Isospora* and *Cystoisospora
(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). Most isosporid species are monoxenous (1-host) parasites in the digestive tracts of vertebrates, although some have recently been found to form encysted (monozoic) stages in the tissues of intermediate hosts. There are three sequential stages in the parasite life-cycle: endogenous multiplication by asexual merogony (= schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which are excreted and undergo asexual sporogony (sporozoite formation). Isosporid oocysts typically contain two sporocysts, each with four sporozoites (1:2:4 configuration). Contemporary phylogenetic studies indicate isosporid coccidia have polyphyletic origins: one group forming sporocysts with Stieda bodies in birds and reptiles being similar to other monoxenous eimeriid coccidia (species retained in the genus *Isospora*), and one group forming sporocysts without Stieda bodies in carnivorous mammals, as well as small encysted stages in the tissues of paratenic hosts, being more closely related to the heteroxenous sarcocystid coccidia (species transferred to genus *Cystoisospora*). Many isosporid species have been associated with clinical disease (coccidiosis) characterized by gastrointestinal perturbations and sometimes extraintestinal lesions.

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:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Isospora* (= *Atoxoplasma*) (parasitic in intestines of birds and lizards)
Species:	various species cause clinical coccidiosis (mostly in neonates)
Family:	Sarcocystidae (heteroxenous, disporocystic oocysts, tissue cyst formation in intermediate/paratenic hosts)
Subfamily:	Cystoisosporinae (monozoic cysts in paratenic transport hosts, sporocysts without Stieda bodies)
	Cystoisospora (formerly mammalian *Isospora*) (parasitic in intestines, sometimes tissues, of mammals)

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**	**Trans-mission***
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [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)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	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)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

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

Numerous species of eimeriid 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 21 genera in the family Eimeriidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genera *Isospora* and *Cystoisospora* form oocysts with a 1:2:4 configuration; that is, oocysts are disporocystic (contain 2 sporocysts) and each sporocyst is tetrasporozoic (contains 4 sporozoites).

Parasite genera	No. spp.	Life-cycle	Hosts	Oocyst configuration
Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1
Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8
Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2
Epieimeria	3	monoxenous	vertebrates (fish)	1:4:2
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4

Isosporan infections have been detected throughout the world, mainly in carnivores (particularly canids and felids) as well as in some omnivores (humans, pigs), lizards and birds. Some 250 species have been described, mostly on the basis of host occurrence and oocyst morphometrics. Most species are considered to be highly host-specific and only parasitize single host species (oioxenous), although some species in birds and reptiles may parasitize closely-related hosts (stenoxenous) or even unrelated hosts (euryxenous). Many hosts also harbour multiple species of coccidia which may vary considerably in morphology, developmental cycle, site of infection and pathogenicity. Historically, there has been considerable confusion in the identification of coccidian genera, particularly since the discovery of species with heteroxenous (two-host) life-cycles alternating between enteric stages in predators and tissue cysts in prey animals. It has recently been demonstrated that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia (*Sarcocystis*, *Frenkelia*, *Hammondia*, *Besnoitia* and *Toxoplasma*) under the name *Cystoisospora.* Many phylogenetic studies have now indicated that *Isospora* spp. from vertebrates may be divided into two major groups: those species that have sporocysts with a Stieda body are closely related to the monoxenous Eimeriidae and occur mainly in birds; while those species that have sporocysts without a Stieda body are most closely associated with the tissue cyst-forming Sarcocystidae and occur in mammals. The latter may also be divided into two types: larger forms with distinct oocyst walls that maintain their integrity within the gastrointestinal tract and sporulate exogenously (species transferred to the genus *Cystoisospora*); and smaller forms with thin membranous oocyst walls that sporulate endogenously and often release their sporocysts within the gastrointestinal tract (species transferred to the genus *Sarcocystis*). Infections by *Cystoisospora* spp. are common in mammals (particularly carnivores), while infections by *Isospora* spp. are common in birds (especially passerines) and lizards (skinks, geckoes and dragons). *Atoxoplasma* infections in birds are currently considered to be *Isospora* infections which have disseminated into extra-intestinal tissues and blood cells.

In the family Eimeriidae, some 360 *Isospora* spp. have been described from a range of wild and captive animals: with 88 species identified in mammals, 162 in birds, 92 in reptiles, 14 in amphibia, 2 in fish, and one in an invertebrate (limacid slug). The website "Coccidia of the World" attempts to catalogue parasite biodiversity (= species richness) together with taxonomic authorities, including numerous host records for un-named species. The following table lists named taxa for which parasite descriptions are consistent with taxonomic guidelines (as stipulated by the International Code of Zoological Nomenclature).

***Isospora* spp.**	**Oocyst size (µm)**	**Definitive hosts**
Mammalian hosts		
I. agrarii	23	Rodentia: murid (striped field mouse)
I. aksaica	26	Artiodactyla: bovid (cattle)
I. almaataensis (*almataensis*)	28 x 26	Artiodactyla: suid (pig)
I. anatolicum	12 x 10	Rodentia: spalacid (lesser mole-rat)
I. aprutina (syn. *I. vulpina* var. *aprutina*)	25 x 21	Carnivora: canid (red fox)
I. aquatici	21 x 18	Eulipotyphla: talpid (eastern mole)
I. araneae (*aranei*)	17	Eulipotyphla: soricid (Eurasian shrew)
I. arvalis		Rodentia: cricetid (common vole)
I. ashtabulensis	20 x 14	Eulipotyphla: talpid (hairy-tailed mole)
I. assensis		Rodentia: sciurid (yellow ground squirrel)
I. aurangabadensis		Rodentia: murid (black rat)
I. batabatica	24 x 21	Rodentia: cricetid (northern water vole)
I. bigemina (large oocyst morphotype = var. *canis*; small oocyst morphotype = var. *cati* = *Toxoplasma?*)	large 19 x 15 small 12 x 8	Carnivora: canid (dog, red fox), felid (cat), mustelid (American mink, polecat)
I. bisoni	29 x 22	Artiodactyla: bovid (gaur)
I. boughtoni	18 x 17	Didelphimorpha: didelphid (North American opossum)
I. brevicauda	17 x 16	Eulipotyphla: soricid (northern short-tailed shrew)
I. californica	24 x 23	Rodentia: cricetid (California mouse, brush mouse, Pinyon mouse, North American deermouse)
I. calomyscus	22 x 18	Rodentia: calomyscid (Zagros Mountains mouse-like hamster)
I. capreoli	43 x 31	Artiodactyla: cervid (roe deer)
I. cebi	21 x 20	Primates: cebid (white-fronted capuchin)
I. chilensis [probably *Sarcocystis* sp.]		Primates: hominid (human)
I. citelli	22 x 21	Rodentia: sciurid (rock squirrel, yellow ground squirrel)
I. clethrionomydis	25	Rodentia: cricetid (bank vole, grey red-backed vole, northern red-backed vole)
I. clethrionomysis	10 x 9	Rodentia: cricetid (bank vole, northern red-backed vole)
I. condylurae	19 x 9	Eulipotyphla: talpid (star-nosed mole)
I. cristatae	16 x 10	Eulipotyphla: talpid (star-nosed mole)
I. dawadimiensis	24 x 21	Rodentia: dipodid (lesser Egyptian jerboa)
I. dymecodi	16 x 13	Eulipotyphla: talpid (True's shrew mole)
I. dyromidis		Rodentia: glirid (forest dormouse)
I. egypti	21 x 18	Rodentia: murid (Shaw's jird)
I. erinacei	30 x 26	Eulipotyphla: erinaceid (European hedgehog)
I. erythrourica	21 x 18	Rodentia: murid (Libyan jird)
I. fennechi	28 x 17	Carnivora: canid (fennec fox)
I. fonsecai	25 x 23	Carnivora: ursid (brown bear)
I. freundi	20	Rodentia: cricetid (European hamster)
I. golemanskii		Rodentia: murid (yellow-necked mouse, wood mouse)
I. hammondi	27 x 19	Rodentia: cricetid (marsh rice rat)
I. hastingsi	31 x 23	Rodentia: cricetid (pinyon mouse)
I. hominis [probably *Sarcocystis* sp.]		Primates: hominid (human)
I. hylomysis	12 x 11	Eulipotyphla: erinaceid (short-tailed gymnure)

