

Giardia

(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 (amoebflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Diplomonads have complex nucleus-associated karyomastigonts and are defined by the possession of two nuclei and unique bilateral symmetry (diplozoic appearance). They typically form reproductive cysts (each containing four nuclei) which facilitate their transmission between hosts. Hexamitids are parasites or commensals in mammals, birds, reptiles and fish. Several parasitic species cause severe clinical disease in man and domestic animals. All species are characterized by their pyriform shape and bilateral symmetry with two equal nuclei lying side by side, two intracytoplasmic granular axonemes and 6-8 flagella. The species *G. duodenalis* causes acute watery diarrhoea in humans and other animals, and protracted infections may lead to failure-to-thrive syndrome in infants.

Classification:

Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Fornicata (diplomonads)
Order: Diplomonadida (with 1-2 karyomastigonts (each with 4 basal bodies/flagella associated with nucleus))
Family: Hexamitidae (2 karyomastigonts arranged in binary axial symmetry)
Genus: *Giardia* (parasitic in digestive tracts of vertebrates)
Species: *G. duodenalis* (causes giardiasis (diarrhoea) in 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 (amoebflagellates), 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)	Transmission*
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)	<i>Giardia</i>	vertebrates (gut)	direct (f-o)
			<i>Hexamita</i> <i>Spironucleus</i>	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)	<i>Histomonas</i>	birds (gut, liver)	direct (f-o)
			<i>Dientamoeba</i>	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	<i>Trichomonas</i>	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	<i>Cochlosoma</i>	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)	<i>Ichthyobodo</i> (= <i>Costia</i>)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	<i>Cryptobia</i>	fish (gills, skin)	direct (w)
			<i>Trypanoplasma</i>	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	<i>Trypanosoma</i>	vertebrates (blood, tissues)	indirect (v-b)
		<i>Leishmania</i>	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: Blastodiniiales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	<i>Amyloodinium</i> <i>Crepidodinium</i> <i>Piscinoodinium</i>	fish (skin)	direct (w)
	Order: Syndiniiales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	<i>Haematodinium</i> <i>Ichthyodinium</i>	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	<i>Perkinsus</i>	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 Fornicata are characterized by the possession of a distinct feeding groove or cytopharyngeal tube. Two classes are recognized: Eupharyngea commonly found in the digestive tracts of animals; and Carpediemonadea found in anaerobic intertidal sediments. The class Eupharyngea contains 2 orders: Diplomonadida with paired karyomastigonts; and Retortamonadida with single karyomastigonts. The diplomonads (meaning 'double monads') are binucleate and most species are found in the alimentary tracts of vertebrate hosts, although several free-living species occur in organically rich waters. Diplomonads typically form reproductive cysts (each containing 4 nuclei) to facilitate their transmission. Their motile vegetative forms (trophozoites) contain 1-2 kinetids, each with 4 kinetosomes but sometimes not all flagellated, and at least one flagellum per kinetid is directed posteriorly and may be associated with the cytopharyngeal tube or groove. Two families are generally recognized, 'monozoic' Enteromonadidae containing *Enteromonas*, *Caviomonas* and *Trimitus*; and 'diplozoic' Hexamitidae containing the genera *Giardia*, *Hexamita*, *Spironucleus*, *Trepomonas* and *Octomitus*. Some consider the enteromonads to be a regressive group with progressive reduction in the number of flagella while others consider them to be ancestral giving rise to the diplozoic hexamitids through the failure of cytokinesis. More recently, it was proposed that the order Diplomonadida be replaced by two new orders, Distomatida

(containing *Trepomonas*, *Hexamita* and *Spiroucleus*) and *Giardiida* (containing *Giardia* and *Octomitus*), both in a novel subclass Diplozoa. Differences in the placement of families and genera within the Diplomonadida (or Fornicata) remain to be reconciled.

