Trichobilharzia, Austrobilharzia
(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 diplostomatids are diverse in morphology and biology, some having bizarre divided bodies, some appearing tubular, and one extraordinary group (the schistosomes) being dioecious, forming separate sexes. Male schistosomes have a unique gynaecophoral canal along the length of the body (schisto-soma = split body), in which a female worm resides. The copulatory partners live together inside visceral blood vessels and are commonly known as blood flukes. Eggs are deposited in the circulation and must penetrate the gut or bladder to be excreted with faeces or urine, or become trapped in host tissues causing severe granulomatous reactions. Schistosomes form multiple sporocyst (no redia) stages in snails which produce fork-tailed cercariae that emerge and actively seek hosts (metacercariae are not formed). Many genera and species have been recorded in birds, but not in association with disease. However, the cercariae can penetrate and migrate in the skin of humans bathing in natural freshwater bodies causing transient dermatitis (swimmer's itch).

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:	Diplostomatida ('strigeids', blood and intestinal flukes mainly of tetrapods, some fish, infection usually by cercarial penetration)
Suborder:	Diplostomata (furcocercous (fork-tailed) cercariae)
Superfamily:	Schistosomatoidea (miracidium penetrates gastropod, bivalve, annelid IH, sporocysts formed, fork-tailed cercariae, penetrates DH)
Family:	Schistosomatidae (blood flukes, cylindrical bodies, in blood vessels of alimentary/urinary tract, separate sexes, male with gynaecophoric canal to hold female)
Genus:	*Trichobilharzia* (parasitic in blood vessels of birds)
Genus:	*Austrobilharzia* (parasitic in blood vessels of birds)
Species:	various species cause dermatitis (swimmer's itch) in 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.

One diplostomatid suborder has been recognized containing 3 superfamilies. The suborder Diplostomata is characterized by species forming furcocercous (fork-tailed) cercariae which either penetrate invertebrate intermediate hosts (forming metacercariae) or directly penetrate vertebrate definitive hosts (forming adults). Members of the superfamily Schistosomoidea do not form metacercariae in second intermediate hosts and their cercariae have been found to develop not only in gastropods but sometimes in bivalves or annelids. Some 430 species have been described in 5 families (Clinostomatidae, Aporocotylidae, Sanguicolidae, Spirorchiidae, Schistosomatidae), the latter 4 families comprising the blood flukes. The family Schistosomatidae contains the blood flukes living in venous blood vessels of tetrapods, the only trematodes that live in the bloodstream of warm-blooded hosts (rich in glucose and amino acids). Schistosomatids are also unique in that the adults are not hermaphroditic but form separate sexes (males resemble rolled leaves with ventral gynaecophoric canals in which the long slender females reside). At present, 15 genera have been classified into 4 subfamilies distinguished by differences in adult morphology and host specificity: Bilharziellinae (short gynaecophoric canal or absent, female genital pore posterior to ventral sucker; *Bilharziella, Trichobilharzia*); Dendritobilharziinae (short canal, anterior pore, dendritic caeca; *Dendritobilharzia*); Gigantobilharziinae (short canal, anterior pore, no ventral sucker; *Gigantobilharzia*); and Schistosomatinae (well-developed canal; *Austrobilharzia* (incl. *Microbilharzia*)*, Ornithobilharzia, Macrobilharzia, Jilinobilharzia, Allobilharzia, Anserobilharzia, Bivitellobilharzia, Heterobilharzia, Schistomatium, Schistosoma* (incl. *Orientobilharzia*) and *Griphobilharzia*). The first 10 genera infect birds, the next 4 genera infect mammals and the last genus infects reptiles.

