Paramphistomum
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult paramphistomids are thick fleshy worms and the ventral sucker is near the posterior end. Paramphistomes are conical (rather than flat) in shape and most occur as parasites in the forestomach of ruminants (rumen/stomach flukes), although some infect the intestines of pigs and horses. Infections by a range of species belonging to several genera have been associated with enteritis and diarrhoea in domestic animals.

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:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida (‘echinostomatids’, plagiorchiids’, mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Pronocephalata (gastropod IH, sporocyst and redia formed; simple-tailed cercariae, encysts in open, metacercariae eaten by DH)
Superfamily:	Paramphistomoidea (rumen flukes, miracidium penetrates gastropod IH)
Family:	Paramphistomidae (thick fleshy worms, conical shape, ventral sucker near posterior end, rediae with appendages, cercariae with two eyespots)
Genus:	*Paramphistomum* (parasitic in rumen/reticulum of cattle/sheep)
Species:	various species cause diarrhoea

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 do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Pronocephalata is characterized by species forming simple-tailed cercariae which encyst in the open and the resultant metacercariae are eaten by herbivorous/omnivorous definitive hosts. One important superfamily is the Paramphistomoidea which contains thick fleshy worms from the stomach and intestines of a wide range of omnivores and herbivores. Adult worms have a pharynx rather than an oral

sucker at the anterior end and a ventral sucker at the posterior end (amphistome arrangement, as distinct from monostome, holostome, distome, echinostome or schistosome). Hundreds of species have been described in over 140 genera in 10 families (Balanorchiidae, Brumptiidae, Cladorchiidae, Diplodiscidae, Gastrodiscidae, Gastrothylacidae, Mesometridae, Microscaphidiidae, Paramphistomidae and Zygocotylidae). Familial designations have been extensively reviewed on the basis of morphotypic and biotypic characters with significant reclassifications of individual genera and species. Hopefully, contemporary molecular characterization studies will help resolve their phylogenetic affinities. Amphistome stomach flukes have been detected in a broad range of definitive hosts encompassing all vertebrate classes (mammals, birds, reptiles, amphibians and fish) widely distributed throughout the world.

Paramphistome families and subfamilies	**Genera**	**Definitive Hosts**
Paramphistomidae		
Paramphistominae	*Calicophoron, Cotylophoron, Explanatum, Gigantocotyle, Paramphistomum* (syn. *Liorchis, Srivastavaia*), *Ugandocotyle*	artiodactyls
Orthocoeliinae	*Bilatorchis, Buxifrons, Gemellicotyle, Gigantoatrium, Glyptamphistoma, Leiperocotyle, Macropharynx, Nilocotyle, Orthocoelium* (syn. *Ceylonocotyle*), *Palamphistomum, Paramphistomoides, Platyamphistoma, Pseudoparamphistoma, Sellsitrema*	artiodactyls
Gastrothylacidae		
	Carmyerius, *Duttiella, Fischoederius*, *Gastrothylax, Velasquezotrema*	artiodactyls
Zygocotylidae		
Olveriinae	*Olveria, Sureshiella*	artiodactyls
Pseudodiscinae	*Macropotrema, Pseudodiscus*	perissodactyls, proboscids, macropodids
Stephanopharynginae	*Stephanopharynx*	artiodactyls
Watsoniinae	*Gastrodiscoides*, *Homalogaster*, *Skrjabinocladorchis, Watsonius*	primates, artiodactyls, rodents
Zygocotylinae	*Choerocotyloides, Wardius, Zygocotyle*	birds, artiodactyls, rodents
Gastrodiscidae		
	Gastrodiscus	proboscids, perissodactyls
Brumptiidae		
	Brumptia, Choerocotyle, Hawkesius	proboscids, rhinocerotids
Balanorchiidae		
	Balanorchis	artiodactyls
Cladorchiidae		
Caballerodiscinae	*Cabellerodiscus, Elseyatrema*	reptiles
Caballeroiinae	*Bancroftrema, Cabelleroia, Platycladorchis*	fish
Chiorchiinae	*Chiorchis, Chiostichorchis, Paraibatrema*	testudines, rodents, sirenia
Cladorchiinae	*Australodiscus, Catadiscus, Cladorchis, Dermatemytrema, Diplodiscus, Progonimodiscus, Pseudodiplodiscus, Taxorchis*	mainly amphibians
Dadaytrematinae	*Alphamphistoma, Anavilhanatrema, Annelamphistoma, Australotrema, Betamphistoma, Cleptodiscus, Dadayius, Dadaytrema, Dadaytremoides, Deltamphistoma, Gammamphistoma, Inpamphistoma, Macrorchitrema, Neocladorchis, Ophioxenus, Pacudistoma, Panamphistomum, Pronamphistoma*	fish, amphibians
Helostomatinae	*Amurotrema, Helostomatis, Protocladorchis*	fish
Megalodiscinae	*Megalodiscus, Opisthodiscus, Pseudopisthodiscus*	mainly amphibians
Microrchiinae	*Brevicaecum, Colocladorchis, Kalitrema, Micramphistoma, Microrchis, Nicollodiscus, Pseudocladorchis*	fish
Nemathophilinae	*Halltrema, Nematophila, Parachiorchis, Pseudoalassostoma*	reptiles
Orientodiscinae	*Australotrema, Basidiodiscus, Orientodiscus, Pretestis, Pseudoorientodiscus, Sandonia*	fish
Osteochilotrematinae	*Osteochilotrema*	fish
Pfenderiinae	*Pfenderius*	proboscids
Pisciamphistominae	*Pisciamphistomum*	fish
Schizamphistominae	*Alassostoma, Alassostomoides, Lobatodiscus, Pseudoalassostomoides, Pseudoceloiptodiscus, Quasichiorchis, Schizamphistomum, Schizamphistomoides, Stunkardia*	mainly reptiles, amphibians

