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PROTOZOOLOGY - REVIEW

Zoonotic giardiasis: an update

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Abstract

Giardia duodenalis is a common intestinal parasite in various hosts, with the disease giardiasis being a zoonosis. The use of molecular typing tools has improved our understanding of the distribution and zoonotic potential of *G. duodenalis* genotypes in different animals. The present review summarizes recent data on the distribution of *G. duodenalis* genotypes in humans and animals in different areas. The dominance of *G. duodenalis* assemblages A and B in humans and common occurrence of host-adapted assemblages in most domesticated animals suggests that zoonotic giardiasis is probably less common than believed and could be attributed mainly to contact with or contamination from just a few species of animals such as nonhuman primates, equines, rabbits, guinea pigs, chinchillas, and beavers. Future studies should be directed to advanced genetic characterization of isolates from well-designed epidemiological investigations, especially comparative analyses of isolates from humans and animals living in the same household or community. This will likely lead to better understanding of zoonotic transmission of *G. duodenalis* in different environmental and socioeconomic settings.

Keywords *Giardia duodenalis* · Giardiasis · Zoonosis · Genotyping · Molecular epidemiology

Introduction

Giardia spp. are common intestinal protozoan parasites in humans and various animals (Dixon 2021). The life cycle of *Giardia* spp. includes two main stages, the trophozoite and the cyst. The infectious cyst, formed in the large intestine of hosts, is relatively resistant to disinfectants and environmental degradation (Einarsson et al. 2016). Numerous cysts are excreted with feces from infected hosts, sustaining the transmission of the pathogen (Dixon 2021). The main clinical manifestations of giardiasis include diarrhea, bloating, malnutrition, weight loss, with most infections being self-limiting (Zahedi et al. 2017). While symptomatic giardiasis frequently requires treatment (Morch and Hanevik 2020), the vast majority of infected individuals in endemic areas remain asymptomatic (Lalle and Hanevik 2018).

It is reported that infection rates in low- and middle-income countries are much higher than those in high-income countries, ranging from 8.0 to 30.0% and 0.4 to 7.5%, respectively (Feng and Xiao 2011). The occurrence of infections is associated with many factors, such as young age, low socioeconomic development, poor hygiene, contact with infected individuals, drinking untreated water, and presence of diarrhea (Dixon 2021). It is estimated that there are 184 million giardiasis cases each year, with the majority occurring in low- and middle-income countries (Kirk et al. 2015). In addition, giardiasis is a major cause for waterborne and foodborne outbreaks of enteric disease in industrialized nations (Einarsson et al. 2016; Ryan et al. 2019). There have been over 300 reported outbreaks of giardiasis in the world since 1954, most of which are related to contaminated water (Baldursson and Karanis 2011; Efstratiou et al. 2017).

Giardiasis has been regarded as zoonosis for quite some time by some researchers (Buret et al. 1990; Faubert 1988; Kasprzak and Pawlowski 1989; Thompson et al. 1988b). This was largely based on the lack of host specificity of

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some isolates in cross transmission studies and finding of genetically identical forms in humans and some animals. Controversies, however, long exist regarding the extent of giardiasis as a zoonosis (Bemrick and Erlandsen 1988; Connaughton 1989; Eckert and Wolff 1979; Gasser 1990; Thompson et al. 1988a). This is largely based on the existence of genetically unique isolates in some animals and the lack of evidence of direct transmission of the pathogen between humans and animals. The present report reviews recent publications in PubMed since our last review (Feng and Xiao 2011) on genetic diversity of the causative agent of giardiasis and the distribution of genotypes and subtypes of the pathogen in humans and animals. Nucleotide from the reported new subtypes within assemblage A at the three widely used genotyping loci were analyzed to re-name them in compliance with the established subtype nomenclature (Caccio et al. 2008; Feng and Xiao 2011). The new subtypes are considered valid only if the same sequence type has been identified in multiple studies or the same nucleotide substitutions are present in multiple sequences in GenBank. Overall, the data generated from this review suggest that zoonotic giardiasis is probably less common than believed and could be attributed mainly to contact with or contamination from just a few species of animals.

Giardia duodenalis genotypes

The causative agent of giardiasis in humans is *G. duodenalis* (synonyms: *G. intestinalis* and *G. lamblia*). In addition to humans, *G. duodenalis* has been found in a broad range of mammals. Other species in mammals include *G. muris* (in rodents), *G. microti* (in muskrats, voles, deer mice), *G. peramelis* (in quenda), and *G. cricetidarum* (in hamsters). In addition, *G. agilis* (in amphibians), *G. ardeae* (in herons and other birds) and *G. psittaci* (in budgerigars and parakeets) have been described in other vertebrates (Ryan and Zahedi 2019). Most studies on the biology and genetics of *Giardia* spp. have been conducted with *G. duodenalis* (Adam 2021).

Eight genotypes have been described in *G. duodenalis* based on sequence analysis of several genes. They are known as assemblages A to H (Ryan and Zahedi 2019). Each assemblage consists of many related subtypes, which form a large cluster in phylogenetic trees built with sequences from individual loci. Some of the assemblages have robust subdivisions in phylogenetic analysis of sequences, forming well-supported subclusters of sequences across multiple genetic loci. These consistent subdivisions at multiple genetic loci are known as sub-assemblages. For example, within assemblage A, there are three common subassemblages known as AI, AII and AIII, which form congruent subclusters in phylogenetic analysis of sequences from multiple genetic loci (Feng and Xiao 2011).

Among the eight assemblages of *G. duodenalis* assemblages A and B have the broadest host ranges, therefore are considered zoonotic (Feng and Xiao 2011). Other genotypes, assemblages C to H, have narrow host ranges (Caccio et al. 2018). Among them, assemblages C and D are mainly found in canine animals, assemblage E mostly infects hoofed mammals such as cattle, sheep, goats, and pigs (Ryan and Zahedi 2019), while assemblages F, G, and H have been mostly reported in felids, rodents, and seals, respectively (Abdel-Moein and Saeed 2016; Caccio et al. 2018; Li et al. 2019). Exceptions, however, occur in infections with these host-adapted *G. duodenalis* genotypes. For instance, assemblages C, D, E, and F have been reported in humans (Abdel-Moein and Saeed 2016; Broglia et al. 2013; Liu et al. 2014b; Soliman et al. 2011; Strkolcova et al. 2015). The number of cases involved has been generally small, except for assemblage E, which has been reported in at least 57 people in several countries (Abdel-Moein and Saeed 2016; Fantinatti et al. 2016; Foronda et al. 2008; Garcia et al. 2021; Helmy et al. 2014; Iwashita et al. 2021; Zahedi et al. 2017). The zoonotic potential of these genotypes needs further assessment.

Molecular typing tools in *G. duodenalis*

Genotyping tools

Three genetic loci, β-giardin (*bg*), triosephosphate isomerase (*tpi*), and glutamate dehydrogenase (*gdh*) genes, are common markers for species differentiation and genotyping of *Giardia* spp. (Feng and Xiao 2011). This generally involves sequence analysis of PCR products from these targets. The SSU rRNA locus is another marker for species differentiation. The conserved nature of that locus however, makes genotyping results of *G. duodenalis* less reliable (Brynildsrud et al. 2018; Feng and Xiao 2011). Phylogenetic analysis of the nucleotide sequences is generally used in supporting genotype identification. Reference sequences of these genes are available for common *G. duodenalis* assemblages (Feng and Xiao 2011).