Parasite genus	**Definitive hosts**	**Location**	**Intermediate hosts (gastropod family)**	**Distribution**
Bilharziella	Anseriformes, Gruiformes, Ciconiformes, Podicipediformes	visceral	freshwater Planorbidae	Europe
Trichobilharzia	Anseriformes (Anatidae)	visceral, nasal	freshwater Lymnaeidae, Physidae	Global
Dendritobilharzia	Anseriformes, Gruiformes, Pelicaniformes, Gaviiformes	visceral	freshwater Planorbidae	Global
Gigantobilharzia	Passeriformes	visceral	freshwater Physidae	North America
Austrobilharzia (incl. *Microbilharzia*)	Charadriiformes	visceral	marine Nassariidae, Batillaridae, Littoriniidae, Potamididae	Global
Ornithobilharzia	Charadriiformes	visceral	marine Batillaridae	Global
Macrobilharzia	Suliformes	visceral	unknown	North America, Africa
Jilinobilharzia	Anseriformes (Anatidae)	visceral	unknown	China
Allobilharzia	Anseriformes (swans)	visceral	unknown	Northern Hemisphere
Anserobilharzia	Anseriformes (geese)	visceral	freshwater Planorbidae	Northern Hemisphere
Bivitellobilharzia	Elephantidae, Rhinocerotidae	visceral	unknown	Africa, Asia
Heterobilharzia	Carnivora, Artiodactyla, Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosomatium	Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosoma (including *Orientobilharzia*)	Primates, Artiodactyla, Rodentia	visceral, nasal	freshwater Planorbidae, Lymnaeidae, Pomatiopsidae	Eurasia, Africa, South America, China
Griphobilharzia	Crocodilia	visceral	unknown	Australia

Many avian schistosome species infect the blood vessels in the viscera or nasal mucosa of waterfowl and shorebirds that have become infected by penetration of cercariae released from aquatic snails. Cercariae from many of these species may also penetrate the skin of humans coming into contact with contaminated water. The parasites do not complete their development in these aberrant hosts but their migration can produce a painful transient creeping dermatitis (colloquially known as swimmer's itch, clam-digger's itch or duck itch), negatively impacting on recreational water use and tourism.

Parasite species	Definitive hosts [adults in blood vessels]	Intermediate hosts [sporocysts in tissues]	Distribution
Bilharziella			
B. littlebi (syn. *Trichobilharzia*)	Passeriformes: parulid (chestnut-sided warbler)		North America
B. polonica (syn. *B. indica, Ornithobilharzia*)	Anseriformes: anatid (duck, mallard, teal, mute swan, goose); Gruiformes: rallid (crested coot); Podicipediformes: podicipedid (great crested grebe)	freshwater Gastropoda: planorbid (*Planorbis corneus, Planorbarius corneus, Bulinus africanus*)	Europe, Africa, Asia, North America
Trichobilharzia			
adults in nasal veins			
T. arcuata	Anseriformes: anatid (wandering whistling duck, muscovy); Columbiformes: columbid (pigeons)	freshwater Gastropoda: lymnaeid (*Lymnaea lessoni*)	Australia
T. aureliani	Podicipediformes: podicipedid (crested grebe, dabchick)		Africa
T. australis	Anseriformes: anatid (Pacific black duck)	freshwater Gastropoda: lymnaeid (*Radix* spp.)	Australia
T. duboisi	Anseriformes: anatid (African pygmy goose)		Africa
T. nasicola	Anseriformes: anatid (yellow-billed duck)		Africa
T. regenti	Anseriformes: anatid (mallard, muscovy); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Radix lagotis, R. labiata, R. peregra, R. ovata, R. auricularia*)	Europe, Middle-East
T. rodhaini	Pelecaniformes: threskiornithid (Hadada ibis)		Africa
T. spinulata	Anseriformes: anatid (Egyptian goose, spur-winged goose)		Africa
adults in viscera			
T. adamsi	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: physid (*Physa coniformis, P. gyrina*)	North America
T. alaskensis	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	North America
T. anatina (syn. *T. berghei*)	Anseriformes: anatid (yellow-billed duck)		Africa
T. brevis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Malaysia
T. brantae	Anseriformes: anatid (Canada goose)		North America
T. burnetti	Anseriformes: anatid (ring-necked duck)		North America
T. cameroni	Anseriformes: anatid (duck); Passeriformes: fringillid (canary); Columbiformes: columbid (pigeon)	freshwater Gastropoda: physid (*Physa gyrina*)	North America
T. cerylei	Coraciiformes: alcedinid (pied kingfisher)		Africa
T. corvi	Passeriformes: corvid (carrion crow, Australian raven); emberizid (yellow bunting); Galliformes: phasianid (chicken)	freshwater Gastropoda: pleurocerid (?)	Asia, Australia
T. elvae	Anseriformes: anatid (black duck, Pekin duck), Passeriformes: fringillid (canary)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	North America
T. filiformis	Anseriformes: anatid (mute swan)		Europe
T. franki	Anseriformes: anatid (mallard)	freshwater Gastropoda: lymnaeid (*Radix auricularia, R. ovata*)	Europe
T. guandongensis	?		Asia
T. horiconensis	Anseriformes: anatid (American wigeon)		North America
T. indica	Anseriformes: anatid (common teal)		India
T. jequitibaensis	Anseriformes: anatid (muscovy)	freshwater Gastropoda: lymnaeid (?), physid (?)	South America
T. jianensis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (?)	Asia
T. kegonsensis	Anseriformes: anatid (canvasback)		North America
T. kowalewski	Anseriformes: anatid (common teal)		Eurasia
T. limnaeae	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (?)	Asia