I. ichneumonis species inquirenda	22 x 19	Carnivora: herpestid (Egyptian mongoose)
I. jakimovi		Carnivora: mustelid (sable)
I. krishnamurthyi		Rodentia: murid (black rat)
I. laguri	28 x 19	Rodentia: cricetid (steppe lemming)
I. lamoillensis	22 x 13	Eulipotyphla: talpid (star-nosed mole)
I. lutreolinae	21 x 18	Didelphimorphia: didelphid (latrine opossum)
I. lyncis (*species inquirenda*)	44 x 32	Carnivora: felid (lynx)
I. marquardti		Lagomorpha: ochotonid (American pika)
I. masoni		Rodentia: cricetid (hispid cotton rat)
I. mcdowelli	10 x 9	Rodentia: cricetid (meadow vole)
I. merionis	24 x 20	Rodentia: murid (midday jird, Vinogradov's jird, Mongolian jird)
I. mexicanasubsimi	24 x 23	Rodentia: cricetid (Mexican vole)
I. motleiensis	14 x 12	Eulipotyphla: talpid (eastern mole)
I. mustelae (*nomen nudum*)	7 x 2	Carnivora: mustelid (European pine marten)
I. neomyi	14	Eulipotyphla: soricid (Mediterranean water shrew, Eurasian water shrew)
I. neurotrichi	14 x 12	Eulipotyphla: talpid (American shrew mole)
I. neyrai	13 x 9	Artiodactyla: suid (pig)
I. ordubadica	20 x 17	Rodentia: murid (Persian jird)
I. orlovi	31 x 18	Artiodactyla: camelid (camel)
I. palustris	18 x 17	Eulipotyphla: soricid (Pacific shrew, northern water shrew, montane shrew, Trowbridge shrew, long-clawed shrew)
I. papionis [probably *Sarcocystis*]	17 x 11	Primates: cercopithecid (chacma baboon)
I. parascalopi	15 x 13	Eulipotyphla: talpid (hairy-tailed mole)
I. peromysci	35 x 21	Rodentia: cricetid (California mouse, North American deermouse, pinyon mouse)
I. putorii	ns	Carnivora: mustelid (stoat)
I. rangiferis	29 x 25	Artiodactyla: cervid (reindeer)
I. rastegaievae	19 x 17	Eulipotyphla: erinaceid (European hedgehog)
I. ratti	23 x 21	Rodentia: murid (brown rat)
I. riccii	23 x 15	Eulipotyphla: talpid (northern mole)
I. saimirae	25 x 22	Primates: cebid (squirrel monkey)
I. samsenis		Rodentia: sciurid (yellow ground squirrel)
I. schmaltzi	26	Eulipotyphla: erinaceid (European hedgehog)
I. sofiae	12 x 11	Eulipotyphla: talpid (European mole)
I. soricis	24 x 17	Eulipotyphla: soricid (Eurasian shrew)
I. spalacensis	15 x 11	Rodentia: spalacid (Middle East blind mole-rat)
I. spermophili		Rodentia: sciurid (suslik)
I. sporopointaea	17 x 11	Eulipotyphla: talpid (European mole)
I. sundarbanensis		Artiodactyla: suid (pig)
I. talpae	18 x 12	Eulipotyphla: talpid (European mole)
I. tamariscini		Rodentia: murid (tamarisk jird)
I. teres	30	Rodentia: cricetid (steppe lemming)
I. tropicalis [= *Sarcocystis* sp.]	16	Carnivora: canid (golden jackal)
I. uralicae	26 x 23	Rodentia: murid (wood mouse)
I. urotrichi	13 x 12	Eulipotyphla: talpid (Japanese shrew mole)
I. vanadica	24 x 19	Rodentia: murid (Persian jird)
I. vinogradovi	27 x 22	Rodentia: murid (Vinogradov's jird)
I. vizcacha		Rodentia: chinchillid (plains viscacha)
I. vulpis	25 x 24	Carnivora: canid (red fox, silver fox, Indian fox)
I. yukonensis		Lagomorpha: ochotonid (collared pika)
Avian hosts		
I. alaudae		Passeriformes: alaudid (Eurasian skylark)
I. albicollis	25 x 20	Passeriformes: turdid (white-necked thrush)
I. ampullacea	27	Passeriformes: sylviid (garden warbler)
I. anseris		Anseriformes: anatid (Canada goose, emperor goose) plus experimental infections in greylag goose, snow goose)

