Invited review

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

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Abstract
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 contamination for 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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Keywords:
Cryptosporidium
Zoonotic
Wildlife
Epidemiology

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http://dx.doi.org/10.1016/j.ijppaw.2015.12.001
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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 diarrhea, 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 Karianis, 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 Karianis, 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 Karianis, 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 people without safe access to drinking water by the end of 2015 (WHO, 2009).

5. Perspectives for the water industry

Conflict of interest

Acknowledgements

References
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. meleagrisidis and C. canis as well as various wildlife species and genotypes have been implicated in zoonotic 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).

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 | Scopthalmus 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        | Kvác et al., 2014b             | Enrochus eurpeaus (European hedgehog) | Hedgehogs, horses | Kvác et al., 2014a |
| C. scrofearum      | Kvác et al., 2013              | Sus scrofa (Pig) | Pigs          | Kvác et al., 2009a, 2009b |
| C. viatorum        | Eline et al., 2012             | Homo sapiens (Human) | Humans | Elwin et al., 2012; Insulander et al., 2013 |
| C. tyzzeri         | Tyzzer, 1912; Ken et al., 2012 | Mus musculus (Mouse) | Rodents | Raskova et al., 2013 |
| C. cuniculus       | Robinson et al., 2010          | Orystologus 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. xiao            | 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         | Jirku et al., 2008             | Duttaphrynus melanostictus (Toad) | Toads | None reported |
| C. fayer           | Ryan et al., 2010              | 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           | Pavulasek, 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 Stjå-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. varanis         | Pavlasek et al., 1995          | Varanus prasinus (Emerald Monitor) | Lizards | None reported |
| C. baileyi         | Current et al., 1986           | Gallus gallus (Chicken) | Birds | Commonly reported in humans |
| C. parvum          | Tyzzer, 1912                   | Bos taurus (Cattle) | Ruminants | Commonly reported in humans |
| C. meleagrisidis   | Slavin, 1955                  | Meleagris gallopavo (Turkey) | Birds and humans | Commonly reported in humans |
| C. serpentinus     | Levine, 1980                   | Elaphe guttata, E. subocularis, Sanzinia madagascarensis (Snakes) | Snakes and lizards | None reported |
| C. felis           | Ieki, 1979                    | Felis catus (Cat) | Cats | Many reports (cf. Lucio-Forster et al., 2010) |
| C. wravari         | Vetterling et al., 1971        | Cavia porcellus (Guinea pig) | Guinea pigs | None reported |
| C. musris          | Tyzzer, 1907; and 1910         | Mus musculus (House mouse) | Rodents | Many reports — Goyet et al., 2001; Gati et al., 2002; Tiangtip and Jongwutiwes, 2002; Gati et al., 2003; Palmer et al., 2003; Gati et al., 2006; Leoni et al., 2006; Muthusamy et al., 2006; Azami et al., 2007; Al-Brikian et al., 2008; Neira et al., 2012; Hasajov et al., 2014; Petrincová et al., 2015; Spanakos et al., 2015 |
| Cryptosporidium species/ genotypes | Wildlife hosts | Zoontic importance | gp60 subtypes reported in wildlife | References |
|-----------------------------------|---------------|--------------------|----------------------------------|------------|
| C. hominis | Fallow deer (*Dama dama*), Dugong (*Dugong dugon*), Chinchillas (*Chinchilla lanigera*), Raboons (*Pachia anubus*), 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*), Eastern 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, IbA16G2R2, IbA17, IbA16G2, IbA13R7, IbA13R8, IbA14R7, IbA20, leA11G3T3, IaA16G2, 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*), Addax (*Addax nasomaculatus*), Arabian oryx (*Oryx leucoryx*), Gemsboks (*Oryx gazella*), Sable antelopes (*sable antelopes*), White-tailed deer (*Odocoileus Virginianus*), Game grey wolves (*Canis lupus*), Raccoon dog (*Nyctereutes procyonoides viverinus*), Rabbit (*Oryctolagus cuniculus*), Nutria (*Myocastor coypus*), Prezewalski’s wild horse (*Equus przewalskii*), Alpaca (*Lama guanico 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 (*Rhinomys sinensis*), Small brown bat (*Myotis lucifugus*), Campbell hamster (*Phodopus campbelli*), Golden hamster (*Mesocricetus auratus*), Capybara (*Hydrochoerus hydrochaeris*), Raccoon dog (*Nyctereutes procyonoides viverinus*), 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 (*Rhinomys sinensis*) | Major | IldA15G1, IldA18G1, IldA19G1, IldA15G2R1, IldA19G2R1, IldA19G3R1, IldA19G4R1, IldA20G3R1, IldA21G3R1, IldA20G4R1, IldA21G4R1, IldA14G1R1, IldA14G2R1, IldA16G3R1, IldA5G3, IldA5G3a, IldA13G1, IldA9G4 (novel subtype) | Morgan et al., 1999a; Arwill et al., 2001; Perez and Le Blancq, 2001; Matsu, et al., 2000; Matsuayashi 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; Ly et al., 2009; Feng, 2010; Gomez-Cousa et al., 2012; Rasavosova et al., 2012; Ye et al., 2012; Dowle et al., 2013; Nolan et al., 2013; Liu et al., 2014; Lv et al., 2009; Reboredo-Fernandez 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, VaA19, VaA13, VaA22, VaA24, VaA26, VaA29, VaA32, VaA22R4, VaA23R3, VaA24R3, VaA25R4, VaA26R4 | 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 | XilA, XilB, XilC, XilD, XilE, XilF | Perez and Le Blancq, 2001; da Silva et al., 2003; Ryan et al., 2003; Feng et al., 2007; Karanis et al., 2007; Ziegler et al., 2007 (continued on next page) |
Table 2 (continued)