T. lonchurae (*Pseudobilharziella*)	Passeriformes: estrildid (mannikin)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Malaysia
T. maegraithi	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Asia
T. mergi	Anseriformes: anatid (red-breasted merganser)	freshwater Gastropoda: lymnaeid (*Radix balthica* (= *R. peregra*, = *R. ovata*))	Iceland
T. ocellata (syn. *T. kossarewi*)	Anseriformes: anatid (duck, teal)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, Stagnicola palustris*), planorbid (*Planorbarius corneus, Planorbis rotundatus*)	Eurasia, North America
T. oregonensis	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: physid (*Physa ampullacea, P. gyrina*)	North America
T. paoi	Anseriformes: anatid (mallard)	freshwater Gastropoda: lymnaeid (*Radix swinhoei, Galba pervia*)	Asia
T. parocellata	Anseriformes: anatid (muscovy duck, Sunda teal, Pacific black duck)	freshwater Gastropoda: lymnaeid (*Lymnaea ovata, L. stagnalis, L. lessoni*)	Europe, Australia
T. physellae	Anseriformes: anatid (mallard); Columbiformes: columbid (pigeon); Passeriformes: fringillid (canary)	freshwater Gastropoda: physid (*Physa parkeri, P. magnalacustris*)	North America
T. querquedulae	Anseriformes: anatid (blue-winged teal, northern shoveler)	freshwater Gastropoda: physid (*Physa gyrina*)	North America
T. salmanticensis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Radix ovata*)	Europe
T. schoutedeni	Anseriformes: anatid (white-backed duck)		Africa
T. stagnicolae	Passeriformes: fringillid (canary); Anseriformes: anatid (duck); Charadriiformes: larid (gull)	freshwater Gastropoda: lymnaeid (*Lymnaea emarginata*)	North America
T. szidati	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. ovata*)	Europe
T. waubesensis	Anseriformes: anatid (American wigeon, ring-necked duck)		North America
T. zongshani	Anseriformes: anatid (duck)		Asia
Austrobilharzia (incl. *Microbilharzia*)			
A. penneri	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Psittaciformes: psittacid (parakeet)	marine Gastropoda: potamidid (*Cerithidea scalariformis*)	North America
A. terrigalensis (syn. *A. variglandis, Microbilharzia*)	Pelecaniformes: ardeid (Pacific reef heron); Charadriiformes: larid (silver gull, brown noddy, sooty tern), scolopacid (ruddy turnstone); Galliformes: phasianid (chicken); Anseriformes: anatid (duck, canvasback, red-breasted merganser, lesser scaup)	marine Gastropoda: littorinid (*Littorina pintado*), planaxid (*Planaxis sulcatus*), batillariid (*Velacumantus australis, Pyrazus (Batillaria) australis*), nassarid (*Ilyanassa* (*Nassa*) *obsoleta*)	Australia, North America
A. odhneri (syn. *Ornithobilharzia, Sinobilharzia*)	Charadriiformes: scolopacid (Eurasian curlew)		China
A. pricei (syn. Ornithobilharzia)	Anseriformes: anatid (Canada goose)		North America
A. hoepplii (syn. *Ornithobilharzia, Microbilharzia*)	Charadriiformes: scolopacid (Swinhoe's snipe)		China
A. lari (syn. *Ornithobilharzia, Microbilharzia*)	Charadriiformes: larid (European herring gull, ring-billed gull, Bonaparte's gull)		Canada
A. bayensis	Charadriiformes: scolopacid (common snipe)		Philippines
Heterobilharzia			
H. americana	Carnivora: canid (dog, coyote), felid (bobcat, mountain lion), procyonid (raccoon), mustelid	freshwater Gastropoda: lymnaeid (*Lymnaea cubensis*,	North America

