Trichostrongylus
(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). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida, including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Trichostronglyus* spp. (black scour and stomach hair worms) cause diarrhoeal diseases that markedly impact production in ruminants worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

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: Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family: Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus: *Trichostrongylus* (parasitic in gut of herbivorous mammals/birds)
Species: various species cause black scours in ruminants

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 with 2 ovaries (some monodelphic or polydelphic), 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 His
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 recognise strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterise taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies, mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Trichostrongylinae contains 6 genera (*Trichostrongylus* (syn. *Buckleya*, *Cobboldostrongylus*, *Gilesia*, *Probostrongylus*); *Graphidioides*, *Graphinema*, *Parostertagia*, *Travassosius*, and *Trichostrongyella*) parasitic in the gastric or intestinal mucosa of ruminants, camelids, rodents, or the caeca of birds. The genus *Trichostrongylus* contains some 60 species of small reddish worms whose excretory pores open into a distinctive ventral notch on the cervical body surface. Infections have been recorded worldwide, particularly in grazing animals, and many species have euryxenous or stenoxenous host ranges often infecting multiple closely-related host species. Most *Trichostrongylus* spp. infect the small intestines of their hosts, although several species infect the stomach (notably *T. axei*). Infections are common in tropical and temperate regions, especially in rural areas with moist loamy soils suitable for egg and larval development. Several species cause considerable problems in domestic livestock industries where morbidity and mortality reduce productivity and treatment is costly. In particular, *T. colubriformis, T. vitrinus* and *T. rugatus* affect sheep production in warm, cool and dry areas respectively, *T. axei* mainly affects cattle production, and *T. tenuis* affects fowl production. Approximately 10 species are known to accidentally infect humans (*T. orientalis* most frequently) when larvae are ingested with unwashed vegetables (some outbreaks traced to farms practising organic farming methods with poorly composted manure). While most infections in humans are not severe, it is estimated that approximately 5.5 million people may be infected annually, with the prevalence being highest in the Middle-East and Asia.

Trichostrongylus species	Definitive Hosts	Location [Clinical signs]	Distribution
T. affinis	Lagomorpha: leporid (European rabbit, eastern cottontail); Rodentia: cricetid (marsh rice rat, hispid cotton rat, cotton mouse, Oldfield mouse, Florida mouse); Primates: hominid (human)		North America, Europe
T. andreevi	Artiodactyla: cervid (roe deer)		Europe
T. angistris	Artiodactyla: bovid (impala, blue duiker, red forest duiker, bushbuck); Copepoda: cyclopid (*Megacyclops viridis*)		Africa
T. anomalus	Artiodactyla: bovid (suni, blue duiker, red forest duiker)		Africa
T. askivali	Artiodactyla: cervid (roe deer, red deer, sambar deer, fallow deer, white-tailed deer), bovid (sheep)	abomasum	Eurasia
T. assadovi	Artiodactyla: bovid (sheep)		Asia
T. asymmetricus	Diprotodontia: macropodid (un-named wallaby sp.)	stomach	zoo
T. auriculatus	Artiodactyla: bovid (steenbok)	small intestines	Africa
T. axei (syn. *Strongylus extenuatus, gracilis, tenuissimus*) (stomach hairworm, stomach bankrupt worm)	Artiodactyla: bovid (cattle, water buffalo, American bison, European bison, sheep, argali, bighorn sheep, mouflon, Cyprus mouflon, goat, mountain goat, chamois, alpine ibex, Iberian ibex, blackbuck, bushbuck, common duiker, blue duiker, red forest duiker, roan antelope, sable antelope, Sharpe's grysbok), antilocaprid (pronghorn), antilocaprid (pronghorn), cervid (moose, roe deer, red deer, fallow deer, marsh deer, mule deer, white-tailed deer, reindeer, caribou, chital), camelid (llama), suid (pig); Perissodactyla: equid (horse, donkey, mule, onager); Lagomorpha: leporid (rabbit); Rodentia: caviid (capybara), sciurid (Richardson's ground squirrel); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)	abomasum, stomach [weight loss, diarrhoea, illthrift]	worldwide
T. brevis	Artiodactyla: bovid (goat); Carnivora: felid (wildcat); Primates: hominid (human)		
T. calcaratus	Artiodactyla: cervid (roe deer ,white-tailed deer), bovid (sheep); Lagomorpha: leporid (European rabbit, eastern cottontail, black-tailed jackrabbit, volcano rabbit); Rodentia: cricetid (muskrat, Florida mouse), sciurid (fox squirrel); Primates: hominid (human)		North America
T. capricola	Artiodactyla: bovid (European bison, sheep, argali, mouflon, Cyprus mouflon, goat, alpine ibex, Iberian ibex, chamois, Pyrenean chamois), cervid (roe deer, moose); Lagomorpha: leporid (Cape hare); Primates: hominid (human)		Europe, North America
T. cesticillus	Primates: cebid (tufted capuchin)		South America
T. chiapensis (syn. *Boehmiella wilsoni*)	Rodentia: sciurid (Deppe's squirrel)		South America
T. colubriformis (syn. *T. instabilis*) (black scour worm, bankrupt worm)	Artiodactyla: bovid (cattle, water buffalo, sheep, bighorn sheep, argali, mouflon, goat, mountain goat, alpine ibex, Iberian ibex, chamois, common tsessebe, impala, goitered gazelle, dama gazelle, Soemmerring's gazelle, sable antelope, lechwe, blackbuck, bushbuck, Maxwell's duiker, common duiker, Sharpe's grysbok), antilocaprid (pronghorn), cervid (roe deer, red deer, mule deer, marsh deer, moose), camelid (llama, bactrian camel, dromedary), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (European rabbit, Cape hare, European hare, Granada hare, mountain hare); Rodentia: murid (Mongolian gerbil), echimyid (coypu), sciurid (European ground squirrel), cricetid (bank vole, muskrat); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)	duodenum [weight loss, diarrhoea, illthrift]	worldwide
T. cramae	Galliformes: phasianid (northern bobwhite quail, turkey, greater prairie chicken); Anseriformes: anatid (Canada goose); Gruiformes: gruid (sandhill crane)	caecum	North America
T. deflexus	Artiodactyla: bovid (cattle, goat, common tsessebe, waterbuck, impala, steenbok, Cape grysbok, common duiker, grey duiker, common eland, nyala, Cape bushbuck, grey rhebok, greater kudu, suni, oribi), suid (desert warthog); Lagomorpha: leporid (scrub hare)		Africa
T. delicatus	Rodentia: sciurid (Abert's squirrel)		North

