

Metagonimus

(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 opisthorchiideans are small to medium spinose flukes living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Heterophyids are parasitic in the intestines of fish-eating birds and mammals and infections by *Heterophyes* and *Metagonimus* spp. have been associated with enteritis and diarrhoea in cats, dogs and humans.

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: Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily: Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family: Heterophyidae (tiny pyriform flukes, in intestines of mammals/birds, two IH (snails and fishes/frogs))
Genus: *Metagonimus* (parasitic in intestines of carnivores)
Species: various species cause diarrhoea in dogs, cats and humans

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
Haplospalchnoidea (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 Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Heterophyidae are found as intestinal parasites in mammals and birds with asexual developmental occurring in molluscs (Prosobranchia) and encysted stages forming mostly in fish and amphibians. The family is characterized by adults with small bodies where the ventral sucker (previously called the acetabulum) is usually enclosed in a genital sinus containing a cirrus-like body (gonotyl) and the male and female reproductive tracts fuse terminally to form a hermaphroditic duct. Some 40 heterophyid genera have been described in 8 subfamilies: Heterophyinae (no genital sinus, posterolateral gonotyl with chitinous rodlets, e.g. *Heterophyes*, *Heterophyopsis*); Metagoniminae (lateral ventral sucker in genital sinus, inconspicuous papilla-like gonotyl, e.g. *Metagonimus*, *Metagonimoides*); Cryptocotylineae (median ventral sucker in muscular genital sinus, papilla-like gonotyl, e.g. *Cryptocotyle*, *Seaphanocephalus*); Apophallinae (well-developed ventral sucker in non-muscular genital sinus, 1-2 papilla-like gonotyls, e.g. *Apophallus*, *Euryhelmsis*); Galactosominae (ventral sucker reduced or absent, globular gonotyl usually with spines, e.g. *Galactosomum*, *Acanthotrema*, *Stictodora*); Centrocestinae (circumoral spines present, well-developed ventral sucker in genital sinus, 1-2 papilla-like gonotyls, e.g. *Centrocestus*, *Ascocotyle*, *Phagicola*, *Pygidiopsis*, *Pygidiopsoides*); Haplorchiinae (rudimentary ventral sucker, large gonotyl with chitinous rodlets superimposed on ventral sucker, single testis, e.g. *Haplorchis*); and Stellanthasminae (small lateral ventral sucker, large spiny gonotyl, distal seminal vesicle forms muscular expulsor, e.g. *Stellanthasmus*, *Procerovum*). The genus *Metagonimus* contains around 9 species of small flukes found in the intestines of piscivorous mammals and birds which become infected by eating fish containing encysted metacercariae. Human infections are most prevalent in riverine and coastal fishing communities where raw fish are traditionally eaten, especially in Asia (Korea, China, Japan, eastern Russia) but also including Indonesia, the Middle-East (Israel and Balkan states) and Spain. The geographic distribution of infections is not confined to regions where snail intermediate hosts are found, as many fish hosts undergo extensive migration. Human infections outside endemic areas can also result from eating pickled fish or sushi imported from endemic areas.

<i>Metagonimus</i> species	Definitive hosts [adults in small intestines]	First intermediate hosts [sporocysts/rediae in tissues]	Second intermediate hosts [metacercariae in tissues]	Distribution
<i>M. hakubaensis</i>	Carnivora: canid (dog), felid (cat), Rodentia: murid (mice, rats), cricetid (hamster); Eulipotyphla: soricid (Japanese water shrew); Galliformes: phasianid (chicken, quail)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira nakasekoeae</i>)	freshwater Petromyzontiformes: petromyzontid (Far Eastern brook lamprey)	Japan
<i>M. katsuradai</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats), cricetid (golden hamster); Lagomorpha: leporid (rabbit); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira libertina</i> , <i>Juga tegulata</i> (= <i>Melania amurensis</i>))	freshwater Cypriniformes: cyprinid (stone moroko, pale chub, napjaru, oily bitterling, kanehira, tamoroko)	Japan, Russia
<i>M. minutus</i>	Primates: hominid (human); Carnivora: canid (dog, red fox), felid (cat); Rodentia: murid (mice); Accipitriformes: accipitrid (black kite)		freshwater Mugiliformes: mugilid (flathead grey mullet)	China, Taiwan
<i>M. miyatai</i> (syn. <i>M. yokogawai</i> Miyata type)	Primates: hominid (human); Carnivora: canid (dog, raccoon dog, red fox), procyonid (raccoon); Rodentia: murid (mice, rats), cricetid (golden hamster); Eulipotyphla: soricid (Japanese water shrew); Accipitriformes: accipitrid (black kite)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira globus</i> , <i>S. libertina</i> , <i>S. dolorosa</i> , <i>Koreanomelania nodifila</i>)	freshwater Osmeriformes: plecoglossid (sweetfish); Cypriniformes: cyprinid (big-scaled redfin, dace, Amur minnow, fat-minnow, pale chub, dark chub, hasu)	Japan, Korea
<i>M. otsurui</i>	Rodentia: cricetid (golden hamster); Eulipotyphla: soricid (Japanese water shrew)		freshwater Gobiiformes: oxudercid (dusky tripletooth goby, tripletooth goby, gobies)	Japan

<i>M. pusillus</i>	Rodentia: murid (brown rat); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (<i>Parajuga subtegulata</i> , <i>P. subextensa</i>)	freshwater Cypriniformes: cyprinid (Amur bitterling)	Russia
<i>M. suifunensis</i>	Rodentia: murid (brown rat)	freshwater Gastropoda: semisulcospirid (<i>Parajuga subtegulata</i> , <i>P. subextensa</i> , <i>P. subcalculus</i> , <i>P. heukelomiana</i> , <i>P. nodosa</i> , <i>P. amurensis</i> , <i>P. buettneri</i>)	freshwater Cypriniformes: cyprinid (Amur bitterling, carp)	Russia
<i>M. takahashii</i> (syn. <i>M. yokogawai</i> var. <i>takahashii</i> , or <i>M. y. Koga</i> type)	Primates: hominid (human); Carnivora: canid (dog, red fox, raccoon dog), felid (cat), procyonid (raccoon); Eulipotyphla: soricid (Japanese water shrew); Rodentia: murid (mice, rats), cricetid (hamster); Lagomorpha: leporid (rabbit); Accipitriformes: accipitrid (black kite); Pelecaniformes: pelecanid (pelican)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira coreana</i> , <i>S. libertina</i> <i>Koreanomelania nodifila</i>)	freshwater Mugiliformes: mugilid (flathead grey mullet); Cypriniformes: cyprinid (carp, crucian carp, goldfish, gudgeon, big-scaled redfin); Perciformes: lateolabracid (Japanese sea bass)	Japan, Korea
<i>M. yokogawai</i> (syn. <i>M. ovatus</i> , <i>M. romanicus</i> , <i>M. dobrogiensis</i>)	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (mice, rats, gerbil), cricetid (golden hamster); Lagomorpha: leporid (rabbit); Artiodactyla: suid (boar); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (kite); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira libertina</i> , <i>S. coreana</i> , <i>S. cancellata</i> , <i>S. laevigata</i> , <i>Koreanomelania nodifila</i>)	freshwater Osmeriformes: plecoglossid (sweetfish), salangid (Japanese icefish), Cypriniformes: cyprinid (goldfish, common carp, chub, Amur fat-minnow, slender bitterling, stone moroko, big-scaled redfin, Pacific redfin); Mugiliformes: mugilid (flathead grey mullet); Gobiiformes: oxudercid (yellowfin goby), odontobutid (dark sleeper); Perciformes: lateolabracid (Japanese seabass); Salmoniformes: salmonid (Japanese huchen)	Asia, Middle- East, Balkans, Spain