I. anthi		Passeriformes: motacillid (meadow pipit)
I. arrui		Passeriformes: fringillid (common linnet)
I. ashmoonmensis		Passeriformes: sylviid (Eurasian blackcap)
I. atrata		Passeriformes: fringillid (black siskin)
I. automoli		Passeriformes: furnariid (olive-backed foliage-gleaner, buff-throated foliage-gleaner)
I. aycardii		Passeriformes: cisticolid (zitting cisticola)
I. balaericae		Gruiformes: gruid (grey crowned crane)
I. bellericae	22 x 20	Gruiformes: gruid (grey crowned crane)
I. bellicosa		Passeriformes: icterid (Peruvian meadowlark)
I. bengalensis	21	Passeriformes: corvid (house crow)
I. bioccai		Passeriformes: fringillid (grey-capped greenfinch)
I. blagburni		Passeriformes: pycnonotid (white-spectacled bulbul)
I. boxae		Passeriformes: passerid (house sparrow)
I. brachyrhynchi		Passeriformes: corvid (American crow)
I. brayi		Passeriformes: zosteropid (Japanese white-eye)
I. buteonis	18 x 15	Accipitriformes: accipitrid (Cooper's hawk, red-tailed hawk, Swainson's hawk, Eurasian sparrowhawk, golden eagle, common buzzard, long-legged buzzard); Falconiformes: falconid (lesser kestrel, common kestrel, American kestrel, peregrine falcon); Strigiformes: tytonid (barn owl), strigid (little owl, long-eared owl, tawny owl),
I. cacici		Passeriformes: icterid (yellow-rumped cacique)
I. cadimi	24 x 23	Passeriformes: thraupid (Brazilian tanager)
I. caerulei		Passeriformes: parid (Eurasian blue tit)
I. calocitta		Passeriformes: corvid (white-throated magpie-jay)
I. canaria		Passeriformes: fringillid (canary)
I. cannabinae		Passeriformes: fringillid (common linnet)
I. capistrata		Passeriformes: leiothrichid (rufous sibia)
I. cardellinae		Passeriformes: parulid (red warbler)
I. cardinalis		Passeriformes: emberizid (black-crested finch)
I. carduelis	28 x 24	Passeriformes: fringillid (goldfinch)
I. certhiae		Passeriformes: certhiid (short-toed treecreeper)
I. ceylonensis		Passeriformes: muscicapid (grey-headed flycatcher)
I. cheeli	14 x 11	Falconiformes: accipitrid (black kite)
I. chloridis	25 x 22	Passeriformes: fringillid (greenfinch, chaffinch)
I. choudari		Galliformes: phasianid (grey junglefowl)
I. cincli		Passeriformes: cinclid (white-throated dipper)
I. concentrica		Passeriformes: dendrocolapid (Amazonian barred woodcreeper)
I. concinnus		Passeriformes: aegithalid (black-throated bushtit)
I. corvi (corviae)	20 x 18	Passeriformes: corvid (large-billed crow)
I. couderti		Passeriformes: sylviid (zitting cisticola)
I. cyanocoracis		Passeriformes: corvid (plush-crested jay)
I. daphnensis		Passeriformes: emberizid (medium ground finch)
I. dilatata	24	Passeriformes: sylviid (Eurasian blackcap, garden warbler, common whitethroat), motacillid (meadow pipit), sturnid (common starling, pied starling)
I. divitis	26 x 23	Passeriformes: icterid (Cuban blackbird)
I. elmahalensis		Passeriformes: pycnonotid (Himalayan bulbul)
I. emberizae	23 x 20	Passeriformes: emberizid (red-headed bunting)
I. erithaci		Passeriformes: turdid (European robin)
I. ernsti		Passeriformes: pycnonotid (white-spectacled bulbul)
I. exigua		Passeriformes: emberizid (small tree finch)
I. fatiguei		Passeriformes: passerid (house sparrow)
I. ficedulae	20	Passeriformes: muscicapid (European pied flycatcher)
I. formarum		Passeriformes: emberizid (slate-coloured grosbeak)
I. fragmentata		Passeriformes: emberizid (small tree finch)
I. fringillae	21	Passeriformes: fringillid (chaffinch)
I. gallicolumbae		Columbiformes: columbid (bronze ground dove)
I. gallinae	24 x 20	Galliformes: phasianid (chicken)
I. gallinarum	29 x 26	Galliformes: phasianid (chicken)
I. garrulae (garrulacis)	21 x 20	Passeriformes: leiothrichid (streaked laughing thrush)

I. garrulusae (garruli)	25 x 21	Passeriformes: corvid (Himalayan jay)
I. geospizae		Passeriformes: emberizid (medium ground finch)
I. ginginiana	23	Passeriformes: sturnid (bank myna)
I. gonnetae		Passeriformes: passerid (house sparrow)
I. graculae		Passeriformes: sturnid (hill myna)
I. gryphoni		Passeriformes: fringillid (American goldfinch)
I. gypsi	20 x 18	Falconiformes: accipitrid (white-rumped vulture)
I. heissini	29	Galliformes: phasianid (turkey)
I. hirundinis	30 x 25	Passeriformes: hirundinid (barn swallow), muscicapid (black redstart, common redstart)
I. hyloctistum		Passeriformes: furnariid (striped woodhaunter)
I. iansmithi		Passeriformes: passerid (house sparrow)
I. indonesianensis		Passeriformes: estrildid (tricoloured munia)
I. ivensae		Passeriformes: estrildid (scaly-breasted munia)
I. jacobfrenkeli		Passeriformes: passerid (house sparrow)
I. koreani		Galliformes: phasianid (common pheasant, green pheasant)
I. kouyatei		Passeriformes: passerid (house sparrow)
I. lacazei	21	Passeriformes: fringillid (goldfinch)
I. landauae		Passeriformes: muscicapid (European pied flycatcher)
I. leiothrixi		Passeriformes: sylviid (red-billed leiothrix)
I. leucogastroides		Passeriformes: estrildid (Javan munia)
I. lickfeldi	24	Passeriformes: sylviid (Eurasian blackcap, garden warbler, common whitethroat)
I. loaei		Passeriformes: estrildid (Javan munia)
I. lonchurae	25 x 22	Passeriformes: estrildid (scaly-breasted munia), sturnid (pied myna)
I. loxopis		Passeriformes: drepanidid (amakihi)
I. lusciniae		Passeriformes: turdid (common nightingale)
I. lyonensis		Passeriformes: estrildid (scaly-breasted munia)
I. lyruri	15	Galliformes: phasianid (black grouse, western capercaillie)
I. magna		Passeriformes: dendrocolapid (Amazonian barred woodcreeper)
I. malabaricae		Passeriformes: sturnid (chestnut-tailed starling)
I. malayaensis		Passeriformes: estrildid (Javan munia)
I. mandari		Anseriformes: anatid (mandarin duck)
I. manoaensis		Passeriformes: zosteropid (Japanese white-eye)
I. mayuri	23 x 21	Galliformes: phasianid (blue peafowl, green peafowl)
I. mcquistioni		Passeriformes: fringillid (grey-capped greenfinch)
I. megalaimae	24	Piciformes: capitonid (coppersmith barbet)
I. mejiro		Passeriformes: zosteropid (Japanese white-eye)
I. melopsittaci		Psittaciformes: psittacid (budgerigar)
I. michaelbakeri		Passeriformes: passerid (house sparrow)
I. mikei		Passeriformes: passerid (house sparrow)
I. miltgeni		Passeriformes: passerid (house sparrow)
I. monedulae	18	Passeriformes: corvid (western jackdaw)
I. muniae	28 x 16	Passeriformes: estrildid (tricoloured munia)
I. nancyae		Passeriformes: passerid (house sparrow)
I. nankinovi	33 x 26	Passeriformes: corvid (Eurasian jay)
I. navarroi	21	Passeriformes: thraupid (Brazilian tanager)
I. nortoni		Passeriformes: fringillid (serin)
I. nucifragae	24 x 21	Passeriformes: corvid (spotted nutcracker)
I. ocellati		Passeriformes: dendrocolapid (ocellated woodcreeper)
I. pari		Passeriformes: parid (grey-crested tit)
I. paroariae		Passeriformes: emberizid (red-crested cardinal)
I. parusae	24 x 21	Passeriformes: parid (grey crested tit)
I. parvae		Passeriformes: muscicapid (red-breasted flycatcher)
I. passeris		Passeriformes: passerid (house sparrow)
I. passerum		Passeriformes: laniid (red-backed shrike)
I. perroncitoi	20	Passeriformes: fringillid (bullfinch)
I. petrochelidon		Passeriformes: hirundinid (American cliff swallow)
I. phaeornis		Passeriformes: muscicapid (Hawaiian thrush)
I. phoenicuri	31 x 20	Passeriformes: turdid (common redstart)
I. pityli		Passeriformes: emberizid (slate-coloured grosbeak)

