Trichuris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most aphasmid nematodes are free-living, although some are parasitic on plants and animals. They possess a non-muscular stichosome oesophagus (slender thin-walled tube) and their life-cycles involve infective L1 (rather than L3) which have a buccal stylet (very common for plant parasites). The males lack a bursa and have only one spicule when present. Three major families of animal parasites are grouped together in the dorylaimian order Trichinellida: trichurids in the caecum/colon of mammals, capillarids in the gut/lungs of mammals/birds, and trichinellids in the intestines and muscles of mammals. Trichurids are known as whipworms because they have a short broad posterior end and a very long narrow whip-like anterior end embedded in the intestinal mucosa. They have simple direct life-cycles involving the faecal-oral transmission of eggs containing infective L1. Eggs excreted with host faeces contaminate soil, food and water supplies and have a characteristic barrel-shape with mucoid polar plugs at each end. Heavy infections by *Trichuris* spp. in humans and domestic animals may cause diarrhoea, anaemia, malnutrition, and occasionally rectal prolapse.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass:	Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)
Order:	Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily:	Trichinelloidea (oesophagus with short muscular anterior portion and long glandular posterior portion)
Family:	Trichuridae (whipworms, sudden transition in width, slender anteriorly, barrel-shaped eggs with polar plugs)
Genus:	*Trichuris* (parasitic in caeca of mammals)
Species:	various species cause trichuriasis in humans and animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Trichinelloidea is characterised by worms having a distinctive oesophagus consisting of a short anterior muscular section and a long posterior glandular section (stichosome) encircled by 1-3 rows of unicellular glands (stichocytes). Adult worms generally have long narrow anterior necks (containing only the stichosome) and stouter posterior bodies (containing the reproductive organs). Female worms produce thick-shelled eggs with bipolar mucoid plugs giving them a lemon- or barrel-shape. Most genera pass unembryonated eggs, but those of some groups (Trichinellidae, Trichosomoididae) embryonate *in utero.* The first-stage larvae (L1) have an oral stylet, similar to their presumed soil-dwelling dorylaimid ancestors. Unlike other parasitic nematodes, the L1 of trichinelloids (rather than L3) is used to infect their final hosts, sometimes after a brief period in an invertebrate intermediate host (such as earthworms) to become infective. Adults worms are endoparasites in most classes of vertebrates, generally occurring within the intestinal mucosa but some infecting epithelia of the urinary, respiratory or integumentary systems. An increasing number of genera have been recognised but their higher classification is confounded as some authorities distinguish 6 families while others have demoted several to subfamily status. The former ranking has been retained in this resource to better help the reader differentiate genera on the basis of recognised apomorphic characters, although future studies may reveal different phylogenetic relationships. The 6 trichinelloid families include: Trichuridae (syn. Trichuroididae), Trichinellidae, Anatrichosomatidae and Trichosomoididae primarily in mammals; Capillariidae in birds, mammals and fish; and Cystoopside in fish and reptiles.

The family Trichuridae contains the whipworms which show a sudden transition in width with the thin anterior portion embedded in the large intestinal epithelia of mammals. Mature worms have 1-3 stichosomes composed of 40-200 stichocytes, male worms have a single spicule and a cirrus with spines or tubercles, and females are oviparous producing distinctive lemon-shaped eggs with mucoid polar plugs. Some 6 genera are recognised: *Trichuris* (syn. *Buckleyuris, Mastigodes, Rudolphia, Salamia, Trichocephalos, Trichocephalus p.p.*), *Capillostrongyloides, Liniscus, Orthothomix, Sclerotrichum* and *Tenoranema.* Infections are transmitted directly when eggs containing infective first-stage larvae (L1) are ingested with contaminated food or water. The genus

Trichuris contains over 110 spp., some of which have been associated with clinical disease in ruminants, marsupials, rodents and primates. The species *T. trichiura* is found in human populations throughout the world, mainly in tropical and subtropical regions. It is estimated that around 10% of the world population (800 million people) may be infected. Parasites are very prevalent in regions where human excrement (nightsoil) is used to fertilise vegetable gardens. Infections are typically over-dispersed, where a few individuals harbour most of the worms. Other whipworm species occur in a range of domestic and wild animals: including *T. ovis*, *T. skrjabini*, *T. discolor* and *T. globulosa* in ruminants; *T. vulpis*, *T. campanula* and *T. serrata* in dogs and cats; *T. suis* in pigs; and *T. muris* in rodents. Zoonotic transmission of *T. vulpis* and *T. suis* to humans has occasionally been reported. Whipworms are more prevalent in animals kept under intensive husbandry situations where hygiene may be poor; such as overcrowded kennels, pens and paddocks.

