Protozoa

Introductory article

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Protozoa may be considered as (mostly) microscopic, essentially single-celled, eukaryotic organisms whose food is obtained by eating other organisms or their products. Some contain algal endosymbionts, or enslave plastids from their prey, and thus gain additional nutritional benefit from photosynthesis. Protozoa are no longer recognised as a taxonomic group and representatives can be found in all but one of the eukaryote supergroups. Protozoa play important roles in the ecology of aquatic habitats and soils, for example, by controlling bacterial populations and releasing nutrients for use by other organisms. As parasites, protozoa have very profound effects on humans, both directly and through their effects on domesticated animals. Some protozoa have shells or skeletal structures that can fossilise and certain types, particularly the foraminifera, are used in biostratigraphy and in locating oil deposits.

History and Introduction

The term protozoa, meaning 'first animals', was coined as a name for the unicellular animal-like organisms by Goldfuss in 1818. Protozoa, in the form of coin-shaped foraminiferan shells, must have been familiar to the ancient Egyptians, as they are seen in the rocks of which the pyramids are built, and similar centimetre-sized individuals are common in the Red Sea today. The effects of protozoan disease were also known to early civilisations; for example, Alexander the Great died of malaria, although the causative organism remained unknown until described by Laveran in 1880 (Mollaret, 1980). As most protozoa, or at least their characteristic structures, are too small to be seen with the naked eye, it was only after the invention of the microscope that the existence and nature of these organisms were realised. The first person to describe living protozoa was the early microscopist, Antony van Leeuwenhoek, whose account of *Euglena* in 1674 and of several other types of freshwater protozoa in 1676, written in letters to The Royal Society of London, are recognisable today (Corliss, 2002; **Figure 1**). **See also**: Euglena; Foraminifera; Leeuwenhoek, Antoni van; Malaria; Protozoan Pathogens of Humans

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Over the following century and a half, numerous unicellular organisms were described by microscopists, notably Müller (1786), Ehrenberg (1838) and Dujardin (1841). Some of these organisms were green and plant-like, whereas others were colourless and often ingested other organisms in an animal-like manner. The former were given the name Algae and the latter Protozoa, although protozoa were also commonly referred to as Infusoria and Rhizopoda. The accumulation of descriptions of these algae and protozoa led to a number of schemes of classification, an early comprehensive scheme being that of Haeckel (1866), whose kingdom (Archephylum) Protista included bacteria and sponges as well as algae and protozoa. By 1880, both Kent (1880–1882) and Bütschli (1880–1889) emphasised the animal-like nature of the protozoa. Bütschli recognised four main groups of protozoa: the amoebae (Sarcodina), Sporozoa (spore-forming parasites), Mastigophora (flagellates) and Infusoria (ciliates), which until the late twentieth century remained the framework of protozoan classification. **See also**: Amoeba

The further study of unicellular organisms, and attempts to classify them on the basis of both structure and physiology, led to a resurrection of the Protista as a taxonomic entity. Several groups, most prominently the euglenid flagellates and the dinoflagellates, contain both photosynthetic representatives classified as Algae and animal-like examples long claimed as Protozoa. Clearly, the separation of animals and plants downward from the animal and plant kingdoms to the unicellular level did not make sense; so many biologists argued that algal and protozoan groups must be united into a single kingdom. A name for this already existed – the Protista of Haeckel (1866). Although some people prefer the earlier name Protoctista, coined by Hogg in 1861 (e.g. Margulis *et al.*, 1989), the vast majority prefer and use the term Protista. **See also**: Dinoflagellates

