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Cryptosporidium and *Giardia* in cats and dogs: What is the real zoonotic risk?

Amanda D. Barbosa [a,b,*], Siobhon Egan [a], Yaoyu Feng [c], Lihua Xiao [c], Una Ryan [a]

[a] Harry Butler Institute, Vector- and Water-Borne Pathogen Research Group, Murdoch University, Murdoch, Western Australia, 6150, Australia
[b] CAPES Foundation, Ministry of Education of Brazil, Brasilia, DF, 70040-020, Brazil
[c] Guangdong Laboratory for Lingnan Modern Agriculture, Center for Emerging and Zoonotic Diseases, College of Veterinary Medicine, South China Agricultural University, Guangzhou, 510642, China

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ABSTRACT

Due to the close bond between humans and companion animals, a thorough understanding of the diversity of *Cryptosporidium* species and *Giardia* assemblages in cats and dogs is essential to determine the potential zoonotic risks. Analysis of molecular studies shows that *C. felis* and *C. canis* are the main species infecting cats and dogs, respectively. These species are largely host-specific, as despite intense association with humans, prevalence of *C. felis* and *C. canis* in humans is low and predominantly in immunocompromised individuals and low-income countries. There have been reports of *C. parvum* in cats and dogs and two reports of *C. hominis* in dogs. In most studies conducted to date, however, the prevalence of zoonotic species was low and may be associated with coprophagy and or/spillback, but this remains to be determined. Results of subtyping studies suggest that for *C. felis* and *C. canis*, some zoonotic transmission may occur but host-adapted subtypes also exist. *Giardia duodenalis* assemblages C and D are commonly reported in dogs, with assemblages F and A most common in cats. Assemblages C, D and F are largely host-specific as there are only a handful of reports of them in humans. Reports of assemblage A and B in cats and dogs may be due to coprophagy or spillback from owners. Despite the extent of pet ownership and the close contact between humans and companion animals worldwide, the overall risk of zoonotic transmission from cats and dogs to humans is uncertain but thought to be low due to *C. canis*, *C. felis* and *G. duodenalis* assemblages C, D and F being predominantly host-specific, the relatively low prevalence of *C. parvum* (and *C. hominis*) in cats and dogs (which may be due to mechanical carriage), and low oo/cyst shedding. Carefully designed epidemiological studies of cats and dogs and their owners using subtyping tools are essential to better quantify the extent of spillover and spillback of *Cryptosporidium* and *Giardia* between pets and their owners.

1. Introduction

Humans and their companion animals, particularly cats and dogs, have had a long and close association over many centuries and provide a wide variety of benefits to their owners and foster carers including increased physical activity, companionship and improvements in mental health (Martins et al., 2023; Zablan et al., 2023). Cat and dog ownership also increases connections with family members and the wider community (Wood et al., 2015), with higher wellbeing and trust, reduced anxiety and reduced screen time particularly in adolescents (Charmaraman et al., 2022; Koyasu et al., 2023).

Pet owner behaviours such as sleeping with pets, allowing pets to lick faces and hands, insufficient/infrequent hand-washing, and feeding raw meat to cats and dogs, can promote the transmission of a variety of zoonotic pathogens from pets to humans. These include *Salmonella* (Davies et al., 2019), antimicrobial resistant bacteria (Jin et al., 2023), ectoparasites and associated zoonotic pathogens (Tahir et al., 2019; Saleh et al., 2021; Mateo et al., 2023), *Toxocara* (Patterson, 2023) and other helminths (Overgaauw et al., 2020; Mateo et al., 2023), and enteric protozoa such as *Cryptosporidium* and *Giardia* (Cai et al., 2021; Meng et al., 2021).

Cryptosporidium oocysts and *Giardia* cysts are immediately infectious when shed in faeces and are environmentally robust (Cai et al., 2021; Ryan et al., 2021a). Transmission of *Cryptosporidium* and *Giardia* in cats and dogs is *via* faecal-oral contamination through coprophagy or ingestion of contaminated food or water. Although frequently

* Corresponding author. Harry Butler Institute, Vector- and Water-Borne Pathogen Research Group, Murdoch University, Murdoch, Western Australia, 6150, Australia.
E-mail address: A.DuarteBarbosa@murdoch.edu.au (A.D. Barbosa).

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asymptomatic in adult cats and dogs, *Cryptosporidium* and *Giardia* can both cause watery diarrhoea, abdominal pain and vomiting in both humans and young pets (Cai et al., 2021; Li et al., 2021a; Ryan et al., 2021a). Fenbendazole and metronidazole are commonly used to treat clinical giardiasis in cats and dogs, but have poor efficacy (Kaufmann et al., 2022). There is no registered treatment available for cryptosporidiosis in cats and dogs (ESCCAP, 2018). Mixed infections with *Giardia* and *Cryptosporidium* and other enteropathogens are common in both dogs and cats, particularly in dogs (Hamnes et al., 2007; Pallant et al., 2015; Xu et al., 2016; Gil et al., 2017; Sommer et al., 2018; López-Arias et al., 2019; Nagamori et al., 2020; Mateo et al., 2023; Murnik et al., 2023).

The 18S ribosomal RNA (rRNA) is the most commonly used locus for identifying *Cryptosporidium* to species level, while the glycoprotein 60 gene (*gp60*) is most widely used for subtyping (Ryan et al., 2021a; Yang et al., 2021). Over 49 *Cryptosporidium* species have been identified to date, with *C. hominis* and *C. parvum* responsible for ~95% of human infections (Ryan et al., 2021a).

Human infections with *Giardia* are caused by *Giardia duodenalis*, a multi-species complex, consisting of eight assemblages. Assemblages A and B predominantly infect humans, assemblages C and D infect mostly dogs, assemblage F infects mainly cats, assemblage G infects rodents and assemblage H infects pinnipeds (Cai et al., 2021; Ryan et al., 2021a). The most commonly used typing loci for *Giardia* are the betagiardin (*bg*), glutamate dehydrogenase (*gdh*), triosephosphate isomerase (*tpi*) genes, and the 18S rRNA locus (Cai et al., 2021; Ryan et al., 2021a). Multilocus sequence typing (MLST) of the *bg*, *gdh* and *tpi* genes has identified three sub-assemblages within assemblage A: sub-assemblage AI (predominantly in livestock, companion animals and some humans); AII (predominantly in humans); and AIII (in wild ruminants) (Cai et al., 2021). In contrast, sub-assemblages within assemblage B, cannot be reliably determined with the currently used loci (Cai et al., 2021).

Due to the close relationship between humans and companion animals, a thorough understanding of the diversity of *Cryptosporidium* species and *Giardia* assemblages in cats and dogs is essential to determine their zoonotic risk and public health implications. This review analyses *Cryptosporidium* species and *Giardia* assemblages reported in cats and dogs globally, and discusses the zoonotic risk posed by the *Cryptosporidium* species and *Giardia* assemblages identified. The majority of the > 350 publications on *Cryptosporidium* and *Giardia* in cats and dogs have been epidemiological surveys, with molecular tools used in more recent years, enabling researchers to type the pathogens to species and subtype level. This review centers on the findings and discussions emerging from these molecular studies.

2. *Cryptosporidium* in cats and dogs

Generally, the overall prevalence of *Cryptosporidium* in cats and dogs globally is < 10%. However, some studies using microscopy and immunological-based detection methods have reported higher prevalences (> 20%) (e.g. Cirak and Bauer, 2004; Hamnes et al., 2007; Ferreira et al., 2017). A recent systematic review of the prevalence of *Cryptosporidium* in cats reported the mean prevalence by microscopy, coproantigens and molecular tools to be 4.2%, 8.2%, and 5.0%, respectively, with an overall mean prevalence of 6% (Meng et al., 2021). In dogs, the overall mean prevalence has been reported at 8% using microscopic detection, 7% using coproantigen detection and 6% using molecular diagnostic methods (Taghipour et al., 2020). For a more complete overview of all studies including microscopy-based analyses, refer to Li et al. (2021a).

Cryptosporidium felis and *C. canis* are the main species infecting cats and dogs globally, respectively (Lucio-Forster et al., 2010; Li et al., 2021a; Meng et al., 2021; Ryan et al., 2021b) (Tables 1 and 2). *Cryptosporidium felis* and *C. canis* are also among the top five *Cryptosporidium* species infecting humans, predominantly in low-income countries (Yang et al., 2021). In cats, in addition to *C. felis,* there have also been some reports of *C. parvum*, *C. canis*, *C. muris*, *C. ryanae*, and rat genotypes III and IV. In dogs, *C. hominis*, *C. parvum*, *C. andersoni*, *C. muris*, *C. scrofarum*, *C. meleagridis*, *C. ubiquitum*, and rat genotypes III and IV have been reported occasionally, in addition to *C. canis*. Many of these species are zoonotic and are listed in Tables 1 and 2. *Cryptosporidium ryanae* and rat genotype III were reported in one and six cats, respectively, in Australia (Yang et al., 2015), most likely due to coprophagy, and rat genotype IV was reported in a single cat in China (Li et al., 2019a). The zoonotic status of *C. andersoni* is uncertain (Yang et al., 2021) and it has not been included in Table 2, but there has been a single report of *C. andersoni* (0.1%; 1/676) in a shelter dog in the UK (Rosanowski et al., 2018). Young age, presence of diarrhoea, and living in pet shops and shelters are risk factors associated with *Cryptosporidium* infection in cats and dogs (Li et al., 2021a; Mateo et al., 2023).

There have been several reports of *C. parvum* in cats involving mostly single reports in individual cats from various countries (Table 1). There have also been a few reports of *C. muris* and rat genotypes III and IV in cats, which may be due to mechanical carriage from ingesting rodents or an accidental infection (Table 1). *Cryptosporidium muris* oocysts from a cat have been shown to be infective to laboratory mice (Pavlásek and Ryan, 2007), indicating that they may retain viability following passage through a cat. Another study indicated that *C. muris* was infectve to cats, as DNA sequencing of paraffin-embedded sections of intestinal and stomach biopsies from a cat with persistant diarrhoea detected *C. muris* in the stomach and *C. felis* in the intestine (FitzGerald et al., 2011). A follow-up study 12 months later on the same cat, detected *C. muris*-like oocysts from endoscopic biopsies but *C. felis* oocysts were not identified (FitzGerald et al., 2011). The identification of *C. muris* and other rodent genotypes in cats is likely due to frequent contact between cats and rodents, with the study by FitzGerald et al. (2011) showing *C. muris* can infect the gastric mucosa of cats. A previous cross-transmission study also reported that cats were "highly susceptible" to *C. muris*, whereas dogs had low susceptibility (Iseki et al., 1989). There has been one report of *C. canis* in one cat, which is likely due to mechanical carriage (Table 1).

There have only been two reports of *C. hominis* in dogs; one in a wild dog in Sydney catchments in Australia (Ng et al., 2011) and the other in a shelter dog faecal sample in Spain (Gil et al., 2017). The parasite was identified by PCR and sequencing at the 18S locus, but in both cases, amplification at the *gp60* locus was not successful (Ng et al., 2011; Gil et al., 2017), suggesting that oocyst numbers were low and may have been present due to coprophagy of human faeces. There have been several reports of *C. parvum* in dogs, with the highest prevalence (10%; 5/50) reported in household dogs in Egypt (Gharieb et al., 2018), and in two puppies with diarrhoea in Egypt (10%; 2/20) (El-Madawy et al., 2010). Another study in Thailand reported *C. parvum* in 6.4% (7/109) of dogs (31.8% of the 22 typed samples) (Tangtrongsup et al., 2017) (Table 2). In the majority of other studies, the prevalence of *C. parvum* has been low (0.3–2.9%) (Table 2).

