Chapter 5
Cryptosporidiosis in Other Vertebrates

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Abstract *Cryptosporidium* has adapted to a broad range of hosts in all major vertebrate classes, and the species associated with humans and livestock represent a small fraction of the diversity in the genus. This review focuses on *Cryptosporidium* and cryptosporidiosis in terrestrial vertebrates other than humans and livestock. As the known host range of *Cryptosporidium* continues to expand, major orders of amphibians (Anura), reptiles (Squamata and Testudines), avians (17 out of 26 orders), and mammals (18 out of 29 orders) are now represented. The greatest *Cryptosporidium* diversity appears to be in mammals, which may be an Artifact of undersampling in other classes, but more likely reflects a different mechanism of *Cryptosporidium* diversification in mammals relative to other classes.

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5.1 Introduction

The emergence of *Cryptosporidium* as a serious human pathogen in the 1980s spurred research efforts to understand the biology and ecology of this enigmatic parasite. While early studies were hindered by a lack of tools to type isolates, the widespread use of genotyping during the last 15 years has begun to uncover the enormous diversity that exists in the genus *Cryptosporidium*.

The major focus of *Cryptosporidium* research over the past 30 years has been the control of cryptosporidiosis in humans and livestock, and the primary motivation to study other vertebrates has been to understand the ecology of human cryptosporidiosis. Wildlife-associated cryptosporidia account for a relatively small but significant proportion of human cryptosporidiosis cases (Feltus et al. 2006; Robinson et al. 2008; Elwin et al. 2011), the recent emergence of *C. cuniculus* as a human pathogen illustrates the connection between wildlife and public health. Rabbit-adapted *C. cuniculus* was not on the public health radar until the misadventures of a rabbit at a UK water treatment facility in 2008 resulted in a waterborne outbreak of cryptosporidiosis (Chalmers et al. 2009). Genetically, *C. cuniculus* is remarkably similar to the major human pathogen *C. hominis*, and the two cannot be differentiated by some routine molecular diagnostics (Robinson et al. 2010). However, prompted by the waterborne outbreak, samples from 3,030 sporadic cryptosporidiosis cases in the UK were reexamined using enhanced diagnostics, and *C. cuniculus* was detected in 1.2 % of samples (Elwin et al. 2012a). Apart from the obvious benefit of knowing the species, and hence the likely source of the *Cryptosporidium* causing human disease, these studies raise interesting and fundamental questions about the biology of *Cryptosporidium*; such as, how does *Cryptosporidium* diversify and how does diversification affect host specificity and disease potential? These questions can be addressed by examining *Cryptosporidium* diversity across the range of vertebrate hosts, not just humans and livestock.

This chapter addresses the occurrence of *Cryptosporidium* in vertebrate hosts other than fish (Chap. 1), humans (Chaps. 2 and 3), and livestock (Chap. 4). Information is organized by vertebrate class (Amphibia, Reptilia, Aves, and Mammalia), and by order within each class. Background information is provided on each order, including orders that do not currently contain identified *Cryptosporidium* hosts. It is hoped that this approach will facilitate the identification of knowledge gaps and will stimulate ideas for future research.

5.2 *Cryptosporidium* and Cryptosporidiosis of Amphibians

To date, *Cryptosporidium* has been detected in only one of the three orders of amphibians: the Anura. It has not been detected in the Caudata, an order that contains more than 550 species in ten families and approximately 30 genera of salamanders, or the Gymnophonia, which are snake-like amphibians with about

180 species in ten families and 35 genera. The Caudata require freshwater for reproduction and they consume invertebrates. Gymnophonia are tropical in distribution, have larvae that may only be partially aquatic, and typically inhabit loose soil layers.

5.2.1 Anura

Anura is the largest order of Amphibians, with over 6,000 species of frogs and toads in 33 families and over 65 genera. Frogs and toads require at least some water for reproduction, but they occupy a wide variety of terrestrial and freshwater habitats. There are no marine species, and only a few inhabit brackish waters. All Anurans consume invertebrate prey, lacking teeth or grinding organs in their digestive tract.

Cryptosporidium fragile, the only amphibian-adapted species described to date, was isolated from the doubtful toad (*Duttaphrynus melanostictus*) originating in Malaysia (Jirků et al. 2008). Oocysts of *C. fragile* measure 6.2 μm (5.5–7.0 μm) × 5.5 μm (5.0–6.5 μm) and are readily lysed in hypertonic solutions. *Cryptosporidium fragile* infects the gastric epithelium and clusters with gastric cryptosporidia in molecular phylogenies (Table 5.1 and Fig. 5.1). Other reports of *Cryptosporidium* and cryptosporidiosis in reptiles have been rare. Cryptosporidiosis was diagnosed in a captive South African clawed frog (*Xenopus laevis*) that was euthanized after becoming grossly emaciated from illness (Green et al. 2003). Endogenous *Cryptosporidium* stages were identified in the gastric mucosa, and oocysts were isolated from water in the infected frog's enclosure. *Cryptosporidium* oocysts also have been reported in a captive Bell's horned frog (*Ceratophrys ornata*) (Crawshaw and Mehren 1987).

5.3 *Cryptosporidium* and Cryptosporidiosis of Reptiles

Cryptosporidium has been detected in two of the four orders of reptiles: Squamata and Testudines. It has not yet been reported in Crocodylia, a small order of 25 species in three families and eight genera, or the Rhynchocephalia, which is represented by two living species: the Brother's Island tuatara (*Sphenodon guntheri*) and the northern tuatara (*Sphenodon punctatus*). Crocodylians, which include crocodiles and alligators, have a two-chambered stomach that is unique among reptiles. The first chamber contains stones and functions much like the avian gizzard, and the second chamber is extremely acidic to facilitate almost complete digestion of prey. Tuataras, which are found only in New Zealand, are similar to the Squamates, but have different dentition and skull characteristics. They feed primarily on invertebrates, but occasionally eat small vertebrates or eggs.

Table 5.1 GenBank accession numbers of representative *Cryptosporidium* small subunit rRNA gene sequences from amphibians and reptiles. A phylogeny constructed from sequences in this table is presented in Fig. 5.1

Class	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
Amphibia	Anura	Toad	**Doubtful toad** (*Duttaphrynus melanostictus*) [EU162751]
Reptilia	Squamata	Lizards	**Central bearded dragon** (*Pogona vitticeps*) [AY382169, AY382170]
			Desert monitor (*Varanus griseus*) [AF112573]
			Leopoard gecko (*Eublepharis macularius*) [AY120915, AY282714, EU553556]
			Savannah monitor (*Varanus exanthematicus*) [AF093500, AY282713]
			Schneiders skink (*Eumeces schneideri*) [AY282715]
			Veiled chameleon (*Chamaeleo calyptratus*) [EU553587]
		Snakes	**Australian taipan** (*Oxyuranus scutellatus*) [AF108866]
			Ball phyton (*Python regius*) [EU553589, EU553590]
			Boa constrictor (*Boa constrictor*) [AY268584]
			Corn snake (*Pantherophis guttatus guttatus*) [EF50204, AF151376]
			Japanese grass snake (*Rhabdophis tigrinus*) [AB222185]
			New Guinea boa snake (*Candoia aspera*) [AY120913]
	Testudines	Tortoises and turtles	**Marginated tortoise** (*Testudo marginata*) [EF547155]
			Pancake tortoise (*Malacochersus tornieri*) [GQ504270]
			Russian tortoise (*Agrionemys horsfieldii*) [GQ504268]
			Indian star tortoise (*Geochelone elegans*) [AY120914]

5.3.1 Squamata

The order Squamata – snakes and lizards – is the largest and most diverse reptilian order, with more than 9,000 species in 50 families. They occupy diverse habitats, though most species inhabit drier terrestrial areas. All are predators that consume a wide variety of prey. Many produce venom or toxins to assist in immobilization of prey, which are swallowed without mastication.

Two *Cryptosporidium* species have been described in the Squamata: *Cryptosporidium serpentis*, which infects the gastric epithelium, and *C. varanii* (syn. *C. saurophilum*), which is an intestinal species (Table 5.1 and Fig. 5.1).

Cryptosporidium serpentis, which was described by Brownstein et al. (1977) and later named by Levine (1980), can cause chronic, insidious, and often fatal hypertrophic gastritis in both immature and mature ophidian hosts (Brownstein et al. 1977; Cranfield and Graczyk 1994; Kimbell et al. 1999). Clinical signs include

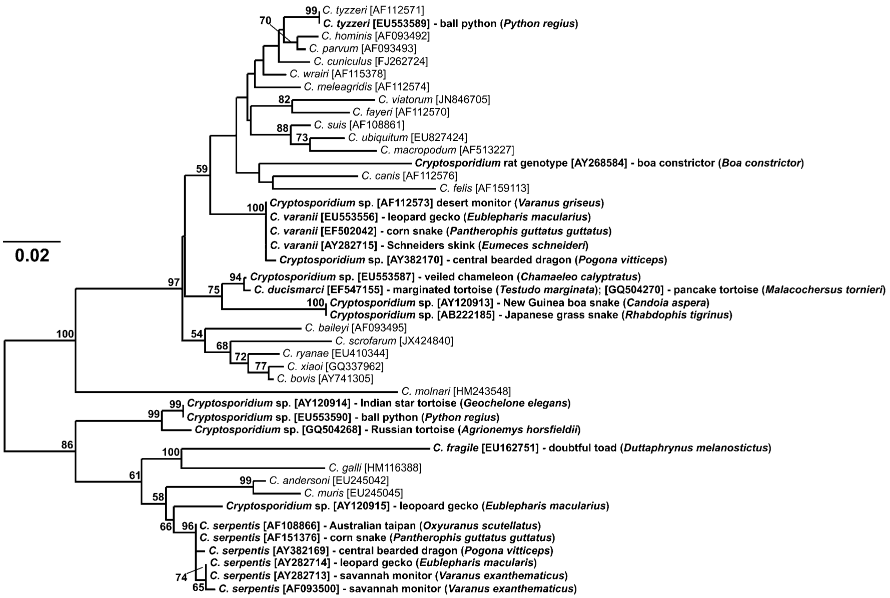

Fig. 5.1 A SSU rDNA-based maximum likelihood (GTRCAT model) tree of *Cryptosporidium* spp. sequences showing clades of cryptosporidia infecting amphibians and reptiles. *Cryptosporidium* sp. detected in amphibians and reptiles are in bold. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown at nodes. Bootstrap values <50 are not shown. Interrupted branches have been shortened fivefold

mid-abdominal swelling and postprandial regurgitation, but not all cases are symptomatic (Brownstein et al. 1977; Cranfield and Graczyk 1994).

Although it is primarily a parasite of snakes (Table 5.2), *C. serpentis* also causes asymptomatic infections in a number of lizard species (Table 5.3). Unsuccessful attempts to experimentally infect Balb/c mice (Fayer et al. 1995), Pekin ducklings (*Anas platyrhynchos*) (Graczyk et al. 1998b), African clawed frogs (*Xenopus laevis*), and wood frogs (*Rana sylvatica*) (Graczyk et al. 1998c) suggest that *C. serpentis* is restricted to reptiles. However, strict reptile-specificity is brought into question by a recent report that *C. serpentis* was isolated from cattle in China, and was infectious for immunosuppressed and non-immunosuppressed Balb/c mice under experimental conditions (Chen and Qiu 2012).

Snakes are not susceptible to experimental infection with cryptosporidia from homothermic animals, including *C. andersoni* (calves), *C. baileyi* (chickens), *C. meleagridis* (turkeys), *C. muris* (mice), *C. muris*-like (Bactrian camels), and *C. wrairi* (guinea pigs), but they are susceptible to other reptilian cryptosporidia (Graczyk and Cranfield 1998). Reports of *C. tyzzeri* (previously mouse genotype I) in a black rat snake (*Elaphe obsoleta obsoleta*), boa constrictor (*Boa constrictor ortoni*), California king snake (*Lampropeltis getulus californiae*), corn snake (*Pantherophis guttatus guttatus*), emerald tree boa (*Corallus caninus*), fox snake

Table 5.2 *Cryptosporidium* spp. identified in snakes

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Boidae	**Amazon tree boa** (*Corallus hortulanus*)	*C. serpentis*	(Morgan et al. 1999c; Xiao et al. 2004)
	Boa constrictor (*Boa constrictor*)	*C. muris*, *C. serpentis*, *C. tyzzeri*, *C. varanii*, rat genotype I	(Xiao et al. 2004; Pedraza-Diaz et al. 2009; Rinaldi et al. 2012)
	Brazilian rainbow boa (*Epicrates cenchria*)	*C. serpentis*	(Graczyk and Cranfield 2000; Sevá Ada et al. 2011b)
	Colombian rainbow (*Epicrates cenchria maurus*)	*C. serpentis*	(Ryan et al. 2003a)
	Emerald tree boa (*Corallus caninus*)	*C. serpentis*, *C. tyzzeri*	(Xiao et al. 2004)
	Green anaconda (*Eunectes murinus*)	*C. serpentis*	(Sevá Ada et al. 2011b)
	Kenyan or East African sand boa (*Eryx colubrinus*)	*Cryptosporidium* sp.	(Pedraza-Diaz et al. 2009)
	Madagascar tree boa (*Sanzinia madagascariensis*)	*C. serpentis*	(Levine 1980)
	New Guinean viper boa (Candoia aspera)	*C. serpentis*, *C. varanii*, *Cryptosporidium* sp.	(Graczyk and Cranfield 2000; Xiao et al. 2004)
	Rosy boa (*Lichanura trivirgata*)	*C. serpentis*	(Ryan et al. 2003a)
Colubridae	**Black rat snake** (*Pantherophis obsoleta obsoleta*)	*C. muris*, *C. serpentis*, *C. tyzzeri*, *C. varanii*, *Cryptosporidium* sp.	(Cranfield and Graczyk 1994; Morgan et al. 1999c; Xiao et al. 2004)
	Brazos water snake (*Nerodia harteri harteri*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Bull snake (*Pituophis melanoleucus melanoleucus*)	*C. serpentis*, *C. varanii*	(Morgan et al. 1999c; Graczyk and Cranfield 2000; Xiao et al. 2004)
	California king snake (*Lampropeltis getulus californiae*)	*C. serpentis*, *C. tyzzeri*	(Xiao et al. 2004; Pedraza-Diaz et al. 2009)
	Common garter snake (*Thamnophis sirtalis*)	*Cryptosporidium* sp.	(Brower and Cranfield 2001)
	Corn snake (*Pantherophis guttatus guttatus*)	*C. muris*, *C. serpentis*, *C. tyzzeri*, *C. varanii*	(Levine 1980; Cranfield and Graczyk 1994; Kimbell et al. 1999; Morgan et al. 1999c; Graczyk and

(continued)

Table 5.2 (continued)

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
			Cranfield 2000; Xiao et al. 2004; Plutzer and Karanis 2007; Pedraza-Diaz et al. 2009; Richter et al. 2011; Sevá Ada et al. 2011b; Rinaldi et al. 2012)
	Diamondback water snake (*Nerodia rhombifer rhombifera*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Eastern indigo snake (*Drymarchon corais couperi*)	*Cryptosporidium* sp.	(Cerveny et al. 2012)
	Fox snake (*Pantherophis vulpina gloydi*)	*C. serpentis*, *C. tyzzeri*	(Xiao et al. 2004)
	Jalisco milk snake (*Lampropeltis triangulum arcifera*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Louisiana pine snake (*Pituophis ruthveni*)	*C. varanii*	(Xiao et al. 2004)
	Milk snake (*Lampropeltis triangulum*)	*C. serpentis*, *C. tyzzeri*, *C. varanii*, *Cryptosporidium* sp.	(Graczyk and Cranfield 2000; Xiao et al. 2004; Pedraza-Diaz et al. 2009; Sevá Ada et al. 2011b)
	Mexican black kingsnake (*Lampropeltis getulus nigritus*)	*C. serpentis*	(Pedraza-Diaz et al. 2009)
	Mexican kingsnake (*Lampropeltis mexicana*)	*C. serpentis*	(Sevá Ada et al. 2011b)
	Pine snake (*Pituophis melanoleucus*)	*C. serpentis*, *C. varanii*, *Cryptosporidium* sp.	(Xiao et al. 2004)
	Prairie king snake (*Lampropeltis calligaster*)	*C. tyzzeri*	(Xiao et al. 2004)
	Rough green snake (*Opheodrys aestivus*)	*Cryptosporidium* sp.	(Brower and Cranfield 2001)
	Ruthven's kingsnake (*Lampropeltis ruthveni*)	*C. serpentis*	(Graczyk and Cranfield 2000)
	Spotted leaf-nosed snake (*Phyllorhynchus decurtatus*)	*C. serpentis*	(Graczyk and Cranfield 2000)

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Table 5.2 (continued)

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
	Texas rat snake (*Elaphe obsolete lindheimeri*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Trans-Pecos rat snake (*Bogertophis subocularis*)	*C. serpentis*	(Levine 1980)
	Tricolor hognose snake (*Lystrophis semicinctus*)	*Cryptosporidium* sp.	(Cerveny et al. 2012)
	Western fox snake (*Pantherophis vulpina vulpina*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Yellow rat snake (*Elaphe obsoleta quadrivittata*)	*C. serpentis*, *C. muris*	(Cranfield and Graczyk 1994; Ryan et al. 2003a)
Elapidae	**Cape coral snake** (*Aspidelaps lubricus lubricus*)	*Cryptosporidium* sp.	(Cerveny et al. 2012)
	Common death adder (*Acanthophis antarticus*)	*C. serpentis*	(Morgan et al. 1999c)
	Eastern/mainland tiger snake (*Notechis scutatus*)	*C. serpentis*	(Morgan et al. 1999c)
	Mulga/king brown snake (*Pseudechis australis*)	*Cryptosporidium* sp.	(Morgan et al. 1999c)
	Red-bellied black snake (*Pseudechis porphyriacus*)	*C. tyzzeri*	(Morgan et al. 1999c)
	Taipan (*Oxyuranus scutellatus*)	*C. serpentis*	(Morgan et al. 1999c; Xiao et al. 2004)
Pythonidae	**Ball python** (*Python regius*)	*C. ducismarci*, *C. muris*, *C. serpentis*, *C. tyzzeri*, tortoise genotype, *Cryptosporidium* sp.	(Xiao et al. 2004; Pedraza-Diaz et al. 2009; Sevá Ada et al. 2011b)
	Burmese python (*Python mollurus*)	*C. serpentis*	(Xiao et al. 2004)
	Boelen's python (*Morelia boeleni*)	*C. serpentis*	(Xiao et al. 2004)
	Green python (*Chondropython viridis*)	*C. serpentis*, *C. varanii*, *Cryptosporidium* sp.	(Xiao et al. 2004)

(continued)

Table 5.2 (continued)

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
	Indian rock python (*Python molurus*)	*C. serpentis*	(Rinaldi et al. 2012)
	Woma python (*Aspidites ramsayi*)	*C. tyzzeri*, *Cryptosporidium* sp.	(Morgan et al. 1999c; Cerveny et al. 2012)
Viperidae	**Bornmueller's viper** (*Vipera bornmuelleri*)	*C. serpentis*	(Xiao et al. 2004)
	Eastern diamondback rattlesnake (*Crotalus adamanteus*)	*C. serpentis*	(Graczyk and Cranfield 2000)
	Jararaca (*Bothropoides jararaca*)	*C. serpentis*	(Sevá Ada et al. 2011b)
	Jararacussu (*Bothrops jararacussu*)	*C. serpentis*	(Sevá Ada et al. 2011b)
	Mountain viper (*Vipera wagneri*)	*C. serpentis*	(Xiao et al. 2004)
	Nikolski viper (*Vipera nikolski*)	*C. serpentis*	(Ryan et al. 2003a)
	Northwestern tropical rattlesnake (*Crotalus durissus culminatus*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Pit viper (*Crotalus viridis viridis*)	*Cryptosporidium* sp.	(Cerveny et al. 2012)
	Timber rattlesnake (*Crotalus horridus*)	*C. serpentis*	(Levine 1980; Heuschele et al. 1986)
	Tropical rattlesnake (*Caudisona durissa*)	*C. serpentis*	(Sevá Ada et al. 2011b)

(*Elaphe vulpina gloydi*), milk snake (*Lampropeltis triangulum*), mangrove monitor (*Varanus indicus*), and prairie king snake (*Lamproletis calligaster*); *C. muris* in a corn snake (*Pantherophis guttatus guttatus*); and rat genotype I in a boa constrictor probably represent passive transmission as a consequence of feeding on infected rodents (Xiao et al. 2004).