I. plectrophenaxia		Passeriformes: calcariid (snow bunting)
I. psittaculae	31 x 26	Psittaciformes: psittacid (Alexandrine parakeet)
I. puella		Passeriformes: irenid (Asian fairy-bluebird)
I. pycnonotus (pycnonoti, pycnonotae)	24 x 20	Passeriformes: pycnonotid (red-whiskered bulbul), leiothrichid (jungle babbler)
I. raggianae		Passeriformes: paradisaeid (Raggiana bird-of-paradise)
I. rajulii		Passeriformes: sturnid (common myna)
I. robini		Passeriformes: turdid (American robin)
I. rochalimai	24 x 20	Passeriformes: corvid (Eurasian magpie)
I. rodhaini	25 x 23	Passeriformes: corvid (carrion crow)
I. rothschildi		Passeriformes: sturnid (Bali myna)
I. rotunda		Passeriformes: emberizid (small tree finch)
I. sagittulae		Passeriformes: formicariid (spotted antbird)
I. scholtysecki		Accipitriformes: accipitrid (Eurasian sparrowhawk); Falconiformes: falconid (saker falcon, lesser kestrel)
I. schwetzi	25 x 23	Passeriformes: corvid (carrion crow)
I. sclerurii		Passeriformes: furnariid (black-tailed leaftosser)
I. seicerci (seicercusae)	25 x 23	Passeriformes: sylviid (grey-hooded warbler)
I. serini		Passeriformes: fringillid (bullfinch)
I. sittae		Passeriformes: sittid (Eurasian nuthatch)
I. solimanae		Coraciiformes: upupid (Eurasian hoopoe)
I. spratti		Passeriformes: passerid (house sparrow)
I. striata		Passeriformes: dendrocolapid (ocellated woodcreeper)
I. strigis	23 x 21	Strigiformes: strigid (short-eared owl)
I. struthionis	31	Struthioniformes: struthionid (ostrich)
I. sturniae	25	Passeriformes: sturnid (chestnut-tailed starling)
I. sylviae	30 x 27	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat)
I. sylvianthina	27 x 24	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat), motacillid (meadow pipit)
I. temenuchi	23 x 21	Passeriformes: sturnid (Brahminy starling)
I. temeraria		Passeriformes: emberizid (medium ground finch)
I. tenuis		Passeriformes: estrildid (Javan munia)
I. thibetana		Passeriformes: fringillid (Tibetan serin)
I. thraupis		Passeriformes: thraupid (palm tanager)
I. tiaris		Passeriformes: emberizid (sooty grassquit)
I. tristis	26 x 22	Passeriformes: sturnid (common myna)
I. tucuruiensis	17	Passeriformes: turdid (white-necked thrush)
I. turdi	19 x 16	Passeriformes: turdid (common blackbird, fieldfare)
I. ubique		Passeriformes: dendrocolapid (wedge-billed woodcreeper)
I. upupae	26	Coraciiformes: upupid (Eurasian hoopoe)
I. vagoi		Passeriformes: estrildid (zebra finch)
I. vanriperorum		Passeriformes: emberizid (northern cardinal)
I. volki	18 x 16	Passeriformes: paradisaeid (Lawe's parotia, brown sicklebill, superb bird-of-paradise, green manucode, greater bird-of-paradise, red-plumed bird-of-paradise, white-plumed bird-of-paradise, lesser bird-of-paradise, blue bird-of-paradise, twelve-wired bird-of-paradise, red bird-of-paradise)
I. wurmbachi	22	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat), phylloscopid (willow warbler), muscicapid (whinchat, African stonechat, European pied flycatcher), motacillid (meadow pipit)
I. xerophila		Passeriformes: ploceid (yellow-crowned bishop, southern red bishop, speckle-fronted weaver, village weaver, black-headed weaver, red-billed quelea)
I. yesi		Passeriformes: passerid (house sparrow)
I. zosteropis	20 x 16	Passeriformes: zosteropid (Oriental white-eye)
Reptilian hosts		
I. abdallahi		Sauria: lacertid (Bosc's fringe-toed lizard)
I. ablephari	26 x 25	Sauria: scincid (snake-eyed skink)
I. acanthodactyli		Sauria: lacertid (Bosc's fringe-toed lizard)
I. albogularis		Sauria: sphaerodactylid (yellow-headed gecko)
I. altiatlantis		Sauria: sphaerodactylid (atlas day gecko)

I. ameivae	19 x 16	Sauria: teiid (ameiva, rainbow whiptail)
I. amphiboluri	25 x 24	Sauria: agamid (eastern bearded dragon, inland bearded dragon)
I. ashkhabadensis [possibly *Sarcocystis*]	17 x 11	Serpentes: viperid (Levantine viper)
I. basilisci	27 x 21	Sauria: corytophanid (brown basilisk)
I. bronchocelae		Sauria: agamid (green crested lizard)
I. calotesi	28	Sauria: agamid (Oriental garden lizard)
I. camillerii	22	Sauria: scincid (ocellated skink)
I. canariensis		Sauria: phyllodactylid (Tenerife wall gecko)
I. cannoni		Sauria: agamid (Tommy roundhead dragon)
I. caryophila		Sauria: agamid (great anglehead lizard)
I. cenchoae	22 x 15	Serpentes: colubrid (blunt-headed vine snake)
I. chalchidis		Sauria: scincid (ocellated skink)
I. chamaeleolidis		Sauria: dactyloid (western bearded anole)
I. chelydrae	10 x 7	Testudines: chelydrid (common snapping turtle)
I. choochotei		Sauria: agamid (Indo-Chinese forest lizard)
I. cnemidophori	28 x 19	Sauria: teiid (rainbow ameiva, green ameiva, rainbow whiptail)
I. colubris	11 x 8	Serpentes: colubrid (western whip snake)
I. cryptoblephari		Sauria: scincid (snake-eyed skink)
I. crotali [probably *Sarcocystis*]	19 x 12	Serpentes: viperid (Gaboon viper, prairie rattlesnake), colubrid (California banded king snake)
I. decipiens		Serpentes: colubrid (South American green racer)
I. deserti		Sauria: agamid (desert agama, Afghan ground agama)
I. dipasi	15	Serpentes: colubrid (slug-eating snake)
I. diplometopon		Sauria: trogonophid (Zarudny's worm lizard)
I. dirumpens [= *Sarcocystis dirumpens*]	16 x 10	Serpentes: viperid (western rattlesnake, long-nosed viper, puff adder), colubrid (Himalayan keelback, eastern racer, western rat snake, eastern fox snake, western gopher snake, grass snake)
I. egerniae	15 x 11	Sauria: scincid (White's skink)
I. eimanae		Sauria: scincid (ocellated skink)
I. fragilis [possibly *Sarcocystis*]	21 x 15	Serpentes: viperid (European asp viper)
I. frenatus		Sauria: gekkonid (common house gecko)
I. gallotiae	17	Sauria: lacertid (Tenerife lizard)
I. gardneri		Sauria: gekkonid (stripeless day gecko)
I. gekkonis		Sauria: gekkonid (gold dust day gecko, Madagascar giant day gecko)
I. goncephali		Sauria: agamid (great anglehead lizard)
I. guarocuyai		Sauria: dactyloid (bark anole)
I. guersae	32 x 30	Serpentes: viperid (Levantine viper)
I. guzarica	18 x 13	Serpentes: colubrid (spotted desert racer)
I. gymnodactyli		Sauria: gekkonid (Turkestan thin-toed gecko)
I. hemidactyli	23	Sauria: gekkonid (tropical house gecko)
I. hendersoni		Sauria: dactyloid (Armour's anole, large-headed anole)
I. insularius		Sauria: tropidurid (Hood lava lizard)
I. jacarei	15 x 13	Crocodilia: alligatorid (broad-snouted caiman)
I. jaracimrmani		Sauria: chamaeleonid (veiled chameleon)
I. jedlickai		Sauria: teiid (common ameiva)
I. kaschcadarinica		Sauria: lacertid (Lalezhar racerunner)
I. kiamichiensis		Serpentes: colubrid (eastern coachwhip)
I. knowlesi	22	Sauria: gekkonid (yellow-belly gecko)
I. lacertae		Sauria: agamid (oriental garden lizard)
I. ladiguensis		Sauria: gekkonid (Seychelles giant day gecko)
I. laverani	12 x 10	Serpentes: colubrid (Montpellier snake)
I. lenti	13 x 10	Serpentes: viperid (jacaraca)
I. leptodeirae	23 x 19	Serpentes: colubrid (southern cat-eyed snake)
I. manchacensis		Sauria: scincid (little brown skink)
I. mesnili	30	Sauria: chamaeleonid (common chameleon)
I. minuta [possibly *Sarcocystis*]	15 x 8	Serpentes: elapid (Asian cobra)
I. muriyu		Sauria: chamaeleonid (Jackson's chameleon)
I. nagasakiensis		Sauria: lacertid (Japanese grass lizard)