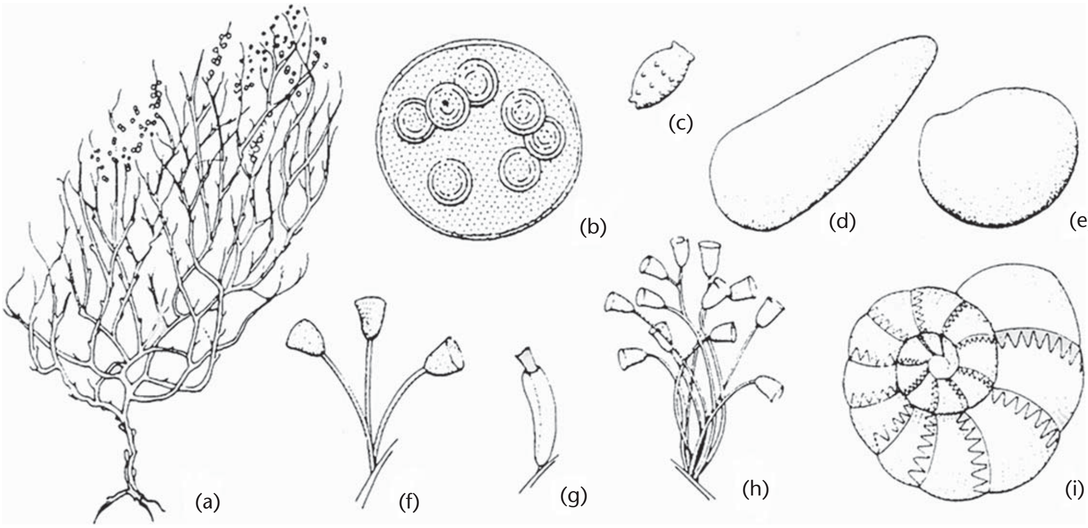

Figure 1 Antony van Leeuwenhoek's draftsman's figures (not drawn to a single scale) of eukaryotic protists: (a) *Anthophysa* (chrysomonad); (b) *Volvox* (chlorophyte); (c) *Coleps* (prostome ciliate); (d) *Cepedea* (opalinid); (e) *Nyctotheroides* (heterotrich ciliate); (f) *Vorticella* (solitary peritrich ciliate); (g) *Cothurnia* (loricate peritirch); (h) *Carchesium* (colonial peritrich); (i) *Elphidium* (formaminiferan). Reproduced from Corliss JO (2002). © Elsevier.

Protists do not have a comprehensive fossil record that can allow phylogenetic analysis, so protistologists have had to rely on structural and biochemical methods of inferring relationships. Comparisons of distinctive structures revealed by electron microscopy, of biochemical pathways studied by methods of classical biochemistry of cultured cells, and of the sequences of monomer units in specific classes of nucleic acid and protein molecules have provided the raw material for phylogenetic analysis among protists. The establishment of patterns of structure by electron microscopy is fundamental to the characterisation of the groups of protists. Analysis of molecular structures, especially comparisons of the sequence of nucleotides in small subunit ribosomal ribonucleic acid (SSU rRNA), has been a main tool for inferring the relationships between these groups, but authorities insist that these relationships should only be accepted after confirmation by other evidence, including structural homology. As a consequence, it is now recommended that the Protista, an assemblage long recognised to be of wider compass than, and not equivalent in status to, the kingdoms Animalia, Fungi and Plantae, should be subdivided. It is now generally agreed that the term protist should revert to being used descriptively for (principally) unicellular eukaryote organisms, rather than as the name of a taxonomic group. Indeed, in recent years eukaryote systematics has undergone a revolution, largely as a result of burgeoning molecular data. This has led to the recognition of at least five supergroups into which most eukaryote lineages have been classified. These are Archeaplastida (also known as Plantae), which includes the green and red algae and the land plants; Opisthokonta, which includes familiar groups such as the animals (Metazoa) and fungi, along with some less familiar heterotrophic protist groups; Amoebozoa which, as the name suggests, comprises various amoeboid groups; Excavata, which comprises exclusively of protist groups, both algal and protozoan, and Sar, which includes the brown seaweeds and various groups that were formerly classified as algae, protozoa or fungi (Adl *et al*., 2012). A sixth supergroup, the Hacrobia, which includes two major protist lineages, the haptophytes and the cryptomonads, has also been suggested (Okamoto *et al*., 2009), although its monophyly is uncertain (Burki *et al*., 2012). Thus, protozoan-like organisms can be found in all parts of the eukaryote tree of life with the exception of the supergroup Archaeplastida. **See also**: Electron Microscopy; Molecular Evolution; Molecular Phylogeny Reconstruction; Phylogeny Based on 16S rRNA/DNA; Protist systematics; Protozoan Evolution and Phylogeny; Protozoan Taxonomy and Systematics

What are Protozoa?

Protozoa are unicellular, heterotrophic eukaryotes. They range in size over some four orders of magnitude, from approximately 1 μm up to 10 mm or more, a bigger range than found among mammals. They are found in all types of habitat where free water is available – in fresh waters, the sea and in soils and sediments, as well as being found as parasites in animals of all types and, to a lesser extent, in plants. The need for free water relates to the fact that active protozoa have an area of naked membrane through which water would be easily lost. However, many protozoa produce resting stages, cysts or spores, protected by a secreted wall, which is usually waterproof. Such resting stages may be found in dry habitats as well as wet ones, and even floating in the air at concentrations averaging $2\,\mathrm{m}^{-3}$ (Corliss and Esser, 1974; Foissner, 2011).

