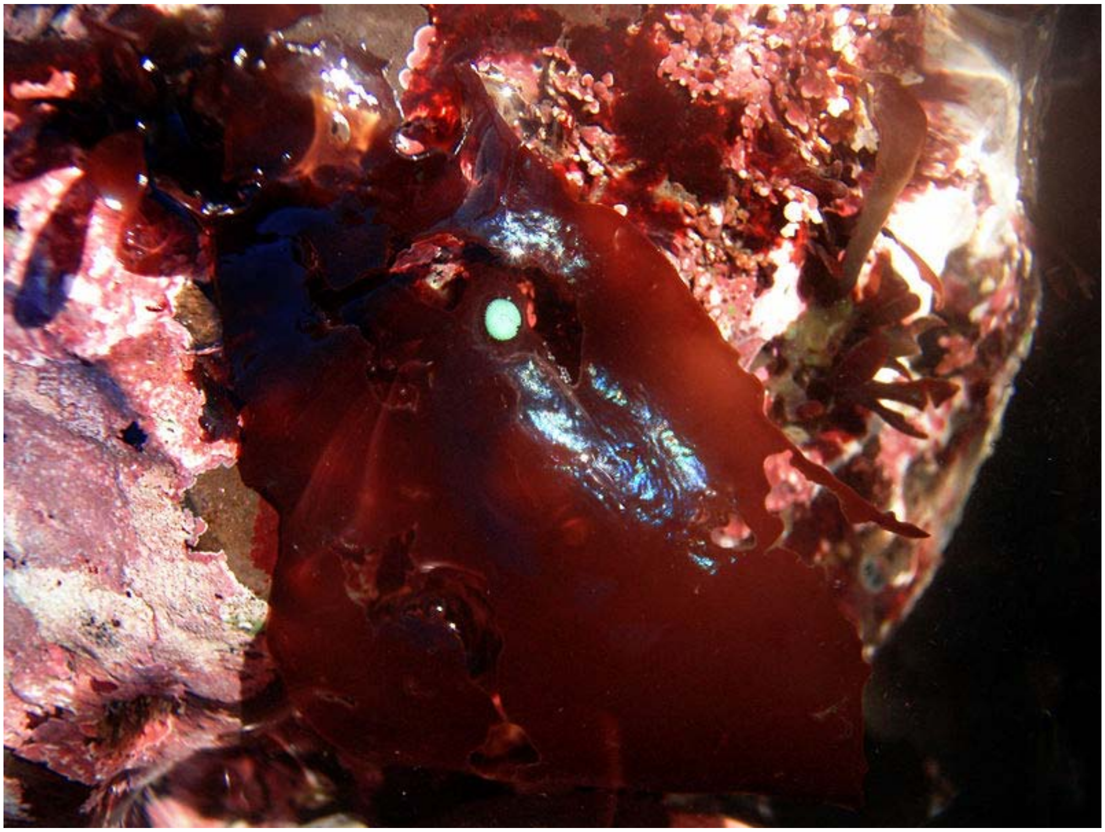
The spores of a sporophyte produce either tetrasporophytes. Monospores produced by this phase germinate immediately, with no resting phase, to form an identical copy of parent. Tetrasporophytes may also produce a carpospore, which germinates to form another tetrasporophyte.

The gametophyte may replicate using monospores, but produces sperm in spermatangia, and "eggs"(?) in carpogonium.

A rather different example is *Porphyra gardneri*:

In its diploid phase, a carpospore can germinate to form a filamentous "conchocelis stage", which can also self-replicate using monospores. The conchocelis stage eventually produces conchosporangia. The resulting conchospore germinates to form a tiny prothallus with rhizoids, which develops to a cm-scale leafy thallus. This too can reproduce via monospores, which are produced inside the thallus itself. They can also reproduce via spermatia, produced internally, which are released to meet a prospective carpogonium in its conceptacle.

Human consumption



Some red algae are iridescent when not covered with water

Several species are used as food. Dulse (*Palmaria palmata*) and *Porphyra* are the best known in the British Isles.

