protozoan

microorganism

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Summary

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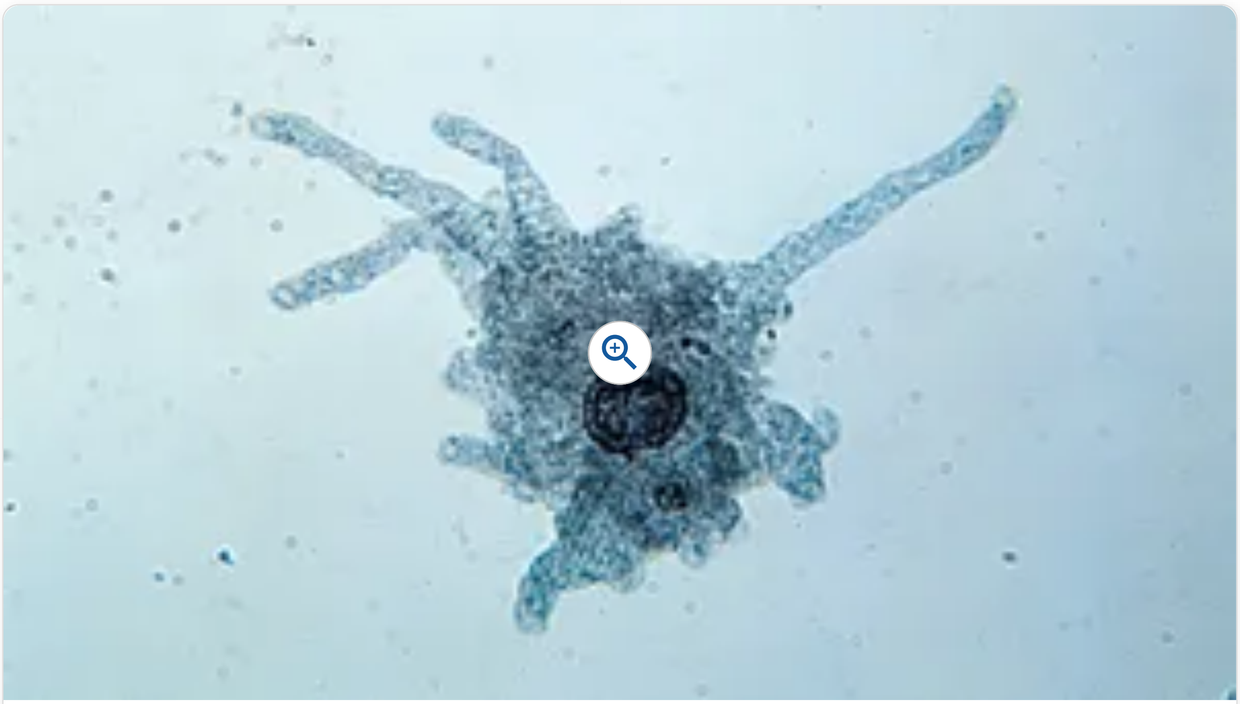
protozoan, organism, usually single-celled and heterotrophic (using organic carbon as a source of energy), belonging to any of the major lineages of protists and, like most protists, typically microscopic. All protozoans are eukaryotes and therefore possess a "true," or membrane-bound, nucleus. They also are nonfilamentous (in contrast to organisms such as molds, a group of fungi, which have filaments called hyphae) and are confined to moist or aquatic habitats, being ubiquitous in such environments worldwide, from the South Pole to the North Pole. Many are symbionts of other organisms, and some species are parasites.

