Teladorsagia
(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. *Teladorsagia* spp. (brown stomach worms) cause diarrhoeal diseases markedly impacting production in sheep 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:	*Teladorsagia* (parasitic in abomasum of ruminants)
Species:	*T. circumcincta* causes scours and illthrift in sheep and goats

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 IH)
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 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 characterize 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 Ostertagiinae (well-developed synlophe, modified bursa)					
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
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
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 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 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 Ostertagiinae was erected for genera with an accessory bursal membrane and other characters include a head region with a small restricted cephalic vesicle, small cervical papillae and prominent transverse striations, and a body with numerous longitudinal cuticular ridges. Some 23 genera have been reported from ruminants, hippopotami, lagomorphs and suids: namely, *Africanostrongylus, Apteragia, Camelostrongylus, Cervicaprastrongylus, Graphidium, Grosspiculagia* (syn. *Ostertagiella*), *Hamulonema, Hyostrongylus* (syn. *Bergheia*), *Longistrongylus* (syn. *Bigalkea, Bigalkenema, Kobusinema*), *Marshallagia, Mazamastrongylus, Orloffia, Ostertagia* (syn. *Capreolagia, Gruhneria, Muflonagia, Ostertagiana, Sjobergia, Skrjabinagia*), *Ostertamia, Paramecistrocirrus, Pseudomarshallagia, Rinadia, Robustostrongylus, Sarwaria, Spiculopteragia* (syn. *Altaevia*), *Spiculopteroides, Teladorsagia* (syn. *Paramecistocirrus*, *Stadelmania*), and *Tunisostertagia.* Some members of the Ostertagiinae have been allocated to 2 groups; one characterised by bursal type 2-1-2 (ray 2 grouped with ray 3, isolation of ray 4, ray 5 grouped with ray 6) including *Graphidium*, *Marshallagia*, *Longistrongylus* and *Ostertagia*; and another characterised by bursal type 2-2-1 (ray 2 grouped with ray 3, ray 4 grouped with ray 5, isolation of ray 6) including *Hyostrongylus*, *Spiculopteragia*, *Teladorsagia* and *Gazellostrongylus*. The genus *Teladorsagia* is further characterised by bursate males with a symmetrical dorsal lobe, a small proconus, spicules with sharply pointed branches, and a genital cone with a Sjoberg organ or short dorsal raylets associated with the accessory membrane. Some 9 species have been described from bovids, camelids and cervids, where they have direct life-cycles with faecal-oral transmission. Several species formerly recorded as *Ostertagia* spp. have been transferred to the genus *Teladorsagia* on the basis of phenotypic and genotypic studies; notably *T. circumcincta*; *T. davtiana* and *T. trifurcata* in sheep (in fact, these 3 species possibly represent a pleomorphic species complex). Worms developing and feeding in the abomasal mucosa may cause disease in weaners and the later emergence of dormant larvae may cause disease in young adults. Infections contribute to significant economic losses in livestock industries through morbidity, mortality and reduced production (meat, milk, fibre). Several species are important pathogens in sheep and goats in all temperate regions, particularly those with high rainfall.