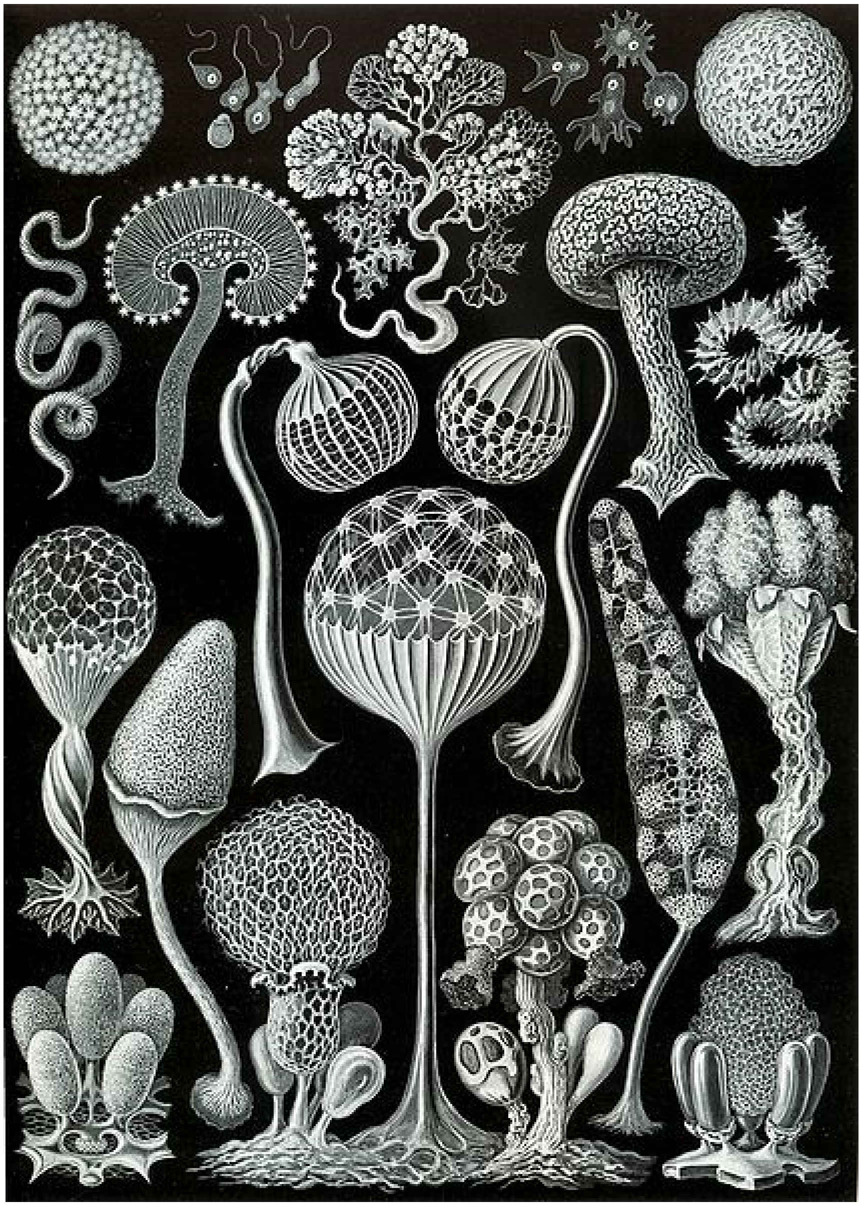
In East and Southeast Asia, agar is most commonly produced from *Gelidium amansii*. In Asia, rhodophytes are important sources of food, such as nori. The high vitamin and protein content of this food makes it attractive, as does the relative simplicity of cultivation, which began in Japan more than 300 years ago.

Chapter 9

Slime Mold

Slime mold *Stemonitis fusca* in Scotland, UK

Fuligo septica, the "dog vomit" slime mold



Mycetozoa from Ernst Haeckel's 1904 *Kunstformen der Natur* (Artforms of Nature)

Slime mold is a broad term describing protists that use spores to reproduce. Slime molds were formerly classified as fungi, but are no longer considered part of this kingdom.

Their common name refers to part of some of these organisms' life cycles where they can appear as gelatinous "slime". This is mostly seen with the myxomycetes, which are the only macroscopic slime molds.

Slime molds have been found all over the world and feed on microorganisms that live in any type of dead plant material. For this reason, these organisms are usually found in soil, lawns, and on the forest floor, commonly on deciduous logs. However, in tropical areas they are also common on inflorescences, fruits and in aerial situations (e.g., in the canopy of trees). In urban areas, they are found on mulch or even in the leaf mold in gutters. One of the most commonly encountered slime molds is the yellow *Physarum polycephalum*, found both in nature in forests in the temperate zones of Earth, as well as in classrooms and laboratories.

Most slime mold are smaller than a few centimeters, but some species may reach sizes of up to several square meters and masses of up to 30 grams. Many have striking colours such as yellow, brown and white.

Taxonomy

Slime molds can generally be divided into two main groups.

- A plasmodial slime mold involves numerous individual cells attached to each other, forming one large membrane. This "supercell" (a syncytium) is essentially a bag of cytoplasm containing thousands of individual nuclei.
- By contrast, cellular slime molds spend most of their lives as individual unicellular protists, but when a chemical signal is secreted, they assemble into a cluster that acts as one organism.

Slime molds, as a group, are polyphyletic. They were originally represented by the subkingdom **Gymnomycota** in the Fungi kingdom and included the defunct phyla Myxomycota, Acrasiomycota and Labyrinthulomycota. Today, slime molds have been divided between several supergroups, none of which are included in the kingdom Fungi.

