Ostertagia
(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. *Ostertagia* spp. (brown stomach worms) cause diarrhoeal diseases (type I and II ostertagiasis) markedly impacting production in cattle 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:	*Ostertagia* (parasitic in abomasum of ruminants)
Species:	various species cause enteric diseases in ruminants (type 1 and type 2 ostertagiasis)

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 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)					
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 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 *Ostertagia* is further characterised by bursate males with a symmetrical dorsal lobe, an enlarged proconus, spicules with short branches and barbed tips, and a genital cone with short dorsal raylets associated with a simple accessory membrane. Over 25 species have been described from bovids and holarctic cervids, where they have direct life-cycles with faecal-oral transmission. Worms developing and feeding in the abomasal mucosa may cause disease in weaners and the synchronous emergence of hypobiotic larvae may later cause disease in yearlings. Infections contribute to significant economic losses in livestock industries through morbidity, mortality and reduced production (meat, milk, fibre). Several species are important pathogens in cattle in most temperate, and some subtropical, regions with winter rainfall.

***Ostertagia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
O. angusdunni	Artiodactyla: bovid (giant eland)		Africa
O. arctica (syn. *Sjobergia, Ostertagiella, Skrjabinagia*)	Artiodactyla: bovid (muskox, mouflon), cervid (roe deer, red deer, fallow deer, reindeer, Svalbard reindeer, Siberian reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou)	abomasum	North America
O. boevi	Artiodactyla: bovid (water buffalo)		
O. callis	Didelphimorphia: didelphid (big-eared opossum)		South America
O. cervi	Artiodactyla: bovid (red deer)		Europe

O. delicata (syn *Delicata cameroni*)	Cingulata: chlamyphorid (southern naked-tailed armadillo)		South America
O. dikmansi (syn. *Skrjaninagia*)	Artiodactyla: cervid (white-tailed deer)	abomasum	North America
O. drozdzi	Artiodactyla: bovid (goat, sheep), cervid (red deer, fallow deer, Altai wapiti)		Europe
O. gruehneri (syn. *Gruhneria*))	Artiodactyla: bovid (cattle, muskox, sheep, mouflon), cervid (roe deer, reindeer, Svalbard reindeer, Siberian tundra reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou)	abomasum	Eurasia
O. harrisi	Artiodactyla: bovid (goat, red forest duiker, grey duiker, Cuvier's gazelle, dama gazelle, nyala)		Africa
O. houdemeri	Artiodactyla: cervid (unspecified deer species)		Indo-China
O. kolchida (syn. *O. lasensis, popovi, rubricervi, Mouflongia podjapolskyi, Grosspiculagia, Sjobergia, Skrjabinagia*) [possibly minor morphotype of *O. leptospicularis*]	Artiodactyla: bovid (cattle, European bison, sheep, mouflon, goat, chamois), cervid (roe deer, red deer, Spanish red deer, sika deer, fallow deer, mule deer, Tule elk, Altai wapiti, reindeer, boreal woodland caribou, moose)	abomasum	North America, Eurasia, New Zealand
O. leptospicularis (syn. *O. capreolagi, capreoli, crimensis, paracapreoli, taurica, Capreolagia antipinni, paraskrjabini, skrjabini, Grosspiculagia*)	Artiodactyla: bovid (cattle, European bison, sheep, argali, mouflon, goat, chamois, alpine ibex, blackbuck), camelid (camel), cervid (red deer, Spanish red deer, mule deer, fallow deer, sika deer, roe deer, Siberian roe deer, Tule elk, Altai wapiti, reindeer, boreal woodland caribou, moose)	abomasum [diarrhoea]	worldwide, esp. Europe, New Zealand
O. lyrata (syn. *O. occidentalis, Camelostrongylus lyratus, Grosspiculagia, Sjobergia, Skrjabinagia, Marshallagia*) (now considered to be a morphological variant of *O. ostertagi*)	Artiodactyla: bovid (cattle, American bison, European bison, muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, chamois, goat, mountain goat, alpine ibex, Iberian ibex), cervid (roe deer, red deer, fallow deer, white-tailed deer)	abomasum [diarrhoea]	worldwide, esp. temperate zones
O. lyrataeformis	Artiodactyla: cervid (roe deer, Siberian roe deer, moose)		Eurasia
O. mossi	Artiodactyla: bovid (sheep), cervid (white-tailed deer, fallow deer, red deer, reindeer)	abomasum	Holarctic
O. muraschkinzevi sp. inq. (syn. *O. nemorhaedi, Grosspiculagia, Camelostrongylus, Longistrongylus*)	Artiodactyla: bovid (Himalayan goral)		Eurasia
O. nianqinqtanggulaensis (syn. *Grosspiculagia, Camelostrongylus*, possibly *Sarwaria*)	Artiodactyla: bovid (sheep, goat)		Eurasia
O. oreamni	Artiodactyla: bovid (mountain goat), cervid (reindeer)		Holarctic
O. ostertagi (brown stomach worm, medium stomach worm) (syn. *O. caprae, Strongylus*)	Artiodactyla: bovid (cattle, Bali cattle, American bison, European bison, sheep, bighorn sheep, Dall sheep, argali, goat, mouflon, Cyprus mouflon, mountain goat, chamois, alpine ibex, Iberian ibex, Cuvier's gazelle, rhim gazelle, kudu, southern reedbuck), antilocaprid (pronghorn), camelid (llama), cervid (roe deer, red deer, Spanish red deer, mule deer, fallow deer, white-tailed deer, sika deer, reindeer, moose); Perissodactyla: equid (horse); Primates: hominid (human)	abomasum/stomach [diarrhoea, illthrift, type I and II diseases]	worldwide, esp. temperate zones
O. oxidentalis	Artiodactyla: bovid (goat)		Eurasia
O. paleobisonica (syn. *Skrjabinagia*)	Artiodactyla: bovid (frozen prehistoric bison)		Russia

