Goussia (fish coccidia)
(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 environmentally-resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). The enteric coccidia are monoxenous (one-host) parasites in the digestive tracts of vertebrates. They undergo three sequential developmental stages: endogenous multiplication by asexual merogony (alternatively known as schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which are excreted and undergo asexual sporogony (forming sporocysts containing infective sporozoites). Many genera are recognized on the basis of oocyst configuration (the number of sporocysts per oocyst, and the number of sporozoites per sporocyst). Eimeriid oocysts typically contain four sporocysts each with two sporozoites (1:4:2 configuration). Infections are prevalent in birds (esp. fowl), reptiles (snakes and lizards), mammals (esp. ruminants) and fish. Many species in several genera (esp. *Goussia*) have been associated with clinical disease (coccidiosis) in fish characterized by gastrointestinal disturbances and extraintestinal tissue 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:	*Goussia* (parasitic in the intestinal mucosa of fish)
Species:	various species cause coccidiosis in fish

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 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 and 3 genera in the family Barrouxiidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genera *Epieimeria* and *Goussia* form oocysts with a 1:4:2 configuration; that is, oocysts are tetrasporocystic (contain 4 sporocysts) and each sporocyst is disporozoic (contains 2 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
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8 (SB-)
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2 (SB+)
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4 (SB+)
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 (SB+)
Epieimeria	5	monoxenous	vertebrates (fish)	1:4:2 (SB+)
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
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4
Family: Barrouxiidae				
Barrouxia	10	monoxenous	invertebrates (arthropods, molluscs)	1:n:1
Crystallospora	1	monoxenous	vertebrates (fish)	1:4:2 (SB-)
Goussia	94	monoxenous	vertebrates (fish, amphibians, reptiles)	1:4:2 (SB-)
Family: Calyptosporiidae				
Calyptospora	5	heteroxenous	vertebrates (fish), invertebrate IH (shrimp)	1:4:2 (SB-)

Some 190 species of fish coccidia have been described in freshwater and marine fish throughout the world but little experimental information is available on their actual host or tissue specificity other than that accompanying clinical records. Numerous *Eimeria* species have been described from fish, with merogony, gamogony and sporogony occurring within host epithelial cells mainly in the intestines but sometimes in the gall bladder, swim bladder, liver or kidney. The genus *Goussia* was erected for unique enteric coccidian species in fish and amphibians which form oocysts with 4 sporocysts whose walls are composed of 2 valves joined by a longitudinal suture. In some species, the suture is associated with a membranous structure but it is delicate and often difficult to observe. Developmental stages are located intracellularly in parasitophorous vacuoles (sometimes deemed extracytoplasmic) which initially have monopodial points of contact with the host cell membrane and later having polypodial (spider-like) points of contact. The genus currently contains some 94 species which occur mainly in fish (freshwater and marine species) as well as a few non-piscine hosts (amphibians, geckos and insects). Most species have monoxenous/homoxenous (one-host) life-cycles, although a few apparently have heteroxenous (2-host) cycles involving tubificid worms as secondary (intermediate or paratenic) hosts.

Goussia species	Oocyst size (µm)	Hosts	Location	Distribution
Species in piscine hosts				
G. acipenseris	10 x 8	freshwater Acipenseriformes: acipenserid (starlet)	intestines, pyloric caeca	Hungary
G. aculeati (syn. *Eimeria*)	14.5 x 11	marine Gasterosteiformes: gasterosteid (three-spined (stickleback)	intestines	Europe
G. alburni (syn. *Eimeria*)	20	freshwater Cypriniformes: cyprinid (gudgeon, roach, rudd)	intestines	Europe
G. anopli	8-9	freshwater Cypriniformes: cyprinid (chubbyhead barb)	foregut	Africa

