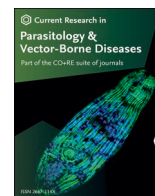




Contents lists available at ScienceDirect

Current Research in Parasitology & Vector-Borne Diseases

journal homepage: www.sciencedirect.com/journal/current-research-in-parasitology-and-vector-borne-diseases

How significant are bats as potential carriers of zoonotic *Cryptosporidium* and *Giardia*?

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ARTICLE INFO

Keywords:

Bats
Cryptosporidium
Giardia
 Reservoir
 Zoonosis
 Public health

ABSTRACT

Bats are known to harbour various pathogens and are increasingly recognised as potential reservoirs for zoonotic diseases. This paper reviews the genetic diversity and zoonotic potential of *Cryptosporidium* and *Giardia* in bats. The risk of zoonotic transmission of *Cryptosporidium* from bats to humans appears low, with bat-specific *Cryptosporidium* genotypes accounting for 91.5% of *Cryptosporidium*-positive samples genotyped from bats worldwide, and *C. parvum* and *C. hominis* accounting for 3.4% each of typed positives, respectively. To date, there have only been sporadic detections of *Giardia* in bats, with no genetic characterisation of the parasite to species or assemblage level. Therefore, the role bats play as reservoirs of zoonotic *Giardia* spp. is unknown. To mitigate potential risks of zoonotic transmission and their public health implications, comprehensive research on *Cryptosporidium* and *Giardia* in bats is imperative. Future studies should encompass additional locations across the globe and a broader spectrum of bat species, with a focus on those adapted to urban environments.

1. Introduction

Chiroptera (bats) are the second largest mammalian order after rodents (representing ~25% of all living mammals) (Irving et al., 2021). Bats are highly diverse and geographically widespread, and have traditionally been sub-divided into two suborders: Megachiroptera or megabats (Old World fruit bats), which fly by vision and Microchiroptera or microbats which use echolocation to fly (Jones et al., 2002; Nikaido et al., 2020). However, molecular data revealed that five lineages of microbats (“Rhinopomatidae, Rhinolophidae, Hipposideridae, Craseonycteridae, and Megadermatidae”) are more closely related to megabats. Therefore, these have been reclassified into a group “Yinpterochiroptera” with megabats, with the remaining microbats classified as “Yangochiroptera” (Tsagkogeorga et al., 2013; Nikaido et al., 2020).

Bats play important roles in ecosystems contributing to seed dispersal, pollination, reducing numbers of pest insects, and recycling nutrients (Russo and Ancillotto, 2015; Ramírez-Francel et al., 2022). These animals have also long been known to host and transmit a variety of pathogens to humans and other animals including Lyssavirus, Hendra and Nipah henipaviruses, Ebola and Marburg filoviruses (Brook and Dobson, 2015), as well as a variety of parasites including helminths

(Moguel-Chin et al., 2023), haemosporidians (Tsague et al., 2022), *Toxoplasma* (Yang et al., 2021), *Leishmania* (Nunes et al., 2017) and *Trypanosoma* (Hamilton et al., 2012; Barbosa et al., 2016; Austen and Barbosa, 2021). Since the discovery of bats as reservoirs of SARS-CoV-1 and more recently a virus closely related to SARS-CoV-2, the cause of the recent COVID-19 pandemic (Zhou et al., 2020), there has been renewed interest in bats as reservoirs of zoonotic infectious diseases.

There are many factors that make bats excellent disease transmitters, including unique immune defense mechanisms which allow them to harbour highly pathogenic organisms asymptotically (Irving et al., 2021; Sia et al., 2022). Bats are also social mammals, living relatively long lives in large roosting colonies. Importantly, these mammals have the ability to fly to different geographical areas allowing pathogen dispersal over long distances, thus facilitating pathogen establishment in naïve bat populations (Nunes et al., 2017; Van Brussel and Holmes, 2022). The ability of bats to travel across wide geographical areas, coupled with phylogenetic analysis of trypanosome lineages, led Hamilton et al. (2012) to propose the “bat seeding” hypothesis which speculates that bats transmitted ancestral *Trypanosoma cruzi* lineages to terrestrial mammals and marsupials.