***Trichuris* species**	**Definitive Hosts [adults in large intestines]**	**Clinical signs**	**Distribution**
T. alcocki	Artiodactyla: cervid (Eld's deer)		India
T. antidorchi	Artiodactyla: bovid (springbok, blesbok)		Africa
T. arvicolae	Rodentia: cricetid (common vole, bank vole, field vole, water vole, southwestern water vole)		Europe, North America
T. baeri	Artiodactyla: giraffid (okapi)		Africa
T. bainae	Rodentia: cricetid (rat-headed rice rat)		South America
T. barbertonensis	Artiodactyla: bovid (cattle, African buffalo, goat, steenbok, impala)		Africa
T. barusi	Rodentia: murid (black rat, Indian gerbil, Indian desert jird)		Asia
T. baskakovi (syn. T. *baskokowi*)	Artiodactyla: cervid (reindeer), bovid (cattle)		Russia
T. bradleyi	Rodentia: octodontid (common degu)		South America
T. buckleyi (now *Buckleyuris*)	Artiodactyla: bovid (steinbok)		Africa
T. bursacaudata	Rodentia: ctenomyid (Talas tuco-tuco)		South America
T. busuluk	Eulipotyphla: talpid (European mole)		Europe
T. cameli	Artiodactyla: camelid (bactrian camel)		Asia
T. campanula	Carnivora: felid (cat)	mostly subclinical	Caribbean
T. capreoli	Artiodactyla: cervid (roe deer, red deer, fallow deer), bovid (mouflon); Rodentia: murid (yellow-necked mouse), cricetid (common vole, European pine vole)	mostly subclinical	worldwide
T. carlieri	Rodentia: murid (fringe-tailed gerbil)		Africa
T. cervicaprae	Artiodactyla: bovid (goat, chamois, blackbuck)		Eurasia
T. chiliensis	Rodentia: cricetid (long-haired grass mouse)		South America
T. citelli	Rodentia: sciurid (California ground squirrel)		North America
T. citellorum	Rodentia: sciurid (long-tailed ground squirrel)		Russia
T. colobae	Primates: cercopithecid (colobus monkey)		Africa
T. contorta	Rodentia: bathyergid (mole-rat)		Africa
T. cutcasheni	Rodentia: sciurid (Caucasian squirrel)		Eurasia
T. cynocephalus	Primates: cercopithecid (Hamadryas baboon)		Africa
T. cyrenaica	Carnivora: canid (red fox, fennec fox)		Europe
T. deseirani	Artiodactyla: bovid (cattle)		Europe
T. didelphis	Didelphimorphia: didelphid (white-eared opossum, Virginnia opossum)		Americas
T. dipodomis	Rodentia: heteromyid (Merriam's kangaroo-rat, chisel-toothed kangaroo-rat, Ord's kangaroo-rat)		North America
T. discolor	Artiodactyla: bovid (cattle, zebu, water buffalo, yak, nilgai, sheep, mountain sheep, bighorn sheep, goat, mouflon, Cyprus mouflon, chamois, Japanese serow), cervid (moose), giraffid (okapi); Rodentia: murid Indian gerbil)	mostly subclinical, sometimes watery diarrhoea	Eurasia, Africa, North America, Australia
T. diversicolor	Artiodactyla: bovid (cattle)		
T. dolichotis	Rodentia: caviid (Patagonian mara)		South America
T. dzejrani	Artiodactyla: bovid (cattle, goitered gazelle)		Russia
T. elatoris	Rodentia: heteromyid (Texas kangaroo-rat, Merriam's kangaroo-rat, Ord's kangaroo-rat)		North America
T. erschovi	Artiodactyla: bovid (cattle)		Russia
T. felis	Carnivora: felid (cat)		Europe