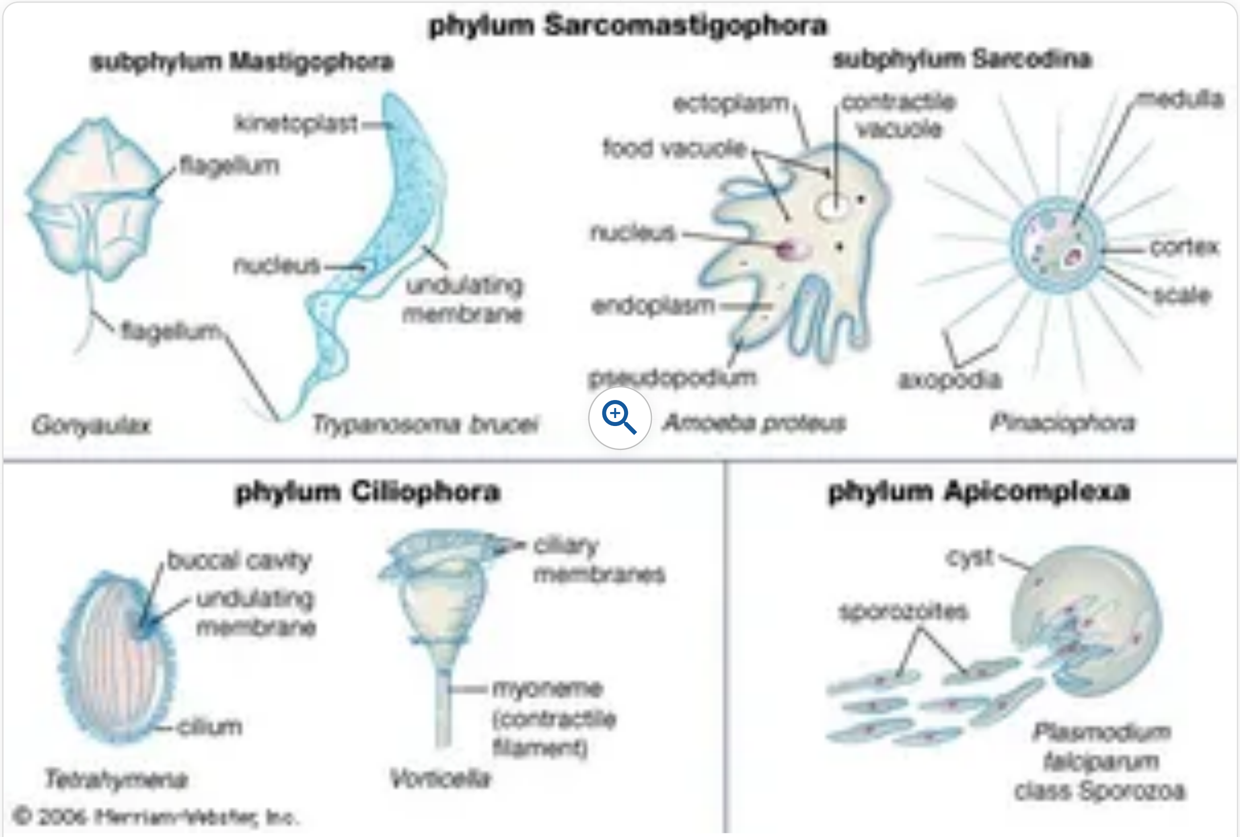


amoeba

Modern ultrastructural, biochemical, and genetic evidence has rendered the term *protozoan* highly problematic. For example, *protozoan* historically referred to a protist that has animal-like traits, such as the ability to move through water as though "swimming" like an animal. Protozoans traditionally were thought to be the progenitors of modern animals, but contemporary evidence has revealed that this is not the case for most protozoans. In fact, modern science has shown that the protozoans represent a very complicated grouping of organisms that do not necessarily share a common evolutionary history. This unrelated, or paraphyletic, nature of the protozoans has caused scientists to abandon the term *protozoan* in formal classification schemes. Hence, the subkingdom Protozoa is now considered obsolete. Today the term *protozoan* is used informally in reference to nonfilamentous heterotrophic protists.

Commonly known protozoans include representative dinoflagellates, amoebas, paramecia, and the malaria-causing *Plasmodium*.

Features of protozoans



representative protozoans

Although protozoans are no longer recognized as a formal group in current biological classification systems, *protozoan* can still be useful as a strictly descriptive term. The protozoans are unified by their heterotrophic mode of nutrition, meaning that these organisms acquire carbon in reduced form from their surrounding environment. However, this is not a unique feature of protozoans. Furthermore, this description is not as straightforward as it seems. For instance, many protists are mixotrophs, capable of both heterotrophy (secondary energy derivation through the consumption of other organisms) and autotrophy (primary energy derivation, such as through the capture of sunlight or metabolism of chemicals in the environment). Examples of protozoan mixotrophs include many chrysophytes. Some protozoans, such as *Paramecium bursaria*, have developed symbiotic relationships with eukaryotic algae, while the amoeba *Paulinella chromatophora* remarkably appears to have acquired autotrophy via relatively recent endosymbiosis of a cyanobacterium (a blue-green alga). Hence, many protozoans either perform photosynthesis themselves or benefit from the photosynthetic capabilities of other organisms. Some algal species of protozoans, however, have lost the ability to photosynthesize (e.g., *Polytomella* species and many dinoflagellates), further complicating the concept of "protozoan."

Protozoans are motile; nearly all possess flagella, cilia, or pseudopodia that allow them to navigate their aqueous habitats. However, this commonality does not represent a unique trait among protozoans; for example, organisms that are clearly not protozoans also produce flagella at various stages in their life cycles (e.g., most brown algae). Protozoans are also strictly non-multicellular and exist as either solitary cells or cell colonies. Nevertheless, some colonial organisms (e.g., *Dictyostelium discoideum*, supergroup Amoebozoa) exhibit high levels of cell specialization that border on multicellularity.