Cryptosporidium and *Giardia* are zoonotic protozoan pathogens of

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<https://doi.org/10.1016/j.crpvbd.2023.100155>

Received 5 October 2023; Received in revised form 8 November 2023; Accepted 16 November 2023

Available online 23 November 2023

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global significance, which infect a wide range of hosts, including bats. Human cryptosporidiosis is a leading cause of diarrhoea worldwide, particularly in children and immunocompromised individuals, and is primarily caused by *Cryptosporidium parvum* and *Cryptosporidium hominis* (Troeger et al., 2017; Ryan et al., 2021). *Giardia* is a genetically diverse parasite of humans and various animals with the species complex, *Giardia duodenalis* (syn. *Giardia lamblia* and *Giardia intestinalis*), being the main species infecting mammals including humans. Within *G. duodenalis*, assemblages A and B are responsible for ~95% of human *Giardia* infections, and are also thought to be zoonotic, whereas the remaining assemblages (C to H) are mainly host-specific (Cai et al.,

2021).

The role of bats in the transmission of *Cryptosporidium* and *Giardia* has been very poorly studied. Both parasites are important causes of gastrointestinal disease, particularly in young children, and are both associated with long-term health sequelae (Hunskar et al., 2021; Boks et al., 2022; Dougherty and Bartelt, 2022; Helmy and Hafez, 2022). There are no vaccines for either parasite and both are frequently refractory to therapy (Lalle and Hanevik, 2018; Khan and Witola, 2023). Considering these enteric pathogens' resilience in the environment and resistance to traditional desinfection measures, a thorough understanding of their transmission routes is essential for public health

Table 1
Cryptosporidium and *Giardia* species and genotypes identified in bats globally.