| Cryptosporidium species/ genotypes | Wildlife hosts | Zoonotic importance | gp60 subtypes reported in wildlife | References |
|-----------------------------------|---------------|---------------------|-----------------------------------|------------|
| *C. muris*                        |               |                     |                                   |            |
| C. muris                          | Wild rats (*Rattus spp.*), Mice (*Mus sp.*), Greater bilbies (*Macrotis lagotis*), Giraffes 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 argentarius*), Bilbies (*Macrotis lagotis*), Bank voles (*Clethrionomys glareolus*), Campbell hamster (*Phodopus campbelli*), Siberian hamster (*Phodopus sungorus*), Golden hamster (*Mesocricetus auratus*), Mountain goats (*Oreamnos americanus*), Cynomolus monkeys (*Macaca fascicularis*), East African mole rat (*Tachyoryctes splendens*), Ringed seal (*Pusa hispida*), Ringed seal (*Phoca hispida*), Large Japanese field mouse (*Apodemus speciosus*), Cynomolus monkey (*Macaca fascicularis*), Slow lorises (*Nycticebus coucang*), Ostriches (*Struthio camelus*), Mountain gorillas (*Gorilla beringei beringei*), Asian house rat (*Rattus norvegicus*), House mouse (*Mus musculus*) | Numerous reports in humans | Chalmers et al., 1997; Hurkova et al., 2003 |
| C. andersoni                      | Bacterian camel (*Camelus bactrianus*), Minor European wisent (*Bison bonasus*), Marmots Campbell hamster (*Phodopus campbelli*), Golden hamster (*Mesocricetus auratus*), Golden takins (*Budorcas taxicolor bedfordi*), Giant panda (*Ailuropoda melanoleuca*), Ostriches (*Struthio camelus*), Mountain gorillas (*Gorilla beringei beringei*), Asian house rat (*Rattus norvegicus*), House mouse (*Mus musculus*) | – | 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 | XIIaA21R11, XIIaA22R9, XIIaA21R10, XIIa20R10, XIIaA19R12, XIIaA22R11 | Dyachenko et al., 2010; Laatamna et al., 2013; Nolan et al., 2013; Kvac et al., 2014a, 2014b; Meredith and Milne, 2000 |
| C. fayeri                         | Southern brown bandicoot (*Isoodon obesulus*), Western-barred bandicoot (*Perameles bougainville*), Koala (*Phascolarctos cinereus*), Red kangaroo (*Macropus rufus*), Eastern grey | Minor | IVA9G4T1R1, IVA9A10, IVA9G1T1, IVA9G1T1, IVA9A12G1T1 | 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 |
| 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) | No reports in humans to date | IXaA4G1T1 | Feng et al., 2011b |
| Opossum genotype I (C. fayeri) | Opossum (Didelphimorphia) | No reports in humans to date | — | Xiao et al., 2002b; Oates et al., 2012 |
| Opossum genotype II | Virginia opossum (Didelphis virginiae) | No reports in humans to date | — | 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; Silverlás et al., 2012; Kurniawan et al., 2013; Adamu et al., 2014; Ryan and Xiao, 2014; Ghaffari and Kanantari, 2014; Sak et al., 2014; Rahmouni et al., 2014; Wang et al., 2014; Stensvold et al., 2015; Vermeulen et al., 2015 |
| C. meleagridis | Mountain gorillas (Gorilla beringei beringei), Brush-tailed rock wallabies (Petrogale penicillata), deermouse (Peromyscus sp.) | Major | IllbA, IlgA (closest match to IlleA13G2R1) | 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; Kvč et al., 2012; Ren et al., 2012; Raskóva et al., 2013; Silva et al., 2013; Swaffer et al., 2014 |
| C. tyzerri | Mice (Mus musculus), Brown rats (Rattus norvegicus), Large-footed bat (Myotis lucifugus), 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 (Panthera pardus), Bobcats (Lynx rufus) | Occasionally reported in humans | IXaA5R2, IXaA6R1, IXaA6R2, IXaA6R3, IXbA6, IXbA6R2 | Power et al., 2004, 2005; Power and Ryan, 2008; Power, 2010; Yang et al., 2011; Nolan et al., 2013 |