In more strict terms, slime molds comprise the group of the mycetozoans (myxomycetes, dictyostelids and protostelids). However, even at this level there are conflicts to be resolved. Recent molecular evidence shows that the first two groups are likely to be monophyletic; however the protostelids seem to be polyphyletic, too. For this reason, scientists are currently trying to understand the relationships among these three groups.

Bikont

- **Acrasiomycota**: slime molds which belong to the super group Excavata as the family Acrasidae. They have a similar life style to Dictyostelids, but their amoebae behave differently and are of uncertain taxonomic position.
- **Labyrinthulomycota**: slime nets which belong to the super group Chromalveolata as the class Labyrinthulomycetes. They are marine and form labyrinthine networks of tubes in which amoeba without pseudopods can travel.
- **Plasmodiophorids**: parasitic protists which belong to the super group Rhizaria. They can cause cabbage club root disease and powdery scab tuber disease. The Plasmodiophorids also form coenocytes but are internal parasites of plants (e.g., Club root disease of cabbages).

Amoebozoa

Slime mold (*Physarum polycephalum*)

- **Mycetozoa**, which includes the defunct phylum Myxomycota, belong to the supergroup Amoebozoa and include:
    - Myxogastria or myxomycetes : syncytial or plasmodial slime molds
    - Dictyosteliida: unicellular slime molds or dictyostelids.
    - Protostelids.

The most commonly encountered are the Myxogastria. A common slime mold which forms tiny brown tufts on rotting logs is *Stemonitis*. Another form which lives in rotting logs and is often used in research is *Physarum polycephalum*. In logs it has the appearance of a slimy web-work of yellow threads, up to a few feet in size. *Fuligo* forms yellow crusts in mulch.

The Dictyosteliida, cellular slime molds, are distantly related to the plasmodial slime molds and have a very different lifestyle. Their amoebae do not form huge coenocytes, and remain individual. They live in similar habitats and feed on microorganisms. When food runs out and they are ready to form sporangia, they do something radically different. They release signal molecules into their environment, by which they find each other and create swarms. These amoeba then join up into a tiny multicellular slug-like coordinated creature, which crawls to an open lit place and grows into a fruiting body. Some of the amoebae become spores to begin the next generation, but some of the amoebae sacrifice themselves to become a dead stalk, lifting the spores up into the air.

The Protostelids have characters intermediate between the previous two groups, but they are much smaller, the fruiting bodies only forming one to a few spores.

Opisthokont

Fonticula is a cellular slime mold which forms a fruiting body in a volcano shape. *Fonticula* is not closely related to either the Dictyosteliida or the Acrasidae. A 2009 paper finds it to be related to *Nuclearia*, which in turn is related to fungi.

Life cycle

Slime mold growing out of a bin of wet paper

They begin life as amoeba-like cells. These unicellular amoebae are commonly haploid and multiply if they encounter their favorite food, bacteria. These amoebae can mate if they encounter the correct mating type and form zygotes which then grow into plasmodia. These contain many nuclei without cell membranes between them, which can grow to be meters in size. One variety is often seen as a slimy yellow network in and on rotting logs.

The amoebae and the plasmodia engulf microorganisms. The plasmodium grows into an interconnected network of protoplasmic strands.

Within each protoplasmic strand the cytoplasmic contents rapidly stream. If one strand is carefully watched for about 50 seconds the cytoplasm can be seen to slow, stop, and then reverse direction. The streaming protoplasm within a plasmodial strand can reach speeds of up to 1.35 mm per second which is the fastest rate recorded for any micro-organism. Migration of the plasmodium is accomplished when more protoplasm streams to advancing areas and protoplasm is withdrawn from rear areas. When the food supply wanes, the plasmodium will migrate to the surface of its substrate and transform into rigid fruiting bodies. The fruiting bodies or sporangia are what we commonly see, they superficially look like fungi or molds but are not related to the true fungi. These sporangia will then release spores which hatch into amoebae to begin the life cycle again.

Plasmodia

The mid sporangial phase of *Enteridium lycoperdon*.

In *Myxomycetes*, the plasmoidal portion of the life cycle only occurs after syngamy, which is the fusion of cytoplasm and nuclei of myxoamoebae or swarm cells. Therefore, all of the nuclei are diploid at this stage and mitosis occurs simultaneously throughout the organism. Myxomycete plasmodia are multinucleate masses of protoplasm that move by cytoplasmic streaming. In order for the plasmodium to move, cytoplasm must be diverted towards the leading edge from the lagging end. This process results in the plasmodium advancing in fan-like fronts. As it moves, plasmodium also gains nutrients through the phagocytosis of bacteria and small pieces of organic matter.