			America
T. dosteri	Artiodactyla: cervid (white-tailed deer)		North America
T. drepanoformis	Artiodactyla: bovid (sheep, goat)	duodenum	Australia
T. duretteae	Rodentia: ctenomyid (Talas tuco-tuco)	small intestines	South America
T. extenuatus	Artiodactyla: bovid (cattle, mouflon, gazelle), cervid (roe deer, red deer)		Europe
T. falculatus	Artiodactyla: bovid (sheep, goat, impala, blue duiker, grey duiker, common tsessebe, sable antelope, Cape grysbok, southern reedbuck bushbuck, grey rhebok, nyala, greater kudu), suid (desert warthog); Lagomorpha: leporid (scrub hare); Primates: cercopithecid (Chacma baboon)		Africa
T. fiberius	Rodentia: cricetid (American muskrat)		North America
T. gaibovi	Artiodactyla: bovid (sheep)		
T. hamatus	Artiodactyla: bovid (common tsessebe)		Africa
T. hypsokysta	Artiodactyla: suid (desert warthog)		Africa
T. instabilis	Artiodactyla: bovid (sheep, impala), suid (desert warthog); Primates: hominid (human)		Africa
T. leiperi	Artiodactyla: bovid (eland)	abomasum, duodenum	Africa
T. lerouxi	Artiodactyla: bovid (cattle); Primates: hominid (human)		Europe
T. longispicularis	Artiodactyla: bovid (cattle, sheep, goat, Pyrenean chamois), cervid (roe deer, mule deer, white-tailed deer, moose), camelid (llama)	small intestines [diarrhoea]	Australia, Americas, Europe
T. longispiculatum	Artiodactyla: bovid (chamois), cervid (moose)		North America
T. magna	Artiodactyla: bovid (greater kudu)		Africa
T. medius	Anseriformes: anatid (mallard, greylag goose), Galliformes: phasianid (black grouse)	small intestines, caecum	Eurasia
T. minor	Artiodactyla: cervid (roe deer)		
T. monnigi	Artiodactyla: bovid (cattle, sheep, roan antelope)		Africa
T. moschatus	Artiodactyla: bovid (suni)	small intestines	Africa
T. orientalis	Artiodactyla: bovid (sheep); Rodentia: hystricid (Indian crested porcupine); Primates: hominid (human)		Asia, Middle East
T. ostertagiaeformis	Artiodactyla: bovid (argali), cervid (roe deer, red deer)		
T. pietersei	Artiodactyla: bovid (goat, Cape grysbok)		Africa
T. pigmentus	Lagomorpha: leporid (Indian hare)		Asia
T. probolurus	Artiodactyla: bovid (sheep, broad-tailed sheep, goat, blackbuck, dorcas gazelle, dama gazelle, dorcas gazelle, Soemmerring's gazelle, Speke's gazelle, goitered gazelle), cervid (roe deer), camelid (bactrian camel, dromedary); Primates: hominid (human)		Africa
T. qilianensis	Artiodactyla: bovid (bharal)		Asia
T. qinghaiensis	Artiodactyla: bovid (yak)		Asia
T. ransomi	Lagomorpha: leporid (eastern cottontail, European rabbit)	small intestines	North America
T. retortaeformis	Lagomorpha: leporid (European rabbit, volcano rabbit, European hare, Granada hare, mountain hare, Tolai hare, snowshoe hare, Cape hare Rodentia: dipodid (great jerboa), murid (yellow-necked mouse, wood mouse), echimyid (coypu), cricteid (muskrat, common vole, Japanese grass vole, southwestern water vole, European water vole, bank vole), caviid (Patagonian mara, Spix's yellow-toothed cavy), chinchillid (southern viscacha), castorid (American beaver), sciurid (red squirrel); Diprotodontia: phalangerid (common brushtail possum); Artiodactyla: bovid (goat), cervid (roe deer)	small intestines [enteritis, mucous exudates]	worldwide
T. rugatus	Artiodactyla: bovid (sheep, bighorn sheep, goat, blue duiker, red duiker, grey rhebok, Cape grysbok); Diprotodontia: phalangerid (common brushtail possum)	duodenum [weight loss, diarrhoea, illthrift]	Africa, Australasia, North America
T. sigmodontis	Rodentia: cricetid (hispid cotton rat, marsh rice rat, golden hamster),	lower small	North

