Echinococcus
(platyhelminth: cestode)

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. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to carnivorous definitive hosts. Adult taeniids have an armed rostellum (except *T. saginata*), elongate gravid segments and are rarely pathogenic. *Echinococcus* spp. form encysted larval stages (unilocular or multilocular cysts) causing space-occupying lesions and disease (hydatidosis) in wild and domestic animals 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:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Taeniidae (scolex often armed, proglottids with single genital pore, fluid-filled cystic metacestodes)
Genus:	*Echinococcus* (parasitic in gut/tissues of canids/omnivores)
Species:	*E. granulosus* (causes hydatid disease in mammals)

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 (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 cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae). Mature taeniid tapeworms have proglottids with unpaired reproductive organs and a single genital pore, and the scolex is often armed with hooks. Taeniids produce round non-operculated eggs with striated shells, the oncospheres are non-ciliated and they form fluid-filled cystic metacestodes (cysticercus, coenurus, strobilocercus, or hydatid cyst). Several genera (*Taenia* (*Multiceps, Taeniarhynchus*), *Hydatigera,*

Echinococcus, Versteria) have been reported predominantly in carnivorous definitive hosts (canids, felids, primates incl. humans) and herbivorous or omnivorous intermediate hosts (artiodactyls, lagomorphs, rodents, primates).

Conventional classification schemes recognize four main *Echinococcus* species: *E. granulosus, E. multilocularis, E. vogeli* and *E. oligarthus,* mostly utilizing canids (and some felids) as definitive hosts and a range of herbivorous mammals as intermediate hosts. *E. granulosus* occurs in most sheep and cattle producing areas around the world, being most prevalent in South America, East Africa, Southeast Asia and China, but being absent in Iceland, Greenland, New Zealand and Tasmania. Canids (dogs, dingoes, wolves, and coyotes) act as definitive hosts for adult worms, while omnivorous/herbivorous mammals (humans, domestic animals and wildlife) serve as intermediate hosts for larval stages (unilocular hydatid cysts). It is estimated that infections may affect around 2-3 million people worldwide, occurring in up to 10% of certain communities in some areas of South America, Africa, and Asia. Infections in domestic animals are prevalent in many rural agricultural zones while the extent of infections in wildlife can only be surmised. Various strains of *E. granulosus* have been identified on the basis of both phenotypic and genotypic differences, with many strains being 'adapted' to particular animals (intermediate host specificity being narrowly stenoxenous rather than strictly oioxenous). This has considerable epidemiological significance for infections in humans; for instance, pig and horse strains in Europe probably do not infect humans, whereas sheep and cattle strains do. More recently, biological and molecular characterization studies have indicated that *E. granulosus sensu lato* (in the broadest sense) may be comprised of several cryptic species: *E. equinus, E. ortleppi, E. canadensis, E. felidis* as well as *E. granulosus sensu stricto* (in the strictest sense). *E. equinus* was already thought to be a subspecies of *E. granulosus* but highly specific for equid intermediate hosts in Europe (most cases in other countries have been traced back to imported European horses). *E. ortleppi* appears to be a cattle genotype/strain found in many countries and transmitted by dogs. *E. canadensis* is composed of several closely-related genotypes (camel, pig and deer strains) found throughout Eurasia and North America and transmitted by wolves and dogs. *E. felidis* was initially thought to be a subspecies of *E. granulosus*, but is now considered to be a separate species in Africa with lions as definitive hosts. A new species, *E. shiquicus,* recently described from China was thought to be closely related to *E. multilocularis* but it forms unilocular minicysts in lagomorphs. *E. multilocularis* commonly cycles between foxes and rodents in Europe and North America, although domestic animals and humans may become infected with larval stages (multilocular hydatid cysts). *E. vogeli* cycles between bush dogs and rodents, and *E. oligarthus* between felids and rodents, in Central and South America, with intermediate hosts (sometimes humans) developing polycystic and unicystic hydatid cysts, respectively.