The Myxomycete plasmodium also has the ability to subdivide and establish separate plasmodia. Conversely, separate plasmodia that are genetically similar and compatible can fuse together to create a larger plasmodium. In the event that conditions become dry, the plasmodium will form a sclerotium, essentially a dry and dormant state. In the event that conditions become moist again the sclerotium absorbs water and an active plasmodium is restored. When the food supply wanes, the Myxomycete plasmodium will enter the next stage of its life cycle forming haploid spores, often in a well-defined sporangium or other spore-bearing structure.

Chapter 10

Ciliate

Ciliates
Temporal range: Ediacaran - Recent

"Ciliata" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification

Domain:	Eukarya

Kingdom:	Chromalveolata
Superphylum:	Alveolata
Phylum:	**Ciliophora** Doflein, 1901 *emend.*

Classes

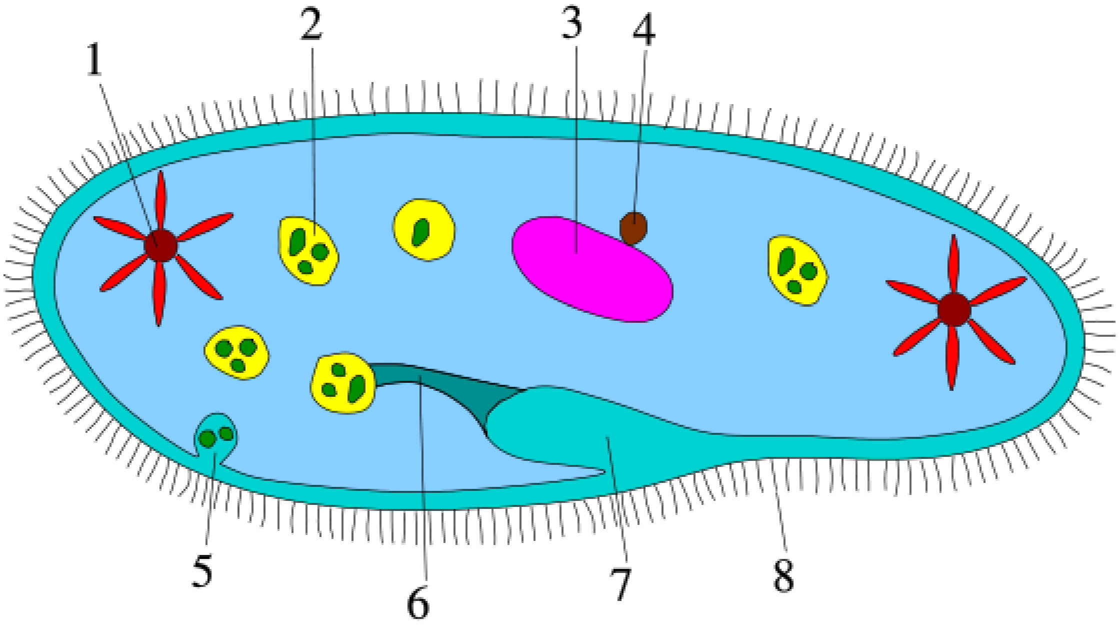
Karyorelictea
Heterotrichea
Spirotrichea
Litostomatea
Phyllopharyngea
Nassophorea
Colpodea
Prostomatea
Oligohymenophorea
Plagiopylea

The **ciliates** are a group of protozoans characterized by the presence of hair-like organelles called cilia, which are identical in structure to flagella but typically shorter and present in much larger numbers with a different undulating pattern than flagella. Cilia occur in all members of the group (although the peculiar suctoria only have them for part of the life-cycle) and are variously used in swimming, crawling, attachment, feeding, and sensation.

The term "Ciliophora" is used in classification as a phylum. Ciliophora can be classified under Protista or Protozoa. The term "Ciliata" is also used, as a class. (However, this latter term can also refer to a type of fish.) Protista classification is rapidly evolving, and it is not rare to encounter these terms used to describe other hierarchical levels.

Ciliates are one of the most important groups of protists, common almost everywhere there is water — in lakes, ponds, oceans, rivers, and soils. Ciliates have many ectosymbiotic and endosymbiotic members, as well as some obligate and opportunistic parasites. Ciliates tend to be large protozoa, a few reach 2 mm in length, and are some of the most complex protozoans in structure.

Cell structure



Cell structure of an ciliophora: 1-contractile vacuole, 2-digestive vacuole, 3-macronucleous, 4-micronucleous, 5-cytoprocto, 6-cytopharynx, 7-cytostome, 8-cilium.

