Tetrahymena
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of buccal (oral) ciliature. Hymenostomes have a paroral membrane located on the right side of the buccal cavity and three membranelles on the left side, while their bodies are mostly covered by uniform somatic ciliature. Tetrahymenids have longitudinal rows of somatic cilia with several rows interrupted by the buccal cavity. Most *Tetrahymena* spp. are free-living aquatic organisms, although some are facultative parasites that may invade the skin and tissues of aquatic animals, sometimes causing lesions and mortalities in fishes.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Hymenostomatida (right paroral dikinetid plus 1-3 left polykinetids)
Order:	Hymenostomatida (preoral suture, somatic monokinetids)
Suborder:	Tetrahymenina (organelle of Lieberkuhn absent)
Family:	Tetrahymenidae (pyriform body, longitudinal ciliary rows)
Genus:	*Tetrahymena* (most free-living aquatic species, some opportunistic parasites in skin/gills/organs of fish)
Species:	several species cause invasive disease ('tet') in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	**Etymology**	**Defining characters**	**Lifestyles***	**Genera covered**
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed as free-living or symbiotic forms, although a few are parasitic mainly in fish. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. The hymenostomes have a well-defined buccal cavity and conspicuous oral ciliature evident as a paroral membrane of dikinetids on the right side and 1-3 left polykinetids (membranelles) on the left side, while their bodies are mostly covered by somatic ciliature. The single order Hymenostomatida contains 2 suborders: Ophryoglenina (cells with dense somatic ciliature, preoral sutures, buccal cavity opening at the bottom of a deep depression, presence of a unique lens-like organelle of Lieberkuhn (watchglass organelle), and teloparakinetal stomatogenesis); and Tetrahymenina (cells with somatic meridional kineties, inconspicuous anteroventral buccal cavities, preoral sutures, absence of organelle of Lieberkuhn, and monoparakinetal stomatogenesis). Tetrahymenines occur mostly as freshwater microphagous forms filter-feeding on bacteria, particulates and solutes, but a few species exhibit polymorphic variation when they transform to macrostome histophagous forms that feed on aquatic hosts (insects, gastropods and fish). Five families are recognized (Curimostomatidae, Glaucomidae, Spirozonidae, Tetrahymenidae, and Turaniellidae) principally on the basis of differences in their somatic and oral ciliature. Tetrahymenids have pyriform bodies, long ciliary rows, oral membranelles that are uniform in width, and 1-3 postoral kineties ending at the posterior margin of the buccal cavity. The family Tetrahymenidae contains 5 genera (*Blepharostoma, Deltopylum, Lambornella, Melacophrya*, and *Tetrahymena*) with the genus *Tetrahymena* (syn. *Cystidium, Leptoglena, Leucophrydium, Leucophrys, Paraglaucoma, Protobalantidium, Roquea, Tetrahymen, Tetrahymenia, Turchiniella*) being characterized by the possession of 20-30 meridional kineties, 2 being postoral while the rest converge anteriorly around an argentophilic pellicular structure (forming an apical loop and preoral suture). The genus contains almost 50 species which are mostly saprozoic in freshwater habitats, although a few species may be facultative parasites on the body surfaces of freshwater fishes, and occasionally invade the skin, muscles and internal organs causing a disease known as 'Tet' in ornamental and farmed fishes.

