Chabertia
(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 chabertiids which have large buccal capsules and infect the large intestines of herbivores. 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 before they return to the lumen and moult into adults. *Chabertia* spp. (large-mouthed bowel worms) are found in the large intestines sometimes causing haemorrhagic enteritis in ruminants worldwide.

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:	Chabertiidae (bowel and nodular worms, two pairs of branches in dorsal ray)
Genus:	*Chabertia* (parasitic in caecum/colon of ruminants)
Species:	various species cause haemorrhagic enteritis in ruminants and pigs

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**
Strongylina (strongyles)				
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
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
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
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

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Chabertiidae contains 4 subfamilies: Chabertinae (globular buccal capsule with leaf crowns, J-shaped ovejector, 11 genera in large intestines of ruminants, rodents, marsupials and primates); Oesophagostominae (cylindrical buccal capsule with leaf crowns and often cervical collar, J-shaped ovejector, 11 genera in large intestines of ruminants, suids, rodents and primates); Cloacinae (cylindrical buccal capsule wit leaf crowns, J-shaped ovejector, 39 genera in stomach of marsupials); and Phascolostrongylinae (cylindrical or globular buccal capsule without leaf crowns but with teeth or cutting plates, Y-shaped ovejector, 6 genera in stomach and intestines of marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Chabertiinae (bowel worms)					
Chabertia (large-mouthed bowel worm)	5	artiodactyls	large intestines	10-26 mm long, stout white body, prominent bell-shaped buccal capsule curved ventrally, vestigial leaf crown in 2 rows, bifurcate dorsal gutter	90-105 x 50-55 µm, ellipsoidal, thin-shelled
Oesophagostominae (nodule worms)					
Oesophagostomum (nodule worms)	52	artiodactyls, primates	large intestines	6-25 mm, white-grey body, cylindrical buccal capsule, prominent leaf crown, cervical collar, larvae provoke nodule formation	58-89 x 34-51 µm, ovoid, thin-shelled

The subfamily Chabertinae contains 11 genera of bowel worms (*Agriostomum, Ancistronema, Castorstrongylus, Chabertia*, *Chabertiella, Colobostrongylus, Corollostrongylus, Cyclodonostomum, Okapistrongylus, Ransomus, Schulzinema,* and *Ternidens*) which are found in mammals worldwide, but are more common in temperate regions where infective larvae are better able to survive mild winters on pasture. Members of the genus *Chabertia* are characterised by their large conspicuous globular buccal capsules which are bent ventrally and associated with 2 rudimentary leaf crowns. Some 5 species have been described from the large intestines of domestic and wild herbivores, and infections have been implicated in productional losses in livestock and sometimes with clinical disease (parasitic gastroenteritis).

***Chabertia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
C. esrchowi	Artiodactyla: bovid (sheep, goat); Proboscidea: elephantid (Indian elephant)	large intestines	Asia
C. gaohanensis	Artiodactyla: bovid (sheep, goat)	large intestines	China
C. ovina (large-mouthed bowel worm) (syn. *Strongylus ovinus, hypostomus, cernuus*)	Artiodactyla: bovid (cattle, American bison, European bison, yak, sheep, bighorn sheep, argali, mouflon, chamois, goat, alpine ibex, goitered gazelle), cervid (roe deer, fallow deer, red deer, mule deer, white-tailed deer), camelid (dromedary), suid (pig)	large intestines [anorexia, enteritis, diarrhoea]	worldwide, esp. temperate zones
C. rishati	Artiodactyla: camelid (camel, sheep, goat)	large intestines	Indo-China
C. shaanxiensis	Artiodactyla: bovid (cattle, sheep, goat)	large intestines	China