Unlike most other eukaryotes, ciliates have two different sorts of nuclei: a small, diploid micronucleus (reproduction), and a large, polyploid macronucleus (general cell regulation). The latter is generated from the micronucleus by amplification of the genome and heavy editing. Division of the macronucleus occurs by amitosis, the segregation of the chromosomes is by a process whose mechanism is unknown. This process is by no means perfect, and after about 200 generations the cell shows signs of aging. Periodically the macronuclei must be regenerated from the micronuclei. In most, this occurs during *conjugation*. Here two cells line up, the micronuclei undergo meiosis, some of the haploid daughters are exchanged and then fuse to form new micronuclei and macronuclei.

Food vacuoles are formed through phagocytosis and typically follow a particular path through the cell as their contents are digested and broken down via lysosomes so the substances the vacuole contains are then small enough to diffuse through the membrane of the food vacuole into the cell. Anything left in the food vacuole by the time it reaches the cytoproct (anus) is discharged via exocytosis. Most ciliates also have one or more prominent contractile vacuoles, which collect water and expel it from the cell to maintain osmotic pressure, or in some function to maintain ionic balance. These often have a distinctive star-shape, with each point being a collecting tube.

Feeding

Most ciliates feed on smaller organisms (heterotrophic), such as bacteria and algae, and detritus swept into the oral groove (mouth) by modified oral cilia. This usually includes a series of membranelles to the left of the mouth and a paroral membrane to its right, both of which arise from *polykinetids*, groups of many cilia together with associated structures. The food is moved by the cilia through the mouth pore into the gullet, which forms food vacuoles.

This varies considerably, however. Some ciliates are mouthless and feed by absorption, while others are predatory and feed on other protozoa and in particular on other ciliates. This includes the suctoria, which feed through several specialized tentacles.

Reproduction

Ciliates can undergo both asexual and sexual reproduction. Asexual reproduction occurs by binary fission. The micronucleus undergoes by mitosis and the macronucleus elongates and splits in half. Both new cells each obtain a copy of the micronucleus and macronucleus. Sexual reproduction involves conjugation, which involve two cells. After conjugation, the two cells divide, forming four new cells.

Specialized structures in cillates

In some forms there are also body polykinetids, for instance, among the spirotrichs where they generally form bristles called *cirri*. More often body cilia are arranged in *mono-* and *dikinetids*, which respectively include one and two kinetosomes (basal bodies), each of which may support a cilium. These are arranged into rows called *kineties*, which run from the anterior to posterior of the cell. The body and oral kinetids make up the *infraciliature*, an organization unique to the ciliates and important in their classification, and include various fibrils and microtubules involved in coordinating the cilia.

The infraciliature is one of the main component of the cell cortex. Another are the *alveoli*, small vesicles under the cell membrane that are packed against it to form a pellicle maintaining the cell's shape, which varies from flexible and contractile to rigid. Numerous mitochondria and extrusomes are also generally present. The presence of alveoli, the structure of the cilia, the form of mitosis and various other details indicate a close relationship between the ciliates, Apicomplexa, and dinoflagellates. These superficially dissimilar groups make up the alveolates.

Fossil record

Until recently, the oldest ciliate fossils known were tintinnids from the Ordovician Period. In 2007, Li *et al.* published a description of fossil ciliates from the Doushantuo Formation, about 580 million years ago, in the Ediacaran Period. These included two types of tintinnids and a possible ancestral suctorian.

