Physaloptera
(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 tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including physalopteroids (with pseudolabia and teeth) found in the stomachs of cats and dogs, and transmitted by beetles, cockroaches and crickets in which L3 develop. Small mammals (esp. rodents), birds and reptiles may also act as paratenic hosts for L3. Infections by *Physaloptera* spp. have been associated with vomiting and anorexia in cats.

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:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Physalopteroidea (stomach worms in mammals, insect IH)
Family:	Physalopteridae (two large lateral pseudolabia, armed with teeth, lips with basal collar, caudal alae on males)
Genus:	*Physaloptera* (parasitic in stomach of cats)
Species:	various species cause vomiting and anorexia in cats

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 (some monodelphic or polydelphic) with 2 ovaries, 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 IHs
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.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Physalopteroidea contains moderately large worms with an anterior collarette and large pseudolabia infecting the alimentary tract of vertebrates and using insects as intermediate hosts for larval development. The single family Physalopteridae is recognised with 3 subfamilies: Physalopterinae (caudal papillae distinct from cuticular ornamentation, caudal alae united on ventral surface, bursa ornamented, parasites of terrestrial vertebrates); Proleptinae (caudal papillae distinct from cuticular ornamentation, caudal alae fading into lateral borders, small area rugosa, parasites of elasmobranchs and marine fishes); and Thubunaeinae (collarette absent, caudal papillae similar to cuticular ornamentation, parasites of reptiles and amphibians). The subfamily Physalopterinae contains 9 genera: *Abbreviata, Kreisiella, Paraphysaloptera, Pentadenoptera* (syn. *Physalopteriata*), *Physaloptera, Pseudabbreviata, Pseudophysaloptera, Skrjabinoptera,* and *Turgida.*

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Physaloptera	135	carnivores, birds, reptiles	stomach, intestines	10-60 mm long, collar, buccal capsule with pseudolabia and teeth, bipartite oesophagus, tail with prepuce-like cuticular extension	44-58 x 29-42 µm, ovoid, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, reptile PH]

The genus *Physaloptera* is characterised by stomach worms possessing a cephalic collarette, large dentate pseudolabia (each with 3 internal teeth), 4 pairs of pedunculate papillae, a prepuce-like cuticular extension on the tail and female worms having two to several uteri. Some workers proposed 2 subgenera: *P.* (*Physaloptera*) (male with closed prepuce-like sheath on posterior end); and *P.* (*Chlamydonema*) (male and female with open prepuce-like sheath at distal end). Other workers recognised several species groups according to female uterus type: namely, didelphic, tridelphic, tetradelphic and polydelphic with 2, 3, 4 or > 4 uteri/uterine branches, respectively. Regrettably, many early descriptions did not include enough detail for species to be classified to subgenus or species group. To date, some 135 *Physaloptera* species have been described from a range of vertebrate definitive hosts; mostly terrestrial reptiles, birds of prey, marsupials, rodents, insectivores, carnivores, and primates (including some reports in humans). The parasites have indirect life-cycles with larvae developing in invertebrate intermediate hosts (esp. insects such as beetles, cockroaches, and crickets) and sometimes being transported by vertebrate paratenic hosts (small rodents, birds, and reptiles).

***Physaloptera* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Intermediate Hosts [plus Paratenic Hosts (PH)]**	**Distribution**
Group Didelphys				
P. abjecta	Serpentes: colubrid (coachwhip, prairie kingsnake)	stomach		North America
P. acuticauda	Accipitriformes: accipitrid (bicoloured hawk, red-tailed hawk, broad-winged hawk, grey-headed hawk, hen harrier); Falconiformes: falconid (peregrine falcon, laughing falcon)	stomach, oesophagus		Holarctic
P. agkistrodontis	Serpentes: viperid (sharp-nosed pitviper)			Asia
P. alata (incl. subspp. *alata*, *chevreuxi*)	Accipitriformes: accipitrid (Eurasian sparrowhawk, besra, shikra, roadside hawk, kestrel hawk, crested goshawk, hen harrier, Montagu's harrier, short-toed snake eagle, booted eagle, common buzzard, European honey buzzard); Falconiformes: falconid (saker falcon, laughing falcon, peregrine falcon, Eleonore's falcon, common kestrel, Eurasian hobby); Galliformes: phasianid (jungle bushquail)	stomach, intestines		Eurasia
P. anomala	Carnivora: felid (jaguar)	stomach		South America
P. apivori	Accipitriformes: accipitrid (European honey buzzard)			Europe
P. bainae	Sauria: teiid (Argentine black-and-white tegu)	stomach		South America
P. banfieldi	Peramelemorphia: peramelid (northern brown bandicoot); Rodentia: murid (fawn-footed mosaic-tailed rat)			Australia
P. bedfordi	Chiroptera: rhinolophid (Geoffroy's horseshoe bat)			Africa
P. bispiculata	Carnivora: felid (cat, wildcat), mustelid (honey badger); Rodentia:	stomach		Africa, Americas

