Echinostoma
(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 echinostomatids often have well-developed scales or spines on the anterior tegument and the ventral sucker is near the oral sucker. Echinostomes ('spiny mouth') are slender worms with a circumoral collar of peg-like spines and they form metacercariae in second intermediate hosts (small aquatic invertebrates, amphibians and fish). Most species are parasites in the intestines of fish-eating birds and mammals, sometimes associated with enteric diseases in waterfowl, domestic carnivores 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:	Echinostomata (miracidium penetrates gastropod IH, redia formed, simple-tailed cercariae, encysts in open or in second IH, metacercariae eaten by DH)
Superfamily:	Echinostomatoidea (slender worms, adult with scales or spines)
Family:	Echinostomidae (in piscivores, adult with collar of peg-like spines, ventral sucker near oral sucker, rediae with appendages, cercariae without eyespots and with simple tail, miracidia with one pair protonephridia)
Genus:	*Echinostoma* (parasitic in gut of birds/mammals)
Species:	various species cause enteritis in birds, carnivores 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
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 Echinostomata contains one superfamily Echinostomatoidea whose members form simple-tailed cercariae that encyst in the open or in second intermediate hosts, and the resultant metacercariae are eaten by definitive hosts. Ten families are recognized (Calycodidae, Cyclocoelidae, Echinostomatidae, Eucotylidae, Fasciolidae, Himasthlidae, Philophthalmidae, Psilostomidae, Rhytidodidae and Typhlocoelidae). The family Echinostomatidae (syn. Cathaemasiidae, including Echinochasmidae) contains 40-50 genera of slender worms with a distinctive collar of peg-like spines. Adult flukes have been found in various organs in fish, reptiles, birds and mammals (including humans) while larval stages develop in freshwater and marine snails, mussels, insects, amphibians and reptiles. A variety of morphotypic and biologic characters have been used to recognize some 45 genera in 10-11 subfamilies, a recent review listing Echinostomatinae (*Bashkirovitrema, Drepanocephalus, Echinodollfusia, Echinoparyphium, Echinostoma* (syn. *Echinostomum*)*, Euparyphium, Hypoderaeum, Isthmiophora* (syn. *Echinocirrus*)*, Longicollia, Lyperorchis, Moliniella, Neoacanthoparyphium, Pameileenia, Parallelotestis, Petasiger* (syn. *Paryphostomum*)*, Prionosoma, Prionosomoides, Singhia*), Echinochasminae (*Dissurus, Echinochasmus, Episthmium, Mehratomum, Microparyphium, Pulchrosomoides, Saakotrema, Stephanoprora, Stephanoprora, Uroproctepisthmium*), Chaunocephalinae (*Chaunocephalus, Balfouria*), Himasthlinae (*Himasthla, Acanthoparyphium, Aporchis, Artyfechinostomum, Caballerotrema, Cloeophora, Curtuteria*), Ignaviinae (*Ignavia*), Nephrostominae (*Nephrostomum, Patagifer*), Pegosominae (*Pegosomum*), Pelmatostominae (*Pelmatostomum*), Singhiatreminae (*Singhiatrema*), Sodalinae (*Sodalis*) and one unplaced (*Ruffetrema*).

The genus *Echinostoma* is speciose with over 120 nominal species recorded worldwide from a wide range of birds, mammals, occasionally reptiles and fish as definitive hosts, freshwater snails as first intermediate hosts, and many aquatic animals (snails, clams, fish, amphibians, planaria and leeches) as second intermediate hosts. Several attempts have been made to revise the systematics of the heterogeneous echinostomes and many phenotypic characters (morphological and biological) have been used to differentiate taxa and identify major groups (possibly species-flocks); the most robust being the number of collar spines on adults and the divisions of paraoesophageal glands in cercariae. The genus *Echinostoma* has been characterized by most workers as comprising adult worms possessing a collar with 27-55 spines (lateral, dorsal and angle spines arranged in 1-2 rows). More recently, a comprehensive comparison of larval and adult stages revealed that the number of spines was consistent between different life-cycle stages and was always uneven (reports of worms with even numbers of spines were considered to represent specimens with spines lost, retracted or supernumerary). Preliminary molecular phylogenetic studies have identified several dominant clades, with strong support found for the 37-collar-spined '*E. revolutum'* group. Infections by *Echinostoma* spp. are prevalent in humans throughout Asia, and zoonotic infections have been recorded throughout Europe, Africa and the Americas. Most human infections occur in children and young women in poor rural areas with limited sanitation and healthcare and where dietary customs include the consumption of raw or insufficiently cooked foods derived from aquatic animals (molluscs, shellfish, amphibians, fish), important sources of supplemental protein in human nutrition. It has been estimated that 40-50 million people throughout the world are at risk of infection by echinostomes, with some 15% developing disease.

***Echinostoma* species**	**Definitive hosts [adults in intestines]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
27-collar-spined				
E. hortense (syn. *Isthmiophora*)	Carnivora: canid (dog), felid (cat), mustelid (Japanese weasel); Rodentia: murid (rats, mice, field mice), cricetid (reed vole); Primates: hominid (human); Suliformes: phalacrocoracid (cormorants); Anseriformes: anatid (duck, mallard, spot-billed duck)	freshwater Gastropoda: lymnaeid (*Lymnaea pervia*, *Radix auricularia*)	freshwater Cypriniformes: cobitid (pond loach, Chinese fine-scaled loach), cyprinid (Chinese minnow, gudgeon); Perciformes: percichthyid (redfin perch); Gobiiformes: odontobutid (dark sleeper), oxudercid (yellowfin goby); Anura: ranid (American bullfrog, tadpoles); Clitellata: hirudinid (leeches); Gastropoda: lymnaeid (snails)	Asia

E. melis (syn. *Isthmiophora, E. trigonocephalum, Euparyphium jassyenese, Eu. spiculator, Eu. suinum*)	Carnivora: mustelid (European badger, European polecat, American mink); Eulipotyphla: erinaceid (European hedgehog); Rodentia: murid (striped field mouse); Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	freshwater Osteichthyes (fish); Anura: ranid (tadpoles)	Eurasia, North America
29-collar-spined				
E. ignavum	Charadriiformes: charadriid (Australian masked plover)			Australia
31-collar-spined				
E. anseris	Anseriformes: anatid (duck)			Asia, North America
E. donosoi		freshwater Gastropoda: ampullariid (*Marisa cornuarietis*)		South America
E. govindum	Charadriiformes: scolopacid (ruff)			India
E. parcespinosum	Gruiformes: rallid (spotted rail, plumbeous rail)			South America
E. sudanense	Pelecaniformes: ardeid (heron), Anseriformes: anatid (duck)			Africa, Europe, North America
33-collar-spined				
E. chasma	Anseriformes: anatid (garganey)			North America
E. operosum	Charadriiformes: scolopacid (common snipe); Suliformes: anhingid (Surinam darter)			Americas
E. stantschinskii	Charadriiformes: scolopacid (common sandpiper)			Japan
35-collar-spined				
E. amurzetica	Anseriformes: anatid (duck)			Asia, North America
E. bhattacharyai	Anseriformes: anatid (duck)			Asia, North America
E. crotophagae	Cuculiformes: cuculid (greater ani, guira cuckoo)			South America
E. distinctum	Passeriformes: icterid (solitary cacique)			South America
E. elongatum	Anseriformes: anatid (ducks); Caprimulgiformes: podargid (tawny frogmouth)			China, Australia
E. emollitum	Cuculiformes: cuculid (pheasant coucal)			Australia
E. grandis	Anseriformes: anatid (duck); Gruiformes: rallid (coot)			Eurasia, North America
E. guirae	Cuculiformes: cuculid (guira cuckoo)			South America
E. parvum	Columbiformes: columbid (rock dove)			South America
E. pekinensis	Anseriformes: anatid (duck)			China, North America
E. porteri	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Rodentia: murid (rats)	freshwater Gastropoda: lymnaeid (*Lymnaea natalensis*)	freshwater Gastropoda: planorbid (*Bulinus* (*Physopsis*) *globosus*, *Bulinus* (*Bulinus*) *forskalii*), lymnaeid (*Lymnaea natalensis*)	Africa