T. feliui	Eulipotyphla: talpid (European mole)		Europe
T. fossor	Rodentia: cricetid (Zacatecan deer mouse), geomyid (Botta's pocket gopher, northern pocket gopher)		Americas
T. fulvi	Rodentia: ctenomyid (tawny tuco-tuco)		South America
T. gazellae	Artiodactyla: bovid (goat)		
T. georgicus	Artiodactyla: bovid (goat, mouflon, sheep)		Africa, Europe
T. gerbillis	Rodentia: murid (North African gerbil, greater Egyptian gerbil, Libyan jird, Shaw's jird, fat sand rat)		Africa
T. germani	Rodentia: murid (large tree mouse, Champion's tree mouse, chesnut tree mouse, gray-bellied tree mouse)		Papua New Guniea
T. giraffae (syn. *Trichocephalus*)	Artiodactyla: giraffid (reticulated giraffe, northern giraffe, okapi)		Africa
T. globulosa	Artiodactyla: bovid (cattle, yak, Indian yak, nilgai, buffalo, goat, sheep, Cyprus mouflon, mouflon, chamois, impala, Dorcas gazelle, Cuvier's gazelle, Soemmering's gazelle, Sharpe's grysbok, roan antelope, sable, waterbuck), camelid (bactrian camel, dromedary), giraffid (reticulated giraffe, Angolan giraffe), cervid (roe deer, red deer, fallow deer, reindeer)	mostly subclinical, sometimes watery diarrhoea	worldwide
T. gracilis	Rodentia: caviid (Brazilian guinea pig), dasyproctid (agouti, red-rumped agouti)		South America
T. guevarai	Artiodactyla: cervid (red deer)		Eurasia
T. gundii	Rodentia: ctenodactylid (gundi)		Africa
T. hyracis	Hyracoidea: procaviid (southern tree hyrax)		Africa
T. hystricis	Rodentia: hystricid (crested porcupine)		Africa
T. indicus	Artiodactyla: bovid (cattle)		Russia
T. infundibulus (*infundibulum*)	Rodentia: hystricid (African crested porcupine); Artiodactyla: bovid (goat, mouflon, sheep)		Africa, Europe
T. laevitestis	Rodentia: cricetid (Azara's grass mouse, hairy-tailed bolo mouse, Argentine swamp rat)		South America
T. landak	Rodentia: hystricid (Sunda porcupine)		Asia
T. lani	Artiodactyla: camelid (dromedary), bovid (sheep), cervid (fallow deer, sika deer, moose)		Asia
T. lenkorani	Rodentia: hystricid (Indian crested porcupine)		Asia
T. leporis (syn. *T. unguiculatus*, *T. sylvilagi*, *T. tineri*)	Lagomorpha: leporid (snowshoe hare, Cape hare, European hare, mountain hare, Tolai hare, European rabbit, volcano rabbit, eastern cottontail), sciurid (Richardson's ground squirrel)	mostly subclinical	North America, Eurasia
T. longispiculus	Artiodactyla: cervid (reindeer, sika deer, roe deer, moose), bovid (sheep, urial, mouflon, long-tailed goral)		Russia
T. madisonensis	Rodentia: sciurid (eastern chipmunk)		North America
T. marsupialis	Didelphimorphia: didelphid (Virginia opossum)		North America
T. massino	Artiodactyla: cervid (reindeer)		Russia
T. mastomysi	Rodentia: murid (Natal multimammate mouse)		Africa
T. media	Artiodactyla: bovid (zebu)		Russia
T. mettami	Rodentia: hystricid (crested porcupine)		Asia
T. minuta	Didelphimorphia: didelphid (water opossum, big-eared opossum, common opossum, Viginia opossum, Linnaeus's mouse opossum); Cingulata: dasypatid (nine-banded armadillo)		Americas
T. muris	Rodentia: murid (house mouse, wood mouse, yellow-necked mouse, typical striped grass mouse, Natal multimammate mouse, African pygmy mouse, Algerian mouse, striped field mouse, Jackson's soft-furred mouse, black rat, Philippine black rat, brown rat, African grass rat, rusty-bellied brush-furred rat, water rat, eastern wood rat, mid-day jird), glirid (woodland dormouse), nesomyid (Gambian pouched rat), hystricid (African brush-tailed porcupine), cricetid (common vole, reed vole, narrow-headed vole, Maximowicz's vole, Muisk vole, European snow vole, Tundra vole, European water vole, European pine vole, bank vole, grey red-backed vole, northern red-	mostly subclinical	worldwide

