

***Sarcocystis* (incl. *Frenkelia*)**

(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. *Sarcocystis* spp. (including former *Frenkelia* spp.) form elongate cysts containing metrocytes then bradyzoites (= cystozoites) predominantly in the striated muscles of numerous omnivores/herbivores (mammals, birds, reptiles). The cysts have elaborate cyst walls and some may become macroscopic in size causing unsightly lesions in the flesh. Precyst merogony (= schizogony) stages in vascular endothelia have occasionally been associated with haemorrhagic clinical diseases in domestic ruminants. Gamogony (male microgametes fertilize female macrogametes) and oocyst formation occurs directly (without merogony) in subepithelial intestinal tissues in a range of carnivores (mammals, birds and reptiles). Sporogony occurs endogenously resulting in the shedding of free sporocysts each with 4 sporozoites. Different species exhibit relative strict host specificity, with particular predator-prey combinations hosting individual species e.g. two species having a dog-sheep cycle.

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: Sarcocystinae (metrocytes present in cysts, simple/elaborate cyst walls)
Genus: *Sarcocystis* (syn. *Frenkelia*) (tissue cyst-forming coccidian parasites of mammals/birds/reptiles)
Species: various species cause acute sarcocystosis and/or chronic sarcosporidiosis in animals

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 endogeny (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-protozoa)						
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 *Sarcocystis* and *Frenkelia* are classified within the subfamily Sarcocystinae as they form 2 generations of zoites within tissue cysts (metrocytes then bradyzoites (sometimes called cystozoites)), the bradyzoites develop directly into gametes, and the isosporid-type oocysts sporulate endogenously before being voided. Recent molecular phylogenetic studies have indicated that these genera may be conspecific and many authorities have transferred all *Frenkelia* spp. into the genus *Sarcocystis*. The parasites are obligatory heteroxenous with cyclic predator-prey transmission usually occurring between carnivorous DHs and herbivorous IHs. Transmission from IH to DH occurs via carnivory (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). Recent studies have also shown some species may exhibit diheteroxenous cycles where the IH and DH are the same host (supporting both tissue cyst and sporocyst formation) or where IH-IH transmission may occur via cannibalism or transplacental infection (or via ingestion of a paratenic host).

Over 220 *Sarcocystis* spp. have been described worldwide, predominantly by the detection of macroscopic and/or microscopic cysts in striated muscles (hence the name sarcocysts) in numerous mammalian, avian and reptilian hosts. Members of the former genus *Frenkelia* have similar cycles to *Sarcocystis* except that they use birds of prey as definitive hosts and they form cysts in nervous tissues of their rodent intermediate hosts. The cysts of most species had unique cyst wall architecture when examined by transmission electron microscopy, and over 80 ultrastructural types/subtypes have been described. Infections by tissue cysts are prevalent in domestic animals in many countries (e.g. 90% of sheep, 60% of cattle), particularly those kept under intensive husbandry in tropical and temperate regions. However, the complete life-cycles have only been determined for around 100 species by the demonstration of sporocyst formation in carnivores fed tissues cysts. Canids and felids were found to be definitive hosts for many species in domestic animals, particularly those species forming micro-cysts being infective for dogs and those forming macro-cysts being infective for cats. Host specificity was relatively strict for both definitive and intermediate hosts, and multiple parasite species have been found in individual host species (e.g. at least 4 species in sheep, and 3 in cattle). Infections in humans are uncommon, but they may serve either as intermediate hosts (in which tissue cysts develop) or definitive hosts (in which sporocysts are formed). [Historically, it should be noted that some parasite species have inadvertently been given 2 names, one under the genus *Sarcocystis* for the tissue cysts found in herbivorous (intermediate) hosts, and another under the genus *Isoospora* for the oocysts/sporocysts found in carnivorous (definitive) hosts. While some attempts have been made to establish nomenclatural priority, it should be noted that few transmission studies have ever been conducted to ascertain that both stages belong to the same species, apart from some experimental studies on several well-known species in domestic animals. Even then, little variation is evident in the morphology of the oocysts and sporocysts, and because some carnivores host multiple parasite species, it is often unclear as to which species the original descriptions referred to. Future molecular characterization studies may help match different life-cycle stages for individual species, but regrettably no type material of oocysts/sporocysts exists for earlier descriptions. I have therefore

listed all *Sarcocystis* spp. according to the morphological (ultrastructural) characteristics of the tissue cysts detected in their different intermediate hosts].

<i>Sarcocystis</i> species	Intermediate hosts (IH)		Definitive hosts (DH)	Distribution
	Species	Cyst wall		
Species with mammalian intermediate hosts				
<i>S. africana</i>	Artiodactyla: hippopotamid (hippopotamus)	type 15b	unknown	Africa
<i>S. alces</i>	Artiodactyla: cervid (moose)	smooth	Carnivora: canid (Arctic fox, red fox)	Europe
<i>S. alceslatrans</i>	Artiodactyla: bovid (Eurasian elk, moose)	type 7b	Carnivora: canid (dog, coyote)	North America, Europe
<i>S. americana</i>	Artiodactyla: cervid (mule deer)	hair-like villar protrusions	unknown	North America
<i>S. arctica</i>	Carnivora: canid (arctic fox, Alaskan wolf)	type 9c	unknown	Norway, Alaska
<i>S. arctosi</i>	Carnivora: ursid (brown bear)	type 1a	unknown	North America, Asia
<i>S. arieticanis</i>	Artiodactyla: bovid (sheep, wild sheep, mouflon, Alpine ibex)	type 7b	Carnivora: canid (dog)	cosmopolitan
<i>S. atheridis</i>	Experimental infection in Rodentia: murid (house mouse, Barbary striped mouse)	macrocyts type 1b	Serpentes: viperid (Nitsche's bush viper)	Africa
<i>S. aucheniae</i> (syn. <i>S. guanicoecanis</i> , <i>S. tilopodi</i>)	Artiodactyla: camelid (llama, guanaco, alpaca)	macrocyts type 21b	Carnivora: canid (dog)	South America, Australia
<i>S. azevedoi</i>	Rodentia: cricetid (large-headed rice rat)	striated wall	unknown	South America
<i>S. baibacinacanis</i> (syn. <i>S. baibacina</i>)	Rodentia: sciurid (grey marmot, steppe marmot, golden marmot)	nr	Carnivora: canid (dog, wolf, red fox)	Central Asia
<i>S. balaenopteralis</i>	Cetacea: balaenopterid (sei whale)	type 1a	unknown	Pacific
<i>S. bertrami</i> (syn. <i>S. equicanis</i> , <i>S. asinus</i>)	Perissodactyla: equid (horse, kiang, Burchell's zebra, ass/donkey)	macrocyts type 11c	Carnivora: canid (dog)	cosmopolitan
<i>S. bettongiae</i> sp. inq.	Diprotodontia: potoroid (burrowing bettong)	nr	unknown	Australia
<i>S. booliati</i>	Eulipotyphla: erinaceid (moonrat)	type 1b	unknown	South-East Asia
<i>S. bovifelis</i>	Artiodactyla: bovid (cattle, gaur, banteng, European bison, American bison)	macrocyts	Carnivora: felid (cat)	Europe
<i>S. bovini</i>	Artiodactyla: bovid (cattle)	finger-like protrusions	unknown	Argentina, New Zealand, China
<i>S. bozemanensis</i>	Rodentia: sciurid (Richardson's ground squirrel)	type 1a	unknown	North America
<i>S. bubalis</i> sp. inq.	Artiodactyla: bovid (Coke's hartebeest)	macrocyts striated wall	unknown	Africa
<i>S. buffalonis</i>	Artiodactyla: bovid (water buffalo)	type 28	Carnivora: felid (cat)	South-East Asia
<i>S. cafferi</i>	Artiodactyla: bovid (African buffalo)	type 23b	unknown	Africa
<i>S. cameli</i>	Artiodactyla: camelid (Arabian camel, Bactrian camel)	type 9j	Carnivora: canid (dog)	Eurasia, Africa
<i>S. camelopardalis</i>	Artiodactyla: giraffid (giraffe)	type 36	unknown	Africa
<i>S. campestris</i>	Rodentia: sciurid (Richardson's ground squirrel, thirteen-lined ground squirrel)	macrocyts type 9a	Carnivora: mustelid (American badger)	North America
<i>S. caninum</i>	Carnivora: canid (dog)	type 9c	unknown	North America
<i>S. canis</i>	Carnivora: canid (dog), ursid (American black bear, polar bear)	only schizonts known (pre-cyst)	unknown	North America