Parasite morphology: *Metagonimus* spp. form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adult flukes. Eggs are ovoid-ellipsoid and small, measuring from 26-36 µm in length by 14-23 µm in width. They are brown-yellow and surrounded by a thick eggshell with a distinct operculum set on thickened opercular shoulders. The eggs are embryonated and contain an ellipsoidal well-developed miracidium which is covered with cilia. Sporocysts have elongate pleomorphic sac-like bodies without organs but containing balls of germinal cells which give rise to rediae by asexual reproduction. Rediae have elongate bodies measuring 700-1050 x 95-150 µm and they possess an anterior mouth with sensory hairs, a spherical pharynx, a short saccular gut and their body cavity contains germinal balls which give rise to daughter rediae or cercariae. Free cercariae are pleurolophocercous with spinose bodies (180-230 x 55-75 µm) containing conspicuous eyespots and a long slender tail (340-400 x 10-14 µm) with lateral fluting (fins), They are brown and have sensory papillae (hairs) located along the lateral body margins. They possess 2 suckers, an anterior oval oral sucker and a larger midbody ventral sucker. Metacercariae are encysted cercariae that have shed their tails and developed thin cyst walls. The cysts are ovoid in shape, measuring 130-500 µm in diameter, and contain yellow-brown pigment granules. The enclosed larvae have spinose teguments and possess an anterior oral sucker with sensory papillae, a ventral sucker located to one side, a short prepharynx, an oval pharynx, a V-shaped excretory bladder and 2 developing testes. Mature flukes are dorsoventrally-flattened and pyriform in shape, small in size ranging 0.5-2.5 x 0.2-0.8 mm, and their tegument is covered with small spines. They possess a small subterminal oral sucker and a larger ventral sucker (not as large as *Heterophyes* spp.) that is unusual in being located submedian and dextral (to right of midline) within a genital sinus. Worms have a short prepharynx, a tubular pharynx opening into 2 saccular caeca that are blind-ended (no anus) and a Y-shaped excretory vesicle. Mature adults are hermaphroditic and possess both male and female reproductive organs. They have 2 globular testes located posteriorly and diagonally adjacent to each other, a large seminal vesicle and receptacle and a short ejaculatory duct opening into the genital pore (cirrus absent). The single globular ovary is connected to a short oviduct, numerous vitellaria located in posterior lateral

fields, and a large tubular uterus that is often filled with eggs and opens into the genital pore. Unlike *Heterophyes* spp., *Metagonimus* worms lack a separate genital sucker but have a ventrogenital complex (combination of ventrogenital sac and ventral sucker) with an inconspicuous papilla-like gonotyl. Characters used to differentiate *Metagonimus* spp. include the locations of the oral and ventral suckers, uterine tubule patterns, vitelline follicle distribution, and morphometrics of the ovary, seminal vesicle and eggs.

Site of infection: Adult flukes infect the small intestines of their definitive hosts, beginning in the mucosa and progressing to the crypts and intervillous spaces. Asexual developmental stages (sporocysts and rediae) occur mostly in the digestive glands of their first intermediate hosts (snails), while metacercariae encyst within the muscles, subcutaneous tissues and sometimes the scales of their second intermediate hosts (fish).

Pathogenesis: The severity of the disease metagonimiasis varies depending on the intensity and duration of infection, the immune status of the host and possibly the frequency of prior exposure leading to protective immune responses. While infections in endemic regions have been shown to accumulate in susceptible hosts over time, milder symptoms often occur in long-term residents than in newly infected patients with similar worm burdens (ranging from hundreds to thousands of worms). Adult flukes feed on to the intestinal mucosa causing irritation, tissue trauma, erosive lesions, necrosis, villous atrophy, crypt hyperplasia, and inflammation. Nevertheless, most light infections are asymptomatic and many moderate infections are subclinical or have only been associated with mild symptoms, such as fatigue, vague epigastric pain, intermittent diarrhoea, nausea, anorexia, and weight loss. Heavier infections cause more severe symptoms, particularly malabsorptive diarrhoea, abdominal pain, ulcers, nausea, vomiting, malaise, anorexia and weight loss. Flukes may penetrate deeply into the small intestinal mucosa, causing villous atrophy, oedema, lymphatic dilatation, crypt hyperplasia with excessive mucus production, and cellular inflammation (neutrophils and eosinophils). Severe infection may lead to mucosal ulceration and malabsorption with hypoalbuminemia, protein loss, impaired vitamin B₁₂ absorption, anaemia, oedema, anasarca, malnutrition and sometimes obstruction. Complications may arise in immunocompromised hosts where worms invade submucosal tissues and deposit eggs which are carried by the circulation and/or lymphatics to internal organs where they may cause emboli, granulomas and/or fibrosis. Cases of myocardial sclerosis, heart valve calcification and cardiac failure attributable to ectopic infections have been reported in humans.

