

## ***Hammondia***

(protist: apicomplexan)

### **Overview**

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (two-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Hammondia* spp. form ellipsoidal cysts containing bradyzoites (= cystozoites) predominantly in the striated muscles of rodents. The cysts have thin cyst walls and may persist in the tissues for years. Merogony (= schizogony), gamogony (male microgametes fertilize female macrogametes) and oocyst formation occurs in the intestinal epithelia of cats or dogs. Sporogony occurs exogenously and mature oocysts contain 2 sporocysts each with 4 sporozoites (1:2:4 configuration). Different species exhibit relative strict host specificity, with particular predator-prey combinations hosting individual species.

### **Classification:**

Domain: Eukaryota (membrane-bound nucleus)  
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)  
Group: Alveolata (with cortical alveoli)  
Phylum: Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))  
Class: Coccidiomorpha [Conoidasida] (with conoid)  
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)  
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)  
Suborder: Eimeriorina (no syzygy, many microgametes)  
Family: Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)  
Subfamily: Toxoplasmatinae (merozoites not present, thin cyst walls)  
Genus: *Hammondia* (tissue cyst-forming coccidian parasites of mammals)  
Species: various species cause lesions/cysts in dogs, cats, cattle and rodents]

**Parasite biodiversity and host range:** Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogony (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as 'haemogregarines' in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Transmission*	
Class: Gregarinomorpha (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)						
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)						
	Cryptosporidiidae (naked sporozoites)	<i>Cryptosporidium</i>	vertebrates	gut, lungs	direct (f-o)	
Class: Coccidiomorpha [Conoidasida] (with conoid)						
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)						
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)						
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	<i>Haemogregarina</i>	reptiles, amphibia, fish	tissues, blood	indirect (v-b)	
		<i>Hepatozoon</i>	mammals, reptiles	tissues, blood	indirect (v-b)	
	Klossiellidae (sporocysts)	<i>Klossiella</i>	mammals	kidney	direct (f-o)	
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	<i>Caryospora</i>	birds, reptiles	gut	direct (f-o)	
		<i>Cyclospora</i>	mammals, reptiles	gut	direct (f-o)	
		<i>Isoospora</i>	birds, reptiles	gut	direct (f-o)	
		<i>Eimeria</i>	vertebrates	gut, tissues	direct (f-o)	
		<i>Epieimeria</i>	fish	gut	direct (f-o)	
		<i>Goussia</i>	fish	gut	direct (f-o)	
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)					
		subfamily Cystoisosporinae (monozoic cysts)	<i>Cystoisospora</i> (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
		subfamily: Sarcocystinae (thick-walls, metrocytes)	<i>Sarcocystis</i> ( <i>Frenkelia</i> )	mammals, birds, reptiles	gut, muscles	indirect (p-p)
		subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	<i>Besnoitia</i>	mammals, reptiles	gut, tissues	indirect (p-p)
	<i>Hammondia</i>		mammals	gut, tissues	indirect (p-p)	
	<i>Neospora</i>		herbivores, dogs	gut, tissues	indirect (p-p)	
		<i>Toxoplasma</i>	vertebrates, cats	gut, tissues	indirect (p-p)	
Class: Aconoidasida (asexual stages without conoid)						
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protzoa)						
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	<i>Plasmodium</i>	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)	
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	<i>Haemoproteus</i>	birds	endothelia, erythrocytes	indirect (v-b)	
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	<i>Leucocytozoon</i> ( <i>Akiba</i> )	birds	tissues, leucocytes	indirect (v-b)	
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	<i>Babesia</i>	mammals	erythrocytes	indirect (v-b)	
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	<i>Theileria</i>	ruminants	leucocytes, erythrocytes	indirect (v-b)	

\* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isoospora* spp. in mammals form encysted

monozytic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	No. spp.	Life-cycle	Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)	Oocyst configuration*
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozytic cysts in PH, sporocysts without Stieda bodies)				
<i>Cystoisospora</i>	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
<i>Sarcocystis</i> (incl. <i>Frenkelia</i> )	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
<i>Toxoplasma</i>	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
<i>Hammondia</i>	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
<i>Neospora</i>	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
<i>Besnoitia</i>	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
<i>Hyaloklossia</i>	1	monoxenous	vertebrates (amphibians)	1:2:4
<i>Nephroisospora</i>	1	monoxenous	vertebrates (bats)	1:2:4

\*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Toxoplasma*, *Hammondia*, *Neospora* and *Besnoitia* are obligatory or facultatively heteroxenous with cyclic predator-prey transmission usually between carnivorous definitive hosts (DH) and herbivorous intermediate hosts (IH). Transmission from IH to DH occurs via carnivorism (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Several species are also di-heteroxenous (less common term di-homoxenous), meaning that infections can be passed horizontally between intermediate hosts by carnivorism (ingestion of tissue cysts in IH or PH) or vertically from mother to offspring (via transplacental or transmammmary infection). These heteroxenous genera within the subfamily Toxoplasmatinae form tissue cysts without metrocytes, the bradyzoites undergo asexual division before gamete formation and the oocysts sporulate exogenously after being voided. More recently, encysted stages of two monoxenous genera (*Hyaloklossia* and *Nephroisospora*) have been found in the tissues of amphibians and bats, prompting their placement in the subfamily Toxoplasmatinae.

The genus *Hammondia* is characterized by the formation of small intracellular cysts in intermediate hosts – the cysts usually conforming to the shape of their host cells (most being elongate ellipsoidal in tubular skeletal muscle cells, and some being ovoidal-sub-spheroidal in brain cells). The cysts are thin-walled and do not bear radial striations nor septae. The cysts are remarkably similar to those of *Toxoplasma*, and the 2 genera do exhibit some degree of immunological cross-reactivity. Experimental studies have shown *Hammondia* spp. to have either canid or felid definitive hosts, where enteroepithelial multiplication (merogony) occurs, followed by gamogony, fertilization and oocyst formation with unsporulated oocysts shed in their faeces. Contemporary molecular characterization studies involving multiple gene sequences have indicated the genus *Hammondia* is paraphyletic with *Neospora* and *Toxoplasma*.

<i>Hammondia</i> species	Intermediate hosts (IH)	Definitive hosts (DH)	Distribution
<i>H. hammondi</i> (syn. <i>Isospora</i> , <i>Toxoplasma</i> )	Rodentia: murid (house mouse, brown rat, multimammate mouse), caviid (guinea pig), cricetid (golden hamster, deer mice); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (goat), cervid (roe deer), suid (pig); Carnivora: canid (dog); Primates: callitrichid (black-and-red tamarin)	Carnivora: felid (cat, wildcat)	cosmopolitan
<i>H. heydorni</i> (syn. <i>Isospora heydorni</i> , <i>I. wallacei</i> , <i>I. bahiensis</i> , <i>I. babiensis</i> , <i>Toxoplasma bahiensis</i> )	Artiodactyla: bovid (cattle, water buffalo, sheep, goats, gazelle), camelid (camels), cervid (moose, wapiti, whitetail); Lagomorpha: leporid (rabbit), Rodentia: murid (gerbil), caviid (guinea pig)	Carnivora: canid (dog, dingo, coyote, red fox, crab-eating fox, Arctic fox), mustelid (mink)	cosmopolitan
<i>H. pardalis</i>	Experimental infection in Rodentia: murid (house mouse)	Carnivora: felid (ocelot, cat, jaguarundi, cougar, jaguar)	Central America
<i>H. triffittae</i>	Artiodactyla: bovid (sheep, goat), cervid (reindeer, moose); Lagomorpha: leporid (rabbit); Carnivora: canid (arctic fox)	Carnivora: canid (red fox, arctic fox)	Europe

