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Invited review

Public health significance of zoonotic *Cryptosporidium* species in wildlife: Critical insights into better drinking water management

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A B S T R A C T

Cryptosporidium is an enteric parasite that is transmitted via the faecal–oral route, water and food. Humans, wildlife and domestic livestock all potentially contribute *Cryptosporidium* to surface waters. Human encroachment into natural ecosystems has led to an increase in interactions between humans, domestic animals and wildlife populations. Increasing numbers of zoonotic diseases and spill over/back of zoonotic pathogens is a consequence of this anthropogenic disturbance. Drinking water catchments and water reservoir areas have been at the front line of this conflict as they can be easily contaminated by zoonotic waterborne pathogens. Therefore, the epidemiology of zoonotic species of *Cryptosporidium* in free-ranging and captive wildlife is of increasing importance. This review focuses on zoonotic *Cryptosporidium* species reported in global wildlife populations to date, and highlights their significance for public health and the water industry.

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1. Introduction

More than 15% of the world's population has no access to safe drinking water (Cauchie et al., 2014). Waterborne parasitic protozoan diseases with worldwide distribution, result in four billion cases of diarrhoea, 1.6 million deaths annually (www.who.int) and 62.5 million Disability Adjusted Life Years (DALYs) worldwide (Wright and Gundry, 2009; WHO, 2009). Yet, despite the latest advances made in water treatment measures, protecting drinking water supplies against waterborne pathogens remains by far, as one of the most challenging concerns for the entire drinking water supply chain worldwide (Cotruva et al., 2004; Betancourt and Rose, 2004; Thompson and Smith, 2011; Plutzer, 2013; Burnet et al., 2014). In response to this, in 2009, the World Health Organization has developed guidelines for water suppliers on how to implement “Water Safety Plans” (WSPs), in the hope of halving the number of people without safe access to drinking water by the end of 2015 (WHO, 2009).

In less developed countries, lack of basic infrastructure for providing safe drinking water is considered a major cause of poor water quality which contributes to the spread of endemic/epidemic waterborne diseases. However, even in industrialized nations, highly advanced infrastructures are not yet a protective factor against outbreaks (Cummins et al., 2010; Smith and Nichols, 2010; Castro-Hermida et al., 2010; Burnet et al., 2014; Smolders et al., 2015). This appears to be largely due to a lack of knowledge about the epidemiology and transmission dynamics of waterborne pathogens (e.g. from animals ranging within the catchments) which leads to poor management practices for drinking water catchments (Gormley et al., 2011; Castro-Hermida et al., 2010).

Waterborne parasitic protozoans are responsible for the majority of waterborne outbreaks worldwide, with socio-economic impacts even in developed countries (Cotruva et al., 2004; Pond, 2005; Baldursson and Karanis, 2011; Cauchie et al., 2014). Of these, *Cryptosporidium* was the etiological agent in 60.3% (120) of the waterborne protozoan parasitic outbreaks that have been reported worldwide between 2004 and 2010 (Baldursson and Karanis, 2011). For the global water industry, therefore, *Cryptosporidium* represents the major public health concern, as its oocyst (the environmentally stable stage) is able to survive and penetrate routine wastewater treatment and is resistant to inactivation by commonly used drinking water disinfectants (Fayer et al., 2001; Baldursson and Karanis, 2011; Burnet et al., 2014). As a result of these waterborne outbreaks of cryptosporidiosis, *Cryptosporidium* testing in source or finished water is now mandatory in most industrialised nations. For example, the U.S. EPA, working with the U.S. public water supply industry, developed and implemented the Long-term Stage 2 Enhanced Surface Water Treatment Rule (LT2ESWTR), known as LT2 to control *Cryptosporidium* in public water supplies (US EPA, 2006). LT2 requires all public water suppliers using surface water sources and serving populations >10,000 to monitor their sources for *Cryptosporidium* by analysing at least 24 consecutive monthly samples. In the UK, the Drinking Water Inspectorate (DWI) requires that water companies carry out risk assessments on all their water supply sites to ascertain the level of risk *Cryptosporidium* poses to the final treated water quality. Those at high risk need additional treatment (in the form of properly controlled coagulation/flocculation filtration systems or membrane or UV treatment systems). The UK regulations also require companies to design and continuously operate adequate treatment and disinfection. A proven failure to comply with this is now an offence (DWI, 2010).

Cryptosporidium species are able to infect a broad range of hosts including humans, domestic and wild animals (mammals, birds, fish, marsupials, reptiles and amphibians) worldwide (Table 1), causing asymptomatic or mild to severe gastrointestinal disease in their host species (Monis and Thompson, 2003; Hunter et al., 2007; Ryan and Power, 2012; Xiao, 2010; Kváč et al., 2014a; Ryan et al., 2014). Current treatment options for cryptosporidiosis are limited and only one drug, nitazoxanide (NTZ), has been approved by the United States (US) Food and Drug Administration (FDA). This drug, however, exhibits only moderate clinical efficacy in children and immunocompetent people, and none in people with HIV (Abubakar et al., 2007; Amadi et al., 2009; Pankiewicz et al., 2015; Gargala, 2008; Rossignol, 2010).

Oocyst transport to surface water can occur by deposition of manure directly in the water or surface runoff. Hence, humans, wildlife and domestic livestock all potentially contribute *Cryptosporidium* contamination to water systems (Ryan et al., 2014). Identification of the sources/carriers of human pathogenic strains is therefore essential for accurate risk assessment and optimal catchment management. However, most studies to date have focused on humans and the potential role of livestock in the epidemiology of zoonotic cryptosporidiosis, while wildlife as a potential risk factor to source water, has only been studied opportunistically. Thus, the aim of this review is to summarize available information about molecular characterisation of *Cryptosporidium* species in wildlife with emphasis on the public health significance of zoonotic species.

2. Taxonomy and zoonotic potential of *Cryptosporidium* species

The application of advanced molecular techniques has led to an improved taxonomy and systematics, and better understanding of *Cryptosporidium* phylogeny (Ryan et al., 2014). Given the morphological similarity of oocysts by microscopy, these advances are crucial for confident identification, description of host/parasite intractions and ultimately accurate risk assessment. Currently, 29 *Cryptosporidium* species have been recognised as valid (Table 1), including the recently described *C. rubeyi* in ground-dwelling squirrels (*Spermophilus* sp.) (Li et al., 2015a). More than 17 species have been identified in humans (Table 1). Of these, *C. parvum* and *C. hominis* are by far the most common species reported in humans worldwide (Xiao, 2010; Ryan and Xiao, 2014) and have been responsible for the majority of waterborne outbreaks typed to date with the exception of a waterborne outbreak in the UK caused by *C. cuniculus* from rabbits (*Oryctolagus cuniculus*) (Chalmers et al., 2009; Xiao, 2010; Ryan et al., 2014).

The most widely molecular markers used for typing of *Cryptosporidium* isolates are the 18S ribosomal RNA (18S rRNA) gene and the 60-kDa glycoprotein (gp60) gene. The latter locus encodes a

Table 1
Valid *Cryptosporidium* species confirmed by molecular analysis.

Species name	Author(s)	Type host(s)	Major host(s)	Reports in humans
C. rubeyi	Li et al., 2015a	*Spermophilus beecheyi* (California ground squirrel)	Squirrels	None reported
C. scophthalmi	Alvarez-Pellitero et al., 2004; Costa et al., 2015	*Scophthalmus maximus* (Turbot)	Turbot	None reported
C. huwi	Ryan et al., 2015	*Poecilia reticulata* (Guppy), *Paracheirodon innesi* (Neon tetra) and *Puntius tetrazona* (Tiger barb)	Fish	None reported
C. erinacei	Kváč et al., 2014b	*Erinaceus europaeus* (European hedgehog)	Hedgehogs, horses	Kváč et al., 2014a
C. scrofarum	Kváč et al., 2013	*Sus scrofa* (Pig)	Pigs	Kváč et al., 2009a, 2009b
C. viatorum	Elwin et al., 2012	*Homo sapiens* (Human)	Humans	Elwin et al., 2012; Insulander et al., 2013
C. tyzzeri	Tyzzer, 1912; Ren et al., 2012	*Mus musculus* (Mouse)	Rodents	Rasková et al., 2013
C. cuniculus	Robinson et al., 2010	*Oryctolagus cuniculus* (European rabbit)	Rabbits	Chalmers et al., 2009; Anon, 2010; Molloy et al., 2010; Chalmers et al., 2011; Anson et al., 2014; Koehler et al., 2014; Chalmers, 2012
C. ubiquitum	Fayer et al., 2010	*Bos taurus* (Cattle)	Ruminants, rodents, primates	Commonly reported (cf. Fayer et al., 2010; Elwin et al., 2012)
C. xiaoi	Fayer et al., 2010	*Ovis aries* (Sheep)	Sheep and goats	Adamu et al., 2014
C. ryanae	Fayer et al., 2008	*Bos taurus* (Cattle)	Cattle	None reported
C. macropodum	Power and Ryan, 2008	*Macropus giganteus* (Kangaroo)	Marsupials	None reported
C. fragile	Jirků et al., 2008	*Duttaphrynus melanostictus* (Toad)	Toads	None reported
C. fayeri	Ryan et al., 2008	*Macropus rufus* (Kangaroo)	Marsupials	Waldron et al., 2010
C. bovis	Fayer et al., 2005	*Bos taurus* (Cattle)	Cattle	Khan et al., 2010; Ng et al., 2012; Helmy et al., 2013
C. suis	Ryan et al., 2004	*Sus scrofa* (Pig)	Pigs	Xiao et al., 2002a; Leoni et al., 2006; Cama et al., 2007; Wang et al., 2013a
C. galli	Pavalasek, 1999; Ryan et al., 2003	*Spermestidae, Frangillidae, Gallus gallus, Tetrao urogallus, Pinicola enucleator* (Birds)	Birds	None reported
C. hominis	Morgan Ryan et al., 2002	*Homo sapiens* (Human)	Humans	Most common species in humans
C. molnari	Alvarez-Pellitero and Sitjà-Bobadilla, 2002	*Sparus aurata* (Gilt-head sea bream) and *Dicentrarchus labrax* (European seabass)	Fish	None reported
C. canis	Fayer et al., 2001	*Canis familiaris* (Dog)	Dogs	Many reports (cf. Lucio-Forster et al., 2010)
C. andersoni	Lindsay et al., 2000	*Bos taurus* (Cattle)	Cattle	Leoni et al., 2006; Morse et al., 2007; Waldron et al., 2011; Agholi et al., 2013; Jiang et al., 2014; Liu et al., 2014
C. varanii	Pavlásek et al., 1995	*Varanus prasinus* (Emerald Monitor)	Lizards	None reported
C. baileyi	Current et al., 1986	*Gallus gallus* (Chicken)	Birds	None reported
C. parvum	Tyzzer, 1912	*Bos taurus* (Cattle)	Ruminants	Commonly reported in humans
C. meleagridis	Slavin, 1955	*Meleagris gallopavo* (Turkey)	Birds and humans	Commonly reported in humans
C. serpentis	Levine, 1980	*Elaphe guttata, E. subocularis, Sanzinia madagascarensus* (Snakes)	Snakes and lizards	None reported
C. felis	Iseki, 1979	*Felis catis* (Cat)	Cats	Many reports (cf. Lucio-Forster et al., 2010)
C. wrairi	Vetterling et al., 1971	*Cavia porcellus* (Guinea pig)	Guinea pigs	None reported
C. muris	Tyzzer, 1907; and 1910	*Mus musculus* (House mouse)	Rodents	Many reports – Guyot et al., 2001; Gatei et al., 2002; Tiangtip and Jongwutiwes, 2002; Gatei et al., 2003; Palmer et al., 2003; Gatei et al., 2006; Leoni et al., 2006; Muthusamy et al., 2006; Azami et al., 2007; Al-Brikan et al., 2008; Neira et al., 2012; Hasajová et al., 2014; Petrincová et al., 2015; Spanakos et al., 2015

precursor protein, that is cleaved to produce mature cell surface glycoproteins (gp45/gp40 and gp15) implicated in zoite attachment to, and invasion of enterocytes (Xiao, 2010; Ryan et al., 2014). Most of the genetic heterogeneity in the gp60 gene is the variation in the number of a tri-nucleotide repeat (TCA, TCG or TCT) in the 5′ end (gp40) of the coding region, although extensive sequence polymorphism is also present in the rest of the gene. The repeats are used to define the subtype families within a species, whereas the remaining polymorphic sites are used to identify subtypes within a subtype family (Ryan et al., 2014).