Family	Genus	Hosts	Pathogenicity
Enteromonadidae	<i>Enteromonas</i>	mammals	nonpathogenic
	<i>Trimitus</i>	frogs, reptiles, fish, insects	nonpathogenic
	<i>Caviomonas</i>	rodents	nonpathogenic
Hexamitidae	<i>Trepomonas</i>	frogs, fish, tortoises	nonpathogenic
	<i>Octomitus</i>	frogs, rodents	nonpathogenic
	<i>Spiroucleus</i>	rodents, birds, fish	pathogenic in birds, fish
	<i>Hexamita</i>	birds, frogs, fish, insects	pathogenic in birds, fish
	<i>Giardia</i>	mammals, birds, frogs, reptiles	pathogenic in mammals, birds

Giardia-like flagellates were first observed in humans by Antony van Leeuwenhoek as early as 1681 but they remained unnamed until 1859 when the name *Cercomonas intestinalis* was proposed by Lambl. Unfortunately, the species name had been used previously in 1850 when revising *Bodo* and *Cercomonas* species. A similar parasite found in rabbits in 1875 was named *Hexamita duodenalis*. The genus name *Giardia* was proposed by Kunstler in 1882 for flagellates in tadpoles, although Blanchard later suggested in 1888 that the genus name be *Lamblia*. Applying the rules of the International Code of Zoological Nomenclature regarding precedence, the name of the species in humans (if identical to that in rabbits) is *G. duodenalis*, although the synonyms *G. intestinalis* and enigmatically *G. lamblia* are still used by some agencies (especially in medical textbooks). The genus *Giardia* is characterized by cells that form binucleate pyriform trophozoites with 2 adjacent karyomastigonts, a ventral adhesive disc, 2 longitudinal axonemes and 2 tangential median bodies, as well as non-flagellated membrane-bound cysts possessing 4 nuclei.

Infections have been detected in numerous host species around the world, sometimes in association with enteric disease (known as giardiasis). The prevalence of giardiasis in humans is greater in developing rather than developed countries, particularly in pre-school and school children (surveys in developing countries ranging from 10-70% compared to 1-6% in developed countries). Infections have been recorded in many domestic and wild animal species, but most reports have not identified the species involved or have simply ascribed them to particular morphotypes. Although some 50 *Giardia* spp. have been described on the basis of host occurrence, many are morphologically indistinguishable. Early comparative studies recognized three species groups on the basis of trophozoite morphology: thin elongate trophozoites with long club-shaped median bodies assigned to the *G. agilis* group found mainly in amphibians; short stout trophozoites with small round median bodies belonging to the *G. muris* group found mainly in rodents (but also birds and reptiles); and medium-sized pyriform trophozoites with claw-shaped median bodies belonging to the *G. duodenalis* group found mainly in mammals (but also birds and reptiles). Currently, another two intermediary morpho-groups are recognized: comprising *G. microti* from muskrats and voles, and *G. ardeae* and *G. psittaci* from birds. Host specificity within each group remains contested. Epidemiological studies have frequently suggested zoonotic and water-borne transmission between mammals. Indeed, common regional names for the disease often suggest animal or water sources of human infection (e.g. beaver fever, backpacker's malady, traveler's diarrhoea). While experimental infections are difficult to perform due to biological, technical and ethical concerns, cross-transmission studies should be attempted where possible to determine the host ranges for clinical isolates. Alternatively, clinical and environmental isolates may be genetically characterized and cross-matched, akin to genetic 'fingerprinting'.

Molecular characterization techniques have identified a range of genotypes which vary in their host occurrence, host specificity and zoonotic potential. It is particularly noteworthy that multiple genotypes have been detected in individual hosts, suggesting parasite infrapopulations retain genetic heterogeneity rather than clonal dominance. Genes used to characterize types have included small subunit ribosomal RNA, glutamate dehydrogenase, triose-phosphate isomerase, elongation factor 1 alpha, variant surface protein and beta-giardin. Three main zoonotic genotypes of *G. duodenalis* have been found in humans (designated A1, A2, B3) while a growing number of other genotypes have been found in domestic animals and wildlife. Dogs and cats may harbour zoonotic genotypes (A and B) as well as species-specific genotypes (C and D for dogs and cats, F for cats only). All *Giardia* positive dogs and cats must therefore be suspected of carrying potentially zoonotic genotypes and treated accordingly. Cattle and other ruminants may also carry non-zoonotic genotypes (E) as may rats (G). When considering host records of infection, it should be remembered that many early works are confounded by incomplete descriptions or generic identifications only, while more recent molecular studies recognized many genotypes, only some of which have been assigned to particular species. In an attempt to redress this situation, it has recently been proposed that some genotypes be afforded separate species status (namely, assemblage A = *G. duodenalis*, B = *G. enterica*, C (or C/D) = *G. canis*, E = *G. bovis*, F = *G. cati*, G = *G. simondi*).

