Ciliophora

Advanced article

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Ciliophora is the name for a phylum of protists commonly called the ciliates or infusorians. These protists are the most complex of cells, having an elaborate cytoskeleton, cilia and two different kinds of nuclei.

Article Contents

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Introduction

Humans have probably observed protozoa assigned to the phylum Ciliophora for hundreds of thousands of years. This is because some of the common marine and freshwater species, like *Mesodinium rubrum* and *Stentor polymorphus*, can grow to populations so dense that they colour the seawater or the pond water red or green, respectively. However, Anton van Leeuwenhoek was probably the first person actually to see ciliates as individual cells when he peered down his revolutionary 'new' microscope in the seventeenth century. In those days, ciliates were called Infusoria, because they were often the most obvious organisms arising in infusions of vegetation. Once modern microscopes became common laboratory instruments in the nineteenth century, there was an explosion of study on the ciliates. During this period, the major groups were identified (Corliss, 1979). **See also**: Leeuwenhoek, Antoni van; Protozoa

The phylum Ciliophora is one of the most homogeneous of protozoan groups, long recognized as monophyletic. There are some 8000 species with about two-thirds of these being free-living and the remainder symbiotic. The free-living forms can be found all over the world (Finlay *et al*., 1998) in almost any habitat where water might accumulate. Ciliates are common in sediments or the benthos of marine and freshwater habitats (Finlay *et al*., 1998), in the plankton of marine (Pierce and Turner, 1992) and freshwater (Fenchel, 1987) environments and in soils (Foissner, 1987). They are even found in some extreme environments, like hot springs and in ice flows from the Arctic and Antarctica. Ciliates are commonly the 'top' organisms in the microbial food web. They feed on bacteria, flagellates and phytoplankton, and are, in their own turn, fed upon by zooplankton, jellyfish and small fish. Thus, they perform a role of transferring energy through aquatic food chains.

Symbiotic ciliates can be commensals, mutualists or parasites. Unique assemblages of commensal forms are found in places as diverse as the intestine of sea urchins and the fermenting stomachs of ruminants. Mutualists are not so common: *Nyctotherus*, which in its turn harbours methanogenic bacteria, lives in the intestinal tract of cockroaches, whose growth is promoted by the presence of these methanogen-carrying ciliates. Parasitic ciliates are rare: *Ichthyophthirius* or 'Ich' creeps into the epithelium of the skin and gills of fishes and causes 'white spot' disease while *Balantidium* can be found invading the intestinal epithelium of pigs and humans. Parasitic invasions by ciliates are being reported more frequently in recent years as fish and shellfish farming become more common, and mortalities have been reported. **See also**: Protozoan Pathogens of domestic and companion animals; Protozoan Symbiosis

Brief Description and Characterization

Ciliates were probably the pinnacle of unicellular eukaryote evolution over 1000 million years ago, before the evolution of the metazoans. They are still some of the most complex and beautiful heterotrophic protists, although some forms (e.g. *Mesodinium*, *Stentor polymorphus*) are autotrophic because they harbour photosynthetic symbionts in their cytoplasm. **See also**: Universal tree of life

Ciliates are characterized by three major features.

1. They exhibit nuclear dimorphism, i.e. they have two different kinds of nuclei in their cytoplasm. The macronucleus is the transcriptionally active nucleus, synthesizing messenger ribonucleic acid (mRNA) that controls the functions of the cell. The macronucleus typically contains many copies of the ciliate genome, which is often highly modified when it develops from the micronucleus following conjugation. The micronucleus is a typical diploid protistan nucleus, i.e. it contains two sets of chromosomes. It functions as the germline deoxyribonucleic acid (DNA) for each species, and undergoes meiosis during conjugation.
2. Conjugation is the second distinctive feature of ciliates. Conjugation is the temporary fusion of two ciliates during which the partners exchange gametic nuclei, which are products of the meiosis of the micronucleus of each partner (**Figure 1**).
3. Ciliates typically have cilia at some time during their life cycle (**Figures 1** and **2**). In some species, these cilia cover the entire cell; in other species, the cilia form compound ciliary organelles called cirri; in some sessile species, the cilia are restricted to the oral region with