Parasite morphology: *Chabertia* spp. form 3 different types of developmental stages: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. Mature females lay eggs which are thin-shelled, clear-coloured, oval-elliptical in shape measuring 90-105 x 50-55 µm and are partially embryonated containing a morula at the 16-32 cell (blastomere) stage of development. L1 are elongate free-living stages measuring around 450 x 20 µm with a striated cuticle bearing a longitudinal lateral line, a cylindrical buccal capsule, a rhabditiform (double-bulbed) oesophagus, intestines comprising 16 cells, and a tapering tail. L2 are similar in morphology but are larger (up to 650 x 30 µm), the cuticle bears 2 lateral lines, and the posterior buccal capsule contains short curved rods. L3 measure around 710-790 µm in length and are ensheathed (retain the L2 cuticle as a protective covering) and have broad round-square heads, small buccal capsules, a strongyliform (non-bulbed) oesophagus, intestines comprising 28-32 rectangular cells, and short conical tails encased in long tail sheath extensions (100-150 µm) of which the last 25% is filamentous. L4 are developing parasitic stages measuring from 1.1-1.8 mm in length and they are beginning to show many adult characteristics, including a well-developed buccal capsule with epaulette-like cranial swellings, an internal cuticular collar, a prominent cervical vesicle near the middle of the oesophageal region, and immature genitalia. Adults are stout white worm ranging in size from 10-26 mm and are readily identified by their enlarged and truncated anterior ends containing a prominent thick-walled buccal capsule which is bent ventrally (visible macroscopically and giving rise to the common name of large-mouthed bowel worm). The buccal capsule is subglobular or bell-shaped (unlike that of *Oesophagostomum* which is cylindrical) and it contains a double row of minute papillae and a dorsal gutter which bifurcates to form the sub-oral canal. The head bears a slightly inflated cephalic vesicle, vestigial corona radiata (internal and external leaf crown much reduced) and a shallow ventral cervical groove. Adult worms are sexually dimorphic, with females being larger than males (14-26 cf. 11-18 mm). Mature males have a well-developed copulatory bursa with 2 long spicules (1.3-1.8 mm) projecting from the posterior end. The bursa comprises 2 lateral lobes supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) and a dorsal lobe supported by a single ray with 4 terminal branches. Males also possess a gubernaculum (~0.2 mm long) and the tail is often spirally coiled. Mature females are didelphic with 2 ovaries, 2 uteri and 2 opposed J-shaped ovejectors leading to a common vulva opening posteriorly near the anus. They are oviparous and produce unembryonated thin-walled eggs.

Site of infection: Endoparasitic stages include exsheathed L3, developing and hypobiotic L4 and adult worms which are all found in the large intestines of their ruminant hosts, especially the proximal colon. Free-living stages include worm eggs, L1, L2 and ensheathed L3 which occur on pastures contaminated by host faeces.

Pathogenesis: Infections by *Chabertia* spp. often occur concomitantly with other nematodes and collectively, moderate infections may contribute to subclinical production losses while heavy infections may cause mild to severe clinical disease (parasitic gastroenteritis). Larvae developing in the mucosa and adults in the lumen feed by drawing a plug of tissue into their large buccal capsules where it is digested. This results in significant traumatic damage to host tissues with petechial haemorrhages, oedema and inflammation. Adult worms frequently move to new feeding sites causing further damage and leaving behind haemorrhagic lesions. The walls of the large intestines become oedematous, thickened and congested, with excess mucus production and ulceration. Blood loss may be sufficient to cause anaemia, and disruptions to the intestinal wall lead to protein and fluid loss with soft or diarrhoeic faeces often containing blood and mucus (and sometimes detached worms), hypoalbuminaemia, weight loss, emaciation and sometimes death. Burdens of 300 worms are often considered to be pathogenic, but adult sheep and cattle develop a strong protective immunity leading to worm expulsion, so they rarely harbour large worm burdens. However, clinical signs may develop during the late prepatent period when developing larvae disrupt the mucosa before adult worms have matured, particularly in young animals under stress. Clinical infections are rarely seen in cattle, while those in sheep occur more frequently in temperate regions, particularly those with winter rainfall.