While tetrahymenids have been known for at least 200 years, they became popular in research laboratories from the 1950's due to their ease of culture and their genetic manipulability. Many publications arose on their biochemistry and physiology, but most research was inadvertently conducted on amicronucleate (asexual) strains which were subsequently characterized by isoenzyme electrophoresis and allocated to phenosets A-E. Following the discovery of conjugation in sexual strains (with micronuclei), many studies described up to 7 different mating types, particularly in what was called the *Tetrahymena pyriformis*-complex, with the identification of numerous strains and varieties (subsequently called syngens). Early workers grouped various *Tetrahymena* spp. into three complexes based on their morphological and life history traits: the *T. pyriformis*-complex with microstomal mouthparts, simple life-cycles alternating between feeding trophonts and dispersal theronts, with occasional resting cyst formation (e.g. *T. pyriformis, setifera, chironomi, americanis, canadensis, malaccensis, asiatica, nanneyi, elliotti, tropicalis*); the *T. patula*-complex comprising the microstome-macrostome transformers, with cycles involving trophonts, theronts and division cysts producing > 2 tomites (e.g. *T. patula, paravorax, vorax, caudata, silvana*); and the *T. rostrata*-complex with larger bodied microstomal forms that are strongly histophagous and/or parasitic, and have cycles involving trophonts, theronts, resting cysts and division cysts producing 2 tomites (e.g. *T. rostrata, limacis, corlissi, stegomyiae*). However, recent molecular (multi-gene) phylogenetic studies have indicated that these complexes are paraphyletic. Instead, two major clades were detected, an 'australis' clade of closely-related species (involving *T. australis, asiatica, capricornis, cosmopolitanis, hegewischi, hyperangularis, nanneyi, patula, pigmentosa, shanghaiensis, sonneborni*); and a 'borealis' clade with less closely-related species (comprising *T. borealis, canadensis, farleyi, malaccensis, pyriformis, thermophila, tropicalis*). Members of both clades show convergence for histophagy, macrostome formation and cyst formation. Comparative genetic studies have shown that some members of these clades exhibit different patterns of conjugation (involving micronuclear meiosis, reciprocal fertilization, and macronucleus assembly) which impacts on their subsequent mating-type determination: with most of the 'australis' clade being synclonal (mating-type determined at fertilization); and several of the 'borealis' clade being karyonidal (mating-type determined during macronuclear development). The following table lists species in groups recognized by contemporary molecular studies, but further studies are required to identify cryptic species and resolve several inconsistencies (esp. synonyms) as well as to determine conjugation types.

***Tetrahymena* species[1,2]**	**Trophont[3] size (µm) [no. kineties]**	**Life-styles (Hosts)**	**Distribution**
***T. pyriformis* group**			
T. leucophrys	microstome 60-94 x 27-54 macrostome 66-99 x 36-71 [19-23]	free-living (freshwater)	North America
T. pyriformis [= amicronucleate phenoset A] [type species] (syn. *T. geleii, Saprophilus oviformis, Leucophrys, Glaucoma*)	10-90 x 10-70 [15-25]	free-living (water, soil) and facultatively parasitic (histophagous) in viscera of terrestrial slugs (Gastropoda: agriolimacid (*Deroceras reticulatum*)), freshwater crayfish (Decapoda: parastacid (*Cherax quadricarinatus*) and fish (Cypriniformes: cyprinid (carp, goldfish, tiger barb, cherry barb, straightfin barb); Cyprinodontiformes: poecilid (guppy, molly); Cichliformes: cichlid (redbelly tilapia, blue-spotted tilapia, angelfish); Characiformes: characid (neon tetra, X-ray tetra); Salmoniformes: salmonid (rainbow trout); Siluriformes: ictalurid (catfish)	North America, Eurasia, Australia
T. setosa (syn. *Glaucoma, T. setifera*)	33-49 x 22-29 [21-26] [caudal cilium]	free-living (freshwater) and facultatively histophagous	North America, Eurasia
T. silvana	not stated[4] macrostome [resting cyst]	free-living (freshwater)	Asia
T. vorax	microstome 30-80 [18-23] macrostome 100-250 [19-28] [reproductive cysts]	free-living (freshwater)	North America

