

## *Caryospora*

(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). *Caryospora* are eimeriid coccidia that were initially thought to be monoxenous (1-host) parasites where merogony (= schizogony), gamogony and sporogony occurred in the digestive tracts of raptorial birds or snakes (definitive hosts). However, recent studies have shown that parasites may undergo complete development in rodent secondary hosts with thin-walled oocysts excysting *in situ* releasing sporozoites which become dormant in monozygic cysts (caryocysts) being infective to new secondary or primary hosts. Mature *Caryospora* oocysts contain a single sporocyst with 8 sporozoites (1:1:8 configuration). Most infections are asymptomatic.

### 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 [Coccidiasida] (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: *Caryospora* (parasitic in gut/tissues of birds/reptiles/mammals)

Species: various species cause enteritis 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 endogony (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

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

Higher taxonomy	Family	Genera	Hosts	Site	Transmission*
Class: Gregarinomorpha (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	<i>Cryptosporidium</i>	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorpha [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	<i>Haemogregarina</i>	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		<i>Hepatozoon</i>	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	<i>Klossiella</i>	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	<i>Caryospora</i>	birds, reptiles	gut	direct (f-o)
		<i>Cyclospora</i>	mammals, reptiles	gut	direct (f-o)
		<i>Isospora</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 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 genus *Caryospora* forms oocysts with a 1:1:8 configuration; that is, oocysts are monosporocystic (contain 1 sporocyst) and each sporocyst is octosporozoic (contains 8 sporozoites).

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

Over 70 *Caryospora* spp. have been described from reptiles (predominantly snakes) and birds (predominantly raptors). The parasites undergo asexual and sexual reproduction in intestinal epithelial cells, culminating in the excretion of oocysts into the external environment. The life-cycle is therefore deemed to be monoxenous (one-host) with transmission to new susceptible hosts occurring when they ingest oocysts. However, several *Caryospora* spp. have also been found to have heteroxenous (2-host) life-cycles involving caryocyst formation in secondary hosts, particularly rodent prey for predatory reptiles and birds. Oocysts ingested by rodents excyst releasing sporozoites which migrate to extra-intestinal tissues (usually skin) where they lead to the formation of dormant caryocysts until ingested by new hosts. Extraintestinal development involving merogony, gamogony and sporogony has also occasionally been observed in companion animals (dogs and cats) in association with disfiguring nodular dermatitis.

<i>Caryospora</i> species	Oocyst size (µm)	Hosts	Distribution
Species in snakes (Serpentes)			
<i>C. ahaetullae</i>	25	colubrid (long-nosed whip snake, Oriental whip snake)	South Asia
<i>C. barnardae</i>	14	colubrid (Malagasy colubrid)	Madagascar
<i>C. bengalensis</i>	22	colubrid (rainbow water snake)	India
<i>C. bigenetica</i>	13	viperid (timber rattlesnake, eastern diamondback rattlesnake, western diamondback rattlesnake, pygmy rattlesnake, massasauga, copperhead); plus heteroxenous cycle involving Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (goat), suid (pig); Rodentia: murid (house mouse, Mongolian gerbil), cricetid (common vole, hispid cotton rat)	North America, Europe
<i>C. bothriechis</i>		viperid (yellow-blotched palm pit viper)	Central America
<i>C. brasiliensis</i>	22 x 21	colubrid (Brazilian green racer, Mboi-obi, Nuazo, culebra)	South America
<i>C. brygooi</i>	20	colubrid (Madagascar cat-eye snake)	Madagascar
<i>C. carajasensis</i>	23 x 22	colubrid (false coral snake)	South America
<i>C. choctawensis</i>		colubrid (flathead snake)	North America
<i>C. cobrae</i>	19 x 17	elapid (Indian cobra)	India
<i>C. colubris</i>	24	colubrid (dwarf colubrid, horseshoe snake, large whip snake,	Europe