***Echinococcus* species**	**Definitive hosts [adults in small intestines] {clinical signs}**	**Intermediate hosts [metacestodes in tissues] {clinical signs}**	**Distribution**
Species causing cystic (unilocular) echinococcosis (CE) (*E. granulosus sensu lato*)			
E. granulosus sensu stricto (genotypes G1-3) (dwarf dog tapeworm, hydatid tapeworm) (probable synonyms: *E. cameroni, E. cepanzoi, E. intermedius, E. iraqii, E. longimanubrius, E. lycaontis, E. minimus, E. patagonicus*)	Carnivora: canid (dog, wolf, fox, jackal, dingo, coyote?), hyaenid (hyaena) {occasionally diarrhoea}	Artiodactyla: bovid (sheep, goat, cattle*, buffalo, yak), camelid (camel), suid (pig), cervid (deer?); Diprotodontia: macropodid (wallaby, kangaroo), vombatid (wombat); Lagomorpha: leporid (rabbit, hare); Primates: cercopithecid (macaques, vervets, baboons), lemurid (lemurs), hominid (human) [unilocular hydatid cysts in liver, lungs, organs] *sterile cysts {space-occupying lesions}	Europe, Middle-East, Africa, Americas, Asia, Australia (except Iceland, New Zealand, Tasmania)
E. equinus (*E. granulosus* genotype G4)	Carnivora: canid (dog, fox)	Perissodactyla: equid (horse, donkey, zebra) [unilocular hydatid cysts in liver, lungs, organs]	Europe, Middle-East, Africa
E. ortleppi (*E. granulosus* genotype G5)	Carnivora: canid (dog, jackal)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), suid (pig); Perissodactyla: equid (zebra) [unilocular hydatid cysts in viscera]	Europe, Africa, Asia, South America
*E. canadensis** (*E. granulosus* genotypes G6-10)	Carnivora: canid (dog, wolf)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig), camelid (camel), cervid (moose, elk, reindeer, caribou, mule deer?); rarely Primates: hominid (human) [unilocular hydatid cysts in viscera]	Middle-East, Africa, Asia, Americas, Europe
*Some workers suggested that *E. canadensis* genotypes could be allocated to 3 species: G6/G7 to *E. intermedius*, G8 to *E. borealis*, and G10 to *E. canadensis;* while others regarded the latter two to be conspecific or even a 'Northern biotype' of *E. granulosus,* and the separation of *E. intermedius* (presumed to have pigs and camels as intermediate hosts) to be premature.			

E. felidis (syn. *E. granulosus felidis*)	Carnivora: felid (lion, African wild cat), hyaenid (spotted hyaena), canis (Cape hunting dog, silver-backed jackal)	Artiodactyla: suid (warthog, bushpig), bovid (wildebeest, buffalo, antelope), giraffid (giraffe), hippopotamid (hippopotamus?); Perissodactyla: equid (zebra) [unilocular hydatid cysts in viscera]	Africa
E. shiquicus	Carnivora: canid (Tibetan fox)	Lagomorpha: ochotonid (pika) [unilocular minicysts in liver and lungs]	Tibet
Species causing polycystic echinococcosis (PE)			
E. vogeli	Carnivora: canid (bush-dog, dog, crab-eating fox)	Rodentia: cuniculid (paca), dasyproctid (agouti), echimyid (coypu); Primates: hominid (gorilla, orangutan, human) [unilocular + polycystic hydatid cysts in liver, lungs, organs] {space-occupying lesions}	Central and South America
Species causing unicystic echinococcosis (UE)			
E. oligarthus (syn. *E. cruzi, E. pampeanus*)	Carnivora: felid (cougar, jaguar, ocelot, jaguarundi, puma, pampas cat, Geoffroy's cat, bobcat, cat)	Rodentia: cuniculid (paca), dasyproctid (agouti), murid (gerbil, spiny rat, climbing rat, cotton rat), Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (cottontail); rarely Primates: hominid (human) (unicystic hydatid cysts in viscera, muscles, skin) [space-occupying lesions]	Central and South America
Species causing alveolar (multilocular) echinococcosis (AE)			
E. multilocularis (dwarf fox tapeworm) [syn. *E. russicensis, E. sibiricensis*]	Carnivora: canid (red fox, arctic fox, sand fox, grey fox, Tibetan fox, corsac fox, wolf, coyote, dog, raccoon dog), felid (cat, lynx)	Rodentia: echimyid (coypu), cricetid (common vole, tundra vole, northern red-backed vole, grey red-backed vole, Hokkaido red-backed vole, meadow vole, northern water vole, bank vole, European pine vole, steppe vole, lemming, muskrat, deermouse), soricid (long-tailed shrews), murid (house mouse, brown rat, Mongolian gerbil), echimyid (coypu), sciurid (ground squirrel), spalacid (Chinese zokor); Lagomorpha: leporid (rabbit), ochotonid (plateau pika); Artiodactyla: suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: cercopithecid (crab-eating macaques), atelid (spider monkey), lemurid (ring-tailed lemur), hominid (gorilla, human) [multilocular (alveolar) hydatid cysts in liver, lungs, organs] {space-occupying lesions}	North America, Asia, Europe