O. ryjikovi	Artiodactyla: bovid (goat, sheep), cervid (fallow deer)		Europe
O. spiculoptera	Artiodactyla: cervid (red deer)		Europe
O. triquetra	Artiodactyla: bovid (grey rhebok)		Africa
O. turkestanica	Artiodactyla: bovid (sheep)		Middle-East
Re-assigned species			
O. aegagri (now *Grosspiculagia*)	Artiodactyla: bovid (sheep, Bezoar goat)		Europe
O. argunica (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Europe
O. asymmetrica (syn. *quadrispiculata*) (now *Spiculopteragia*)	Artiodactyla: cervid (fallow deer)		Europe
O. belockani (now *Marshallagia*)	Artiodactyla: bovid (wild goat)		Russia
O. bisonis (syn. *O. orloffi, bellae, kazakhstanica*, *Camelostrongylus*) (now *Orloffia*)	Artiodactyla: bovid (cattle, American bison, sheep. Barbary sheep), antilocaprid (pronghorn), cervid (mule deer, moose)	abomasum	North America
O. bubalis (now *Sarwaria*)	Artiodactyla: bovid (cattle)		South America
O. bullosa (now *Pseudostertagia*)	Artiodactyla: antilocaprid (pronghorn), cervid (mule deer), bovid (sheep, bighorn sheep)	abomasum	North America
O. butschnevi (syn. *Skrjabinagia*, *Marshallagia*) (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Eurasia
O. dahurica (syn. *O. hsiungi, Orloffia buriatica*) (now *Orloffia*)	Artiodactyla: bovid (goat, sheep, cattle)	abomasum	Asia
O. erschovi (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Europe
O. elongata (now *Pseudomarshallagia*)	Artiodactyla: bovid (sheep)		Africa
O. gansuensis (now *Grosspiculagia*)	Artiodactyla: bovid (sheep)		Asia
O. kenyensis (now *Hamulonema*)	Artiodactyla: bovid (Damara dik-dik, Grant's gazelle)		Africa
O. lanceata (now *Grosspiculagia*)	Artiodactyla: bovid (bharal)		Asia
O. marshalli (syn. *O. brigantiaca*, *O. tricuspis*) (now *Marshallagia*)	Artiodactyla: bovid (mountain goat, sheep, bighorn sheep, chamois, Pyrenean chamois)	abomasum, duodenum	Europe, North America
O. mentulata (now *Camelostrongylus*)	Artiodactyla: camelid (dromedary), bovid (rhim gazelle)		Middle-East, Africa
O. mongolica (now *Marshallagia*)	Artiodactyla: bovid (goat, sheep, antelope)		Eurasia
O. ningshaanensis (now *Grosspiculagia*)	Artiodactyla: bovid (takin)		Asia
O. odocoilei (now *Mazamastrongylus*)	Artiodactyla: cervid (white-tailed deer)		North America
O. okapiae (now *Bergheia*)	Artiodactyla: giraffid (okapi)		Eurasia
O. ransomi (now *Delicata*)	Cingulata: chlamyphorid (southern naked-tailed armadillo)		South America
O. sogdiana (now *Marshallagia*)	Artiodactyla: bovid (goat)		Russia
O. trifida (now *Marshallagia*)	Artiodactyla: bovid (sheep, argali, goat, goitered gazelle, steppe saiga), camelid (dromedary)		Asia