Developmental cycle and mode of transmission: Chabertiid worms have simple direct monoxenous life-cycles involving faecal-oral transmission. Female worms lay partially embryonated eggs (up to 3,000-5,000 per day) which are excreted with host faeces into the external environment. In warm and moist conditions, the eggs hatch in several days releasing free-living L1 which feed on faecal bacteria. These larvae moult to form free-living L2 which also feed on bacteria before moulting to L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. Development from egg to L3 generally takes around 5 weeks in favourable conditions of warmth and moisture, but may take longer in cooler conditions. Eggs and larvae are also able to survive for long periods in cold conditions, even withstanding temporary freezing. Infections are more prevalent in temperate regions, particularly those with winter rainfall. Sheathed L3 exhibit both horizontal migration (dispersing from faecal pellets) and vertical migration (ascending vegetation) in moist conditions (e.g. following rainfall or heavy dew). Ruminants become infected when they ingest infective L3 on contaminated pastures. Ingested L3 exsheath in small intestine and then invade glands in the ileum, caecum and colon where they moult to L4 around 7 days later (they do not undertake extra-intestinal migration). L4 may be released from mucosal tissues to continue their development, or they may undergo developmental arrest (hypobiosis) in the intestinal wall, emerging much later to resume development. In either case, L4 liberated into the gut lumen congregate in the caecum where moult to young adults (sometimes designated L5). Direct development from infection to L5 takes around 24-25 days, whereas delayed development involving hypobiotic larvae usually occurs over winter, with larvae emerging in early spring. The young adults move to the colon where they mature and mate. The prepatent period (time from infection to first egg excretion) ranges from 42-56 days.

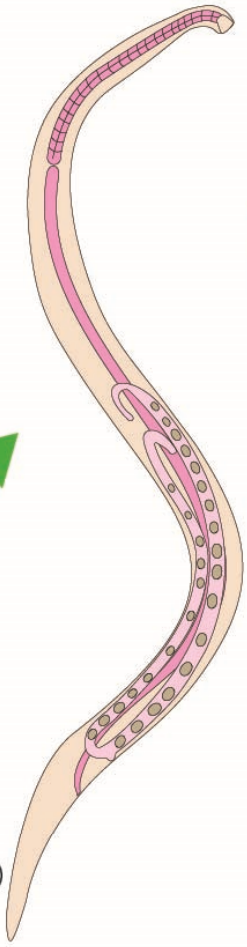
Differential diagnosis: The diagnosis of infections on the basis of clinical symptomatology is difficult as many infectious agents may cause similar nonspecific signs of gastroenteritis and loss of condition. Although expelled worms may be observed in diarrhoeic faeces in heavy acute infections, most diagnoses are based on the microscopic detection of worm eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions. Regrettably, the morphological features of the worm eggs are not sufficiently characteristic to differentially diagnose infections, as the eggs appear similar to many other trichostrongyle genera. In addition, many of the clinical signs may be caused by developing larvae before adult worms have matured and thus may appear during the late prepatent period when egg counts are negative or low. Recourse may be made to the coproculture of faecal samples to harvest L3 which can be identified by their morphological characteristics (sheathed L3 with broad rounded head, filariform oesophagus, intestines comprising 32 cells, and long filamentous tail sheath). Infections may also be diagnosed at necropsy by the detection of grey punctate lesions and/or adult worms in mucosal tissues. Molecular biological techniques have been used to differentiate various parasite species following the polymerase chain reaction (PCR) amplification of parasite DNA (nuclear ribosomal DNA, especially internal transcribed spacer regions 1 and 2, and the complete mitochondrial genome).

Treatment and control: A range of broad-spectrum anthelmintics have been used to successfully treat *Chabertia* infections in domestic livestock, including the macrocyclic lactones (avermectins (ivermectin, abamectin), milbemycins (moxidectin)), benzimidazoles (thiabendazole), imidazothiazoles (levamisole) and tetrahydropyrimidines (morantel), with most drugs being effective against adult worms, and less so against larval stages. Many veterinary health agencies recommend that producers monitor for drug resistance using faecal egg count reduction tests, and that they reduce treatment frequency by systematic dosing (seasonally or by cohort) or strategic dosing (on a needs basis). A variety of preventive control measures may also be used at the farm level to

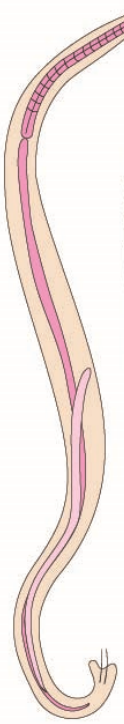
reduce the faecal-oral transmission of infections. Pasture contamination by worm eggs and free-living larvae may be minimalized by improving sanitation (draining pastures, providing clean water, and not giving supplementary feed on the ground), reducing stocking rates, quarantining new livestock, moving treated animals to clean ungrazed pastures, using rotational grazing for different cohorts (especially pregnant livestock and neonates) or mixed grazing with other animal species, and periodically spelling pastures, especially over hot dry summers.