	backed vole, field vole, root vole, yellow steppe lemming, Chinese striped hamster, gray hamster), sciurid (long-tailed ground squirrel); Eulipotyphla: soricid (Indian musk shrew)		
T. myocastoris	Rodentia: echimyid (coypu)		South America
T. navonae	Rodentia: cricetid (Montane grass mouse, blackish grass mouse)		South America
T. neomi	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
T. neotomae	Rodentia: cricetid (dusky-footed woodrat)		North America
T. nodosus (syn. *Trichocephalus*)	Rodentia: murid (mouse)		Europe
T. nutria	Rodentia: echimyid (coypu)		South America
T. odocoileus	Artiodactyla: cervid (white-tailed deer)		North America
T. opaca	Rodentia: cricetid (muskrat, meadow vole), erethizontid (bristle-spined rat)	intestines	Americas
T. oreamnos	Artiodactyla: bovid (mountain goat, Rocky Mountain goat)		North America
T. ovis	Artiodactyla: bovid (cattle, American bison, sheep, bighorn sheep, argali, tahr, mouflon, Cyprus mouflon, Afghan urial, chamois, goat, mountain goat, blackbuck, alpine ibex), cervid (sika deer, roe deer, red deer, maral, Iberian red deer, fallow deer, marsh deer, black-tailed deer, boreal woodland caribou, reindeer, moose), camelid (bactrian camel, dromedary), suid (pig), giraffid (reticulated giraffe)	mostly subclinical, sometimes watery diarrhoea, often with blood	worldwide
T. palaeformis	Primates: cercopithecid (green monkey)		Africa
T. pampeana	Rodentia: ctenomyid (Azara's tuco-tuco, Talas tuco-tuco)		South America
T. pardinasi	Rodentia: cricetid (Buenos Aires leaf-eared mouse, yellow-rumped leaf-eared mouse)		South America
T. parvispicularis	Rodentia: thryonomyid (greater cane rat)		Africa
T. parvispiculum	Artiodactyla: bovid (cattle, sheep, goat)		Africa, Australia
T. pedetei	Rodentia: pedetid (South African springhare)		Africa
T. peramelis	Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot)		Australia
T. perognathi	Rodentia: heteromyid (pocket mouse, California pocket mouse)		North America
T. peromysci	Rodentia: cricetid (California mouse)		North America
T. petteri	Rodentia: murid (Jackson's soft-furred mouse)		Africa
T. procaviae	Hyracoidea: procaviid (rock hyrax)		Africa, Middle-East
T. raoi	Artiodactyla: camelid (camel)		India
T. rhinopiptheroxella	Primates: cercopithecid (Sichuan snub-nosed monkey)		Asia
T. rhinopithecus	Primates: cercopithecid (Yunnan snub-nosed monkey)		Asia
T. rhombomydis (syn. *T. rhombomidis*)	Rodentia: cricetid (gray hamster), murid (midday jird, great gerbil)		Russia
T. robusti	Rodentia: ctenomyid (tawny tuco-tuco)		South America
T. rupicaprae	Artiodactyla: bovid (chamois)		Europe
T. schumakovitschi	Artiodactyla: bovid (Rocky Mountain bighorn sheep, mountain goat)		North America
T. serrata	Carnivora: felid (cat, wildcat), canid (dog)	mostly subclinical	Americas
T. skrjabini	Artiodactyla: bovid (sheep, mouflon, chamois, goat, ibex, cattle), camelid (camel, dromedary), giraffid (okapi), cervid (red deer, fallow deer)	mostly subclinical	Eurasia, Africa, North America, Australia
T. spalacis	Rodentia: spalacid (lesser mole-rat), murid (great gerbil)		Africa, Russia
T. spiricollis	Artiodactyla: giraffid (reticulated giraffe)		Africa
T. suis	Artiodactyla: suid (pig, wild boar, Japanese boar, Sardinian wild boar); Rodentia: cricetid (muskrat), castorid (American beaver); Primates: hominid (human)	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia	worldwide
T. surka	Rodentia: sciurid (long-tailed marmot)		Asia