Parasite species	Hosts	Trophozoite size (and features)	Distribution
<i>G. duodenalis</i> (= assemblage A)	<p>Primates: hominid (human, gorilla), atelid (southern brown howler monkey); Carnivora: canid (dog, red fox, coyote, African painted dog, wolf), felid (cat, jaguar), phocid (grey seal, harp seal, harbor seal, hooded seal), otariid (Australian sea lion); Artiodactyla: bovid (cattle, water buffalo, muskox, sheep, goat, camelid (alpaca), cervid (moose, fallow deer, reindeer, red deer, roe deer, white-tailed deer), suid (pig); delphinid (common dolphin), phocoenid (harbour porpoise), balaenopterid (minke whale); Perissodactyla: equid (horse); Rodentia: murid (mice), mustelid (ferret), castorid (beaver), chinchillid (chinchilla); Lagomorpha: leporid (rabbit); Dasyuromorphia: dasyurid (common planigale); Diprotodontia: macropodid (red kangaroo, western grey kangaroo, Parma wallaby, tammar wallaby, swamp wallaby, yellow-footed rock-wallaby, quokka), potoroid (long-nosed potoroo, rufous rat-kangaroo), phascolarctid (koala); vombatid (southern hairy-nosed wombat); phalangerid (common brushtail possum, mountain brushtail possum); Peramelemorphia: peramelid (quenda); Dasyuromorphia: dasyurid (Tasmanian devil); Galliformes: phasianid (chicken); Anseriformes: anatid (common eider); Charadriiformes: larid (herring gull, gull), Lamniformes: lamnid (mako shark); Perciformes: latid (barramundi), sparid (black bream), sciaenid (mulloway), lutjanid (snapper); Mugiliformes: mugilid (sea mullet); Sauria: lacertid (Iberian rock lizard); Bivalvia: tellinid (<i>Macoma</i> clams)</p>	12-15 x 6-8 μm (claw-shaped median bodies)	worldwide
<i>G. enterica</i> (= assemblage B)	<p>Primates: hominid (human, chimpanzee, gorilla), cercopithecoid (mandrill, macaque, Japanese macaque, vervet monkey, red colobus monkey), callitrichid (pygmy marmoset, cotton-top mandarin); Artiodactyla: bovid (cattle, muskox, sheep, gazelle), cervid (red deer, roe deer), suid (pig), delphinid (common dolphin, Atlantic white-sided dolphin, Risso's dolphin), phocoenid (harbour porpoise); Perissodactyla: equid (horse); Carnivora: canid (dog, red fox, coyote, African painted dog, wolf), felid (cat), phocid (grey seal, harp seal, harbor seal), otariid (Australian sea lion); Rodentia: castorid (beaver), cricetid (muskrat), chinchillid (chinchilla), mustelid (ferret), caviid (guinea pig), capromyid (Desmarest's hutia); Hyracoidea: procaviid (rock hyrax); Lagomorpha: leporid (rabbit); Diprotodontia: macropodid (red kangaroo, Parma wallaby, tammar wallaby, western grey kangaroo); Dasyuromorphia: dasyurid (tiger quoll, Tasmanian devil); Galliformes: phasianid (chicken); Struthioniformes: struthionid (ostrich); Charadriiformes: larid (herring gull, gull); Anseriformes: anatid (common eider); Perciformes: latid (barramundi), sparid (black bream), sciaenid (mulloway), lutjanid (snapper); Mugiliformes: mugilid (sea mullet); Osmeriformes: galaxiid (western minnow); Lamniformes: lamnid (mako shark), alopiid (thresher shark); Sauria (lacertid (Iberian rock lizard)</p>	12-15 x 6-8 μm (claw-shaped median bodies)	worldwide
<i>G. canis</i> (= assemblages C/D)	<p>Carnivora: canid (dog, fox, coyote, African painted dog), felid (cat), phocid (harbour seal); Artiodactyla: bovid (cattle), suid (pig), kogiid (pygmy sperm whale), delphinid (striped dolphin); Rodentia: chinchillid (chinchilla), murid (mice, bush rat); Diprotodontia: macropodid (kangaroo); Peramelemorphia: peramelid (southern brown bandicoot); rarely Primates: hominid (human)</p>	12-15 x 6-8 μm (claw-shaped median bodies)	worldwide