**Parasite morphology:** *Hammondia* spp. form 5 different types of developmental stages: meronts and tissue cysts in intermediate hosts; and meronts, gamonts and oocysts in definitive hosts. Meronts (also called schizonts) are asexual proliferative stages that appear as intracellular rounded basophilic bodies (5-20 µm in diameter) in host cells. They undergo internal division (endodyogeny) to produce numerous (up to 20) merozoites (usually called tachyzoites) which are slender elongate cells (4-9 x 2-3 µm). Ultrastructural studies have shown that *Hammondia* tachyzoites contain a central nucleus, an anterior conoid and typical apicomplexan organelles, including several (up to 8) rhoptries that are electron-dense (electron-lucent in *Toxoplasma* tachyzoites) as well as micronemes and dense granules. Tissue cysts are located in striated muscle cells, and they range in size from 100-340 x 40-95 µm, depending on their maturity. They are bound by a thin smooth primary cyst wall (< 0.5 µm) consisting of a thickened unit membrane (cyst wall similar to that of *Toxoplasma* but thinner than that of *Neospora*). The cysts are aseptate (lacking internal compartments) and mature cysts contain numerous (hundreds) of cystozoites (usually called bradyzoites) which have formed by endogenous division. Bradyzoites are elongate slender cells ranging in size from 6-8 x 2-3 µm. Ultrastructural studies have shown them to contain a posterior nucleus, an anterior conoid, few (< 8) rhoptries but numerous micronemes and dense granules, and pellicular membranes with 22 subpellicular microtubules. In definitive hosts, parasites form both asexual and sexual developmental stages prior to oocyst formation. Meronts (schizonts) appear as rounded basophilic bodies (5-12 µm) located intracellularly within host enterocytes. They undergo asexual division by endodyogeny to form numerous (up to 16) merozoites that are slender elongate stages (4-5 x 1-3 µm). Gamonts then appear as rounded basophilic bodies (8-10 µm) in host cells, developing into macrogametocytes (female) with single nuclei and multiple cytoplasmic vacuoles, and microgametocytes (male) with multiple (up to 8) uninucleated microgametes (1-2 µm) evident around the periphery. Following gamete fertilization, the resultant zygote begins oocyst formation by developing external membranous walls from internal cytoplasmic wall-forming bodies. Unsporulated oocysts are excreted in host faeces as spherical stages (10-14 x 10-13 µm) containing a central granulated sporoblast but lacking a micropyle, polar granules or an oocyst residuum. Sporulation occurred in the external environment with oocysts forming 2 sporocysts (6-8 x 4-6 µm), each containing 4 sporozoites (4-7 x 1-2 µm) and a sporocyst residuum but lacking Stieda and sub-Stieda bodies. The resultant oocyst:sporocyst:sporozoite configuration was 1:2:4 (usually referred to as isosporid-type). Morphological studies have shown *Hammondia* sporozoites to possess a crystalloid body (like other coccidia but absent in *Toxoplasma*).

**Site of infection:** *Hammondia* spp. first form schizonts in the intestinal lamina propria, muscles, Peyer's patches, and mesenteric lymph nodes mainly of herbivorous/omnivorous intermediate hosts, followed by cyst formation in their striated muscles, mainly skeletal but sometimes cardiac. Infections have been recorded in some 23 mammalian species, including artiodactylans (bovids, camelids, cervids, suids), rodents (caviids, cricetids, murids), lagomorphs (leporids), carnivores (canids) and primates (callitrichids). Schizonts, gametocytes, and developing oocysts are found in enterocytes in the intestinal mucosa of carnivorous definitive hosts (canids, felids and mustelids). *Hammondia* spp. exhibit many similarities to the closely-related species *Toxoplasma gondii*, but detailed comparative studies have conclusively proven that they are structurally, biologically, antigenically, and genetically distinct. *Hammondia* spp. have a much smaller intermediate host range, and they can utilize either canids or felids as definitive hosts.

**Pathogenesis:** Infections by *Hammondia* spp. are not considered to be pathogenic and they have not been associated with clinical disease in either intermediate or definitive hosts. Nonetheless, intracellular parasite proliferation ultimately causes lysis of the host

cell and cyst formation in skeletal muscles may result in small space-occupying lesions. The resultant damage, however, appears to be insufficient to cause enough structural and/or functional deficits in their hosts to induce clinical disease. The only exceptions have been several cases where enteric infections by *H. heydorni* are thought to have caused anorexia and diarrhoea in immunosuppressed dogs.