Only a few studies have subtyped the *C. parvum* detected in dogs. Among them, subtypes IIaA15G2R1 and IIaA17G2R1 have been detected in dogs in the UK (Smith et al., 2010; Rosanowski et al., 2018), and subtype IIaA15G2R1 in dogs in Germany (Murnik et al., 2022). These are common subtypes in cattle and humans (Feng and Xiao, 2017; Holzhausen et al., 2019; Santín, 2020; Guo et al., 2021, 2022; Yang et al., 2021). In the study by Smith et al. (2010), IIaA17G2R1 was detected in the single farm dog sampled, and was the dominant subtype detected in cattle on the farm. Epidemiological analysis indicates that dogs are at a higher risk of being infected with *C. parvum* from cattle when living in areas on or near cattle farms (Moreira et al., 2018). In the study of shelter dogs in the UK (Rosanowski et al., 2018), the authors reported that "some of the dogs arriving at the shelter, may have been roaming as strays prior to submission, with the potential that the environment was more contaminated than for owned dogs". The study in Germany, which identified IIaA15G2R1 in two dogs (Murnik et al., 2022), was conducted in Saxony, and IIaA15G2R1 was the most

Table 1
Zoonotic *Cryptosporidium* and *Giardia* species and assemblages identified in cats globally.

Species/Assemblage	Hosts	Prevalence	Country	Reference
Cryptosporidium				
C. felis	Domestic cats	1.3% (2/162)	Australia	Sargent et al. (1998)
	Domestic cat	–	Australia	Morgan et al. (1998)
	Shelter & domestic cats	1.7% (18/1063)	Australia	Palmer et al. (2008a, b)
	Various	2.3% (8/345)	Australia	Yang et al. (2015)
	Domestic cats	1.7% (5/298)	Austria	Hinney et al. (2015)
	Shelter cats	1.5% (2/130)	Austria	Joachim et al. (2023)
	Cryptosporidium-positive domestic cats	100% (7/7)	Brazil	Thomaz et al. (2007)
	Domestic cats	6.1% (3/49)	Brazil	Alves et al. (2018)
	Domestic cats	5.4% (3/55)	Brazil	de Oliveira et al. (2021)
	Various	1.9% (1/52)	China	Li et al. (2015)
	Domestic cats	3.8% (6/160)	China	Xu et al. (2016)
	Domestic cats	2.3% (8/346)	China	Li et al. (2019b)
	Wide range	5.0% (21/418)	China	Li et al. (2019a)
	Domestic cats	0.6% (1/171)	China	Wang et al. (2021)
	Domestic cat	10.9% (5/46)	Colombia	Santín et al. (2006)
	Domestic cats	100% (1/1)	Czech Republic	Hajdušek et al. (2004)
	Domestic & stray cats	4.3% (11/255)	Czech Republic, Poland, Slovakia	Kváč et al. (2017)
	Domestic cats	2.8% (9/317)	Denmark	Enemark et al. (2020)
	Domestic cats	0.7% (1/134)	Egypt	Elmahallawy et al. (2023)
	Domestic & shelter cats	1.5% (4/264)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	1.4% (2/140)	Iran	Ranjbar et al. (2018)
	Domestic dogs	0.6% (2/300)	Iran	Homayouni et al. (2019)
	Stray cats	5.3% (7/132)	Iran	Karimi et al. (2023)
	Shelter cats	1.5% (1/65)	Italy	Gil et al. (2017)
	Domestic dogs	0.1% (1/705)	Italy	Simonato et al. (2017)
	Domestic cats	1.8% (19/1079)	Japan	Yamamoto et al. (2009)
	Domestic cats	12.7% (7/55)	Japan	Yoshiuchi et al. (2010)
	Domestic & pet shop cats	1.4% (4/286)	Japan	Ito et al. (2017)
	Domestic cats	1.0% (1/101)	Poland	Piekara-Stępińska et al. (2021)
	Shelter cats	0.6% (1/158)	South Korea	Kwak and Seo (2020)
	Domestic cats	2.9% (1/34)	Spain	de Lucio et al. (2017)
	Temple cats	2.5% (2/80)	Thailand	Koompapong et al. (2014)
	Domestic & shelter cats	1.5% (1/66)	Thailand	Tangtrongsup et al. (2020)
	Stray cats	3.0% (12/399)	Turkey	Köseoğlu et al. (2022)
	Cat colony cats	100% (18/18)	USA	Fayer et al. (2006)
	Domestic cats	4.8% (12/250)	USA	Ballweber et al. (2009)
C. parvum	Domestic cats	2.0% (1/49)	Brazil	Alves et al. (2018)
	Domestic cat	100% (1/1)	Chile	Neira et al. (2010)
	Various	1.9% (1/52)	China	Li et al. (2015)
	Wide range	0.7% (3/418)	China	Li et al. (2019a)
	Domestic cats	14.3% (1/7)	Costa Rica	Scorza et al. (2011)
	Domestic cats	3.7% (5/134)	Egypt	Elmahallawy et al. (2023)
	Domestic cats	5.3% (1/19)	Germany	Sotiriadou et al. (2013)
	Domestic & shelter cats	1.5% (1/66)	Thailand	Tangtrongsup et al. (2020)
C. canis	Domestic cats	3.0% (1/133)	Iran	Karimi et al. (2023)
C. muris	Domestic cat	100% (1/1)	Australia	FitzGerald et al. (2011)
	Various	0.3% (1/345)	Australia	Yang et al. (2015)
	Wide range	0.3% (1/418)	China	Li et al. (2019a)
	Domestic cat	2.2% (1/46)	Colombia	Santín et al. (2006)
	Domestic cat	100% (1/1)	Czech Republic	Pavlásek and Ryan (2007)
Giardia				
Assemblage A	*Giardia*-positive cats	33.3% (6/18)	Australia	Read et al. (2004)
	Various	0.3% (1/345)	Australia	Yang et al. (2015)
	Domestic cats	1.3% (4/298)	Austria	Hinney et al. (2015)
	Shelter cats	1.5% (2/130)	Austria	Joachim et al. (2023)
	Giardia-positive domestic cats	42.1% (8/19)	Brazil	Souza et al. (2007)
	Domestic cats	100% (1/1)	Brazil	Volotão et al. (2007)
	Giardia-positive domestic cats	61.5% (8/13)	Canada	McDowall et al. (2011)
	Various	3.6% (8/219)	Canada	Hoopes et al. (2015)
	Stray cats	7.8% (8/102)	China	Zheng et al. (2015)
	Domestic cats	1.2% (2/160)	China	Xu et al. (2016)
	Stray cats	2.8% (3/104)	China	Pan et al. (2018)
	Wide range	0.3% (1/418)	China	Li et al. (2019a)
	Domestic cats	0.3% (1/346)	China	Li et al. (2019b)
	Domestic cats	28.6% (2/7)	Costa Rica	Scorza et al. (2011)
	Giardia-positive domestic cats	5.5% (1/18)	Czech Republic	Lecová et al. (2020)
	Domestic cats	2.5% (8/317)	Denmark	Enemark et al. (2020)
	Giardia-positive cats	43.0% (68/158)	Europe	Sprong et al. (2009)
	Domestic cats	10.5% (2/19)	Germany	Sotiriadou et al. (2013)
	Domestic cats	1.4% (2/145)	Germany	Sommer et al. (2018)
	Domestic & shelter cats	2.3% (6/264)	Greece	Kostopoulou et al. (2017)
	Kennel cat	100% (1/1)	Italy	Berrilli et al. (2004)
	Stray & domestic cats	37.0% (10/27)	Italy	Papini et al. (2007)

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Table 1 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Domestic cats	1.7% (3/181)	Italy	Paoletti et al. (2011)
	Domestic cats	9.0% (14/156)	Italy	Zanzani et al. (2014)
	Sheltered cats	1.5% (1/65)	Italy	Gil et al. (2017)
	Stray cats	27.8% (37/133)	Italy	Guadano Procesi et al. (2022)
	Giardia-positive cats	100% (3/3)	Italy, Croatia	Cacciò et al. (2008)
	Cats from cat café's and petshops	0.6% (2/321)	Japan	Suzuki et al. (2011)
	Giardia-positive domestic cat	100% (1/1)	Mexico	Ponce-Macotela et al. (2002)
	Various	1.0% (2/200)	Mexico	Veyna-Salazar et al. (2023)
	Domestic cats	1.6% (1/60)	Netherlands	Overgaauw et al. (2009)
	Domestic cats	3.0% (1/33)	Poland	Piekarska et al. (2016)
	Household & kennel cats	9.0% (2/22)	Portugal	Ferreira et al. (2011)
	Giardia-positive cats	27.7% (5/18)	Sweden	Lebbad et al. (2010)
	Domestic & shelter cats	1.5% (1/66)	Thailand	Tangtrongsup et al. (2020)
	Domestic cats	3.3% (4/122)	UK	Krumrie et al. (2022)
	Domestic cats	2.4% (6/250)	USA	Vasilopulos et al. (2007)
	Giardia-positive domestic cats	32.4% (12/37)	USA	Saleh et al. (2019)
Assemblage B	*Giardia*-positive cats	11.1% (2/18)	Australia	Read et al. (2004)
	Giardia-positive domestic cats	7.7% (1/13)	Canada	McDowall et al. (2011)
	Domestic cats	3.7% (6/160)	China	Xu et al. (2016)
	Giardia-positive cats	1.9% (3/158)	Europe	Sprong et al. (2009)
	Domestic & shelter cats	0.4% (1/264)	Greece	Kostopoulou et al. (2017)
	Stray cats	0.7% (1/132)	Iran	Karimi et al. (2023)
	Symptomatic cats	29.4% (30/102)	Turkey	Sursal et al. (2020)
	Domestic cats	8.0% (8/100)	Turkey	Önder et al. (2021)
	Domestic cats	3.3% (4/122)	UK	Krumrie et al. (2022)
Assemblage C	*Giardia*-positive cats	11.1% (2/18)	Australia	Read et al. (2004)
	Stray cats	1.0% (1/102)[b]	China	Zheng et al. (2015)
	Domestic cats	1.3% (2/160)	China	Xu et al. (2016)
	Domestic cats	9.0% (1/11)	China	Liu et al. (2017)
	Giardia-positive cats	3.2% (5/158)	Europe	Sprong et al. (2009)
	Domestic & shelter cats	0.4% (1/264)	Greece	Kostopoulou et al. (2017)
	Domestic cats	1.4% (2/146)	Italy	Mancianti et al. (2015)
	Domestic & shelter cats	6.1% (4/66)	Thailand	Tangtrongsup et al. (2020)
Assemblage D	*Giardia*-positive cats	38.8% (7/18)	Australia	Read et al. (2004)
	Shelter & domestic cats	0.1% (1/1063)	Australia	Palmer et al. (2008a, b)
	Domestic cats	0.6% (1/160)	China	Xu et al. (2016)
	Giardia-positive cats	1.9% (3/158)	Europe	Sprong et al. (2009)
	Domestic cats	1.9% (3/156)	Italy	Zanzani et al. (2014)
	Domestic cats	80.0% (8/10)	Romania	Adriana et al. (2016)
	Domestic & shelter cats	1.5% (1/66)	Thailand	Tangtrongsup et al. (2020)
Assemblage E	*Giardia*-positive cats	5.5% (1/18)	Australia	Read et al. (2004)
	Giardia-positive cats	1.3% (2/158)	Europe	Sprong et al. (2009)
	Giardia-positive cats	5.5% (1/18)	Sweden	Lebbad et al. (2010)
Assemblage F	Shelter & domestic cats	0.7% (7/1063)	Australia	Palmer et al. (2008a, b)
	Various	2.6% (9/345)	Australia	Yang et al. (2015)
	Domestic cats	3.3% (10/298)	Austria	Hinney et al. (2015)
	Shelter cats	7.7% (10/130)	Austria	Joachim et al. (2023)
	Giardia-positive domestic cats	57.9% (11/19)	Brazil	Souza et al. (2007)
	Various	1.9% (1/52)	China	Li et al. (2015)
	Stray cats	1.0% (1/102)	China	Zheng et al. (2015)
	Domestic cats	4.4% (7/160)	China	Xu et al. (2016)
	Domestic cats	9.0% (1/11)	China	Liu et al. (2017)
	Stray cats	2.8% (3/104)	China	Pan et al. (2018)
	Domestic cats	2.6% (9/346)	China	Li et al. (2019b)
	Wide range	3.3% (14/418)	China	Li et al. (2019a)
	Domestic cats	1.2% (2/171)	China	Wang et al. (2021)
	Domestic cats	6.3% (1/16)	China	Wu et al. (2022)
	Domestic cats	6.5% (3/46)	Columbia	Santín et al. (2006)
	Giardia-positive domestic cats	88.8% (16/18)	Czech Republic	Lecová et al. (2020)
	Domestic & stray cats	6.3% (16/255)	Czech Republic, Poland, Slovakia	Kváč et al. (2017)
	Domestic cats	0.6% (2/317)	Denmark	Enemark et al. (2020)
	Giardia-positive cats	48.7% (77/158)	Europe	Sprong et al. (2009)
	Domestic cats	9.6% (14/145)	Germany	Sommer et al. (2018)
	Domestic & shelter cats	2.3% (6/264)[a]	Greece	Kostopoulou et al. (2017)
	Domestic cats	1.0% (3/300)	Iran	Homayouni et al. (2019)
	Stray cats	0.7% (1/132)	Iran	Karimi et al. (2023)
	Giardia-positive cat	100% (1/1)	Italy	Lalle et al. (2005a)
	Domestic cats	2.8% (5/181)	Italy	Paoletti et al. (2011)
	Domestic cats	6.2% (9/146)	Italy	Mancianti et al. (2015)
	Shelter cats	1.5% (1/65)	Italy	Gil et al. (2017)
	Giardia-positive cat	100% (1/1)	Japan	Itagaki et al. (2005)
	Domestic cats	1.8% (1/55)	Japan	Yoshiuchi et al. (2010)
	Cats from cat café's and petshops	6.2% (20/321)	Japan	Suzuki et al. (2011)
	Domestic cats	12.1% (4/33)	Poland	Piekarska et al. (2016)
	Shelter cats	3.8% (6/158)	South Korea	Kwak and Seo (2020)
	Domestic cats	5.9% (2/34)	Spain	de Lucio et al. (2017)