***T. thermophila* group**			
T. elliotti [= amicronucleate phenoset B]	not stated [selfing]	free-living (freshwater)	Americas, Eurasia
T. malaccensis	not stated [karyonidal]	free-living (freshwater)	Malaysia
T. thermophila (syn. *T. pyriformis* syngen 1)	50 [karyonidal]	free-living (freshwater and briny pond)	North America
***T. tropicalis* group**			
T. aquasubterranea	37-53 x 18-27 [17-19]	free-living (well groundwater)	Africa
T. furgasoni (syn. *T. pyriformis* strain W [= amicronucleate phenoset C], *T. lwoffi* [= amicronucleate phenoset E])	not stated	free-living (freshwater)	North America
T. tropicalis (syn. *T. pyriformis* syngen 9)	not stated	free-living (freshwater)	North America, Pacific
***T. borealis* group**			
T. borealis (syn. *T. pyriformis* syngen 3)	not stated [karyonidal]	free-living (freshwater)	North America, Europe
T. canadensis (syn. *T. pyriformis* syngen 7)	not stated [karyonidal]	free-living (freshwater)	North America, Malaysia
T. mimbres	35-48 x 17-26 [16-18]	free-living (hot springs)	North America, China
T. rostrata (syn. *Paraglaucoma*]	35-90 x 24-56 free-living [26-39], parasitic [35-58] [caudal cilium] [resting cysts] [reproductive cysts]	free-living (edaphic in soil, litter, moss) and facultatively parasitic (histophagous) in viscera of terrestrial slugs/snails (Gastropoda: agriolimacid (*Deroceras reticulatum, laeve*, *panormitanum*), arionid (*Arion circumscriptus*, *intermedius*), clausiliid (*Macrogastra latestriata*), cochlicopid (*Cochlicopa lubrica*), discid (*Discus rotundatus*), helicid (*Helix aspersa*), milacid (*Milax gagates*, *Tandonia sowerbyi*), oleacinid (*Poiretia algira*), valloniid (*Vallonia pulchella*), vitrinid (*Vitrina pellucida*), zonitid (*Zonitoides nitidus*), and possibly the skin of cultured fish (Salmoniformes: salmonid (Atlantic salmon)	North America, Europe, Australia
***T. americanis* group**			
T. americanis (syn. *T. pyriformis* syngen 2)	not stated [resting cysts] [synclonal]	free-living (freshwater)	Americas, Asia
T. asiatica	not stated [synclonal]	free-living (freshwater)	Asia
T. australis (syn. *T. pyriformis* syngen 11)	20-50 x 10-30 [19-22] [synclonal]	free-living (freshwater)	Australia, Americas, Eurasia
T. capricornis (syn. *T. pyriformis* syngen 12)	not stated [synclonal]	free-living (freshwater)	Australia
T. cosmopolitanis (syn. *T. pyriformis* syngen 4)	not stated	free-living (freshwater)	North America, Eurasia
T. empidokyrea	32-52 x 18-32 [16-19]	parasitic (histophagous) in insects (Diptera: culicid (*Aedes* adult mosquitoes))	North America
T. hegewischi (syn. *T. pyriformis* syngen 5)	not stated [synclonal]	free-living (freshwater)	North America