G. arinae	17.5 x 12.5	freshwater Cypriniformes: cyprinid (sabre carp)	faeces	Russia
G. arrawarra	14.3-15.1 x 10.1-10.9	marine Perciformes: sillaginid (sand whiting)	intestines	Australia
G. aurati (syn. *Eimeria*)	20 x 16	freshwater Cypriniformes: cyprinid (goldfish)	intestines	USA
G. auxidis (syn. *Eimeria*)	17-37	marine Scombriformes: scombrid (bullet tuna, albacore, slender tuna, skipjack tuna, yellowfin tuna, blue mackerel); Beloniformes: scomberesocid (Pacific saury)	kidney, liver, spleen	Pacific
G. balatonica	22 x 14	freshwater Cypriniformes: cyprinid (white bream)	intestines	Europe
G. bayae	22-30 x 18-25	freshwater Moroniformes: moronid (white perch)	liver, gallbladder	Atlantic
G. bettae	7.5-8.5	freshwater Anabantiformes: osphronemid (Siamese fighting fish)	foregut	Asia
G. bigemina (syn. *Eimeria*)	28	marine Trachiniformes: ammodytid (lesser sand eel)	intestines	Atlantic
G. biwaensis	8-9	freshwater Cypriniformes: cyprinid (pike gudgeon)	foregut	Japan
G. bohemica	15 x 13	freshwater Cypriniformes: cyprinid (gudgeon)	intestines	Europe
G. callinani (syn. *Eimeria*)	8.4-9.2	freshwater Gobiiformes: eleotrid (empire gudgeon)	intestines	Australia
G. carassici (syn. *Eimeria*)	18	freshwater Cypriniformes: cyprinid (goldfish)	intestines	Asia
G. carpelli (syn. *Eimeria cyprini*)	10	freshwater Cypriniformes: cyprinid (common bleak, bighead carp, European carp, Crucian carp, silver carp, common barbel, goldfish, gudgeon, sunbleak, Marmara chub, common dace, Eurasian minnow, stone moroko, common roach, tench); Scorpaeniformes: abyssocottid (Herzenstein's rough sculpin, Vitim sculpin), cottocomephorid (bighead sculpin, Kessler's sculpin) [plus indirect transmission via sporozoites in Oligochaeta: naidid (sludge worm *Tubifex tubifex*, red worm *Limnodrilus hoffmeisteri*)]	intestinal epithelia (enteritis)	Europe
G. caseosa	40-47	marine Gadiformes: macrourid (roughhead grenadier)	intestines, swim bladder, gall bladder (granulomas)	Atlantic
G. centropomi	19.1 x 17.6	marine Perciformes: centropomid (common snook)	intestines	North America
G. cernui	15-22.5	freshwater Perciformes: percid (Eurasian ruffe)	faeces	Russia
G. chalupskyi (syn. *Eimeria*)	10.5-11.5	freshwater Cypriniformes: cyprinid (Marmara chub)	faeces	Europe
G. cheni	9	freshwater Cypriniformes: cyprinid (bighead carp, silver carp, black carp)	intestinal epithelia	Far East, China
G. cichlidarum (syn. *Eimeria*)	31 x 27	freshwater Cichliformes: cichlid (redbelly tilapia, blue tilapia, mango tilapia, Nile tilapia)	swim bladder	Middle-East, Africa
G. clupearum (syn. *Coccidium, Eimeria, E. wenyoni*)	14-30	marine Beloniformes: belonid (garfish); Clupeiformes: clupeid (European pilchard, Atlantic herring, Pacific herring, European pilchard, European sprat, Japanese sardine, Pontic shad, round sardinella, Madeiran sardinella), engraulid (European anchovy); Carangiformes: carangid (false scad,	liver, gonads, stomach, intestines (inflammation, necrosis)	cosmopolitan

		lookdown, Atlantic horse mackerel); Gadiformes: gadid (blue whiting, pouting); Mulliformes: mullid (West African goatfish); Scombriformes: scombrid (Atlantic mackerel, Atlantic chub mackerel, bullet tuna, little tunny); Spariformes: sparid (two-banded seabream, red porgy, blackspot picarel)		
G. cruciata (syn. *Coccidium, Eimeria*)	17-26	marine Carangiformes: carangid (Atlantic horse mackerel, Mediterranean horse mackerel, Cape horse mackerel, Cunene horse mackerel, Chilean jack mackerel, blue jack mackerel, rough scad, white trevally)	liver, pancreas, pyloric caeca (hepatic lesions)	Atlantic, Mediterranean, Pacific, Adriatic
G. cultrati	22.5-30	freshwater Cypriniformes: cyprinid (sabre carp)	faeces	Russia
G. dakarensis	13-17	marine Perciformes: haemulid (parrot grunt, bigeye grunt), polynemid (lesser African threadfin))	liver	Atlantic
G. decapteri	13-18.5	marine Carangiformes: carangid (false scad)	liver	Africa
G. degiustii	24 x 19	freshwater Cypriniformes: cyprinid (shiners, minnows)	spleen, swim bladder, kidney, intestines (splenic lesions)	Canada
G. desseri	13-20	freshwater Perciformes: percid (zander, Volga pikeperch)	intestines (nodules)	Eurasia
G. echinata	18-19.3 x 9.4-11.7	marine Clupeiformes: clupeid (Atlantic herring)	intestines, caeca	Atlantic
G. emissolei	16-22 x 11.5-18	marine Carcharhiniformes: leptochariid (barbeled houndshark)	intestines	Africa
G. erythroculteri (syn. *Eimeria*)	37 x 26	freshwater Cypriniformes: cyprinid (redfin culter)	kidney	China
G. ethmalotis	30-37	marine Clupeiformes: clupeid (Bonga shad)	liver	Africa
G. exoceti	23-30 x 22-25	marine Beloniformes: exocoetid (fourwing flyingfish)	liver	Africa
G. floridana	19-21 x 14-18	marine Perciformes: sciaenid (red drum)	intestines, caeca	North America
G. gadi (syn. *Eimeria, E. jadviagae*)	20-33	marine Gadiformes: gadid (haddock, Atlantic cod, saithe, pollock), lotid (fourbeard rockling), macrourid (bigeye grenadier, blue grenadier)	swim bladder (eventually filled with viscoid exudates)	North Sea, Atlantic, Baltic
G. gasterostei (syn. *Eimeria, Coccidium*)	17	freshwater Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback)	liver	Europe
G. girellae (syn. *Eimeria*)	20.1-28.8 x 12.5-16.3	marine Perciformes: kyphosid (rudderfish)	intestines, liver, spleen, gills (moribund)	North America
G. grygieri	10-11	freshwater Cypriniformes: cyprinid (pike gudgeon)	foregut	Asia
G. gymnocephali	25	freshwater Perciformes: percid (Eurasian ruffe)	intestines	Russia
G. iroquoina	10	freshwater Cypriniformes: cyprinid (common shiner, hornyhead chub, blacknose shiner, rosyface shiner, bluntnose minnow, fathead minnow, eastern blacknose dace, creek chub)	intestinal epithelia	Canada
G. janae (syn. *Eimeria*)	18 x 13	freshwater Cypriniformes: cyprinid (Eurasian dace, Marmara chub)	intestines	Eurasia
G. kessleri	11 x 8	freshwater Gobiiformes: gobiid (round goby, bighead goby, monkey goby)	intestines	Eurasia
G. koertingi	15.8-16.5 x	freshwater Cypriniformes: cyprinid	intestines	Europe