***Teladorsagia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
T. boreoarcticus	Artiodactyla: bovid (muskox, Greenland muskox), cervid (reindeer, barren ground caribou)		Holarctic
T. circumcincta (brown stomach worm) (syn. *Ostertagia, Ostertagiella, Stadelmania, Strongylus, S. vicarius, cervicornis p.p., instabilis, turkestanica*)	Artiodactyla: bovid (cattle, muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, Cyprus mouflon, goat, mountain goat, chamois, Pyrenean chamois, alpine ibex, Iberian ibex, antelope, common tsessebe, common duiker, red forest duiker, bushbuck, Cuvier's gazelle, Cape grysbok), antilocaprid (pronghorn), camelid (camel, llama), cervid (roe deer, red deer, mule deer, southern mule deer, white-tailed deer, black-tailed deer, reindeer, Svalbard reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou, moose); Rodentia: murid (Mongolian gerbil); Primates: hominid (human)	abomasum [weight loss, diarrhoea]	worldwide
T. dactylospicula (syn. *Skrjabinagia*)	Artiodactyla: bovid (cattle)	abomasum	Asia
T. davtiani (syn. *T. grigoriani*) (considered by some to be a morphological variant of *T. circumcincta*)	Artiodactyla: bovid (sheep, bighorn sheep, Dall sheep, goat, mountain goat, chamois, Iberian ibex, Cuvier's gazelle, muskox), cervid (mule deer, roe deer, reindeer)	abomasum [weight loss, diarrhoea]	worldwide
T. kasakhstanica (syn. *Ostertagia*)	Artiodactyla: bovid (American bison)		North America
T. kegeni	Artiodactyla: bovid (sheep)		Eurasia
T. pinnata (syn. *Ostertagia*)	Artiodactyla: bovid (sheep, mouflon, chamois, alpine ibex, Iberian ibex), cervid (roe deer)		Europe
T. trifurcata (syn. *Ostertagia, Stadelmania*) (considered to be a morphological variant of *T. circumcincta*)	Artiodactyla: bovid (cattle, water buffalo, muskox, Greenland muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, chamois, Pyrenean chamois, goat, mountain goat, alpine ibex, Iberian ibex), antilocaprid (pronghorn), cervid (roe deer, red deer, fallow deer, mule deer, white-tailed deer, reindeer, Svalbard reindeer, boreal woodland caribou), camelid (llama)	abomasum [weight loss, diarrhoea]	worldwide
T. vietnamica (syn. *Spiculopteragia, Spiculopteroides, Mazamastrongylus*)	Artiodactyla: cervid (Indian muntjac)		Asia
Re-assigned species			
T. hamata (syn. *Ostertagia, Spiculopteragia, Apteragia, Teladorsagia*) (now *Hamulonema*)	Artiodactyla: bovid (springbok, bontebok, Speke's gazelle, gemsbok, grey rhebok)		Africa
T. peruvianus (syn. *Spiculoperagia*) (now *Mazamastrongylus*)	Artiodactyla: camelid (alpaca, vicugna, guanaco)		South America
T. pursglovei (now *Mazamastrongylus*)	Artiodactyla: cervid (white-tailed deer)		North America

Parasite morphology: *Teladorsagia* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 consecutive stages termed L1 to L4); and adult worms. Newly laid eggs have a symmetrical ellipsoidal shape and range in size from 60-100 x 40-50 µm. They are thin-walled and contain a morula (8-16 cell stage) that almost fills the egg. First-stage larvae (L1) are 300-500 µm long and have a rounded head, a bulbed (rhabditiform) oesophagus, and a conical pointed tail. They moult to form L2 which are also rhabditiform but are slightly bigger measuring up to 750 µm in length. These larvae moult to form L3 which retain the L2 cuticle as a close-fitting protective sheath. Infective L3 measure from 797-910 µm in length and have a round head, tubular (strongyliform) oesophagus, intestines comprising 16 cells, and a sharply-tapering tail with a short non-filamentous tail sheath extension (30-60 µm). Following ingestion, L3 exsheath and moult in gastric glands to form L4 around 1 mm long. Eventually, L4 emerge onto the mucosal surface and moult to form young adult worms (sometimes designated L5) which mature and mate. Adults are elongate slender worms 10-15 mm in length and usually appearing brown to red in colour. They have a small cephalic vesicle with a tiny buccal cavity lacking teeth (neodont formation absent). Worms are bound by well-developed cuticular synlophes whose anterior regions have transverse striations while the rest of the body have numerous longitudinal ridges. Adults lack an excretory notch (present in the genus *Trichostrongylus*) but they have 2 small cervical papillae projecting above the body surface (smaller and located more posteriorly than in the genus *Haemonchus*). They have a strongyliform oesophagus leading to elongate intestines ending in a subterminal anus/cloaca. Adult worms are sexually dimorphic, with females being larger than males. Mature males have a large copulatory bursa with 2 large lateral lobes and a small symmetrical dorsal lobe (cf. asymmetrical in *Haemonchus*). The lateral lobes have 5 lateral rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 configuration (ventral rays together, anterolateral and mediolateral rays close together, and posterolateral rays separate). The genital cone has a small proconus (ventral swelling) and a small accessory bursal membrane. Detailed studies have also shown that male worms of several species may exhibit different morphological types ('morphs') whereby the genital cone may simply be supported by 2 divergent rays (e.g. *T. circumcincta*) or modified to form Sjoberg's organ resembling a pair of posterior sessile papillae (e.g. *T. davtiani, T. trifurcata*). Males also possess a gubernaculum with a telamon and 2 spicules which vary in shape (long and thin or short and broad) but whose posterior ends are split into 2-3 pointed processes (crab-claw like). Mature females are didelphic with 2 ovaries connected to uteri opening into a posterior vulva covered by medium-sized flap (unlike the large and prominent vulva flap in *Haemonchus*). Female tails have a small number of annular cuticular bands at the tip but they lack a terminal spine.