Parasite morphology: Tapeworms form three different developmental stages: eggs; larvae; and adults. Adult worms are small (1-7 mm long) and have a scolex and strobila ranging from 3-7 proglottids. The scolex has four lateral suckers and a non-retractable rostellum armed with a double crown of recurved hooks (28-50 in *E. granulosus*, 26-36 in *E. multilocularis*). All adults are hermaphroditic and contain both male and female reproductive organs. While the gonads in anterior segments are immature, they are mature and functional in posterior segments. The caudal segment is gravid and the uterus is filled with eggs. The eggs are typical for most taeniid species and are small and round (30-43 µm in diameter), thick-shelled and contain a hexacanth (6-hooked) non-ciliated embryo (oncosphere). Larval (metacestode) stages are lacunate (internal channel forms during development) and they become encysted in tissues as hydatid cysts (bladder-worms) which produce multiple infective stages known as protoscoleces (scoleces invaginated into their neck portions and already containing suckers and developing hooks) either directly from the inner

germinal layer of the cyst wall, or by forming brood sacs by endogenous (internal) or exogenous (external) budding of the germinal layer (detached sacs freely floating in vesicular fluid known as hydatid sand). *E. granulosus* forms fluid-filled unilocular cysts with endogenous budding to form brood capsules, *E. vogeli* forms fluid-filled polycystic cysts with exogenous budding to form new cysts and endogenous budding to form septae, and *E. multilocularis* forms fluid-free multilocular or alveolar cysts with exogenous budding to form multiple cysts.

Site of infection: The small adult tapeworms attach to the mucosa of the small intestines in dogs, sometimes in their thousands. The larval stages (hydatids) most commonly infect visceral tissues and organs, especially the liver and lungs, in their mammalian intermediate hosts, although cysts may be found in many other locations, including the brain and long bones.

Pathogenesis: The adult stages are considered benign and do not cause disease in their definitive hosts, as the small tapeworms do not invade or feed on host tissues. Large numbers of worms (thousands) have been found in asymptomatic canid hosts, and only rarely have heavy infections been associated with any clinical signs (enteritis, diarrhoea). The larval (metacestode) stages which encyst within visceral tissues in intermediate hosts initially do not cause clinical disease, but they may cause significant pathological changes as the cysts grow and put pressure on surrounding tissues producing chronic space-occupying lesions. *Echinococcus* spp. form different types of cysts, either discrete single-compartment (unilocular) cysts which exhibit expansive growth or budding multi-compartmented (multilocular) cysts which can infiltrate organs and even disseminate to other tissues and organs. *E. granulosus s.l.* causes cystic echinococcosis (CE, also known as unilocular echinococcosis or cystic hydatid disease), *E. multilocularis* causes alveolar echinococcosis (AE, also called multilocular or multivesicular echinococcosis, or alveolar hydatid disease), while *E. vogeli* and *E. oligarthus* cause polycystic echinococcosis (PE, recently called neotropical PE). Because only discrete cysts of *E. oligarthus* have been detected in humans, this disease has also been called unicystic echinococcosis (UE). Cysts may grow around 1 mm per month and are often 1-7 cm in diameter when discovered, but some may eventually measure up to 20-30 cm in diameter with litres of fluid containing thousands of protoscoleces. Cysts in humans develop over many years before symptoms become apparent, while most domestic livestock are slaughtered before cysts become large enough to cause clinical signs (although longer-lived animals such as horses may develop clinical disease). However, CE may cause significant economic losses in agriculture from the condemnation of animal organs at meat inspection, and possibly from reduced meat, milk and fibre production during the course of infection and disease. Organ enlargement may be accompanied by a variety of clinical signs depending on the size and location of the cysts. CE generally involves the liver and lungs, and less frequently the bones, kidneys, spleen, muscles, central nervous system and eyes. Cysts in the liver may cause pressure atrophy, compression, hepatomegaly, cholestatic jaundice, anaemia, portal hypertension, ascites, cirrhosis, abdominal distention, pain, nausea, vomiting and indigestion. Cysts in the lung may cause chronic cough, haemoptysis (coughing up blood), dyspnoea (difficulty breathing), chest pain, pneumothorax and abscess formation (from secondary bacterial infection). Cysts in the brain or spinal cord can provoke acute inflammatory responses and numerous neurological sequelae, including epilepsy, seizures and blindness. Cysts in the bones can destroy internal structure and result in spontaneous fractures. Cysts in the heart can cause pericardial effusion, heart block or other arrhythmias, and sudden death. Infections may also be accompanied by non-specific signs such as anorexia, weight loss and weakness. Cyst rupture has been associated with acute clinical signs (such as peritonitis and pneumothorax), and the sudden release of hydatid fluid may cause severe allergic reactions (such as asthma, pruritus, urticaria and anaphylactic shock). Protoscoleces released from ruptured cysts can regress and form new hydatid cysts throughout the body. Some cysts formed are sterile and never produce brood capsules, while others become sterile after bacterial infection or calcification. AE is less common than CE but is more serious and can be fatal if left untreated. It is characterized by the slow development of a primary tumour-like lesion usually in the liver (often misdiagnosed as hepatocellular carcinoma) and then larval metastases may spread to other organs (such as the spleen, lungs or brain) by dissemination via the blood and lymphatic systems. Clinical signs include weight loss, abdominal pain, general malaise and progressive hepatic failure. Larval stages of *E. multilocularis* may also exhibit incomplete atypical development in humans by forming sheets of thin membranes (with no identifiable cestode structures) which bisect the liver disrupting structure and function. Several hundred cases of PE have been recorded in humans, with multi-chambered interconnected cysts typically developing in the liver (often leading to hepatic insufficiency) and then spreading in the peritoneal and pleural cavities and invading other organs. Only three cases of UE have been reported in humans, two involving discrete cysts behind the eyes and one in the heart.