T. hyperangularis (syn. *T. pyriformis* syngen 10)	not stated [synclonal]	free-living (freshwater)	North America, Europe
T. nanneyi	not stated [synclonal]	free-living (freshwater)	North America
T. nipissingi (syn. *T. pyriformis* syngen 14)	not stated [synclonal]	free-living (freshwater)	North America
T. patula (syn. *Leucophrys*)	microstome 45 x 28 [32-41] macrostome 80-160 [35-45] [reproductive cysts]	free-living (freshwater)	North America
T. shanghaiensis	33-60 x 21-30 [16-20]	free-living (freshwater)	Asia
T. sonneborni (syn. *T. pyriformis* syngen 13)	not stated [synclonal]	free-living (freshwater)	North America, Europe
Miscellaneous group			
T. caudata	microstome 54-61 x 26-37 macrostome 81-101 x 58-81 [17-26] [caudal cilium] [resting cyst]	free-living (freshwater)	Asia
T. chironomi	40 x 23 [23-28] [selfing]	parasitic in haemolymph of insects (Diptera: chironomid (*Chironomus plumosus* larvae)	Europe, North America
T. corlissi	30-70 x 20-45 [23-31] [caudal cilium] [resting cysts] [reproductive cysts]	free-living (freshwater), facultatively parasitic (histophagous) in skin, muscles and body cavity of fish (Anabantiformes: osphronemid (dwarf gourami, kissing gourami); Cyprinodontiformes: poecilid (guppy, molly, platyfish); Cichliformes: cichlid (mango tilapia); Characiformes: characid (tetras); Perciformes: percichthyid (golden perch); Siluriformes: ictalurid (bullhead catfish) and amphibians (Urodela: plethodontid (*Pseudotriton* larvae)	North America, Europe, Australia
T. dimorpha	microstome 33-49 x 25-38 [19-24] macrostome 56-89 x 41-70 [30-66]	parasitic in haemolymph of insects (Diptera: simuliid (*Simulium equinum* larvae, pupae, adults, *S. ornatum* larva)	Europe
T. farahensis	26-43 x 21-36	free-living (wastewater)	Pakistan
T. farleyi	42-56 x 14-26 [15-17]	parasitic in urinary tract of vertebrate (Carnivora: canid (dog))	North America
T. limacis (syn. *Paraglaucoma*)	28-68 x 17-42 free-living [24-32] parasitic [26-46] [selfing]	terrestrial, parasitic (histophage) in viscera of slugs/snail (Gastropoda: agriolimacid (*Deroceras reticulatum, laeve*), arionid (*Arion hortensis*, *Prophysaon andersoni*, *Monadenia fidelis*), daudebardiid (*Daudebardia rufa*), helicid (*Helix pomatia*), hygromiid (*Trichia lubomirskii*, *Perforatella dibothrion*), limacid (*Lehmannia marginatus*, *valentiana*, *Limacus flavus*, *maximus*), milacid (*Milax gagates*, *Tandonia budapestensis*), succineid (*Oxyloma pfeifferi*, *Succinea oblonga*), vitrinid (*Vitrina pellucida*), zonatid (*Nesovitrea hammonis*, *Oxychilus depressus*)	Europe, North America, Africa
T. paravorax	microstome 80 x 40 [22-30] macrostome 100-200 [24-28] [caudal cilium]	free-living (freshwater)	Europe

	[selfing]		
T. rotunda	41-89 x 40-80 [50-66]	parasitic in haemolymph of insects (Diptera: simuliid (*Simulium venustum* larvae, pupae, adults, *S. tuberosum* larvae))	North America
T. sialidos	32-51 x 18-33 [22-27] [selfing]	parasitic in haemolymph of insects (Megaloptera: sialid (*Sialis lutaria* larvae))	Europe
Uncharacterized species			
T. bergeri	50-70 x 25-30 [26-33] [reproductive cysts]	free-living (freshwater) and facultatively histophagous	Europe
T. edaphoni	40-50 x 20 [18-20] [resting cysts]	free-living (terrestrial, spruce forest)	Europe
T. glochidiophila	bactivore 30-49 x 19-27 histophage 41-59 x 19-31 [23-26] [caudal cilium?]	freshwater, parasitic (histophagous) in mantle cavity of mollusc larvae (Bivalvia: unionid (*Lampsilis siliquoidea* glochidia larvae))	North America
T. mobilis (syn. *Saprophilus*)	30-40 [22]	free-living (activated sludge) and facultatively histophagous (experimentally on fragmented mealworms *Tenebrio molitor*)	Europe
T. pigmentosa (syn. *T. pyriformis* syngen 6, 8)	not stated [synclonal]	free-living (freshwater)	North America, Europe, Africa
T. stegomyiae (syn. *Lambornella*)	60 [25-30] [resting cysts]	parasitic in haemolymph of insects (Diptera: culicid (*Aedes* larvae))	Africa

[[1]Environmental and clinical isolates of tetrahymenids not identified to species have not been included in this table]
[[2]Three species (*T. faurei, T. glaucomaeformis* and *T. parasitica*) are considered *nomen dubium* due to incomplete/inadequate descriptions, and are excluded from most species lists]
[[3]Selfing = intraclonal conjugation; synclonal = exconjugant mating-type determined at fertilization; karyonidal = exconjugant mating-type determined during macronuclear development]
[[4]Not stated = no morphometrics given in species description]