E. uncatum	Cuculiformes: cuculid (greater ani, smooth-billed ani, squirrel cuckoo)			South America
E. uitalica	Galliformes: phasianid (common pheasant)			Russia
E. valentini	Suliformes: phalacrocoracid (Indian cormorant)			Pakistan
37-collar-spined (*Echinostoma* '*revolutum'* group)				
E. acuticauda	Pelecaniformes: threskiornithid (straw-necked ibis)			Australia
E. atrae	Gruiformes: rallid (black coot)			Pakistan
E. caproni (syn. *E. liei, E. togoensis, E. parasensei*)	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Columbiformes: columbid (pigeon); Passeriformes: fringillid (finch); Falconiformes: falconid (falcon); Rodentia: murid (mice, jirds, rats, roof rat), cricetid (golden hamster); Eulipotyphla: soricid (Egyptian giant shrew); Lagomorpha: leporid (rabbit)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata, Bulinus*)	freshwater Gastropoda (snails), Bivalvia (clams), Anura (tadpoles)	Africa
E. chloephagae	Anseriformes: anatid (upland goose)			South America
E. cinetorchis	Carnivora: canid (dog); Primates: hominid (human); Rodentia: murid (rats, mice)	freshwater Gastropoda: viviparid (*Cipangopaludina chinensis*), lymnaeid (*Austropeplea ollula*), planorbid (*Hippeutis* (*Helicorbis*) *cantori*, *Segmentina hemispaerula, S. nitidella*, *Gyraulus convexiusculus*)	freshwater Gastropoda: planorbid (*Segmentina hemispaerula*, *S. nitidella, Gyraulus convexiusculus*, *Hippeutis* (*Helicorbis*) *cantori, H. cantori, Planorbis compressus*), lymnaeid (*Radix auricularia, Lymnaea japonica*), physid (*Physa* (*Physella*) *acuta*), viviparid (*Cipangopaludina chinensis*); Bivalvia: cyrenid (*Corbicula*, basket clams); Cypriniformes: cobitid (pond loach, muddy loach); Anura: ranid (dark-spotted frog, American bullfrog)	Asia
E. deserticum	Rodentia: murid (African grass rat)	freshwater Gastropoda: planorbid (*Bulinus trancatus, B. globosus*)	freshwater Gastropoda (snails)	Africa
E. echinatum (syn. *E. lindoense, E. barbosai, E. robustum*)	Rodentia: murid (rats, mice); Primates: hominid (human); Columbiformes: columbid (spotted dove); Anseriformes: anatid (duck, mallard, mottled duck, goldeneye, wigeon, muscovy, shelduck, ferruginous duck, gadwall, pochard, shoveler, whooper swan, mute swan, greylag goose); Podicipediformes:	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*), planorbid (*Planorbarius*, *Planorbis corneas*, *Anisus*, *Gyraulus*, *Biomphalaria glabrata*), viviparid	freshwater Gastropoda: viviparid (*Idiopoma javanica*); Bivalvia: cyrenid basket clams (*Corbicula lindoensis, C. sucplanta*), unspecified mussels	South America, Europe, Asia, Australia?

	podicipedid (great crested grebe, little grebe); Suliformes: phalacrocoracid (red-legged cormorant, pygmy cormorant); Pelecaniformes: ardeid (black-crowned night heron, crowned heron, squacco heron); Gruiformes: gruid (common crane)	(*Viviparus* (*Paludina*) *vivipara*, *V. achatina*)		
E. erraticum	Columbiformes: columbid (pigeon, ground dove); Gruiformes: rallid (common gallinule, coot, russet-crowned crake); Pelecaniformes: ardeid (yellow-crowned night heron); Cuculiformes: cuculid (smooth-billed ani)	freshwater Gastropoda: planorbid (*Biomphalaria*, *Drepanotrema*)	freshwater Gastropoda: physid (*Physa rivalis*), planorbid (*Planorbis*)	Europe
E. friedi	Rodentia: murid (rats, mice), cricetid (hamster); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*, *L. corvus*, *Radix*), planorbid (*Gyraulus chinensis*, *Biomphalaria*, *Bulinus*)	freshwater Gastropoda: lymnaeid (*Lymnaea*), planorbid (*Gyraulus*)	Europe
E. jurini (syn. *E. bolschewense, E. sisjakowi, E. orlovi*)	Rodentia: cricetid (golden hamster, muskrat), murid (rats, mice); Columbiformes: columbid (pigeon)	freshwater Gastropoda: viviparid (*Viviparus contectus, V. viviparus, V. acerosus*)	freshwater Gastropoda: physid (*Physa acuta, P. fontinalis*), viviparid (*Viviparus viviparus*, *V. contectus*), lymnaeid (*Lymnaea stagnalis, L. tomentosa, L. truncatula, L. palustris, L. peregra, L. auricularia*), planorbid (*Planorbarius corneus, Planorbis planorbis, Biomphalaria glabrata, B. alexandrina*), bithynid (*Bithynia tentaculata, B. leachi*); Bivalvia (thick-shelled river mussels, zebra mussels); Anura: ranid (European grass frog, marsh frog); Testudines: emydid (European pond turtle)	Eurasia
E. londonense	Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Planorbis corneus*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*, *L. pereger*), planorbid (*Planorbis corneus*)	Europe
E. luisreyi	Rodentia: murid (mice), cricetid (hamster)	freshwater Gastropoda: physid (*Physa marmorata*)	freshwater Gastropoda: physid (*Physa*), planorbid (*Biomphalaria*)	Central/South America

E. mendax	Anseriformes: anatid (black-necked swan, white-faced whistling duck)			South America
E. miyagawai	Anseriformes: anatid (duck, tufted duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: planorbid (*Planorbis planorbis*, *Planorbarius corneus*, *Anisus vortex*), lymnaeid (*Lymnaea*)	freshwater Gastropoda (snails)	Europe, Asia, Australia, New Zealand
E. nasincovae	Rodentia: cricetid (golden hamster)	freshwater Gastropoda: planorbid (*Planorbarius corneus*)		Europe
E. novaezealandense	Anseriformes: anatid (Canada goose, duck, black swan)			New Zealand
E. nudicaudatum	Columbiformes: columbid (pigeon)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	Europe
E. paraensei	Rodentia: cricetid (hamster, scaly-footed water-rat), murid(mice, rats)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*), physid (*Physa rivalis, P. marmorata, P. gyrina, Glyptophysa*)	freshwater Gastropoda (snails)	Central and South America, Australia
E. parvocirrus	Anseriformes: anatid (muscovy duck); Passeriformes: fringillid (canary)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*), physid (*Physa marmorata*); Anura: bufonid (cane toad, tadpoles)	Central and South America
E. revolutum (syn. *E. audyi, E. paraulum, E. ivaniosi, E. columbae, E. neglectum, E. nephrocystis, E. microrchis, E. echinocephalum?*)	Anseriformes: anatid (duck, black duck, tufted duck, mallard, spot-billed duck, greater scaup, goose, pied goose, white-fronted goose, Canada goose, black swan, green goose teal, falcated teal); Columbiformes: columbid (pigeon, little cuckoo dove); Podicipediformes: podicipedid (crested grebe); Galliformes: phasianid (chicken); Passeriformes: sturnid (starling), estrildid (Java sparrow, black-headed munia, spotted munia); turdid (thrush); Falconiformes: falconid (falcon, Eurasian hobby); Accipitriformes: accipitrid (northern goshawk, lesser spotted eagle, common buzzard, rough-legged buzzard, short-toed snake eagle, red kite); Strigiformes: strigid (little owl, tawny owl), tytonid (barn owl); Ciconiiformes: ciconiid (white stork); Gruiformes: rallid (common gallinule); Charadriiformes: larid (black-backed gull); Rodentia: cricetid (hamster), echimyid (coypu), murid (rat); Carnivora: felid (cat);	freshwater Gastropoda: lymnaeid (*Lymnaea elodes, perega, rubiginosa, stagnalis, Radix Auricularia, peregra, Stagnicola palustris*), viviparid (*Filopaludina*), physid (*Physa occidentalis*), planorbid (*Segmentina*)	freshwater Gastropoda (pulmonate and prosobranch snails) physid (*Physa occidentalis*), lymanaeid (*Lymnaea*); Bivalvia (mussels, basket clams) cyrenid (*Corbicula producta*); Anura: ranid (frogs, tadpoles); Testudines (turtles)	Eurasia, Americas, Africa, Australia