Koudela and Modrý (1998) identified and named the species *C. saurophilum* from five lizard species: the desert monitor (*Varanus griseus*), emerald monitor (*Varanus prasinus*), leopard gecko (*Eublepharis macularius*), Schneider's skink (*Eumeces schneideri*), and skink (*Mabuya perrotetii*). Pavlásek and Ryan (2008) subsequently showed that *C. saurophilum* was indistinguishable from *C. varanii*, a species described 4 years earlier in an emerald monitor (Pavlásek et al. 1995), and proposed that *C. varanii* should take precedence as the species name. *Cryptosporidium varanii* (syn. *saurophilum*) infects the intestine and cloaca of a number of lizard species (Table 5.3), causing weight loss and abdominal swelling (Koudela and Modrý 1998). In contrast to *C. serpentis* in snakes, the disease is observed in

Table 5.3 *Cryptosporidium* spp. identified in lizards

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Agamidae	**Bearded dragon** (*Pogona vitticeps*)	*C. serpentis*, *C. varanii*	(Xiao et al. 2004)
	Damara rock agama (*Agama planiceps*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Frilled lizard (*Chlamydosaurus kingui*)	*C. serpentis*, *Cryptosporidium* sp.	(Pedraza-Diaz et al. 2009; Rinaldi et al. 2012)
	Ground agama (*Agama aculeata*)	*Cryptosporidium* sp.	(Upton et al. 1989)
Chamaeleonidae	**Giant Madagascar chameleon** (*Chamaeleo oustaleti*)	*C. serpentis*	(Pedraza-Diaz et al. 2009)
	Mountain chameleon (*Chamaeleo montium*)	*C. serpentis*, *C. varanii*	(Xiao et al. 2004)
	Veiled chameleon (*Chamaeleo calyptratus*)	*C. ducismarci*, *C. varanii*, *Cryptosporidium* sp.	(Koudela and Modrý 1998; Pedraza-Diaz et al. 2009; Rinaldi et al. 2012)
Gekkonidae	**African fat-tailed gecko** (*Hemiteconyx caudicintus*)	*C. varanii*	(Pedraza-Diaz et al. 2009)
	Gargoyle gecko (*Rhodocodactylus auriculatus*)	*C. serpentis*, *C. varanii*	(Xiao et al. 2004)
	Gecko (Gekkoninae sp.)	*C. parvum*, *C. varanii*	(Xiao et al. 2004)
	Giant ground gecko (*Chondrodactylus angulifer*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Leopard gecko (*Eublepharis macularius*)	*C. parvum*, *C. serpentis*, *C. varanii*, *Cryptosporidium* sp.	(Koudela and Modrý 1998; Xiao et al. 2004; Pedraza-Diaz et al. 2009; Richter et al. 2011; Rinaldi et al. 2012)
	Madagascar giant day gecko (*Phelsuma madagascariensis grandis*)	*Cryptosporidium* sp.	(Upton et al. 1989)
	Mediterranean house gecko (*Hemidactylus turcicus turcicus*)	*Cryptosporidium* sp.	(Upton et al. 1989)
Gerrhosauridae	**Plated lizard** (*Gerrhosaurus* sp.)	*C. varanii*	(Xiao et al. 2004)

(continued)

Table 5.3 (continued)

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Iguanidae	**Green iguana** (*Iguana iguana*)	*C. varanii*, *C. parvum*, avian genotype V	(Xiao et al. 2004: Kik et al. 2011)
Lacertidae	**European green lizard** (*Lacerta viridis*)	*C. varanii*	(Koudela and Modrý 1998)
Scincidae	**Ocellated skink** (*Chalcides ocellatus*)	*C. varanii*	(Koudela and Modrý 1998)
	Schneider's skink (*Eumeces schneideri*)	*C. varanii*	(Koudela and Modrý 1998)
	Skink (*Mabuya perrotetii*)	*C. serpentis*, *C. varanii*	(Koudela and Modrý 1998; Xiao et al. 2004)
Varanidae	**Crocodile monitor** (*Varanus salvadori*)	*C. muris*	(Ryan et al. 2003a)
	Desert monitor (*Varanus griseus*)	*C. serpentis*, *C. varanii*	(Koudela and Modrý 1998) (Ryan et al. 2003a; Xiao et al. 2004)
	Emerald monitor (*Varanus prasinus*)	*C. varanii*, *C. serpentis*	(Pavlásek et al. 1995; Koudela and Modrý 1998)
	Mangrove monitor (*Varanus indicus*)	*C. tyzzeri*	(Xiao et al. 2004)
	Monitor sp. (*Varanus* sp.)	*C. varanii*, *C. parvum*	(Xiao et al. 2004)
	Nile monitor (*Varanus niloticus*)	*C. serpentis*	(Xiao et al. 2004)
	Savannah monitor (*Varanus exanthematicus*)	*C. serpentis*	(Morgan et al. 1999c; Xiao et al. 2004)

juveniles but not adults (Koudela and Modrý 1998). Oocysts are smaller than *C. serpentis* at 5.0 μm (4.4–5.6 μm) × 4.7 μm (4.2–5.2 μm) with a shape index of 1.09 (1.04–1.12) (Koudela and Modrý 1998). Under experimental conditions, *C. varanii* was not infectious for snakes, birds, or mice (Koudela and Modrý 1998); however, natural *C. varanii* infections have been detected in at least nine snake species from three families (Table 5.2).

Other *Cryptosporidium* taxa identified in Squamata include a genotype sharing 99 % identity with *C. serpentis* from a leopard gecko (Richter et al. 2011), avian genotype V from a green iguana (*Iguana iguana*) (Kik et al. 2011), *C. ducismarci* and the tortoise genotype from a ball python (Pedraza-Diaz et al. 2009), *C. ducismarci* from a veiled chameleon (Pedraza-Diaz et al. 2009), and a genotype from a New Guinea boa (*Candoia aspera*) and Japanese grass snake (*Rhabdophis tigrinus*) sharing 98 % similarity with *C. ducismarci* and avian genotype II (Xiao et al. 2002; Kuroki et al. 2008).

5.3.2 *Testudines*

The order Testudines is comprised of 250 species of turtles in 14 families and more than 20 genera. All species possess a bony and cartilaginous carapace. Turtles are found in a great variety of habitats, including dry upland regions as well as marine and fresh waters. Diet is similarly varied, with mostly omnivorous species, but also some herbivorous and carnivorous species.

Cryptosporidium ducismarci (previously known as *Cryptosporidium* sp. ex *Testudo marginata* CrIT-20) has been proposed as a new *Cryptosporidium* species (Traversa et al. 2008; Traversa 2010). This species, which infects the intestinal epithelium of *Testudo marginata*, also has been detected in an asymptomatic veiled chameleon and ball phyton in Spain (Pedraza-Diaz et al. 2009) and in the pancake tortoise (*Malacochersus tornieri*) and Russian tortoise (*Testudo horsfieldi*) in the US (Griffin et al. 2010). Biological data, including descriptions of pathology, and oocyst morphometry data are lacking for this species description.

The *Cryptosporidium* tortoise genotype has been identified in an asymptomatic Indian star tortoise (*Geochelone elegans*) at the Lisbon Zoo (Alves et al. 2005). The SSU rRNA sequence of the isolate identified by Alves et al. (2005) is identical to a sequence previously reported by Xiao et al. (2002) in an Indian star tortoise at the St. Louis Zoo (GenBank accession no. AY120914), and a sequence from an environmental isolate in Maryland, USA (Yang et al. 2008). In a study of pet reptiles, Pedraza-Diaz et al. (2009) detected *Cryptosporidium* sp. in 17.6 % of tortoise samples and identified the *Cryptosporidium* tortoise genotype in a Hermann's tortoise (*Testudo hermanni*) and a ball python (*Python regius*).

5.4 *Cryptosporidium* and Cryptosporidiosis of Birds

GenBank accession numbers and phylogenetic relationships among representative *Cryptosporidium* small subunit rRNA sequences from birds are presented in Table 5.4 and Fig. 5.2. Three avian-associated *Cryptosporidium* species are recognized: *Cryptosporidium meleagridis*, *Cryptosporidium baileyi*, and *Cryptosporidium galli*. These species infect a broad range of birds; however, they differ in host range and site of infection. *Cryptosporidium meleagridis* also causes disease in humans (McLauchlin et al. 2000; Alves et al. 2003; Cama et al. 2003).

Cryptosporidium meleagridis is primarily a parasite of intestinal epithelial cells of birds, particularly turkeys (Slavin 1955; Sreter and Varga 2000). *Cryptosporidium baileyi* inhabits the respiratory tract, bursa of Fabricius, and cloaca of the domestic chicken and a broad range of other birds (Current et al. 1986; Sreter and Varga 2000). Endogenous stages of *C. galli* are localized on glandular epithelial cells of the proventriculus (Ryan et al. 2003b).

The three avian species can be distinguished based on oocyst morphology. Oocysts of *C. meleagridis* are the smallest of the three, measuring

Table 5.4 GenBank accession numbers of representative *Cryptosporidium* small subunit rRNA gene sequences from avians. A phylogeny constructed from sequences in this table is presented in Fig. 5.2

Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
Anseriformes	Waterfowl: geese and ducks	**Black duck** (species unspecified) [AF316630] **Goose** (species unspecified) [AY120912, EF641009, FJ607874, FJ607886, FJ607887, FJ607896, FJ607898, FJ607910, FJ607918] **Canada goose** (*Branta canadensis*) [AY324635, AY324637–AY324639, AY324641, AY324643, AY504512–AY504517] **Goose** (*Anser anser f. domestica*) [FJ984564] **Mallard** (*Anas platyrhynchos*) [GU082388]
Charadriiformes	Gulls and woodcock	**Eurasian woodcock** (*Scolopax rusticola*) [AY273769] **Kelp gull** (*Larus dominicanus*) [GQ355891]
Columbiformes	Pigeons and doves	**Fan-tailed pigeon** (*Columba livia*) [HM116382] **Pigeon** (species unspecified) [EU032319–EU032324] **Rufous turtle dove** (*Streptopelia orientalis*) [HM116384]
Falconiformes	Black vulture	**Black vulture** (*Coragyps atratus*) [GQ227474]
Galliformes	Fowl: chickens, turkey, quail, Indian peafowl	**Chicken** (*Gallus gallus domesticus*) [AF093495, JX548291, JX548292, JX548299, GQ227476, AY168847, AY168848] **Cockatiel** (*Nymphicus hollandicus*) [GQ227477] **Indian peafowl** (*Pavo cristatus*) [GQ227478] **Quail** (*Coturnix coturnix*) [JQ217141, JQ217142] **Quail** (species unspecified) [AF316631] **Turkey** (*Meleagris gallopavo*) [AF112574]
Gruiformes	Coot	**Eurasian coot** (*Fulica atra*) [FJ984565]
Passeriformes	Perching birds: finches, canaries, sparrows, nightingale, waxwings, corvids	**Atlantic canary** (*Serinus canaria*) [GU074388, GU074389] **Aurora finch** (*Pytilia phoencoptera*) [AF316627–AF316629] **Blackbilled magpie** (*Pica pica*) [HM116380]

(continued)

Table 5.4 (continued)

Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
		Bohemian waxwing (*Bombycilla garrulus*) [HM116383, HM116388]
		Canary (*Serinus canaria*) [GQ227479, EU543269]
		Common myna (*Acridotheres tristis*) [HM116374]
		Crested lark (*Galerida cristata*) [HM116379]
		Gold finch (*Carduelis carduelis*) [AY168846]
		Gouldian finch (*Erythrura gouldiae*) [AF316623–AF316625, HM116377]
		Java sparrow (*Padda oryzivora*) [GU074384]
		Lesser seed finch (*Oryzoborus angolensis*) [EU543270]
		Plum-headed finch (*Neochmia modesta*) [AF316626]
		Red-billed Leiothrix (*Leiothrix lutea*) [HM116375]
		Red-billed blue magpie (*Urocissa erythrorhyncha*) [HM116386]
		Silver eared leiothrix (*Leiothrix argentauris*) [HM116387]
		Society finch (*Lonchura striata domestica*) [GU074390]
		White Java sparrow (*Padda oryzivora*) [HM116376]
		Zebra finch (*Taeniopygia guttata*) [HM116378]
Psittaciformes	Parrots, cockatiels, lovebirds	**Cockatiel** (*Nymphicus hollandicus*) [AB471645–AB471648, EU543268, GQ227477, GQ227481, GU074385–GU074387, HM116381, HM116385]
		Indian rose parakeet (*Psittacula krameri*) [AF180339]
		Peach-faced lovebird (*Agapornis roseicollis*) [GQ227480]
Struthioniformes	Ostrich	**Ostrich** (*Struthio camelus*) [DQ002931]

4.5–6.0 μm × 4.2–5.3 μm with a shape index (length/width) of 1.0–1.3. *Cryptosporidium baileyi* oocysts measure 6.0–7.5 μm × 4.8–5.7 μm with a shape index of 1.1–1.8 (Lindsay et al. 1989), and oocysts of *C. galli* measure 8.2 × 6.3 μm with a shape index of 1.3 (Ryan et al. 2003b). Relatively little is known about the biology of other cryptosporidia infecting birds.

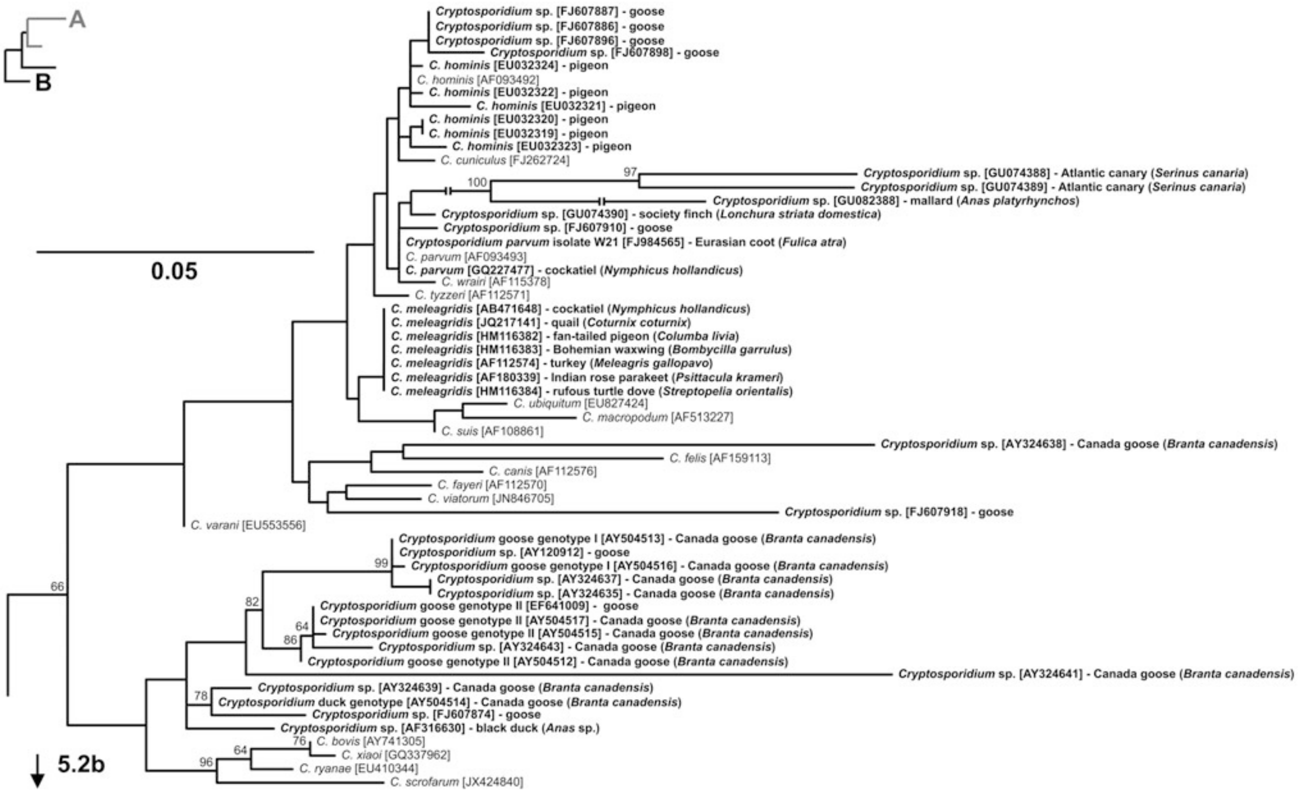

Fig. 5.2 (continued)

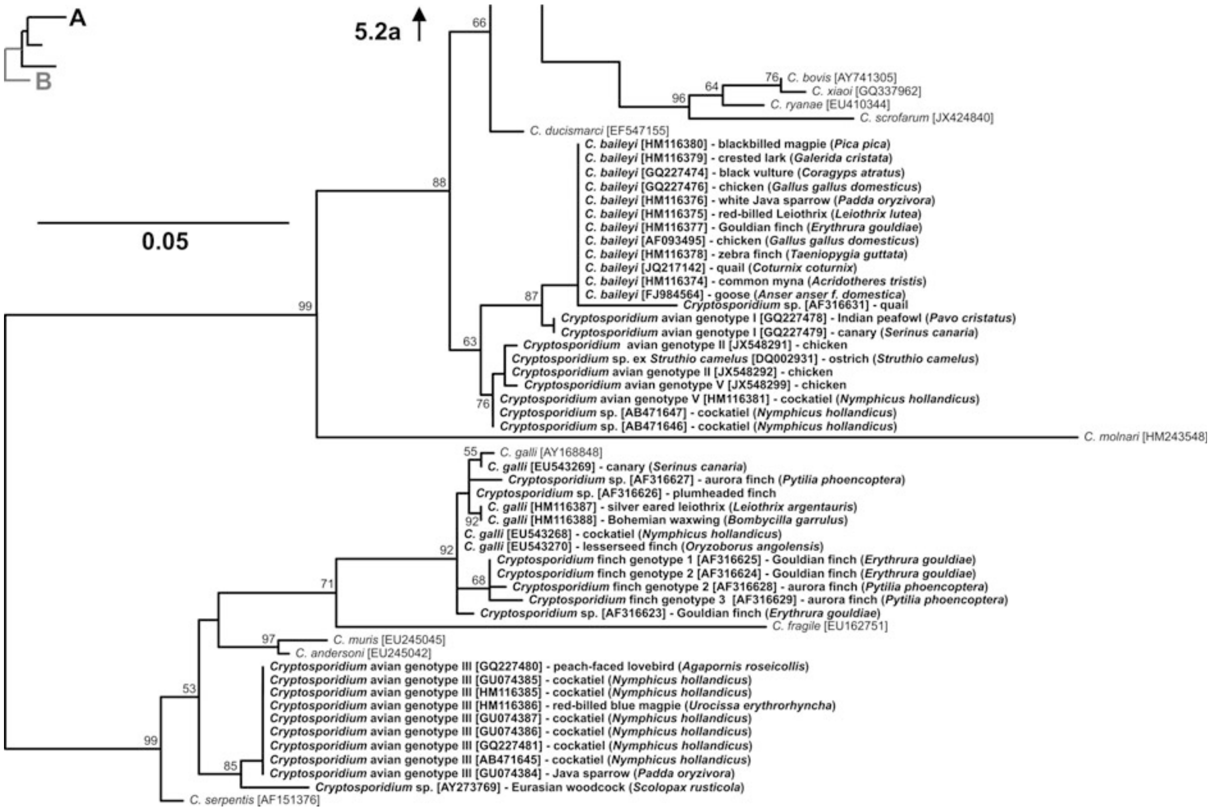

Fig. 5.2 A SSU rDNA-based maximum likelihood (GTRCAT model) tree of *Cryptosporidium* spp. sequences showing clades of cryptosporidia infecting avians. *Cryptosporidium* sp. detected in avians are in bold. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown at nodes. Bootstrap values <50 are not shown. Interrupted branches have been shortened fivefold

Cryptosporidium has been reported in 17 out of 26 avian orders. Members of the following orders have not yet been identified as hosts:

Tinamiformes: This is a very old avian lineage comprising one family, nine genera, and 47 species. Members are ominvorous, feeding on a variety of seeds and invertebrates. Many species occur in forests or open grasslands, but they generally prefer dryland habitats.

Gaviiformes: This order comprises one family, one genus, and five species of aquatic birds that primarily inhabit North America and Eurasia. They feed on fish, amphibians, or aquatic invertebrates and inhabit both freshwater and marine environments during their annual cycle.

Podicipediformes: This order comprises 22 species in one family and six genera of aquatic birds. Molecular phylogenies indicate that they are closely related to loons and flamingoes. They feed on fish, amphibians, and aquatic invertebrates.

Procellariiformes: This order comprises four families, 26 genera, and about 112 species of seabirds. All inhabit offshore marine environments and most return to land only for nesting. Although, most feed exclusively on marine invertebrates or fish, a couple of species scavenge carrion on islands.

Opisthocomiformes: This order comprises one species, genus, and family of tropical birds that inhabit swamps and mangroves of South America. They feed on vegetable matter (seeds, nuts, leaves, and fruits), and have well-developed ceca that facilitates fermentation in the digestive tract.

Cuculiformes: This is a medium sized order comprising six families, 30 genera, and 143 species. Members inhabit Africa, Asia, Australasia, Eurasia, and the Americas (South, Central, and North).

Apodiformes: This order comprises two families containing approximatley 24 genera and 100 species of small birds. They mostly inhabit the northern hemisphere and can be found in a variety of habitats. They feed aerially on insects.

Trochiliformes: These small, nectar-feeding birds include hermits and hummingbirds. There are approximately 330 species in one family with about 100 genera. The majority of species occur in tropical and subtropical Central and South America.

Trogoniformes: Trogons comprise approximately 39 species in one family with six to eight genera. They inhabit tropical forests, where they feed mainly on insects or fruit.

5.4.1 Struthioniformes

The order Struithioniformes (including cassowaries, emus, kiwis, ostriches, and rheas) is comprised of some of the oldest avian species. There are about 12 species in five families and six genera. All are flightless, forage on insects or vegetation, and lay large eggs with thick shells. Ceca are often well developed in these species.