Within a single cell membrane, protozoa possess a variety of organelles which perform all of the necessary functions of their life. As heterotrophs, they must take in organic molecules in some form, either as soluble molecules that pass through the membrane, or in particulate form by formation of a food vacuole within which the food particle is digested. The organic molecules taken in are partly converted to body structures and partly broken down in respiratory processes, which in aerobic protozoa involve the mitochondria, to release energy in a form that can be used to drive active processes in the cell. The enzymes to perform these processes, as well as the structural molecules of the cell, are formed in the cytoplasm at ribosomes, many of them associated with membranes of the endoplasmic reticulum system, using information derived from the nuclear genes. Smaller protozoa contain a single nucleus, and a single (haploid) or double (diploid) set of chromosomes, according to the species and the stage in the life cycle. Many larger protozoa contain additional nuclear material, either as multiple haploid or diploid nuclei, as polyploid nuclei or as multiple nuclei of different types, such as the diploid micronuclei and polyploid macronuclei of ciliates; it seems likely that there is some limit to the amount of cytoplasm that a single set of genes can control. The endoplasmic reticulum, and a specialised part of it called the Golgi complex, forms a compartment within the cell that has functions in secretion and membrane synthesis, including the packaging of digestive enzymes in lysosomes for delivery to food vacuoles. **See also**: Protozoan Sexuality

Most protozoa are motile, for purposes of food capture and/or locomotion, and possess specialised organelles of motility. All protozoa probably have both types of contractile mechanism found in eukaryote cells, that is, those based on microfilaments and those based on microtubules. The former are responsible for various cytoplasmic movements, ranging from slow shape changes and the formation of food vacuoles to some exceedingly rapid contractions. The latter are responsible for the movement of chromosomes during nuclear division as well as the bending of cilia and flagella, and some other shape changes. **See also**: Protozoan Organelles of Locomotion

Protozoa often contain symbiotic organisms or organelles of one sort or another. Frequently, these symbionts are bacteria whose influence on the life of the host cell is unknown, although they play important roles in the energy metabolism of anaerobic protozoa (Görtz, 2008; Fenchel and Finlay, 1992). In other cases they are other protists, or the remnants of protists; notable among these are the symbiotic algae that aid the nutrition of various green or brown ciliates and amoebae, and the plastids derived from remnants of symbiotic algae acquired by the ancestors of photosynthetic euglenids and dinoflagellates (Keeling, 2004). **See also**: Protozoan Symbioses

Finally, the cells of protozoa may contain structural elements deposited as an internal skeleton or as a thickened pellicle under the surface membrane, or they may secrete a protective shell, or theca, adhering tightly to the outside of the cell or a looser protective lorica.

The Diversity of Protozoa

The presence, type and organisation of the various cellular organelles, and the way they are used, provide the enormous diversity of protozoa. **See also**: Protozoan Diversity and Biogeography; Protozoan Organelles of Locomotion

Amoeboid or Pseudopodial Forms

Light microscopy reveals that some protozoa produce pseudopodia, which they use to surround and engulf potential food particles, to move over surfaces by cytoplasmic streaming or as fine filaments which aid flotation. These are amoeboid protozoa, and the shape of the pseudopodia, and the presence of any supporting skeleton of silica or protein fibres or of a secreted calcareous or siliceous shell or spines, characterise the various subgroups. Many, but not all, amoeboid forms are found within the supergroup Amoebozoa, including the classes Tubulinea, which typically have tubular pseudopodia and may be either naked (e.g. *Amoeba proteus*) or with a shell or test that is either proteinaceous or agglutinated (e.g. *Arcella*, *Difflugia*: **Figure 2a**); Discosea, which have flattened pseudopodia (e.g. *Vannella*) and Archamoebae, which are microaerophilic or anaerobic (e.g. *Entamoeba*). Amoeboid forms also include the slime moulds, of which there are two types. In the cellular slime moulds (e.g. *Dictyostelium*), small amoeboid cells aggregate together to form a multicellular mass, capable of migration as a colony until it reaches a suitable site for some cells to differentiate to form a stalk, and other cells migrate to the top of the stalk and form spores. In the syncytial slime moulds (e.g. *Physarum*), the colony grows as a multinucleate plasmodium, without any internal membranes, in which the internal cytoplasm flows to and fro; sporangia eventually grow from this, with a stalk and a cluster of spores at the top. The form of the stalked sporangia suggested to earlier writers that the slime moulds were related to fungi; however, this is a case of convergent evolution and no slime moulds are classified among the fungi. Slime moulds are generally smaller than a few centimetres, but some species may reach sizes of up to several square metres and masses of up to 30 g (Zhulidov *et al*., 2002). Examples of naked amoebae, testate amoebae and slime moulds can also be found in other supergroups, for example, Excavata and Sar. **See also**: Rhizopoda; Slime Moulds

Other types of pseudopodia include the needle-shaped axopodia and thin, net-like filopodia. The axopodia of the planktonic actinopod protozoa are supported by bundles of microtubular fibres. These are found largely in the freshwater Heliozoa (sun animalcules, e.g. *Actinophrys*; **Figure 2b**), where there is usually no additional skeleton, although secreted external spines may be present; in the marine Radiolaria (e.g. *Aulacantha*), where there is an additional internal skeleton of silica; and in the marine Acantharia (e.g. *Acanthometra*), where the internal skeletal

