Cooperia
(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. *Cooperia* spp. (wire worms) contribute to illthrift reducing production in sheep and cattle 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:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Cooperia* (parasitic in small intestines of ruminants)
Species:	various species cause scours and illthrift in cattle and sheep

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 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
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled

The subfamily Cooperiinae was established for genera with a cephalic vesicle and contains 10 genera (*Chabaudstrongylus*, *Cooperia*, *Cooperioides*, *Gazellostrongylus*, *Impalaia* (syn. *Anthostrongylus, Minutostrongylus*), *Megacooperia*, *Minutostrongylus*, *Neocooperia, Ortleppstrongylus*, *Paracooperia* (syn. *Schwartziella*), *Paracooperioides, Pseudostertagia* and *Tapironema*) which are parasitic in the small intestines of ruminants (bovids, giraffids, camelids, cervids). The genus *Cooperia* contains small wire-worms with small cephalic vesicles, reduced buccal capsules with three or fewer cutting plates or teeth, and the males have a fully developed bursa (type 2-2-1) with lyre-shaped dorsal rays, no gubernaculum or telamon, and 2 spicules not joined posteriorly. Some 24 species have been described mainly from bovids, giraffids and camelids. All species have direct life-cycles involving the faecal-oral transmission of pasture stages. Infective larvae do not undergo tracheal migration in their hosts, but some may undergo arrested development (hypobiosis) in host tissues. Several *Cooperia* spp. are important pathogens of domestic ruminants, causing significant production losses through reduced weight gain, poor reproductive performance, morbidity and mortality. Infections are more common in cooler areas with high winter rainfall as the exogenous stages of the parasites (eggs and larvae) prefer moist conditions.

***Cooperia* species**	**Definitive Hosts**	**Location [clinical signs[**	**Distribution**
C. acutispiculum	Artiodactyla: bovid (greater kudu, bushbuck)		Africa
C. asamati	Artiodactyla: bovid (cattle)		
C. aserbaidjanica	Artiodactyla: bovid (cattle)		Asia
C. borgesi sp. inq.	Artiodactyla: bovid (cattle, sheep, reedbuck)		Africa
C. chabaudi	Artiodactyla: bovid (bay duiker)	small intestines	Africa
C. connochaeti	Artiodactyla: bovid (blue wildebeest, Livingstone's eland, impala, puku)	abomasum, small intestines	Africa
C. curticei (syn. *C. fieldingi p.p., Strongylus curticei, ventricosus p.p.*)	Artiodactyla: bovid (cattle, water buffalo, sheep, argali, mouflon, goat, roan antelope, sable antelope, lechwe, Kafue lechwe, Sharpe's grysbok, blesbok, gemsbok, springbok, waterbuck, black wildebeest, impala), cervid (roe deer, red deer, white-tailed deer); Diprotodontia: phalangerid (common brushtail possum)	small intestines [inappetence]	worldwide
C. erschovi sp. inq.	Artiodactyla: bovid (cattle)	pancreas	China
C. fuelleborni	Artiodactyla: bovid (impala, common tsessebe, roan antelope, sable antelope, waterbuck, topi, Sharpe's	small intestines	Africa