	cricetid (South American water rat, hispid cotton rat); Lagomorpha: ochotonid (American pika)			
P. bonnei	Sauria: teiid (tegu (sapakara))	stomach		South America
P. brachycerca	Accipitriformes: accipitrid (lizard buzzard)	stomach		Africa
P. brevivaginata	Chiroptera: miniopterid (common bentwing bat), vespertilionid (greater mouse-eared bat, lesser mouse-eared bat, grey long-eared bat, Kuhl's pipistrelle)	stomach		Europe
P. canis	Carnivora: canid (black-backed jackal), felid (Southern African wildcat), viverrid (common genet, Cape genet)			Africa
P. cerdocyona	Carnivora: canid (crab-eating fox)	subcutis		Africa
P. chamaeleontis	Sauria: chamaeleonid (slender chameleon)	stomach		Africa
P. P. clausa	Carnivora: canid (culpeo, gray fox, South American gray fox); Eulipotyphla: erinaceid (north African hedgehog, European hedgehog, northern white-breasted hedgehog, southern white-breasted hedgehog, long-eared hedgehog, desert hedgehog)	stomach	[PH: Sauria: lacertid (sand lizard, European green lizard); Rodentia: dipodid (southern birch mouse)]	South America, Africa
P. crosi	Accipitriformes: accipitrid (Bonnelli's eagle); Coraciiformes: coraciid (European roller); Strigiformes: strigid (Eurasian eagle-owl)	stomach		Eurasia
P. cruzsilvai	Accipitriformes: accipitrid (white-bellied sea-eagle)			Asia
P. galinieri	Accipitriformes: accipitrid (unspecified eagle)	stomach, oesophagus		Eurasia
P. getula	Rodentia: cricetid (South American water rat), murid (mouse, black rat, Polynesian rat)	stomach		Americas, Asia, Africa
P. herthameyerae	Didelphimorphia: didelphid (agile gracile opossum)	stomach		South America
P. hispida	Rodentia: cricteid (hispid cotton rat, marsh rice rat, cotton mouse, Oldfield mouse, Florida mouse), murid (brown rat)	stomach	Blattodea: blattid (cockroach, *Blatella germanica*); Coleoptera: carabid (ground beetle, *Harpalus*); Dermaptera: forficulid (earwig, *Forficula auricularia*)	Americas
P. immerpaini	Eulipotyphla: erinaceid (Southern African hedgehog)			Africa
P. limbata	Eulipotyphla: talpid (eastern mole, prairie mole, Missouri valley mole, hairy-tailed mole), soricid (northern short-tailed shrew); Rodentia: geomyid (plains pocket gopher)	stomach, intestines		North America
P. liophis	Serpentes: colubrid (military ground snake)	stomach		South America
P. longissima	Serpentes: colubrid (unspecified snakes)			Australia
P. losseni	Accipitriformes: accipitrid (white-collared kite)	pharyngeal cavity		South America
P. lumsdeni	Primates: galagid (bush baby)			Africa
P. lutzi	Sauria: teiid (giant ameiva,			South

	Brazilian whiptail lizard), tropidurid (neotropical ground lizard, Amazon lava lizard)			America
P. malayensis	Carnivora: felid (junglecat, bushcat, tiger), hyaenid (striped hyena)	stomach, intestines		Malaysia
P. masoodi	Primates: lorisid (slender loris)	stomach		Eurasia
P. massino	Rodentia: dipodid (Gobi jerboa, Mongolian five-toed jerboa), murid (mouse), sciurid (Siberian chipmunk, Tarbagan marmot, long-tailed ground squirrel, Sherman's fox squirrel); Lagomorpha: ochotonid (Daurian pika)			Africa, Europe
P. maxillaris	Carnivora: mephitid (striped skunk, hooded skunk, Molina's hog-nosed skunk), canid (gray fox); Pelecaniformes: pelecanid (brown pelican)	stomach	Orthoptera: gryllid (fall field cricket); Blattodea: blattid (unspecified cockroach) [plus PH: Anura: ranid (northern leopard frog); Serpentes: colubrid (common garter snake)]	Americas
P. mexicana	Accipitriformes: accipitrid (buzzard)			North America
P. mirandai	Didelphimorphia: didelphid (brown four-eyed opossum)			South America
P. monodens	Serpentes: boid (boa constrictor)	stomach, intestines		South America
P. murisbrasiliensis	Rodentia: cricetid (web-footed marsh rat, hispid cotton rat), murid (Polynesian rat), sciurid (Brazilian squirrel)	stomach, small intestines		cosmopolitan
P. myotis	Chiroptera: miniopterid (common bentwing bat), rhinolophid (greater horseshoe bat, lesser horseshoe bat), vespertilionid (common noctule, lesser mouse-eared bat, greater mouse-eared bat, serotine bat, Bechstein's bat, Daubenton's bat, Nathusius's pipistrelle)			Eurasia
P. ngoci	Eulipotyphla: erinaceid (short-tailed gymnure); Rodentia: murid (mouse, rat)			Asia
P. obtusissima	Sauria: iguanid (Mexican spiny-tailed iguana); Serpentes: colubrid (indigo snake)	stomach		Americas
P. papillotruncata	Pilosa: choloepodid (Linnaeus's two-toed sloth), myrmecophagid (collared anteater)	stomach		South America
P. phrynosoma	Sauria: phrymnosomatid (Texas horned lizard, regal horned lizard)	stomach		Americas
P. (C.) praeputialis (syn. *P. (C.) felineus*)	Carnivora: felid (cat, sand cat, fishing cat, Pallas's cat, wildcat, South African wildcat, bobcat, lynx, Canada lynx, Iberian lynx, leopard cat, cougar, leopard, clouded leopard, ocelot, jaguarundi), canid (dog, wolf, maned wolf, red fox, corsac fox, Iberian fox), viverrid (common genet)	stomach [vomiting, anorexia]	Orthoptera: anostostomatid (king cricket), gryllid (Jamacian field cricket, *Acheta assimilis,* trilling cricket, *Gryllus*, striped cricket, *Miogryllus*), rhaphidophorid (camel cricket, *Ceuthophilus*); Dictyoptera: blattid (American cockroach, *Periplaneta americana*, Australian cockroach, *P. australasiae*); ectobiid	worldwide