| C. macropodum | Red kangaroo (Macropus rufus), Eastern grey kangaroo (Macropus giganteus), Swamp wallaby (Wallabia bicolor), Western grey kangaroos (Macropus fuliginous) | No reports in humans to date | — | Robinson et al., 2011; Helmy et al., 2013; García-Pressedo et al., 2013b; Sak et al., 2013; Qi et al., 2015b; Qin et al., 2014 |
| C. bosis | Yaks, foxes, Gorillas (single report), Roe deer (Capreolus capreolus) | Occasionally reported in humans | — | Feng et al., 2012; Garcia-Pressedo et al., 2013b |
| C. ryanae | Roe deer (Capreolus capreolus), Water buffaloes (Bubalis bubalis) | No reports in humans to date | — | Atwill et al., 2004; Feng et al., 2007, 2011b; Lv et al., 2009 |
| C. wrairi | Gaines pig (Cavia porcellus), California ground squirrels (Spermophilus beecheyi), California ground squirrel (S. adamsi) | No reports in humans to date | VIIaA13T1, VIIaA17T1, VIIaA16T1 | García-Pressedo et al., 2013a; Ng-Hublin et al., 2013; Nemec et al., 2013; Budager et al., 2015; Parsons et al., 2015 |
| C. scrofarum | Asian house rat (Rattus tanezumi), Brown rat (Rattus norvegicus), Eurasian wild boars (Sus scrofa) | Occasionally reported in humans | — | García-Pressedo et al., 2013a; Ng-Hublin et al., 2013; Nemec et al., 2013; Budager et al., 2015; Parsons et al., 2015 |
| C. suis | Chimpanzees (Pan troglodytes schweinfurthii), Eurasian wild boars (Sus scrofa), Rodents | Occasionally reported in humans | — | Nemec et al., 2012, 2013; Budager 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), Fulvous roundleaf bat (Hipposideros fulvus), Lechznauri's rousette (Rousettus leschenaultii) | No reports in humans to date | — | Kwč et al., 2015 |
| Bat genotype III | Big brown bat (Epistesicus fuscus) | No reports in humans to date | — | Kwč et al., 2015 |
| Bat genotype IV | Western barbastelle (Barbastella barbastellus) | No reports in humans to date | — | Feng et al., 2007 |
| Beaver genotype | North American beaver (Castor canadensis) | No reports in humans to date | — | Hill et al., 2008 |
| Brushtail possum I | Brushtail possum (Trichasurus vulpecula) | No reports in humans to date | — | (continued on next page)
### 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 mouse (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., 2015; Guo et al., 2015 |
| **Chipmunk genotype II**         | Eastern chipmunk (Tamias striatus), Black-footed ferret (Mustela nigripes), Red squirrel (Sciurus vulgaris) | No reports in humans to date | – | Lv et al., 2009 |
| **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 (Mustelafer), Siberian chipmunk (Tamias sibiricus), River otters (Lutra 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; Květ 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 II 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 | – | Anwell 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 przewalskii), Four-toed hedgehog (Ateles geoffroyi) | Identified in humans in the UK | VlaA11G3, VlaA13 | Ryan et al., 2003; Robinson et al., 2008; Abe and Matsubara, 2015 |
| **Mink genotype**                | River otter (Lontra canadensis), American minks (Mustela vison), Ermine (Mustela erminea) | Several reports in humans | XaA5G1 | Feng et al., 2007, Wang et al., 2008; Feng et al., 2011b; Ng-Hublin et al., 2013, 2014; 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, Silva et al., 2013 |
| **Mouse genotype III**           | House mouse (Mus musculus) | No reports in humans to date | – | Foo et al., 2007; Silva et al., 2013, Silva et al., 2013 |