	12.8-13.5	(common barbel)	(nodular coccidiosis)	
G. kuehae	37-40 x 28-30	estuarine Perciformes: latid (barramundi)	intestines	Australasia
G. langdoni (syn. *Eimeria*)	10.5-12	freshwater Perciformes: percichthyid (golden perch)	intestines, caeca	Australia
G. leucisci (syn. *G. scardinii, freemani Eimeria leucisci*)	25 x 22	freshwater Cypriniformes: cyprinid (Siberian dace, carp bream, common bleak, common roach, common rudd, white bream, common shiner)	kidney interstitium, renal tubules	Europe, North America
G. lomi (syn. *Eimeria*)	14.3-16.8	freshwater Perciformes: percichthyid (Murray cod)	intestines	Australia
G. luciae (syn. *Eimeria*)	9.5-10.8	marine Perciformes: mullid (red mullet)	intestines	Europe
G. lucida (syn. *Eimeria, E. scylli, Coccidium*)	10.5-11.5	marine Carcharhiniformes: triakid (smooth-hound, dusky smooth-hound), scyliorhinid (lesser spotted dogfish, nursehound), squalid (spiny dogfish, longnose spurdog)	intestines	Europe
G. luciopercae	30-35 x 30	freshwater Perciformes: percid (zander)	intestines	Russia
G. lusca	28.8-35.4	marine Gadiformes: gadid (pouting)	liver	Europe
G. malayensis	33-38	freshwater Cyprinodontiformes: aplocheilid (blue panchax)	foregut	Asia
G. metchnikovi (syn. *Eimeria, E. macroresidualis*)	25	freshwater Cypriniformes: cyprinid (white-finned gudgeon, gudgeon, Kessler's gudgeon, Amur whitefin gudgeon)	spleen, kidney, liver (splenic lesions)	Europe
G. microcanthi	11.7-13.5 x 10.1-11.7	marine Perciformes: kyphosid (stripey)	intestines	Australia
G. minuta (syn. *Eimeria*)	10	freshwater Cypriniformes: cyprinid (tench), percid (redfin perch)	kidney, liver	Europe
G. molnarica	14-16 x 9-10	freshwater Siluriformes: clariid (African sharptooth catfish)	intestines	Africa
G. motellae	14	marine Gadiformes: lotid (three-bearded rockling)	intestines, caeca	Europe
G. mylopharyngodoni (syn. *Eimeria*)	13	freshwater Cypriniformes: cyprinid (black carp)	intestines, liver, kidney	Eurasia
G. nipponica	10-12	marine Cypriniformes: cyprinid (big-scaled redfin)	foregut	Asia
G. notemigonica	21	freshwater Cypriniformes: cyprinid (golden shiner)	kidney, spleen swim bladder	Canada
G. notropicum	9	freshwater Cypriniformes: cyprinid (common shiner)	intestines	Canada
G. pannonica	11 x 9	freshwater Cypriniformes: cyprinid (white bream)	intestines	Eurasia
G. peleci	37.5-45 x 35-42.5	freshwater Cypriniformes: cyprinid (sabre carp)	intestines	Russia
G. pigra (syn. *Eimeria*)	18 x 14	freshwater Cypriniformes: cyprinid (common rudd)	intestinal epithelia	France
G. platichthyus	30-35 x 27.5-30	marine Pleuronectiformes: pleuronectid (European flounder)	faeces	Europe
G. pogonognathi	10-13	freshwater Beloniformes: zenarchopterid (forest halfbeak)	foregut	Asia
G. polylepidis	15-23 x 14-20	freshwater Cypriniformes: cyprinid (Iberian nase)	swim bladder, kidney	Europe
G. sasyki	7.5-11.3	freshwater Clupeiformes: clupeid (Black Sea sprat)	intestines, gall bladder	Europe
G. senegalensis	15.5-19	marine Perciformes: lutjanid (African forktail snapper)	liver	Africa
G. sinensis (syn. *Eimeria*)	12	freshwater Cypriniformes: cyprinid (bighead carp, silver carp)	intestines (enteritis)	Asia, Europe
G. soumbediounensis	10-14.5	marine Carcharhiniformes: leptochariid (barbeled houndshark)	intestines	Africa