The descriptive guidelines presented above exclude many organisms, such as flagellated photosynthetic taxa (formerly Phytomastigophora), that were considered protozoans by older classification schemes. Organisms that fit the contemporary definition of a protozoan are found in all major groups of protists that are recognized by protistologists, reflecting the paraphyletic nature of protozoans.

Discover how individual cilia employ viscous drag to coordinate power and recovery strokes for locomotion

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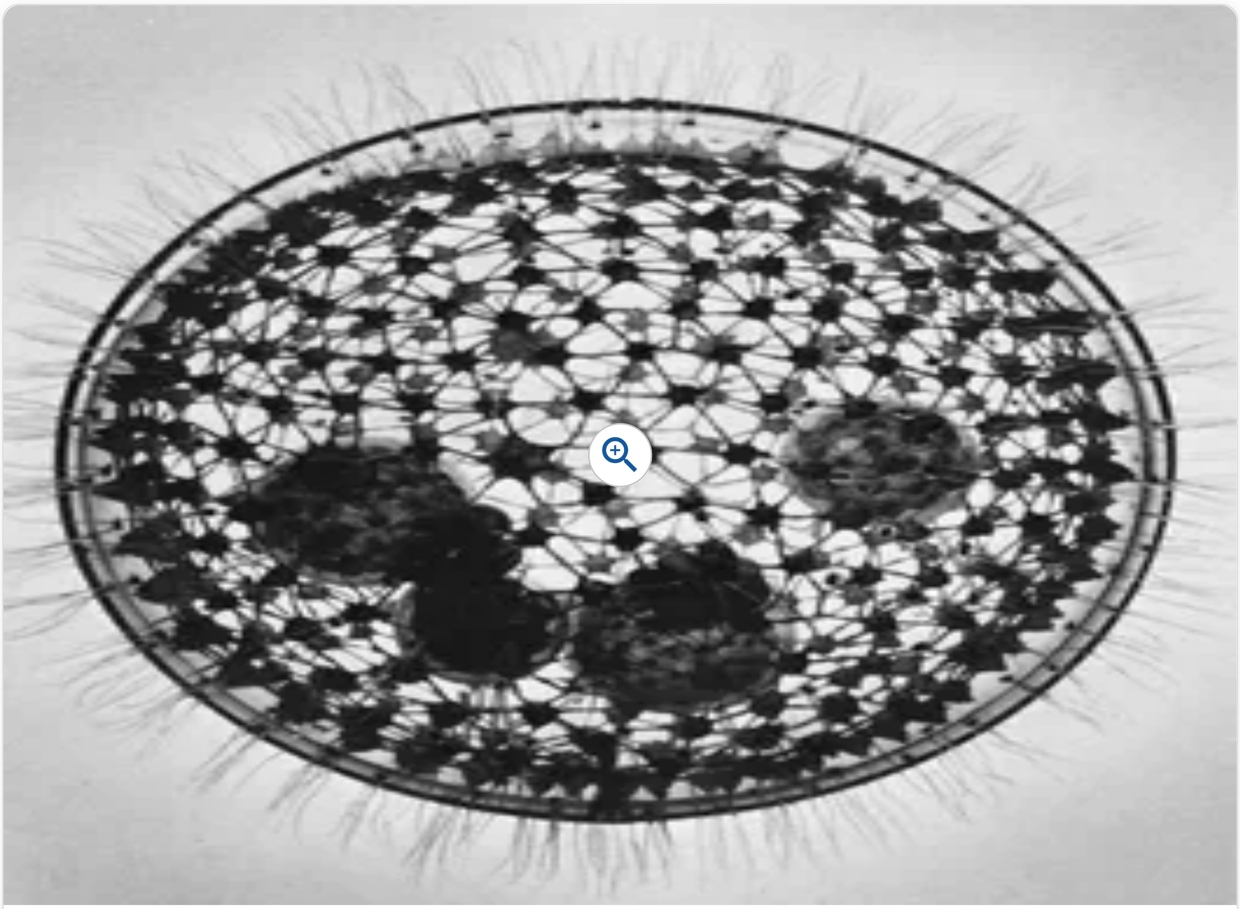
The most important groups of free-living protozoans are found within several major evolutionary clusters of protists, including the ciliates (supergroup Chromalveolata), the lobose amoebae (supergroup Amoebozoa), the filose amoebae (supergroup Rhizaria), the cryptomonads (supergroup Chromalveolata), the excavates (supergroup Excavata), the opisthokonts (supergroup Opisthokonta), and the euglenids (Euglenozoa). These groups of organisms are important ecologically for their role in microbial nutrient cycles and are found in a wide variety of environments, from terrestrial soils to freshwater and marine habitats to aquatic sediments and sea ice. Significant protozoan parasites include representatives from Apicomplexa (supergroup Chromalveolata) and the trypanosomes (Euglenozoa). Organisms from these groups are the causative agents of human diseases such as malaria and African sleeping sickness. Owing to the prevalence of these human pathogens, and to the ecological importance of the free-living protozoan groups mentioned above, much is known about these groups. This protozoan groups mentioned above, much is known about these groups. This article therefore concentrates on the biology of these comparatively well-characterized protozoans. At the end of this article is a summary of the contemporary protistan classification scheme.