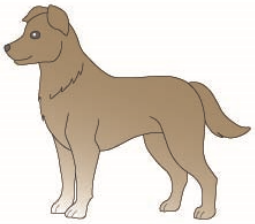
Developmental cycle and mode of transmission: Tapeworms have an indirect life-cycle involving predator-prey transmission between definitive (carnivorous) and intermediate (herbivorous/omnivorous) mammalian hosts. Mature tapeworms release numerous thick-shelled eggs from gravid segments (proglottids), although occasionally the hindmost segment may break off and be shed as a package of eggs. The eggs are very resistant to external environmental conditions and can survive for several weeks or months on pastures or fomites, unless they are exposed to hot dry conditions. The eggs have a sticky coat and may adhere to animal fur and other objects. Birds and insects (beetles, flies) may also act as mechanical vectors. Herbivores and omnivores become infected by ingesting eggs; either on herbage, in water, or by hand-to-mouth transfer. Following ingestion, the eggs hatch releasing the oncosphere which uses its three pairs of hooks to penetrate the gut, enter the circulation and settle in various organs and tissues (frequently in the liver after being filtered out by portal capillaries). Over many months, they form fluid-filled hydatid cysts (unilocular or multilocular depending on the parasite species) and eventually produce multiple infective protoscoleces (directly from the germinal membrane or via brood sacs formed by endogenous or exogenous budding). This asexual reproduction of the metacestode stage is a unique feature for the genus *Echinococcus*. When mature cysts in offal or carcases are eaten by carnivorous

definitive hosts, the cyst wall is digested away freeing the protoscoleces, which evaginate and attach to the small intestinal mucosa. They mature to adult worms in about 8 weeks and may live for 5-20 months. Various *Echinococcus* species, strains and genotypes have been recognized based on differences in parasite morphology, development, biochemistry, genetics and host specificity. Most appear to be adapted to particular intermediate host species and do not develop well in other host species. Infections are particularly well adapted to pastoral cycles involving farm dogs and domestic livestock (notably sheep and cattle), as well as sylvatic cycles involving wild carnivores (wolves, coyotes, dingoes) and free-ranging herbivores (such as deer, moose and wallabies). Spill-over may occur between sylvatic and pastoral cycles. Infections in human populations occur more frequently in rural areas, particularly where local traditions are conducive to transmission; e.g. feeding dogs offal, eating dog intestines, not burying the dead, and even using dog faeces to tan hides.