	grysbok, Coke's hartebeest, common duiker, greater kudu, common eland, sheep, cattle, blesbok, African buffalo)		
C. hippotragusi sp. inq.	Artiodactyla: bovid (cattle, roan antelope, reedbuck, oribi)		Africa
C. hrenktahnsa	Artiodactyla: bovid (yak)		Asia
C. hungi	Artiodactyla: bovid (goat, sheep, African buffalo, blue wildebeest, Coke's hartebeest, common tsessebe, sable antelope, steenbok, nyala, greater kudu, bushbuck, Sharpe's grysbok, southern reedbuck, waterbuck, common duiker, common eland, impala, topi, suni), suid (desert warthog); Lagomorpha: leporid (scrub hare)	abomasum, small intestines	Africa
C. laterouniformis	Artiodactyla: bovid (blackbuck, water buffalo)	small intestines	Asia
C. minor sp. inq.	Artiodactyla: bovid (cattle)		Africa
C. neitzi	Artiodactyla: bovid (sable antelope, Sharpe's grysbok, Livingstone's eland, kudu, greater kudu, bushbuck, grey duiker, sheep)	small intestines	Africa
C. okapi (syn. *C. okapiae*)	Artiodactyla: giraffid (okapi)	small intestines	Africa
C. oncophora (wire worm) (syn. *C. bisonis, harkeri, Strongylus radiatus p.p., ventricosus p.p., oncophorus*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, sheep, bighorn sheep, argali, mouflon, goat, European bison, American bison), camelid (dromedary, llama, vicuna, alpaca), cervid (roe deer, fallow deer, red deer, mule deer, white-tailed deer)	small intestines, stomach [inappetence, diarrhoea]	worldwide
C. pectinata (syn. *C. nicolli*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, zebu, European bison, water buffalo, African buffalo, sheep, argali, mouflon, goat, common tsessebe, Livingstone's eland, Coke's hartebeest, greater kudu, bushbuck, sable antelope, impala), camelid (dromedary), cervid (roe deer, fallow deer, red deer, white-tailed deer)	small intestines [inappetence, diarrhoea]	worldwide
C. pigachei	Artiodactyla: bovid (mountain reedbuck)		Africa
C. punctata (cattle bankrupt worm) (syn. *C. africana, brasiliensis, fieldingi p.p., Strongylus punctatus, bovis*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, Bali cattle, zebu, water buffalo, African buffalo, European bison, sheep, goat, chamois, Sharpe's grysbok, Coke's hartebeest, greater kudu, sable antelope, Livingstone's eland, suni), cervid (roe deer, fallow deer, red deer, marsh deer, chital, white-tailed deer), suid (pig)	abomasum, small intestines, pancreas [inappetence, diarrhoea]	worldwide
C. reduncai sp. inq.	Artiodactyla: bovid (reedbuck)		Africa
C. rotundispiculum	Artiodactyla: bovid (impala, blue duiker, red forest duiker, grey duiker, suni, gemsbok, common duiker, common eland, nyala, Cape bushbuck, greater kudu, Bohor reedbuck)	abomasum, small intestines	Africa
C. schistopapillatus	Artiodactyla: bovid (greater kudu)		Africa
C. spatula	Artiodactyla: bovid (cattle, sheep), cervid (white-tailed deer)		North America
C. spatulata	Artiodactyla: bovid (cattle, zebu, sheep)	small intestines	Australasia, North America, Africa
C. surnabada (syn. *C. zurnabada, mcmasteri*) (now considered to be a morphological variant of *C. onchophora*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, American bison, European bison, sheep, bighorn sheep, goat), camelid (llama), cervid (red deer, roe deer, mule deer)	small intestines [inappetence, diarrhoea]	Europe, Americas, Australia
C. svanetica	Artiodactyla: bovid (cattle)	small intestines	Russia
C. verrucosa	Artiodactyla: bovid (common eland, impala, Coke's hartebeest, Kirk's dik-dik)	abomasum, small intestines	Africa
C. yoshidai	Artiodactyla: bovid (impala, red forest duiker, common tsessebe, sable antelope, Bohor reedbuck, southern reedbuck, greater kudu)	abomasum, small intestines	Africa

Re-assigned species			
C. alata (now *Pithecostrongylus*)	Primates: cercopithecid (macaque)		Africa
C. antidorca (now *Cooperioides*)	Artiodactyla: bovid (springbok, Grant's gazelle, Thomson's gazelle, sheep)		Africa
C. caballeroi (now *Chabaudstrongylus*)	Artiodactyla: tragulid (mouse-deer)		Asia
C. dubosti (now *Chabaudstrongylus*)	Artiodactyla: tragulid (water chevrotain)		Africa
C. elegans (now *Molineus*)	Primates: cebid (Guianan squirrel monkey)	small intestines	South America
C. falsa (now *Macielia*)	Cingulata: chlamyphorid (southern naked-tailed armadillo)	stomach	South America
C. hamiltoni (syn. *C. kenyensis*) (now *Cooperioides*)	Artiodactyla: bovid (impala, suni, sheep)	small intestine	Africa
C. hepaticae (now *Cooperioides*)	Artiodactyla: bovid (impala)		Africa
C. macieli (now *Macielia*)	Cingulata: dasypodid (nine-banded armadillo)	stomach	South America
C. nodulosa (syn. *Schwartziella*) (now *Paracooperia*)	Artiodactyla: bovid (carabao)	small intestines	Philippines
C. serrata (syn. *Schwartziella*) (now *Paracooperia*)	Artiodactyla: bovid (springbok, sheep)		Africa