Species/Genotype/Assemblage	Hosts	Prevalence	Country	Reference
<i>Cryptosporidium</i>				
<i>C. hominis</i>	Grey-headed flying fox (<i>Pteropus poliocephalus</i>)	0.7% (2/281)	Australia	Schiller et al. (2016)
<i>C. parvum</i>	Western small-footed bats (<i>Myotis ciliolabrum</i>)	50.0% (1/2)	USA	Kváč et al. (2015)
	Common pipistrelle (<i>Pipistrellus</i>)	9.1% (1/11)	Czech Republic	Kváč et al. (2015)
<i>C. tyzzeri</i>	Large-footed bat (<i>Myotis adversus</i>)	100% (1/1)	Australia	Morgan et al. (1999)
Unnamed <i>Cryptosporidium</i> bat genotype (OQ132822)	Little yellow-shouldered Mesoamerican bat (<i>Sturnira parvidens</i>)	9.1% (1/11)	Costa Rica	Carbonara et al. (2022)
Bat genotype I (KC445650, KC445651)	Chinese rufous horseshoe bat (<i>Rhinolophus sinicus</i>)	5.4% (4/74)	China	Wang et al. (2013)
Bat genotype I (KC445654)	Stoliczka's trident bat (<i>Aselliscus stoliczkanus</i>)	7.8% (4/51)	China	Wang et al. (2013)
Bat genotype II (KC445652)	Fulvous roundleaf bat or fulvous leaf-nosed bat (<i>Hipposideros fulvus</i>)	7.2% (5/69)	China	Wang et al. (2013)
Bat genotype II (KC445655)	Leschenault's rousette (<i>Rousettus leschenaultia</i>)	5.7% (3/53)	China	Wang et al. (2013)
Bat genotype III (KR819166, KR819167)	Big brown bat (<i>Eptesicus fuscus</i>)	18.2% (2/11)	USA	Kváč et al. (2015)
Bat genotype IV (KR819168, KR819169)	Common pipistrelle (<i>Pipistrellus</i>)	18.2% (2/11)	Czech Republic	Kváč et al. (2015)
Bat genotype V (LC089977)	Cave nectar bat (<i>Eonycteris spelaea</i>)	2.2% (1/45)	Philippines	Murakoshi et al. (2016)
Bat genotype VI (LC089976)	Lesser short-nosed fruit bat (<i>Cynopterus brachyotis</i>)	2.2% (1/45)	Philippines	Murakoshi et al. (2016)
Bat genotype VII (LC089979)	Philippine forest horseshoe bat (<i>Rhinolophus inops</i>)	2.2% (1/45)	Philippines	Murakoshi et al. (2016)
Bat genotype VIII (KX118594)	Grey-headed flying-fox (<i>Pteropus poliocephalus</i>)	0.3% (1/281)	Australia	Schiller et al. (2016)
Bat genotype IX (KX118595)	Grey-headed flying-fox (<i>Pteropus poliocephalus</i>)	0.3% (1/281)	Australia	Schiller et al. (2016)
Bat genotype X (KX118596)	Grey-headed flying-fox (<i>Pteropus poliocephalus</i>)	0.7% (2/281)	Australia	Schiller et al. (2016)
Bat genotype XI (KX118597)	Grey-headed flying-fox (<i>Pteropus poliocephalus</i>)	1.4% (4/281)	Australia	Schiller et al. (2016)
Bat genotype XII (LC276360, LC276361)	Northern bat (<i>Eptesicus nilssonii</i>)	66.6% (2/3)	Japan	Murakoshi et al. (2018)
Bat genotype XIII (previously bat genotype II) (LC089978)	Greater musky fruit bat (<i>Ptenochirus jagori</i>)	2.2% (1/45)	Philippines	Murakoshi et al. (2016)
Bat genotype XIV (MK007969-MK007971)	Straw-coloured fruit bat (<i>Eidolon helvum</i>)	4.6% (5/109)	Nigeria	Li et al. (2018)
Bat genotype XV (MK007972)	Straw-coloured fruit bat (<i>Eidolon helvum</i>)	0.9% (1/109)	Nigeria	Li et al. (2018)
Bat genotype XVI (MH553322, MH553323)	Flat-faced fruit-eating bat (<i>Artibeus planirostris</i>)	7.9% (6/76)	Brazil	Batista et al. (2019)
Bat genotype XVI	White-lined broad-nosed bat (<i>Platyrrhinus lineatus</i>)	4.3% (1/23)	Brazil	Batista et al. (2019)
Bat genotype XVI	Great fruit-eating bat (<i>Artibeus lituratus</i>)	7.2% (1/14)	Brazil	Batista et al. (2019)
Bat genotype XVI-like (OQ132820)	Jamaican fruit bat (<i>Artibeus jamaicensis</i>)	5.0% (1/20)	Costa Rica	Carbonara et al. (2022)
Bat genotype XVI-like (OQ132821)	Pacific tent-making bat (<i>Uroderma convexum</i>)	11.1% (1/9)	Costa Rica	Carbonara et al. (2022)
Bat genotype XVII (MH553324, MH553325)	Flat-faced fruit-eating bat (<i>Artibeus planirostris</i>)	1.3% (1/76)	Brazil	Batista et al. (2019)
Bat genotype XVII	Dark fruit-eating bat (<i>Artibeus obscurus</i>)	16.7% (1/6)	Brazil	Batista et al. (2019)
Bat genotype XVIII (MH553326)	Seba's short-tailed bat (<i>Carollia perspicillata</i>)	8.3% (1/12)	Brazil	Batista et al. (2019)
Bat genotype XIX (OP346577- OP346579)	Seba's short-tailed bat (<i>Carollia perspicillata</i>)	16.6% (4/24)	Colombia	Silva-Ramos et al. (2023)
Bat genotype XIX-like (OQ132823)	Seba's short-tailed bat (<i>Carollia perspicillata</i>)	10.0% (1/10)	Costa Rica	Carbonara et al. (2022)
Bat genotype XX (OP346576)	Trinidadian funnel-eared bat (<i>Natalus tumidirostris</i>)	8.7% (2/23)	Colombia	Silva-Ramos et al. (2023)
<i>Giardia</i>				
Not typed	Lesser bulldog bat (<i>Noctilio albigentris</i>)	7.1% (1/14)	Brazil	Lima et al. (2018)
Not typed	Velvety free-tailed bat (<i>Molossus</i>)	21.7% (5/23)	Brazil	Lima et al. (2018)
Not typed	Insectivorous bats	3.3% (1/30)	Nepal	(Adhikari et al., 2020)
Unknown ^a	Fringe-lipped bat (<i>Trachops cirrhosis</i>)	100% (1/1)	Costa Rica	Carbonara et al. (2022)
Not applicable ^b	Straw-coloured fruit bats (<i>Eidolon helvum</i>)	0% (0/109)	Nigeria	Li et al. (2018)

^a 18S sequence too short to type.

^b No positive samples identified.

interventions. As a result of the morphological overlap between *Cryptosporidium* oocysts of most species (Fall et al., 2003) and also morphological similarities between *Giardia* cysts and trophozoites of different species and assemblages (Hillman et al., 2016), genetic identification is essential. This review will examine available evidence on the genetic diversity and prevalence of zoonotic species of *Cryptosporidium* and *Giardia* in bats.