3. Wildlife associated outbreaks and water contamination

Relatively little is known about the distribution of zoonotic and non-zoonotic *Cryptosporidium* species and subtypes in wildlife populations (Appelbee et al., 2005; Ziegler et al., 2007; Ryan et al., 2014). Conclusive molecular evidence, linking contamination of water supplies by wild animals in catchments with outbreaks of cryptosporidiosis in human populations is scant. However, a recent waterborne outbreak in the UK caused by *C. cuniculus* from rabbits has highlighted the importance of wildlife in the dissemination of *Cryptosporidium* to drinking water sources and the associated human health risk (Chalmers et al., 2009; Elvin et al., 2012).

A wide range of *Cryptosporidium* species and genotypes have been identified in drinking source water, storm water runoff, stream sediment, wastewater and seawater in various geographic locations including *C. hominis*, *C. parvum*, *C. andersoni*, *C. muris*, *C. cuniculus*, *C. meleagridis* and *C. canis* as well as various wildlife

Table 2
Cryptosporidium species and genotypes identified by molecular tools in wild terrestrial mammals and their zoonotic importance.

Cryptosporidium species/ genotypes	Wildlife hosts	Zoonotic importance	gp60 subtypes reported in wildlife	References
C. hominis	Fallow deer (*Dama dama*), Dugong (*Dugong dugon*), Chinchillas (*Chinchilla lanigera*), Baboons (*Pabio anubis*), Chimpanzees (*Pan troglodytes schweinfurthii*), Red colobus (*Procolobus rufomitratus*), Black-and-white colobus (*Colobus guereza*), Rhesus macaque (*Macaca mulatta*), Cynomolgus monkey (*Macaca fascicularis*), Francois' leaf monkey (*Trachypithecus francoisi*), Lemurs (*Lemur sp.*), Bandicoots (*Isoodon obesulus*), Bushtail possums (*Trichosurus vulpecula*), Estern grey kangaroos (*Macropus giganteus*), Brush-tailed rock-wallabies (*Petrogale penicillata*), Wild dingo (*Canis lupus dingo*), Squirrel monkey (*Saimiri sciureus*)	Main *Cryptosporidium* species infecting humans	IbA12G3, IbA10G2R2, IiA17, IfA12G2, IaA13R7, IaA13R8, IaA14R7, IdA20, IeA11G3T3, IfA16G2, IkA7G4 (novel subtype)	Morgan et al., 2002; Salyer et al., 2012; Ye et al., 2012; Ng et al., 2011; Dowle et al., 2013; Nolan et al., 2013; Karim et al., 2014; Ryan et al., 2014; Liu et al., 2015b; Parsons et al., 2015; Zahedi et al., 2015
C. parvum	Alpaca (*Lama pacos*), Swamp deer (*Cervus duvauceli*), Red deer (*Cervus elaphus*), Roe deer (*Capreolus capreolus*), Fallow deer (*Dama dama*), Addaxes (*Addax nasomaculatus*), Arabian oryx (*Oryx leucoryx*), Gemsboks (*Oryx gazella*), Sable antelopes (*sable antelopes*), White-tailed deer (*Odocoileus Virginianus*), Game grey wolves (*Canis lupus*), Racoon dog (*Nyctereutes procyonoides viverrinus*), Rabbit (*Oryctolagus cuniculus*), Nutria (*Myocastor coypus*), Prezewalski's wild horse (*Equus przewalskii*), Alpaca (*Lama quanico pacos*), Eastern grey squirrel (*Sciurus carolinensis*), Ground Squirrels (*Spermophilus beecheyi*), Siberian chipmunk (*Tamias sibiricus*), Hamsters (*Cricetinae*), Wood mice (*Apodemus sylvaticus*), White-footed mouse (*Peromyscus leucopus*), Yellow-bellied marmot (*Marmota flaviventris*), Bamboo rats (*Rhizomys sinensis*), Small brown bat (*Myotis lucifugus*), Campbell hamster (*Phodopus campbelli*), Golden hamster (*Mesocricetus auratus*), Capybara (*Hydrochoerus hydrochaeris*), Racoon dog (*Nictereutes procyonoides viverrinus*), Red fox (*Vulpes vulpes*), Rhesus macaques (*Macaca mulatta*), Toque macaques (*Macaca sinica sinica*), Grey langurs (*Semnopithecus priam thersites*), Purple-faced langurs (*Trachypithecus vetulus philbricki*), Common dolphins (*Delphinus delphis*), Golden takins (*Budorcas taxicolor bedfordi*), Eastern grey kangaroos (Macropus giganteus), Asian house rat (*Rattus tanezumi*), Brown rat (*Rattus norvegicus*), Bamboo rats (*Rhizomys sinensis*)	Major	IIdA15G1, IIdA18G1, IIdA19G1, IIaA15G2R1, IIaA19G2R1, IIaA19G3R1, IIaA19G4R1, IIaA20G3R1, IIaA20G3R2, IIaA20G4R1, IIaA21G3R1, IIaA16G2R1, IIaA14G1R1, IIaA14G2R1, IIaA16G3R1, IIcA5G3, IIcA5G3a, IIoA13G1, IIpA9 (novel subtype)	Morgan et al., 1999a; Atwill et al., 2001; Perez and Le Blancq, 2001; Matsui et al., 2000; Matsubayashi et al., 2004; Ryan et al., 2003, 2004; Ekanayake et al., 2007; Feng et al., 2007; Meireles et al., 2007; Paziewska et al., 2007; Starkey et al., 2007; Ziegler et al., 2007; Cinque et al., 2008; Lv et al., 2009; Feng, 2010; Gómez-Couso et al., 2012; Ravaszova et al., 2012; Ye et al., 2012; Dowle et al., 2013; Nolan et al., 2013; Liu et al., 2014; Lv et al., 2009; Reboredo-Fernández et al., 2014; Bodager et al., 2015; Liu et al., 2015a; Montecino-Latorre et al., 2015; Qi et al., 2015; Wang et al., 2015; Wells et al., 2015; Zahedi et al., 2015; Zhao et al., 2015a, 2015b
C. cuniculus	European rabbit (*Oryctolagus cuniculus*), Eastern grey kangaroo (*Macropus giganteus*) (single report)	Responsible for several waterborne outbreaks and sporadic cases of cryptosporidiosis in the UK and has been identified in a human in Australia	VaA18,VbA18, VbA19, VbA21, VaA22, VbA24, VbA26, VbA29, VbA32, VbA22R4, VbA23R3, VbA24R3, VbA25R4,VbA26R4	Xiao et al., 2002a; Ryan et al., 2003;Chalmers, 2012; Nolan et al., 2010; Robinson et al., 2010; Elwin et al., 2012; Zhang et al., 2012; Nolan et al., 2013; Kapuke et al., 2014; Koehler et al., 2014; Liu et al., 2014; Puleston et al., 2014
C. ubiquitum	Swamp deer (*Cervus duvauceli*), Deer mouse (*Peromyscus*), Eastern grey squirrels (*Sciurus carolinensis*), Red	Emerging human pathogen	XIIa, XIIb, XIIc, XIId, XIIe, XIIf	Perez and Le Blancq, 2001; da Silva et al., 2003; Ryan et al., 2003; Feng et al., 2007; Karanis et al., 2007; Ziegler

(*continued on next page*)

Table 2 (*continued*)

Cryptosporidium species/ genotypes	Wildlife hosts	Zoonotic importance	gp60 subtypes reported in wildlife	References
	squirrel (*Sciurus vulgaris*), Eastern chipmunk (Tamias striatus), Lemur (Lemuroidea), North American beaver (*Castor canadensis*), Woodchuck (*Marmota monax*), Raccoon (*Procyon lotor*), White-tailed deer (*Odocoileus virginianus*), Sika deer (*Cervus Nippon*), Roe deer (*Capreolus capreolus*), Blesbok (*Damaliscus pygargus phillipsi*), Ibex (*Capara sibirica*), Nyala (*Niyala anagasii*), Coquerel's sifaca (*Propithecus coquereli*), Large Japanese field mouse (*Apodemus speciosus*), Foxes			et al., 2007; Wang et al., 2008; Fayer et al., 2010; Cinque et al., 2008; Feng, 2010; Robinson et al., 2010, 2011; Feng et al., 2012; Abu Samraa et al., 2013; Nolan et al., 2013; Murakoshi et al., 2013; Li et al., 2014; Ma et al., 2014; Perec-Matysiak et al., 2015; Qi et al., 2015a, 2015b; Stenger et al., 2015b
C. muris	Wild rats (*Rattus* sp.), Mice (*Mus* sp.), Greater bilblies (*Macroties lagotis*), Girrafes house mice (*Mus musculus*), Eastern grey squirrel (*Sciurus carolinensis*), Golden hamster (*Mesocricetus auratus*), Rock hyrax (*Procavia capensis*), Large footed mouse-eared bat (*Myotis adversus*), Japanese field mouse (*Apodemus argenteus*), Bilbies (*Macrotis lagotis*), Bank voles (*Clethrionomys glareolus*), Campbell hamster (*Phodopus campbelli*), Siberian hamster (*Phodopus sungorus*), Golden hamster (*Mesocricetus auratus*), Mountain goats (*Oreamnos americanus*), Cynomolgus monkeys (*Macaca fascicularis*), East African mole rat (*Tachyoryctes splendens*), Ringed seal (*Pusa hispida*), Donkey (*Giraffa camelopardalis*), Ringed seal (*Phoca hispida*), Large Japanese field mouse (*Apodemus speciosus*), Cynomolgus monkey (*Macaca fascicularis*), Slow loris (*Nycticebus coucang*), Ostriches (*Struthio camelus*), Mountain gorillas (*Gorilla beringei beringei*), Asian house rat (*Rattus tanezumi*), Brown rat (*Rattus norvegicus*), House mouse (*Mus musculus*)	Numerous reports in humans	Chalmers et al., 1997; Hurkova et al., 2003	Dubey et al., 2002; Morgan et al., 1999a; Xiao et al., 2002a, 2004b; Warren et al., 2003; Nakai et al., 2004; Hikosaka and Nakai, 2005; Santín et al., 2005; Azami et al., 2007; Brikan et al., 2008; Kvac et al., 2008; Lupo et al., 2008; Lv et al., 2009; Kodadkova et al., 2010; Feng, 2010; Murakoshi et al., 2013; Yang et al., 2011, 2013; Ng-Hublin et al., 2013; Karim et al., 2014, Qi et al., 2014; Sak et al., 2014; Du et al., 2015; Laatamna et al., 2015; Petrincová et al., 2015, Zhao et al., 2015b
C. andersoni	Bacterian camel (*Camelus bactrianus*), European wisent (*Bison bonasus*), Marmots Campbell hamster (*Phodopus campbelli*), Golden hamster (*Mesocricetus auratus*), Golden takins (*Budorcas taxicolor bedfordi*), Giant panda (*Ailuropoda melanoleuca*), *Macaca mulatta* (*Rhesus macaque*), American mink (*Mustela vison*)	Minor	–	Matsubayashi et al., 2005; Wang et al., 2008; Lv et al., 2009; Stuart et al., 2013; Du et al., 2015; Wang et al., 2015; Zhao et al., 2015a
C. felis	Rhesus macaques (*Macaca mulatta*); Pallas's cat (*Felis Manul*)	Numerous reports in humans	–	Lucio-Forster et al., 2010; Ye et al., 2012; Beser et al., 2015; Ebner et al., 2015; Li et al., 2015c
C. canis dog genotype	Unidentified fox, Coyote (*Canis latrans*)	Numerous reports in humans	–	Xiao et al., 2002a; Ryan et al., 2004; Zhou et al., 2004; Trout et al., 2006; Ziegler et al., 2007; Elwin et al., 2012; Koompapong et al., 2014
C. canis fox genotype	Fox	No reports in humans to date	–	Zhou et al., 2004; Swaffer et al., 2014
C. canis coyote genotype	Coyotes	No reports in humans to date	–	Xiao et al., 2002a; Zhou et al., 2004
C. erinacei	European hedgehog (*Erinaceus europaeus*), Horses	One report in humans	XIIIaA21R11, XIIIaA22R9, XIIIaA21R10, XIIIa20R10, XIIIaA19R12, XIIIaA22R11	Dyachenko et al., 2010; Laatamna et al., 2013; Nolan et al., 2013; Kváč et al., 2014a, 2014b; Meredith and Milne, 2009
C. fayeri	Southern brown bandicoot (*Isodon obesulus*), Western-barred bandicoot (*Permeles bougainville*), Koala (*Phascolarctos cincerus*), Red kangaroo (*Macropus rufus*), Eastern grey	Minor	IVaA9G4T1R1, IVaA10, IVaA7, IVbA9G1T1, IVcA8G1T1, IVdA7G1T1, IVfA12G1T1	Power et al., 2005; Ryan et al., 2008; Yang et al., 2008, 2011; Power, 2010; Waldron et al., 2010; Feng et al., 2011b; Nolan et al., 2013; Swaffer et al., 2014; Vermeulen et al., 2015