			(German cockroach, *Blatella germanica*) [plus PH: Anura: bufonid (European green toad); Sauria: agamid (steppe agama), sphaerodactylid (frog-eyed gecko), varanid (desert monitor); Serpentes: colubrid (diadem snake, spotted desert racer), lamprophiid (arrow snake), viperid (painted carpet viper, lebetine viper); Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: murid (mouse)]	
P. pseudopraeputialis	Carnivora: felid (cat)	stomach		Philippines
P. rapacis	Accipitriformes: accipitrid (steppe eagle)			Africa
P. rara (syn. *P. felidis*) (oesophageal worm)	Carnivora: canid (dog, coyote, wolf, red fox, gray fox), felid (cat, bobcat, cougar, ocelot), mustelid (badger), procyonid (raccoon), ursid (American black bear, Florida black bear)	stomach, intestines [vomiting, anorexia]	Coleoptera: carabid (ground beetle, *Harpalus*), tenebrionid (flour beetle, *Tribolium confusum*); Blattodea: ectobiid (German cockroach, *Blatella germanica*), Orthoptera: gryllid (Jamacian field cricket, *Acheta assimilis*), acridid (red-legged grasshopper, *Melanoplus femurrubrum*) [plus PH: Serpentes: viperid (prairie rattlesnake); Rodentia: murid (mouse); Anura: ranid (northern leopard frog)]	North America, Egypt
P. reevesi	Accipitriformes: accipitrid (Eurasian sparrowhawk, crested goshawk)			Eurasia
P. retusa	Sauria: anguid (southern alligator lizard, Mexican alligator lizard, snake lizard), crotaphytid (long-nosed leopard lizard), iguanid (Lutz's tree iguana), liolaemid (Lutz's tree iguana), phrynosomatid (western fence-lizard, eastern fence-lizard, common side-blotched lizard, torquate lizard, rosebelly lizard, bluebelly lizard, zebra-tailed lizard, canyon lizard, cleft lizard, plateau spiny lizard, crevice spiny lizard, blue spiny lizard, desert spiny lizard, granite spiny lizard, Mexican emerald spiny lizard, Boccourt's spiny lizard, Yarrow's spiny lizard, plateau lizard, sage brush lizard, mesquite lizard), scincid (western skink, Paraguay mabuya), teiid (giant ameiva, rainbow ameiva, canyon spotted whiptail, rainbow whiptail, Brazilian whiptail, Spix's whiptail),	stomach, intestines	[PH: Anura: bufonid (granular toad, leaf litter toad)]	Americas

	tropidurid (Amazon lava lizard); Serpentes: colubrid (hog-nosed snake)			
P. semilanceolata	Carnivora: procyonid (white-nosed coati)	stomach		South America
P. seurati	Eulipotyphla: erinaceid (Algerian hedgehog, desert hedgehog)	stomach		Africa
P. sibirica	Carnivora: canid (wolf, red fox, corsac fox), felid (lynx), mustelid (European badger, mountain weasel, Siberian weasel)		[PH: Rodentia: glirid (garden dormouse)]	Eurasia
P. spinicauda	Rodentia: sciurid (Nelson's antelope squirrel)			North America
P. squamatae	Sauria: dactyloid (brown anole), leiocephalid (northern curly-tailed lizard), phrynosomatid (Florida scrub lizard), scincid (little brown skink), teiid (Caribbean ameiva); Serpentes: viperid (eastern copperhead, Texas copperhead)			Americas
P. subalata	Accipitriformes: accipitrid (bicoloured hawk, crane hawk)	stomach		South America
P. tacapensis	Rodentia: ctenodactylid (common gundi)	stomach		Eurasia
P. terdentata	Carnivora: felid (cougar, tiger)	stomach		South America
P. thalacomys	Peramelemorphia: peramelid (eastern barred bandicoot), thylacomyid (lesser bilby)			Australia
P. tupinambae	Sauria: teiid (Argentine black-and-white tegu)	stomach		South America
Group Tridelphys				
P. cebi	Primates: cercopithecid (hamadryas baboon, crab-eating macaque)	stomach		South America
P. coelebs	Afrosoricida: tenrecid (tenrec)			Madagascar
Group Tetradelphys				
P. bluntschlii	Afrosoricida: tenrecid (tenrec)	stomach		Madagascar
P. colubri	Serpentes: colubrid (smooth snake)	intestines		Australia
P. ericuli	Afrosoricida: tenrecid (spiny tenrec)			Madagascar
P. (C.) lagothricis	Primates: atelid (spider monkey)			Africa
P. magnipapilla	Pilosa: myrmecophagid (collared anteater)	stomach		South America
P. singhi	Primates (unspecified South American monkey)			South America
P. simplicidens	Sauria: scincid (sleepy lizard)			Australia
P. tumefaciens	Primates: cercopithecid (stump-tailed monkey, crab-eating macaque)	stomach		Asia
Group Polydelphys				
P. capensis	Rodentia: sciurid (Cape ground squirrel)	stomach		Africa
P. dilatata	Carnivora: felid (cougar, margay); Primates: atelid (brown woolly monkey), callitrichid (golden lion tamarin, marmoset), pitheciid (black bearded saki, titi monkey)	intestines, stomach		South America
P. torresi	Didelphimorphia: didelphid (common opossum); Lagomorpha: cuniculid (lowland paca); Rodentia: dasyproctid (agouti), cricetid (rice rat)	stomach		South America
P. turgida	Didelphimorphia: didelphid	stomach	Blattodea: blattid (German	Americas