T. sylvilagi	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, Japanese hare, Cape hare, European hare)		worldwide
T. syrca	Rodentia: sciurid (Tarbagan marmot)		China
T. tarandi	Artiodactyla: cervid (reindeer)		Russia
T. tenuis	Artiodactyla: camelid (dromedary, llama, vicuna), bovid (goat)	mostly subclinical, sometimes diarrhoea	worldwide
T. thrichomysi	Rodentia: echimyid (common punare)		South America
T. travassosi	Rodentia: cricetid (black-footed pygmy rice rat)		South America
T. trichiura (syn. *Trichocephalus trichiuris, T. dispar*) [human whipworm]	Primates: hominid (human, eastern gorilla, eastern chimpanzee), cercopithecid (grivet, Skye's monkey, Campbell's mona monkey, blue monkey, king colobus, western red colobus, Japanese macaque, southern pig-tailed macaque, crab-eating macaque, togue, baboon, yellow baboon, chacma baboon, Guinea baboon, northern plain gray langur, purple-faced leaf monkey), cebid (patas monkey); Artiodactyla: bovid (sheep), suid (pig); Gadiformes: gadid (Alaska pollock) [plus carriage by Diptera: calliphorid (oriental latrine fly), muscid (house fly)]	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia, illthrift, finger clubbing, tenesmus, rectal prolapse	worldwide, esp. tropics
T. ursinus	Primates: cercopithecid (chacma baboon)		Africa
T. vondwei	Artiodactyla: bovid (goat, sheep, mouflon)		Africa, Europe
T. vulpis [dog whipworm]	Carnivora: canid (dog, golden jackal, coyote, wolf, maned wolf, racoon dog, swift fox, red fox, Japanese red fox, Iberian fox), felid (cat), mustelid (European polecat); Primates: hominid (human)	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia	worldwide

Parasite morphology: Whipworms form 3 different developmental stages; eggs, larvae and adults. The eggs are usually yellow-brown (bile-stained), barrel- to lemon-shaped and measure 50-93 µm in length by 22-42 µm in width. They have smooth outer shells and distinctive mucoid bipolar opercular plugs (one at each end). Eggs are typically unembryonated in faecal samples and develop infective larvae in the external environment. The elongate larval stages measure from 115-155 µm in length and have a rounded cephalic end with a sharp protrusible stylet. Adult worms have elongated tubular bodies with a long thin (0.1-0.2 mm wide) anterior end (up to 2/3rds of body length) that suddenly becomes thicker (up to 0.5 mm wide) at the posterior end (hence the common name whipworm). The thin anterior portion contains the stichosome oesophagus and the thicker posterior portion contains the intestines and reproductive organs (both sexes have a single gonad). The mouth is a simple opening without lips but provisioned with a minute spear (stylet) protruding from the small buccal capsule. The moniliform oesophagus is thin, tubular, capillary-like and surrounded by a single row of 40-200 glandular stichocytes (whole structure referred to as stichosome pharynx). Adult female worms measure from 30-80 mm in length and the uterus (containing many lemon-shaped eggs) ends in a ventral midbody vulva, sometimes with a protruding spiny ridge. Adult male worms are smaller measuring 23-60 mm in length and they have a tightly coiled posterior end with a single spicule 8.5-11.0 mm long surrounded by a spiny protrusible sheath (sometimes called a cirrus). *Trichuris* spp. have conventionally been differentiated on the basis of host occurrence, egg and worm morphometrics, and spicule, cloacal and uterine structure. *T. trichiura* from humans and *T. suis* from pigs are remarkably similar in appearance (despite some reports of differences in the sizes of eggs, infective larvae, spicules and the presence/absence of caudal papillae), but recent molecular characterization studies have confirmed their separate classification.

Site of infection: Juvenile worms develop in glands of the caecal and colonic mucosa where they moult and grow. Adult worms have their anterior ends embedded in tunnels in the mucosa with their posterior ends dangling into the lumen.

Pathogenesis: Infections may cause trichuriasis (whipworm disease), one of the most important geohelminthiases (soil-transmitted helminthiases) widespread in tropical regions. Small worm burdens (< 100) rarely cause disease, while heavier infections may produce a variety of conditions, ranging from local enteric disturbances to systemic conditions and occasionally death. Infections tend to be over-dispersed in host populations, with a few hosts harbouring heavy infections (especially small children). The anterior ends of the adult worms are embedded in the gut mucosa where they are constantly probing back and forth feeding on fluids, digested tissues and possibly blood. Worms may also release cytolytic enzymes to assist in tissue digestion. Collectively, this may cause significant mechanical and chemical trauma to the mucosa with chronic haemorrhage leading to dysentery and anaemia. Heavy infections may cause haemorrhagic colitis and/or diphtheritic inflammation of the caecal mucosa, both associated with epithelial desquamination, necrosis, excess mucus production, congestion and submucosal oedema. This may result in intermittent watery diarrhoea often with fresh blood and mucus, dehydration, anaemia and anorexia. Pathogenesis has been related to host inflammatory responses, involving markedly reduced cell-mediated responses and elevated IgE responses, characteristic of local