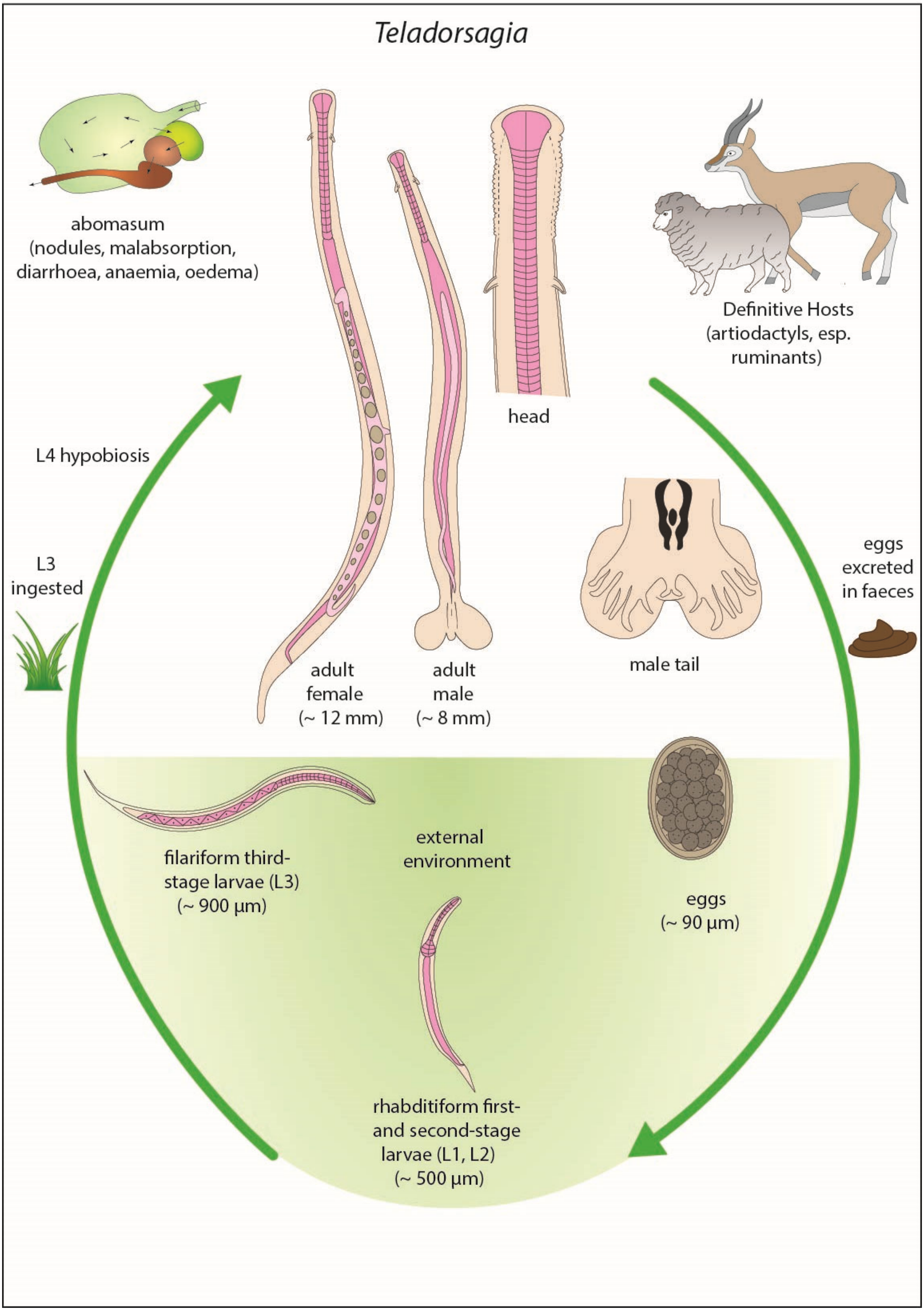
Site of infection: Adult worms occur on the mucosal surface of the abomasum of their ruminant hosts, while developing larvae infect the gastric pits and glands. Pastures become contaminated with worm eggs which release free-living larvae that eventually become infective for grazing animals.