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Table 1 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Giardia-positive cats	66.6% (12/18)	Sweden	Lebbad et al. (2010)
	Domestic cats	31.1% (38/122)	UK	Krumrie et al. (2022)
	Cat colony cats	44.4% (8/18)	USA	Fayer et al. (2006)
	Domestic cats	4.4% (11/250)	USA	Vasilopulos et al. (2007)
	Giardia-positive cat	100% (1/1)	USA	Miska et al. (2009)
	Giardia-positive domestic cats	56.7% (21/37)	USA	Saleh et al. (2019)
Mixed F and A	*Giardia*-positive domestic cats	30.8% (4/13)	Canada	McDowall et al. (2011)
	Domestic & shelter cats	1.5% (4/264)	Greece	Kostopoulou et al. (2017)
	Giardia-positive domestic cats	10.8% (4/37)	USA	Saleh et al. (2019)
Other mixtures	Stray cats	A + B (n = 2)	Italy	Guadano Procesi et al. (2022)

[a] 4 samples typed as assemblage A at 18S locus.

prevalent subtype in calves in the same area in a previous study (Holzhausen et al., 2019). In another study, *C. parvum* subtype IIcA5G3b was identified in two street dogs in Nigeria (Ayinmode et al., 2018b). The *C. parvum* IIc subtype family almost exclusively infects humans (Yang et al., 2021), suggesting that its presence in dogs may have been due to coprophagy of human faeces by the dogs.

There have been two reports of *C. muris* in dogs (Table 2). Oocysts of *C. muris* directly isolated from the stomach of infected mice have previously been orally inoculated in dogs with very few oocysts (7–12) detected between 7 and 12 days post-infection, and a few *C. muris* life-cycle stages were identified in the gastric mucosa of one dog (Aydin and Ozkul, 1996). These findings suggest that dogs may not be a natural host of *C. muris*, which is consistent with a study by Iseki et al. (1989). In one study in Texas, *Cryptosporidium* antigens were detected in 70% (49/70) of kennel dogs (Lupo et al., 2008), with six of the positives being amplified at the 18S locus and identified as *C. muris* and "*C. muris*-like". Oocysts were also identified in these six samples (Lupo et al., 2008). The actual prevalence of *C. muris* in the study remains unknown, but the reported 70% prevalence is likely an over-estimate, as there have been numerous reports of false positives by *Cryptosporidium* enzyme antigen tests, especially considering the fact that most coproantigen kits are not expected to detect *C. muris* (CDC, 1999; Doing et al., 1999; Katanik et al., 2001).

There has also been a single report of *C. scrofarum* in one shelter dog in Greece (Kostopoulou et al., 2017), *C. meleagridis* in a domestic dog in the Czech Republic, and *C. ubiquitum* and rat genotype IV in individual dogs in China (Li et al., 2019a). These are all likely due to coprophagy.

Cryptosporidium oocyst shedding from cats and dogs appears to be low (Asahi et al., 1991; Cox et al., 2005; Hamnes et al., 2007; Labana et al., 2018; Smith et al., 2020). For example, oocyst concentrations ranging from 0 to 17 and 0–5000 oocysts per gram of faeces (OPG) have been reported in cats and dogs, respectively, using direct immunofluorescence microscopy (DFA) (Cox et al., 2005). A more recent larger study of 869 dogs reported median *Cryptosporidium* oocyst excretion of 3.8×10 OPG using DFA (Smith et al., 2020). In comparison, livestock, particularly cattle, shed much higher numbers of oocysts, with calves shedding $> 5.5 \times 10^6$ oocysts per day and $> 3 \times 10^{10}$ oocysts over a 6-day period (Nydam et al., 2001). Infected lambs can shed up to 3.7×10^9 OPG (Yang et al., 2014), while humans can shed up to 10^8 oocysts in a single bowel movement (Goodgame et al., 1993).

3. *Giardia* in cats and dogs

The prevalence of *Giardia* in cats (~1.3–44.4%) and dogs (~1–57.9%) varies widely but is generally < 10% (Feng and Xiao, 2011; Bouzid et al., 2015; López-Arias et al., 2019; Nagamori et al., 2020; Cai et al., 2021; Sui et al., 2022) (Tables 1 and 2). In one meta-analysis, the global prevalence of *Giardia* was calculated at 2.61% (112,513/4,309,451) in dogs and 2.33% (5807/248,195) in cats (Bouzid et al., 2015). In China, the overall prevalence of *Giardia* in dogs has been estimated at 12.3% by molecular testing (Zhao et al., 2022). Factors that influence the prevalence of *Giardia* include age, presence of diarrhoea, socioeconomic situation, and origin of the samples (e.g. household pets *versus* kennel/shelter dogs/cats) and the number of doses of anthelmintic administered each year (Bugg et al., 1999; Bouzid et al., 2015; Cai et al., 2021; French et al., 2023; Murnik et al., 2023).

The highest prevalence of *Giardia* in dogs and cats has been reported from young animals (< 6 months) (Bouzid et al., 2015), in dogs from low- to middle-income areas, and from kennel/shelter dogs, where the potential for transmission is greater due to high densities of animals, continuous environmental contamination and frequent introduction of new animals. For example, the overall prevalence of *Giardia* in dogs was 44.4% (16/36) (Kuthyar et al., 2021) in Argentina, and 41.1% (69/168) in shelter dogs in Italy (Agresti et al., 2021). In another study from Spain, the highest prevalence was detected in breeding (45.8%; 11/24) and shelter dogs (40.4%; 88/218) (Adell-Aledon et al., 2018). In China, a recent study reported a prevalence of 40.3% (60/149) in shelter dogs compared to only 3.0% (6/199) in household dogs (Liao et al., 2020). Similarly in Portugal, 47.0% (23/49) of kennel dogs were *Giardia*--positive, but household dogs (n = 97) were negative (Ferreira et al., 2011). In cats, in one study in Italy, an overall prevalence of 37% (10/27) was reported for stray and domestic cats and all were assemblage A (Papini et al., 2007), and in the USA, 44.4% of colony cats were positive for *Giardia* (Fayer et al., 2006). However, another study reported similar prevalences of *Giardia* in shelter/breeding cats and household cats (Sommer et al., 2018).

Microscopy-based screening studies generally under-report the prevalence of *Giardia* due to sporadic shedding of cysts and the poor sensitivity of flotation assays and miscoscopy (Thompson, 2004). Many of the studies conducted the initials screens for *Giardia* by microscopy and then genotyped the positives samples, which can also underestimate the true prevalence. For example, one study detected *Giardia* in 57.9% (165/285) of kennel dogs by qPCR analysis of the 18S rRNA gene, compared to only 14.6% (39/268) detected by microscopy (Simonato et al., 2015). However, of the qPCR-positive samples, only 64% (106/165) were confirmed by nested PCR, and of these, only 74.5% (79/106) produced sequences (Simonato et al., 2015), emphasising the importance of sequencing to confirm positives.

Assemblages C and D are the most commonly reported *Giardia* in dogs, while assemblages F and A are most common in cats (Tables 1 and 2) (Ramírez-Ocampo et al., 2017; Cai et al., 2021; Zhao et al., 2022). In addition to assemblages C and D, assemblages A, B, E and F have also been reported in dogs. Similarly, assemblages B, C, D and occasionally E have also been reported in cats (Tables 1 and 2). Although assemblages C and D dominate in dogs, assemblages A and B (which infect humans) have also been detected. The detection of assemblages A and B in dogs and cats is thought to be mainly due to coprophagy and/or spill-back from human contact (Feng and Xiao, 2011; Cai et al., 2021), but this remains to be conclusively determined.

Despite the presence of host-adapted assemblages, assemblages A and B are common in cats and dogs (Tables 1 and 2). Between them, studies conducted in China revealed that assemblage A was the dominant assemblage in stray cats and dogs (Pan et al., 2018), and in police and farm dogs (92.6% of typed isolates; 25/27) (Li et al., 2013).

Table 2
Zoonotic *Cryptosporidium* and *Giardia* species and assemblages identified in dogs globally.