Table 2 (*continued*)

Cryptosporidium species/ genotypes	Wildlife hosts	Zoonotic importance	gp60 subtypes reported in wildlife	References
	kangaroo (*Macropus giganteus*), Yellow footed rock wallaby (*Petrogale xanthopus*), Western grey kangaroo (*Macropus fuliginosus*), Koalas (*Phascolarctos cinereus*)			
Opossum genotype I (*C. fayeri*)	Opossum (*Didelphimorphia*)	No reports in humans to date	XIaA4G1T1	Feng et al., 2011b
Opossum genotype II	Virginia opossum (*Didelphis virginiae*)	No reports in humans to date	–	Xiao et al., 2002b; Oates et al., 2012
C. meleagridis	Mountain gorillas (*Gorilla beringei beringei*), Brush-tailed rock wallabies (*Petrogale penicillata*), deermouse (*Peromyscus* sp.)	Major	IIIbA, IIIgA (closest match to IIIeA19G2R1)	Morgan et al., 2000; Cama et al., 2003; Gatei et al., 2006; Leoni et al., 2006; Muthusamy et al., 2006; Feng et al., 2007; Elwin et al., 2012; Silverlås et al., 2012; Kurniawan et al., 2013; Adamu et al., 2014; Ryan and Xiao, 2014; Ghaffari and Kalantari, 2014; Sak et al., 2014; Rahmouni et al., 2014; Wang et al., 2014; Stensvold et al., 2015; Vermeulen et al., 2015
C. tyzerri	Mice (*Mus musculus*), Brown rats (*Rattus norvegicus*), Large-footed bat (*Myotus adversus*), Yellow-necked mouse (*Apodemus flavicollis*), Bank vole (*Myodes glareolus*), Common vole (*Microtus arvalis*), Red panda (*Ailurus fulgens*), Leopard (*Panthera pardus*), Takin (*Budorcas taxicolor*), Prairie bison (*Bison bison*), Lesser panda (*Ailurus fulgens*), Black leopards (*Pantera pardus*), Bobcats (*Lynx rufus*)	Occasionally reported in humans	IXaA5R2, IXaA6R1, IXaA6R2, IXaA6R3, IXbA6, IXbA6R2	Morgan et al., 1999a, Xiao et al., 2002a; Bajer et al., 2003; Alves et al., 2005; Foo et al., 2007; Karanis et al., 2007; Ziegler et al., 2007; Lv et al., 2009; Feng et al., 2011b; Carver et al., 2012; Kváč et al., 2012; Ren et al., 2012; Rasková et al., 2013; Silva et al., 2013; Swaffer et al., 2014
C. macropodum	Red kangaroo (*Macropus rufus*), Eastern grey kangaroo (*Macropus giganteus*), Swamp wallaby (*Wallabia bicolor*), Western grey kangaroos (*Macropus fuliginosus*)	No reports in humans to date	–	Power et al., 2004, 2005; Power and Ryan, 2008; Power, 2010; Yang et al., 2011; Nolan et al., 2013
C. bovis	Yaks, foxes, Gorillas (single report), Roe deer (*Capreolus capreolus*)	Occasionally reported in humans	–	Robinson et al., 2011; Helmy et al., 2013; García-Presedo et al., 2013b; Sak et al., 2013; Qi et al., 2015b; Qin et al., 2014
C. ryanae	Roe deer (*Capreolus capreolus*), Water buffaloes (*Bubalus bubalis*)	No reports in humans to date	–	Feng et al., 2012; García-Presedo et al., 2013b
C. wrairi	Guinea pig (*Cavia porcellus*), California ground squirrels (*Spermophilus beecheyi*)	No reports in humans to date	VIIaA13T1, VIIaA17T1, VIIaA16T1	Atwill et al., 2004; Feng et al., 2007, 2011b, Lv et al., 2009
C. scrofarum	Asian house rat (*Rattus tanezumi*), Brown rat (*Rattus norvegicus*), Eurasian wild boars (*Sus scrofa*)	Occasionally reported in humans	–	García-Presedo et al., 2013a; Ng-Hublin et al., 2013, Nemeic et al., 2013; Bodager et al., 2015; Parsons et al., 2015
C. suis	Chimpanzees (*Pan troglodytes schweinfurthii*), Eurasian wild boars (*Sus scrofa*), Rodents	Occasionally reported in humans	–	Nemeic et al., 2012, 2013; Bodager et al., 2015; Parsons et al., 2015
C. suis-like	Asian house rat (*Rattus tanezumi*)	No reports in humans to date	–	Ng-Hublin et al., 2013
C. rubeyi	California ground squirrel (*S. beecheyi*), Belding's ground squirrel (*S. beldingi*), Golden Mantled ground squirrel (*S. lateralis*)	No reports in humans to date	–	Pereira et al., 2010; Li et al., 2015a
Bear genotype	Black bear (*Ursus americanus*)	No reports in humans to date	–	Xiao et al., 2000
Bat genotype I	Chinese rufous horseshoe bat (*Rhinolophus sinicus*), Stoliczka's trident bat (*Aselliscus stoliczkanus*)	No reports in humans to date	–	Wang et al., 2013b
Bat genotype II	Chinese rufous horseshoe bat (*Rhinolophus sinicus*), Fulvus roundleaf bat (*Hipposideros fulvus*), Leschenault's rousette (*Rousettus leschenaultii*)	No reports in humans to date	–	Wang et al., 2013b
Bat genotype III	Big brow bat (*Eptesicus fuscus*)	No reports in humans to date	–	Kváč et al., 2015
Bat genotype IV	Western barbastelle (*Barbastella barbastellus*)	No reports in humans to date	–	Kváč et al., 2015
Beaver genotype	North American beaver (*Castor canadensis*)	No reports in humans to date	–	Feng et al., 2007
Brushtail possum I	Brushtail possum (*Trichasuris vulpecula*)	No reports in humans to date	–	Hill et al., 2008

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Table 2 (*continued*)

Cryptosporidium species/ genotypes	Wildlife hosts	Zoonotic importance	gp60 subtypes reported in wildlife	References
Chipmunk genotype I	Chipmunk sp. (*Tamias* sp.), Eastern grey squirrel (*Sciurus carolinensis*), Deer mice (*Peromyscus maniculatus*)	Emerging human pathogen	XIVaA18G2T1, XIVaA18G2T2	Jiang et al., 2005; Feltus et al., 2006; Feng et al., 2007; ANOFEL, 2010; Insulander et al., 2013; Lebbad et al., 2013; Guo et al., 2015
Chipmunk genotype II	Eastern chipmunk (*Ramias striatus*)	No reports in humans to date	–	Feng et al., 2007; Stenger et al., 2015a
Chipmunk genotype III	Siberian chipmunk (*Tamias sibiricus*)	No reports in humans to date	–	Lv et al., 2009
Deer mouse genotype I	Deer mouse (*Peromyscus*)	No reports in humans to date	–	Xiao et al., 2002b; Feng et al., 2007, 2011b
Deer mouse genotype II	Deer mouse (*Peromyscus*)	No reports in humans to date	–	Xiao et al., 2002b; Feng et al., 2007
Deer mouse genotype III	Deer mouse (*Peromyscus*)	No reports in humans to date	–	Feng et al., 2007; Stenger et al., 2015b
Deer mouse genotype IV	Deer mouse (*Peromyscus*)	No reports in humans to date	–	Feng et al., 2007
Ferret genotype	Ferret (*Mustelidae*), Siberian chipmunk (*Tamias sibiricus*), River otters (Lontra canadensis), Black-footed ferret (*Mustela nigripes*), Red squirrel (*Sciurus vulgaris*)	No reports in humans to date	VIIIaA5G2	Xiao et al., 2002a; Abe and Iseki, 2003; Gaydos et al., 2007; Kváč et al., 2008; Lv et al., 2009; Feng et al., 2011b
Giant panda genotype	Giant panda (*Ailuropoda melanoleuca*)	No reports in humans to date	–	Liu et al., 2013
Squirrel genotypes I–III	Golden-mantled ground squirrels (*Callospermophilus lateralis*), Belding's ground squirrels (*Urocitellus beldingi*), California ground squirrels (*Otospermophilus beecheyi*), Black-tailed prairie dog (*Cynomys ludovicianus*)	No reports in humans to date	–	Atwill et al., 2004; Pereira et al., 2010; Stenger et al., 2015b
Hamster genotype	Siberian hamster (*Phodopus sungorus*)	No reports in humans to date	–	Lv et al., 2009
Horse genotype	Przewalski's wild horse (*Equus przewalski*), Four-toed hedgehog (*Atelerix albiventris*)	Identified in humans in the UK	VIaA11G3, VIbA13	Ryan et al., 2003; Robinson et al., 2008; Abe and Matsubara, 2015
Mink genotype	River otter (*Lontra canadensis*), American minks (*Mustela vison*), Ermine (*Mustela ermine*)	Several reports in humans	XaA5G1	Feng et al., 2007, Wang et al., 2008; Feng et al., 2011b; Ng-Hublin et al., 2013; Stuart et al., 2013; Ebner et al., 2015
Mouse genotype II	House mouse (*Mus musculus*)	No reports in humans to date	–	Foo et al., 2007; Silva et al., 2013
Mouse genotype III	House mouse (*Mus musculus*)	No reports in humans to date	–	Silva et al., 2013
Muskrat genotype I	Muskrat (*Ondatra zibethicus*), Boreal red-backed vole (*Myodes rutilus*)	No reports in humans to date	–	Xiao et al., 2002a; Zhou et al., 2004; Feng et al., 2007
Muskrat genotype II	Muskrat (*Ondatra zibethicus*), Red fox (*Vulpus vulpus*), Deer mouse (*Peromyscus maniculatus*), Meadow vole (*Microtus pennsylvanicus*)	No reports in humans to date	–	Ziegler et al., 2007; Robinson et al., 2011
Naruko genotype	Large Japanese field mouse (*Apodemus speciosus*)	No reports in humans to date	–	Murakoshi et al., 2013
Rat genotype I	Brown rat (*Rattus norvegicus*)	No reports in humans to date	–	Ng-Hublin et al., 2013
Rat genotype II	Brown rat (*Rattus tanezum*), Wild black rat (*Rattus rattus*), Brown rat (*Rattus norvegicus*).	No reports in humans to date	–	Lv et al., 2009; Paparini et al., 2012; Ng-Hublin et al., 2013; Silva et al., 2013
Rat genotype III	Asian house rat (*Rattus tanezumi*), Wild black rat (*Rattus rattus*).	No reports in humans to date	–	Lv et al., 2009; Paparini et al., 2012; Ng-Hublin et al., 2013; Silva et al., 2013
Rat genotype IV	Tanezumi rat (*Rattus tanezumi*), Asian house rat (*Rattus tanezumi*), Brown rat (*Rattus norvegicus*)	No reports in humans to date	–	Ng-Hublin et al., 2013
Seal genotypes I and II	Ringed seals (*Phoca hispida*), Harbour seals (*Phoca vituline*), Hooded seal (*Cystophora cristata*)	No reports in humans to date	–	Santín et al., 2005; Bass et al., 2012
Seal genotype III	Harp seal (*Pagophilus groenlandicus*)	No reports in humans to date	–	Bass et al., 2012
Seal genotype IV (similar to skunk genotype)	Southern elephant seal (*Mirounga leonina*)	No reports in humans to date	–	Rengifo-Herrera et al., 2011, 2013
Seal genotype V (Weddell seal genotype)	Weddel seal (*Leptonychotes weddellii*)	No reports in humans to date	–	Rengifo-Herrera et al., 2013
Shrew genotype		No reports in humans to date	–	