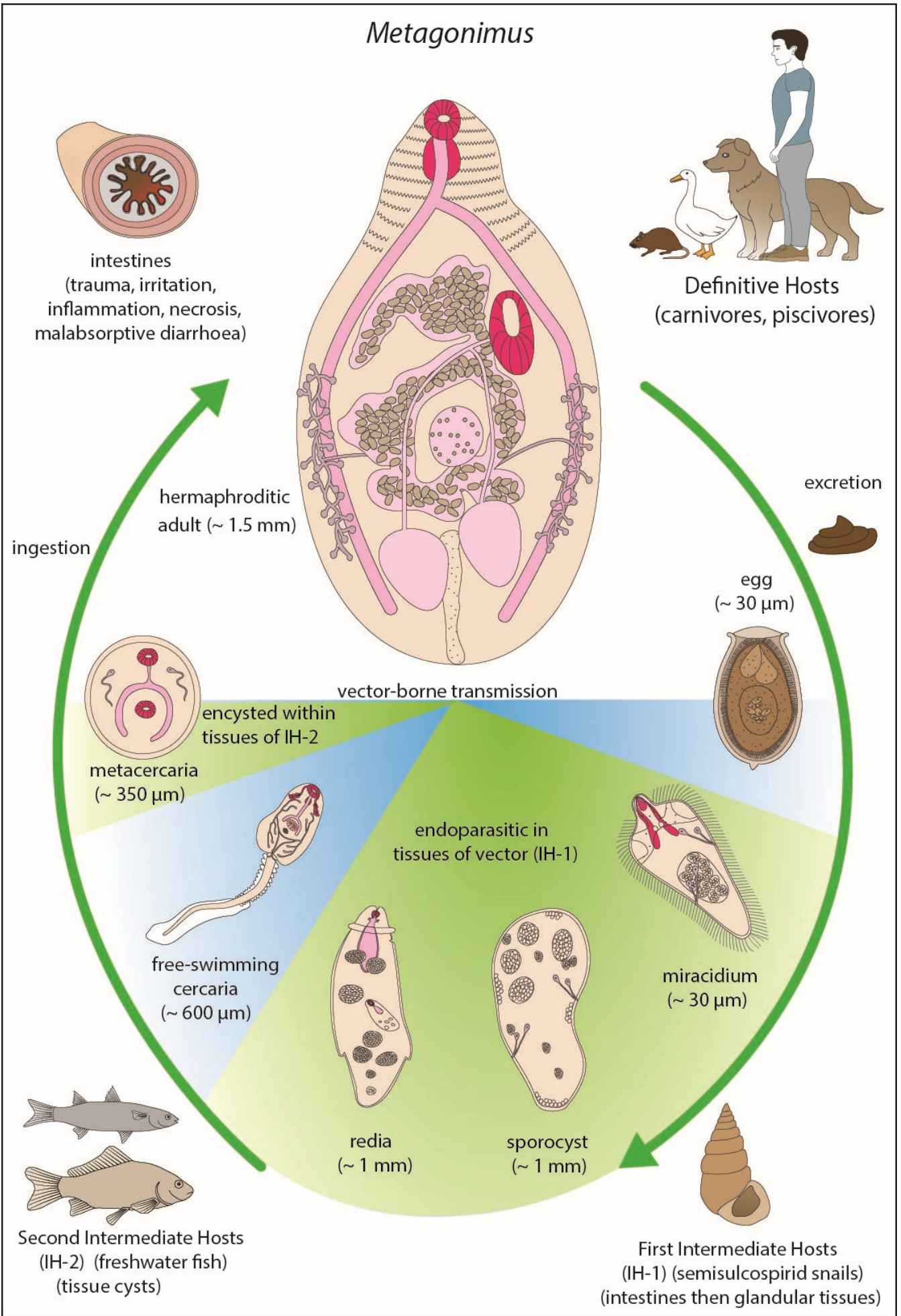
Developmental cycle and mode of transmission: *Metagonimus* spp. have indirect heteroxenous life-cycles involving cyclic transmission between 3 different types of hosts: adult worms in mammals and birds (definitive hosts); larval stages in snails (first intermediate hosts) and infective stages in fish (second intermediate hosts). Adult flukes lay embryonated eggs into the host gut lumen and they are voided with host faeces into the external environment. Eggs are ingested by freshwater snails feeding on aquatic plants in contaminated waters. Intermediate host specificity is high and only semisulcospirid snails (*Parajuga*, *Semisulcospira*, *Juga*, *Koreanomelania*) act as suitable first intermediate hosts. These gilled snails have robust high-spired or turreted shells with opercula and are found in many rivers, streams and lakes throughout Asia. The eggs hatch in the snail gut releasing the contained miracidium which penetrates the gut wall shedding its cilia and forming a sporocyst in the digestive gland. Mother sporocysts feed by absorption (they lack digestive organs) whilst their germ balls produce multiple rediae by asexual reproduction. Rediae are released into adjacent snail tissues where they feed (they possess mouths and guts) while their germ balls produce numerous cercariae. Mature cercariae are released from the rediae and exit the snail into the surrounding waters where they use their tails to swim about seeking fish hosts. Upon contact, the cercariae penetrate the skin of the fish shedding their tails and forming metacercarial cysts in fish tissues (scales, subcutis, muscles). Various species of freshwater (some brackish-water) fish act as suitable second intermediate hosts, including Osmeriformes (plecoglossids, salangids), Cypriniformes (cyprinids), Mugiliformes (mugilids), Gobiiformes (oxudercids, odontobutids), Perciformes (lateolabracids), Salmoniformes (salmonids) and Petromyzontiformes (petromyzontid lampreys). Infections are transmitted to piscivorous definitive hosts when they ingest fish tissues. Metacercariae are thought to remain viable in live fish for up to 2.5 years and they can survive in raw, undercooked, lightly preserved or pickled fish products for several days. Following ingestion, the metacercariae excyst in the host duodenum releasing the juvenile worms which attach to the mucosa and mature into adults around 1 week later. The prepatent period (time from infection to first release of eggs) ranges from 2-3 weeks and adult worms may produce from 14-280 eggs per day and live in vertebrate hosts for up to 18 months.

Differential diagnosis: Infections may be suggested on the basis of symptomatology and history of exposure (residence or travel in endemic regions, dietary intake of under-processed fish), but most clinical signs are nonspecific and other aetiological agents may be implicated. Coprological tests are usually conducted to confirm diagnoses by the microscopic detection of worm eggs in faecal samples, either in smears (direct smear, glycerin-jelly mounts, cellophane thick smears, Kato-Katz thick smears) or concentrates (formalin-ether sedimentation, some floatation techniques). Multiple samples from consecutive days should be examined due to intermittent or low egg excretion, although the differential diagnosis of fluke species (and genera) is difficult due to their similar appearance. Adult worms may be recovered for microscopic examination following anthelmintic treatment or by using purgatives or endoscopy. Infections by metacercariae in fish may be detected at necropsy by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. Several immunoserological tests have been developed to detect host serum antibodies, including intradermal and indirect fluorescent-antibody tests and enzyme immunoassays, but they have often

yielded poor specificity due to the use of crude worm antigens. Chromosome karyotyping techniques have been used in research settings to differentiate between several *Metagonimus* spp. (*M. miyatai*, *M. yokogawai*, *M. takahashii*) but they have not found widespread application. More recently, molecular biological techniques have been used to characterize various species by polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), simple sequence repeats PCR (SSR) or sequencing nuclear (28S ribosomal RNA, internal transcribed spacer region 1) or mitochondrial (cytochrome c oxidase subunit 1) genes.

Treatment and control: The drug of choice for treating *Metagonimus* infections is the isoquinoline anthelmintic praziquantel, despite some minor side-effects, such as nausea, vomiting, headaches, dizziness and insomnia. Alternative anthelmintics include the salicylanilides (niclofolan and niclosamide) and halogenated phenols (bithionol) but they were not as effective. The potential for re-infection following chemotherapy is high in endemic regions so various control strategies have been explored to break transmission cycles. The prevention of water contamination by faecal material is paramount in domestic and aquaculture settings and many attempts have been made to reduce snail populations in ponds used for fishing. However, the widespread use of toxic chemicals in aquatic ecosystems should not be considered due to environmental concerns. It is better to improve sanitary practices around water bodies and prevent definitive hosts from consuming unprocessed fish products. Public education campaigns should encourage people, especially in endemic areas, to fully cook fish and eliminate raw or undercooked fish meals from their dietary practices, despite some dishes being regarded as traditional delicacies. Many salting, smoking and pickling processes practiced in endemic communities do not effectively kill metacercariae, and freezing only renders them nonviable if fish products are deep-frozen (-20°C for at least 7 days). Experimental studies have also shown that gamma-irradiation of fish at 200 Gy also destroys metacercariae.