Several other *Ostertagia* spp. described in ruminants (*O. bakuriani, O. murmani, O. petrovi, O. tatiani, O. tundra,* and *O. volgaensis*) are considered *species inquirenda* as their descriptions appear to be based on teratologically changed specimens (esp. with respect to spicule and bursa morphology). Several species prevalent in sheep have also been transferred to the genus *Teladorsagia;* notably *T. circumcincta*; *T. davtiana* and *T. trifurcata* (indeed, these 3 species possibly represent a pleomorphic species complex).

Parasite morphology: *Ostertagia* spp. form 3 different stages in their developmental cycles: eggs; larvae (moulting through 4 consecutive stages termed L1 to L4); and adult worms (males and females). Freshly laid eggs have a symmetrical ellipsoidal shape and range in size from 60-100 x 38-50 µm. They are thin-walled and contain a morula (8-16 cell stage) that almost fills the egg. First-stage larvae (L1) are elongate measuring from 300-500 µm in length and have rounded heads and conical pointed tails. L1 have a small buccal capsule and rhabditiform (bulbed) oesophagus used to feed on free-living bacteria. They moult to form L2 which are also free-living rhabditiform larvae but are longer (up to 750 µm). In turn, they moult to form infective L3 which are ensheathed (retain the L2 cuticle) and are thus non-feeding stages. L3 measure from 850-928 µm in length and have a squared head, strongyliform (flask-shaped) oesophagus, intestines comprising 16 cells, the gut ending in a single terminal cell, and a smooth sharply-tapering tail with a short tail sheath extension (45-83 µm) of which the last 10% may be filamentous. Once ingested, L3 exsheath and invade gastric glands where they moult to form L4 almost 1 mm long (some of which may exhibit developmental arrest). Eventually, they re-emerge to the gut lumen and moult to form young adult worms (sometimes designated L5) which mature and mate. Adults are long slender worms ranging in length from 6-15 mm and are 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*) and they have 2 small cervical papillae projecting above the body surface (but 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 (8-15 x 0.14 mm compared to 6-9 x 0.12 mm). Mature females are didelphic with 2 ovaries connected to uteri opening into posterior vulva often covered by small skirt-like 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. Mature males have a large copulatory bursa with 2 large lateral lobes and a 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 2-1-2 configuration (ventral rays together, anterolateral ray separate, mediolateral and posterolateral rays together). The bursa has an enlarged proconus, and the genital cone has 2 lobes with short dorsal raylets associated with a simple accessory membrane. Males also possess a gubernaculum and have 2 large well-sclerotized spicules usually curved with short branches and barbed tips. Early studies considered spicule morphology to be distinctive for individual *Ostertagia* spp. (e.g. stout and rod-like with expanded tips in *O. ostertagi*, robust and rectangular in *O. lyrata*, or stout and branched near the middle in *O. trifurcata*), but recent studies have indicated that different morphological types ('morphs') may occur within several *Ostertagia* spp.