Species/Assemblage	Hosts	Prevalence	Country	Reference
Cryptosporidium				
C. canis	Shelter & domestic dogs	0.3% (4/1400)	Australia	Palmer et al. (2008a,b)
	Wild dogs	20.5% (9/44)	Australia	Ng et al. (2011)
	Wild dogs	3.1% (1/32)	Australia	Nolan et al. (2013)
	Wild dogs	100% (2/2)	Australia	Zahedi et al. (2018)
	Cryptosporidium-positive dogs	100% (5/5)	Australia, USA	Morgan et al. (2000b)
	Cryptosporidium-positive domestic dogs	100% (9/9)	Brazil	Thomaz et al. (2007)
	Domestic dogs	3.1% (4/128)	Brazil	Alves et al. (2018)
	Domestic dogs	4.7% (3/64)	Brazil	de Oliveira et al. (2021)
	Domestic, shelter & pet shop dogs	1.9% (4/209)	Canada	Uehlinger et al. (2013)
	Various	1.7% (5/294)	Canada	Julien et al. (2019)
	Domestic dogs	0.3% (3/860)	Canada	Smith et al. (2020)
	Various	3.8% (29/770)	China	Jian et al. (2014)
	Domestic dogs	1.6% (5/315)	China	Gu et al. (2015)
	Domestic dogs	8.0% (39/485)	China	Xu et al. (2016)
	Dogs with diarrhoea	4.1% (20/485)	China	Yu et al. (2018)
	Various	2.9% (19/651)	China	Liao et al. (2020)
	Domestic dogs	4.6% (12/262)	China	Wang et al. (2021)
	Domestic dogs	1.6% (10/604)	China	Cao et al. (2022)
	Domestic dogs	1.8% (4/218)	Egypt	Elmahallawy et al. (2023)
	Stray & domestic dogs	5.0% (15/300)	Egypt	Khalifa et al. (2023)
	Domestic dogs	2.0% (3/150)	Finland	Rimhanen-Finne et al. (2007)
	Domestic dogs	2.6% (3/116)	France	Osman et al. (2015)
	Domestic dogs	9.4% (33/349)	Germany	Murnik et al. (2022)
	Domestic & shelter dogs	0.2% (2/807)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	0.6% (2/315)	Iran	Homayouni et al. (2019)
	Kennel & domestic dogs	0.4% (1/240)	Italy	Giangaspero et al. (2006)
	Kennel dogs	1.0% (3/285)	Italy	Simonato et al. (2015)
	Domestic dogs	0.1% (1/705)	Italy	Simonato et al. (2017)
	Domestic dogs	9.3% (13/140)	Japan	Abe et al. (2002)
	Domestic dogs	0.1% (1/906)	Japan	Yamamoto et al. (2009)
	Domestic dogs	3.9% (3/77)	Japan	Yoshiuchi et al. (2010)
	Kennel dogs	21.1% (66/314)	Japan	Itoh et al. (2019)
	Domestic dog	100% (1/1)	Nigeria	Ayinmode et al. (2018a)
	Domestic dogs	1.1% (3/264)	Poland	Piekara-Stępińska et al. (2021)
	Domestic dogs	3.6% (2/55)	Spain	de Lucio et al. (2017)
	Shelter dogs	2.6% (5/194)	Spain	Gil et al. (2017)
	Domestic dogs	1.6% (4/252)	Spain	Mateo et al. (2023)
	Temple dogs	2.1% (2/95)	Thailand	Koompapong et al. (2014)
	Domestic dogs	13.8% (15/109)	Thailand	Tangtrongsup et al. (2017)
	Domestic & shelter dogs	2.6% (8/301)	Thailand	Tangtrongsup et al. (2020)
	Monastery dogs	0.7% (4/540)	Thailand	Khine et al. (2021)
	Shelter dogs	4.2% (28/676)	UK	Rosanowski et al. (2018)
	Domestic dogs	0.8% (1/129)	USA	Wang et al. (2012)
	Domestic dogs	4.8% (4/84)	USA	Scorza and Lappin (2017)
	Domestic dogs	33.3% (1/3)	Vietnam	Iwashita et al. (2021)
C. hominis	Wild dogs	2.3% (1/44)	Australia	Ng et al. (2011)
	Shelter dogs	0.5% (1/194)	Italy	Gil et al. (2017)
C. parvum	Domestic dogs	1.6% (2/128)	Brazil	Alves et al. (2018)
	Domestic dogs	3.1% (2/64)	Brazil	de Oliveira et al. (2021)
	Various	0.3% (2/651)	China	Liao et al. (2020)
	Domestic dogs	1.7% (1/58)	Costa Rica	Scorza et al. (2011)
	Domestic dogs	50.0% (1/2)	Czech Republic	Hajdušek et al. (2004)
	Stray dogs	10.0% (2/20)	Egypt	El-Madawy et al. (2010)
	Domestic dogs	10.0% (5/50)	Egypt	Gharieb et al. (2018)
	Domestic dogs	1.2% (1/81)	Germany	Sotiriadou et al. (2013)
	Domestic dogs	0.6% (2/349)	Germany	Murnik et al. (2022)
	Kennel & privately-owned dogs	2.9% (7/240)	Italy	Giangaspero et al. (2006)
	Domestic dogs	1.4% (10/705)	Italy	Simonato et al. (2017)
	Street dogs	1.5% (3/203)	Nigeria	Ayinmode et al. (2018b)
	Domestic dogs	0.8% (2/264)	Poland	Piekara-Stępińska et al. (2021)
	Domestic dogs	0.4% (1/252)	Spain	Mateo et al. (2023)
	Domestic dogs	6.4% (7/109)	Thailand	Tangtrongsup et al. (2017)
	Domestic & shelter dogs	0.3% (1/301)	Thailand	Tangtrongsup et al. (2020)
	Farm dog	100% (1/1)	UK	Smith et al. (2010)
	Shelter dogs	0.3% (2/676)	UK	Rosanowski et al. (2018)
C. muris	Wide range	0.2% (1/601)	China	Li et al. (2019b)
	Street dogs	1.0% (2/203)	Nigeria	Ayinmode et al. (2018b)
	Kennel dogs	8.6% (6/70)	USA	Lupo et al. (2008)
C. scrofarum	Domestic & shelter dogs	0.1% (1/807)	Greece	Kostopoulou et al. (2017)
C. meleagridis	Domestic dogs	50.0% (1/2)	Czech Republic	Hajdušek et al. (2004)
C. ubiquitum	Wide range	0.4% (1/267)	China	Li et al. (2015)

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Table 2 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
Giardia				
Assemblage A	Domestic dogs	13.8% (5/36)	Argentina	Kuthyar et al. (2021)
	Shelter & domestic dogs	0.07% (1/1400)	Australia	Palmer et al. (2008a, b)
	Wild dogs	6.8% (3/44)	Australia	Ng et al. (2011)
	Wild dogs	3.1% (1/32)	Australia	Nolan et al. (2013)
	Various	3.5% (40/1159)	Belgium	Claerebout et al. (2009)
	Stray dogs	36.8% (7/19)	Brazil	Volotão et al. (2007)
	Giardia-positive stray dogs	100% (60/60)	Brazil	Fantinatti et al. (2018)
	Dogs from a remote indigenous community	8.4% (13/155)	Canada	Himsworth et al. (2010)
	Dogs in indigenous communities	13.8% (32/231)	Canada	Schurer et al. (2012)
	Domestic, shelter & pet shop dogs	1.4% (3/209)	Canada	Uehlinger et al. (2013)
	Domestic dogs	2.4% (5/209)	China	Li et al. (2012)
	Police & farm dogs	12.2% (25/205)	China	Li et al. (2013)
	Domestic dogs	3.2% (7/216)	China	Zheng et al. (2014)
	Giardia-positive domestic dogs	40.0% (8/20)	China	Tan et al. (2016)
	Domestic dogs	4.7% (23/485)	China	Xu et al. (2016)
	Stray dogs	4.9% (26/527)	China	Pan et al. (2018)
	Domestic dogs	0.2% (1/604)	China	Cao et al. (2022)
	Domestic dogs	18.2% (2/11)[b]	Côte d'Ivoire	Berrilli et al. (2012)
	Giardia-positive domestic & kennel dogs	2.7% (2/96)	Croatia	Beck et al. (2012)
	Domestic dogs	10.2% (10/98)	Cuba	Puebla et al. (2017)
	Stray & domestic dogs	0.6% (2/300)	Egypt	Khalifa et al. (2023)
	Giardia-positive dog samples	22.8% (137/600)	Europe	Sprong et al. (2009)
	Giardia-positive domestic dogs	60.0% (33/55)	Germany	Leonhard et al. (2007)
	Domestic dogs	6.2% (5/81)	Germany	Sotiriadou et al. (2013)
	Giardia-positive domestic dogs	19.5% (24/123)	Germany	Pallant et al. (2015)
	Domestic dogs	0.5% (2/376)	Germany	Sommer et al. (2018)
	Domestic dogs	6.5% (2/31)	Germany	Rehbein et al. (2019)
	Domestic dogs	2.3% (9/386)	Germany	Murnik et al. (2023)
	Domestic & shelter dogs	0.9% (7/807)[a]	Greece	Kostopoulou et al. (2017)
	Domestic dogs	4.9% (5/101)	India	Traub et al. (2004)
	Domestic dogs	0.5% (1/212)	India	Utaaker et al. (2018)
	Domestic dogs	0.3% (1/315)	Iran	Homayouni et al. (2019)
	Giardia-positive domestic dogs	11.8% (2/17)	Italy	Berrilli et al. (2004)
	Domestic & kennel dogs	0.8% (2/240)	Italy	Paoletti et al. (2008)
	Domestic dogs	6.3% (8/127)	Italy	Scaramozzino et al. (2009)
	Stray dogs	64.3% (9/14)	Italy	Marangi et al. (2010)
	Domestic dogs	0.3% (2/655)	Italy	Pipia et al. (2014)
	Sheltered dogs	3.6% (7/194)	Italy	Gil et al. (2017)
	Shelter dogs	9.5% (16/168)	Italy	Agresti et al. (2021)
	Domestic dogs	19.5% (44/225)	Jamaica	Lee et al. (2017)
	Giardia-positive domestic dogs	66.6% (14/21)	Japan	Itagaki et al. (2005)
	Shelter dogs	1.0% (2/202)	Korea	Shin et al. (2015)
	Giardia-positive domestic dogs	100% (2/2)	Mexico	Ponce-Macotela et al. (2002)
	Giardia-positive domestic dogs	100% (11/11)	Mexico	Eligio-Garcia et al. (2005)
	Puppies	100% (5/5)	Mexico	Lalle et al. (2005b)
	Various	1.1% (2/189)	Netherlands	Uiterwijk et al. (2020)
	Domestic dogs	3.5% (2/58)	Nicaragua	Roegner et al. (2019)
	Domestic dogs	1.4% (5/348)	Spain	Adell-Aledon et al. (2018)
	Domestic dogs	0.4% (1/252)	Spain	Mateo et al. (2023)
	Giardia-positive dog samples	3.6% (1/28)	Sweden	Lebbad et al. (2010)
	Temple dogs	2.2% (5/229)	Thailand	Inpankaew et al. (2007)
	Temple dogs	14.4% (33/229)	Thailand	Traub et al. (2009)
	Monastery dogs	0.4% (2/540)	Thailand	Khine et al. (2021)
	Domestic dogs	0.7% (1/152)	The Netherlands	Overgaauw et al. (2009)
	Giardia-positive shelter dogs	2.4% (1/41)	UK	Upjohn et al. (2010)
	Domestic dogs	1.9% (1/52)	UK	Krumrie et al. (2022)
	Giardia-positive domestic dogs	11.1% (1/9)	Unknown	Read et al. (2004)
	Giardia-positive domestic dogs	28.0% (36/128)	USA	Covacin et al. (2011)
	Domestic dogs	13.3% (16/120)	USA	Munoz and Mayer (2016)
Assemblage B	Domestic dog	100% (1/1)	Argentina	Minvielle et al. (2008)
	Various	0.3% (4/1159)	Belgium	Claerebout et al. (2009)
	Domestic dogs	3.1% (1/32)	Brazil	Colli et al. (2015)
	Domestic dogs	2.2% (2/94)	Cambodia	Inpankaew et al. (2014)
	Domestic dogs	1.9% (6/315)	China	Gu et al. (2015)
	Domestic dogs	0.2% (1/485)	China	Xu et al. (2016)
	Giardia-positive domestic & kennel dogs	23.3% (17/96)	Croatia	Beck et al. (2012)
	Giardia-positive dog samples	8.8% (53/600)	Europe	Sprong et al. (2009)
	Giardia-positive domestic dogs	6.5% (8/123)	Germany	Pallant et al. (2015)
	Domestic & shelter dogs	5.7% (46/807)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	2.0% (2/101)	India	Traub et al. (2004)
	Domestic dogs	0.5% (1/212)	India	Utaaker et al. (2018)
	Kennel dogs	0.3% (1/318)	Italy	Simonato et al. (2015)
	Sheltered dogs	4.1% (8/194)	Italy	Gil et al. (2017)
	Domestic dogs	0.1% (1/705)	Italy	Simonato et al. (2017)
	Shelter dogs	3.6% (6/168)	Italy	Agresti et al. (2021)