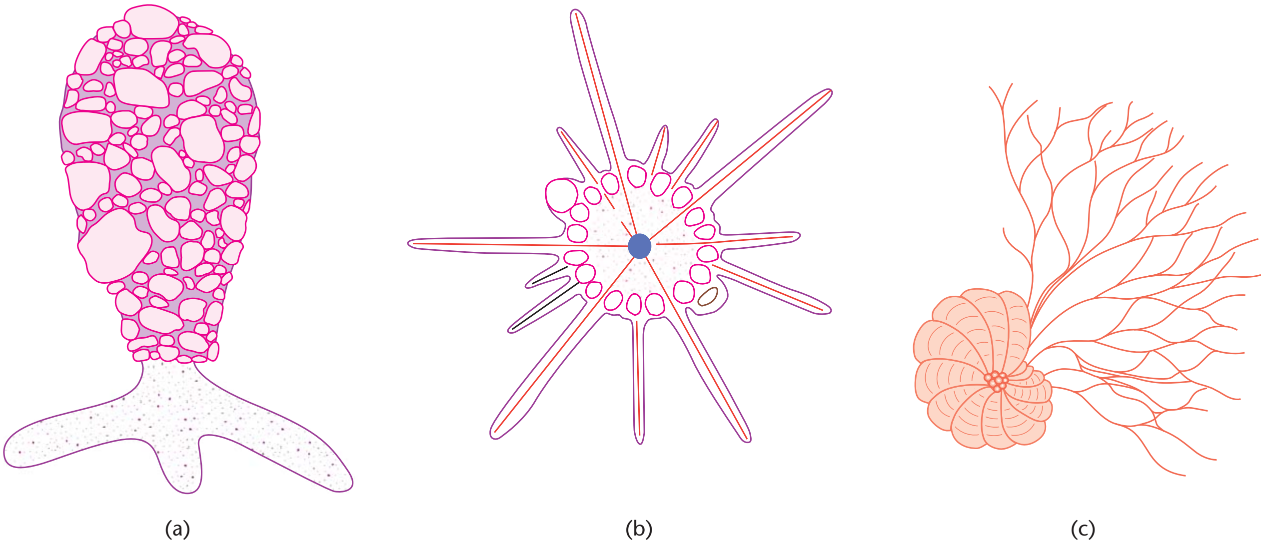

Figure 2 The form of pseudopodia in three types of amoeboid protozoa. (a) The testate amoeba *Difflugia* (approximately 250 μm long) has broadly lobed pseudopodia; these emerge from a shell into which sand grains are incorporated. (b) The heliozoan *Actinophrys* (cell body 40 μm diameter) has axopodia supported by bundles of microtubular fibres. (c) The foraminiferan *Elphidium* (shell up to 500 μm across) has fine reticulopodia forming a network.

spines are made of strontium sulfate. Thin, branching filopodia, which are studded with granules carried in the streaming cytoplasm, emerge from the shells of foraminifera (e.g. *Elphidium*; **Figure 2c**) to form a feeding network. In this planktonic and benthic, largely marine group the secreted shell may be calcareous, siliceous or organic, with or without the adhering particles collected from the environment. Amoeboid protozoa with shells and skeletons have left an important fossil record, the foraminifera providing particularly useful stratigraphical information on account of their small size and abundance (Jones, 1996). Such microfossils are also used in reconstructing past climate change. **See also**: Amoeba; Fossil Record; Silica

Ciliated and Flagellated Forms

Many protozoa propel water by waving fine hair-like projections called cilia or flagella; the former normally occur in large numbers and propel water parallel to the cell surface, whereas flagella are typically borne singly (or as two or four) and beat to propel water away from or towards the cell. Water propulsion generally provides locomotion, unless the cell is anchored to a surface, and also provides a water current from which food particles can be extracted by some intercepting surface. **See also**: Cilia and Flagella

Ciliate protozoa (Ciliophora) form a large and distinctive group in which cilia are arranged in various characteristic functional patterns associated with different modes of feeding or locomotion. The cilia are anchored in the cell cortex by fibre systems of characteristic types; the form of this 'infraciliature' and the distribution of the cilia and the extent to which the cilia are grouped into compound structures are used to distinguish different subgroups. In some of these, rows of cilia cover almost the whole cell surface, either with only simple cilia (e.g. *Holophrya*) or with simple cilia over most of the surface and compound cilia associated with the cell mouth for food collection (e.g. *Tetrahymena*; **Figure 3**). In others, the cilia may be more or less confined to one surface of the body, and again may be all simple (e.g. *Chilodonella*) or all compound (e.g. *Euplotes*). All the ciliates mentioned so far feed on particles (or on prey organisms ranging from bacteria to small metazoans) collected from water currents generated by cilia. Adult suctorian ciliates (e.g. *Discophrya*), however, lack cilia, and catch swimming protozoa, usually ciliates, on adhesive tentacles before sucking out their cytoplasmic contents (their larval cells are ciliated, but nonfeeding). Ciliates, typically, possess a unique nuclear dualism, generally with one or more diploid micronuclei and one or more polyploid macronuclei, and generally the pellicle of the cell has multiple membranes, including an inner pair that forms the alveoli. Of the four traditional protozoan groups originally proposed by Bütschli (1880–1889), only the ciliates are recognised as a monophyletic (natural) group. **See also**: Ciliophora; *Euplotes* (Dorsoventrally-Flattened Ciliates); Paramecium; Suctorians