Cryptosporidium infections in ostriches can be subclinical (Gajadhar 1993), or characterized by a prolapsed phallus/cloaca (Bezuidenhout et al. 1993; Santos et al. 2005), and edema/necrosis of the pancreas (Jardine and Verwoerd 1997). In Brazil, ostriches with a prolapsed cloaca shed oocysts of *Cryptosporidium* avian genotype II measuring 6.0 μm (5.0–6.5 μm) × 4.8 μm (4.2–5.3 μm) with a shape index of 1.31 (Santos et al. 2005; Meireles et al. 2006). *Cryptosporidium* avian genotype II is not infectious for 1-day-old chicks under experimental conditions (Meireles et al. 2006), although it has been detected in a naturaly infected chicken (GenBank accession no. JX548291; unpublished). *Cryptosporidium* avian genotype II was detected in 23 % of farmed ostriches (*Struthio camelus*) in Vietnam (Nguyen et al. 2013). The highest prevalence and oocyst shedding intensity was observed in birds aged 61–90 days; younger and older birds had a lower prevalence and shed fewer oocysts (Nguyen et al. 2013). Oocysts from subclinical *Cryptosporidium* infections in ostriches being imported into Canada measured 4.6 μm (3.9–6.1 μm) × 4.0 μm (3.3–5.0 μm) with a shape index of 1.15 (range 1.0–1.4) (Gajadhar 1993), which is similar to oocysts of *C. meleagridis*. Oocysts were not infectious for suckling mice, chickens, turkeys, or quail (Gajadhar 1993, 1994). *Cryptosporidium baileyi* oocysts were identified in an ostrich from the Czech Republic (Ryan et al. 2003a). *Cryptosporidium* sp. was detected in 60 % of farmed ostriches and rheas originating from Belgium, France, Netherlands Portugal, and Spain (Gordo et al. 2002).

5.4.2 Anseriformes

Waterfowl, including ducks, geese and swans, form the order Anseriformes, with about 162 species in three families and 52 genera. These birds are omnivorous, feeding on combinations of vegetation and invertebrates, with a few groups feeding on small aquatic vertebrates.

Three species and five named genotypes of *Cryptosporidium* have been identified in ducks, geese, mergansers, and swans (Table 5.5). In addition, five unnamed genotypes have been reported in Canada geese (*Branta canadensis*) (Jellison et al. 2004), however, sequences have not been deposited in GenBank, and it is not clear if they differ from subsequently named genotypes. Canada geese have also been shown to host the human pathogens *C. hominis* and *C. parvum*, and the rodent-specific muskrat genotype I (Graczyk et al. 1998d; Zhou et al. 2004b; Jellison et al. 2009). It is hypothesized that birds serve as mechanical vectors for mammalian cryptosporidia, and this is supported by data showing that *C. parvum* does not infect Canada geese or Pekin ducks (*Anas platyrhynchos*) under experimental conditions but oocysts remain viable following passage (Graczyk et al. 1996b, 1997).

Cryptosporidium has been reported to cause varying degrees of respiratory distress in ducks and geese (O'Donoghue et al. 1987). *Cryptosporidium baileyi* has been identified in the bursa of Fabricius and cloaca of ducks with mild symptoms (Lindsay et al. 1989), and the bursa of Fabricius and conjunctiva of domestic geese with no clinical symptoms (Chvala et al. 2006).

Table 5.5 *Cryptosporidium* spp. identified in Anseriformes species

Host species (scientific name)	*Cryptosporidium* taxa	References
American widgeon (*Anas americana*)	*Cryptosporidium* sp.	(Kuhn et al. 2002)
Black swan (*Cygnus atratus*)	*Cryptosporidium* sp.	(Rohela et al. 2005)
Blue-winged teal (*Anas discors*)	*Cryptosporidium* sp.	(Kuhn et al. 2002)
Canada goose (*Branta canadensis*)	*C. hominis*, *C. hominis*-like, *C. parvum*, muskrat genotype I, duck genotype, goose genotype I, goose genotype II, 5 unnamed genotypes	(Graczyk et al. 1998d; Jellison et al. 2004, 2009; Zhou et al. 2004b)
Common merganser (*Mergus merganser*)	*Cryptosporidium* sp.	(Kuhn et al. 2002)
Domestic goose (*Anser anser f. domestica*)	*C. baileyi*	(Chvala et al. 2006)
Green-winged teal (*Anas cercca carolinensis*)	*Cryptosporidium* sp.	(Kuhn et al. 2002)
Hooded merganser (*Lophodytes cucullatus*)	*Cryptosporidium* sp.	(Kuhn et al. 2002)
Mallard (*Anas platyrhynchos*)	*Cryptosporidium* sp.	(O'Donoghue et al. 1987; Kuhn et al. 2002)
Swan goose (*Anser cygnoides*)	*Cryptosporidium* sp.	(Rohela et al. 2005)

5.4.3 Galliformes

There are approximately 290 species in five families and 80 genera of gallinaceous birds. These terrestrial species feed mostly on seeds and small insects. This group has been extensively domesticated for agricultural purposes, and many species have been introduced to areas well outside of their historic range.

A number of gallinaceous birds including the domestic chicken (*Gallus gallus domesticus*), grouse (*Tetrastes bonasia rupestris*), and capercaillie (*Tetrao urogallus*), are natural hosts of *C. galli* (Ryan et al. 2003b; Ng et al. 2006).

Non-genotyped cryptosporidia have been detected in the common quail (*Coturnix coturnix*), common peafowl (*Pavo cristatus*), great argus (*Argusianus argus*), great currasow (*Crax rubra*), red-legged partridge (*Alectoris rufa*), and ring-necked pheasant (*Phasianus colchicus*) (O'Donoghue et al. 1987; Rohela et al. 2005; Lim et al. 2007). Infections in the common quail and ring-necked pheasant have been associated with clinical signs of respiratory disease, and oocysts recovered from these hosts were infectious for chickens (O'Donoghue et al. 1987).

Cryptosporidium meleagridis caused an outbreak of respiratory and diarrheal cryptosporidiosis with greater than 50 % mortality in red-legged partridges (*Alectoris rufa*) on a game farm in Spain (Pages-Mante et al. 2007).

5.4.4 Phoenicopteriformes

Phoenicopteriformes is a small order of five species in one family and three genera of flamingoes. These long-legged wading birds use a specialized bill to filter-feed invertebrates or algae from shallow waters. The intestine is relatively long compared to other avian species.

In the only report from this order, *C. galli* was identified in a Cuban flamingo (*Phoenicopterus ruber*) from the Czech Republic (Ng et al. 2006).

5.4.5 Sphenisciformes

Sphenisciformes is comprised of 17 penguin species in one family and six genera. Penguins are flightless birds of the southern oceans, feeding on fish and krill in offshore areas. Very little is known about cryptosporidiosis in this group of birds.

Cryptosporidium oocysts have been detected in 6.6 % (11/167) of stools from the Adelie penguin (*Pygoscelis adeliae*) from the Antarctic territory (Fredes et al. 2007), and in 32.8 % (21/64) of gentoo penguins (*Pygoscelis papua*) from Ardley Island, King George Island, South Shetland Islands, and the Antarctic Specially Protected Area no. 150 (Fredes et al. 2008).

5.4.6 Pelecaniformes

Pelecaniformes includes waterbirds comprising approximately 65 species in eight families and ten genera. These birds feed mostly on aquatic vertebrates. A gular pouch is usually present, and prey is often swallowed whole. Almost all inhabit marine waters for part of their annual cycle.

There have been just two reports of *Cryptosporidium* from the order Pelecaniformes. *Cryptosporidium baileyi* and a non-genotyped *Cryptosporidium* sp. were reported in a cormorant and great cormorant (*Phalacrocorax carbo*), respectively (Jellison et al. 2004; Plutzer and Tomor 2009).

5.4.7 Ciconiiformes

There are approximately 116 ciconiiform species in three families and 39 genera. All are long-legged wading birds, feeding in aquatic environments on a variety of invertebrates and vertebrates.

Cryptosporidium has been reported in a marabou stork (*Leptoptilos crumeniferus*) from a zoo in Malaysia (Rohela et al. 2005) and 12.5 % (3/24) of white storks (*Ciconia ciconia*) from Poland (Majewska et al. 2009). The species infecting white storks was identified as *C. parvum* using fluorescence in situ hybridization.

5.4.8 Falconiformes

There are approximately 304 species in three to five families and 83 genera of falconiform birds. These birds feed on vertebrate prey or carrion. Most nest in trees or cliffs and are terrestrial in their habits.

Cryptosporidium baileyi and *C. parvum* have been identified in Falconiforms, and both are associated with disease. *Cryptosporidium parvum* caused anorexia, mild respiratory difficulties, and mild bilateral ocular discharge in a 3-month old gyrfalcon (*Falco rusticolus*), and *C. baileyi* caused mild bilateral conjunctivities and sinusitis in a 13-year-old gyrfalcon × Saker falcon hybrid (*Falco rusticolus* × *Falco cherrug*) (Barbon and Forbes 2007). Both raptors recovered following treatment with paromomycin. *Cryptosporidium baileyi* similarly caused an upper respiratory tract infection in three mixed-bred falcons (*Falco rusticolus* × *Falco cherrug*) (van Zeeland et al. 2008). One of the birds had epiglottal swelling and laryngeal stridor, and two had nasal discharge and sneezing. Oocyst shedding was not detected in any of the birds. *Cryptosporidium baileyi* also was identified in a Saker falcon (*Falco cherrug*) with inflammation of the middle ears, conjunctivae, third eyelids, choanae, larynx, trachea, salivary glands of the tongue, syrinx, and turbinates (Bougiouklis et al. 2012), and in a captive black vulture (*Coragyps atratus*) (Nakamura et al. 2009).

5.4.9 Charadriiformes

Charadriiformes is a diverse order of shorebirds, with about 367 species distributed among 17 families and 88 genera. Most species feed on invertebrate prey, and utilize marine habitats during part of their annual cycle.

Cryptosporidium sp. has been reported in black-headed gulls (*Chroicocephalus ridibundus*) (Pavlásek 1993; Smith et al. 1993; Ryan et al. 2003a), herring gulls (*Larus argentatus*) (Smith et al. 1993; Bogomolni et al. 2008), and kelp gulls

(*Larus dominicanus*) (GenBank accession no. GQ355891; unpublished). Smith et al. (1993) detected *Cryptosporidium* oocysts measuring 4.7 μm (4.4–5.2 μm) × 5.2 μm (4.7–5.8 μm) in feces from gulls trapped at two refuse sites and other locations in Scotland, and found no difference in *Cryptosporidium* prevalence between the black-headed gull and the herring gull. *Cryptosporidium baileyi* was identified as a cause of significant morbidity and mortality in 28–100 % of black-headed gulls in the Czech Republic (Pavlásek 1993). *Cryptosporidium baileyi* from black-headed gulls infected 4-day-old chickens (*Gallus gallus f. domestica*), causing 40 % mortality (Pavlásek 1993). The intestinal locations of developmental stages are similar to those in the black-headed gull (Pavlásek 1993). *Cryptosporidium baileyi* was reported in a black-headed gull, and a novel *Cryptosporidium* genotype (GenBank accession no. AY273769) was identified in a wild-caught Eurasian woodcock (*Scolopax rusticola*) from the Czech Republic (Ryan et al. 2003a).

5.4.10 Gruiformes

Gruiformes contains 212 species distributed among 11 families and 61 genera. Most species inhabit marshland areas, and feed on invertebrates, seeds, or other vegetation. Ceca and hindgut fermentation are common in this group.

Cryptosporidium baileyi has been identified in a crane from the Czech Republic (Ng et al. 2006). In Korea, a 4-month old white naped crane (*Grus vipio*) that died from a disseminated *Eimeria* infection also had an incidental *Cryptosporidium* infection of the cloaca (Kim et al. 2005). In Hungary, Plutzer and Tomor (2009) identified *C. parvum* in a wild Eurasian coot (*Fulica atra*) (GenBank accession no. FJ984565).

5.4.11 Columbiformes

Pigeons and doves make up the order Columbiformes. Although there are 308 species worldwide, only one or two families containing 42 genera are recognized. These birds occupy a diverse range of terrestrial habitats, feeding almost exclusively on seeds and grains.

There have been relatively few reports of *Cryptosporidium* in pigeons (Ozkul and Aydin 1994; Rodriguez et al. 1997; Abreu-Acosta et al. 2009; Qi et al. 2011; Radfar et al. 2012). *Cryptosporidium hominis* has been reported in rock pigeons (*Columba livia*) on Tenerife, one of the Canary Islands, suggesting that pigeons can play a role in the transmission of human-pathogenic cryptosporidia (Abreu-Acosta et al. 2009). In a study of *Cryptosporidium* in birds at pet stores in China, Qi et al. (2011) detected *C. meleagridis* in a fan-tailed pigeon and a rufous turtle dove (*Streptopelia orientalis*).

5.4.12 Psittaciformes

Birds in the order Psittaciformes order, which contains 364 species from 85 genera in the family Psittacidae, inhabit trees in dense, tropical or subtropical forests, and feed almost exclusively on fruits and seeds. Although there have been few studies of psittaciforms in their natural environment, captive psittaciforms host a number of *Cryptosporidium* species and genotypes (Table 5.6). The greatest diversity of taxa has been detected in the cockatiel (*Nymphicus hollandicus*), which hosts four species (*C. baileyi*, *C. galli*, *C. meleagridis*, and *C. parvum*) and three genotypes (avian genotypes II, III, and V) (Abe and Iseki 2004; Ng et al. 2006; Antunes et al. 2008; Nakamura et al. 2009; Abe and Makino 2010; Qi et al. 2011; Gomes et al. 2012). The galah (*Eolophus roseicapilla*), which is in the same subfamily as the cockatiel, also hosts avian genotype II (Ng et al. 2006).

Although most cases of *Cryptosporidium* infection in psittaciform birds have been asymptomatic, there have been reports of clinical disease. Latimer et al. (1992) diagnosed cryptosporidiosis in four cockatoos with psittacine beak-and-feather disease. *Cryptosporidium* infection was confined to the bursa of Fabricius in three of the birds, and was more widespread in the intestine of the fourth. All birds had intermittent diarrhea. Makino et al. (2010) detected avian genotype II in 35 % (13/37) of infected peach-faced lovebirds (*Agapomis roseicollis*). All birds had symptoms of infection including weight loss and chronic vomiting.

5.4.13 Strigiformes

The owls make up a small order of about 180 species in two families and 29 genera. All species are predators of small vertebrates, principally rodents. Most species are nocturnal and inhabit forested areas, though a few nest underground in burrows.

In a study of 12 adult owls held in captivity in south Brazil, da Silva et al. (2009) isolated *Cryptosporidium* oocysts measuring 5–6 μm × 4–5 μm from a barn owl (*Tyto alba*), great horned owl (*Bubo virginianus*), and striped owl (*Phinoptynx clamator*). Owls showed no clincal signs of disease.

Molina-Lopez et al. (2010) diagnosed ocular and respiratory cryptosporidiosis in 16 wild fledgling scops owls (*Otus scops*) up to 2 months after they were admitted to a wildlife rehabilitation center in Catalonia, northern Spain; the owls were born in the wild and were healthy when they arrived at the center. Blepharoedema, conjunctival hyperaemia, and mucopurulent ocular discharge were diagnosed unilaterally in 75 % (12/16) of the birds and bilaterally in 25 % (4/16). Five owls (31 %) developed diffuse epithelial corneal edema, one exhibited mild anterior exudative uveitis, and another developed rhinitis. *Cryptosporidium baileyi*, measuring 6.5–7.0 μm × 5.0–5.5 μm, was identified in samples from two birds that were

Table 5.6 *Cryptosporidium* spp. identified in Psittaciformes species

Host species (scientific name)	*Cryptosporidium* taxa	References
Alexandrine parakeet (*Psittacula eupatria*)	Avian genotype II, *Cryptosporidium* sp.	(Ng et al. 2006; Papini et al. 2012)
Blue-fronted Amazon (*Amazona aestiva*)	*Cryptosporidium* sp.	(Papini et al. 2012)
Budgerigar (*Melopsittacus undulatus*)	*Cryptosporidium* sp.	(Nakamura et al. 2009)
Cockatiel (*Nymphicus hollandicus*)	*C. baileyi*, *C. galli*, *C. meleagridis*, *C. parvum*, avian genotype II, avian genotype III, avian genotype V	(Abe and Iseki 2004; Ng et al. 2006; Antunes et al. 2008; Nakamura et al. 2009; Abe and Makino 2010; Qi et al. 2011; Gomes et al. 2012)
Eastern rosella (*Piatycercus eximius*)	*Cryptosporidium* sp.	(Papini et al. 2012)
Eclectus parrot (*Eclectus roratus*)	Avian genotype II	(Ng et al. 2006)
Galah (*Eolophus roseicapilla*)	Avian genotype II	(Ng et al. 2006)
Goffin's cockatoo (*Cacatua goffini*)	*Cryptosporidium* sp.	(Nakamura et al. 2009)
Indian ring-necked parrot (*Psittacula krameri*)	*C. meleagridis*	(Morgan et al. 2000b)
Major Mitchell's cockatoo (*Lophochroa leadbeateri*)	Avian genotype II	(Ng et al. 2006)
Peach faced lovebirds (*Agapomis roseicollis*)	Avian genotype III	(Makino et al. 2010)
Princess parrot (*Polytelis alexandrae*)	Avian genotype II	(Ng et al. 2006)
Red-bellied macaw (*Orthopsittaca manilata*)	*Cryptosporidium* sp.	(Nakamura et al. 2009)
Red-crowned Amazon (*Amazona viridigenalis*)	*C. baileyi*	(Ryan et al. 2003a)
Rose-ringed parakeet (*Psittacula krameri*)	*C. meleagridis*	(Ryan et al. 2003a)

(continued)

Table 5.6 (continued)

Host species (scientific name)	*Cryptosporidium* taxa	References
Salmon-crested cockatoo (*Cacatua moluccensis*)	*Cryptosporidium* sp.	(Rohela et al. 2005)
Sun conure (*Aratinga solstitialis*)	Avian genotype II	(Ng et al. 2006)
Turquoise parrot (*Neophema pulchella*)	*C. galli*	(Ng et al. 2006)
White-eyed parakeet (*Aratinga leucophthalma*)	Avian genotype II	(Sevá Ada et al. 2011a)

euthanized due to the severity of their disease. The remaining owls recovered following a 15-day treatment with azithromycin.

5.4.14 Caprimulgiformes

This small order of insectivorous birds has about 118 species in five families and 22 genera. Most feed nocturnally, on the wing. These species generally occur near upland forests, and almost all species nest on the ground.

Cryptosporidium muris has been detected in the tawny frogmouth (*Podargus strigoides*); although, the bird may have been a mechanical vector (Ryan et al. 2003a; Ng et al. 2006).

5.4.15 Piciformes

The piciform birds include woodpeckers and toucans, with approximately 398 species in five to nine families and eight genera. Most species occur in forests of the Americas, and almost all nest in cavities. The woodpeckers feed mostly on insects, but toucans are fruigivorous and the honeyguides have the unique ability to eat beeswax.

Cryptosporidium infection has been reported in a channel-billed toucan (*Rhamphastus vitellinus*), chestnut-eared aracari (*Pteroglossus castanotis*), and Toco toucan (*Ramphastos toco*) (Ryan et al. 2003a; Nakamura et al. 2009). The channel-billed toucan was infected with *C. baileyi* (Ryan et al. 2003a).

5.4.16 Coraciiformes

Hornbills, kingfishers, and rollers make up the order Coraciiformes, which has about 209 species in 11 families and 51 genera that are found mostly in Eurasia. These birds are generally omnivorous, feeding on a variety of invertebrates, small vertebrates, or fruits and seeds. The coraciiform birds typically inhabit forests, but ground dwelling species occur in sub-Saharan Africa. Most nest in cavities or burrows.

To date, only a few species from the order Coraciiforme have been identified as hosts for *Cryptosporidium*. *Cryptosporidium galli* was identified in a captive rhinocerous hornbill (*Buceros rhinoceros*) in the Czech Republic (Ng et al. 2006). In Malaysia, *Cryptosporidium* sp. was detected in a wrinkled hornbill (*Aceros corrugatus*) and a wreathed hornbill (*Aceros undulates*) at the Kuala Lumpur National Zoo and Zoo Negara, respectively (Rohela et al. 2005; Lim et al. 2007).

5.4.17 Passeriformes

Passeriformes is the largest avian order, with over 5,700 species in approximately 96 families and more than 1,200 genera. All species have feet for perching, and they occupy a wide range of habitats from dense forests to open grasslands. Fruits, seeds and invertebrates are the dominant foods in their diet.

Passerines are relatively frequent hosts of *Cryptosporidium* sp., some of which are human pathogens (Table 5.7). Yet, despite having more than 50 % of the avian diversity, passerines host only four species (*C. baileyi*, *C. galli*, *C. meleagridis*, and *C. parvum*) and three genotypes (avian genotypes I, III, and IV) of *Cryptosporidium* (Table 5.6).

Australian passerines infected with avian genotypes I, III, and IV showed no clinical signs; whereas, birds from the Czech Republic, which were primarily infected with *C. baileyi* and *C. galli*, had diarrhea and anorexia (Ng et al. 2006).