	bear), otariid (California sea lion, Steller sea lion), phocid (Hawaiian monk seal), Rodentia: chinchillid (long-tailed chinchilla), Artiodactyla: delphinid (striped dolphin), Perissodactyla: equid (horse)	stages)		
<i>S. capracanis</i>	Artiodactyla: bovid (goat), plus molecular detection in sheep	type 14	Carnivora: canid (dog, wolf, coyote, red fox, corsac fox, wood fox, crab-eating dog, raccoon dog)	cosmopolitan
<i>S. capreolicanis</i> (syn. <i>capreoli</i>)	Artiodactyla: cervid (European roe deer)	type 6	Carnivora: canid (dog, swift fox, red fox, raccoon dog)	Europe
<i>S. capricornis</i>	Artiodactyla: bovid (Japanese serow)	type 27	unknown	Japan
<i>S. caviae sp. inq.</i>	Rodentia: caviid (guinea pig)	nr	unknown	South America
<i>S. cernae</i>	Rodentia: cricetid (common European vole)	type 1	Falconiformes: falconid (Eurasian kestrel)	Europe
<i>S. cervicanis</i>	Artiodactyla: cervid (red deer)	type 8a	Carnivora: canid (dog, coyote)	Europe
<i>S. citellibuteonis</i>	Rodentia: sciurid (yellow ground squirrel)	type 1	Accipitriformes: accipitrid (Eurasian buzzard)	Europe
<i>S. citellivulpes</i>	Rodentia: sciurid (yellow ground squirrel)	macrocysts type 9	Carnivora: canid (red fox, corsac fox), mustelid (steppe polecat)	Central Asia
<i>S. clethrionomyelaphis</i>	Experimental infections in Rodentia: cricetid (bank vole, common vole, Gunther's vole, tundra vole)	type 9	Serpentes: colubrid (striped Aesculapian rat snake), plus experimental infection in colubrid (steppe rat snake, corn snake, western rat snake, four-lined snake, ladder snake)	Europe, Middle-East, North America
<i>S. clethrionomysi</i>	Rodentia: cricetid (grey-sided vole)	thick	unknown	Japan
<i>S. cornagliai</i>	Artiodactyla: bovid (Alpine ibex, chamois)	type 24	unknown	Europe
<i>S. corsaci sp. inq.</i>	Carnivora: canid (corsac fox), diheteroxenous	nr	Carnivora: canid (corsac fox)	Central Asia
<i>S. cricetuli</i>	Rodentia: cricetid (Chinese hamster)	nr	unknown	Asia
<i>S. crotali</i>	Rodentia: murid (house mouse)	type 1a	Serpentes: viperid (Mojave rattlesnake)	North America
<i>S. cruzi</i> (syn. <i>bovicanis</i>)	Artiodactyla: bovid (cattle, bison, wisent, gaur, banteng, water buffalo) [causes Dalmeny disease in cattle]	type 7a	Carnivora: canid (dog, coyote, red fox, crab-eating fox, wolf, raccoon dog, crab-eating dog), procyonid (raccoon)	cosmopolitan
<i>S. cuniculorum</i> (syn. <i>S. cuniculi</i>)	Lagomorpha: leporid (rabbit, European hare, mountain hare)	type 10b	Carnivora: felid (cat)	Europe, Australia, New Zealand
<i>S. cymruensis</i> (syn. <i>S. rodentifelis</i>)	Rodentia: murid (house mouse, brown rat, black rat, greater bandicoot rat, Oriental house rat), cricetid (bank vole), also diheteroxenous (rodent-rodent transmission via cannibalism,	type 1c	Carnivora: felid (cat)	Asia, Europe

	paratenic hosts, transplacental)			
<i>S. danzani</i>	Artiodactyla: bovid (Mongolian gazelle)	type 29a	unknown	Asia
<i>S. dasypi</i>	Cingulata: dasypodid (nine-banded armadillo)	type 11	unknown	Americas
<i>S. didelphidis</i>	Didelphimorpha: didelphid (black-eared opossum)	macrocysts	unknown	South America
<i>S. diminuta</i>	Cingulata: dasypodid (nine-banded armadillo)	type 11	unknown	Americas
<i>S. dirumpens</i>	Rodentia: murid (house mouse, Natal multimammate mouse, Mongolian gerbil, pale gerbil, Barbary striped grass mouse, brown rat, grey-headed thicket rat), cricetid (golden hamster, Djungarian hamster)	type 1b	Serpentes: viperid (puff adder, rhinoceros viper, horned viper, Gaboon viper)	Africa
<i>S. dispersa</i>	Rodentia: murid (house mouse)	type 18a	Strigiformes: tytonid (barn owl, masked owl), strigid (long-eared owl)	Europe
<i>S. dogeli</i>	Lagomorpha: ochotonid (Daurian pika)	macrocysts	unknown	Asia
<i>S. dubeyella</i>	Artiodactyla: suid (desert warthog)	type 30	unknown	South Africa
<i>S. elongata</i>	Artiodactyla: cervid (red deer)	thin finger-like protrusions	unknown	Europe
<i>S. entzerothi</i>	Artiodactyla: cervid (European roe deer)	macrocysts type 10a	unknown	Europe
<i>S. eothenomysi</i>	Rodentia: cricetid (Yunnan red-backed vole)	type 18a	unknown	China
<i>S. erdmanae</i>	Carnivora: mephitid (striped skunk)	nr	Carnivora: canid (dog)	North America
<i>S. espinosai</i>	Rodentia: cricetid (North American deer mouse)	type 1h	Strigiformes: strigid (Northern saw-whet owl)	North America
<i>S. eutamias</i>	Rodentia: sciurid (chipmunk)	nr	unknown	Asia
<i>S. eversmanni</i>	Carnivora: mustelid (steppe polecat)	nr	unknown	Central Asia
<i>S. fayeri</i>	Perissodactyla: equid (horse, donkey, onager, plains zebra)	type 11a	Carnivora: canid (dog)	cosmopolitan
<i>S. fedoseenkoi</i>	Rodentia: cricetid (great gerbil)	type 9	unknown	Central Asia
<i>S. felis</i>	Carnivora: felid (cat, bobcat, Florida panther, Florida cougar, cheetah, Geoffroy's cat, oncilla, margay, colocolo, lion, jaguarundi)	type 9c	unknown	North America
<i>S. ferovis</i>	Artiodactyla: bovid (bighorn sheep)	type 3a	Carnivora: canid (coyote)	North America
<i>S. fusiformis</i> (syn. <i>S. blanchardi</i> , <i>S. siamensis</i> , <i>S. bubali</i>)	Artiodactyla: bovid (water buffalo)	macrocysts type 21b	Carnivora: felid (cat)	Eurasia, Africa, South America
<i>S. galuzoi</i>	Lagomorpha: ochotonid (alpine pika)	macrocysts	unknown	Central Asia
<i>S. garnhami</i>	Didelphimorpha: didelphid (black-eared opossum, gray four-eyed opossum)	macrocysts type 9m	unknown	Americas
<i>S. gazellae</i>	Artiodactyla: bovid (red-fronted gazelle, Grant's gazelle, Thomson's gazelle, springbok)	macrocysts type 14	unknown	Africa
<i>S. gerbillechis</i>	Rodentia: cricetid (lesser Egyptian gerbil, pale gerbil), murid (Shaw's jird, fat sand rat,	macrocysts type 1b	Serpentes: viperid (Arabian saw-scaled viper)	Egypt

	fat-tailed gerbil)			
<i>S. gigantea</i> (syn. <i>S. ovifelis</i>)	Artiodactyla: bovid (sheep, bighorn, goat)	macrocyts type 21a	Carnivora: felid (cat), canid (red fox)	cosmopolitan
<i>S. giraffae</i>	Artiodactyla: giraffid (giraffe)	macrocyts type 34	unknown	South Africa
<i>S. glareoli</i> (syn. <i>Toxoplasma glareoli</i> , <i>Iso spor a buteonis</i> , <i>Frenkelia buteonis</i> , <i>F. clethrionomyobuteonis</i> , <i>F. glareoli</i>) [recently transferred from genus <i>Frenkelia</i> to <i>Sarcocystis</i> on the basis of genotypic studies]	Rodentia: cricetid (common vole, bank vole, northern red-backed vole, grey-sided vole, field vole, European water vole), murid (Eurasian field mouse)	non-lobate cysts type 1a	Accipitriformes: accipitrid (common buzzard, rough legged buzzard)	Europe, Japan
<i>S. gracilis</i>	Artiodactyla: cervid (European roe deer, Siberian roe deer); bovid (cattle)	type 1g	Carnivora: canid (red fox, Arctic fox, raccoon dog)	Europe
<i>S. greineri</i>	Didelphimorphia: didelphid (Virginia opossum)	type 9b	unknown	North America
<i>S. grueneri</i> (<i>gruneri</i> , <i>grüneri</i>)	Artiodactyla: cervid (reindeer, red deer, reindeer, sika deer, fallow deer)	type 8a	Carnivora: canid (dog, Arctic fox, red fox, raccoon dog)	Eurasia
<i>S. gusevi sp. inq.</i>	Artiodactyla: bovid (Marco Polo sheep)	nr	unknown	Central Asia
<i>S. hardangeri</i>	Artiodactyla: cervid (reindeer, red deer)	macrocyts type 26	unknown	Europe
<i>S. hemioni</i>	Artiodactyla: cervid (mule deer)	type 10d	unknown	North America
<i>S. hemionilatrantis</i>	Artiodactyla: cervid (mule deer, European roe deer)	type 17	Carnivora: canid (dog, coyote)	North America
<i>S. hippopotami</i>	Artiodactyla: hippopotamid (hippopotamus)	type 33	unknown	South Africa
<i>S. hircicanis</i>	Artiodactyla: bovid (goat), cervid (mule deer)	type 7a	Carnivora: canid (dog)	cosmopolitan
<i>S. hirsuta</i> (syn. <i>S. bovisfelis</i>)	Artiodactyla: bovid (cattle, gayal, banteng, bison, wisent)	macrocyts type 28	Carnivora: felid (cat, wildcat)	cosmopolitan
<i>S. hjorti</i>	Artiodactyla: cervid (red deer, moose)	thin hair-like protrusions	Carnivora: canid (red fox, Arctic fox)	Europe
<i>S. hoarensis</i>	Experimental infections in Rodentia: murid (house mouse, Natal multimammate mouse, pale gerbil, Mongolian gerbil), cricetid (golden hamster, Djungarian hamster)	macrocyts type 42	Serpentes: viperid (puff adder, rhinoceros viper), plus experimental infection in viperid (horned adder, Gaboon viper)	Mediterranean
<i>S. hofmanni</i>	Carnivora: mustelid (European badger), procyonid (raccoon)	macrocyts type 10b	unknown	Europe
<i>S. hominis</i> (syn. <i>boviahominis</i>)	Artiodactyla: bovid (cattle, gayal, banteng, bison, wisent, water buffalo)	type 10b	Primates: hominid (human, chimpanzee), cercopithecoid (rhesus macaque, long-tailed macaque, yellow baboon)	Americas, Europe, Asia
<i>S. hueti</i>	Carnivora: otariid (California sea lion)	type 1e	unknown	North America
<i>S. hydrurgae</i>	Carnivora: phocid (leopard seal)	type 1e	unknown	Antarctic
<i>S. inghami</i>	Didelphimorphia: didelphid (Virginia opossum)	type 9n	unknown	North America
<i>S. ippeni</i>	Artiodactyla: camelid (Arabian camel)	type 32	unknown	Africa
<i>S. jaypeedubeyi</i>	Rodentia: cricetid (meadow	type 9o	unknown	North America

