Dictyocaulus
(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 lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Unlike most lungworms, dictyocaulids have direct life-cycles where adults in the lungs lay eggs or larvae which are swallowed and passed in faeces as L1. They develop to L3 in the external environment and are ingested by hosts where they exsheath, penetrate the intestinal wall and migrate via the lymphatic-vascular systems to the lungs. *Dictyocaulus* infections have been associated with respiratory clinical signs in many ruminants, sometimes progressing to pneumonia.

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:	Dictylocaulidae (lungworms, direct cycle, infection by ingestion of L3)
Genus:	*Dictyocaulus* (parasitic in respiratory tract of ruminants)
Species:	various species cause pneumonia in ruminants (incl. husk in cattle)

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**
Metastrongylina (lungworms)				
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
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
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

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 5 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Larvae
Dictylocaulidae					
Dictylocaulus (lungworms)	13	ruminants, equids	respiratory tract	25-100 mm long, small buccal capsules, male bursa with large lobes, short stout spicules, direct cycle, eggs laid in lungs swallowed, L1 passed in faeces	larvae 290-450 µm, anterior knob, short tail spike

The family Dictyocaulidae contains 2 subfamilies: Mertensinematinae containing 3 genera (*Mertensinema*, *Borrellostrongylus* (syn. *Parabatrachostrongylus*) and *Zygocaulus*) parasitic in the digestive tracts of amphibians and reptiles; and Dictyocaulinae containing 2 genera (*Dictyocaulus* (syn. *Micrurocaulus*) and *Bronchonema*) parasitic in the trachea, bronchi and bronchioles of ruminants and horses. These lungworms have direct life-cycles with infective larvae on pastures ingested by grazing herbivores. The genus *Dictyocaulus* contains some 13 species, many of which have been associated with respiratory clinical diseases in domestic and wild ruminants, particularly bovids and cervids. The lungworms vary in their host specificity, most being stenoxenous (infect closely-related hosts) but they do demonstrate strong preferences for particular host species. Most parasite species are also considered to be cosmopolitan, presumably due to the widespread translocations of domestic livestock, but they do exhibit variations in their regional distribution and seasonal abundance. For example, the species *D. viviparus* occurs mainly in cattle and buffalo in subtropical and temperate regions, mostly in moist elevated areas (forests and farms at altitudes between 1,000-2,000 m).

***Dictyocaulus* species**	**Hosts**	**Location [Clinical signs**	**Distribution**
D. africanus	Artiodactyla: bovid (hartebeest, tiang)	lungs	Africa
D. arnfieldi (equine lungworm)	Perissodactyla: equid (horse, donkey, onager), tapirid (Indian tapir)	lungs [persistent cough, nasal discharge]	worldwide
D. cameli	Artiodactyla: camelid (bactrian camel, dromedary)	lungs	worldwide
D. capreolus	Artiodactyla: cervid (moose, roe deer), bovid (cattle)	lungs	worldwide
D. cervi	Artiodactyla: cervid (red deer)	lungs	Europe
D. eckerti	Artiodactyla: cervid (roe deer, fallow deer, red deer, sika deer, reindeer, Indian hog deer, Indian muntjac, moose), bovid (cattle, muskox)	bronchi, trachea	worldwide, esp. temperate zones
D. filaria (syn. *D. sibiricus*, *unequalis*) (sheep lungworm)	Artiodactyla: bovid (sheep, mouflon, urial, chamois, argali, goat, Iberian ibex, cattle, water buffalo, American bison, kafue lechwe), cervid (fallow deer, red deer, moose), camelid (dromedary); Lagomorpha: leporid (rabbit); Rodentia: murid (mouse, gerbil)	lungs [cough, unthriftiness]	worldwide
D. hadweni	Artiodactyla: bovid (American bison), cervid (moose)	lungs	North America
D. khawi sp. inq.	Artiodactyla: suid (pig)	lungs	
D. magnus (syn. *Bronchonema*)	Artiodactyla: bovid (blesbok, springbok)	lungs	Africa
D. murmanensis	Artiodactyla: cervid (reindeer)	lungs	Eurasia
D. noerneri (possible syn. of *D. viviparus* or *D. eckerti*)	Artiodactyla: cervid (red deer, roe deer, fallow deer)	lungs	worldwide
D. pandionis	Perissodactyla: equid (onager)	lungs	Africa
D. viviparus (syn. *D. bisonis*) (bovine lungworm)	Artiodactyla: bovid (cattle, zebu, muskox, water buffalo, European bison, sheep, bighorn sheep, mouflon, argali, chamois, Tatra chamois, impala, kafue lechwe, nyala, greater kudu, southern reedbuck, common duiker, red forest duiker, grey duiker), cervid (roe deer, fallow deer, sika deer, Japan rusa, red deer, central European red deer, reindeer, Arctic reindeer, boreal woodland caribou, Rocky Mountain elk, mule deer, black-tailed deer, white-tailed deer, western moose), camelid (bactrian camel)	bronchi, trachea [cough (husk), unthriftiness]	worldwide, esp. temperate zones