Subtyping tools

Sequence analysis of the *bg*, *tpi*, and *gdh* genes is also used in subtyping human-pathogenic *G. duodenalis* genotypes. Other more variable markers such as microsatellites are available (Ankarklev et al. 2018; Durigan et al. 2018; Wielinga et al. 2015). Between the two common *G. duodenalis* genotypes in humans, assemblage A appears to be less polymorphic, producing several subtypes at each of the three commonly used genetic loci. Subtypes differ from each by one to a few single nucleotides (Feng and Xiao 2011). Among common subtypes of assemblage A, A1 and

A5 subtypes are mainly found in animals, A2-A4 subtypes mostly in humans, and A6 mostly in wild ruminants (Feng and Xiao 2011). Other less common subtypes are found at these genetic loci, including several newly established ones (A7-A12 at the *tpi* locus and A7-A9 at the *bg* locus and at the *gdh* locus; Table 1). However, there are not enough data to indicate whether there are apparent host preference and geographic distribution in these new subtypes.

Assemblage B is more polymorphic than assemblage A, with the generation of numerous subtypes at each of the three common genotyping loci. Unlike in assemblage A, however, there is no consistent segregation of isolates in phylogenetic analysis of the sequences among the three widely used genetic loci (Brynildsrud et al. 2018; Xiao and Feng 2017). Recently, a novel multilocus sequence typing (MLST) tool was developed using three new genetic markers (Seabolt et al. 2021). This new methodology for typing assemblage B was based on genomics analysis of all core genes and comparisons of their phylogenetic trees with the tree based on whole genomic sequences. Three genetic loci (*6pgd*, a hypothetical protein, and *phkg2*) with low sequence heterozygosity and better agreement with the topology of whole genome-based phylogeny were identified (Seabolt et al. 2021). Sixty-eight isolates were successfully typed using these three loci, with the formation of robust subgroups compared with the result using the traditional markers (Seabolt et al. 2021). The utility of this new MLST tool needs verifications from analysis of additional assemblage B isolates from other hosts and areas.

Assemblage E is also highly polymorphic. Although many assemblage E subtypes were found in recent studies, there has been no evidence of the formation of host-specific subgroups at the *bg*, *tpi*, and *gdh* loci (Feng et al. 2019; Naguib et al. 2018; Qi et al. 2016; Wang et al. 2014; Wang et al. 2017b; Wegayehu et al. 2017; Zhao et al. 2015). The utility of the recently identified new genotyping markers for assemblages A and B has not been assessed for assemblage E. Sequence polymorphism is apparently also present among assemblages C and D isolates, although the utility of subtyping these pathogens has not been demonstrated (Li et al. 2015b; Zhang et al. 2016; Zhang et al. 2017b).

Multilocus genotyping tools

In *G. duodenalis*, the result of genotyping at the *bg*, *tpi*, and *gdh* loci sometimes may be inconsistent, making it a common practice to use multiple markers in genotyping isolates, which can generate more robust clustering of isolates using concatenated sequence data (Brynildsrud et al. 2018; Feng and Xiao 2011). The sequence data generated from these loci are analyzed for single nucleotide substitutions (SNPs) in assemblage A, B, and E isolates (Xiao and Feng 2017). Moreover, the MLST data generated have been analyzed for population genetic structures of *G. duodenalis* in humans and animals using various software packages (Choy et al. 2015; Durigan et al. 2017; Gabin-Garcia et al. 2017).

As indicated above, MLST characterizations of isolates have led to the identification of three major sub-assemblages (AI, AII, and AIII) of assemblage A, with 9–12 subtypes (A1, A2, A3, etc.) at individual loci (Brynildsrud et al. 2018). Sequences of sub-assemblages form congruent subclusters of isolates in phylogenetic analyses, leading to consistent subtype identification across these genetic loci, such as A1 or A5 subtypes commonly seen in sub-assemblage AI at each of the three genetic loci (*bg*, *gdh*, and *tpi*), A2 subtype commonly seen in sub-assemblages AII at all three genetic loci, and A6 subtype seen in sub-assemblage AIII at all three genetic loci (Table 2). Therefore, sequence data from all three genetic loci are required to establish the subassemblage identity of assemblage A isolates. Apparent host-adaption has been observed among the three classical sub-assemblages; sub-assemblage AI is mainly found in animals, sub-assemblage AII is most found in humans, while sub-assemblage AIII has been almost exclusively found in wild ruminants especially deer (Feng and Xiao 2011).

In contrast, the initial identification of sub-assemblages BIII and BIV-based results of allozyme electrophoretic analysis is not supported by MLST analysis (Brynildsrud et al. 2018; Xiao and Feng 2017). The analysis of MLST data has led to the identification of a host-adapted subpopulation of assemblage B in Old World monkeys (Chen et al. 2019b; Karim et al. 2015). This is yet supported by the characterization of isolates using MLST analysis of the newly identified genetic markers, which have generated more robust phylogenetic relationships among assemblage B isolates (Seabolt et al. 2021).

Multilocus sequence analysis of the *bg*, *tpi*, and *gdh* genes has been commonly used in subtyping assemblage E isolates from ruminants. A study conducted in Qinghai, China had identified different subpopulations between Tibetan sheep and yaks sharing pastures. However, it had also identified a subpopulation shared between the two species of animals (Jin et al. 2017). Some studies had identified geographically segregated assemblage E subpopulations (Cui et al. 2018; Qi et al. 2016; Wang et al. 2016a; Wang et al. 2016b; Zhong et al. 2018). The high infection rates and presence of multiple subtypes on most study farms make the MLST-based subtyping of assemblage E isolates problematic (Feng et al. 2019; Wang et al. 2019; Wang et al. 2017b). The common occurrence of genetic recombination among isolates on individual farms further indicates that subtyping based on a few genetic loci is probably not meaningful for assemblage E (Wang et al. 2019).

Table 1 Subtypes of *Giardia duodenalis* assemblage A at three commonly used genetic loci (2000–2021)

