Protists

Protists are defined as unicellular eukaryotes (see page 30). Many form filaments (such as some fungi), are colonial or aggregate into larger clusters of cells. They are divided into the Archaeplastida (green algae, red algae and ancestors of higher plants), the Amoebozoa (many amoeboid species), the Opisthokonta (collar cells, fungi and ancestors of animals), Stramenopiles, Alveolata, Rhizaria and Excavata. Typically, they have one nucleus and soil species have a contractile vacuole for regulating water and ion concentrations. Many species have a swimming dispersal stage with one or more cilia. Cysts form in sub-optimum living conditions or when prey are scarce. Although many protists can be identified under the microscope to family or genus level, species identification is made through DNA sequence analysis (see pages 64-65). [27]

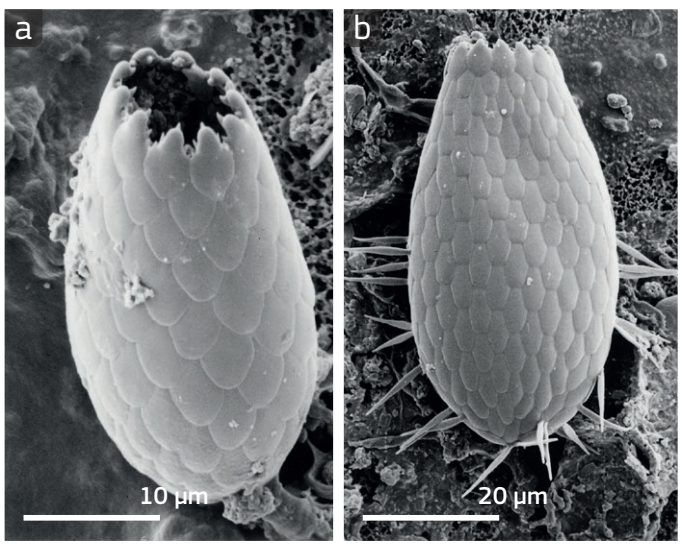
Rhizaria

Morphology

Cells typically produce very thin hair-like extensions called filopodia that can branch and merge together again, forming a complex network in some species. They tend to grow flat on surfaces and their filopodia can extend into small crevices in the soil searching for bacteria. When detached from surfaces, they swim with two cilia. They can also move by amoeboid locomotion or gliding on surfaces. Soil species form resting cysts that enable them to survive adverse environmental conditions. There are many variations of this basic morphology as it is a diverse group.

Taxonomy

This supergroup has one major soil lineage: the Cercozoa [28]. The Cercozoa (common name cercomonads) consist of a diverse variety of species of small bacterial-feeding unicells less than 10 µm in size. One subgroup common in soils is the Silicofilosea that secrete silica scales on their surface. The Silicofilosea also include the Euglyphida that form vase-shaped protective layers (known as tests) outside the cell. Other Cercozoa include Vampyrellida that feed on fungal hyphae (see box on page 39), the Phytomyxea that are parasites of plants and Stramenopiles (see page 37) and Ascetospora that are parasites on soil invertebrates.



The filose testate amoebas (**a**) *Euglypha rotunda* and (**b**) *Euglypha compressa* are Rhizaria species abundant in soil. (YE, SS)

Microhabitat

Rhizaria live on the surfaces of soil and organic matter particles where they select bacteria to ingest. Species may have depth preferences in the soil. Some prefer organic matter and litter on the surface of the forest floor. Others, such as Vampyrellida, prefer to penetrate fungal hyphae or spores. Those species with cilia can explore their habitat by swimming. The filopodia can extend into very small crevices (< 1 µm) to search for bacterial prey.

Diversity, abundance and biomass

There are hundreds or even thousands of soil Cercozoa species that cannot be distinguished by microscopy and, therefore, many genera remain to be described. These are usually the most common active protists in soils, and abundances vary with moisture as well as with the abundance of bacteria or other prey. Densities may reach more than one million cells per gramme of soil but are usually 10^3 - 10^5 per gramme.