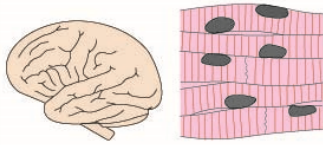
**Developmental cycle and mode of transmission:** Experimental cross-transmission studies have demonstrated that *Hammondia* spp. have an obligatory heteroxenous (2-host) life-cycle involving predator-prey transmission of tissue cysts from intermediate hosts (herbivores/omnivores) to definitive hosts (carnivores), and faecal-oral transmission of oocysts from definitive hosts to intermediate hosts. Following ingestion, oocysts excyst in the small intestines of herbivores/omnivores releasing infective sporozoites which penetrate the gut wall. They infect cells in or near the intestines and undergo asexual proliferation forming schizonts which produce numerous tachyzoites over 7-10 days. The host cells break down releasing the tachyzoites which then infect striated muscle fibres around 14 days after infection. Here they form encapsulated tissue cysts which undergo internal division to produce hundreds of bradyzoites over several weeks. When infected flesh is consumed by cats or dogs, the tissue cysts are digested in the gut releasing the infective bradyzoites which invade intestinal enterocytes within 1-3 days. They form intracellular schizonts which divide asexually to produce numerous merozoites that are released to invade neighbouring cells. The parasites then form female and male gamonts which produce gametes from 4-7 days after infection: female macrogametocytes forming single egg-like macrogametes; and male microgametocytes forming several sperm-like flagellated microgametes. Fertilization occurs by gamete fusion resulting in zygotes that begin oocyst formation. Developing oocysts produce membranous oocyst walls from endogenous wall-forming bodies before they are excreted unsporulated in host faeces. The prepatent period (time from infection to first oocyst excretion) ranges from 5-17 days, while the patent period (duration of oocyst excretion) ranges from 10-28 days. The oocysts undergo sporulation in the external environment over 2-3 days whereby each oocyst forms 2 sporocysts, each of which produces 4 sporozoites (resulting in a 1:2:4 isosporid-type configuration). Sporulated oocysts contaminate food and water sources and are infective to suitable intermediate hosts when inadvertently consumed. Unlike *Toxoplasma*, *Hammondia* spp. do not infect extraintestinal organs in their definitive hosts, and they do not exhibit transplacental or congenital infections in either intermediate or definitive hosts.

**Differential diagnosis:** Infections by *Hammondia* spp. are asymptomatic and are generally detected in hosts incidentally by the detection of tissue cysts in histological sections of post-mortem material. *Hammondia* cysts are morphologically similar to those of *Toxoplasma* and *Neospora*, but the different genera can sometimes be distinguished by careful examination of the cyst wall (thicker in *Neospora*), bradyzoite ultrastructure (electron-dense rhoptries in *Hammondia*, electron-lucent in *Toxoplasma*) and by differential staining with antisera tagged with fluorochrome or chromogenic labels (little cross-reactivity between genera). Infections in definitive hosts are diagnosed by the microscopic detection of oocysts in faecal samples following concentration by sedimentation/floatation techniques. Several serological tests (fluorescent and enzyme immunoassays) have been developed to detect specific host antibodies against parasite antigens, but many *Hammondia* infections only stimulate low levels of antibodies in their hosts and they sometimes cross-react with *Toxoplasma* antigens. Attempts to cultivate parasites *in vitro* in tissue culture (e.g. feline kidney cells) met with partial success but continuous culture of tachyzoites was not achieved as the parasites began cyst formation and were 'outgrown' by host cells. Several *in vivo* bioassays were developed in rodent models, but infections ensued only after feeding oocysts rather than tachyzoites or bradyzoites (in contrast to *Toxoplasma* where all 3 stages triggered infections). *Hammondia* cysts are more frequently found in striated muscles of experimentally-infected mice (while *Toxoplasma* cysts occur more frequently in the brain). Contemporary molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (large subunit ribosomal DNA, internal transcribed spacer region 1). Comparative phylogenetic studies have clearly differentiated between *Hammondia*, *Neospora* and *Toxoplasma* species, and shown the 3 genera to be very closely-related (paraphyletic).

