Trichomonads (enteric species in mammals, birds, reptiles, amphibia, fish, invertebrates)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Many *Trichomonas* spp. have been reassigned to different genera based on the number of free anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Most trichomonad species are endocommensals in mammals, birds, reptiles and insects but several species are parasitic in the alimentary or urogenital tracts of man and domestic animals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Excavata (with conspicuous ventral feeding groove)
Group:	Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum:	Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class:	Trichomonadea (single mastigont, comb-like structure absent, infrakinetosomal body absent)
Order:	Trichomonadida (lamelliform undulating membrane, B-type costa)
Family:	Trichomonadidae (5-6 flagella, cone-like axostyle)
Genus:	*Trichomonas* (parasites/commensals in tubular organs of vertebrates)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Trichomonad taxonomy can be very confusing as many *Trichomonas* spp. have now been reassigned to sister genera based on the number of anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Recent ultrastructural and molecular biological studies have also led to the placement of the genus *Tritrichomonas* into a separate class (Tritrichomonadea) as the cells contain unique comb-like structures and infrakinetosomal bodies at the bases of their recurrent flagella (both lacking in members of the class Trichomonadea). Several genera (*Hypotrichomonas* and *Trichomitus*) were assigned to another class (Hypotrichomonadea) as their cells contained comb-like structures but lacked infrakinetosomal bodies.

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found exclusively in invertebrate hosts (such as termites and cockroaches) are not listed.

The class Trichomonadea contains a diverse range of cells with single karyomastigonts giving rise to 2-6 flagella, with one being recurrent but lacking a comb-like structure and infrakinetosomal body. Two orders are recognized: Honigbergiella (undulating membrane absent or lamelliform without supporting costa); and Trichomonadida (most with lamelliform undulating membrane supported by B-type costa and stout cone-like axostyles). The family Trichomonadida contains some 10 genera (*Cochlosoma, Lacusteria, Pentatrichomonas, Pentatrichomonoides, Pseudotrichomonas, Pseudotrypanosoma, Tetratrichomonas, Trichomitopsis, Trichomonas* and *Trichomonoides*) which vary in their cellular, organellar and flagellar configurations, zoogeography (host ranges), and biological characteristics (heterotrophs ranging from mutualists to commensals to parasites). Trichomonads (*sensu latu* = in the broadest sense) usually exhibit strong site specificity (tissue tropism) and occur in the alimentary, urogenital or respiratory tracts of their hosts, where they may cause very different types of disease. Several specialized species living in the urogenital tracts of vertebrates may cause severe inflammatory diseases, with *Trichomonas vaginalis* causing vaginitis in humans, and *Tritrichomonas foetus* causing bovine infertility. A few species living in the upper respiratory and alimentary tracts of birds may cause life-threatening diseases, including *Trichomonas gallinae* causing canker in birds. In contrast, those inhabiting the intestinal tracts of vertebrate and invertebrate hosts are often considered to be symbiotes or commensals (rather than parasites) as most infections appear benign. Rather than try to cover trichomonad biodiversity and their disparate clinical significance in one comprehensive section, it has been elected to showcase representatives in 4 separate sections, targeting:

- urogenital infections by *Tritrichomas foetus* in cattle;
- urogenital infections by *Trichomonas vaginalis* in humans;
- oral infections by *Trichomonas gallinae* in birds; and
- enteric infections by *Trichomonas, Tetratrichomonas* and *Pentatrichomonas* spp. in a wide range of hosts.

A large number of trichomonad species have been reported in the digestive tracts from a wide range of vertebrates (mammals, birds, reptiles, amphibia, fish) and invertebrates (wood-eating termites and cockroaches, leeches, snails). Most infections have not been associated with clinical disease and many trichomonads are considered to be harmless commensals or symbiotes (even mutualists in insects). While trichomonads are often encountered in clinical samples, they are generally regarded to be incidental detections unrelated to aetiology. Nonetheless, several species have tentatively been associated with mild clinical signs in a small number of hosts, including *Trichomonas tenax* and *Pentatrichomonas hominis* in humans, and *Tetratrichomonas gallinarum* in birds.