Amoebozoa

Morphology

The Amoebozoa is another group of unicellular organisms whose cells are covered by a very thin protein layer with or without microscales. [29, 30]

Taxonomy

The Amoebozoa is a supergroup that contains bacterial-feeding amoeboid species. Several lineages contain mostly aggregative species referred to as 'social amoebae', such as the Myxogastria and the Dictyostelia, but aggregative species occur in other protists as well. In Arcellinida the cell is inside a vase- or helmet-shaped structure made of protein, sometimes amended with soil particles bound together by proteins.

Social amoebae

- Social amoebae occur among protists and not just in Amoebozoa.
- They are found in a wide variety of colours; more than 900 species of slime mould occur all over the world.
- Some species may reach sizes of several square metres and masses of up to 30 grammes.
- They live in any type of dead plant material and contribute to the decomposition process.

Fuligo septica is commonly known as the dog vomit slime mould or scrambled egg slime because of its peculiar yellowish colour. It grows on decaying wood but can also grow on plant leaves. (SI)

Microhabitat

Amoeboid species occur on moist surfaces and live in water microfilms where they forage for palatable bacteria or other prey. Some species prefer wet conditions, others occur in drier conditions, some have depth and litter preferences, and some are known colonisers and occur in disturbed soils where other species are absent. Amoeba are very effective at scouring surfaces for bacteria. A small number feed on fungal hyphae or prey on protists or microinvertebrates.

An Ameabozoa specimen from the Vannellidae family. Flattened, fan-shaped amoebae of this family were recognised as an important major amoebozoan taxon only in 2004. (YE)

Diversity, abundance and biomass

Although most genera have probably been described, and about 3 000 species have been identified, many species still remain to be discovered. When active, there can be as many as 100 000 cells per gramme of soil, but more typically numbers are 10^3 - 10^4, depending on the ecosystem.

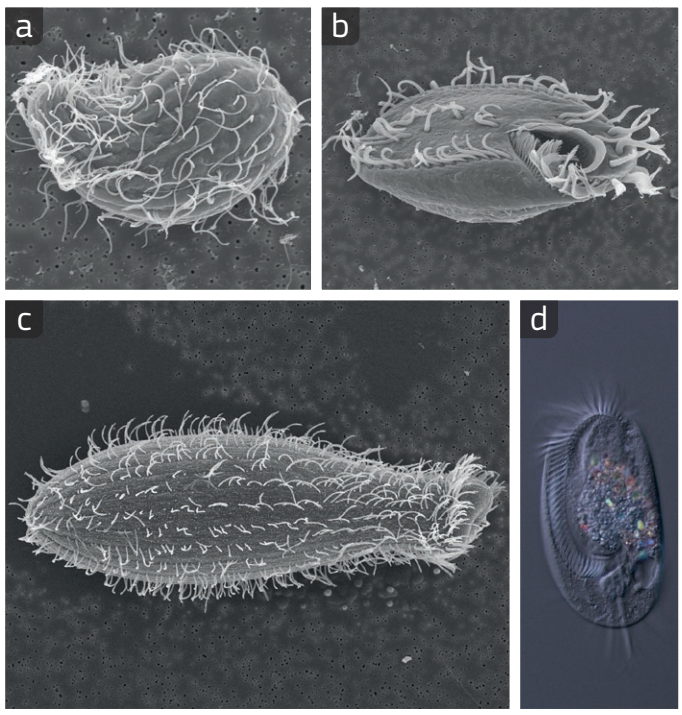
Alveolata

Morphology

The Alveolata is a group of protists characterised by folded membranes underneath their cell membranes (called alveoli) [31]. Ciliophora (the only soil-inhabiting Alveolata) have two types of nuclei: a small inactive nucleus with condensed chromosomes, which becomes active only during reproduction, and a large nucleus that is always active and holds many copies of the chromosomes. Most species have rows of cilia that beat in a coordinated manner, and a specialised funnel structure for capturing and ingesting prey. They also often have specific defensive or aggressive structures, called ejectosomes. These are made of mucus that is ejected from the cell. A complex network of vacuoles inside the cell regulates the digestion of food and the water balance.