Solenorchiinae	*Solenorchis*	dugongs
Stichorchiinae	*Stichorchis*	rodents, artiodactyls
Transvassosiniinae	*Travassosinia, Zetamphistoma*	fish
Mesometridae		
	Centroderma, Elstia, Mesometra, Neowardula, Parawardula, Wardula	fish
Microscaphidiidae (syn. Angiodictyidae)		
	Angiodictyum, Curumai, Denticauda, Deuterobaris, Dictyangium, Doodytrema, Hexangitrema, Hexangium, Microscaphidium, Neoctangium, Neodeuterobaris, Neohexangitrema, Octangioides, Octangium, Paradeuterobaris, Podocnemitrema, Polyangium, Polygorgyra, Pseudohexangium, Pseudoparabaris	testudines

Most of the known paramphistomoids of ruminants (commonly known as paramphistomes) belong to 2 families Paramphistomidae and Gastrothylacidae. The family Paramphistomidae comprises the rumen flukes whose adults lack a ventral pouch, and some 20 genera have been classified in 2 major subfamilies: the Paramphistominae (Laurer's canal crosses excretory duct); and the Orthocoeliinae (Laurer's canal and excretory duct do not cross). Some classifications include other subfamilies within the Paramphistomidae but subsequent reviews have reassigned them elsewhere. Notably, the subfamily Pseudodiscinae was transferred to the family Zygocotylidae; the subfamily Cladorchiinae to the family Cladorchiidae (although the genus *Olveria* was established in a new subfamily Olveriinae in the family Zygocotylidae); and the subfamily Gastrodiscinae was split with the genus *Gastrodiscus* placed in the family Gastrodiscidae and the genera *Gastrodiscoides* and *Homalogaster* allocated to the subfamily Watsoniinae in the family Zygocotylidae. The family Gastrothylacidae contains rumen flukes whose adults possess a ventral pouch, and 4 genera are recognized. Various species of rumen flukes impact on domestic livestock industries by causing morbidity and production losses (rarely mortality).

Amphistome species	**Definitive hosts [location]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Infective stages**	**Distribution**
Family: Paramphistomidae				
Subfamily: Paramphistominae (Laurer's canal crosses excretory duct)				
Paramphistomum				
P. bothriophoron	Artiodactyla: bovid (zebu)			Africa
P. cephalophi	Artiodactyla: bovid (black-fronted duiker) [small intestines]			Africa
P. cervi (rumen fluke)	Artiodactyla: bovid (cattle, banteng, buffalo, bison, yak, sheep, argali, goat, ibex, roan antelope, hartebeest, waterbuck, kob, lechwe, gemsbok, oryx, reedbuck), cervid (moose, red deer, roe deer, fallow deer, reindeer, sika, sambar, chital, muntjac); Perissodactyla: equid (Przewalski's horse) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Planorbis planorbis, P. carinatus, Anisus cornetus, A. leucostomus, A. septemgyratus, A. spirorbis, A. vortex, Armiger crista, Ar. inermis, Bathyomphalus contortus, Choanophalus anophalus, Gyraulus albus, G. ehrenbergi, G. gredleri, Hippeutis complanatus, Segmentina nitida, Indoplanorbis exustus, Helicorbis, Polypylis*)	metacercariae on herbage	Eurasia, Americas
P. clavula	Artiodactyla: bovid (zebu, buffalo)			Africa
P. epiclitum (syn. *P. indicum p.p., P.*	Artiodactyla: bovid (cattle, zebu, buffalo, guar, sheep, goat, sable	freshwater Gastropoda: planorbid	metacercariae on herbage	India, Southeast