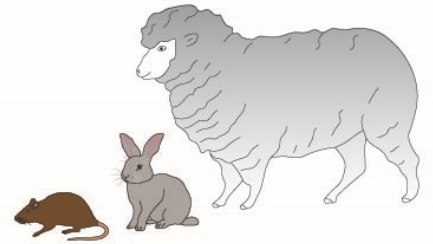
**Treatment and control:** Natural infections by parasitic cysts are generally detected incidentally in the course of histological studies on naturally-infected intermediate hosts, where parasite development has not been associated with any clinical disease requiring treatment. Several attempts have been made to treat experimental infections in rodents using antiprotozoal and antibiotic drugs, but none have been effective. In contrast, experimental infections in definitive hosts have been reported to respond to treatment with coccidiostats, such as sulfonamides (sulfadiazine) or triazinones (ponazuril, toltrazuril, diclazuril), with the apparent suppression of oocyst development. While natural infections are unlikely to occur in modern laboratory rodent colonies, care should be taken not to introduce infected rodents (by serological screening, culling and wild rodent control), excluding carnivores (using barriers), providing clean food (heat-processed pellets) and water (filtered/chlorinated), and regularly cleaning cages and equipment.

# Hammondia

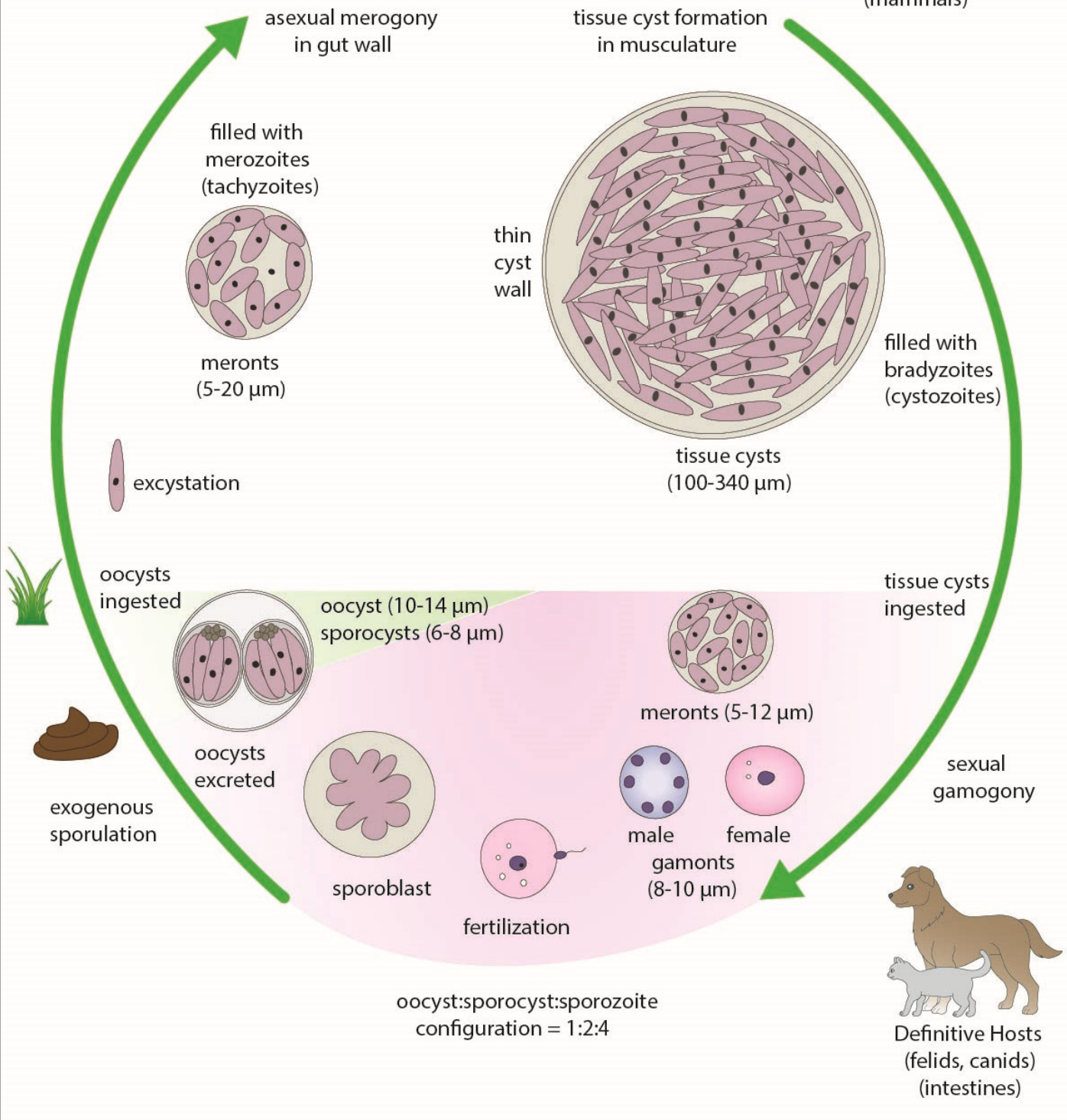
heteroxenous (2-host) cycle  
 predator-prey transmission  
 (predator ingests tissue cysts in prey)  
 (prey ingests sporocysts shed by predator)