Parasite morphology: *Dictyocaulus* spp. form 3 different morphological stages during their development: eggs, larvae (4 successive stages designated L1-L4); and adult worms. Freshly laid eggs are thin-shelled and ovoid measuring 75-138 x 51-90 µm, and are already embryonated containing a fully developed larva. Freed L1 are small stout stages measuring 290-450 µm with rounded heads, a club-shaped oesophagus spanning the anterior third to half of the body, intestinal cells with dark granules (usually obscuring anatomical details), and a smooth round tapering tail (*D. filaria* L1 also possess a small anterior cuticular knob and a short tail spike, while *D. arnfieldi* L1 have a terminal protuberance, and those of other lungworm genera have more elaborate tail ornamentations). L2 are free-living stages measuring up to 500-600 µm with rounded heads, granular intestinal cells and blunt conical tails. L3 differ in that they have retained the L2 cuticle as a close-fitting protective sheath measuring 400-500 µm, and they have a rounded head, an elongate flask-shaped (strongyliform) oesophagus, intestines with few granules, and a short sharply conical tail. L4 are endoparasitic stages which have developed many adult characteristics, with males measuring 800-890 µm and females 780-1,080 µm in length. Adult lungworms are slender milky-white worms 25-100 mm long with an oval oral opening surrounded by a buccal ring (triangular or reniform in shape), a small anterior buccal capsule with heavily chitinized walls, and single basal buccal tooth. The mouth lacks lips and leaf crowns, but a few species have a small cephalic vesicle (*D. eckerti, D. cervi*). The cuticle bears numerous longitudinal ridges (synlophe) and the intestines often appear as a dark internal band. Adult worms are sexually dimorphic, with males being smaller than females (25-80 cf. 43-100 mm). Mature males have a fully developed caudal copulatory bursa which is non-lobulated and appears bell-shaped (not divided into lateral and dorsal lobes, but confluent). The supporting rays have a unique configuration in that the ventral rays are partly fused and separate from the lateral rays, and the dorsal ray is split to its base. Males have a gubernaculum, telamon and 2 short boot-shaped spicules (0.2-0.6 mm long) made of spongy porous material and bearing either large lateral alae or 1-2 small branching processes. Mature females are didelphic with 2 ovaries and uteri (opposed in amphidelphic configuration) opening into a common midbody vulva, sometimes with raised lips. Females have pointed tails and produce eggs that embryonate *in utero* to contain a fully developed L1.

Site of infection: Adult lungworms infect the respiratory tracts of their hosts, residing mainly in the bronchi, but sometimes extending down to the bronchioles or up to the trachea. Earlier developing larval stages migrate from the gut to the lungs via the circulation and/or lymphatics before invading alveolar air-spaces and forming young adults which ascend the bronchi. Free-living (preparasitic) larval stages develop on pastures and soils contaminated with host faecal material.