| **Muskrat genotype I**           | Muskrat (Ondatra zibethicus), Boreal red-backed voles (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 vulpes), 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 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 vitulina), 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), Humpback seal (Megaptera novaeangliae) | No reports in humans to date | – | Bass et al., 2012 |
| **Seal genotype IV**             | Southern elephant seal (Mirounga leonina) | No reports in humans to date | – | Rengifo-Herrera et al., 2011, 2013 |
| **Shrew genotype**               | Weddel seal (Leptonychotes weddellii) | No reports in humans to date | – | Rengifo-Herrera et al., 2013 |
| **Shrews and genotypes**         | No reports in humans to date | – | – | – |
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 (Appelbee 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 IaA12G3 in Rhesus macaques, subtype IIa17 in Cynomolgus monkeys and Rhesus monkeys and subtype IIA12G2 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 IIA10G2 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, cameldids, equids, canids, non-human primates and marine mammals (Table 2) (Morgan et al., 1995a; 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; Paziweska 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 (Ila to Ilo (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 IlldA15G1, IlldA18G1, IlldA19G1 have been reported from golden takins, lemurs, chipmunks and hamsters, and IlldA15G2R1, IlldA19G2R1, IlldA19G3R1, IlldA19G4R1, IlldA20G4R1, IlldA20G3R2 and IlldA21G3R1 have been reported from deer and Eastern grey kangaroos (Lv et al., 2009; Bodager et al., 2015; Montecinio-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 Iman 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 (Charlimers et al., 2011; Wong and Ong, 2006; Fayer et al., 2010; Gieloszyk 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-Soud et al., 2013; Mi et al., 2013; Murakoshi et al., 2013; Li et al., 2014; Ma et al., 2014; Perec-Matyasi 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, *C. ubiquitum* 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 XIIIb) (Li et al., 2014). However, as persons in the United States usually have little direct contact with wild rodents, the authors 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, felds, suids, giraffidae, 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; Tangtip and Jongwutwes, 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-Brikian et al., 2008; Neira et al., 2012; Hasajov et al., 2014; Petircovcic et al., 2015; Spanakos et al., 2015; Huruova 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 10⁸ *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 × 10⁸ to 4.1 × 10¹⁰ 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 been 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., 2015). Several studies have reported that C. andersoni is the dominant species in source and tap water (Feng et al., 2011; Nicholls 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 mammals, respectively (Lindsay et al., 2000). It has only occasionally been 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., 2015). Several studies have reported that C. andersoni is the dominant species in source and tap water (Feng et al., 2011; Nicholls 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 (Atelurex albiventris) in 1998 (Graczyk et al., 1998). An isolate from a European hedgehog originating from Denmark was typed in 2002 (Enermark 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; Kvác 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; Kvác et al., 2014b). Previously reported C. erinacei isolates include XIIIaA20R10 (KF055453), XIIIaA21R10 (GQ214085), XIIIaA22R9 (KC305644), XIIIaA19R12 (GQ214081), and XIIIaA22R11 (GQ255940) (Kvác et al., 2014b).

