Gaigeria
(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 ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals, esp. humans and companion animals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts. Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. *Gaigeria* spp. cause mild-severe hookworm disease (anaemia) in sheep in southern continents, except Australia.

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:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Gaigeria* (parasitic in small intestines of sheep)
Species:	*G. pachyscelis* causes anaemia in 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**
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
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
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

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs	Transmission
Bunostominae						
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	108-115 x58-61 µm, ellipsoidal, thin-shelled	transdermal
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal
Ancylostominae						
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Globocephalus	18	artiodactyls, rodents, primates	caecum, small intestines	3-9 mm long, large buccal capsule without cutting plates or teeth, larval pulmonary migration	60-75 x 35-41 µm, ovoid, thin-shelled	oral, transdermal
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal

The subfamily Bunostominae contains 12 genera classified in 2 tribes: Bunostominea containing worms with anterodorsally directed heads with pronounced dorsal inclination, oral opening with well-developed cutting plates, no buccal collar, long oesophagus (*Bunostomum* (syn. *Bustomum*, *Monodontus*), *Bathmostomum*, *Bunostomoides, Brachyclonus*, *Cameronecator*, *Gaigeria*, *Grammocephalus*, *Monodontus*, *Necator*, *Rhinoceratonema*) in elephants, rhinoceros, procyonids, ruminants, rodents, tayasuids, tapirs, and primates; and Acheilostominea containing worms with anterodorsally directed heads with slight dorsal inclination, oral opening with inconspicuous or no cutting plates, buccal collar, short oesophagus (*Acheilostoma*, *Tetragomphius*) in rodents, mustelids and procyonids. The genus *Gaigeria* is monotypic and contains a single species *G. pachyscelis* infecting ruminants in Africa, India and Indonesia. Adult worms have exceptionally large dorsal bursal lobes, the dorsal cone is not supported by subdorsal plates and the female ovejectors have short vestibula. This species is a voracious bloodsucker and is probably the most pathogenic hookworm.

Parasite species	Hosts	Location [Clinical signs]	Distribution
Gaigeria pachyscelis (syn. *G. ullissiponensis*)	Artiodactyla: bovid (zebu, sheep, goat, blue wildebeest, grey duiker, nyala, impala, nilgai, blackbuck, steenbok), suid (African bush pig); Rodentia: caviid (guinea pig), murid (mouse)	small intestines [anaemia]	Africa, Americas, Asia

Parasite morphology: *Gaigeria* forms 3 different types of morphological stages in its developmental cycle: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. The eggs are thin-shelled ellipsoidal stages measuring 108-115 x 58-61 µm and contain a developing embryo (morula) at the 4-8 cell (blastomere) stage of development. L1 and L2 are free-living (pre-parasitic) stages measuring from 350-600 µm in length that have rounded heads, rhabditiform (double-bulbed) oesophagi, and tapering tails. L3 are ensheathed stages (still encased in the L2 cuticle) measuring from 630-720 µm in length, including a long sheath tail extension (128-135 µm) which is filamentous for the last 50% of its length. Infective L3 have a bullet-shaped head, strongyliform oesophagus with a prominent caudal bulb, intestines comprising 16 cells, and a sharply-tapering tail. L4 are transient parasitic stages that have begun to show adult worm characteristics, particularly with regard to mouth and genitalia (male bursa and female vulva). Adults are small white hookworms measuring from 10-45 mm long with anterodorsally directed heads with a pronounced dorsal inclination (hook). They have large subglobular to funnel-shaped buccal capsules armed with pair of well-developed ventral cutting plates around the oval mouth and a pair of elongate subventral lancets (each with several cusps). The buccal capsule also contains a short dorsal cone (not supported by subdorsal plates) containing the duct of the dorsal oesophageal gland (in ancylostomins, the duct is contained within a dorsal groove). Adult worms are sexually dimorphic, with males being smaller than females (10-20 x 0.5-0.6 mm cf. 17-45 x 0.6-0.8 mm). Mature males have a well-developed copulatory bursa consisting of 2 short lateral lobes joined together ventrally, each supported by 6 rays (formed by muscular elements following nerve channels to terminal papillae) arranged such that the short anterolateral rays are separated from the other laterals, and the externodorsal rays arise from the main stem of the dorsal ray) and an exceptionally large symmetrical dorsal lobe (supported by a dorsal ray which bifurcates with each short branch terminating in small digitations). Males do not possess a gubernaculum but they have 2 elongate equal spicules (1.2-1.3 mm) with recurved (kinked or barbed) tips. Mature females are didelphic with 2 ovaries and uteri connected by ovejectors with short vestibula to a common vulva located anterior to the midbody. Females have bluntly rounded tails that do not have terminal spines.