(syn. for original <i>S. microti</i>) [name replaced to overcome homonym caused by transfer of <i>Frenkelia microti</i> to genus <i>Sarcocystis</i>]	vole, long-tailed vole)			
<i>S. jorrini</i>	Artiodactyla: cervid (fallow deer)	macrocysts type 15	unknown	Spain
<i>S. kalvikus</i>	Carnivora: mustelid (wolverine)	macrocysts type 1a	unknown	North America, Eurasia
<i>S. kirkpatricki</i>	Carnivora: procyonid (raccoon)	type 11b	unknown	North America
<i>S. kitikmeotensis</i>	Carnivora: mustelid (wolverine)	type 9h	unknown	North America, Eurasia
<i>S. klaseriensis</i>	Artiodactyla: giraffid (giraffe)	type 35	unknown	South Africa
<i>S. kortei</i>	Primates: cercopithecid (rhesus macaque, bonnet macaque, patas monkey, diademed monkey, sooty mangabey, Angolan talapoin)	type 10	unknown	Asia, Africa
<i>S. lamacanis sp. inq.</i> (syn. <i>S. lamacenis</i>)	Artiodactyla: camelid (llama, alpaca)	nr	Carnivora: canid (dog)	South America
<i>S. lampropeltii</i>	Rodentia: cricetid (prairie vole)	type 1a	Serpentes: colubrid (speckled kingsnake)	North America
<i>S. leporum</i>	Lagomorpha: leporid (eastern cottontail, mountain cottontail, marsh rabbit)	macrocysts type 10b	Carnivora: procyonid (raccoon), felid (cat)	North America
<i>S. levinei</i>	Artiodactyla: bovid (water buffalo)	macrocysts type 7a	Carnivora: canid (dog)	Asia, South America
<i>S. lindemanni</i>	Primates: hominid (humans)	nr	unknown	equatorial
<i>S. lutrae</i>	Carnivora: mustelid (American mink, beech marten, Eurasian badger, Eurasian otter, European polecat), canid (Arctic fox)	type 1a	unknown	Europe
<i>S. markusi</i>	Primates: cercopithecid (vervet monkey)	type 9i	unknown	Africa
<i>S. marmosae</i>	Didelphimorpha: didelphid (Linnaeus's mouse opossum)	finger-like villi	unknown	South America
<i>S. medusiformis</i>	Artiodactyla: bovid (sheep, argali)	macrocysts type 20	Carnivora: felid (cat)	Australia, New Zealand, Europe
<i>S. melampi</i>	Artiodactyla: bovid (common impala)	type 40	unknown	Africa
<i>S. melis</i>	Carnivora: mustelid (European badger, least weasel)	type 1f	unknown	Europe
<i>S. menglaensis</i>	Artiodactyla: tragulid (Williamson's mouse deer)	type 10f	unknown	China
<i>S. mephitisi</i>	Carnivora: mephitid (striped skunk)	type 9m	unknown	North America
<i>S. micros</i>	Artiodactyla: bovid (sheep)	type 27	Carnivora: canid (dog)	China
<i>S. microti</i> (syn. <i>Frenkelia microti</i>) [recently transferred to genus <i>Sarcocystis</i> on the basis of genotypic studies] [homonym overcome by renaming original <i>S. microti</i> as <i>S. jaypeedubeyi</i>]	Rodentia: cricetid (short-tailed vole, common vole, American vole, prairie vole, Syrian hamster, European hamster), murid (wood mouse, yellow-necked mouse, striped field mouse, house mouse, Natal multimammate mouse, brown rat), chinchillid (long-tailed chinchilla); Lagomorpha: leporid (rabbit)	lobulated cysts type 1a	Accipitriformes: accipitrid (common buzzard, red tailed hawk)	Northern Hemisphere
<i>S. miescheriana</i>	Artiodactyla: suid (pig)	type 10b	Carnivora: canid (dog)	cosmopolitan

[type species] (syn. <i>S. suicanis</i>)			wolf, red fox, golden jackal, raccoon dog), procyonid (raccoon)	
<i>S. mihoensis</i>	Artiodactyla: bovid (sheep)	macrocysts type 39	Carnivora: canid (dog)	Japan
<i>S. mongolica</i>	Artiodactyla: bovid (Mongolian gazelle)	macrocysts type 1c	unknown	Mongolia
<i>S. montanaensis</i>	Rodentia: cricetid (prairie vole, meadow vole, long-tailed vole)	type 1a	Serpentes: viperid (southern copperhead)	North America
<i>S. moulei</i> (syn. <i>S. caprifelis</i>)	Artiodactyla: bovid (goat)	macrocysts type 21	Carnivora: felid (cat)	Eurasia, Africa
<i>S. mucosa</i>	Diprotodontia: macropodid (allied rock wallaby, brush-tailed rock wallaby, Bennett's wallaby, Tasmanian pademelon)	macrocysts type 13	unknown	Australia
<i>S. murinotechis</i>	Rodentia: murid (black rat, bush rat, eastern swamp rat, long-tailed mouse, broad-toothed mouse), plus experimental infection in murid (house mouse, brown rat)	type 9b	Serpentes: elapid (black tiger snake)	Australasia
<i>S. muris</i> (syn. <i>S. musculi</i>)	Rodentia: murid (house mouse), plus diheteroxenous (rodent-rodent via cannibalism)	macrocysts type 1a	Carnivora: felid (cat), mustelid (ferret), plus sporocyst production in experimentally infected Rodentia: murid (mice)	cosmopolitan
<i>S. muriviperae</i>	Experimental infection in Rodentia: murid (house mouse)	type 18b	Serpentes: viperid (Palestinian viper), colubrid (black whipsnake)	Middle-East
<i>S. nelsoni sp. inq.</i>	Artiodactyla: bovid (waterbuck, kob, puku)	macrocysts	unknown	Africa
<i>S. neotomafelis</i>	Rodentia: cricetid (Southern Plains woodrat)	macrocysts type 1c	Carnivora: felid (cat)	Mexico
<i>S. nesbitti</i>	Primates: cercopithecoid (rhesus macaque, long-tailed macaque, sooty mangabey, baboon), possibly hominid (human)	type 1	unknown	Africa, Indo-Asia
<i>S. neurona</i>	Perissodactyla: equid (horse, causes equine protozoal myeloencephalitis (EPM), zebra); Carnivora: procyonid (raccoon), mustelid (ferret, sea otter, mink, fisher), mephitid (striped skunk), felid (cat, bobcat), canid (dog), ailurid (red panda), phocid (Pacific Harbor seal), otariid (California sea lion), Artiodactyla: phocoenid (Pacific Harbor porpoise), Cingulata: dasypodid (nine-banded armadillo), Passeriformes: icterid (brown-headed cowbird), Pelecaniformes: threskiornithid (straw-necked ibis); experimental infections in Rodentia: murid (KO mice); DNA detection by PCR in other marine mammals (seals, dolphins, whales)	type 11	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, common opossum)	Americas
<i>S. novaki sp. inq.</i>	Artiodactyla: bovid (cattle)	type 24	unknown	Central Asia