Natural history

Size range and diversity of structure



glass model of *Volvox*

Protozoans range in diameter from a few thousandths of a millimetre to several millimetres. Because the group contains many unrelated or loosely related organisms, enormous diversity in structure and form exists.

Flagellated protozoans

dinoflagellate

The flagellated protozoans range from a simple oval cell with one or more flagella to the structural sophistication of the collared flagellates (choanoflagellates, supergroup Opisthokonta). The collared flagellates lack photosynthetic pigments and are therefore colourless. They have a single flagellum surrounded by a delicate circular collar of fine pseudopodia (microvilli) on which they trap food particles. In some marine species the whole cell is enclosed in an elaborate, open latticelike basket formed from strands of silica. Although some dinoflagellates (supergroup Chromalveolata) still contain plant pigments and rely to a greater or lesser degree on photosynthesis, many members have lost the ability to photosynthesize. All dinoflagellates are surrounded by a cell wall armour with a complicated pattern and possess two flagella, one of which beats in a transverse plane around the equator of the cell while the other beats in a longitudinal plane.

Many other flagellated protozoans can develop stalks that connect them to a substrate, either as single cells (e.g., the genus *Paraphysomonas*) or as colonies (e.g., the genus *Codosiga*). Other flagellated taxa may exist as colonies (e.g., the genus *Codosiga*). Other flagellated taxa may exist as

Amoebae and pseudopodia

The amoebae also are extremely diverse. Amoebae are defined based on pseudopodia type: those with thin, or filose, pseudopods, which may be reinforced by stiff microtubule proteins, are classified in the supergroup Rhizaria (e.g., foraminiferans and radiolarians), whereas those with lobose pseudopods, which are blunt and are not reinforced, are classified in the supergroup Amoebozoa. Both groups of amoebae can be "naked" or housed inside a shell, or test, composed of organic or inorganic materials.

The naked amoebae are the simplest of the amoebae. They have no defined shape and extend one or many lobose pseudopodia. Many of these lobose amoebae, including those in the genera *Mastigamoeba* and *Mastigella*, also possess flagella in the vegetative (resting) phase. At the opposite extreme are the complex foraminiferans, which live inside multichambered calcareous shells up to several millimetres in diameter. The filose pseudopodia of foraminiferans are known as reticulopodia and extend from the aperture of the largest chamber of the shell, forming a complicated, sticky branching network. Rhizarian amoebae that are known commonly as radiolarians form shells from silica or strontium sulfate; in some the shell has so many holes that the structure resembles a sponge. The polyphyletic heliozoans, or sun protozoans, have radiating pseudopodia (axopodia) that extend like spokes from the central body; microtubules support an outer layer of cytoplasm. Many heliozoans are members of Rhizaria; however, some are placed in Chromalveolata.

Ciliated protozoans

The ciliates are the most structurally homogeneous group, although even they have evolved considerable variation on the cilia-covered cell. In some species (e.g., the hypotrich *Euplotes*) the cilia are combined to form thick conical structures, called cirri, which the ciliate uses to crawl along surfaces, rather like small limbs. In other species the cilia virtually disappear from the main body of the cell, but the circle of cilia around the mouth becomes well developed (as in the oligotrich *Strombidium* and the tintinnid ciliates). The peritrich ciliates have developed stalks and attach to plants and animals as a means of dispersal. Many peritrichs (e.g., *Epistylis*) form branching colonies.

The suctorian ciliates have completely lost their cilia in the adult phase. They have instead developed a stalk and many tentacles, which they use to capture passing prey, usually other ciliates. Because they cannot swim, they produce motile ciliated offspring, which settle elsewhere and then transform into the feeding stage, thus avoiding overcrowding.