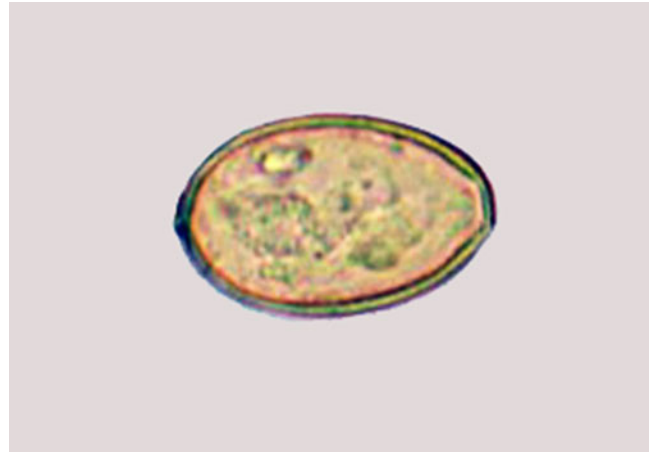
Metagonimus



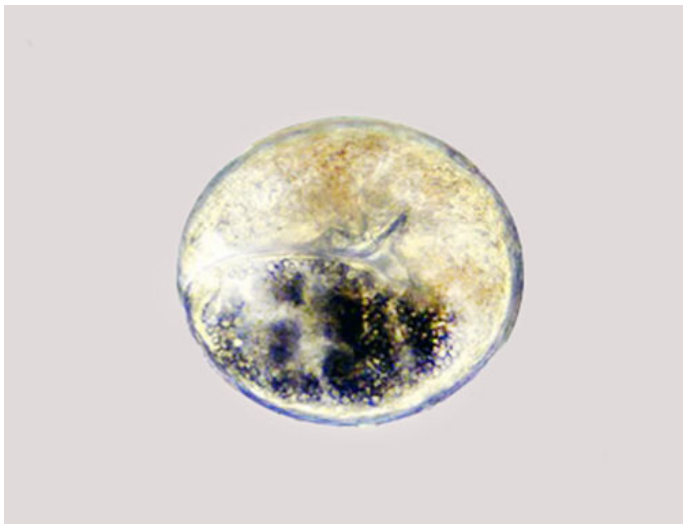


wiki

Metagonimus adult worm



Metagonimus egg



Metagonimus metacercaria

other taxa sister to *Heterophyes/Metagonimus*

Parasite species	Definitive hosts [adults in tissues]	First intermediate hosts [sporocysts/rediae in tissues]	Second intermediate hosts [metacercariae in tissues]	Distribution
Subfamily: Cryptocotylinae (median ventral sucker (acetabulum) in muscular genital sinus, papilla-like gonotyl)				
<i>Cryptocotyle</i>				
<i>C. badamshini</i>	Carnivora: phocid (Caspian seal)			Russia
<i>C. concava</i> (<i>concovum</i>)	Carnivora: felid (cat) mammals birds		brackish water Gobiiformes: gobiid (knot goby, round goby, monkey goby)	Korea, Russia
<i>C. cryptocotyloides</i>	Gaviiformes: gaviid (black-throated loon)			Russia
<i>C. delamurei</i> (syn. <i>Ciureana</i>)	Carnivora: otariid (northern fur seal)			Russia
<i>C. jejuna</i>	Carnivora: canid (dog); Charadriiformes: larid (gull)		brackish water Gobiiformes: gobiid (knot goby, round goby, monkey goby)	Russia
<i>C. lata</i>	Anseriformes: anatid (duck)	freshwater Gastropoda: bithyniid (<i>Boreoelona ussuriensis</i>)	freshwater Cypriniformes: cyprinid (swamp minnow); Anura: ranid (Dybowski's frog, tadpoles)	Russia
<i>C. lingua</i> (syn. <i>C. americana</i> , <i>C. macrorhina</i>)	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat), procyonid (raccoon), phocid (harbor seal, northern elephant seal), otariid (California sea lion); Rodentia: murid (rat); Charadriiformes: larid (black-backed gull, European herring gull, tern); Pelecaniformes: ardeid (heron)	marine Gastropoda: littorinid (<i>Littorina littorea</i>)	marine Gobiiformes: gobiid (two-spotted goby); Perciformes: labrid (Ballan wrasse); Mugiliformes: mugilid (thicklip grey mullet)	Greenland, Eurasia, North America
<i>C. quinqueangularis</i>	Carnivora: felid (cat)			Russia
<i>C. ransomi</i> sp. inq.	Carnivora: canid (dog); Rodentia: murid (brown rat)			Russia
<i>C. thapari</i>	Carnivora: mustelid (giant otter, neotropical river otter)			South America
Subfamily: Centrocestinae (circumoral spines present, well-developed ventral sucker (acetabulum) in genital sinus, 1-2 papilla-like gonotyls)				
<i>Centrocestus</i>				
<i>C. armatus</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Lagomorpha: leporid (rabbit); Rodentia: murid (rats, mice), cricetid (hamster); Pelecaniformes: ardeid (large egret, heron); Accipitriformes: accipitrid (kite)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira libertina</i>)	freshwater Cypriniformes: cyprinid (bitterling, rosy bitterling, stone moroko, pale chub, dark chub), cobitid (pond loach); Gobiformes: oxudercid (Amur goby); Siluriformes: bagrid (yellowhead catfish)	Russia, Korea, Japan
<i>C. caninus</i> (syn. <i>C. longus</i> , <i>C. yokogawai</i> , <i>C. asadai</i>)	Carnivora: canid (dog), felid (cat); Rodentia: murid (mouse); Primates: hominid (human); Pelecaniformes: ardeid (egret, heron)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira</i>)	brackish water Mugiliformes: mugilid (flathead grey mullet); Cypriniformes: cyprinid (European carp, goldfish, Chinese barb, dace), cobitid (pond loach); Gobiiformes: oxudercid (yellowfin goby); Abantiformes: channid (small snakehead), osphronemid	Asia

			(paradise fish); Perciformes: leiognathid (ponyfish); Beloniformes: hemiramphid (halfbeak); Anura: dicoglossid (rice field frog), bufonid (Asian toad)	
<i>C. cuspidatus</i>	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (rats); Galliformes: phasianid (chicken); Accipitriformes: accipitrid (yellow-billed kite)		freshwater Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (eastern happy)	Middle East, Asia
<i>C. formosanus</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats); Lagomorpha: leporid (rabbit); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (night heron, green heron, heron, pond heron, great egret)	freshwater Gastropoda: semisulcospirid (<i>Semisulcospira libertina</i>), thiarid (<i>Stenomelania newcombi</i> , <i>Melanoides tuberculata</i>)	freshwater Anabantiformes: anabantid (climbing perch), channid (striped snakehead); Characiformes: characid (blind cave fish); Cypriniformes: cyprinid (goldfish, mudcarp, barb, hardlip barb, repasson, hampala, common carp, forktail blenny, minnow, pla-kamung, swamp barb, Java barb, pale chub), nemacheilid (stone loach), cobitid (pond loach); Perciformes: percid (fountain darter); Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (blue tilapia, Nile tilapia, redbelly tilapia); Anura: ranid (Asian grass frog), bufonid (Asian toad)	Asia, Philippines, North America, Hawaii
<i>C. kurokawai</i>	Primates: hominid (human)		freshwater fish?	Japan
<i>C. nycticoracis</i>	Pelecaniformes: ardeid (black-crowned night heron, grey heron); Suliformes: phalacrocoracid (great cormorant); Accipitriformes: accipitrid (black kite); Carnivora: felid (cat)			Japan
<i>C. polyspinosus</i>	Carnivora: canid (dog)		brackish water Anabantiformes: channid (blotched snakehead), anabantid (climbing perch); Siluriformes: clariid (catfish); Cypriniformes: cobitid (weather loach)	Japan
<i>Pygidiopsis</i>				
<i>P. ardeae</i>	Pelecaniformes: ardeid (grey heron); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Carnivora: canid (dog)		marine Pleuronectiformes: pleuronectid (plaice, flounder)	Europe
<i>P. australis</i>	Galliformes: phasianid (chicken); Rodentia: murid (mouse)			South America
<i>P. anterouteria</i> (syn. <i>Caiguira</i>)	Charadriiformes: recurvirostrid (black-winged stilt); Carnivora: felid (cat)			South America
<i>P. cambodiensis</i>	Rodentia: cricetid (golden hamster)		marine Mugiliformes: mugilid (largescale mullet)	Asia
<i>P. crassus</i>	Galliformes: phasianid (chicken); Rodentia: murid (mouse)			South America
<i>P. genata</i>	Primates: hominid (human); Carnivora: felid (cat), canid (wolf, dog, fox); Eulipotyphla: soricid (shrew); Rodentia: murid (rats,	freshwater Gastropoda: thiarid (<i>Melanoides tuberculata</i>),	brackish-water Cypriniformes: cyprinid (Jordan himri); Cyprinodontiformes: poeciliid (western mosquitofish);	Middle East, Eurasia