(syn. *Turgida*)	(Virginia opossum, big-eared opossum, brown four-eyed opossum, bare-tailed woolly opossum); Carnivora: mustelid (American badger); Primates: cercopithecid (gelada)		cockroach, *Blatella germanica*); Orthoptera: gryllid (field cricket, *Acheta pennsylvanicus*)	
Group undetermined				
P. accipiteri	Accipitriformes: accipitrid (shikra)			India
P. ackerti	Didelphimorphia: didelphid (Virginia opossum)	stomach		North America
P. aduensis	Rodentia: murid (Peters's striped mouse)			Africa
P. (C.) agarwali	Carnivora: felid (tiger)			
P. amphibia	Anura: ranid (fanged river frog)	stomach		Eurasia
P. anadonta	Eulipotyphla: erinaceid (long-eared hedgehog)	stomach		Eurasia
P. bedfordi	Chiroptera: rhinolophid (Geoffroy's horseshoe bat)			Africa
P. bellicosa	Sauria: chamaeleonid (southwestern Madagascar chameleon)			Madagascar
P. bilabiata	Passeriformes: laniid (lesser grey shrike)	intestines		Eurasia
P. brevispiculum	Carnivora: felid (cat, wildcat, rusty spotted cat, African wildcat, leopard cat), mustelid (honey badger), viverrid (small Indian civet)	stomach	Dermaptera: labidurid (earwig, *Labidura riparia*) [plus PH: Sauria: agamid (Indian spiny-tailed lizard), gekkonid (yellow-belly gecko); Anura: bufonid (Indian marbled toad); Rodentia: sciurid (Indian palm squirrel)]	Africa, Asia
P. buteonis	Accipitriformes: accipitrid (red-tailed hawk)			North America
P. cahuidei	Carnivora: mephitid (Molina's hog-nosed skunk)			South America
P. calunensis	Rodentia: cricteid (small vesper mouse)	stomach		South America
P. cesticillata	Carnivora: canid (fennec fox)	stomach		Egypt
P. circularis	Rodentia: murid (black rat)	stomach		Africa
P. citilli (*citelli*)	Rodentia: sciurid (European ground squirrel)	stomach		Eurasia
P. confusa	Serpentes: elapid (tiger snake)		[PH: Anura: hylid (Australian green tree frog, Peron's tree frog), limnodynatsid (pobblebonk, spotted grass frog), pelodryadid (golden bell frog)	Australia
P. crassa	Passeriformes: alaudid (Eurasian skylark)	intestines		Eurasia
P. dentata	Sauria: agamid (steppe agama, secret toadhead agama); Serpentes: viperid (common European viper)	intestines, mouth		Russia
P. digitata	Carnivora: felid (cougar)	stomach		South America
P. dispar	Eulipotyphla: erinaceid (African hedgehog, North African hedgehog)	stomach		Africa
P. dogieli	Rodentia: murid (Libyan jird, Persian jird, Tristam's jird), sciurid (long-tailed ground squirrel)			Eurasia
P. elegantissima	Carnivora: mustelid (honey badger)	stomach		Africa