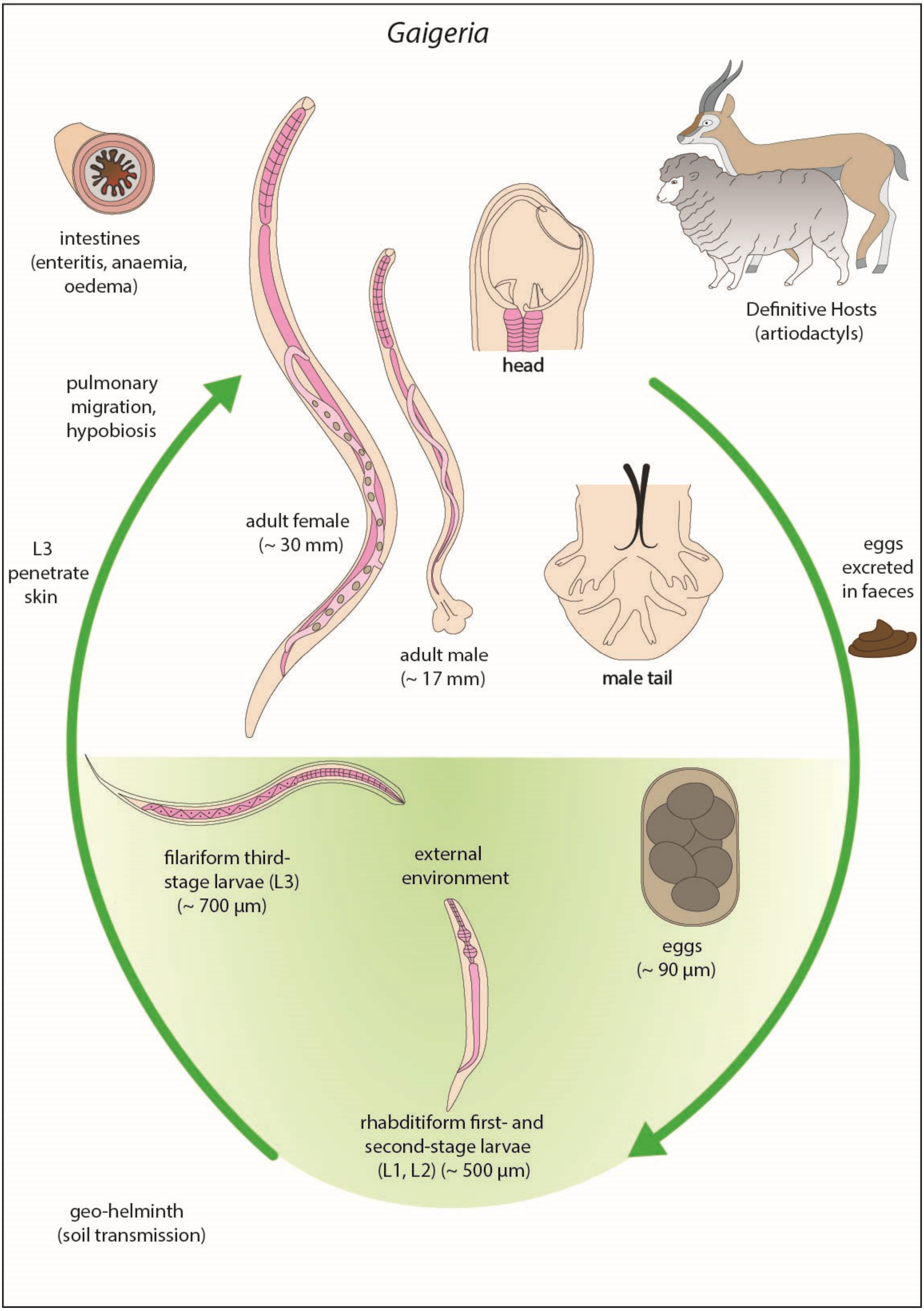
Site of infection: Adult worms infect the small intestines (mainly the duodenum) of their herbivorous hosts, while earlier larval developmental stages undergo a pulmonary migration through the lungs before settling in the gut. Free-living larval stages contaminate the external environment after developing from hatched eggs.

