

Protozoa

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Publication year: 2014

A group of eukaryotic microorganisms traditionally classified as one of the five animal kingdoms.

Although the name signifies primitive animals, some protozoa (phytoflagellates and slime molds) show enough plantlike characteristics to justify claims that they are plants. This apparent conflict may be reconciled to some extent by considering protozoa as descendants of microorganisms which preceded plants and animals. Such an assumption might account for *Euglena gracilis*, a green flagellate which can fix carbon dioxide (CO₂) in light as algae do but, unlike algae, can also carry on a plantlike fixation in darkness. In addition, *E. gracilis* can fix carbon dioxide by pathways characteristic of animals. Inclusion of such metabolically unspecialized organisms, along with certain photoautotrophic chlorophyll-bearing species, might imply that the phylum is partly an arrangement for taxonomic convenience rather than a phylogenetically homogeneous group.

Protozoa are almost as widely distributed as bacteria. Free-living types occur in soil, wet sand, and in fresh, brackish, and salt waters. Protozoa of the soil and sand live in films of moisture on the particles. Habitats of endoparasites vary. Some are intracellular, such as malarial parasites in vertebrates, which are typical Coccidia in most of the cycle. Other parasites, such as *Entamoeba histolytica*, invade tissues but not individual cells. Most trypanosomes live in the blood plasma of vertebrate hosts. Many other parasites live in the lumen of the digestive tract or sometimes in coelomic cavities of invertebrates, as do certain gregarines. *See also:* COCCIDIA; GREGARINIA; TRYPANOSOMATIDAE.

Many protozoa are uninucleate, others binucleate or multinucleate, and the number also may vary at different stages in a life cycle. Size ranges from less than 3 micrometers to a number of centimeters, as in various Mycetozoia. Colonies are known in flagellates, ciliates, and Sarcodina. Although marked differentiation of reproductive and somatic zooids characterizes certain colonies, such as *Volvox*, protozoa have not developed tissues and organs.

Taxonomy

Various systems of classification have been proposed, and none is yet accepted by all protozoologists. One of those sponsored by the Society of Protozoologists follows:

Phylum Protozoa

Subphylum Sarcomastigophora

Superclass Mastigophora

Class Phytamastigophorea

Order Chrysomonadida

Order Silicoflagellida

Order Coccolithophorida

Order Heterochlorida

Order Cryptomonadida

Order Dinoflagellida

Order Eбриida

Order Euglenida

Order Chloromonadida

Order Volvocida (Phytomonadida)

Class Zoomastigophorea

Order Choanoflagellida

Order Bicosoecida

Order Rhizomastigida

Order Kinetoplastida

Order Retortamonadida (Protomastigida)

Order Diplomonadida

Order Oxymonadida

Order Trichomonadida

Order Hypermastigida

Superclass Sarcodina

Class Rhizopodea

Subclass Lobosia

Order Amoebida

Order Arcellinida

Subclass Filosia

Order Aconchulinida

Order Gromiida

Subclass Granuloreticulosia

Order Athalamida

Order Foraminiferida

Order Xenophyophorida

Subclass Mycetozoia

Order Acrasida

Order Eumycetozoida

Order Plasmodiophorida

Subclass Labyrinthulia

Class Piroplasma

Class Actinopodea

Subclass Radiolaria

Order Porulosida

Order Oculosida

Subclass Acantharia

Order Acanthometrida

Order Acanthophractida

Subclass Heliozoia

Order Actinophryida

Order Centrohelida

Order Desmothoracida

Subclass Proteomyxidia

Subphylum Sporozoa

Class Telosporea

Subclass Gregarina

Order Archigregarinida

Order Eugregarinida

Order Neogregarinida

Subclass Coccidia

Order Protococcida

Order Eucoccida

Suborder Adeleina

Suborder Eimeriina

Suborder Haemosporina

Class Toxoplasmea

Order Toxoplasmoda

Class Haplosporea

Order Haplosporida

Order Sarcosporida

Order Entodiniomorphida

Subphylum Cnidospora

Class Myxosporidea

Order Myxosporida

Order Actinomyxida

Order Helicosporida

Class Microsporidea

Class Ciliatea

Subclass Holotrichia

Order Gymnostomatida

Order Trichostomatida

Order Chonotrichida

Order Apostomatida

Order Astomatida

Order Hymenostomatida

Order Thigmotrichida

Subclass Peritrichia

Subclass Suctoria

Order Suctorida

Subclass Spirotrichia

Order Heterotrichida

Order Oligotrichida

Order Tintinnida

Order Entodiniomorphida

Order Odontostomatida

Order Hypotrichida

Morphology

A protozoan may be a plastic organism (ameboid type) but changes in form are often restricted by the pellicle. In *Trypanosoma lewisi*, parallel microtubules beneath the pellicle may support this layer and may also, as probably contractile structures, cause the typical undulations of these flagellates. Although protozoan form varies considerably, there is a tendency toward universal symmetry in floating species and radial symmetry in sessile types. Bilateral symmetry is rare; most swimmers show appreciable spiral torsion.

A protective layer is often secreted outside the pellicle, although the pellicle itself may be strengthened by incorporation of minerals. Secreted coverings may fit closely, for example, the cellulose-containing theca of Phytomonadida and Dinoflagellida, analogous to the cell wall in higher plants. The dinoflagellate theca (**Fig. 1a**) may be composed of plates arranged in a specific pattern. Tests, as seen in Rhizopodea (Arcellinida, Gromida, Foraminiferida), may be composed mostly of inorganic material, although organic (chitinous) tests occur in certain species. Siliceous skeletons, often elaborate, characterize the Radiolaria (**Fig. 1d** and **Fig. 2a-e**). A vase-shaped lorica, from which the anterior part of the organism or its appendages may be extended, occurs in certain flagellates (**Fig. 1b**) and ciliates (**Fig. 1c**). Certain marine ciliates (Tintinnida) are actively swimming loricate forms.

Colonies and aggregates

An important feature of colonies is the material which holds the component zooids together. In spheroid colonies (**Fig. 3**) a matrix is secreted during development of the colony. Spheroid colonies of a few Radiolaria (*Colozoum*), unusually large examples, may measure 4–6 cm across. In arboroid colonies (**Fig. 4b** and **f**) a branching pattern is produced by a branching stalk (**Fig. 4b**) or by attachment of loricae to one another (**Fig. 1b**). Dispersal of such colonial species sometimes involves migratory stages. In certain spheroid colonies of *Pleodorina* (**Fig. 3b** and **c**) and *Volvox*, reproductive and somatic zooids are differentiated. More often members of a colony are similar. In

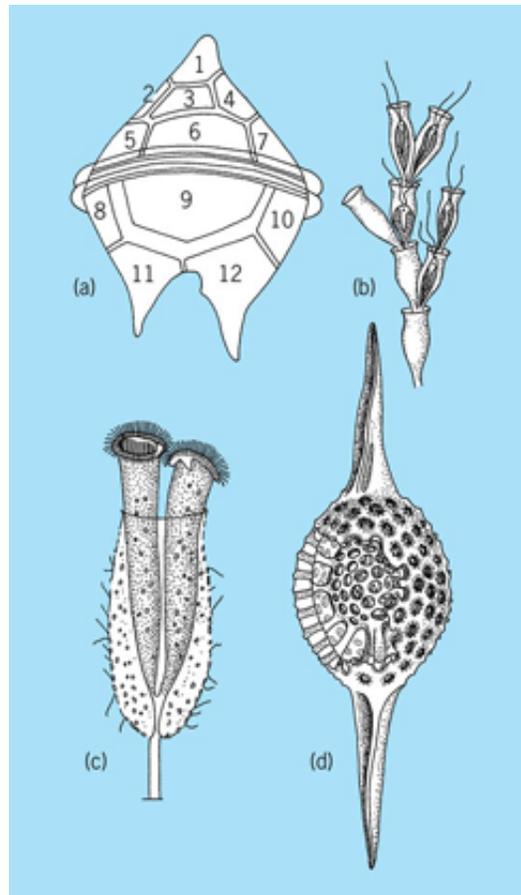


Fig. 1 External coverings of protozoa. (a) Theca of dinoflagellate (*Peridinium*), showing separate plates. (b) Lorica of a colonial chryomonad, *Dinobryon*. (c) Two zooids within a lorica of a peritrich, *Cothurnia*. (d) A radiolarian skeleton, siliceous type. (After L. H. Hyman, *The Invertebrates*, vol. 1, McGraw-Hill, 1940)

in addition to colonial types, certain protozoa may form aggregates by not separating promptly after fission. Palmella stages of Phytomonadida, analogous to spheroid colonies, are aggregates of nonflagellated organisms. Chains of *Gonyaulax catenella* and certain other Dinoflagellida are another type of aggregate.