Table 2 (*continued*)

Cryptosporidium species/ genotypes	Wildlife hosts	Zoonotic importance	gp60 subtypes reported in wildlife	References
	Northern short-tailed shrew (*Blarina brevicauda*), Wildebeest (*Connochaetes*), White-toothed shrew (*Crocidura russula*), Common shrew (*Sorex araneus*), Masked shrew (*Sorex scinereus*), Pygmy shrew (*Sorex minutus*), Brewer's mole (*Parascalops brewer*), Ermine (*Mustela ermine*)			Torres et al., 2000; Alves et al., 2005; Feng et al., 2007; Ziegler et al., 2007
Skunk/skunk-like genotype	Striped skunk (*Mephitis mephitis*), Raccoon (*Procyon lotor*), Eastern grey squirrel (*Sciurus carolinensis*), River otter (*Lontra canadensis*), Raccoon (*Procyon lotor*), Southern elephant seal (*Mirounga leonina*), Raccoon (*Procyon lotor*), Shunk (*Mephitis mephitis*), American red (*Tamiasciurus hudsonicus*), Fox squirrel (*Sciurus niger*)	Has been reported in humans	–	Xiao et al., 2002b; Zhou et al., 2004; Feng et al., 2007; Ziegler et al., 2007; Robinson et al., 2008; Chalmers et al., 2009; Feng et al., 2011b; Rengifo-Herrera et al., 2011; Elwin et al., 2012; Stenger et al., 2015b
Vole genotype	Meadow vole (*Microtus pennynsylvanicus*)	No reports in humans to date	–	Feng et al., 2007
Wildbeast genotype	Black wildbeast (*Connochaetos*)	No reports in humans to date	–	Alves et al., 2005

adapted genotypes and unidentified “environmental sequences” which probably represent as yet unidentified wildlife genotypes and which also highlight the potential for contamination of water supplies by wildlife (Zhou et al., 2004; Jiang et al., 2005; Yang et al., 2008; Jellison et al., 2004; Nichols et al., 2010; Koompapong and Sukthana, 2012; Van Dyke et al., 2012; Xiao et al., 2012; Galván et al., 2014; Li et al., 2014; Mahmoudi et al., 2015). For example, studies on *Cryptosporidium* contamination from wildlife from New York watersheds have shown that wildlife are the major source of *Cryptosporidium* in protected drinking source water, including some emerging human pathogens such as *C. ubiquitum* and chipmunk genotype I (Jiang et al., 2005; Feng et al., 2007).

3.1. *Cryptosporidium in mammals*

Due to the morphological similarity of *Cryptosporidium* oocysts from different host species, initial findings of *Cryptosporidium* infections in wild animals were assumed to be due to *C. parvum* leading to an overestimation of the potential role of wildlife as reservoirs of human disease (Appelbeea et al., 2005). However, with the assistance of advanced molecular techniques, many of these species were identified as host-adapted genotypes (Table 2). Both wild terrestrial and marine mammals have been studied as potential reservoirs for human-infectious *Cryptosporidium* species and genotypes using molecular tools (Table 2). The prevalence of *Cryptosporidium* in wild placental mammal hosts has been reported in detail in a recent review (Feng, 2010) and varies widely between mammalian hosts.

3.1.1. *Cryptosporidium hominis*

Although humans are the major host species for *C. hominis*, it has been reported in a number of wildlife hosts including a dugong and non-human primates (Table 2) (Xiao et al., 1999; Ye et al., 2012; Karim et al., 2014; Bodager et al., 2015; Parsons et al., 2015). *C. hominis*/*Cryptosporidium parvum*-like sequences were identified in red and black-and-white colobus monkeys in Uganda (Salyer et al., 2012). However, typing was obtained using a short fragment of the *Cryptosporidium* oocyst wall protein (COWP) gene, which is not reliable for differentiating *Cryptosporidium* species. In Australia, a number of recent studies have also identified *C. hominis*/*C. parvum*-like isolates at the 18S locus in marsupials including bandicoots, brushtail possums, eastern grey kangaroos and brush-tailed rock-wallabies (Hill et al., 2008; Ng et al., 2011; Dowle et al., 2013; Vermeulen et al., 2015). However, despite efforts, the identification of *C. hominis*/*C. parvum* could not be confirmed at other loci. This might be due to low numbers of oocysts and the multi copy nature of the 18S rRNA gene. Another study reported a *C. hominis*-like sequence at the 18S locus in a wild dingo, but was also unable to confirm this at other loci (Ng et al., 2011).

Subtyping of *C. hominis* at the gp60 locus has identified nine subtype families (Ia to Ij) (Ryan et al., 2014). To date, few *C. hominis* subtypes have been reported in wild mammals but include subtype IbA12G3 in Rhesus macaques, subtype IiA17 in Cynomolgus monkeys and Rhesus monkeys and subtype IfA12G2 in baboons and Mitumba chimpanzees (Feng et al., 2011b; Karim et al., 2014; Bodager et al., 2015; Parsons et al., 2015).

Recently, *C. hominis* has been identified and enumerated from eastern grey kangaroos and cattle faecal samples from Sydney catchments and characterised at multiple loci (Zahedi et al., 2015). In that study, *C. hominis* isolates were typed at three loci (18S, a novel mucin-like glycoprotein that contains a C-type lectin domain and the gp60 gene) (Zahedi et al., 2015). The *C. hominis* IbA10G2 subtype was identified in the marsupials and cattle (Zahedi et al., 2015), which is the main subtype associated with outbreaks of cryptosporidiosis by *C. hominis* (Xiao, 2010).

3.1.2. *C. parvum*

C. parvum was first described in mice (Tyzzer, 1912) and is primarily a parasite of artiodactyls and humans (Xiao, 2010). *C. parvum* has however been frequently reported in wildlife, infecting a broad range of wild species including various rodents, bovids, camelids, equids, canids, non-human primates and marine mammals (Table 2) (Morgan et al., 1999a; Atwill et al., 2001; Perez and Le Blancq, 2001; Matsubayashi et al., 2004; Ryan et al., 2004; Appelbee et al., 2005; Feng et al., 2007; Meireles et al., 2007; Paziewska et al., 2007; Starkey et al., 2007; Ziegler et al., 2007; Gómez-Couso et al., 2012; Ye et al., 2012; Abu Samraa et al., 2013; Liu et al., 2013; García-Presedo et al., 2013b; Reboredo-Fernández et al., 2014; Montecino-Latorre et al., 2015; Wells et al., 2015; Matsui et al., 2000).

Few studies have identified *C. parvum* in captive wild mammals but red deer, fallow deer, addaxes, Arabian oryx, gemsboks, and sable antelopes are among mammals to be infected with *C. parvum* in captivity (Perez and Le Blancq, 2001; Ryan et al., 2003; Hajdusek et al., 2004; Abe et al., 2006; Feng et al., 2007; Meireles et al., 2007; Matsubayashi et al., 2004; Bodager et al., 2015; Wang et al., 2015; Zhao et al., 2015a).

Subtyping of *C. parvum* at the gp60 locus has identified fourteen subtype families (IIa to IIo (Ryan et al., 2014)). Few studies which identified *C. parvum* in wild mammals have conducted typing at the gp60 locus but a variety of *C. parvum* subtypes including IIdA15G1, IIdA18G1, IIdA19G1 have been reported from golden takins, lemurs, chipmunks and hamsters, and IIaA15G2R1, IIaA19G2R1, IIaA19G3R1, IIaA19G4R1, IIaA20G3R1, IIaA20G4R1, IIaA20G3R2 and IIaA21G3R1 have been reported from deer and Eastern grey kangaroos (Lv et al., 2009; Bodager et al., 2015; Montecino-Latorre et al., 2015; Zhao et al., 2015a; Zahedi et al., 2015). These are all *C. parvum* subtypes that have been reported in humans (Xiao, 2010).

3.1.3. *Cryptosporidium cuniculus*

C. cuniculus (previously known as rabbit genotype) was first described in rabbits by Inman and Takeuchi (1979), who described the microscopic detection and ultra-structure of endogenous *Cryptosporidium* parasites in the ileum of an asymptomatic female rabbit. Molecular characterisation of *C. cuniculus* was first conducted on rabbit faecal samples from the Czech Republic (Ryan et al., 2003) and *C. cuniculus* was formally re-described as a species in 2010 (Robinson et al., 2010). Since then, it has been described from rabbits across a wide geographic area including Australia, China, the UK, the Czech Republic, Poland, France and Nigeria (Ryan et al., 2003; Nolan et al., 2010; Shi et al., 2010; Chalmers et al., 2011; Zhang et al., 2012; Nolan et al., 2013; Liu et al., 2014; Koehler et al., 2014; Puleston et al., 2014; Zahedi et al., 2015). *C. cuniculus* has a close genetic relationship with *C. hominis* and its zoonotic potential became clear in 2008, when it was responsible for a drinking-water associated outbreak of cryptosporidiosis in the UK (Chalmers et al., 2009; Robinson et al., 2011; Puleston et al., 2014) and has also been identified in many sporadic human cases of cryptosporidiosis (Robinson and Chalmers, 2011; Chalmers et al., 2011; Elwin et al., 2012; Koehler et al., 2014). It is also the third most commonly identified *Cryptosporidium* species in patients with diarrhoea in the UK (Chalmers et al., 2011). Subtyping at the gp60 locus has identified two distinct subtype families, designated Va and Vb (Chalmers et al., 2009). Most cases described in humans relate to clade Va and the first waterborne outbreak was typed as VaA22 (Robinson et al., 2008; Chalmers et al., 2009). *C. cuniculus* has been reported in rabbits and humans (subtypes VaA9–VaA22 and VbA20–VbA37 – see Wang et al., 2012) but has recently been identified in marsupials (subtype VbA26) (and a human – subtype VbA25) in Australia (Nolan et al., 2013; Koehler et al., 2014). The widespread occurrence of *C. cuniculus* genotypes in rabbits and the fact that it has been now been identified in marsupials in Australia suggests that *C. cuniculus* might be a species more ubiquitous than previously thought, and might be able to spread to other mammals as well as humans. Therefore, there is a need to diligently monitor for *C. cuniculus* in the vicinity of drinking water catchments and in drinking water.

3.1.4. *Cryptosporidium ubiquitum*

C. ubiquitum (previously cervine genotype, cervid, W4 or genotype 3) was first identified by Xiao et al. (2000) in storm water samples in lower New York State (storm water isolate W4, GenBank accession no. AF262328). Subsequently, Perez and Le Blancq (2001) identified this genotype in white-tailed deer-derived isolates from lower New York State and referred to it as genotype 3. Since then it has been described in a wide variety of hosts worldwide including humans and was formally described as a species in 2010 (Fayer et al., 2010). *C. ubiquitum* is of public health concern because of its wide geographic distribution and broad host range (Li et al., 2014). In addition to domestic animals (in particular sheep) and wildlife, *C. ubiquitum* has been frequently reported from drinking source water, storm water runoff, stream sediment and wastewater in various geographic locations, suggesting potential contamination of water sources with oocysts of *C. ubiquitum* shed by animals inhabiting water catchments (Nolan et al., 2013; Li et al., 2014). *C. ubiquitum* is considered an emerging zoonotic pathogen (Li et al., 2014), as it has been identified in many human cases of cryptosporidiosis in the United Kingdom, Slovenia, the United States, Canada, Spain, New Zealand, Venezuela and Nigeria (Charlmers et al., 2011; Wong and Ong, 2006; Fayer et al., 2010; Cieloszyk et al., 2012; Elwin et al., 2012; Blanco et al., 2015; Qi et al., 2015a).