3.1.9. Cryptosporidium fayeri and Cryptosporidium macrodum

The two main species identified in a wide range of marsupials are C. fayeri and C. macrodum (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. macrodum 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 km² 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 IVaAG4T1R1, 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. macrodum, 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; Silverlás 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 (IIa to IIg) (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. meleagris          | Turkey (Meleagris gallopavo), Indian ring-necked parrot (Pitucacula kameri), Turkeys, American coot (Fulica americana), Domestic chicken (Gallus gallus), Japanese quail (Coturnix 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 (Symuscius australis), Cocktails (Nymphicus hollandicus), Whooping crane (Grus vipio), Grey-bellied bulbul (Pycnonotus spp.), Black vulture (Coragyps atratus), Saffron finch (Sicalis flaveola), Mixed-bred falcons (Falcoristoculus x Falco cherrug), Red-shelduck (Tadornaferruginea), Red-billed leiothrixes (Leiothrix lutea), Pekin ducks (Anas platyrhynchos), Buff-fronted seedeater (Sporophila frontalis), Java sparrows (Padda oryzivora), Mynas (Acridotheres tristis), Zebra finches (Taeioppygia guttata), Crested Lark (Galerida cristina), Gouldian finch (Chloebia gouldiae), Black-billed magpie (Pica pica), Ostriches (Struthio camelus), Quails (Coturnixcoturnix japonica), Red grouse (Lagopus lagopus scoticus), Red-winged cran (Grus japonensis) | Cloaca, bursa, trachea, Preventriculus | 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; Hamidinajet et al., 2014; Wang et al., 2014; Li et al., 2015c; Maca and Pavlasek, 2015 |
| C. galli              | Chicken (Gallus gallus), Finches (Spermostidae and Fringillidae), Capercaillie (Tetroa argylli), Pine grosbeak (Pinicola enucleator), Turquise parrots (Neopheme pulchella), Cuban flamingo (Phoenicopterus ruber), Rhinoceros hornbill (Bucerorh rhinocerous), Red-cowled cardinal (Paroaria dominicana), Zebra finches (Taeniopygia guttata), Chocolate parson finches (Pephila cincta), Chestnut finches (Lonchura castaneothorax), Painted firetail finches (Ehmsma picta), Canaries (Serinus sp.), Glesters (Serinus canaria), Green-winged saltatros (Saltator similis), Slate-collar seedeater (Sporophila chicasteca), Great-billed seed-fench (Oryzoborus maximiliani), Ultermarine grosbeak (Cyanomopsa brissinai), Bohemian waxywing (Bombycilla garrulus), Silver-eared Mesia (Leiothrix argentans), Cockatiel (Nymphicus hollandicus), Chopi blackbird (Gnorimopsar choji), Green-winged saltator (Saltator similis), Rufous-collared sparrows (Zonotrichia capensis) | – | Ng et al., 2006; Nakamura et al., 2009 |
| Avian genotype I      | Red factor canary (Serinus canaria), Canary (S. canaria), Indian peafowl (Pavo cristatus) | – | Meireles et al., 2006; Ng et al., 2006; Nakamura et al., 2009; Seva et al., 2011; Nguyen et al., 2013 |
| Avian genotype II     | Ecretus (Ecretus roratus), Galah (Elophus roseicapilla), Cockatiel (Nymphicus hollandicus), Major Mitchell Cockatoo (Cacatua lead beater), Ostriches (Struthio camelus), White-eyed parakeet (Aratinga leucophthalma) | – | 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 III    | Galah (Elophus roseicapilla), Cockatiel (Nymphicus hollandicus), Java sparrow (Padda oryzivora), Son canure (Aratinga solstitialis), Peach faced lovebirds (Agapornis roseicollis), Seagull (Laridae sp), Blue-fronted amazon (Amazona australis), Cockatell (Nymphicus hollandicus), Rufous-collared sparrows (Zonotrichia capensis), Lovebird (Agapornis species), Cockatiel (Nymphicus hollandicus) | – | Abe and Makino, 2010; Qi et al., 2011 |