I. naiae [possibly *Sarcocystis*]	17 x 9	Serpentes: elapid (Cape cobra); viperid (timber rattlesnake)
I. natricis	14	Serpentes: colubrid (common grass snake)
I. necasi		Sauria: chamaeleonid (giant one-horned chameleon)
I. neivai [*species inquirenda*]	20 x 12	Serpentes: viperid (jararaca)
I. oudrii		Sauria: phyllodactylid (Oudri's fan-footed gecko)
I. pachydactyli		Sauria: gekkonid (Bibron's sand gecko)
I. phisalixae	31 x 14	Serpentes: colubrid (four-lined snake)
I. phrynocephali	26	Sauria: agamid (sun-watcher toad-head agama)
I. platyurusi		Sauria: gekkonid (frilled house gecko)
I. ptyodactyli		Sauria: phyllodactylid (Levante fan-fingered gecko)
I. rayi	26	Sauria: agamid (green fan-throated lizard)
I. reui		Sauria: dactyloid (long-snouted anole)
I. rodriguesae	25 x 21	Testudines: testudinid (yellow-footed tortoise)
I. roudabushi [= *Sarcocystis* sp.]	20 x 12	Serpentes: colubrid (western gopher snake, eastern racer, black rat snake)
I. rustamovi		Sauria: agamid (reticulated toad-headed agama)
I. schlegeli		Sauria: gekkonid (common house gecko)
I. scinci		Sauria: scincid (five-lined skink, broadhead skink)
I. seychellensis		Sauria: scincid (Seychelles skink)
I. spilogaster		Sauria: scincid (Kalahari tree skink)
I. stenodactyli		Sauria: gekkonid (short-fingered gecko)
I. tahuayoensis		Sauria: dactyloid (slender anole)
I. testudae	26	Testudines: testudinid (Horsfield's tortoise)
I. thavari		Sauria: gekkonid (stump-toed gecko)
I. tigris		Sauria: chamaeleonid (Seychelles tiger chameleon)
I. turkmenica	*nomen nudum*	Serpentes: boid (dwarf sand boa)
I. uptoni		Sauria: gekkonid (common house gecko)
I. varani	nd	Sauria: varanid (desert monitor)
I. viridanae		Sauria: scincid (West canary skink)
I. wildi		Sauria: chamaeleonid (flap-necked chameleon)
I. wilkiei	33 x 29	Crocodilia: crocodylid (American crocodile)
I. wilsoni	17	Serpentes: colubrid (flathead snake)
I. xantusiae	26	Sauria: xantusiid (granite night lizard, desert night lizard)
Amphibian hosts		
I. brumpti	24 x 16	Anura: bufonid (European green toad)
I. cogginsi	19 x 15	Anura: hylid (western chorus frog)
I. cruzi	21 x 17	Anura: hylid (dwarf tree frog, neotropical nasal tree frog, red-snouted tree frog, Venezuela snouted tree frog)
I. delicatus	14 x 8	Anura: hylid (Strecker's chorus frog, Illinois chorus frog)
I. fragosum	19	Anura: microhylid (western narrow-mouthed toad)
I. hightoni	23	Lissamphibia: plethodontid (western slimy salamander)
I. hylae	33 x 23	Anura: hylid (European tree frog)
I. jeffersonianum	20	Urodela: ambystomatid (Jefferson salamander)
I. lieberkuehni (*species inquirenda*)	nr	Anura: ranid (edible frog, northern leopard frog, marsh frog, European grass frog)
I. neos	26 x 22	Anura: ranid (moor frog)
I. ranae (*nomen nudum*)	nr	Anura: ranid (green frog)
I. stomaticae	26 x 18	Anura: bufonid (Indian marbled toad)
I. wenyoni	18 x 12	Anura: bufonid (Asian black-spined toad, Indian cricket frog, Asian bullfrog)
I. wladimirovi	21 x 18	Anura: hylid (European tree frog)
Piscine hosts		
I. sinensis	32 x 22	freshwater Cypriniformes: cyprinid (sharpbelly)
I. lotae	26	freshwater Gadiformes: lotid (burbot)
Invertebrate hosts		
I. rara [type species]	ns	Gastropoda: limacid (land slugs)

Another 47 species have been transferred to the genus *Cystoisospora* classified in the subfamily Cystoisosporinae in the family Sarcocystidae.