	Primates: hominid (human)			
E. rodriguesi	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Rodentia: cricetid (hamster), murid (mice)	freshwater Gastropoda: physid (*Physa rivalis*)	freshwater Gastropoda: physid (*Physa rivalis*), planorbid (*Biomphalaria glabrata*)	Brazil
E. serratum (syn. *Echinoparyphium*)	Anseriformes: anatid (duck)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)		Australia
E. trivolvis (syn. *E. rodriguesi, E. armigerum, E. coalitum, E. callawayensis, E. multispinosum, Echinoparyphium contiguum*)	Anseriformes: anatid (duck, mallard, pintail, wigeon, teals, mottled duck, shoveler duck, shelduck, goldeneye, black duck, tufted duck, goose, emden goose, greylag goose, magpie goose, bean goose, scaup, ring-necked duck, fulvous whistling duck, common scoter, muscovy, mute swan, whooper swan,); Galliformes: phasianid (chicken, partridge); Passeriformes: icterid (grackle), corvid (carrion crow, jackdaw); Charadriiformes: larid (black-headed gull); Phoenicopteriformes: phoenicopterid (flamingo); Podicipediformes: podicipedid (great crested grebe); Columbiformes: columbid (mourning dove, pigeon); Accipitriformes: accipitrid (rough-legged buzzard); Strigiformes: strigid (horned owl); Rodentia: caviid (guinea pig), cricetid (golden hamster, muskrat), murid (mice, rats); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, red fox), felid (cat): Artiodactyla: suid (pig); Primates: hominid (human)	freshwater Gastropoda: planorbid (*Helisoma trivolvis, Biomphalaria*), lymnaeid (*Lymnaea*), physid (*Physa*), bithyniid (*Bithynia*)	freshwater Gastropoda (pulmonate and prosobranch snails); Bivalvia (mussels); Rhabditophora (planarians); Anura (bullfrogs, green frogs, leopard frogs, tadpoles); Testudines (turtles); Osteichthyes (fish)	Americas, Europe
39-collar-spined				
E. aphylactum	Gruiformes: rallid (purple gallinule); Primates: callitrichid (Geoffroy's tamarin)			South America
E. platensis	Rodentia: cricetid (Argentine swamp rat)			South America
E. rufinae	Anseriformes: anatid (red-crested pochard)			Eurasia, North America
E. uralensis	Charadriiformes: scolopacid (woody sandpiper, Eurasian curlew, little curlew)		freshwater Gastropoda: bithynid (*Bithynia tentaculata, B. trocheli*), lymnaeid (*Lymnaea stagnalis*)	Russia
41-collar-spined				
E. alepidotum	Gruiformes: rallid (azure gallinule)			Brazil
E. angustitestis	Carnivora: canid (dog); Primates: hominid (human)		freshwater fish	Asia
E. rafiae	Pelecaniformes: ardeid (little egret)			Pakistan
E. turkestanica	Anseriformes: anatid (duck)			Eurasia, North America
43-collar-spined				

E. academica	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. aegyptiacum	Rodentia: murid (albino rat)			Japan
E. azerbaidjanicum	Galliformes: phasianid (chicken)			India
E. coronale	Passeriformes: corvid (carrion crow)			Russia
E. dietzi	Anseriformes: anatid (duck)			Eurasia, North America
E. macrorchis	Rodentia: murid (field mice, rats), cricetid (field vole); Eulipotyphla: talpid (mole); Charadriiformes: scolopacid (common snipe); Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Lymnaea luteola*)	freshwater Gastropoda: viviparid (*Cipangopaludina chinensis, C. malleata, C. japonica*), planorbid (*Segmentina nitidella*; Anura: ranid (frog)	Asia
E. malayanum (syn. *Artyfechinostomum*)	Carnivora: canid (dog), Artiodactyla: suid (pig); Rodentia: murid (mice, rats), cricetid (hamsters); Primates: hominid (human)	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Gyraulus convexisuculus*)	freshwater Gastropoda: lymnaeid (*Radix, Bullastra* (*Lymnaea cumingiana*), ampullariid (*Pila scutata*), planorbid (*Indoplanorbis exustus, Gyraulus convexisuculus*), Anura: dicroglassid (skittering frog, tadpoles); Osteichthyes (fish)	Southeast Asia, India
45-collar-spined				
E. attenuatum	Gruiformes: rallid (king rail, mangrove rail)			North America
E. australasianum	Gruiformes: gruid (brolga)			Australia
E. coromandum	Pelecaniformes: ardeid (cattle egret)			Germany (ex: India)
E. exile	Columbiformes: columbid (rock dove); Gruiformes: rallid (American purple gallinule)			South America
E. gotoi	Anseriformes: anatid (mallard, spot-billed duck)			Asia
E. jacanae	Charadriiformes: jacanid (wattled jacana)			South America
E. lahorensis	Galliformes: phasianid (chicken)			Pakistan
E. pindchi (formerly *Euparyphium*)	Podicipediformes: podicipedid (little grebe)			India
E. siticulosum	Tinamiformes: tinamid (undulated tinamou, variegated tinamou, yellow-legged tinamou)			South America
47-collar-spined				
E. chloropodis	Gruiformes: rallid (coots, gallinules, common moorhen); Anseriformes: anatid (duck)			Eurasia, North America
E. corvi	Passeriformes: corvid (carrion crow)			Japan
E. garzetti	Pelecaniformes: ardeid (little egret)			Pakistan
E. hilliferum	Gruiformes: pallid (Australasian swamphen)			Australia
E. hystricosum	Passeriformes: estrildid (white-headed munia, spotted munia);	freshwater Gastropoda:	freshwater Gastropoda:	Malaya

	Columbiformes: columbid (zebra dove)	lymnaeid (*Lymnaea rubiginosa*)	lymnaeid (*Lymnaea rubiginosa*), planorbid (*Gyraulus convexisulcus, Indoplanorbis exustus*)	
E. militare	Charadriiformes: scolopacid (Eurasian curlew, jack snipe); Gruiformes: rallid (spotted crake)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*), viviparid (*Viviparus* (*Paludina*) *vivipara*)		Eurasia
E. necopinum	Pelecaniformes: threskiornithid (bald ibis)			Brazil
E. rousseloti	Gruiformes: rallid (Allen's gallinule)			Africa
E. sarcinum	Gruiformes: gruid (common carne); Anseriformes: anatid (duck)			Eurasia, Africa, North America
E. travassosi	Passeriformes: corvid (gray crow)			Russia
49-collar-spined				
E. coecale	Galliformes: phasianid (chicken)			India
E. condignum	Caprimulgiformes: caprimulgid (scissor-tailed nightjar)			Brazil
E. ilocanum (syn. *Euparyphium*)	Carnivora: felid (cat), canid (dog); Rodentia: murid (rats, rice field rat); Primates: cercopithecid (baboon), hominid (human)	freshwater Gastropoda: planorbid (*Gyraulus, Hippeutis*)	freshwater Gastropoda: ampullariid (*Pila conica*), viviparid (*Viviparus javanicus*), lymnaeid (*Lymnaea rubiginosa*)	Asia, Philippines
51-collar-spined				
E. sindhenses	Pelecaniformes: ardeid (western cattle egret)			Pakistan
E. transfretanum	Gruiformes: rallid (red-gartered coot)			Brazil
Reptile species				
E. jacaretinga	Crocodilia: alligatorid (caiman)			Brazil
E. ornatum (= *Stephanoprora ornata*)	Crocodilia: crocodylid (Nile crocodile)			Egypt
E. umbonatum (= *Allechinostomum crocodili*)	Crocodilia: crocodylid (Nile crocodile, Siamese crocodile)			Africa, Southeast Asia
Piscine species				
E. annulatum	Gymnotiformes: gymnotid (electric eel)			South America
E. cristatum	Scombriformes: stromateid (blue butterfish)			Mediterranean
E. dujardinii	Pleuronectiformes: pleuronectid (European plaice), scophthalmid (turbot)			Europe
E. fallax	Trachiniformes: uranoscopid (Atlantic stargazer)			Atlantic
E. hispidum	Acipenseriformes: acipenserid (European sea sturgeon, starry sturgeon, sterlet)			Eurasia
E. pristis	Gadiformes: gadid (blue whiting)			Atlantic
E. scabrum	Gadiformes: lotid (common ling), gadid (Atlantic cod)			Atlantic
As yet unplaced				
E. apiculatum	Strigiformes: strigid (brown owl, tawny owl, short-eared owl)			North America