Parasite species†	**Size (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Trichomonadea** (single karyomastigont) [4-6F-CLS-IKB(+CA in most genera, TA or reduced in others)]					
Order: Trichomonadida [5-6F+LUM+BC]					
Family: Trichomonadidae [+CA]					
Trichomonas [5F(=4A+R)+LUM-RF+BC]					
Trichomonas agilis	10-14 x 7-9	Isoptera: kalotermitid (termite *Calotermes brouni*)	hindgut		New Zealand
Trichomonas alexeieffi		Sauria: anguid (slow worm)			Europe
Trichomonas anthropopitheci		Primates: hominid (chimpanzee)			Africa
Trichomonas aotus		Primates: aotid (three-striped night monkey)	intestines		Americas
Trichomonas aragaoi		Edentata: myrmecophagid (southern tamandua)			South America
Trichomonas aulacodi		Rodentia: thryonomyid (greater cane rat)			Africa
Trichomonas avium		Gruiformes: aramid (cayenne wood rail); Cuculiformes: cuculid (ani, guira cuckoo); Piciformes: galbulid (nunbird)			Americas
Trichomonas boae		Serpentes: boid (boa constrictor)			South America
Trichomonas bonasae		Galliformes: tetraonid (ruffed grouse)			Europe
Trichomonas bramae		Strigiformes: strigid (spotted owlet)			Asia
Trichomonas brevicollis		Isoptera: kalotermitid (termite *Calcaritermes brevicollis*)	hindgut		Central America
Trichomonas brixi [+AF]	4-11 x 2-8	Carnivora: canid (dog), felid (cat)	oral cavity		Europe
Trichomonas cartagensis		Isoptera: kalotermitid (termite *Glyptotermes contracticornis*)	hindgut		Central America
Trichomonas chagasi		Rodentia: caviid (rock cavy)			South America
Trichomonas chordeilis		Caprimulgiformes: caprimulgid (night hawk)			Americas
Trichomonas coccyzi		Cuculiformes: cuculid (yellow-bellied cuckoo)			Americas
Trichomonas corvus		Passeriformes: corvid (eastern American crow)			North America
Trichomonas costulata [+RF+AF]+costula		Isoptera: kalotermitid (termite *Cryptotermes havilandi*)	hindgut		India, Brazil
Trichomonas cryptonucleata		Rodentia: sciurid (woodchuck)			North America
Trichomonas cynomysi		Rodentia: sciurid (prairie-dog)			North America
Trichomonas digranula		Rodentia: sciurid (woodchuck)			North America
Trichomonas duboscqui		Anura: discoglossid (painted frog)			Europe

Trichomonas equibuccalis [+AF]	6-9 x 6	Perissodactyla: equid (horse, donkey)	mouth	non-pathogenic	worldwide
Trichomonas flagelliphora		Rodentia: caviid (guinea pig)			
Trichomonas frugivori		Rodentia: murid (black rat)			India
Trichomonas fulicae		Gruiformes: rallid (American coot)			Americas
Trichomonas gallinae	covered in separate section				
Trichomonas gigantea		Isoptera: archotermopsid (termite, *Porotermes adamsoni*)	hindgut		Australia
Trichomonas hegneri		Galliformes: tetraonid (European partridge), phasianid (California quail)			Europe, North America
Trichomonas hoarei		Pelecaniformes: phalacrocoracid (cormorant)			Africa
Trichomonas holmgreni		Isoptera: kalotermitid (termite *Neotermes holmgreni*)	hindgut		Central America
Trichomonas iowensis		Caprimulgiformes: caprimulgid (night hawk)			Americas
Trichomonas labella		Isoptera: termitid (termite *Microtermes hispaniolae*)	hindgut		Central America
Trichomonas lacertae		Sauria: scincid (golden skink), xantusiid (desert night lizard), agamid (starred agama), lacertid (land lizard, wall lizard, green lizard), iguanid (crested desert lizard, chuckawalla lizard, brush lizard, zebra-tailed lizard, collared lizard, horned lizard, sand lizard)			Eurasia, Africa, Americas
Trichomonas lanceolata		Caprimulgiformes: caprimulgid (nacunda nightjar)			Africa
Trichomonas landei		Charadriiformes: scolopacid (sanderling)			North America
Trichomonas lavieri		Rodentia: cricetid (pine vole)			North America
Trichomonas leucuri		Rodentia: hystricid (Indian crested porcupine)	caecum		India
Trichomonas lighti		Isoptera: termitid (termites *Amitermes minimus, emersoni, silvestrianus, coachellae, wheeleri*)	hindgut		North America
Trichomonas limacis		Gastropoda: limacid (land snail)			Europe
Trichomonas linearis		Isoptera: termitid (termite *Orthognathotermes wheeleri*)	hindgut		Americas
Trichomonas mabuiae		Sauria: scincid (golden skink)			Asia
Trichomonas macropi		Diprotodontia: macropodid (kangaroo, rock kangaroo, Woodward wallaroo, black-faced kangaroo, great grey kangaroo, black tree kangaroo)			Australia
Trichomonas macrostoma		Isoptera: hodotermitid (termite *Hodotermes mossambicus*)	hindgut		Africa
Trichomonas megastoma		Rodentia: erethiozontid (hairy tree porcupine)			Americas
Trichomonas muris		Rodentia: murid (house mouse, wood mouse, brown rat), sciurid (ground squirrel, thirteen-striped ground squirrel), cricetid (bank vole, field mouse, white-footed mouse)			Americas, Eurasia