5.5 *Cryptosporidium* and Cryptosporidiosis of Mammals

Oocyst size and gastrointestinal localization of *Cryptosporidium* species reported in wild mammals are shown in Table 5.8. In contrast to cryptosporidia of domestic animals, oocyst morphometry, infection site, and course of infection are unknown for many *Cryptosporidium* genotypes infecting wild mammals, including bear, beaver, brushtail possum II, chipmunk II and III, *C. bovis*-like, *C. hominis*-monkey, *C. muris*-like, *C. ryanae*-variant, *C. suis*-like, deer, deer mouse I–IV, elephant seal, fox, giant panda, guinea pig, hamster, hedgehog, horse, kangaroo I, mink, mouse II,

Table 5.7 *Cryptosporidium* spp. identified in Passeriformes species

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Alaudidae	**Crested lark** (*Galerida cristata*)	*C. baileyi*	(Qi et al. 2011)
Bombycillidae	**Bohemian waxwing** (*Bombycilla garrulous*)	*C. galli*, *C. meleagridis*	(Qi et al. 2011; Sevá Ada et al. 2011a)
Cardinalidae	**Green-winged saltator** (*Saltator similis*)	*C. galli*	(Sevá Ada et al. 2011a)
Corvidae	**Black-billed magpie** (*Pica pica*)	*C. baileyi*	(Qi et al. 2011)
	Hooded crow (*Corvus cornix*)	*Cryptosporidium* sp.	(Plutzer and Tomor 2009)
	Red-billed blue magpie (Urocissa erythrorhyncha)	Avian genotype III	(Qi et al. 2011)
Estrildidae	**Aurora finch** (*Pytilia hypogrammica*)	*Cryptosporidium* sp.	(Morgan et al. 2001)
	Australian diamond firetail finch (*Stagonoplura bella*)	*Cryptosporidium* sp.[a]	(Blagburn et al. 1990)
	Bengalese finch (*Lonchura striata domestica*)	*C. parvum*[b]	(Gomes et al. 2012)
	Black-throated finch (*Poephila cincta*)	*Cryptosporidium* sp.	(Gardiner and Imes 1984)
	Bronze mannikin finch (*Lonchura cucullata*)	*Cryptosporidium* sp.	(Lindsay et al. 1991)
	Chestnut finch (*Lonchura castaneothorax*)	*C. galli*	(Ng et al. 2006)
	Diamond firetail finch (*Stagonopleura guttata*)	*Cryptosporidium* sp.	(Lindsay et al. 1991)
	Gouldian finch (*Erythrura gouldiae*)	*C. baileyi*, *C. galli*	(Morgan et al. 2001; Qi et al. 2011)
	Java sparrow (*Padda oryzivora*)	*C. baileyi*, avian genotype III	(Qi et al. 2011; Gomes et al. 2012)
	Painted firetail finch (*Emblema pictum*)	*C. galli*	(Ng et al. 2006)
	Parson's finch (*Poephila cincta*)	*C. galli*	(Ng et al. 2006)
	Plum-headed finch (*Neochmia modesta*)	*Cryptosporidium* sp.	(Morgan et al. 2001)
	Red-face aurora finch (*Pytilia hypogrammica*)	*Cryptosporidium* sp.	(Morgan et al. 2001)
	Zebra finch (*Taeniopygia guttata*)	*C. galli*, *C. baileyi*	(Ng et al. 2006; Qi et al. 2011)
Fringillidae	**Canary** (*Serinus canaria*)	*C. galli*, avian genotype I	(Ng et al. 2006; Nakamura et al. 2009)
	Goldfinch (*Carduelis tristis*)	*C. galli*	(Sevá Ada et al. 2011a)
	Pine grosbeak (*Pinicola enucleator*)	*C. galli*	(Ryan et al. 2003b)
	White lored euphonia (*Euphonia chrysopasta*)	*Cryptosporidium* sp.	(Lindsay et al. 1991)

(continued)

Table 5.7 (continued)

Family	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Hirundinidae	**Cliff swallow** (*Petrochelidon pyrrhonota*)	*Cryptosporidium* sp.	(Ley et al. 2012)
Icteridae	**Chopi blackbird** (*Gnorimopsar chopi*)	*Cryptosporidium* sp.	(Nakamura et al. 2009)
	Crested oropendola (*Psarocolius decumanus*)	*C. baileyi*	(Ryan et al. 2003b)
	Red-rumped cocique (*Cacicus haemorrhous*)	*C. baileyi*	(Ryan et al. 2003b)
Leiothrichidae	**Red-billed leiothrix** (*Leiothrix lutea*)	*C. baileyi*	(Qi et al. 2011)
	Silver-eared mesia (*Leiothrix argentauris*)	*C. galli*	(Qi et al. 2011)
Ploceidae	**Eastern golden-backed weaver** (*Ploceus jacksoni*)	*C. baileyi*	(Ng et al. 2006)
Pycnonotidae	**Gray-bellied bulbul** (*Pycnonotus cyaniventris*)	*C. baileyi*	(Ng et al. 2006)
Sturnidae	**Common myna** (*Acridotheres tristis*)	*C. baileyi*	(Qi et al. 2011)
Thraupidae	**Double-collared seedeater** (*Sporophila caerulescens*)	*Cryptosporidium* sp.	(Nakamura et al. 2009)
	Lesser seed finch (*Oryzoborus* sp.)	*C. galli*	(Antunes et al. 2008; Nakamura et al. 2009)
	Red-cowled cardinal (*Paroaria dominicana*)	*C. galli*	(Ng et al. 2006)
	Saffron finch (*Sicalis flaveola*)	*C. baileyi*, *C. galli*	(Nakamura et al. 2009; Sevá Ada et al. 2011a)
	Slate-coloured seedeater (*Sporophila schistacea*)	*C. galli*	(Sevá Ada et al. 2011a)
Turdidae	**Rufous-bellied thrush** (*Turdus rufiventris*)	*C. galli*, *Cryptosporidium* sp.	(Sevá Ada et al. 2011a)
Zosteropidae	**Japaneese white eye** (*Zosterops japonicus*)	Avian genotype IV	(Ng et al. 2006)

[a] Associated with clinical disease

[b] *C. parvum* was identified using molecular tools; however, oocysts from the sample measured 7.2 μm × 5.8 μm, which suggests that another species was also present

muskrat I and II, opposuum II, raccon, rat I–IV, Sbey/Sbld A, Sbey B, Sbey/Sbld/Sltl C, Sbld D, seal I and II, shrew, skunk, vole, W12, W18, and many other unnamed genotypes (Fig. 5.3).

Table 5.9 shows GenBank accession numbers for representative SSU rRNA gene sequences from mammal-associated cryptosporidia. *Cryptosporidium* has been identified in the three major groups of mammals: the egg-laying mammals (Protheria), marsupials (Metatheria), and placental mammals (Eutheria).

Table 5.8 Oocyst morphology and infection site of *Cryptosporidium* taxa detected in wild mammals

Cryptosporidium taxa	Oocysts size (μm)	Infection site	Reference
C. andersoni	6.0–8.1 × 5.0–6.5	Abomasum	(Lindsay et al. 2000)
C. baileyi	6.0–7.5 × 4.8–5.7	Brusa of Fabricius, cloaca	(Lindsay et al. 1989)
C. canis	3.68–5.88 × 3.68–5.88	Small intestine	(Fayer et al. 2001)
C. cuniculus	5.55–6.40 × 5.02–5.92	Small intestine	(Robinson et al. 2010)
C. fayeri	4.5–5.1 × 3.8–5.0	ND	(Ryan et al. 2008)
C. felis	4.6 × 4.0 (3.2–5.1 × 3.0–4.0)	Small intestine	(Iseki 1979)
C. macropodum	4.5–6.0 × 5.0–6.0	ND	(Power and Ryan 2008)
C. muris	7.5–9.8 × 4.6–6.3	Stomach	(Upton and Current 1985)
C. parvum	5.2–5.7 × 4.7–5.3	Small intestine	(Vítovec et al. 2006)
C. scrofarum	4.81–5.96 × 4.23–5.29	Small intestine	(Kváč et al. 2013a)
C. suis	6.0–6.8 × 5.3–5.7	Large intestine	(Vítovec et al. 2006)
C. tyzzeri	4.64 ± 0.05 × 4.19 ± 0.06	Small intestine	(Ren et al. 2012)
C. ubiquitum	4.71–5.32 × 4.33–4.98	Small intestine	(Fayer et al. 2010)
C. wrairi	5.4 × 4.6 (4.8–5.6 × 4.0–5.0)	Small intestine	(Tilley et al. 1991)
Brushtail genotype I	3.92 ± 0.25 × 4.12 ± 0.34	ND	(Hill et al. 2008)
Chipmunk genotype I	5.3–6.6 × 4.7–5.9	ND	(Kváč et al. 2008a)
Ferret genotype	4.9–6.0 × 4.7–5.6	ND	(Kváč et al. 2008a)

ND not determined

5.6 Egg-Laying Mammals

Monotremata, which is the only order of egg-laying mammals, contains two families, three genera, and five species. All lack teeth as adults, forage on insects or other invertebrates, and are native to Australia and New Guinea.

The only report of *Cryptosporidium* from this order has been in a short-beaked echidna (*Tachyglossus aculeatus*), a species that inhabits Australia and New Guinea (O'Donoghue 1995).

5.7 Marsupials

Marsupials comprise seven orders of about 334 species primarily inhabiting Australia and surrounding islands, and South America. *Cryptosporidium* has thus far been detected in species from the orders Dasyuromorphia, Peramelemorphia, and Diprotodontia in Australia, and Didelphimorphia in South America. Members

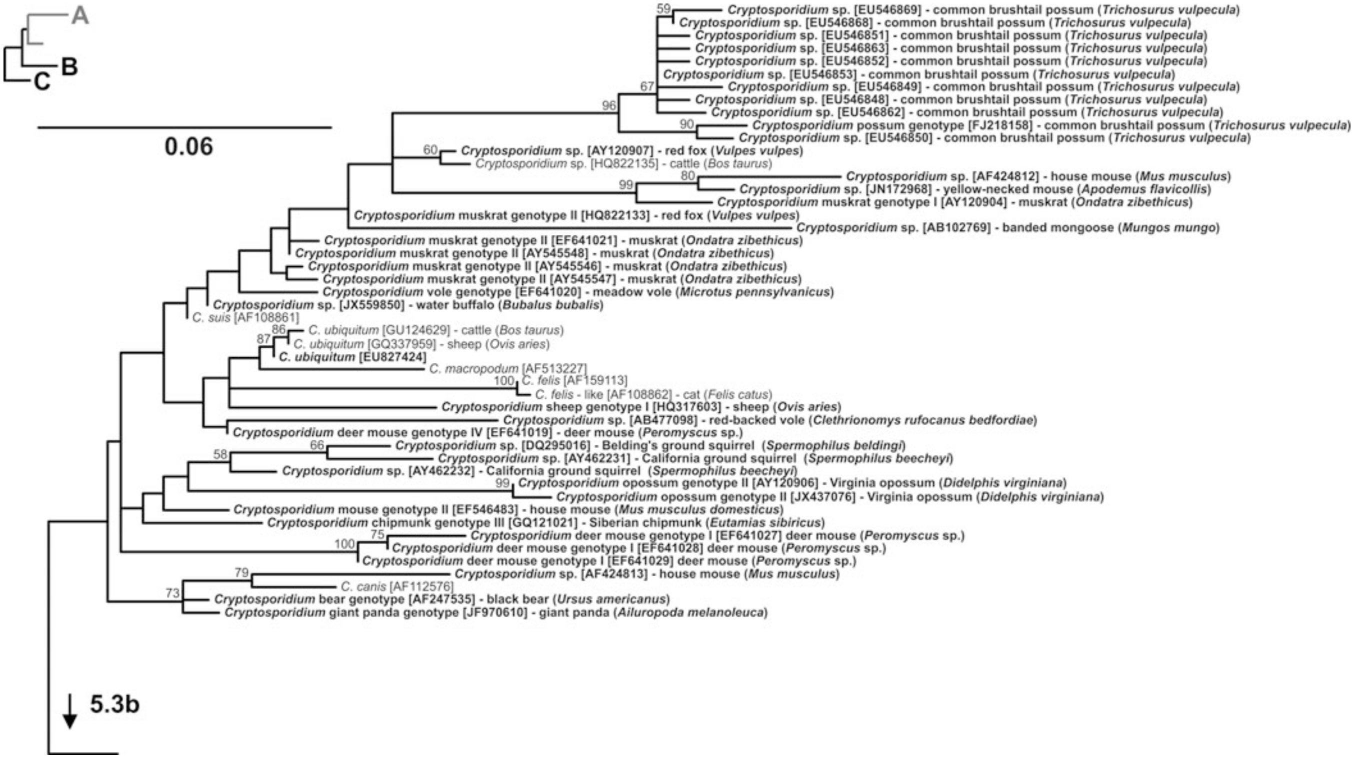

Fig. 5.3 (continued)

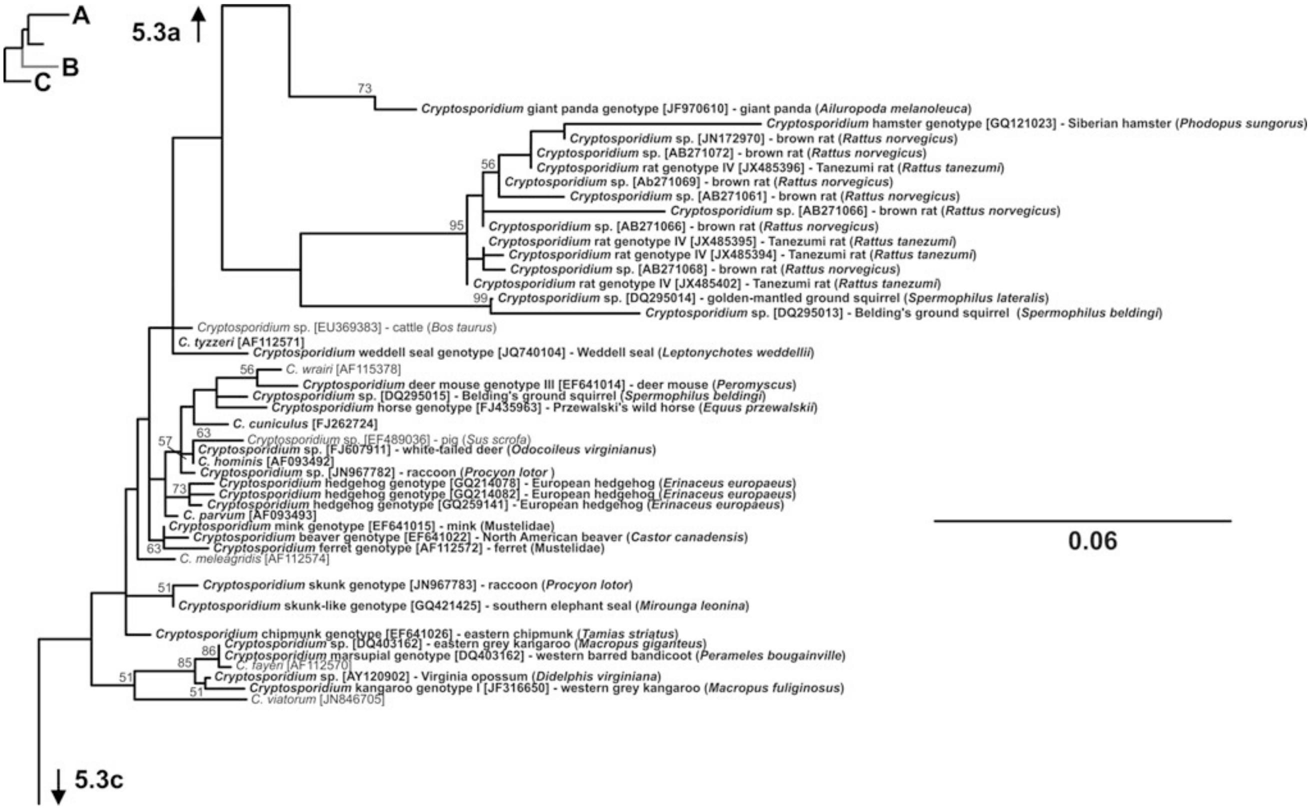

Fig. 5.3 (continued)

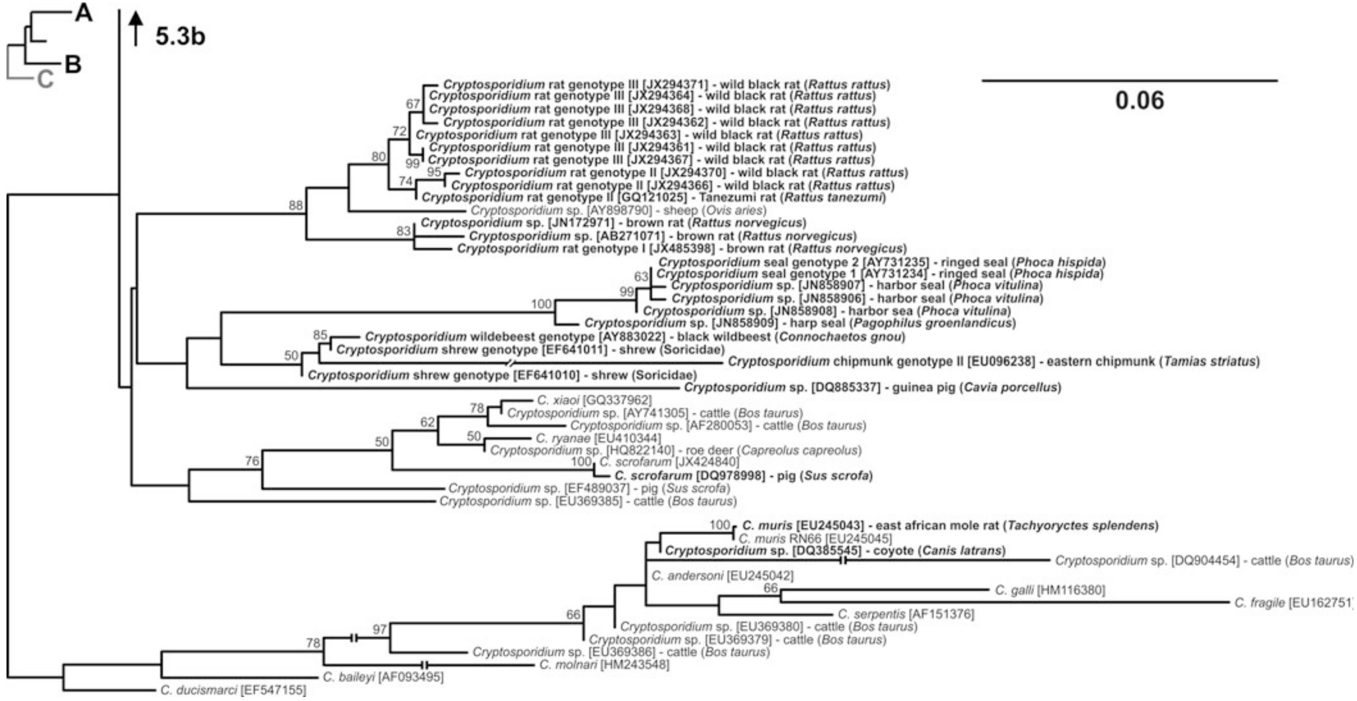

Fig. 5.3 A SSU rDNA-based maximum likelihood (GTRCAT model) tree of *Cryptosporidium* spp. sequences showing clades of cryptosporidia infecting mammals. *Cryptosporidium* sp. detected in mammals are in bold. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown at nodes. Bootstrap values <50 are not shown. Interrupted branches have been shortened fivefold

Table 5.9 Select GenBank accession numbers for *Cryptosporidium* small subunit rRNA gene sequences from mammals. Hosts are separated by taxonomic order and common name groupings

Infraclass	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
Placental mammals	Artiodactyla	Ungulates: sheep, cows, pigs, deer, alpine ibex, Black wildebeest, water buffalo	**Alpine ibex** (*Capra ibex*) [EF613340] **Black wildbeest** (*Connochaetos gnou*) [AY883022] **Deer** [AY120910, FJ607911, FJ607928] **Roe deer** (*Capreolus capreolus*) [HQ822140] **Sika deer** (*Cervus nippon*) [DQ898159] **Water buffalo** (*Bubalus bubalis*) [JX559850] **Wild boar** (*Sus scrofa*) [U96770]
	Carnivora	Bears	**Black bear** (*Ursus americanus*) [AF247535] **Giant panda** (*Ailuropoda melanoleuca*) [JF970610, JN790957]
		Canines: dog, foxes, coyote	**Coyote** (*Canis latrans*) [DQ385545] **Dog** (*Canis lupus*) [AF112576] **Red fox** (*Vulpes vulpes*) [AY120907, HQ822133] **Raccoon dog** (*Nyctereutes procyonoides viverrinus*) [AB104730]
		Cats	**Cat** (*Felis catus*) [AF108862, AF112575, AF159113]
		Mongoose	**Banded mongoose** (Mungos mungo) [AB102769]
		Skunk, raccoons, otter, mink, ferret	**Ferret** (*Mustela*) [AF112572] **Mink** (*Mustela vison*) [EF428186, EF428187, EF428189, EF641015] **Raccoon** (*Procyon lotor*) [AY120903,FJ607943, GQ426097, JN967782–JN967784] **River otter** (*Lontra canadensis*) [DQ288166]

(continued)

Table 5.9 (continued)

Infraclass	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
		Seals	**Harbor seal** (*Phoca vitulina*) [JN858906–JN858908]
			Harp seal (*Pagophilus groenlandicus*) [JN858909]
			Hooded seal (*Cystophora cristata*) [JN858905]
			Southern elephant seal (*Mirounga leonina*) [GQ421425, JQ740100–JQ740102]
			Ringed seal (*Phoca hispida*) [AY731234, AY731235]
			Weddell seal (*Leptonychotes weddellii*) [JQ740103, JQ740104]
	Hyracoidea	Hyrax	**Rock hyrax** (*Procavia capensis*) [AF161579]
	Erinaceomorpha	Hedgehogs	**European hedgehog** (*Erinaceus europaeus*) [GQ214078, GQ214082, [GQ259141]
	Soricomorpha	Shrews and moles	**Shrew** (Soricidae) [EF641010, EF641011]
	Lagomorpha	Rabbits	**European rabbit** (*Oryctolagus cuniculus*) [AY120901, AY273771, FJ262725, GQ865536, HQ397716]
	Perissodactyla	Horse	**Prezewalski's wild horse** (*Equus przewalskii*) [FJ435963]
	Non-human Primates	Lemur	**Black-and-white colobus** (*Colobus guereza*) [F342450]
			Coquerel's sifaka (*Propithecus verreauxi coquereli*) [AF442484]
			Gray lagur (*Semnopithecus entellus thersites*) [EF446673 EF446678]
			Mountain gorilla (*Gorilla gorilla gorilla*) [JQ837801]
			Olive baboon (*Papio anubis*) [JF681172–JF681174]