<i>G. bovis</i> (= assemblage E)	Artiodactyla: bovid (cattle, yak, water buffalo, sheep, goat), cervid (fallow deer, moose), camelid (alpaca), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog, fox), felid (cat); Primates: hominid (human), cercopithecoid (red colobus monkey); Rodentia: murid (ash-grey mouse), Peramelemorphia: peramelid (southern brown bandicoot); Perciformes: latid (barramundi), sciaenid (mulloway); Sauria: lacertid (Bocage's wall lizard)	12-15 x 6-8 μm (claw-shaped median bodies)	worldwide
<i>G. cati</i> (= assemblage F)	Carnivora: felid (cat, lion); Rodentia: murid (bush rat); rarely Primates: hominid (human); Artiodactyla: phocoenid (harbour porpoise), delphinid (striped dolphin)	12-15 x 6-8 μm (claw-shaped median bodies)	worldwide
<i>G. simoni</i> (= assemblage G)	Rodentia: murid (rats, mice), castorid (beaver)	12-15 x 6-8 μm (claw-shaped median bodies)	Europe, Australia
Assemblage H (un-named)	Carnivora: phocid (grey seal, harbor seal); Charadriiformes: larid (gull)	not determined	North America
<i>G. peramelis</i> (= queda genotype)	Peramelemorphia: peramelid (southern brown bandicoot)	not determined	Australia
<i>G. muris</i>	Rodentia: murid (mice, rats, gerbil), cricetid (hamster, common vole)	9-12 x 5-7 μm (rounded median bodies)	worldwide
<i>G. cricetarum</i>	Rodentia: cricetid (Djungarian hamster, Campbell's dwarf hamster, golden hamster)	12-18 x 8-12 μm (round median bodies)	China
<i>G. microti</i>	Rodentia: cricetid (California vole, muskrat); Perciformes: latid (barramundi)	12-15 x 6-8 μm (cysts with 2 trophozoites)	North America
<i>G. ardeae</i>	Pelecaniformes: ardeid (grey heron, Cooi heron, rufous heron, black-crowned night heron, great blue heron), threskiornithid (glossy ibis); Accipitriformes: cathartid (turkey vulture); Suliformes: anhingid (American darter)	10 x 6.5 μm (round-rod median bodies)	North America
<i>G. psittaci</i>	Psittaciformes: psittaculid (budgerigar), psittacid (barred parakeet)	14 x 6 μm (claw-shaped median bodies, lack flange/groove)	Central and North America
<i>G. agilis</i>	Anura: pipid (toads), ranid (frogs) [tadpoles]	20-30 x 4-5 μm (club-shaped median bodies)	Americas, Africa, Europe
<i>G. varani</i>	Sauria: varanid (Nile monitor, Bengal monitor)	12-16 x 8-10 μm (median bodies rare)	Asia, India (North America?)

Other *Giardia* species that have been described (prior to molecular characterization techniques becoming available) include: *G. wenyoni* from Primates: lorid (slender loris), *G. bradyi* from Pilosa: bradypodid (pale-throated sloth), *G. caprae* from Artiodactyla: bovid (goat, sheep), *G. equii* from Perissodactyla: equid (horse), *G. dasi* from Carnivora: viverrid (palm civet), *G. hegneri* from Carnivora: viverrid (Malay civet), *G. irarae* from Carnivora: mustelid (tayra), *G. suricatae* from Carnivora: herpestid (meerkat), *G. otomyis* from Rodentia: murid (South African vlei rat), *G. beckeri* from Rodentia: sciurid (ground squirrel), *G. caviae* from Rodentia: caviid (guinea-pig), *G. chinchillae* from Rodentia: chinchillid (chinchilla), *G. viscaciae* from Rodentia: chinchillid (viscacha), *G. ondatrae* from Rodentia: cricetid (muskrat), *G. pitymysi* from Rodentia: cricetid (Savi's pine vole), *G. botauri* from Pelecaniformes: ardeid (American bittern), *G. floridae* from Pelecaniformes: ardeid (little blue heron) *G. herodiadis* from Pelecaniformes: ardeid (intermediate egret), *G. hyderabadensis* from Pelecaniformes: ardeid (cattle egret), *G. nycticori* from Pelecaniformes: ardeid (black-crowned night heron), *G. pseudoardeae* from Pelecaniformes: ardeid (great blue heron), *G. beltrani* from Passeriformes: passerid (house sparrow), *G. marginalis* from Passeriformes: lariid (red-backed shrike), *G. melospizae* from Passeriformes: passerellid (swamp sparrow), *G. sturnellae* from Passeriformes: icterid (western meadowlark), *G. recurvirostrae* from Charadriiformes: recurvirostrid (avocet), *G. sanguinis* from Accipitriformes: accipitrid (black-winged kite), *G. tucani* from Piciformes: ramphastid (Ariel toucan), *G. serpentis* from Serpentes: viperid (Cape viper), and *G. denticis* [possibly *Hexamita*] from Perciformes: sparid (Carpenter seabream). In one extraordinary case, *Giardia* trophozoites were even detected inside the mouth and anterior gut of hookworms (*Ancylostoma caninum*) recovered from a dog (probably the result of accidental uptake rather than an instance of hyperparasitism).