Genetic locus	Subtype	Reference sequence	Host	References
tpi	A1	L02120, EU014517, EF688040	Sheep, dog, cattle, human gull	Benhassine et al. (2020), Feng and Xiao (2011), Wang et al. (2011), Zahedi et al. (2017) and Zheng et al. (2014)
	A2	U57897	Human	Costache et al. (2020), Feng and Xiao (2011), Wang et al. (2011) and Zahedi et al. (2017)
	A3	EU041754	Human	Lalle et al. (2009)
	A4	AB509382, JQ928710	Human, sheep, cat, ferret	Feng and Xiao (2011), Lebbad et al. (2010) and Zhang et al. (2012)
	A5	EU781000, AB509383, JQ837805[a], JQ837806[a]	Sheep, gorilla, human, cat	Feng and Xiao (2011), Sak et al. (2013) and Thompson (2004)
	A6	EU781002, DQ650648, MT060488[a]	Deer, human, cat	Costache et al. (2020), Feng and Xiao (2011) and Solarczyk et al. (2012)
	A7	EU014501[a], EU518563[a]	Human, gull	Lasek-Nesselquist et al. (2008) and Teodorovic et al. (2007)
	A8	FJ890961[a], HQ259661[a]	Monkey, deer	Beck et al. (2011b) and Levecke et al. (2009)
	A9	MK639172[a]	Sheep, monkey	Karim et al. (2015) and Peng et al. (2020)
	A10	AB569394[a], AB569398[a]	Cat, human	Suzuki et al. (2011)
	A11	MH673809[a]	Lemur, human	Karim et al. (2015) and Yu et al. (2019b)
	A12	MH673818[a]	Human, macaque	Ye et al. (2014) and Yu et al. (2019b)
bg	A1	X85958, X14185	Cattle, human, chinchilla, pig, sheep, dog, fish, fox	Budu-Amoako et al. (2012a), Feng and Xiao (2011), Gomez-Munoz et al. (2012), Minetti et al. (2015), Pantchev et al. (2014), Schurer et al. (2012) and Wang et al. (2016a, 2017a)
	A2	FJ560582, DQ116610, AY072723	Hunan, dog, cat	Adell-Aledon et al. (2018), de Lucio et al. (2015), Feng and Xiao (2011), Minetti et al. (2015), Pan et al. (2018) and Segui et al. (2018)
	A3	EU188631, FJ971416, EU188635, FJ971415, AY072724	Human, dog	Adell-Aledon et al. (2018), Cooper et al. (2007), de Lucio et al. (2015), Feng and Xiao (2011), Kosuwin et al. (2010) and Robertson et al. (2006)
	A4	AY545642	Cattle	Lalle et al. (2005)
	A5	AB469365, AY655702[a], GQ329671[a]	Cattle, sheep, human, pig, ferret, chipmunk, deer, dog, cat	Deng et al. (2018), Feng and Xiao (2011), Garcia-Presedo et al. (2013), Liu et al. (2014a), Liu et al. (2019), Peng et al. (2020) and Wang et al. (2017a)
	A6	EU621373, EU626198[a], DQ648777[a]	Deer	Feng and Xiao (2011), Robertson et al. (2007) and Solarczyk et al. (2012)
	A7	EU642897[a]	Cat, goat	Geurden et al. (2008), Lebbad et al. (2010) and Lebbad et al. (2011)
	A8	EU769205[a]	Chinchilla	Pantchev et al. (2014)
	A9	HQ538712[a], HQ538713[a]	Deer	Solarczyk et al. (2012)
gdh	A1	EF685701, EF685696[a]	Cattle, cat, sheep, dog, human	Feng and Xiao (2011), Lasek-Nesselquist et al. (2010), Liu et al. (2014a), Souza et al. (2007) and Zheng et al. (2014)

Table 1 (continued)

Genetic locus	Subtype	Reference sequence	Host	References
	A2	EF507674, EF507675, EU362964	Human	Feng and Xiao (2011)
	A3	EU278608	Human	Lalle et al. (2009)
	A4	EF507651, EF507676	Human	Feng and Xiao (2011) and Minetti et al. (2015)
	A5	M84604	Cattle, sheep, human, marine animals, cat	Feng and Xiao (2011), Lasek-Nesselquist et al. (2008) and Souza et al. (2007)
	A6	DQ100288	Deer, human	Costache et al. (2020), Feng and Xiao (2011), Solarczyk et al. (2012) and Thompson 2004)
	A7	KT948091[a], KY432844[a]	Human, cattle	Wang et al. (2017b), Yu et al. (2019b)
	A8	AB469364[a], AB508813[a], AB569380[a]	Pig, cattle, horse, ferret, cat	Abe et al. (2010), Li et al. (2020a), Liu et al. (2019), Paz e Silva et al. (2012), Qi et al. (2016), Santin et al. (2013), Suzuki et al. (2011) and Wang et al. (2017a)
	A9	MF671910[a]	Chipmunk	Deng et al. (2018)

[a]New subtype determined by comparative analysis of sequences

Whole genome sequencing and comparative genomics

As whole genome sequencing (WGS) becomes affordable in recent years, comparative genomics analysis has been increasingly used in advanced genetic characterizations of *G. duodenalis* (Capewell et al. 2021). Combined with a cyst purification procedure, WGS analysis of *G. duodenalis* in clinical samples has become possible (Hanevik et al. 2015). The genomes of assemblages A to E have been sequenced (Franzen et al. 2009; Jerlstrom-Hultqvist et al. 2010; Kooyman et al. 2019; Morrison et al. 2007). They are approximately the same in size (± 11.5 Mb) and encode similar number of genes (± 5300). Among them, assemblages A and E are genetically related, forming a large cluster together with assemblage B. In contrast, assemblages C and D form a separate cluster in phylogenetic analysis of whole genome sequences (Kooyman et al. 2019).

WGS and comparative genomics analysis have been used for high-resolution tracking of infection and contamination sources in giardiasis outbreaks (Prystajecky et al. 2015; Tsui et al. 2018). Results of these comparative genomics analyses have confirmed the zoonotic transmission of assemblage B and sub-assemblage AI (Tsui et al. 2018). These studies have also identified the common concurrence of both assemblages A and B in drinking water-associated outbreaks of giardiasis (Prystajecky et al. 2015; Tsui et al. 2018).

Allelic sequence heterozygosity and mixed infections in *G. duodenalis*: implications for typing

Whole genome sequence analysis has identified the presence of allelic sequence heterozygosity (ASH) in *G. duodenalis* (Morrison et al. 2007; Poxleitner et al. 2008). This ASH is present in single trophozoites and cysts of assemblage B at the commonly used genotyping loci (Ankarklev et al. 2012). ASH has been found to be higher in the genomes of assemblages B (> 0.43%), C (0.89%) and D (0.74%) than assemblages A (< 0.01–0.037%) and E (0.002%) (Kooyman et al. 2019). There are no data on genome characteristics especially ASH of assemblages F, G, and H. Based on phylogenetic relationship of *G. duodenalis*, it is expected that assemblage F has low ASH as assemblages A and E while assemblage G and H have relatively higher ASH as assemblages B, C and D (Kooyman et al. 2019).

The presence of ASH in the genome of some assemblages of *G. duodenalis* could be due to the occurrence of genetic recombination (Franzen et al. 2009). *G. duodenalis* has four copies of the genome in each of the two nuclei. Recombination is known to occur between the two nuclei duration encystation is a process called karyogamy or diplomixis

Table 2 Definition of multilocus subtypes in assemblage A[a] (2000–2021)

Sub-assemblage	Multi-locus subtype	Subtype			Reference sequence			Host (positive number)	References
		gdh	*bg*	*tpi*	*gdh*	*bg*	*tpi*		
AI	AI-1	A1	A1	A1	XM773614, EF507606, FJ792421	XM763377, AY258617, X85958, DQ904426	L02120, AY655704, AF069556, EF688040, FJ792413	Cattle (2), human (2), cat (1), sheep (1)	Caccio et al. (2008), Dan et al. (2019), Feng et al. (2019), Gomez-Munoz et al. (2012), Souza et al. (2007) and Wielinga and Thompson (2007)
	AI-2	A5	A5	A5	M84604	AB469365	AB509383	Cat (1)	Caccio et al. (2008)
	AI-3	A1	A5	A1	EF507606, KR075940, KJ668144, MF671911	AB469365, KR075938, KU668890, MF671918	L02120, JX845464, JX845453, MF671916	Cattle (7), goat (3), chipmunk (1)	Bartley et al. (2019), Chen et al. (2019a), Deng et al. (2018) and Wang et al. (2019)
	AI-4	A5	A1	A5	KP635111	KP635115	KP635106	Sheep (5)	Wang et al. (2016a)
	AI-5	A8	A5	A5	AB469364	AB469365	AB509383	Ferret (1)	Abe et al. (2010)
	AI-6	A8	A5	A1	AB508813	AB508814	AB509384	Ferret (1)	Abe et al. (2010)
	AI-7	A9	A5	A5	MF671910	MF671918	MF671915	Chipmunk (1)	Deng et al. (2018)
	AI-8	A1	A5	A5	MF671911	MF671917, MF671918	MF671915	Chipmunk (2)	Deng et al. (2018)
AII	AII-1	A2	A2	A2	AY178737, KC313924, KY320581	AY072723, KY432854	U57897, KC313923, KY658185	Human (34), cattle (1)	Huey et al. (2013), Minetti et al. (2015) and Yu et al. (2019a)
	AII-2	A3	A3	A2	EU278608	FJ971410	U57897	Human (2)	Minetti et al. (2015)
	AII-3	A3	A2	A2	EU278608	AY072723	U57897	Human (4)	Caccio et al. (2008)
	AII-4	A4	A3	A2	JX994237	FJ971410	U57897	Human (9)	Minetti et al. (2015)
	AII-5	A2	A3	A2	AY178737, KC313924, KC313925	AY072724, KC313946, KC313948	U57897	Human (6)	Minetti et al. (2015)
	AII-6	A3	A3	A3	EU278608	AY072724	EU041754	Human (1)	Caccio et al. (2008)
	AII-7	A3	A3	A4	EU278608	AY072724	AB509382	Human (1)	Caccio et al. (2008)
	AII-8	A4	A2	A2	JX994237	AY072723	U57897	Human (6)	Minetti et al. (2015)
	AII-9	A7	A2	A11	KT948091	MG736240	MH673809	Human (1)	Yu et al. (2019b)
	AII-10	A7	A2	A12	KT948091	MG736240	MH673818	Human (1)	Yu et al. (2019b)
	AII-11	A7	A2	A2	KY432844	AY072723	U57897	Cattle (1)	Wang et al. (2017b)
AIII	AIII-1	A6	A6	A6	HM150751	EU626198	HM150750	Red deer (1)	Solarczyk et al. (2012)