	(mink); Rodentia: castorid (beaver), echimyid (coypu); Lagomorpha: leporid (swamp rabbit); Didelphimorphia: didelphid (opossum); Artiodactyla: cervid (white-tailed deer)	*Pseudosuccinea columella*)	
Gigantobilharzia			
G. acotylea	Charadriiformes: larid (common gull, lesser black-backed gull, little gull, black-headed gull, common tern, white-winged tern); Passeriformes: hirundinid (sand martin); Podicipediformes: podicipedid (great crested grebe); Anseriformes: anatid (duck)	aquatic Gastropoda: physid (*Physa fontinalis*), planorbid (*Anisus spirorbis*)	Europe
G. adami	Anseriformes: anatid (African pygmy goose)		Africa
G. ardeola	Pelecaniformes: ardeid (Malagasy pond heron)		Madagascar
G. elongata	Podicipediformes: podicipedid (pied-billed grebe)	freshwater Gastropoda: planorbid (*Gyraulus parvus*)	North America
G. gyrauli	Passeriformes: icterid (red-winged blackbird, yellow-headed blackbird, brown-headed cowbird, common grackle)	freshwater Gastropoda: planorbid (*Gyraulus parvus*), physid (*Physa* sp.)	North America
G. huronensis	Passeriformes: fringillid (American goldfinch), cardinalid (northern cardinal)	freshwater Gastropoda: physid (*Physa gyrina)*	North America
G. huttoni	Psittaciformes: psittacid (parakeets)	marine Gastropoda: bullid (*Haminoea antillarum*)	North America
G. lawayi	Charadriiformes: larid (European herring gull, ring-billed gull, Bonaparte's gull)		North America
G. nettapi	Anseriformes: anatid (African pygmy goose)		Africa
G. plectropteri	Anseriformes: anatid (spur-winged goose)		Africa
G. sturniae	Passeriformes: corvid (carrion crow), sturnid (chestnut-cheeked starling)	freshwater Gastropoda: planorbid (*Segmentina nitidella, Polypylis hemisphaerula*)	Japan
G. tantali	Ciconiiformes: ciconiid (yellow-billed stork)		Africa
G. vittensis	Charadriiformes: larid (common gull)	freshwater Gastropoda: planorbid (*Anisus leucostomus*)	Europe
Ornithobilharzia			
O. canaliculata (syn. *O. intermedia, O. kowalewskii*)	Charadriiformes: larid (gulls, terns); Procellariiformes: procellariid (puffin); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	marine Gastropoda: batillariid (*Batillaria minima*)	Eurasia, Americas

