Giardia duodenalis Infections in Humans and Other Animals in China

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Giardia duodenalis is an important zoonotic pathogen in both public and veterinary health, and has been genotyped into at least eight assemblages (A–H), each with a distinct host range. In recent years, this intestinal protozoan parasite has been identified widely in humans and various other animals, and has even been recorded in environmental contaminants. Along with whole genome sequencing of G. duodenalis, multilocus sequence typing is increasingly being used to characterize G. duodenalis isolates. Here, we review the epidemiology, genotyping, and subtyping of G. duodenalis from humans and a wide range of other animals, as well as from wastewater, in China.

Keywords: G. duodenalis, humans, animals, prevalence, assemblage, multilocus sequence typing, China, zoonotic

INTRODUCTION

Giardia is one of the most common intestinal parasites of both humans and a diverse range of other animals (Feng and Xiao, 2011). The parasite was first discovered by Antonie van Leeuwenhoek over 300 years ago (Dobell, 1920), and since then, six Giardia species have been described. Among them, Giardia agilis, Giardia ardeae, Giardia psittaci, Giardia muris, and Giardia microti infect animals ranging from amphibians to rodents and birds, whereas the broad range of hosts for Giardia duodenalis (syn. Giardia intestinalis and Giardia lamblia) includes humans and domestic, farmed, and wild animals (Monis et al., 2009; Feng and Xiao, 2011; Ryan and Cacciò, 2013). Giardiasis, which is caused by Giardia duodenalis, is an important zoonotic disease for both public and veterinary health (Ryan and Cacciò, 2013).

The G. duodenalis life cycle is simple in that it comprises rapidly multiplying trophozoites (attached to intestinal epithelial cells) and cysts that are resistant to environmental degradation, which are excreted with feces and transmitted onwards via the fecal-oral route (Lv et al., 2013; Einarsson et al., 2016). G. duodenalis has long been considered to reproduce asexually by simple binary fission, but there is increasing evidence from epidemiological, molecular genetics, and whole genome sequencing studies that Giardia is capable of sexual reproduction (Cooper et al., 2007; Morrison et al., 2007; Poxleitner et al., 2008; Nolan et al., 2010; Gabin-García et al., 2017).

Molecular biological analysis of G. duodenalis has benefited from understanding the taxonomy, population genetics, and epidemiology of this pathogen, and such studies are essential to the effective control of giardiasis in clinical practice (Cacciò and Ryan, 2008). In terms of its genetic variation, G. duodenalis isolates genotypically fall into one of at least eight assemblages (A–H), each of which have a distinct host range (Cacciò and Ryan, 2008; Sprong et al., 2009; Feng and Xiao, 2011; Ryan and Cacciò, 2013). There is also genetic diversity within these assemblages. For example, sub-assemblages AI, AII, and AIII fall within assemblage A (Feng and Xiao, 2011) and BIII and BIV form assemblage B (Monis et al., 2003), while various sub-assemblages form assemblage E (Zhang et al., 2012c).

Multilocus genotyping (MLG) analysis using both conserved (e.g., ssrDNA, cf, h2b, h4) and variable (e.g., tpi, gdh, bg) genes was originally used to assess the G. duodenalis assemblages...
Nowadays, variable genes such as \textit{tpi}, \textit{gdh}, and \textit{bg} are used to characterize \textit{G. duodenalis} isolates from humans and other animals and determine the genotype or subtype. These analyses provide sufficient resolution to assess the disease burden arising from zoonotic transmission of the parasite (Cacciò et al., 2008; Sprong et al., 2009; Wang et al., 2014b; Wang H. et al., 2016). To date, four genetically distinct \textit{G. duodenalis} isolates (WB, AI; AS175, AII; P15, E, and GS, B) have been studied genomically (Franzén et al., 2009; Jerlström-Hultqvist et al., 2010; Adam et al., 2013) and transcriptomically (Franzén et al., 2013). Differences between the genomic and transcriptomic profiling results may explain the differences observed in host preferences and clinical presentation of \textit{G. duodenalis} infection (Franzén et al., 2009, 2013; Jerlström-Hultqvist et al., 2010; Adam et al., 2013).