Pathogenesis: Light lungworm infections may remain asymptomatic or cause subclinical conditions possibly contributing to poor growth with associated production losses (reduced meat, milk and/or fibre production). Heavier infections, however, may cause clinical respiratory disease varying in severity depending on the parasite species (some species more virulent than others), host susceptibility (permissive species, young naive animals), and the dynamics (intensity) and kinetics (phase) of infection. The species *D. viviparus* causes parasitic bronchitis in cattle (also known as verminous pneumonia, husk, hoose or fog fever), while other species cause little or sporadic episodic disease in small ruminants and equids. The parasites live in the upper respiratory tract where developing larvae and adult worms cause traumatic damage to the mucosa exacerbated by host inflammatory responses, both leading to partial occlusion of the airways and respiratory distress typified by coughing, dyspnoea (shortness of breath, laboured breathing), hyperpnoea (rapid breathing), pulmonary oedema, emphysema and pneumonia. Hypersensitivity reactions may also develop in hosts following re-infection. Pathogenesis has been associated with 3 consecutive phases of infection: often described as the prepatent, patent and post-patent (or recovery) phases. In the first week after infection, ingested larvae penetrate the gut and migrate to the lungs but rarely cause clinical signs. However, the developing larvae cause damage to alveoli and bronchioles during the prepatent phase (from 8-25 days after infection) with inflammation (alveolitis, bronchiolitis and finally bronchitis) and cellular infiltrates (especially eosinophils) occluding airways and causing atelectasis (alveolar collapse) resulting in tachypnoea and coughing. Heavy infections may be fatal after 15 days due to respiratory failure with severe interstitial emphysema and pulmonary oedema. During the patent phase of infection (from 26-60 days after infection), disease is caused by a combination of bronchitis and pneumonia. The development of worms in the bronchi and distal trachea causes severe catarrhal bronchitis with epithelial hyperplasia, cellular infiltrates and excess mucus production (worms becoming embedded in white frothy mucus). Pneumonia develops when the congestion spreads to the lungs, particularly in areas around infected bronchi which collapse when aspirated eggs and larvae elicit dense cellular infiltrates (polymorphs, macrophages and multinucleated giant-cells) with interstitial emphysema, pulmonary oedema, alveolar epithelialization and hyaline membrane formation. Clinical signs progress from an occasional cough when exercised to a deep harsh cough at rest (with squeaks and crackles on auscultation), dyspnoea (animals adopting an 'air-hunger' disposition with mouth-breathing and outstretched necks), hyperpnoea and tachypnoea (> 60 respirations per minute), tenacious nasal discharges, excessive salivation, anorexia, unthriftiness with poor growth and weight loss, sometimes proving fatal. Most animals recover slowly in a post-patent phase (from 60-90 days after infection) when adult worms are expelled by adaptive (acquired) immune responses and inflammation subsides with improved respiration, less frequent coughing, and animals resuming weight gain. Lesions may persist in some animals, mostly involving bronchial/peribronchial fibrosis with surrounding alveolar epithelialization, sometimes leading to sporadic mortalities due either to post-patent bronchitis (proliferation of type 2 pneumocytes with emphysema and oedema associated with degenerating worms) or acute interstitial pneumonia (due to secondary bacterial infections in damaged lungs). Young animals are most susceptible to clinical infections due to their immature immune systems, while adult animals develop strong protective immune responses unless malnourished or immunocompromised. Infective larvae that have become trapped in lymph nodes generate some resistance to infection (but it rapidly weakens and only lasts around 6 months), whereas developing larvae and worms in the lungs stimulate more persistent cellular and humoral responses (lasting for 2 years or

more if maintained by repeated exposure). Occasionally, the massive uptake of larvae may establish infections quicker than the immune system can respond, thus leading to the phenomenon known as re-infection syndrome. Infections are more prevalent and severe in cattle farmed under intensive conditions, particularly dairy or dairy-cross calves during their first grazing season on permanent or semipermanent pastures. Infections in deer are variable in presentation, with animals often tolerating high worm burdens until subject to nutritional or behavioural stress due to poor season or frequent herding. Animals may quickly lose condition and die with little or no warning. Infections in sheep and horses are rarely associated with disease, although some horses may develop atypical lesions involving raised circumscribed pulmonary lesions (30-50 mm in diameter) containing worms and mucopurulent discharge.