Pathogenesis: Infections by *Teladorsagia* spp. are a significant cause of diarrhoea and ill-thrift in sheep and goats around the world, particularly in cool temperate regions. Light-moderate infections may be symptomatic but still cause subclinical production losses, while heavier infections (> 10,000 worms) may cause severe disease in young susceptible animals (due to their immunological immaturity). While adult worms live on the surface of the abomasum and feed on host blood, most damage is caused by earlier larval stages penetrating, developing and re-emerging from the mucosa resulting in extensive structural and functional changes. L3 invade the gastric pits and glands of the abomasum where they moult and develop to L4 which cause small space-occupying lesions evident as white raised umbilicated nodules 1–2 mm in diameter, each nodule having a central opening. Sometimes the nodules become confluent and covered with tenacious mucus. The abomasal mucosa becomes inflamed and hyperaemic (diffuse hyperplastic abomasitis), sometimes with small abscesses or scar tissue in the gastric pits (rarely imparting a leathery cobblestone appearance). The larvae cause pressure necrosis in the glandular epithelium resulting in hyperplasia and metaplasia with rapid turnover of mucosal cells. There is a marked loss of zymogen (Chief) cells (which produce pepsinogen) and parietal cells (which produce hydrochloric acid) and they are replaced by rapidly-dividing undifferentiated mucus neck cells. The reduction in acid production causes the abomasal pH to rise (from 2 to 7) so pepsinogen is not activated to pepsin and food digestion is impaired. The integrity of the mucosal lining is also compromised as cells in affected glands lose their tight intercellular junctions resulting in the leakage of fluids and proteins into tissues, the circulation and the gut lumen. Such leakage causes local oedema in the abomasum, sometimes extending into the small intestine, as well as generalized swellings such as submandibular oedema (bottle jaw), anasarca and ascites (particularly in Angora goats). Collectively, these changes produce a protein-losing gastroenteropathy (PLGE) with maldigestion and malabsorption leading to an intermittent diarrhoea with hindquarter staining ('dagginess' in sheep and 'dirty-tail' in cattle). The increased abomasal pH stimulates the production of gastrin resulting in hypergastrinaemia which exacerbates inappetence and weight loss. Changes in the abomasal environment diminish its bacteriostatic activity leading to bacterial overgrowths and diarrhoea. Adult worms feed on host blood through the mucosa, often causing small petechial haemorrhages with blood loss and progressive anaemia. The combination of diarrhoea, malabsorption, hypoproteinaemia and anaemia in small ruminants results in reduced growth rates, inappetence, anorexia, loss of body condition, emaciation, and even death. Infections contribute to significant production losses (meat, milk, fibre) due host morbidity, mortality and even reduced reproductive performance. Clinical infections generally cause an acute or subacute disease syndrome (termed type I disease) when larvae undergo normal uninterrupted development in the gastric glands emerging 2-3 weeks later. This disease frequently occurs in weaners grazing pastures for the first time and is characterised by marked weight loss with intermittent diarrhoea. However, infections by a few species may sometimes cause a more chronic form of disease (similar to type II ostertagiasis) when larvae undergo short periods of arrested or protracted development in gastric glands emerging several months later (some consider this to be a prolonged histotrophic stage rather than true hypobiosis). This type II syndrome occurs sporadically in young adult animals in temperate and subtropical regions with winter rainfall, and is typified as progressive loss of condition and emaciation. Adult animals exposed to low dose infections do eventually acquire strong protective immunity, but at a slower rate than that found for other nematodes.