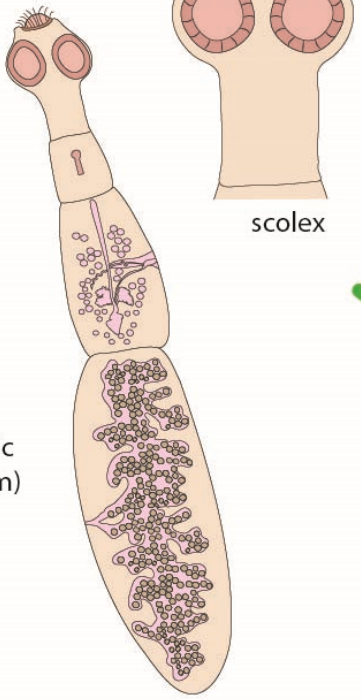
Differential diagnosis: Infections in dogs may be diagnosed by the detection of eggs, and occasionally worms, in faecal samples. Eggs, however, are morphologically indistinguishable from those of *Taenia* spp. Purgation with arecoline prior to faecal testing has been discontinued due to safety concerns for both definitive hosts and diagnosticians. Immuno-coprological tests have also been developed to detect parasite antigens in faecal samples. Infections in intermediate hosts are generally diagnosed well after the larvae have encysted. Clinical symptoms of a slow-growing tumour accompanied by eosinophilia are suggestive. Cysts may be visualized by various medical imaging techniques; including X-rays, ultrasound, computerized axial tomography (CAT) scans, and magnetic resonance imaging (MRI). Biopsies (fine needle aspiration of cyst fluid) can be used to assist diagnosis, but there is always the attendant risk of cyst rupture or leakage leading to allergic reactions or further cyst development. Cyst fluid can be examined microscopically for protoscoleces or tested for parasite antigens by enzyme immunoassays or for parasite DNA by polymerase chain reaction (PCR) assays. Several immunological tests (complement fixation, agglutination, enzyme immunoassays, immunoblots, immunochromatography) have been developed to detect host antibodies or parasite antigens (e.g. Em16, Em 18, antigen B) in host serum or faecal samples. Best results were obtained using semi-defined or recombinant antigens, although some cross-reactivity problems were encountered and some people simply do not develop detectable antibody levels. An intradermal (Casoni) test using hydatid fluid has also been used in surveys. Molecular tests are also being developed to characterize parasite DNA by PCR amplification of nuclear (18S ribosomal RNA, internal transcribed spacers (ITS), elongation factor 1-α (*ef1a*)) or mitochondrial (cytochrome c oxidase subunit 1 (*cox1*), cytochrome b (*cob*), large subunit ribosomal RNA (*rrnL*), NADH dehydrogenase subunit 1 (*nad1*)) genes, and by restriction fragment length polymorphism (RFLP), single strand conformational polymorphism (SSCP) or microsatellite analyses.

Treatment and control: Despite some promising indications, the treatment of hydatid disease with conventional anthelmintic drugs has not proven wholly effective, being complicated by the large size and inaccessible location of cysts and their thick, possibly impenetrable, walls. Variable results have been obtained using select isoquinolines (praziquantel) and benzimidazoles (mebendazole), while albendazole and niclosamide have been less effective. The only remaining treatment option is for the surgical removal of cysts, provided they are in favourable sites. Surgeons must take care not to rupture cysts as protoscoleces may spread to new sites to form more cysts. Scolecidal chemicals, such as cetrimide, may also be used during surgery to sterilize excision sites. Where cystectomy is contraindicated, surgeons may use the puncture-aspiration-injection-reaspiration (PAIR) technique to puncture cysts under ultrasound guidance, aspirate cyst fluid, inject scolecides and reaspirate contents. Infections by adult worms in dogs can be successfully treated with praziquantel, and it is advisable to confine dogs and/or use purgatives to facilitate the collection and disposal of infected faeces. Preventing dogs from becoming infected involves eliminating offal and other potentially infected material from their diets, curbing their hunting behaviour, properly disposing of carcases in the field, and culling wild and feral dogs. Several countries have developed highly successful hydatid eradication campaigns based around dog management and treatment. Oncospheres have proven to be highly immunogenic and intermediate hosts may become immune to reinfection after primary exposure. This has prompted studies on vaccine development using defined oncosphere antigens, with considerable success reported using recombinant vaccines to prevent hydatid formation in domestic herbivores. Vaccination trials are continuing as some measure of control may be possible in livestock involved in pastoral cycles, although there will be access problems vaccinating wildlife involved in sylvatic cycles.