In wildlife, *C. ubiquitum* has been reported sporadically in rodents, wild ruminants, carnivores, marsupials and primates (Table 2) (Perez and Le Blancq, 2001; da Silva et al., 2003; Ryan et al., 2003; Feng et al., 2007; Feng, 2010; Karanis et al., 2007; Ziegler et al., 2007; Wang et al., 2008; Fayer et al., 2010; Cinque et al., 2008; Robinson et al., 2011; Feng et al., 2011b; Abu Samraa et al., 2013; Mi et al., 2013; Murakoshi et al., 2013; Li et al., 2014; Ma et al., 2014; Perec-Matysiak et al., 2015; Qi et al., 2015a, 2015b; Stenger et al., 2015b; Vermeulen et al., 2015).

Because *C. ubiquitum* is genetically distant from *C. hominis* and *C. parvum*, until recently, gp60 homologs had not been sequenced. However, the gp60 gene of *C. ubiquitum* was identified by whole-genome sequencing and six subtype families (XIIa–XIIf) within *C. ubiquitum* were identified (Li et al., 2014). Application of this new tool to human, animal, and environmental (water) isolates has suggested that sheep and rodents are a key source of *C. ubiquitum* transmission to humans, through either direct human contact with infected animals or by contamination of drinking source water (Li et al., 2014). For example, in the US, all *C. ubiquitum* specimens from humans characterized belonged to the same subtype families found in wild rodents in the US (XIIb, XIIc and XIId) (Li et al., 2014). However, as persons in the United States usually have little direct contact with wild rodents, the authots concluded that transmission of *C. ubiquitum* to humans from rodents was likely to come from drinking untreated water contaminated by wildlife (Li et al., 2014).

3.1.5. *Cryptosporidium muris*

C. muris is a gastric parasite and was first identified in the gastric glands of mice in 1907 by Tyzzer (1907). Since then, molecular tools have shown that it has a wide host range, including various mammals (rodents, canids, felids, suids, giraffida, equids, non-human primates and marsupials) and birds (Tables 1 and 2). *C. muris* is considered a zoonotic species as there have been numerous reports of *C. muris* in humans and one report in human sewage (Guyot et al., 2001; Gatei et al., 2002; Tiangtip and Jongwutiwes, 2002; Gatei et al., 2003; Palmer et al., 2003; Gatei et al., 2006; Leoni et al., 2006; Muthusamy et al., 2006; Azami et al., 2007; Al-Brikan et al., 2008; Neira et al., 2012; Hasajová et al., 2014; Petrincová et al., 2015; Spanakos et al., 2015; Hurkova et al., 2003).

In a recent human infectivity study, *C. muris* was examined in six healthy adults (Chappell et al., 2015). Volunteers were challenged with 10^5 *C. muris* oocysts and monitored for 6 weeks for infection and/or illness. All six patients became infected. Two patients experienced a self-limited diarrhoeal illness. *C. muris* oocysts shed during the study ranged from 6.7×10^6 to 4.1×10^8, and *C. muris*-infected subjects shed oocysts longer than occurred with other species studied in healthy volunteers. Three volunteers shed oocysts for 7 months (Chappell et al., 2015). The authors concluded that healthy adults are susceptible to *C. muris*, which can cause mild diarrhoea and result in persistent, asymptomatic infection (Chappell et al., 2015), which confirms the zoonotic status of *C. muris* and highlights the public health risks of finding *C. muris* in wildlife in drinking water catchments.

3.1.6. *Cryptosporidium andersoni*

Like *C. muris*, *C. andersoni* is also a gastric parasite and primarily infects the abomasum of cattle and to a lesser extent, sheep and goats (Ryan et al., 2014; Wang et al., 2012). *C. andersoni* produces oocysts that are morphologically similar to, but slightly smaller than those of *C. muris* (7.4–8.8 × 5.8–6.6 μm vs 8.2–9.4 × 6.0–6.8 μm, respectively) and was originally mistakenly identified in cattle as *C. muris* based on its oocyst size. In 2000, it was described as a new species based on the location of endogenous stages in the abomasum, its host range, and genetic distinctness at multiple loci (Lindsay et al., 2000). It has only occasionally being detected in wild animals (Table 2) (Ryan et al., 2004; Wang et al., 2008, 2015; Lv et al., 2009; Feng et al., 2010; Zhao et al., 2015a). Several studies have reported that *C. andersoni* is the dominant species in source and tap water (Feng et al., 2011; Nichols et al., 2010), suggesting that cattle may be the primary source of contamination. Interestingly, in a recent study, it was found at a prevalence of 15.6% (19/122) and 0.5% (1/200) in captive and wild giant pandas, respectively in China (Wang et al., 2015). It is occasionally detected in humans (Leoni et al., 2006; Morse et al., 2007; Waldron et al., 2011; Agholi et al., 2013; Jiang et al., 2014; Liu et al., 2014). Two studies in China by the same research group have reported that *C. andersoni* was the most prevalent *Cryptosporidium* species detected in humans (Jiang et al., 2014; Liu et al., 2014). However, further research is required to better understand the zoonotic importance of *C. andersoni*.

3.1.7. *Cryptosporidium canis*

C. canis (previously dog genotype 1) was first identified as the dog genotype by Xiao et al. (1999) and described as a species in 2001 (Fayer et al., 2001), on the basis that *C. canis* oocysts were infectious for calves but not mice and were genetically distinct from all other species. *C. canis* and its sub-genotypes (*C. canis* fox genotype and *C. canis* coyote genotype) have been reported in dogs, foxes and coyotes (Table 2) (Xiao et al., 2002a; Zhou et al., 2004; Fayer, 2010; Feng, 2010). *C. canis* has also been reported worldwide in humans (Lucio-Forster et al., 2010; Fayer, 2010; Elwin et al., 2012; Mahmoudi et al., 2015; Parsons et al., 2015).

3.1.8. *Cryptosporidium erinacei*

Little is known about epidemiology and pathogenicity of zoonotic *C. erinacei* in wildlife. *C. erinacei* (previously known as hedgehog genotype) was first identified morphologically in a captive four-toed hedgehog (*Ateletrix albiventris*) in 1998 (Graczyk et al., 1998). An isolate from a European hedgehog originating from Denmark was typed in 2002 (Enemark et al., 2002) and shown to be distinct. Subsequent studies have identified *C. erinacei* in hedgehogs, horses and humans (Dyachenko et al., 2010; Laatamna et al., 2013; Kváč et al., 2014a, 2014b; Meredith and Milne, 2009). At the gp60 locus, *C. erinacei* isolates are identified as subtype family XIII (Dyachenko et al., 2010; Laatamna et al., 2013; Lv et al., 2009; Kváč et al., 2014b). Previously reported *C. erinacei* subtypes include XIIIaA20R10 (KF055453), XIIIaA21R10 (GQ214085), XIIIaA22R9 (KC305644), XIIIaA19R12 (GQ214081), and XIIIaA22R11 (GQ259140) Kváč et al., 2014b).

3.1.9. *Cryptosporidium fayeri and Cryptosporidium macropodum*

The two main species identified in a wide range of marsupials are *C. fayeri* and *C. macropodum* (previously marsupial genotype I and II) (Table 2) (Morgan et al., 1997; Power et al., 2004, 2005; Power and Ryan, 2008; Ryan et al., 2008; Nolan et al., 2010; Power, 2010; Ng et al., 2011a; Yang et al., 2011; Ryan and Power, 2012; Nolan et al., 2013; Vermeulen et al., 2015; Zahedi et al., 2015). Neither of these species is associated with diarrhoea in their marsupial hosts (Ryan and Power, 2012). *C. macropodum* has not been reported in humans but cryptosporidiosis caused by *C. fayeri* has been reported in a 29-year-old female patient in Australia (Waldron et al., 2010). The woman was immunocompetent but suffered prolonged gastrointestinal illness. The patient resided in a national forest on the east coast of New South Wales, Australia, an area where marsupials are abundant. She had frequent contact with partially domesticated marsupials (Waldron et al., 2010). Identification of *C. fayeri* in a human patient is a concern for water catchment authorities in the Sydney region. The main water supply for Sydney, Warragamba Dam, covers 9050 km^2 and is surrounded by national forest inhabited by diverse and abundant marsupials. At the gp60 locus, the subtype family IV has been identified with 6 subtypes (IVa–IVf) (Power et al., 2009). Subtyping of the human-derived isolate of *C. fayeri* identified IVaA9G4T1R1, which has also been identified in eastern grey kangaroos in Warragamba Dam, suggesting possible zoonotic transmission (Power, 2010; Waldron et al., 2010).

In addition to *C. fayeri* and *C. macropodum*, there have been several other host-adapted genotypes identified in Australian marsupials. Possum genotype I has been described in brushtail possums, a host species found in a range of habitats throughout Australia (Hill et al., 2008) and the novel kangaroo genotype I in western grey kangaroos (Yang et al., 2011). Possum genotype I and kangaroo genotype I have not been reported in humans or other animals and their zoonotic potential is unknown.

3.1.10. *Cryptosporidium meleagridis*

Although primarily a bird parasite (see section 3.2.1 and Table 3), *C. meleagridis* has been identified in deermice, mountain gorillas and marsupials (Feng et al., 2007; Sak et al., 2014; Vermeulen et al., 2015). It is also the third most prevalent species infecting humans (Morgan et al., 2000; Cama et al., 2003; Gatei et al., 2006; Muthusamy et al., 2006; Leoni et al., 2006; Berrilli et al., 2012; Elwin et al., 2012; Neira et al., 2012; Silverlås et al., 2012; Kurniawan et al., 2013; Sharma et al., 2013; Wang et al., 2014; Adamu et al., 2014; Ghaffari and Kalantari, 2014; Ryan and Xiao, 2014; Ghaffari and Kalantari, 2014; Rahmouni et al., 2014; Wang et al., 2014; Stensvold et al., 2014, 2015). In some studies, *C. meleagridis* prevalence is similar to that of *C. parvum* (Gatei et al., 2002; Cama et al., 2007). The ability of *C. meleagridis* to infect humans and other mammals, and its close relationship to *C. parvum* and *C. hominis* at multiple loci, has led to the suggestion that mammals actually were the original hosts, and that the species has later adapted to birds (Xiao et al., 2002a,). Subtyping at the gp60 locus has identified seven subtype families (IIIa to IIIg) (Stensvold et al., 2015). More details on transmission dynamics will be discussed in section 3.2.1.

3.1.11. Other *Cryptosporidium* species and genotypes reported in wild mammals

A number of other *Cryptosporidium* species and genotypes have been identified in wildlife (Table 2). Most are host-adapted genotypes that are not of public health significance, however several have been identified in humans (Table 2). Of these, the chipmunk genotype I is considered an emerging human pathogen (Jiang et al., 2005; Feltus et al., 2006; Feng et al., 2007; ANOFEL, 2010; Insulander et al., 2013; Lebbad et al., 2013; Guo et al., 2015). At the gp60 locus, 15 different subtypes have been identified but subtypes differ only in the number of tandem repeats (TCA/TCG/

Table 3
Cryptosporidium species and genotypes in avian hosts confirmed by molecular analysis (Modified from Ryan and Xiao, 2014).