Parasitic protozoans

Although the parasitic protozoans tend to be less structurally complex than free-living forms, considerable variation may occur during the course of their life cycles. *Plasmodium*, the malarial parasite that lives inside the liver and red blood cells of humans and the gut of its insect vector (the *Anopheles* mosquito), undergoes various changes in form through its asexual and sexual phases of development. Among the parasitic flagellates, the trypanosomes and their relatives (kinetoplastids), morphological variation occurs during the various stages of the life cycle in both the mammalian and insect hosts. Among species of *Leishmania*, which cause visceral leishmaniasis (kala-azar), cutaneous leishmaniasis (Oriental sore), and mucocutaneous leishmaniasis (espundia), two distinctly different forms occur. Rounded, nonflagellated forms called amastigotes feed and divide inside macrophage cells in different regions of the human body, while in the gut of the insect vector there occurs a flagellated form called a promastigote. Members of the genus *Trypanosoma*, which cause sleeping sickness and other diseases, have flagellated forms with different morphologies. At some stage in the life cycle, all assume the trypomastigote form—i.e., slender with part of the flagellum running over the body and attached to it by a finlike extension to form an undulating membrane. They may also occur as amastigote (stumpy flagella) or promastigote forms.

promastigote forms.

Distribution and abundance

oligotrich; *Halteria grandinella*

Protozoans have colonized a wide array of aquatic and terrestrial habitats from the Arctic and Antarctic to equatorial zones. In soils and bogs, protozoans form part of a complex microbial community. They live in the moisture films surrounding soil particles, so that they are actually aquatic organisms, even though living in a terrestrial environment. Between 10,000 and 100,000 organisms per gram of soil may inhabit fertile land; the relative proportions of each group vary depending on soil type and latitude. In Antarctic soils flagellates and testate (shell-dwelling) amoebae predominate, while in temperate woodland soils ciliates are more numerous.

In the open waters of lakes, estuaries, and the ocean, protozoans form an important component of the floating (planktonic) community. They are often present in densities of tens of thousands per litre of water. Most planktonic protozoa feed on bacteria, algae, other protozoans, and small animals. The most common planktonic protozoans include a variety of flagellated taxa, ciliates—especially oligotrichs and tintinnids (which live inside small tubes, or loricae)—and the exclusively marine foraminiferans and radiolarians. Foraminiferans have been found at depths of 4,000 metres (about 13,120 feet), and some protozoans have been observed around hydrothermal vents on the ocean floor.

Ecological and industrial importance of protozoans

Protozoans play important roles in the fertility of soils. By grazing on soil bacteria, they regulate bacterial populations and maintain them in a state of physiological youth—i.e., in the active growing phase. This enhances the rates at which bacteria decompose dead organic matter. Protozoans also excrete nitrogen and phosphorus, in the form of ammonium and orthophosphate, as products of their metabolism, and studies have shown that the presence of protozoans in soils enhances plant growth.

Protozoans play important roles in wastewater treatment processes, in both activated sludge and slow percolating filter plants. In both processes, after solid wastes are removed from the sewage, the remaining liquid is mixed with the final sludge product, aerated, and oxidized by aerobic microorganisms to consume the organic wastes suspended in the fluid. In the activated sludge process, aerobic ciliates consume aerobic bacteria, which have flocculated (formed loose aggregates, making them easily separated from liquid). In the percolating filter process, substrates are steeped in microorganisms, such as fungi, algae, and bacteria, which provide food for oxidizing protozoans. In the final stages of both processes, solids settle out of the cleaned effluent in the settlement tank. Treatment plants with no ciliates and only small numbers of amoebae and flagellates produce turbid effluents containing high levels of bacteria and suspended solids. Good-quality, clean effluents are produced in the presence of large ciliated protozoan communities because they graze voraciously on dispersed bacteria and because they have the ability to flocculate suspended particulate matter and bacteria.