	echimyid (coypu), murid (Mongolian gerbil)	intestine, caecum	America
T. skrjabini	Artiodactyla: bovid (sheep, argali, mouflon), cervid (roe deer); Rodentia: sciurid (European ground squirrel); Primates: hominid (human)	abomasum, small intestines	Russia
T. subtilis	Artiodactyla: bovid (sheep, broad-tailed sheep, dorcas gazelle), camelid (bactrian camel, dromedary); Primates: cercopithecid (hamadryas baboon), hominid (human)		Africa
T. suis	Artiodactyla: suid (pig)		
T. tenuis (syn. *T. pergracilis*)	Galliformes: phasianid (chicken, Indian peafowl, turkey, ring-necked pheasant, grey partridge, rock partridge, chukar, red-legged partridge, willow ptarmigan, rock ptarmigan, common quail, northern bobwhite quail, mountain quail, black grouse, red grouse); Anseriformes: anatid (mottled duck, mallard, greater white-fronted goose, greylag goose, snow goose, mute swan); Casuariiformes: casuariid (emu)	caecum, small intestines [enteritis, diarrhoea]	North America, Eurasia
T. texanus	Rodentia: sciurid (black-tailed prairie dog)	small intestines	North America
T. thomasi	Artiodactyla: bovid (impala, red forest duiker, bushbuck, common tsessebe, greater kudu), suid (desert warthog); Lagomorpha: leporid (scrub hare)		Africa
T. vitrinus (black scour worm)	Artiodactyla: bovid (cattle, European bison, sheep, broad-tailed sheep, argali, goat, mouflon, Cyprus mouflon, chamois, Pyrenean chamois, alpine ibex, Iberian ibex, Cuvier's gazelle, dama gazelle, dorcas gazelle, goitered gazelle), cervid (roe deer, red deer, fallow deer, mule deer, reindeer, moose), camelid (bactrian camel, dromedary, llama); Lagomorpha: leporid (European rabbit); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)	duodenum [weight loss, diarrhoea, illthrift]	temperate regions
T. yoshidai	Rodentia: caviid (Brazilian guinea pig)		South America