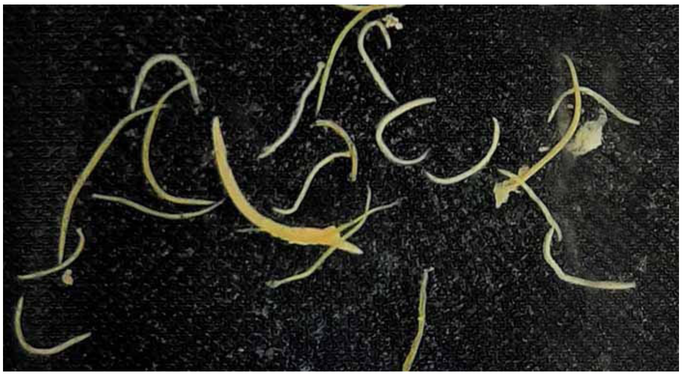
Pathogenesis: The species *G. pachyscelis* has a reputation as a voracious bloodsucker and some consider it to be the most pathogenic hookworm. Infections with < 30 worms have been associated with clinical disease in small ruminants, and infections with > 100 worms may cause death within several weeks. Adult worms attach to the intestinal mucosa and feed on host tissues and blood with their large buccal capsules and cutting plates. Worms frequently detach and move to new feeding sites leaving behind haemorrhagic lesions in a swollen and inflamed mucosa covered with mucus. Blood loss causes a progressive anaemia and disrupted mucosal function contributes to oedema (ascites and submandibular bottle-jaw), maldigestion, hypoproteinaemia, intermittent diarrhoea, cachexia, rapid loss of condition, emaciation, weakness and death. Young animals are most susceptible to clinical disease, while prior exposure may provide some protective immunity to surviving adult animals.

Developmental cycle and mode of transmission: Like other hookworms, these parasites have direct monoxenous life-cycles whereby hosts become infected by the percutaneous (transdermal) penetration of infective L3 from the environment. Female worms lay eggs (up to 600-800 per day) which are excreted with host faeces. The eggs hatch under suitable warm and moist conditions releasing free-living rhabditiform L1 which moult to similar L2. These stages then moult to form strongyliform L3 which retain the L2 cuticle as a protective sheath. Nevertheless, these L3 are highly susceptible to desiccation and do not survive long without adequate moisture. Definitive hosts become infected when infective L3 come into contact with their skin which they quickly penetrate invading dermal tissues. The larvae migrate to the lungs via the circulation, penetrate into alveolar air-spaces and moult to L4 which ascend the mucociliary escalator to the trachea where they are swallowed and carried to the gut. They moult in the small intestines to young adults which feed and develop into mature adults over several weeks. The prepatent period (time from infection to first excretion of eggs) ranges from 56-70 days. Transplacental and transmammary transmission has not been reported. High worm burdens are sometimes found in tropical regions at the end of the dry season, apparently due to maturation of hypobiotic larvae. Infections are more common in tropical and subtropical regions where pastures may be moist for most of the year, while heavy infections are uncommon in temperate regions with hot summers.

Differential diagnosis: While infections may be suspected on the basis of clinical signs (severe anaemia), other aetiological agents may be responsible (including other hookworms and some trichostrongyles). Infections are conventionally diagnosed by the detection of the large characteristic eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions. Coprocultures may also be used to harvest L3 which can tentatively be identified by their morphological characteristics (short ensheathed L3 with 16 intestinal cells and long filamentous tails), but incubation times of up to a week are often required. Infections may also be diagnosed by the detection of adult worms in gut samples collected post-mortem from dead or sacrificed animals. Several immunoserological tests (mostly enzyme immunoassays) have been developed to detect specific host antibodies against adult worm antigens, but they have varied in their sensitivity and specificity due to some cross-reactivity with other nematodes.

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections, including benzimidazoles (albendazole, oxfendazole, fenbendazole, mebendazole), macrocyclic lactones (ivermectin, doramectin, moxidectin), and imidazothiazoles (levamisole). Treatment is usually repeated on a regular basis to stop hosts becoming re-infected, although strategic drenching before and after weaning, and then on a needs-basis, have been recommended to combat the emergence of drug resistance. A variety of farm management strategies may be used to minimise transmission between livestock, mostly by reducing environmental contamination by worm eggs and larvae (remove faeces from holding areas, regularly clean pens, provide dry bedding, drain wet pastures, spell pastures over hot dry periods) and managing grazing (separate young and adult cohorts, cyclic or rotational grazing, mixed grazing, avoid overstocking, quarantine new livestock). Preliminary studies on vaccine development using irradiated larvae demonstrated variable protection in some animals as evidenced by reduced worm burdens and less severe disease following pathogenic challenge.


Gaigeria
intestines
(enteritis, anaemia,
oedema)
Definitive Hosts
(artiodactyls)
head
pulmonary
migration,
hypobiosis
adult female
(~ 30 mm)
adult male
(~ 17 mm)
male tail
L3
penetrate
skin
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 700 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 500 µm)
geo-helminth
(soil transmission)

 *Gaigeria* adult worm	