thapari, P. malayi, Cotylophoron madrasense, C. chauhani)	antelope), cervid (chital) [rumen]	(*Indoplanorbis exustus*)		Asia
P. gotoi	Artiodactyla: bovid (cattle, buffalo, blackbuck, sheep) [rumen]	freshwater Gastropoda: planorbid (*Segmentina nitidella, Gyraulus largielli*)		Southeast Asia, Egypt
P. gracile (syn. *P. indicum p.p., P. bombayiensis*)	Artiodactyla: bovid (cattle, zebu, nilgai, buffalo, sheep) [rumen]			Indochina
P. hiberniae	Artiodactyla: bovid (cattle, buffalo, argali), cervid (red deer) [rumen]	freshwater Gastropoda: planorbid (*Anisus leucostomus*)		United Kingdom
P. ichikawai (syn. *Cotylophoron vigisi*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (roe deer, red deer, sika) [rumen]	freshwater Gastropoda: planorbid (*Helicorbis australiensis, H. suiffunensis, Anisus centrifugus, A. minusculus, A. spirorbis, A. subfilialis, Gyraulus corinna, G. filialis, Hippeutis complanatus, Planorbis carinatus, Segmentina nitida, S. semiglobosa, S. hemisphaerula*)	metacercariae on herbage	Eurasia, South America, Australia, New Zealand
P. leydeni (syn. *P. scotiae, P. julimarinorum, P. nicabrasilorum, P. procapri, Cotylophoron skrjabini p.p.*)	Artiodactyla: bovid (cattle, bison, buffalo, argali, goa), cervid (red deer, roe deer, red deer, reindeer, sika, moose) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Anisus leucostoma, A. septemgyratus, A. spirorbis, A. vortex, Armiger crista, Bathyomphalus contortus, Gyraulus albus, G. gredleri, Hippeutis complanatus, Planorbis planorbis, Segmentina nitida*)		Europe, Asia, Americas
P. liorchis	Artiodactyla: cervid (red brocket, gray brocket, brown brocket, white-tailed deer, moose, marsh deer, sambar, pampas deer), bovid (cattle, buffalo, goat, argali) [rumen])	freshwater Gastropoda: planorbid (*Helisoma campanulata, H. trivolvis*)		Americas, Southeast Asia
P. phillerouxi	Artiodactyla: bovid (zebu, buffalo)			Africa
Explanatum				
E. anisocotyle (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, goat)			Indochina
E. bathycotyle (syn. *Paramphistomum*)	Artiodactyla: cervid (chital), bovid (cattle, buffalo, goat, argali)	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)		Indochina
E. explanatum (syn. *Paramphistomum fraternum, P. siamense*)	Artiodactyla: bovid (cattle, banteng, bison, buffalo, yak, sheep, argali, goat, hartebeest, blackbuck, reedbuck, bontebok, roan antelope), cervid (sambar)	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)	metacercariae on herbage	Asia, India, Middle-East, Africa
E. symmeri	Artiodactyla: bovid (buffalo)			Africa
Cotylophoron				
C. bareilliense	Artiodactyla: bovid (cattle, buffalo,			India,

(syn. *C. skrjabini*)	sheep, goat)			Philippines, South America
C. chauhani	Artiodactyla: bovid (sheep, goat)			India
C. cotylophorum (syn. *C. indicum, C. guongdongense, Paramphistomum cotylophorum*)	Artiodactyla: bovid (cattle, buffalo, yak, sheep, goat, impala, hartebeest, Harvey's duiker, tsessebe, Thomson's gazelle, roan antelope, royal antelope, sable antelope, klipspringer, waterbuck, bushbuck, marshbuck, kob, lechwe, puku, oribi, argali, steinbok, reedbuck, bohor reedbuck, duiker, eland, nyala, kudu), cervid (chital, gray brocket), hippopotamid (hippopotamus); Proboscidea: elephantid (African elephant); Perissodactyla: equid (zebra) [rumen, reticulum]	freshwater Gastropoda	metacercariae on herbage	Africa, Southeast Asia, India, Australia
C. dilipticus	Artiodactyla: bovid (cattle)			Africa
C. fulleborni (syn. *C. kwantungensis, C. noveboracensis, C. shangkiangensis, C. sinuointestinum*)	Artiodactyla: bovid (cattle, buffalo, impala, duiker, bongo)			Africa
C. jacksoni	Artiodactyla: bovid (cattle, hartebeest, sable antelope, waterbuck)			Africa
C. macrosphinctris	Artiodactyla: bovid (buffalo, hartebeest, oribi)			Africa
C. madrasensis	Artiodactyla: bovid (sheep)			India
C. panamense	Artiodactyla: bovid (cattle, sheep)			America
C. travassosi	Artiodactyla: bovid (cattle)			Brazil
C. xiangjiangense	Artiodactyla: bovid (buffalo)			China
Ugandocotyle				
U. pisum (syn. *Paramphistomum*)	Artiodactyla: hippopotamid (hippopotamus) [stomach, intestines]			Africa
Calicophoron				
C. bothriophoron (syn. *Amphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, waterbuck, reedbuck)			Africa, India
C. calicophorum (syn. *C. fusum, C. orientalis, C. ovillum, C. zhejiangense, Paramphistomum calicophorum, P. cauliorchis, P. crassum, P. erschovi, P. ijimai*)	Artiodactyla: bovid (cattle, buffalo, tamaraw, sheep, goat, impala, moose, hartebeest, wildebeest, roan antelope, sable antelope, waterbuck, lechwe, springbok, bontebok, eland, nyala, kudu), cervid (chital, sika, sambar, red deer, muntjac, fallow deer, reindeer) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Gyraulus scottianus* (syn. *Pygmanisis pelorius*), *G. corinna, G. pulcher, Anisus spirorbis, Bulinus tropicus, Planorbis kahuika, P. planorbis, Helicorbis suiffunensis*)	metacercariae on herbage	Africa, Eurasia, India, Australia, New Zealand
C. clavula (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, goat, impala, hartebeest, waterbuck, reedbuck, kob, puku, oribi, roan antelope, sable antelope)	freshwater Gastropoda: planorbid (*Bulinus abyssinicus*)		Africa
C. daubneyi (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, gemsbok), cervid (roe deer, red deer) [rumen]	freshwater Gastropoda: lymnaeid (*Galba trunculata, Lymnaea peregra*)	metacercariae on herbage	Africa, Europe
C. microbothrioides (syn. *Paramphistomum microbothrium, Ceylonocotyle petrowi*)	Artiodactyla: bovid (cattle, bison, sheep), cervid (sika, sambar, muntjac)	freshwater Gastropoda: planorbid (*Anisus minusculus*), lymnaeid (*Galba trunculata, Lymnaea peregra, L. cubensis, L. humilis*)		Europe, Asia, North America
C. microbothrium	Artiodactyla: bovid (cattle, buffalo,	freshwater Gastropoda:	metacercariae on	Africa,