Taxonomy

There are three main supergroups in the Alveolata (Apicomplexa, Dinoflagellata and Ciliophora), but only Ciliophora (ciliates) are found free-living in the soil. Most ciliates ingest bacteria, but some ingest other protists or are specialised symbionts or parasites (see box on page 33). Colpodellida prey on other protists and can reach higher numbers by feeding on soil invertebrate corpses. The Colpodea includes most of the ciliates found in high abundance when soil samples are kept in the laboratory. Many genera emerge from cysts when sufficient moisture and bacteria are present and then reproduce. Colpodids are very diverse and can be identified to the genus or family level (see page 29) through microscopy. The other genera that occur in some abundance in soils belong to the order Hypotrichea. These are also diverse but rarely dominant in terms of abundance. The Colpodid to Hypotrich ratio (also called the Colpodid to Stichotrich ratio) is used as an indicator of environmental quality.



Examples of Alveolata: (**a**) *Colpoda steinii* shows a shape that resembles a kidney; (**b**) *Steinia* sp. with a pointed tail (left side), typical of this genus; (**c**) *Spathidium sp.* with its ovoid body, typical of this genus; (**d**) a specimen of the ciliate group Hypotrichia showing the details of the oral structure and associated bristles, scientifically named cilia. (SS, YE)

Microhabitat

As soil dries, the ciliates' habitat becomes restricted to water films on surfaces. They detect prey by chemical-sensing and swim toward the signal, or away from toxic molecules. Their dispersal is by water infiltration through soil pores, or in the air if dry soil is disturbed.

Diversity, abundance and biomass

More than 1 500 species of soil ciliates have been described, but many more remain undescribed so far. One study from Namibia revealed 365 species, of which 128 were new species, from 73 soil samples. Temperate soils typically hold 20 - 30 species per gramme of soil, but most are inactive. In moist soils with plenty of bacteria or prey, there can be 10 000 active cells per gramme declining to none in very dry soils. Although the biomass of ciliates per gramme of soil is very low, when active they can ingest several hundred bacterial cells per minute.

Stramenopiles

Morphology

Stramenopiles are unicellular organisms with two cilia that beat in different directions: a front one that includes tiny hairs (visible on electron microscope images) that pulls the cell, and a trailing one that pushes the cell. In some groups, however, the trailing cilium is missing. Other groups are usually filamentous and only the dispersal cell is ciliated. Terrestrial species form resting cysts in the soil, and in some sexual species dispersal spores are produced after sexual reproduction. [32, 33]

Taxonomy

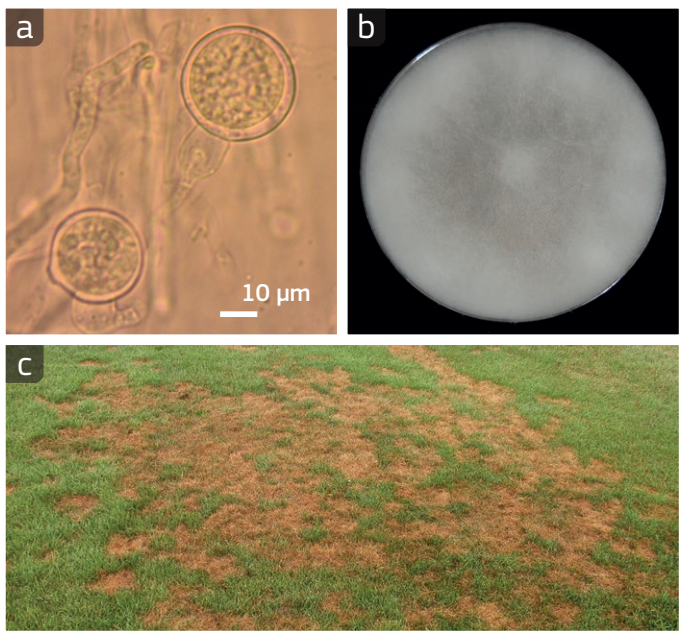
This supergroup includes the brown algae and several groups previously thought to be fungi, such as Hyphochytriales and Peronosporomycetes, which are commonly found in soils. Some species of true brown algae occur in alpine soils (for example, *Vaucheria*), but they are typically rare or absent. Most terrestrial species have lost the ability to photosynthesise (see box on page 35) and appear colourless. They absorb nutrients from the living or decomposing tissues into which they grow.