Parasite morphology: These avian schistosomes form 5 different stages in their developmental cycles: eggs, miracidia, sporocysts, cercariae and adults. Eggs may be spindle-shaped, cresentic or ellipsoidal, measuring around 180 µm in length (depending on species), often with a small projection or hook at one end. As they mature, they embryonate to contain a well-developed miracidium. Hatched miracidia are pyriform in shape, measure ~110 µm in length, and are covered by a mosaic of ciliated plates often arranged in 4 tiers and separated by ridges, some with lateral horns. They contain prominent apical and lateral glands and the posterior body is filled with clusters of germinal cells. Sporocysts are pleomorphic sac-like structures without any conspicuous organ systems other than balls of germinal cells that undergo asexual reproduction to produce another generation of sporocysts. Daughter sporocysts produce cercariae measuring up to 1mm in length which have elongate tubular bodies (~300 µm long) with distinctive furcocercous (forked) tails (stem 250-500 µm long, 2 prongs each 150-250 µm long). The cercarial body has an anterior head organ, prominent penetration glands located around the ventral sucker (previously called the acetabulum), 1-2 pigmented eyespots (ocellate), a spiny tegument but is apharyngate. Adult flukes have long, slender filiform bodies, measuring from 3-10 mm in length and 20-100 µm in diameter, and the posterior end is spatulate. The tegument is often covered by tubercles or spines and they possess oral and ventral suckers. The digestive tract lacks a pharynx, but has a long oesophagus which bifurcates into 2 caeca with then recombine posteriorly. Schistosomes are not hermaphroditic but dioecious forming separate males and females. Adult worms are invariably found in male-female pairs, with male worms possessing short gynaecophoric canals that partly contain female worms. Males have numerous posterior testes, an elongate seminal vesicle between the ventral sucker and gynaecophoric canal, a small cirrus and a genital pore located at the anterior end of the canal. Females have a single elongate coiled ovary located anteriorly and connected to a well-developed posterior seminal receptacle and numerous vitellaria, an anterior ootype and an elongate uterus that opens immediately posterior to the ventral sucker. Fertilized female worms generally only contain a single egg in the uterus.

Site of infection: Adult schistosomes live in blood vessels in visceral organs or the nasal mucosa of their definitive hosts (birds). Asexual developmental stages (sporocysts) develop in the tissues, predominantly the hepatopancreas, of their intermediate hosts (aquatic snails).

Pathogenesis: Most avian schistosomes are not pathogenic in their definitive hosts, but some species have been associated with significant tissue injuries in birds, caused by migration of cercariae, schistosomula, adult flukes, eggs or miracidia. Migrating stages cause tracking trauma, focal lesions, petechial haemorrhages, inflammation, cellular infiltration and other host immune responses. Parasites may become trapped in host tissues where they provoke fibrosis and granuloma formation. Most fluke species migrate through the viscera of their hosts, but those species with a predilection for nasal mucosa migrate through nervous tissue (esp. white matter) and may cause neuromotor disorders. Outbreaks of trichobilharziasis have been recorded in ducks and geese with significant morbidity (esp. leg paralysis and balance disorders) and low mortality. The impact of infections on wild bird species is not known although miscellaneous case reports have been published. Avian schistosomes have also been associated with clinical disease in humans and other mammals, when cercariae penetrate the skin causing painful transient creeping dermatitis (colloquially known as swimmer's itch, clam-digger's itch or duck itch), more intense in sensitized hosts. Symptoms include erythema, oedema, thickening and itching of immersed skin, followed by the development of pruritic hyperaemic papules which may become vesicular. Scratching the affected areas may result in secondary bacterial infections. In repeated infections, cellular infiltration (neutrophils, eosinophils, macrophages, lymphocytes, mast cells) is more severe and may lead to the formation of large abscesses, epidermal and/or dermal necrosis. Cases of cercarial dermatitis can occur in both fresh and brackish water environments. Several parasite species seem to be responsible for the majority of dermatitis outbreaks in humans, particularly *Trichobilharzia franki*, *T. physellae*, *T. querquedulae* and *Austrobilharzia variglandis* associated with aquatic environments used for tourism and recreational purposes. Interestingly, while experimental studies have shown that avian schistosomes do not mature in nonpermissive (incompatible) mammalian hosts, they have also recently shown that not all parasites are trapped and eliminated in the skin, but may wander for extended periods through nervous tissues and viscera, possibly contributing to more complications than previously thought.