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Table 2 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Domestic dogs	8.6% (5/58)	Nicaragua	Roegner et al. (2019)
	Domestic dogs	0.8% (1/128)	Poland	Piekarska et al. (2016)
	Household & kennel dogs	1.6% (2/126)	Portugal	Ferreira et al. (2011)
	Domestic dogs	2.3% (8/348)	Spain	Adell-Aledon et al. (2018)
	Temple dogs	3.9% (9/229)	Thailand	Traub et al. (2009)
	Domestic dogs	10.8% (51/473)	Turkey	Gultekin et al. (2017)
	Giardia-positive domestic dogs	22.2% (2/9)	Unknown	Read et al. (2004)
	Giardia-positive domestic dogs	40.6% (52/128)	USA	Covacin et al. (2011)
Assemblage C	*Giardia*-positive domestic dogs	90.9% (10/11)	Australia	Monis et al. (1998, 2003)
	Shelter & domestic dogs	2.9% (41/1400)	Australia	Palmer et al. (2008a, b)
	Wild dogs	11.4% (5/44)	Australia	Ng et al. (2011)
	Shelter dogs	1.4% (1/70)	Austria	Joachim et al. (2023)
	Various	2.2% (26/1159)	Belgium	Claerebout et al. (2009)
	Giardia-positive domestic dogs	29.9% (7/27)	Brazil	Souza et al. (2007)
	Domestic dogs	3.1% (1/32)	Brazil	Colli et al. (2015)
	Domestic dogs	1.4% (2/147)	Brazil	Paim Arruda Trevisan et al. (2020)
	Giardia-positive domestic dogs	16.6% (2/12)	Brazil	Silva et al. (2022)
	Domestic dogs	4.3% (4/94)	Cambodia	Inpankaew et al. (2014)
	Giardia-positive domestic dogs	30.6% (23/75)	Canada	McDowall et al. (2011)
	Domestic, shelter & pet shop dogs	4.8% (10/209)	Canada	Uehlinger et al. (2013)
	Various	0.7% (2/294)	Canada	Julien et al. (2019)
	Domestic dogs	1.6% (14/860)	Canada	Smith et al. (2020)
	Police & farm dogs	1.0% (2/205)	China	Li et al. (2013)
	Domestic dogs	0.5% (1/216)	China	Zheng et al. (2014)
	Wide range	2.6% (7/267)	China	Li et al. (2015)
	Giardia-positive domestic dogs	25.0% (5/20)	China	Tan et al. (2016)
	Domestic dogs	5.4% (26/485)	China	Xu et al. (2016)
	Domestic dogs	15.8% (3/19)	China	Liu et al. (2017)
	Stray dogs	5.7% (9/159)	China	Zhang et al. (2017)
	Stray dogs	3.4% (18/527)	China	Pan et al. (2018)
	Wide range	4.5% (27/601)	China	Li et al. (2019b)
	Various	0.8% (5/651)	China	Liao et al. (2020)
	Domestic dogs	1.5% (4/262)	China	Wang et al. (2021)
	Domestic dogs	2.3% (14/604)	China	Cao et al. (2022)
	Domestic dogs	2.9% (13/448)	China	Sui et al. (2022)
	Domestic dogs	3.8% (4/105)	China	Wu et al. (2022)
	Domestic dogs	3.0% (3/100)	Colombia	Hernandez et al. (2021)
	Domestic dogs	9.1% (1/11)	Côte d'Ivoire	Berrilli et al. (2012)
	Giardia-positive domestic & kennel dogs	36.9% (27/73)	Croatia	Beck et al. (2012)
	Giardia-positive domestic dogs	38.8% (21/54)	Czech Republic	Lecová et al. (2020)
	Domestic & shelter dogs	3.0% (50/1645)	Eastern European countries	Sommer et al. (2015)
	Domestic dogs	0.5% (1/218)	Egypt	Elmahallawy et al. (2023)
	Giardia-positive dog samples	31.8% (191/600)	Europe	Sprong et al. (2009)
	Domestic dogs	2.0% (3/150)	Finland	Rimhanen-Finne et al. (2007)
	Giardia-positive dogs	76.9% (30/39)	France	Kaufmann et al. (2022)
	Giardia-positive domestic dogs	35.9% (33/92)	Germany	Barutzki et al. (2007)
	Giardia-positive domestic dogs	36.4% (20/55)[b]	Germany	Leonhard et al. (2007)
	Giardia-positive domestic dogs	42.3% (52/123)	Germany	Pallant et al. (2015)
	Domestic dogs	10.1% (38/376)	Germany	Sommer et al. (2018)
	Domestic dogs	3.2% (1/31)	Germany	Rehbein et al. (2019)
	Domestic dogs	11.2% (43/386)	Germany	Murnik et al. (2023)
	Domestic & shelter dogs	5.7% (46/807)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	2.2% (5/229)	Hungary	Szénási et al. (2007)
	Domestic dogs	4.2% (9/212)	India	Utaaker et al. (2018)
	Domestic dogs	0.9% (3/315)	Iran	Homayouni et al. (2019)
	Giardia-positive domestic dogs	64.7% (11/17)	Italy	Berrilli et al. (2004)
	Domestic & kennel dogs	1.2% (3/240)	Italy	Paoletti et al. (2008)
	Domestic dogs	11.0% (14/127)	Italy	Scaramozzino et al. (2009)
	Domestic dogs	2.6% (17/655)	Italy	Pipia et al. (2014)
	Domestic dogs	2.4% (6/253)	Italy	Zanzani et al. (2014)
	Domestic dogs	3.0% (15/502)	Italy	Paoletti et al. (2015)
	Kennel dogs	17.2% (49/285)	Italy	Simonato et al. (2015)
	Domestic dogs	1.3% (9/705)	Italy	Simonato et al. (2017)
	Stray dogs	2.3% (6/262)	Italy	Liberato et al. (2018)
	Dogs with primary chronic enteropathy	2.2% (1/47)	Italy	Perrucci et al. (2020)
	Shelter dogs	1.2% (2/168)	Italy	Agresti et al. (2021)
	Giardia-positive domestic dogs	4.8% (1/21)	Japan	Itagaki et al. (2005)
	Pet shop puppies	0.5% (9/1794)	Japan	Itoh et al. (2011)
	Shelter dogs	0.5% (1/202)	Korea	Shin et al. (2015)
	Domestic dogs	1.4% (9/640)	Korea	Kim et al. (2019)
	Various	9.0% (17/189)	Netherlands	Uiterwijk et al. (2020)
	Domestic dogs	2.0% (2/100)	Nicaragua	Lebbad et al. (2008)
	Domestic dogs	5.2% (3/58)	Nicaragua	Roegner et al. (2019)
	Domestic dogs	1.5% (9/605)	Peru	Cooper et al. (2010)
	Domestic & shelter dogs	0.7% (1/148)	Poland	Solarczyk and Majewska (2010)
	Sled dogs	8.0% (2/25)	Poland	Bajer et al. (2011)

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Table 2 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Domestic dogs	14.0% (18/128)	Poland	Piekarska et al. (2016)
	Household & kennel dogs	11.9% (15/126)	Portugal	Ferreira et al. (2011)
	Domestic dogs	3.7% (3/80)	Portugal	Pereira et al. (2021)
	Domestic dogs	20.5% (8/39)	Romania	Adriana et al. (2016)
	Domestic dogs	5.4% (3/55)	Spain	de Lucio et al. (2017)
	Domestic dogs	0.3% (2/348)	Spain	Adell-Aledon et al. (2018)
	Domestic dogs	1.6% (4/252)	Spain	Mateo et al. (2023)
	Giardia-positive dog samples	28.6% (8/28)	Sweden	Lebbad et al. (2010)
	Domestic dogs	2.4% (1/42)	Taiwan	Liang et al. (2012)
	Stray dogs	5.9% (7/118)	Taiwan	Tseng et al. (2014)
	Temple dogs	0.4% (1/229)	Thailand	Inpankaew et al. (2007)
	Temple dogs	2.2% (5/229)	Thailand	Traub et al. (2009)
	Domestic dogs	7.3% (8/109)	Thailand	Tangtrongsup et al. (2017)
	Domestic & shelter dogs	0.3% (1/301)	Thailand	Tangtrongsup et al. (2020)
	Monastery dogs	1.3% (7/540)	Thailand	Khine et al. (2021)
	Stray dogs	3.8% (4/104)	Trinidad and Tobago	Mark-Carew et al. (2013)
	Giardia-positive shelter dogs	24.4% (10/41)	UK	Upjohn et al. (2010)
	Domestic dogs	19.2% (10/52)	UK	Krumrie et al. (2022)
	Giardia-positive domestic dogs	44.4% (4/9)	Unknown	Read et al. (2004)
	Giardia-positive domestic dogs	100% (15/15)	USA	Sulaiman et al. (2003)
	Giardia-positive dog samples	33.3% (1/3)	USA	Miska et al. (2009)
	Giardia-positive domestic dogs	14.8% (19/128)	USA	Covacin et al. (2011)
	Domestic dogs	0.8% (1/129)	USA	Wang et al. (2012)
	Shelter dogs	0.1% (1/672)[b]	USA	Johansen et al. (2014)
	Domestic dogs	4.8% (10/209)	Vietnam	Nguyen et al. (2018)
Assemblage D	*Giardia*-positive domestic dogs	9.1% (10/11)	Australia	Monis et al. (1998, 2003)
	Shelter & domestic dogs	3.1% (44/1400)	Australia	Palmer et al. (2008a, b)
	Various	4.2% (49/1159)	Belgium	Claerebout et al. (2009)
	Giardia-positive domestic dogs	74.1% (20/27)	Brazil	Souza et al. (2007)
	Kennel dogs	16.5% (16/97)	Brazil	Fava et al. (2016)
	Domestic dogs	4.3% (4/94)	Cambodia	Inpankaew et al. (2014)
	Giardia-positive domestic dogs	68.0% (51/75)	Canada	McDowall et al. (2011)
	Domestic, shelter & pet shop dogs	9.1% (19/209)	Canada	Uehlinger et al. (2013)
	Various	1.0% (3/294)	Canada	Julien et al. (2019)
	Domestic dogs	1.5% (13/860)	Canada	Smith et al. (2020)
	Domestic dogs	8.6% (18/209)	China	Li et al. (2012)
	Domestic dogs	0.5% (1/216)	China	Zheng et al. (2014)
	Domestic dogs	1.3% (4/315)	China	Gu et al. (2015)
	Giardia-positive domestic dogs	35.0% (7/20)	China	Tan et al. (2016)
	Domestic dogs	11.9% (58/485)	China	Xu et al. (2016)
	Domestic dogs	15.8% (3/19)	China	Liu et al. (2017)
	Stray dogs	5.7% (9/159)	China	Zhang et al. (2017)
	Stray dogs	2.5% (13/527)	China	Pan et al. (2018)
	Dogs with diarrhoea	3.1% (15/485)	China	Yu et al. (2018)
	Wide range	4.3% (26/601)	China	Li et al. (2019b)
	Various	2.1% (14/651)	China	Liao et al. (2020)
	Domestic dogs	12.2% (32/262)	China	Wang et al. (2021)
	Domestic dogs	1.2% (7/604)	China	Cao et al. (2022)
	Domestic dogs	3.1% (14/448)	China	Sui et al. (2022)
	Domestic dogs	1.0% (1/105)	China	Wu et al. (2022)
	Domestic dogs	3.0% (3/100)	Columbia	Hernandez et al. (2021)
	Domestic dogs	3.4% (2/58)	Costa Rica	Scorza et al. (2011)
	Domestic dogs	18.2% (2/11)	Côte d'Ivoire	Berrilli et al. (2012)
	Giardia-positive domestic & kennel dogs	36.9% (27/73)	Croatia	Beck et al. (2012)
	Giardia-positive domestic dogs	59.2% (32/54)	Czech Republic	Lecová et al. (2020)
	Domestic & shelter dogs	4.1% (68/1645)	Eastern European countries	Sommer et al. (2015)
	Domestic dogs	0.4% (4/986)	Egypt	Abdelaziz and Sorour (2021)
	Domestic dogs	1.4% (3/218)	Egypt	Elmahallawy et al. (2023)
	Stray & domestic dogs	1.6% (5/300)	Egypt	Khalifa et al. (2023)
	Giardia-positive dog samples	35.8% (215/600)	Europe	Sprong et al. (2009)
	Domestic dogs	2.6% (4/150)	Finland	Rimhanen-Finne et al. (2007)
	Giardia-positive dogs	23.1% (9/39)	France	Kaufmann et al. (2022)
	Giardia-positive domestic dogs	54.3% (50/92)	Germany	Barutzki et al. (2007)
	Giardia-positive domestic dogs	3.6% (2/55)	Germany	Leonhard et al. (2007)
	Giardia-positive domestic dogs	56.1% (69/123)	Germany	Pallant et al. (2015)
	Domestic dogs	12.5% (47/376)	Germany	Sommer et al. (2018)
	Domestic dogs	6.5% (2/31)	Germany	Rehbein et al. (2019)
	Domestic dogs	10.4% (40/386)	Germany	Murnik et al. (2023)
	Domestic & shelter dogs	2.7% (22/807)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	6.5% (15/229)	Hungary	Szénási et al. (2007)
	Domestic dogs	3.3% (7/212)	India	Utaaker et al. (2018)
	Domestic dogs	0.6% (2/315)	Iran	Homayouni et al. (2019)
	Giardia-positive domestic dogs	5.8% (1/17)	Italy	Berrilli et al. (2004)
	Domestic & kennel dogs	10.4% (25/240)	Italy	Paoletti et al. (2008)
	Domestic dogs	3.2% (4/127)	Italy	Scaramozzino et al. (2009)
	Domestic dogs	3.5% (23/655)	Italy	Pipia et al. (2014)