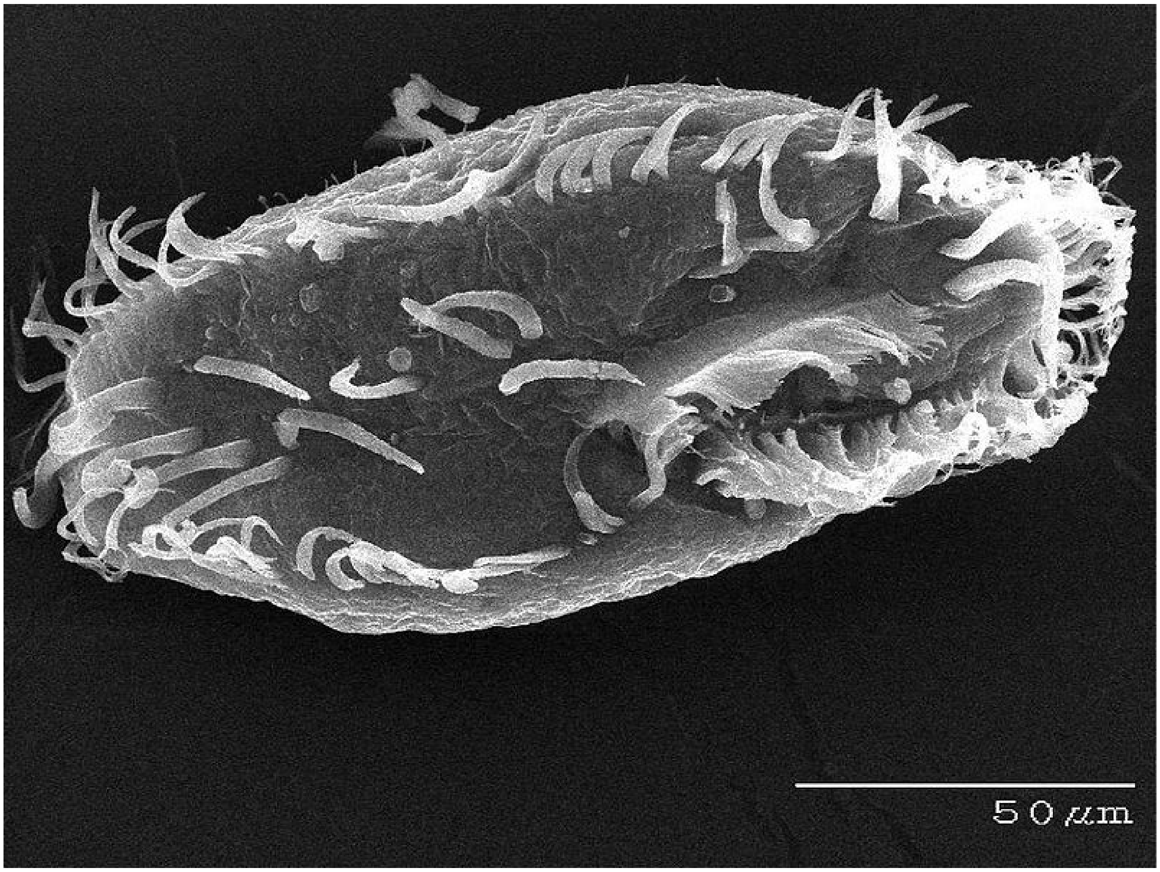
Classification

Stentor roeseli

Subphylum Postciliodesmatophora

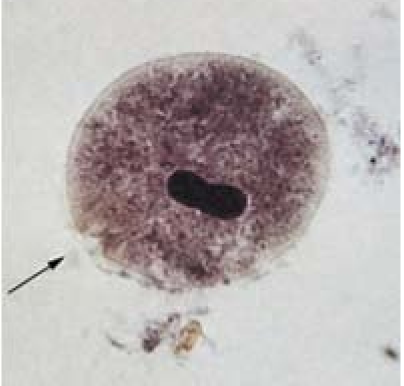
- Class Karyorelictea
- Class Heterotrichea (e.g. *Stentor*)

Subphylum Intramacronucleata



Oxytricha trifallax

- Class Spirotrichea
    - Subclass Choreotrichia (e.g. *Tintinnidium*)
    - Subclass Oligotrichia (e.g. *Halteria*)
    - Subclass Stichotrichia (e.g. *Stylonychia*)
    - Subclass Hypotrichia (e.g. *Euplotes*)



A trophozoite of *Balantidium coli*

- Class Litostomatea
  - Subclass Haptoria (e.g. *Didinium*)
  - Subclass Trichostomatia (e.g. *Balantidium*)
- Class Phyllopharyngea
  - Subclass Phyllopharyngia (e.g *Chilodonella uncinata*
  - Subclass Rhynchodia
  - Subclass Chonotrichia
  - Subclass Suctoria (e.g. *Podophrya*)
- Class Nassophorea
- Class Colpodea (e.g. *Colpoda*)
- Class Prostomatea (e.g. *Coleps*)
- Class Oligohymenophorea
  - Subclass Peniculia (e.g. *Paramecium*)
  - Subclass Hymenostomatia (e.g. *Tetrahymena*)
  - Subclass Scuticociliatia
  - Subclass Peritrichia (e.g. *Vorticella*)
  - Subclass Astromatia
  - Subclass Apostomatia
- Class Plagiopylea