The flagellates also use their flagella in distinctive ways in swimming and food collection, but other features of cell shape, pellicle or skeletal organisation and other special organelles are also used to distinguish the groups from one another. Dinoflagellates are one of the most familiar groups of flagellates which, together with the ciliates, are classified within a major Sar lineage called the alveolates. Dinoflagellates are best known as brown photosynthetic flagellates, but approximately half of this large group are heterotrophs and some are parasites; all have a distinctive arrangement (at least at some part of the life cycle) of one (posterior) longitudinal flagellum and a second

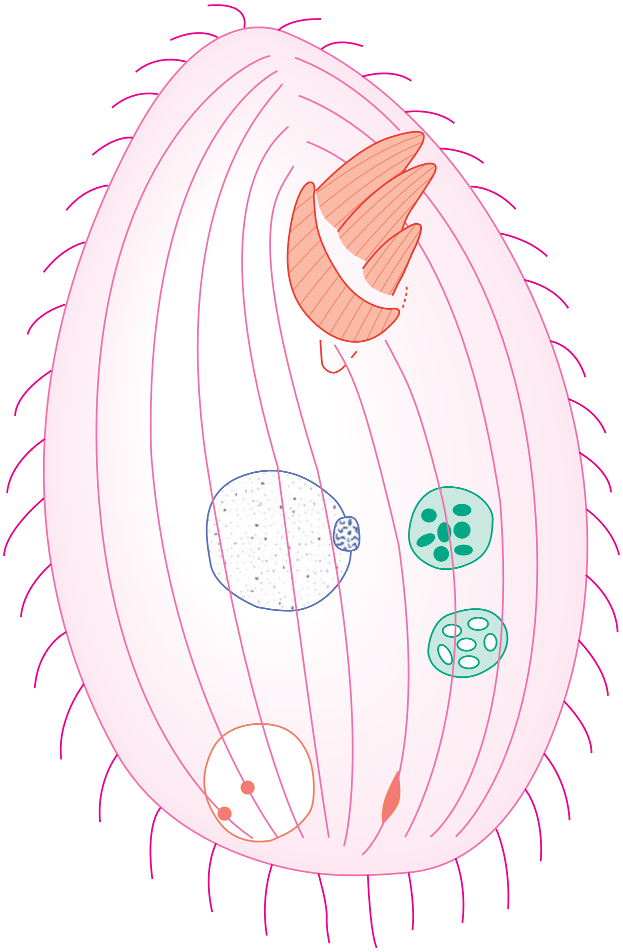

Figure 3 The ciliate *Tetrahymena* has rows of simple cilia and a group of three membranelles and one membrane around the cell mouth (cell approximately 50 μm long).

(transverse) flagellum, which is wound around the body, usually in an equatorial groove. Dinoflagellates also have a complex pellicle, including a system of alveoli, and unusual nuclei in which condensed, banded chromosomes are visible throughout the cell cycle. **See also**: Dinoflagellates; Mitosis

One characteristic flagellar pattern found on swimming cells is the presence of one anterior flagellum, which possesses two rows of stiff hairs along opposite sides thus enabling the flagellum to pull water towards the cell, and one posterior flagellum, which is smooth and trails more or less passively behind. This 'heterokont' condition typifies the unicellular Stramenopiles (supergroup Sar), as well as the gametes and zoospores of multicellular members of this group. Moreover, within the Sar supergroup are the cercomonads which are colourless amoeboid forms that may also possess flagella, usually with one projecting forwards and the other trailing behind. They are usually small (approximately 10 μm long) and commonly found in soil and freshwater where they feed on bacteria. **See also**: Chromista

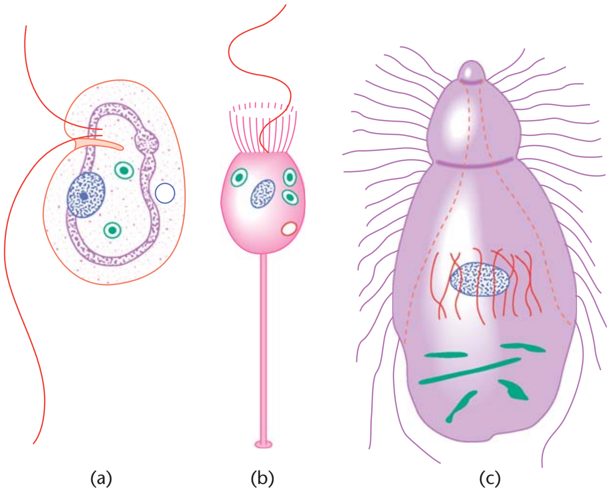

Figure 4 Examples of flagellate protozoa. (a) The kinetoplastid flagellate *Bodo* is approximately 10 μm long. (b) The collar flagellate *Codosiga* (cell 15 μm long) is attached by a stalk and has a single flagellum emerging from the centre of the collar. (c) The hypermastigote flagellate *Trichonympha* (approximately 200 μm long) has numerous flagella and ingests wood fragments at the posterior end.