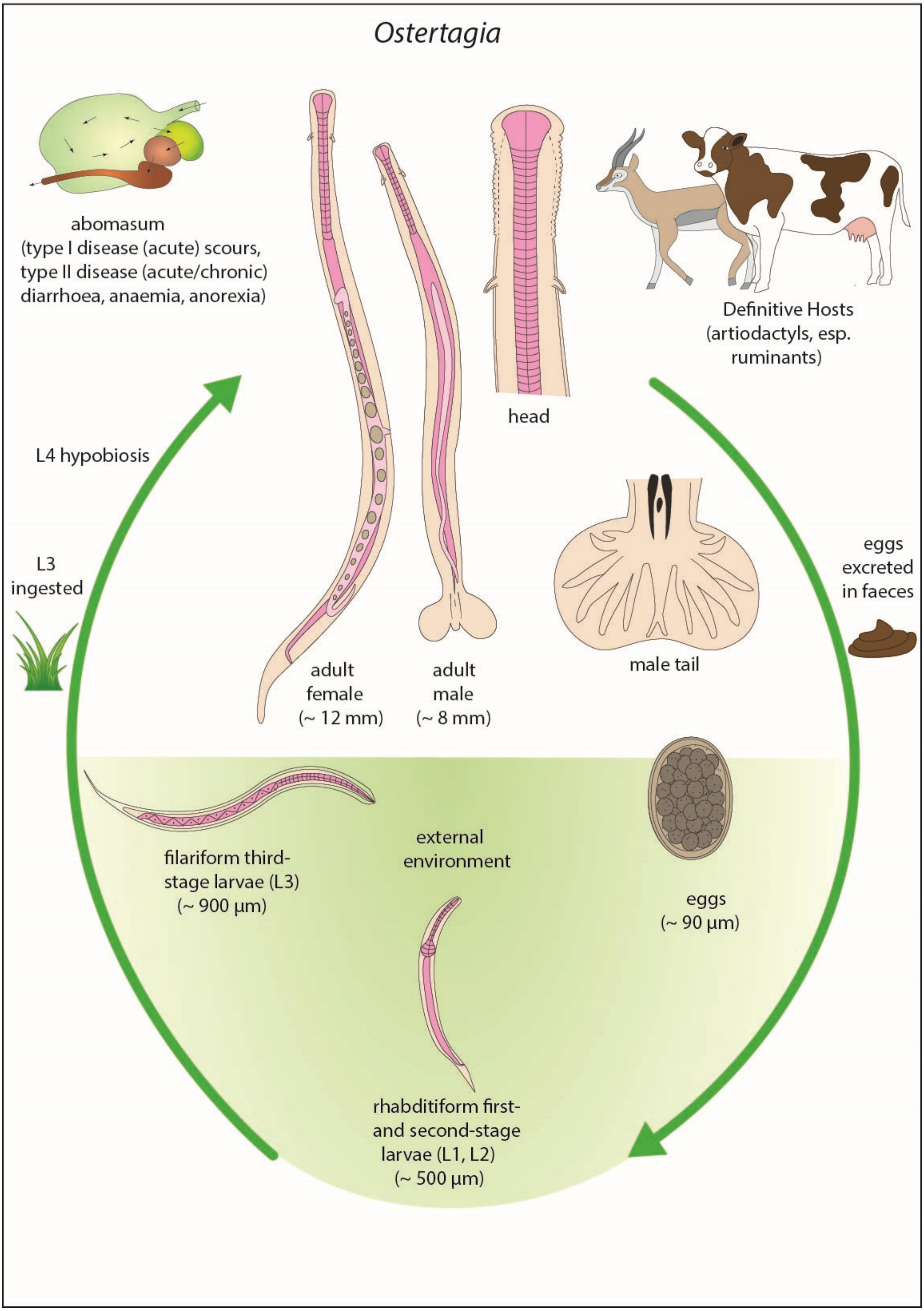
Site of infection: Infective larvae (L3) invade the gastric pits and glands of their ungulate hosts, mainly in the fundus and pylorus of the abomasum, where they moult to L4 before re-emerging onto the mucosal surface to moult and mature into adult worms. Pastures become contaminated with larvae that hatch from worm eggs voided with host faeces.