<i>S. ochotonae</i>	Lagomorpha: ochotonid (Daurian pika, plateau pika)	type 1a	unknown	China
<i>S. odocoileocanis</i>	Artiodactyla: cervid (whitetail, sika deer), bovid (cattle, sheep)	type 17	Carnivora: canid (dog, wolf, coyote, red fox, grey fox)	North America
<i>S. odoi</i>	Artiodactyla: cervid (white-tailed deer)	type 10a	Carnivora: felid (cat)	North America
<i>S. oreamni</i>	Artiodactyla: bovid (Rocky Mountain goat)	type 29	unknown	North America
<i>S. orientalis sp. inq.</i>	Artiodactyla: bovid (Siberian ibex)	macrocyts	unknown	Siberia
<i>S. oryzomyos</i>	Rodentia: cricetid (large-headed rice rat)	striated wall	unknown	South America
<i>S. ovalis</i>	Artiodactyla: cervid (moose, red deer)	macrocyts type 26	Passeriformes: corvid (hooded crow, magpie)	Europe
<i>S. oviformis</i>	Artiodactyla: cervid (European roe deer)	macrocyts	unknown	Europe
<i>S. peromysci</i>	Rodentia: cricetid (North American deer mouse)	hairy protrusions	unknown	North America
<i>S. phacochoeri</i>	Artiodactyla: suid (warthog)	type 29b	unknown	South Africa
<i>S. pilosa</i>	Artiodactyla: cervid (sika deer)	type 7a	unknown	Europe
<i>S. pitymysi sp. inq.</i>	Rodentia: cricetid (Savi's pine vole)	nr	unknown	Europe
<i>S. poephagi</i>	Artiodactyla: bovid (yak)	macrocyts type 28	Carnivora: felid (cat) unknown	China
<i>S. poephagicanis</i>	Artiodactyla: bovid (yak)	macrocyts type 6/7	Carnivora: canid (dog)	China
<i>S. porcifelis sp. inq.</i>	Artiodactyla: suid (pig)	macrocyts thin striated wall	Carnivora: felid (cat)	Russia, Romania, Japan, India
<i>S. proechimyos</i>	Rodentia: echimyid (Guyenne spiny rat)	striated wall	unknown	South America
<i>S. pseudois</i>	Artiodactyla: bovid (naur)	type 14	unknown	China
<i>S. putorii</i>	Rodentia: cricetid (common European vole, field vole)	macrocyts type 9b	Carnivora: mustelid (common ferret, least weasel, stoat, mink)	Europe
<i>S. rangi</i>	Artiodactyla: cervid (reindeer)	type 7a	Carnivora: canid (Arctic fox, red fox)	Europe
<i>S. rangiferi</i>	Artiodactyla: cervid (reindeer, red deer)	macrocyts type 15a	unknown	Europe
<i>S. rauschorum</i>	Rodentia: cricetid (Richardson's collared lemming)	type 1h	Strigiformes: strigid (snowy owl)	North America
<i>S. rhombomys</i>	Rodentia: cricetid (great gerbil)	type 1	Carnivora: canid (red fox)	Central Asia
<i>S. richardii</i>	Carnivora: phocid (harbour seal)	macrocyts	unknown	Bering Sea
<i>S. rommeli</i>	Artiodactyla: bovid (cattle)	slender villar protrusions	Carnivora: felid (cat)	Asia
<i>S. idahoensis</i>	Rodentia: murid (North American deer mouse)	thin wall	Serpentes: colubrid (Great Basin gopher snake)	North America
<i>S. roudabushi</i>	unknown		Serpentes: colubrid (gopher snake, black rat snake, fox snake)	North America
<i>S. rzepecyzkii</i>	Rodentia: murid (bush rat)	nr	Serpentes: boid (carpet python)	Australia
<i>S. russuli sp. inq.</i>	Eulipotyphla: soricid (greater white-toothed shrew)	nr	unknown	Central Asia
<i>S. saiga sp. inq.</i>	Artiodactyla: bovid (saiga antelope)	nr	unknown	Central Asia
<i>S. scandinavica</i>	Artiodactyla: cervid (moose)	nr	unknown	Europe
<i>S. scotti</i>	Rodentia: murid (house mouse)	type 1	Strigiformes: strigid	Eurasia

			(tawny owl)	
<i>S. sebeki</i>	Rodentia: muris (house mouse, wood mouse)	type 1b	Strigiformes: strigid (tawny owl)	Eurasia
<i>S. sehi</i>	Rodentia: erethizontid (North American porcupine)	type 1e	unknown	North America
<i>S. sibirica</i>	Artiodactyla: cervid (Siberian roe deer)	type 27	unknown	Asia
<i>S. sigmodontis</i>	Rodentia: cricetid (cotton rat)	macrocyts type 4	unknown	North America
<i>S. silva</i>	Artiodactyla: cervid (European roe deer, moose)	macrocyts type 10a	unknown	Europe
<i>S. sinensis</i> (syn. <i>S. dubeyi</i> or <i>vice versa</i>)	Artiodactyla: bovid (water buffalo)	type 10c	Carnivora: felid (cat)	Asia
<i>S. singaporensis</i> (replacement name for <i>S. orientalis</i> Zaman & Colley, 1975)	Rodentia: murid (brown rat, black rat, dusky rat, long-haired rat, Malaysian field rat, Polynesian rat, ricefield rats, bandicoot rats, yellow-haired hill rat, fraternal hill rat, Sulawesi giant rat, Musschenbroek's spiny rat, Bartel's spiny rat, yellow-tailed rat)	type 19	Serpentes: pythonid (reticulated python, rock python, Timor python, black-headed python)	Australasia
<i>S. speeri</i>	experimental infection in Rodentia: murid (immunodeficient mice)	macrocyts type 38	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, common opossum)	North America
<i>S. sui hominis</i> (syn. <i>porci hominis</i>)	Artiodactyla: suid (pig)	macrocyts type 31	Primates: hominid (human, chimpanzee), cercopithecid (rhesus monkey, long-tailed macaque, yellow baboon)	Europe, India, Japan
<i>S. sulawesiensis</i>	Rodentia: murid (yellow-haired hill rat, fraternal hill rat, Sulawesi giant rat)	type 5	unknown	Indonesia
<i>S. svanai</i>	Carnivora: canid (dog, Pampas fox)	type 1a	unknown	North America
<i>S. sybillensis</i> (syn. <i>S. cervi</i>)	Artiodactyla: cervid (elk, red deer)	type 12	Carnivora: canid (dog, coyote)	Europe, North America
<i>S. taeniata</i>	Artiodactyla: cervid (Canadian moose, red deer, sika deer)	type 7a	unknown	Americas, Europe
<i>S. talpini sp. inq.</i>	Rodentia: cricetid (northern mole vole)	nr	unknown	Central Asia
<i>S. tamanduae sp. inq.</i>	Pilosa: myrmecophagid (collared anteater)	nr	unknown	South America
<i>S. tarandi</i>	Artiodactyla: cervid (reindeer, red deer)	type 10e	unknown	Europe
<i>S. tarandivulpes</i>	Artiodactyla: cervid (reindeer)	type 17	Carnivora: canid (Arctic fox, red fox, dog, raccoon dog)	Europe
<i>S. taugulusi</i>	Artiodactyla: tragulid (Williamson's mouse deer)	type 24	unknown	China
<i>S. tenella</i> (syn. <i>ovicanis</i>)	Artiodactyla: bovid (sheep, wild sheep, mouflon, chamois)	type 14	Carnivora: canid (dog, wolf, dingo, coyote, red fox, jackal, raccoon dog)	cosmopolitan
<i>S. terrestri sp. inq.</i>	Rodentia: cricetid (northern water vole)	hirsute protrusions	unknown	Central Asia
<i>S. tupaia</i>	Scandentia: tupaiid (northern treeshrew)	type 1a	unknown	China

<i>S. tropicalis sp. inq.</i>	unknown	nr	Carnivora: canid (golden jackal)	India
<i>S. truncata</i>	Artiodactyla: cervid (red deer)	thick finger-like protrusions	unknown	Europe
<i>S. undulati</i>	Rodentia: sciurid (long-tailed ground squirrel)	macrocysts	Carnivora: canid (red fox, corsac fox), mustelid (steppe polecat)	Central Asia
<i>S. ursusi</i>	Carnivora: ursid (American black bear)	type 9g	unknown	North America
<i>S. villivillosi</i>	Rodentia: murid (brown rat, black rat, ricefield rats, Malayan field rat, Polynesian rat, long-haired rat, dusky rat, bandicoot rats)	type 22	Serpentes: pythonid (reticulated python, Timor python, rock python, black-headed python)	Asia
<i>S. vulpis sp. inq.</i>	Carnivora: canid (red fox)	nr	unknown	Central Asia
<i>S. wapiti</i>	Artiodactyla: cervid (wapiti)	type 2	Carnivora: canid (dog, coyote)	Europe
<i>S. wetzeli</i> (syn. <i>Isospora wetzeli</i>)	unknown		Carnivora: canid (red fox)	Europe
<i>S. woodhousei</i>	Artiodactyla: bovid (Grant's gazelle, Thomson's gazelle, springbok, Kirk's dik-dik, eland, kewel)	type 29a	unknown	Africa
<i>S. youngi</i>	Artiodactyla: cervid (mule deer)	type 16	unknown	North America
<i>S. zamani</i>	Rodentia: murid (brown rat, black rat, Polynesian rat, Annandale's rat, bandicoot rat)	type 18c	Serpentes: pythonid (reticulated python)	Asia
<i>S. zuoi</i>	Rodentia: murid (brown rat)	type 17	Serpentes: colubrid (king rat snake)	China
Species with avian intermediate hosts				
<i>S. accipitris sp. inq.</i>	Experimental infection in Passeriformes: fringillid (canary)	nr	Accipitriformes: accipitrid (northern goshawk)	Europe
<i>S. alectoributeonis</i>	Galliformes: phasianid (chukar)	macrocysts	Accipitriformes: accipitrid (common buzzard)	Europe
<i>S. alectorivulpes</i>	Galliformes: phasianid (chukar)	type 9/10	Carnivora: canid (red fox, corsac fox)	Europe
<i>S. albifronsi</i>	Anseriformes: anatid (white-fronted goose)	type 9a	Carnivora: canid (Arctic fox)	Europe
<i>S. ammodrami sp. inq.</i>	Passeriformes: passerellid (grassland sparrow)	nr	unknown	South America
<i>S. anasi</i>	Anseriformes: anatid (mallard)	type 9a	unknown	Europe
<i>S. aramidis sp. inq.</i>	Gruiformes: rallid (slaty-breasted wood rail)	nr	unknown	South America
<i>S. calchasi</i>	Columbiformes: columbid (pigeon); plus captive Psittaciformes: psittaculid (princess parrot), cacatuid (long-billed corella, galah), plus experimental infections in Columbiformes: columbid (pigeon), Passeriformes: parid (great tit), Psittaciformes: cacatuid (cockateil)	type 1a	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe, North America
<i>S. cheeli sp. inq.</i>	unknown	nr	Accipitriformes: accipitrid (black kite)	India
<i>S. chloropusae</i>	Gruiformes: rallid (common moorhen)	type 10	unknown	Egypt
<i>S. colii sp. inq.</i>	Coliiformes: coliid (red-faced mouse bird)	macrocysts	unknown	nr