(syn. *Paramphistomum*)	sheep, goat, ibex, impala, hartebeest, bontebok, tsessebe, red-fronted gazelle, Thomson's gazelle, roan antelope, waterbuck, reedbuck, kob, lechwe, puku, serow, gemsbok, oribi, eland, nyala, kudu), camelid (camel), cervid (roe deer, red deer) [rumen]	planorbid (*Bulinus tropicus, B. truncatus, B. liratus, B. mariei, B. forskalii, B. natalensis, B. octoploidus, Physopsis globosus, P. nasutus*)	herbage	Europe
C. papilligerum (syn. *Paramphistomum*)	Artiodactyla: cervid (Eld's deer)			Asia
C. papillosum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep)			India, Asia
C. phillerouxi (syn. *Paramphistomum togolense, P. vangrenbergeri*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, impala, tsessebe, roan antelope, sable antelope, waterbuck, kob, puku, kudu, reedbuck)	freshwater Gastropoda: planorbid (*Bulinus cercinus, B. forskalii, B. senegalensis*)		Africa
C. raja	Artiodactyla: bovid (cattle, buffalo, sheep, goat, impala, hartebeest, wildebeest, tsessebe, Thomson's gazelle, roan antelope, sable antelope, waterbuck, reedbuck, lechwe, puku, gemsbok, eland, bushbuck, kudu)	freshwater Gastropoda: planorbid (*Physopsis globosus*)		Africa
C. shillongensis	Artiodactyla: bovid (sheep, goat)			India
C. sukari (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)	freshwater Gastropoda: planorbid (*Biomphalaria pfeifferi*)		Africa
C. sukumum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, wildebeest, tsessebe, roan antelope, waterbuck, reedbuck, lechwe, eland)			Africa
C. wuchengense	Artiodactyla: bovid (buffalo)			China
Subfamily: Orthocoeliinae (Laurer's canal and excretory duct do not cross)				
Orthocoelium				
O. arambuloi	Artiodactyla: bovid (cattle, buffalo)			Indonesia, Philippines
O. bovini (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle)			India
O. brevicaeca (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, buffalo)			China
O. dawesi (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, sheep, goat)			India
O. dicranocoelium (syn. *Ceylonocotyle tamilensis, Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat) [rumen]	freshwater Gastropoda: bithyniid (*Digoniostoma pulchella*)	metacercariae on herbage	India, Southeast Asia
O. dinniki	Artiodactyla: bovid (cattle, buffalo, sheep, goat)			India, Asia
O. gigantopharynx (syn. *Ceylonocotyle hsui, C. chinensis*)	Artiodactyla: bovid (blackbuck, buffalo)			India, Southeast Asia
O. indonesiense	Artiodactyla: bovid (cattle, sheep)			Indonesia
O. narayanai (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, buffalo)			India
O. orthocoelium (syn. *O. saccocoelium, Paramphistomum chinensis, P. spinicephalus, Chenocoelium kiangsiensis*)	Artiodactyla: bovid (cattle, buffalo, goat, sheep)			India, Asia
O. parastreptocoelium (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, buffalo)			China

O. parvipapillatum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)			India
O. scoliocoelium (syn. *Ceylonocotyle cheni, C. longicoelium, Cotylophoron ovatum, Paramphistomum, P. shipley*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (chital, barasingha, muntjac, red deer) [rumen]	freshwater Gastropoda: bithyniid (*Bulimus* (*Bithynia*) *pulchella, Digoniostoma pulchella*), planorbid (*Anisus natalensis, Gyraulus convexiusculus, Indoplanorbis exustus*), lymnaeid (*Lymnaea luteola*)	metacercariae on herbage	Africa, India, Asia
O. serpenticaecum	Artiodactyla: bovid (swamp buffalo)			Philippines
O. sinuocoelium (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle)			China
O. streptocoelium (syn. *Ceylonocotyle, Paramphistomum, P. malayi*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, Thomson's gazelle, waterbuck, bushbuck), cervid (barasingha, muntjac, sambar) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus gilberti, G. isingi, G. waterhousei, G. chinensis*)	metacercariae on herbage	Australia, India, Asia
O. thapari	Artiodactyla: bovid (cattle, buffalo)			India
Family: Gastrothylacidae				
Gastrothylax				
G. caraphilensis	Artiodactyla: bovid (cattle)			Philippines
G. compressus (syn. *G. glandiformis, G. indicus*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat,), cervid (barasingha, sambar)			India, Asia
G. crumenifer (syn. *G. orientalis, G. chinensis, Paramphistomum magnum*)	Artiodactyla: bovid (cattle, buffalo, yak, banteng, bison, sheep, goat, blackbuck, nilgai, lechwe, sitatunga), cervid (chital, hog deer, barasingha, Philippine deer, sambar) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus, G. albus, G. ehrenbergi, Armiger crista, Planorbis planorbis, P. sieversi*)	metacercariae on herbage	India, Asia, southern Africa
G. globoformis	Artiodactyla: bovid (buffalo)			China
G. magnadiscus	Artiodactyla: bovid (buffalo)			China
G. zhonghuaensis	Artiodactyla: bovid (cattle, buffalo)			China, Philippines
Carmyerius				
C. bubalis (syn. *C. gretillati, Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, hartebeest, bongo)			Africa, China
C. bulbosus	Artiodactyla: bovid (buffalo), cervid (sambar)			Asia
C. chabaudi	Artiodactyla: bovid (Thomson's gazelle)			Africa
C. cruciformis (syn. *Gastrothylax*)	Artiodactyla: hippopotamid (hippopotamus)			Africa
C. diplopharyngialis	Artiodactyla: bovid (?)			Africa
C. endopapillatus (syn. *C. papillatus*)	Artiodactyla: bovid (cattle, buffalo, Thomson's gazelle, roan antelope, waterbuck, kob, reedbuck), hippopotamid (hippopotamus)			Africa
C. exoporus	Artiodactyla: bovid (cattle, buffalo, sheep, tsessebe, sitatunga, roan antelope)	freshwater Gastropoda: planorbid (*Anisus natalensis*)		Africa
C. graberi	Artiodactyla: bovid (cattle, buffalo, sheep, red-fronted gazelle, Thomson's gazelle, hartebeest, waterbuck, bohor reedbuck, harnessed bushbuck)			Africa
C. gregarius	Artiodactyla: bovid (cattle, buffalo,	freshwater Gastropoda:		India, Asia,