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Table 2 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Domestic dogs	2.0% (5/253)	Italy	Zanzani et al. (2014)
	Domestic dogs	0.4% (2/502)	Italy	Paoletti et al. (2015)
	Domestic dogs	10.2% (29/285)	Italy	Simonato et al. (2015)
	Domestic dogs	1.6% (11/705)	Italy	Simonato et al. (2017)
	Stray dogs	7.2% (19/262)	Italy	Liberato et al. (2018)
	Dogs with primary chronic enteropathy	10.6% (5/47)	Italy	Perrucci et al. (2020)
	Giardia-positive domestic dogs	100% (6/6)	Italy	Ciuca et al. (2021)
	Giardia-positive domestic dogs	100% (4/4)	Japan	Abe et al. (2003)
	Giardia-positive domestic dogs	28.6% (6/21)	Japan	Itagaki et al. (2005)
	Domestic dogs	2.6% (2/77)	Japan	Yoshiuchi et al. (2010)
	Pet shop puppies	1.1% (20/1794)	Japan	Itoh et al. (2011)
	Domestic dogs	1.4% (9/640)	Korea	Kim et al. (2019)
	Various	25.9% (49/189)	Netherlands	Uiterwijk et al. (2020)
	Domestic dogs	5.0% (5/100)	Nicaragua	Lebbad et al. (2008)
	Domestic dogs	5.2% (3/58)	Nicaragua	Roegner et al. (2019)
	Domestic dogs	5.3% (32/605)	Peru	Cooper et al. (2010)
	Domestic & shelter dogs	0.7% (1/148)	Poland	Solarczyk and Majewska (2010)
	Domestic dogs	1.6% (2/128)	Poland	Piekarska et al. (2016)
	Household & kennel dogs	9.5% (12/126)	Portugal	Ferreira et al. (2011)
	Domestic dogs	13.7% (11/80)	Portugal	Pereira et al. (2021)
	Domestic dogs	27.6% (29/39)	Romania	Adriana et al. (2016)
	Domestic dogs	3.7% (13/348)	Spain	Adell-Aledon et al. (2018)
	Domestic dogs	1.6% (4/252)	Spain	Mateo et al. (2023)
	Giardia-positive dog samples	50.0% (14/28)	Sweden	Lebbad et al. (2010)
	Domestic dogs	7.1% (3/42)	Taiwan	Liang et al. (2012)
	Stray dogs	3.4% (4/118)	Taiwan	Tseng et al. (2014)
	Temple dogs	1.3% (3/229)	Thailand	Inpankaew et al. (2007)
	Temple dogs	5.7% (13/229)	Thailand	Traub et al. (2009)
	Domestic dogs	11.0% (12/109)	Thailand	Tangtrongsup et al. (2017)
	Domestic & shelter dogs	6.0% (18/301)	Thailand	Tangtrongsup et al. (2020)
	Monastery dogs	1.3% (7/540)	Thailand	Khine et al. (2021)
	Stray dogs	20.2% (21/104)	Trinidad and Tobago	Mark-Carew et al. (2013)
	Giardia-positive shelter dogs	70.7% (29/41)	UK	Upjohn et al. (2010)
	Giardia-positive domestic dogs	22.2% (2/9)	Unknown	Read et al. (2004)
	Giardia-positive dog samples	66.6% (2/3)	USA	Miska et al. (2009)
	Giardia-positive domestic dogs	16.4% (21/128)	USA	Covacin et al. (2011)
	Domestic dogs	1.5% (2/129)	USA	Wang et al. (2012)
	Domestic dogs	0.8% (1/120)	USA	Munoz and Mayer (2016)
	Domestic dogs	4.8% (10/209)	Vietnam	Nguyen et al. (2018)
Mixed C& D	Domestic dogs	2.7% (1/36)	Argentina	Kuthyar et al. (2021)
	Shelter & domestic dogs	0.1% (2/1400)	Australia	Palmer et al. (2008a, b)
	Domestic, shelter & pet shop dogs	0.5% (1/209)	Canada	Uehlinger et al. (2013)
	Domestic & stray dogs	8.5% (80/940)	China	Qi et al. (2016)
	Wide range	0.8% (5/601)	China	Li et al. (2019b)
	Domestic dogs	1.1% (5/448)	China	Sui et al. (2022)
	Giardia-positive domestic dogs	1.8% (1/54)	Czech Republic	Lecová et al. (2020)
	Giardia-positive dogs	2.6% (1/39)	France	Kaufmann et al. (2022)
	Giardia-positive domestic dogs	8.7% (8/92)	Germany	Barutzki et al. (2007)
	Domestic dogs	3.1% (12/386)[b]	Germany	Murnik et al. (2023)
	Domestic & shelter dogs	1.9% (15/807)	Greece	Kostopoulou et al. (2017)
	Domestic dogs	0.4% (1/229)	Hungary	Szénási et al. (2007)
	Giardia-positive domestic dogs	5.8% (1/17)	Italy	Berrilli et al. (2004)
	Domestic dogs	0.6% (3/502)	Italy	Paoletti et al. (2015)
	Various	7.4% (14/189)	Netherlands	Uiterwijk et al. (2020)
	Domestic dogs	1.0% (1/100)	Nicaragua	Lebbad et al. (2008)
	Domestic dogs	4.3% (26/605)	Peru	Cooper et al. (2010)
	Domestic dogs	0.8% (1/128)	Poland	Piekarska et al. (2016)
	Domestic dogs	5.0% (4/80)	Portugal	Pereira et al. (2021)
	Domestic dogs	2.6% (1/39)	Romania	Adriana et al. (2016)
	Domestic dogs	0.4% (1/252)	Spain	Mateo et al. (2023)
	Giardia-positive dog samples	17.8% (5/28)	Sweden	Lebbad et al. (2010)
	Domestic dogs	0.9% (1/109)	Thailand	Tangtrongsup et al. (2017)
	Giardia-positive shelter dogs	2.4% (1/41)	UK	Upjohn et al. (2010)
	Domestic dogs	0.8% (1/129)	USA	Wang et al. (2012)
	Shelter dogs	24.4% (164/672)	USA	Johansen et al. (2014)
	Domestic dogs	2.3% (7/300)	USA	Hascall et al. (2016)
	Domestic dogs	10.7% (9/84)	USA	Scorza and Lappin (2017)
Assemblage E	Wild dogs	4.5% (2/44)	Australia	Ng et al. (2011)
	Domestic dogs	1.4% (2/143)	Brazil	Harvey et al. (2023)
	Domestic, shelter & pet shop dogs	0.5% (1/209)	Canada	Uehlinger et al. (2013)
	Various	0.3% (1/294)	Canada	Julien et al. (2019)
	Wide range	1.9% (5/267)	China	Li et al. (2015)
	Giardia-positive dog samples	0.8% (5/600)	Europe	Sprong et al. (2009)
	Domestic dogs	0.6% (1/150)	Finland	Rimhanen-Finne et al. (2007)
	Domestic dogs	0.5% (2/376)	Germany	Sommer et al. (2018)
	Domestic dogs	0.5% (1/212)	India	Utaaker et al. (2018)

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Table 2 (*continued*)

Species/Assemblage	Hosts	Prevalence	Country	Reference
	Domestic dogs	2.6% (1/39)	Romania	Adriana et al. (2016)
	Stray dogs	1.0% (1/104)	Trinidad and Tobago	Mark-Carew et al. (2013)
Assemblage F	*Giardia*-positive domestic dogs	16.6% (2/12)	Brazil	Silva et al. (2022)
	Dogs with diarrhoea	0.2% (1/485)	China	Yu et al. (2018)
	Various	0.1% (1/651)	China	Liao et al. (2020)
	Giardia-positive domestic dogs	4.9% (6/123)	Germany	Pallant et al. (2015)
	Domestic dogs	0.5% (2/376)	Germany	Sommer et al. (2018)
	Domestic dogs	15.4% (8/52)	UK	Krumrie et al. (2022)
Other mixtures	Domestic dogs	C + A (1/36)	Argentina	Kuthyar et al. (2021)
	Wild dogs	A + E (3/44)	Australia	Ng et al. (2011)
	Domestic dogs	A + C (1/147)	Brazil	Paim Arruda Trevisan et al. (2020)
	Domestic, shelter & pet shop dogs	A + C (1/209) B + D (1/209) D + E (1/209)	Canada	Uehlinger et al. (2013)
	Domestic dogs	5.1% (11/216)[b]	China	Zheng et al. (2014)
	Domestic dogs	A + B (4/105) A + D (1/105) A + B + D (2/105)	China	Wu et al. (2022)
	Giardia-positive domestic dogs	A + D (1/92)	Germany	Barutzki et al. (2007)
	Domestic dogs	A + B (1/31)	Germany	Rehbein et al. (2019)
	Giardia-positive domestic dogs	A + C (2/17)	Italy	Berrilli et al. (2004)
	Temple dogs	A + B (3/229) A + D (1/229)	Thailand	Inpankaew et al. (2007)
	Domestic dogs	A + B (38/473)	Turkey	Gultekin et al. (2017)

[a] Also contained mixtures with C and D.
[b] Various mixtures.