P. galvaoi	Rodentia: cricetid (terraced rice rat)	stomach		South America
P. georginapedreirae	Serpentes: elapid (coral snake)			
P. goytaca	Rodentia: cricteid (goytaca)	stomach		South America
P. guiarti	Carnivora: phocid (Weddell seal)	stomach		Antarctica
P. incurva	Eulipotyphla: erinaceid (southern African hedgehog)	stomach, intestines		Africa
P. inermis	Rodentia: sciurid (Prevost's squirrel)	stomach		Eurasia
P. inflata	Accipitriformes: accipitrid (Harris's hawk)	stomach, oesophagus		Central America
P. lagarda	Sauria: teiid (red tegu)			South America
P. longispicula	Rodentia: echimyid (common punare)	stomach		South America
P. massimo	Rodentia: sciurid (fox squirrel, thirteen-lined ground squirrel)			North America
P. megalostoma	Accipitriformes: accipitrid (Eurasian sparrowhawk)	proventriculus		Eurasia
P. mephites	Carnivora: mephitid (skunk)			South America
P. mydai	Carnivora: mephitid (stink badger)	stomach		Asia
P. nasilionis	Macroscelidea: macroscelidid (elephant shrew)	connective tissue		Africa
P. pacitae	Carnivora: felid (cat)	stomach		Philippines
P. papuensis	Peramelemorphia: peramelid (spiny bandicoot)			Australasia
P. parvicollaris	Peramelemorphia: peramelid (long-nosed bandicoot)			Australia
P. peragale	Peramelemorphia: thylacomyid (lesser bilby)			Australia
P. peramelis	Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot), thylacomyid (lesser bilby)			Australia
P. pyramidalis	Pilosa: choloepodid (Linnaeus's two-toed sloth)			South America
P. quadridentata	Accipitriformes: accipitrid (broad-winged hawk)			North America
P. rauschi	Carnivora: mustelid (American badger)			North America
P. ruwenzorii	Rodentia: murid (Abyssinian grass rat, Natal multimammate mouse)	intestines		Africa
P. sarcophili	Dasyuromorphia: dasyurid (northern quoll, tiger quoll, Tasmanian devil)			Australia
P. sciuri	Rodentia: sciurid (Mentawai squirrel)	stomach, intestines		Asia
P. sonsinoi	Sauria: agamid (desert agama)	stomach		Europe
P. spiralis	Sauria: amphisbaenid (worm lizard)	stomach		South America
P. tadorna	Anseriformes: anatid (common shelduck)			Eurasia
P. tigrinae	Anura: ranid (Indian bullfrog)			India
P. torquata	Carnivora: mustelid (American badger, wolverine); Rodentia: cricteid (hispid cotton rat)	stomach		America
P. transfuga	Carnivora: canid (dog), felid (cat); Primates: hominid (human)		Coleoptera (unspecified beetle)	
P. troughtoni	Rodentia: murid (bush rat)			Australia
P. truncata	Galliformes: phasianid (junglefowl)	stomach		South

				America
P. upembae	Gruiformes: rallid (African swamphen)			Africa
P. variegata	Serpentes: colubrid (eastern racer, eastern hognose snake); Sauria: anguid (eastern glass lizard)			North America
P. versicoli	Sauria: agamid (oriental garden lizard)			Asia
P. vigisiana	Galliformes: phasianid (chicken)			Russia
P. visakhapatnamensis	Rodentia: sciurid (Indian palm squirrel)			Asia
P. zigodontomis	Rodentia: cricetid (cane mouse)			Asia
Species inquirenda				
P. brevicauda sp. inq.	Galliformes: phasianid (red-billed spurfowl)	intestines		Africa
P. hieracideae sp. inq.	Falconiformes: falconid (brown hawk)			Australia
P. malleus sp. inq.	Passeriformes: corvid (hooded crow, Eurasian magpie)			Eurasia
P. papilloradiata sp. inq.	Carnivora: canid (wolf)	pectoral cavity		Eurasia
P. spirula sp. inq.	Hyracoidea: procaviid (rock hyrax, Cape hyrax)	large intestines		Eurasia
Re-assigned species				
P. abbreviata (now *Abbreviata*)	Sauria: agamid (sand lizard), anguid (European glass lizard), lacertid (ocellated lizard, European green lizard, Iberian emerald lizard, Iberian wall lizard); Serpentes: colubrid (water snake)	stomach		North Africa, Europe
P. africana (now *Abbreviata*)	Rodentia: murid (striped mouse, white-nosed rat, Pretoria rat), octodontid (cane rat), sciurid (gray-footed squirrel)			Africa
P. aloisii-sabaudiae (now *Abbreviata*)	Sauria: agamid (black-necked agama)	intestines		Africa
P. amaniensis (now *Abbreviata*)	Sauria: agamid (dragon lizard)			Africa
P. antarctica (syn. *P. alba*) (now *Abbreviata*)	Serpentes: pythonid (diamond python), elapid (death adder); Sauria: scincid (western blue-tongued lizard, eastern blue-tongued lizard), varanid (lace monitor)	stomach, oesophagus		Australia
P. bancrofti (syn. *P. natricus, physignathi*) (now *Abbreviata*)	Sauria: agamid (Australian water dragon), gekkonid (broad-tailed gecko); Serpentes: colubrid (Bismarck keelback)			Australia, New Zealand
P. britanica (now *Abbreviata*)	Sauria: agamid (unspecified agamid)	intestines		Africa
P. bulbosa (now *Cyrnea*)	Galliformes: phasianid (green peafowl)	stomach		Asia
P. calotisi (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. capensis (now *Abbreviata*)	Rodentia: sciurid (Cape ground squirrel)			Africa
P. caucasica (syn. *P. mordens*) (now *Abbreviata*)	Primates: cercopithecid (hamadryas baboon, yellow baboon, chacma baboon, Barbary macaque, rhesus macaque), hominid (orangutan, human)	stomach, oesophagus, intestines	Blattodea: blattid (German cockroach, *Blatella germanica*); Coleoptera (unspecified beetle); Orthoptera: acridid (desert locust, *Schistocerca gregaria*)	Africa