Species name	Major host(s)	Site of infection	References
C. meleagridis	Turkey (*Meleagris gallopavo*), Indian ring-necked parrot (*Psittacula kameri*), Red-legged partridge (*Alectoris rufa*), Cocktails (*Nymphicus hollandicus*), Bohemian waxwing (*Bombycilla garrulous*), Rufousturle dove (*Streptopelia orientalis*), Fan-tailed pigeon (*Columba livia*), Chicken (*Gallus gallus*), Quails (*Coturnixcoturnix japonica*), Pekin ducks (*Anas platyrhynchos*), Domestic Pigeons (*Columba livia domestica*), European turtle dove (*Streptopelia turtur*), Red-legged partridge (*Alectoris rufa*)	Intestine	Morgan et al., 2000; Glaberman et al., 2001; Abe and Iseki, 2004; Abe and Makino 2010; Wang et al., 2010; Qi et al., 2011; Berrilli et al., 2012; Wang et al., 2012; Baroudi et al., 2013; Wang et al., 2014; Koompapong et al., 2014; Maca and Pavlasek, 2015; Reboredo-Fernandez et al., 2015
C. baileyi	Turkey (*Meleagris gallopavo*), Chicken (*Gallus gallus*), Brown squail (*Synoicus australis*), Cocktails (*Nymphicus hollandicus*), Whooping crane (*Grus vipio*), Grey-bellied bulbul (*Pycnonotus* spp.), Black vulture (*Coragyps atratus*), Saffron finch (*Sicalis flaveola*), Mixed-bred falcons (*Falcorusticolus x Falco cherrug*), Reddy Shelduck (*Tadornaferruginea*), Red-billed leiothrixes (*Leiothrix lutea*), Pekin ducks (*Anas platyrhynchos*), Buffy-fronted seedeater (*Sporophila frontalis*), Javva sparrows (*Padda oryzivora*), Mynas (*Acridotheres tristis*), Zebra finches (*Taeniopygia guttata*), Crested Lark (*Galerida cristana*), Gouldian finch (*Chloebia gouldiae*), Black-billed magpie (*Pica pica*), Ostriches (*Struthio camelus*), Quails (*Coturnixcoturnix japonica*), Red grouse (*Lagopus lagopus scotica*), Red-crowned crane (*Grus japonenis*)	Cloaca, bursa, trachea	Morgan et al., 2001; Abe and Iseki, 2004; Ng et al., 2006; Huber et al., 2007; Kimura et al., 2004; Nakamura et al., 2009; Abe and Makino, 2010; Wang et al., 2010; Qi et al., 2011; Wang et al., 2012; Baroudi et al., 2013; Baines et al., 2014; Hamidinejat et al., 2014; Wang et al., 2014; Li et al., 2015c; Maca and Pavalasek, 2015
C. galli	Chicken (*Gallus gallus*), Finches (*Spermestidae* and *Fringillidae*), Capercaille (*Tetrao urogallu*), Pine grosbeak (*Pinicola enuncleator*), Turqoise parrots (*Neophema pulchella*), Cuban flamingo (*Phoenicopterus ruber ruber*), Rhinoceros hornbill (*Buceros rhinoceros*), Red-cowled cardinal (*Paroaria dominicana*), Zebra finches (*Taeniopygia guttata*), Chocolate parson finches (*Peophila cincta*), Chesnut finches (*Lonchura castaneothorax*), Painted firetali finches (*Ebmlema picta*), Canaries (*Serinus* sp.), Glosters (*Serinus canaria*), Green-winged saltatros (*Saltator similis*), Slate-collard seedeater (*Sporophila schistaceca*), Great-billed seed-fench (*Oryzoborus maximiliani*), Ultermarine grosbeak (*Cyanocompsa brissonii*), Bohemian waxwing (*Bombycilla garrulous*), Silver-eared Mesia (*Leiothrix argentauris*), Cockatiel (*Nymphicus hollandicus*), Chopi blackbird (*Gnorimopsar chopi*), Green-winged saltator (*Saltator similis*), Rufous-collared sparrow (*Zonotrichia capensis*)	Preventriculus	Ryan et al., 2003; Ng et al., 2006; Antunes et al., 2008; Nakamura et al., 2009; da Silva et al., 2010; Qi et al., 2011; Nakamura et al., 2014
Avian genotype I	Red factor canary (*Serinus canaria*), Canary (*S. canaria*), Indian peafowl (*Pavo cristatus*)	–	Ng et al., 2006; Nakamura et al., 2009
Avian genotype II	Eclectus (*Eclectus roratus*), Galah (*Eolophus roseicapilla*), Cockatiel (*Nymphicus hollandicus*), Major Mitchel Cockatoo (*Cavcatua lead beater*), Ostriches (*Struthio camelus*), White-eyed parakeet (*Aratinga leucophthalma*)	–	Meireles et al., 2006; Ng et al., 2006; Nakamura et al., 2009; Seva et al., 2011; Nguyen et al., 2013
Avian genotype III	Galah (*Eolophus roseicapilla*), Cockatiel (*Nymphicus hollandicus*), Java sparrow (*Padda oryzivora*), Son conure (*Aratinga solstitialis*), Peach faced lovebirds (*Agapornis roseicollis*), Seagull (*Laridae* sp), Blue-fronted amazon (*Amazona aestival*), Cockatiel (*Nymphicus hollandicus*), Rufous-collared sparrow (*Zonotrichia capensis*), Lovebird (*Agapornis species*), Cockatiel (*Nymphicus hollandicus*)	–	Ng et al., 2006; Nakamura et al., 2009; Makino et al., 2010; Koompapong et al., 2014; Nakamura et al., 2014; Ravich et al., 2014; Li et al., 2015c; Gomes et al., 2012
Avian genotype IV	Japanese white-eye (*Zosterops japonica*)	–	Abe and Makino, 2010; Qi et al., 2011
Avian genotype V	Cockatiel (*Nymphicus hollandicus*), Budgerigar (*Melopsittacus undulates*)	–	Abe and Makino, 2010; Qi et al., 2011; Zhang et al., 2015
Duck genotype	Black dock (*Anus rubripes*), Canada geese (*Branta canadensis*)	–	Jellsison et al., 2004; Zhou et al., 2004
Eurasian woodcock genotype	Eurasian woodcock (*Scolopax rusticola*)	–	Ryan et al., 2003; Ng et al., 2006
Goose genotype I	Canada geese (*Branta canadensis*)	–	Xiao et al., 2002b; Jellison et al., 2004; Zhou et al., 2004
Goose genotype II	Canada geese (*Branta canadensis*)	–	Jellison et al., 2004; Zhou et al., 2004
Goose genotype III	Canada geese (*Branta canadensis*)	–	Jellison et al., 2004
Goose genotype IV	Canada geese (*Branta canadensis*)	–	Jellison et al., 2004
Goose genotype V	Canada geese (*Branta canadensis*)	–	Jellison et al., 2004

TCT) and comprise a single subtype family (XIVa). Analysis indicates that subtypes from humans and wildlife are genetically similar and zoonotic transmission might play a potential role in human infections (Guo et al., 2015). The skunk and mink genotypes have also been reported in a few human cases of cryptosporidiosis (Robinson et al., 2008; Chalmers et al., 2009; Rengifo-Herrera et al., 2011; Elwin et al., 2012; Ng-Hublin et al., 2013; Ebner et al., 2015).

3.2. *Cryptosporidium in birds*

The mobility of migratory birds, together with their distribution and ability to form large colonies, makes them potentially suitable to spread pathogens. Due to their easy access to drinking water catchments and other water sources, wild birds are believed to be a potential risk to drinking water safety. The epidemiology of avian cryptosporidiosis, in particular zoonotic *Cryptosporidium* species infecting birds is therefore of public health importance. Currently only three avian *Cryptosporidium* spp. are recognised; *C. meleagridis, C. baileyi* and *C. galli* (Table 3) (Ryan and Xiao, 2014).

3.2.1. *C. meleagridis*

C. meleagridis infects the intestinal (small and large intestine and bursa) epithelial cells of a wide range of birds (Table 3) (Ryan and Xiao, 2014). It was first detected in a wild turkey (*Meleagris gallopavo*) by Tyzzer in 1929, but named as a valid *Cryptosporidium* species in 1955 (Slavin, 1955). *C. meleagridis* oocysts have been experimentally infected into broiler chickens, ducks, turkeys, calves, pigs, rabbits, rats and mice (Darabus and Olariu, 2003; Ryan and Xiao, 2014). It has also been reported as one of the most commonly detected human-infectious *Cryptosporidium* species in wastewater (Feng et al., 2007, 2011a; Li et al., 2012).

Molecular analysis has revealed that *C. meleagridis* has relatively low host specificity, and many *C. meleagridis* subtypes at other loci have been found in both birds and humans and both anthroponotic and zoonotic transmission routes have been suggested (Cama et al., 2003; Elwin et al., 2012; Silverlås et al., 2012). Subtyping at the gp60 locus has identified seven subtype families (IIIa–IIIg) and the likely occurrence of cross-species transmission of *C. meleagridis* between birds and humans (Wang et al., 2014). Human volunteer studies have shown that healthy adults can be infected and become ill from ingestion of *C. meleagridis* oocysts (Chappell et al., 2011). In the study by Chappell et al., five volunteers were challenged with 10^5 *C. meleagridis* oocysts and monitored for six weeks for faecal oocysts and clinical manifestations. Four volunteers had diarrhoea; three had detectable faecal oocysts; and one infected volunteer remained asymptomatic. All infections were self-limited and oocysts were cleared within $\leq$12 days of challenge (Chappell et al., 2011).

3.2.2. *Cryptosporidium baileyi*

C. baileyi is generally associated with the respiratory form of cryptosporidiosis in birds and has been predominantly reported in broiler chickens. Compared to *C. meleagridis*, *C. baileyi* is capable of infecting a larger spectrum of avian hosts (Table 3), targeting various sites of infection mostly associated with digestive and respiratory tracts (Ryan and Xiao, 2014). Experimental cross-transmission of *C. baileyi* to other birds has been successfull, however there has been no reports of cross-transmission between birds and other vertebrates (Lindsay and Blagburn, 1990; Cardozo et al., 2005), except for a single unsubstantiated report of human infection with *C. baileyi* which did not include any molecular analysis (Ditrich et al., 1991). Therefore, *C. baileyi* is not considered to be of public health significance.

3.2.3. *Cryptosporidium galli*

Unlike other avian species, *C. galli* is a gastric species with endogenous developmental stages occurring in the glandular epithelial cells of the proventriculus (Pavlásek, 1999, 2001; Ryan et al., 2003; Ng et al., 2006; Ryan and Xiao, 2014). It predominantly infects birds of the family Spermestidae, Fringilidiae and domestic chickens (*Gallus gallus*), and seems to be more prevalent among songbirds (Table 3). Successful experimental cross-transmission of *C. galli* to other chickens have been reported, however the full extent of its host range is still unknown (Ryan, 2010). It has not been reported in humans.

3.2.4. *Other Cryptosporidium species and genotypes reported in birds*

In addition to *C. meleagridis*, other zoonotic species of *Cryptosporidium* reported in birds include *C. hominis*, *C. parvum*, *C muris* and *C. andersoni* (Zylan et al., 2008; Jellison et al., 2009; Ryan, 2010; Reboredo-Fernandez et al., 2015; Gomes et al., 2012). In addition, twelve genotypes; avian genotypes I–V, the black duck genotype, the Eurasian woodcock genotype and goose genotypes I–V have been reported (Table 3). To date, there is no evidence of human cryptosporidiosis caused by these genotypes.

3.3. *Cryptosporidium in fish and marine mammals*

Cryptosporidium has been described in both fresh and marine water piscine species with parasitic stages located either on the stomach or intestinal surface, or deep within the epithelium (Table 4). The first account of *Cryptosporidium* in a piscine host was *Cryptosporidium nasorum*, identified in a Naso tang, a tropical fish species (Hoover et al., 1981). However, currently only three species are recognized; *C. molnari*, *C. scophthalmi* and *C. huwi* (previously known as piscine genotype I) (Alvarez-Pellitero and Sitja-Bobadilla, 2002; Alvarez-Pellitero et al., 2004; Palenzuela et al., 2010; Costa et al., 2015; Ryan et al., 2015), none of which have been reported in humans. In fish hosts, *Cryptosporidium* fish species and genotypes are typically located either in the stomach or intestine and the parasite can cause clinical manifestations, such as emaciation, decrease in growth rate, anorexia, whitish faeces, abdominal swelling, and ascites (Alvarez-Pellitero et al., 2004; Ryan et al., 2015). Most studies on *Cryptosporidium* in fish have been reported in farmed or aquarium fish (Table 4) and little data are currently available regarding the molecular identification of *Cryptosporidium* species and genotypes in wild fish populations and, in particular, in edible fish (Palenzuela et al., 2010; Reid et al., 2010; Barugahare et al., 2011; Gibson-Keuh et al., 2011; Koinari et al., 2013; Certard et al., 2015).