		western whip snake)	
<i>C. coniophanis</i>	19 x 18	colubrid (black striped snake)	Central America
<i>C. conophae</i>	20	colubrid (road guarder snake)	Central America
<i>C. constanciae</i>	21 x 19	elapid (Amazonian coral snake)	South America
<i>C. corallae</i>	22	boid (emerald tree boa)	South America
<i>C. demansiae</i>	20	elapid (yellow-faced whip snake)	Australia
<i>C. dendrelaphis</i>	21 x 20	colubrid (common tree snake)	Australia
<i>C. durrelli</i>	19 x 18	boid (Round Island boa)	Mauritius
<i>C. duszynskii</i>	26 x 24	colubrid (corn snake, red corn snake, Texas rat snake, black rat snake, prairie kingsnake)	North America
<i>C. epicratesi</i>	23 x 21	boid (Brazilian rainbow boa)	South America
<i>C. gracilis</i>	24 x 23	colubrid (flat headed snake)	North America
<i>C. guatemalensis</i>	24 x 23	colubrid (scarlet kingsnake)	Central America
<i>C. hermae</i>	22 x 21	colubrid (western striped sand snake)	Africa
<i>C. heterodermus</i>	20	colubrid (variable green snake)	Africa
<i>C. japonicum</i>	19	colubrid (tiger keelback)	Asia
<i>C. jararacae</i>	14	viperid (coffee palm viper, fer-de-lance, jararaca)	South America
<i>C. kalimantanensis</i>	15 x 11	colubrid (mangrove snake)	Malaysia
<i>C. lampropeltis</i>	23	colubrid (prairie kingsnake, desert kingsnake, red milk snake)	North America
<i>C. legeri</i>	30 x 26	colubrid (striped sand snake)	Africa
<i>C. maculatus</i>	12	viperid (spotted night adder)	Africa
<i>C. madagascariensis</i>	26 x 24	colubrid (Madagascar cat-eye snake, Malagasy colubrid)	Madagascar
<i>C. masticophis</i>	14 x 13	colubrid (eastern coachwhip, southern black racer)	North America
<i>C. matatu</i>	20	viperid (horned bush viper)	Africa
<i>C. maxima</i>	43 x 42	colubrid (Forskal's sand snake)	Middle-East
<i>C. mayorum</i>	26 x 24	colubrid (road guarder snake)	Central America
<i>C. micruri</i>	16	elapid (Amazonian coral snake)	South America
<i>C. minuta</i>	12	colubrid (Madagascar hognose snake)	Madagascar
<i>C. najadae</i>	21 x 15	colubrid (Dahl's whip snake)	Middle-East
<i>C. najae</i>	15	elapid (red spitting cobra)	Africa
<i>C. paraensis</i>	17	colubrid (false coral snake)	South America
<i>C. peruensis</i>	29 x 26	colubrid (Argentine vine snake)	South America
<i>C. psammophi</i>	29 x 27	colubrid (western striped sand snake)	Africa
<i>C. pseustesii</i>	26 x 25	colubrid (yellow bellied puffing snake)	South America
<i>C. regentensis</i>	17 x 16	elapid (eastern green mamba, western green mamba)	Africa
<i>C. relictiae</i>	19 x 18	colubrid (Florida crowned snake)	North America
<i>C. saudiarabiensis</i>	43 x 41	viperid (African carpet viper)	Africa
<i>C. serpentis</i>	17	colubrid (Madagascar hognose snake, Madagascar cat-eye snake, Madagascar colubrid)	Madagascar
<i>C. simplex</i>	15	viperid (European asp viper, Russell's viper, nose-horned viper, northern viper, Kaznakov's viper, Palestine viper, Ottoman viper); plus heteroxenous cycle involving Artiodactyla: bovid (goat); Rodentia: murid (house mouse), cricetid (hispid cotton rat)	Europe, North America
<i>C. tantillae</i>	20 x 19	colubrid (Florida crowned snake)	North America
<i>C. telescopus</i>	15 x 11	colubrid (European cat snake)	Europe
<i>C. veselyi</i>	19	colubrid (long nosed whip snake)	India
<i>C. weyerdae</i>	16 x 15	colubrid (western striped sand snake)	Africa
<i>C. zuckermanae</i>	17	colubrid (spotted whip snake)	Eurasia
<i>C. zacapensis</i>	23 x 22	colubrid (neotropical whip snake)	Central America
Species in lizards (Sauria)			
<i>C. ernsti</i>		dactyloid (Carolina anole)	North America
<i>C. gekkonis</i>	20	gekkonid (Tokay gecko)	India
<i>C. varani</i> <i>nomen dubium</i>		varanid (ornate monitor)	Africa
Species in turtles (Testudines)			
<i>C. cheloniae</i>	33.8-40.1 x 11-14.6	cheloniid (green sea turtle)	Australia, Caribbean
Species in birds (Aves)			
<i>C. aquilae</i>		Accipitriformes: accipitrid (golden eagle)	Holarctic
<i>C. arcayae</i>		Accipitriformes: accipitrid (roadside hawk, broad winged hawk)	Americas
<i>C. argentati</i>	20 x 17	Charadriiformes: larid (European herring gull)	Europe