Parasite morphology: All *Tetrahymena* spp. form at least 2 developmental stages (feeding trophonts and dispersal theronts), while some species may also form resting cysts and/or reproductive (division) cysts ('tomonts'). The trophonts are broad ovoid to pyriform stages, bluntly pointed anteriorly and rounded posteriorly. They swim slowly, feed constantly and become darkened in colour by the growing abundance of food vacuoles. They vary considerably in size depending on species and nutritional status, becoming larger as they feed to repletion (particularly in favourable culture conditions). Trophonts of most species range from 10-100 µm in length, but some may enlarge and grow up to 250 µm long. Cells have both specialized oral (buccal) and somatic (body) ciliation. The oral apparatus is located subapically in the anterior body and consists of a buccal cavity leading to the cytostome, both being surrounded by a paroral undulating membrane on the right side and by 3 serially-arranged membranelles on the left side. Most species have small (ca. 10 x 6 µm) mouthparts (microstome forms) facilitating saprozoic filter-feeding (on solutes and particulates, including bacteria). Some species, however, are able to transform into larger cells (100-250 µm) with enlarged (ca. 30 x 20 µm) mouthparts (macrostome forms), sometimes with deep cytopharyngeal pouches that grossly distort their anterior ends. These enlarged mouthparts allow the ciliates to prey on other ciliates as carnivores (even cannibals) and/or to become histophagous (facultative or obligate parasites of invertebrates (insects, gastropods) and vertebrates (fish)). Transformation from microstome to macrostome forms is generally reversible depending on environmental conditions and food availability. The trophont body is covered in longitudinal (meridional) rows (kineties) of ciliary basal bodies (kinetosomes) giving rise to short eukaryotic cilia (microtubular core with 2 single central microtubules and 9 peripheral doublets). The number of somatic kineties varies from 15-66 (most with 20-30) depending on the ciliate species, trophont maturity and the occurrence of macrostome forms. Trophonts have a straight pre-oral suture with 1-3 postoral kineties beginning at the posterior margin of the buccal cavity, and some species may possess a single caudal cilium. Cells possess a large spherical-ovoid central macronucleus with an adjacent small dense micronucleus, and a single terminal contractile vacuole with 2-6 pores (2-3 in microstomal forms, 3-6 in macrostomes). Theronts act as dispersal stages and they are generally smaller than trophonts and have narrow elongate bodies with rounded posterior ends and pointed anterior ends often curved slightly to the right. These cells are highly active and they swim rapidly spirally up and down in the water column frequently changing direction. In the absence of food, the theronts of some species (e.g. *T. americanis, T. caudata, T. corlissi, T. rostrata, T. silvana,* and *T. stegomyiae*) form small inactive resting cysts (18-20 µm in diameter) encapsulated by cyst walls formed by secretions of mucocysts. Several species may also form larger (35-40 µm) division (reproductive) cysts known as tomonts which divide internally to form 2-8 (rarely 16) tomites (often observed rotating within cysts), with *T. bergeri* and *T. corlissi* forming 2 tomites, and *T. patula* and *T. vorax* forming > 2 tomites. When food becomes available, both types of cysts undergo excystment, with resting cysts releasing stages that develop into trophonts while division cysts release tomites that may form trophonts or theronts.

Site of infection: Most *Tetrahymena* spp. are free-living filter-feeding ciliates usually found in freshwater bodies. The trophonts of a few species, however, have been found to infect the haemolymph of insects, the mantle cavities and viscera of slugs and snails, or the external surfaces (skin and gills) of fish and sometimes their internal tissues (muscles and viscera). Infections have been commonly reported in cultured freshwater fish and tropical ornamental species. However, many reports only identified the parasites as belonging to the genus *Tetrahymena,* so little is known about the identity, host range or specificity of the species that actually infect fish. Four species (*T. corlissi, T. pyriformis, T. rostrata,* and *T. faurei*) have been reported as being histophagous in fish, but even their identification to species level has often been presumptive. *T. corlissi* is probably the most common and pathogenic species in fish, while the remaining 3 species have usually been associated with terrestrial gastropods (snails and slugs) and only occasionally with fish. *T. pyriformis* is widespread but has many congeners with similar morphological characteristics (e.g. species included in the classical (biologic) *T. pyriformis*-complex and the contemporary (molecular) *T. pyriformis* group). *T. rostrata* has been tentatively linked to rare cranial lesions in some cultured salmonids, while *T faurei* reported as parasitic in carp, catfish and trout is generally considered *nomen dubium* due to the lack of sufficient descriptive data. Theronts are free-swimming planktonic stages; while resting and division cysts are inactive stages that usually sink onto benthic substrates.