Trichomonas mystromyis		Rodentia: murid (white-tailed rat)			Europe
Trichomonas ninaekohlyakimovi		Clitellata: hirudinid (leech)			Europe
Trichomonas ortyxis		Galliformes: tetraonid (European partridge), phasianid (valley quail)			Europe, North America
Trichomonas oti		Strigiformes: strigid (screech owl)			Americas
Trichomonas parva		Rodentia: murid (brown rat, house mouse)			Europe
Trichomonas phasiani		Galliformes: phasianid (ring-necked pheasant, bobwhite quail)	intestines	diarrhoea, dehydration	Europe
Trichomonas pisobiae		Charadriiformes: scolopacid (least sandpiper, pectoral sandpiper, semipalmated sandpiper)			North America
Trichomonas porzanae		Gruiformes: rallid (sora rail)			North America
Trichomonas sanguisugae		Clitellata: hirudinid (horse leech)			Europe
Trichomonas sigalasi		Charadriiformes: scolopacid (dunlin)			Holarctic
Trichomonas singhii		Rodentia: murid (gerbil)			India
Trichomonas tapiri		Perissodactyla: tapirid (tapir)			Americas
Trichomonas tatusi		Edentata: dasypodid (nine-banded armadillo)			Americas
Trichomonas tenax (syn. *Trichomonas buccalis*) [-RF+AF]	4-16 x 2-15	Primates: hominid (human), rarely Carnivora: canid (dog), plus experimental infection in Primates: cercopithecid (macaques); Carnivora: felid (cat), Rodentia: murid (mice)	oral cavity, submaxillary glands (atypically respiratory tract)	periodontal disease, pleural empyema	worldwide
Trichomonas termitidis (possibly *Trichomonoides trypanoides*)		Isoptera: rhinotermitid (termites *Rhinotermes, Schedorhinotermes*)	hindgut		
Trichomonas termopsidis [+AF]	11-55 x 7-29	Isoptera: archotermopsid (termites *Zootermopsis angusticollis, nevadensis, laticeps*)	hindgut		North America
Trichomonas tritonis		Urodela: salamandrid (marbled newt)			Europe
Trichomonas vaginalis	covered in separate section				
Trichomonas vermiformis		Isoptera: hodotermitid (termite *Anacanthotermes murgabicus*)	hindgut		Africa
Trichomonas vitali		Anura: bufonid (cane toad)			Americas
Trichomonas wenrichi		Rodentia: sciurid (woodchuck)			North America
Trichomonas sp.		Perciformes: sparid (salema porgy)	intestines		Europe
Trichomitopsis [5F(=4A+R)+RF+BC+UM+A]					
Trichomitopsis termitis (syn. *Trichomonas termitis*)	30-83 x 15-64	Isoptera: archotermopsid (termite *Archotermopsis wroughtoni*)	hindgut		India
Tetratrichomonas (possible syn. *Trichomonoides*) [5F(=4A+R)+RF] (pseudocyst formation)					
Tetratrichomonas anatis (syn. *Trichomonas*)	13-27 x 8-18	Anseriformes: anatid (ducks)	posterior intestines	non-pathogenic	worldwide
Tetratrichomonas anseris	8-14 x 4-7	Anseriformes: anatid (goose)	caecum	non-pathogenic	worldwide