In addition to the three recognized species of *Cryptosporidium* in piscine hosts, numerous *Cryptosporidium* species and genotypes have been reported in fish including; piscine genotypes 2 to 8, unnamed novel genotypes ($n = 5$), rat genotype III, *C. parvum*, *C. hominis*, *C. xiaoi* and *C. scrofarum* (Table 4). Of these, only *C. parvum*, *C. hominis* and *C. scrofarum* are of public health interest. *Cryptosporidium scrofarum* was identified in a whiting (Reid et al., 2010); *C. parvum* was found in School whiting, Nile tilapias, a Silver barb, Arctic char and European whitefish and *C. hominis* was reported in Mackerel scad (Reid et al., 2010; Gibson-Kueh et al., 2011; Koinari et al., 2013; Certad et al., 2015). In one of the most recent studies, *C. parvum* was identified in freshwater fish from Lake Geneva (Lac Léman) by both histology and molecular analysis (Certad et al., 2015). In that study, the overall prevalence of *Cryptosporidium* was 36.6% (15/41); the prevalence of *C. parvum* and *C. molnari* was 86.7% (13/15) and 6.7% (1/15), respectively, while 6.7% (1/15) were mixed *C. parvum* and *C. molnari* infections (Certad et al., 2015). Histological analysis identified *C. parvum*

Table 4
Cryptosporidium sp. reported in fish using molecular tools (modified from Ryan et al., 2014).

Species	Host	Site of infection	Reference
C. molnari	Gilthead sea bream (*Sparus aurata*), European sea bass (*Dicentrarchus labrax*), Murray cod (*Maccullochella peelii peelii*)	Stomach (and intestine)	Palenzuela et al., 2010; Barugahare et al., 2011; Certad et al., 2015
C. scophthalmi	Turbot (*Scophthalmus maximus*)	Intestine	Costa et al., 2015
C. huwi (previously piscine genotype 1)	Guppy (*Poecilia reticulata*)	Stomach	Ryan et al., 2004; Ryan et al., 2015
Piscine genotype 2	Angelfish (*Pterophyllum scalare*)	Stomach	Murphy et al., 2009
Piscine genotype 3	Mullet (*Mugil cephalus*)	Intestine	Reid et al., 2010
Piscine genotype 4	Golden algae eater (*Crossocheilus aymonieri*), Kupang damsel (*Chrysiptera hemicyanes*), Oscar fish (*Astronatus ocellatis*), Neon tetra (*Paracheirodon innesi*)	Intestine	Reid et al., 2010; Morine et al., 2012
Piscine genotype 5	Angelfish (*Pterophyllum scalare*), Butter bream (*Monodactylidae*), Golden algae eater (*Crossocheilus aymonieri*)	–	Zanguee et al., 2010
Piscine genotype 6/genotype 6-like	Guppy (*Poecilia reticulata*), Gourami (*Trichogaster trichopterus*)	–	Zanguee et al., 2010; Morine et al., 2012
Piscine genotype 7	Red eye tetra (*Moenkhausia sanctaefilomenae*)	–	Morine et al., 2012
Piscine genotype 8	Oblong silver biddy (*Gerres oblongus*)	–	Koinari et al., 2013
Rat genotype III, *C. hominis, C. parvum, C. xiaoi* and *C. scrofarum*	Whiting (*Sillago vittata*), Barramundi (*Lates calcarifer*), Arctic char (*Salvelinus alpinus*), Nile tilapias (*Oreochromis niloticus*), Silver barb (*Puntius gonionotus*), Mackerel scad (*Decapterus macarellus*), European whitefish (*Coregonus lavaretus*), School whiting (*Sillago vittata*)	–	Reid et al., 2010; Gibson-Kueh et al., 2011; Koinari et al., 2013; Certad et al., 2015
Novel un-named genotypes (n = 5)	Orange clownfish (*Amphiprion percula*), Azure damsel (*Chrysiptera hemicyanea*), Blue tang (*Paracanthurus hepatus*), Platyfish (*Xiphophorus maculatus*), Oscar (*Astronotus ocellatus*), Goldfish (*Carassius auratus*)	–	Yang et al., 2015

developmental stages in the stomach and intestine suggesting that *C. parvum* was infecting the fish, rather than being passively carried which has important public health implications.

Subtyping of *Cryptosporidium* isolates in fish has identified *C. parvum* subtype IIaA18G3R1 in School whiting from Australia (Reid et al., 2010), three *C. parvum* subtypes (IIaA14G2R1, IIaA15G2R1 and IIaA19G4R1) in Nile tilapia, silver barb and mackerel scad and a *C. hominis* subtype (IdA15G1) in mackerel scad in Papua New Guinea (Koinari et al., 2013), and *C. parvum* subtypes IIaA15G2R1, IIaA16G2R1 and IIaA17G2R1 in Arctic char and European whitefish from France (Certad et al., 2015). All of these *C. parvum* subtypes are zoonotic and commonly found in cattle and humans (Xiao, 2010). The identification of the *C. hominis* subtype probably reflects human sewage contamination of the water. Clearly further studies in this area are required to better understand the transmission dynamics of *Cryptosporidium* in fish.

3.4. *Cryptosporidium in amphibians and reptiles*

Little is known about *Cryptosporidium* species infecting amphibians. Of the three orders of amphibians; *Anura*, *Caudata* and *Gymnophonia*, *Cryptosporidium* has been only reported in Anura which includes frogs and toads and only one species, *C. fragile* is recognised (Table 5) (Jirků et al., 2008). In transmission experiments, *C. fragile* was not infective in one fish species (*Poecilia reticulate*), four amphibian species (*Bufo bufo*, *Rana temporaria*, *Litoria caerulea* and *Xenopus laevis*), one species of reptile (*Pantherophis guttatus*) and SCID mice (Jirků et al., 2008). This species has not been reported in humans.

Cryptosporidium infections are ubiquitous in reptiles and have been reported in more than 57 reptilian species (O'Donoghue, 1995; Ryan and Xiao, 2014). Unlike in other animals in which *Cryptosporidium* infection is usually self-limiting in immunocompetent individuals, cryptosporidiosis in reptiles is frequently chronic and sometimes lethal in some snakes. Both intestinal and gastric cryptosporidiosis has been described in snakes and lizards. To date, two species are recognised; *C. serpentis* (gastric) and *C. varanii* (*C. saurophilum*) (intestinal) (Levine, 1980; Pavlasek et al., 1995; Koudela and Modry, 1998; Pavlásek and Ryan, 2008); neither of which have been reported in humans, but *C. serpentis* has been identified in cattle (Azami et al., 2007; Chen and Qiu, 2012). A new intestinal species, *Cryptosporidium ducismarci* (tortoise genotype II) has been reported in several species of tortoises, snakes and lizards (Traversa, 2010). Because only molecular data are presented, this species is regarded as a nomen nudum, pending the support of morphological and biological data.

C. parvum, *C. muris* and *Cryptosporidium tyzzeri* are also commonly reported in reptiles, particularly snakes but this is thought to be due to mechanical transmission due to predation of infected rodents and is not thought to present a substantial zoonotic risk (Morgan et al., 1999; Xiao et al., 2004b; Pedraza-Diaz et al., 2009; Díaz et al., 2013; da Silva et al., 2014). In addition, various host-adapted genotypes have been identified including tortoise genotype I and snake genotypes I and II (cf. Ryan and Xiao, 2014), which have not been reported in humans (Table 5) (Xiao et al., 2004b; Pedraza-Diaz et al., 2009; Traversa, 2010; Seva Ada et al., 2011; Richter et al., 2011; Rinaldi et al., 2012; da Silva et al., 2014; Abe and Matsubara, 2015). There is also a single report of avian genotype V from green iguanas (*Iguana inguana*) (Kik et al., 2011).

4. The role of urbanisation in the transmission of zoonotic ***Cryptosporidium*** species from wildlife

The risk of waterborne outbreaks of cryptosporidiosis depends on a complex interplay of factors, associated with both the environment and the biology and ecology of host and parasite. *Cryptosporidium* detection in an animal faecal sample does not necessarily mean active infection in the host, nor does this guarantee that the parasite prevalence and the host-population dynamics are conducive to an outbreak. For these reasons the epidemiological potential of detection of *Cryptosporidium* in wildlife cannot be easily and fully extrapolated. An increased epidemiological risk, however, can be identified when there is an overlap between humans and the distribution and dispersal of animal hosts. This is largely due to human encroachment into wildlife-populated areas, which, by extension, also includes conversion of natural environments to drinking water catchments. Similarly, urban environments may also represent attractive new habitats for animals harbouring zoonotic *Cryptosporidium* spp. Thus, it is clear

Table 5
Amphibian and reptile *Cryptosporidium* species and genotypes and their hosts confirmed by molecular analyses (modified from Ryan et al., 2014).

Species/genotype	Amphibian/Reptile host species	Site of infection	Reference
C. fragile	Black-spined toads (*Duttaphrynus melanostictus*)	Stomach	Jirků et al., 2008
C. serpentis	Amazon tree boa (*Corallus hortulanus*), Black rat snake (*Elaphe obsoleta obsolete*), Bornmueller's viper (*Vipera bornmuelleri*), Bull snake (*Pituophis melanoleucus melanoleucus*), California kingsnake (*Lampropeltis getulus californiae*), Cornsnake (*Elaphe guttata guttata*), Common death adder (*Acanthophis antarticus*), Desert monitor (*Varanus griseus*), Eastern/Mainland Tiger snake (*Notechis scutatus*), Frilled lizard (*Chlamydosaurus kingui*), Giant madagascar or Oustalet's chameleon (*Chamaeleo oustaleti*), Leopard gecko (*Eublepharis macularius*), Mexican black kingsnake (*Lampropeltis getulus nigritus*), Milk snake (*Lampropeltis triangulum*), Mountain viper (*Vipera wagneri*), Python (*Python molurus*), Savannah monitor (*Varanus exanthematicus*), Skink (*Mabuya perrotetii*), Taipan (*Oxyuranus scutellatus*), Red-tailed boa (*Boa constrictor constrictor*), Rainbow boa (*Epicrates cenchria cenchria*)	Stomach	Kimbell et al., 1999; Morgan et al., 1999b; Hajdusek et al., 2004; Xiao et al., 2004b; Pedraza-Díaz et al., 2009; Richter et al., 2011; Sevá-Ada et al., 2011; Rinaldi et al., 2012; Díaz et al., 2013; da Silva et al., 2014; Abe and Matsubara, 2015
C. varanii	African fat-tailed gecko (*Hemitheconyx caudicinctus*), Leopard gecko (*Eublepharis macularius*), Boa constrictor (*Boa constrictor*), Cornsnake (*Elaphe guttata guttata*), Leopard gecko (*Eublepharis macularius*), Desert monitor (*Varanus griseus*), Gecko (*Gekkoninae* sp.), Green iguana (*Iguana iguana*), *Lampropeltis* sp; Louisiana pine snake (*Pituophis ruthveni*), Plated lizard (*Gerrhosaurus* sp.), Schneider's Skink (*Eumeces schneideri*), Taipan (*Oxyuranus scutellatus*), Baron's green racer (*Philodryas baroni*), Yellow anaconda (*Eunectes notaeus*), Cornsnake (*Elaphe guttata guttata*), Mato Grosso lancehead (*Bothrops matogrossensis*)	Intestine and Cloaca	Koudela and Modry, 1998; Morgan et al., 1999b; Hajdusek et al., 2004; Xiao et al., 2004b; Plutzer and Karanis, 2007; Pedraza-Díaz et al., 2009; Richter et al., 2011; da Silva et al., 2014; Abe and Matsubara, 2015
Lizard genotype/*C. serpentis*-like	Leopard gecko (*Eublepharis macularius*), Cornsnake (*Pantherophis guttatus*), Chinese wonder gecko (*Teratoscincus scincus*)	–	Xiao et al., 2004b; Richter et al., 2011, Abe and Matsubara, 2015
Tortoise genotype I	Indian star tortoises (*Geochelone elegans*), Herman's tortoise (*Testudo hermanii*), Ball python (*Python regius*), Russian tortoise (*Agrionemys [Testudo] horsfieldii*)	Stomach	Xiao et al., 2002b, 2004b, Alves et al., 2005; Pedraza-Díaz et al., 2009; Griffin et al., 2010; Richter et al., 2012
Tortoise genotype II (*C. duismarci*)	Marginated tortoise (*Testudo marginata*), Ball python (*Python regius*), Veiled chameleon (*Chamaeleo calyptratus*), Pancake tortoise (*Malacochersus tornieri*), Russian tortoise (*Agrionemys [Testudo] horsfieldii*)	Intestine	Traversa et al., 2008; Pedraza-Díaz et al., 2009; Griffin et al., 2010; Traversa, 2010; Richter et al., 2012
Snake genotype I	New Guinea Viper boa (*Candoia asper*), Japanese grass snakes (*Rhabdophis tigris*)	–	Xiao et al., 2002b; Kuroki et al., 2008
Snake genotype II	Boa constrictor (*Boa constrictor ortoni*)	–	Xiao et al., 2004b

that wildlife-associated *Cryptosporidium* is an increasing concern for cryptosporidiosis in humans.