Chabertia

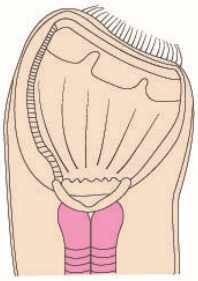
intestines
(haemorrhagic
enteritis, anaemia)



adult
female
(~ 25 mm)

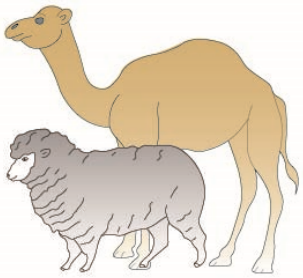


adult
male
(~ 15 mm)



head

male tail
(lateral)

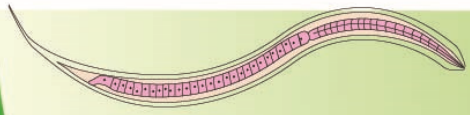


Definitive Hosts
(artiodactyls)

hypobiosis

L3
ingested

eggs
excreted
in faeces



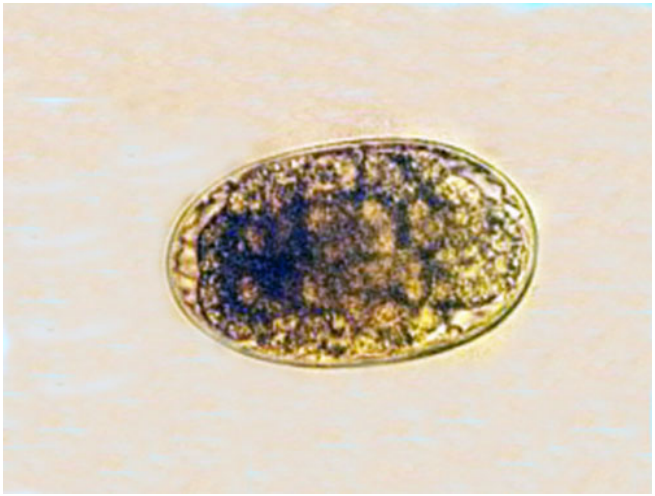
filariform third-
stage larvae (L3)
(~ 750 µm)

external
environment

eggs
(~ 100 µm)

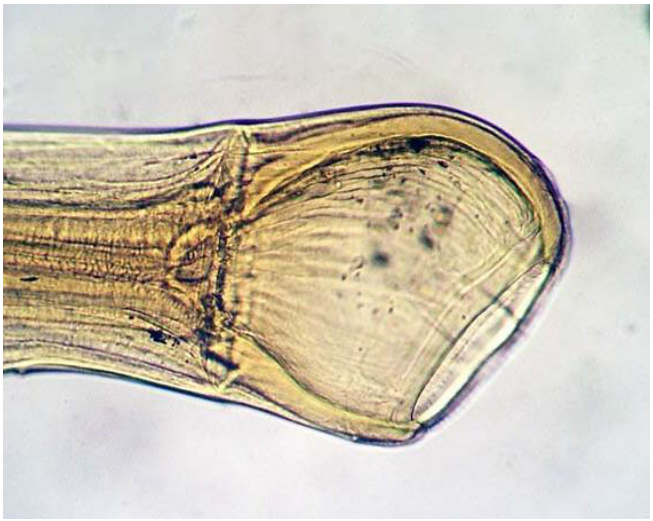
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 500 µm)

Chabertia adult worms



Chabertia worm egg

Chabertia adult worm, male bursa



Chabertia adult worm, head