G. subepithelialis (syn. *Eimeria*)	16-21 x 13-18	freshwater Cypriniformes: cyprinid (common carp, tench) [plus indirect transmission via oocysts/sporozoites in Oligochaeta: naidid (sludge worm *Tubifex*)]	intestines (nodular coccidiosis)	Europe
G. sparis (syn. *Eimeria*)	9.4-14.6	marine Perciformes: sparid (redbanded seabream, gilthead bream, bluespotted seabream)	intestines	Eurasia
G. spraguei	16.2-16.8	marine Gadiformes: gadid (Atlantic cod, haddock)	kidney tubules	Canada
G. squali (syn. *Eimeria*)	24-36 x 20-29	marine Squaliformes: squalid (spiny dogfish)	spiral valve	North America
G. suliculiformis	22	freshwater Cypriniformes: cyprinid (gudgeons)	serosa of swim bladder, intestines, liver, kidney	Eurasia
G. szekelyi	14-15.5	freshwater Gobiiformes: gobiid (round goby, monkey goby)	intestines	Europe
G. thelohani (syn. *Eimeria*, *Coccidium*)	16-23	marine Perciformes: labrid (East Atlantic peacock wrasse), sparid (yellowfin bream, goldlined seabream)	liver	Europe, Australia
G. trachinoti	9.5-12	marine Carangiformes: carangid (pompani)	liver	Africa
G. trichogasteri (syn. *Eimeria*)	12.5-22.5	freshwater Anabantiformes: osphronemid (snakeskin gourami)	foregut	Asia
G. truttae (syn. *Eimeria*)	12.3-13	anadromous and freshwater Salmoniformes: salmonid (masu, rainbow trout, brown trout, brook trout, grayling)	caeca	North America
G. vanasi (syn. *Eimeria*)	15-17 x 11-13	freshwater Cichliformes: cichlid (blue tilapia, Nile tilapia, mango tilapia, Mozambique tilapia, banded tilapia, southern mouthbrooder)	foregut	Africa
G. vargai (syn. *Eimeria*)	12.6-20	freshwater Acipenseriformes: acipenserid (sterlet)	intestines	Europe
G. vimbae	15-22.5	marine Cypriniformes: cyprinid (vimba bream)	intestines	Russia
G. wakabayashii	8-9	freshwater Gobiiformes: gobiid (numa-chichibu)	foregut	Japan
G. zarnowskii (syn. *Eimeria*)	19 x 9	freshwater Gasterosteiformes: gasterosteid (three-spined stickleback)	intestines	Europe
Species in non-piscine hosts				
G. flaviviridis (syn. *Eimeria*)	18-35 x 10-16	terrestrial Sauria: gekkonid (yellow-belly gecko)	gall bladder	Asia
G. hyalina (syn. *Coccidium, Eimeria*)	10-17	freshwater Coleoptera (unspecified beetle)	Malpighian tubules	Europe
G. hyperolisi	7-9.8	freshwater Anura: hyperoliid (tadpoles of common reed frog)	gut mucosa	Africa
G. lacazei (syn. *Bananella*, *Eimeria*, *Coccidium schneideri*)	30-40	terrestrial Chilopoda: lithobiid (*Lithobius forficatus, martini* centipedes)	intestines	Holarctic
G. neglecta	8.5-12.5	freshwater Anura: ranid (tadpoles of edible frog, marsh frog, little water frog, grass frog)	intestines	Europe
G. noelleri	10.5-11.5 x 8-11	freshwater Anura: ranid (common frog, agile frog)	intestines	Eurasia

The genus *Epieimeria* was erected for *Eimeria*-like coccidian species whose developmental stages are attached to the surface of intestinal epithelial cells protruding into the lumen (considered to be an epi-cellular location). Oocysts form 4 sporocysts, each with an apical pore and a Stieda body. Sporogony may exogenously after oocysts are excreted from the host, or intercellularly when

oocysts infiltrate the mucosa and accumulate in the viscera or body cavities where they sporulate and are liberated only after death of the host. The genus contains 5 species which have been recorded in marine fish and anadromous eels.