<i>S. columbae</i>	Columbiformes: columbid (wood pigeon)	type 1a	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
<i>S. cornixi</i>	Passeriformes: corvid (hooded crow)	type 1g	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
<i>S. corvusi</i>	Passeriformes: corvid (jackdaw)	type 1d	unknown	Central Asia
<i>S. debonei sp. inq.</i>	Passeriformes: icterid (cowbird)	nr	unknown	North America
<i>S. falcatala</i>	Passeriformes: cardinalid (rose-breasted grosbeak), icterid (cowbirds, grackles), meropid (carmine bee-eater); Cuculiformes: cuculid (guira cuckoo), Strigiformes: strigid (great horned owl), Accipitriformes: accipitrid (bald eagle, golden eagle); Columbiformes: columbid (Luzon bleeding-heart pigeon, Pinon's imperial pigeon, nutmeg imperial pigeon, Victoria crowned pigeon); Psittaciformes: psittacid (African grey parrot, burrowing parrot, Cuban amazon, vinaceous amazon, eclectic parrot, Meyer's parrot, Alexandrine parrot, ring-necked parakeet, thick-billed parrot), psittaculid (Weber's lorikeet, green naped lorikeet, ornate lorikeet, rainbow lorikeet, red lory, Duivenbode's lory, yellow-streaked lory, cardinal lory, violet-necked lory, yellow-bibbed lory, chattering lory, black-capped lory, Derbyan parakeet), cacatuid (Moluccan cockatoo, bare-eyed cockatoo, white cockatoo), and experimentally Columbiformes: columbid (pigeon), Passeriformes: fringillid (finch, canary), passerid (sparrow); Psittaciformes: psittaculid (budgerigar); Galliformes: numidid (guineafowl)	macrocyts type 11b	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, big-eared opossum, common opossum)	Americas
<i>S. garzettae</i>	Pelecaniformes: ardeid (little egret)	type 5	unknown	South Africa
<i>S. halioti</i>	unknown	nr	Accipitriformes: accipitrid (white-tailed sea eagle)	Norway
<i>S. horvathi</i> (syn. <i>S. gallinarum</i>)	Galliformes: phasianid (chicken)	macrocyts, striated wall	Carnivora: canid (dog), felid (cat)	Europe, Australasia, North America
<i>S. jacarinae sp. inq.</i>	Passeriformes: thraupid (blue-black grassquit)	nr	unknown	South America
<i>S. kaiserae</i>	Columbiformes: columbid (laughing dove)	type 9j	unknown	South Africa
<i>S. kirmsei</i>	Galliformes: phasianid (Siamese fireback)	type 9	unknown	Asia

<i>S. lari</i>	Charadriiformes: larid (great black-backed gull)	type 1d	Accipitriformes: accipitrid (white-tailed eagle)	Europe
<i>S. lindsayi</i>	experimental infection in Psittaciformes: psittaculid (budgerigar)	type 11d	Didelphimorphia: didelphid (white-eared opossum, big-eared opossum)	South America
<i>S. nontenella sp. inq.</i>	Accipitriformes: accipitrid (common buzzard)	nr	unknown	Eurasia
<i>S. oliverioi sp. inq.</i>	Psittaciformes: psittacid (green-rumped parrotlet)	nr	unknown	South America
<i>S. otus</i>	Accipitriformes: accipitrid (Eurasian buzzard), Strigiformes: strigid (long-eared owl)	hirsute protrusions	unknown	Germany
<i>S. peckai</i>	Galliformes: phasianid (common pheasant)	finger-like protrusions	Carnivora: canid (dog), felid (cat)	Europe
<i>S. phoeniconaii</i>	Phoenicopteriformes: phoenicopterid (lesser flamingo)	macrocyts type 9l	unknown	Africa
<i>S. ramphastosi</i>	Piciformes: ramphastid (keel-billed toucan)	macrocyts type 9e	unknown	ex: Central America
<i>S. rileyi</i>	Anseriformes: anatid (mallard, northern pintail, American wigeon, green-winged teal, northern shoveler, blue-winged teal, mottled duck, American black duck, wood duck, gadwall, lesser scaup, redhead, greater scaup, canvasback, Eurasian teal, Sunda teal, bufflehead, goldeneye, Eurasian wigeon, white-winged scoter, common eider)	macrocyts type 23	Carnivora: mephitid (striped skunk); canid (red fox, raccoon dog); Didelphimorphia: didelphid (North American opossum)	North America, Europe
<i>S. setophagae</i>	Passeriformes: parulid (American redstart)	macrocyts	unknown	North America
<i>S. spaldingae</i>	Pelecaniformes: ardeid (great blue heron, striated heron, great egret, little blue heron, white ibis, yellow-crowned night-heron)	macrocyts type 9	unknown	North America
<i>S. sulfuratusi</i>	Piciformes: ramphastid (keel-billed toucan)	type 9f	unknown	Central America
<i>S. turdusi</i> (incl. <i>turdi nomen nudum</i>)	Passeriformes: turdid (common blackbird)	type 18b	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
<i>S. wenzeli</i>	Galliformes: phasianid (chicken)	type 9k	Carnivora: canid (dog), felid (cat)	Europe, China, Australasia
<i>S. wobeseri</i>	Anseriformes: anatid (barnacle goose, mallard)	type 1d		Europe
Species with reptilian intermediate hosts				
<i>S. acanthocolubri</i>	Sauria: lacertid (fringe-toed lizard, Bosc's fringe-toed lizard, leopard fringe-toed lizard)	macrocyts type 9d	Serpentes: colubrid (diadem snake)	Egypt
<i>S. ameivamastigodryasi</i>	Sauria: teiid (giant ameiva)	type 1b	Serpentes: colubrid (Rio tropical racer, Boddaert's tropical racer)	Brazil
<i>S. atlanticae</i>	Sauria: lacertid (Atlantic lizard), diheteroxenous	type 37	Sauria: lacertid (Atlantic lizard)	Canary Islands
<i>S. atractaspidis sp. inq.</i>	Serpentes: lamprophiid (Ogaden burrowing asp)	nr	unknown	Africa

<i>S. bunopusi</i>	Sauria: gekkonid (rock gecko)	type 1a	unknown	Saudi Arabia
<i>S. chalcidicolubris</i>	Sauria: scincid (ocellated skink, Gran Canarian skink, Canarian cylindrical skink)	type 1e	Serpentes: colubrid (spotted whip snake, Balkan racer, green whip snake, Dahl's whip snake)	Mediterranean
<i>S. chamaeleonis</i>	Sauria: chamaeleonid (Fischer's chameleon)	nr	unknown	Africa
<i>S. ctenosauris sp. inq.</i>	unknown	nr	Sauria: iguanid (black iguana)	Central America
<i>S. dugesii</i>	Sauria: lacertid (Madeiran wall lizard), diheteroxenous	type 17	Sauria: lacertid (Madeiran wall lizard)	Mediterranean
<i>S. gallotiae</i>	Sauria: lacertid (Tenerife lizard), diheteroxenous	type 37a	Sauria: lacertid (Tenerife lizard)	Canary Islands
<i>S. gongyli</i>	Sauria: lacertid (ocellated lizard)	type 9d	Serpentes: colubrid (diadem snake)	Sicily
<i>S. kinosterni</i>	Testudines: kinosternid (scorpion mud turtle)	thin wall	unknown	South America
<i>S. lacertae</i>	Sauria: lacertid (European wall lizard)	macrocyts type 37a	Serpentes: colubrid (smooth snake)	Europe
<i>S. lacertaetae</i> (syn. <i>S. utae</i>)	Sauria: lacertid (common side-blotched lizard)	smooth	unknown	North America
<i>S. mitrani</i>	Sauria: scincid (Arabian sand skink)	macrocyts type 9d	unknown	Saudi Arabia
<i>S. platydactyli</i>	Sauria: phyllodactylid (Moorish gecko)	macrocyts striated wall	unknown	Mediterranean
<i>S. platydactyliscleropori</i>	Sauria: iguanid (western fence lizard)	thick wall	unknown	North America
<i>S. podarcicolubris</i>	Sauria: lacertid (ruin lizard, Tyrrhenian wall lizard, Erhard's wall lizard, Iberian wall lizard, Lilford's wall lizard, Dalmatian wall lizard, Milos wall lizard, Peloponnese wall lizard, Ibiza wall lizard, common wall lizard, sand lizard, Brown's rock lizard, Carpetane rock lizard, Anatolian rock lizard, Italian wall lizard, jewelled lacerta, sharp-snouted rock lizard, Balkan green lizard, Caucasus emerald lizard, meadow lizard, Armenian lizard, viviparous lizard, blue-throated keeled lizard)	type 9m	Serpentes: colubrid (green whip snake, Balkan racer, large whip snake, Dahl's whip snake, spotted whip snake, false smooth snake)	Europe
<i>S. pythonis</i>	Serpentes: pythonid (carpet python)	thin	unknown	Australia
<i>S. schneideri</i>	Sauria: scincid (barber skink)	type 1b	unknown	Egypt
<i>S. scelopori</i>	Sauria: iguanid (western fence lizard)	striated wall	unknown	North America
<i>S. simonyi</i>	Sauria: lacertid (El Hierro giant lizard), diheteroxenous	type 37a	Sauria: lacertid (El Hierro giant lizard)	Canary Islands
<i>S. stehlinii</i>	Sauria: lacertid (Gran Canaria giant lizard), diheteroxenous	type 7c	Sauria: lacertid (Gran Canaria giant lizard)	Spain
<i>S. stenodactylicolubris</i>	Experimental infections in Sauria: phyllodactylid (Sinai fan-fingered gecko), gekkonid (Jordan short-fingered gecko)	type 4	Serpentes: colubrid (Dahl's whip snake), plus experimental infection in colubrid (Roger's racer)	Middle-East
<i>S. turcicii</i>	Sauria: gekkonid (Mediterranean house gecko)	type 9d	unknown	Saudi Arabia
Species with piscine intermediate hosts				