<i>C. biarmicusis</i>		Falconiformes: falconid (lanner falcon)	Africa, Eurasia
<i>C. boeri</i>		Falconiformes: falconid (Eurasian kestrel)	Europe
<i>C. bubonis</i>		Strigiformes: strigid (great horned owl) plus heteroxenous cycle involving Rodentia: murid (mouse)	Americas
<i>C. circi</i>		Accipitriformes: accipitrid (western marsh harrier)	Eurasia
<i>C. falconis</i>	33	Falconiformes: falconid (peregrine falcon, Eurasian hobby, European kestrel)	Eurasia
<i>C. gloriae</i>	32 x 28	Passeriformes: icterid (Cuban blackbird)	Cuba
<i>C. henryae</i>	39 x 32	Strigiformes: strigid (Eurasian eagle-owl); Accipitriformes: cathartid (turkey buzzard), accipitrid (black kite), Falconiformes: falconid (kestrel, hobby)	cosmopolitan
<i>C. jiroveci</i>		Passeriformes: muscicapid (European robin)	Palaearctic
<i>C. kansasensis</i>		Accipitriformes: accipitrid (Swainson's hawk)	North America
<i>C. kutzeri</i> (syn. <i>C. falconis</i> p.p., <i>henryi</i> p.p.)		Falconiformes: falconid (lanner falcon, Saker falcon, Laggar falcon, prairie falcon, peregrine falcon, gyrfalcon, Eurasian hobby, European kestrel)	Eurasia, Americas
<i>C. lindsayi</i>		Accipitriformes: accipitrid (red tailed hawk)	North America
<i>C. megafalconis</i>		Falconiformes: falconid (Saker falcon, gyrfalcon, Eurasian falcon)	Europe
<i>C. neofalconis</i>		Falconiformes: falconid (lanner falcon, prairie falcon, peregrine falcon, Eurasian hobby, European kestrel)	Eurasia, Americas
<i>C. strigis</i>		Strigiformes: tytonid (barn owl)	cosmopolitan
<i>C. tremula</i>		Accipitriformes: cathartid (turkey vulture)	Americas
<i>C. undata</i>	33 x 29	Charadriiformes: larid (European herring gull), alcid (tufted puffin, common murre)	Holarctic
<i>C. uptoni</i>		Accipitriformes: accipitrid (red tailed hawk)	North America
Species in mammals (Mammalia)			
<i>C. microti</i> <i>nomen dubium</i>	10 x 9	Rodentia: cricetid (meadow mouse)	North America

**Parasite morphology:** *Caryospora* spp. form 3 different types of sequential developmental stages (meronts, gamonts, and oocysts) in host cells, but some species may occasionally form a fourth stage (caryocysts) in certain hosts. Meronts (schizonts) appear as basophilic bodies located within parasitophorous vacuoles in host cells. They range in size (5-20 x 4-10 µm) and divide internally to form up to 25 merozoites. The merozoites are tightly packed in some meronts or loosely packed in other, occasionally being radially arranged in a wheel-spoke configuration around a central eosinophilic body. The merozoites were larger in some meronts than others (4 x 1.6 cf. 2.4 x 1.2 µm), suggesting the occurrence of 2 meront generations or asynchronous development or overlapping infections (most natural infections contained mixtures of the different types of meronts). Gamonts were also located in parasitophorous vacuoles in host cells, and they exhibited sexual differentiation into macrogametocytes (female) and microgametocytes (male), the former being more plentiful than the latter. Macrogametocytes were elongate ellipsoidal stages (10-37 x 9-14 µm) aligned along the long axis of the host cell. They were bound by a thin wall and contained fine eosinophilic granular cytoplasmic reticulum, a small round central eosinophilic nucleus with a basophilic nucleolus, and they become heavily vacuolated as they matured to uninucleate macrogametes. Microgametocytes were oval-round stages (10-43 x 9-27 µm) that often displaced the host cell nucleus laterally. They were bound by a thin wall and became multinucleated as they developed numerous (> 20) basophilic rod-like microgametes (1-4 µm long) that were biflagellated. Gamete fertilization produced non-motile zygotes that commenced oocyst formation by producing thick membranous oocyst walls. Developing oocysts contained a central sporoblast that produced a single sporocyst enclosed by membranous sporocyst walls. Each sporocyst formed 8 vermiform sporozoites with central nuclei and posterior refractile bodies. The resultant oocyst:sporocyst:sporozoite configuration was 1:1:8, which is considered to be characteristic for the genus *Caryospora*. Mature oocysts were spherical-ovoid in shape, lacked micropyles and residual bodies, and ranged in diameter from 10-43 µm depending on the parasite species. The sporocysts were subspherical-ovoid in shape, ranged in diameter from 8-35 µm, possessed a residual body, and those of most species contained a Stieda body evident as a prominent anterior dome. The sporozoites varied considerably in size (4-20 x 1-12 µm) and shape, with those of some species being short and stubby, and those of other species being long and slender, sometimes crescentic. Merogony, gamogony and oocyst formation have also been reported in some mammalian hosts, but the oocysts were thin-walled and only produced a few sporozoites which became encysted in host tissues. These so-called caryocysts appeared as small rounded stages (10-18 x 10-16 µm) within parasitophorous vacuoles in macrophages and connective tissue cells, and they usually contained one (sometimes 2 or 3) robust sporozoites (4-6 x 2-3 µm).