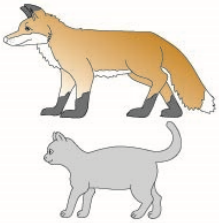
Echinococcus



intestines
(rarely enteritis,
diarrhoea)



scolex



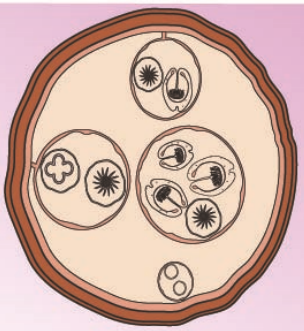
Definitive Hosts
(carnivores)

predator-prey
transmission
through
ingestion
of larvae
from cysts

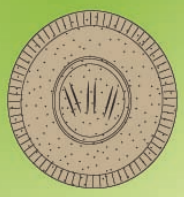
hermaphroditic
adults (~ 5 mm)

excretion
of eggs in
faeces

external
environment

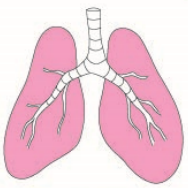


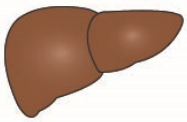
hydatid cyst
(~ 10-70 mm)



egg
(~ 40 µm)

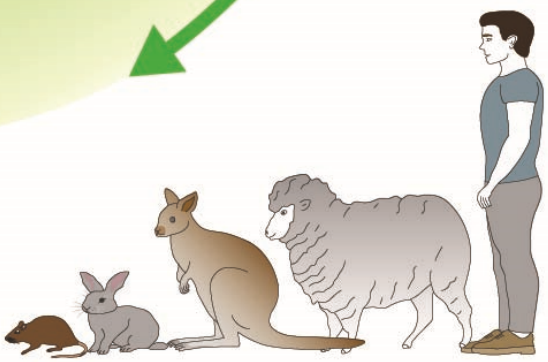
oncosphere
(~ 40 µm)





viscera
(space-occupying lesions,
hydatid disease)

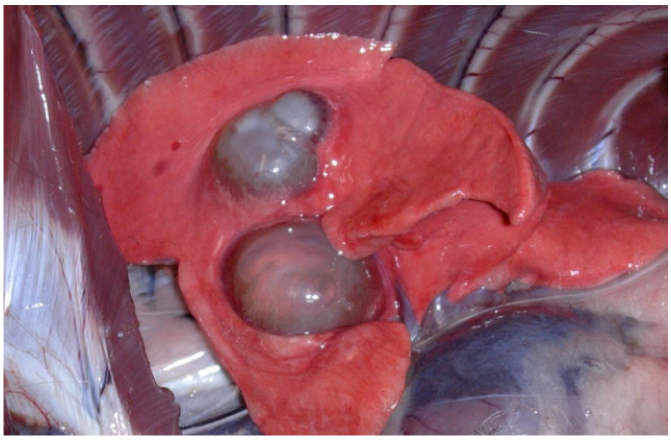
Intermediate Hosts
(primates, ungulates,
rodents, lagomorphs)



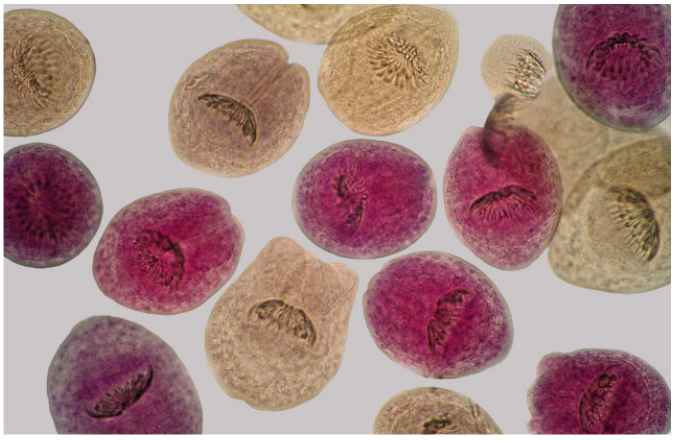
Echinococcus adult worm

Echinococcus scolex

Echinococcus egg



Echinococcus hydatid cysts in lung of kangaroo



Echinococcus protoscoleces from hydatid cyst