| Avian genotype IV     | Japanese white-eye (Zosterops japonica) | – | Abe and Makino, 2010; Qi et al., 2011 |
| Duck genotype | Black duck (Anas rubripes), Canada geese (Branta canadensis) | – | Jellison 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 Tyyzer 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 anthropoontic and zoonotic transmission routes have been suggested (Cama et al., 2003; Elwin et al., 2012; Silverlas et al., 2012). Subtyping at the gp60 locus has identified seven subtype families (Ila—Ilg) 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 10³ 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 oo-
cysts were cleared within <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 successful, 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 (Pavlasek, 1999, 2001; Ryan et al., 2003; Ng et al., 2006; Ryan and Xiao, 2014). It predominantly infects birds of the family Spernsetidae, Fringillidae 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 Nasto ang, 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 Cryp-
osporidium 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; Cerfard 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 tilapia, 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; Cerfard 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 (Cerfard et al., 2015). In that study, the overall prevalence of Crypto-
osporidium 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 (Cerfard et al., 2015). Histological analysis identified C. parvum...
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 IlA18G3R1 in School whiting from Australia (Reid et al., 2010), three C. parvum subtypes (IlA14G2R1, IlA15G2R1 and IlA19G4R1) 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 IlA15G2R1, IlA16G2R1 and IlA17G2R1 in Arctic char and European whitefish from France (Cerdà 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 Gymnophiona, Cryptosporidium has been only reported in Anura which includes frogs and toads and only one species, C. fragile is recognised (Table 5) (Jirku et al., 2008). In transmission experiments, C. fragile was not infective in one fish species (Poecilia reticulata), four amphibian species (Bufo bufo, Rana temporaria, Litoria caerulea and Xenopus laevis), one species of reptile (Pantherophis guttatus) and SCID mice (Jirku 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. varani (C. saurophillum) (intestinal) (Levine, 1980; Pavlasek et al., 1995; Koudela and Modry, 1998; Pavlasek 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; Diaz 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 iguana) (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...
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; Kväč 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 day⁻¹ (Owings et al., 1977; Boellstorff and Owings, 1995), which when combined with shedding of up to 2 × 10⁹ oocysts animal⁻¹ day⁻¹ results in rates of environmental loading equivalent to 1 × 10⁹ oocysts hectare⁻¹ day⁻¹ (Atwill et al., 2004). Further analysis of squirrel populations however suggests 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