***Epieimeria* species**	**Oocyst/sporocyst sizes (µm)**	**Hosts**	**Location (Disease)**	**Distribution**
E. anguillae (syn. *Eimeria*) (type species)	oo: 8.0-12.8 sp: 5.6-8.8 x 2.4-5.6	freshwater Anguilliformes: anguillid (New Zealand longfin eel, long-finned eel, short-finned eel, European eel, American eel), congrid (European conger)	intestines, caeca (mucosal degeneration, emaciation)	Holarctic, Australia, New Zealand
E. isabellae	oo: 12-14 sp: 7.6-8.4 x 5-6	marine Anguilliformes: congrid (conger eel)	intestines	Mediterranean
E. lomae	oo: 10-12 sp: 6.5-7.5 x 4-5	marine Scorpaeniformes: scorpaenid (black scorpionfish)	pyloric caeca	Adriatic
E. ocellata	oo: 8.8-11 x 8-11 sp: 6-8 x 4-5	marine Perciformes: sciaenid (red drum)	intestines	North America
E. puytoraci	oo: 13-14.5 sp: 8.5-10 x 4.5-5.5	marine Labriformes: labrid (East Atlantic peacock wrasse)	intestines	Adriatic

The genus *Calyptospora* was originally created for the species *Eimeria funduli* when it was found that the sporocysts were radically different from those of typical Eimeria spp. in that they lacked Stieda and sub-Stieda bodies and were covered by a thin veil supported by tentacle-like sporopodia. The sporocysts possessed an anterior apical opening sometimes associated with an incomplete longitudinal fissure (which does not divide the sporocyst into 2 valves like *Goussia* spp.). The parasites usually develop in the livers of fish hosts and they are thought to have monoxenous (one-host) cycles where transmission occurs via the excretion and subsequent ingestion of oocysts. However, some species may have heteroxenous (2-host) life-cycles where oocysts ingested by shrimp (paratenic or intermediate) hosts have been found to excyst releasing sporozoites which invade the gut wall ready to be ingested by predatory fish.

***Calyptospora** species*	**Oocyst/sporocyst size (µm)**	**Hosts**	**Location**	**Transmission**	**Distribution**
C. empristica	19.6-24.5	freshwater Cyprinodontiformes: fundulid (starhead topminnow)	liver, pancreas	possibly indirect (sporozoites in Decapoda: palaemonid (*Palaemon kadiakensis*)	North America
C. funduli (syn. *Eimeria*) (type species)	oo: 19-31 sp: 9-11 x 5-7	marine; Cyprinodontiformes: fundulid (Gulf killifish, saltmarsh topminnow, Bayou killifish, longnose killifish, mummichog, inland silverside); Batrachoidiformes: batrachoidid (Gulf toadfish)	liver, pancreas, intestines, ovary, dermis (hepatic and pancreatic lesions)	direct (oocyst ingestion) and indirect (sporozoites in Decapoda: palaemonid (*Palaemonetes pugio, vulgaris, paludosus, kadiakensis, Macrobrachium ohione*)	North America
C. gonzaguensis	19.6	freshwater Characiformes: triportheid (dusky narrow hatchetfish)	liver, gall bladder, adipose tissue		South America
C. paranaidji	22.1	freshwater Cichliformes: cichlid (blue peacock wrasse)	liver		South America
C. serrasalmi	23.5-25.5	freshwater Characiformes: serrasalmid (black piranha, redeye piranha, peppered piranha)	liver		South America
C. spinosa	21.1-23.4	freshwater Cichliformes: cichlid (pike cichlid)	liver, gonads		South America
C. tucunarensis	23-26	freshwater Cichliformes: cichlid (butterfly peacock bass)	liver		South America

*Note that the genus *Calyptospora* may also refer to pucciniomycete fungi (Basidomycota)

The genus *Crystallospora* was created for a single species (originally *Coccidium crystalloides*) which produced highly unusual crystal-like sporocysts that were dodecahedral in shape and composed of 2 hexagonal pyramidal valves joined at their bases by a suture. Infections have only been detected in marine fish (rockling) around coastal Europe.

***Crystallopsora* species**	**Oocyst size (µm)**	**Hosts**	**Location**	**Transmission**	**Distribution**
C. crystalloides (syn. *C. thelohani, Coccidium, Eimeria*)	oo: 20-24 sp: 15 x 9.5	marine, Gadiformes: lotid (shore rockling, three-bearded rockling)	intestines	direct	Atlantic, Mediterranean