(syn. *Trichomonas*)					
Tetratrichomonas brumpti (syn. *Trichomonas*)		Testudines: testudinid (Ceylon terrapin, radiated tortoise, African spurred tortoise, Chaco tortoise)	digestive tract	non-pathogenic	Eurasia, Africa
Tetratrichomonas buttreyi		Artiodactyla: suid (pig)	large intestines	non-pathogenic	Europe
Tetratrichomonas canistomae (syn. *Trichomonas*)	7-12 x 3-4	Carnivora: canid (dog)	oral cavity	non-pathogenic	North America, Europe
Tetratrichomonas didelphidis (syn. *Trichomonas*)	5-11 x 3-9	Didelphimorpha: didelphid (opossum)	intestines	non-pathogenic	Americas
Tetratrichomonas felistomae (syn. *Trichomonas*)	6-11 x 3-4	Carnivora: felid (cat)	oral cavity	non-pathogenic	North America
Tetratrichomonas gallinarum (syn. *Trichomonas, Trichomonas pullorum*) [+RF+AF]	6-15 x 3-10	Galliformes: phasianid (chickens, turkeys, guineafowl, quail, chukar, pheasant), Anseriformes: anatid (ducks, geese), plus experimental subcutaneous assays in Rodentia: murid (mice), atypical infection in Primates: hominid (human)	caecum, liver (atypically human respiratory tract)	mostly asymptomatic, possibly typhlo-hepatitis	worldwide
Tetratrichomonas macacovaginae (syn. *Trichomonas*)		Primates: cercopithecid (rhesus monkey)	vagina		Asia
Tetratrichomonas microti (syn. *Trichomonas*)	4-9	Rodentia: murid (rats, mice), cricetid (hamsters, voles)	large intestines	non-pathogenic	worldwide
Tetratrichomonas ovis (syn. *Trichomonas, Ditrichomonas ovis*) [+RF+AF]	6-9 x 4-8	Artiodactyla: bovid (sheep)	rumen, caecum	non-pathogenic	North America
Tetratrichomonas pavlovi (syn. *Trichomonas, Trichomonas bovis*)	11-12 x 6-7	Artiodactyla: bovid (cattle)	caecum	non-pathogenic	Europe
Tetratrichomonas prowazeki (syn. *Trichomonas*)		Clitellata: hirudinid (horse leech); Perciformes: sparid (sea bream); Urodela: salamandrid (giant newt, common newt, salamander, northern crested newt); Anura: discoglossid (midwife toad), leptodactylid (swamp frog), ranid (pond frogs), bufonid (toads); Crocodila: crocodylid (marsh crocodile); Serpentes: colubrid (grass snakes, garter snakes)			India, Americas, Eurasia
Pentatrichomonas [6F(=5A+R)+RF+BC]					
Pentatrichomonas alleni		Passeriformes: corvid (Himalayan crow)	alimentary tract	non-pathogenic	Himalayas
Pentatrichomonas capellae	8-14 x 4-9	Charadriiformes: charadriid (snipe)	caecum		
Pentatrichomonas centropi	7-14 x 5-12	Cuculiformes: cuculid (crow pheasant)	caecum		
Pentatrichomonas hominis (syn. *Cercomonas hominis, Monocercomonas*	6-20 x 3-14	Primates: hominid (human), callitrichid (marmoset), cercopithecid (macaques); Artiodactyla: suid (pig), bovid (cattle, water buffalo, goat);	large intestines (atypically respiratory tract)	non-pathogenic	worldwide