The *Irish Potato Famine*

- The *Irish Potato Famine*, a period of mass starvation, disease and emigration in Ireland between 1845 and 1852, was caused by *Phytophthora infestans*, a Peronosporomycetes.
- Originally from the Toluca Valley in Mexico, once introduced through infected potatoes, it spread rapidly to much of northern and central Europe.
- Because prior to 1980 they were considered to be fungi, we still lack an effective chemical compound to treat stramenopile parasites since fungicides (aiming to disrupt fungi) do not work.

Microhabitat

Hyphochytriales are found in moist soil environments. They absorb dissolved nutrients with a network of filaments that extend from the cell. Terrestrial species of Peronosporomycetes are decomposers of organic matter or live as plant parasites. They feed by extending filaments into plant tissues. They are economically important because they include species that cause some of the most damaging plant diseases, such as *Pythium* (which causes the damping-off disease in greenhouses), downy mildews and white blister rusts. Diatomea are typically aquatic species that can be found in riparian or regularly flooded soils, and sometimes inside rotting tree logs. Their role and presence in soils is poorly documented. The motile stage is usually a small swimming cell with two cilia, while sexual reproduction leads to the growth of a thick walled spore for dispersal.



(**a**) The structures producing spores, sporangia, of *Pythium aphanidermatum*. (**b**) In the laboratory it is possible to grow *Pythium aphanidermatum* and see its filamentous root. (**c**) *Pythium* species are responsible for plant diseases, such as the 'Pythium blight', a highly destructive turfgrass disease. (LG, JKA)

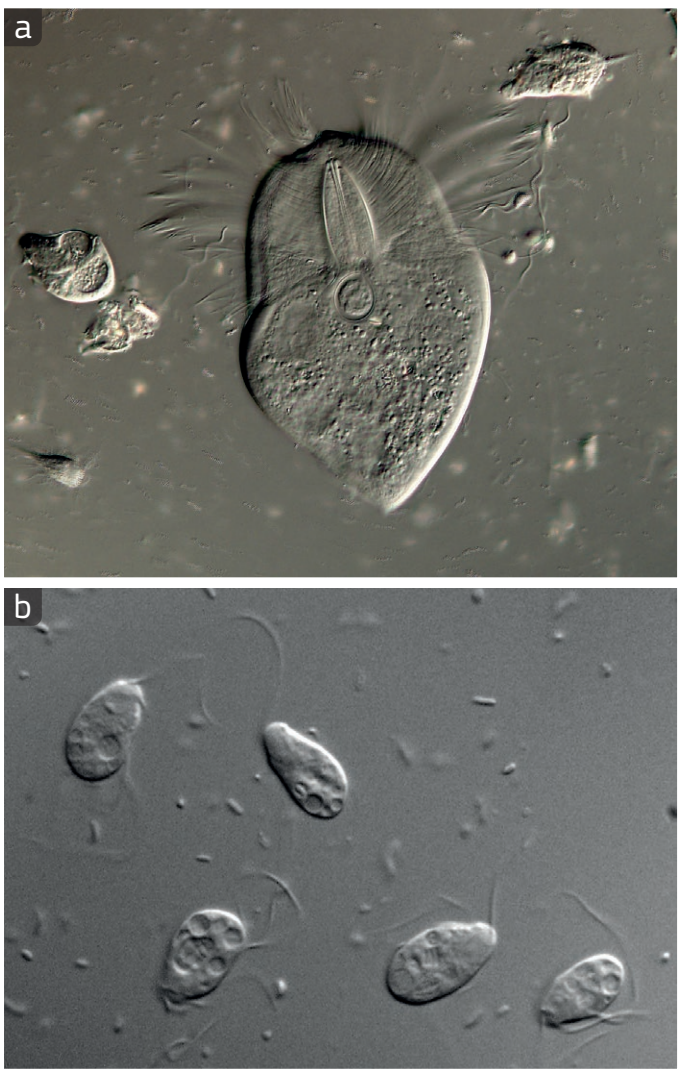
Diversity, abundance and biomass

Only approximately 25 genera of Hyphochytriales are known to science, but many still remain to be described. Fewer than 700 species of Peronosporomycetes are described, but there are likely to be 1 000 - 10 000 species.