Parasite morphology: Piscine coccidia belonging to the genera *Goussia*, *Epieimeria*, *Calyptospora* and *Crystallospora* undergo merogony (asexual multiplication), gamogony (formation of gamonts then gametes) and sporogony (formation of oocysts, sporocysts and sporozoites) in their developmental cycles, somewhat similar to *Eimeria* spp. However, the locations of the developmental stages in host tissues and the structure of the oocysts and sporocysts differ markedly from that of typical *Eimeria* spp. Meronts, gamonts and oocysts of *Goussia, Epieimeria, Calyptospora* and *Crystallospora* are generally small, appearing as rounded colourless-basophilic bodies ranging in diameter from 5-25 µm. They are located within membrane-bound parasitophorous vacuoles within host cells (intracellular, but extracytoplasmic) and many species are located epicellularly; that is, attached to the luminal surface of epithelial cells by finger-like attachment organelles (monopodial or polypodial). Meronts are rounded basophilic stages that divide asexually to form numerous merozoites. Gamonts are also rounded stages, but female gamonts (macrogamonts) are lightly stained uninucleate vacuolated stages, while male gamonts (micro-gamonts) are basophilic and become multinucleate as they form several microgametes. Fertilization produces a zygote, evident as an immature oocyst with a thin fragile oocyst envelope lacking a micropyle. Oocysts mature (sporulate) to produce 4 sporocysts, each with 2 sporozoites (typical eimeriid 1:4:2 configuration). Members of the genus *Epieimeria* form ovoid to ellipsoidal sporocysts with polar plugs and/or Stieda bodies (like *Eimeria* spp.), while members of the genus *Goussia* form sporocysts without Stieda bodies but with walls consisting of 2 cup-like valves joined along a longitudinal suture (sometimes associated with a delicate membranous structure). The sporocysts of *Calyptospora* spp. lack Stieda and sub-Stieda bodies but are surrounded by amorphous material covered by a thin veil supported by tentacle-like sporopodia. The sporocysts have an apical opening often associated with a short longitudinal fissure. The single *Crystallospora* sp. forms unusual crystal-like sporocysts consisting of 2 hexagonal pyramidal valves joined along a transverse suture line.

Site of infection: Most piscine coccidia infect the intestinal mucosa (epithelium and/or submucosa), but developmental stages may sometimes be found in extra-intestinal tissues and organs (stomach, caeca, gall bladder, liver, spleen, pancreas, kidneys, swim bladder, spleen, gills, and gonads). A total of 88 *Goussia* spp. have been described from the intestines, and sometimes extra-intestinal tissues, in 156 fish species: with 32 species recorded in 79 marine fish species belonging to 29 families in 14 orders, and 56 parasite species in 77 freshwater fish species belonging to 19 families in 14 orders. Another 6 *Goussia* spp. have also been found in the guts of several amphibians, a few insects (centipedes, beetle) and a lizard (gecko). Sporozoite developmental stages of several species have also been detected in freshwater oligochaetes (tubificids) which may act as secondary hosts (paratenic or intermediate hosts). Seven *Calyptospora* spp. have been found in the livers, and sometimes other organs, in 15 fish species (8 freshwater, 7 marine) belonging to 5 families in 4 orders. Sporozoites have also been detected in the guts of 5 species of palaemonid shrimp which act as secondary hosts. Five *Epieimeria* spp. have been described attached to the surface of intestinal epithelial cells (epicellular location) in 10 fish species (6 freshwater, 4 marine) belonging to 5 families in 4 orders. Oocysts are usually voided into the external environment, although those of some species accumulate in the viscera or body cavities and are only liberated after the death of the host. Only one *Crystallospora* sp. has been reported in the intestines of 2 species of marine rockling.

Pathogenesis: Infections in fish ranged from asymptomatic-subclinical to causing mild-severe disease, sometimes with mortalities. The parasites formed both asexual and sexual developmental stages intracellularly within host cells which ultimately led to host cell lysis to liberate parasite progeny. The resultant structural losses to host tissues was sometimes severe enough to result in functional abnormalities and disease expression. Many parasite species exhibit strong tissue tropism (site specificity), with development occurring in or on intestinal epithelial cells (intracytoplasmic or epicytoplasmic) or in visceral (extra-intestinal) organs, although several species may develop in multiple locations, sometimes apparently in sequence (e.g. *Goussia girellae* in rudderfish). Infections in the gastro-intestinal tract usually cause regressive epithelial changes (dystrophy, necrosis, desquamation) and mild-severe inflammatory responses, with affected fish sometimes showing inappetence, darkened bodies and protracted low grade mortalities. Examples of enteric disease include diffuse enteritis caused by *Goussia carpelli* and *G. sinensis* in carp and *G. clupearum* in pilchards, and nodular coccidiosis caused by *G. subepithelialis* in carp, *G. desseri* in perch, and *G. koertingi* in barbels. Extra-intestinal infections may result in necrotic lesions sometimes with granuloma formation: e.g. hepatic lesions caused by *Calyptospora funduli* in killifish and *G. cruciata* in mackerel, splenic lesions by *G. degiustii* in minnows and *G. metchnikovi* in gudgeon, kidney lesions by *G. leucisci* in cyprinids and *G. spraguei* in haddock, and swim bladder lesions by *G. gadi* in cod and *G.*

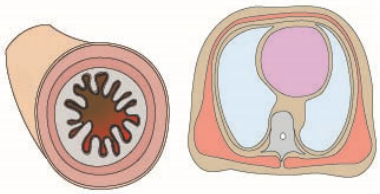
caseosa in grenadier. Clinical infections and disease are more prevalent and severe in young fish (fry to fingerling stages) and some infections appear to be seasonal with peaks occurring in spring (thought to be associated with host reproductive cycles, and possibly with the seasonal abundance of putative secondary hosts (such as oligochaetes and shrimp).