Parasite morphology: *Cooperia* spp. exhibit sequential development through 3 distinct biological stages: eggs; larvae (4 stages encoded L1-L4); and adult worms. Gravid females lay thin-walled eggs measuring 65-95 x 29-44 μm which are prolate ellipsoidal in shape with nearly parallel sides. Freshly laid eggs contain a morula composed of 16-32 cells almost filling the interior. First-stage larvae (L1) are pre-parasitic free-living feeding stages measuring from 300-375 μm in length. They have a rounded head, rhabditiform (bulbed) oesophagus, intestines dilated anteriorly and posteriorly with an undulating lumen, and sharply pointed tails. L2 are similarly free-living feeding stages but they measure 500-800 μm long and their intestines are less serpentine. In contrast, L3 are non-feeding stages that are still encased in the L2 cuticle as a protective sheath. The ensheathed L3 usually measure from 711-924 μm in length, but those of some species may range from 550-1,050 μm depending on maturity. The sheath has an annulated appearance and a long tail sheath extension (35-116 μm) of which the posterior 20-25% is filamentous. The larvae themselves have a round-square head with 2 distinctive refractile bodies, a strongyliform (non-bulbed) oesophagus, intestines comprising 16 cells, and a blunt tail. Parasitic L4 are elongate measuring from 1.9-4.6 mm in length and their genital primordia have begun to form distinctive reproductive organs (with the vulva and bursa becoming conspicuous). Early L4 of some species may undergo arrested development (hypobiosis) in host tissues. Adult worms are commonly called 'wire-worms' due to their comma or watch-spring appearance (with 1-2 tight coils). They are small slender worms measuring from 4-15 mm in length and are red-brown or pink-white in colour. They typically have an anterior cuticular inflation (cephalic vesicle) giving the head a bulbous or cylindrical appearance, a reduced buccal capsule, tiny cervical papillae, a cylindrical strongyliform oesophagus and a distinctive synlophe with prominent anterior transverse striations giving way to a small number of longitudinal cuticular ridges. Adults have an excretory pore located near the distal oesophagus (but lack the excretory notch characteristic of the genus *Trichostrongylus*). Adult worms are sexually dimorphic, with females being larger than males (5-15 mm cf. 4-9 mm long). Mature females are didelphic with 2 ovaries (rarely some are monodelphic) connected to uteri opening into a posterior vulva with a well-developed ovejector and small vulvar flaps. They have long tapering tails that are sharply pointed and lack terminal spines. Male worms have a large pronounced copulatory bursa with 2 lateral lobes supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) with a 2-2-1 configuration (divergent ventral and lateral rays separated from posterolateral ray) and a shorter symmetrical dorsal lobe with dorsal rays forming a distinctive lyre-shape. Mature males do not have a gubernaculum or telamon, but have 2 short thick spicules not joined posteriorly. Spicule structure appears to be species-specific (e.g. bow-like with terminal feet for *C. oncophora*, posterior bifurcation and conical tips for *C. surnabada*, medial wing-like projection with ridges for *C. curticei*).

Site of infection: Parasites infect the small intestines of their hosts, particularly the duodenum, but sometimes extending to the large intestines, abomasum, and rarely the pancreas. Larval stages develop in small intestinal crypts (sometimes undergoing development arrest), whereas adult worms coil up amongst mucosal villi. Worm eggs are excreted onto pastures where free-living larval stages eventually develop into infective L3.