Annually, 280 million people worldwide are estimated to have clinically-diagnosable giardiasis (Feng and Xiao, 2011; Ryan and Cacciò, 2013; Einarsson et al., 2016; Squire and Ryan, 2017), and infection rates are higher in developing countries (Feng and Xiao, 2011; Ryan and Cacciò, 2013). Giardiasis is generally a self-limiting clinical illness characterized by watery diarrhea, abdominal cramps, bloating, weight loss, and malabsorption (Feng and Xiao, 2011; Einarsson et al., 2016). However, asymptomatic infections occur more frequently than symptomatic ones (Himsworth et al., 2010; Feng and Xiao, 2011; Ryan and Cacciò, 2013; Wegayehu et al., 2016). In China, approximately 28.5 million giardiasis cases are estimated to occur in humans per year (Feng and Xiao, 2011), although the true incidence is likely underestimated as there are many undetected and/or unreported cases. In recent years, \textit{G. duodenalis} has been identified in humans, non-human primates (NHPs), ruminants, companion animals, domestic animals, wildlife, and even in the environment in China (Liu et al., 2011; Wang et al., 2011, 2014b; Li N. et al., 2012; Zhang et al., 2012c; Liu A. et al., 2014; Liu H. et al., 2014; Li J. et al., 2015; Qi et al., 2016a,b; Wang H. et al., 2016). Here, the epidemiology, genotyping, and subtyping of \textit{G. duodenalis} in humans and various other animals in China are summarized and reviewed.

\textbf{G. DUODENALIS IN HUMANS}

Investigations and case reports on \textit{G. duodenalis} infections in humans are common in China (Table 1). Sporadic reports of human giardiasis have been documented since 1962, although a number of giardiasis cases were recoded in 1983 in Xi’an (Zhang and Li, 1983). The large number of epidemiological investigations conducted at the start of this century suggested that the average infection rate was 0.85\% (197/23,098), with the highest infection rate (9.46\%, 774) reported by one study carried out in Shanghai (Wang L. et al., 2013). Differences in the observed rates of infection may be due, in part, to the age of the patients. In China, children <15 years of age were the most affected, with the peak infection rate occurring in those aged 5–10 years (Yu et al., 1994; Lv et al., 2013). A similar observation was made in Malaysia, where children under 15 years old were more likely to be infected with \textit{G. duodenalis} (Mohammed Mahdy et al., 2009; Anuar et al., 2014).

Despite its widespread occurrence, molecular epidemiological data for \textit{G. duodenalis} infections in humans from China is limited. According to the few available genotyping studies, both assemblage A (subtypes AI and AII) and B isolates have been found in China, with subtype AII and assemblage B being the dominant genotypes (Yong et al., 2000; Wang et al., 2011; Wang L. et al., 2013; Wang T. et al., 2017). Interestingly, a canid-specific assemblage C strain, which was first identified in Egypt (Soliman et al., 2011), was found in 16 \textit{Giardia}-positive diarrheal outpatients in Shanghai (Liu H. et al., 2014). MLG analysis of assemblage AII and B isolates from Shanghai identified six and 11 sequence types, respectively (Wang L. et al., 2013). No significant gender-specific association for \textit{G. duodenalis} infections or assemblage distribution has been reported in China (Liu H. et al., 2014; Wang T. et al., 2017).

\textbf{G. DUODENALIS IN NHPS}

The prevalence of \textit{G. duodenalis} infections in NHPs varies markedly between different studies (Table 2). The average rate of infection for NHPs was 4.49\% (172/3,827), with the highest rate recorded by a study conducted in Hunan Province (44.00\%, 33/75). However, variability in the feeding habitats, health status, and age of the subjects, as well as differences in the geographic location and diagnostic techniques used in the studies probably contribute to the discrepant infection rates (Li J. et al., 2017).

Thus far, assemblage A, B, and E strains have been identified in NHPs, with assemblage B dominant in China (Karim et al., 2014, 2015). Only one study, from Shaanxi Province, identified an assemblage E isolate in NHPs in China (Du et al., 2015), although an assemblage E isolate has also been found in a red colobus monkey in western Uganda (Johnston et al., 2010). MLG has also been used for genotyping \textit{G. duodenalis} in NHPs. Like humans, several assemblage A (subtypes AI and AII) and B (subtype BIV) subtypes have been identified in NHPs, with subtype BIV identified as the dominant subtype (Karim et al., 2014, 2015). A total of 15 MLG genotypes (two known and 13 novel) were reported in one study, although the two known MLG genotypes were not significant from a public health perspective (Karim et al., 2015).