The supergroup Excavata contains various lineages of protozoan protists whose members are typically flagellated. These include the euglenoids, kinetoplastids and parabasalians. The familiar green *Euglena* and other photosynthetic genera are included with a number of colourless flagellates of similar organisation in the euglenoid group, most of which are gliding cells moving over substrata on one (posterior) flagellum while the other flagellum projects forwards. Euglenoid cells have a stiffened pellicle, and those members of this group that ingest food particles also have a well-defined mouth. Closely related to euglenoid flagellates, and with somewhat similar body organisation and/or flagellation, are the kinetoplastids, an entirely colourless group which includes the sleeping sickness parasite *Trypanosoma* as well as free-living members like *Bodo* (**Figure 4a**). The parabasalians are almost all parasites or gut symbionts. The name refers to the presence of a system of (parabasal) fibres and massive Golgi bodies associated with the flagellar bases. Members of one subgroup of these flagellates typically have very large numbers of flagella and are only found in the hindguts of wood-eating insects like termites, where the lack of oxygen means that mitochondria would not be useful; these 'hypermastigote' (**Figure 4c**) and 'polymastigote' flagellates have hydrogenosome organelles, which are thought to have been derived from the mitochondria and which are involved in anaerobic respiration (Hiort *et al*., 2010). Another subgroup are the trichomonads (e.g. *Trichomonas*), with one recurrent flagellum associated with an undulating membrane and (usually) three free, forward flagella; these cells are generally small and include species parasitic in humans and other mammals. **See also**: Algal Photosynthesis; Euglena; Trichomonads; Trypanosoma

In a further distinctive group of flagellates (the Choanamonada of the supergroup Opisthokonta) there is only a single flagellum, whose base is surrounded by a 'collar' of filaments; these collar flagellates (e.g. *Codosiga*; **Figure 4b**) share their cell organisation with the flagellate cells of sponges, and there is growing evidence that the ancestor of the Metazoa was a choanomonad-like organism (Carr *et al.*, 2008). There are also flagellate members of the chlorophyte algae, most of which are green, but a few are colourless, which are now grouped with land plants and green seaweeds in the Chloroplastida (supergroup Archaeplastida): these flagellate cells have cell walls and two (sometimes four) similar flagella that move in breaststroke fashion. Two other well-known flagellated groups are the haptophytes (= haptomonads or prymnesiophytes) and the cryptophytes (= cryptomonads) of the putative supergroup Hacrobia. The haptophyte flagellates, including the coccolithophores, are characterised by the possession of two similar flagella and an adhesive coiled organelle called a haptonema, which looks like a flagellum but does not beat. The cryptophyte flagellates likewise have two nearly similar flagella. Both groups have members that take in organic food. **See also**: Cryptomonads; Haptophyta; Porifera (Sponges)

Parasitic Forms

Parasites can obtain a plentiful supply of food, provided they can solve problems of two types: they must successfully gain entry to a suitable host, and they must develop ways of evading the host's defences. These evasion techniques are numerous and varied among protozoa, and details should be sought in descriptions of particular parasites, but the diversity of methods of infection can be used in conjunction with structural features as a basis for classifying parasitic protists. Two characteristics of parasites are almost universal: massive reproduction to produce enormous numbers of infective individuals, and the production of resting infective stages, spores or cysts with a resistant coat, which gives protection from dehydration and from attack by digestive enzymes of the host, as most parasites depend on ingestion by the host in order to gain entry. The name Sporozoa was devised to include those parasitic protozoa that produce infective spores. However, structural study revealed that these organisms belong to several groups, and that some parasitic protozoa do not produce spore stages because they are transmitted between hosts by vector organisms, in the way that malaria is carried by mosquitoes. In addition, some parasites, including both spore-forming species and forms with naked infective stages, are found among the amoeboid, flagellate and ciliate groups, and resistant spores or cysts are formed by free-living protists of most groups, and not just parasites. More precision was therefore required. **See also**: Antigenic Variation in Microbial Evasion of Immune Responses; Protozoan Cysts and Spores; Protozoan Pathogens of Domestic and Companion Animals; Protozoan Pathogens: Identification; Protozoan Pathogens of Humans