Pathogenesis: While many infections are light and remain asymptomatic, mild-moderate infections may cause significant subclinical production losses and heavy infections (> 40,000 worms) may produce clinical disease. When infections occur concomitantly with other gut nematodes (especially *Haemonchus* and *Ostertagia*), the combined clinical effects (gastroenteritis, diarrhoea, malnutrition) can be severe. Developing larval stages burrow beneath the small intestinal mucosa forming tunnels which eventually rupture to release young adults into the lumen. Adult worms coil among the intestinal villi and forage along the mucosa (earlier reports of them feeding on host blood have not been substantiated, but adults have been observed to bury their bulbous heads in the mucosa apparently for anchorage). Collectively, larval and adult stages cause mucosal damage resulting in inflammation (catarrhal enteritis), cellular infiltration, epithelial loss, lesion formation, villus atrophy and some petechial haemorrhages which contribute to malabsorption with fluid and protein loss. Infected animals exhibit intermittent watery diarrhoea, dehydration, hypoproteinaemia, oedema, inappetence, anorexia and failure to thrive with reduced growth rates and poor weight gain or weight loss. *Cooperia* spp. vary in their pathogenicity, with *C. pectinata* and *C. punctata* considered to be most pathogenic (large numbers can be fatal in calves) and *C. oncophora* to be mildly pathogenic (causing mild diarrhoea). Young animals (< 8 months old) are most susceptible to clinical infections but they rapidly acquire a strong but partial protective immunity by 12 months of age. The resumption of development of hypobiotic larvae in older animals (yearlings) is not usually associated with a second wave of disease (as occurs for some *Ostertagia* spp.). While adult animals generally show few clinical signs of infection, but may continue to act as carriers with low but persistent egg excretion.

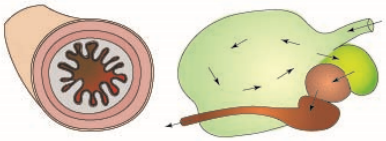
Developmental cycle and mode of transmission: *Cooperia* spp. are monoxenous parasites with direct life-cycles involving the faecal-oral transmission of infective larvae on pastures. Gravid female worms lay 1,000-3,000 eggs per day which are passed into the external environment with host faeces. The eggs embryonate and hatch after several days releasing free-living L1 which feed on faecal bacteria. The larvae then moult to L2 that also feed on bacteria before moulting to ensheathed non-feeding L3 (they retain the L2 cuticle as a protective sheath). L3 are very active stages that migrate outwards from faecal material and upwards onto vegetation. They develop in 1-6 weeks depending on prevailing environmental conditions, with development occurring in moist conditions with temperatures ranging from 5-33°C. Infective L3 may survive on pastures for up to 1 year, and are able to tolerate cold conditions. They are ingested on herbage by grazing animals and exsheath in the gut before invading crypts in the small intestines. Here they moult to L4 and then to young adults over 8-10 days before emerging onto the intestinal mucosa to feed, mature and mate. The prepatent period (time from infection to the first release of eggs) ranges from 11-22 days depending on species (11-19 days for *C. punctata*, 14-15 days for *C. curticei*, and 17-22 days for *C. oncophora*). The larvae of several *Cooperia* spp. may also exhibit arrested development (hypobiosis) at the early L4 stage (particularly when preparasitic L3 are exposed to cold conditions), only resuming development months later when environmental conditions are more suitable. Hypobiosis occurs during late autumn and winter in cool temperate zones, during spring and summer in warm temperate zones, and during prolonged dry seasons in subtropical regions.

Differential diagnosis: Infections cause nonspecific clinical signs (gastroenteritis) which could be attributed to a wide range of infectious agents. Indeed, *Cooperia* infections often occur concomitantly with other gut nematodes that have similar host ranges and modes of transmission. Infections are often diagnosed by the direct detection of worm eggs in faecal samples, normally following their concentration by sedimentation in water and/or floatation in saturated salt or sugar solutions (eggs are buoyant in media with high specific gravities). Several coprological techniques have been quantitated by counting the number of eggs present in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) and calculating the number of eggs per gram of faeces (epg). Unfortunately, faecal egg counts show poor correlations with worm burdens and the severity of clinical disease, as they do not account for larval stages, male worms, or females not producing eggs due to their immaturity, senescence or immune-induced suppression of egg production. The eggs of *Cooperia* spp. are small in size and ellipsoidal in shape with flattened sides, but otherwise do not exhibit any reliable characteristics to differentiate species or even other trichostrongyle genera (notably *Trichostrongylus, Haemonchus, Ostertagia* and *Teladorsagia*). Faecal samples may be incubated for several days to harvest L3 which can be identified by their morphological characteristics (annulated sheath with long tapering tail, squared head with refractile bodies, strongyliform oesophagus, and intestines comprising 16 cells). Infections may also be diagnosed by the detection of adult worms in gut samples obtained post-mortem from dead or sacrificed animals. The stomach and intestines may be ligated, perfused with saline and mucosal washes or digests examined for characteristic worms (red colouration, coiled spring appearance, prominent bursa and spicules). More recently, molecular biological techniques have been used to characterize different species by the polymerase chain reaction (PCR) amplification of nuclear genes (encoding ribosomal RNA and internal transcribed spacers I and II).