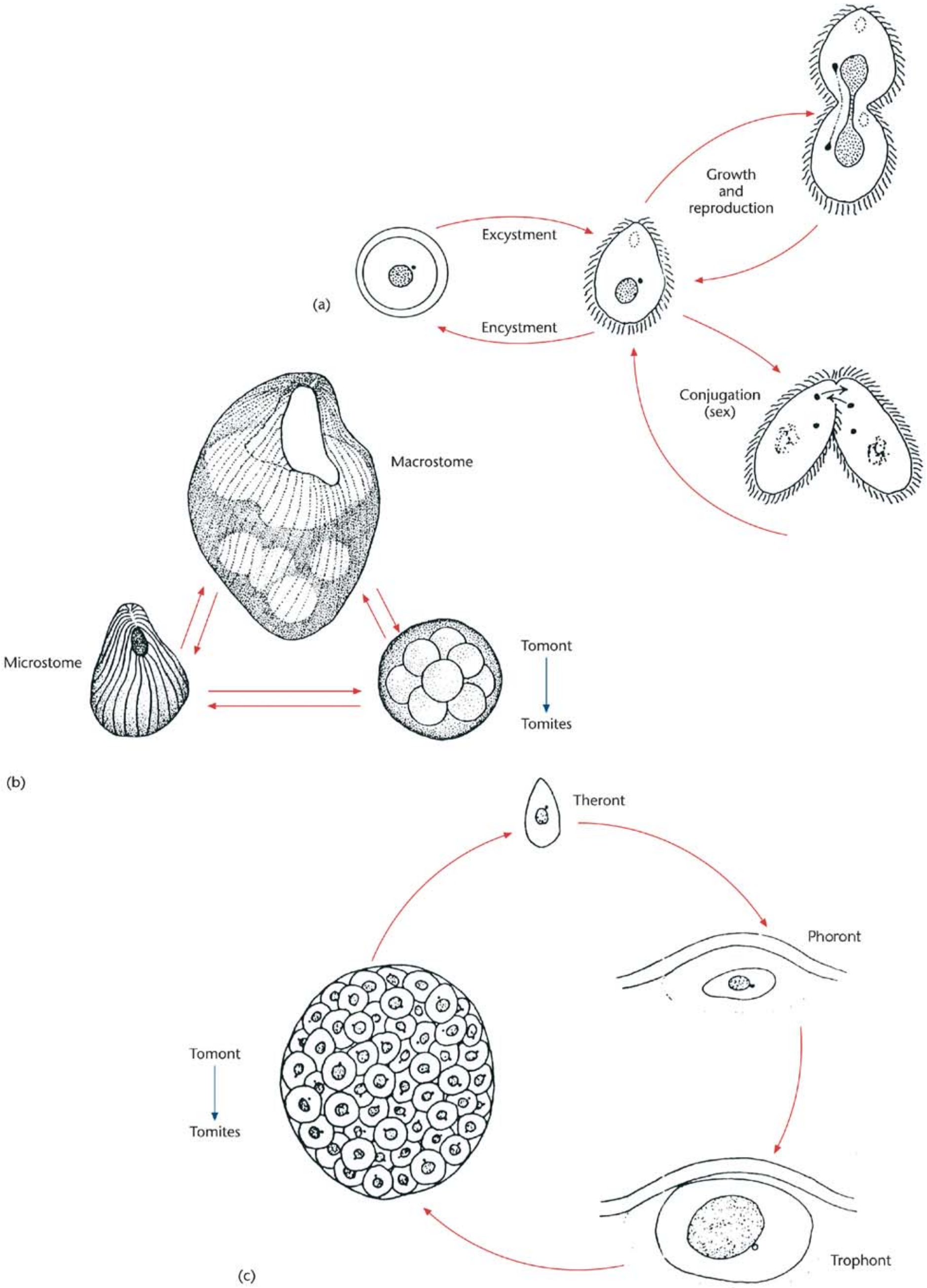

Figure 1 Life cycles of ciliated protozoa. (a) A generalized life cycle of a ciliate showing three major phases: (1) growth and reproduction during which the ciliate feeds and undergoes binary fission; (2) conjugation usually stimulated by starvation conditions, during which the ciliates undergo meiosis and exchange gametic nuclei before separating and (3) encystment and excystment during which the ciliate secretes a cyst wall about itself to survive harsh conditions, like desiccation or the absence of food. (b) The life cycle of the hymenostome *Tetrahymena patula*, which has a microstome phase that eats bacteria, a macrostome phase that eats microstomes and other smaller ciliates when the bacterial food supply is depleted and a tomont or dividing phase that undergoes sequential binary fissions in a cyst to produce tomites. The tomites escape the cyst when bacteria are again abundant. (c) The life cycle of the hymenostome *Ichthyophthirius multifiliis*, the parasite that causes white-spot disease of the skin of fishes. The theront, a small cell, burrows into the skin of a fish to become a phoront that begins feeding as a trophont stage. The trophont may reach over 1 mm in diameter at which time it falls off the fish on to the bottom to become a tomont. Here, the tomont divides sequentially by binary fission to produce sometimes 1000 tomites, which break out of the division cyst to become the next generation of theronts. Based on Lynn and Small (1989) and Lynn and Small (2002).

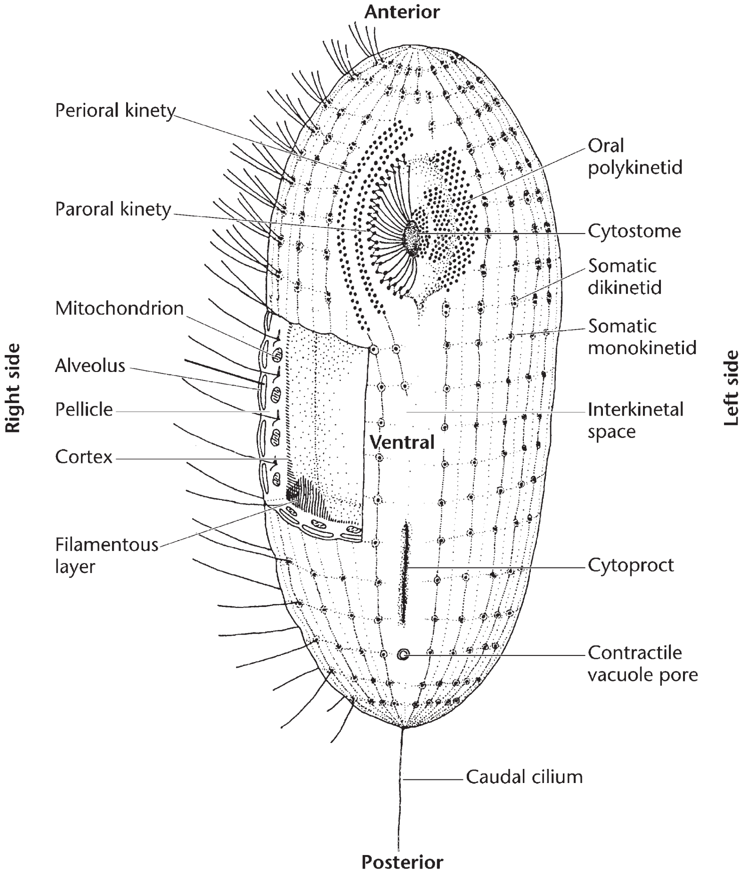

Figure 2 Generalized drawing of the ventral surface of a ciliated protozoon. The body can be divided into somatic and oral regions. The oral region illustrated here has two oral polykinetids and one paroral kinety, and adjacent to this are some specialized perioral kineties that aid in feeding. Refer to Figure 6 for some illustrations of more oral structures. The somatic cortex is covered by a pellicle that includes the alveoli (see Figure 3). The pellicle is part of the cortex, the outer portion of the cell in which are embedded the somatic mono- and dikinetids and the mitochondria. The cortex may be separated from the endoplasm by a filamentous layer. There are typically three openings to the outside: the cytostome or cell mouth through which food passes into the food vacuole; the cytoproct through which undigested food passes from the food vacuole and the contractile vacuole pore out of which excess water and some wastes are passed from the contractile vacuole. Based on Lynn and Small (1989).

> body or somatic cilia only appearing when the ciliate disperses, while in other sessile species, such as the suctorians, cilia are absent at all stages but the dispersal stage.

Thus, if a protist exhibits these three features – nuclear dimorphism, conjugation and presence of cilia – it must be a ciliate.