P. constricta (now *Spiroxys*)	Serpentes: colubrid (common water snake)	stomach		North America
P. contorta (now *Spiroxys*)	Testudines: emydid (pond slider, chicken turtle, eastern box turtle), kinosternid (eastern mud turtle)	stomach		North America
P. funambuli (now *Abbreviata*)	Rodentia: sciurid (northern palm squirrel)			Asia
P. gemina (now *Abbreviata*)	Carnivora: felid (cat)	stomach, intestines		Egypt
P. gracilis (now *Abbreviata*)	Sauria: lacertid (unspecified lizard)			Africa
P. guptae (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. kotlani (syn. *P. soricina, riukiuana*) (now *Pseudophysaloptera formosana*)	Eulipotyphla: soricid (common shrew, alpine shrew, bicoloured shrew, Eurasian pygmy shrew, Asian house shrew, Laxmann's shrew, moonrat); Rodentia: sciurid (squirrel, long-tailed ground squirrel, tropical ground squirrel)	stomach		Eurasia
P. indica (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. johnsoni (now *Abbreviata*)	Sauria: varanid (monitor lizard)			Asia
P. joyeuxi (now *Abbreviata*)	Artiodactyla: suid (warthog)			Africa
P. kherai (now *Abbreviata*)	Sauria: varanid (yellow monitor)			Asia
P. leptosoma (now *Abbreviata*)	Sauria: agamid (North African spiny-tailed lizard, Moroccan spiny-tailed lizard), varanid (desert monitor)	stomach, oesophagus		Africa
P. mucronata (now *Ascaris*)	Crocodilia: alligatorid (American alligator)			North America
P. multipapillata (now *Abbreviata*)	Primates: cercopithecid (hamadryas baboon)			Africa
P. musculi (now *Abbreviata*)	Rodentia: murid (mouse)			Sri Lanka
P. numidica (now *Abbreviata*)	Rodentia: murid (North African gerbil)	stomach		Africa
P. ortleppi (now *Abbreviata*)	Sauria: chamaeleonid (flap-necked chameleon)			Africa
P. ovata (now *Cyrnea*)	Accipitriformes: accipitrid (black sparrowhawk)	ventriculus		Africa
P. pallaryi (now *Abbreviata*)	Sauria: agamid (Bibron's agama)	stomach, intestines		Africa
P. paradoxa (syn. *P. affinis, algeriensis*) (now *Abbreviata*)	Sauria: varanid (white-throated monitor, rock monitor, gray monitor); Serpentes: colubrid (whipsnake), psammophiid (hissing sand snake), viperid (horned viper)	stomach, intestines		Africa
P. poicilometra (now *Abbreviata*)	Primates: cercopithecid (blue monkey, mangabey, guenon)	stomach		Africa
P. polydentata (now *Abbreviata*)	Sauria: gekkonid (tropical house gecko)			Africa
P. ranae (now *Abbreviata*)			[larvae: Anura: ranid (American bullfrog, southern leopard frog, northern leopard frog), bufonid (Woodhouse's toad)]	Americas
P. rotundata	Otidiformes: otidid (MacQueen's	intestines		Asia

(now *Habronema*)	bustard)			
P. saginata (now *Spiroptera*)	Caprimulgiformes: caprimulgid (goatsucker); Passeriformes: corvid (crow)			
P. striata (now *Cyrnea*)	Ciconiiformes: ciconiid (white-stork); Serpentes: colubrid (dice snake)	stomach		Eurasia
P. tasmani (now *Abbreviata*)	Sauria: chamaeleonid (chameleon)			Africa
P. tenuicollis (now *Ascaris*)	Accipitriformes: pandionid (osprey)	intestine		Europe
P. terrapenis (now *Abbreviata*)	Testudines: chelydrid (common snapping turtle), emydid (western box turtle, western painted turtle, Blanding's turtle)			North America
P. thaparus (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. vandenbrandeni (now *Abbreviata*)	Carnivora: felid (wildcat)			Africa
P. varani (syn. *P. quadrovaria*) (now *Abbreviata*)	Sauria: varanid (yellow monitor, Bengal monitor, Indian monitor, Nile monitor), phrynosomatid (eastern fence lizard); Serpentes: colubrid (big-eye rat snake)	stomach, intestines		Asia, North America

Parasite morphology: *Physaloptera* spp. form 3 different types of morphological stages during their development: namely, eggs; larvae; and adult worms. The eggs range in size from 42-58 x 29-42 μm and are oval-elliptical in shape with slightly flattened sides. They are bound by a thick smooth shell thickened at the poles and are embryonated when laid. The parasites form 4 successive larval stages, usually encoded L1 to L4. The eggs contain coiled L1 which measure 150-250 μm in length and have conical heads with a subterminal left hook and 1-2 pairs of median scales, a bipartite oesophagus (with a posterior bulb), long sac-like intestines, and conical tails. L2 have elongate cylindrical bodies up to 1.2 mm long, laterally flattened mouths with cephalic and labial papillae, small buccal capsules, a divided oesophagus, and conical tails. L3 range in length from 1.5-4.2 mm and have adult cephalic characteristics (2 massive pseudolabia, each with an external tooth and 3 internal teeth), flattened mouths with labial papillae no longer identifiable, a divided oesophagus and conical tails. L4 are transient parasitic stages that have begun to develop sexual characteristics in the form of genital primordia. Adults are pink robust worms with cylindrical bodies ranging from 10-60 mm in length and are bound by thick cuticles with fine transverse striations. Most species possess an anterior cuticular recess appearing as a cervical collarette, broad caudal alae, and a preputial-like sheath extending posteriorly (closed distally in males of the subgenus *P.* (*Physaloptera*), but open in both males and females of the subgenus *P.* (*Chlamydonema*)). The anterior mouth is laterally flattened and possesses 2 large triangular lateral pseudolabia, each armed with 3 flattened internolateral teeth and a single conical externolateral tooth. The buccal capsule is atrophied and not well-developed or absent, and the bipartite oesophagus has a short anterior muscular and a long posterior glandular section. Adults worms are sexually dimorphic, with males being smaller than females (10-45 cf. 15-60 mm). Mature males have coiled tails with a specialised ventral cuticular patch of tubercles (area rugosa), well-developed caudal papillae (4 cloacal pairs), 2 caudal alae which join ventrally (forming an ornamental caudal bursa), and 2 well-developed subequal spicules (left spicule longer). Mature female worms have a single vulva opening anterior to the midbody but connected to 2 or more uteri/uterine branches (didelphic with 2, tridelphic with 3, tetradelphic with 4, polydelphic with > 4). Gravid females produce embryonated eggs containing fully developed larvae.