Developmental cycle and mode of transmission: The life-cycles of most coccidian species infecting fishes remain to be definitively determined, but most are assumed to have monoxenous (one-host) life-cycles involving the faecal-oral transmission of oocysts voided by infected hosts being ingested by new susceptible hosts. Ingested oocysts excyst in the fish gut releasing the infective sporozoites which invade host tissues. They form meronts (schizonts) which undergo asexual proliferation by internal (endogenous) division to form numerous merozoites. Depending on the parasite species, there may be several cycles of merogony before sexual development begins. Sexually-dimorphic gamonts form macrogametocytes (female) that mature into single macrogametes while microgametocytes (male) produce several flagellated ('sperm-like') microgametes. Fertilization occurs by gamete fusion producing zygotes which begin oocyst formation by producing membranous oocyst walls. The oocysts undergo an asexual sporulation process to produce 4 sporocysts, each of which contains 2 sporozoites. Sporulation often occurs exogenously after oocysts are excreted from the host. However, some species undergo endogenous (intercellular) sporulation when oocysts infiltrate the mucosa and accumulate in the viscera or body cavities where they sporulate and are liberated only after the death of the host. The whole life-cycle may be completed as quickly as 15 days or may take up to 7 months. In addition, some parasite species also exhibit heteroxenous (2-host) transmission involving secondary hosts which act either as paratenic hosts (transporting parasite stages without development) or as true intermediate hosts (supporting parasite asexual development). Several *Goussia* spp. (e.g. *G. carpelli, G. subepithelialis*) may be transmitted directly between carp by oocyst ingestion, but they may also be transmitted indirectly to fish by the ingestion of infected tubificid oligochaetes living in pond sediments. It is not yet known whether the oligochaetes support parasite development or not, although it has been shown that some ingested oocysts excyst in the oligochaete gut releasing sporozoites into the lumen with some also invading intestinal epithelial cells. Infections are readily transmitted to fry feeding on infected worms. Several *Calyptospora* spp. (e.g. *C. funduli, C. empristica*) in minnows have been shown to be transmitted indirectly between fish by the ingestion of infected palaemonid shrimp which harbour sporozoites in their gut walls. Following the ingestion of shrimp by the predatory fish, the sporozoites penetrated the fish gut wall and were carried to the liver where they underwent asexual and sexual development.

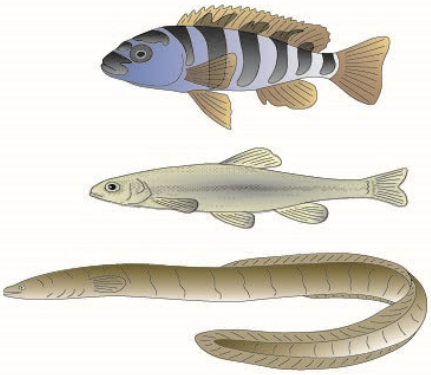
Differential diagnosis: Infections are diagnosed by the direct microscopic detection of parasites in tissue or faecal samples. Wet mounts of gut content, mucosal smears or tissue squashes may be examined by high-contrast microscopy (bright-field, phase- or interference-contrast) for endogenous stages and developing oocysts. Thin sections of fixed tissues may also be examined after staining with routine histological stains. Fresh faecal samples may be examined as wet mounts or following concentration by sedimentation-floatation techniques. Molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (usually small subunit (18S) ribosomal DNA). While *in vivo* parasite culture has not been used for diagnostic purposes, experimental studies have successfully infected carp fry by feeding them tubificid oligochaetes exposed to Goussia carpelli oocysts.

Treatment and control: Various coccidiostatic and coccidiocidal drugs have been developed for the treatment of avian and mammalian coccidiosis, and some are used off-label for the treatment of piscine coccidiosis. Aquarium fish may be treated by topical or systemic applications either individually or in small batches, whereas aquaculture and mariculture facilities with larger fish populations rely on in-feed medications. Clinical infections in fish by several *Goussia* spp. have responded to treatment with some anticoccidial drugs (diclazuril, lasalocid, robenidine, maduramicin, orazole, furazolidone, furanace) but not with others (amprolium, toltrazuril, monensin, narasin, salinomycin), while fish infected with *Calyptospora* sp. were responsive to monensin. Various treatments produced some side-effects and several drugs required lengthy with-holding periods when used in food animals. Various strategies have been suggested to prevent infections by reducing oocyst contamination in culture facilities. Fish should be screened for infections before their introduction into culture, with positive fish held in isolation for treatment or culling. Dead or dying fish should be removed from ponds promptly and disposed of by incineration or burial. Water flow and quality should be managed to reduce the accumulation of sediments and organic wastes in ponds and prevent their colonization by oligochaetes which may act as paratenic hosts for some coccidian species. Infected ponds should be drained, dried and disinfected (with lime) to kill any contaminating oocysts. Fish may become more susceptible to infection and disease when stressed (and immuno-compromised), so husbandry procedures should endeavour to avoid stressful situations (such as overcrowding, over-handling, poor diets, and poor water quality).