**Table 5**

| Species/genotype | Amphibian/Reptile host species | Site of infection | Reference |
|------------------|-------------------------------|------------------|-----------|
| C. fragile       | Black-spined toads (Duttaphrynus melanostictus) | Stomach | Jirku et al., 2008 |
| C. serpentis     | Amazon tree boa (Corallus hortulanus), Black rat snake (Elaphe obsoleta obsoleta), Bornmuller’s viper (Vipera bornmuelleni), Bull snake (Pituophis melanoleucus melanoleucus), California kingsnake (Lampropeltis getulus californiae), Cornsnake (Elaphe guttata guttata), Common death adder (Acanthophis antarcticus), Desert monitor (Varanus girensis), Eastern/Mainland Tiger snake (Notechis scutatus), Filled lizard (Chlamydosaurus kingii), Giant madagascar or Oustalet’s chameleon (Chamaeleo oustaleti), Leopard gecko (Eublepharis macularius), Mexican black kingsnake (Lampropeltis getulus nigrita), Milk snake (Lampropeltis triangulum), Mountain vipers (Vipera oceanus), Python (Python molurus), Savannah monitor (Varanus exanthematicus), Skink (Mabuya perroteti), Taipan (Oxyuranus scutellatus), Red-tailed boa (Boa constrictor constrictor), Rainbow boa (Epibras cenchria cenchria) | 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 |
| C. varanii       | African fat-tailed gecko (Hemideinae caudicinctus), Leopard gecko (Eublepharis macularius), Boa constrictor (Boa constrictor), Cornsnake (Elaphe guttata guttata), Leopard gecko (Eublepharis macularius), Desert monitor (Varanus girensis), Gecko (Gekkoninae sp.), Green iguana (Iguana iguana), Lampropeltis sp; Louisiana pine snake (Pituophis rutilieni), Plated lizard (Gerrhosaurus sp.), Schneider’s Skink (Zamurex schneideri), Taipan (Oxyuranus scutellatus), Baron’s green racer (Pholidoros baroni), Yellow anaconda (Eunectes notaeus), Cornsnake (Elaphe guttata guttata), Mato Grosso lancehead (Bothrops marxoglossis) | – | Xiao et al., 2004b; Richter et al., 2011, Abe and Matsubara, 2015 |
| Lizard genotype/C. serpents-like | Leopard gecko (Eublepharis macularius), Cornsnake (Pantherophis guttatus), Chinese wonder gecko (Teratoscincus scincus) | – | Xiao et al., 2002b, 2004b, Alves et al., 2005; Pedraza-Díaz et al., 2009; Griffin et al., 2010; Richter et al., 2012 |
| Tortoise genotype I | Indian star tortoises (Geochelone elegans), Hermann’s tortoise (Testudo hermanni), Ball python (Python regius), Russian tortoise (Agrionemys Testudo horsfieldii) | Stomach | Xiao et al., 2000b, 2004b; Alves et al., 2005; Pedraza-Díaz et al., 2009; Griffin et al., 2010; Richter et al., 2012 |
| Tortoise genotype II (D. diurca) | Marginated tortoise (Testudo marginata), Ball python (Python regius), Veiled chameleon (Chamaeleo calyptratus), Pancake tortoise (Malacochersus tornieri), Russian tortoise (Agrionemys Testudo horsfieldii) | Intestine | Traverse et al., 2008; Pedraza-Díaz et al., 2009; Griffin et al., 2010; Traverse, 2010; Richter et al., 2012 |
| Snake genotype I | New Guinea Viper boa (Candoia asper), Japanese grass snakes (Rhodophis tigris) | – | Xiao et al., 2002b, 2004b; Kuroki et al., 2008 |
| Snake genotype II | Boa constrictor (Boa constrictor ontoni) | – | Xiao et al., 2004b |
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 10²) (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; Racki 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 ddPCR 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 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 informative data for modelling and quantitative microbial risk assessments (QMRA) of wildlife in various catchments.

Conflict of interest
None.

Acknowledgements
The authors are grateful for funding for our current Cryptosporidium research from the Australian Research Council Linkage Grant number LP130100035.

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