<i>S. salvelini</i> sp. inq.	Salmoniformes: salmonid (brook trout)		unknown	North America
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Parasite morphology: *Sarcocystis* spp. undergo 3 different developmental cycles in their hosts: typically involving 2 generations of asexual merogony (sometimes called schizogony) followed by tissue cyst formation in intermediate hosts; and then one generation of sexual gamogony (gamete formation) with fertilization producing zygotes (oocysts) that undergo sporogony (sporozoite formation) in definitive hosts. Meronts appear as pleomorphic basophilic bodies located within host endothelial cells: first-generation meronts (M1) in arterioles and second-generation meronts (M2) in capillaries. The meronts undergo internal (endogenous) division to form multiple merozoites (sometimes called tachyzoites). Undifferentiated M1 meronts appear as ovoid-ellipsoidal bodies (10-20 x 5-10 μm) which form elongate differentiated bodies (10-35 x 5-20 μm) containing numerous (10-40) uninucleate merozoites (1-8 x 0.5-3.0 μm). Undifferentiated M2 meronts appear as ovoid bodies (11-16 x 5-10 μm) which form elliptical thin-walled differentiated bodies (12-35 x 3-16 μm) containing numerous (3-50) uninucleate merozoites (1.5-5 x 0.5-2 μm). Tissue cyst (sarcocyst) formation occurs in striated muscles with the appearance of small elongate basophilic bodies (14-33 x 3-6 μm) that begin internal divisions. Cysts are initially thin-walled and microscopic in size (38-110 x 7-15 μm) containing numerous (14-85) undifferentiated spherical (3-5 x 1-3 μm) cells (metrocytes) around the periphery. Maturing cysts become larger (28-184 x 15-36 μm) and may cause host cell distention (the cysts of several species may grow to become macroscopically visible, up to 1 cm in diameter). The cysts are oval-elongate and cylindrical in shape (originally called Meischer's tubules) and are often white-cream in colour. Most cysts are septate and divided into compartments by an internal network of fibrils. Cysts contain several (0-40) spherical (2-5 x 2-4 μm) metrocytes as well as numerous (8-140) crescent-shaped bradyzoites (sometimes called cystozoites) initially being elongate (4-11 x 1.5 μm) but maturing to become banana-shaped (8-15 x 1-4 μm). Ultrastructural studies reveal the bradyzoites to possess an anterior conoid associated with electron-dense organelles (rhoptries and micronemes), lateral micropores, and rigid pellicles with 22 subpellicular microtubules. The cysts are bound by a thin primary cyst wall, comprising a thickened unit membrane with vesicle-like invaginations and species-specific protrusions. The primary cyst walls of some species appear thick (1.5-2.5 μm) and striated due to the presence of prominent radial protrusions. A few species (e.g. *S. gigantea*) also possess a secondary cyst wall consisting of amorphous granular and fibrillar material apparently deposited around the cyst by the host. Ultrastructural studies have, so far, identified 77 different cyst wall types for over 180 *Sarcocystis* spp. Sexual stages (both microgamonts (male) and macrogamonts (female)) develop directly in intestinal cells of definitive hosts, without any preceding asexual multiplication (merogony/schizogony). Macrogamonts form macrogametocytes that appear as ovoid (10-20 μm) lightly-basophilic cells that mature into single macrogametes with prominent lipid bodies and amylopectin granules. Microgamonts form microgametocytes that appear as ovoid-elongate (7 x 5 μm) darkly-basophilic cells which undergo internal division to form multiple (3-11) slender uninucleate microgametes (4 x 0.5 μm) which often appear as rosettes around the periphery. Microgametes are biflagellated and contained a compact nucleus, mitochondrion and 8-10 microtubules. Fertilization involves fusion of a macrogamete and a microgamete creating a zygote that develops into an oocyst. Developing oocysts form thick refractile membranous walls from eosinophilic wall-forming bodies and then begin sporogonous division. The inner mass (sporont) divides into 2 sporoblasts that each form a membrane-bound sporocyst, within which 4 sporozoites are formed (resulting in a typical 1:2:4 oocyst:sporocyst:sporozoite configuration, usually referred to as *Isospora*-like). *Sarcocystis* oocysts, however, are unusual in that endogenous sporulation occurs within the lamina propria of the gut (rather than exogenously outside the host) and the resultant oocysts are thin-walled and often break apart so that free sporocysts are passed into the gut lumen. The sporocysts are small and oval (13-19 x 8-11 μm), lack Stieda bodies and contain 4 crescent-shaped sporozoites and a granular residual body.

Site of infection: In intermediate hosts, parasites first undergo several cycles of asexual proliferation in the endothelial cells of the host vasculature (arterioles then capillaries) followed by tissue cyst formation usually within striated (skeletal and cardiac) musculature. Some species also show an affinity for neural tissue, including peripheral nerve fibres and ganglia, cardiac Purkinje fibres, and white and grey matter in the spinal cord, cerebellum and cerebrum (notably *S. neuronae* in horses). In definitive hosts, gamogony and sporogony occurs in subepithelial locations in the small intestines culminating in the excretion of free sporocysts. The genus *Sarcocystis* is biodiverse with many species occurring in many hosts (mammals, birds and reptiles), but the host specificity of individual species is often narrow, being confined to a small number of intermediate hosts and fewer definitive hosts. Some 88 *Sarcocystis* spp. have been found to form sarcocysts in around 227 mammalian hosts, comprising 62 artiodactylan species (bovid, camelid, cervid, delphinid, giraffid, hippopotamid, phocoenid, suid, tragulid), 7 perissodactyls (equids), 1 cetacean (balaenopterid), 1 cingulate (dasypodid), 9 lagomorphs (leporid, ochotonid), 1 pilosan (myrmecophagid), 1 scandentian (tupaiid), 4 didelphimorphs (didelphids), 5 diprotodonts (macropodid, potoroid), 2 eulipotyphlans (erinaceid, soricid), 82 rodents (caviid, chinchillid, cricetid, echimyid, erethizontid, murid, sciurid), 42 carnivores (ailurid, canid, felid, mephitid, mustelid, otariid, phocid, procyonid, ursid), and 10 primates (cercopithecoid, hominid). Definitive hosts are known for only 85 of these parasite species, with sporocyst production found in 22 carnivore species (canid, felid, mustelid, procyonid), 3 didelphimorphs (didelphid), 5 primates (hominid, cercopithecoid), 1 rodent (murid), 26 snake species (bovid, colubrid, elapid, pythonid, viperid), and 13 bird species (accipitrid, falconid, corvid, strigid, tytonid). Another 37 parasite species have been found to form sarcocysts within some 100 avian hosts belonging to 28 families from 14 orders; including 4 Accipitriformes (accipitrid); 23 Anseriformes (anatid); 1 Charadriiformes (larid); 1 Coliiformes (coliid); 7 Columbiformes (columbid); 1 Cuculiformes (cuculid); 4 Galliformes (numidid, phasianid); 2 Gruiformes (rallid); 7 Pelecaniformes (ardeid); 1 Phoenicopteriformes (phoenicopterid); 1 Piciformes (ramphastid); 31 Psittaciformes (cacauid, psittacid, psittaculid); 2 Strigiformes (strigid); and 11 Passeriformes (cardinalid, corvid, fringillid, icterid, meropid, parid, parulid, passerellid, passerid, thraupid, turdid). Definitive hosts have been identified for only 17 parasite species of

birds, with sporocyst formation reported in 7 mammalian carnivore species (canid, felid, mephitid), 5 didelphimorphs (didelphid), and 6 birds of prey (accipitrids). Around 25 *Sarcocystis* spp. have been reported to form sarcocysts in around 50 reptilian hosts, including 47 lizard species belonging to 7 families (mostly lacertids but also chamaeleonids, gekkonids, iguanids, phyllodactylids, scincids and teiids), 2 snakes species belonging to 2 families (lamprophiid and pythonid), and one tortoise species from one family (kinosternid). Definitive hosts are known only for 15 of these parasite species, all involving reptiles with sporocyst production found in 6 lizard species belonging to 2 families (iguanids and lacertids) and 13 snake species belonging to 2 families (mostly colubrids and one viperid).