[a]Modified based on (Feng and Xiao 2011)

Several new multilocus subtypes of assemblage A have been added based on recent epidemiologic data

(Poxleitner et al. 2008). Diplomixis could be less efficient in the assemblages A and E, contributing to their ASH values (Franzen et al. 2009).

The genetic recombination is further facilitated by the high occurrence of infections with mixed assemblages or subtypes. It has been estimated that only 75% and 50% of assemblage A or B cases of human giardiasis represent single strain infections, respectively (Woschke et al. 2021). The common occurrence of mixed assemblages and subtypes could facilitate the occurrence of meiotic recombination between different isolates (Cooper et al. 2007). The presence of ASH within isolates and frequent occurrence of infections with mixed assemblages make it difficult to genotype and subtype *G. duodenalis* reliably (Feng and Xiao

2011; Woschke et al. 2021). In addition to the use of MLST tools, they may require the use of separate assemblage-specific genotyping tools in the analysis of clinical samples (Woschke et al. 2021).

G. duodenalis genotypes in humans

Human giardiasis has been commonly documented in many areas, with infection rates ranging from 0.42 to 56.9% (Table S1). Patients including both children and adults had high infection rates of 43.6% in Turkey and 56.9% in Egypt (Cicek and Sakru 2015; Yu et al. 2019a). Moreover, high infection rates (more than 47%) occurred in children under 6 years old in Brazil and Mozambique (Correa et al. 2020; Fantinatti et al. 2016; Messa et al. 2021). Patients with diarrhea generally have higher infection rates (Table S1). However, in one recent report from Brazil, a high infection rate was seen in asymptomatic persons (Correa et al. 2020).

Two *G. duodenalis* genotypes, assemblages A and B, are responsible for most giardiasis cases in humans (Fig. 1a). In recent studies, *G. duodenalis* in 3202 human samples were genotyped by PCR and sequence analysis of three genetic loci. There were more infections by assemblage B (1786 cases) than by assemblage A (1255 cases) (Table S1). In Western Asia, however, infections of assemblage A are more common than those of assemblage B (Table S1). Likewise, in South America, more data were obtained from assemblage A than assemblage B (228 cases versus 118 cases), except for three studies in Brazil (Koster et al. 2021; Nunes et al. 2018; Segui et al. 2018). At the subtype level, most of the assemblage A isolates found in humans belonged to sub-assemblage AII, with the dominance of subtype A2 at each of the three genetic loci (Fig. 2a). In New Zealand, one study reported the rare sub-assemblage AIII in human isolates (Garcia et al. 2021). Several new subtypes defined at individual loci in this review were from humans (Table S15).

Although assemblage E is generally considered a host-specific genotype in hoofed animals, it has been reported in humans in Brazil (15 cases), Egypt (25 cases), Vietnam (7 cases), Australia (6 cases), and New Zealand (1 case) in recent studies (Abdel-Moein and Saeed 2016; Fantinatti et al. 2016; Garcia et al. 2021; Iwashita et al. 2021; Zahedi et al. 2017). In addition, one isolate from Egypt was identified as assemblage C (Soliman et al. 2011). Assemblages D and F detected in a few human samples previously have not been reported in recent studies.

G. duodenalis genotypes in farm animals

G. duodenalis genotypes in bovine animals

Cattle are common hosts of *G. duodenalis* (Santin 2020). The prevalence of *G. duodenalis* in cattle varied between 1.1% and 74.2% in recent publications (Table S2). In two

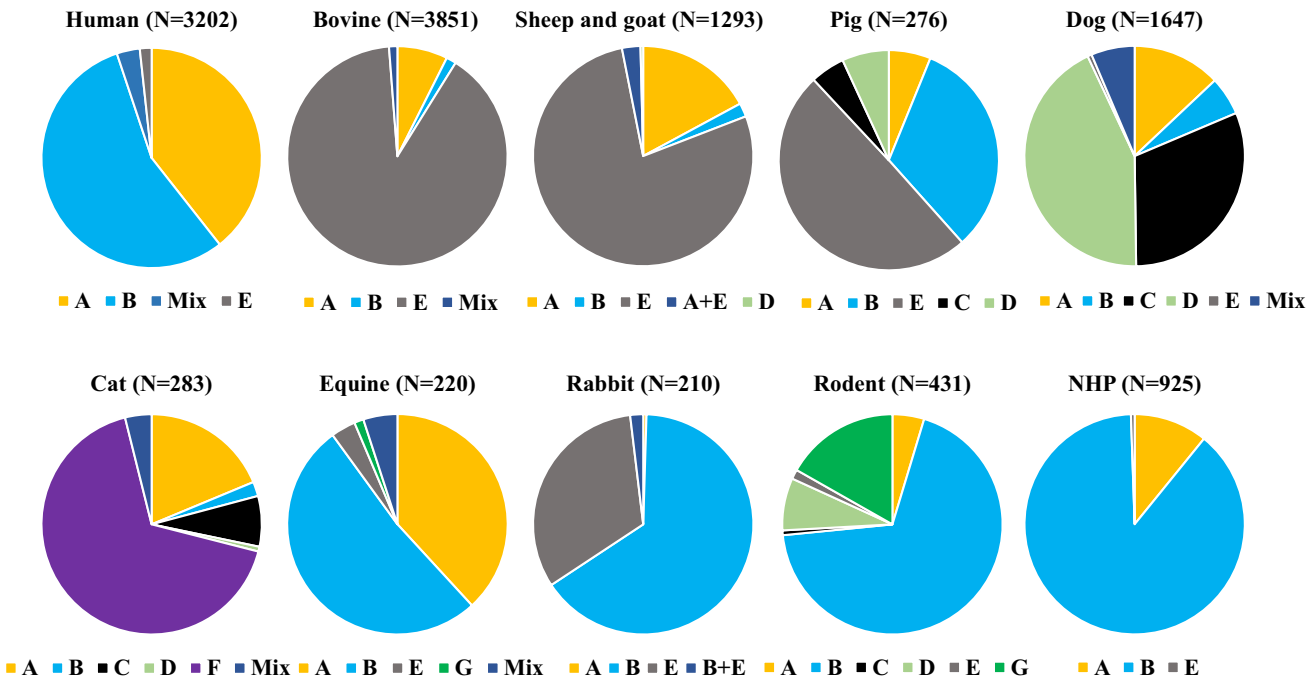

Fig. 1 Distribution of *Giardia duodenalis* assemblages in humans, cattle, sheep and goats, pigs, dogs, cats, horses, rabbits, rodents, and nonhuman primates (NHPs) in reports during 2011–2021