**Site of infection:** Infections are commonly found in the digestive tracts of reptiles and birds, with 54 parasite species reported in snakes (colubrids, elapids, viperids, boids), 2-3 species in lizards, one in turtles, and 20 species in birds, mostly birds of prey (Accipitriformes, Falconiformes and Strigiformes) but also some Charadriiformes (gulls, puffins) and Passeriformes (robins). These hosts are considered to be primary (predatory) hosts in which parasites completed asexual proliferation and sexual reproduction culminating in the excretion of oocysts. Natural and experimental infections have also been detected in extraintestinal tissues

(usually dermal tissues) in various mammals, usually small rodents which are normally prey for predatory reptiles or birds, but sometimes in carnivores (dogs, cats) and experimentally in ungulates (pigs, goats). These hosts are considered to be secondary (prey) hosts (and not intermediate or paratenic hosts) as the parasites complete both asexual and sexual development, culminating in the formation of dormant sporozoites (caryocysts) in host tissues.

**Pathogenesis:** Even though parasite developmental stages infect and lyse host enterocytes in primary hosts, most infections are asymptomatic as the cumulative damage was not severe enough to cause disease. Heavy infections by some species, however, may cause enough damage to manifest in disease (coccidiosis), with focal haemorrhagic lesions, epithelial hyperplasia and inflammation (enteritis) producing clinical signs, including diarrhoea, regurgitation, reduced appetite, weight loss, depression, and even acute death. Clinical infections have been reported primarily in birds, and occasionally in reptiles (especially green turtles). Natural infections have also been reported in secondary hosts, including rodents (rats, mice) and carnivores (dogs, cats), and experimental infections in ungulates (pigs, goats). Some of the infections in dogs and cats have been associated with an unusual clinical disease involving progressive pyogranulomatous dermatitis, panniculitis (inflammation of subcutaneous fat), oedema, and perivascular to interstitial infiltrates of neutrophils and macrophages that coalesce into papules and nodules. Parasite developmental stages found within lesions included meronts, gamonts, unsporulated and sporulated thin-walled oocysts and caryocysts.

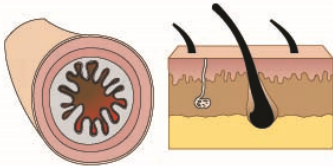
**Developmental cycle and mode of transmission:** *Caryospora* spp. are eimeriid coccidia that were initially thought to only have monoxenous (one-host) life-cycles where merogony, gamogony and sporogony occurred in the digestive tracts of primary hosts (raptorial birds, snakes). Over 1-2 weeks, parasites underwent asexual proliferation followed by sexual reproduction in host enterocytes, leading to the formation of thick-walled oocysts that were excreted in host faeces. Sporulation was often (but not always) completed exogenously when sporocysts formed numerous infective sporozoites. The prepatent period (time from infection to first oocyst excretion) ranged from 8-13 days, and the patent period (duration of oocyst excretion) ranged from 9-18 days, sometimes longer. Transfer between hosts was direct and accomplished by the faecal-oral transmission of oocysts shed in faeces contaminating food and water supplies to be ingested by new hosts. Some *Caryospora* species, however, were also found to have facultatively or obligatory heteroxenous (2-host) life-cycles involving mammalian prey animals (usually rodents) as alternate hosts. By definition, these hosts were not paratenic (transport) hosts as parasites developed further in their tissues, and they were not intermediate hosts as the parasites completed both asexual and sexual development. They have therefore frequently been referred to as secondary (prey) hosts. Parasite development typically took place in extraintestinal sites (usually the skin) resulting in the production of thin-walled oocysts which underwent endogenous sporulation forming small numbers of sporozoites. Oocyst excystation occurred *in situ* releasing small robust sporozoites which became dormant in host tissues as caryocysts. The caryocysts were found to be infective to new secondary or primary hosts, with transmission occurring via predation.