Site of infection: Adult worms infect the stomachs of their final hosts (mammals, birds, reptiles) where they are found attached to the mucosal wall. Infective larvae develop within the gut wall of invertebrate intermediate hosts (insects), and they may also be carried in the tissues of small vertebrate paratenic hosts.

Pathogenesis: While light infections often remain subclinical, heavier infections may cause disease typified by gastritis and emesis (vomiting). Worms attach to the stomach wall using their anterior collarettes and sublabial teeth but do not appear to feed on host tissues, but rather on stomach content. Nevertheless, they frequently detach to move to new locations leaving behind small erosive lesions which continue to haemorrhage and may ulcerate. The mucosa becomes inflamed (catarrhal gastritis with mucus production), hosts may vomit stomach content, and the faeces may appear dark in colour due to the presence of blood (melena). Continued blood loss in heavy infections may result in anaemia and animals may become anorexic and progressively lose body weight and condition.

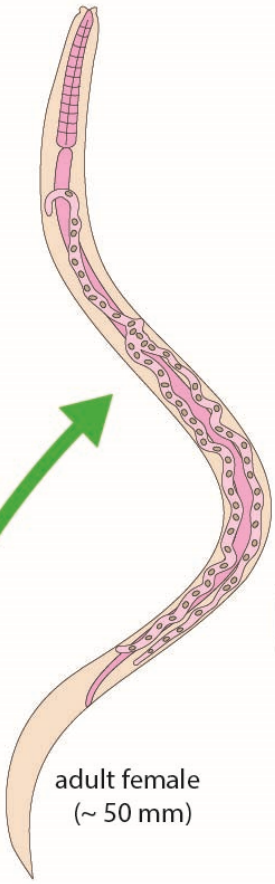
Developmental cycle and mode of transmission: *Physaloptera* spp. have indirect heteroxenous life-cycles involving adult worm formation in predatory or scavenging vertebrates (definitive hosts), larval development in coprophagous insects (intermediate hosts), and often larval carriage in small insectivorous vertebrates (paratenic hosts). Embryonated eggs laid by gravid females in the stomach are excreted with host faeces (sometimes vomitus) into the external environment where may survive for short periods in moist conditions. The eggs are ingested by a range of insects (cockroaches, beetles, grasshoppers, crickets, earwigs) which act as intermediate hosts supporting larval development. Ingested eggs hatch in the gut releasing L1 which penetrate the gut wall inducing the formation of local syncytia (hypertrophied multinucleate epithelial cells) which eventually become encapsulated by loose fibrous connective tissue. Enclosed L1 moult twice to form L3 by 30-35 days and the growing capsules often become pedunculate and bulge into the haemocoel. Larvae do not undergo arrested development in the insect intermediate hosts but continue growing and reach an advanced stage of sexual development. Infective L3 may also re-encapsulate in the gut wall of a range of vertebrate paratenic hosts (rodents, birds, reptiles, amphibians) which have consumed infected insects. Final hosts become infected when they ingest infective L3 contained within the tissues of intermediate or paratenic hosts. Ingested L3 develop directly in the gut without undertaking any local or somatic migration. They moult twice to form subadults (sometimes termed L5) which then mature to adult worms. The prepatent period (time from infection to the first excretion of eggs) varies considerably depending on parasite species, ranging from 56-70 days in those with rapid development, from 73-90 days in those with moderate development, and from 131-156 days in those with slow development.

Differential diagnosis: Clinical infections may be suggested in hosts exhibiting signs of gastritis involving vomiting, melena and anaemia, but differential diagnosis requires the direct detection of parasites. Immature worms may be found in vomitus of puppies or kittens, but mature worms are usually firmly attached to the mucosa. Endoscopic examination (gastroscopy) has been used to detect stomach worms *in situ*. Worm eggs may be detected by coprological examination of faecal samples, but the characteristic eggs (thick-shelled, elliptical, embryonated) are not very buoyant and are best detected by sedimentation rather than floatation. Adult worms may also be detected at post-mortem by dissection of the stomach mucosa. Modern molecular biological techniques have been used to examine parasite phylogenetic relationships following polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA).