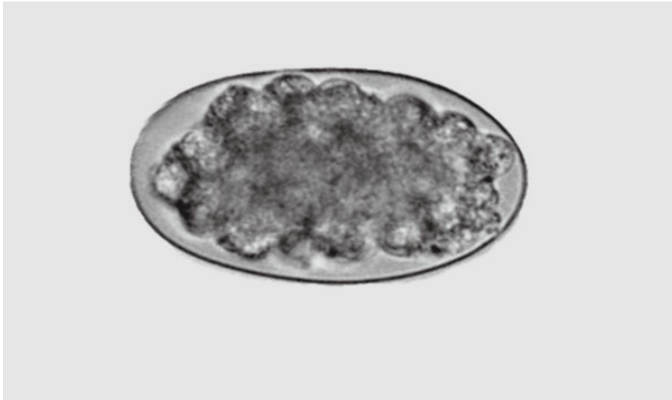
Pathogenesis: Infections by *Ostertagia* spp. may be subclinical but are frequently associated with clinical disease in susceptible grazing animals. While adult worms live on the surface of the abomasum and feed on host blood, most damage is caused by earlier larval stages penetrating, developing and 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. Most nodules occur in the fundic region, but they may extend over the whole abomasal mucosa. They are usually found as discrete isolated lesions, but tend to coalesce in heavy infections giving the mucosa a cobblestone appearance. The larvae cause pressure necrosis in the glandular epithelium resulting in hyperplasia (initially focal but becoming more generalized over time) 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 ensuing maldigestion and rapid transit of poorly processed digesta manifest as watery diarrhoea with loss of body condition. 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 oedema with ascites (fluid accumulation in the abdomen) and bottlejaw (submandibular oedema). Collectively, these changes produce a protein-losing gastroenteropathy (PLGE) with malabsorption and watery diarrhoea presenting as scours (with 'dagginess' in sheep and 'dirty-tail' in cattle). The increased abomasal pH stimulates gastrin production, 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 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 to host morbidity, mortality and even reduced reproductive performance. Infections may cause 2 types of disease: most producing type I ostertagiasis (an acute disease occurring several weeks after infection); and some causing type II ostertagiasis in cattle (acute or chronic disease occurring months after infection). Type I disease occurs when larvae undergo normal uninterrupted development in the gastric glands and emerge approximately 18 days after infection. It often occurs in weaners grazing pastures for the first time and is characterised by persistent scours (profuse watery green-coloured diarrhoea) with soiled hindquarters, dull rough coats, bottle jaw and anaemia. It usually occurs simultaneously in many animals (reflecting their common exposure) and is associated with high morbidity but low mortality. Type II disease occurs mostly in cattle when L4 undergo prolonged arrested development (hypobiosis) in gastric glands, eventually emerging (often synchronously) several months later in yearlings. Disease may be acute (profuse diarrhoea, rapid loss of condition, dehydration and often death) or more chronic (progression of signs over several weeks, with intermittent diarrhoea, excessive thirst, anaemia, anorexia, weight loss). It generally occurs only in a few animals within a herd at once (reflecting the irregular development of larvae), and is associated with lower morbidity but higher mortality. Type II disease occurs more frequently in beef cattle than in dairy cattle, and it varies in its seasonal occurrence (late winter or spring in cool temperate regions, spring and early summer in warm temperate regions, and autumn in regions with hot dry summers). Both types of disease occur mainly in young animals (weaners and yearlings) due not only to their immunological immaturity but also apparently to active impairment or immunosuppression of particular cellular and humoral responses. Adult animals exposed to low dose infections do eventually acquire strong protective immunity, but usually at a slower rate than that found for other nematodes. There is also some evidence that certain stressors may precipitate disease; particularly parturition, lactation, stock translocations, nutritional changes (both decreased and increased levels) and sudden bad weather.

Developmental cycle and mode of transmission: *Ostertagia* spp. have direct monoxenous life-cycles involving faecal-oral transmission. Gravid females produce 50-200 eggs per day which are passed in host faeces to contaminate the external environment. Eggs embryonate and hatch releasing free-living rhabditiform larvae (L1) which feed on bacteria before moulting. The resultant L2 are also free-living rhabditiform stages that feed before moulting, but in this case, the L3 retain the L2 cuticle as an encapsulating protective sheath. L3 do not feed and have a small closed buccal capsule and a strongyliform oesophagus. Eggs and larvae may survive for long periods in faecal material, but are susceptible to desiccation and temperature extremes. Under warm and moist environmental conditions, L3 may develop in as little as 5 days, but typically take longer under suboptimal conditions (usually 10-14 days). They also exhibit horizontal migration (dispersing out of faecal deposits) and vertical migration (ascending herbage into dew droplets when sunlight levels are low). Infective L3 ingested by grazing hosts exsheath in the stomach and invade the gastric glands in the abomasum where they undergo histotrophic development moulting to L4 and subsequently to young adults (sometimes designated L5) after 9-11 days. Young worms emerge from the gastric glands around 18 days after infection and they feed and complete their development to sexually-mature adults on the mucosal surface. The prepatent period (time from infection to first egg excretion) ranges from 18-28 days. The course of infection by certain *Ostertagia* spp. (mostly in cattle) may be greatly prolonged when developing larvae inhibit or arrest their development for several months, usually as early L4 inside gastric glands. This process is known as hypobiosis and usually occurs over seasons when external environmental conditions are not conducive for parasite development and survival on pastures (over winter or summer in temperate and subtropical regions depending on rainfall patterns). The exact mechanisms governing larval hypobiosis are not known, but may involve host physiological changes in response to seasonal reproduction, day length, climatic variation, level of nutrition, abomasal crowding and developing host immunity. 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. Hypobiosis is by no means a universal feature as it does not occur in regions with more frequent rainfall.