(syn. *Gastrothylax*)	sheep, blackbuck, bushbuck)	planorbid (*Bulinus truncatus, B. forskalii*)		Africa
C. mancupatus (syn. *C. dollfusi, C. minutus, Wellmanius wellmani, Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, goat, waterbuck, roan antelope, eland, bushbuck)	freshwater Gastropoda: planorbid (*Bulinus liratus, B. mariei, Anisus natalensis*)		Africa
C. multivitellarius	Artiodactyla: bovid (Thomson's gazelle)			Africa
C. parvipapillatus (syn. *C. gregarius p.p.*)	Artiodactyla: bovid (cattle, sheep, goat, tsessebe, waterbuck, kob)	freshwater Gastropoda: planorbid (*Physopsis globosus*)		Africa
C. schoutedeni	Artiodactyla: bovid (buffalo, black-fronted duiker, waterbuck, kob, reedbuck, bongo), hippopotamid (hippopotamus)			Africa
C. spatiosus (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, reedbuck, waterbuck, kob,lechwe, puku, hartebeest, tsessebe, Thomson's gazelle, roan antelope, eland, bushbuck, sitatunga), cervid (muntjac) [rumen]		metacercariae on herbage	Africa, India, Southeast Asia
C. synethes (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, goat), cervid (sambar)			Southeast Asia
C. wenyoni (syn. *Gastrothylax*)	Artiodactyla: bovid (Nile lechwe)			Africa
Fischoederius				
F. bubalis	Artiodactyla: bovid (buffalo)			China
F. cobboldi (syn. *F. poyangensis, Gastrothylax)*	Artiodactyla: bovid (cattle, buffalo, gayal, banteng, yak, nilgai, sheep, goat), cervid (sambar) [rumen]	freshwater Gastropoda	metacercariae on herbage	India, Asia
F. elongatus (syn. *F. ceylonensis, F. compressus, F. fischoederi, F. siamensis, Gastrothylax elongatus)*)	Artiodactyla: bovid (cattle, banteng, gayal, anoa, buffalo, sheep, goat), cervid (chital, Philippine deer, Javan rusa, sambar, muntjac, water deer, reindeer); rarely Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Radix luteola*, *Lymnaea luteola, L. acuminata*), planorbid (*Gyraulus euphraticus, G. pulcher*)	metacercariae on herbage	India, Asia
F. japonicus (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo), cervid (sambar, muntjac)			Asia
F. ovatus (syn. *F. ovis*)	Artiodactyla: bovid (cattle, buffalo, sheep)			China
F. philippinensis	Artiodactyla: bovid (cattle, buffalo, goat)			Philippines
F. skrjabini	Artiodactyla: bovid (cattle, buffalo), cervid (moose, roe deer, red deer)			Asia
Family: Gastrodiscidae				
Gastrodiscus				
G. aegyptiacus (syn. *Cotylogaster cochleariformis, Distoma, G. sonsini, G. minor, G. polymastos, G. equi*)	Artiodactyla: bovid (cattle), suid (pig, forest hog, desert warthog); Perissodactyla: rhinocerotid (white rhinoceros), equid (horse, donkey, mule, zebras, Przewalski's horse) [caecum, colon]	freshwater Gastropoda: planorbid (*Bulinus forskalii, B. senegalensis*)	metacercariae on herbage	Africa, India, Asia, Australia
G. secundus	Proboscidea: elephantid (Asian elephant); Perissodactyla: equid (donkey, Przewalski's horse) [caecum, colon]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus*)	metacercariae on herbage	India, Asia, Egypt