	mice), cricetid (hamster); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (kite); Anseriformes: anatid (duck); Suliformes: phalacrocoracid (cormorant)	melanopsid (<i>Melanopsis costata</i>)	Mugiliformes: mugilid (thinlip mullet); Cichliformes: cichlid (Nile tilapia)	
<i>P. himantopae</i> (syn. <i>Caiguira</i>)	Charadriiformes: recurvirostrid (black-necked stilt)			North America
<i>P. macrostomum</i>	Rodentia: cricetid (hamster), murid (rat)	brackish water Gastropoda: cochliopid (<i>Heleobia australis</i>)	freshwater Cyprinodontiformes: poeciliid (January carpling, molly), anablepid (Rio de la Plata onesided livebearer)	South America
<i>P. marivillai</i>	Accipitriformes: accipitrid (sea eagle)			Philippines
<i>P. pelecani</i>	Pelecaniformes: pelecanid (pelican)			China
<i>P. phalacrocoracis</i>	Suliformes: phalacrocoracid (common cormorant)			Japan
<i>P. piclaumoreli</i>	Charadriiformes: larid (common tern)			Africa
<i>P. plana</i>	Pelecaniformes: ardeid (green heron)			North America
<i>P. summa</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat), procyonid (raccoon); Rodentia: murid (rats, mice)	brackish-water Gastropoda: potamidid (<i>Tympanotonus microptera</i> (= <i>Cerithidea fluvialitis</i>), <i>Cerithidea cingulata</i>)	brackish-water Mugiliformes: mugilid (flathead gray mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby, mudskipper, walking goby); Perciformes: lateolabracid (Japanese seabass); Clupeiformes: clupeid (dotted gizzard shad)	Asia
<i>Ascocotyle</i>				
<i>A. (Phagicola) angeloii</i>	Pelecaniformes: ardeid (least bittern); Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: cochliopid (<i>Littoridina (Heleobia) castellanosae</i>)	freshwater Cyprinodontiformes: anablepid (onesided livebearer)	South America
<i>A. (Phagicola) ampullacea</i>	Carnivora: procyonid (raccoon)		freshwater Cyprinodontiformes: poeciliid (western mosquitofish)	North America
<i>A. angrense</i>	Pelecaniformes: ardeid (striated heron, green heron, tricolored heron, yellow-crowned night heron, black-crowned night heron, great egret, snowy egret); Anseriformes: anatid (wood duck); Galliformes: phasianid (chicken); Suliformes: sulid (northern gannet); Charadriiformes: larid (herring gull); Carnivora: canid (dog, Alaskan fox), felid (cat), procyonid (raccoon); Rodentia: cricetid (muskrat, hamster), murid (mouse, rat)		freshwater Cyprinodontiformes: poeciliid (top minnow, sailfin molly, black molly), cyprinodontid (sheepshead pupfish), fundulid (longnose killifish, Gulf killifish, golden topminnow, mummichog, saltmarsh topminnow, striped killifish, rainwater killifish)	Americas
<i>A. arnoldoi</i>	Rodentia: murid (mouse); Carnivora: canid (dog), felid (cat); Procellariiformes: diomedeid (albatross)			South America
<i>A. (Phagicola) ascolonga</i>	Carnivora: canid (dog), felid (cat)		brackish water Cichliformes: cichlid (tilapia, Galilean comb)	Middle East
<i>A. (A.) branchialis</i>			Anura: ranid (edible frog,	Europe

			tadpoles)	
<i>A. byrdi</i>	Accipitriformes: cathartid (turkey vulture)			North America
<i>A. (Phagicola) cameliae</i>	Sphenisciformes: spheniscid (Magellanic penguin)			South America
<i>A. (A.) chandleri</i>			brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish), fundulid (longnose killifish), poeciliid (sailfin molly)	North America
<i>A. (A.) coleostoma</i>	Pelecaniformes: pelecanid (pelican); Primates: hominid (human)			Middle East
<i>A. (Phagicola) diminuta</i>	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Pelecaniformes: ardeid (great egret, snowy egret); Carnivora: procyonid (raccoon); Rodentia: murid (mouse, rat), cricetid (hamster)	brackish water Gastropoda: hydrobiid (<i>Pyrgophorus coronatus</i> , <i>Littoridina castellanosae</i> , <i>L. parchappei</i>)	brackish water Cyprinodontiformes: poeciliid (Yucatan molly, Peten molly, top minnow, variatus platy), fundulid (longnose killifish, Gulf killifish), cyprinodontid (goldspotted killifish)	Americas
<i>A. (A.) felippei</i> (syn. <i>A. puertoricensis</i>)	Pelecaniformes: ardeid (least bittern)		freshwater Cyprinodontiformes: poeciliid (guppy)	Americas
<i>A. (A.) gemina</i>	Gruiformes: rallid (mangrove rail); Galliformes: phasianid (chicken); Anseriformes: anatid (duck)	freshwater Gastropoda: hydrobiid (<i>Litterodinops monroensis</i>)	brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish),	North America
<i>A. (Leighia) hadra</i>	Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: hydrobiid (<i>Littoridina parchappei</i>)	freshwater Cyprinodontiformes: poeciliid (ten-spotted livebearer), anablepid (onesided livebearer)	South America
<i>A. intermedius</i>	Accipitriformes: accipitrid (Indian fishing eagle)			India
<i>A. langeniiformis</i>	Rodentia: cricetid (muskrat)			North America
<i>A. (A.) leighi</i>	Carnivora: procyonid (raccoon); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (tricolored heron, great egret)		brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish), poeciliid (sailfin molly); Cichliformes: cichlid (Bay snook)	Americas
<i>A. (Phagicola) longa</i>	Carnivora: canid (dog, Alaskan fox); Rodentia: cricetid (hamster); Primates: hominid (human); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (eagle); Sphenisciformes: spheniscid (Magellanic penguin)	brackish water Gastropoda: cochliopid (<i>Heleobia australis</i>)	brackish water Mugiliformes: mugilid (liza)	Americas, Africa, Europe, Middle-East
<i>A. (Phagicola) longicollis</i>	Carnivora: canid (dog), felid (cat)		brackish water Mugiliformes: mugilid (mullet); Cichliformes: cichlid (tilapia)	Middle East
<i>A. (Phagicola) macrostomus</i>	Galliformes: phasianid (chicken); Accipitriformes: cathartid (turkey vulture)		brackish water Cyprinodontiformes: poeciliid (Yucatan molly)	North America
<i>A. mcintoshi</i>	Pelecaniformes: threskiornithid (American white ibis); Galliformes: phasianid (chicken)	brackish water Gastropoda: hydrobiid (<i>Littoridinops</i>)	brackish water Cyprinodontiformes: poeciliid (sailfin molly, western mosquitofish)	North America