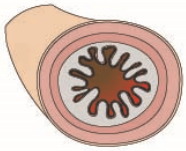
tissue anaphylactic responses. Whipworm infections are more common in children due to their poor hygiene practices, particularly in impoverished rural regions where toilet facilities are sparse. Persistent infections have been associated with malnutrition, growth retardation, and reduced cognitive function in children. Chronic infections may also cause finger (and occasionally toe) clubbing evident as odd thickening of the ends of the digits. Heavy infections may produce tenesmus (urgency) causing the host to strain and possibly suffer rectal prolapse (recto-rectal intussusception). Infections in pigs and dogs may be pathogenic causing severe typhlitis whereas infections in ruminants and other animals are usually subclinical but may cause problems when animals are stressed (e.g. in feedlots or under drought conditions).

Developmental cycle and mode of transmission: Whipworms have a direct developmental cycle whereby embryonated eggs are directly infective to the definitive host. Infections are transmitted by the faecal-oral route, involving the ingestion of eggs with contaminated food, water or soil. Fertilised female worms produce numerous eggs (sporadic production from none up to 3,000-10,000 per day) which are excreted with host faecal material. The eggs embryonate in around 10 days and develop infective larvae in about 3 weeks in moist shady soil (or in as little as 2 weeks in warm conditions or up to 4 months in cold conditions). Eggs are dispersed in the environment by anthropogenic activities as well as by wind, water and insects (house flies can act as mechanical vectors). The eggs are resistant to environmental conditions and may remain viable under suitable conditions for up to 4-5 years. They may contaminate soil, water and foodstuffs that are consumed by definitive hosts. When ingested, infective larvae emerge from the eggs in the small intestines and enter the crypts of Lieberkuhn where they penetrate basal cells and tunnel within the epithelium back towards the lumen. They continue to invade the mucosa as they move to the lower intestines where they complete moulting and form adults. Patent infections may develop in 5-12 weeks and can persist for 1-4 years. Infections may also accumulate in hosts as they are constantly re-infected from their heavily-contaminated environments.

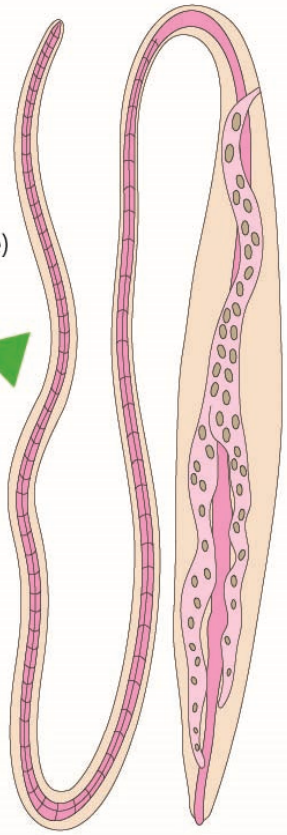
Differential diagnosis: Infections may be indicated by clinical history and symptomatology but are routinely confirmed by the microscopic detection of characteristic eggs by coprological examination of faecal samples, usually following concentration by centrifugation in saturated heavy metal salt or sugar solutions (preferable to use high specific gravity solutions as whipworm eggs are relatively dense). Because eggs may be shed intermittently, repeat samples should be examined. In individuals with rectal prolapse, worms can be seen macroscopically attached to the mucosa. Colon endoscopy has also been used to reveal the presence of worms. Several immunoserological tests (enzyme immunoassays, Western blots) have been developed in research laboratories to detect specific host antibodies or parasite antigens, but they have demonstrated variable cross-reactions with other helminths and cannot reliably differentiate between recent or previous infection. Molecular biological techniques have recently been developed to discriminate species by polymerase chain reaction (PCR) amplification of specific gene sequences (small subunit (SSU) ribosomal RNA and internal transcribed spacer regions (ITS1, ITS2)).