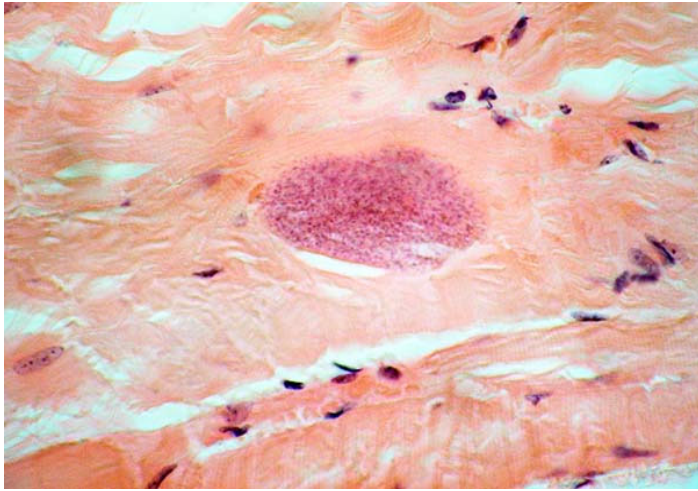


brain, muscles  
 (subclinical space-occupying lesions)

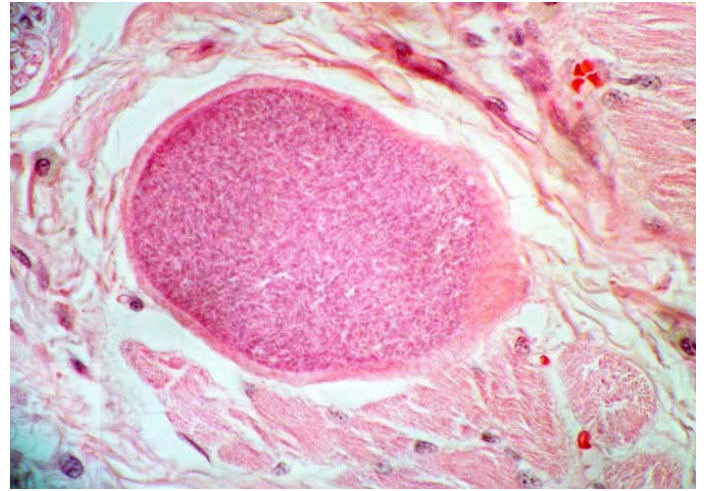


Intermediate Hosts  
 (mammals)





*Hammondia* cyst in mouse muscle



*Hammondia* cyst in mouse muscle