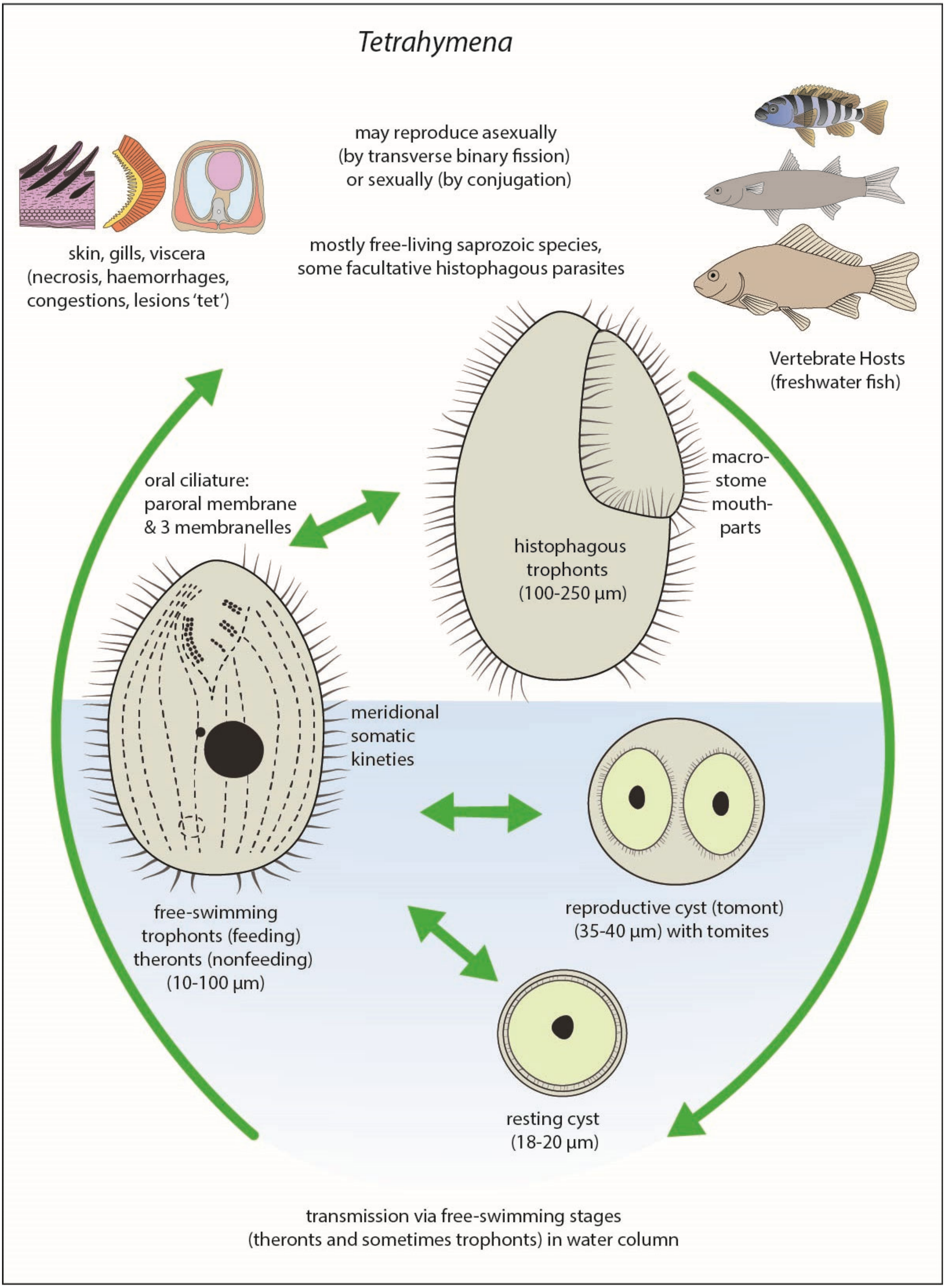
Pathogenesis: Free-swimming tetrahymenids occur as filter-feeders in freshwater lakes, ponds and streams, but the trophonts of some species are attracted to hosts by chemokinesis (involving host peptides) and can switch from free-living to epizoic (attaching to host) ranging from commensalistic (no harm to host) to parasitic (harms host). The ciliates feed on fish surfaces using their microstome mouthparts or transform to histophagous forms with macrostome mouthparts and invade tissues. They may ingest solutes, cellular debris, particulate material and even host cells (including erythrocytes). Light infections in fish may be asymptomatic or subclinical, but parasites may proliferate rapidly resulting in heavy infections causing superficial and/or systemic disease (colloquially called 'Tet'). Infections of the skin initially produce small white patches with masses of ciliates in copious mucus, but often progress to deeper invasion with tissue necrosis, epidermal sloughing, lifting of scales, haemorrhage, oedema, granular lesions and open wounds. Infections of the gills may result in extensive necrosis, epithelial hyperplasia and sloughing, congestion with excessive mucus production and respiratory distress. Ciliates that develop macrostome mouthparts become histophagous and invade internal tissues, including somatic musculature, body cavity organs and sometimes central nervous tissues. This may produce considerable necrosis and degeneration resulting in focal expanding lesions contributing to dysfunctional changes (loss of equilibrium, fin clamping, lethargy) and mortalities. Infections are rarely associated with inflammatory reactions and while some fibroblast responses have been recorded, they have not led to any significant fibrosis. Occasionally, masses of ciliates accumulating around the rim of the eye socket may cause a condition known as 'spectacled eye', and intraocular infections may lead to exophthalmos ('pop-eye'). Systemic infections may cause death in 1-3 weeks, with female fish succumbing before male fish. Fry are particularly susceptible to clinical disease, particularly those with injured integuments.