Treatment and control: Whipworms are resistant to many anthelmintic treatments due to their relative inaccessibility in the host mucosa. Nonetheless, several groups of nematocidal drugs are effective against whipworms, with some notable exceptions. Benzimidazoles (mebendazole, albendazole, flubendazole, fenbendazole) have proven effective in various hosts (although thiabendazole produces unpleasant side-effects) and tetrahydropyrimidines (oxantel, pyrantel) and depsipeptides (emodepside) also have good activity. These drugs may not be effective against immature stages so repeat treatments may be required. Domestic animals have been successfully treated using macrocyclic lactones (avermectins, milbemycins) and imidazothiazoles (levamisole by injection), but infections in some hosts (mostly camelids) appear to be refractory. Other conventional de-wormers, such as diethylenediamines (piperazine) and diphenylethers (nitroscanate), are not effective against whipworm. Any eggs contaminating the environment may still be viable for several years so patients may quickly become re-infected, therefore so regular de-worming treatments may be mandated. It is difficult to decontaminate environmental sources as the eggs are very resistant to most chemical disinfectants. Some success has been reported using strong bleach solutions, steam-cleaning and/or flame guns to decontaminate concrete holding facilities. Alternatively, stock at risk may be translocated to cleaner surroundings. It is essential to reduce exposure by maintaining high standards of hygiene and sanitation with sewage containment or regular removal of faeces. Prevention of infections is best achieved by prohibiting the use of excrement (night-soil) as fertiliser (or ensuring it is processed by suitable microbial biocomposting prior to use) and thoroughly washing vegetables, salads and fruits with clean water prior to consumption. Control measures include education programmes to improve personal hygiene and sanitary conditions, and regular deworming campaigns.

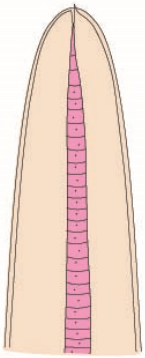
Trichuris



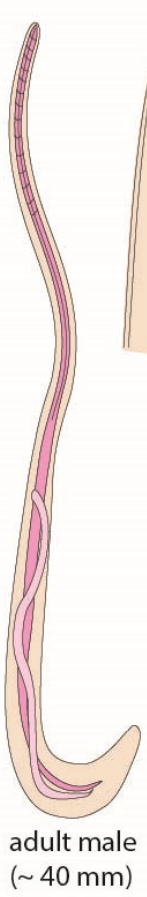
intestines
(diarrhoea, anaemia,
malnutrition, prolapse)



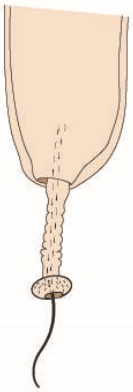
adult female
(~ 70 mm)



head



adult male
(~ 40 mm)



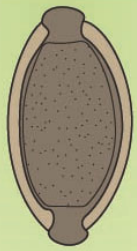
male
tail

Definitive Hosts
(primates, ruminants,
rodents, marsupials)

first-stage larvae (L1)
(~ 120 µm)

eggs
ingested

larva develop
within eggs



eggs
(~ 80 µm)

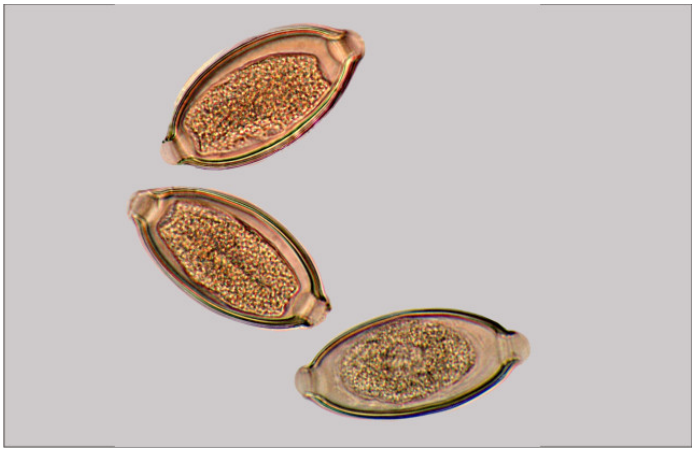
external
environment

eggs
excreted
in faeces

faecal-oral transmission

Trichuris adult worms

Trichuris adult worms



Trichuris worm eggs

Trichuris sections of worms in colon