**Differential diagnosis:** Infections are usually detected by the coprological examination of faecal concentrates (sediments, floats) for the presence of distinctive oocysts. Endogenous developmental stages are usually detected at post-mortem by the microscopic examination of histological sections, sometimes aided by immunolabelling with antiserum conjugated to fluorochrome or enzyme tags. Molecular biological techniques have been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) or mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

**Treatment and control:** There have been several attempts to treat natural infections in birds and reptiles, with the application of sulphonamides (sulfadimidine), thiamine analogues (amprolium), nitroimidazoles (metronidazole) and triazinones (toltrazuril, ponazuril) producing reasonable results, although some treatments produced adverse side-effects requiring supportive therapy or dietary supplementation. Dogs and cats with disfiguring nodular dermatitis have been successfully treated with combinations of trimethoprim-sulfamethoxazole or pyrimethamine and clindamycin with the resolution of lesions within 6 weeks (although some animals relapsed following the discontinuation of treatment). Various preventive strategies have been recommended to break both faecal-oral and predator-prey transmission cycles, including regular health surveillance to detect infected individuals for treatment, quarantine or culling, better sanitation to reduce faecal oocyst contamination, improved hygiene to disinfect holding facilities, rodent control to prevent the ingress of wildlife into colonies, and curbing the hunting/scavenging behaviours of pets and captive predators.

# Caryospora

monoxenous (1-host) cycle  
[sometimes heteroxenous involving secondary host]

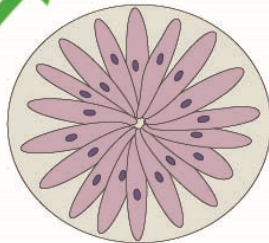


gut, skin  
(enteritis, lesions,  
nodular dermatitis)



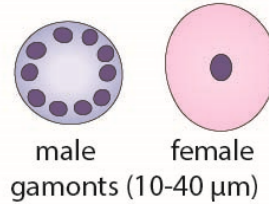
Definitive Hosts  
(birds, reptiles,  
some mammals)

asexual merogony  
(several cycles)

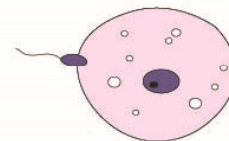


meront  
(5-20 μm)

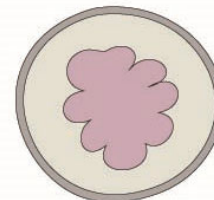
sexual  
gamogony



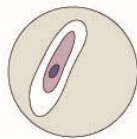
male female  
gamonts (10-40 μm)



fertilization



sporoblast



monozytic  
caryocyst  
(10-18 μm)



excystation  
(sporozoites  
released)

ingested

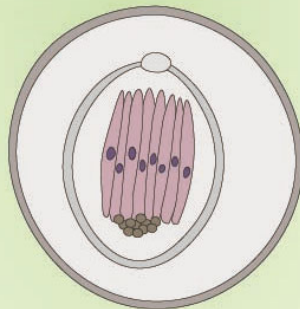
oocyst:sporocyst:sporozoite  
configuration = 1:1:8

excreted



Secondary Hosts  
(some species infect  
small prey (rodents)  
producing thin-walled  
oocysts which release  
sporozoites that encyst  
(as caryocysts) in skin and  
are infective to predators)

oocyst  
(10-43 μm)



sporocyst  
(8-35 μm)

exogenous  
sporulation

mostly direct transmission via ingestion of thick-walled oocysts  
contaminating environment (soil, water, food)



*Caryospora* oocysts in snake faeces