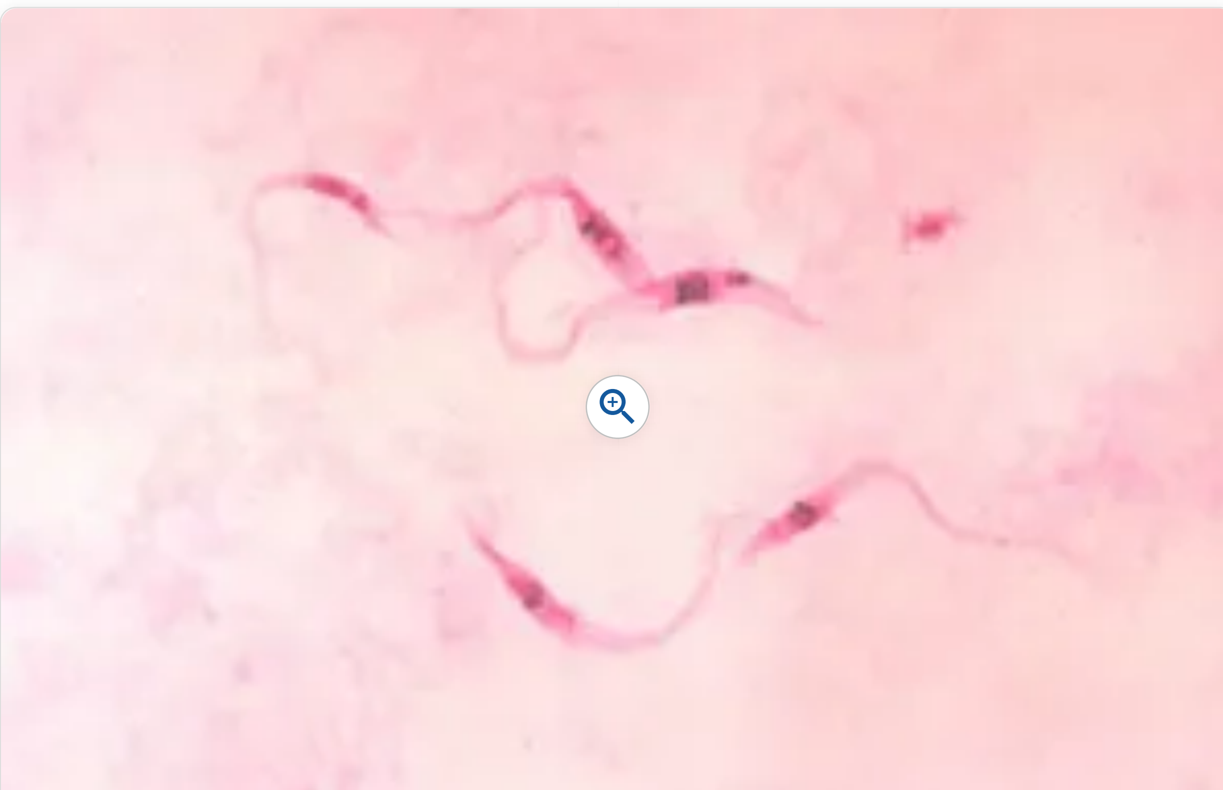
Protozoans probably play a similar role in polluted natural ecosystems. Indeed, there is evidence that they, by feeding on oil-degrading bacteria, increase bacterial growth in much the same way that they enhance rates of decomposition in soils, thereby speeding up the breakdown of oil spillages.

Some radiolarians and foraminiferans harbour symbiotic algae that provide their protozoan hosts with a portion of the products of photosynthesis. The protozoans reciprocate by providing shelter and carbon and essential phytonutrients. Many ciliates contain endosymbiotic algae, and one species, *Mesodinium rubrum*, has formed such a successful relationship with its red-pigmented algal symbiont that it has lost the ability to feed and relies entirely on symbiosis for its livelihood. *Mesodinium* often forms dense red blooms, or red tides, when it reaches high densities in water. Among the ciliates with endosymbionts, *Mesodinium* is the only completely photosynthetic species. Other ciliates achieve photosynthesis in another way. Although they do not have symbiotic algae, they consume plantlike flagellates, sequester the organelles that contain the plant pigments, and use them for photosynthesis. These organelles are known as plastids. Because the isolated plastids eventually age and die, they must be replaced continuously.

Protozoans and disease

Parasitic protozoans have invaded and successfully established themselves in hosts from practically every animal phylum. The best-studied parasitic species are those of medical and agricultural relevance. The trypanosomes, for example, cause a number of important diseases in humans. African sleeping sickness is produced by two subspecies of *Trypanosoma brucei* —namely, *T. brucei gambiense* and *T. brucei rhodesiense*. The life cycle of *T. brucei* has two hosts: a human (or other mammal) and the bloodsucking tsetse fly, which transmits the parasite between humans.