hominis, Trichomonas intestinalis, Pentatrichomonas felis, Trichomonas felis) [+RF+AF]		Carnivora: canid (dog); felid (cat); Rodentia: caviid (guinea pig); Serpentes: boid (boa); Strigiformes: strigid (owl); plus experimental infections in Rodentia: murid (rats, mice), cricetid (hamster)			
Pentatrichomonas ketupae [*nomen nudum*]	7-136 x 6-11	Strigiformes: strigid (brown fish owl)	intestines	non-pathogenic	India
Pentatrichomonas lobivanellae [*nomen nudum*]	6-13 x 4-8	Charadriiformes: charadriid (red-wattled lapwing)	caecum	non-pathogenic	India
Class: **Hypotrichomonadea** (single mastigont) [4F+CLS-IKB+LUM+AC+CA]					
Order: Hypotrichomonadida (as for class)					
Family: Hypotrichomonadidae (syn. Trichomitidae) (2 genera)					
Hypotrichomonas					
Hypotrichomonas acosta	10-35	Serpentes: boid (boa), colubrid (indigo snake, racers, hog-nosed snakes, rat snakes, king snakes, grass snakes, garter snakes, gopher snakes), helodermatid (beaded lizards); Testudines (turtle)	intestines		Americas, Africa
Hypotrichomonas hemidactyli		Sauria: gekkonid (house gecko)			India
Hypotrichomonas osmaniae		Sauria: varanid (monitor lizard)			India
Hypotrichomonas venkataramiahii		Sauria: varanid (monitor lizard)			India
Trichomitus [4F(=3A+R)+RF+UM+AC]					
Trichomitus batrachorum (syn *Tritrichomonas, Trichomonas, T. natricis*)	10-15	Anura: ranid (edible frog, Indian bullfrog, common frog, green frog), hylid (European tree frog), pipid (clawed frog), bufonid (natterjack toad, Asiatic toad, common toad); Urodela: ambystomatid (mole salamanders), salamandrid (salamanders, crested newts); Serpentes: colubrid (grass snakes, gopher snakes, garter snakes); Sauria: iguanid (horned lizard), lacertids (green lizards), scincid (skink lizard), gekkonid (Leschenault's leaf-toed gecko); Serpentes: colubrid (long-nosed snake); plus molecular detection in Artiodactyla: suid (pig)	intestines		worldwide
Trichomitus fecalis [+AF]	5-14 x 4-6	Primates: hominid (human), plus experimental infection in Anura (tadpoles, frogs)	faeces		North America
Trichomitus marmotae (syn. *Trichomonas*)	10-15	Rodentia: sciurid (squirrels, woodchuck)			North America
Trichomitus rotunda [+AF]	7-12 x 4-8	Artiodactyla: suid (pig)	caecum, colon	non-pathogenic	worldwide
Trichomitus trypanoides (syn. *Trichomonas trypanoides*) [+AF]	16	Isoptera: rhinotermitid (termites *Reticulitermes lucifugus, tibialis, flavipes*)	hindgut		North America
Trichomitus wenyoni	4-16	Rodentia: murid (rats, mice),	large intestines	non-	worldwide

(syn. *Tritrichomonas*)		cricetid (hamster); Primates: cercopithecid (macaques)		pathogenic	

†Coding: + = present; - = absent; #F = total number of flagella; #A = number of anterior flagella; R = recurrent flagellum; RF = recurrent flagellum extending posteriorly as free flagellum; UM = undulating membrane; LUM = lamelliform undulating membrane; RUM = rail-type undulating membrane; C = costa; AC = A-type costa; BC = B-type costa; A = axostyle; AF = axostyle protrudes posteriorly; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: Trichomonads forms motile trophic stages (trophozoites) that have multiple flagella: *Trichomonas* and *Tetratrichomonas* spp. having 4 anterior flagella plus a recurrent flagellum, and *Pentatrichomonas* having 5 (sometimes 3 or 4) anterior flagella plus a recurrent flagellum. Trophozoites usually have thin elongate pyriform bodies ranging from 5-20 µm in length (6-15 µm for *Tetratrichomonas gallinarum*, 5-16 µm for *Trichomonas tenax,* 8- 20 µm for *Pentatrichomonas hominis).* All stages contain a single prominent anterior nucleus located adjacent to a distinctive parabasal body formed by dictyosomes (Golgi complexes). The nucleus and parabasal body are associated with small dense basal bodies (kinetosomes) forming a single karyomastigont unit (ancestral unit with 4 kinetosomes). The kinetosomes give rise to the anterior tuft of flagella which projects forwards for 5-15 µm. An independent neighbouring kinetosome gives rise to the recurrent flagellum (directed posteriad) which is attached longitudinally to the cell body forming an undulating membrane. The recurrent flagellum of *Trichomonas* spp. does not extend beyond the posterior margin of the cell, while that of *Tetratrichomonas* and *Pentatrichomonas* spp. projects beyond the posterior margin as a free flagellum. The undulating membrane is lamelliform in appearance (rather than rail-like) and it is underpinned by a slender elongate rod-like structure in the cell cytoplasm known as the costa, which is striated with a periodicity known as B-type (rather than A-type). Trophozoites swim in fluids with a distinctive wobbly jerky movement, with the undulating membrane imparting a quivering/shimmering appearance to the cell body. Trophozoites also possess a slender longitudinal hyaline rod-like structure known as an axostyle which is composed of concentric rows of microtubules forming a cone (rather than a tube). The axostyle begins near the nucleus and runs posteriorly through the cell body, protruding through the posterior end and terminating in a sharp point. The axostyle is often lined with unique membrane-bound structures known as hydrogenosomes (formerly called siderophil granules) which are anaerobic energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-level phosphorylation with release of hydrogen ions). Trichomonads do not form encapsulated cysts, although some cells (particularly *Tetratrichomonas* spp.) may round up and lose their flagella forming what has been called pseudocysts. Some regard these stages to be resistant transmissive forms while others consider them to simply be degenerate forms.