Pathogenesis: Many *Sarcocystis* spp. have not been associated with any clinical disease, with infections in both intermediate hosts (herbivores) and definitive hosts (carnivores) remaining asymptomatic or subclinical. Some species, however, have been linked to disease (initially called sarcosporidiosis, but now sarcocystosis): either systemic due to merogony and tissue cyst formation in intermediate hosts, or enteric due to gamogony in definitive hosts. Infections by tissue cysts (sarcocysts) are often latent without any overt pathology, even though they may elicit mild inflammation with cyst destruction (sometimes calcification) and host cell repair (e.g. muscular myophagia). Sarcocysts are often detected incidentally in wildlife, but some heavy infections by macroscopic cysts cause unsightly streaks in skeletal muscle bundles (notably in waterfowl and rodents). Infections by cysts are quite prevalent in domestic animals (especially ungulates), but occasionally chronic infections may cause muscle atrophy and myositis/myocarditis resulting in weakness, lameness, muscle pain, swelling and rarely paralysis. In some countries, infections by macroscopic cysts are classified as carcass lesions by meat inspection services, resulting in enforced carcass trimming or meat condemnation from human consumption, with attendant economic losses. Humans have occasionally been found infected with sarcocysts (around 100 cases worldwide), with some infections associated with malaise, nausea, muscle cramps, pain, swelling, weakness and fatigue. It is only relatively recently that experimental studies have shown that asexual stages preceding cyst formation may cause acute systemic disease in intermediate hosts due to vascular endothelial damage. First and second generation meronts lyse host endothelial cells (arterioles then capillaries) causing petechial haemorrhages throughout most organs and tissues. Heavy experimental infections in domestic livestock may cause acute transient disease around 4 weeks after infection with severe acute vasculitis, massive perivascular infiltration of mononuclear cells and multi-organ haemorrhages resulting in profound anaemia, fever, weakness, recumbency, sudden mortality, and reproductive losses through abortion and stillbirth in pregnant animals (but the parasites do not cross the placenta). Surviving animals sometimes developed subacute disease, exhibiting inappetence, weight loss, loss of hair or wool breakage, poor or stunted growth, muscle atrophy, lethargy, and weakness. Subclinical infections have also been associated with weaner illthrift, reduced weight gain, poor wool growth and reduced milk production. Experimental studies demonstrated that animals developed strong protective immune responses, with animals surviving acute disease becoming resistant to lethal challenge and disease. Acute disease is rarely seen in field conditions, presumably due to early low-dose exposures (e.g. trickle infections) protecting animals while allowing some parasites to develop and persist in host musculature (a state known as premunitive immunity). Nonetheless, natural infections have been linked to several instances of acute sarcocystosis in cattle (colloquially called Dalmeny disease) and an unusual aggressive form of disease in horses causing equine protozoal myeloencephalitis (EPM) with parasites occurring behind the blood-brain barrier in the spinal cord and brain resulting in neurologic disorders, encephalitis, seizures, paralysis and depression. Infections by sexual developmental stages (gamonts) and oocyst formation generally do not cause clinical signs in definitive hosts (primates, carnivores, snakes, birds), but some may cause enteric disease due to intestinal lesions, inflammation, epithelial flattening, villus atrophy and crypt hyperplasia resulting in abnormal function. Clinical signs include malabsorption, watery diarrhea, abdominal pain and distension, stomach ache, nausea, vomiting, fever and sometimes eosinophilia, rapid pulse and difficulty in breathing. Disease is usually mild and self-limiting with spontaneous recovery, but may occasionally be severe, particularly in immunocompromised patients, with protracted diarrhoea leading to dehydration and complications such as jaundice, cholestatic hepatitis, pruritic rashes and weakness.

Developmental cycle and mode of transmission: *Sarcocystis* spp. have heteroxenous (2-host) life-cycles involving predator-prey transmission between carnivorous definitive hosts (in which sexual development of the parasite occurs) and herbivorous/omnivorous intermediate hosts (in which asexual development occurs). Definitive hosts become infected by consuming meat containing tissue cysts whereas intermediate hosts become infected by ingesting sporocysts excreted by the definitive hosts. Once ingested, sporocysts are triggered to excyst by biochemical cues (low oxygen, pH and bile enzymes) facilitating the release of the contained sporozoites. Parasites then undergo asexual (merogonous) multiplication within host tissues: the site of development, number of generations, and number of progeny varying for each parasite species. Typically, motile sporozoites move through the gut wall into the circulation where they infect the endothelial cells of small arteries and arterioles throughout the body. They form first-generation meronts (M1) within 6-19 days of infection which produce numerous merozoites that are released by host cell lysis. These merozoites are swept downstream where they infect endothelial cells in capillaries in numerous sites (lymphatic, respiratory, urinary, digestive, nervous, muscular, reproductive, endocrine and dermal tissues and organs). They form second-generation meronts (M2) from 21-36 days after infection which produce numerous merozoites that are also released by host cell lysis. Merozoites then enter striated muscle cells, rounding up to form merocytes and initiating cyst formation. Developing cysts are evident within 40-45 days of infection and they exhibit rapid merocyte division over 5-10 days with cystozoite and cyst wall formation occurring thereafter. The cyst maturation process takes around 2 months or so until the contained bradyzoites become infectious. The cysts may persist for months, even years, within host muscles where they are walled off from the immune system. When mature cysts are ingested by carnivores consuming infected flesh, the cyst wall is digested in the gut facilitating the release of the contained bradyzoites. The motile bradyzoites invade the lamina propria of the small intestines within 3-6 hours and commence

sexual reproduction by gamogony (without any preceding asexual multiplication like other coccidia). Male and female gamonts develop into gametocytes which produce gametes in 1-2 days. Female gametocytes produce one uninucleate macrogamete, while male gametocytes produce several biflagellated microgametes which are released to find and fertilize receptive macrogametes. The resultant zygote develops into an oocyst within the gut wall, which then undergoes endogenous sporulation forming sporocysts and sporozoites while resident within the lamina propria of the gut wall. The *Isospora*-like oocysts (with 1:2:4 configuration) are thin-walled and break open so that free sporocysts are released into the gut lumen and excreted with host faeces. These sporocysts are immediately infectious for intermediate hosts via contaminated food and water (and do not require an exogenous maturation phase like some other coccidia). The prepatent period (time from infection to sporocyst excretion) ranges from 7-14 days, and the patent period (duration of sporocyst excretion) ranges from days to weeks depending on both host and parasite species. Humans may act as definitive or definitive hosts for several *Sarcocystis* spp.: developing enteric infections after eating raw or undercooked beef or pork containing mature sarcocysts of *S. hominis* (syn. *S. bovihominis*) or *S. suis* and shedding sporocysts 11-18 days later; or developing muscle cysts after consuming sporocysts voided by definitive hosts with predator-primate cycles (e.g. pythons with monkey prey). It is hoped that modern molecular genotypic characterization studies will help to identify these heteroxenous parasites.

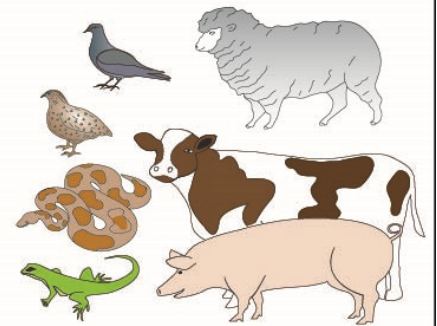
Differential diagnosis: Infections are conventionally diagnosed by the detection of parasite developmental stages in host samples by microscopy. Enteric infections are diagnosed by the demonstration of characteristic sporocysts in faecal smears or concentrates (following floatation in high specific gravity salt or sugar solutions), in post-mortem gut scrapings (following enzymatic digestion to liberate parasites from subepithelial locations) or in gut tissues (stained histological sections). Different *Sarcocystis* spp. cannot be identified on the basis of sporocyst morphology as they are all very similar in size, shape and appearance. Muscle infections are diagnosed either by the detection of sarcocysts in biopsy or autopsy material (by macroscopic examination of fresh tissues or by microscopic examination of fresh squash (trichinoscopic) preparations or fixed stained histological sections) or the detection of bradyzoites in muscle digest sediments (following pepsin-acid digestion of ground meat samples). Medical imaging techniques (including computed tomography (CT) and magnetic resonance imaging (MRI)) have occasionally been used to demonstrate sarcocysts in host muscles (especially calcified cysts). A range of immunoserological techniques have also been developed to detect specific host antibodies against parasite antigens (including complement fixation, haemagglutination, immunofluorescence and enzyme immunoassays), with the detection of specific IgM or IgG antibodies indicating acute or chronic infections respectively. Polyclonal and monoclonal antibodies have been produced and used in immuno-histochemical studies to locate parasites in tissues. Immunoblotting techniques have also been used to detect parasite antigens in the cerebrospinal fluid from horses suffering from equine protozoal myeloencephalitis (EPM). Modern molecular biological techniques have recently been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear (18S and 23S ribosomal DNA) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: A variety of chemicals have been used in attempts to treat infections in livestock, companion animals and miscellaneous wildlife. Treatment of enteric infections in carnivores is often not required as they are usually asymptomatic, transient and self-limiting. In exceptional cases, animals with clinical signs have responded well to treatment with anti-coccidial drugs, including ionophores (maduramicin), triazinones (toltrazuril, diclazuril), sulfonamides (sulfadiazine, co-trimoxazole), quinazolinones (halofuginone) and even some nitroimidazoles (tinidazole). Animals also benefited from supportive rehydration therapy, as well as concurrent antibiotic treatment for secondary bacterial infections. The treatment of livestock with chronic infections by tissue cysts is also not warranted as they do not cause clinical signs and the parasites are locked away in membrane-bound intracellular cysts. However, livestock experiencing acute clinical disease due to pre-cyst parasite proliferation within the vasculature have responded reasonably well to treatment with several anticoccidial drugs, including thiamine analogues (amprolium), ionophores (salinomycin), triazinones (toltrazuril, diclazuril), folic acid antagonists (pyrimethamine), diaminopyrimidines (trimethoprim), sulfonamides (sulfadiazine) and sulfanilamides (sulfamethoxazole). While treatment did not eliminate parasites, it significantly reduced their numbers thus curtailing overt pathology and providing sufficient time for the development of protective host immune responses. A variety of preventive control measures may be adopted to reduce the risk of parasite transmission between livestock and companion animals, mostly based around good hygiene and sanitation. Domestic carnivores should not have access to animal carcasses and they should be prevented from hunting and from defaecating on pastures or fodder stores (outbreaks of Dalmeny disease have been attributed to the contamination of supplementary fodder by cats used to control rodent populations in haysheds). Meat infected with sarcocysts should not be fed to farm dogs and cats, but could be thoroughly cooked or deep-frozen to kill infectious bradyzoites. Livestock should have access to clean water that has not been contaminated by carnivore faeces, with conventional water treatment by chlorination and/or filtration effectively killing sporocysts. Despite common-sense interventions, parasite control may prove difficult due to the apparent ubiquitous nature of the organisms. In many instances, eradication and control may not be appropriate because lightly infected hosts are protected against acute disease, afforded by the development of premunitive immunity (where parasites are not eradicated but small numbers persist in tissues providing protection against superinfection). Hosts and parasites are said to have achieved enzootic stability which, paradoxically, could be upset by control programs if parasite numbers are reduced to the point that hosts no longer develop protective immunity and become susceptible to acute disease.