***Cystoisospora* species**	**Oocyst size (µm)**	**Definitive hosts [and transport hosts]**	**Distribution**
Species in mammals (Mammalia)			
C. africana (syn. *Isospora africana*)	26	Carnivora: mustelid (Saharan striped polecat)	Africa
C. altaica (syn. *Isospora altaica*)	33 x 28	Carnivora: mustelid (mountain weasel)	Asia
C. arctopitheci (syn. *Isospora arctopitheci, I. scorzai, I. callimico, I. endocallimici, I. natalensis*)	28 x 24	Primates: callithrichid (black-tufted marmoset, Geoffroy's tamarin, red-crested tamarin, Goeldi's marmoset), cebid (white-headed capuchin, squirrel monkey), pithecid (red bald-headed uakari); hominid (human), plus experimental infections in Primates: aotid (three-striped night monkey), atelid (black-headed spider monkey, black howler monkey), cebid (squirrel monkey), galagid (Senegal bushbaby); Carnivora: canid (dog), procyonid (ring-tailed coati, kinkajou), mustelid (tayra), felid (cat); Didelphimorphia: didelphid (southern opossum) [plus tissues of experimental transport hosts Rodentia: murid (house mouse); Galliformes: phasianid (chicken)]	worldwide
C. belli (syn. *Isospora hominis p.p.*)	32 x 14	Primates: hominid (human), plus experimental infection in hylobatid (gibbon)	worldwide
C. buriatica (syn. *Isospora buriatica*)	25 x 19	Carnivora: canid (corsac fox, Bengal fox, red fox, Arctic fox)	Asia, India
C. burrowsi (syn. *Isospora burrowsi*)	20 x 17	Carnivora: canid (dog) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat)]	Europe, North America
C. canis (syn. *Isospora canis*)	38 x 30	Carnivora: canid (dog, coyote, red fox, golden jackal) [plus tissues of experimental transport hosts Rodentia: murid (house mouse), Artiodactyla: camelid (one-humped camel), bovid (sheep); Carnivora: felid (cat)]	worldwide
C. canivelocis (syn. *Isospora canivelocis*)	33 x 28	Carnivora: canid (swift fox, red fox, Artic fox)	Eurasia, North America
C. chobotari (syn. *Isospora chobotari*)	17 x 14	Carnivora: procyonid (raccoon)	North America
C. dasguptai (syn. *Isospora dasguptai*)	21 x 17	Carnivora: herpestid (Indian gray mongoose, small Asian mongoose)	India
C. dutoiti (syn. *I. dutoiti*) [possibly *Hammondia* or *Neospora*]	12 x 10	Carnivora: canid (golden jackal)	Russia
C. eversmanni (syn. *Isospora eversmanni*)	20	Carnivora: mustelid (steppe polecat, European polecat)	Asia
C. felis (syn. *Isospora felis, I. bengalensi, I. cati, I. leopardi, I. nandankani, I. pantheri, I. pardusi*)	40 x 30	Carnivora: felid (cat, jungle cat, wildcat, ocelot, serval, tiger, Bengal tiger, lion, clouded leopard, leopard, leopard cat, jaguar, lynx) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat), cricetid (golden hamster), Artiodactyla: bovid (cattle); Carnivora: canid (dog), felid (cat); Galliformes: phasianid (chicken)]	worldwide
C. frenkeli (syn. *Isospora frenkeli*)	28 x 22	Carnivora: felid (cat) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat)]	South America
C. garnhami (syn. *Isospora garnhami*)	29 x 25	Carnivora: herpestid (dwarf mongoose, long-nosed kusimanse, Indian gray mongoose)	Africa
C. gottschalki (syn. *Isospora lutrae p.p.*)	33 x 26	Carnivora: mustelid (European otter)	Europe

C. goussevi (syn. *Isospora goussevi*)	22 x 17	Carnivora: mustelid (least weasel)	
C. herpestei (syn. *Isospora herpestei*)	20 x 15	Carnivora: herpestid (small Asian mongoose, Indian gray mongoose)	India
C. hoarei (syn. *Isospora hoarei*)	17 x 15	Carnivora: herpestid (dwarf mongoose, Indian gray mongoose)	Africa
C. hoogstraali (syn. *Isospora hoogstraali*)	38 x 33	Carnivora: mustelid (Saharan striped polecat)	Africa
C. israeli	29 x 21	Carnivora: otariid (brown fur seal)	Israel
C. laidlawi (syn. *Isospora laidlawi*)	34 x 29	Carnivora: mustelid (European polecat, American mink); canid (red fox) [plus tissues of transport host Rodentia: murid (house mouse)]	Eurasia, North America
C. leonina (syn. *Isospora leonina*)	32 x 28	Carnivora: felid (lion)	India
C. levinei (syn. *Isospora levinei*)	27 x 25	Carnivora: hyaenid (striped hyena)	India
C. lutrae (syn. *Isospora lutrae*)	32 x 30	Carnivora: mustelid (European otter)	Europe
C. martessii (syn. *Isospora martessii*)	27 x 19	Carnivora: mustelid (sable)	Siberia
C. melis (syn. *Isospora melis*)	30 x 24	Carnivora: mustelid (Eurasian badger)	Europe
C. mirungae (syn. *Isospora mirungae*)	20 x 12	Carnivora: phocid (southern elephant seal)	Europe
C. mungoi (syn. *Isospora mungoi*)	34 x 27	Carnivora: herpestid (Indian gray mongoose)	India
C. neorivolta (syn. *Isospora neorivolta*)	13 x 11	Carnivora: canid (dog, coyote)	North America
C. nivalis (syn. *Isospora nivalis*)	21 x 18	Carnivora: mustelid (least weasel)	Asia
C. ohioensis (syn. *Isospora ohioensis*)	24 x 21	Carnivora: canid (dog, coyote, wolf, dingo, red fox, raccoon dog) [plus tissues of experimental transport hosts Rodentia: murid (house mouse); Carnivora: felid (cat); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (sheep)]	worldwide
C. pavlodarica (syn. *Isospora pavlodarica*)	24 x 21	Carnivora: canid (red fox, Arctic fox)	Asia
C. pavlovskyi (syn. *Isospora pavlovskyi*)	39 x 30	Carnivora: mustelid (steppe polecat)	Asia
C. pellerdyi (syn. *Isospora pellerdyi, I. knowlesi, I. dubeyi*)	28 x 23	Carnivora: herpestid (grey mongoose)	India
C. rivolta [syn. *Isospora rivolta, I. felina, I. mohini, I. novocati*]	25 x 20	Carnivora: felid (cat, wildcat, jungle cat, tiger, Bengal tiger, serval, clouded leopard, leopard, leopard cat, lion, cheetah) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat), cricetid (golden hamster), Artiodactyla: bovid (cattle), Carnivora: canid (dog), Galliformes: phasianid (chicken)]	worldwide
C. sengeri (syn. *Isospora sengeri*)	20 x 15	Carnivora: mustelid (eastern spotted skunk)	North America
C. spilogales (syn. *Isospora spilogales*)	34 x 26	Carnivora: mustelid (eastern spotted skunk)	North America
C. suis (syn. *Isospora suis*)	23 x 18	Artiodactyla: suid (pig)	worldwide
C. theileri (syn. *Isospora theileri*) [possibly *Sarcocystis*]	21 x 18	Carnivora: canid (golden jackal)	Russia
C. timoni	26 x 25	Carnivora: herpestid (slender-tailed meerkat)	Africa
C. triffitti	12 x 11	Carnivora: canid (Arctic fox, red fox)	Asia