Differential diagnosis: Infections may be strongly indicated on the basis of clinical signs (scours, oedema, anaemia, poor development) and history (appropriate host cohorts, region, season and grazing history), but other aetiological agents may confound diagnosis (notably other gastrointestinal nematodes). Several clinical parameters may provide indirect evidence of infection, including haematology (for progressive anaemia) and blood biochemistry (for hypoalbuminaemia and elevated plasma pepsinogen). There is a strong correlation between the degree of abomasal pathology and the amount of pepsinogen leaking into the circulation, peaking during the course of infection when larvae disrupt mucosal integrity. Coprological tests are best used to confirm 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). Faecal eggs counts > 500 epg are often considered to be suggestive for chemotherapeutic intervention, but egg counts do not always correlate well with actual 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, nor hosts experiencing changes in the rate of passage of digesta (egg numbers often higher in diarrhoeic faeces). Clinical signs may also be more evident before egg production occurs (i.e. during the prepatent period) when hosts are infected by developing larvae rather than mature worms. Unfortunately, egg morphometrics cannot be used to differentially diagnose *Ostertagia* infections as their eggs are very similar to those of other trichostrongyle nematodes (particularly *Trichostrongylus*, *Haemonchus* and *Teladorsagia* spp.). For generic diagnosis, 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 *Ostertagia* spp. by the polymerase chain reaction (PCR) amplification of specific gene sequences from nuclear DNA (mostly 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 livestock with most 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, including the benzimidazoles (albendazole, fenbendazole, oxfendazole) and macrocyclic lactones (ivermectin, milbemycin) when used at standard dosages, and the probenzimidazole (febantel) when used at higher doses. Anthelmintics do not have any persistent residual activity so to prevent treated animals from quickly becoming re-infected when returned to contaminated pastures, repeat treatments are recommended. Young susceptible animals are generally treated around weaning when they first begin to graze, and are then re-treated after periods when larvae may undergo arrested development (usually as yearlings in the spring/summer in temperate zones, or autumn/winter in subtropical regions). Adult animals are usually not treated as they develop strong protective immune responses. However, the emergence and widespread distribution of drug resistance to benzimidazoles and macrocyclic lactones has presented a significant problem to control programmes. It is recommended that drug resistance testing (faecal egg count reduction tests) be conducted on representative animals to select the most effective drug for mass treatments, that drugs be administered correctly (avoiding under-dosing) and that they be used strategically (as required) or systematically (in cyclic rotation) to avoid the development of drug resistance. Recent studies have also indicated that leaving some animals untreated provides 'refugia' for drug-susceptible worms and facilitates low-dose infections for the acquisition of natural protective immunity. Preliminary studies on vaccine development with membrane-bound proteins and excretory-secretory products of *O. ostertagi* have provided some encouraging results with vaccinated animals having lower worm burdens, but sometimes having more hypobiotic larvae. 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. Various biological control strategies are under investigation, including seeding pastures with nematode-trapping fungi, and providing supplementary feed rich in tannins. 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 separated from adults, stocking rates should be kept low where possible, 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).


Ostertagia
abomasum
(type I disease (acute) scours,
type II disease (acute/chronic)
diarrhoea, anaemia, anorexia)
head
Definitive Hosts
(artiodactyls, esp.
ruminants)
L4 hypobiosis
L3
ingested
eggs
excreted
in faeces
male tail
adult
female
(~ 12 mm)
adult
male
(~ 8 mm)
external
environment
filariform third-
stage larvae (L3)
(~ 900 µm)
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 500 µm)

 *Ostertagia* adult worms	 *Ostertagia* worm egg
 *Ostertagia* adult worm, male bursa	 *Ostertagia* adult worm, head