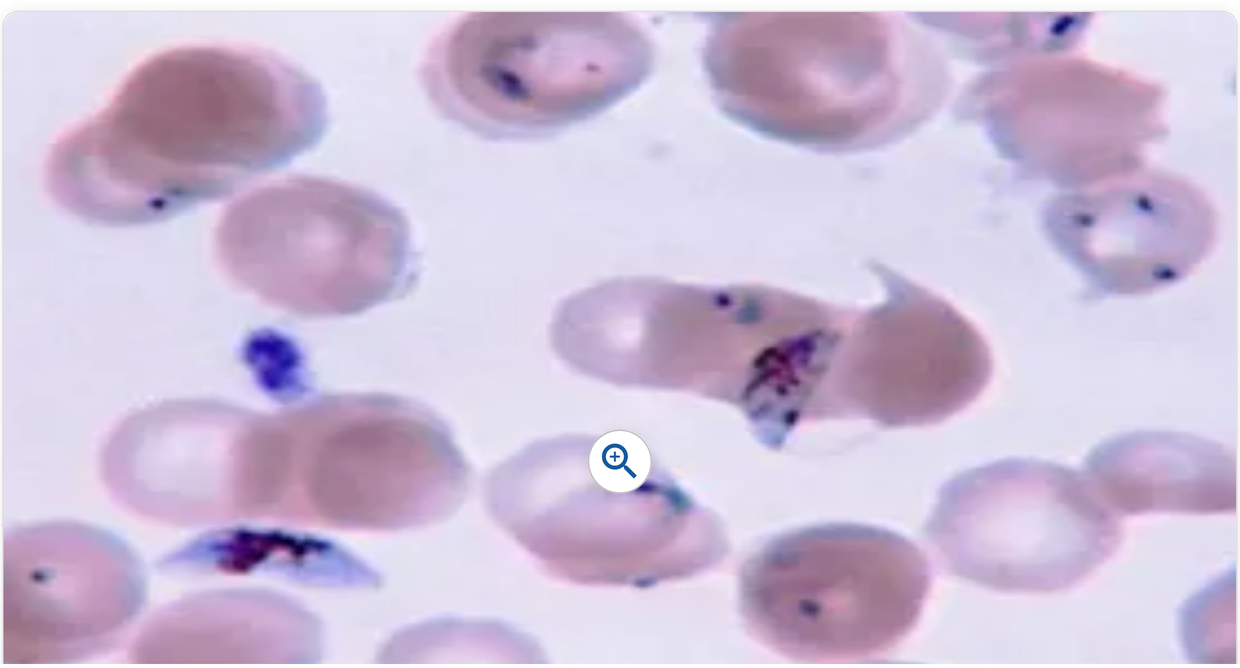
Trypanosomes live in the blood plasma and the central nervous system of humans and have evolved an ingenious way of fooling the immune system of the host. Upon contact with a parasite, the immune system generates antibodies that recognize the specific chemical and physical nature of the parasite and actively neutralize it. Just as the host's immune system is beginning to win the battle against the parasite and the bulk of the population is being recognized and destroyed by host antibodies, the parasite is able to shed its glycoprotein coat, which is attached to the cell surface, and replace it with a coat containing different amino acid sequences. Thus, the parasite essentially changes its makeup. These alternate forms are known as antigenic variants, and it has been estimated that each species may have as many as 100 to 1,000 such variants. The host must produce a new set of antibodies against each new variant, and in the meantime the parasite has time to replenish its numbers. Ultimately, unless the disease is treated, the parasite wins the battle and the host dies. Such antigenic variation makes the development of an effective vaccine against certain parasitic protozoan diseases virtually impossible.

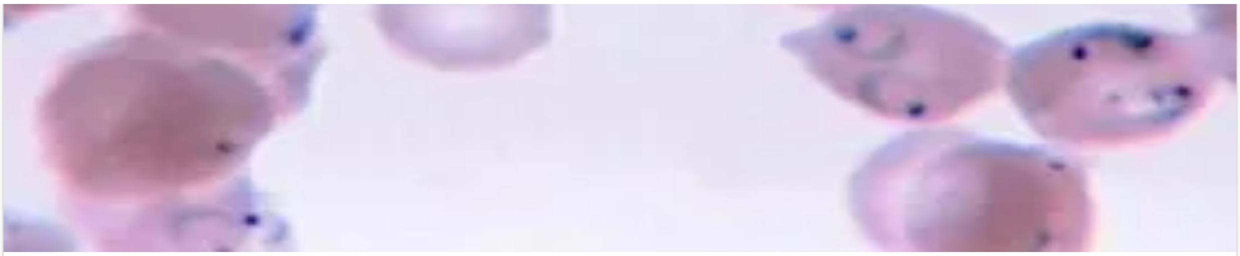


Trypanosoma cruzi

A close relative of *T. brucei*, *Trypanosoma cruzi*, causes Chagas disease, or American trypanosomiasis. Vector hosts include bugs of the genus *Rhodnius* and other arthropods, such as lice and bedbugs. In humans the nonflagellated (amastigote) form of the parasite lives inside macrophage cells, the cells of the central nervous system, and muscle tissue, including the heart, where it grows and divides. Short trypomastigote flagellated forms periodically appear in the blood, where they are readily taken up by the bloodsucking vector hosts. These flagellated forms do not divide in the blood; reproduction occurs only in the amastigote intracellular forms.