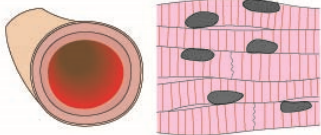
Sarcocystis

heteroxenous (2-host) cycle

predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)

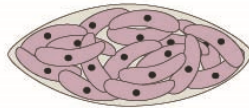


Intermediate Hosts
(mammals, esp. herbivores,
birds, reptiles)

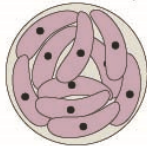


blood vessels, muscles
(petechial haemorrhages,
space-occupying lesions)

asexual merogony in
vascular endothelia
(arterioles then capillaries)

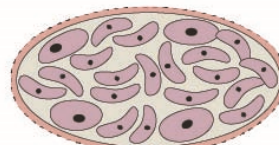


meronts
(10-35 μm)



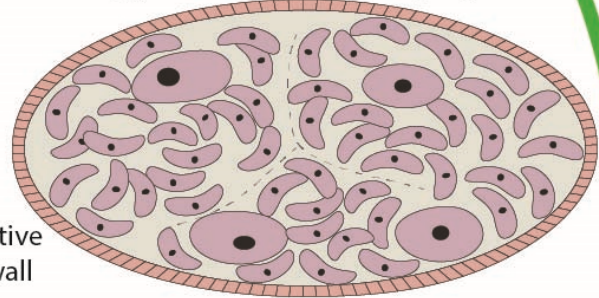
excystation

tissue cyst formation
in striated musculature



peripheral meronts (rounded)

numerous bradyzoites
(cystozoites) (banana-shaped)

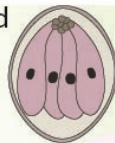


distinctive
cyst wall

tissue cysts ('sarcocysts')
(30 μm - 1 cm)

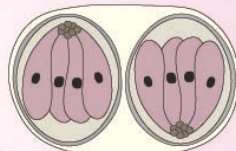


sporocysts
ingested



sporocyst
(13-19 μm)

sporocysts
excreted



endogenous
sporogony &
sporulation

oocyst



sporoblast

oocyst:sporocyst:sporozoite
configuration = 1:2:4

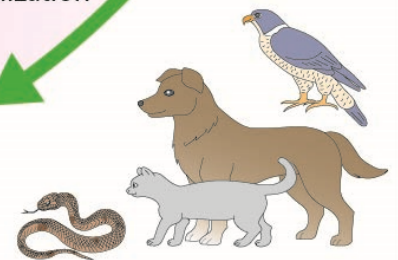
male gamonts (10-20 μm)
female gamonts (10-20 μm)



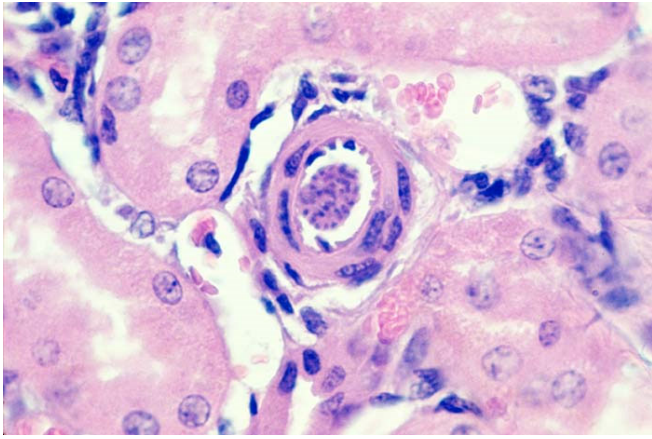
fertilization

tissue cysts
ingested

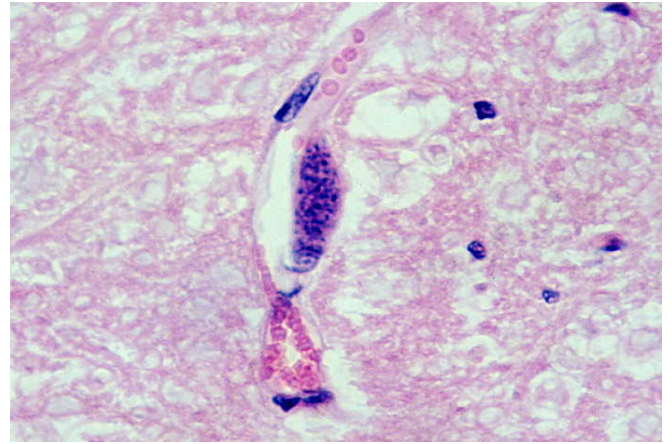
sexual
gamogony



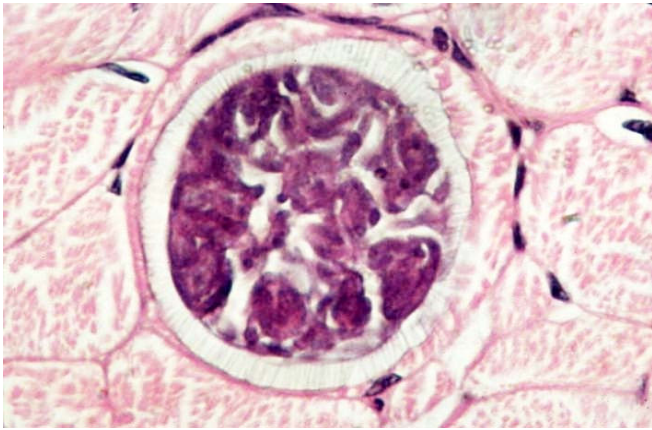
Definitive Hosts
(carnivores)
(intestines)



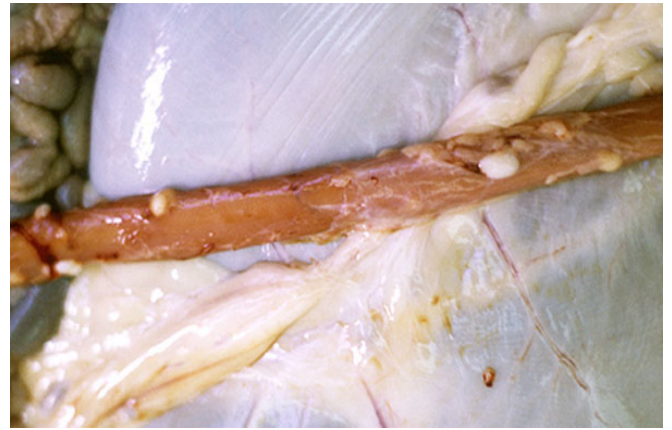
Sarcocystis schizont in sheep kidney arteriole



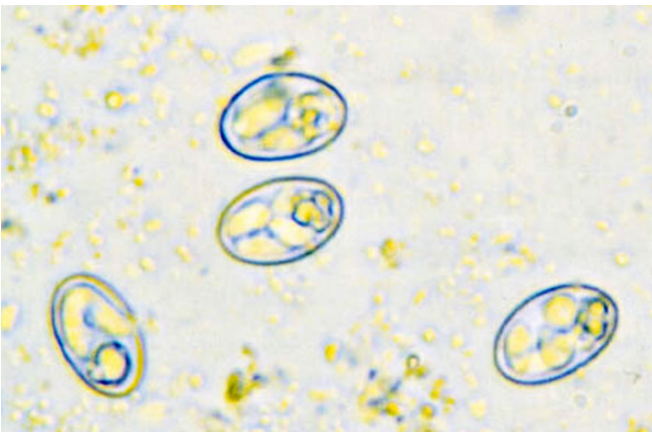
Sarcocystis schizont in sheep brain capillary



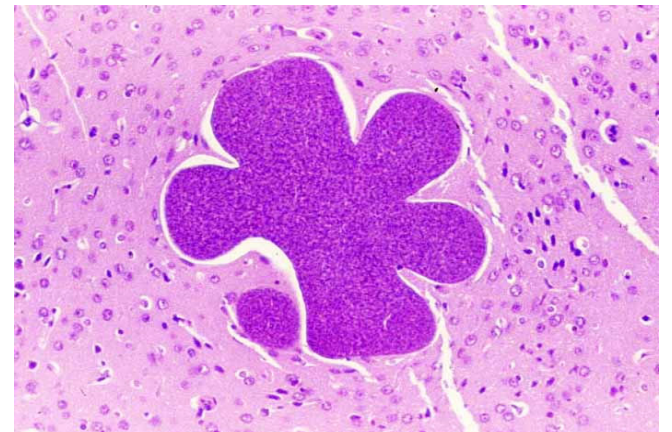
Sarcocystis thick-walled cyst in sheep muscle



Sarcocystis macrocysts on sheep oesophagus



Sarcocystis sporocysts from dog faeces



Sarcocystis (*Frenkelia*) cyst in rodent brain