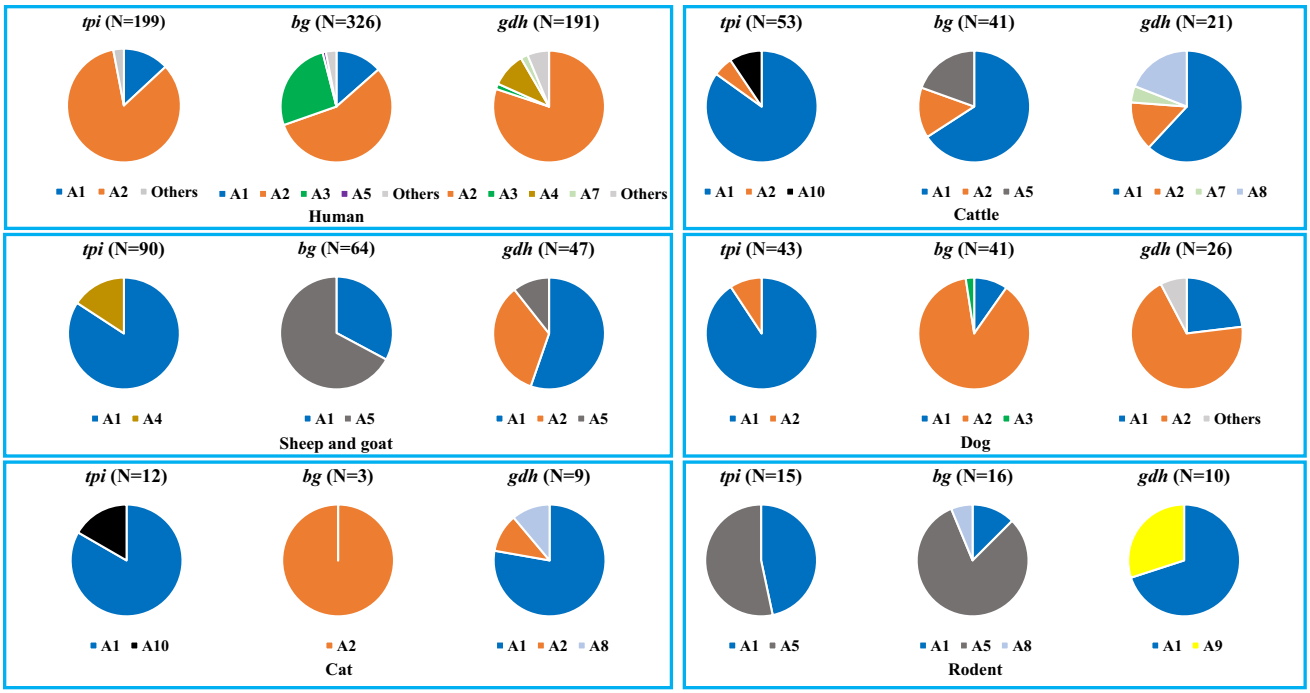

Fig. 2 Distribution of subtypes of *Giardia duodenalis* assemblage A in humans, cattle, sheep and goats, dogs, cats, and rodents by genetic locus in reports during 2011–2021

reports from China, pre-weaned calves under 9 weeks had extremely high infection rates of *G. duodenalis* (60.1% and 74.2%) (Feng et al. 2019; Wang et al. 2017b). Pre-weaned calves generally have higher infection rates than post-weaned calves and adult cattle (Cui et al. 2018; Li et al. 2016; Naguib et al. 2018; Wang et al. 2014, 2019). In at least one study, calves with diarrhea had a higher occurrence of *G. duodenalis* (Wang et al. 2019).

The prevalent genotype of *G. duodenalis* in cattle is assemblage E, with assemblages A and B occurring sporadically (Fig. 1b). Other assemblages are rarely seen, with occasional reports of assemblage D in China (one case) and assemblage F in Spain (four cases) (Cardona et al. 2015; Lam et al. 2020). These occasional reports of rare genotypes were frequently based on data from a single genetic locus.

Assemblage A accounts for a small proportion of *G. duodenalis* infections in cattle in recent studies (Fig. 1b). Among them, subtype A1 dominated at the three genetic loci, leading to the identification of sub-assemblage AI (Fig. 2b). In contrast, assemblage B, another zoonotic genotype, was only found in a few studies. Two studies, however, reported the common occurrence of assemblage B in cattle. In one study in Heilongjiang, China, assemblage B was reported in 18 cattle (Liu et al. 2012). In another study in the United Kingdom, assemblage B was detected in 12 cattle (Bartley et al. 2019).

Giardia duodenalis infections are well-documented in yaks (*Bos grunniens*), although the infection rates reported are generally lower than in cattle (≤10.4%). Assemblage E was reported as the dominant genotype in yaks (Table S2). Similarly, assemblage E has been reported in water buffalo (*Bubalus bubalis*) in several studies (Abeywardena et al. 2014, 2013; de Aquino et al. 2020; Helmy et al. 2014; Russell et al. 2020). In one study in Australia, assemblage A predominated in water buffalo in *G. duodenalis* infections (Abeywardena et al. 2013).

G. duodenalis genotypes in sheep and goats

The prevalence of *G. duodenalis* in sheep and goats appears slightly lower than in cattle, with infection rates ranging from 0.7 to 33.8% in recent studies (Table S3). Lambs and goat kids generally had higher *G. duodenalis* infection rates than old animals (Benhassine et al. 2020; Peng et al. 2016; Wang et al. 2016a; Wegayehu et al. 2017; Yin et al. 2018). In one study, lambs with diarrhea had higher *G. duodenalis* infection rate than those without diarrhea (Benhassine et al. 2020).

As in cattle, assemblage E is the dominant *G. duodenalis* genotype in sheep and goats, followed by assemblage A (Fig. 1c). Like in cattle, most of the assemblage A isolates in sheep and goats belonged to sub-assemblage AI, although sub-assemblage AII was reported in some studies (Fig. 2c). Other assemblages have been rarely detected in recent years. In one study in Algeria, four samples from sheep were identified as positive for assemblage D (Sahraoui et al. 2019). In

one study in Spain, 11 infections with assemblage B were found in sheep and lambs (Castro-Hermida et al. 2011). Nine infections with assemblage B and one with assemblage D were reported in goats in India (Utaaker et al. 2017). The latter, however, was based on sequence analysis of the SSU rRNA locus.

G. duodenalis genotypes in pigs

Giardia duodenalis infections have been reported frequently in pigs, with infection rates ranging from 0.6 to 26.9% (Table S4). Most studies reported higher occurrence of *G. duodenalis* in weaners and fattening pigs than in piglets (Lee et al. 2020; Petersen et al. 2015; Siwila and Mwape 2012). In one study, no correlation was observed between fecal consistency and cyst excretion levels (Petersen et al. 2015).