Site of infection: Trichomonads occur in the digestive tracts of a wide range of animals, with *Trichomonas* spp. recorded in 10 families of birds, 16 families of mammals, 6 families of reptiles, 3 families of amphibia, 5 families of termites, one leech family, and one snail family; *Tetratrichomonas* spp. in 8 mammal families, 2 bird families, 3 reptile families, 5 amphibian families, one fish family, and one leech family; and *Pentatrichomonas* spp. in 10 mammal families, 4 bird families, and one reptile family. Most species are considered to be harmless commensals in vertebrates or mutualistic symbiotes in insects. Several species, however, have tentatively been associated with clinical disease in a few hosts, including *Trichomonas tenax* and *Pentatrichomonas hominis* in humans, and *Tetratrichomonas gallinarum* in birds. Trophozoites are found within the lumina of tubular organs: *Trichomonas tenax* in the mouths of humans (between the teeth, in pus pockets, tooth cavities, tartar, tonsillar crypts), rarely in the trachea and lungs; *Pentatrichomonas hominis* in the large intestines and caecum of humans, sometimes in the stomach; and *Tetratrichomonas gallinarum* in the large intestines of poultry (chickens, turkeys, guinea fowl, quail, ducks, geese).

Pathogenesis: Most infections are asymptomatic and have not been associated with any clinical disease, even when trophozoites are present in abundance in the lumen of the digestive tract. Infections by a few species have occasionally been linked with clinical conditions involving irritation and inflammation of mucosal membranes when trophozoites contact epithelial surfaces, sometimes invading atypical locations. The species *Tetratrichomonas gallinarum* usually causes latent infections in the large intestines of poultry, but may sometimes cause lesions in the caecum and liver with microvillous atrophy, papule formation and necrotic enteritis resulting in diarrhoea with yellow frothy liquid caecal exudates. The parasite is regarded as a potential causative agent of enterohepatitis especially in turkeys, and infections are thought to aggravate other disease conditions (such as histomoniasis and typhlohepatitis in galliform birds). Infections in ducks have been associated with reduced egg production and increased mortalities in female birds. The species *Trichomonas tenax* is often reported as a harmless commensal in the mouth of humans, feeding on microorganisms and cellular debris. However, trophozoites invading the respiratory system have been associated with debilitating pulmonary diseases (bronchiectasis, abscesses, and possibly carcinomas) in individuals with poor dental hygiene, malnutrition and alcoholism. The species *Pentatrichomonas hominis* is usually regarded to be an endocommensal in the large intestines of humans, but when parasites invade the respiratory tract by aspiration or through bronchoenteral fistulas, they may cause necrotizing pulmonary abscesses and pleural effusions. Atypical infections by *Trichomonas vaginalis* and *Tritrichomonas foetus* have been recorded in the respiratory tract of patients with empyema and pulmonary diseases (such as acute respiratory distress syndrome).

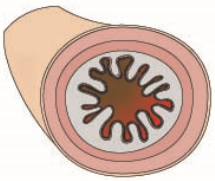
Developmental cycle and mode of transmission: Trichomonads have simple monoxenous (one-host) life cycles involving the asexual multiplication of trophozoites within hosts and their transmission to new susceptible hosts by intimate contact or the ingestion of recently contaminated food or water. The parasites do not form true encapsulated cysts, and only a few species (particularly *Tetratrichomonas* spp.) form rounded nonflagellated stages (called pseudocysts) that are either degenerate forms or may be environmentally-resistant forms. Trophozoites divide by longitudinal binary fission and they do not survive for long outside of host tissues. Nonetheless, a few experimental studies have found that trophozoites expelled from hosts may survive in moist food and drinking water for several hours. Infections by *Tetratrichomonas gallinarum* are thought to be transmitted via the consumption of contaminated food and water, and experimental infections have been achieved by oral and cloacal inoculation. Trophozoites of *Trichomonas tenax* cannot survive passage through the stomach of humans, so most transmission occurs by direct oral contact, such as kissing or sharing eating/drinking utensils. Trophozoites of *Pentatrichomonas hominis* are excreted in human faecal samples thus supporting faecal-oral transmission but only involving freshly contaminated food or water. Trophozoites have recently been detected in or on filth flies suggesting the possibility of passive transport by paratenic hosts, but only within the small window of opportunity of limited trophozoites survival.