Family: Zygocotylidae				
Subfamily: Pseudodiscinae				
Pseudodiscus				
P. collinsi (syn. *Amphistoma, P. stenleyi*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, mule, donkey, Przewalski's horse); Proboscidea: elephantid (Asian elephant) [caecum, colon]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus*)	metacercariae on herbage	India
Macropotrema				
M. pertinax	Diprotodontia: macropodid (agile wallaby)			Australia
Subfamily: Olveriinae				
Olveria				
O. indica (syn. *O. thapari*)	Artiodactyla: bovid (cattle, buffalo, sheep) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)	metacercariae on herbage	India
O. bosi	Artiodactyla: bovid (cattle, buffalo, sheep)		metacercariae on herbage	India
Subfamily: Watsoniinae				
Homalogaster				
H. paloniae (syn. *H. poirieri, H. philippiensis, H. taiwana*)	Artiodactyla: bovid (cattle, buffalo, gayal, banteng, sheep, goat, blackbuck, lechwe), cervid (Javan rusa, muntjac); Proboscidea: elephantid (Asian elephant) [large intestines]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Polypylis* (*Segmentina*) *hemisphaerula*)	metacercariae on herbage	Asia, Australasia, Africa
Watsonius				
W. watsoni (syn. *Amphistoma, Cladorchis, Gastrodiscus, Paramphistomum, Pseudodiscus*)	Primates: cercopithecid (grivet, crab-eating macaque, mandrill), hominid (human)			Africa
W. noci (syn. *Chiorchis, Prochiorchis*)	Primates: cercopithecid (rhesus macaque)			Asia
W. macaci	Primates: cercopithecid (rhesus macaque)			Asia
W. deschiensi	Primates: cercopithecid (mandrill, hamadryas baboon)			Africa
W. capri	Artiodactyla: bovid (goat)			Pakistan
Gastrodiscoides (considered in detail separately in next section)				
G. hominis (syn. *Amphistoma, Gastrodiscus*) (colonic fluke)	Rodentia: cricetid (water vole, muskrat), murid (bandicoot rats, ricefield rat, brown rat, black rat), echimyid (coypu); Artiodactyla: suid (pig, bushpig, warthog), tragulid (mouse-deer); Primates: cercopithecid (crab-eating macaque, Philippine long-tailed macaque, rhesus macaque, Sumatran surili), hominid (orangutan, human)	freshwater Gastropoda: planorbid (*Helicorbis coenosus*, *Anisus acronicus*), lymnaeid (*Lymnaea stagnalis*)	on herbage (esp. water caltrop)	India, Asia, Russia, Africa

Parasite morphology: Paramphistomes form 7 different developmental stages in their life-cycles: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adults. Eggs are yellow-green to white, oval to spherical and vary considerably in size depending on the parasite species: most ranging from 100-170 µm in length by 60-100 µm in width (e.g. *Explanatum explanatum, Cotylophoron cotylophorum, Calicophoron calicophorum, Orthocoelium scoliocoelium, Pseudodiscus collinsi, Homalogaster paloniae, Gastrothylax crumenifer, Carmyerius spatiosus, Fischoederius cobboldi*); a few species produce larger eggs measuring 170-200 x 100-120 µm (e.g., *Gastrodiscus aegyptiacus*); and several species produce smaller eggs measuring 35-100 x 30-60 µm (e.g., *Paramphistomum cervi*). The eggs are enveloped within transparent eggshells which are thin in species developing in freshwater and thicker in species developing in marine/brackish-water. The eggs taper anteriorly to a small operculum and have a knob-like posterior polar thickening. They embryonate in the external environment forming miracidia which are released when the eggs hatch. Miracidia have elongated streamlined bodies, measuring 110-200 µm long by 35-50 µm wide, and are covered with ciliated epidermal plates, often arranged anteriorly in staggered longitudinal rows. They have a prominent terminal papilla and a primitive gut with elongated cellular masses. Sporocysts appear as elongated sac-like structures up to 1.5 mm in length without internal organs but with germ balls undergoing asexual reproduction to form rediae. Two redial generations are formed, with mother rediae forming daughter rediae which then form cercariae. Each developing redia is sausage-shaped measuring from 140-750 µm long by 45-140 µm wide (daughters are larger) and they have a mouth, pharynx, saccular gut, and 3 pairs of flame cells. Cercariae have light brown ovoid bodies measuring from 200–900 µm in diameter with an elongate unforked tail measuring 450–900 µm in length and containing a conspicuous excretion tube. The amphistome cercariae have 2 eyespots, a pharynx with a pair of well-developed oral pouches, an oesophagus with a muscular bulb, 2 simple intestinal caeca, and a prominent posterior ventral sucker. Metacercariae consist of the cercarial body which has encysted after shedding its tail. They appear brown and are hemispherical measuring 200-300 µm in length. Adult paramphistomes have thick fleshy bodies that are mostly conical but somewhat flattened to form pyriform 'jelly-bean' shapes. They are often orange to pink-red and are variable in size depending on species; ranging from 3-20 mm in length by 1-8 mm in width. Many species are medium-sized measuring 6-14 x 2-5 mm (e.g. *Paramphistomum cervi, Explanatum explanatum Cotylophoron cotylophorum*), some are larger measuring 11-20 x 5-8 mm (e.g. *Gastrothylax crumenifer*), and some smaller measuring 2-5 x 1-2 mm (e.g. *Orthocoelium scoliocoelium*). Adult worms are covered with a smooth tegument (without spines) and they have a muscular apparatus (the pharynx) at the anterior oral opening, and a well-developed muscular ventral sucker located at the posterior end (amphistome arrangement). They contain internal organs constituting digestive, reproductive, excretory, lymphatic and nervous systems. The digestive system comprises 3 parts: the anterior pharynx (with primary pharyngeal sacs or pharyngeal bulb and secondary pharyngeal sacs); the middle oesophagus (with or without muscular thickening); and the posterior caeca (blind-ended bifurcated gut). The excretory system is stenosome in type, consisting of solenocytes, capillaries, 2 main canals, connecting vesicle, excretory bladder and excretory pore. Adult flukes are hermaphroditic, possessing both male and female reproductive organs, most lying between the intestinal caeca except the extensive vitelline follicles. Female organs comprise an oval-conical ovary, oviduct, Laurer's canal, vitellaria, Mehlis' gland, ootype, uterus with muscular distal end (metraterm) opening into a hermaphroditic sac, while male organs consist of 2 large lobulated testes, vasa efferentia, a vas deferens, an ejaculatory duct (some species in lower vertebrates also have a cirrus sac) with erectile genital papilla (instead of a cirrus). The genital papilla is surrounded by a depression known as the genital atrium with walls strengthened by muscular elements around the genital pore (terminal genitalium). Species belonging to the family Gastrothylacidae also have a blind ventral pouch associated with the atrium. Paramphistome genera are distinguished primarily on the basis of differences in the types of pharynx (5 main types with numerous subtypes), terminal genitalium (4 main types with numerous subtypes) and ventral sucker (3 main types with numerous subtypes). Adult amphistomes of most warm-blooded vertebrates are oviparous (produce eggs) whereas those of cold-blooded vertebrates may be ovoviviparous (eggs hatching internally) or viviparous (bearing live young).