Flagella

These organelles occur in active stages of Mastigophora and flagellated stages of certain Sarcodina and Sporozoa. A flagellum consists of a sheath enclosing a matrix in which an axoneme extends from the cytoplasm to the flagellar tip. In certain groups the sheath shows lateral fibrils (mastigonemes) which increase the surface area and also may modify direction of the thrust effective locomotion. In electron micrographs axonemes show two central and nine pairs of peripheral microtubules. The base (blepharoplast) in certain species may contain only nine peripheral triplets. The blepharoplast is considered a self-replicating structure from which new flagella arise in fission. Flagellar number ranges from one or two for most free-living species to many as seen on certain

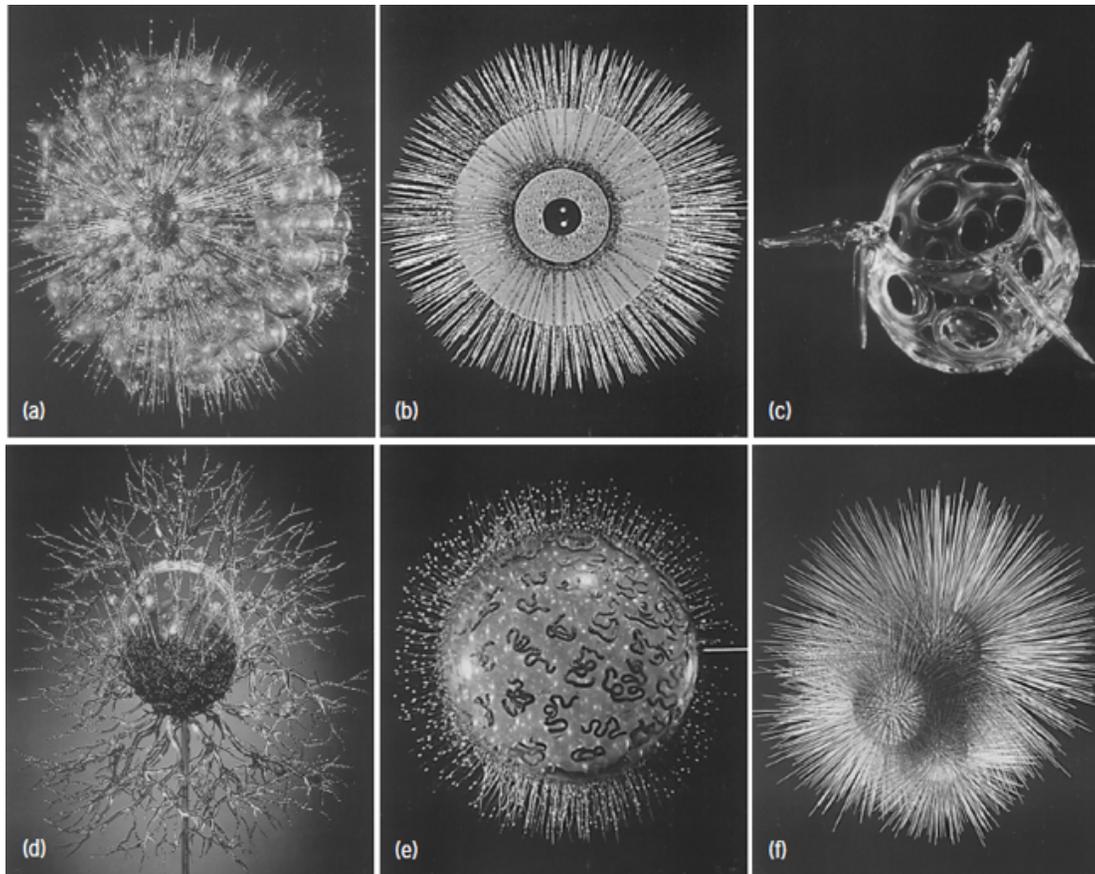


Fig. 2 Glass models of marine protozoa. Radiolarian types: (a) *Trypanosphaera transformata* (Indian Ocean); (b) *Actissa princeps* (Indian and Pacific oceans); (c) *Peridium spinipes* (Pacific Ocean); (d) *Lithocircus magnificus* (Atlantic Ocean); (e) *Collozoum serpentinum* (Atlantic Ocean). (f) Foraminiferan type: the pelagic *Globigerina bulloides* (which is found in all seas). (American Museum of Natural History)

symbionts of termites and wood roaches. Most flagella extend forward in swimming; others extend posteriorly, sometimes driving the body forward, sometimes serving as a ski in gliding, or forming the margin of an undulating membrane. Certain organelles, as the kinetoplast (Kinetoplastida), axostyle, parabasal body (Trichomonadida), or sometimes other structures, may be attached to or adjoin the blepharoplasts. *See also*: CILIA AND FLAGELLA; KINETOPLASTIDA.

Flagellar movements include planar sinusoidal waves, helical waves, and lateroposterior strokes. When a planar wave travels from base to tip, the force is directed basally, pushing the organism (*Ceratium* and others). However, a base-to-tip beat pulls *Ochromonas*, a chrysomonad, the mastigonemes changing a potential push into a pull. The flagellate is pulled (trypanosomes) when a planar wave travels from tip to base. Helical waves from tip to base (trichomonad undulating membrane) push the flagellate. A similar wave, from tip to base, pulls in *Peranema*. Lateroposterior beating (*Monocercomonas neosepsorum* and certain other trichomonads) more or less resembles a breast stroke in human swimming. An unusual jet propulsion observed for *Medusochloris* sp., a

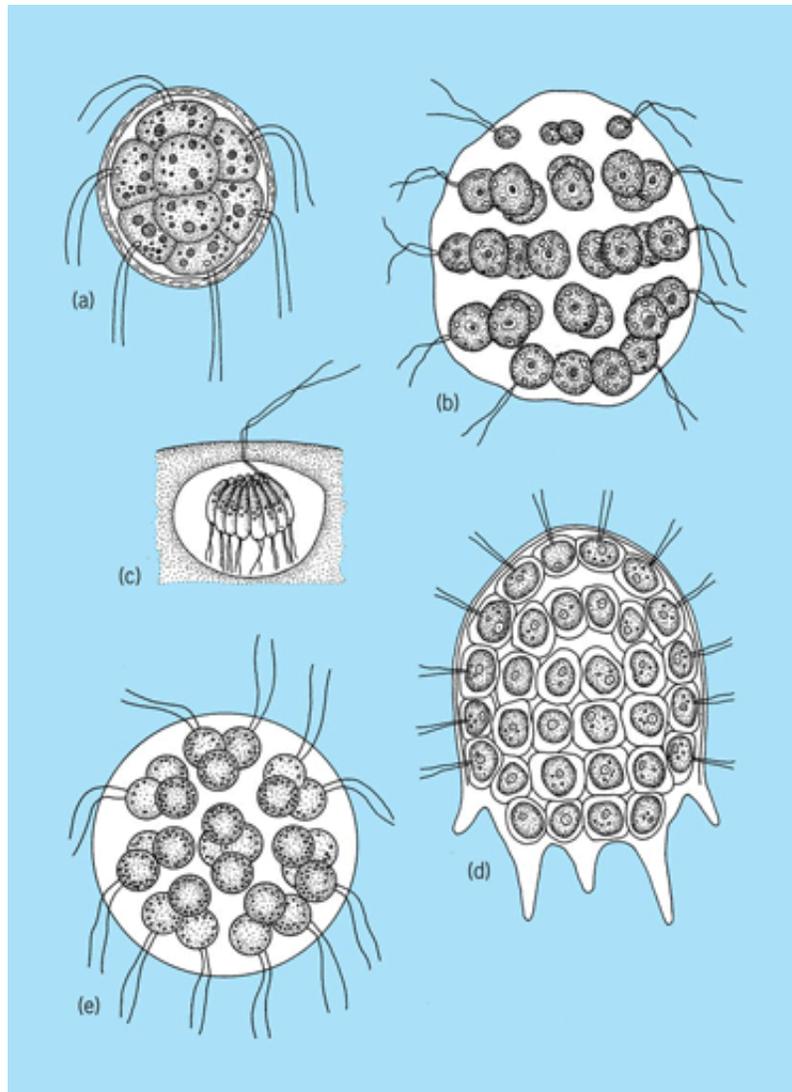


Fig. 3 Colonies of Phytomonadida. (a) *Pandorina*. (b) *Pleodorina illinoisiensis*. (c) Sperm packet, *Pleodorina*. (d) *Platydorina caudata*. (e) *Eudorina*. (After L. H. Hyman, *The Invertebrates*, vol. 1, McGraw-Hill, 1940)

phytomonad, involves contractions of a medusa-shaped body. Another substitute for flagellar drive is seen in *Mixotricha paradoxa*, a parasite of an Australian termite. Most of the body is covered with “brackets,” each of which bears a posterior pit into which the tip of a spirochete fits. Coordinated undulations of the spirochetes in metachronal waves, beginning at the anterior end of the flagellate, drive the organism smoothly forward. See also: MASTIGOPHORA.