Three main groups of entirely parasitic spore-producing protists that appeared to be protozoa were recognised by light microscopists on the basis of the type of spore, and of the form of the infective cell that emerges from the spore, backed up by features of the life cycle of the parasite. These distinguishing features have been supported and refined by ultrastructural comparisons using electron microscopy. The largest and most important group initially kept the name Sporozoa, and was characterised by the emergence from the relatively simple spore (**Figure 5a**) of a spindle-shaped 'sporozoite' (**Figure 5b**), which moves by gliding. Examples of such sporozoans include *Cryptosporidium*, which infects man and domestic animals, and *Eimeria*, an important parasite of birds. Similar sporozoite cells are injected into humans with the saliva of mosquitoes, infecting them with malaria (*Plasmodium*). A more accurate characterisation of these infective cells (and some other cells of these parasites) is the possession of an 'apical complex' of structures, only visible by electron microscopy, which are associated with the penetration of host cell membranes; recognition of this fact led to this group being named the Apicomplexa, although the words 'Sporozoa' and 'sporozoan' remain widely used. The Apicomplexa are known to have evolved from within the same lineage as ciliates and dinoflagellates and thus forms the third major group of alveolates (Sar supergroup). **See also**: Apicomplexa; Cryptosporidiosis; Eimeria; Plasmodium

In two other types of intracellular parasites long (but no longer) classed as Protozoa, the spores are more complex and contain eversible threads that play a role in infection of a new host (**Figure 5c** to **5f**). These are the Microsporidia, which probably evolved from zygomycete fungi and is now classified among the fungi, and the Myxozoa, which are a group of multicellular parasites that are now known to be severely modified members of the metazoan phylum Cnidaria (Adl *et al.*, 2012; Holland *et al.*, 2011; Keeling, 2003; Okamura *et al.*, 2002; Siddall *et al.*, 1995). **See also**: Microsporidians; Myxozoa

The Lives of Protozoa and Their Importance to Humans

Protozoa occupy a wide variety of ecological niches. Their small size enables them to grow and reproduce quickly under suitable conditions on relatively modest nutrient supplies, and permits rapid dispersal by currents in water or air or by migrating animals. Their activities are also ecologically important in a diversity of ways and have extensive influence on humans and their environment.

Among the photosynthetic protozoa, the largely freshwater euglenids can turn ponds and puddles, and even banks of mud, temporarily green, but probably have limited ecological importance. By contrast, the photosynthetic dinoflagellates exert important influences in at least three

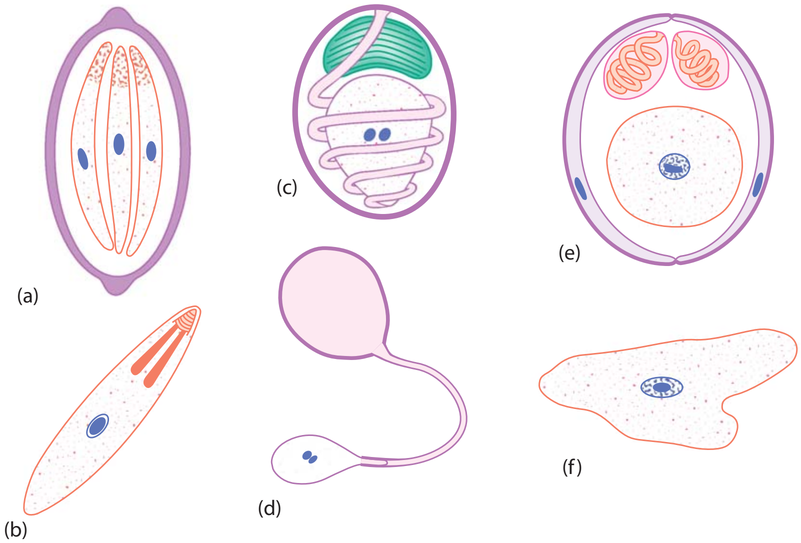

Figure 5 Spores and infective cells of parasitic protozoa and other microeukaryotic groups formerly classified as protozoa. (a) A spore of an apicomplexan (approximately 20 μm long) containing several sporozoites; these emerge as gliding cells (b) with an apical complex, seen here at the upper end. (c) A microsporidian spore (approximately 4 μm long) contains a laminated structure and an inverted and coiled polar thread surrounding the infective cell; on germination of the spore the tubular polar thread everts and penetrates a host cell so that when the infective amoeboid cell passes through the tube (d) it enters the cytoplasm of the host cell. (e) A myxozoan spore (approximately 20 μm long) with a multicellular spore case containing two polar capsules and a single infective cell; the latter emerges as an amoeboid cell (f) in the gut of the host.

ways. First, in the sea, and sometimes in freshwater lakes, the primary production by dinoflagellates forms a substantial component of the annual total planktonic production. Second, the photosynthetic activity of dinoflagellates that are symbiotic in animals, particularly in corals, some molluscs and planktonic radiolaria and foraminifera, enables these animal hosts to live and compete strongly in low-nutrient habitats. Third, a number of the photosynthetic dinoflagellates, particularly those producing blooms visible as 'red tides', synthesise toxic products that are responsible for fish kills and for paralytic shellfish poisoning of people eating molluscs that have fed on the blooms of dinoflagellates. Other types of flagellate, ciliate and amoeboid protozoa may contain symbiotic algae, enabling them to compete more successfully and either to occupy habitats with very low nutrient levels or to form blooms, like the red ciliate *Mesodinium*, which can become so dense in inshore waters and estuaries that their respiratory demand at night can suffocate other plankton. **See also**: Eutrophication of Lakes and Rivers; Harmful Algal Blooms