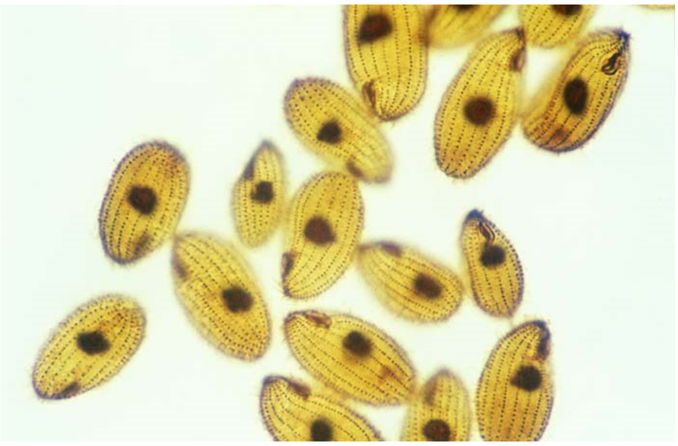
Developmental cycle and mode of transmission: Tetrahymenids are essentially free-living ciliates, with microstomal species feeding mainly on bacteria, but some able to reversibly transform to macrostomal carnivorous forms and/or histophagous parasites (most facultative, but some obligate) with direct transmission to aquatic/terrestrial invertebrates (insects, gastropods) or vertebrates (fish). Different species have different life-cycles, involving cyclic transformation between feeding trophonts (which may divide asexually by binary fission when food is available) and active free-swimming theronts (which do not feed or divide, but disperse seeking food). When food is scarce, theronts may sometimes forming resting cysts (containing immotile stages), division (reproductive) cysts (tomonts) which divide asexually to produce tomites (that mature to theronts or trophonts when released), or mate sexually by the process of conjugation (involving micronuclear meiosis, reciprocal fertilization, and new macronucleus assembly). Studies have shown that up to 7 different sexes (mating types) may be produced; with a few able to undergo intraclonal conjugation ('selfing') but most committed to cross-breeding with exconjugant mating-types determined at fertilization (synclonal) or during macronuclear assembly (karyonidal). Members of the *T. pyriformis*-complex generally exhibit simple cycles, with small microstomal trophonts from both amicronucleate and micronucleate species growing and dividing by binary fission when food is available. Under starvation conditions, the trophonts form theronts for dispersion (some also form resting cysts) and micronucleate species may also undergo conjugation. Members of the *T. patula*-complex include larger species which may reversibly form macrostome mouthparts and prey on other ciliates (as carnivores, and even cannibals); some even developing huge cytopharyngeal pouches. When food is depleted, several of these species form reproductive cysts in which multiple (2-16) tomites are formed. Members of the *T. rostrata*-complex are also larger bodied species, which are strongly histophagous and/or parasitic. In unfavourable conditions, some produce both resting and reproductive cysts (usually only yielding 2 tomites). The transmission of parasitic species between piscine hosts occurs directly via free-swimming stages, both dispersal theronts and sometimes feeding trophonts (particularly in crowded conditions).