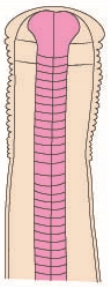
Treatment and control: A variety of anthelmintic drugs have been used to effectively treat clinical infections, including benzimidazoles (fenbendazole, oxfendazole, albendazole), prebenzimidazoles (febantel, netobimin, thiophanate), imidazothiazole (levamisole), and macrocyclic lactones (ivermectin). Regrettably, drug resistance to benzimidazoles and macrocyclic lactones has become widespread, so it is recommended that drug resistance monitoring be instituted (faecal egg count reduction tests) and that treatments be applied strategically (as required) or systematically (regularly and in rotation). In particular, young livestock should be treated during their first grazing season, whereas adult animals acquire protective immunity and usually do not display clinical signs. Control programmes should also include stock and pasture management practices at the farm level to reduce pasture contamination by worm eggs and larvae. New livestock should be isolated and treated in quarantine, stocking rates should be kept low, different

cohorts should be grazed in rotation, treated animals should be placed on clean pastures, different host species may be grazed together or alternately, and pastures should be spelled periodically, particularly over adverse seasons (e.g. hot summers). While some studies have shown that pastures seeded with a nematode-trapping fungus (*Athrobotrys oligospora*) later contained fewer infective larvae, environmental constraints (narrower temperature ranges and moisture requirements) appear to limit widespread application.

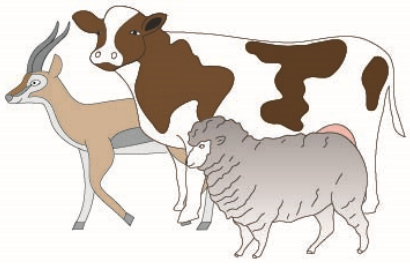
Cooperia



intestines, stomach
(gastroenteritis, diarrhoea,
malnutrition)



head



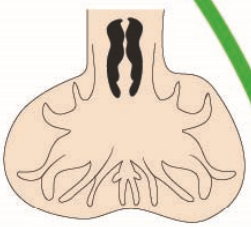
Definitive Hosts
(artiodactyls)

L4 hypobiosis

L3
ingested

adult
female
(~ 15 mm)

adult
male
(~ 9 mm)



male tail

eggs
excreted
in faeces

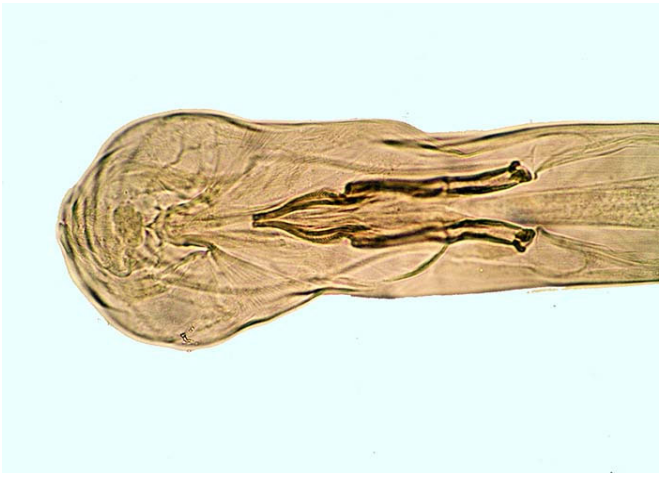
filariform third-
stage larvae (L3)
(~ 900 µm)

external
environment

eggs
(~ 90 µm)

rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 600 µm)

Cooperia adult worm, head



Cooperia adult worm, male bursa

Cooperia worm egg