During the last 100 years in many countries of the world, there have been dramatic changes in natural/rural landscapes due to urbanization (Mackenstedt et al., 2015). Although urbanization is one of the leading causes of species extinction (McKinney, 2006), for adaptable species, urban and periurban areas can be very attractive due to increased food and water resources (waste food, pet food, garden produce, water tanks etc) (Mackenstedt et al., 2015). In these environments, wildlife species may reach far higher population densities than in more natural or rural landscapes (Bradley and Altizer, 2007), potentially increasing the faecal–oral transmission of oocysts between wildlife and humans and contamination of drinking water catchments.

Shifting boundaries between wildlife and humans have been responsible for the emergence of species like *C. ubiquitum* and chipmunk genotype I in human populations. For example, squirrels host *C. ubiquitum*, chipmunk genotype I, the skunk genotype and other *Cryptosporidium* genotypes associated with human disease (Feng et al., 2007; Kváč et al., 2008; Ziegler et al., 2007; Stenger et al., 2015b), and because they frequently share habitats with humans they may be a significant reservoir of human infection. Squirrels can reach relatively high densities in suitable habitats, resulting in high rates of environmental loading of *Cryptosporidium* oocysts (Atwill et al., 2001). For example, California ground squirrels can reach densities as high as 92 adults hectare^{-1} (Owings et al., 1977; Boellstorff and Owings, 1995), which when combined with shedding of up to 2×10^5 oocysts animal^{-1} day^{-1} results in rates of environmental loading equivalent to 1×10^7 oocysts hectare^{-1} day^{-1} (Atwill et al., 2004). Further analysis of squirrel populations however has suggested that most tree squirrels host zoonotic species and genotypes while ground squirrels host species and genotypes that are tribe-specific and unlikely to cause human disease, despite overlapping ranges (Stenger et al., 2015b). This highlights the importance of extensive molecular epidemiological studies of wildlife to better understand the public health risks.

While urban-environment-induced increases in wildlife population densities are conducive to elevated rates of *Cryptosporidium* transmission, the host specificity of some wildlife species and genotypes may limit the potential for spillover of wildlife genotypes to sympatric populations of humans. For example, in Australia, the common brushtail possum is one of the most abundant native marsupials in urban environments, having successfully adapted to utilise anthropogenic resources (Hill et al., 2008). A higher *Cryptosporidium* prevalence in urban compared to woodland possum populations (11.3 versus 5.6%) has been reported, but the majority of possums sampled shed low numbers of host adapted (possum genotype) oocysts (1 to 10^2) (Hill et al., 2008). However, the finding a *C. fayeri* clinical infection in a human, which had previously been thought to be a host-adapted species (Waldron et al., 2010), highlights our lack of knowledge about the human infectious potential of many species and genotypes of *Cryptosporidium* infecting wildlife.

5. Perspectives for the water industry

Management of *Cryptosporidium* public health risks for the drinking water industry requires the implementation of a holistic approach including research, monitoring *Cryptosporidium* oocysts in animals and source water and catchment management (e.g., access protection, vegetation cover, etc). As watersheds are vulnerable to contamination with both zoonotic and non-zoonotic species from wildlife, sensitive detection of *Cryptosporidium* oocysts in water and correct identification of oocysts to the species/genotype level are essential for source water management and risk assessment (Li et al., 2015b). The routine practice of assessing *Cryptosporidium* contamination of catchments and drinking water supplies using total oocyst counts based on the U.S. Environmental Protection Agency (EPA) Method 1622/1623, cannot differentiate *Cryptosporidium* species and cannot reliably access viability (infectivity). This microscopy-based method, therefore overestimates the human health risk, as wildlife in catchments frequently carry non-zoonotic genotypes and species and not all oocysts are viable.

The introduction of molecular identification techniques has therefore been an important advance for water management and quantification of the risk to drinking water supplies from *Cryptosporidium*-infected wildlife (Nolan et al., 2013; Zahedi et al., 2015). Identification of *Cryptosporidium* to the species/genotype level is especially challenging for environmental (faecal and water) samples because of the usual presence of very low numbers of oocysts and high concentrations of PCR inhibitors and non-target organisms (Li et al., 2015b). It is essential however, for the assessment of the public health importance of *Cryptosporidium* oocysts from wildlife. Recently, the use of fluorescence resonance energy transfer (FRET) probes combined with melt curve analysis has been used for rapid and sensitive differentiation of zoonotic from non-zoonotic species in water samples (Li et al., 2015b). Another study of a drinking water supply in Australia, found no *C. hominis* in any water sample tested, but *Cryptosporidium* genotypes associated with native and non-native wildlife made up 70% of all isolates typed (Swaffer et al., 2014). Similarly, Ruecker et al. (2012) reported that non-zoonotic wildlife species and genotypes of *Cryptosporidium* accounted for 64.3% of *Cryptosporidium* identified in environmental water samples in Canada and that only 7.2% of human-infectious species were detected. A low prevalence of *C. hominis* and *C. parvum* was also reported by Nolan et al. (2013) in Melbourne catchments, who detected *C. hominis* and *C. parvum* in only 0.6% of samples, despite screening >2000 animal faecal samples. However, the human-infectious potential of many wildlife-adapted *Cryptosporidium* is currently unknown and the UK outbreak caused by *C. cuniculus* should act as a caution against assuming these unusual species and genotypes are not significant (Chalmers et al., 2009; Robinson et al., 2011).

Accurate, quantitative identification of *Cryptosporidium* in wildlife excreta is an essential starting point for estimating catchment loads (Davies et al., 2003). Quantitative PCR (qPCR) (real-time PCR) therefore represents an invaluable tool that enables rapid, high-throughput and cost-effective detection and quantitation of *Cryptosporidium* oocysts and is increasingly being used to monitor oocyst shedding by animals in catchments (Yang et al., 2014a). Due to the intrinsic constraints of qPCR however, standards of known concentration are required to generate calibration curves used to estimate the concentration of pathogens in a sample (Hindson et al., 2013; Rački et al., 2014). Therefore the quantification of the target molecules in the unknown sample is only as good as that of the standards used. Droplet digital PCR (ddPCR) (Hindson et al., 2013) is the third-generation implementation of conventional PCR that facilitates the quantitation of nucleic acid targets without the need for calibration curves (Vogelstein and Kinzler, 1999). A recent study compared ddPCR with qPCR for the quantitative detection of *Cryptosporidium* DNA in animal and human faecal samples (Yang et al., 2014b) and revealed that ddPCR appeared to be less sensitive to inhibitors than qPCR and that inaccurate calibration of qPCR standards resulted in qPCR overestimating the numbers of oocysts present (Yang et al., 2014b). This has important implications for catchment risk management. However, qPCR is cheaper and provides better throughput and therefore using ddPCR to precisely quantify qPCR standards would be one way to combine the advantages of the two technologies and provide more accurate assessment of *Cryptosporidium* catchments loads from wildlife faecal samples.

Besides quantitative considerations, measuring the infectivity is also important for adjusting the risk profile of oocysts from wildlife in source waters (Swaffer et al., 2014). For example, a recent study has shown that the infectivity fraction of oocysts within source water samples in South Australian catchments was low (~3.1%), which provided a much more accurate water quality risk assessment (Swaffer et al., 2014). This low infectivity fraction is consistent with source water infectivity reported by Di Giovanni et al. (1999) of 4.9% and Lalancette et al. (2012) of 0%. The ability to routinely measure oocyst infectivity has been hampered by a number of issues including the distribution and low numbers of oocysts, costs and reproducibility (Di Giovanni and LeChevallier, 2005; Swaffer et al., 2014). However, recent improvements in cell culture immunofluorescence assays have led to the development of a single format assay that provides information on method performance (recovery rate), oocyst number, oocyst infectivity and genotype of infectious oocysts, overcoming these obstacles (King et al., 2015). This assay should therefore enable a more comprehensive understanding of *Cryptosporidium* risk for different water sources, assisting in the selection of appropriate risk mitigation measures (King et al., 2015). It is however important to remember that the detection of non-viable oocysts in the 10–20 L of the water column that is usually sampled, does not mean that other oocysts in the water body are also non-viable.

Factors that affect the viability of *Cryptosporidium* oocyst load in faecal samples from wildlife in the catchment and water (runoffs, water column and sediments), include solar inactivation, desiccation, temperature and residence time in catchments and these dynamics should be factored into risk assessments (Hijen et al., 2006; King and Monis, 2007; Monis et al., 2014). Transport, including hydrodynamically-driven accumulation, settlement, dispersion, dilution etc. can also affect oocyst concentrations in the water, either positively or negatively. Peak flow periods (when the maximum area of catchment is contributing to stream flow), are a major driver behind the transport of oocysts to surface water.

Therefore monitoring the distribution of *Cryptosporidium* during elevated flow conditions caused by rainfall run-off is important given the demonstrated positive and significant correlation between *Cryptosporidium* concentration with flow and turbidity (Swaffer et al., 2014). Measuring the infectivity of different wildlife-derived *Cryptosporidium* species under different climactic conditions is therefore crucial for accurate risk assessment of public health implications, particularly as more extreme precipitation is predicted globally (IPCC, 2013 – www.ipcc.ch) (Ryan et al., 2014).

There are still many research gaps in our understanding of the public health significance of wildlife in drinking water catchments and taxonomic and molecular epidemiological studies on *Cryptosporidium* spp. in wildlife, especially those in watersheds are still scarce. Whole genome studies in *Cryptosporidium* species will assist with the development of gp60 and other typing tools to better access the zoonotic potential and transmission dynamics of *Cryptosporidium* in wildlife. Morphological and biological data including pathogenicity and oocyst shedding rates are not yet available for some common zoonotic *Cryptosporidium* species and genotypes in wildlife. There is also a need to confirm if molecular detection of zoonotic *Cryptosporidium* species in wildlife is commonly associated with actual infections or mechanical transmission (Ryan et al., 2014). *C. cuniculus* is the only species besides *C. hominis* and *C. parvum*, known to be associated with a waterborne outbreak of human cryptosporidiosis, yet little is known about the prevalence and oocyst shedding rates of *C. cuniculus* in rabbits.

The evolution of methods to enumerate and genotype oocysts and determine oocyst infectivity provides much-needed tools to refine the human health risk from wildlife in catchments and future studies will provide water quality managers with much more accurate and informed data for modelling and quantitative microbial risk assessments (QMRA) of wildlife in various catchments.

Conflict of interest

None.

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