Life cycles

Ciliates have life cycles that vary depending upon the adaptive strategy of the species. A typical life cycle has three major phases (**Figure 1a**). If there are prey organisms present, the ciliate feeds and undergoes growth and reproduction. Reproduction is typically by transverse binary fission (cytokinesis, division of the cell) accompanied by mitosis of the micronucleus and bipartitioning of the macronucleus (Raikov, 1996). Often, when food becomes limiting, this is a signal for ciliates to become sexually active and enter the conjugation phase of the life cycle (**Figure 1a**). Ciliate geneticists have taken advantage of this adaptive strategy to induce sexual processes in the laboratory so that they can be explored as cellular and molecular processes. If there are no partners nearby, ciliates – like many other protists – can undergo encystment, forming a protective wall around the cell to inhibit desiccation, and then undergoing excystment when optimal conditions again arise (**Figure 1a**). It is in the cyst stage that ciliates are most probably dispersed to distant habitats by wind and animals. **See also**: Binary fission in bacteria; Protozoan cysts and spores

There are many variations on this basic life cycle (see Corliss, 1979). Two interesting ones are demonstrated by *Tetrahymena patula* and *Ichthyophthirius multifiliis* (**Figure 1b** and **1c**). *T. patula* can develop into a large-mouthed form or macrostome (**Figure 1b**) if small-sized prey organisms disappear and only larger-sized ones abound. It can even become cannibalistic, eating its 'brothers and sisters'. *Ichthyophthirius* is a parasite of the epithelium of fishes. A small-sized theront or hunter searches out a fish and burrows beneath its surface epithelial cells where it ingests fluids and cells of the fish, growing into a large trophont. The trophont falls off the fish to the bottom of the pond, becomes a tomont, and divides many times to yield sometimes over 1000 tomites (**Figure 1c**). Sessile ciliates, like the suctorians and *Vorticella*, have life cycles characterized by dispersal stages called swarmers. **See also**: *Tetrahymena*

Cell structure

There is a considerable diversity in cell morphology among the different groups or classes of ciliates. Nevertheless, the vast majority of ciliates exhibit similar basic features (**Figure 2**). The cilia distributed over the cell surface can be divided into somatic and oral types.

The somatic cilia cover the cell surface or body, usually in longitudinal files or rows called kineties. The unit structure of a kinety is the kinetid, which can be composed of one kinetosome and its cilium, a monokinetid, or two kinetosomes and their cilia, a dikinetid (**Figure 2**). The somatic kinetids are used to propel the ciliate through the water in search of food or to escape predators. Some somatic kinetids, the perioral kinetids, become more complex near the oral region, functioning to aid in food capture (**Figure 2**). **See also**: Cilia and flagella

The oral cilia can be organized as simple dikinetids surrounding the cell mouth or cytostome. Sometimes, these dikinetids can be restricted to one side of the oral region, often the right side; they are called the paroral kinety or paroral membrane, whose cilia are used to filter food particles from the water. The water is drawn to the oral region by the beating of the cilia of compound ciliary organelles, called oral polykinetids (**Figure 2**). In ciliates like *Euplotes* and *Stentor* these oral polykinetids can number over 30, forming a conspicuous adoral zone that spirals around the anterior end of the cell. Food particles are driven through the cytostome into a forming food vacuole, which buds off from the base of the oral cavity and circulates through the cytoplasm. After the ingested food has been digested, it is egested through a permanent cell anus or cytoproct (**Figure 2**). During ingestion, water from the environment is sequestered in the food vacuole. This water, together with water that continuously crosses the cell membranes, is sequestered by a tubular system in the cytoplasm, accumulated in the contractile vacuole, and expelled through the permanent contractile vacuole pore.

The cell surface of a ciliate is covered by a cell membrane or plasmalemma, which is underlain by unit membrane-bound sacs, called alveoli (**Figures 2** and **3**). A layer of microtubules and a fibrous epiplasmic layer can be found beneath the alveoli. Together these form the pellicle (**Figure 3**). A more detailed examination in the electron microscope reveals the substructure of the kinetids. The somatic kinetids are typically composed of a kinetosome or basal body of nine triplets of microtubules, two of which extend as the nine doublets of the ciliary shaft. Three fibrillar structures are associated with the kinetosomes, and together with it form a kinetid. (1) A transverse ribbon of microtubules typically extends leftwards across the longitudinal axis of the ciliate. (2) A postciliary ribbon of

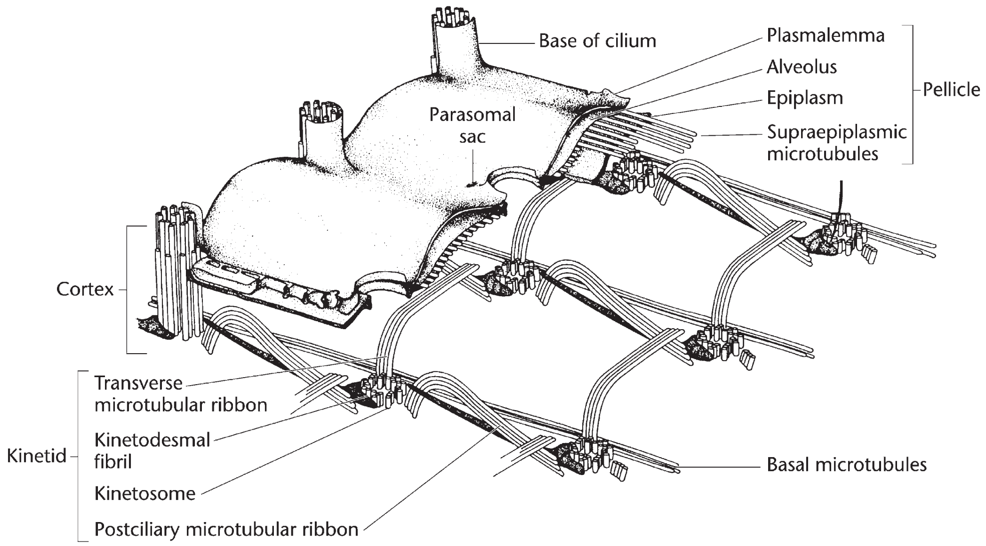

Figure 3 A patch of the cortex of a ciliate that shows the subcomponents of the pellicle and the kinetid. The microtubular and filamentous components of the cortex are elements of the cytoskeleton that provide support for the form of the ciliate. Based on Lynn and Small (1989).