Like in cattle, sheep, and goats, assemblage E was the main *G. duodenalis* genotype in pigs (Fig. 1d). Some assemblage A infections were seen, with AI as the dominant sub-assemblage (Table S15). Assemblage B was reported at high frequency in a few studies. In one study conducted in Nigeria, assemblage E was detected in 69.8% of 53 *G. duodenalis*-positive samples in pigs, while assemblage B was detected in 26.4% of *G. duodenalis*-positive samples (Akinkuotu et al. 2019). In two studies conducted in Canada and China, assemblage B accounted for far more infections than assemblage E (Farzan et al. 2011; Jing et al. 2019). In addition, assemblages C and D were reported in one study in Korea and three studies in China (Lam et al. 2020; Lee et al. 2020; Liu et al. 2019; Zou et al. 2019). The identification of these unusual genotypes in the Korean study, however, was based on sequence analysis of the SSU rRNA gene, which is known to be unreliable in genotyping *G. duodenalis*.

G. duodenalis genotypes in companion animals

G. duodenalis genotypes in dogs and cats

Giardia duodenalis is common in dogs, with the infection rates varying between 1.9 and 57.9% in recent studies (Table S5). Symptomatic dogs had higher infection rates in two studies (Bouzid et al. 2015; Shin et al. 2015). In one study in Spain, *G. duodenalis* infection rates were significantly different among hunting, breeding, and sheltered dogs (Adell-Aledon et al. 2018). Some studies reported higher infection rates in sheltered dogs (Johansen et al. 2014; Kostopoulou et al. 2017; Shin et al. 2015). This might be attributed to heavy environmental contamination with cysts due to the repeated use of kennels, higher animal density, and continuous introduction of new animals (Adell-Aledon et al. 2018). In one study in the United States, puppies had higher infection rates than adults (Johansen et al. 2014).

In dogs, assemblages C and D are the predominant genotypes, followed by zoonotic assemblage A (Fig. 1e, Table S5). Based on the distribution of assemblage A and canine-specific assemblages, there could be two transmission cycles in *G. duodenalis* in canine animals (Feng and Xiao 2011). The transmission with canine-specific assemblages dominates in dogs in most settings, especially those in crowded kennels with poor hygiene (Feng and Xiao 2011). In contrast, the transmission of assemblage A mainly occurs between household dogs and humans (Feng and Xiao 2011). At the subtype level, A1 was the dominant subtype at the *tpi* locus, while A2 was the dominant subtype at the *bg* and *gdh* loci (Fig. 2d). Therefore, the sub-assemblage identity of assemblage A in canine animals remains unclear. The use of more advanced multilocus genotyping tools in the characterization of canine isolates is needed to resolve this issue before we can have a better understanding of the zoonotic potential of assemblage A from dogs.

Assemblage B has been reported sporadically in dogs (Feng and Xiao 2011). The occurrence of assemblage B, however, might be underestimated in previous reports. In one recent study in Spain, assemblage B accounted for 42.1% (8/19) of *G. duodenalis* infections in dogs, whereas assemblages C and D were only detected altogether in 4 samples (Gil et al. 2017). In Turkey, assemblage B sequences were found in 51 of 89 canine samples genotyped (Gultekin et al. 2017). The increased occurrence of assemblages A and B in dogs in recent years could be the result of cross-species transmission of *G. duodenalis* between humans and dogs.

The occurrence of *G. duodenalis* in cats varied between 1.3 and 27.3% (Table S6), lower than in dogs described above. Living condition is a risk factor affecting the prevalence of *G. duodenalis* in cats. In one report from Canada, the prevalence of *G. duodenalis* was higher in rural cats than in free-roaming cats (Hoopes et al. 2015). In addition, significantly higher infection rates were reported in shelter and stray cats than in pet cats (Kvac et al. 2017; Yang et al. 2015).

Cats are mainly infected with *G. duodenalis* assemblage F, followed by assemblage A (Fig. 1f). In one report from Canada, however, all eight samples genotyped had assemblage A (Hoopes et al. 2015). Among the small numbers of samples identified as having assemblage A, sub-assemblage AI was mostly found, with several new subtypes being found at the *tpi* and *gdh* loci (Fig. 2e). Assemblages B, C, and D were detected in small numbers of samples in recent investigations (Table S6).

G. duodenalis genotypes in equines

The infection rates of *G. duodenalis* in equines ranged from 1.5 to 17.4% (Table S7). It was reported that donkeys had higher infection rates than horses (Li et al. 2020a). This report also demonstrated that donkeys of 6–12 months and horses over 12 months had higher infection rates than other age groups. One study of horses in Turkey, however, reported no significant age- and sex-associated differences in *G. duodenalis* infection rates (Demircan et al. 2019).

In recent studies, most *G. duodenalis*-positive samples from horses had assemblages A and B (Fig. 1d). Among recent studies, one in Turkey reported that all 25 *G. duodenalis*-positive samples had assemblage A (Demircan et al. 2019), while two other studies in Italy and Colombia reported assemblage B as the dominant genotype (Santin et al. 2013; Traversa et al. 2012). In contrast, higher genotype diversity was detected in horses in China, with assemblages A (n = 9), B (n = 22), E (n = 4), and G (n = 3) being found in four small-scale studies (Deng et al. 2017; Li et al. 2020a; Qi et al. 2015b; Zhang et al. 2019). In one study conducted in four countries (Belgium, The Netherlands, Germany, and Greece), assemblages A ($n = 14$), B ($n = 14$), E ($n = 3$), and mixed infections of A and B ($n = 8$) were identified in horses (Kostopoulou et al. 2015). The assemblage A isolates in horses mainly belonged to sub-assemblage AI (Table S15). Assemblage B appears to be especially common in donkeys and was the dominant *G. duodenalis* assemblage in two studies in China (Li et al. 2020a; Zhang et al. 2017a).

G. duodenalis genotypes in rabbits

The prevalence of *G. duodenalis* in rabbits varied greatly between 1.9 and 72.3% in reported studies (Table S8). In Nigeria, rabbits under 25 weeks had high prevalence of 72.3%, even though all animals were asymptomatic (Akinkuotu et al. 2018). Age may be a risk factor of *G. duodenalis* infections in rabbits. One study indicated that young rabbits were most likely infected with *G. duodenalis* (Zhang et al. 2018). Infection rates of *G. duodenalis* in rabbits differ further among breeds and living settings (Li et al. 2020b). Two studies reported that rabbits raised outdoors had infection rates significantly higher than those raised indoors (Jiang et al. 2018; Li et al. 2020b).

Results of recent characterizations of isolates suggest the zoonotic assemblage B dominates in rabbits (Fig. 1h). Only one study reported a high occurrence of assemblage E in rabbits (Li et al. 2020b). In the same study, assemblage A was reported in one rabbit.

G. duodenalis genotypes in rodents

The occurrence of *G. duodenalis* in rodents is extremely common. Recent studies recorded infection rates of 6.0% to 66.3% (Table S9). The infection rates in chinchillas were mostly over 27.1% (Table S9). In one study in Belgium, chinchillas had the highest infection rate of 66.3% (Fernandez-Alvarez et al. 2014). The high infection rate in chinchillas was attributed to intensive rearing of the animals (Levecke et al. 2011). Young chinchillas and those participating in shows, had a higher occurrence of *G. duodenalis* (Levecke et al. 2011). In another study of *G. duodenalis* in bamboo rats, animals under 6 months were more likely to be infected. In addition, infection rates in bamboo rats differed among farms, indicating hygiene and management practices could be other factors affecting the prevalence of infections (Ma et al. 2018). One study in China, however, reported no significant age-associated difference in infection rates in pet chinchillas (Qi et al. 2015a).