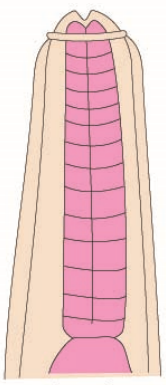
Treatment and control: Infections have been successfully treated using a range of anthelmintic drugs, including benzimidazoles (fenbendazole), tetrahydropyrimidines (pyrantel) and macrocyclic lactones (ivermectin). Infections responded best to sustained treatment over 5 days or repeated treatment over several weeks. Few preventive strategies are practicable in natural situations involving wildlife, but commonsense measures may be taken to limit transmission in domestic or peridomestic situations. Efforts should be made to routinely remove potential sources of contamination (faeces and vomitus), decontaminate animal holding facilities (regular cleaning and disinfection), reduce insect populations (using barriers and insecticides), exclude potential paratenic hosts (close-mesh screens and fencing) and prevent parasite uptake by final hosts (prevent hunting and scavenging, and providing clean food and water).

Physaloptera

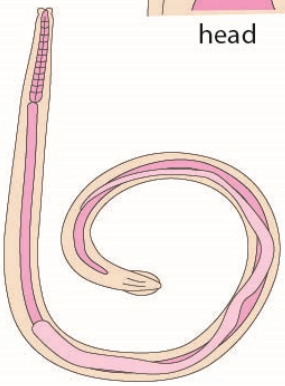
stomach
(gastritis, emesis)



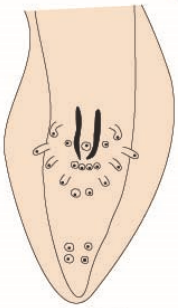
adult female
(~ 50 mm)



head



adult male
(~ 30 mm)



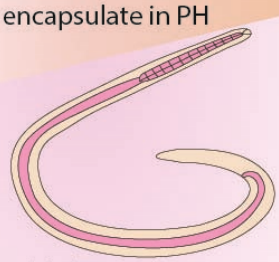
male tail

Definitive Hosts
(carnivores, birds,
reptiles)

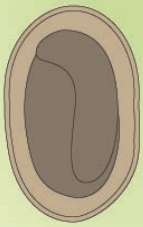
eggs
excreted
in
faeces

IH/PH
ingested

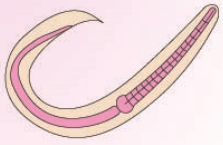
L3 may also encapsulate in PH



third-stage larvae
(L3) (~ 3 mm)



eggs
(~ 50 µm)



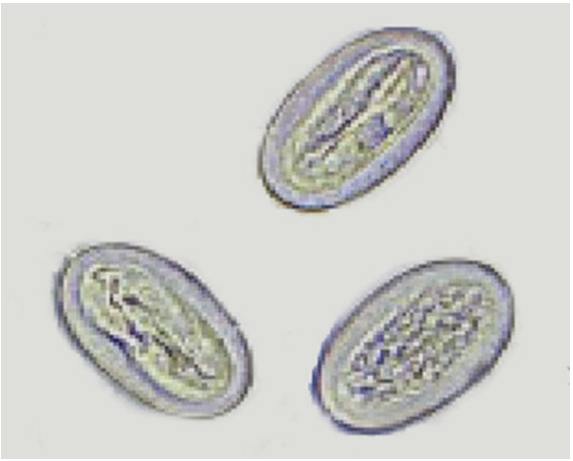
first-stage larvae
(L1) (~ 200 µm)

Paratenic Hosts (PH)
(rodents, birds, reptiles, frogs)
(gut wall)

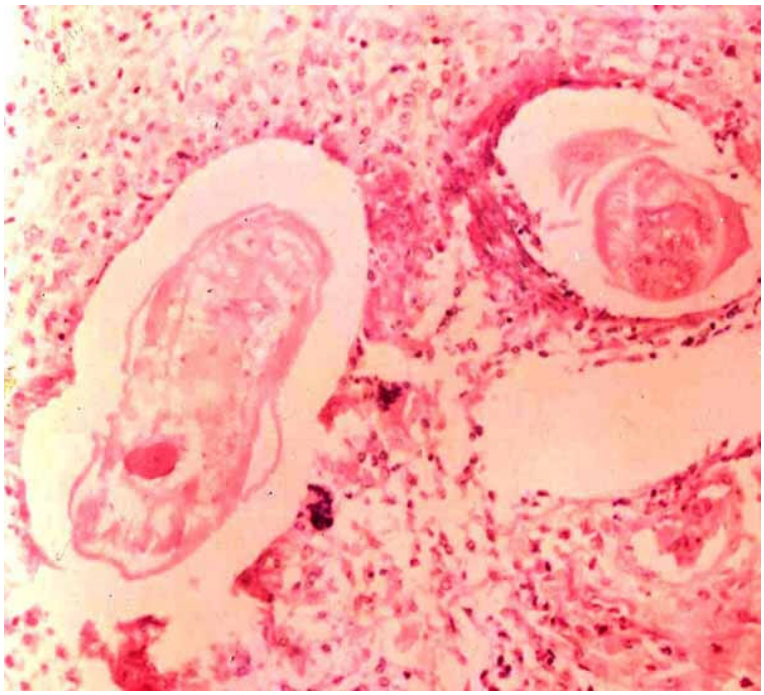
eggs ingested
by IH

Intermediate Hosts (IH)
(insects)
(gut wall)

Physaloptera adult worm



Physaloptera worm eggs



Physaloptera lesion