microtubules typically extends posteriorly along the length of the kinety. (3) A kinetodesmal fibril extends anteriorly or laterally to the right (**Figure 3**). These fibrillar structures provide support for the cell surface and maintain the characteristic form of each ciliate species. All these fibrillar elements together with those of the pellicle form the cortex of a ciliate cell. **See also**: Alveolates; Tubulin and microtubules

The structure of the fibrillar associates of the somatic kinetid differs from one group of ciliates to another (**Figure 4**). It is this variation in structure that has served as the basis for the modern characterization of the major

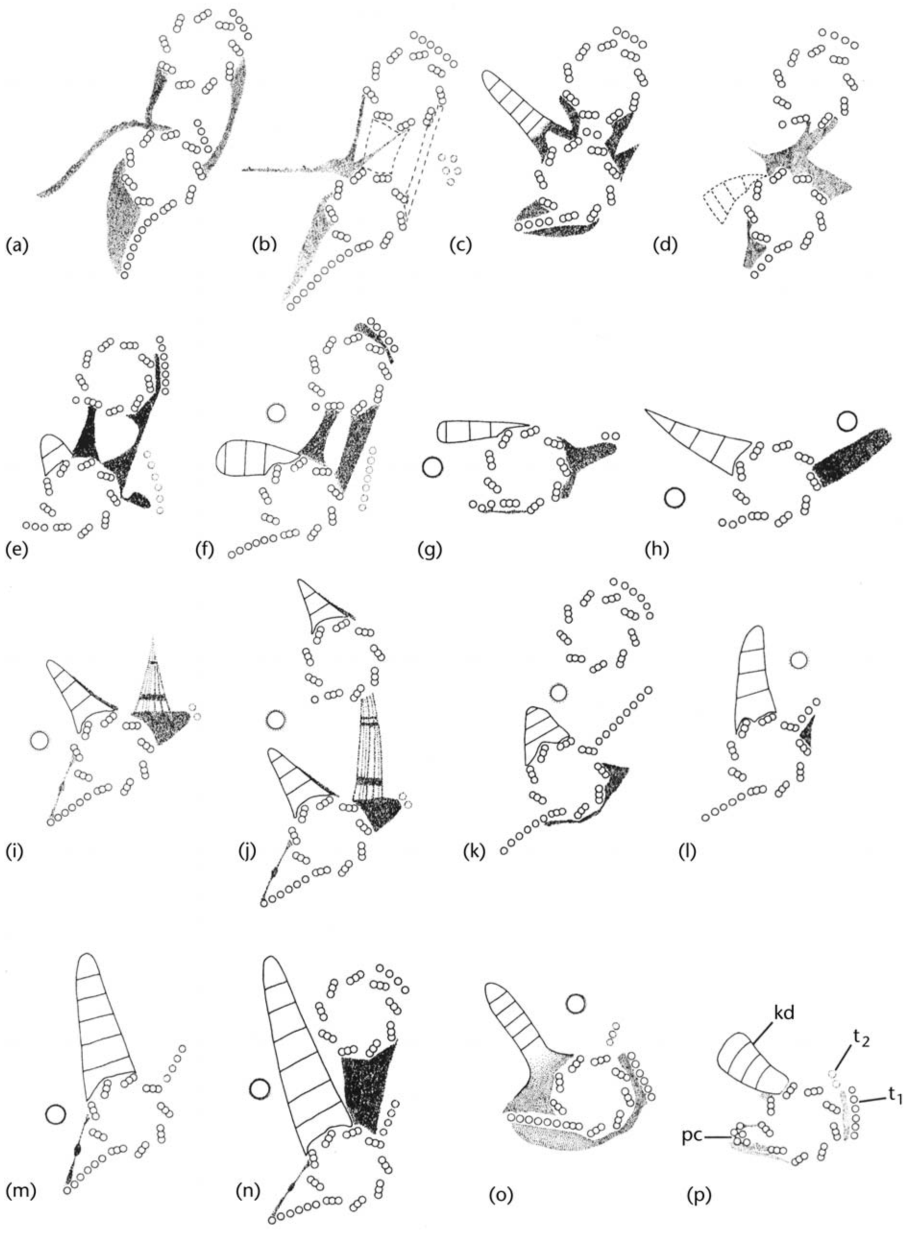

Figure 4 Transverse sections of the somatic kinetids of representative genera from the major classes of ciliates. (a, b) Subphylum Postciliodesmatophora. (a) Class Karyorelictea – *Geleia*. (b) Class Heterotrichea – *Climacostomum*. (c–p) Subphylum Intramacronucleata. (c, d) Class Spirotrichea – *Protocruzia* (c) and *Stylonychia* (d). (e, f) Class Colpodea – *Sorogena* (e) and *Pseudoplatyophrya* (f). (g, h) Class Phyllopharyngea – *Hypocoma* (g) and the suctorian *Trichophrya* (h). (i, j) Class Nassophorea – monokinetid (i) and dikinetid of *Nassula* (j). (k, l) Class Oligohymenophorea – dikinetid of *Colpidium* (k) and monokinetid of *Ichthyophthirius* (l). (m, n) Class Prostomatea – monokinetid (m) and dikinetid of *Coleps* (n). (o, p) Class Litostomatea – *Lepidotrachelophyllum* (o) and *Isotricha* (p). kd, kinetodesmal fibril; pc, postciliary microtubular ribbon; t1 and t2, transverse microtubular ribbons. Based on Lynn (1996a).

lineages of ciliates (Lynn and Corliss, 1991; Lynn and Small, 1989; Lynn and Small, 2002). Some lineages are characterized as having somatic monokinetids while others have somatic dikinetids (**Figure 4**).

Place in Overall Taxonomic Scheme

The ciliates have long been recognized as a monophyletic group. For many years, the suctorians were not considered ciliates (Corliss, 1979). However, along with other ciliates, they are known to show nuclear dimorphism, to conjugate, and to have cilia during their dispersal phase. The structure of suctorian kinetids has the fibrillar associates typical of ciliates (**Figure 4**).