E. asiatica	Anseriformes: anatid (duck)			North America
E. bancrofti	Gruiformes: rallid (Eurasian coot)			India
E. bilobum	Gruiformes: rallid (Eurasian coot), Pelecaniformes: threskiornithid (Eurasian spoonbill, white ibis)			Eurasia, Australia
E. chishtii	Accipitriformes: accipitrid (black kite)			India
E. cinctum	Charadriiformes: charadriid (lapwings)			Europe
E. crecci	Anseriformes: anatid (duck)			North America
E. danubiana	Gruiformes: rallid (Eurasian coot)			Europe
E. denticulatum	Charadriiformes: larid (common tern, black tern, sandwich tern)			Northern Hemisphere
E. dilatatum	Galliformes: phasianid (junglefowl)			Asia
E. echiniferum	Charadriiformes: scolopacid (ruff)			Europe
E. echymiperae	Peramelemorphia: peramelid (spiny bandicoot)			Papua New Guinea
E. egregium (syn. *Dietziella*)	Pelecaniformes: threskiornithid (bald ibis); Anseriformes: anatid (piken duck)			Brazil, Middle-East
E. ferox	Ciconiiformes: ciconiid (white stork, black stork);Pelecaniformes: ardeid (brown bittern)			Europe, Africa
E. fotedari	Passeriformes: acrocephalid (clamorous reed warbler)			India
E. fulicae	Anseriformes: anatid (duck)			North America
E. koisarensis	Anseriformes: anatid (duck)			North America
E. leptosomum	Charadriiformes: scolopacid (dunlin, sanderling)			Eurasia
E. minimus	Anseriformes: anatid (duck)			North America
E. nephrocephalum	Passeriformes: muscicapid (rock thrush)			
E. nordiana	Anseriformes: anatid (greater scaup)			Europe
E. novum	Anseriformes: anatid (duck)			North America
E. ralli	Gruiformes: rallid (water rail)			Japan
E. spinulosum	Podicipediformes: podicipedid (great crested grebe); Anseriformes: anatid (garganey); Charadriiformes: alcid (black guillemot), larid (herring gull, glaucous gull, black-headed gull), scolopacid (curlew); Suliformes: phalacrocoracid (spectacled cormorant); Anseriformes: anatid (goldeneye)			Northern Hemisphere
E. stromi	Anseriformes: anatid (duck)			North America
E. turdi	Passeriformes: turdid (Tickell's thrush)			India
E. uncinatum	Gruiformes: rallid (moorhen)			

Parasite morphology: *Echinostoma* spp. form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adults. Eggs are typically oval-elliptical in shape and variable in size depending on the species, ranging from 58-150 µm in length by 36-88 µm in width. They are surrounded by a thin refractory tanned eggshell (yellow-brown or silver-white in colour) with an operculum (often small and inconspicuous) at one end and a small abopercular wrinkle, knob or thickening at the other end. Unembryonated ectolecithal eggs are passed in faeces, but embryonate in water to contain miracidia which are released upon hatching. Free-swimming miracidia are elongate measuring 65-120 x 45-70 µm, broad anteriorly and tapering posteriorly. They possess ciliated epidermal plates, apical papilla, 2 eyespots, and a pair of protonephridia with 2 excretory ducts and pores. In snails, they transform to non-ciliated contractile pleomorphic sacs (sporocysts) initially measuring around 100 µm long but growing to 200-250 µm. Sporocysts do not have defined organs but contain germ balls which form larval embryos (rediae) by asexual reproduction. Rediae are motile colourless elongate larvae measuring 0.5–2.0 x 0.07–0.2 mm and they possess an anterior mouth, pharynx, saccular gut, an anterior collar-like tegumentary ring, and 2 posterior stumpy locomotor appendages (ambulatory buds). There are 2-3 rediae generations with small mother rediae producing slightly larger daughter rediae and some forming grand-daughter redia. Daughter and grand-daughter rediae ultimately produce cercariae. Larval cercariae measure 0.2–0.6 x 0.1–0.2 mm and are gymnocephalous with elongate bodies and simple cylindrical tails with finger-like tips. They are active swimmers and have oral and ventral suckers, an oral collar of spines, anterior cystogenous penetration glands and several finfolds (dorsal, ventral and ventrolateral). Metacercariae are tail-less cercariae that have encysted becoming surrounded by several cyst wall layers (thick outer wall, thin inner opaque wall). The cysts are spherical measuring from 100-200 µ in diameter and contain stages similar to immature worms with collar spines, excretory granules and an oesophagus. Adult trematodes have elongate-oval ventrally-curved bodies ranging in size from 2.5-30 mm in length by 0.6–6.0 mm in width, depending on species. The tegument is spinose (covered with scale-like spines), the number and size of which is reduced in the posterior half of the body. *Echinostoma* adults are characterized by the possession of a prominent circumoral collar armed with 27-55 large spines (up to 110 µm long) arranged in 1-2 ventrally interrupted rows. The oral and ventral suckers are well developed and the gut comprises a mouth, prepharynx, pharynx, oesophagus, and 2 blind caeca. Adult worms are hermaphroditic, with smooth or lobate testes in tandem in the posterior half of the body, and spherical or ovoid ovaries in the anterior body. Other male organs comprise the vas efferentia, vas deferens, cirrus sac (with seminal vesicle, ejaculatory duct, cirrus and prostate gland) terminating in a median genital pore. Other female organs consist of an oviduct (with seminal receptacle), numerous vitelline follicles (with ducts), an ootype (oviduct enlargement) surrounded by glandular tissue (Mehlis' gland) and a uterus also terminating in the genital pore.

Site of infection: Adult echinostomes infect the small intestines of their definitive hosts, including domestic and wild mammals (carnivores, rodents, primates) and aquatic birds (many families). In heavy infections, adults can also be found in stomach, liver, gall-bladder and pancreas of their vertebrate hosts. Larval sporocysts and rediae infect the tissues and organs of their first intermediate hosts (aquatic snails). Sporocysts often form near the site of miracidial penetration (foot, head) but rediae move to the heart and then the digestive gland-gonad complex. Encysted metacercariae form in the tissues of their second intermediate hosts (molluscs, crustaceans, fish and amphibians), particularly in the kidney-pericardial region of molluscs, the gills and gonads in clams, the kidneys and cloaca of frogs, and the skin and muscles of fish.