Assemblage A was also the dominant assemblage in dogs in Japan (66.6%; 14/21 typed isolates) (Itagaki et al., 2005) and in Germany (60%; 33/55 typed isolates) (Leonhard et al., 2007). Assemblage A was the only assemblage identified in slum and stray dogs in Brazil (Volotão et al., 2007; Fantinatti et al., 2018), domestic dogs in Jamaica (Lee et al., 2017), and dogs in indigenous communities in Saskatchewan, Canada (32/32 typed isolates) (Schurer et al., 2012). Subtyping of assemblage A in cats and dogs has identified mostly sub-assemblage AI, which is mainly confined to animal hosts (Lalle et al., 2005b; Souza et al., 2007; Volotão et al., 2007; Marangi et al., 2010; Zheng et al., 2015; Saleh et al., 2019; Mateo et al., 2023). However, some studies have identified sub-assemblage AII in cats and dogs (e.g. Claerebout et al., 2009; Traub et al., 2004; Gil et al., 2017; Ito et al., 2017; Agresti et al., 2021; Guadano Procesi et al., 2022), which is mainly human-associated and even sub-assemblage AIII (Claerebout et al., 2009; Guadano Procesi et al., 2022), which is wild ruminant-associated (Klotz et al., 2022). Differences in sub-assemblage A assignment may be related to the typing locus used, as a meta-analysis revealed that subtyping assemblage A at multiple loci produced divergent results, with sub-assemblage AI dominating amongst assemblage A identified in dogs, when the *tpi* locus was used, and sub-assemblage AII dominating at the *bg* locus (Cai et al., 2021). Therefore, the identity of A sub-assemblages in cats and dogs is unclear.

Assemblage B has been reported less frequently in cats and dogs than assemblage A (Feng and Xiao, 2011; Cai et al., 2021) (Tables 1 and 2). However, assemblage B was identified as the dominant assemblage in these animals in some studies. For example, in Spain, assemblage B was detected in 42.1% (8/19) of typed *Giardia*-positive dogs, followed by assemblage A (7/19), with assemblages C and D only detected in 4 samples (Gil et al., 2017). A study in the USA, also reported assemblage B as the dominant assemblage (41% of typed samples) in household dogs, followed by assemblage A (28% of typed samples) (Covacin et al., 2011). In Turkey, assemblage B was reported in all 89 typed *Giardia*-positive dogs, but 42.7% (38/89) of these were mixed infections with assemblage A (Gultekin et al., 2017). Moreover, also in Turkey, assemblage B was the only assemblage detected in 30 typed *Giardia*-positive symptomatic cats (Sursal et al., 2020). Interestingly, in a study conducted in Romania, assemblage D was the only assemblage detected in 80% (8/10) of cats screened (Adriana et al., 2016). In that study, seven of the cats positive for assemblage D resided in the same house, and although dogs were not present, all cats had outdoor access (Adriana et al., 2016).

Many of these studies, particularly earlier studies, have relied on one locus for identification of *Giardia* assemblages in cats and dogs. Due to discordance in genotyping results between loci, however, it is possible for *Giardia* isolates from cats and dogs to be typed as ‘zoonotic’ at one locus but ‘host-specific’ at another (Cacciò and Ryan, 2008), which makes interpretation difficult. In many studies, where multiple loci were used, there was significant discordance between loci (e.g. Covacin et al., 2011; Beck et al., 2012; Johansen et al., 2014; Pallant et al., 2015; Kostopoulou et al., 2017), with one study reporting that the 18S locus preferentially amplified assemblages B, D and C, whereas the *bg* locus preferentially amplified assemblages A and B (Covacin et al., 2011).

Giardia cyst excretion is highly variable and sporadic and relatively few studies have examined cyst excretion in dogs and cats. In DFA analysis, cyst concentrations ranging from 0 to 7143 and 0–6061 (median 835) cysts per gram of faeces (CPG) have been reported in cats and dogs, respectively (Cox et al., 2005). Another study of *Giardia* cyst shedding in 104 dogs and 21 cats from Germany, reported that 92.3% (96/104) of dogs and 76.2% (16/21) of cats, shed low numbers of cysts (< 50 cysts per slide) (Sommer et al., 2018). In Canada, a study of 869 dog faecal samples from urban parks reported median *Giardia* cyst excretion rates of 1.0×10^4 CPG (Smith et al., 2020). Similarly, studies of *Giardia*-positive dogs in Italy (Ciuca et al., 2021) and France (Kaufmann et al., 2022) reported a mean of 2×10^4 CPG (2.7×10^3–4.8×10^4) and a geometric mean excretion of 2.1×10^5 CPG, respectively. A more recent study of *Giardia* in dogs and cats in Egypt using qPCR reported that 56% (47/84) of the *Giardia* positives from dogs and 90.7% (39/43) of the *Giardia* positives from cats had high qPCR CT values indicating “light infections” (Elmahallawy et al., 2023). In comparison, cattle can shed $> 1 \times 10^6$ *Giardia* cysts per day (Nydam et al., 2001), while infected humans can shed 10^8–10^9 cysts per day (Danciger and Lopez, 1975; Rendtorff, 1979).

4. Zoonotic risk of cryptosporidiosis and giardiasis from cats and dogs

The dominant *Cryptosporidium* species and *Giardia* assemblages infecting cats are *C. felis* and assemblages F and A, compared with *C. canis* and assemblages C and D in dogs (Tables 1 and 2). Although

Table 3
Reports of *Cryptosporidium felis*, *C. canis* and *Giardia* assemblages C, D and F in humans globally.

Species/ Assemblage	No. of cases	Comment	Country	Reference
Cryptosporidium				
C. felis	2	HIV+ patients	Algeria	Semmani et al. (2023)
	1	21-year-old female with diarrhoea	Australia	Ebner et al. (2015)
	5	HIV+ patients	Brazil	Lucca et al. (2009)
	4	School children	Brazil	Pacheco et al. (2022)
	2	Sporadic cases	Canada	Guy et al. (2021)
	2	Hospitalised children (median 36 months-old)	China	Feng et al. (2012)
	8	1 HIV+, 4 with diarrhoea, 2 with non-gastrointestinal illnesses	China	Liu et al. (2020)
	3	Kindergarten children aged 2–6 years	China	Wang et al. (2022b)
	1	Average age 5 years	Colombia	Higuera et al. (2020)
	2	1 child and 1 HIV+ patient	Colombia	Uran-Velasquez et al. (2022)
	1	*C. felis* identified in owner's cat	Colombia	Potes-Morales and Crespo-Ortiz (2023)
	5	HIV+/AIDS patients	Ethiopia	Adamu et al. (2014)
	6	HIV+ patients	France	Guyot et al. (2001)
	15	10 HIV+ patients, 3 transplant patients	France	ANOFEL Cryptosporidium National Network (2010)
	10	Immunodeficient individuals	France	Costa et al. (2018)
	6	40% immunodeficient patients	France	Costa et al. (2020)
	2	AIDS patients	Hatai	RaccurtBrasseur et al. (2006)
	1	HIV+ patients	India	Muthusamy et al. (2006)
	3	Patients with diarrhoea; many had underlying clinical conditions	India	Khalil et al. (2017)
	1	HIV+ patients	Jamaica	Gatei et al. (2008)
	2	Children aged < 5 years	Kenya	Gatei et al. (2006)
	1	HIV+/AIDS patients	Malaysia	Lim et al. (2011)
	4	Children aged 3–14 years	Mozambique	Muadica et al. (2021)
	1	HIV+/AIDS patients	Nigeria	Ukwah et al. (2017)
	1	All children; not associated with diarrhoea	Peru	Xiao et al. (2001)
	24	3.3% of typed positives from HIV+/AIDS patients	Peru	Cama et al. (2003)
	9	HIV+ patients	Peru	Cama et al. (2006)
	6	HIV+ patients	Peru	Cama et al. (2007)
	4	Children aged < 3 years	Peru	Cama et al. (2008)
	1	HIV+ patients	Portugal	Alves et al. (2001)
	4	HIV+ patients	Portugal	Matos et al. (2004)
	1	HIV+ patient	Spain	Cieloszyk et al. (2012)
	1	–	Spain	Abal-Fabeiro et al. (2014)
	1	37-year-old immunocompetent female with a range of underlying health issues and used inhaled steroids, pet cat also had *C. felis*	Sweden	Beser et al. (2015)
	4	Sporadic cases - one had travelled to Asia	Sweden	Lebbad et al. (2021)
	3	HIV+ patients	Switzerland	Morgan et al. (2000a)
	3	HIV+ patients	Thailand	Gatei et al. (2002)
	1	HIV+ patients	Thailand	Tiangtip and Jongwutiwes (2002)
	1	HIV+/AIDS patients	Thailand	Srisuphanunt et al. (2011)
	7	HIV+ patients	Thailand	Sannella et al. (2019)
	1	Primary school children	Thailand	Sutthikornchai et al. (2021)
	4	One HIV+ patient, one had a severe underlying condition, one aged 1 year	UK	Pedraza-Días et al. (2001)
	6	2 were known to be immunocompromised	UK	Leoni et al. (2006)
	4	0.01% (4/8000) of typed cases	UK	Chalmers et al. (2009b)
	38	0.3% (38/14,469) of typed cases, 6/38 were immunocompromised	UK	Elwin et al. (2012b)
	1	HIV+ patients	USA	Pieniazek et al. (1999)
	3	Rural Nebraska; age range 7 months to 79 years	USA	Loeck et al. (2020)
	10	New York City residents. 1.8% (10/547) of typed samples	USA	Alderisio et al. (2023)
	1	Patients with diarrhoea	Zambia	Mulunda et al. (2020)
	2	One patient infected while on holiday in India and second patient had "contact with a kitten with diarrhoea 3 weeks before disease onset"	Sweden	Insulander et al. (2013)
C. canis	1	School children (10% prevalence)	Angola	Dacal et al. (2018)
	1	HIV+ patients	Brazil	Lucca et al. (2009)
	5	Symptomatic children attending hospital	Cambodia	Moore et al. (2016)
	1	Hospitalised children (median 36 months-old)	China	Feng et al. (2012)
	2	Both with non-gastrointestinal illnesses	China	Liu et al. (2020)
	18	40% (12/30) of dog owners and 24% of (6/25) dog shelter workers	Egypt	Khalifa et al. (2023)
	2	HIV+/AIDS patients	Ethiopia	Adamu et al. (2014)
	4	3 HIV+ patients	France	ANOFEL Cryptosporidium National Network (2010)
	3	40% immunodeficient patients	France	Costa et al. (2020)
	1	HIV+ patients	Jamaica	Gatei et al. (2008)
	1	Critically ill child in hospital with additional co-infections	Jordan	Hijjawi et al. (2010)
	3	Children aged < 5 years	Kenya	Gatei et al. (2006)
	2	Children (24- and 14 months old)	New Zealand	Learmonth et al. (2004)
	1	Children aged 6 months to 6 years	Nigeria	Molloy et al. (2010)
	2	All children; not associated with diarrhoea	Peru	Xiao et al. (2001)
	36	4% of typed samples from HIV+/AIDS patients	Peru	Cama et al. (2003)
	12	HIV+ patients	Peru	Cama et al. (2006)

(*continued on next page*)

Table 3 (*continued*)