Ciliates are now acknowledged to constitute a phylum taxonomically, related to two other phyla that have membrane-bound alveoli in the pellicle. Along with the ciliates the two sister phyla, the Apicomplexa and the Dinozoa, are called the alveolates. In addition to the presence of alveoli, these three phyla are highly similar with respect to sequences of the small subunit ribosomal RNA (SS-rRNA) genes (**Figure 5**). **See also**: Alveolates; Apicomplexa; Phylogeny based on 16S rRNA/DNA; Protozoan taxonomy and Systematics

Major Subtaxa and Well-known Species

The ciliates are now divided into 11 major lineages or classes (**Table 1**). These classes were initially characterized by differences in the pattern of the somatic kinetid (**Figure 4**). To a lesser extent, oral structures and the patterns of cell division (Foissner, 1996; Lynn and Small, 2002) can also be used to characterize these classes. However, even within one class, for example the class Colpodea,

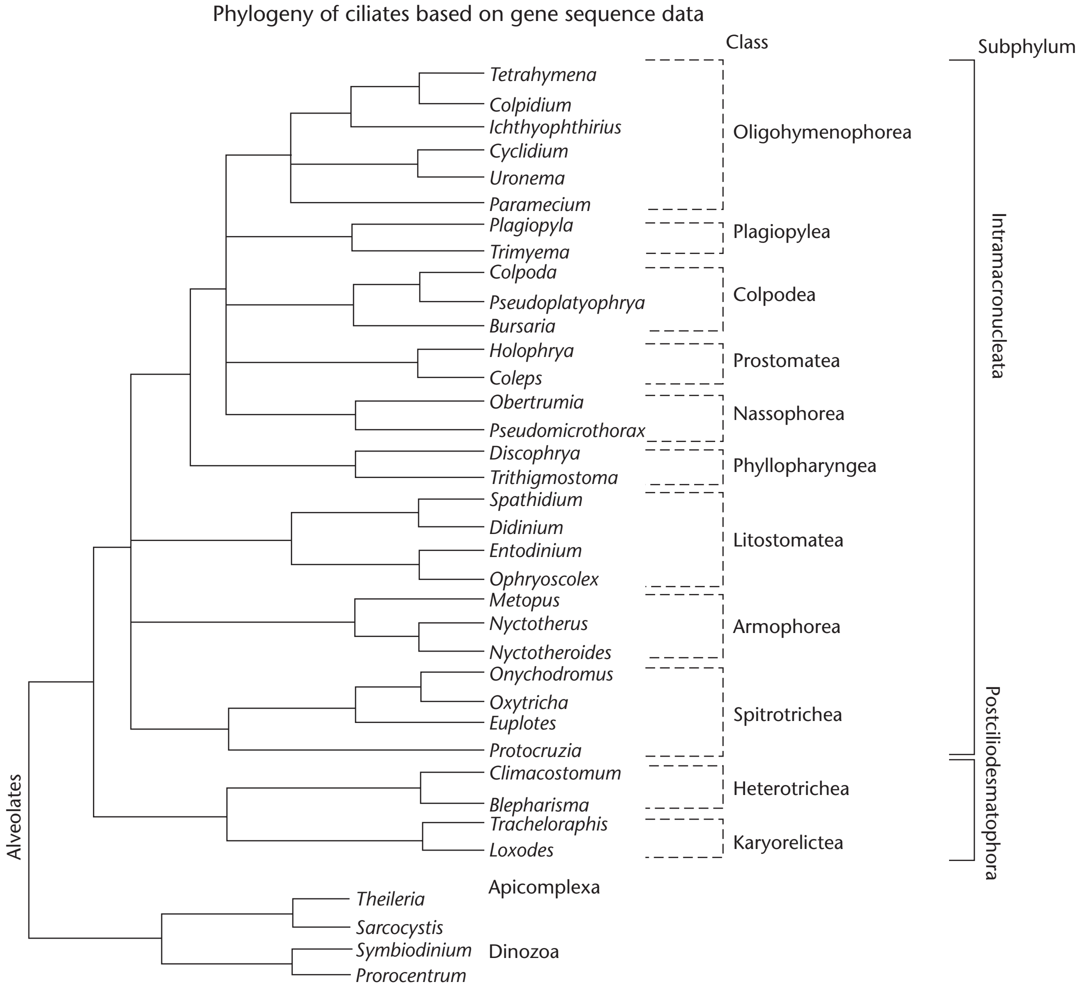
Phylogeny of ciliates based on gene sequence data

Figure 5 A phylogeny based on phylogenies derived from comparisons of the nucleotide sequences of ss-rRNA genes. The other two alveolate phyla Apicomplexa and Dinozoa serve as outgroups to root the ciliate portion of the tree.

Table 1 Classification of the phylum Ciliophora with representative genera, some of which are available from culture collections or biological supply houses

Phylum Ciliophora (Doflein, 1901)

- Subphylum Postciliodesmatophora, Gerassimova and Seravin, 1976
  - Class Karyorelictea, Corliss, 1974
    - *Loxodes*, *Tracheloraphis*
  - Class Heterotrichea, Stein, 1859
    - *Blepharisma*, *Spirostomum*, *Stentor*
- Subphylum Intramacronucleata, Lynn, 1996
  - Class Spirotrichea, Bütschli, 1889
    - *Protocruzia*
    - *Euplotes*, *Oxytricha*, *Stylonychia*
    - *Halteria*, *Strombidium*, *Tintinnopsis*
  - Class Armophorea, Jankowski, 1964
    - *Caenomorpha, Metopus*
    - *Clevelandella, Nyctotherus, Nyctotheroides*
  - Class Litostomatea, Small and Lynn, 1981
    - *Didinium*, *Dileptus*, *Protospathidium*, *Spathidium*
    - *Balantidium*, *Entodinium*, *Ophryoscolex*
  - Class Phyllopharyngea, de Puytorac *et al*., 1974
    - *Chilodonella*, *Trithigmostoma*, *Spirochona*
    - *Discophrya*, *Heliophrya*, *Tokophrya*
  - Class Nassophorea, Small and Lynn, 1981
    - *Nassula*, *Pseudomicrothorax*
  - Class Colpodea, Small and Lynn, 1981
    - *Bursaria*, *Colpoda*, *Platyophrya*, *Sorogena*
  - Class Prostomatea, Schewiakoff, 1896
    - *Coleps*, *Cryptocaryon*, *Holophrya*
  - Class Plagiopylea, Small and Lynn, 1985
    - *Plagiopyla*, *Trimyema*
  - Class Oligohymenophorea, de Puytorac *et al*., 1974
  - Scuticociliates
    - *Anophryoides*, *Cinetochilum*, *Cyclidium*, *Glauconema*, *Homalogastra*, *Metanophrys, Miamiensis*, *Parauronema*, *Potomacus*, *Pseudocohnilembus*
  - Peniculines
    - *Paramecium*
  - Peritrichs
    - *Carchesium*, *Epistylis*, *Opisthonecta*, *Rhabdostyla*, *Vorticella*
  - Hymenostomes
    - *Colpidium*, *Glaucoma*, *Ichthyophthirius*, *Tetrahymena*

oral structures can be found that are reminiscent of the oral structures found in other classes (**Figure 6**).