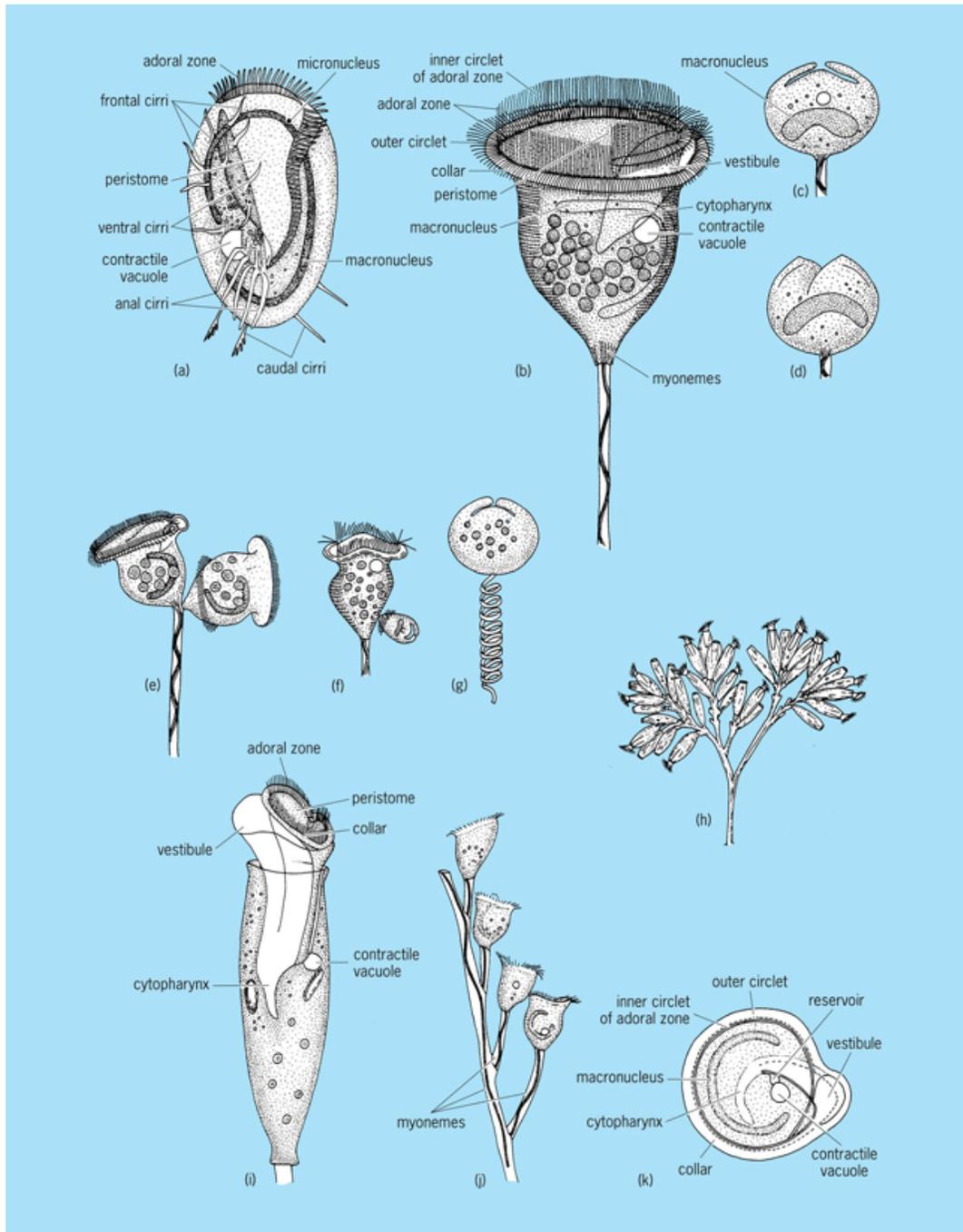


Fig. 4 Hypotricha and Peritricha. (a) *Euplotes*. (b) *Vorticella*. (c–e) Stages of fission in *Vorticella*. (f) Macro- and microconjugants in *Vorticella*. (g) *Vorticella*, stalk contracted. (h) Arboroid colony, *Opercularia*. (i) Zooid from *Opercularia* colony. (j) Portion of colony (*Carchesium*) showing stalk muscle. (k) Peristome of *Vorticella*, seen from above. (After L. H. Hyman, *The Invertebrates*, vol. 1, McGraw-Hill, 1940)

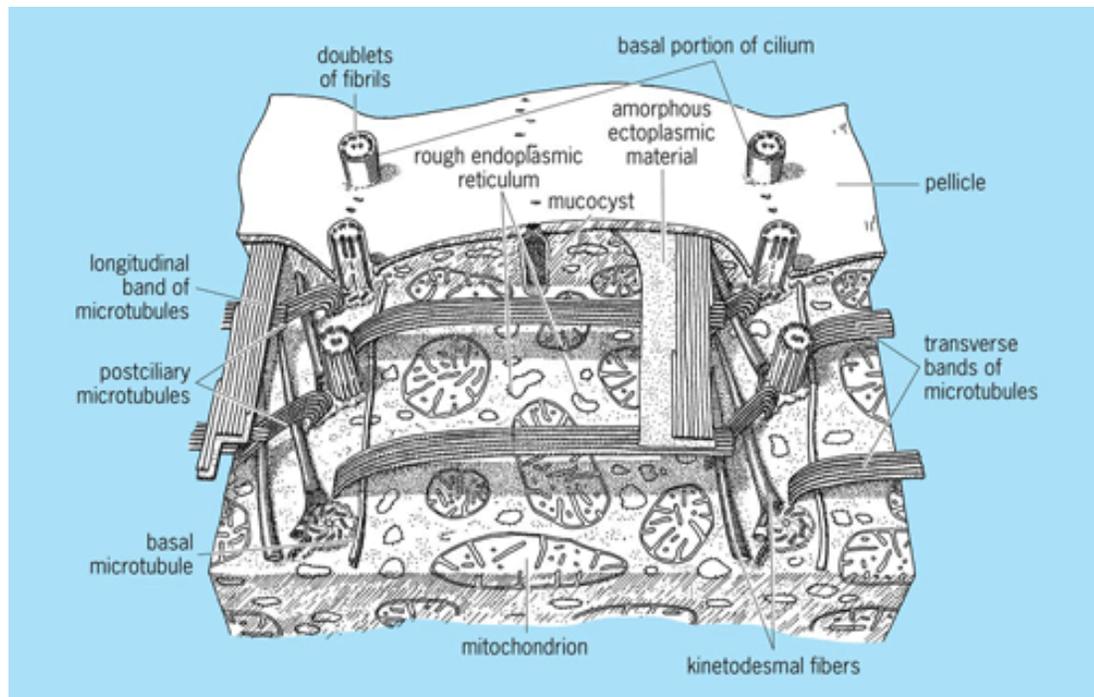


Fig. 5 Schematic of cortex of *Tetrahymena pyriformis*. (After R. D. Allen, *J. Protozool.*, 14:553–565, 1967)

Cilia

Although typically shorter than flagella, cilia are similar in structure, even to the fibrillar triplets in the base (basal granule and kinetosome). Multiplicity of cilia entails complex fibrillar systems. It has been suggested that several sets of fibrils help support the cortex and ciliary system. A more delicate fibril, or tubule (**Fig. 5**), running along each row of basal granules (*Tetrahymena*) seemingly offers little support and may, as suggested, function in coordination (**Fig. 5**). Such ciliates as hypotrichs, with compound organelles, may have quite complex fibrillar systems. Compound ciliary organelles represent fused bundles or rows of cilia, with the basal granules detectable in basal plates of the organelles. Membranes (longitudinal rows) occur along the right margin of the buccal cavity, if they are present. Membranelles (transverse rows) often form an adoral zone (**Fig. 4a**) along the left margin of the buccal cavity. Cirri (**Fig. 4a**), typically ventral, are fused tufts of cilia, several to 50 or more in large cirri, important in locomotion.

Cortical myonemes (**Fig. 6**) are well developed in certain large ciliates (*Spirostomum* and *Stentor*). Similar cortical myonemes, composed of several to a dozen or more fibrils, occur in various gregarines. Ectoplasmic myonemes of certain ciliates also show longitudinal fibrils. Analogous stalk “muscles” occur in the stalks of *Vorticella* and certain colonial ciliates (*Carchesium* and *Zoothamnium*). See also: CILIOPHORA.

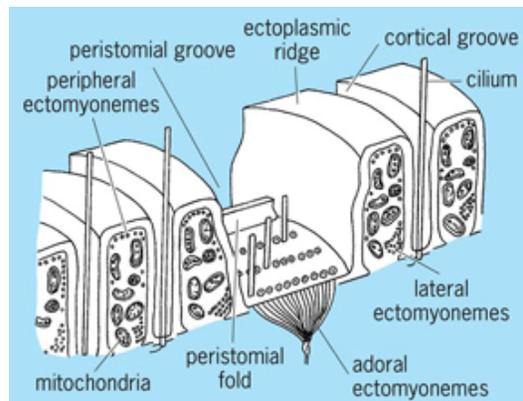


Fig. 6 Diagrammatic reconstruction of the cortex of *Spirostomum ambiguum*. (After H. E. Finley, C. A. Brown, and W. A. Daniel, *J. Protozool.*, 11:264, 1964)

Pseudopodia

Two major types have been described, the contraction-hydraulic and the two-way flow types. The first are lobopodia with rounded tips and ectoplasm denser than endoplasm. The larger ones commonly contain granular endoplasm and clear ectoplasm.