		<i>monroensis</i>)		
<i>A. (Leighia) megalcephala</i>	Pelecaniformes: ardeid (great egret)		brackish water Cyprinodontiformes: poeciliid (Yucatan molly)	North America
<i>A. (Phagicola) minuta</i>	Carnivora: canid (dog), felid (cat); Pelecaniformes: ardeid (grey heron)			Middle East
<i>A. (Phagicola) nana</i>	Pelecaniformes: pelecanid (American white pelican), ardeid (great egret, great blue heron, least bittern); Galliformes: phasianid (chicken); Accipitriformes: accipitrid (black hawk); Suliformes: sulid (northern gannet); Carnivora: canid (Alaskan fox), procyonid (raccoon); Didelphimorphia: didelphid (Virginia opossum); Rodentia: murid (mouse), cricetid (muskrat, Syrian hamster)		freshwater Cichliformes: cichlid (Mayan cichlid, Jack Dempsey, firemouth cichlid, golden cichlid); Characiformes: characid (banded astyanax); Cyprinodontiformes: poeciliid (Yucatan molly)	Americas
<i>A. (A.) nunezae</i>	Pelecaniformes: ardeid (great egret); Galliformes: phasianid (chicken)		freshwater Cichliformes: cichlid (firemouth cichlid, Jack Dempsey)	America
<i>A. (A.) pachycystis</i>	Carnivora: procyonid (raccoon), felid (cat)	brackish water Gastropoda: hydrobiid (<i>Littoridinops tenuipes</i>)	brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish)	North America
<i>A. (A.) patagoniensis</i>	Carnivora: otariid (South American sea lion); Sphenisciformes: spheniscid (Magellanic penguin)		marine Atheriniformes: atherinopsid (silversides)	South America
<i>A. (Phagicola) pindoramensis</i>	Pelecaniformes: ardeid (least bittern, stripe-backed bittern, great blue heron, striated heron, yellow-crowned night heron, black-crowned night heron), threskiornithid (roseate spoonbill); Suliformes: phalacrocoracid (Neotropic cormorant); Accipitriformes: pandionid (osprey); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Rodentia: cricetid (marsh rice rat, golden hamster), murid (mouse); Carnivora: canid (dog)		brackish water Cyprinodontiformes: poeciliid (January carp, Catemaco molly, shortfin molly, guppy, swordtail); Cichliformes: cichlid (tilapia)	Americas
<i>A. pithecofagicola</i>	Accipitriformes: accipitrid (monkey-eating eagle)			Philippines
<i>A. (A.) secunda</i>	Galliformes: phasianid (chicken)	freshwater Gastropoda: hydrobiid (<i>Heleobia castellanosae</i> , <i>H. parchappei</i>)	freshwater Cyprinodontiformes: poeciliid (tenspotted livebearer, western mosquitofish), anablepid (onesided livebearer)	South America
<i>A. (A.) sexidigita</i>	Galliformes: phasianid (chicken)		marine Cyprinodontiformes: fundulid (California killifish)	North America
<i>A. (A.) tenuicollis</i>	Pelecaniformes: ardeid (great egret, American bittern, little blue heron, tricolored heron); Accipitriformes: accipitrid (black hawk); Galliformes: phasianid (chicken)	brackish water Gastropoda: hydrobiid (<i>Pyrgophorus coronatus</i>)	brackish water Cyprinodontiformes: fundulid (mummichog), poeciliid (southern platyfish, Peten molly, Yucatan molly, broadspotted molly, western mosquitofish,	Americas, Middle East

			speckled mosquitofish, sailfin molly, ten-spotted livebearer); Characiformes: characid (Mexican tetra); Perciformes: centrarchid (warmouth); Cichliformes: cichlid (Jack Dempsey, yellowjacket cichlid, sepelkirjoahven, Pantani cichlid, redhead cichlid)	
<i>A. (A.) tertia</i>	Galliformes: phasianid (chicken)	freshwater Gastropoda: hydrobiid (<i>Heleobia castellanosae</i> , <i>H. parchappei</i>)	freshwater Cyprinodontiformes: poeciliid (tenspotted livebearer, western mosquitofish), anablepid (onesided livebearer)	South America
Subfamily: Galactosominae (ventral sucker (acetabulum) reduced or absent, globular gonotyl usually with spines)				
<i>Stictodora</i>				
<i>S. (S.) adulecentia</i>	Charadriiformes: larid (gull)			Japan
<i>S. allicoli</i>	Charadriiformes: larid (Indian skimmer)			India
<i>S. (S.) caballeroi</i>	Charadriiformes: larid (ring-billed gull)			North America
<i>S. cablei</i>	Charadriiformes: larid (royal tern)			North America
<i>S. (S.) diplacantha</i>	Suliformes: phalacrocoracid (pied cormorant)			Australia
<i>S. (S.) fuscata</i>	Carnivora: felid (cat), canid (dog); Primates: hominid (human)		brackish-water Mugiliformes: mugilid (flathead grey mullet, largescale mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby)	Japan, Korea
<i>S. (S.) guerreroi</i>	Charadriiformes: larid (black-headed gull)			Philippines
<i>S. (S.) hainanensis</i>	Carnivora: canid (dog)			China
<i>S. (S.) japonica</i>	Anseriformes: anatid (red-breasted merganser)			Japan
<i>S. (Galactosomoides) johnsoni</i>	Suliformes: sulid (brown booby); Charadriiformes: larid (royal tern)			Central America
<i>S. (S.) lari</i>	Charadriiformes: larid (black-tailed gull); Carnivora: felid (cat), canid (dog); Primates: hominid (human)	brackish-water Gastropoda: batillariid (<i>Velacumantus australis</i>)	estuarine Perciformes: gobiid (southern longfin goby, pale mangrove goby); Atheriniformes: atherinid (smallmouth hardyhead); Syngnathiformes: syngnathid (hairy pipefish); Cyprinodontiformes: poeciliid (western mosquitofish)	Japan, Korea, Russia, Vietnam, Australia
<i>S. (S.) lariformicola</i>	Charadriiformes: larid (herring gull, laughing gull, ring-billed gull, royal tern)			North America
<i>S. (S.) macrotestis</i>	Charadriiformes: scolopacid (wandering tattler)			Russia
<i>S. (S.) manilensis</i>	Carnivora: felid (cat), canid (dog); Rodentia: murid (mouse, rat)			Philippines
<i>S. (S.) mergi</i>	Anseriformes: anatid (red-breasted merganser)			Japan
<i>S. (S.) morosovi</i>	Charadriiformes: larid (Mediterranean gull)			Russia
<i>S. (S.) palmifera</i>			marine Perciformes: sillaginid (trumpeter whiting)	Philippines