Differential diagnosis: Infections are diagnosed by the microscopic detection of motile ciliates in wet mounts of skin or other tissues. Trophonts are best observed using high-contrast microscopy or they can be counter-stained with methyl green-pyronin.

Generic and specific identification involves enrobing ciliates onto albuminized slides and subjecting them to silver staining (silver proteinate (protargol), silver nitrate, silver carbonate) to reveal their distinctive patterns of oral and somatic ciliation (ciliary basal bodies are strongly argentophilic). Ciliates can be readily cultivated *in vitro* in a variety of media, including plant infusions (hay, rye, lettuce), axenic cultures (proteose-peptone, skim-milk, chemically-defined) and monoxenic cultures (with feeder bacteria). This has facilitated numerous studies on ciliate physiology, reproduction, and genetics, including the determination of mating compatibilities to discriminate species (often impractical as living stocks of multiple mating types are required but many isolates are either asexual or sexually immature). Molecular studies have examined isoenzyme electrophoretic profiles for many isolates, but consistent differences between species were only found occasionally. More recently, molecular biological techniques have been used to characterize isolates following the polymerase chain reaction (PCR) amplification of specific gene sequences, with low interspecific variation noted for nuclear genes (small and large subunit ribosomal DNA, internal transcribed spacer regions) and greater variability found for faster-evolving mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: Ectozoic infections on the superficial aspects of fish have responded to treatments with various chemical baths (e.g. formalin, potassium permanganate, methylene blue), but there are no effective treatments for endozoic systemic infections. Several anthelmintics (e.g. niclosamide, albendazole) and anti-malarials (e.g. chloroquine) have shown some efficacy in killing parasites in aquaria. Preventive measures have focussed on reducing contamination by ciliates in culture systems and avoiding conditions predisposing to infections and disease. Animals should be screened prior to their introduction into facilities, with suspect fish quarantined or culled. Fish should be reared in clean water sources (filtered and chlorinated if possible) with regular flushing and water exchange. Care should be taken to avoid over-feeding as accumulated organic wastes increases the likelihood of biofouling and bacterial blooms that are conducive to ciliate growth. Dead and dying fish should be promptly removed and carcases disposed of by burying on land or incineration. Contaminated tanks should be drained, disinfected, and dried before restocking. Management practices should endeavour to avoid stressful (immunocompromising) situations that affect host susceptibility, such as poor water quality, poor nutrition, excessive handling, overcrowding, concomitant infections and injuries. Experimental vaccination studies using live attenuated ciliates or lysates, with or without adjuvants and/or boosters, have given variable results with some protection linked to increased lysozyme activity in challenged fish.


Tetrahymena
may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)
mostly free-living saprozoic species,
some facultative histophagous parasites
skin, gills, viscera
(necrosis, haemorrhages,
congestions, lesions 'tet')
Vertebrate Hosts
(freshwater fish)
oral ciliature:
paroral membrane
& 3 membranelles
macro-
stome
mouth-
parts
histophagous
trophonts
(100-250 µm)
meridional
somatic
kineties
free-swimming
trophonts (feeding)
theronts (nonfeeding)
(10-100 µm)
reproductive cyst (tomont)
(35-40 µm) with tomites
resting cyst
(18-20 µm)
transmission via free-swimming stages
(theronts and sometimes trophonts) in water column



Tetrahymena trophonts from aquarium

Tetrahymena trophont from fish skin (silver stain)

Tetrahymena trophonts from fish skin (silver stain)