Parasite morphology: *Giardia* parasites form two developmental stages: trophozoites and cysts. The trophozoites are pyriform (10-30 µm long) and appear to have bilateral symmetry due to the possession of two adjacent karyomastigonts (nuclear-flagellar basal body units). Each trophozoite therefore possesses two nuclei (which are identical) and eight flagella (two anterior, two lateral, two ventral and two caudal). The trophozoites also have a prominent ventral adhesive disc, two longitudinal axonemes and two tangential curved median bodies. Cysts are ovoid to ellipsoid (11-14 µm in length by 7-10 µm in width), membrane-bound (sometimes imparting a halo-appearance) and contain four nuclei, axonemes and median bodies.

Site of infection: Flagellated trophozoites are found in the small intestines of their hosts, especially the duodenum. Trophozoites have been observed swimming with a distinct corkscrew motion in luminal content as well as adhering to the gut mucosal surface with their ventral adhesive discs (when they detach, they leave distinct oval impressions in the microvillous layer). Trophozoites are occasionally passed together with cysts in stool samples, but the trophozoites do not survive long in the external environment (unlike cysts which are very hardy).

Pathogenesis: *Giardia* spp. may cause asymptomatic infections, acute transient diarrhoea for 1-2 weeks or chronic protracted diarrhoea for more than two weeks. Infections interfere with the normal absorptive functioning of the small intestines, thereby causing osmotic overload of the large intestines resulting in watery or foul-smelling mucoid diarrhoea that may be acute, chronic or intermittent. Attached parasites may physically blanket the small intestinal mucosa significantly reducing the surface area for absorption. Infections damage and increase the turnover rate of epithelial cells culminating in villous atrophy which further reduces the surface area for absorption. Various parasite products have been shown to have detrimental effects on intestinal mucosal cells; including the induction of apoptosis, disruption of the microvillous layer (brush border), disruption of tight cell junctions, and increased membrane permeability. These factors contribute to malabsorption of fats and other nutrients resulting in watery diarrhoea and steatorrhea accompanied by dehydration, intestinal pain (bloating and cramps), flatulence, malaise and sometimes headache. Many patients also become lactose intolerant over the course of infection. Most clinical infections are self-limiting and resolve spontaneously but some persist for months with intermittent diarrhoea (frothy yellow or greasy foul-smelling stools), weight loss, retarded growth and 'failure-to-thrive' syndrome. Chronic infections have also been associated with food allergies, arthritis, chronic fatigue and irritable bowel syndrome. Young individuals are most susceptible to clinical infections and focal outbreaks are common in child day-care centres and among intensively-reared and housed young animals. Not all infected individuals, however, develop clinical signs but may remain asymptomatic carriers excreting cysts contributing to environmental contamination.