2. Diversity of *Cryptosporidium* species and genotypes in bats

Relatively few studies have examined the prevalence and diversity of *Cryptosporidium* spp. in bats with only ~3% of bat species screened for *Cryptosporidium* to date (Schiller et al., 2016). *Cryptosporidium* has currently been genetically characterised in 23 species of bats from six families (Hipposideridae, Natalidae, Phyllostomidae, Pteropodidae, Rhinolophidae and Vespertilionidae) in studies in Australia, Brazil, Colombia, Costa Rica, China, the Czech Republic, Japan, Nigeria and the Philippines (Table 1). The overall prevalence of *Cryptosporidium* in bats is variable with prevalences ranging from 2.1% (Kvác et al., 2015) to 16.3% (Batista et al., 2019).

Three *Cryptosporidium* spp. (*C. hominis*, *C. parvum* and *C. tyzzeri*), 20 bat genotypes (bat genotype I-XX), and one unnamed bat genotype have been reported in bats (Table 1). A simplified phylogenetic depiction of *Cryptosporidium* sequences derived from bats (Fig. 1), reveals that the majority of bat genotypes identified to date exhibit significant divergence from both *C. parvum* and *C. hominis*, indicating minimal zoonotic risk. Of the 20 known bat genotypes, most have been described from individual hosts, but some are common to several species. For example, bat genotype I has been identified in Chinese rufous horseshoe bats and

Stoliczka's trident bats, bat genotype II has been identified in *Fulvus* roundleaf bats and Leschenault's rousette bats, with bat genotypes XVI and XVI-like having the broadest host range as they have been reported in five species of bat; three species of *Artibeus* fruit bats, a white-lined broad-nosed bat and a Pacific tent-making bat in studies from Brazil and Costa Rica (Table 1). In 2016, Murakoshi et al. (2016) reported detecting bat genotype II in a Greater musky fruit bat; however, this was subsequently recognised as a separate genotype and renamed bat genotype XIII (LC089978) (Li et al., 2018).

Phylogenetic analyses of sequences recently obtained in a study in Costa Rica (Carbonara et al., 2022) revealed that four bat-like genotypes were identified: bat genotype XVI-like sequences from a Jamaican fruit bat and a Pacific tent-making bat (99.6% and 97% identity respectively), a bat genotype XIX-like sequence (98.7% similarity) in a Seba's short-tailed bat and an unnamed bat sequence was identified from a little yellow-shouldered Mesoamerican bat (OQ132822), that had the highest similarity to bat genotype XVIII (87.5%) (Table 1). Longer 18S sequences from the unnamed bat sequence need to be generated before its phylogenetic relationships to other bat genotypes can be determined. Phylogenetic analysis has also shown some groupings amongst the bat genotypes; for example bat genotype V (from a Cave nectar bat) and bat genotype XI (from a grey-headed flying-fox), which are both fruit bats form a clade together. Similarly, bat genotypes VIII, IX and X (all from grey-headed flying-fox) also clustered together. Bat genotypes II, XIII, XIV and XV again all from fruit bats grouped together in another clade (Li et al., 2018). The most recently described bat genotype XIX had the highest identity to bat genotype XII (97.9%), while bat genotype XX unusually grouped in a clade with the gastric parasites *C. andersoni* and *C. muris* (Silva-Ramos et al., 2023). The remaining bat genotypes are