Protozoa that depend for their nutrition on the absorption of dissolved organic molecules only thrive in special situations. Most protozoa that live as parasites or as symbionts within other organisms obtain their nourishment in this way, and have their ecological influence through their detrimental or beneficial effects on their hosts, rather than having any direct environmental impact. Many free-living protozoa are probably able to use dissolved organic molecules, but they have a low surface area to volume ratio compared with bacteria, which specialise in this form of nutrition, and probably never compete successfully with bacteria. Some species of protozoa do flourish, however, in situations where the decomposing activities of bacteria and fungi provide a temporary abundance of dissolved organic molecules. **See also**: Protozoan Symbioses; Soils and Decomposition

More successful in these situations are the protozoa that feed on the bacteria themselves. Bacterivorous amoebae (including foraminifera), flagellates and ciliates are able to detach bacteria from surfaces, where the bacteria tend to grow best, but there are many ciliates and flagellates that capture suspended bacteria. In open waters, and especially in the sea, small flagellates are credited with the ability to control the concentration of planktonic bacteria, bacterial numbers stabilising at between 10^5 and $10^6\,\mathrm{mL}^{-1}$ and flagellate numbers approximately $10^3\,\mathrm{mL}^{-1}$, in the absence of substantial organic inputs. Bacterivorous ciliates are rarely as important, except where there is local organic enrichment, because the ciliates require higher bacterial concentrations in order to thrive. One such example is biological wastewater treatment processes where bacterial grazing by ciliates is essential for maintaining effluent quality (Curds, 1973). Bacterivorous protozoa are important in several ways, both in aquatic habitats and in soils: the cropping of bacteria helps to maintain bacterial populations in active growth; protozoa limit bacterial numbers, including those of pathogens; protozoa 'package' organic material into larger particles, capable of being efficiently grazed by small metazoa, thereby helping to channel bacterial biomass into the consumer parts of aquatic food webs; the digestion of bacterial biomass by protozoa and their subsequent metabolism releases approximately 75% of mineralised nutrients in a form that can be used in growth by plants and bacteria. **See also**: Protozoan Ecology

Ciliates and the larger dinoflagellates are important grazers on planktonic algae. In temperate and some polar waters, blooms of larger planktonic algae for a brief season provide an excess of food, much of which is cropped by metazoa and their larvae, or sinks to the sea floor to nourish the benthos. However, most of the time and in most waters smaller algae predominate, and protozoa are the main grazers, cropping virtually the whole of the daily production of photosynthetic flagellates and diatoms of the plankton. This grazing also packages organic matter into a form that is preferred by many predators, with a higher protein to carbohydrate ratio, and recycles a proportion of mineral nutrients that can sustain plant growth. Benthic algae similarly provide food for ciliates and dinoflagellates, and also for amoebae and other larger flagellates like euglenids.

Although some of the grazing protozoa that eat algae are purely herbivorous, others are omnivores that will eat other protozoa and detritus, or even small metazoa, as well as algae. Thus the larger ciliates, such as *Stentor*, are omnivores catching rotifers and small larvae, as well as flagellates and small ciliates, in their powerful feeding current. Heliozoa and radiolaria catch crustaceans and even fish eggs and small larvae as well as protozoan prey, which make contact with their extended axopodia. By contrast, some protozoa pursue (e.g. *Didinium* chasing *Paramecium*) or lie in wait for (e.g. a suctorian trapping a ciliate on its tentacles) a much more limited range of prey.

Most animals and many plants are subject to infection by parasitic or symbiotic protozoa. Examples of the benefits of symbiotic protozoa are the flagellates that help wood-eating insects to digest wood, and the ciliates that abound in the rumen of ruminant mammals and assist in their digestion; in both cases volatile fatty acids are the main protozoan product that is used by the host. Examples of protozoan parasites directly harmful to humans include apicomplexans like the malarial parasites (*Plasmodium* spp.) and *Toxoplasma*, flagellates like *Trypanosoma*, which cause sleeping sickness and Chagas disease, and amoebae that cause forms of dysentery and meningitis. Many more infect domestic animals, for example, mammals, birds and even insects like bees and silkworms, and wild animals like fish that are cropped by humans, causing epidemics and/or loss of production. Less direct effects are exerted by parasitic protozoa on animals of ecological importance, for example, those that influence major food chains or human food supply; these may be beneficial when they infect pests, for example, locusts. **See also**: Protozoan Pathogens of Domestic and Companion Animals; Protozoan Pathogens of Humans

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