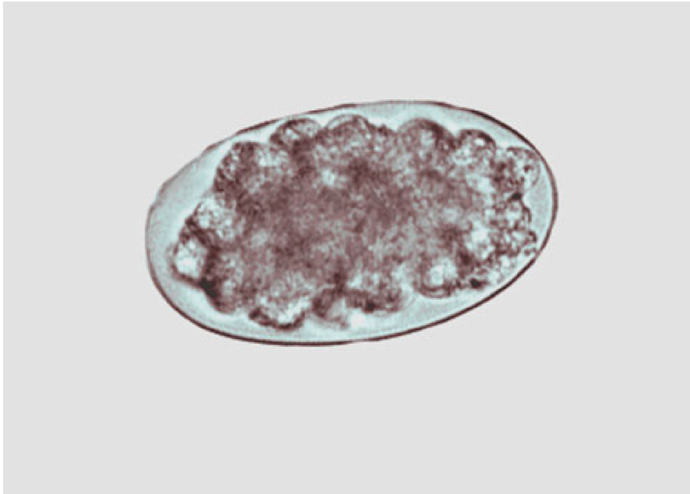
Developmental cycle and mode of transmission: *Teladorsagia* spp. have direct monoxenous life-cycles with horizontal transmission occurring between individuals by the faecal contamination of pastures by eggs and the oral ingestion of infective larvae by grazing animals. Females produce 10-200 eggs per day which are passed in host faeces. The eggs embryonate and hatch releasing rhabditiform larvae (L1) which are free-living and feed on bacteria in faecal material. The larvae moult to form rhabditiform L2 which are also free-living and feed on bacteria. These larvae moult to form strongyliform L3 which retain the L2 cuticle as an encapsulating protective sheath and do not feed. Eggs and larvae may survive for long periods in faecal material, particularly in regions with cooler climates, but they are susceptible to desiccation. L3 may develop from eggs in 10-14 days, but may take longer in suboptimal conditions. When moisture is available (following rainfall or morning dew), mature L3 exhibit horizontal migration (dispersing out of faecal deposits) and vertical migration (ascending herbage into water droplets). Infective L3 are ingested on herbage by grazing hosts and they exsheath in the stomach and invade the gastric glands in the abomasum. Here they form nodules and moult to L4 before emerging onto the mucosal surface some 9-11 days later and moulting to young adults which feed and mature. The prepatent period (time from infection to first egg excretion) ranges from 18-21 days, and adult worms live for several months before dying or being expelled by host immune responses. In infections by certain species, some larvae may still be found in the mucosa 8-12 weeks after infection, apparently undergoing arrested development (hypobiosis) although some authorities consider them to be prolonged histotrophic stages. Their delayed development occurs over seasons when external environmental conditions are not conducive for parasite development and survival on pastures (generally over winter in temperate regions). The exact mechanisms involved are not known, but appear to include host reproductive physiology (pregnancy, parturition and lactation), metabolism (level of nutrition), immunity (innate and acquired responses) as well as external environmental conditions (day length, temperature and rainfall patterns). Pregnant animals often exhibit a sharp periparturient rise in worm egg production which leads to heavy larval contamination of pastures around the time their weaning offspring begin grazing.

Differential diagnosis: Infections may be suggested by clinical symptomatology with appropriate history, but other gastroenteric pathogens may cloud diagnoses. Blood biochemistry may show reduced albumin and elevated pepsinogen levels consistent with abomasal damage and fluid leakage. While there is a strong correlation between the degree of abomasal pathology and the amount of pepsinogen leaking into the circulation, levels often peak early in the course of infection when only larvae are present. Coprological tests may be used to detect patent infections by the microscopic detection of worm eggs in faecal samples, usually following concentration by sedimentation in water and/or floatation in high specific gravity sugar or salt solutions. Some techniques may be quantitated by counting the number of worm eggs in aliquots of diluted faeces in volumetric McMaster or Whitlock chambers and then calculating the number of eggs per gram of faeces (epg). However, faecal eggs counts do not correlate well with worm burdens as they do not take into account developing larvae, male worms, immature or senescent females or those in which egg production has been reduced by immunological mechanisms. Unfortunately, egg morphometrics cannot be used to differentially diagnose infections as *Teladorsagia* eggs are very similar to those of other trichostrongyle nematodes (particularly *Trichostrongylus*, *Haemonchus* and *Ostertagia*). Recourse is sometimes made to coprocultures whereby faecal material is incubated in funnels or petri dishes for several days to harvest L3 stages which can then be identified by their morphological characteristics (squared head, strongyliform oesophagus, intestines comprising 16 cells, and a tapering tail with a short sheath). Infections may also be diagnosed by the collection and identification of adult worms from gut samples collected at post-mortem from dead or sacrificed animals. Total worm counts may also be conducted by ligating the abomasum and intestines, perfusing them with saline and then counting worm numbers in mucosal washes (and sometimes mucosal digests (warm pepsin-hydrochloric acid) to free larval stages). Several serological tests have been developed to detect specific host antibodies against worm antigens, but problems have been encountered with test sensitivity and specificity, including cross-reactions with other nematodes. Molecular biological techniques have also been used to characterize adult worms, larvae and even eggs of different *Teladorsagia* spp. by the polymerase chain reaction (PCR) amplification of specific gene sequences from nuclear DNA (large and small subunit ribosomal DNA and internal transcribed spacers I and II).