Other

- Genus *Cryptocaryon*

Chapter 11

Mesomycetozoea and Opalinidae

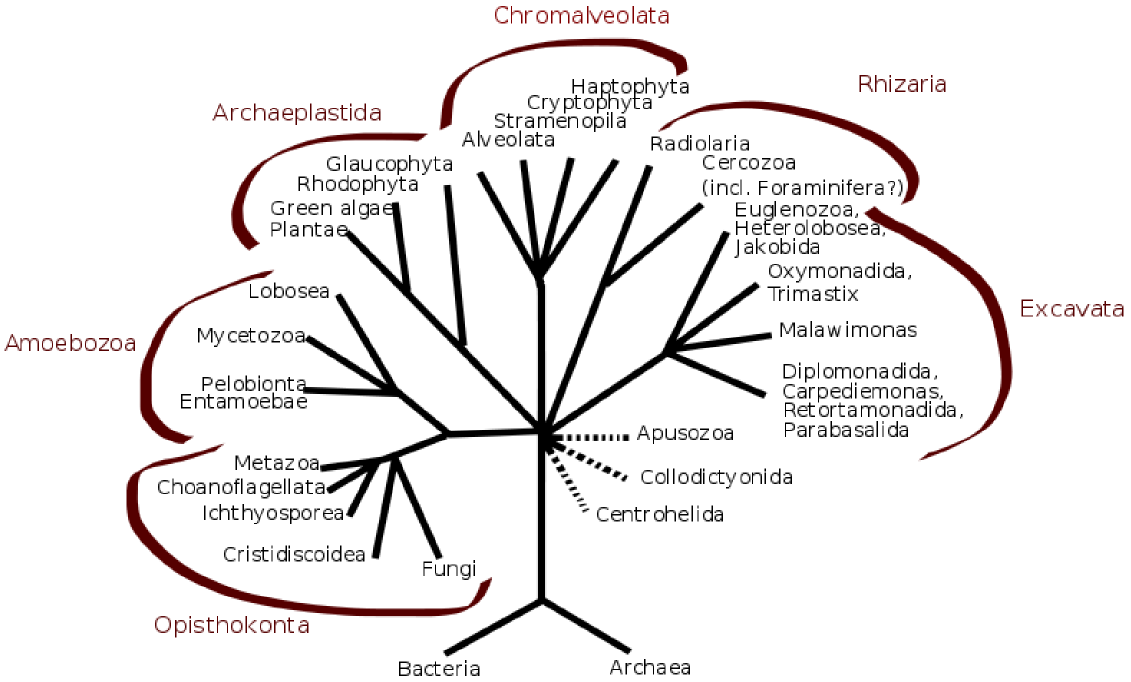
Mesomycetozoea

Mesomycetozoea	
Scientific classification	
Domain:	Eukarya
(unranked)	Opisthokonta
(unranked)	Choanozoa or Holozoa
Class:	**Mesomycetozoea**
Orders	
Dermocystida Ichthyophonida	

The **Mesomycetozoea** (or **DRIP** clade, or **Ichthyosporea**) are a small group of protists, mostly parasites of fish and other animals.

Significance

They are not particularly distinctive morphologically, appearing in host tissues as enlarged spheres or ovals containing spores, and most were originally classified in various groups of fungi, protozoa, and algae. However, they form a coherent group on molecular trees, closely related to both animals and fungi and so of interest to biologists studying their origins. In a 2008 study they emerge robustly as the sister-group of the clade Filozoa, which includes the animals.



Eukaryota tree. Note "Ichthyosporea" at bottom left, in Opisthokont clade. "Metazoa" are animals, and Choanoflagellates are closely aligned. Fungi is at other end of Opisthokont clade, with Cristidiscoidea closely aligned. Ichthyosporea is in the middle ("Meso-") of the fungi ("-myceto-") and the animals ("-zoea").

Terminology

The name DRIP is an acronym for the first protozoa identified as members of the group, Cavalier-Smith later treated them as the class **Ichthyosporea**, since they were all parasites of fish.

- order Dermocystida
    - "D": *Dermocystidium*. One species, *Rhinosporidium seeberi*, infects birds and mammals, including humans.
    - "R": the "rosette agent", now known as *Sphaerothecum destruens*
- order Ichthyophonida
    - "I": *Ichthyophonus*
    - "P": *Psorospermium*

Since other new members have been added, Mendoza *et al.* suggested changing the name to Mesomycetozoea, which refers to their evolutionary position. Note the name Mesomycetozoa (without a second e) is also used to refer to this group, but Mendoza *et al.* use it as an alternate name for the phylum Choanozoa.

Opalinidae

Opalinidae

Scientific classification

Kingdom:	Chromalveolata
Division:	Heterokontophyta
Class:	Opalinea
Order:	Slopalinida
Family:	**Opalinidae** Claus 1874

Genera

- *Cepedea*
- *Opalina*
- *Protoopalina*
- *Protozelleriella*
- *Zelleriella*

The **opalines** are a small group of peculiar protists, currently assigned to the family Opalinidae, in the order Slopalinida. Their name is derived from the opalescent appearance of these microscopic organisms when illuminated with full sunlight (p. 247). Most opalines live as endocommensals in the large intestine and cloaca of anurans (frogs and toads), though they are sometimes found in fish, reptiles, molluscs and insects. The unusual features of the opalines, first observed by Antoine van Leeuwenhoek in 1683, has led to much debate regarding their phylogenetic position among the protists.

Taxonomy and phylogeny

The relationships opalines and other protists has been a subject of great controversy since the late 19th century, and is not completely resolved at present. Initially, microscopists believed that the thousands of rhythmically beating hair-like structures which cover their surface were cilia, and they placed the opalines in Ciliophora. In the early 20th century other aspects of opaline biology clearly differentiated them from the ciliates and they were placed in Sarcomastigophora, with the amoebae and flagellates. In the 1980s, detailed ultrastructural studies of *Opalina ranarum* revealed that they share many features with the heterokonts of the family Proteromonadidae. A new order—Slopalinida Patterson 1985—was proposed to include the members of the families Proteromonadidae Grassé 1952 and Opalinidae Claus 1874. In 2004, the first reliable opaline genetic sequence data supported the monophyletic nature of the order Slopalinida. The authors of that study considered the opalines to be a family (Opalinidae) within the order Slopalinida.