(continued)

Table 5.9 (continued)

Infraclass	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
			Purple-faced lagur (*Trachypithecus vetulus philbricki*) [EF446679]
			Red colobus (*Procolobus rufomitratus*) [JF342488–JF342495]
			Rhesus macaque (*Macaca mulatta*) [HM234173, JX000568–JX000570]
			Toque macaque (*Macaca sinica sinica*) [EF446672; EF446674–EF446677]
	Rodentia	Mice and rats	**Brown rat** (*Rattus norvegicus*) [AB271061, AB271062, AB271064, AB271066, AB271068, AB271069, AB271071–AB271073, JX485398, EU245045, JN172970, JN172971]
			Deer mouse (*Peromyscus* sp.) [AY120905, EF641014, EF641019, EF641027–EF641030]
			Mouse (species unspecified) [AF108863, AF112571]
			House mouse (*Mus musculus*) [AF424812, AF424813]
			House mouse (*Mus domesticus*) [EF546483]
			Tanezumi rat (*Rattus tanezumi*) [GQ121025, JX485394–JX485396, JX485402]
			Wild black rat (*Rattus rattus*) [JX29435–JX294371]
			Yellow-necked mouse (*Apodemus flavicolis*) [JN172968]
		Squirrels: chipmunks, tree and ground squirrels	**Belding's ground squirrel** (*Spermophilus beldingi*) [DQ295013, DQ295015, DQ295016]
			California ground squirrel (*Spermophilus beecheyi*) [AY462231–AY462233, DQ295012]

(continued)

Table 5.9 (continued)

Infraclass	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
			Golden-mantled ground squirrel (*Spermophilus lateralis*) [DQ295014]
			Eastern gray squirrel (*Sciurus carolinensis*) [EU096237]
			Eastern chipmunk (*Tamias striatus*) [EU096238, EF641026]
			Red squirrel (*Sciurus vulgaris*) [EU250844, EU250845]
			Siberian chipmunk (*Eutamias sibiricus*) [GQ121021]
		Muskrats, voles, hamster	**Boreal red-backed vole** (*Myodes gapperi*) [EF641012, EF641013, or EF641016][a]
			Meadow vole (*Microtus pennsylvanicus*) [EF641020]
			Muskrat (*Ondatra zibethicus*) [AY120904, AY545546–AY545548, EF641021][b]
			Red-backed vole (*Clethrionomys rufocanus bedfordiae*) [AB477098]
			Siberian hamster (*Phodopus sungorus*) [GQ121023]
			Brazilian porcupine (*Coendou prehensiles*) [HM209375]
		Guinea pigs, porcupine	**Brazilian porcupine** (*Coendou prehensiles*) [HM209375]
			Guinea pig (*Cavia porcellus*) [AF115378, DQ885337]
		Beaver	**North American beaver** (*Castor canadensis*) [EF641022]
Marsupials	Didelphimorphia	American opossums	**Opossum** (*Didelphis virginiana*) [AY120902, AY120906, JX437075–JX437079]

(continued)

Table 5.9 (continued)

Infraclass	Order	Common names/groups	Host species (scientific name) and GenBank accession numbers
	Diprotodontia	Kangaroos, possums, koala	**Eastern grey kangaroo** (*Macropus giganteus*) [AF513227, AY237630, DQ403162]
			Common brushtail possum (*Trichosurus vulpecula*) [EU546848–EU546853, EU546862, EU546863, EU546868 EU546869, FJ218158]
			Red Kangaroo (*Macropus rufus*) [AF108860, AF112570]
			Western grey kangaroo (*Macropus fuliginosus*) [JF316650, JF316651]
	Peramelemorphia	Bandicoot	**Western barred bandicoot** (*Perameles bougainville*) [DQ403162]

[a] It is not clear from the GenBank entries which of these three sequences was isolated from the boreal red-backed vole

[b] It is not clear from the GenBank entries which of these three sequences was isolated from the muskrat

of the Notoryctemporphia, which contains two species of marsupial moles (*Notoryctes typhlops* and *Notoryctes caurinus*) that are native to Australia; the Microbiotheria, which contains a single species (*Dromiciops gliroides*) that is native to the southwestern part of South America; and the Paucituberculata, which contains six species of shrew opossum (*Rhyncholestes raphanurus*, *Lestoros inca*, *Caenolestes caniventer*, *Caenolestes condorensis*, *Caenolestes convelatus*, and *Caenolestes fuliginosus*) that are native to South America, have yet to be identified as hosts for *Cryptosporidium*.

5.7.1 Dasyuromorphia

This order of carnivorous species includes the Tasmanian Devil (*Sarcophilus harrisii*), numbat (*Myrmecobius fasciatus*), and the shrew-like antechinus species.

To date, only the brown antechinus (*Antechinus staurtii*) has been identified as a host for *Cryptosporidium* (Barker et al. 1978).

5.7.2 Peramelemorphia

This order of omnivorous marsupials, which includes bandicoots and bilbies, is found in Australia and New Guinea.

Cryptosporidium sp. and *C. fayeri* have been reported in a southern brown bandicoot (*Isoodon obesulus*) and western-barred bandicoot (*Peremeles bougainville*), respectively (O'Donoghue 1995; Power 2010). *Cryptosporidium muris* was detected in greater bilbies (*Macrotis lagotis*) at a captive breeding colony in Australia. Although some animals cleared the infection within 2 months, others remained infected for 6 months (Warren et al. 2003). Mice trapped in the pens of infected bilbies were positive for *C. muris* and were considered to be the likely source of the infection.

5.7.3 Diprotodontia

Diprotodontia, a large and diverse order of herbivorous marsupials that are native to Australia and surrounding islands, hosts a number of *Cryptosporidium* species and genotypes. *Cryptosporidium fayeri*, which was first isolated from a koala (*Phascolarctos cincereus*) (Morgan et al. 1997), has been reported in the red kangaroo (*Macropus rufus*), eastern grey kangaroo (*Macropus giganteus*), and yellow-footed rock wallaby (*Petrogale xanthopus*) (Ryan et al. 2008). *Cryptosporidium macropodum* (previously marsupial genotype II) has been reported in the red kangaroo, eastern grey kangaroo, western grey kangaroo, and swamp wallaby (*Wallabia bicolor*). Neither *C. fayeri* nor *C. macropodum* are known to cause clinical disease in diprodonts or any other marsupial. The *Cryptosporidium* kangaroo genotype I, which was identified in the western grey kangaroo (Yang et al. 2011), clusters with the opossum genotype in a neighbour-joining phylogeny of SSU rRNA sequences (Fig. 5.3b). Brushtail possum genotypes I and II have been identified in the brushtail possum (*Trichasuris vulpecula*) (Power et al. 2003; Hill et al. 2008). Non-genotyped *Cryptosporidium* sp. have been reported in the red-necked wallaby (*Macropus rufogriseus*), pademelon (*Thylogale billardierii*), and koala (Jakob 1992; O'Donoghue 1995).

5.7.4 Didelphimorphia

The didelphimorphs (opossums) are native to the American continent.

The *C. fayeri*-opossum genotype (previously opossum genotype I; this genotype is 99 % similar to *C. fayeri* at the SSU rRNA locus), *C. fayeri* (identified by RFLP analysis), and opossum genotype II have been reported in Virginia opossums (*Didelphis virginiana*) from California and New York, USA (Xiao et al. 2002;

Ziegler et al. 2007b). *Cryptosporidium* also has been detected in the white-eared opossum (*Didelphis albiventris*) (Zanette et al. 2008).

5.8 Placental Mammals

Of the 21 orders of placental mammals, 13 contain species that have been identified as hosts for *Cryptosporidium*. The following eight orders have yet to be identified as hosts:

Cingulata and Pilosa: These two orders – totalling 19 species in five families and 18 genera – constitute the superorder Xenarthra. Representatives of these orders include armadillos (Cingulata), anteaters (Cingulata), and sloths (Pilosa). Many species are now extinct. The habitats and diets within the group are quite varied. Most are omnivores, but many are insectivores or herbivores.

Macroscelididae, **Afrosordida**, **and Tublidentata**: These are three of the six orders in the superorder Afrotheria. They include tenrecs (Afrosoricida), elephant shrews (Macroscelidia), and aardvarks (Tubulidentata).

Pholidota: This order compromises about eight species in one family and one genus. They are insectivores, inhabiting Africa and southern areas of Asia.

Dermoptera: These comprise a small family of two genera and two arboreal species of gliding mammals, colugos, in Southeast Asia.

Scandentia: These are native of Indonesia and comprise two families, five genera, and 20 species. These small omnivores, commonly referred to as treeshrews, are found in densely forested habitats.

5.8.1 Hyracoidea

Hyracoidea (hyraxes) are in the superorder Afrotheria. They have a digestive system that is similar in function to that of ruminants.

A single species, *C. muris*, has been identified in the rock hyrax (*Procavia capensis*) (Graczyk et al. 1996a; Xiao et al. 1999a).

5.8.2 Sirenia

The order Sirenia, which contains aquatic herbivores such as the dugong and manatee, is most closely related to elephants in the order Proboscidea.

Reports of *Cryptosporidium* in the sirenians have been rare. Hill et al. (1997) described a case of intestinal cryptosporidiosis in a dugnong (*Dugong dugon*) from Queensland, Australia. Three dugongs died as a consequence of the disease and a fourth, the subject of the study, was humanely euthanized (Hill et al. 1997). Sequence analysis of SSU rRNA and acetyl CoA synthethase genes amplified from preserved tissue specimens revealed that the dugong was infected with *C. hominis* (Morgan et al. 2000a).

5.8.3 Proboscidea

There have been few studies of *Cryptosporidium* in the herbivorous elephants that comprise the order Proboscidea.

Cryptosporidium sp. has been detected in African elephants (*Loxodonta africana*) at Kruger National Park, South Africa (6/144 positive) (Abu Samra et al. 2011) and the Barcelona Zoo (Gracenea et al. 2002).

5.8.4 Erinaceomorpha

Hedgehogs (Erinceomorpha) contain 24 species in one family (Erinceidae) and ten genera. Some recent phylogenies include this group in the order Soricomorpha (moles and shrews); hedgehogs are similar to shrews in many ways, including an omnivorous diet that may include carrion.

Cryptosporidium can cause clinical and sometimes fatal infections in hedgehogs. Graczyk et al. (1998a) reported fatal cryptosporidiosis in juvenile African hedgehogs (*Ateletrix albiventris*) housed at the Baltinore Zoo. *Cryptosporidium* developmental stages were detected in the ileum, jejunum, and colon, and moderate to severe villous atrophy was detected in the ileum and jejunum. Meredith and Milne (2009) reported on a case of cryptosporidiosis in an adult European hedgehog (*Erinaceus europaenus*) with hemorrhagic diarrhoea. Similar to the juvenile African hedgehogs, moderate to severe villous atrophy was detected in the ileum and jejunum. Sturdee et al. (1999) detected *Cryptosporidium* oocysts in feces of a free-living European hedgehog from the UK with an estimated infection intensity of 3,000 oocysts per gram. *Cryptosporidium* spp. was detected in 30.0 % (56/188) of European hedgehogs in Germany (Dyachenko et al. 2010). *Cryptosporidium parvum* from gp60 subtype families IIa and IIc, and *Cryptosporidium* hedgehog genotype from gp60 subtype family XIIa (previously VIIa) were identified in positive samples. Although *Cryptosporidium* positive hedgehogs had diarrhea, any association between a *Cryptosporidium* sp. and clinical signs was not determined.

5.8.5 *Soricomorpha*

The Soricomorpha (moles and shrews) represent about 420 species in four families and 44 genera. These are small omnivorous mammals, though invertebrates (especially insects) form a large component of the diet. Many are nocturnal or fossorial. Shrews and moles occupy a variety of habitats, and often live in close association with water.

Cryptosporidium has been reported in the greater white-toothed shrew (*Crocidura russula*), common shrew (*Sorex araneus*), masked shrew (*Sorex cinereus*), northern short-tailed shrew (*Blarina brevicauda*), pygmy shrew (*Sorex minutus*), and Brewer's mole (*Parascalops brewer*) (Siński 1993; Sturdee et al. 1999; Torres et al. 2000; Ziegler et al. 2007a). The shrew genotype (also known as W5) has been identified in 2/5 northern short-tailed shrews in New York (Feng et al. 2007). It is not known to what extent *Cryptosporidium* infection of shrews is associated with clinical disease.

5.8.6 *Cetacea*

Cetaceans include approximately 90 species in 11 families and 40 genera of dolphins and whales. There are two main groups. The Mysticeti (baleen whales) have baleen rather than teeth for filtering invertebrates from water or bottom sediments. The Odontoceti (toothed whales) have teeth and generally are piscivorous. Most species inhabit marine waters, but a few occur in coastal rivers. Cetaceans are most closely related to the hippopotamus.

Cryptosporidium has been detected in fecal samples from 5.1 % (2/39) of bowhead whales (*Balaena mysticetus*) and 24.5 % (12/49) of North Atlantic right whales (*Eubalaena glacialis*) (Hughes-Hanks et al. 2005). Isolates were not genotyped.

5.8.7 *Artiodactyla*

The Artiodactyl mammals include about 240 species in 10 families and 89 genera. These even-toed ungulates include three main groups that differ in their digestive system: Suiformes (pigs) have non-ruminating stomachs, Tylopoda (camels) have three-chambered ruminating stomachs, and Ruminantia (deer, antelope, cows, and hippos) have four-chambered ruminating stomachs. They occupy a wide variety of habitats, but many utilize grasslands or savannahs.

5.8.7.1 Pigs

Most research has focused on the domestic pig, and there is relatively limited data regarding *Cryptosporidium* and cryptosporidiosis in wild pigs (described variously as wild boars and feral pigs). Although domestic pigs can host several *Cryptosporidium* taxa, including *C. felis*, *C. hominis*, *C. meleagridis*, *C. muris*, *C. parvum*, *C. scrofarum*, *C. suis*, *C. tyzzeri*, *Cryptosporidium* sp. Eire w65.5, *Cryptosporidium* rat genotype, and *C. suis*-like (Morgan et al. 1999a; Ebeid et al. 2003; Chen and Huang 2007; Kváč et al. 2009a, c), only *C. parvum*, *C. suis*, and *C. scrofarum* have been detected in wild pigs (Table 5.10) (Atwill et al. 1997; Němejc et al. 2012; Garcia-Presedo et al. 2013). The occurrence of non-adapted cryptosporidia in domestic pigs, and their absence from wild pigs, may be a consequence of farming operations that place pigs in close proximity to humans and cattle (e.g. *C. parvum*), cats (*C. felis*), and rodents (*C. tyzzeri*, *C. muris*, and rat genotype).

Similar to domestic pigs, it appears that shedding of *Cryptosporidium* oocysts by wild pigs is associated with age and population density. Atwill et al. (1997) reported a 4.2-fold greater likelihood of oocyst shedding in animals younger than 8 months compared to older animals. Also, wild pigs from sites with $\geq$2.0 wild pigs/km^2 had approximately a tenfold greater likelihood of shedding *Cryptosporidium* oocysts compared to animals from sites with $\leq$1.9 feral pigs/km^2.

There is no association between diarrhea in wild pigs and the presence of cryptosporidia, and infection intensity is generally less than 2,000 oocyts per gram of feces (Castro-Hermida et al. 2011a; Němejc et al. 2012).

5.8.7.2 Camels and Llamas

Camels are susceptible to infection with two closely related gastric cryptosporidia, *C. muris* and *C. andersoni*, which prior to 2001 were considered a single species, *C. muris* (Lindsay et al. 2000). A key difference between these species is that only *C. muris* is infectious for neonatal mice under experimental conditions (Lindsay et al. 2000). Therefore, when Anderson (1991) isolated *C. muris*-like oocysts from a camel and demonstrated their infectivity for 2–20-day-old mice, it is probable that the isolate was *C. muris*, and not *C. andersoni*. Molecular studies have subsequently shown that *C. muris* from a Bactrian camel clusters with *C. muris* from mice, a hamster, and a rock hyrax in phylogenies constructed from SSU rRNA, Internal transcribed spacer region 1, and HSP-70 sequences (Xiao et al. 1999a; Morgan et al. 2000c).

A *C. andersoni* isolate with oocysts measuring 7.0–7.2 μm × 5.1–5.2 μm (shape index: 1.37–1.39) from a 3-year-old Bactrian camel did not infect immunosuppressed or immunocompetent calves, immunosuppressed or immunocompetent Kun-ming mice, or severe combined immunodeficiency mice (Wang et al. 2007).

Table 5.10 *Cryptosporidium* spp. identified in wild pigs

Cryptosporidium taxa	Country	Prevalence	Reference
Cryptosporidium sp.	Spain	11.5 % (20/175)	(Castro-Hermida et al. 2011a)
	Spain	ND	(Gómez et al. 2000)
	USA	ND	(Pereira et al. 1998)
C. parvum[a]	Spain	11.1 % (3/27)	(Garcia-Presedo et al. 2013)
	USA	5.4 % (12/221)	(Atwill et al. 1997)
C. scrofarum	Austria	2.3 % (1/44)[b] 13.6 % (6/44)[c]	(Němejc et al. 2013)
	Czech Republic	0 % (0/193)[b] 13.0 % (25/193)[c]	(Němejc et al. 2012)
	Czech Republic	1.7 % (4/231)[b] 11.3 % (26/231)[c]	(Němejc et al. 2013)
	Poland	2.3 % (3/129)[b] 7.8 % (10/129)[c]	(Němejc et al. 2013)
	Slovak Republic	0 % (0/56)[b] 1.8 % (1/56)[c]	(Němejc et al. 2013)
	Spain	70.4 % (19/27)[c]	(Garcia-Presedo et al. 2013)
C. suis	Austria	2.3 % (1/44)[b] 11.4 % (5/44)[c]	(Němejc et al. 2013)
	Czech Republic	0 % (0/193)[b] 13.0 % (25/193)[c]	(Němejc et al. 2013)
	Czech Republic	0.9 % (2/231)[b] 10.8 % (25/231)[c]	(Němejc et al. 2013)
	Poland	0 % (0/129)[b] 0.8 % (1/129)[c]	(Němejc et al. 2013)
	Slovak Republic	0 % (0/56)[b] 3.6 % (2/56)[c]	(Němejc et al. 2013)
	Spain	18.5 % (5/27)[c]	(Garcia-Presedo et al. 2013)

[a] Although, the sequence obtained from the feral pig isolate was confirmed as *C. parvum* by the appropriate location of and 100 % sequence homology with two internal probes and three internal primers, in retrospect is impossible to determinate the species and genotypes

[b] Determined using microscopy and

[c] Determined using PCR

ND not determined

Kváč et al. (2008b) infected two out of three lambs and three out of three goat kids with *C. muris* isolate CB03, which originated from a naturally infected Bactrian camel. *Cryptosporidium muris* CB03 was also infectious for Balb/c mice and southern multimammate mice (*Mastomys coucha*). Developmental stages were detected in the *plicae spirales curvature major* in the abomasum of infected lambs and kids. Gastric glands were slightly dilated, and covered with cuboidal and metaplased cells. Infiltration or congestion in the *lamina propria* was not detected, and there was no diarrhea.

Oocysts isolated from rectal samples of camels at a slaughterhouse in Iran had a diameter of 4.56 ± 0.65 μm (range: 4.20–5.70 μm), which is consistent with the morphology of intestinal cryptosporidia (Razawi et al. 2009). However, the isolates were not genotyped so this could not be confirmed. Ryan et al. (2003a) identified *C. parvum* in an alpaca (*Lama pacos*), and Gómez et al. (2000) detected *Cryptosporidium* sp. in a guanaco (*Lama guanicoe*).

A study of dromedary camels (*Camelus dromedaries*) in Iran showed a high *Cryptosporidium* prevalence in animals younger than 1 year (20 %) relative to adult camels (6.5 %) (Yakhchali and Moradi 2012). Another study in Iran showed a relatively high prevalence of *Cryptosporidium* sp. (20.3 %; 61/300) in asymptomatic camels (Sazmand et al. 2012).

5.8.7.3 Giraffe and Okapi

Cryptosporidium muris and *Cryptosporidium* sp. have been detected in giraffes (*Giraffa camelopardalis*) from zoos in the Czech Republic and Spain, respectively (Gómez et al. 1996; Kodádková et al. 2010). The *C. muris* isolate was identical to isolates from the rock hyrax and Bactrian camel at the SSU rRNA locus, and was not infectious for Balb/c mice under experimental conditions (Kodádková et al. 2010).