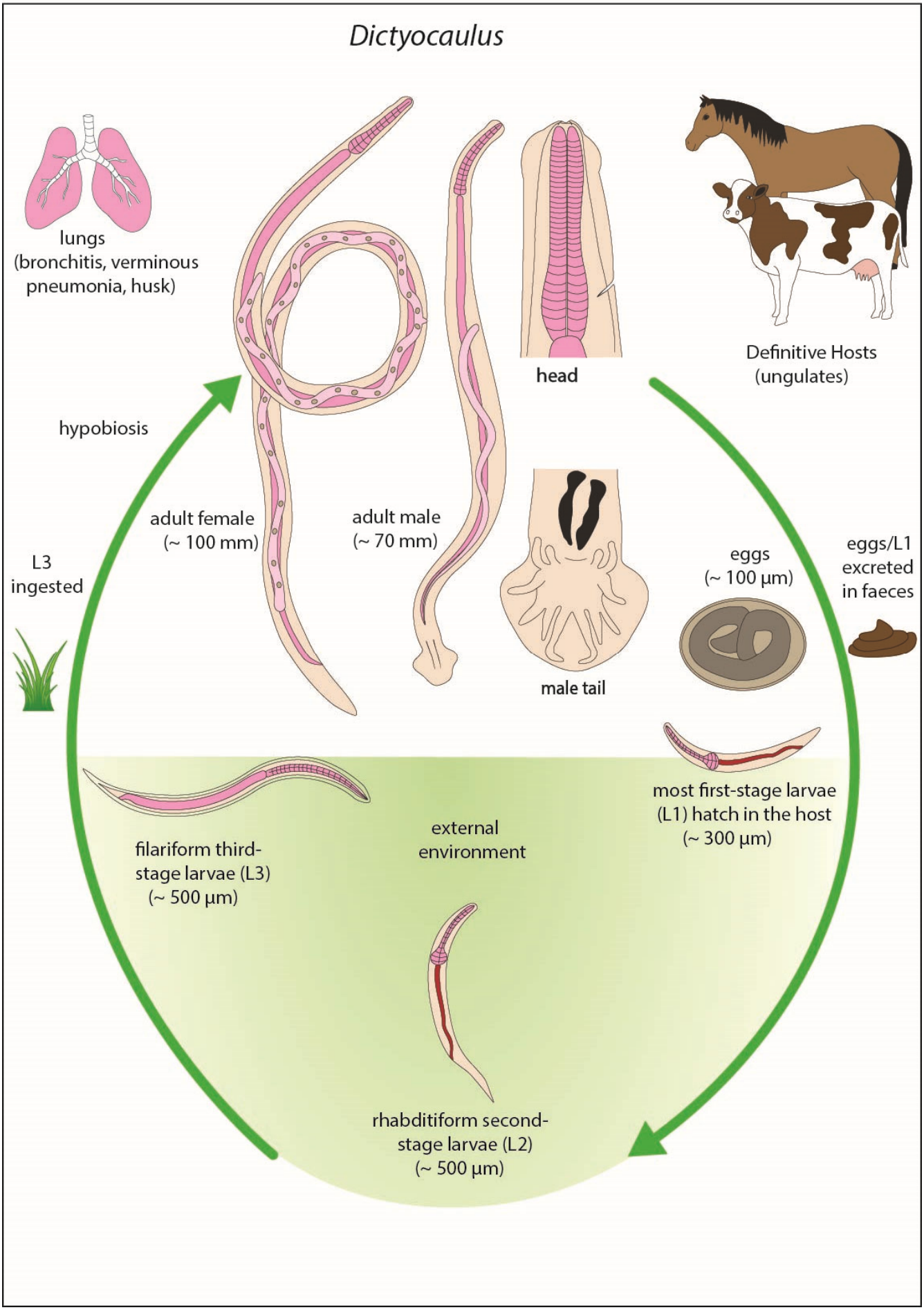
Developmental cycle and mode of transmission: *Dictyocaulus* spp. have direct monoxenous (one-host) life-cycles with faecal-oral transmission involving larval stages on pastures. Gravid female lungworms lay fully embryonated (larvated) eggs which hatch almost immediately in the airways releasing L1 which ascend the trachea to be swallowed and passed in host faeces. Some eggs may be swallowed intact and hatch in the intestines, while the eggs of a few species (e.g. *D. arnfieldi*) pass through the gut to be shed in faeces where they hatch shortly thereafter. The free-living L1 contain numerous food granules and are not rhabditiform and do not feed on bacteria. They moult to L2 within several hours and then to ensheathed L3 in 4-7 days in favourable environmental conditions, but take longer in suboptimal conditions. L3 are sensitive to heat and desiccation and survive only days in dry conditions, but they are quite resistant to cold and can survive on moist pastures and soils for months (overwintering in temperate regions). Infective L3 migrate horizontally out of faecal material onto surrounding vegetation, with those of some species (mainly in cattle) invading the sporangia of fungi (*Pilobolus* spp.) growing in faeces to be broadcast over several metres when the sporangia explode during sporulation. Grazing animals become infected when they ingest infective L3 on contaminated vegetation. The L3 exsheath in the gut and invade the wall of the abomasum or small intestines. They enter the lymphatics and move to the mesenteric lymph nodes where they remain for 5-6 days and moult to L4 without significant growth. The L4 migrate via the thoracic duct to the anterior vena cava, the heart and then the pulmonary arteries in the lungs where they penetrate into alveoli about 1 week after infection. Here they grow markedly and move to the bronchioles where they moult several days later to young adults (sometimes designated L5). Immature adults move up to the bronchi where they mature and mate, with gravid females laying embryonated eggs. The prepatent period (time from infection to the first excretion of eggs/larvae) varies from 3-5 weeks (8-14 weeks for *D. arnfieldi* in equids), and the adult worms live only for 7-10 weeks before being expelled by host immune responses. In some instances, the prepatent period may be extended for several months when developing stages (late L4 and early L5) undergo delayed maturation (developmental arrest or hypobiosis) overwinter in lymph nodes or bronchioles before resuming development in spring. Most cattle become infected as young animals (2-5 months of age) during their first grazing season on spring pastures, especially dairy or dairy-cross calves turned out after being housed indoors over winter. Clinical infections are more prevalent in livestock in temperate regions with mild climates, high rainfall and abundant permanent grass, whereas disease occurs intermittently in tropical areas particularly after heavy rainfall when animals congregate on raised damp areas.