Subphylum Postciliodesmatophora

Gene sequences of both SS-rRNA and large subunit ribosomal RNA (LS-rRNA) have confirmed these classes, but also strongly suggest that there are two major subphyletic radiations (Lynn, 1996b; Lynn, 2004). The subphylum Postciliodesmatophora, which includes the heterotrich genera *Stentor* and *Climacostomum* and the karyorelictean genera *Loxodes* and *Tracheloraphis* (**Figure 5**), is characterized by having somatic kinetids whose postciliary ribbons of microtubules typically form conspicuous overlapping fibres. The macronuclei of karyorelicteans do not divide but are formed anew at each cell division from a product of micronuclear division. On the other hand, the macronuclei of heterotrichs do divide, but use bundles of microtubules that assemble outside the macronuclear envelope, the so-called extramacronuclear microtubules. The presence of these extramacronuclear microtubules has led some to argue that division of macronuclei evolved twice within the phylum (Lynn, 1996b).

The class Karyorelictea (**Figure 5**, **Table 1**) includes genera such as *Tracheloraphis* and *Loxodes*. *Tracheloraphis* and its relatives are typically found in marine sands where they crawl between the sand grains ingesting bacteria and other food particles. *Loxodes* is an unusual karyorelictean as it is found in freshwaters, but typically in habitats with very low oxygen concentrations (Fenchel, 1987).

The class Heterotrichea (**Figure 5**, **Table 1**) includes both marine and freshwater species. These typically large ciliates, such as *Blepharisma*, *Stentor* and *Spirostomum*, have an extensive spiralling zone of oral polykinetids that extend out over the anterior end. The polykinetidal cilia create feeding currents that bring prey, such as flagellates and other ciliates, into the oral cavity for ingestion (Fenchel, 1987). **See also**: *Stentor*

Subphylum Intramacronucleata

The second subphylum of the ciliates, the Intramacronucleata, includes the remaining nine classes of ciliates, which divide their macronuclei using microtubules that assemble inside the macronuclear envelope, the so-called intramacronuclear microtubules (Lynn, 1996b; Lynn, 2004). Unlike the subphylum Postciliodesmatophora in which there is some similarity in somatic kinetid structure (**Figure 4**), intramacronucleates exhibit a tremendous diversity in somatic kinetid structure (**Figure 4**) and show a rapid burst of diversification in molecular phylogenies (**Figure 5**). It is primarily on the basis of these somatic kinetid features together with features of the oral region and the pattern of oral development or stomatogenesis that the classes within the subphylum Intramacronucleata are characterized (Lynn and Corliss, 1991; Lynn and Small, 1997; Lynn and Small, 2002).

The class Spirotrichea (**Figure 5**, **Table 1**) includes a diverse assemblage of forms found in a wide variety of habitats from ponds to lakes to the oceans, and even in soils. Spirotrichs are found on the bottom of these water bodies and swimming in the water column as plankton. *Euplotes*, *Oxytricha* and *Stylonychia* are some common genera, which have oral polykinetids arranged like the heterotrichs. However, their somatic cilia are combined into cirri, compound ciliary structures composed of 50 or more cilia, which are used like little legs by these ciliates as they 'walk' along the substrate. Other spirotrichs, like *Halteria*, *Strombidium* and *Tintinnopsis*, are common in the plankton, where they feed upon bacteria and phytoplankton, and are in turn ingested by zooplankton. *Tintinnopsis* is a representative of an unusual group of ciliates called the tintinnids. These ciliates secrete a lorica or 'house', in which they sit and which they propel using their oral cilia. Tintinnids are one group of ciliates to have been fossilized; fossil tintinnid loricae date back over 200 million years (Lynn and Small, 1989). Another spirotrich ciliate is *Protocruzia* associated with the spirotrichs by its SS-rRNA sequence. This unusual ciliate has a dividing macronucleus that appears to exhibit chromosome-like structures when it divides, reminiscent of a micronucleus (Corliss, 1979; Raikov, 1982). *Protocruzia* may represent the ancestral state of the intramacronucleate macronucleus. **See also**: *Euplotes* (dorsoventrally-flattened Ciliates)

The class Armophorea (**Table 1**) is one of the two riboclasses in the phylum (Lynn, 2004). 'Riboclasses' are groups that do not demonstrate any obvious morphological shared-derived characters, and yet they are strongly supported by gene sequence data. The class is divided into two major groups. One group, represented by *Caenomorpha* and *Metopus*, includes free-living ciliates found in habitats with low or no oxygen. The other group includes *Clevelandella, Nyctotherus* and *Nyctotheroides* endosymbionts in the intestinal tract of insects, frogs and other invertebrates. The ciliates in this class are all anaerobes or microaerophils, and use hydrogenosomes as 'respiratory organelles' rather than mitochondria (Boxma *et al*., 2005).

The class Litostomatea (**Figure 5**, **Table 1**) includes two very different groups of ciliates: *Didinium* and *Dileptus* are free-living ciliates found in marine and freshwater habitats while *Entodinium* and *Ophryoscolex* represent a diverse assemblage of ciliates found in the intestinal tracts of vertebrates, such as deers, cows, horses, elephants and even gorillas. The only ciliate to cause disease in humans, *Balantidium*, is placed in this class. These ciliates typically have an anterior oral region with simple oral ciliature, typically composed of mono- or dikinetids. *Didinium* and *Dileptus* capture their prey, which can be other ciliates like *Paramecium*, using organelles called toxicysts. Toxicysts are rod-like organelles that are ejected from the ciliate into its prey, much like a harpoon. Not only do toxicysts capture the prey, but they also have hydrolytic enzymes that immobilize the prey and begin to digest its cytoplasm. **See also**: Balantidiosis; *Paramecium*