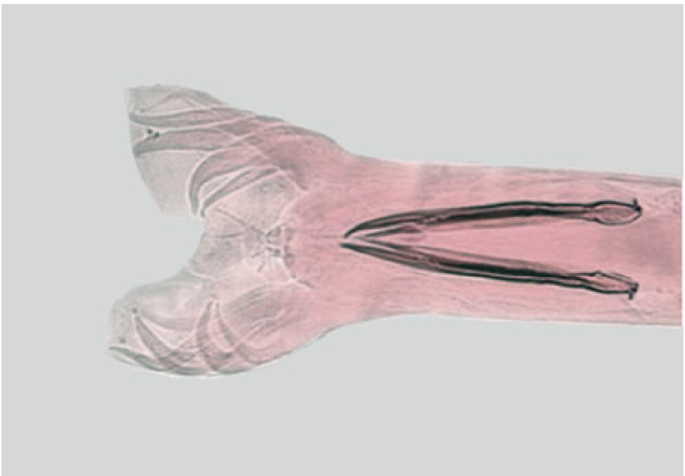
Treatment and control: A broad range of anthelmintic drugs have been used to treat clinical infections in livestock, with most drugs being effective against adult worms, including benzimidazole-methylcarbamates (albendazole, fenbendazole, oxfendazole, parbendazole), benzimidazole-thiazolyl (thiabendazole), probenzimidazoles (febantel, netobimin, thiophanate), imidazothiazole (levamisole), tetrahydropyrimidine (morantel) and macrocyclic lactones (avermectins such as doramectin, eprinomectin, ivermectin, and milbemycins such as milbemycin and moxidectin). However, only some of these drugs were effective against hypobiotic larvae, notably the benzimidazoles (albendazole, fenbendazole, oxfendazole) and macrocyclic lactones (ivermectin, milbemycin). Repeated treatments are required as anthelmintics do not have any persistent residual activity and animals quickly become re-infected when returned to contaminated pastures. Pregnant animals should be treated to avoid a periparturient rise in egg production, and young susceptible animals should be treated around weaning when they first begin to graze, and then re-treated at the end of the season when larval hypobiosis or prolonged development may have occurred (usually late winter or early spring). Adult animals are usually not treated as they gradually acquire strong protective immune responses and show an age-resistance to clinical infection. Regrettably, many countries have now reported the emergence of widespread drug resistance to benzimidazoles and macrocyclic lactones. Authorities recommend that drug resistance testing (faecal egg count reduction tests) be conducted on representative animals to select the most effective drug for mass treatment, that drugs be administered correctly (avoiding under-dosing) and that they are used strategically (as required) or systematically (in cyclic rotation) to avoid the development of drug resistance. Recent work has also shown that leaving some animals untreated provides 'refugia' for drug-susceptible worms and facilitates low-dose infections for the acquisition of natural protective immunity. Genetic studies have also shown that individual animals vary in their innate resistance to infection, and experimental breeding programmes have successfully selected some resistant lines of animals without compromising production parameters. However, the most effective control programmes at the farm level include stock and pasture management practices shown to reduce environmental contamination by worm eggs and decrease the development and survival of larvae on pastures. Treated animals should be immediately moved to clean areas (spelled or recently ungrazed pastures), new livestock should be treated in quarantine, different cohorts should be grazed sequentially or in rotation (but young susceptible animals should be kept separate from adults), stocking rates should be kept low, different host species may be grazed together (mixed grazing) or alternately (e.g. sheep one year, cattle the next), and pastures should be spelled periodically, particularly over adverse seasons (e.g. hot summers).


Teladorsagia
abomasum
(nodules, malabsorption,
diarrhoea, anaemia, oedema)
head
Definitive Hosts
(artiodactyls, esp.
ruminants)
L4 hypobiosis
L3
ingested
eggs
excreted
in faeces
adult
female
(~ 12 mm)
adult
male
(~ 8 mm)
male tail
filariform third-
stage larvae (L3)
(~ 900 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 500 µm)

Teladorsagia adult worms



Teladorsagia worm egg



Teladorsagia adult worm, male bursa