Site of infection: Most paramphistomes occur as parasites in the gastrointestinal tracts of ruminants, with juvenile (sub-adult) stages in the small intestines and/or abomasum migrating to the rumen or reticulum to develop as adults (hence the common name of rumen or stomach flukes). Some species infect the small intestines of non-ruminants, such as pigs and horses. Asexual generations form in tissues of aquatic snails, mainly bithyniids, planorbids and lymnaeids. Miracidia and cercariae are free-swimming aquatic stages, while metacercariae encyst on herbage.

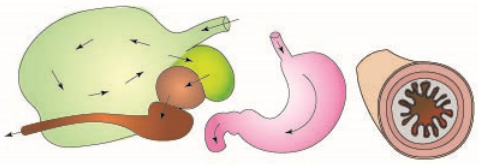
Pathogenesis: Infections by small numbers of paramphistome flukes rarely cause disease, but large numbers of immature flukes developing and migrating in the small intestinal mucosa may cause severe clinical disease, especially in young ruminants as adult animals develop immunity with repeated exposure. Juvenile worms cause traumatic damage to the mucosa by adhering using their posterior sucker. Continuous attachment and detachment during migration amplifies the damage and may result in mucosal irritation, enteritis, ulceration, haemorrhage, foetid diarrhoea (scours), dehydration, anorexia, rapid weight loss, loss of electrolytes and hypoproteinaemia (often with submandibular oedema and sometimes generalized oedema such as hydrothorax, hydropericardium, ascites, lung oedema), anaemia, lethargy, recumbency and death. In addition, the development of young flukes may be retarded in heavy infections so they remain in the small intestine for months causing severe disease through cumulative damage. The parasites are considered to be a leading cause of livestock morbidity in tropical and subtropical regions, with considerable production and economic losses. Moderate infections by immature flukes have also been associated with reduced weight gain, lower milk production and ill-thrift. Recent studies have indicated that infections by mature flukes in the stomach may also be responsible for production losses by causing atrophy and ulceration of ruminal papillae at attachment sites.

Developmental cycle and mode of transmission: Paramphistomes have indirect life-cycles involving transmission between vertebrate definitive hosts and molluscan intermediate hosts by aquatic developmental stages. Eggs passed with host faeces embryonate in water over several weeks and then hatch releasing their enclosed miracidia (hatching may be delayed in cold water). The miracidia are ciliated and swim about in water seeking molluscan hosts, apparently using chemotactic cues to home in on snail mucus and then penetrating soft tissues. Paramphistomes develop in aquatic snails (mostly planorbids, lymnaeids and bithyniids) which act as intermediate hosts for the massive asexual reproduction of larval cercariae. Parasite distribution is largely delimited by the distribution of suitable snail hosts, with higher incidence recorded in wet high rainfall and irrigation areas. Miracidia move to the heart, shed their ciliated plates and form sporocysts in surrounding mantle tissues. Sporocysts contain little other than balls of germinal cells which develop into rediae which are feeding stages with functional mouths and guts. Two generations of rediae are formed, with mother rediae migrating to the digestive gland, gut, gonads or mantle tissue where their germ balls form daughter rediae which eventually release cercariae to complete their development in snail tissues over several days. The prepatent period in snails (time from infection to first release of cercariae) ranges from 35-65 days and infected snails can shed cercariae for over 1 year. Mature cercariae released from the snail pulmonary aperture swim about actively for several hours but then shed their tails and encyst as metacercariae on subaquatic vegetation. Metacercariae may remain viable for up to 6 months under favourable environmental conditions (wet humid). When ingested on herbage by grazing animals, the metacercariae excyst in the duodenum and the immature flukes attach to the small intestinal mucosa for 3-6 weeks before migrating to the stomach(s) where they develop into mature adults. The prepatent period in vertebrates (time from infection to first release of eggs) ranges from 55-75 days and adult flukes may live for up to 1 year. Animals are usually exposed to subclinical trickle infections (slow and continuous) under normal grazing conditions, but heavy infections and severe disease may ensue when numerous metacercariae are ingested over short periods from grazing wetlands, marshlands, flooded or irrigated pastures, saturated pastures or around lakes and rice paddies.