<i>S. (S.) perpendiculum</i>	Charadriiformes: larid (gull); Carnivora: canid (dog), felid (cat)			Japan
<i>S. (S.) petrowi</i>	Charadriiformes: larid (gull)			Russia
<i>S. (S.) pusilla</i>	Charadriiformes: larid (gull)			Japan
<i>S. (S.) sawakinensis</i>	Charadriiformes: larid (gull); Procellariiformes: procellariid (Cory's shearwater)			Middle-East, Russia, Philippines
<i>S. (S.) sclerogonocotyla</i>	Pelecaniformes: ardeid (purple heron)			Middle-East
<i>S. (S.) thaparai</i>	Carnivora: felid (cat)			Middle East
<i>S. ubelakeri</i>	Carnivora: otariid (California sea lion)			North America
Acanthotrema				
<i>A. acanthotrema</i> (syn. <i>Stictodora</i>)	Charadriiformes: larid (royal tern)			Central America
<i>A. armata</i>	Charadriiformes: larid (Audouin's gull)			Europe
<i>A. cursitans</i> (syn. <i>Stictodora</i>)	Rodentia: cricetid (marsh rice rat); Carnivora: procyonid (raccoon); Didelphimorphia: didelphid (opossum)	brackish water Gastropoda: potamidid (<i>Cerithidea scalariformis</i>)	Cyprinodontiformes: fundulid (killifish)	North America
<i>A. felis</i>	Carnivora: felid (cat); Primates: hominid (human)		brackish water Gobiiformes: oxudercid (yellowfin goby)	Korea
<i>A. hancocki</i>	Galliformes: phasianid (chicken)			North America
<i>A. martini</i>	Charadriiformes: larid (black skimmer)			North America
<i>A. tanayensis</i> (syn. <i>Stictodora</i>)	Carnivora: felid (cat)			Philippines
<i>A. tridactyla</i> (syn. <i>Stictodora</i>)	Galliformes: phasianid (chicken); Carnivora: felid (cat)			Middle-East
Subfamily: Heterophyinae (no genital sinus, posterolateral gonotyl with chitinous rodlets)				
Heterophyopsis				
<i>H. continua</i> (syn. <i>Heterophyes expentans</i>)	Primates: hominid (human); Carnivora: felid (cat), canid (dog); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Charadriiformes: larid (seagull); Gaviiformes: gaviid (black-throated loon)		fresh and brackish water Cypriniformes: cyprinid (common carp); Mugiliformes: mugilid (flathead gray mullet); Clupeiformes: clupeid (shad, spotted sardine); Gobiiformes: oxudercid (yellowfin goby, mudskipper, walking goby); Osmeriformes: plecoglossid (sweetfish); Perciformes: serranid (dusky-tail grouper, orange-spotted grouper), lateolabracid (Asian seabass); Anguilliformes: congrid (white- spotted conger)	Asia
Subfamily: Stellantchasmae (small lateral ventral sucker (acetabulum), large spiny gonotyl, distal seminal vesicle forms muscular expulsor)				
Procerovum				
<i>P. calderoni</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Galliformes: phasianid (chicken)	brackish water Gastropoda: thiarid (<i>Thiara riquetti</i>)	marine and freshwater Gobiiformes: gobiid (tank goby, robust mangrove goby); Anabantiformes: channid (striped snakehead), anabantid (climbing perch); Perciformes: gerreid (whipfin silver-biddy), eleotrid (olive flathead gudgeon), ambassid (Buru glass perchlet), terapontid (trumpeter	Asia, Egypt

			perch), siganid (streaked spinefoot), polynemid (fourfinger threadfin); Mugiliformes: mugilid (gray mullet); Gonorynchiformes: chanid (milkfish); Cyprinodontiformes: poeciliid (sailfin molly); Scorpaeniformes: platycephalid (bartail flathead); Beloniformes: hemiramphid (halfbeak)	
<i>P. cheni</i>	Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: thiarid (<i>Melanoides tuberculata</i>)	freshwater Anabantiformes: osphronemid (paradisefish)	China
<i>P. varium</i>	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (water rat, mouse); Pelecaniformes: pelecanid (Australian pelican), ardeid (great egret, yellow-billed egret, white-faced heron, nankeen night heron); Accipitriformes: accipitrid (whistling kite); Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	brackish water Gastropoda: thiarid (<i>Melanoides (Thiara) tuberculata</i>)	brackish water Mugiliformes: mugilid (flathead grey mullet, eastern keelback mullet); Scorpaeniformes: platycephalid (bartail flathead); Cyprinodontiformes: poeciliid (sailfin molly); Perciformes: scatophagid (spotted scat); Gonorynchiformes: chanid (milkfish); Gobiiformes: oxudercid (maned goby); Beloniformes: hemiramphid (halfbeak); Anabantiformes: anabantid (climbing perch)	Asia, India, Australia
<i>Stellantchasmus</i>				
<i>S. aspinosus</i>	Rodentia: murid (Australian water rat, rat); Carnivora: felid (cat); Suliformes: phalacrocoracid (little pied cormorant); Galliformes: phasianid (chicken)			Australia
<i>S. batillans</i>	Rodentia: murid (Australian water rat); Anseriformes: anatid (duck)			Australia
<i>S. falcatus</i>	Carnivora: canid (dog), felid (cat); Primates: hominid (human); Artiodactyla: suid (pig); Rodentia: murid (rat, mouse); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (nankeen night heron); Accipitriformes: accipitrid (whistling kite)	brackish-water Gastropoda: thiarid (<i>Stenomelania newcombi</i> , <i>Melanoides tuberculata</i> , <i>Thiara granifera</i>)	brackish and freshwater Mugiliformes: mugilid (thinlip mullet, flathead grey mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby); Anabantiformes: anabantid (climbing perch); Beloniformes: zenarchopterid (wrestling halfbeak)	Asia, Oceania
<i>S. gallinae</i>	Galliformes: phasianid (chicken)			Vietnam
Subfamily: Haplorchiinae (rudimentary ventral sucker (acetabulum), large gonotyl with chitinous rodlets superimposed on ventral sucker, single testis)				
<i>Haplorchis</i>				
<i>H. butei</i> (<i>nom. nud.?</i>)	Accipitriformes: accipitrid (long-legged buzzard)			India
<i>H. gyanpuri</i>	Accipitriformes: accipitrid (black kite)			India
<i>H. parapumilio</i>	Suliformes: phalacrocoracid (pygmy cormorant)			Indonesia
<i>H. parataichui</i>	Carnivora: felid (cat)		freshwater Atheriniformes: melanotaeniid (Pacific blue-eye)	Australia
<i>H. paravanissimus</i>	Pelecaniformes: ardeid (rufous night heron), pelecanid (Australian pelican), Accipitriformes: accipitrid (whistling kite); Suliformes:			Australia

	phalacrocoracid (little black cormorant)			
<i>H. pearsoni</i> (<i>sp. inq.</i>)	Strigiformes: strigid (brown fish owl)			Sri Lanka
<i>H. popelkiae</i>	Testudines: chelid (northern snapping turtle, red-faced turtle)			Australia
<i>H. pumilio</i> (syn. <i>H. taihokui</i> , <i>H. milvi</i> , <i>H. pleurolophocerca</i> , <i>Monorchotrema taihokui</i>)	Primates: hominid (human), cercopithecoid (crab-eating macaque (= cynomolgus monkey)); Carnivora: canid (dog, fox), felid (cat); Eulipotyphla: soricid (African giant shrew); Rodentia: murid (mice, rat, water rat), cricetid (hamster), caviid (guinea pig); Lagomorpha: leporid (rabbit); Pelecaniformes: ardeid (night heron, yellow-billed egret), pelecanid (great white pelican, grey pelican), threskiornithid (red-naped ibis); Suliformes: phalacrocoracid (little pied cormorant); Accipitriformes: accipitrid (black kite); Charadriiformes: larid (gull), scolopacid (whimbrel); Columbiformes: columbid (pigeon); Anseriformes: anamid (duck)	freshwater Gastropoda: potamidid (<i>Pirenella conica</i>), thiarid (<i>Thiara granifera</i> (= <i>Melania reiniana</i> , <i>M. obliquegranosa</i> , <i>Melanooides tuberculata</i> , <i>Me. chinensis</i>), semisulcospirid (<i>Semisulcospira libertina</i>)	fresh and brackish water Cypriniformes: cyprinid (hampala barb, spotted barb, Mekong flying barb, barb, grass carp); Cyprinodontiformes: poeciliid (mosquitofish); Mugiliformes: mugilid (mullet, thinlip mullet); Anabantiformes: channid (striped snakehead), anabantid (climbing perch), osphronemid (paradisefish); Gobiiformes: oxudercid (goby), gobiid (tank goby); Centrarchiformes: terapontid (silver perch); Perciformes: siganid (spinefoot), anabantid (climbing gourami), gerreid (whipfin silver-biddy); Cichliformes: cichlid (tilapia, happy); Percomorpha: ambassid (Buru glass perchlet)	Middle-East, Asia, Australia
<i>H. solus</i>	Serpentes: colubrid (green tree snake)			India
<i>H. sprengi</i>	Carnivora: felid (cat); Rodentia: murid (water rat, rat); Suliformes: phalacrocoracid (little black cormorant, little pied cormorant, pied cormorant); Pelecaniformes: pelecanid (Australian pelican), ardeid (great egret, plumed egret, white-faced heron); Galliformes: phasianid (chicken)			Australia
<i>H. tagoreai</i> (<i>nom. nud.?</i>)	Carnivora: canid (dog)			India
<i>H. taichui</i> (syn. <i>H. microrchis</i>)	Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats), caviid (guinea pig), cricetid (hamster); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (cattle); Primates: hominid (human); Pelecaniformes: ardeid (night heron, egret), pelecanid (spot-billed pelican), threskiornid (red-naped ibis); Accipitriformes: accipitrid (black kite, brahminkite)	freshwater Gastropoda: thiarid (<i>Thiara granifera</i> (= <i>Melania reiniana</i> , <i>M. obliquegranosa</i> , <i>M. juncea</i> , <i>Melanooides tuberculata</i> , <i>Tarebia granifera</i>), semisulcospirid (<i>Semisulcospira libertina</i>)	freshwater Mugiliformes: mugilid (keelback mullet); Cypriniformes: cyprinid (dace, goldfish, common carp, grass carp, repasson, hampala, thinlip barb, spotted barb, swamp barb, Java barb, marginated barb, srang, stone moroko, rosy bitterling, pale chub, Burmese trout, Siamese mud carp); Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (tilapia)	Asia, India, Middle-East
<i>H. vanissimus</i>	Primates: hominid (human); Carnivora: canid (dog); Suliformes: phalacrocoracid (little black cormorant); Accipitriformes: accipitrid (whistling kite); Pelecaniformes: ardeid (Nankeen night heron)		freshwater fish?	Philippines, Australia
<i>H. wellsii</i>	Coraciiformes: alcedinid (ruddy kingfisher)			Taiwan