Rodents may be potential reservoirs of zoonotic *G. duodenalis* since assemblage B is the dominant genotype in these animals (Fig. 1i). In one study in China, all 52 *G. duodenalis*-positive samples from bamboo rats were identified as having assemblage B (Ma et al. 2018). Six recent studies reported assemblage B as the dominant *G. duodenalis* in chinchillas (Table S9). Assemblage B has been found in beavers in China and Canada (Li et al. 2015a; Prystajecky et al. 2015). In Croatia, one Prevost's squirrel and one Patagonian cavy were identified as having assemblage B (Beck et al. 2011a). Assemblage A, however, was found in some chipmunks and chinchillas in China (Deng et al. 2018; Pantchev et al. 2014; Qi et al. 2015a). Most of the assemblage A isolates from rodents belonged to sub-assemblage AI (Fig. 2f). Assemblage G was found in chipmunks, rats, mice, and some wild rodents, but this rodent-specific assemblage was not as prevalent as assemblage B (Fig. 1i). Assemblage C was found in one muskrat and two chinchillas (Adriana et al. 2016; Veronesi et al. 2012). In addition, assemblages D and E were identified in 33 and 6 chinchillas in Romania, respectively (Gherman et al. 2018). The occurrence of them was attributed to contact with ruminants and guard dogs on the studied farms (Gherman et al. 2018). In one study in Belgium, direct PCR analysis of the *bg* gene identified only assemblage B in chinchillas, but the use of assemblage-specific PCR revealed the presence of assemblages A, C, and E as well (Levecke et al. 2011).

G. duodenalis genotypes in wildlife

Various wild animals, including non-human primates (NHPs), carnivores, and wild mammals, are susceptible to *G. duodenalis* infection (Feng and Xiao 2011). Several recent studies have reported data on the prevalence and

genotype identity of *G. duodenalis* in these wild animals in various areas (Tables S10–S12).

Giardia duodenalis is common in NHPs, with infection rates in recent studies ranging from 4.8 to 57.8% (Table S10). Several reports showed a high occurrence of *G. duodenalis* in captive and farmed NHPs (Chen et al. 2019b; Karim et al. 2015; Karim et al. 2014; Zhong et al. 2017). The keeping of large numbers of susceptible animals in confined spaces may facilitate the transmission of *G. duodenalis* among NHPs (Zhong et al. 2017). One study in China reported the likely waterborne transmission of *G. duodenalis* in rhesus macaques in a public park (Ye et al. 2012). The relationship between *G. duodenalis* infection and age of NHPs is not clear. The majority of *G. duodenalis* isolates from NHPs were identified as assemblage B, with some occurrence of assemblage A (Fig. 1j). The latter was found in some NHPs in China (Karim et al. 2015; Ye et al. 2014), Thailand (Sricharern et al. 2016), Malaysia (Anuar et al. 2014), Norway (Brynildsrud et al. 2018), Brazil (David et al. 2014), and Central African Republic (Sak et al. 2013). In one report from Malaysia, assemblage A was the dominant genotype (62 cases) in orangutans (Anuar et al. 2014). In addition, five cases of assemblage E infections were found in NHPs (Brynildsrud et al. 2018). At the subtype level, in addition to the occurrence of A1, A2, and other common subtypes at individual loci, several new subtypes of assemblage A have been found in NHPs (Table S15). The common occurrence of assemblage B suggests that *G. duodenalis* from NHPs has high zoonotic potential.

Giardia duodenalis infections have been documented in deer, with infection rates ranging from 0.7% to 23.0% (Table S11). There are limited data on the risk factors and patterns of *G. duodenalis* infection in deer. One study conducted in China found that musk deer under one year accounted for 60% of *G. duodenalis* infections (Song et al. 2018). In published studies, assemblage A was the dominant *G. duodenalis* genotype in various deer, although assemblages B, C and E were present in some (Table S11). The assemblage A isolates subtyped belonged to sub-assemblages AIII and AI (Table S15). Although assemblage A was frequently found in deer, the presence of host-adapted subtypes indicates that isolates from deer may have limited zoonotic potential.

In recent reports, several isolates from wild carnivores were genotyped (Table S12). Assemblage D appears to be the dominant assemblage in wild canids. Altogether, it has been identified in 14 wolves, one raccoon dog, and one fox. Assemblage A has been seen in seven wolves. In contrast, assemblage B has been seen in three wolves and one jackal (Table S12). In one European study, only assemblages A and B were detected in one ferret each (Pantchev et al. 2014). Two infections with assemblage E were found in wild dogs, but the diagnosis was based on the analysis of the SSU rRNA locus (Ng et al. 2011). Among wild felids, only 10 isolates of leopards, Siberian tigers, jaguars, cheetahs, servals, lynx, and lions were genotyped, with the finding of five *G. duodenalis* genotypes (Table S12).

In the first report of *G. duodenalis* in captive masked palm civets, most infected animals had assemblage B (Yu et al. 2020). All 18 cases of *G. duodenalis* infections in wild raccoons in one study were identified as having assemblage B (Solarczyk et al. 2021). The high occurrence of assemblage B suggests civets and raccoons may be potential reservoirs of zoonotic *G. duodenalis*. More epidemiological studies are needed to understand the prevalence and genotype identity of *G. duodenalis* in these animal species.

Giardia duodenalis has been reported in marine animals in at least three studies (Delport et al. 2014; Reboredo-Fernandez et al. 2015b, 2014). In one study, the infection rate in captive sea lions living in the zoo was higher than in wild animals (36.8% versus 10.3%) (Delport et al. 2014). In these captive animals, exposure to humans and unnatural habitats might have led to higher transmission of *G. duodenalis*. Results of limited genotyping efforts indicate that marine animals can be infected with assemblages A, B, C, and F. Assemblage B was the dominant genotype in Australian sea lions, but this result was based on analysis of the SSU rRNA locus (Delport et al. 2014). By contrast, assemblage A was found in six dolphins and one whale in Spain (Reboredo-Fernandez et al. 2014). Additionally, assemblage C was found in one pygmy sperm whale at the *ITS* locus, and assemblage F was found in one harbor porpoise and two striped dolphins at the SSU rRNA locus (Reboredo-Fernandez et al. 2015b). To better understand the distribution of *G. duodenalis* genotypes in marine animals, more molecular data based on the commonly used genetic loci (*bg*, *tpi*, and *gdh*) are needed.

Data on *G. duodenalis* infection in other wild mammals are scarce. In Australia, eight cases of assemblage B infection and one case of assemblage D infection were found in brush-tailed rock-wallabies, Tasmanian devils, and quenda (Hillman et al. 2019; Vermeulen et al. 2015; Wait et al. 2017). In only one study in Australia, based on sequence analysis of the SSU rRNA locus, assemblages A, B, C, and D were respectively detected in eight, two, four, and four kangaroos (Ng et al. 2011). Assemblages A, B, and E were found in wild boars in several countries (Beck et al. 2011b; Li et al. 2017; Stojecki et al. 2015). More extensive molecular characterizations are required to understand the host specificity and zoonotic potential of *G. duodenalis* in these wild mammals described above.

G. duodenalis genotypes in birds

Assemblages A and B were frequently found in various birds in several countries (Table S13), although some of the identifications were based on data from the SSU rRNA or *ITS* locus

(Reboredo-Fernandez et al. 2015a). In one study conducted in Cote d'Ivoire, assemblages A, B, and the mix infection of A and B were found in 7, 7, and 4 chicken samples, respectively (Berrilli et al. 2012). In one study in China, however, all *G. duodenalis*-positive pet birds had assemblage E (Dong et al. 2021). In contrast, another study conducted in China identified assemblages B and E in 19 and 4 wild birds, respectively (Jian et al. 2021). The distribution of *G. duodenalis* genotypes in birds could be affected by geographic locations and living conditions.