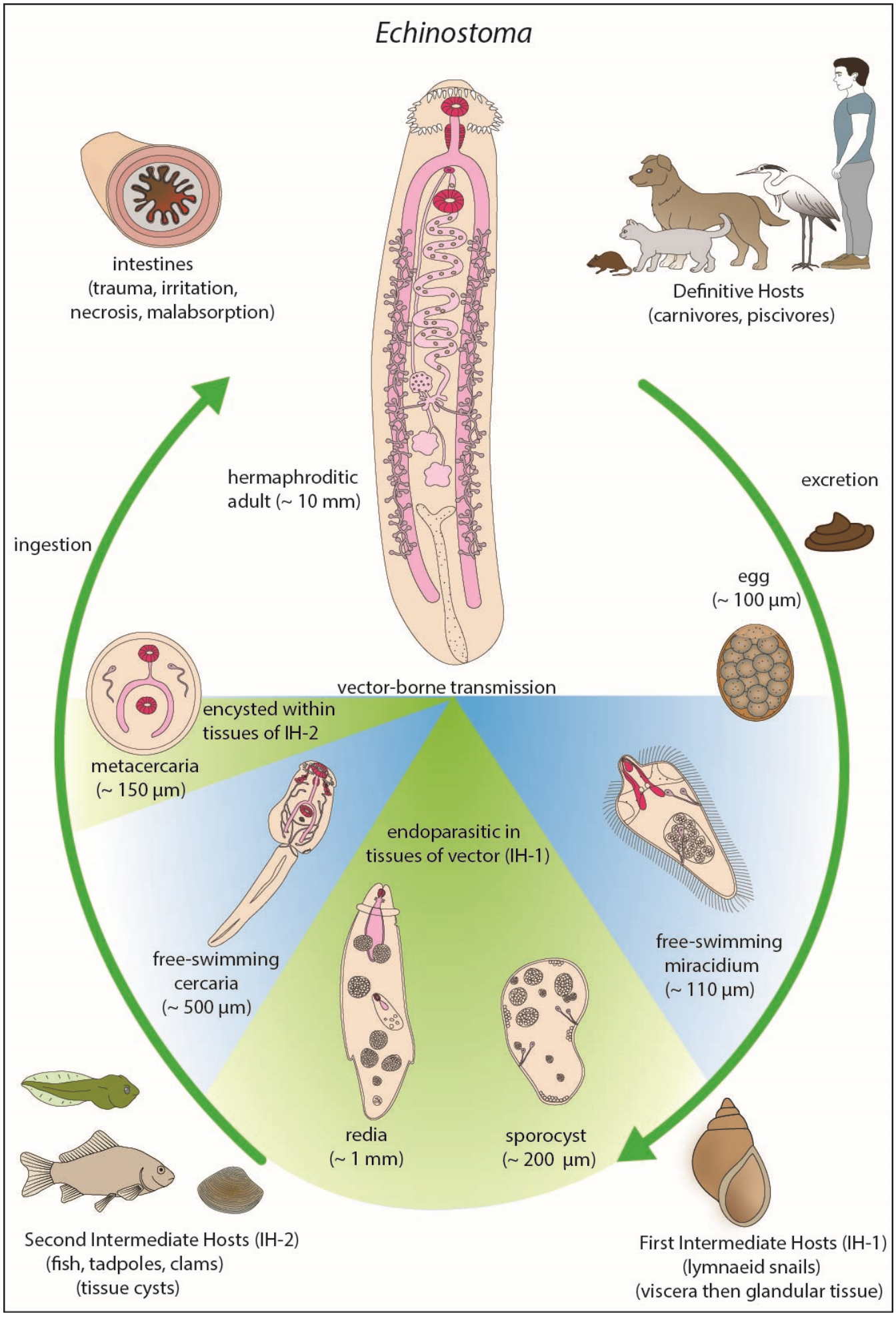
Pathogenesis: Trematodes have mouths (oral suckers) and saccular guts (blind caeca lacking an anus) which are used to feed on the intestinal mucosa of their vertebrate hosts. Light infections may be asymptomatic or subclinical, while heavier infections may cause clinical manifestations attributable to trauma/irritation at the site of attachment and to host immune/allergic responses to the flukes and their metabolites. Young and adult flukes attach to the mucosa using their oral and ventral suckers and collar spines to penetrate to subepithelial layers. They feed using their oral suckers to imbibe and pinch off tissue plugs which causes tissue damage, ulceration and inflammation. This may result in epithelial desquamation, villous blunting and atrophy, crypt hyperplasia, necrosis, enteritis, cellular infiltration, oedema, haemorrhages and vascular congestion. Adult flukes also secrete and excrete many metabolites (e.g. digestive enzymes, waste products) into the host gut which trigger physiological and immunological responses, including diarrhoea, anaemia and malabsorption with inflammatory, allergenic and hypersensitivity reactions. Light to moderate infections have been associated with intermittent diarrhoea, epigastric and abdominal pain, intestinal colic and flatulence, postprandial burning, headaches, dizziness, anorexia, weight loss, fatigue, mild anaemia and eosinophilia. Heavy infections may produce profuse watery diarrhoea, mucosal ulceration and haemorrhages, catarrhal enteritis, oedema, severe epigastric pain and abdominal discomfort, anorexia, malnutrition, weight loss, emaciation, weakness and a developing anaemia with elevated white blood cell counts, including eosinophilia. In heavy infections, adult worms may migrate up the common bile duct to the liver, gall-bladder and pancreas damaging tissues, causing haemorrhages and forming granulomas. While infections are unlikely to cause death in humans, they have severe consequences for patients in remote rural communities with limited healthcare by causing chronic diarrhoea with dehydration and malnutrition as well as predisposing them to other opportunistic infections, which collectively may prove fatal. In animals, heavy infections have been associated with severe disease and mortality, particularly in domestic fowl exhibiting haemorrhagic diarrhoea and emaciation.

Developmental cycle and mode of transmission: *Echinostoma* spp. have indirect life-cycles involving 3 different types of hosts: adult trematodes infecting definitive hosts (vertebrates), asexual stages multiplying within first intermediate hosts (molluscs), and metacercariae encysting within second intermediate hosts (vertebrates and invertebrates). Transmission from definitive to

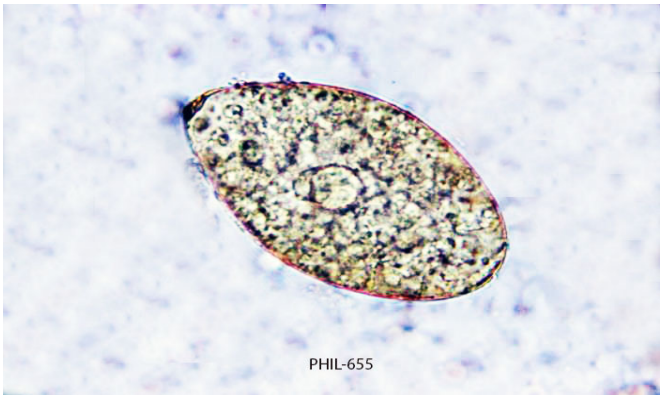
intermediate hosts involves free-swimming aquatic stages, while parasites move from second intermediate to definitive hosts by predator-prey transmission. Eggs produced by adult flukes are passed with host faeces to contaminate the external environment. Those deposited in water embryonate over 2-3 weeks depending on temperature (longer in colder water) and some have been observed to remain viable for up to 5 months. Most eggs hatch around 3 weeks releasing a non-feeding ciliated miracidium which swims around for 2-15 hours seeking a suitable aquatic snail host using positive phototaxis (swim to light), negative geotaxis (swim up) as well as chemotaxis (swim towards macromolecules secreted in snail mucus). *Echinostoma* spp. have been found within ampullariid, lymnaeid, physid, planorbid and viviparid snails, and their host specificity is generally confined to a few related snail species. The snails act as first intermediate hosts as the miracidia penetrate their tissues and undergo massive asexual multiplication forming several larval generations (a single sporocyst generation then 2 rediae generations). Sac-like sporocysts are formed within organs (usually the heart cavity) within 2 days and their germ balls produce first-generation (mother) rediae after 5 days. These rediae migrate to the gonads and/or digestive gland and produce second-generation (daughter) rediae which in turn produce numerous cercariae within 28-42 days of initial infection. Cercariae migrate to the mantle cavity and exit the host via the sinuses. They are free-swimming stages that periodically swim to the surface of the water and then sink to the bottom for up to 5 days. They may infect a wide range of second intermediate hosts, including the same or different snail species, bivalves (river mussels, basket clams), amphibians (including tadpoles) or fish (particularly cyprinids). When cercariae penetrate host tissues, they shed their tails and encyst as metacercariae. Definitive hosts living in or near fresh-water or brackish-water habitats become infected when they eat infective metacercariae within the tissues of prey. Metacercariae excyst in the ileum releasing immature flukes which migrate to the lower small intestines where they attach to the gut wall and develop into adult flukes over 1-3 weeks. Mature flukes may produce from 300-2,000 eggs per day and they may live for several months. Human infections are most often associated with the consumption of raw or undercooked fish, clams or snails, particularly in specialized dishes in Asian cuisine: e.g. lab-pla or plasom (raw fish), kinilaw (raw fish or snails dipped in salt and vinegar), kukhol or kiambu-ay (raw fish in coconut milk), tinola (lightly boiled fish), gintaan (fish stewed in coconut milk), sinugba (charcoal-grilled fish), sashimi (raw sliced fish), and sushi (raw fish roll in rice).

Differential diagnosis: Echinostome infections may be diagnosed by the detection of worm eggs in faecal samples, but the identification of particular species relies on the examination of whole adult worms recovered from hosts. Coprological tests may detect eggs in faecal smears (e.g. Kato-Katz thick smears, merthiolate-iodine-formalin fixation) or following their concentration by sedimentation (in water) and/or floatation (in saturated salt or sugar solutions). Adult flukes may be recovered from hosts ante-mortem following anthelmintic treatment or by endoscopic biopsy around the duodenal bulb, or post-mortem by dissection. *Echinostoma* spp. are differentiated mainly on the basis of the number and arrangement of the circumoral spines and the topography of the genital systems in adult flukes. Haematological and biochemical tests conducted on blood and urine samples have associated infections with reductions in erythrocyte parameters (anaemia), plasma choline, formate, acetate, lactate, urine creatine, increases in eosinophil counts, plasma glucose and distortions in neutral lipid and amino acid profiles, but such changes are mostly nonspecific and may be attributable to other causes. Enzyme immunoassays have been developed to detect class-specific host antibodies in serum samples (typified by early transient increases in IgM and secretory IgA, followed by more persistent IgG responses) as well as to detect parasite copro-antigens in faecal samples. These immunological tests were reported to vary considerably in their sensitivity and specificity, with cross-reactions found between various trematode species. Molecular biological techniques have recently been used to characterize DNA from adult flukes, metacercariae and eggs of various echinostome species (particularly those with 37 collar spines); mostly following polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD) or particular gene sequences (nuclear DNA (small (18S) and large (28S) subunit ribosomal RNA and internal transcribed spacers 1 and 2) and mitochondrial DNA (nicotinamide adenine dinucleotide dehydrogenase subunit 1, and cytochrome c oxidase subunit 1).