Excavata

Morphology

The general body-type in this very diverse group is a small cell with a cilium directed backwards that generates locomotion and directs food (mostly bacteria) toward a feeding groove on the ventral surface, as observed in Fornicata. Many groups have reduced mitochondrial function and prefer micro-aerophilic (low oxygen) or anaerobic (no oxygen) environments. In contrast to many Excavata groups, the Kinetoplastea (commonly called kinetoplastids) have a characteristic mitochondrion with a large amount of DNA. Many kinetoplastid species rely on dissolved nutrients for food (they are osmotrophic). In Parabasalia, the single body-type is replicated hundreds of times to form large multiciliated cells. Both Parabasalia and Preaxostyla have elaborate supporting cytoskeletal elements that provide shape and assist in locomotion. The Heterolobosea are generally amoeboid species with two or four cilia that are used to move in search of food, but some have lost either the ciliated stage or the amoeboid stage. The Euglenids are typically spindle-shaped cells covered by a flexible pellicle; and they can be photosynthetic or not, with the non-photosynthetic species feeding on bacteria or other protists. [34]



Examples of Excavata: (**a**) Parabasalia shows the cilia arranged in clusters near the anterior of the cell; (**b**) *Monocercomonas* spp. can also be found in the digestive tract of wood-eating insects, such as termites. (VH, IC)

Taxonomy

The Excavata is a supergroup, with genera that occur in soil included in six phyla: Fornicata, Parabasalia, Preaxostyla, Discoba, Heterolobosea and Euglenozoa.

Microhabitat

Heterolobosea are found in every ecosystem but are rarely the dominant protists, except in some disturbed soils. The Euglenida, both photosynthetic and heterotrophic genera, occur in soils that are regularly moist or water-saturated (e.g. in wet soil and in riparian areas). Among the Discoba, some free-living species occur in the order Jakobida, such as those of the genus *Andalucia*.

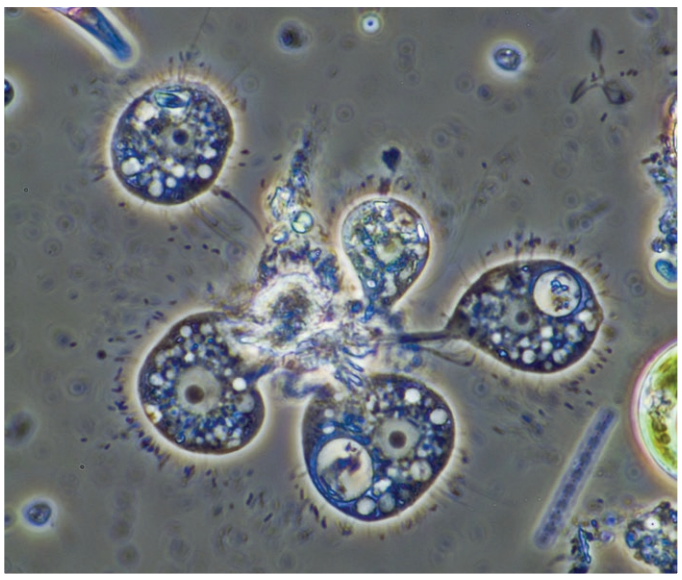
Diversity, abundance and biomass

There are approximately 562 described species of Parabasalia and Preaxostyla, more than 80 species of Heterolobosea and more than 1 520 species of Euglenozoa.