Parasite morphology: Trichostrongylid nematodes form 3 different morphological stages in their developmental cycles: eggs; larvae; and adult worms. Freshly laid eggs are described as being typically 'strongyle' in that they are ellipsoidal with slightly pointed uneven poles, bound by thin smooth colourless shells (the inner membrane sometimes wrinkled) and contain a discrete central morula (early-stage embryo) usually consisting of 8-32 cells (blastomeres). Eggs vary in size from 73-125 x 31-72 µm, with narrower size ranges recorded for individual species (e.g. *T. colubriformis* 79-101 x 39-47 µm, *T. retortaeformis* 85-91 x 46-56 µm, *T. vitrinus* 93-118 x 41-52 µm, *T. axei* 79-92 x 31-41 µm). There are 4 sequential larval stages (designated L1-L4), the first 3 being exogenous (developing in the external environment) and the fourth being endogenous (occurring within the host). The first 2 larval stages (L1 and L2) are free-living pre-parasitic stages measuring from 320-400 µm in length. They are characterized by the possession of a rhabditiform pharynx or oesophagus (stout with a caudal bulb) used to feed on bacteria and particulate material. Although the third larval stage (L3) is free-living, it is ensheathed (retains the L2 cuticle as a thin protective sheath) and does not feed externally. They measure from 619-796 µm in length and are characterized by having tapering round heads, a strongyliform (flask-shaped) oesophagus, intestines comprising 16 cells, tapering tails (smooth in the abomasal species *T. axei*, digitate in the intestinal species) and short tail sheath extensions (18-56 µm). L3 are infective to their final hosts in which they develop to L4 and then immature worms (sometimes called pre-adults or L5) which subsequently mature. Adults are slender hair-like worms measuring from 2-10 mm long with rounded heads and tapering tails. Most species are colourless although some may be grey, light brown or pale red in colour. Trichostrongyles have rudimentary or no buccal capsules (compared to well-developed buccal capsules of strongyles) usually lacking lips and teeth are rarely present. *Trichostrongylus* spp. lack cephalic vesicles (unlike *Nematodirus* and *Cooperia*) and they have very small or no cervical papillae. Adult worms are characterized by the presence of a conspicuous ventral notch in the cervical region where the excretory pore is located (notch absent in *Haemonchus* and *Ostertagia*). Worms are surrounded by a thick cuticle with a synlophe (pattern of longitudinal ridges) reduced to annular striations. The oesophagus is relatively short and lacks a caudal bulb while the intestines have well-developed microvilli and a distinctive zig-zag lumen. Mature worms are sexually dimorphic, with females being larger than males (3-10 mm x 55-80 µm cf. 2-9 mm x 50-70 µm). Male worms have a well-developed symmetrical bursa (copulatory clasping organ) with a short dorsal lobe supported by 3 simple rays (comprising muscular elements following nerve channels to terminal papillae) and 2 long lateral lobes each supported by 6 rays (in a popular annotation system the rays have a 1-4 configuration with the ventroventral ray separated from the next 4 rays, while in another annotation scheme ray 2 is separated from rays 3-6). They also have a boat-shaped gubernaculum and 2 stout ridged brown spicules measuring 74-156 µm in length. The spicules vary in morphology depending on the species and may be equal in length (*T. capricola*), unbranched and barbed (*T. colubriformis*) or pointed (*T. vitrinus*); subequal in length and barbed (*T. falculatus*) or blunted (*T. longispicularis*); or markedly unequal in length (*T. axei, T. rugatus*) and barbed (*T. retortaeformis*). Female worms have blunted conical tails and are didelphic with 2 opposed uteri and paired genital tubes opening into a vulva (lacking a flap) usually located just posterior to the midbody. Gravid worms only contain a few (4-5) eggs aligned pole-to-pole *in utero*.