G. duodenalis genotypes in shellfish

Four assemblages have been identified in shellfish (Table S14). Assemblage A was found in three oysters in Brazil and 19 mussels in Italy (Giangaspero et al. 2014; Leal et al. 2018; Tedde et al. 2019). In contrast, assemblage B was found in one blue mussel in Argentina and one green-lipped mussel in New Zealand (Coupe et al. 2018; Torrecillas et al. 2021). In California, assemblages B, C, and D were found in 1,1, and 2 mussels, respectively (Adell et al. 2014). Little evidence indicates *G. duodenalis* infection actually occurs in shellfish since shellfish can concentrate *Giardia* cysts through the filter-feeding system (Ryan et al. 2019). Findings of cysts in shellfish or successful genotyping may only reflect environmental contamination.

These data suggest these filter-feeding shellfish destined for human consumption have the potential to infect humans if they are eaten raw or under-cooked. Thus far, eating shellfish has been implicated as the cause of two outbreaks of giardiasis (Ryan et al. 2019).

Role of zoonotic infection in giardiasis epidemiology

The common occurrence of *G. duodenalis* in humans and various animals around the world has raised concerns on the zoonotic transmission of this pathogen. Data from several recent epidemiological studies have supported the potential role of zoonotic transmission in the epidemiology of human giardiasis. In one study in Brazil, contact with hooved animals (cattle, pigs, and horses) was associated with human giardiasis in a slum community (Fantinatti et al. 2016). Several other reports also indicated possible transmission of *G. duodenalis* between cattle and humans (Abdel-Moein and Saeed 2016; Budu-Amoako et al. 2012b; Iwashita et al. 2021; Khan et al. 2011). Household dogs were considered another infection source for human giardiasis in several studies (Garcia-Cervantes et al. 2017; Lee et al. 2017; Quadros et al. 2016; Ratanapo et al. 2008). These data, however, have provided only circumstantial evidence on the possible occurrence of zoonotic transmission of *G. duodenalis*.

The use of molecular typing tools has improved our understanding of the role of these animals in the epidemiology of human giardiasis (Feng and Xiao 2011). As humans are mainly infected with assemblages A and B, discussions about zoonotic transmission of *G. duodenalis* are naturally centered around infections with these two assemblages. In one study in India, subtype A1 (at the *bg* gene) was found in both calves and farm workers on the same farm, supporting the likely occurrence of zoonotic transmission of *G. duodenalis* between calves and humans (Khan et al. 2011). In Mexico, assemblage A was detected in schoolchildren, family members and pet dogs living in the same area based on PCR–RFLP analyses of the *vsp417* and *gdh* genes (Garcia-Cervantes et al. 2017).

In Cambodia, however, humans and dogs living in the same village mostly had different *G. duodenalis* genotypes, prompting the authors to conclude a low risk of zoonotic transmission of the pathogen from dogs to humans existed in the areas studied (Inpankaew et al. 2014). Although infections with assemblage E have been found in both farm animals and humans living in the same household or community in Egypt, Brazil, and Vietnam (Abdel-Moein and Saeed 2016; Fantinatti et al. 2016; Iwashita et al. 2021), the hoofed livestock-adapted nature of the genotype indicates that they could represent extreme cases of giardiasis. In addition, the occurrence of the same genotype/subtype in humans and animals in the same community only indicates a possibility of cross-species transmission of *G. duodenalis*. More firm conclusions can be made only if identical subtypes of *G. duodenalis* have been found in both humans and animals living in the same households and the infections have occurred first in animals and then later in humans.

Compared with hoofed livestock, dogs, and cats, which are commonly infected with host-adapted *G. duodenalis* genotypes, the common occurrence of zoonotic assemblages A and B in equine animals, rabbits, guinea pigs, chinchillas, and NHPs suggests that concerns about the zoonotic transmission of *G. duodenalis* probably should be directed to these animals (Fig. 1, Tables S7–S10). Some of the animals are increasingly kept as companion animals and pets or have increased contact with humans in recent years. Unfortunately, few epidemiological studies have assessed the potential role of contacting these animals as a risk factor for human giardiasis or compared the genetic identity of *G. duodenalis* between humans and these animals living in the same households. Few studies have measured the intensity and duration of cyst shedding among *G. duodenalis* assemblages in naturally infected animals. This could be another factor affecting zoonotic transmission of *G. duodenalis.*

Among all animals of concern, the strongest evidence of zoonotic transmission of *G. duodenalis* came from molecular

epidemiological characterizations of isolates from beavers in North America, where giardiasis is known by many as "beaver fever". As reviewed previously, beavers are known to be commonly infected with assemblages A and B (Xiao and Feng 2017). Data from recent comparative genomics analysis have supported the long-suspected role of them as an amplification host or reservoir host for *G. duodenalis* in watersheds (Prystajecky et al. 2015; Tsui et al. 2018). These data confirm that beavers are a zoonotic source of human giardiasis through contaminated drinking source water.

Conclusions and prospectives

Our understanding of the zoonotic potential and public health implications of *G. duodenalis* in various animals has been greatly improved by the usage of molecular characterization tools (Xiao and Feng 2017). This has led to the identification of major animal groups, such as NHPs, equine animals, rabbits, guinea pigs, chinchillas, and beavers, that are commonly infected with the human-pathogenic *G. duodenalis* assemblage B. Although the other major human-infective genotype, assemblage A, has been found in various animals such as livestock, companion animals, rodents, and wild mammals, it frequently accounts for less than 10% *G. duodenalis* infections in these animals. They are in fact mostly infected with host-adapted *G. duodenalis* assemblages, which are rarely found in humans. The smaller human disease burden by assemblage A and host-adaptation at the sub-assemblage and subtype levels have further reduced the public health significance of assemblage A from animals. As a result, zoonotic transmission of assemblage A is likely less common than previously believed.

Future research efforts on zoonotic transmission of *G. duodenalis* should be directed more on assemblage B rather than assemblage A as done previously. This would require the development of high-resolution typing tools for this genotype with extensive ASH at the established genotyping loci. Currently, the identification of host-adapted subpopulations within assemblage B has been hampered by inconsistent classifications of isolates across genetic loci because of ASH. To this end, a novel MLST technique targeting three genetic loci without ASH has been established recently (Seabolt et al. 2021). Population genetic characterization of *G. duodenalis*, however, would require the use of more genetic loci. Ideally, comparative genomics analysis should be used in high-resolution typing of isolates, especially in the identification of genetic determinants for host-adaptation and virulence. Thus far, it has been only used in characterization of small numbers of isolates from waterborne outbreaks in Canada (Prystajecky et al. 2015; Tsui et al. 2018).

Genotyping alone will unlikely resolve key issues in zoonotic transmission of *G. duodenalis*. Affirmative identification of zoonotic *G. duodenalis* infection requires the finding of animal contact or consumption of water and food contaminated by animals as a risk factor as well as advanced genetic comparison of isolates from both humans and the associated animals. This in turn requires the use of well-designed epidemiological investigations (such as cohort and case–control studies and outbreak investigations) and simultaneous sampling of humans and animals. Currently, very few reports of such studies are available, especially those involving the major reservoir hosts of zoonotic assemblage B. Future studies should focus on assessing the likely involvement of horses, exotic pets, and NHPs in the zoonotic transmission of *G. duodenalis* to humans and advanced genetic characterization of human and animal isolates from the same household and community in both endemic and epidemic settings.

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Declarations

Conflict of interest The authors declare no competing interests.

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