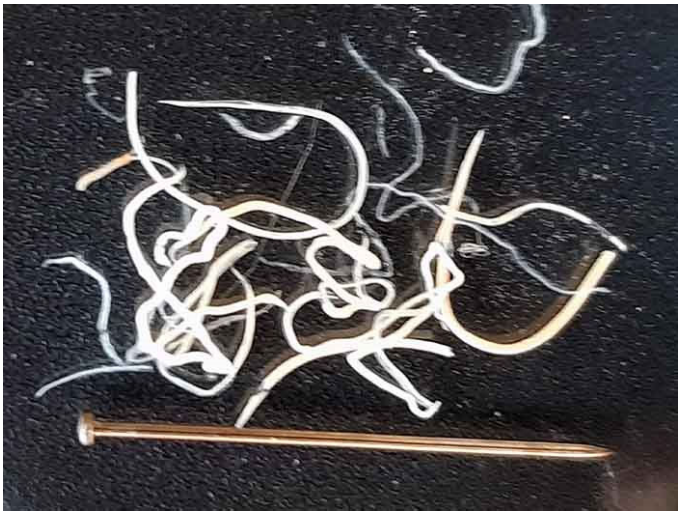
Differential diagnosis: Infections are strongly indicated on the basis of clinical signs (respiratory distress involving coughing) and relevant history (young naive animals, spring grazing, endemic region). However, the occurrence and severity of clinical signs varies considerably according to host species, being worse in cattle, sporadic in deer, and rare in small ruminants and equids. Coughing may be induced or become more pronounced in animals subject to mild exercise (e.g. chasing around a paddock) and physical examinations involving auscultation may help reveal sounds of bronchopneumonia. Infections are conventionally diagnosed by the detection of L1 in faecal samples (usually following their harvest by Baermann filtration), and sometimes by the detection of embryonated eggs in faecal concentrates (usually centrifugal floats). Counts of > 100 larvae per gram of faeces are considered significant, although larger numbers (> 1,000) may be present during patency. L1 appear as lethargic stages with rounded heads, granular intestines and bluntly pointed tails. Tracheal washes may also be examined for eggs, larvae and sometimes adults, and bronchoscopy may reveal parasites in the upper respiratory tract. At necropsy, worms may be detected in the bronchi upon dissection. Several immunoserological tests (mostly enzyme immunoassays) have been developed to detect specific host antibodies against *D. viviparus* antigens. They have generally yielded good sensitivity and specificity, with a few false positives, and seroconversion was shown to take around 4-6 weeks but only persisted for 4-7 months. Molecular biological techniques have been used to characterize parasite species following the polymerase chain reaction (PCR) amplification (including multiplex PCR and real-time PCR) of nuclear gene sequences (particularly the internal transcribed spacer 2 of ribosomal RNA).