According to the contraction-hydraulic theory, pseudopodia of *Amoeba proteus* arise as a result of pressure from the contracting ectoplasm on the endoplasm, forcing the latter forward, away from the posterior contraction. Local weakening of the ectoplasm results in a bulge, or developing pseudopodium. Endoplasm reaching the tip of the growing pseudopodium is diverted to the ectoplasm and converted into gel, thus becoming part of the ectoplasm. In the meantime, ectoplasm at the other end is being converted into endoplasm, which flows forward again under pressure from the ectoplasm.

Two-way flow pseudopodia include reticulopodia of Foraminiferida and related types, filoreticulopodia of Radiolaria, and axopodia of certain Heliozoia. Axopodia of some genera show an axoneme composed of microtubules extending from the centroplast; in others, of a cylinder surrounded by microtubules. In addition, similar filoreticulopodia (no axonemes) occur in Radiolaria and certain other groups. In all these, cytoplasmic flow in opposite directions occurs on opposite sides of a pseudopodium. *See also:* HELIOZOIA; RADIOLARIA; SARCODINA.

Trichocysts

At maturity these lie in the cortex of certain ciliates and flagellates. Mucocysts (**Fig. 5**) seem homogeneous in some ciliates in electron micrographs; in others, there is a dense inner zone. The mucocysts of *Tetrahymena pyriformis* show inclusions forming a “houndstooth” pattern. Analogous mucocysts occur in Euglenida and Dinoflagellida. These inclusions probably serve in secretion of cyst walls and similar materials. Filamentous

trichocysts (*Paramecium* and *Frontonia*) in the cortex are homogeneous bodies attached to a differentiated tip. During discharge there is formed a cross-striated shaft, ending in a dense tip. Discharged trichocysts are replaced by endoplasmic formation of new ones which, as they mature, are moved to the usual cortical location. Similar trichocysts occur in *Oxyrrhis*, a dinoflagellate. Cross striations of the shaft show a particular periodicity (55 nanometers) in various ciliates. Fibrillar trichocysts of *Paramecium* may be extruded partially to anchor a feeding ciliate. Toxicysts of *Dileptus* show, after discharge, a nonstriated tubule with a rodlike tip. Before discharge a capsule contains telescoping tubules and is closed apically by a cap. New toxicysts arise from endoplasmic vesicles which migrate to an adoral position during development. Toxicysts may, upon contact, induce paralysis of lysis of various Protozoa and sometimes paralysis of rotifers. Such organelles aid carnivores in capture of prey.

Inclusions

In addition to nuclei, food vacuoles (gastrioles) in phagotrophs, chromatophores and stigma in many phytoflagellates, water-elimination vesicles in many Protozoa, and sometimes other organelles, the cytoplasm may contain mitochondria, Golgi material, pinocytotic vacuoles, stored food materials, endoplasmic reticulum, and sometimes pigments of various kinds.

Chromatophores. These contain chlorophylls and commonly additional pigments such as carotenes and xanthophylls. Accessory pigments, varying with the group, may be abundant enough to produce yellowish-green, brown, and even blue or red chromatophores. In different species, chromatophores range from a large one (**Fig. 7e, f, and i**) to a number of flattened bodies (**Fig. 7g and k**). A chromatophore contains, within a double membrane, electron-opaque lamellae separated by transparent material in which granules may be embedded. Deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), chemically different from nuclear DNA and cytoplasmic RNA, occur in chromatophores of *Euglena gracilis*. DNA has been reported also from chromatophores of *Chlamydomonas moewusii*. Certain strains of *E. gracilis* have been bleached by exposure to high temperature (about 97°F or 36°C), maintenance in darkness, or treatment with streptomycin, erythromycin, pyribenzamine, and a nitrosoguanidine, among other drugs. Bleaching has been temporary or permanent with different treatments. Certain antibiotics damage chloroplast DNA (preventable by supplementary hydroxylamine). Plastids, containing starch but no chlorophyll, lie below the cortical mitochondria in *Polytoma uvella*. See also: CHROMATOPHORE.

Pyrenoids, ranging from a single body to a cluster, are associated with the chromatophore in certain phytoflagellates but not in others (**Fig. 7b, c, and j**). Taxonomic distribution may be erratic; for example, certain species of *Euglena* have pyrenoids but others do not. In *Chlamydomonas* the pyrenoid, lying within a chloroplast, is surrounded by starch granules. Electron micrographs show delicate tubules extending from the pyrenoid to the lamellae of the chloroplast.

Stigma. A stigma (**Fig. 7d**) occurs in many green flagellates and a few of their colorless relatives. Observations on behavior have suggested that the stigma functions in orientation with relation to a light source. Also, stigmaless

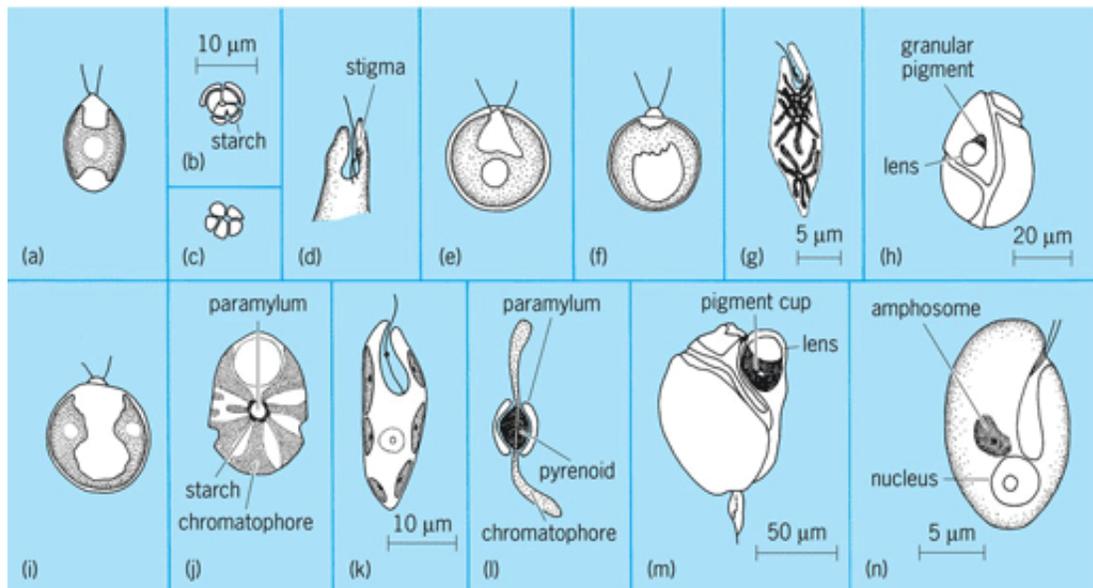


Fig. 7 Chromatophores, ocellus, amphosome, and pyrenoids. (a) Chromatophores in *Chlamydomonas agloeiformis*. (b, c) Compound pyrenoids of *Pyramidomonas*, with adherent starch. (d) Stigma of *Euglena*. (e) Chromatophores in *Chlamydomonas umbonata*. (f) Chromatophores in *Chlamydomonas inversa*. (g) Chromatophores in *Euglena geniculata*. (h) Ocellus in *Protopsis*. (i) Chromatophores in *Chlamydomonas bicocca*. (j) Chromatophore in *Peridinium umbonatum*. (k) Chromatophores in *Colacium*. (l) Chromatophore having a pyrenoid and a paramylum. (m) Ocellus in *Erythrospira*. (n) Amphosome (stained) in *Cryptomonas*. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

mutants (*Chlamydomonas*) respond to light more erratically than the green parent stock. Whether the stigma is a photoreceptor or merely a shield for a photosensitive organelle is debatable. A typical stigma shows globules containing carotenoid pigment. The organelle lies on the wall of the reservoir, as in *Euglena*, or may be adherent to or lie within a chromatophore, as in the phytomonads. The pigment globules (100 nm or larger) are packed into one or more plates forming the stigma. In experimentally bleached *Euglena*, the fate of the stigma is not closely correlated with that of the chromatophores. A more complex ocellus of certain dinoflagellates (Fig. 7b and m) shows a lenslike body in a pigmented cup. See also: PHOTORECEPTION.

Cytoplasmic pigments. These occur in many phytoflagellates and certain other protozoa, such as *Blepharisma* and *Stentor*, ranging from violet to red. Reddish pigments are common in Euglenida and Phytomonadida. In *Haematococcus pluvialis* production of such pigments (largely astaxanthin) in abundance results in a “hematocyst” in which the green color is masked. In *Euglena rubra* a similar pigment, normally endoplasmic, is moved to the periphery upon exposure to bright light or temperatures near 104°F (40°C). Red blooms may develop in ponds during hot summers.