Differential diagnosis: Infections are conventionally diagnosed by the microscopic detection of trichomonads in clinical samples. Motile trophozoites may be detected in wet mounts of excretions, exudates, tissue swabs, impressions or scrapings by high-contrast bright-field, phase-contrast or interference-contrast microscopy. Live parasites move with a characteristic jerky rolling motion and the undulating membrane gives a shimmering appearance to the cell body. Trophozoites may also be detected in fixed smears following staining with Giemsa, silver, iron haematoxylin, malachite green, methylene blue, or acradine orange, but fixation often causes cells to condense or lyse. Tissue samples may also be collected at necropsy and histological sections examined for parasites after staining with haematoxylin and eosin, Giemsa, periodic acid-Schiff or immunohistochemical stains using polyclonal or monoclonal antibodies. Trophozoites may also be cultured *in vitro* from clinical samples by anaerobic cultivation in axenic or monoxenic liquid/semiliquid media, such as Diamond's medium or InPouch TF media culture kits. Some trichomonad species have also been grown on cell lines maintained in tissue cultures: e.g. *Tetratrichomonas gallinarum* grows on monkey kidney cells, chicken liver (LMH) cells or quail (QT35) fibroblasts. Enzyme immunoassays have been developed to detect specific host antibodies against *Tetratrichomonas gallinarum* in poultry, and modern molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (large and small subunit ribosomal RNA and internal transcribed spacers 1 and 2). Molecular characterization has led to the recognition of 5 groups (A-E) and 11 subgroups (A1, A2, B1, B2, B3, C1, C2, C3, D1, D2, E) amongst *Tetratrichomonas gallinarum* isolates.

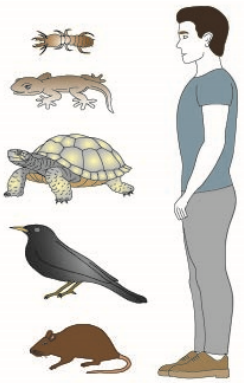
Treatment and control: Clinical infections have generally responded well to chemotherapy using nitroimidazole drugs (metronidazole, dimetridazole), although their application may cause some adverse side-effects and there are growing concerns about the emergence of drug-resistant strains of parasites. Preventive measures designed to minimize contamination and reduce the risk of transmission basically involves regular health monitoring, quarantine, strict hygiene and sanitation, water treatment, food hygiene, and good husbandry (maintaining nutrition and avoiding stressors). Management practices in commercial poultry production should include regularly changing feed and water, cleaning containers and drying fomites in holding facilities, separating cohorts without co-mingling, and avoiding stressors (such as over-crowding, poor nutrition and concomitant infections). In humans, better oral hygiene is recommended to control the spread of *Trichomonas tenax*, and proper sanitation, water treatment and good food hygiene should be employed to prevent the faecal-oral transmission of *Pentatrichomonas hominis.*

Pentatrichomonas (6 flagella)*
Tetratrichomonas (5 flagella)*
Trichomitopsis (5 flagella)*
Trichomonas (5 flagella)*
Trichomitus (4 flagella)*