Goussia
Calyptospora
Crystallospora



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

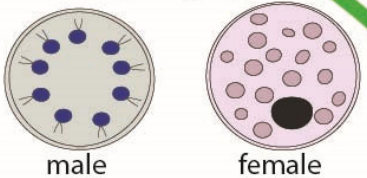


Definitive Hosts
(marine and
freshwater fish)

intestines, viscera
(enteritis, nodules,
lesions)

asexual merogony
(several cycles)

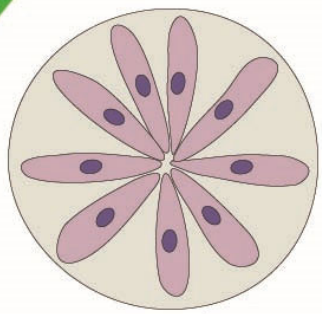
sexual
gamogony



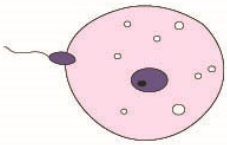
male

female

gamonts (5-15 µm)

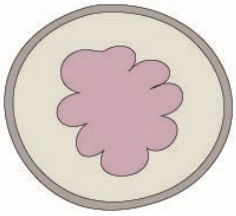


meronts
(5-25 µm)



fertilization

excystation
(sporozoites
released)



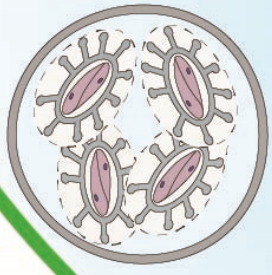
sporoblast

ingested

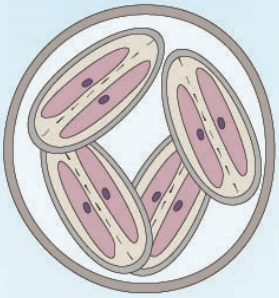
oocyst:sporocyst:sporozoite
configuration = 1:4:2

excreted

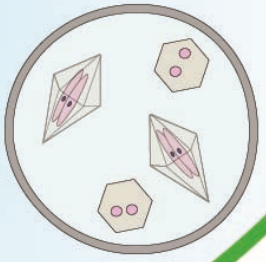
Calyptospora
(sporopodia)



Goussia
(valved sporocysts)



Crystallospora
(pyramidal sporocysts)

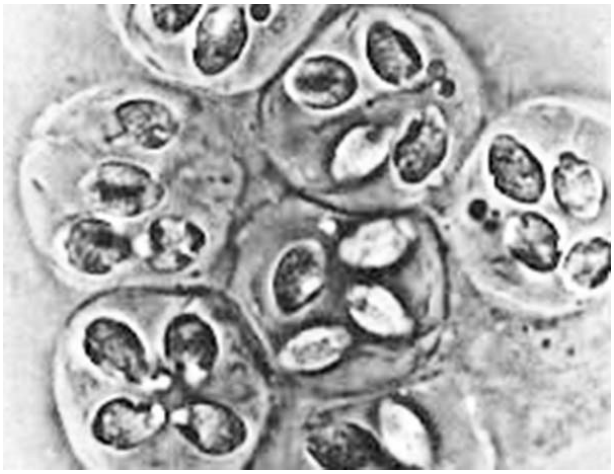
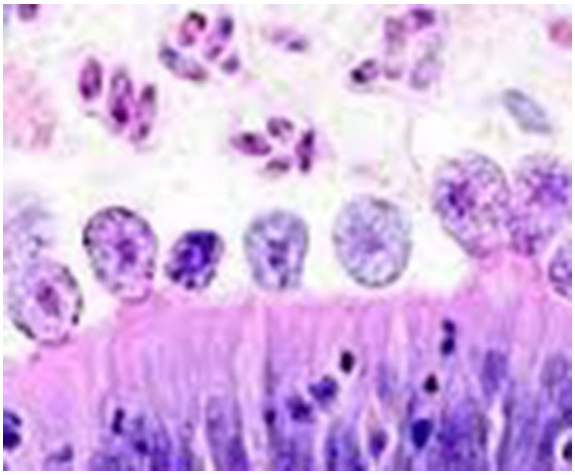


exogenous
sporulation

oocysts (10-35 µm)

Possible Paratenic Hosts
(tubificid oligochaetes)
(tissues)

faecal-oral transmission via oocysts
contaminating aquatic environment

	
Goussia oocysts from fish gut	*Goussia* development on fish gut