(syn. *Isospora triffitti*) [possibly *Hammondia* or *Neospora*?]			
C. ursi (syn. *Isospora ursi*)	37 x 25	Carnivora: ursid (sloth bear)	India
C. viverrae (syn. *Isospora viverrae*)	23 x 19	Carnivora: viverrid (African civet)	Africa
C. viverrina (syn. *Isospora viverrina*)	32 x 27	Carnivora: felid (fishing cat)	India
C. vulpina (syn. *Isospora vulpina*)	25 x 21	Carnivora: canid (red fox, Bengal fox, Arctic fox, dog), plus experimental infection in tissues of Rodentia: murid (house mouse)	Europe, North America
C. zorillae (syn. *Isospora zorillae*)	12 x 10	Carnivora: mustelid (Saharan striped polecat)	Africa

Parasite morphology: Coccidian parasites form three developmental stages: schizonts (meronts), gamonts and oocysts. Schizonts first appear as small basophilic rounded cells (mother meronts) located intracellularly within host cells. The meronts form numerous daughter merozoites by endogenous division of the nucleus followed by cytokinesis. Mature schizonts range in diameter from 10-50 µm and appear as membrane-bound clusters of small basophilic bodies (similar to bunches of grapes). Gamonts exhibit sexual differentiation, with microgamonts (male) apparent as multinucleate basophilic stages ultimately shedding small biflagellated microgametes; and macrogamonts (female) evident as uninucleate eosinophilic cells with a single ovoid nucleus. Developing oocysts contain numerous eosinophilic wall-forming bodies which give rise to the tough outer oocyst walls. Unsporulated oocysts contain a developing sporoblast which eventually undergoes sporulation forming sporocysts which contain the infective sporozoites. Isosporid oocysts exhibit a characteristic 1:2:4 configuration, that is, each oocyst contains 2 sporocysts each containing 4 sporozoites. Oocysts are generally ovoid to ellipsoid in shape, range from 10-40 µm in length by 10-30 µm in width, and vary in their possession of specialized structures, such as oocyst spines, projections, micropyles, micropyle caps, residua, polar granules, sporocyst sporopodia, ridges, sutures, residua, Stieda bodies, sub-Stieda or para-Stieda bodies, sporozoite nuclei, refractile bodies and striations.

Site of infection: Parasites undergo merogony and gamogony in the small intestinal mucosa, located intracellularly within the cytoplasm of epithelial cells (although some reptilian species exhibit intranuclear development). They undergo several cycles of schizogony, each culminating in host cell lysis releasing merozoites. Ultimately, gamonts are formed which mature to produce micro- and macro-gametes that undergo fertilization forming a non-motile zygote (oocyst) which is excreted with host faeces. The monozoic cysts of *Cystoisospora* spp. are thought to be encysted sporozoites (cystozoites) located within host cells (mainly in lymphoid tissue of rodent hosts). These zoites do not undergo further development or multiplication, so their rodent hosts are considered to be paratenic (transport) hosts rather than intermediate hosts. The zoites are infective to definitive carnivorous hosts when they feed on rodent host tissues. *Atoxoplasma* infections in birds may also involve extraintestinal stages in various host tissues and in mononuclear cells.

Pathogenesis: Most enteric species are only mildly pathogenic but can cause transient diarrhoea, colic, weight loss and fever. When mature, endogenous developmental stages of the parasite lyse their host epithelial cells lining small intestinal villi, producing villous atrophy, crypt hypertrophy, inflammation, malabsorption and sometimes petechial haemorrhages. There is substantial epidemiological evidence that the severity of infections may be exacerbated by concomitant viral disease or other immunosuppressive agents. Young animals (puppies, kittens, piglets, etc.) are most susceptible to disease but develop a strong specific protective immunity thereafter. Some species in birds may cause disseminated infections which have been associated with severe disease and death. Atoxoplasmosis is a chronic wasting disease of passerine birds, especially captive canaries and finches, and is unusual in that extra-intestinal stages (merozoites) may disseminate within the host in blood cells (mostly lymphocytes).

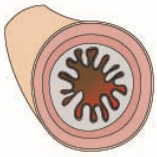
Developmental cycle and mode of transmission: Infections are passed between hosts by the faecal-oral transmission of infective oocysts contaminating the external environment, including food and water supplies. Oocysts are excreted unsporulated from definitive hosts and undergo exogenous sporulation over several days in the external environment. Following ingestion by susceptible hosts, the oocysts and sporocysts excyst in the intestines releasing their contained sporozoites which invade host cells and undergo merogony and gamogony. *Cystoisospora* spp. are also thought to also utilize predator-prey transmission when dormant stages (cystozoites) in paratenic hosts (e.g. rodents) are ingested by carnivorous definitive hosts.

Differential diagnosis: Although clinical signs generally coincide with parasite patency (period during which oocysts are produced), longitudinal samples should be examined whenever possible as asexual developmental stages of virulent species may cause gut damage before oocyst formation. Infections are usually diagnosed by the coprological examination of host faeces for coccidial oocysts (concentrated using various sedimentation-flotation techniques). *Cystoisospora* and *Isospora* species form medium-sized oocysts (20-50 μm) whereas *Sarcocystis, Toxoplasma, Hammondia* and *Neospora* species form smaller oocysts (10-15 μm). Faeces from carnivores can also be pretreated with ether/chloroform to remove fatty material. Unstained oocysts are best observed by light microscopy using suboptimal transmitted illumination (condenser wound down to introduce diffraction), phase-contrast or interference-contrast optics. Alternatively, oocysts can be stained with Giemsa or acid-fast stains of dried smears or with fluorescence dyes (auramine-rhodamine) in wet preparations. Fresh faecal samples may only contain unsporulated oocysts so differential specific diagnosis may sometime require short-term storage to facilitate sporulation (2% potassium dichromate is often used to suppress microflora during storage, and refrigeration can slow the process down if required for field samples).

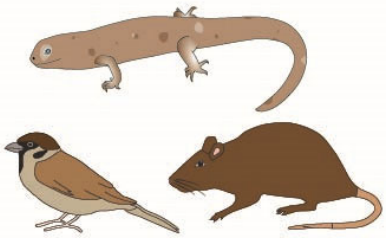
Treatment and control: Coccidiostatic drugs, particularly toltrazuril and sulfonamides (trimethoprim-sulfamethoxazole), are effective for therapeutic use, acting against endogenous developmental stages to limit infections. However, commencement of treatment when oocysts are being voided is not often followed by rapid resolution of clinical signs as the damage has already been done and the drug has been used too late in the course of infection. Control measures include good sanitation, proper effluent disposal, isolation of infected individuals and avoiding crowding, particularly in intensive husbandry situations, breeding establishments, kennels and rescue centres. Oocysts passed in faeces take several days to sporulate and become infectious, so the judicious daily removal of waste from animal containment facilities has great effect in reducing contamination. Conventional disinfectants (bleaches and detergents) are ineffective against coccidian oocysts, although some ammonia-based products and steam-cleaning have been shown to kill infective oocysts. Nevertheless, the process of cleaning aids decontamination by removing oocysts from holding facilities. Vermin should be excluded from kennels, and carnivores should be discouraged from hunting and scavenging.