Developmental cycle and mode of transmission: Infections are passed between hosts by the faecal-oral transmission of encysted parasite stages. When trophozoites pass through the colon, they form non-flagellated cysts which are excreted and contaminate the environment. The cysts are said to be reproductive in that they undergo nuclear division as they mature becoming quadrinucleate. Cysts passed in host faeces are immediately infectious. Following their ingestion by a new host, they excyst in the small intestine releasing two trophozoites which attach to the microvillous layer (brush border) of the intestinal epithelial cells (beneath the mucus layer). The trophozoites subsequently feed and multiply asexually by binary fission (a type of mitosis). Excystation stimuli include various post-gastric digestive conditions (bile salts, enzymes, pH, microaerophilic conditions, etc.). Most infections are transmitted accidentally by 'hand-to mouth' contact whereby faecal contaminants on fomites (objects) are transferred to the mouth (e.g. contaminated fingers, utensils, clothing, etc.). The cysts are quite resistant to external environmental conditions and can survive for months, particularly in cool moist conditions. The cysts also contaminate water supplies and cause infections when subsequently ingested with drinking water or the consumption of food-stuffs diluted or washed with contaminated water. *Giardia* cysts have been detected on many food types, including fruit, vegetables, dairy products, meat and shellfish. Infections have also been associated with recreational water use, including swimming pools, lakes and water-theme parks. Many countries have recorded marked seasonal differences in the occurrence of giardiasis, with latitudinal variation depending on both climatic conditions (shown to be conducive to cyst survival) and animal husbandry practices (when susceptible neonates are most abundant). Disease was more prevalent in the rainy season in tropical countries, during autumn in subtropical countries and during spring in countries with temperate climates.

Differential diagnosis: Distinctive cysts of the parasite may be detected by routine coprological examination of faecal smears stained with iodine, trichrome or iron haematoxylin, or by microscopy of faecal concentrates prepared by sedimentation/flotation techniques. The sensitivities of these diagnostic tests are poor due to the intermittent excretion of the small cysts, so multiple faecal samples should be examined over several days. Endoscopic techniques (gastroscopy through to duodenum) have been used in chronic cases to detect trophozoites in intestinal aspirates or biopsy material. A string test has also been used to recover and examine bile-stained mucus for trophozoites. More recently, sensitive and specific immunological techniques (enzyme immuno-assays, immuno-chromatography, and fluorescent-labelling) have been developed to detect parasite antigens in faecal preparations (copro-antigen tests). Monoclonal antibody immuno-reagents are also used in many countries to detect cysts in environmental samples (water sources and food preparations) using immuno-magnetic separation techniques, enzyme immuno-assays or fluorescent-activated cell sorting. Many countries have now introduced molecular diagnostic tools to genotype isolates using polymerase chain reaction (PCR) techniques to amplify parasite DNA [small subunit ribosomal RNA (*18S rRNA*), glutamate dehydrogenase (*gdh*),

triose phosphate isomerase (*tpi*), beta-giardin (*bg*), elongation factor 1-alpha (*ef1a*) and variable surface protein (*vsp*) genes], thus allowing the molecular epidemiology of infections to be investigated.

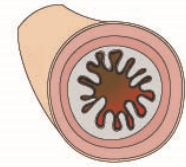
Treatment and control: Metronidazole is the drug of choice for giardiasis despite mild side-effects (such as nausea), but it should not be used in pregnant women due to the risk of birth defects. Recently, there are growing problems with the emergence of metronidazole-resistant parasite strains in several countries. Other nitroimidazole derivatives (tinidazole), nitrofurans (furazolidone), acridine drugs (quinacrine) and microtubule inhibitor anthelmintics (albendazole, fenbendazole, febantel) have been reported effective. Conventional water treatment procedures (filtration and chlorination) are not wholly effective against *Giardia* cysts as they are quite small and resistant to many chemical disinfectants. Control depends largely on good sanitation, proper effluent disposal and effective water treatment (well-maintained sand filtration or microfiltration, optimum chlorination or ozonation, boil water alerts during outbreaks). Hygienic conditions should be maintained, particularly where susceptible hosts are crowded together in intensive facilities (daycare centres, nursing homes, kennels, dairies, etc.). Giardiasis is a notifiable disease in many developed countries, with outbreaks eliciting actionable investigations and interventions by public health agencies. This facilitates better risk assessment, disease management, health education, public awareness and more effective prevention and control programs.

Giardia

division by longitudinal binary fission



Vertebrate Hosts
(mammals, birds, reptiles, amphibians)



intestines
(malabsorption, diarrhoea, failure-to-thrive)