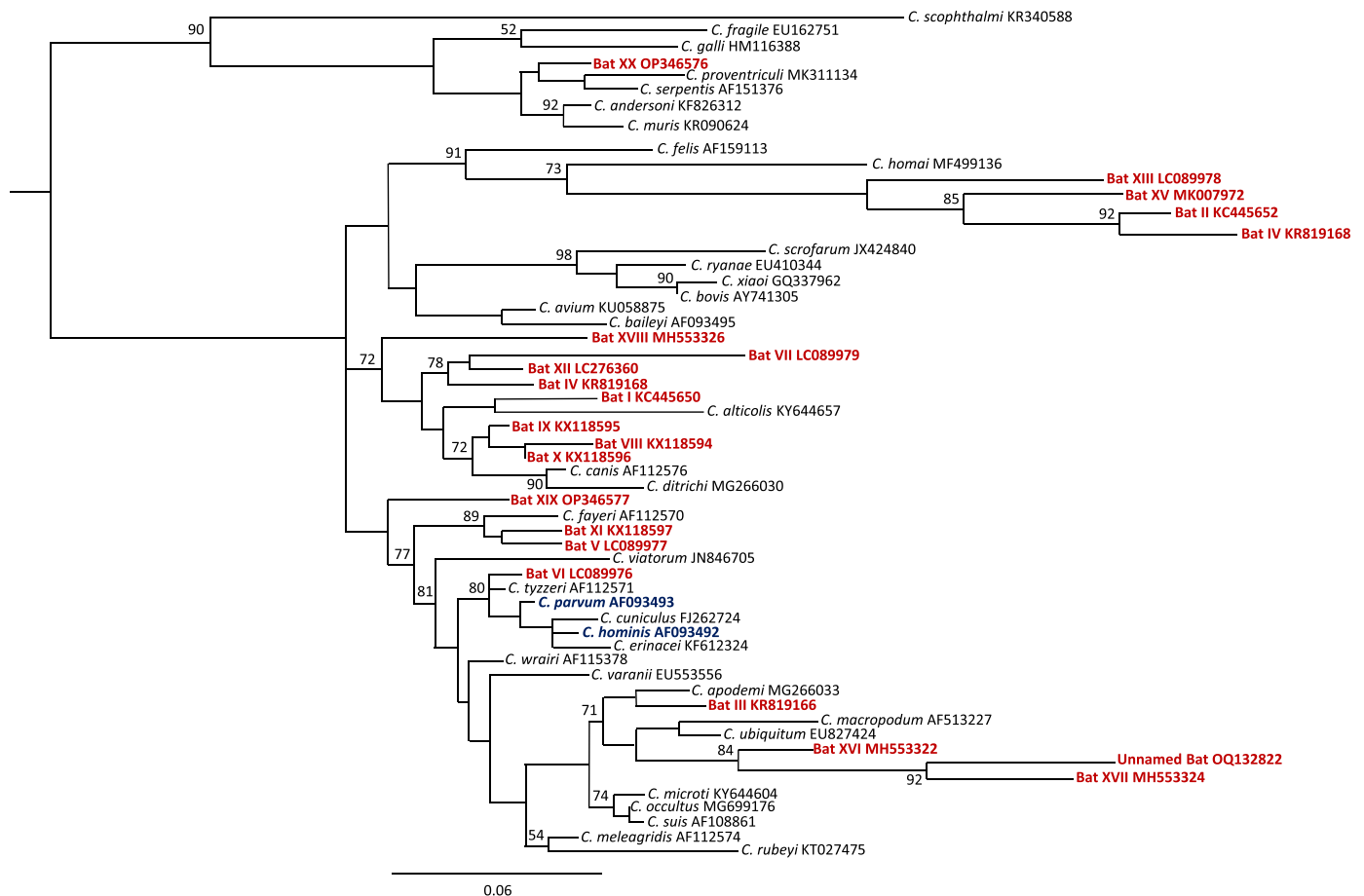


Fig. 1. Maximum likelihood analysis of 18S rDNA sequences from bats (red) and main human-pathogenic *Cryptosporidium* spp. (blue) based on partial sequences (451 bp). Created in Geneious version 2023.1 (by Biomatters), available from <https://www.geneious.com>.

dispersed throughout the intestinal clade. The phylogeny of bat-derived *Cryptosporidium* isolates is currently poorly resolved and longer 18S sequences and phylogenetic analysis at multiple loci is required to better understand their phylogenetic relationships but they are all likely separate species. The 20 bat genotypes are thought to be host-specific as there have been no reports in humans, although *Cryptosporidium* bat genotype II was reported from a water treatment plant in Colombia (0.9%; 1/110) (Sánchez et al., 2018).

Cryptosporidium hominis was identified in two (2%; 2/102) captive grey-headed flying foxes from Tolga, Queensland and 0/179 wild flying foxes (overall prevalence 0.7%; 2/281) (Schiller et al., 2016). Typing at the *gp60* locus identified *C. hominis* subtype Iba9G2 in one of these samples (Schiller et al., 2016), which is one of the most commonly reported *C. hominis* subtypes in people in Australia and globally (Waldron et al., 2009). Overall in that study, *Cryptosporidium* spp. were detected in 3.2% (9/281) of flying fox faecal samples, with a higher prevalence in captive (5.9%; 6/102) compared to wild bats (1.7%; 3/179) (Schiller et al., 2016), with all the remaining *Cryptosporidium* positives identified as bat-specific genotypes VIII-XI (see Table 1).