*one flagellum recurrent and
forming undulating membrane



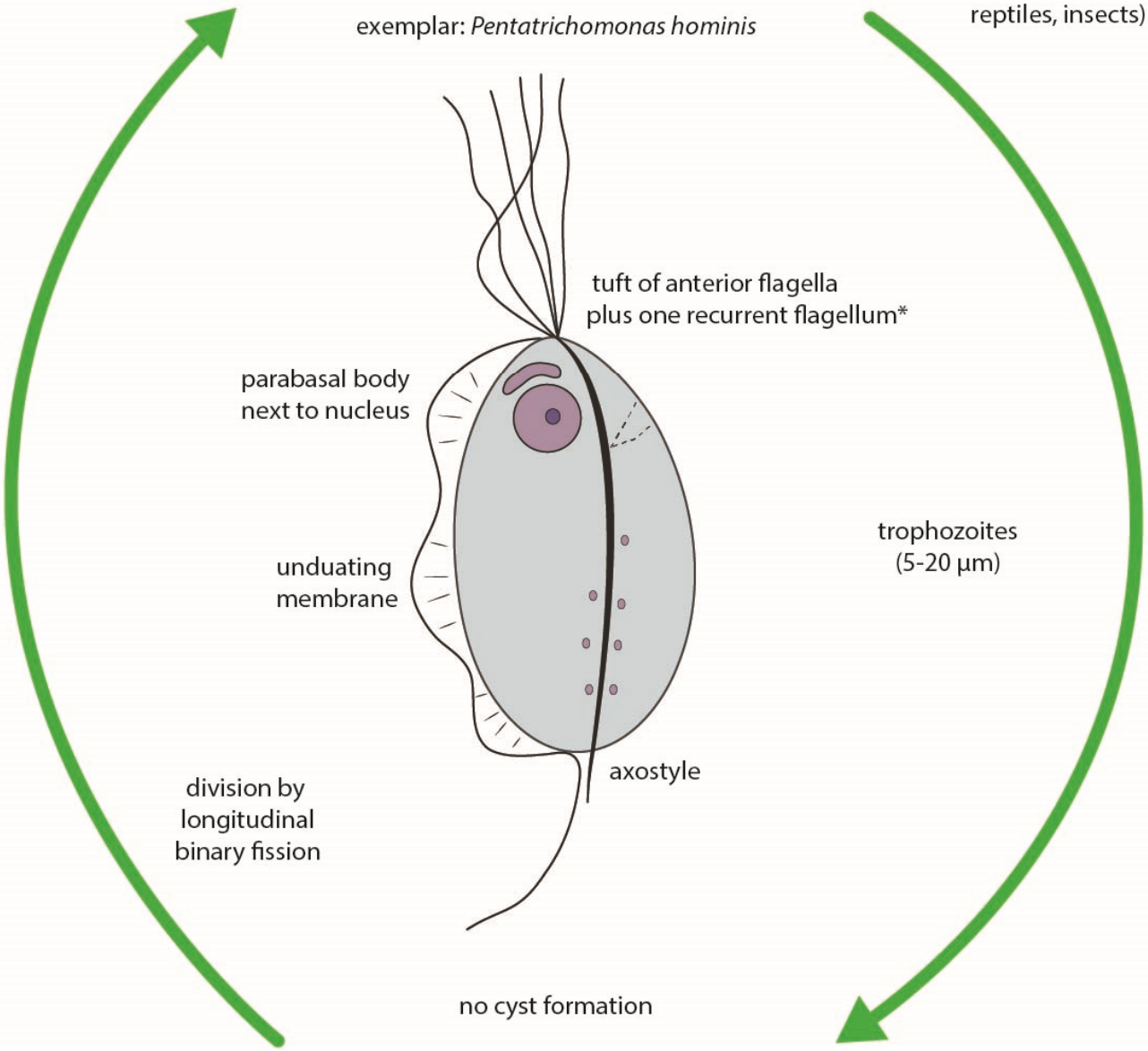
alimentary tract
(rare gut pertubations)



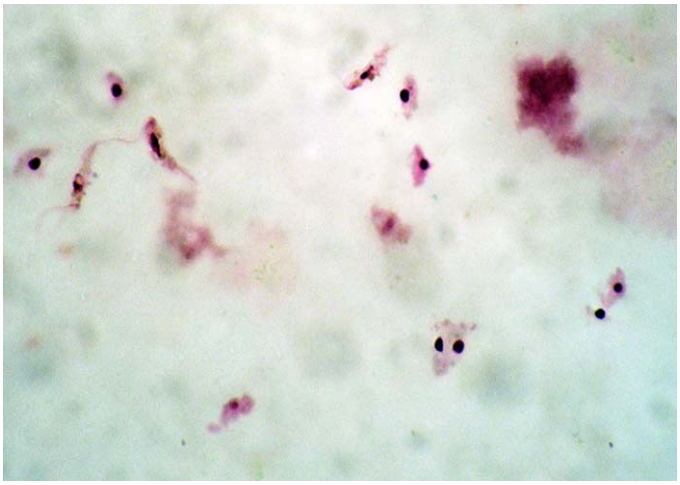
Hosts
(mammals, birds,
reptiles, insects)

most species not associated with disease
(often considered to be endocommensals)

exemplar: *Pentatrichomonas hominis*



direct transmission by transfer of trophozoites
during close contact (courtship, grooming, allo-feeding)
or possibly via contaminated fomites



Trichomonas trophozoites from termite hindgut

Trichomonas trophozoite from snake gut