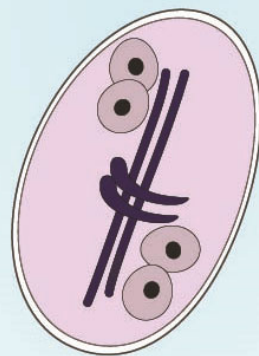
trophozoite
(10-30 μm)

bilateral symmetry
2 nuclei
ventral adhesive disc
8 flagella
2 axonemes
median body



cysts ingested

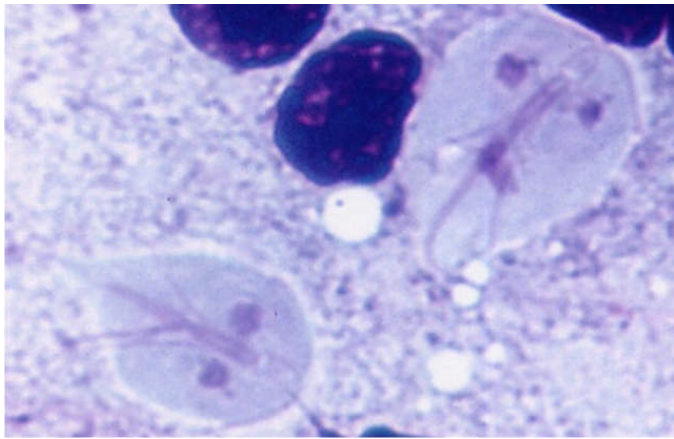
cysts passed in faeces



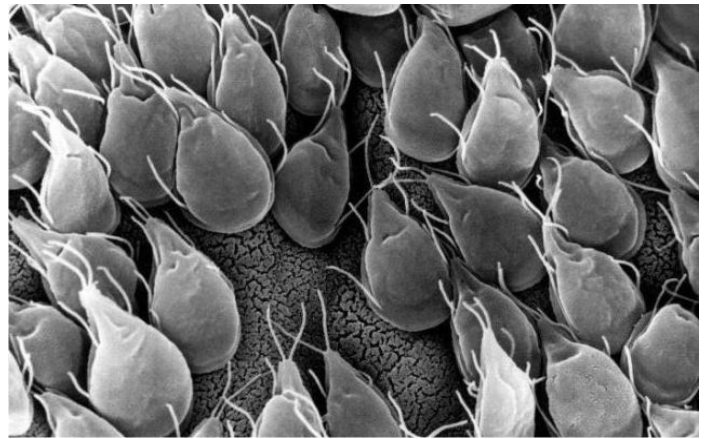
4 nuclei
longitudinal rods
median bodies

cyst
(11-14 μm)

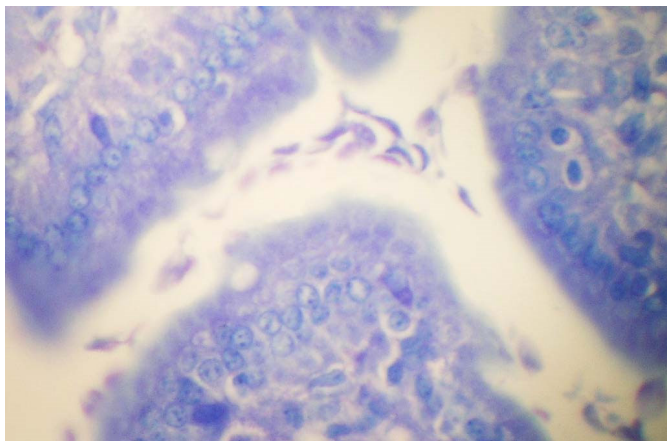
faecal-oral transmission between hosts
by cysts contaminating external environment
(soil, water, food, fomites)



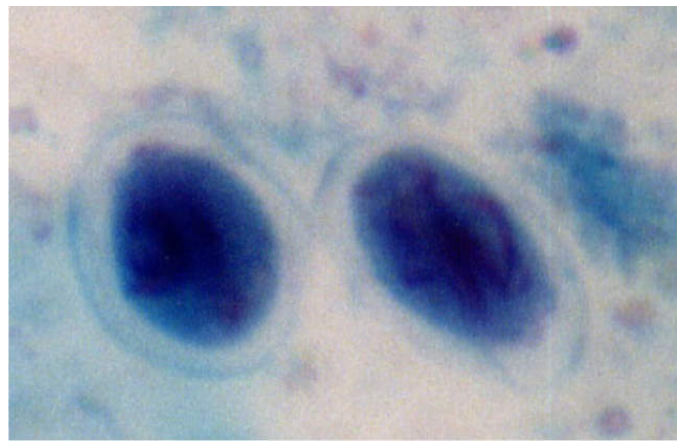
Giardia trophozoites



Giardia trophozoites on gut wall



Giardia trophozoites in gut lumen



Giardia cysts in faeces