Cryptosporidium parvum was identified by restriction fragment length polymorphism (RFLP) in a big brown bat (*Eptesicus fuscus*) from New York state watershed (Ziegler et al., 2007), but was not confirmed by sequencing and is not included in Table 1. In another study that screened 281 faecal samples from 22 species of bats, two *C. parvum* positives (0.7% prevalence) were identified by PCR and sequencing; one from a common pipistrelle bat from the Czech Republic and one from a western small-footed bat from the USA (Kváč et al., 2015). *Cryptosporidium tyzzeri* was identified in one large-footed bat from New South Wales, Australia (Morgan et al., 1999).

3. *Giardia* in bats

It is currently unknown whether bats carry zoonotic *Giardia* spp. There have only been a few reports of *Giardia* in bats however this parasite was not characterised to species or assemblage levels in those studies (Lima et al., 2018; Adhikari et al., 2020; Carbonara et al., 2022) (Table 1). *Giardia* has been reported in a lesser bulldog bat and a velvety free-tailed bat in Brazil at a prevalence of 7.1% and 21.7% respectively (Lima et al., 2018), and in one fringe-lipped bat in Costa Rica (Carbonara et al., 2022). The prevalence of *Giardia* in bats from Nepal was 3.3% (1/30) in insectivorous bats (Adhikari et al., 2020). In a study conducted in Nigeria, none of the 109 straw-coloured fruit bats tested were positive for *Giardia* (Li et al., 2018).

4. Zoonotic risk of *Cryptosporidium* and *Giardia* from bats

Bat-specific *Cryptosporidium* genotypes account for 91.5% of *Cryptosporidium*-positive samples typed from bats, with *C. parvum* and *C. hominis* accounting for 3.4% each of the typed positives and *C. tyzzeri*, a rodent-associated species, accounting for 1.7% of positives (Fig. 2). The identification of *C. hominis* and *C. parvum* in bats, is most likely due to mechanical carriage, as no oocysts were detected in the two *C. parvum* positives reported by Kváč et al. (2015), and oocysts were not demonstrated in the study which identified *C. hominis* in flying foxes in Australia (Schiller et al., 2016). Evidence of active *C. hominis* and *C. parvum* infections in bats is needed to confirm if bats can be infected by these two species. Similarly, *C. tyzzeri* is primarily a rodent species, and the identification of *C. tyzzeri* in a bat (Morgan et al., 1999), may also have been due to mechanical carriage. The risk of zoonotic transmission of *Giardia* from bats is currently unknown as very few studies have been conducted and no samples have been genetically typed. This is a major knowledge gap.

Many bat species are very sensitive to ecological disturbances, particularly urbanization, which has negative impacts on many bat species including population size and diversity reductions (Russo and Ancillotto, 2015). Loss of resources can also force adaptable bat species

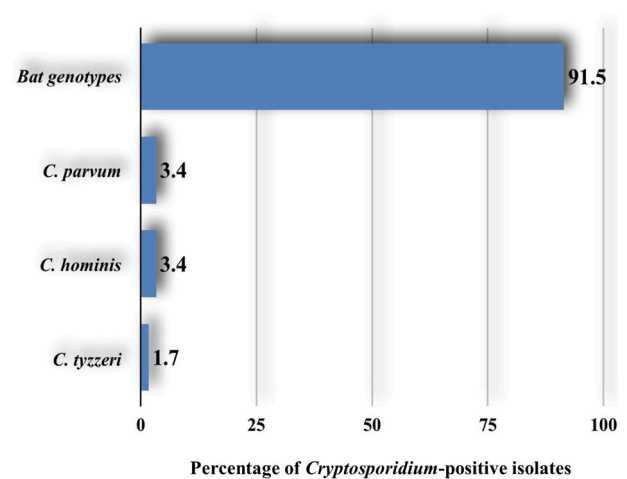


Fig. 2. *Cryptosporidium* species and genotypes in bats globally as a percentage of all positive isolates typed.

to expand into urban environments to take advantage of new food resources (Russo and Ancillotto, 2015; Nunes et al., 2017; Yabsley et al., 2021). It is well-recognised that growing contact between wildlife and humans can result in wildlife becoming reservoirs of zoonotic disease, increasing the risk of emergence of zoonotic diseases in humans (Gibb et al., 2020). In general, urbanization does not appear to have made a major impact on the prevalence of zoonotic *Cryptosporidium* spp. in bats, as to date, most studies on *Cryptosporidium* in bats have examined samples from urban or close to urban areas (Ziegler et al., 2007; Wang et al., 2013; Murakoshi et al., 2016, 2018; Schiller et al., 2016; Li et al., 2018; Carbonara et al., 2022; Silva-Ramos et al., 2023), yet predominantly bat-adapted *Cryptosporidium* genotypes have been identified in bats (Table 1 and Fig. 2).