There are currently about 200 recognized species of opalines in 5 genera: *Opalina* Purkinje and Valentin 1835, *Protoopalina* Metcalf 1918, *Cepedea* Metcalf 1920, *Zelleriella* Metcalf 1920, and *Protozelleriella* Delvinquier et al. 1991. Two additional genera, *Hegneriella* Earl 1971 and *Bezzenbergeria* Earl 1973, have not been considered as valid by subsequent authors (p. 249) The 5 recognized genera differ in terms of the number of nuclei, the appearance and location of the falx (two short, sickle-shaped rows of flagella), and whether the long rows of flagella (called "kineties") cover the body evenly or if there is a "bald spot". Due to the differences in body shape among the different life cycle stages within a species, the use of overall body shape - whether flat or cylindrical - to differentiate the genera has been de-emphasized.

Life cycle

Like many parasites, the life cycle of opalines is rather complex . The most comprehensive study published so far concluded that the life cycles of 10 *Opalina* species, 1 *Zelleriella* species and 1 *Protoopalina* species are all "remarkably similar" (p. 321). A more recent study found that *Cepedea couillardi* fits the standard opaline life cycle model described below, while that of *Opalina proteus* is completed entirely in the tadpole stage of the host. Very little is known about the life cycles of opalines in fish, reptile or arthropod hosts.

Asexual phase in adult anuran host. The basic opaline life cycle begins with the large, multinucleate **trophonts** in the adult anuran cloaca. Through much of the year, the trophonts grow and divide continually to yield more trophonts. Nuclear divisions maintain the appropriate number of nuclei during this phase. As the host's breeding season approaches, the trophonts enter a phase known as **palintomy** -- a series of cell divisions with little or no overall growth or nuclear divisions. The resulting opalines, which become gradually smaller with fewer nuclei per individual, are called **tomonts**. At some point the small tomonts undergo encystment, and the **cysts** are released into the environment (i.e. the breeding pool of the anuran host) along with the feces.

Sexual and asexual phases in larval anuran host. Once cysts are eaten by foraging tadpoles, they excyst (hatch) to yield **gamonts**. The gamonts divide further, including a meiotic division, to yield halpoid **gametes**. Each gamete has only one nucleus and may be either a **microgamete** or a **macrogamete**. Conjugation occurs between one microgamete and one macrogamate, to yield a diploid **zygocyst** with one nucleus. The zygocyst has two possible fates. It may be shed along with the feces of the tadpole host; and if eaten by another tadpole, it will excyst (hatch) to yield more gamonts in the new host. Alternatively, the zygocyst may excyst in its original host and grow into a multinucleate **protrophont**. In this case, the protrophont grows into a trophont and the whole cycle starts over again. The cycle from protrophont to cyst may occur in either the tadpole or adult hosts. Some evidence suggests that the life cycle transitions of opalines may be governed by the hormonal cycles of the host.

Hosts and commensal lifestyle

Lacking a mouth, opalines feed by taking in nutrients from their surroundings by pinocytosis. While the opalines are often referred to as "parasites", two lines of evidence suggest that they are actually commensals which do no harm to their anuran hosts.

1. They are found almost exclusively in the large intestine and cloaca. Since the anuran absorbs the nutrients from its food in the small intestine, the opalines are probably not depriving their hosts of nutrients. It is believed that the opalines are simply living off the "left-over" nutrients in the feces, possibly supplemented by the biochemical contributions of the rich bacterial flora which also reside there.
2. Anuran hosts containing many thousands of opalines appear to be completely healthy, with no obvious irritation or other pathological signs on their intestinal or cloacal walls.

Only about a dozen reports of opalines in fishes have been published, and even fewer on opalines from reptile or salamander hosts. Their scarcity outside of anuran hosts had led many to speculate that the others are just incidental infestations—maybe the infested snake had just eaten an infested frog, for example. However, opalines have been found in saltwater fish which have no access to anurans. Also, the populations of opalines in fish hosts are often very high, suggesting that they are probably reproducing in the fish host.

The pathogenicity (if any) of opalines in fish hosts is not yet known. One study found no irritation or other pathological signs on the rectal epithelium of *Symphysodon aequifasciata* infested with *Protoopalina symphysodonis*, but stated that "most infected animals died".

In vitro culture of opalines

Successful culturing of opalines in artificial media for periods of 1 month or more has been reported. This technique will aid tremendously in future studies of all aspects of opaline biology.