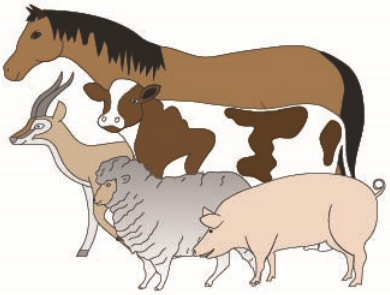
Differential diagnosis: Infections may be suspected on the basis of clinical symptomatology and history of exposure, i.e. when diarrhoea, illthrift and mortalities occur in livestock in endemic regions. Confirmation of diagnosis is afforded by the microscopic detection of fluke eggs in faecal samples, often following filtration (using sieves), sedimentation (in water) and contrast staining (with methylene blue or methyl green rather than iodine). However, clinical disease is often caused by immature stages migrating through the intestinal mucosa, which may occur before any adults have matured in the stomach and produced eggs. Infections may be diagnosed at post-mortem by the detection of immature stages from suspicious haemorrhagic lesions in the intestinal mucosa, or by the detection of adult worms in the stomach. Immunodiagnostic tests may become available in the future as research studies have developed enzyme immunoassays to detect host antibodies in serum, saliva and milk samples using protein extracts from whole worms. Molecular diagnostic techniques may also become more widely available, with the polymerase chain reaction (PCR) amplification of specific nuclear genes (ribosomal RNA and internal transcribed spacer region 2) and mitochondrial genes (cytochrome c oxidase subunit 1) already being used to examine phylogenetic and geographic variation between adults of a growing number of species.

Treatment and control: Clinical infections have been successfully treated using a range of anthelmintic drugs, including salicylanilides (oxyclozanide, niclosamide, resorantel), probenzimidazoles (febantel), benzimidazoles (albendazole), halogenated phenols (bithionol, hexachlorophene) and halogenated hydrocarbons (hexachloroethane, carbon tetrachloride). In particular, the salicylanilides proved to be most effective against both immature and mature worms when multiple doses were given several days apart. Regular drenching also provides prophylactic protection against infections, especially during periods when pastures are wet and snails vectors abound. Various control strategies have been used to reduce parasite transmission between hosts, particularly by avoiding faecal contamination of water sources (exclusion fences, waste management), reducing snail populations (drain affected areas, repair leaking dams and troughs, use molluscicides) and managing grazing livestock (barrier fences, herd/flock rotation, not grazing weaners with adults, and avoiding wet pastures prior to winter when they are more heavily contaminated). More recently, vaccination studies have demonstrated some promise in the control of infections as cattle, sheep and goats were found to develop some protective immunity against clinical challenge that persisted for at least a year.

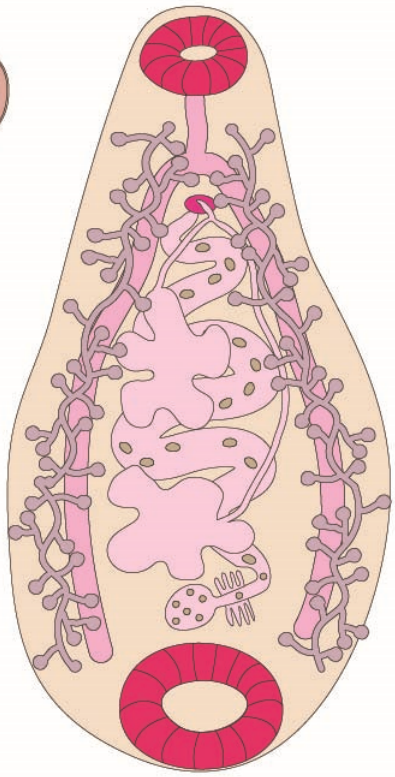
Paramphistomum



stomach(s), intestines
(trauma, irritation, diarrhoea,
anorexia, oedema)



Definitive Hosts
(ruminants,
some monogastrics)

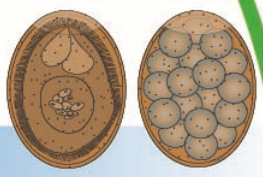


ingestion

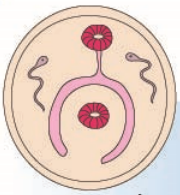
hermaphroditic
adult (~ 15 mm)

excretion

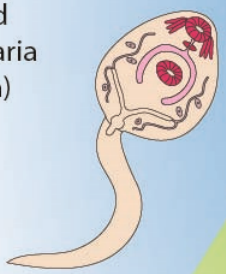
eggs
(~ 150 µm)



vector-borne transmission



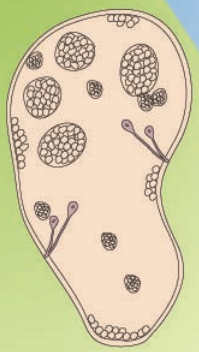
encysted
metacercaria
(~ 250 µm)



endoparasitic in
tissues of vector

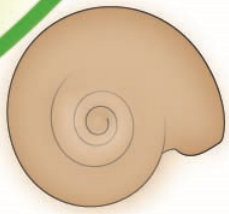
free-swimming
miracidium
(~ 150 µm)

free-swimming
cercaria
(~ 700 µm)



redia
(~ 0.5 mm)

sporocyst
(~ 1 mm)



Intermediate Hosts
(planorbid snails)
(viscera and glandular tissue)

Paramphistomum adult worms

Paramphistomum adult worms

Paramphistomum adult worms

Paramphistomum cercaria