The only bat species in which *C. hominis* was reported was the Australian grey-headed flying-fox (Schiller et al., 2016). In Australia, there are four native species of fruit bats (*Pteropus* spp.) which have readily adapted to urban ecosystems, with most major east coast cities and towns now persistently occupied by flying foxes (Tait et al., 2014; McCarthy et al., 2021; Yabsley et al., 2021). The grey-headed flying-fox is the only endemic species, and is the main fruit bat species found across New South Wales, Victoria and South Australia (Australian Government, 2021), where they form large tree roost colonies containing up to 50,000 individuals, frequently close to humans in parks (Tait et al., 2014; Australian Government, 2021).

Individuals within colonies are highly mobile (Welbergen et al., 2020) and there is a risk of bats becoming reservoirs of human-infectious diseases. *Salmonella enterica* has been detected in grey-headed flying-foxes in New South Wales (McDougall and Power, 2021; Van Brussel et al., 2023); however, they are not considered major reservoirs for *Salmonella*, as the prevalence is very low (0.4%; 1/254) (McDougall and Power, 2021). Similarly, enteropathogenic *Escherichia coli* (EPEC) has been detected in 17.4% of grey-headed flying-fox faecal samples collected from New South Wales and South Australia; however, whole genome sequencing suggested that the bats were carrying mostly bat-specific lineages of EPEC (McDougall et al., 2023).

Growing contact between bats and humans also increases the potential for spill-back of human-infectious pathogens such as *Cryptosporidium* spp. into bats. In the study by Schiller et al. (2016), the prevalence of *C. hominis* was low 0.7% (2/281) compared to bat-specific genotypes (2.8%; 8/281). Importantly, it is unknown if the detection of *C. hominis* in the bats was due to mechanical transmission between humans and bats or was an actual infection, as oocysts were not screened for in the bat faecal samples (Schiller et al., 2016). It is also important to note that *C. hominis* was only detected in captive grey-headed flying foxes and not wild flying foxes, where the potential for spill-back from humans was

higher compared to wild flying foxes (Schiller et al., 2016). However, the potential for bats to become an important reservoir of human-infectious *Cryptosporidium* in urban areas needs to be examined in more detail.

Management of bat colonies is complex and previous studies on viral pathogens in bats have shown that culling and/or disturbing bat colonies did not eliminate the risk of zoonotic spill-over (e.g. Streicker et al., 2012; Amman et al., 2014). Integrated and coordinated, evidence-based management plans, particularly ecological solutions such as habitat repair, are required to reduce the risk of zoonotic transmission from bats while still supporting their essential ecosystem services (Sokolow et al., 2019).

5. Conclusions

To date, relatively few studies have examined the prevalence and diversity of *Cryptosporidium* in bats. However, current evidence suggests that bats are predominantly infected with bat-specific genotypes and there is a lack of evidence of active infection of bats with zoonotic *Cryptosporidium* species. Future studies in additional countries on a wider range of bat species will likely identify many more bat-adapted genotypes. Additionally, studies focussed on urban-adapted bats are required to better understand the potential for spill-back of human infectious *Cryptosporidium* spp. into bats. Nothing is known about the prevalence of zoonotic *Giardia* in bats, therefore screening and genotyping of *Giardia*-positive samples are essential to understand the zoonotic risk of *Giardia* from these animals.

Funding

This work was funded by Water Research Australia (WaterRA), project number 1156 and the 111 Project of China (D20008).

Ethical approval

Not applicable.

CRedit authorship contribution statement

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.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Given their role as Guest Editor, Amanda Barbosa had no involvement in the peer review of this article and has no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to Dr Frank Katzer (Co-Editor) and Professor Aneta Kostadinova (Editor-in-Chief).

Data availability

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

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