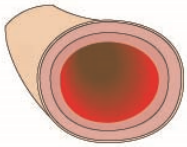
Developmental cycle and mode of transmission: Like other digenetic trematodes, avian schistosomes have indirect heteroxenous life-cycles involving transmission between definitive (bird) and intermediate (snail) hosts with free-swimming aquatic larval stages. Adult flukes living in blood vessels of birds deposit eggs into the circulation where they release proteolytic enzymes to pass through different tissue layers to reach the gut or nasal mucosa. Eggs of visceral species reach the gut lumen and are excreted with host faeces where they hatch releasing their enclosed miracidia. Eggs of nasal species reach the nasal cavity and hatch when they come into contact with water when the host feeds/drinks (an exception is the species *T. regenti* whose eggs hatch directly in the mucosa and the freed miracidia await contact with water). Once in water, the ciliated miracidia swim for up to 24 hours actively seeking snail hosts using chemotactic cues. A small range of aquatic snails act as suitable intermediate hosts; including freshwater lymnaeids, physids, planorbids (rarely pleurocerids) and marine potamidids, littorinids, planaxids, batillariids, nassarids and bullids. The miracidia penetrate snail tissues in the head-foot region shedding their cilia and developing into sac-like sporocysts. The parasites undergo 2 generations of asexual reproduction whereby mother sporocysts produce daughter sporocysts which migrate to the hepatopancreas before producing cercariae. The prepatent period in snails (time from infection to first release of cercariae) ranges from 3-10 weeks. Cercariae emerge from snails into water and use their forked tails to swim about seeking vertebrate hosts. A range of migratory and territorial bird species act as suitable definitive hosts, notably those associated with aquatic ecosystems such as waterfowl and shorebirds. Cercariae penetrate the skin shedding their tails and transforming into schistosomula which migrate via the circulation, lymphatics or peripheral nerves to their final predilection sites (blood vessels in the viscera or nasal mucosa). Cercariae may also cause transient infections in non-permissive vertebrate hosts, mostly mammals swimming or bathing in contaminated waters.

Differential diagnosis: Infections in avifauna are usually diagnosed at post-mortem by the detection of adult flukes in tissues from dead birds, often incidentally as the worms are located in cryptic sites. The detection of eggs in faecal samples, nasal swabs, aspirates or exudates is often difficult due to their low numbers, sporadic excretion and short longevity (eggs may hatch internally or upon contact with water). Furcocercariae may also be recovered from snail hosts following their dissection or after their emergence in wet cultures. Clinical infections in aberrant hosts (mammals) present with cercarial dermatitis, usually manifest by characteristic allergenic reactions (creeping eruptions). Blood tests often reveal a concurrent systemic eosinophilia and elevated IgE levels. A small number of serological tests have been developed to detect specific host antibodies to cercarial antigens, including complement fixation, immunofluorescence and enzyme immunoassays, but they often yield low sensitivity and specificity. Researchers have detected differences between several common types of cercariae by karyotypic studies, while molecular characterization techniques have discriminated between adult and larval stages of several *Trichobilharzia* spp. by polymerase chain reaction (PCR) amplification of nuclear genes (5.8S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial genes (cytochrome c oxidase subunit 1, NADH dehydrogenase subunits 2, 4 and 6).