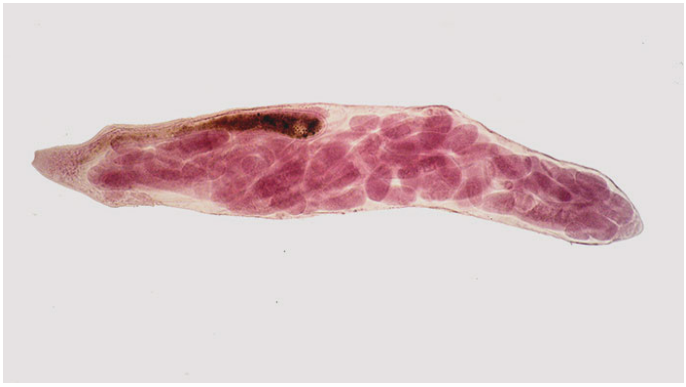
Treatment and control: A range of anthelminthics have proven effective in treating echinostomiasis in humans, including the broad-spectrum benzimidazoles (albendazole, mebendazole), isoquinolines (praziquantel), halogenated phenols (bithionol), salicylanilides (nicolsamide, rafoxanide, oxyc1ozanide) and substituted dihydroxybenzene (hexylresorcinol). Most drugs had few side-effects, mostly nausea, abdominal pain, headaches and dizziness. Recent experiments have also reported some success *in vitro* using the trematodicide clorsulon, the anthelmintic tribendimidine and the antiprotozoal artemisinin (dihydroartemisinin). The halogenated hydrocarbons (tetrachloroethylene and carbon tetrachloride) have been used to treat infections in birds and some mammals, but their use in humans in contraindicated due to toxic or adverse interactions with dietary components. Despite regular treatment programmes in many endemic regions, re-infection was found to be common as the parasites may be maintained in sylvatic or peridomestic cycles involving aquatic birds and mammals. Preventive measures are based on breaking transmission cycles by reducing faecal contamination of water bodies (through proper effluent treatment and disposal), reducing intermediate host snail populations (using molluscicides or draining swampy fields), and avoiding the consumption of raw or improperly cooked foods (notably fish, clams, snails and frogs). Public health education campaigns may be used to inform at-risk groups although their impact may be eroded in endemic rural communities by poor living conditions, the lack of alternative food sources and entrenched dietary customs.


Echinostoma
intestines
(trauma, irritation,
necrosis, malabsorption)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 10 mm)
excretion
ingestion
egg
(~ 100 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 150 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 500 µm)
free-swimming
miracidium
(~ 110 µm)
redia
(~ 1 mm)
sporocyst
(~ 200 µm)
Second Intermediate Hosts (IH-2)
(fish, tadpoles, clams)
(tissue cysts)
First Intermediate Hosts (IH-1)
(lymnaeid snails)
(viscera then glandular tissue)

Echinostoma adult worm

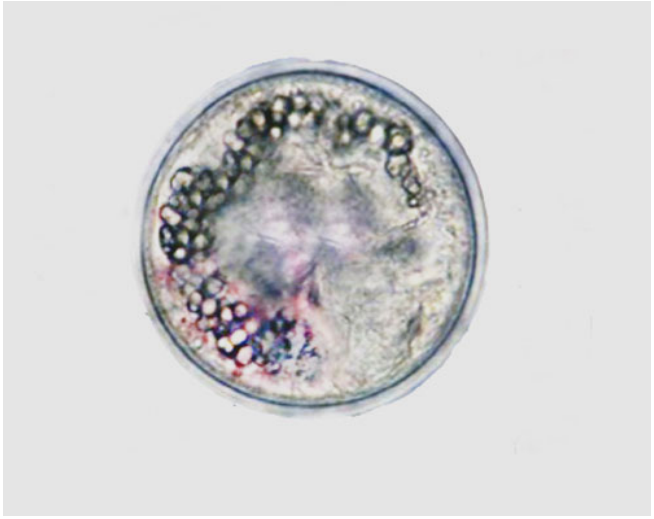


Echinostoma egg

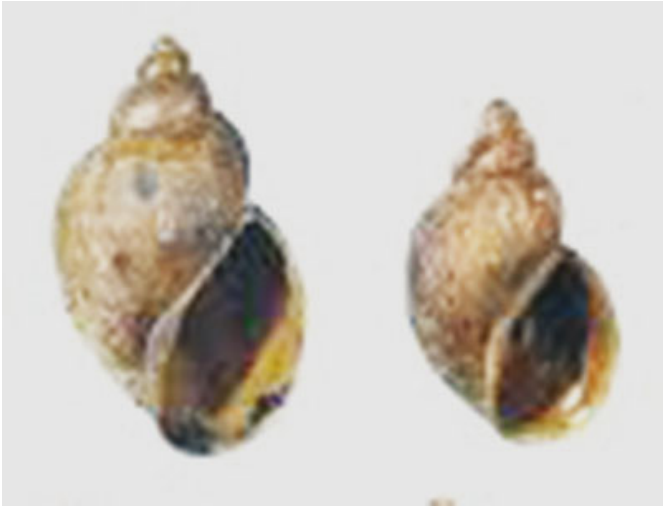


Echinostoma redia

Echinostoma cercaria



Echinostoma metacercaria



Echinostoma lymnaeid snail vectors

Sister genera to *Echinostoma*

Parasite species	Definitive hosts [adults in intestines]	First intermediate hosts [sporocysts/rediae in tissues]	Second intermediate hosts [metacercariae in tissues]	Distribution
Subfamily: Echinochasminae				
Echinochasmus				
E. accipeteri	Accipitriformes: accipitrid (shikra)			Pakistan
E. amphibolus (syn. *E. botauri*)	Pelecaniformes: ardeid (Eurasian bittern, black-crowned night heron); Suliformes: phalacrocoracid (great cormorant); Gruiformes: rallid (common moorhen)			Europe, Pakistan
E. antigonus	Gruiformes: gruid (sarus crane)			India
E. bagulai	Pelecaniformes: ardeid (Indian pond heron)	freshwater Gastropoda: thiarid (*Thiara tuberculata*)	freshwater Cyprinodontiformes: aplocheilid (blue panchax), poeciliid (western mosquitofish); Beloniformes: adrianichthyid (medaka); Anabantiformes: channid (spotted snakehead)	Asia, India
E. beleocephalus	Passeriformes: sittid (Eurasian nuthatch); Pelecaniformes: ardeid (black-crowned night heron, grey heron); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Parafossarulus*)	freshwater Cypriniformes: cyprinid (goldfish); Anura: ranid (*Rana dubowskii* tadpoles); freshwater Gastropoda: bithyniid (*Parafossarulus*)	Europe
E. coaxatus (syn. *E. squamatus)*	Anseriformes: anatid (mallard); Podicipediformes: podicipedid (black-necked grebe, red-necked grebe, great crested grebe); Ciconiiformes: ciconiid (white stork); Columbiformes: columbid (pigeon)	freshwater Gastropoda: bithyniid (*Bithynia tentaculata*)	freshwater Cypriniformes: cyprinid (spined loach, Caspian roach, rudd, tench, bleak, silver bream); Perciformes: percid (European perch); Gasterosteiformes: gasterosteid (Ukrainian stickleback); Gobiformes: gobiid (bighead goby, round goby)	Eurasia, North America
E. cohensi	Charadriiformes: larid (European herring gull)			Europe
E. colymbi (= *E. schigini*) (= *Episthmium*?)	Podicipediformes: podicipedid (grebes)			Eurasia
E. dietzevi	Pelecaniformes: threskiornithid (roseate spoonbill); Anseriformes: anatid (teal); Podicipediformes: podicipedid (great crested grebe, black-necked grebe)			Europe, North America
E. donaldsoni	Pelecaniformes: pelecanid (brown pelican, American white pelican);	freshwater Gastropoda: amnicolid (*Amnicola limosa, A.*	freshwater fish	North America