Certain ciliates also produce cytoplasmic pigments. Of these the pink pigments, similar to hypericin of plants, of *Blepharisma undulans* are converted by bright light into products toxic to microorganisms, including

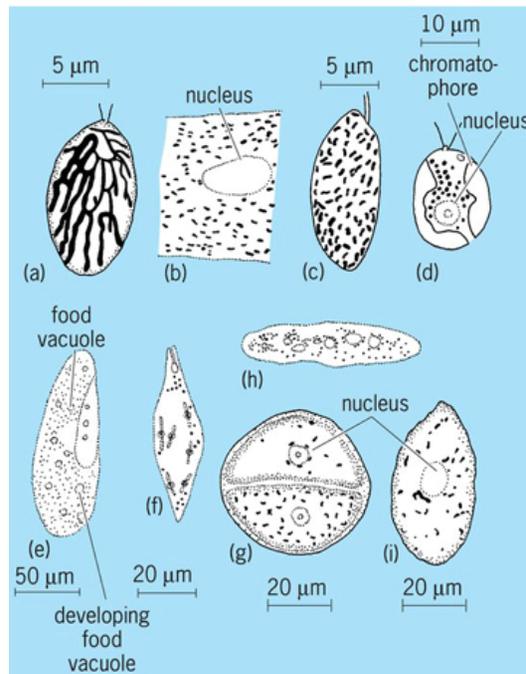


Fig. 8 Mitochondria, granules, and osmiophilic inclusions. Mitochondria (a) in *Polytoma*; (b) in *Protoopalina*; and (c) in *Chilomonas*. Granules (d) in *Chlamydomonas*; (e) in *Paramecium*; and (f) in *Euglena*. Osmiophilic inclusions (g) in *Gregarina*, gametocytes in cyst; (h) in *Paramecium*; (i) in *Protoopalina*. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

Blepharisma. Pigment extracts, tested in light, show similar toxicity. An analogous material, ichthyotoxin, produced by a flagellate (*Prymnesium parvum*), is inactivated in bright light.

Mitochondria. Although apparently absent in certain anaerobes, these normally occur in aerobic protozoa **Fig. 8a-c**. These inclusions are usually elongated and may fuse into nets in certain species (**Fig. 8a**). Morphology may be influenced by the condition of the organism. When reproduction slows down in a culture of *Tetrahymena pyriformis*, the previous ovoid and peripheral mitochondria round up and become more widely distributed. Also, ribosomes which are normally clumped along mitochondrial villi tend to disappear. DNA has been detected in mitochondria of several species. Oxidative phosphorylation seems to be associated with protozoan mitochondria (*Euglena*), as would be expected. *See also:* MITOCHONDRIA.

Electron micrographs indicate two general kinds of protozoan mitochondria. In one, folds of the inner membrane form cristae extending into the central lumen; this variety, characteristic of higher animals, occurs in certain phytoflagellates (*Euglena* and chrysomonads) and apparently certain trypanosomes. The kinetoplast may be continuous with such a mitochondrion, and metamorphosis from a leishmanial to a leptomonad stage may involve an increase in the size and complexity of trypanosomid mitochondria. In the other type (amebas, ciliates, and certain parasitic flagellates), cristae are replaced by microvilli.

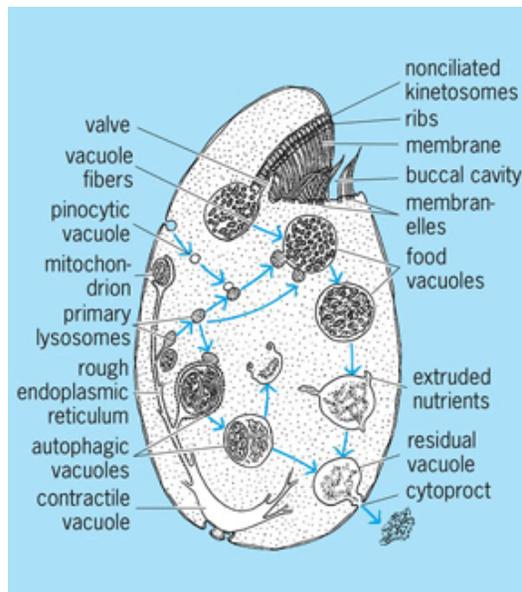


Fig. 9 Digestive pathways in *Tetrahymena pyriformis*. (After A. M. Elliot, *J. Protozool.*, 13:311, 1966)

Lysosomes. Small vacuoles (0.5–1.0 μm) in *Tetrahymena pyriformis* (**Fig. 9**) are considered lysosomes containing acid hydrolases (not yet involved in digestion) and probably arising from the rough endoplasmic reticulum. *See also:* ENDOPLASMIC RETICULUM; LYSOSOME.

Golgi material. In electron micrographs a typical Golgi body is a stack of flattened vesicles, sometimes up to 30 (*Peranema*). Although the identity of protozoan Golgi material is confused in older literature, some of the described Golgi elements should prove to be such. Although functional significance in Protozoa is not yet certain, some workers favor a secretory activity of these inclusions. *See also:* GOLGI APPARATUS.

Food reserves. Polysaccharides are often stored as visible inclusions. These include glucose polymers: paramylum of Euglenida, leucosin of Chrysomonadida, starches of Cryptomonadida, Phytomonadida, and Dinoflagellida; and glycogens of Sarcodina, Zoomastigophorea, and ciliates. Protozoan glycogens resemble liver and muscle glycogen but differ in molecular weight and number of glucose residues in unit chains. Lipids may be stored as small to large globules which are characteristic of old rather than young laboratory cultures. A few flagellates, like certain diatoms, accumulate oils responsible for undesirable flavors and odors of drinking water. Nitrogenous reserves include chromatoid bodies, described in axenic cultures of trophozoites of *Entamoeba invadens* and cysts of certain other species. These inclusions arise before encystment by aggregation of small vesicles into bodies of characteristic form. Such inclusions aid in differentiating encysted *E. histolytica* and *E. coli*. Protein and RNA have been reported from chromatoid bodies, each of which contains small (about 20 nm) globules, interpreted by some workers as ribosomes. In electron micrographs (*E. invadens*) these inclusions show fibrils in a closely packed helical arrangement. Chromatoid bodies gradually disappear as the cyst matures. *See also:* AMOEBIDA.

Water expulsion vesicle. This organelle (**Figs. 10** and **11**), commonly termed a contractile vacuole, is characteristic of fresh-water protozoa and occurs also in certain marine and parasitic phagotrophs. Such vesicles show cyclic increase in volume, followed by collapse during which the contents are discharged. Motion pictures show no contraction of the “contractile” vacuole in *Amoeba proteus* (**Fig. 11**). Instead, cytoplasmic pressure increases with accumulating fluid until the vesicle is forced to the surface and its proximal surface is thrown into folds as the cortex ruptures to release the contents through a pore. The result is collapse of the vesicle. Electron micrographs of *Tetrahymena pyriformis* suggest a similar collapse of the vesicle as its contents are discharged through the pores. Accumulation of fluid in the enlarging vesicle is aided by collecting tubules (**Fig. 10f** and **g**) which may, as in *T. pyriformis*, extend through much of the cytoplasm as a “nephridial” system apparently continuous with the endoplasmic reticulum. The major function of the vesicle is elimination of excess water, which may be traced to ingestion (phagotrophs), endosmosis, or metabolic origin. Cyclic activity of the vesicle may be accelerated by adding ATP to the medium. Since there is no evidence that only pure water is secreted into the collecting tubules, it is possible that soluble materials also are eliminated by the vesicle.

Sensory vacuoles. These occur in certain parasitic and free-living ciliates (**Fig. 10c-e**). The similarity to statocysts of certain invertebrates inspired the assumption implied by the name.

Nuclei. Dimorphic nuclear equipment (micronucleus and macronucleus) is typical of ciliates. Analogous dimorphism is known in a few Foraminiferida but has not been observed in various others. Except for possibly similar cases yet to be investigated carefully, protozoa outside the ciliates contain one kind of nucleus, although the number ranges from one to many. The polyploid macronucleus of ciliates develops from a diploid derivative of the synkaryon (conjugation and autogamy), presumably by repeated replication of chromosomes in a macronuclear anlage. Filamentous “chromosomes” containing DNA have been described in macronuclei of *Blepharisma*. Later development involves increase in volume and sometimes elongation (*Euplotes* and *Vorticella*) or constriction into nodes (*Stentor* and some strains of *Blepharisma*). Micronuclear differentiation may involve a slight decrease in size. Both kinds of nuclei may contain about twice as much RNA as DNA, while the macronuclear content may be about 40 times that of the micronucleus (*Paramecium*).

In protozoa other than ciliates, nuclei vary in size and content of chromatin and nucleoli (or endosomes). Nuclear division is mitotic except in the ciliate macronucleus. It is not certain that the polyploid “somatic” nuclei of various Foraminiferida ever divide normally.