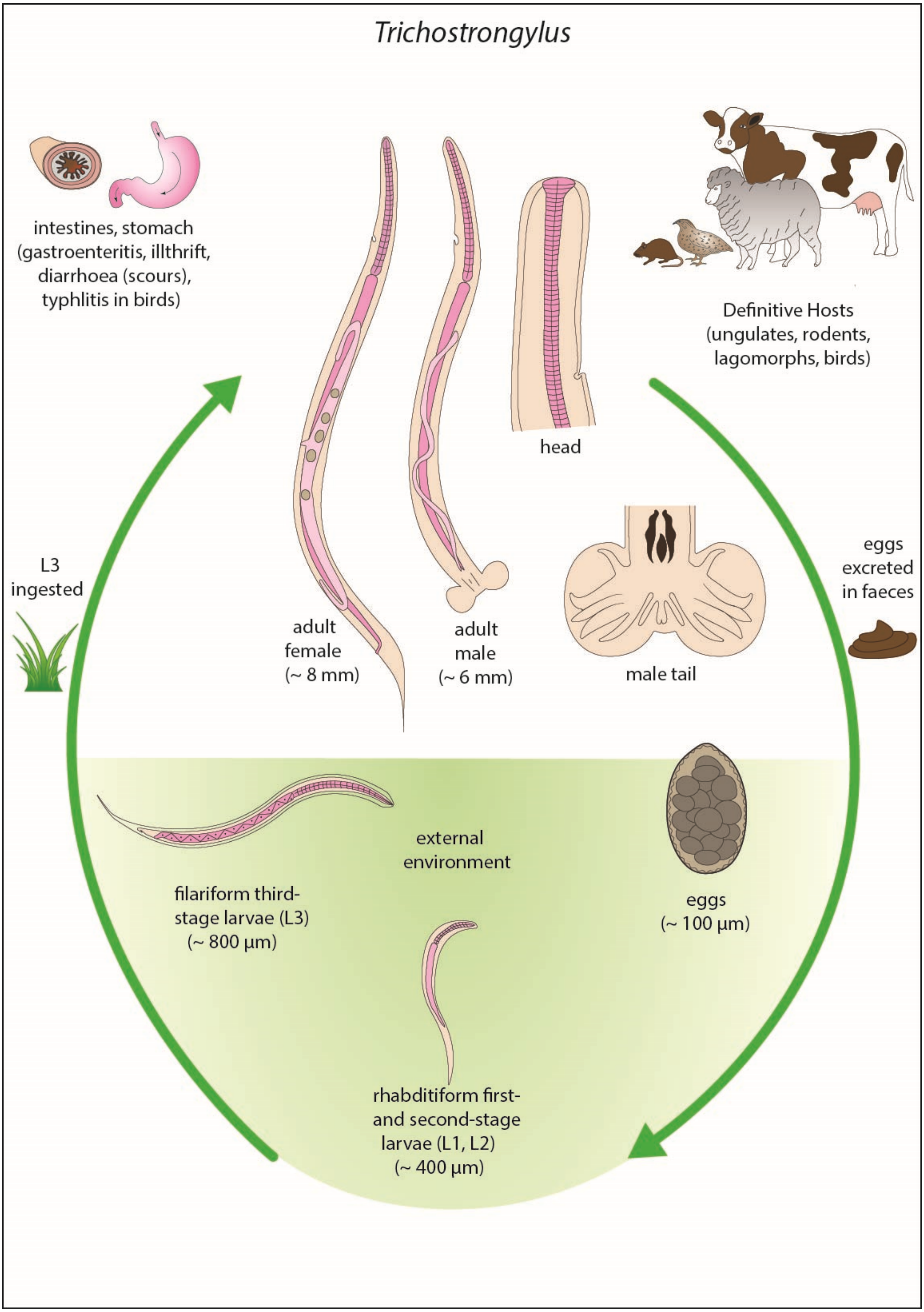
Site of infection: Adult worms of different *Trichostrongylus* species vary in their predilection site of infection: many species (such as *T. colubriformis, T. rugatus, T. vitrinus*) infecting the mucosal lining of the anterior small intestine (usually the duodenum of ruminants); several species (e.g. *T. tenuis, T. sigmodontis*) infecting the caecum (mainly in birds and rodents), and several species (esp. *T. axei*) infecting the stomach (glandular part in monogastrics (pigs, horses) or the abomasum (fourth stomach) in ruminants).