	Columbiformes: columbid (pigeon); Podicipediformes: podicipedid (pied-billed grebe)	*lustrica*)		
E. euryporus	Accipitriformes: accipitrid (buzzard, western marsh harrier, pallid harrier, red kite, black kite); Pelecaniformes: ardeid (grey heron, great egret, little egret)			Eurasia, Africa
E. famelicus	Ciconiiformes: ciconiid (lesser adjutant)			Sri Lanka
E. fujianensis	Carnivora: canid (dog), felid (cat); Artiodactyla: suid (pig); Rodentia: murid (rats); Primates: hominid (human)	freshwater Gastropoda: viviparid (*Bellamya aeruginosa*)	freshwater Cypriniformes: cyprinid (stone moroko, common carp)	China
E. gorsakii	Pelecaniformes: ardeid (Japanese night heron)			Japan
E. japonicus	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Pelecaniformes: ardeid (egret); Carnivora: canid (dog), felid (cat); Rodentia: murid (rats, mice); Primates: hominid (human)	freshwater Gastropoda: bithyniid (*Parafossarulus striatulus, P. manchouricus, Boreoelona*)	freshwater Cypriniformes: cyprinid (stone moroko, Manchurian gudgeon); Osmeriformes: osmerid (pond smelt); Anura: ranid (Dybowski's frog, tadpoles)	Asia, Europe
E. jamshorensi	Pelecaniformes: ardeid (Indian pond heron)			Pakistan
E. jiufoensis	Primates: hominid (human)			China
E. liliputanus	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat), mustelid (badger), procyonid (raccoon), birds?	freshwater Gastropoda: viviparid (*Bellamya aeruginosa*), bithyniid (*Parafossarulus striatulus*)	freshwater Cypriniformes: cyprinid (stone moroko, goldfish) [plus drinking water containing cercariae]	Middle-East, China
E. leopoldinae	Galliformes: phasianid (chicken)	aquatic Gastropoda: hydrobiid (*Pyrgophorus coronatus*)	brackish water Cichliformes: cichlid (Mayan cichlid, firemouth cichlid, Nile tilapia)	Mexico
E. macrocaudatus	Galliformes: phasianid (chicken); Anseriformes: anatid (duck)	aquatic Gastropoda: hydrobiid (*Pyrgophorus coronatus*)	freshwater Characiformes: characid (Mexican tetra); Cyprinodontiformes: poeciliid (variegated platy, Yucatan molly)	Mexico
E. mathevossianae (syn. *Schiginella*)	Anseriformes: anatid (pochard, goldeneye)			Russia
E. mazharuddini	Passeriformes: sturnid (bank myna)			Pakistan
E. megavitellus	Pelecaniformes: ardeid (Indian pond heron)			India
E. mergi (syn. *Stephanoprora mergi*, *Mesorchis mergi*) (incl. subspp. *E. m. mergi, E. m. palaearcticus*)	Anseriformes: anatid (merganser)			Europe, North America
E. microacetabulum	Charadriiformes: larid (European herring gull)			Russia
E. militaris	Pelecaniformes: ardeid (grey heron)			Europe
E. milvi	Accipitriformes: accipitrid (black kite)			Japan

E. mirus	Anseriformes: anatid (common eider)			Europe
E. mohiuddini	Pelecaniformes: ardeid (Indian pond heron)			Pakistan
E. mordax	Podicipediformes: podicipedid (great crested grebe); Pelecaniformes: pelecanid (Dalmatian pelican)			Eurasia, Africa
E. muraschkinzevi	Pelecaniformes: pelecanid (Dalmatian pelican)			Russia
E. narayani	Accipitriformes: accipitrid (black kite)			India
E. passeri	Passeriformes: passerid (house sparrow)			Pakistan
E. perfoliatus	Carnivora: canid (dog, red fox), felid (cat); Artiodactyla: suid (pig); Rodentia: murid (rats); Primates: hominid (human); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Parafossarulus manchouricus*, *Bithynia leachi*), lymnaeid (*Lymnaea stagnalis*)	freshwater Cypriniformes: cyprinid (goldfish, carp, pale chub, dark chub, stone moroko)	Asia, Europe
E. prakashi	Pelecaniformes: ardeid (black-crowned night heron)			Pakistan
E. reniovarus	Passeriformes: corvid (house crow)			India
E. ruficapensis	Pelecaniformes: ardeid (black-crowned night heron); Podicipediformes: podicipedid (little grebe)			Europe
E. schwartzi	Anseriformes: anatid (ducks); Rodentia: murid (mouse)		freshwater Cyprinodontiformes: fundulid (mummichog)	North America
E. skrjabini	Gaviiformes: gaviid (red-throated loon); Podicipediformes: podicipedid (great crested grebe)			Europe
E. spinulosus	Anseriformes: anatid (ducks)			Europe
E. swabiensis	Accipitriformes: accipitrid (black kite)			Pakistan
E. tobi	Accipitriformes: accipitrid (black kite)			Japan
E. vindhianae	Accipitriformes: accipitrid (Asian tawny eagle)			India
E. zubedakhaname	Passeriformes: tyrannid (pied water tyrant); Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken)	freshwater Gastropoda: ampullariid (*Pomacea glauca*)	freshwater Cyprinodontiformes: poeciliid (rainbow fish)	Americas
Episthmium				
E. bilqeesae	Pelecaniformes: ardeid (little egret)			Pakistan
E. bursicola (syn. *Uroproctepisthmium*)	Pelecaniformes: ardeid (grey heron)			Europe
E. caninum	Carnivora: canid (dog), felid (cat); Primates: hominid (human)		freshwater fish	Asia
E. colymbi	Pelecaniformes: ardeid (little egret)			Pakistan
Subfamily: Echinostominae				

Euparyphium				
E. albuferensis	Rodentia: murid (rats, mice), cricetid (hamster)	freshwater Gastropoda: planorbid (*Gyraulus chinensis*)	freshwater Gastropoda: planorbid (*Gyraulus chinensis*), lymnaeid (*Lymnaea trunculata, L. peregra, L. palustris*), physid (*Physa acuta*)	Europe
E. beaveri (syn. *Isthmiophora*)	Carnivora: mustelid (mink, otter); Lagomorpha: leporid (snowshoe hare)	freshwater Gastropoda: lymnaeid (*Stagnicola* (*Lymnaea*) *angulata*)	freshwater Anura (tadpoles, frogs)	North America
E. capitaneum (syn. *E. anhingae*)	Suliformes: anhingid (darter)			North America
E. guerreroi	Rodentia: murid (brown rat)			
E. inermis (syn. *Isthmiophora*)	Carnivora: mustelid (North American river otter)			North America
E. lukjanovi (syn. *Isthmiophora*)	Artiodactyla: bovid (goitered gazelle)			Russia
E. melis (syn. *Isthmiophora*)	Carnivora: felid (cat), canid (fox), mustelid (European polecat, mink, badger, otter); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (rats)	freshwater Gastropoda: lymnaeid (*Lymnaea*)	freshwater Cypriniformes: cobitid (loach); Anura: ranid (tadpoles)	Europe
E. murinum	Rodentia: murid (rats); Anseriformes: anatid (ducks); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*), planorbid (*Gyraulus chinensis*), lymnaeid (*Lymnaea ollula*	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*), planorbid (*Gyraulus chinensis, Segmentina hemisphaerula, Hippeutis cantori*), lymnaeid (*Lymnaea ollula*), bithynid (*Parafossarulus striatulus*), viviparid (*Viviparus*); Anura: ranid (tadpoles)	Philippines, China
E. paramurinum	Rodentia: caviid (guinea pig)	freshwater Gastropoda: viviparid (*Vivipara angularis*)	freshwater Gastropoda: viviparid (*Vivipara angularis*)	Philippines
E. vietnamensis	Carnivora: mustelid (Eurasian otter)			Vietnam
Echinoparyphium				
E. aconiatum	Galliformes: phasianid (ruffed grouse); Charadriiformes: scolopacid (black-tailed godwit); Anseriformes: anatid (ducks)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. corvus*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. corvus, Stagnicola turricula, Radix peregra, R. auricularia*), bithyniid (*Bithynia tentaculata, B. troscheli*), planorbid (*Planorbarius corneus, Planorbis planorbis*), physid (*Physella acuta*)	Eurasia, North America
E. agnatum	Anseriformes: anatid (mallard)			Europe
E. baculoides	Charadriiformes: larid (whiskered tern)			Eurasia
E. baculus	Anseriformes: anatid (smew, scaup, goldeneye, northern shoveler, velvet scoter); Gaviiformes: gaviid (black-throated loon)			Eurasia
E. bagulai	Anseriformes: anatid (Indian spot-billed duck)	freshwater Gastropoda: lymnaeid	freshwater Gastropoda: lymnaeid (*Lymnaea luteola*)	India