Nutrition

In protozoan feeding, either phagotrophic (holozoic) or saprozoic (osmotrophic) methods predominate in particular species. In addition, chlorophyll-bearing flagellates profit from photosynthesis; in fact, certain species have not been grown in darkness and may be obligate phototrophs.

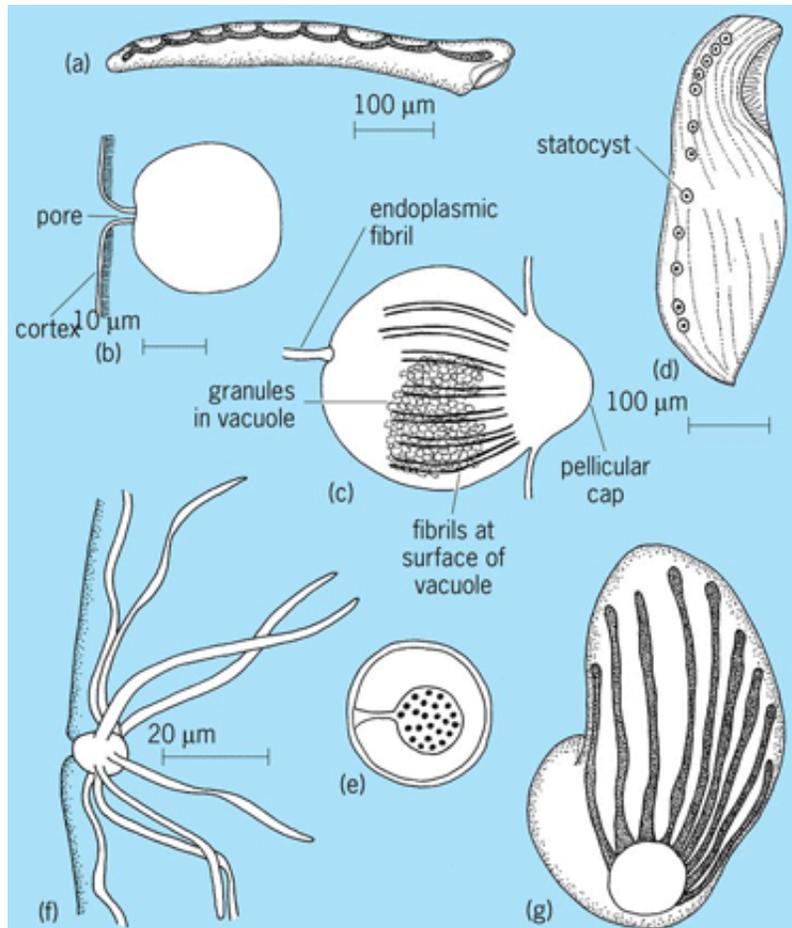


Fig. 10 Water expulsion vesicles and sensory vacuoles of protozoa. (a) Contractile tube in *Haptophrya*, an intestinal ciliate from a salamander. (b) Water expulsion vesicle and pore in *Eudiplodinium*, a parasitic ciliate from ruminants. (c–e) Sensory vacuoles of *Blepharoprosthium* and *Loxodes*. (f, g) Water expulsion vesicle and contributory canals in *Paramecium* and *Tillina*. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

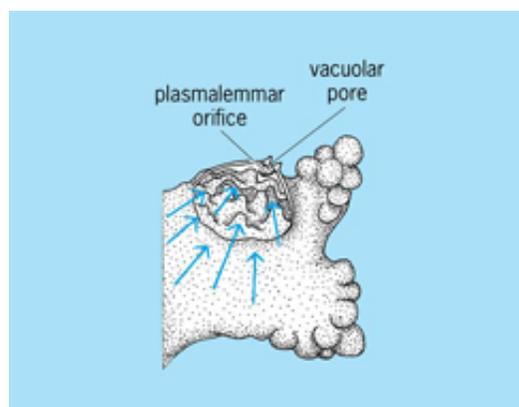


Fig. 11 Water elimination vesicle in *Amoeba proteus*, based on tracings of photomicrographs. Arrows indicate movement of granules. Endoplasm gets pushed against vesicle membrane, producing wrinkles. (After Wigg, Bovee, and Jahn, *J. Protozool.*, 14:104, 1967)

Phagotrophic

Ingestion of food, followed by digestion in vacuoles, is characteristic of Sarcodina, ciliates, and many flagellates. Digestion follows synthesis of appropriate enzymes and their transportation to the food vacuole. Ingestion of nonnutritive latex particles also leads to acid-phosphatase activity of the “food” vacuoles. Primary lysosomes, which can fuse with the food vacuole, may transport hydrolases from the rough endoplasmic reticulum, as suggested for *Tetrahymena* (Fig. 9). Even a few Sporozoa, the malarial parasites and certain gregarines, are known to ingest host proteins or sometimes tissue cells or portions of them. Details of ingestion vary. Formation of food cups, or gulletlike invaginations, to enclose prey is common in more or less ameboid organisms, such as various Sarcodina, many flagellates, and at least a few Sporozoa. Entrapment in a sticky reticulopodial net occurs in Foraminiferida and certain other Sarcodina. A persistent cytostome and gullet are involved in phagotrophic ciliates and a few flagellates. A small cytostome and gullet in *Trypanosoma mega* suggest ability to ingest food, although importance of this activity in trypanosomes is still uncertain. Many ciliates (Fig. 9) have buccal organelles (membranes, membranelles, and closely set rows of cilia) arranged to drive particles to the cytostome. Particles pass through the cytostome into the cytopharynx (gullet), at the base of which food vacuoles (gastrioles) are formed. Digestion occurs in such vacuoles. An additional feature, reported in *Paramecium* and *Tetrahymena*, is entanglement of particles in mucus secreted by the peristomial cortex or buccal cavity. The effect is a clumping of particles into larger aggregates. In many less specialized ciliates the cytostome opens at the surface of the body. Such organisms (*Didinium* and *Perispira*) usually ingest large prey, such as other Protozoa. In some cases rodlike trichites surrounding the cytopharynx appear analogous to toxicysts of certain other ciliates.

Saprozoic

By definition this involves passage of dissolved foods through the cortex. It is uncertain to what extent diffusion is responsible, but enzymatic activities presumably are involved in uptake of various simple sugars, acetate and butyrate in *Polytoma* and even potassium and phosphate ions. In addition, external factors, for example, the pH of the medium, may strongly influence uptake of fatty acids and phosphate.

Pinocytosis

This process resembles phagocytosis in miniature but with ingestion apparently limited to materials in solution. First recognized in *Amoeba proteus*, the process has since been described in other amebas, certain ciliates, and *Eimeria* (Sporozoa). Pinocytosis is stimulated by “inducers,” such as proteins, certain salts, and toluidine blue. In the process small vacuoles are formed at the base of a tubular invagination from a surface, either cortex or the wall of cytopharynx. The vacuoles drift into the endoplasm and mingle with other inclusions. In certain ciliates, a similar process yields secondary vacuoles from a food vacuole. In certain malarial parasites, but not in others, such pinocytosis precedes completion of digestion. *See also*: ENDOCYTOSIS.

Nutritional requirements

Establishment of a strain in axenic cultures in defined media make possible a determination of specific food requirements. In nature, these requirements are met by the available diet which includes other microorganisms and materials dissolved in the external medium. *See also:* AXENIC CULTURE.

Mineral requirements. Certain materials, including calcium, silicon, and strontium salts, are needed for tests and other skeletal structures, and metal ions are needed in traces for enzyme systems. Trace requirements of one species or another include calcium, cobalt, copper, iron, potassium, magnesium, manganese, phosphorus, sulfur, and zinc. Although indispensable status is uncertain, aluminum, barium, boron, iodine, silicon, sodium, and vanadium have each stimulated growth of one or more species.

Nitrogenous foods. Nitrogen requirements of many phytoflagellates are met by an ammonium salt or by either a nitrate or an ammonium salt. Other protozoa need specific amino acids which they cannot synthesize, the number ranging from 1 (*Perenema*) to 7 for an amoeba (*Hartmannella rhysodes*), 13 for *Paramecium multimicronucleatum*, and at least 15 for *Leishmania tarentolae*. In a few cases, radioactive amino acids have been used in tracing their fate in metabolism. In analogous fashion, labeled food organisms have been used to identify species ingested by Foraminiferida in laboratory aquariums. In addition to amino acids, certain protozoa need a purine, or sometimes both a purine and a pyrimidine. *See also:* AMINO ACIDS; PURINE; PYRIMIDINE.

Carbon requirements. The only carbon source needed by certain chlorophyll-bearing flagellates is CO₂. In fact, *Gymnodinium breve*, a dinoflagellate occurring in “red tides,” apparently cannot use any organic compound which has been tested and seems to be an obligate phototroph. *Euglena gracilis*, in contrast, can grow in darkness in a good medium. Requirements of heterotrophs, as a group, may be met by a polysaccharide, by a fatty acid, by an acid of the tricarboxylic acid (TCA) cycle, or by an alcohol. Suitability varies with the species.