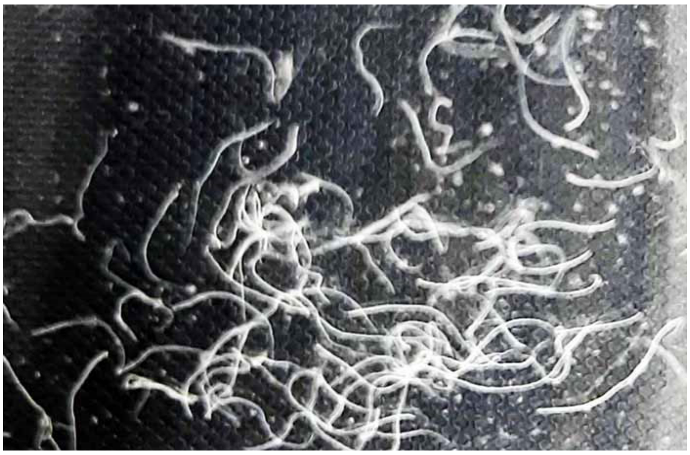
Pathogenesis: Infections by *Trichostrongylus* spp. vary considerably in their impact on their hosts; ranging from subclinical to clinical and even fatal. Pathogenesis depends on the intensity of infection (larval challenge and worm burden), host susceptibility (greatest in young naive animals) and parasite virulence (some species being more pathogenic than others). Parasite developmental stages burrow and feed in the gut mucosa causing traumatic damage and provoking host inflammatory responses. Light to moderate infections often remain subclinical even though various host production parameters may be affected, including impaired growth and weight gain, inferior wool production, reduced milk production and poor reproductive performance. Heavier infections may result in mild-severe gastroenteritis with significant morbidity (especially weaner illthrift) and mortality. Most *Trichostrongylus* spp. infect the small intestines (especially the duodenum and proximal jejunum) where larval and adult worms burrow between villi forming subepithelial tunnels, often congregating in small focal areas. Structural changes include epithelial metaplasia with increased cell turnover, mucous hyperplasia, oedema, catarrhal inflammation and villous atrophy. Functional changes include protein loss into the intestine (leading to hypoalbuminaemia and hypoproteinaemia), reduced levels of brush border enzymes (alkaline phosphatase, dipeptidase), maldigestion and malabsorption, altered levels of gut hormones (secretin), increased gastrointestinal motility, episodic diarrhoea in young animals (black scours, soft dark-coloured faeces producing dags) or chronic diarrhoea in older animals leading to dehydration, inappetence, anorexia and illthrift. Intestinal disease is worsened when tunnels rupture (often synchronously) to release young adults resulting in petechial haemorrhages and the further loss of plasma proteins contributing to mild anaemia. Reduced calcium and phosphorus levels may also result in osteoporosis and osteomalacia. Heavy infections (> 20,000 worms) may cause high mortalities, particularly in undernourished weaners. In sheep, the disease is common in lambs under 5 months of age whereas older animals exposed to > 3,000 worms develop a solid cell-mediated immunity which is premunitive (leading to worm expulsion) and protective (resistance to larval challenge). Immune sheep have increased numbers of basophils, eosinophils and mast cells in the lamina propria and they secrete substances in the intestinal mucus which paralyses larvae. Some *Trichostrongylus* spp. (notably *T. axei*) infect the stomach of their hosts (abomasum in ruminants) where developing stages burrow in the gastric mucosa causing hyperaemia and gastritis. Heavy infections are required to produce disease and studies have shown that challenges with > 40,000 larvae may be fatal in certain sheep breeds. Larval stages cause catarrhal gastritis/abomasitis whereas adult worms cause wart-like mucosal thickenings and gastric erosions covered with tenacious mucus. Affected areas may coalesce to present as a diffuse hypertrophic gastritis, evident macroscopically as circumscribed proliferative areas later devoid of epithelium. Chronic infections in horses may result in pale raised thickenings, occasionally with pedunculated or polypoid growths, projecting into the gastric lumen. Functional changes include increases in abomasal pH, abomasal and serum pepsinogen, and a decrease in available nitrogen with the development of foul-smelling ingesta, mucosal oedema, hypoproteinaemia, sometimes diarrhoea and/or anaemia. Clinical signs may develop rapidly and include reduced appetite, anorexia, progressive weight loss, general loss of body condition, emaciation, weakness and death. Infections by *T. tenuis* may cause severe typhlitis in a range of birds, particularly ground-feeding galliform birds (including domestic and game birds). Various species have been found to cause transient infections in humans, usually being asymptomatic but sometimes involving gastrointestinal problems (abdominal pain, diarrhoea, anorexia, emaciation) and/or generalized systemic problems (anaemia, eosinophilia, headache, fatigue).