The class Phyllopharyngea (**Figure 5**, **Table 1**) is named because the cytopharynx of these ciliates is lined with leaf-like ribbons or phyllae (= *phyllos* in Greek) of microtubules. Phyllopharyngeans are divided into two major groups, free-swimming forms like *Chilodonella* and *Trithigmostoma*, which are typically associated with the sediments and other substrates in marine and freshwater habitats, and sessile forms like the chonotrichs and suctorians. Chonotrichs, such as *Spirochona*, are ectosymbionts on crustaceans where they attach to appendages and mouthparts of their host and obtain food particles and bacteria from the host. Suctorians, such as *Discophrya*, *Heliophrya* and *Tokophrya*, attach to substrates and to hosts, like crustaceans, insects and even turtles. These ciliates were named because they have long tentacles supported by the phyllae. The tentacles have extrusive organelles called haptocysts at their tips, which capture prey, usually other ciliates, and 'suck' or transport their cytoplasm into the cell body of the suctorian. Suctorians and chonotrichs produce ciliated swarmers by cell division, and these swarmers swim to other habitats or hosts to disperse the species. **See also**: Suctorians

The class Nassophorea (**Figure 5**, **Table 1**) includes marine and freshwater ciliates that are typically associated with the sediments. They are named after a very prominent basket of microtubular bundles that supports the cytopharynx, called the nasse in French (Corliss, 1979; Lynn and Small, 2002). Nassophoreans, such as *Nassula* and *Pseudomicrothorax*, use the nasse to ingest filamentous cyanobacteria, which are transported into the cytoplasm by the action of small arms attached to the microtubules of the nasse.

The class Colpodea (**Figures 5** and **6**; **Table 1**) includes species that are typically able to form protective capsules called cysts, in which the ciliate can remain dormant, often for periods of years. Colpodeans, such as *Colpoda*, *Platyophrya* and *Sorogena*, are primarily restricted to freshwater habitats and soils where they feed on bacteria, flagellates and other ciliates. *Sorogena* is unusual among ciliates in that individual ciliates aggregate when their food, *Colpoda*, becomes scarce to form a complex aggregate cyst called a sorocarp that sits on a small stalk. The sorocarp is then blown by the wind, taking its hundreds of 'passengers' to a new habitat. One of the largest ciliates, *Bursaria*, is found in this class. *Bursaria* was for many years thought to be a heterotrich, like *Stentor*, because it has many oral polykinetids spiralling towards its cytostome (**Figure 6**). However, its ultrastructure and SS-rRNA gene sequences clearly demonstrate that it is a colpodean (Lynn, 1996b; Lynn and Corliss, 1991; Lynn and Small, 2002). In fact, a number of colpodeans were misclassified by earlier researchers because their oral structures (**Figure 6**) appeared similar to the oral structures of ciliates that we now know belong to different classes based on the structure of the somatic kinetid (**Figure 4**) and gene sequences (**Figure 5**). **See also**: *Stentor*

The class Prostomatea (**Figure 5**, **Table 1**) includes marine and freshwater ciliates that are associated with the bottom and are also found in the water column as plankton. The prostomes, as the name suggests, have an oral region at the anterior end of the cell body. Oral ciliature is simple,