<i>H. yokogawai</i> (syn. <i>H. vagabundi</i> , <i>Monorchotrema</i>)	Primates: hominid (human), cercopithecoid (crab-eating macaque (= cynomolgus monkey)); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle); Rodentia: murid (mouse, water rat); Accipitriformes: accipitrid (whistling kite, black kite); Pelecaniformes: ardeid (night heron, cattle egret), pelecanid (spot-billed pelican), threskiornithid (red-naped ibis); Passeriformes: corvid (rufous treepie)	freshwater Gastropoda: thiarid (<i>Stenomelania newcombi</i> , <i>Melanoides (Thiara) tuberculata</i>)	brackish water Mugiliformes: mugilid (flathead grey mullet, eastern keelback mullet); Perciformes: siganid (streaked spinefoot), ambassid (Buru glass perchlet), gerreid (silver biddy), mullid (red mullet); Anabantiformes: anabantid (climbing perch), channid (snakehead); Cypriniformes: cyprinid (goldfish, mud carp, beardless barb, spotted hampala barb, serrated anal-spine carp), cobitid (weather loach); Cyprinodontiformes: poeciliid (western mosquitofish); Suliformes: clariid (Hong Kong catfish), ariid (Manila sea catfish); Beloniformes: hemiramphid (long-billed halfbeak); Cichliformes: cichlid (Nile tilapia); Decapoda: penaeid (shrimp)	Asia, India, Australia, Mediterranean
Subfamily: Apophallinae (well-developed ventral sucker (acetabulum) in non-muscular genital sinus, 1-2 papilla-like gonotyls)				
Apophallus				
<i>A. bacalloti</i>	Anseriformes: anatid (duck); Passeriformes: fringillid (canary)		freshwater Gasterosteiformes: gasterosteid (three-spined stickleback); Cyprinodontiformes: poeciliid (western mosquitofish)	Europe
<i>A. brevis</i>	Charadriiformes: larid (ring-billed gull, herring gull); Gaviiformes: gaviid (common loon); Carnivora: felid (cat); Rodentia: murid (rat)	freshwater Gastropoda: amnicolid (<i>Amnicola limosa</i>)	freshwater Perciformes: percid (yellow perch); Salmoniformes: salmonid (trout)	North America
<i>A. crami</i>	Charadriiformes: larid (California gull)			North America
<i>A. donicus</i>	Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (white rat, gerbil), cricetid (golden hamster); Lagomorpha: leporid (rabbit); Primates: hominid (human); Galliformes: phasianid (chicken); Charadriiformes: larid (black-headed gull, sandwich tern); Accipitriformes: accipitrid (common buzzard); Anseriformes: anatid (merganser); Pelecaniformes: ardeid (black-crowned night heron); Ciconiiformes: ciconiid (white stork); Strigiformes: strigid (owl); Columbiformes: columbid (wood dove, pigeon); Siluriformes: ictalurid (channel catfish)	freshwater Gastropoda: lithoglyphid (<i>Fluminicola virens</i>)	freshwater Cypriniformes: cyprinid (bleak, roach, blackside dace, speckled dace, redbreast shiner, squawfish, white bream, common bream, rudd, gudgeon, northern pikeminnow), catostomid (largescale sucker); Salmoniformes: salmonid (coho salmon, rainbow trout); Perciformes: percid (European perch, zander, ruffe, striped ruffe, zingel)	Europe, North America
<i>A. eccentricus</i>	Carnivora: canid (dog)			Philippines
<i>A. imperator</i>	Pelecaniformes: ardeid (great blue heron); Anseriformes: anatid (common merganser, hooded merganser)	freshwater Gastropoda: amnicolid (<i>Amnicola limosa</i>), planorbid (<i>Helisoma</i>)	freshwater Salmoniformes: salmonid (brook char, brown trout); Perciformes: percid (perch); Cypriniformes: catostomid (sucker)	North America
<i>A. itascensis</i>			freshwater Perciformes: percid (yellow perch); Cypriniformes:	North America

			cyprinid (eastern shiner)	
<i>A. lerouxi</i>	Charadriiformes: scolopacid (red shank)			Europe
<i>A. microsoma</i>	Galliformes: phasianid (chicken)		Salmoniformes: salmonid (coho salmon)	North America
<i>A. microtestis</i>	Pelecaniformes: ardeid (black-crowned night heron)			Europe
<i>A. muhlingi</i> (syn. <i>A. major</i>)	Charadriiformes: larid (black-headed gull, lesser black-headed gull), recurvirostrid (stilt); Pelecaniformes: pelecanid (pelican), ardeid (heron); Suliformes: phalacrocoracid (cormorant); Gaviiformes: gaviid (loon); Carnivora: canid (dog), felid (cat)	freshwater Gastropoda: lithoglyphid (<i>Lithoglyphus naticoides</i>)	brackish water Cypriniformes: cyprinid (crucian carp, common bream, silver bream, dace, bitterling, rudd); Perciformes: percid (perch)	Europe
<i>A. similis</i>	Carnivora: phocid (harbour seal)			North America
<i>A. venustus</i>	Carnivora: canid (dog, Arctic fox), felid (cat), procyonid (raccoon); Pelecaniformes: ardeid (blue heron); Charadriiformes: larid (gulls)	terrestrial Gastropoda: endodontid (<i>Goniobasis livescens</i>)	freshwater Lepisosteiformes: lepisosteid (garpike); Cypriniformes: cyprinid (carp), catostomid (sucker); Siluriformes: bagrid (catfish); Perciformes: centrarchid (smallmouth bass)	North America
<i>A. zalophi</i> (syn. <i>Pricetrema</i>)	Carnivora: otariid (sea lion)			North America