Developmental cycle and mode of transmission: Trichostongyles have simple direct monoxenous life-cycles involving faecal-oral transmission between hosts. Female worms lay eggs which are voided with host faeces into the external environment where they embryonate and hatch within several days. Rhabditiform L1 are released which feed on bacteria and then moult to form rhabditiform L2 which also feed on bacteria. After 5-10 days, the larvae moult to form infective filariform L3 which are ensheathed (retain L2 cuticle), non-feeding and relatively resistant to desiccation (can dry out and become active again when rehydrated). The developmental time from egg to L3 depends on prevailing environmental conditions (especially temperature and moisture), varying from 1-3 weeks in temperate conditions (longer in colder conditions). Rainfall and heavy dew help release larvae from dung pellets and newly hatched larvae are often found on the soil underneath vegetation where they are protected. L3 actively migrate both horizontally over the soil surface (dispersal up to 10 cm) as well as vertically up blades of grass during periods of sunlight (contaminating edible pastures). Definitive hosts become infected by ingesting infective L3 with food or water. The L3 exsheath in the gut and migrate into the mucosa becoming partially embedded where they moult to L4 before returning to the lumen, moulting to young adults (L5) and maturing into male and female adult worms. After mating, mature females lay some 10-200 eggs per day and may live for up to 1 year. The prepatent period (time from infection to first egg production) ranges from 18-28 days. *Trichostronglyus* spp. vary in their geographical distribution and seasonal abundance, mostly in association with regional climatic conditions. For example, species found in sheep vary considerably between regions, with *T. colubriformis* being most prevalent in summer rainfall zones, *T. vitrinus* in winter rainfall zones, and *T. rugatus* in lower rainfall zones. *T. axei* is widespread in temperate zones and has a broader host specificity with cross-transmission occurring when mixed grazing practices are used or when stock are introduced to contaminated paddocks. *T. tenuis* in also prevalent in temperate zones and while parasites develop faster in birds (prepatent period of 7-8 days), infections tend to occur seasonally as some ingested L3 exhibit arrested development (hypobiosis) over winter. Several species may opportunistically infect humans when infective L3 are ingested with contaminated vegetables (raw, unwashed, or washed in contaminated water), particularly crops fertilized in fresh animal manure (widely practiced in rural areas of South-East Asia).

Differential diagnosis: Trichostrongylosis may be suspected on the basis of clinical presentation (gastroenteritis, diarrhoea/scours, anorexia, eosinophilia) and pertinent history (notably afflicting weaners during winter and spring), although other aetiological agents may cause similar diseases (e.g. ostertagiasis, fascioliasis, metabolic disorders, etc). Infections are conventionally confirmed by the direct detection of parasites either antemortem (eggs in faeces) or postmortem (worms in gut). Various coprological techniques may be used to microscopically detect trichostrongyle eggs in faecal samples, usually following concentration by sedimentation in water and then floatation in high specific gravity sugar or heavy-metal salt solutions. Several quantitative techniques have been developed whereby aliquots of diluted faeces are examined in volumetric chambers (McMaster or Whitlock slides) and the number of eggs counted is extrapolated to eggs per gram of faeces (epg). Caution is advised when interpreting faecal egg counts for *Trichostrongylus* infections as they do not correlate well with the intensity of infection; not accounting for larval numbers, male worms, immature or spent female worms, immunological suppression of egg production, nor variable fecundity over time and between species. Egg counts also vary depending on the rate of passage and water content of digesta, often being reduced in diarrhoeic animals and increased in animals starved overnight. Nonetheless, faecal egg counts are routinely used as rough guides to the level of infection when deciding whether to treat animals or not. Faecal egg count reduction tests are also used to determine whether resistance is present to anthelmintic drugs or not. Coprological tests, however, cannot differentiate between many strongyle genera because their eggs are relatively similar in size, shape and appearance (although experienced workers can differentiate trichostrongyle eggs from hookworm eggs (the latter are smaller and do not have pointed ends) and even allocate most trichostrongyle eggs to collective genus-groups (including *Trichostrongylus/Ostertagia*, sometimes separating *Haemonchus*). To differentiate genera, recourse is sometimes made to culturing faecal samples (Baermann apparatus or Petri dishes) until L3 emerge which are then harvested and examined microscopically for characteristic morphotypic features (L3 of *Trichostrongylus* are around 650 µm long, ensheathed, with a tapered head, 16 intestinal cells and a nonpointed tail with a short sheath). Unfortunately, coproculture takes 1-2 weeks before results become available and it also requires expertise to identify L3s. Infections may also be diagnosed by detecting adult worms in gut samples collected at post-mortem after sacrificing some sick or unthrifty animals. The abomasum and small intestines are collected intact, ligated, preferably filled with warm physiological saline for several hours to help release worms (sometimes the mucosa is digested in pepsin-hydrochloric acid solutions), the washings sieved and examined microscopically for characteristic worms (adult *Trichostrongylus* spp. lacking cephalic vesicles but both sexes with distinctive excretory notches in oesophageal region). The technique can be quantitated by counting the number of worms in aliquots and extrapolating to estimate total worm counts. Infections by 10,000 worms have been associated with significant production losses in sheep, and infections by 20,000 worms have proven fatal in weaners. Several research laboratories have developed serological tests (especially enzyme immunoassays) to detect specific host antibodies against parasite antigens harvested from larval and adult worms, but several problems have been experienced with sensitivity, specificity and cross-reactivity. Modern molecular biological techniques have been used to differentiate species (eggs, larvae and adults) by the polymerase chain reaction (PCR) amplification of parasite DNA (especially the internal transcribed spacer regions (ITS1 and 2) of nuclear ribosomal DNA).