Isospora

monoxenous
(1-host)
cycle



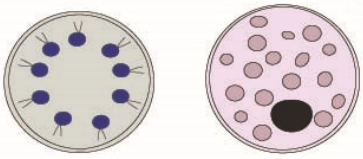
intestines
(malabsorption,
diarrhoea)



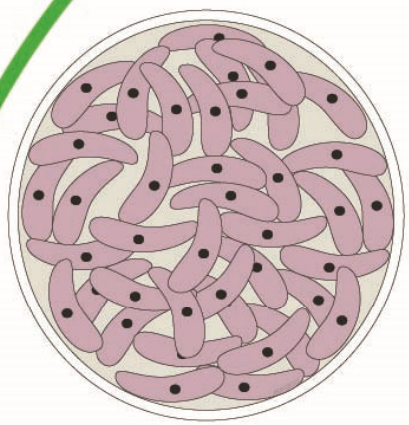
Definitive Hosts
(mammals, birds,
reptiles)

asexual merogony
(several cycles)

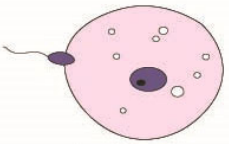
sexual
gamogony



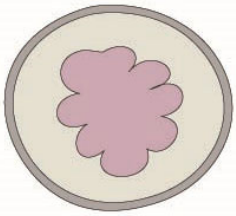
male female
gamonts (5-20 µm)



meronts
(10-50 µm)



fertilization



sporoblast

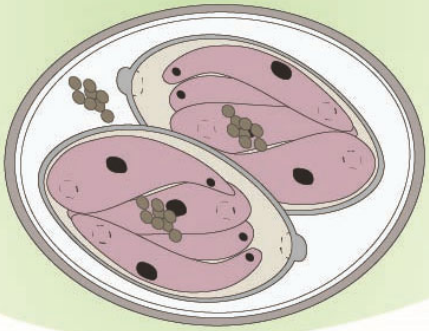
excystation
(sporozoites
released)

ingested

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

excreted

oocyst
(10-40 µm)



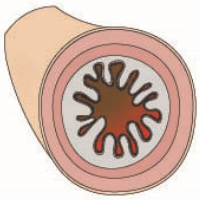
sporocysts with
Stieda bodies

exogenous
sporulation

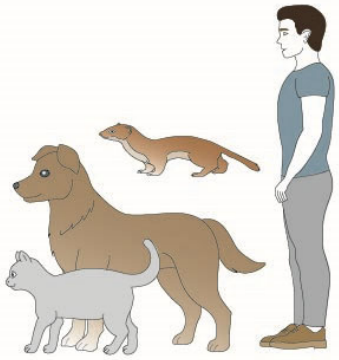
faecal-oral transmission via oocysts
contaminating environment (soil, water, food)

Cystoisospora

monoxenous (1-host) cycle
(sometimes heteroxenous
involving another host))



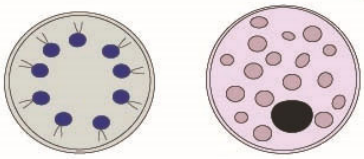
intestines
(malabsorption,
diarrhoea)



Definitive Hosts
(mammals, mainly
carnivores)

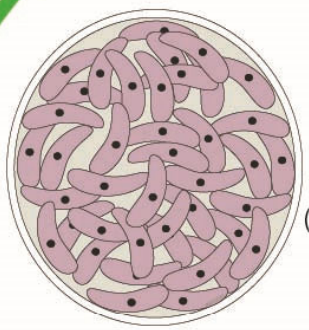
asexual
merogony
(several
cycles)

sexual
gamogony

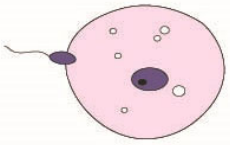


male gamonts (5-20 µm)

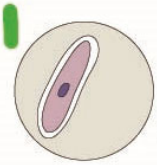
female



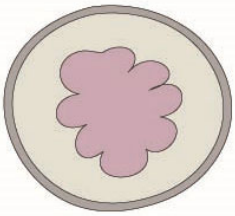
meronts
(10-50 µm)



fertilization



encysted
sporozoite
(cystozoite)



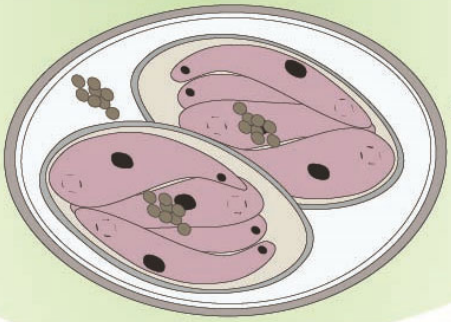
sporoblast

excystation
(sporozoites
released)

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

ingested

excreted



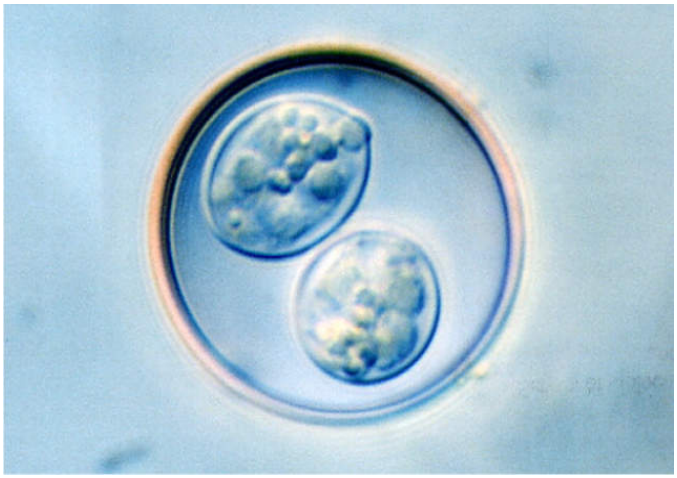
oocyst
(10-40 µm)

sporocysts lack
Stieda bodies

exogenous
sporulation

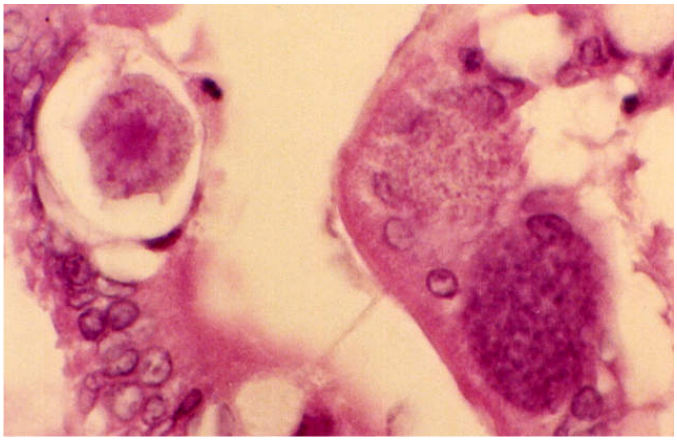
Paratenic Hosts (mainly rodents)
(some predator-prey transmission
involving encysted sporozoites
('cystozoites') in prey tissues)

mainly faecal-oral transmission via oocysts
contaminating environment (soil, water, food)



Isospora oocyst from lizard faeces

Isospora oocyst from bird faeces



Cystoisospora gamonts in dog gut