5.8.7.4 Deer and Moose

Cryptosporidium parvum, *C. ubiquitum*, and the *Cryptosporidium* deer genotype have been detected at varying rates in deer and moose worldwide. *Cryptosporidium parvum* and *C. ubiquitum* have been reported in 12.5 % (4/32) of swamp deer (*Cervus duvauceli*) from Nepal (Feng et al. 2012), in a roe deer from England (Robinson et al. 2011), in a red deer (*Cervus elaphus*) from the Czech Republic (Hajdušek et al. 2004), and in a sika deer (*Cervus nippon*) from China (Wang et al. 2008a). The *Cryptosporidium* deer genotype, which is closely related to *C. ryanae*, has been reported in white-tailed deer (*Odoileus virginianus*) from the US (Xiao et al. 2002). *Cryptosporidium* sp. has been detected in 1.3 % (2/149) and 6 % (3/49) of caribou (*Rangifer tarandus*) from Canada and Alaska, respectively; 8.3 % (2/24), 8.8 % (4/35), and 5.0 % (72/360) of white-tailed deer from the US; 7.9 % (3/38) of black-tailed deer (*Odocoileus hemionus columbianus*) from the US; 25 % (10/40) of tule elk (*Cervus canadensis* ssp. nannodes) from the US; 1.3 % (3/224), 9.1 % (2/22), and 6.2 % (18/291) of roe deer (*Capreolus capreolus*) from Spain, Poland, and Norway, respectively; 14.4 % (17/118), 0.3 % (1/289), 41.5 % (135/325), and 100 % (2/2) of red deer from Poland, Norway, Ireland, and the US, respectively; and 3.3 % (15/455) of moose (*Alces alces*) from Norway (Simpson 1992; Fayer et al. 1996; Deng and Cliver 1999; Rickard et al. 1999; Skerrett and Holland 2001; Siefker et al. 2002; Hamnes et al. 2006; Ziegler et al. 2007b; Johnson et al. 2010; Castro-Hermida et al. 2011b). Other deer that have been identified as hosts of *Cryptosporidium* sp., include the fallow deer (*Dama dama*), axis deer (*Axis axis*), barasingha deer (*Cervus duvauceli*), Eld's deer, muntjac deer, sambar (*Rusa* *unicolor*), Thorold's deer (*Cervus albirostris*), and Père David's deer (*Elaphurus davidianus*) (Heuschele et al. 1986; Sturdee et al. 1999).

5.8.7.5 Bovids

Cryptosporidium has thus far been identified in wild bovid species representing eight of the ten bovid subfamilies (Table 5.11). It has not yet been identified in the Tibetan antelope (*Pantholops hodgsonii*) or grey rhebok (*Pelea capreolus*), which are the sole representatives of the Pantholopinae and Peleinae subfamilies, respectively. Most studies of wild bovid species have been limited to captive animals outside their native habitat.

In a study of cryptosporidiosis in wild bovids, *Cryptosporidium* developmental stages were identified in the small intestine, cecum, spiral colon, and colon (Van Winkle 1985). Four mountain gazelles (*Gazella cuvieri*) at the Munich Zoo with cryptosporidiosis had anorexia and weight loss but no diarrhea (Pospischil et al. 1987). *Cryptosporidium* developmental stages were detected in the abomasum only. The mucosa was hyperplastic and diffusely infiltrated with small lymphocytes, and the mucosal glands were elongated and hypercellular.

Hippopotamus

Cryptosporidium sp. has been detected in a pygmy hippopotamus (*Choeropsis liberiensis*) at the Barcelona Zoo (Gómez et al. 2000).

5.9 Chiroptera

Bats represent a diverse order of flying mammals with over 1,100 species in 18 families and 202 genera. The group is split into the Megachiropterans, which are large, fruit or nectar-eating bats that lack certain ear structures, and the Microchiropterans, which are small, omnivorous or insectivorous species that utilize echolocation and possess associated ear structures. Most (but not all) bats hibernate, and are generally associated with forest habitats.

Despite representing about 20 % of the mammalian fauna, few bat species have been identified as hosts for *Cryptosporidium*. Cryptosporidiosis was diagnosed in a big brown bat (*Eptesicus fuscus*) from Oregon, USA (Dubey et al. 1998). In New York, *Cryptosporidium* sp. and *C. parvum* were identified in a small brown bat (*Myotis lucifugus*) and big brown bat, respectively (Ziegler et al. 2007b). *Cryptosporidium tyzzeri* was detected in a large-footed bat (*Myotus adversus*) from New South Wales, Australia (Morgan et al. 1999b).

Table 5.11 *Cryptosporidium* in wild bovids grouped by subfammily

Subfamily	Host species (scientific name)	*Cryptosporidium* taxa	Reference
Aepycerotinae	**Impala** (*Aepyceros melampus*)	*C. ubiquitum*, *Cryptosporidium* sp.	(Abu Samra et al. 2011; 2013) (Heuschele et al. 1986)
Alcelaphinae	**Black wildebeest** (*Connochaetes gnou*)	Similar to shrew genotype (W5), *Cryptosporidium* sp.	(Mtambo et al. 1997; Alves et al. 2005)
	Blesbok (*Damaliscus dorcas philipsi*)	*C. ubiquitum*	(Ryan et al. 2003a)
	Blue wildebeest (*Connochaetes taurinus*)[a]	*C. parvum*	(Gómez et al. 1996; Morgan et al. 1999b)
Antilopinae	**Addra gazelle** (*Gazella dama ruficollis*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Blackbuck (*Antilope cervicapra*)	*Cryptosporidium* sp.	(Van Winkle 1985; Heuschele et al. 1986)
	Dorcas gazella (*Gazella dorcas neglecta*)[a]	*Cryptosporidium* sp.	(Gómez et al. 1996)
	Mountain gazelle (*Gazella cuvieri*)[a]	*Cryptosporidium* sp.	(Pospischil et al. 1987)
	Persian gazelle (Gazella subgutturosa)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Slender-horned gazelle (*Gazella leptoceros*)[a]	*C. parvum*, *Cryptosporidium* sp.	(Heuschele et al. 1986; Geurden et al. 2009)
	Springbok (*Antidorcas marsupialis*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Thomson's gazelle (*Eudorcus thomsonii*)	*Cryptosporidium* sp.	(Canestri-Trotti 1989)
Bovinae	**African buffalo** (*Syncerus caffer*)	*C. ubiquuitum*, *C. bovis*, *Cryptosporidium* sp.	(Gómez et al. 1996; Mtambo et al. 1997; Abu Samra et al. 2011; 2013)
	Bison, American (*Bison bison*)[a]	*C. tyzzeri*, *Cryptosporidium* sp.	(Alves et al. 2005; Geurden et al. 2009)
	Bison, European (*Bison bonasus*)[a]	*C. andersoni*, *Cryptosporidium* sp.	(Paziewska et al. 2007) (Ryan et al. 2003a)
	Bongo antelope (*Tragelaphus eurycerus*)[a]	*C. parvum*, *Cryptosporidium* sp.	(Geurden et al. 2009) (Gómez et al. 2000)

(continued)

Table 5.11 (continued)

Subfamily	Host species (scientific name)	*Cryptosporidium* taxa	Reference
	Eland (*Taurotragus oryx*)[a]	*C. parvum*, *Cryptosporidium* sp.	(Heuschele et al. 1986; Geurden et al. 2009)
	Lowland anoa (*Bubalus depressicornis*)[a]	*Cryptosporidium* sp.	(Gómez et al. 2000)
	Nilgai (*Boselaphus tragocamelus*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Nyala (*Tragelaphus angasi*)[a]	*C. ubiquitum*	(Ryan et al. 2003a)
	Water buffalo (*Bubalus bubalis*)	*C. ryanae* variant	(Feng et al. 2012)
	Yak (*Bos mutus*)[a]	*C. parvum*, *Cryptosporidium* sp.	(Geurden et al. 2009) (Karanis et al. 2007)
	Zebu (*Bos primigenius indicus*)	*C. ryanae* variant	(Feng et al. 2012)
Caprinae	**Alpine ibex** (*Capra ibex*)[a]	*C. ubiquitum*	(Karanis et al. 2007)
	Angora goat (*Capra hircus*)	*Cryptosporidium* sp.	(Mason et al. 1981)
	Armenian mouflon (*Ovis orientalis gmelini*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Barbary sheep (*Ammotragus lervia*)[a]	*C. tyzzeri*	(Karanis et al. 2007)
	Mouflon sheep (*Ovis musimon*)[a]	*C. ubiquitum*, *Cryptosporidium* sp.	(Gómez et al. 2000; Ryan et al. 2003a)
	Takin (*Budorcas taxicolor*)[a]	*C. tyzzeri*	(Karanis et al. 2007)
	Turkomen markhor (*Capra falconeri*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Urial (*Ovis orientalis*)	*Cryptosporidium* sp.	(Ducatelle et al. 1983)
Hippotraginae	**Addax** (*Addax nasomaculatus*)	*Cryptosporidium* sp.	(Van Winkle 1985) (Heuschele et al. 1986)
	Fringe-eared oryx (*Oryx beisa callotis*)	*Cryptosporidium* sp.	(Van Winkle 1985)
	Sable antelope (*Hippotragus niger*)[a]	*C. parvum*, *Cryptosporidium* sp.	(Hajdušek et al. 2004) (Van Winkle 1985; Heuschele et al. 1986)
	Scimitar-horned oryx (*Oryx dammah*)	*Cryptosporidium* sp.	(Van Winkle 1985) (Heuschele et al. 1986)

(continued)

Table 5.11 (continued)

Subfamily	Host species (scientific name)	*Cryptosporidium* taxa	Reference
	White antelope (*Addax nasomaculatus*)	*Cryptosporidium* sp.	(Van Winkle 1985)
Reduncinae	**Nile lechwe** (*Kobus megaceros*)[a]	*Cryptosporidium* sp.	(Heuschele et al. 1986)
	Waterbuck (*Kobus ellipsiprymnus*)	*Cryptosporidium* sp.	(Gómez et al. 1996)

[a] Wild bovids under captive condition

5.10 Perissodactyla

The Perissodactyl mammals include about 16 species in three families and six genera. These are odd-toed ungulates that include horses, tapirs and rhinoceroses. The digestive system is much simpler than that of the ruminants, with cellulose broken down by fermentation in the latter portion of the gut. They occupy mainly grassland or savannah habitat.

5.10.1 Equids

Equids include the zebra, ass, kiang, and wild horse. *Cryptosporidium* was detected in 28 % (7/25) of zebras (*Equus zebra*) at Mikumi National Park in Tanzania (Mtambo et al. 1997). *Cryptosporidium* horse genotype was identified in a Przewalski's wild horse foal at the Prague Zoo (Ryan et al. 2003a). Although, no other cryptosporidia have been reported in wild Equids, domestic horses have been identified as hosts for *C. parvum*, *Cryptosporidium* horse genotype, and *Cryptosporidium* hedgehog genotype (Laatamna et al. 2013).

5.10.2 Rhinoceros and Tapirs

Cryptosporidium sp. has been reported in a southern white rhinoceros (*Ceratotherium simum simum*), rhinoceros (*Rhinoceros unicornis*), and a South American tapir (*Tapirus terrestris*) at the Barcelona Zoo (Wang and Liew 1990; Gómez et al. 1996, 2000).

5.11 Carnivora

5.11.1 Fin-Footed Mammals (Pinnipedia)

Cryptosporidium muris, which was isolated from a ringed seal (*Phoca hispida*) in Northern Quebec, Canada (Santín et al. 2005), remains the only species identified in Pinnipeds to date. *Cryptosporidium* sp. has been reported in the ringed seal (*Phoca hispida*), harbor seal (*Phoca vitulina*), harp seal (*Pagophilus groenlandicus*), Weddell seal (*Leptonychotes weddellii*), California sea lion (*Zalophus californianus*), grey seal (*Halichoerus grypus*), and southern elephant seal (*Mirounga leonina*) (Deng et al. 2000; Hughes-Hanks et al. 2005; Santín et al. 2005; Bogomolni et al. 2008; Rengifo-Herrera et al. 2011, 2013; Bass et al. 2012). In a neighbor-joining phylogeny, SSU rRNA gene sequences from the ringed seal (seal genotype I, GenBank accession no. AY731234 and seal genotype II, GenBank accession no. AY731235), harbor seal (GenBank accession nos. JN858906–JN858908), harp seal (GenBank accession no. JN858909), and hooded seal (GenBank accession no. JN858905) form a separate clade that is most closely related to a group containing sequences from the shrew (Soricidae), wildebeest (*Connochaetes gnou*), and eastern chipmunk (*Tamias striatus*) (Fig. 5.3c). Isolates from southern elephant seals (*Mirounga leonina*) on the west coast of the Antarctic Peninsula shared 99 % identity with a skunk genotype and *C. tyzzeri* at the SSU locus and are named southern elephant seal genotype (Rengifo-Herrera et al. 2011, 2013). Isolates from the Weddell seal are most closely related to the ferret genotype and *C. parvum* (99 % identity at the SSU locus). *Cryptosporidium* sp. detected in California sea lions (*Zalophus californianus*) from the northern California coastal area share 98 % identity with *C. parvum* at the COWP locus (Deng et al. 2000).

5.11.2 Domestic Dogs

There have been few molecular studies of *Cryptosporidium* in dogs (Table 5.12). *Cryptosporidium canis* is the most frequently identified species in dogs (Abe et al. 2002) and it appears to be relatively host adapted. Other species found in dogs include *C. parvum* (Hajdušek et al. 2004), *C. muris* (Ellis et al. 2010), and *C. meleagridis* (Hajdušek et al. 2004). *Cryptosporidium muris* caused chronic gastritis in an 18-month male, mixed-breed dog (Ellis et al. 2010). It appeared that the dog had a concurrent infection with *Helicobacter*.

In a study of parasites infecting sled dogs in Poland, Bajer et al. (2011) found a higher prevalence of *Cryptosporidium* in dogs infected concurrently with *Giardia* (35.5 %) than in dogs without *Giardia* (2.7 %). In contrast, *Cryptosporidium* prevalence was three times lower in dogs infected with nematodes. Other studies have shown a higher prevalence of *Cryptosporidium* in dogs with diarrhea (Mirzaei

Table 5.12 Prevalence of *Cryptosporidium* in dogs from different countries

Country	Prevalence	Cryptosporidium taxa	Reference
Australia	10.9 % (54/493)	*Cryptosporidium* sp.	(Bugg et al. 1999)
Argentina	2.2 % (48/2,193)	*Cryptosporidium* sp.	(Fontanarrosa et al. 2006)
	1.0 % (1/100)	*Cryptosporidium* sp.	(Soriano et al. 2010)
Brazil	–	*C. canis*	(Thomaz et al. 2007)
	9.6 % (43/450)	*Cryptosporidium* sp.	(Lallo and Bondan 2006)
	4.9 % (4/81)	*Cryptosporidium* sp.	(Mandarino-Pereira et al. 2010)
Canada	74.3 % (52/70)	*Cryptosporidium* sp.	(Shukla et al. 2006)
	3.2 % (5/155)	*Cryptosporidium* sp.	(Himsworth et al. 2010)
Costa-rica	1.7 % (1/58)	*Cryptosporidium* sp.	(Scorza et al. 2011)
Czech Republic	ND	*C. meleagridis*, *C. parvum*	(Hajdušek et al. 2004)
Iran	2.0 % (11/548)	*Cryptosporidium* sp.	(Mirzaei 2012)
Iran	5.2 % (4/77)	*Cryptosporidium* sp.	(Beiromvand et al. 2013)
Japan	3.9 % (3/77)	*C. canis*	(Yoshiuchi et al. 2010)
Korea	9.7 % (25/257)	*Cryptosporidium* sp.	(Kim et al. 1998)
Netherlands	8.6 % (13/152)	*Cryptosporidium* sp.	(Overgaauw et al. 2009)
Poland	13 % (14/108)	*Cryptosporidium* sp.	(Bajer et al. 2011)
Spain	5.1 % (4/79)	*Cryptosporidium* sp.	(Dado et al. 2012)
	6.3 % (32/505)	*Cryptosporidium* sp.	(Gracenea et al. 2009)
USA	10.2 % (5/49)	*Cryptosporidium* sp.	(Jafri et al. 1993)
	17 % (17/100)	*Cryptosporidium* sp.	(Juett et al. 1996)
	3.8 % (5/130)	*Cryptosporidium* sp.	(Hackett and Lappin 2003)
	2.0 % (4/200)	*Cryptosporidium* sp.	(el-Ahraf et al. 1991)
	2.3 % (3/129)	*C. canis*	(Wang et al. 2012)
	ND	*C. muris*	(Ellis et al. 2010)
	12.0 % (6/50) with diarrhea; 2.0 % (1/50) without diarrhea	*Cryptosporidium* sp.	(Tupler et al. 2012)
	2.5 % (3/120)	*Cryptosporidium* sp.	(McKenzie et al. 2010)

ND not determined

2012; Tupler et al. 2012), and dogs less than 1-year-old (Mirzaei 2012). It is not known if the association with diarrhea is dependent on the *Cryptosporidium* species/genotype causing the infection.

Cryptosporidium canis does occasionally cause human disease (Leoni et al. 2006; Hijjawi et al. 2010), and a UK study found that dogs are the most likely companion animals to shed *Cryptosporidium* (46/139) (Smith et al. 2009).

5.11.3 Raccoon Dogs

Cryptosporidium parvum has been identified in a raccoon dog (*Nyctereutes procyonoides viverrinus*) at a zoo in Osaka, Japan (Matsubayashi et al. 2005).

5.11.4 Foxes

Cryptosporidium has been reported in the two genera of true foxes: *Vulpes* and *Urocyon*. Current (1989) identified *Cryptosporidium* sp. in the gray fox (*Urocyon cinereoargenteus*), which is native to southern parts of North America and northern parts of South America. *Cryptosporidium canis* fox genotype ($n = 4$), *C. canis* ($n = 1$), and muskrat genotype I ($n = 1$) were identified in 6/76 *Cryptosporidium* positive samples from unidentified fox species in Maryland, USA (Zhou et al. 2004a). *Cryptosporidium* was detected in 38.7 % (24/62) and 8.1 % (10/124) of red foxes (*Vulpes vulpes*) from the Slovak Republic and Ireland, respectively (Nagano et al. 2007; Ravaszová et al. 2012). Two of the isolates from the study in Ireland were identified as *C. parvum* by sequence analysis of the SSU rRNA and gp60 loci. In contrast to the relatively high prevalence reported in the Slovak Republic, *Cryptosporidium* sp. was detected in only 2.2 % (6/269) and 8.7 % (2/23) of red foxes from Norway and England, respectively (Sturdee et al. 1999; Hamnes et al. 2007).

5.11.5 Wolves

Two large Canadian studies were consistent in showing a relatively low prevalence of *Cryptosporidium* in gray wolves. The prevalence was 1.7 % in a study of 1,558 fecal samples from wolves in British Columbia (Bryan et al. 2012), and 1.2 % in a study of 601 fecal samples from wolves in Manitoba (Stronen et al. 2011). In contrast, 54.9 % of fecal samples (28/51) from wolves in northeast Poland were positive for *Cryptosporidium* (Kloch et al. 2005). A subsequent study in the same region of Poland reported a prevalence of 35.7 %, and *C. parvum* was identified by sequence analysis of the COWP gene (GenBank accession number: AF266273) (Paziewska et al. 2007).

5.11.6 Coyotes

Cryptosporidium has been detected in 27 % (6/22) and 26.3 % (5/19) of fecal samples from coyotes (*Canis latrans*) in northeastern Pennsylvania (Trout et al. 2006) and New York (Ziegler et al. 2007a), respectively. One isolate from the Pennsylvania study shared 99.7 % sequence identity with *C. muris* at the SSU rRNA locus, and the remaining five isolates were identical to the *C. canis* coyote genotype (Trout et al. 2006). In a study of coyotes in southern Alberta and Saskatchewan, Canada, *Cryptosporidium* was not found during winter, and the prevalence was 17.4 % during summer. SSU rRNA sequences from two of the isolates were identified as the *C. canis* coyote genotype (Thompson et al. 2009).

5.11.7 Bears

Cryptosporidium has been detected in three of the five genera in the family Ursidae (*Ailuropoda*, *Helarctus*, and *Ursus*). There have been no reports in the sloth bear (*Melursus ursinus*) or spectacled bear (*Tremarctos ornatus*), which are the only extant representatives of their genera.

Cryptosporidium has been reported in two captive Malayan sun bears (*Helarctos malayanus*) at a zoological park in Taiwan (Wang and Liew 1990).

Cryptosporidium has been detected in black bears (*Ursus americanus*), brown bears (*Ursus arctos*), and polar bears (*Ursus maritimus*) in the genus *Ursus* (Siam et al. 1994; Duncan et al. 1999; Xiao et al. 2000; Ravaszová et al. 2012). Xiao et al. (2000) identified the *Cryptosporidium* bear genotype in a black bear and showed that it is most closely related to *C. canis* at the SSU rRNA and HSP-70 loci.

Karanis et al. (2007) detected *C. tyzzeri* (previously mouse genotype I) in a lesser panda (*Ailurus fulgens*). An isolate from a giant panda (*Ailuropoda melanoleuca*) was named the *Cryptosporidium* giant panda genotype based on sequences of the SSU rRNA, actin, COWP, and HSP-70 genes. Although the study has not been published, the sequences are available in GenBank under the accession numbers JF970610, JN969985, JN588570, and JN588571.

5.11.8 Raccoons

A number of studies have identified *Cryptosporidium* in raccoons (*Procyon lotor*) (Snyder 1988; Perz and Le Blancq 2001; Zhou et al. 2004a; Ziegler et al. 2007a;

Chavez et al. 2012). Zhou et al. (2004a) identified the skunk genotype in 3.9 % (2/51) of raccoon samples collected in the Chesapeake Bay area of Maryland, USA. *Cryptosporidium* was detected in 11 out of 44 fecal samples from raccoons in Colorado, USA. Five out of six of the isolates that were genotyped were identified as the skunk genotype, and one was identified as *C. parvum* (Chavez et al. 2012).

Cryptosporidium also causes clinical disease in raccoons. A juvenile raccoon, estimated to be between 6 and 12-months-old was found in a moribund condition in Fort Collins, Colorado. The animal was emaciated and dehydrated, and had diarrhea and a mucoid oculonasal discharge. *Cryptosporidium* sp. was identified on intestinal villi (Martin and Zeidner 1992).