Treatment and control: Lungworms infections may be treated with a range of anthelmintic drugs, but care should be taken to avoid excessive dosing which may interfere with the development of natural protective immunity as well as predispose towards the emergence of drug resistance. Treatment appears to be most effective against mature stages within the respiratory tree, but is less effective against developing or hypobiotic stages in host tissues. It is therefore recommended that longer-acting drugs, such as some benzimidazoles (albendazole, oxfendazole, fenbendazole) and macrocyclic lactones (ivermectin, eprinomectin, abamectin, moxidectin) be used, with follow-up treatment as required. Many animal health authorities also recommend that strategic dosing be used to prevent heavy pasture contamination and to protect young animals while they acquire protective immune responses. Treatment may initially worsen clinical signs due to parasite death and host inflammatory responses, so some supportive therapy may be required in the form of non-steroidal anti-inflammatory agents, antibiotics to ameliorate secondary bacterial pneumonia, electrolyte replacement for dehydrated animals, dietary supplementation to reduce nutritional stress, and even sheltered housing in

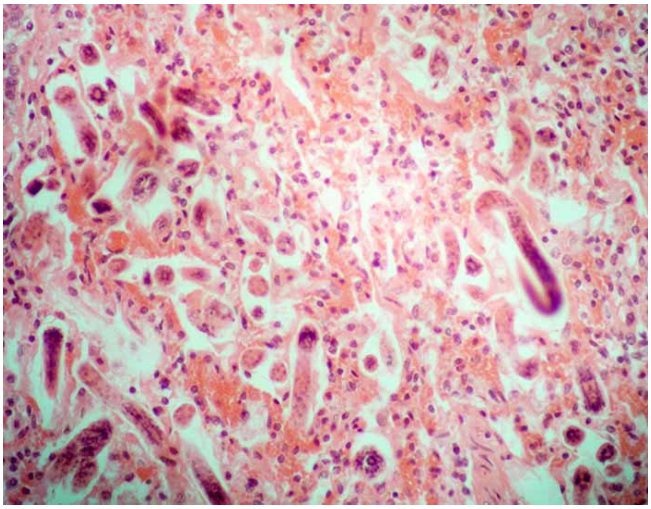
poor weather conditions. Despite treatment, some animals may experience relapses of respiratory signs due to the severity and poor resolution of lung pathology. An alternative, or better yet a supplement, to drug treatment is that of vaccination, as this parasitic disease is one of the few for which effective vaccines have been developed, predominantly for use in cattle. Two doses of live attenuated (gamma-irradiated) larvae 2-4 weeks apart stimulates the development of strong protection against disease, but does not completely eradicate existing infections (generating a concomitant or premunitive immunity, rather than a sterile immunity). Vaccination is primarily targeted at young animals in their first grazing season, but is effective in older animals, including pregnant breeders. It is most effective on farms in endemic areas, particularly when remembering that vaccinated animals need further exposure to infection by low levels of pasture larvae in order to develop a natural acquired immunity. Various preventive strategies have been applied, usually at the farm level, to reduce transmission rates, principally involving improved sanitation (faecal removal, cleaning pens), maintaining good hygiene (clean water, food troughs for supplementary feed), stock management (closed herds, quarantining imports, avoid overstocking, separating cohorts) and pasture management (rotational and/or mixed grazing, draining wet pastures, spelling pastures). Several studies on biological control using nematode-trapping fungi or dung beetles demonstrated modest reductions in pasture larval contamination, but no methods have yet been commercialized.

Dictyocaulus



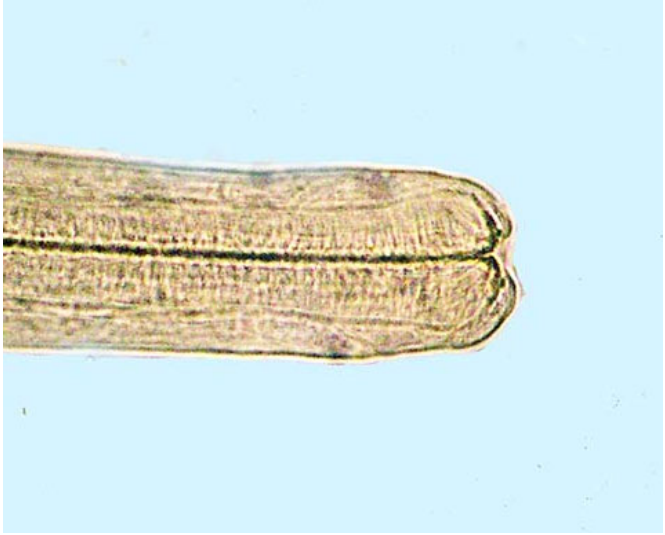


Dictyocaulus adult worms



Dictyocaulus lung lesion

Dictyocaulus adult worm, male bursa



Dictyocaulus adult worm, head