Growth factors. Organic substances, such as vitamins, are needed in traces. A few phytoflagellates, namely, certain species of *Brachiomonas*, *Chlamydomonas*, and *Chlorogonium*, are known to synthesize all required vitamins. Other protozoa need one or more vitamins and sometimes other growth factors. Loss of an ability to synthesize a particular growth factor (niacin or thioctic acid) has occurred in *Tetrahymena pyriformis* after prolonged maintenance of strains in laboratory cultures. Certain amoebas (*Acanthamoeba* and *Hartmannella*) need only three vitamins (B₁₂, biotin, and thiamine); similar requirements are known for certain phytoflagellates. A ciliate, *Glaucoma chattoni*, needs biotin, folic acid, nicotinic acid, pantothenic acid, pyridoxine, riboflavin, thiamine, thioctic acid, plus certain lipids. Less common requirements include ethanol or methanol for *Tetrahymena setifera*, chlorine for certain European strains of *T. pyriformis*, and a pteridine for *Critbidia fasciculata*. Identification of vitamin requirements was followed by use of certain protozoa in biological assays—vitamin B₁₂ (*Ochromonas malbamensis*, *Euglena gracilis*), thiamine (*O. malbamensis*), pyridoxine (*Tetrahymena pyriformis*), biotin (*Ochromonas danica*), nicotinic acid (*T. pyriformis*), and pantothenic acid (*T. pyriformis*). *See also:* VITAMIN.

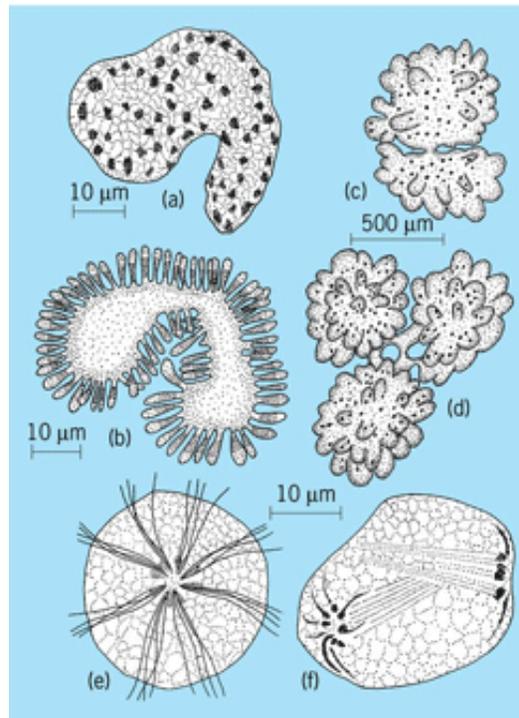


Fig. 12 Schizogony and plasmotomy. (a) Schizogony in *Ovivora thalassemae*. (b) Schizont of *O. thalassemae*. (c, d) Plasmotomy in *Pelomyxa carolinensis*. (e) *Coronympha octonaria*, vegetative stage showing nuclei and flagellar groups. (f) Nuclear groups at end of telophase, as they appear just before plasmotomy in *C. octonaria*. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

Reproduction

Reproduction occurs after a period of growth which ranges, in different species, from less than half a day to several months (certain Foraminiferida). General methods include binary fission, budding, plasmotomy, and schizogony. Fission, involving nuclear division and replication of organelles, yields two organisms similar in size. Budding produces two organisms, one smaller than the other. In internal budding (certain Suctoria) a bud is formed within a brood pouch, an almost closed invagination in the “parental” body. The bud, after it develops cilia, is expelled through a “birth pore” as a sort of larva which, after a few hours of activity, undergoes metamorphosis (losing cilia, developing tentacles) into a typical suctorian. In external budding, the bud is formed at the surface of the “parental” body. In plasmotomy (**Fig. 12c and d**), a multinucleate organism divides into several, each containing a number of nuclei. Schizogony, characteristic of Sporozoa, follows repeated nuclear division, yielding many uninucleate buds (**Fig. 12a and b**). In some cases, as in *Eimeria bovis*, the schizont first divides into several multinucleate forms, in each of which the nuclei approach the surface to take part in schizogony (merogony).

Reproduction includes formation of new organelles, either by division of old structures or by neof ormation, sometimes preceded by resorption of an old organelle. Blepharoplasts and basal granules, in particular, seem to be self-replicating. Formation of a new mouth (stomatogenesis) in ciliates often involves origin of an anlage from basal granules of one or more ciliary rows and its differentiation into new buccal organelles. Even the formation of a new pellicle in Euglenida may involve formation of new pellicular strips between adjacent strips of the original pellicle.

Life cycles

Simple life cycles include a cyst and an active (trophic) stage undergoing growth and reproduction. In certain free-living and parasitic species, no cyst is developed. Dimorphic cycles show two active stages; polymorphic show several. The former include adult and larva (Suctorina); flagellates and ameba (certain Mastigophora and Sarcodina); flagellate and palmella (nonflagellated; certain Phytomonadida); and ameba and plasmodium (Mycetozoa especially).

Encystment

This process involves resorption of locomotor and feeding organelles, loss of water, often rounding up of the body, and secretion of one or more cyst membranes. The wall usually is composed of secreted materials (proteins, carbohydrates, keratin, and others), although foreign particles may be cemented into a wall. Precystic activities may include storage of reserves. Protective cysts (**Fig. 13a-d**), with fairly thick walls, often resist desiccation. Dried cysts of *Colpoda cucullus* have remained viable for 5 years; those of certain amebas and flagellates, for 49 years in dry soil samples. Within reproductive cysts (**Fig. 13e and f**) fission, budding or schizogony, sometimes gametogenesis, and syngamy occur in various species. The usually thin-walled reproductive cysts afford relatively little protection.

Excystment involves absorption of water leading to rupture of cyst membranes and, when necessary, development of organelles for feeding and locomotion.

Sexual activities

These involve production of haploid (gametic) nuclei and their fusion into a synkaryon (zygotic nucleus). Meiosis occurs at different stages in life cycles. In haploid organisms (Phytomonadida, certain flagellates of termites and wood roaches, Coccidia, malarial parasites, and gregarines) the zygote is the only diploid stage. Meiosis occurs as the zygotic nucleus divides. In these haploid cycles a heterozygous condition can exist only in the zygote. Diploid cycles, in which meiosis occurs during gametogenesis, are found in ciliates, Heliozoa (*Actinophryx* and *Actinosphaerium*), and in certain Hypermastigida. In several flagellates of the wood roach, sexual activity is stimulated by ecdysone (molting hormone) of the host. A few Foraminiferida show an alternation of generations

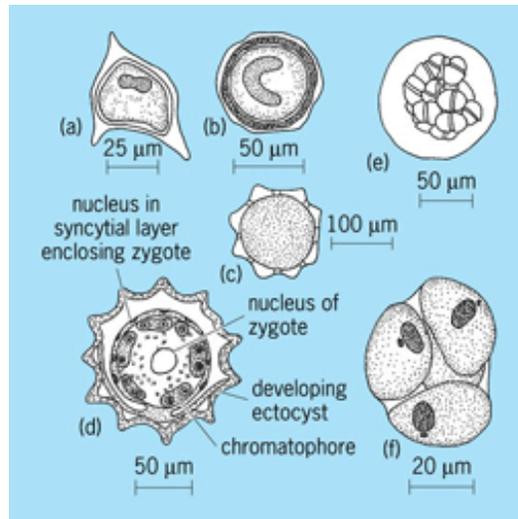


Fig. 13 Protective and reproductive cysts. (a) Protective cyst of *Ceratium*; (b) of *Didinium*; (c) of *Bursaria*. (d) Encysted zygote of *Volvox*. (e) Reproductive cyst of *Gyrodinium*, a dinoflagellate and (f) of *Colpoda*, a ciliate. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

involving a haploid gamete-producing phase and a diploid phase with ordinary reproduction (**Fig. 14**). See also: ECDYSONE.

Sexual activities include syngamy, autogamy, and conjugation. Syngamy involves fusion of two gametes which may be morphologically similar (isogamy) or different (anisogamy). Autogamy occurs within a single organism; haploid nuclei are formed and subsequently fuse into a synkaryon. Conjugation involves pairing of ciliates (**Fig. 15**), apparently following appearance of specific protein-containing substances at the surface, including cilia. Pairing in *Tetrahymena* includes fusion of the two pellicles and formation of channels joining the conjugants. In tests with radioactive foods, cytoplasmic materials (RNA and proteins) passed from one conjugant to the other. Pairing stimulates nuclear activities. Old macronuclei gradually degenerate as a rule, although fragments may be exchanged occasionally in *Stylonychia*. The micronucleus undergoes three divisions, the second being reductional. The third produces gametic nuclei which, in *Tetrahymena*, arise from one haploid nucleus. A migratory gametic nucleus, whose status is apparently determined by position, passes from each conjugant to its mate, where fusion with the stationary nucleus occurs. The resulting synkaryon, in different species, divides one or more times and the products become macro- and micronuclei. Reorganization may involve one or more fissions which restore nuclear numbers to normal. In this sense, a pair of conjugants produces two or more ciliates. In the peritrichs, with micro- and macroconjugants, only the latter survives.