Relatives of the trypanosomes, species of the genus *Leishmania*, cause a variety of diseases worldwide, known as leishmaniasis. Like *T. cruzi*, these are intracellular parasites of the macrophage cells. The intermediate, or vector, hosts are a variety of sand fly species (subfamily Phlebotominae). In cutaneous leishmaniasis the infected macrophages remain localized at the site of the infection, causing an unsightly lesion, but in visceral leishmaniasis the infected macrophages are carried by the blood to the visceral organs. This latter disease is characterized by enlargement of the spleen and liver, leading to the distended abdomen that is typical of kala-azar. In mucocutaneous leishmaniasis the initial skin infection spreads to the mucous membranes of the face (the nose, mouth, and throat), producing a lesion that can cause destruction of part of the face.





blackwater fever

[Malaria](), which is caused by the apicomplexan protozoan *Plasmodium*, remains a serious disease despite measures that can be taken to control and

Form and function

The protozoan cell

The protozoan cell carries out all of the processes—including feeding, growth, reproduction, excretion, and movement—necessary to sustain and propagate life. The cell is enclosed in a membrane called the plasma membrane. Like all membranous structures in the eukaryotic cell, the plasma membrane is composed of mostly lipid and some protein molecules. The plasma membrane is a barrier between the cell cytoplasm and the outside liquid environment. Some substances, such as oxygen, readily pass through the membrane by diffusion (passive transport), while others must be transported across at the expense of energy (active transport). Cilia and flagella arising from the cell are also sheathed in the cell membrane; this is in contrast to bacterial flagella, which are not surrounded by a membrane.

The cell also has internal membranes, which are not as thick as the plasma membrane. Among these are the endoplasmic reticulum, whose membranes separate compartments of the cell, thereby allowing different conditions to be maintained in various parts—e.g., separation of deleteriously reactive substances. Enzymes are arranged on the surface of the endoplasmic reticulum; one such enzyme system catalyzes the activity of the ribosomes during protein synthesis. The Golgi apparatus is a cluster of flattened vesicles, or cisternae, associated with the endoplasmic reticulum. The vesicles are involved in membrane maturation and the formation and storage of the products of cell synthesis, as in the formation of scales on the surface coat of some flagellates, for example. The scales are formed within the Golgi and are transported by the vesicles to the plasma membrane, where they are incorporated onto the surface of the cell. The Golgi apparatus is poorly evident in most ciliates and absent from some amoebae.

All protozoans possess at least one nucleus, and many species are multinucleate. The genetic material DNA (deoxyribonucleic acid) is contained within the chromosomes of the nucleus. Each nucleus is bounded by two unit membranes possessing pores that permit the passage of molecules between the cytoplasm and the nucleoplasm. Most ciliates have two types of nuclei: micronuclei and macronuclei. The macronucleus is the somatic, or nonreproductive, nucleus. It is large and it is polyploid, meaning that it contains more than two sets of chromosomes (the condition of two sets of chromosomes is described as diploid). In contrast, the micronucleus is germinal (responsible for transfer of genetic information during sexual reproduction) and diploid. The macronucleus can be quite variable in shape, resembling in some species a string of beads or a horseshoe. It directs the normal functioning of the cell and usually disintegrates during sexual reproduction, to be re-formed from the products of micronuclear division after the sexual phase is completed.

Almost all protozoans contain double-membrane mitochondria; the inner membrane forms flattened, tubular, or discoidal extensions (cristae) into the mitochondrial interior in order to increase the surface area of the respiratory machinery, and the outer membrane forms the boundary of the organelle. Mitochondria are the sites of cellular respiration in most eukaryotes. Species

organelles, about 1–2 micrometres (μm; 1 micrometre = 3.9×10^{-5} inch) in length, are believed to be the site of fermentative processes. They contain enzymes that oxidize pyruvate to acetate and carbon dioxide, resulting in the release of hydrogen sulfide under anaerobic conditions.

Organisms that live in a liquid environment with a lower concentration of ions than is found in the interior of their cells—an osmotically hypotonic environment—gradually gain water if they equilibrate with their habitat. If this process remains unchecked, the cell swells and bursts. In protozoans the maintenance of the osmotic gradient between the cell cytoplasm and the environment is achieved by the contractile vacuole. These membrane-bound organelles are situated close to the plasma membrane. They swell with water periodically and then suddenly contract and disappear, forcing their contents from the cell in repeated cycles. In some amoebae and some flagellated taxa the contractile vacuole is formed when smaller vesicles combine with the main vacuole. In the ciliates the contractile vacuole is fed by a complex system of feeder canals, which are in turn fed by a complex network of vesicles and fine tubules within the cytoplasm.

Protozoans have transitory food or digestive vacuoles. The number of these membrane-bound cell organelles depends on the feeding habits of the organism. Some species may have many, whereas others may contain only one or two at any one time. In ciliates the food vacuoles form at the base of the cytopharynx, whereas in species without a cell "mouth," or cytostome, the vacuoles form near the cell membrane at the site where food is ingested.

Within the cell, structural proteins of various types form the cytoskeleton (cell skeleton) and the locomotory appendages. They include microfilaments formed of a contractile protein also found in the muscles of animals (actin) and cylindrical microtubules formed from filaments of the protein tubulin. Microtubules are particularly important in the structural formation and functioning of cilia and flagella. Filopodia of certain rhizarian species are supported by microtubules.