Treatment and control: A range of anthelmintic drugs have been used to effectively treat *Trichostrongylus* spp. infections, but the emergence of drug resistance has become a common problem. In commercial herds/flocks, faecal egg count reduction tests should be conducted to determine drug efficacy. Various authorities recommend regular (periodic) or strategic (as required) dosing, with cyclic rotation of white (benzimidazoles), clear (levamisoles, tetrahydropyrimidines), macrocyclic lactones (avermectins) and even cocktail (mixed) drenches to combat the development of drug resistance. It has also recently been suggested that some animals be left untreated as ‘refugia’ for susceptible worms as well as allowing for the development of naturally acquired immunity. Anthelmintics act to kill susceptible worms and some are also effective against hypobiotic larvae. Various formulations are either administered orally (drenches), subcutaneously (injected) or even intraruminally (as capsules or boluses that break down to release drugs continuously or in pulses). Careful consideration should be given to regulations and advisory notices concerning drug usage, as some have unpleasant side effects (nausea, bloating, diarrhoea), some have lengthy with-holding periods in production animals, and others are contra-indicated during pregnancy. Infected hosts also respond well to nutrient and protein supplementation during treatment. Regrettably, most anthelmintics have little residual activity, so animals can become re-infected when returned to contaminated pastures - thus giving rise to the conventional practices of ‘drench and move to clean pasture’ and ‘drench at regular intervals’. Studies have shown that the best times to treat sheep is before lambing (to counter the periparturient rise in egg production and minimise pasture contamination) and around weaning (when animals are at their highest risk of disease due to dietary stress, increased grazing and immature immunity) Adult animals generally develop strong protection against challenge infections (concomitant or premunitive immunity rather than sterile immunity as some worms persist within protected hosts). Hosts also exhibit marked variability in their innate genetic resistance to infections, and experimental breeding programs have been successful in selecting resistant livestock, mostly without negatively affecting production parameters. Many environmental factors (especially temperature and moisture) affect the development and survival of eggs, free-living L1 and L2, and ensheathed L3 present in faecal material and on pasture. Nematode control programs should therefore include pasture management practices shown to minimise contamination and reduce the survival/infectivity of free-living stages (rotational grazing of cohorts, mixed grazing with other host species, screening and quarantining introduced livestock, spelling pastures, particularly over dry summers). However, caution is advised when using communal or mixed grazing strategies against *T. axei* infections as this species has a broad host specificity which facilitates cross-transmission between a wide range of herbivores (ruminants and monogastrics). The transmission of infections to humans has been shown to be reduced in regions with proper sewage systems, access to clean water, restricting the use of manure to fertilise vegetable crops, instituting good food hygiene (washing and cooking vegetables) and improving hygiene (washing hands before meals and after contact with animals).

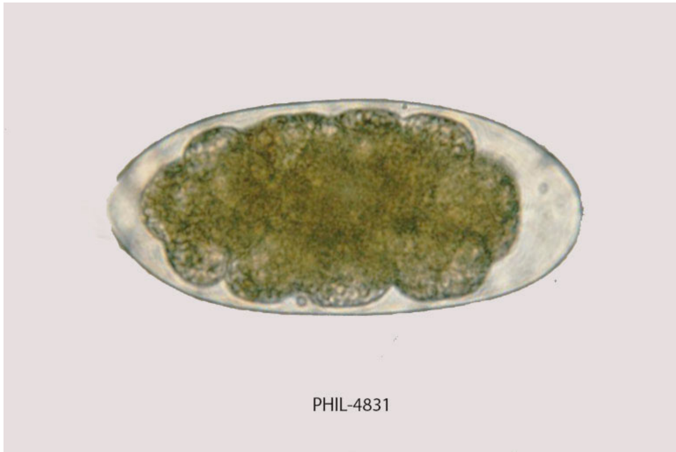

Trichostrongylus
intestines, stomach
(gastroenteritis, illthrift,
diarrhoea (scours),
typhlitis in birds)
Definitive Hosts
(ungulates, rodents,
lagomorphs, birds)
head
adult
female
(~ 8 mm)
adult
male
(~ 6 mm)
male tail
L3
ingested
eggs
excreted
in faeces
external
environment
filariform third-
stage larvae (L3)
(~ 800 µm)
eggs
(~ 100 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 400 µm)



Trichostrongylus adult worms

Trichostrongylus adult worm, head

Trichostrongylus adult worm, male bursa



Trichostrongylus egg

Trichostrongylus third-stage larvae