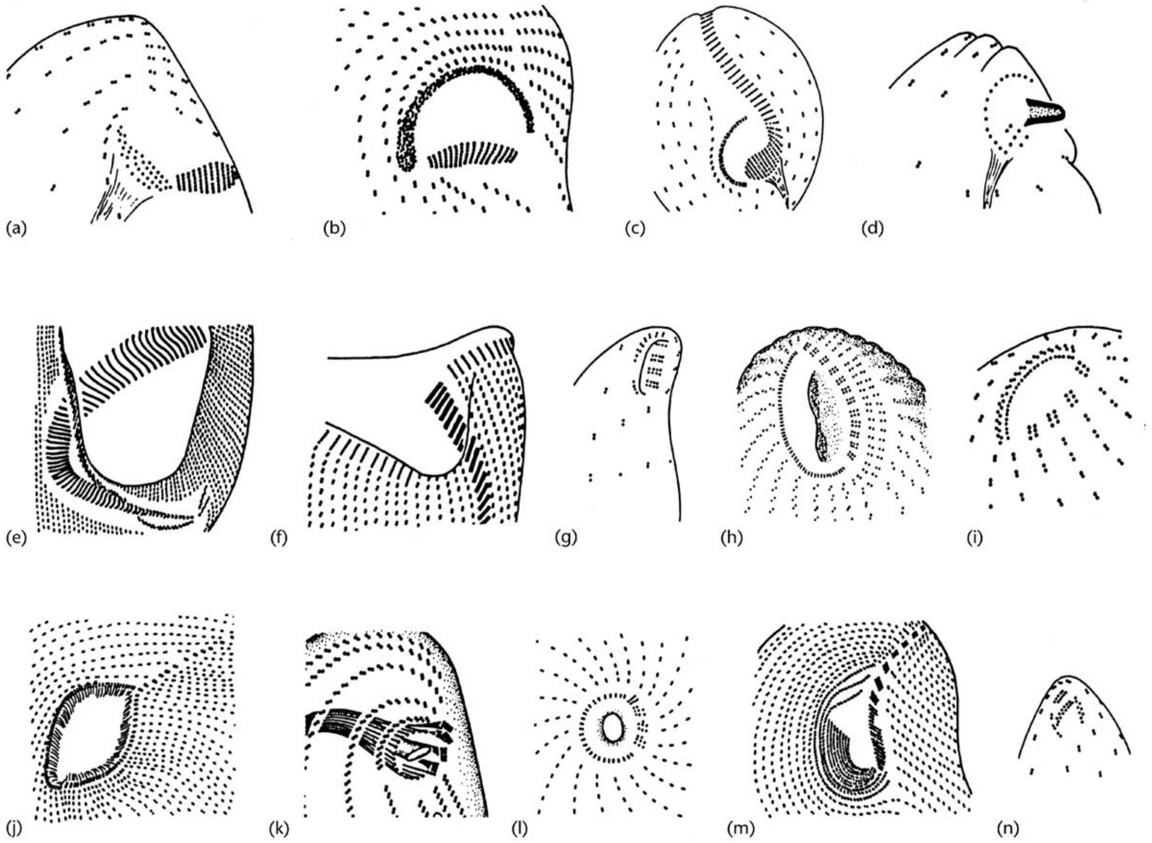

Figure 6 A demonstration of the diversity of oral structures of genera in the class Colpodea. Some of these ciliates represent oral features that are convergent on oral features of ciliates from other classes. (a) *Colpoda* with two oral polykinetids. (b) *Hausmanniella* also with two oral polykinetids. (c) *Bardeliella* with a left oral polykinetid that extends out over the anterior end as a series of rows of cilia. (d) *Grossglockneria* whose everted cytopharynx is used to pierce fungal cells and ingest their cytoplasm, like a suctorian's tentacle. (e, f) *Bursaria* (e) and *Bursaridium* (f) whose extensive series of left oral polykinetids placed them in the class Heterotrichea for many years. (g) *Cyrtolophosis* with its small number of oral polykinetids and small cell size was once considered a member of the class Oligohymenophorea. (h) *Platyophrya* with paroral and multiple left oral polykinetids. (i) *Sagittaria* similar to *Platyophrya*. (j) *Rostrophrya* with small polykinetids extending out on to the somatic surface was initially thought to be a member of the class Nassophorea. (k) *Pseudochlamydonella* whose ventral oral cavity and basket-like cytopharynx are similar to those structures in the class Phyllopharyngea. (l) *Sorogena* with its simple, ring-like anterior oral apparatus was initially classified as a member of the class Prostomatea. (m) *Bryophrya* shows some similarities to *Rostrophrya* and nassophoreans although it has a deep oral cavity. (n) *Trihymena*, a colpodean with a simple oligohymenophorean-like oral apparatus. Based on Lynn (1996a) and Foissner (1993).

usually of dikinetids, but complemented sometimes by specialized kineties, called brosse (= brush in French) kineties, which may be used in detecting prey. Prostomes, such as *Coleps*, *Holophrya* and their relatives, eat bacteria, flagellates and other ciliates. However, they can also feed on dead or dying invertebrates and are called histophagous, or tissue-eating (= *histos* in Greek) for this reason. A prostome, *Cryptocaryon*, causes a white-spot disease of marine fishes. This is similar to the fish disease caused by the freshwater oligohymenophorean *Ichthyophthirius* (see below).

The class Plagiopylea, the second riboclass in the phylum (**Figure 5**, **Table 1**), includes a small assemblage of ciliates whose phylogenetic affinities were unclear until sequences of SS-rRNA suggested that they were related to the class Oligohymenophorea, described below. Plagiopyleans are typically found in marine and freshwater sediments, particularly where oxygen concentrations are low or absent. Some are even symbionts in the intestines of sea urchins, another anaerobic habitat. These ciliates are able to survive here because their mitochondria have evolved to generate hydrogen, and are now called hydrogenosomes. The hydrogen, in turn, is consumed by methanogenic bacteria that live in association with the hydrogenosomes, providing some carbon for their ciliate host.

The class Oligohymenophorea (**Figure 5**, **Table 1**) is probably the most speciose class of ciliates. These ciliates are found virtually anywhere there is moisture – in soils, hot springs, temporary puddles, small ponds, lakes and oceans. The four major subclasses in this taxon are the scuticociliates, peniculines, peritrichs and hymenostomes. Many of these ciliates are easily cultivated and this has made them favourite research subjects: two of the most researched genera of ciliates belong to this class – the peniculine *Paramecium* and the hymenostome *Tetrahymena* (Nanney, 1980). Oligohymenophoreans are named because they have only a few (= *oligos* in Greek) membranes (= *hymen* in Greek) in their oral cavity. Typically they have a paroral kinety or membrane on the right side and three oral polykinetids on the left side of the oral cavity, hence *Tetrahymena* or four membranes. Most oligohymenophoreans are bacteriovorous. Peritrich ciliates, such as *Carchesium* and *Vorticella*, can be found abundantly in sewage treatment plants where they consume faecal coliforms. However, some *Tetrahymena* species can be histophagous while others can be parasitic, as can some scuticociliates, such as *Philasterides*. Probably the most famous parasitic ciliate, although most people do not recognize it as a protozoon, is the hymenostome *Ichthyophthirius*, the parasite of fish that causes white-spot disease of the epithelium and gills. Diseases caused by ciliates may be on the increase as the aquaculture industry expands and provides more opportunities for ciliates to take advantage of overcrowded invertebrates and vertebrates, which also may be less physically fit than their free-ranging relatives. **See also**: *Paramecium*; *Tetrahymena*; Protozoan pathogens of domestic and companion animals; *Vorticella*

This brief survey of the diversity of ciliates has omitted mention of a number of smaller, but no less interesting groups. More detailed information can be found in Corliss (1979), Lynn and Corliss (1991) and Lynn and Small (2002).

Phylogenetic and Evolutionary Considerations

There is probably more known about the comparative morphology and molecular evolution of ciliate groups than any other group of protists. Thus, our confidence in the phylogeny and evolution within this group is fairly high, even though there still remain many unanswered questions. Ciliates have a fossil record that certainly dates back over 200 million years: some fossil tintinnids are this old (Lynn and Small, 1989). However, the phylum is undoubtedly much older. Reid and John (1981) argued that chitinozoa, which are found in Proterozoic deposits over 600 million years old, may be tintinnid cysts. Wright and Lynn (1997) used a molecular clock calibrated on the evolution of the SS-rRNA genes and calculated that ciliates might be 1980–2200 million years old, dating back to the Palaeoproterozoic. If true, the ciliates were undoubtedly the ‘masters of the seas’ in that microbial age. The molecular evidence suggests that the major lineages, now subphyla and classes, radiated very shortly after the emergence of the ‘protociliate’. A burst of evolutionary diversification is a common feature of the emergence of most groups of organisms and unfortunately confounds our understanding of how evolution might have occurred. **See also**: Fossil record; Molecular phylogeny reconstruction; Origin of life

Ciliates are alveolates, and so related to the dinoflagellates. Thus, dinoflagellates and ciliates undoubtedly share a common ancestor. Given this, what might the ancestral ciliate have looked like? Eisler (1992) has argued that the somatic kineties of ciliates arose from the migration of the kinetosomes of a paroral kinety of dikinetids associated with the cytostome of the ‘protociliate’. This ancestor would also probably have evolved some kind of nuclear dimorphism with a macronucleus, probably nondividing like the karyorelicteans, and a dividing micronucleus. How this evolution proceeded is still not resolved, but it is our hope that further comparative study of other genes of ciliates will reveal more clearly the sequence of evolution of the major groups in this intriguing phylum of protists. **See also**: Protozoan evolution and phylogeny

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