Autogamy occurs in certain ciliates and a few parasitic flagellates, *Barbulanympha*, for example. Since the gametic nuclei arise from one nucleus, the resulting synkaryon is homozygous.

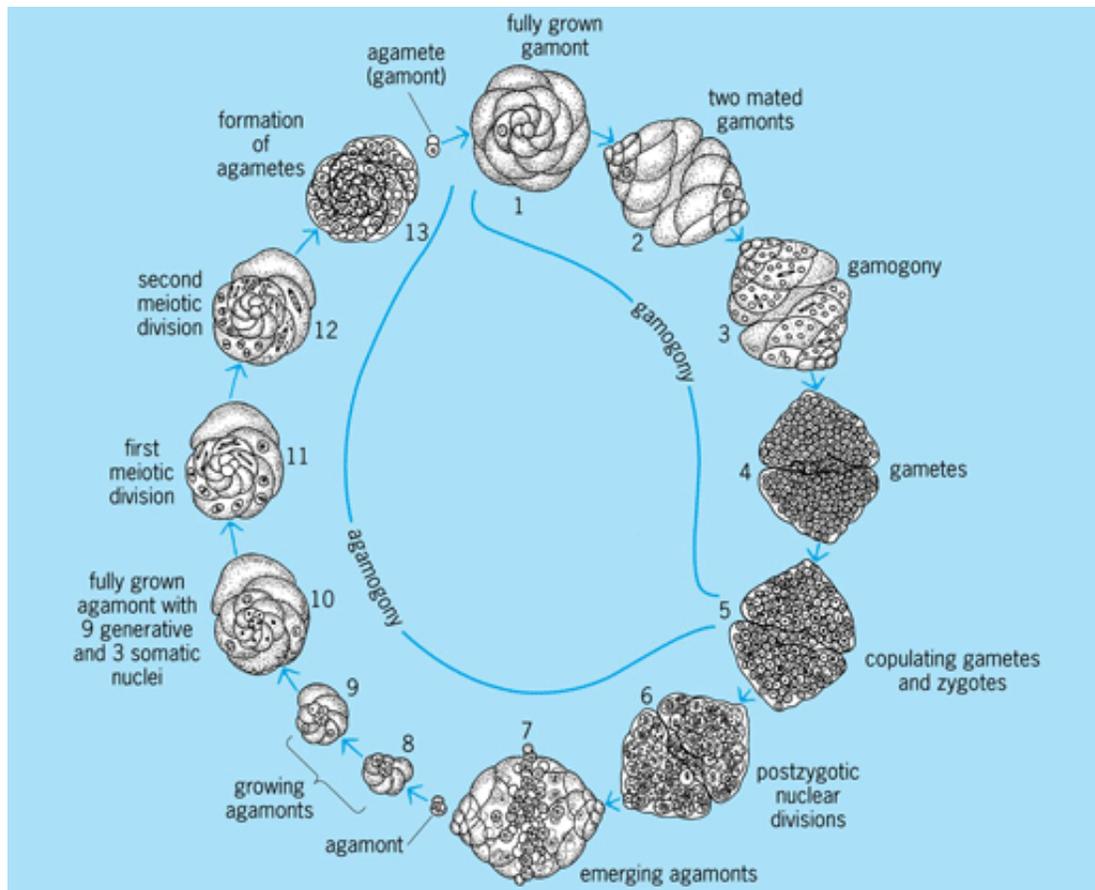


Fig. 14 Life cycle of *Glabratella sulcata*, showing alternation of haploid phase (gamogony) and diploid phase (agamogony). Two meiotic divisions (11 and 12) precede the production of young haploid organisms (13). (After K. G. Grell, *Research in Protozoology*, vol. 2, Pergamon Press, 1968)

Normal conjugation involves ciliates of complementary mating types, two or more belonging to a syngen, originally termed “variety.” Each species contains a number of syngens. Typically, mating types within one syngen can conjugate normally. Abortive conjugation, sometimes fatal, follows pairing of ciliates from different syngens.

Syngamy in Phytomonadida typically requires two kinds of gametes (+ and –). Syngens analogous to those of ciliates have been reported in certain Phytomonadida. In *Astrephomene* at least, different syngens may have different chromosome counts. In dioecious species (*Chlorogonium* and some species of *Chlamydomonas*) the two gametes come from different clones; each zygote produces two clones of each “sex.” In monoecious types (several species of *Chlamydomonas* and *Haematococcus pluvialis*) a single clone produces both types of gametes. In colonial phytomonads gametes may be isogamous (*Gonium* and *Pandorina*) or anisogamous (*Eudorina* and *Volvox*). Differentiation of male colonies in *Volvox aureus* is induced by a rather thermostable protein-containing substance. In less specialized genera (*Gonium*) all zooids become gametes; at the other extreme (*Volvox* and *Eudorina*) gametes arise in the posterior half of the colony.

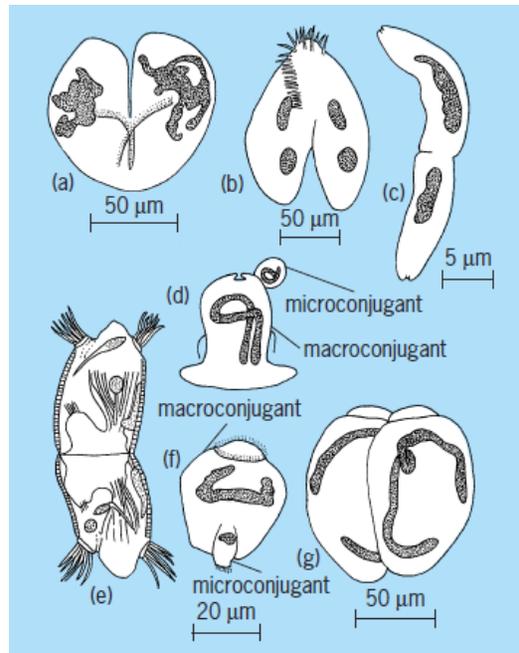


Fig. 15 Early conjugation, just after fusion of conjugants. (a) *Nyctotherus*. (b) *Pleurotricha*. (c) *Ancistrocoma*. (d) *Cycloposthium*. (e) *Scyphidia*. (f) *Vorticella*. (g) *Euplotes*. (After R. P. Hall, *Protozoology*, Prentice Hall, 1953)

According to the concept of a “physiological life cycle,” laboratory strains of ciliates pass through phases of youth; maturity, when conjugation is possible; senescence, when conjugation is impossible; and death. Senescence supposedly is averted by opportune occurrence of conjugation. Although certain species apparently can live indefinitely without conjugation, it is possible that autogamy replaces conjugation in rejuvenating such ciliates.

Parasitic Protozoa

Parasites occur in all major groups. Sporozoa are exclusively parasitic, as are some flagellate orders (Trichomonadida, Hyperamastigida, and Oxymonadida), the Opalinata, Piroplasma, and several ciliate orders (Apostomatida, Astomatida, and Entodiniomorphida). Various other groups contain both parasitic and free-living types. Protozoa also serve as hosts of other Protozoa, certain bacteria, fungi, and algae. An unusual addition is *Leptomonas karyophilus*, a trypanosomid flagellate which invades the macronucleus of *Paramecium trichium*. Such symbionts as *Chlorella paramecii* in *Paramecium bursaria* are considered symbiotes. A similar example is a bacterial symbiont of *Crithidia oncopelti*, which apparently contributes products to nitrogen metabolism of the host.

Many protozoan symbionts, called commensals, are more or less harmless. Cellulose-digesting flagellates of termites and ciliates of ruminants are symbiotic in the sense that they benefit their hosts. In addition to helpful digestive activities, rumen ciliates are potential food for the herbivores.

Pathogens

Relatively few parasites are distinctly pathogenic, causing amebiasis, visceral leishmaniasis (kala azar), African sleeping sickness, Chagas' disease, malaria, tick fever of cattle, dourine of horses, and other diseases. *See also:* MALARIA.

Harmful effects may be produced in different ways. Tissue cells are invaded and destroyed in Chagas' disease, leishmaniasis, coccidiosis, and malaria. Tissues may be destroyed, as in abscesses and ulcers involving *Entamoeba histolytica*. Although a potent "toxotoxin" is reported for *Toxoplasma gondii* and a Chagas toxin from *Trypanosoma cruzi*, little is yet known about possible toxins of protozoan parasites.

Epidemiology

Transfer may involve direct migration of parasites living in aquatic hosts; direct contact (osculatory, venereal); ingestion with contaminated food or drink; and vector transfer, as in malaria or Chagas' disease. Variations include placental transfer from mother to fetus, known in malaria and Chagas' disease; ovarian transfer, to eggs in ovary, as in ticks infected with *Babesia bigemina*; and lacteal transfer, from female to suckling young, reported in laboratory trypanosomiasis. *See also:* MEDICAL PARASITOLOGY.

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