5.11.9 Ferrets

Rehg et al. (1988) reported cases of subclinical cryptosporidiosis in 40 % of ferrets at an animal research facility in Tennessee. Subsequent studies identified the *Cryptosporidium* ferret genotype in the black-footed ferret (*Mustela nigripes*) and domestic ferret (*Mustela putorius furo*) in the USA and Japan (Xiao et al. 1999b; Sulaiman et al. 2000; Abe and Iseki 2003). The ferret genotype is genetically closely related to *C. parvum*, sharing 99 %, 98 %, 98 %, and 97 % identity at the SSU rRNA, actin, COWP, and HSP-70 genes, respectively. Ferret genotype isolates from the USA (Sulaiman et al. 2000) and Japan (Abe and Iseki 2003) have identical sequences, suggesting that this genotype is geographically conserved.

Cryptosporidium also causes clinical disease in ferrets. Gómez-Villamandos et al. (1995) reported an outbreak of fatal cryptosporidiosis in captive 11–12 month-old non-pregnant female ferrets (*Mustela putorius furo*) kept on a goat farm. Animals died 48–72 h after the onset of signs, which included anorexia, depression, and diarrhea. *Cryptosporidium* developmental stages were identified in feces and tissue, but the species/genotype causing the infection was not identified.

5.11.10 Otters

Cryptosporidium has been detected in the European or wild otter (*Lutra lutra*), river otter (*Lontra canadensis*), and sea otter (*Enhydra lutris nereis*) (Feng et al. 2007; Gaydos et al. 2007; Méndez-Hermida et al. 2007; Oates et al. 2012). In Spain, *Cryptosporidium* oocysts were detected in 17 out of 437 fecal samples from wild otters (Méndez-Hermida et al. 2007). In the USA, nine river otters from the Puget Sound Georgia Basin were positive for the *Cryptosporidium* mink genotype (Gaydos et al. 2007), and a river otter in New York was positive for the *Cryptosporidium* skunk genotype (Feng et al. 2007). *Cryptosporidium* sp. was detected in a single sea otter in California (Oates et al. 2012).

5.11.11 Mink and Martens

Rademacher et al. (1999) isolated *Cryptosporidium* oocysts measuring 3–5 μm from captive beech martens (*Martes foina*) with episodes of diarrhea. *Cryptosporidium* oocysts (4.5–5.5 μm) were also detected in 24.2 % (8/33) of fecal samples from captive American minks (*Mustela vison*) in Spain. The animals did not show clinical signs associated with cryptosporidiosis. Three isolates had COWP sequences that differed from the ferret genotype by a single nucleotide polymorphism (Gómez-Couso et al. 2007). In China, eight *Cryptosporidium* isolates were obtained from 469 fecal samples of American minks (*Mustela vison*) originated from a farm in Hebei Province in China. Six of the eight *Cryptosporidium*-positive samples contained a novel genotype, the *Cryptosporidium* mink genotype, that was most closely related to the *Cryptosporidium* ferret genotype (Wang et al. 2008b). In New York, one of four mink (*Mustela vison*) in a watershed study was positive for *Cryptoporidium* mink genotype, and an ermine (*Mustela erminea*) had a mixed infection with *Cryptosporidium* shrew genotype (also known as W5 genotype) and W18 genotype (Feng et al. 2007). Also in New York, Ziegler et al. (2007a) detected *Cryptosporidium* sp. in one of three ermine (*Mustela erminea*) and in one of 58 American mink (*Musela vison*).

5.11.12 Skunk

Cryptosporidium has been detected in the striped skunk (*Mephitis mephitis*) in New York, USA (Perz and Le Blancq 2001; Ziegler et al. 2007a), and the *Cryptosporidium* skunk genotype has been described from this host (Xiao et al. 2002; Feng et al. 2011). *Cryptosporidium* prevalence in the striped skunk in New York was 14 % (12/86) (Ziegler et al. 2007a).

5.11.13 Badger

Cryptosporidium has been reported in 15.4 % (4/26) of European badgers (*Meles meles*) in England (Sturdee et al. 1999). The *Cryptosporidium* species/genotype infecting badgers is not yet known.

Table 5.13 Prevalence of *Cryptosporidium* in cats from different countries

Country	Prevalence	*Cryptosporidium* taxa	Reference
Argentina	2.2 % (48/2,193)	*Cryptosporidium* sp.	(Fontanarrosa et al. 2006)
Canada	7.1 % (5/70)	*Cryptosporidium* sp.	(Shukla et al. 2006)
Germany	5.3 % (1/19)	*Cryptosporidium* sp.	(Sotiriadou et al. 2013)
Japan	12.7 % (7/55)	*C. felis*	(Yoshiuchi et al. 2010)
Korea	9.7 % (25/257)	*Cryptosporidium* sp.	(Kim et al. 1998)
Netherlands	8.6 %	*Cryptosporidium* sp.	(Overgaauw et al. 2009)
Spain	6.3 % (32/505)	*Cryptosporidium* sp.	(Gracenea et al. 2009)
UK	5.9 % (3/51)	*Cryptosporidium* sp.	(Smith et al. 2009)
USA	5.3 % (11/206)	*Cryptosporidium* sp.	(Hill et al. 2000)
	4.7 % (16/344)	*Cryptosporidium* sp.	(Mekaru et al. 2007)
	3.8 % (10/263)	*Cryptosporidium* sp.	(Spain et al. 2001)
	6.4 % (11/173)	*Cryptosporidium* sp.	(Nutter et al. 2004)
	12.0 % (30/250) – IFA	*Cryptosporidium* sp.	(Ballweber et al. 2009)
	4.8 % (12/250) – PCR	*C. felis*	

5.11.14 Banded Mongoose

The banded mongoose (*Mungos mungo*) has been identified as a host of a *Cryptosporidium* genotype that is most closely related to the bear genotype at the SSU rRNA and HSP-70 loci (Abe et al. 2004).

5.11.15 Domestic Cat

Two *Cryptosporidium* species, *C. felis* and *C. muris*, have been reported in domestic cats (*Felis catus*). *Cryptosporidium felis* was first identified in cats in Japan (Iseki 1979) and has since been reported in cats worldwide. *Cryptosporidium muris* has been reported in cats less frequently (Santín et al. 2006; Pavlásek and Ryan 2007; FitzGerald et al. 2011). FitzGerald et al. (2011) reported a *C. felis*/*C. muris* coinfection in a cat with chronic diarrhea. *Cryptosporidium muris* was identified within the glands of the gastric mucosa. Interestingly, the cat appeared to be persistently infected with *C. muris*, but not *C. felis*. *Cryptosporidium felis* has been identified as an infrequent cause of human cryptosporidiosis (Pedraza-Diaz et al. 2001; Caccio et al. 2002; Caccio 2005; Leoni et al. 2006). The prevalence of *Cryptosporidium* sp. in cats from different countries is shown in Table 5.13.

5.11.16 Wild Cats

Cryptosporidium tyzzeri has been identified in black leopards (*Pantera pardus*) (Karanis et al. 2007). *Cryptosporidium* sp. also has been reported in bobcats (*Lynx rufus*) in California (Carver et al. 2012) and New York, USA (Ziegler et al. 2007a).

5.12 Lagomorpha

Lagomorpha (rabbits, hares and pikas) includes about 87 species in two families and 12 genera. The phylogeny of the lagomorphs is not well understood. They have four upper incisors, and all are herbivorous. All produce both a hard fecal pellet and a soft, grease-like pellet derived from the cecum. The soft pellet is reingested, and contains a much higher concentration of vitamins and minerals than the uningested hard pellet. Lagomorphs occupy both forested and grassland areas.

Rabbits are the major host of *C. cuniculus* (previously *Cryptosporidium* rabbit genotype). *Cryptosporidium cuniculus* is closely related to *C. hominis*, sharing 99.5, 100, 99.9, and 99.5 % nucleotide sequence identity at the SSU rRNA, COWP, actin, and HSP-70 loci, respectively (Robinson et al. 2010). It emerged as a human pathogen in 2009 when it was identified as the cause of a waterborne cryptosporidiosis outbreak in Northhamptonshire, England (Robinson et al. 2010). A subsequent study identified *C. cuniculus* in 1.2 % of 3,030 samples from human cryptosporidiosis cases in the UK during the period 2007–2008 (Chalmers et al. 2011). In a comprehensive review of the literature on *Cryptosporidium* in rabbits, which will not be duplicated here, Robinson and Chalmers (2010) noted that in studies employing genotyping tools, *C. cuniculus* was the only species/genotype detected. More recently, *C. cuniculus* was the only species detected in rabbits in Australia (Nolan et al. 2010, 2013) and China (Shi et al. 2010; Zhang et al. 2012), and prevalence was highest in younger (1–3-month-old) rabbits (Shi et al. 2010).

5.13 Rodentia

Rodents comprise about 40 % of the mammalian diversity, with over 2,200 species in 31 families and 481 genera. Five suborders are typically recognized: Myomorpha (mice, rats, gerbils, and relatives), Sciuromorpha (tree squirrles and relatives), Castorimorpha (beavers, gophers, and relatives), Anumaluromorpha (scaly-tailed squirrels, and springhares), and Hystricomorpha (gundis, capybaras, and relatives). With such diversity, rodents occupy a wide range of habitats, and generalizations regarding their natural history are difficult. All rodents have two upper and two lower incisors that grow continuously (and are self-sharpening) but lack canines. Most species are herbivorous or omnivorous.

5.13.1 Muridae

Old world mice and rats comprise the subfamily Murinae in the largest mammal family, the Muridae. Gerbils, which also are members of the family Muridae, have yet to be identified as a natural host for *Cryptosporidium*, although they are susceptible to experimental infections (Baishanbo et al. 2005; Kváč et al. 2009d).

Four *Cryptosporidium* species (*C. tyzzeri*, *C. muris*, *C. parvum*, and *C. scrofarum*) and six genotypes (*C. suis*-like genotype, rat genotypes I–IV and mouse genotype II) have been reported as natural infections in several species of *Mus*, *Apodemus*, and *Rattus* in Australia, China, the Czech Republic, Germany, Kenya, New Zealand, the Philippines, Poland, Portugal, Spain, the UK, and the US (Table 5.13). The *C. suis*-like genotype and *C. scrofarum* were reported in rats in the Philippines; *C. suis*-like genotype was found exclusively in Asian house rats, and *C. scrofarum* was additionally identified in brown rats (Ng-Hublin et al. 2013). The *C. suis*-like genotype, which is 99.7 % similar to *C. suis* at the SSU rRNA locus, has additionally been reported in cattle and humans (Ong et al. 2002; Langkjær et al. 2007; Robinson et al. 2011). *Cryptosporidium scrofarum* is a pig-adapted species that also has been reported in cattle and humans (Kváč et al. 2009b; Ng et al. 2011). *Cryptosporidium muris*, a rodent adapted species, has been detected the domestic mouse (*Mus musculus domesticus*) in the UK (Chalmers et al. 1997), the Algerian mouse (*Mus spretus*) in Spain (Torres et al. 2000), and the East African mole rat (*Tachyoryctes splendens*) in Kenya (Kváč et al. 2008b). *Cryptosporidium* mouse genotype II has been identified in 11 domestic mice in Australia (Foo et al. 2007). Rat genotypes I–IV have been reported in various rat species in Australia, China, and the Philippines (Table 5.14). Although *C. tyzzeri* (previously mouse genotype I) has been reported in the yellow-necked mouse, voles, snakes, and rats (Morgan et al. 1998, 1999b; Bajer et al. 2003; Xiao and Ryan 2004; Karanis et al. 2007), the house mouse is considered the major host for this species (Ren et al. 2012).

The fate of the house mouse (*Mus musculus*) has been intimately connected to humans since the establishment of a commensal relationship at the dawn of civilization. Two house mouse subspecies, *Mus musculus musculus* and *Mus musculus domesticus*, diverged approximately 0.5 million years ago in the Middle East (Geraldes et al. 2008; Duvaux et al. 2011; Auffray and Britton-Davidian 2012; Bonhomme and Searle 2012). *Mus m. musculus* spread to northern Eurasia and migrated westward through Europe. *Mus m. domesticus* expanded westward through Asia Minor to southern and western Europe, northern Africa, and the New World (Boursot et al. 1993; Guénet and Bonhomme 2003; Rajabi-Maham et al. 2008; Duvaux et al. 2011; Auffray and Britton-Davidian 2012; Bonhomme and Searle 2012; Cucchi et al. 2012). About 6,000 years ago, westward migrating

Table 5.14 *Cryptosporidium* spp. identified in species of old world mice and rats

Host (scientific name)	*Cryptosporidium* taxa	Reference
Algerian mouse (*Mus spretus*)	*C. muris*, *C. parvum*	(Torres et al. 2000)
Asian house rat (*Rattus tanezumi*)	*C. scrofarum*, *C. tyzzeri*, *C. suis*-like, rat genotypes II–IV	(Lv et al. 2009; Ng-Hublin et al. 2013)
Black rat (*Rattus rattus*)	*C. parvum*, rat genotypes II–III, *Cryptosporidium* sp.	(Miyaji et al. 1989; Yamura et al. 1990; Webster and Macdonald 1995; Chilvers et al. 1998; Torres et al. 2000; Paparini et al. 2012)
Brown rat (*Rattus norvegicus*)	*C. tyzzeri*, *C. scrofarum*, *C. muris*, rat genotypes I–IV, *Cryptosporidium* sp.	(Iseki 1986; Miyaji et al. 1989; Yamura et al. 1990; Quy et al. 1999; Kimura et al. 2007; Lv et al. 2009; Ng-Hublin et al. 2013)
House mouse (*Mus musculus*)	*C. tyzzeri*, *C. muris*, mouse genotype II, *Cryptosporidium* sp.	(Klesius et al. 1986; Chalmers et al. 1997; Chilvers et al. 1998; Xiao et al. 1999b; Foo et al. 2007; Ziegler et al. 2007a; 2007b; Lv et al. 2009; Kváč et al. 2013b)
Japanese field mouse (*Apodemus speciosus*)	*Cryptosporidium* sp.	(Nakai et al. 2004; Hikosaka and Nakai 2005)
Striped field mouse (*Apodemus agrarius*)	*Cryptosporidium* sp.	(Siński et al. 1998)
East African mole rat (*Tachyoryctes splendens*)	*C. muris*	Kváč et al. 2008b
Wood mouse (*Apodemus sylvaticus*)	*C. parvum*, *C. muris*, *Cryptosporidium* sp.	(Chalmers et al. 1997; Torres et al. 2000; Hajdušek et al. 2004)
Yellow-necked mouse (*Apodemus flavicollis*)	*C. tyzzeri*, *C. parvum*, *Cryptosporidium* sp.	(Siński 1993; Torres et al. 2000; Bajer et al. 2002; 2003; Bednarska et al. 2003)

M. m. musculus and eastward-migrating *M. m. domesticus* reestablished contact in central Europe, and formed a stable, narrow (approximately 20 km wide) hybrid zone that stretches 2,500 km from Norway to the Black Sea (Macholán et al. 2003; Jones et al. 2011; Ďureje et al. 2012). This hybrid zone affords a rare opportunity to study speciation through the interactions between two subspecies that have been separated for about 500,000 years.

The hybrid zone was recently used to test the hypothesis that the house mouse-adapted species *C. tyzzeri* is coevolving with subspecies of *M. musculus*. *Cryptosporidium tyzzeri* isolates from naturally infected *M. m. musculus* and *M. m. domesticus* in the hybrid zone differed genetically, morphometrically, and biologically (Kváč et al. 2013b), which supports the coevolution hypothesis.

5.13.2 Cricetidae

Cricetidae, which includes muskrats, deer mice, voles, cotton rats, and hamsters, are the second largest family of mammals with greater than 681 species in 130 genera. To date, members of this family have been reported as hosts for four *Cryptosporidium* species (*C. muris*, *C. parvum*, *C. andersoni*, and *C. ubiquitum*) and ten genotypes (vole genotype, muskrat genotypes I and II, W12, hamster genotype, chipmunk genotype I, and deer mouse genotypes I–IV) (Table 5.15).

Within the Cricetidae, *C. muris* and *C. andersoni* have been detected only in hamsters (Ryan et al. 2003a; Lv et al. 2009). *Cryptosporidium andersoni*, a ruminant adapted species, was detected in 5.9 % (8/136) of pet hamsters from three different species in China (Lv et al. 2009), suggesting that hamsters may be a significant host for *C. andersoni*, at least in that country. *Cryptosporidium muris* and *C. parvum* are the only *Cryptosporidium* species or genotypes known to infect members of both the Muridae and Cricetidae family. These species also are found in the family Sciuridae (see below).

5.13.3 Sciuridae

Five species (*C. andersoni*, *C. baileyi*, *C. muris*, *C. parvum*, and *C. ubiquitum*) and ten genotypes have been detected in the family Sciuridae, which includes squirrels and chipmunks (Table 5.16). In addition to *C. parvum* and *C. muris*, which are found in Muridae, Cricetidae, and Sciuridae, two species (*C. andersoni* and *C. ubiquitum*) and two genotypes (chipmunk genotype I and deer mouse genotype III) are common to the Cricetidae and Sciuridae (Fig. 5.4).

5.13.4 Hystricomorpha

Hystricomorphs include the guinea pig, capybara, and chinchilla, which were the first rodents to colonize South America about 40 million years ago, probably from Africa, and they remained the only rodents in South America until the arrival of murids about five million years ago (Antoine et al. 2012).

Table 5.17 shows the *Cryptosporidium* sp. that have been reported in Hystricomorphs. *Cryptosporidium wrairi* is found only in guinea pigs (Vetterling et al. 1971; Lv et al. 2009), and the prevalence of infection can be as high as 85 % in pet guinea pigs (Lv et al. 2009). Guinea pigs also host a guinea pig genotype

Table 5.15 *Cryptosporidium* spp. identified in the Cricetidae

Host (scientific name)	*Cryptosporidium* taxa	Reference
Bank vole (*Myodes glareolus*)	*Cryptosporidium* sp.	(Siński 1993; Laakkonen et al. 1994; Chalmers et al. 1997; Bull et al. 1998; Siński et al. 1998; Torres et al. 2000; Bajer et al. 2002; Bednarska et al. 2007)
Campbell hamster (*Phodopus campbelli*)	*C. andersoni*, *C. muris*, *C. parvum*	(Lv et al. 2009)
Common vole (*Microtus arvalis*)	*Cryptosporidium* sp.	(Siński et al. 1998; Bednarska et al. 2007)
Cotton rat (*Sigmodon hispidus*)	*Cryptosporidium* sp.	(Elangbam et al. 1993)
Deer mouse or white-footed mice (*Peromyscus* spp.)	*C. parvum*, *C. ubiquitum*, muskrat genotype II (W16), chipmunk genotype I (W17), deer mouse genotypes I–IV	(Perz and Le Blancq 2001; (Xiao et al. 2002; Feng et al. 2007; Ziegler et al. 2007a, b)
Golden hamster (*Mesocricetus auratus*)	*C. andersoni*, *C. muris*, *C. parvum*	(Ryan et al. 2003a; Lv et al. 2009)
Meadow vole (*Microtus pennsylvanicus*)	Vole genotype (W15), muskrat genotype II (W16)	(Feng et al. 2007; Ziegler et al. 2007a; 2007b)
Muskrat (*Ondatra zibethicus*)	Muskrat genotype I (W7), muskrat genotype II (W16)	(Siński et al. 1998; Perz and Le Blancq 2001; Xiao et al. 2002; Zhou et al. 2004a; Feng et al. 2007; Ziegler et al. 2007b)
Siberian hamster (*Phodopus sungorus*)	*C. andersoni*, *C. muris*, *C. parvum*, hamster genotype	(Lv et al. 2009)
Southern red-backed vole (*Myodes gapperi*)	*C. parvum*, vole cluster, muskrat genotype I (W7), Muskrat genotype II (W16), W12	(Feng et al. 2007; Ziegler et al. 2007a, b)

(GenBank Accession nos. DQ885337 and DQ885338) that is only 93 % similar to *C. wrairi* at the SSU rRNA locus. *Cryptosporidium parvum* has been identified in capybara (*Hydrochoerus hydrochaeris*) in Brazil (Meireles et al. 2007); however, it is likely that the infections resulted from exposure of capybara to water polluted by anthroponotic activities.

Table 5.16 *Cryptosporidium* spp. identified in the Sciuridae – chipmunks and squirrels

Host (scientific name)	*Cryptosporidium* taxa	Reference
American red squirrel (*Tamiasciurus hudsonicus*)	*C. ubiquitum*, chipmunk genotype I	(Ziegler et al. 2007a, b)
Bobak marmot (*Marmota bobac*)	*C. andersoni*	(Ryan et al. 2003a)
Belding's ground squirrel (*Spermophilus beldingi*)	Sbey/Sbld A, Sbey/Sbld/Sltl C, Sbld D	(Pereira et al. 2010)
California ground squirrels (*Spermophilus beecheyi*)	Sbey/Sbld A, Sbey B, Sbey/Sbld/Sltl C	(Atwill et al. 2001; 2004)
Eastern chipmunk (*Tamias striatus*)	*C. andersoni*, *C. baileyi*, *C. ubiquitum*, chipmunk genotypes I–II	(Perz and Le Blancq 2001; Feng et al. 2007; Ziegler et al. 2007a, 2007b)
Eastern grey squirrel (*Sciurus carolinensis*)	*C. baileyi*, *C. muris*, *C. parvum*, *C. ubiquitum*, chipmunk genotype I, deer mouse genotype III, skunk genotype	(Sundberg et al. 1982; Feng et al. 2007; Ziegler et al. 2007a, 2007b)
Eurasian red squirrel (*Sciurus vulgaris*)	*C. ubiquitum*, ferret genotype, chipmunk genotype I (W17)	(Bertolino et al. 2003; Feng et al. 2007; Kváč et al. 2008a; Lv et al. 2009)
Fox squirrel (*Sciurus niger*)	*C. ubiquitum*, *Cryptosporidium* sp.	(Current 1989) (Stenger et al. unpublished)
Golden-mantled ground squirrel (*Spermophilus lateralis*)	Sbey/Sbld/Sltl C	(Pereira et al. 2010)
Siberian chipmunk (*Tamias sibiricus*)	*C. muris*, *C. parvum*, chipmunk genotype III, Ferret genotype	(Matsui et al. 2000; Lv et al. 2009)
Southern flying squirrel (*Glaucomys volans*)	*Cryptosporidium* sp.	(Current 1989)
Thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*)	*Cryptosporidium* sp.	(Current 1989)
Woodchuck or Groundhog (*Marmota monax*)	*C. ubiquitum*	(Feng et al. 2007; Ziegler et al. 2007b)

5.13.5 Beaver and Gophers

Cryptosporidium has been detected in the American and European beavers and the plains pocket gopher (Table 5.18). Combining the data from three studies in the eastern US (Fayer et al. 2006; Feng et al. 2007; Ziegler et al. 2007b), the prevalence of *Cryptosporidium* in American beavers (*Castor Canadensis*) was 4.0 % (7/176).