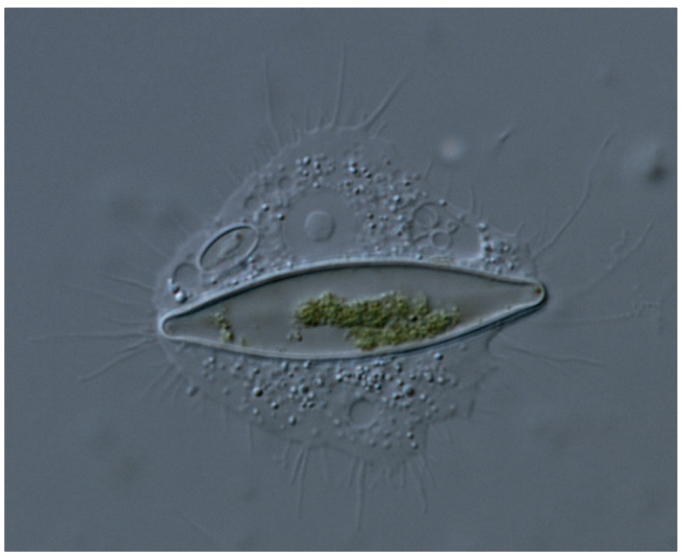
Other protists

Nuclearia, *Ancyromonas* and others

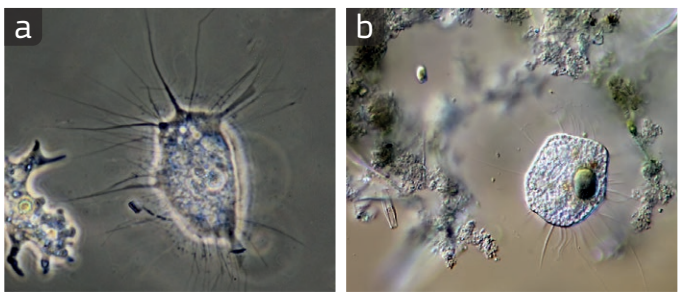
There are several genera that belong to the base of the Opisthokonta, the group that includes animals and fungi. These genera are common in soil, though rarely abundant, and contribute to the ingestion of bacteria. These include *Nuclearia*, *Fonticula*, and the *Rozella*. Several genera found in soils cannot yet be placed into our classification system. They are placed as *incertae sedis* in the eukaryotes. These include *Ancyromonas*, *Breviata* and Apusomonadida.



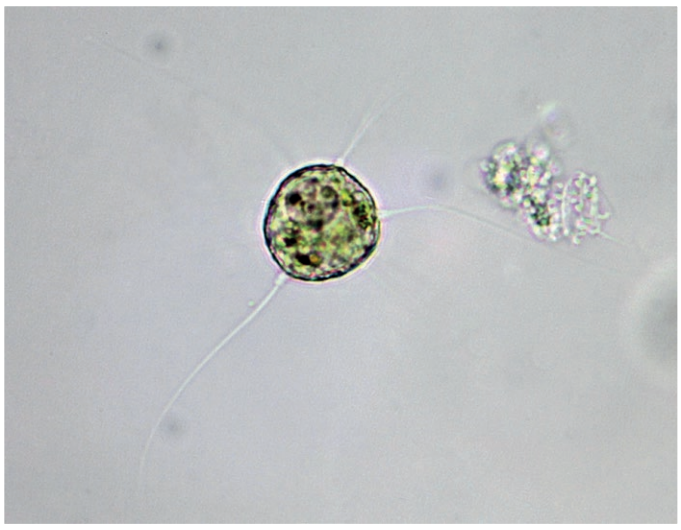
Five specimens of *Nuclearia thermophila* probably feeding on the same prey. This species can be found in peat bogs. (FS)



A species of *Nuclearia* with ingested diatom. (YE)



Diversity of the genus *Nuclearia*: (**a**) *Nuclearia flavocapsulata* usually feeds on bacteria, algae, or detritus; (**b**) *Nuclearia delicatula* feeds by penetrating damaged or old cells of algae or by actively ingesting bacteria. (FS)



A specimen of *Artodiscus saltans*. It can be found in sediments of clear lakes and rivers. Its presence has also been reported in flooded pastures. (FS)