		(*Lymnaea luteola*)		
E. chinensis	Anseriformes: anatid (duck)			China
E. cinctum	Anseriformes: anatid (duck); Charadriiformes: scolopacid (black-tailed godwit)	freshwater Gastropoda: lymnaeid (*Lymnaea*)	freshwater Gastropoda: lymnaeid (*Lymnaea*); Anura: ranid (frogs); Testudines (turtles)	Europe
E. clerci (syn. *Echinostoma*?)	Anseriformes: anatid (domestic duck); Charadriiformes: scolopacid (black-tailed godwit)			India
E. combesi	Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: planorbid (*Bulinus truncatus*), physid (*Physa acuta*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, Planorbarius metidjensis*), physid (*Physa acuta*); Anura: ranid (marsh frog tadpoles)	Africa
E. contiguum	Rodentia: cricetid (muskrat)			North America
E. dollfusi (syn. *Paryphostomum*?)	Suliformes: anhingid (Indian darter)			India
E. dunni	Anseriformes: anatid (duck); Columbiformes: columbid (pigeon); Passeriformes: estrildid (white-capped munia, spotted munia, Java sparrow)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*), planorbid (*Gyraulus convexiusculus, Indoplanorbis exustus*), viviparid (*Bellamya ingallsiana*)	Malaysia
E. elegans	Anseriformes: anatid (ducks); Pelecaniformes: ardeid (western cattle egret); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Passeriformes: fringillid (canary); Rodentia: murid (rats); Carnivora: felid (cat)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. tropica*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. globosus, B. tropica, Biomphalaria glabrata*), physid (*Physa acuta*)	Africa
E. ellisi	Anseriformes: anatid (duck, black swan)	freshwater Gastropoda: planorbid (*Glyptophysa*)		Australia, New Zealand
E. flexum	Anseriformes: anatid (blue-winged teal, black scoter), Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	freshwater Gastropoda: lymnaeid (*Lymnaea* (*Stagnicola*) *palustris*)	freshwater Gastropoda: lymnaeid (*Lymnaea* (*Stagnicola*) *palustris*), viviparid (*Viviparus bengalensis*), physid (Physa); Anura (ranid, hylid tadpoles)	North America
E. gallinarum	Galliformes: phasianid (chicken)			China
E. gizzardai	Anseriformes: anatid (black swan)			India
E. indicum	Accipitriformes: accipitrid (Egyptian vulture)			India
E. groenlandicum	Charadriiformes: scolopacid (purple sandpiper)			Greenland
E. hirundonis (syn. *Euparyphium*)	Passeriformes: hirundinid (red-rumped swallow)			Taiwan
E. hydromys	Rodentia: murid (Australian water rat, dusky rat)	freshwater Gastropoda: planorbid (*Plananisis* (*Gyraulus*) *isingi*)	Anura: ranid (tadpoles)	Australia
E. ichthyophilum	Pelecaniformes: ardeid (grey heron)			Eurasia
E. kashmirensis	Galliformes: phasianid			India

	(chicken)			
E. limosorum	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. longicirrus	Anseriformes: anatid (mute swan)			India
E. macrovitellatum	Suliformes: phalacrocoracid (great cormorant)			Russia
E. megacirrus	Galliformes: phasianid (chicken); Rodentia: murid (mouse)		freshwater Bivalvia: hyriid (*Diplodon chilensis*); and Platyhelminthes: temnocephalid (*Temnocephala chilensis*) ectosymbiotic on Decapoda: aeglid (Patagonian crab)	South America
E. mordvilkowi	Charadriiformes: charadriid (northern lapwing, plovers, killdeers), scolopacid (black-tailed godwit)	freshwater Gastropoda: valvatid (*Valvata piscinalis*)	freshwater Gastropoda: valvatid (*Valvata piscinalis*)	Eurasia
E. montgomeriana	Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Bulinus africanus*)		Africa
E. nordianum	Anseriformes: anatid (Eurasian wigeon)			Eurasia
E. oscitansi	Ciconiiformes: ciconiid (Asian openbill stork)			Asia
E. paracinctum	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. petrowi (syn. *Neoacanthoparyphium*?)	Anseriformes: anatid (duck, goose); Galliformes: phasianid (chicken)		freshwater Gastropoda: viviparid (*Viviparus viviparous*)	Russia
E. phasianinum	Galliformes: phasianid (pheasant)			Russia
E. politus (syn. *Echinostoma*?)	Charadriiformes: scolopacid (green sandpiper)			Europe
E. poulini	Anseriformes: anatid (black swan)			New Zealand
E. pseudorecurvatum	Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Planorbis planorbis*)	freshwater Gastropoda: planorbid (*Planorbis planorbis*); Anura (frogs, tadpoles)	Europe
E. ralphaudyi	Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Passeriformes: fringillid (finch); Rodentia: murid (mouse, rat), cricetid (hamster)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. forskalii, B. sericinus*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. forskalii, B. sericinus*)	Africa
E. recurvatum (syn. *E. bioccalerouxi*)	Anseriformes: anatid (mallard, greater scaup, tufted duck, spot-billed duck, brahmany duck, graylag goose); Podicipediformes: podicipedid (greater crested grebe); Galliformes: phasianid (chicken, pheasant, ruffed grouse, turkey); Columbiformes: columbid (pigeon); Charadriiformes: larid (southern black-backed gull, red-billed gull), charadriid (common ringed plover), scolopacid (common	freshwater Gastropoda: lymnaeid (*Radix peregra, R. auricularia, Lymnaea peregra, L. stagnalis*), valvatid (*Valvata piscinalis*), physid (*Physa fontinalis)*, planorbid (*Planorbis carinatus, Planorbarius corneus, Bulinus truncatus*)	freshwater Gastropoda: lymnaeid (*Radix auricularia, Lymnaea peregra, L stagnalis*), physid (*Physa fontinalis*), planorbid (*Planorbis planorbis, Biomphalaria glabrata*); Bivalvia (clams, mussels); Anura: ranid (European grass frog, tadpoles); Cypriniformes: cobitid (loach)	worldwide

	snipe, black-tailed godwit); Accipitriformes: accipitrid (common buzzard); Rodentia: murid (rats): Carnivora: canid (dog); Primates: hominid (human)			
E. rubrum	Galliformes: phasianid (pheasant); Accipitriformes: accipitrid (red-tailed hawk); Rodentia: cricetid (golden hamster)	freshwater Gastropoda: physid (*Physa gyrina, P. occidentalis)*		North America
E. scapteromae	Rodentia: cricetid (Argentine swamp rat)			South America
E. schulzi	Columbiformes: columbid (pigeon)			Europe
E. serratum	Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)	Australia
E. sinorchis	Anseriformes: anatid (garganey), Passeriformes: corvid (azure-winged magpie)			Europe
E. speotyto	Strigiformes: strigid (burrowing owl)			North America
E. spiniferum	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: planorbid (*Planorbarius corneus*)		Asia
E. spinosus	Charadriiformes: charadriid (spur-winged plover)			India
E. syrdariense	Galliformes: phasianid (chicken)			Russia
E. westsibiricum	Galliformes: phasianid (chicken)			Russia
Hypoderaeum				
H. batanguensis	Gruiformes: rallid (moorhen)			Eurasia
H. conoideum	Anseriformes: anatid (duck, mallard, garganey, scaup, northern shoveler, merganser, swan, goose); Podicipediformes: podicipedid (grebes); Galliformes: phasianid (chicken, turkey); Columbiformes: columbid (pigeon); Primates: hominid (humans)	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Planorbis corneus*), lymnaeid (*Radix rubiginosa, Lymnaea peregra, L. auricularia, L. trunculata, L. stagnalis, L. ovata, L. limosa, L. tumida, L. corvus*)	freshwater Gastropoda: lymnaeid (*Lymnaea trunculata, L. stagnalis, L. limosa, L. tumida, L. ovata*), planorbid (*Planorbis planorbis, P. corneus*); Bivalvia (clams, mussels); Anura (frogs, tadpoles)	Eurasia
H. cubanicum	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea tumida*)	freshwater Gastropoda: lymnaeid (*Lymnaea tumida*), planorbid (*Planorbis planorbis*)	Cuba
H. dingeri	Anseriformes: anatid (duck, goose)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*), lymnaeid (*Gastrothylax crumenifer*)		Thailand
H. essexensis	Anseriformes: anatid (duck)			England
H. gnedini	Anseriformes: anatid (red-necked duck, pouting duck, green-winged duck, mallard, spotted duck, white-browed			China, Russia

	duck, red-headed duck); Galliformes: phasianid (chicken)			
H. longitestis (syn. *Euparyphium, Vermatrema*)	Anseriformes: anatid (black swan)			India
H. magnocirrusa	Anseriformes: anatid (pintail)			India
H. mainpuria	Anseriformes: anatid (shoveler)			Europe
H. microspina	Anseriformes: anatid (pintail)			India
H. sinensis	Anseriformes: anatid (duck)			China
H. skrjabini	Anseriformes: anatid (duck)			Russia
H. vigi	Anseriformes: anatid (greater scaup); Charadriiformes: scolopacid (little stint, dunlin)			Eurasia