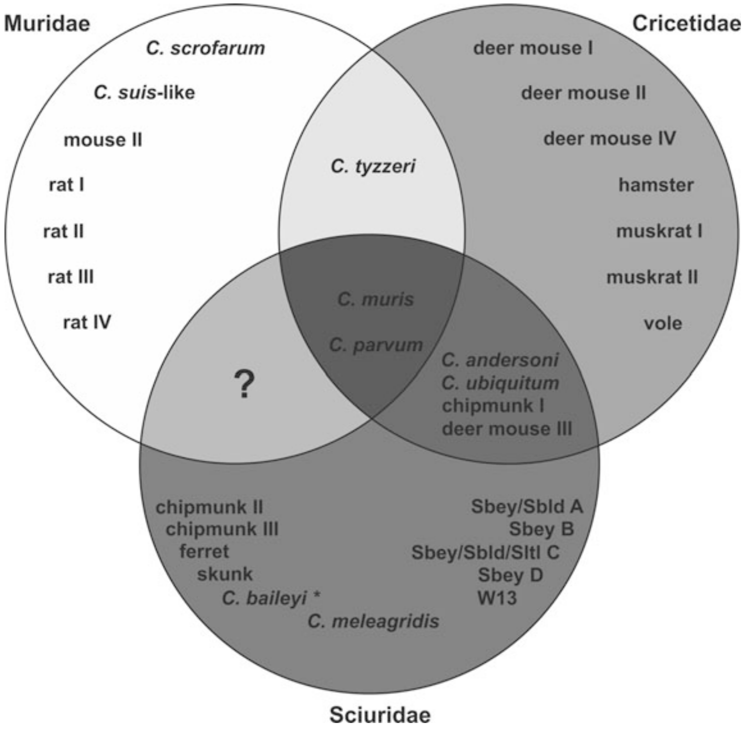

Fig. 5.4 Venn diagram showing group specific and overlapping *Cryptosporidium* taxa from the muridae, cricetidae, and scuridae. **C. baileyi* is generally associated with avian hosts

In Europe, *Cryptosporidium* was detected in 19.2 % (10/52) of European beavers (*Castor fiber*) in northeastern Poland (Paziewska et al. 2007). *Cryptosporidium ubiquitum* and a novel beaver genotype were identified in beavers in New York. The beaver genotype clusters with mink and ferret genotypes in a neighbor-joining phylogeny of SSU rRNA sequences, (Fig. 5.3b) and is most similar to a ferret-like genotype, sharing 99.6 % identity at the SSU rRNA locus.

5.14 Non-Human Primates

There are about 375 species of non-human primates in 15 families and 68 genera. All are omnivorous, and occupy both forest and open grassland habitats. There is potential for *Cryptosporidium* transmission between humans and endangered non-human primates in areas where the two live in close proximity (Nizeyi et al. 1999, 2002; Graczyk et al. 2001). Yet, knowledge of *Cryptosporidium* and cryptosporidiosis in our closest relatives remains relatively poor, and few studies

Table 5.17 *Cryptosporidium* spp. identified in hystricomorphs

Host (scientific name)	*Cryptosporidium* taxa	Reference
Capybara (*Hydrochoerus hydrochaeris*)	*C. parvum*	(Meireles et al. 2007)
Chinchilla (*Chinchilla laniger*)	*Cryptosporidium* sp.	(Yamini and Raju 1986)
Guinea pig (*Cavia porcellus*)	*C. wrairi*, guinea pig genotype	(Vetterling et al. 1971; Xiao et al. 1999b; Huber et al. 2007; Lv et al. 2009)
Indian crested porcupine (*Hystrix indica*)	*Cryptosporidium* sp.	(Fayer et al. 2000)
North American porcupine (*Erethizon dorsatum*)	*Cryptosporidium* sp.	(Ziegler et al. 2007a, 2007b)
Nutria/coypu (*Myocastor coypus*)	*Cryptosporidium* sp.	(Ryan et al. 2003a)

Table 5.18 *Cryptosporidium* spp. identified in the beaver and gophers

Host (scientific name)	*Cryptosporidium* taxa	Reference
American beaver (*Castor canadensis*)	*C. ubiquitum*, beaver genotype	(Fayer et al. 2006; Feng et al. 2007; Ziegler et al. 2007b)
European beaver (*Castor fiber*)	*Cryptosporidium* sp.	(Siński et al. 1998; Paziewska et al. 2007)
Plains pocket gopher (*Geomys bursarius*)	*Cryptosporidium* sp.	(Current 1989)

have genotyped isolates (Table 5.19). Among those that have, the potential for zoonotic transmission is clearly evident in the species detected.

Cryptosporidium parvum has been identified in the mountain gorilla (*Gorilla gorilla beringei*) from Uganda; toque macaque (*Macaca sinica sinica*), gray lagur (*Semnopithecus entellus thersites*), and purple-faced lagur (*Trachypithecus vetulus philbricki*) from Sri Lanka; and rhesus macaque (*Macaca mulatta*) from China (Graczyk et al. 2001; Ekanayake et al. 2007; Ye et al. 2012). *Cryptosporidium hominis* has been reported in rhesus macaques from the US and China and olive baboons (*Papio anubis*) from Kenya (Feng et al. 2011; Li et al. 2011; Ye et al. 2012). Isolates from the red-tailed guenon, red colobus, and black-and-white colobus were indistinguishable from *C. hominis*, *C. parvum* and *C. cuniculus* at the COWP locus (Salyer et al. 2012). Other *Cryptosporidium* taxa detected in primates include *C. felis* in rhesus macaques at a park in China (Ye et al. 2012) and a *Cryptosporidium* sp. closely related to *C. suis* in a Coquerel's sifaka (*Propithecus coquereli*) in the US (da Silva et al. 2003).

The clinical signs of cryptosporidiosis in infant non-human primates resemble those seen in human infants. Cryptosporidiosis was diagnosed in 81/157 infant primates, predominantly pigtailed macaques (*Macaca nemestrina*), housed in a nursery unit at the Washington Regional Primate Research Center. The mean age at onset of oocyst shedding was 38 ± 25 days, and animals shed oocysts for

Table 5.19 *Cryptosporidium* spp. identified in non-human primates

Host (scientific name)	Country	*Cryptosporidium* taxa	Reference
Captive – zoo			
Black-and-white ruffed lemur (*Lemur variegatus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Black-capped squirrel monkey (*Saimiri sciureus boliviensis*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Black lemur (*Eulemur macaco*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000; Gracenea et al. 2002)
Bonnet macaque (*Macaca radiata*)	Malaysia	*Cryptosporidium* sp.	(Lim et al. 2008)
Brown spider monkey (*Ateles belzebuth hybridus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Brown lemur (*Lemur macacomayottensis*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Campbell's mona (*Cercopithecus campbelli*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Collared mangabey (*Cercocebus torquatus lunulatus*)	Spain	*Cryptosporidium* sp.	(Gracenea et al. 2002)
Common marmoset (*Calithrix jacchus*)	USA	*Cryptosporidium* sp.	(Kalishman et al. 1996)
Cotton-top tamarin (*Saguinus oedipus*)	USA	*Cryptosporidium* sp.	(Heuschele et al. 1986)
Drill (*Mandrillus leucophaeus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Gray langur (*Semnopithecus*)	Malaysia	*Cryptosporidium* sp.	(Lim et al. 2008)
Lesser slow loris (*Nycticebus pygmaeus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Mangabey (*Cercocebus albigena*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992, 2000; Gracenea et al. 2002)
Marimonda spider monkey (*Ateles belzebuth*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Olive baboon (*Papio anubis*)	Italy	*Cryptosporidium* sp.	(Fagiolini et al. 2010)
Patas monkey (*Erythrocebus patas*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Pig-tailed macaque (*Macaca leonina*)	Malaysia	*Cryptosporidium* sp.	(Lim et al. 2008)
Red ruffed lemur (*Vaecia variegate rubra*)	USA	*Cryptosporidium* sp.	(Heuschele et al. 1986)
Ring-tailed lemur (*Lemur catta*)	Spain Italy	*Cryptosporidium* sp.	(Gómez et al. 2000) (Fagiolini et al. 2010)
Siamang (*Hylobates syndactylus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000; Gracenea et al. 2002)
Southern talapoin monkey (*Miopithecus talapoin*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Stump-tailed macaque (*Macaca arctoides*)	Malaysia	*Cryptosporidium* sp.	(Lim et al. 2008)

(continued)

Table 5.19 (continued)

Host (scientific name)	Country	*Cryptosporidium* taxa	Reference
Talapoin monkey (*Cercopithecus talapoin*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Tibetan Macaque (*Macaca thibetana*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Velvet monkey (*Cercopithecus aethiops*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
Western gorilla (*Gorilla gorilla gorilla*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000; van Zijll Langhout et al. 2010)
White-collared monkey (*Cercocebus torquatus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 1992)
White-crowned mangabeys (*Cercocebus torquatus lunulatus*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
White-faced saki (*Pithecia pithecia*)	Spain	*Cryptosporidium* sp.	(Gómez et al. 2000)
Captive – non-zoo			
Crab-eating macaque (*Macaca fascicularis*)	USA	*C. muris*-like	(Dubey et al. 2002)
Coquerel's sifaka (*Propithecus coquereli*)	USA	*Cryptosporidium* sp.	(Charles-Smith et al. 2010) (da Silva et al. 2003)
Rhesus macaque (*Macaca mulatta*)	USA	*Cryptosporidium* sp.	(Yanai et al. 2000)
	USA	*Cryptosporidium* sp.	(Osborn et al. 1984; Feng et al. 2011; Ye et al. 2012)
	Not reported	*C. hominis* monkey genotype	Feng et al. 2011;
Southern pig-tailed macaque (*Macaca nemestrina*)	USA	*Cryptosporidium* sp.	(Miller et al. 1990a)
Free living			
Black-and-white colobus (*Colobus guereza*)	Uganda	*Cryptosporidium* sp.	(Salzer et al. 2007; Salyer et al. 2012)
Gray lagur (*Semnopithecus entellus thersites*)	Sri Lanka	*C. parvum*, *Cryptosporidium* sp.	(Ekanayake et al. 2006)
Green monkey (*Cercopithecus aethiops*)	Ethiopia	*Cryptosporidium* sp.	(Legesse and Erko 2004)
Mountain gorilla (*Gorilla beringei beringei*)	Uganda	*Cryptosporidium* sp.	(Nizeyi et al. 1999; Sleeman et al. 2000; Graczyk et al. 2001)
	Rwanda	*C. parvum*	Graczyk et al. 2001)
		Cryptosporidium sp.	Sleeman et al. 2000,

(continued)

Table 5.19 (continued)

Host (scientific name)	Country	*Cryptosporidium* taxa	Reference
Olive baboon (*Papio anubis*)	Kenya	*Cryptosporidium* sp.	(Muriuki et al. 1997, 1998; Hope et al. 2004; Legesse and Erko 2004; Li et al. 2011)
		C. hominis	Li et al. 2011)
	Uganda	*Cryptosporidium* sp.	Hope et al. 2004
	Ethiopia	*Cryptosporidium* sp.	Legesse and Erko 2004
Purple-faced lagur (*Trachypithecus vetulus*)	Sri Lanka	*Cryptosporidium* sp.	(Ekanayake et al. 2006)
		C. parvum	(Ekanayake et al. 2007)
Rhesus macaque (*Macaca mulatta*)	China	*C. felis*, *C. hominis*, *C. parvum*	Ye et al. 2012
Red colobus (*Procolobus tephrosceles*)	Uganda	*Cryptosporidium* sp.	(Salzer et al. 2007, Salyer et al. 2012)
Red-tailed guenon (*Cercopithecus ascanius*)	Uganda	*Cryptosporidium* sp.	(Salzer et al. 2007) (Salyer et al. 2012)
Savanna chimpamzee (*Pan troglodytes schweinfurthii*)	Tanzania	*Cryptosporidium* sp.	(Gonzalez-Moreno et al. 2013) (Ekanayake et al. 2006)
Toque macaque (*Macaca sinica*)	Sri Lanka	*Cryptosporidium* sp.	Ekanayake et al. 2007)
Vervet monkey (*Chlorocebus pygerythrus*)	Kenya	*Cryptosporidium* sp.	(Muriuki et al. 1997, 1998)
Western gorilla (*Gorilla gorilla gorilla*)	Gabon	*Cryptosporidium* sp.	(van Zijll Langhout et al. 2010)

7–78 days. All but one of the animals had clinical symptoms of enteric infection, which included severe diarrhea and dehydration. The outbreak was confined to the nursery and no cases were detected among juvenile or adult animals (Miller et al. 1990a). A follow-up study (Miller et al. 1990b) characterized the course of experimental infections in pigtailed macaques infected with 10 or 2×10^5 oocysts from naturally infected macaques (the species/genotype of the isolate was not reported). Infected animals suffered clinical enteritis, watery stools, lethargy, and loss of appetite. Animals infected with 10 and 2×10^5 oocysts began shedding oocysts on day 8 and day 7, respectively, and there was no difference in the duration of intense oocyst shedding or clinical symptoms between the treatments.

Cryptosporidiosis in immunocompromised non-human primates resembles cryptosporidiosis in immunocompromised humans with respect to extraintestinal involvement. Kaup et al. (1994) diagnosed biliary and pancreatic cryptosporidiosis in several rhesus monkeys following an experimental simian immunodeficiency virus (SIV) infection. Yanai et al. (2000) reported moderate to severe bronchopneumonia with cryptosporidiosis in macaques experimentally infected with SIV. Endogenous stages were detected in the trachea, lungs, bile ducts, pancreas, and intestine. Conjunctival infections were detected in six SIV-infected, immunodeficient rhesus monkeys (Baskin 1996). Although conjunctival cryptosporidiosis has been reported in birds, there have been no reported cases in humans. Singh et al. (2011) examined the time during an SIV infection when a self-limiting *Cryptosporidium parvum* infection becomes persistent due to mucosal immune defects. One group of SIV-infected macaques was challenged with *C. parvum* during acute SIV infection and the second group was challenged during the chronic infection phase. Interestingly, persistent cryptosporidiosis developed during acute SIV infection.

5.15 Diversity of *Cryptosporidium* in Different Vertebrate Classes

The diversity of mammalian cryptosporidia appears to reflect mammal diversity. We compared *Cryptosporidium* diversity in the order Rodentia – the most diverse order of mammals – to diversity in other mammalian orders. Figure 5.5 presents 68 mammalian *Cryptosporidium* taxa (species and genotypes) in a Venn diagram with two sets: 'Rodentia' and 'other mammals' Among the taxa that are members of both sets (the intersection), *C. andersoni*, *C. scrofarum*, and the ferret genotype primarily infect non-rodent hosts and are therefore included with 'other mammals'. Similarly, *C. tyzzeri* and *C. muris* are primarily parasites of rodents and are included with the Rodentia set. *Cryptosporidium baileyi* was excluded from the analysis because it primarily infects avian hosts. Forty percent (27/67) of mammalian *Cryptosporidium* taxa are associated with the order Rodentia, which reflects the diversity of Rodentia within mammals (Rodentia contains 40 % of mammalian species). Three percent (2/67) of *Cryptosporidium* taxa (*C. parvum* and *C. ubiquitum*) can be considered generalists, and 57 % (38/67) of taxa are associated with non-rodent mammals. These data suggest that cryptosporidia diverged in close association with mammal species.

In contrast to mammals, it appears that the diversity of avian cryptosporidia does not reflect avian diversity. The order Passeriformes comprises about 50 % of avian species; species diversity in the Passeriforme order is comparable to that of the entire mammal class. Figure 5.6 presents 17 *Cryptosporidium* taxa from avians in a Venn diagram with two sets: 'Passeriformes' and 'other avians'. Muskrat genotype I, *C. hominis*, *C. hominis*-like, *C. muris*, and *C. parvum* were excluded from the analsysis because they are not considered avian-associated taxa. Seventeen percent (2/12) of avian *Cryptosporidium* taxa are exclusively found in passerines (avian genotypes I and IV), 50 %

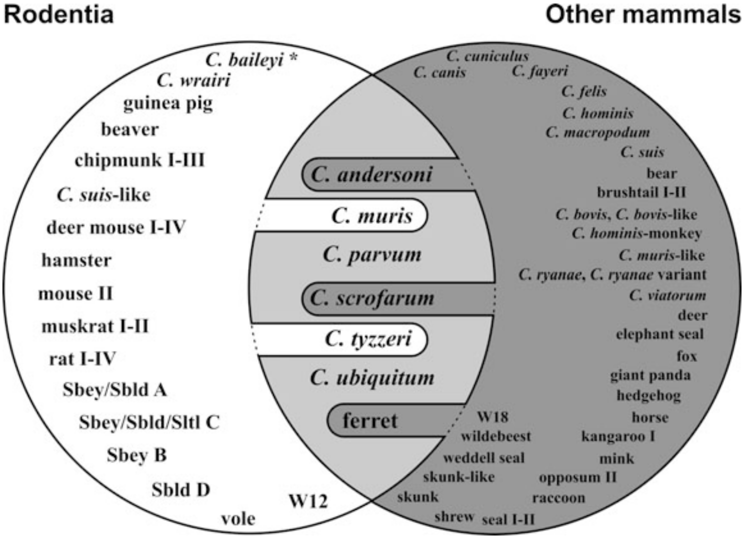

Fig. 5.5 Venn diagram showing group-specific and overlapping *Cryptosporidium* taxa in rodent and non-rodent mammal groups. **C. baileyi* is generally associated with avian hosts

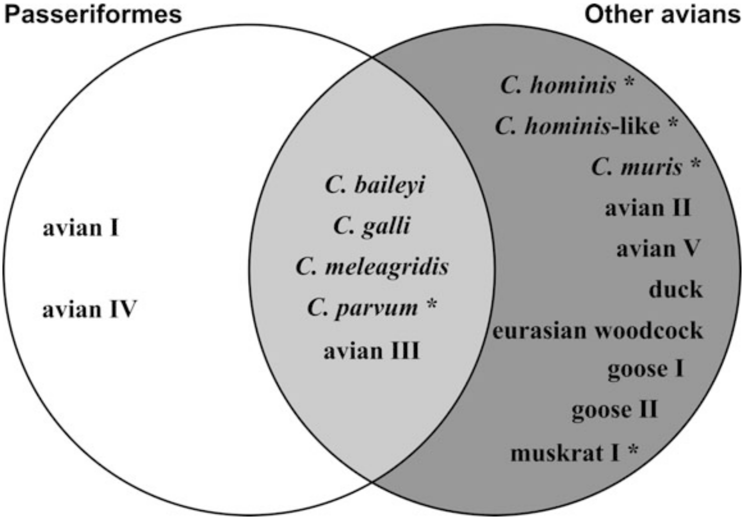

Fig. 5.6 Venn diagram showing group-specific and overlapping *Cryptosporidium* taxa from passerine and non-passerine bird groups

(6/12) are found only in non-passerine orders, and 33 % (4/12; *C. baileyi*, *C. meleagridis*, *C. galli*, and avian genotype III) infect multiple avian orders and can be considered generalists. From these data, it can be hypothesized that the mechanisms of *Cryptosporidium* diversification in avians and mammals are fundamentally different.

The diversity of *Cryptosporidium* in reptiles and amphibians appears to be low. Despite a comparable faunal diversity with birds, and considerably greater faunal diversity than mammals, relatively few *Cryptosporidium* taxa have been reported in reptiles or amphibians.

5.16 Gaps in Knowledge and Suggestions for Future Work

- *Cryptosporidium* remains poorly characterized in many vertebrate orders. For example, Chiroptera (bats), an order that comprises 20 % of mammal species, has not been well studied. If *Cryptosporidium* diversity reflects bat diversity, then we should expect to find many bat-adapted *Cryptosporidium* taxa.
- *Cryptosporidium viatorum* is a recently described species that has thus far been identified only in cases of human cryptosporidiosis in the UK ($n = 10$) and Sweden ($n = 2$); all cases were associated with travel to countries in the Indian subcontinent, Africa, and South America (Elwin et al. 2012b; Insulander et al. 2013). Studies are needed to determine if there is a major animal host for this species. Greater sampling in general, particularly of animals in their natural habitat, will help to help to identify emerging sources of human disease.
- Relatively little is known about the general biology of many of the *Cryptosporidium* genotypes identified. Experimental evidence of infection characteristics and host specificity will enhance understanding of the biological diversity and will clarify taxonomy.

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