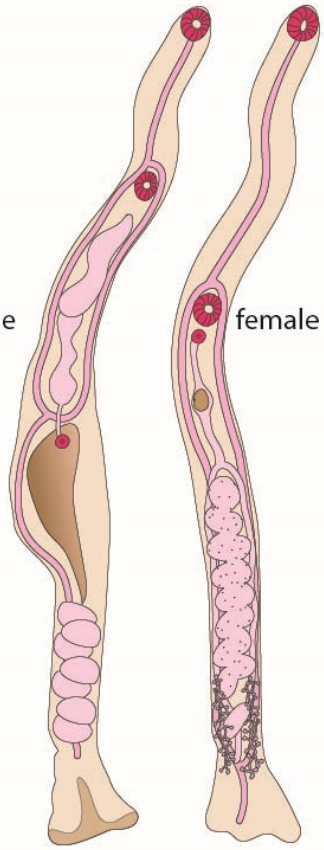
Treatment and control: Clinical infections in birds have responded well to treatment with the broad-spectrum anthelmintic praziquantel, although advanced cases (particularly those involving neurological signs) did not fully resolve. Nonetheless, drug treatment significantly reduced egg production and excretion in individuals not cured. The prevention of infections is based around breaking the transmission cycle between snails and birds, thus reducing the numbers of infective cercariae present in water. Various attempts have been made to reduce the contamination of water bodies by parasite eggs and miracidia, either by treating birds or relocating them. While some success has been reported in small scale peridomestic situations, efforts to control wild bird

populations are untenable. Greater success has been achieved in reducing snail populations by chemical, mechanical and biological control, but the widespread application of molluscicides may have untoward toxicological and environmental consequences. Disturbing snail habitats in shallow ponds and lakes by mechanized tilling or raking has proven effective in reducing snail numbers, particularly when carried out during their breeding seasons. Removing aquatic vegetation, introducing natural predators (e.g. fish) and temporarily draining small ponds have also been successful in reducing snail numbers. Considerable effort has been made in several endemic areas (especially those frequented by tourists) to prevent cercariae from infecting humans. Advisory notices, and even legal regulations, have attempted to prohibit or restrict human access to contaminated waters, but they are often ignored by swimmers and bathers. Most cases of cercarial dermatitis involve skin openly exposed to water, prompting studies that have shown some protection may be afforded by protective clothing, thoroughly drying the skin immediately after water contact, and coating the skin with vaseline or recently-developed chemical repellents.

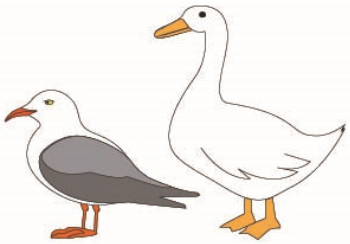
Trichobilharzia, Austrobilharzia



blood vessels
(viscera, nasal mucosa)
(cercarial dermatitis,
egg granulomas,
fibro-obstructive disorders)



adults
(~ 7 mm)



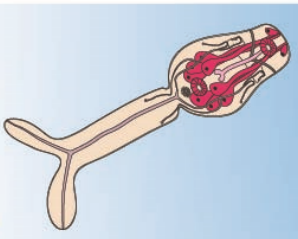
Definitive Hosts
(freshwater waterfowl,
marine shore birds)

excretion
(faeces,
nasal mucus)

eggs
(~ 180 µm)

skin
penetration

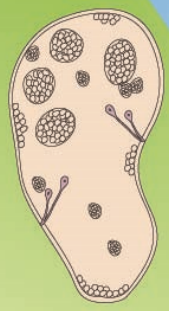
vector-borne transmission



endoparasitic in
tissues of vector

free-swimming
cercaria
(~ 1 mm)

free-swimming
miracidium
(~ 110 µm)



redia
(~ 1 mm)

sporocyst
(~ 1 mm)

Intermediate Hosts (freshwater lymnaeid snails, marine potamidid snails)
(visceral then glandular tissues)

Trichobilharzia eggs

Trichobilharzia cercaria