Species/ Assemblage	No. of cases	Comment	Country	Reference
	6	HIV+ patients	Peru	Cama et al. (2007)
	2	32-month-old female, 6.5-year-old brother (and household dog)	Peru	Xiao et al. (2007)
	4	Children aged < 3 years	Peru	Cama et al. (2008)
	2	HIV+ patients	Thailand	Gatei et al. (2002)
	1	HIV+/AIDS patients	Thailand	Srisuphanunt et al. (2011)
	12	HIV+ patients	Thailand	Sannella et al. (2019)
	1	Child aged 2 years	UK	Pedraza-Días et al. (2001)
	1	Child aged 1 year; had returned from Africa	UK	Leoni et al. (2006)
	1	0.01% (1/8000) of typed cases	UK	Chalmers et al. (2009a)
	1	0.007% (1/14,469) of typed cases	UK	Elwin et al. (2012b)
	1	HIV+ patients	USA	Pieniazek et al. (1999)
	1	Rural Nebraska; age range 7 months to 79 years	USA	Loeck et al. (2020)
	3	New York City residents. 0.5% (3/547) of typed samples	USA	Alderisio et al. (2023)
	1	HIV+ patients	Venezuela	Certad et al. (2006)
	2	1 human diarrheal and 1 non-diarrheal sample	Vietnam	Iwashita et al. (2021)
Giardia				
Assemblage C	5	Children attending a day-care centre	Brazil	Durigan et al. (2014)
	6	Immunocompromised patients	Brazil	Jeske et al. (2022)
	16	Typing only conducted at 1 locus	China	Liu et al. (2014)
	3	HIV+/AIDS patients	China	Jiang et al. (2023)
	1	Adult immunocompromised male with cancer and diarrhoea	Egypt	Soliman et al. (2011)
	1	44-year-old female with chronic diarrhoea; was not a pet owner	Slovakia	Štrkolcová et al. (2015)
Assemblage D	2	Travel returnees from Southeastern Asia	Germany	Broglia et al. (2013)
	1	Rural village, lack of water and sanitation. Only typed at 1 locus	Argentina	Candela et al. (2021)
	1	Immunocompromised patients	Brazil	Jeske et al. (2022)
Assemblage F	1	10-month-old child	Brazil	Silva et al. (2022)
	3	Children. Mixed A and F	Ethiopia	Gelanew et al. (2007)
	3	Children living with poor sanitation	Slovakia	Pipiková et al. (2022)
	1	Primary school children	Thailand	Sutthikornchai et al. (2021)

C. felis, *C. canis*, and assemblages C, D and F are considered to be of limited zoonotic potential, this risk is not negligible as there have been numerous reports of *C. felis* and *C. canis* in humans, as well as a few reports of assemblages C, D and F in humans (Table 3). The prevalence of *C. felis* and *C. canis* in humans is usually low (1–3% of cryptosporidiosis cases); however, a few studies have reported higher prevalences; 5–40% for *C. canis* and 7.1–37.5% for *C. felis* cryptosporidiosis cases, mostly in children or HIV-positive individuals (Moore et al., 2016; Dacal et al., 2018; Sannella et al., 2019; Uran-Velasquez et al., 2022; Wang et al., 2022b; Khalifa et al., 2023).

Cryptosporidium canis and *C. felis* are however, largely host-specific, as the prevalence of *C. felis* and *C. canis* in humans is usually low, despite the close contact between humans and companion animals. For example, in the USA, ~14% of households own a cat and ~22.2% of households own a dog, equating to 111.6 million households (APPA, 2022). Across Europe, 26% of households own one or more cats and 25% own one or more dogs, equating to ~127.2 million cats and 104.4 million dogs (FEDIAF, 2023). In Australia, 48% of Australian households have dogs and 33% of households have cats across both urban and rural areas (Animal Medicines Australia). The majority of reports of *C. felis*, *C. canis* and assemblages C, D and F in humans have been in immunologically immature children or immunocompromised adults and predominantly in low-income countries (Table 3). Therefore, the zoonotic risk from *C. felis*, *C. canis* and assemblages C, D and F in immunocompetent humans is probably low.

There have been several reports suggesting possible zoonotic transmission between owners and pets using genotyping analysis of human and animal samples from the same household or workplace (Xiao et al., 2007; Beser et al., 2015). For example, *C. felis* was characterised in a 37-year-old immunocompetent woman and her cat in Sweden (Beser et al., 2015) and *C. canis* was identified in a 2.5 year-old child, her 6.5 year-old brother and their dog in Peru (Xiao et al., 2007). In a recent study in Egypt, *C. canis* was identified in 12 domestic dog owners and 6 dog shelter workers (Khalifa et al., 2023).

The recent development of *gp60* subtyping tools for *C. felis* and *C. canis* has facilitated studies of zoonotic transmission of these two pathogens (Rojas-Lopez et al., 2020; Jiang et al., 2021). Results of these studies have identified both zoonotic and human-adapted subtypes in *C. felis.* Therefore, subtypes XIXc, XIXd and XIXe have been reported only in humans, while the remaining two subtypes (XIXa and XIXb) have been reported in both humans and cats (Jiang et al., 2020; Rojas-Lopez et al., 2020; Guy et al., 2021; Li et al., 2021b; Joachim et al., 2023). In total, nine *C. canis* subtype families (XXa to XXi) have been identified (Jiang et al., 2021; Murnik et al., 2022; Wang et al., 2022a; Elmahallawy et al., 2023; Mateo et al., 2023). The limited typing to date in *C. canis* has supported potential zoonotic transmission (Jiang et al., 2021), including re-analysis of samples from a suspected case of zoonotic transmission of *C. canis* in a household (Xiao et al., 2007), with *C. canis* subtype XXa4 identified from the 2.5 year-old female index case, her 6.5-year-old brother and their dog (Jiang et al., 2021). Similarly, subtyping has confirmed zoonotic transmission of *C. felis* between two human cases and their cats in Sweden (Rojas-Lopez et al., 2020).

Cats and particularly dogs can also be infected with *C. parvum*, which is a more significant public health risk. However, in most studies where *C. parvum* was detected, with a few exceptions, the occurrence rate was low and it is unknown if dogs and cats are mechanically carrying *C. parvum* due to coprophagy of human or cattle faeces or actually infected. It is possible that cats and particularly dogs from rural locations close to ruminants, may have a higher prevalence of *C. parvum.* Zoonotic transmission of *C. parvum* from cats and dogs has been suggested (Neira et al., 2010; Gharieb et al., 2018). For example, *C. parvum* was detected in children and their pet dogs in Egypt (Gharieb et al., 2018) and in a pregnant immunocompetent woman and her cat (Neira et al., 2010). The direction of transmission, i.e. spillover from pets to humans or spillback from humans to pets, in these studies is unknown. In contrast, a study in Spain reported no evidence supporting zoonotic transmission between owners and their pet cats and dogs (de Lucio et al., 2017). Similarly, in households in Peru, only *Giardia* assemblages A and B were identified in humans, while assemblages C and D were identified in their dogs, with the exception of one dog with a mixed assemblage B/D infection (Cooper et al., 2010). There have only been two reports of *C. hominis* in dogs and in both cases, PCR analysis of a second locus was unsuccessful, indicating very low oocyst numbers (Ng et al., 2011; Gil et al., 2017).

As with *Cryptosporidium*, several studies have suggested possible transmission of *Giardia* from pets to owners (Traub et al., 2004; Palmer et al., 2008b; Marangi et al., 2010; Quadros et al., 2016; Rehbein et al., 2019; Kuthyar et al., 2021; Harvey et al., 2023; Khalifa et al., 2023), particularly in socially-deprived areas. For example, in a low socioeconomic community in southern Italy, sub-assemblage AI was identified in nine of 14 dogs and six of 14 children (Marangi et al., 2010). In Argentina, assemblage A was detected in 12 humans and five pet dogs (Kuthyar et al., 2021). In one study in Brazil, assemblage E was the only assemblage detected in dogs, and assemblages A, B and E were recovered from children from the same rural community (Harvey et al., 2023). Another study of *Giardia*-positive samples from humans, dogs and cats in Brazil, identified assemblage F in one human and assemblages C, D and F in dogs and F in one cat (Silva et al., 2022). These studies are suggestive of zoonotic transmission but have not been confirmed by finding identical multilocus subtypes in both humans and their companion animals. Furthermore, it would also be necessary to demonstrate that the animals acquired the infection prior to human infection (Cai et al., 2021). Other studies have found no evidence of transmission between companion animals and their owners (Hopkins et al., 1997; Inpankaew et al., 2014; Wu et al., 2022). For example, one study examined *Giardia* assemblages in dogs and humans in rural Cambodia and found the occurrence of different assemblages between the two host species, leading to the conclusion that the risk of zoonotic transmission was low (Inpankaew et al., 2014). Another recent study in Egypt detected assemblages A and D in domestic and shelter dogs but assemblage A only in their owners and dog shelter workers (Khalifa et al., 2023).

Many of the typing studies conducted to date on *Giardia* in cats and dogs are problematic due to (i) high levels of mixed infections with multiple *Giardia* assemblages, (ii) the use of only one locus or lack of agreement between multiple loci, and (iii) the high levels of allelic sequence hetrerozygosity (ASH) in assemblages C and D, which make assemblage assignment unreliable (Morrison et al., 2007; Franzén et al., 2009; Kooyman et al., 2019; Veldhuis et al., 2022; Klotz et al., 2023). Therefore, it is difficult to draw firm conclusions on the zoonotic potential of *Giardia* infections in companion animals. It has been suggested that in dogs, two main transmission cycles exist, with assemblage C and D predominating, particularly in kennel/shelter dogs, and assemblage A and occasionally assemblage B transmission between dogs and humans in households (Cai et al., 2021). In agreement with this, a case-control study in the UK, reported a significant correlation between dog ownership and assemblage A infection in humans (Minetti et al., 2015). Others argue that overall, humans and pets are preferentially infected with sub-assemblages AII and AI, respectively (Feng and Xiao, 2011).

5. Conclusions

Our understanding of the zoonotic transmission of *C. felis* and *C. canis* from cats and dogs to humans will be improved by the recent development of molecular typing tools, with preliminary evidence supporting some level of zoonotic transmission (Rojas-Lopez et al., 2020; Jiang et al., 2020, 2021; Guy et al., 2021; Li et al., 2021a). Most molecular-based household transmission studies to date, however, have focussed on middle to high-income countries, where the prevalence of *C. felis* and *C. canis* in humans is low. Relatively few studies have been conducted in dogs and cats in low-income countries, where the prevalence of *C. felis* and *C. canis* is much higher in humans. Overall, the risk of zoonotic transmission from cats and dogs to humans is uncertain but likely to be low due to the relatively low zoonotic risk from *C. canis*, *C. felis* and assemblages C, D and F, the overall low prevalence of *C. parvum* (and *C. hominis*) in cats and dogs, and low oocyst shedding (Lucio-Forster et al., 2010; de Lucio et al., 2016; Rehbein et al., 2019; Li et al., 2021a; Cai et al., 2021). This would be even more the case for *G. duodenalis* in cats and dogs due to differences in host preferences of this parasite at the assemblage and sub-assemblage levels. Future epidemiological studies should concentrate on applying the most recently developed *Cryptosporidium* and *Giardia* multi-locus sub-typing tools, as well as whole genome sequencing, to longitudinal *Giardia*-positive samples from cats and dogs and their owners, before a clearer understanding of the extent of spillover and/or spillback of *Cryptosporidium* and *Giardia* between pets and their owners can be determined.

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Amanda D. Barbosa: Writing – original draft, Writing – review & editing. **Siobhon Egan:** Writing – review & editing. **Yaoyu Feng:** Writing – review & editing, Funding acquisition. **Lihua Xiao:** Writing – review & editing, Funding acquisition. **Una Ryan:** Writing – original draft, Writing – review & editing, Project administration, Funding acquisition, All authors read and approved the final manuscript.

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Data availability

The data supporting the conclusions of this article are included within the article.

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