Phylogenetic analysis has suggested the possibility of geographical segregation and host-adaptation amongst assemblage B strains in NHPs in China. The role of NHPs in the transmission of \textit{G. duodenalis} to humans is not clear. It is believed that the frequent occurrence of assemblage B strains in captive NHPs may be associated with transmission from human sources, or an indication of adaptation to primate host (Sprong et al., 2009; Karim et al., 2015).

\textbf{G. DUODENALIS IN CATTLE}

In cattle, \textit{G. duodenalis} infections vary in their prevalence and genotypic distribution according to region and cattle species (Table 3). The first documentation of \textit{G. duodenalis} infection in dairy cattle occurred in 2006 in Guangdong Province (Xiao et al.,...
| Locations     | Patient group                     | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References                      |
|---------------|-----------------------------------|-----------|--------------|------------------|---------------------|---------------------------------|
| Shaanxi: Xi’an| Patients                          | 19\(^a\)  | Case reports | A (4)            | All (4)             | Zhang and Li, 1983              |
| Anhui         |                                    | 10\(^b\)  | Genotypes identified | B (4)       | All (4)             | Yong et al., 2000               |
| Sichuan       | Diarrhea patients                 | 2\(^a\)   | Case reports | A (4)            | All (4)             | Chen, 2001                      |
| Henan         | Inpatients                        | 18\(^a\)  | Genotypes identified | A (12)    | All (8); All (4)    | Wang et al., 2011               |
| Hebei: Chengde| Resident                          | 216       | 3 (1.39%)    | A (3)            | All (3)             | Chen et al., 2000               |
| Anhui: Huainan| School pupils                     | 1,332     | 81 (6.08%)   | A (42); AII (4)  | All (4)             | Fu et al., 2004                 |
| Hainan: Haikou| Elementary school students        | 535       | 8 (1.50%)    | A (42); AII (4)  | All (4)             | Gan et al., 2006                |
| Henan: KaiFeng| Patients                          | 6,093     | 10 (0.16%)   | A (42); AII (4)  | All (4)             | Wang et al., 2009               |
| Henan: Zhengzhou| Patients                        | 4,836     | 11 (0.23%)   | A (42); AII (4)  | All (4)             | Sun et al., 2010                |
| Henan: Zhengzhou| Children patients               | 1,996     | 12 (0.60%)   | A (42); AII (4)  | All (4)             | Xu et al., 2011                 |
| Anhui: Fuyang| HIV positive patients             | 302       | 4 (1.32%)    | A (42); AII (4)  | All (4)             | Tian et al., 2012               |
| Anhui: Fuyang| HIV negative individuals         | 303       | 4 (1.32%)    | A (42); AII (4)  | All (4)             | Tian et al., 2012               |
| Shanghai      | Children with various congenital or inherited diseases | 74\(^b\) | 7 (9.46%)    | A (42); AII (4)  | All (4)             | Wang L. et al., 2013            |
| Shanghai      | Children attending the endocrinology | 283     | 4 (1.41%)    | A (42); AII (4)  | All (4)             | Wang L. et al., 2013            |
| Shanghai      | children attending general surgeries | 216     | 0            | A (42); AII (4)  | All (4)             | Wang L. et al., 2013            |
| Shanghai      | Children                          | 3,472     | 25 (0.72%)   | A (42); AII (4)  | All (4)             | Wang L. et al., 2013            |
| Shanghai      | Diarrhea outpatients             | 252       | 17 (6.75%)   | A (42); AII (4)  | All (4)             | Liu H. et al., 2014             |
| Hubei: Chibi  | Kindergarten children             | 20        | 1 (5.00%)    | A (42); AII (4)  | All (4)             | Yuan et al., 2015               |
| Shanghai      | Diarrhea patients                 | 95        | 1 (1.05%)    | B (1)            | All (4)             | Liu H. et al., 2015             |
| Tibet: Lhasa  | Resident                          | 1,015     | 4 (0.39%)    | B (1)            | All (4)             | Liu et al., 2016                |
| Guangdong: Shenzhen | Diarrhea children         | 126       | 0            | A (42); AII (4)  | All (4)             | Shen et al., 2016               |
| Guangdong: Shenzhen | Diarrhea adults patients      | 286       | 0            | A (42); AII (4)  | All (4)             | Shen et al., 2016               |
| Yunnan: Kunming| Diarrhea patients < 18            | 126       | 0            | A (42); AII (4)  | All (4)             | Shen et al., 2016               |
| Yunnan: Kunming| Diarrhea children                | 850       | 0            | A (42); AII (4)  | All (4)             | Zhang S. X. et al., 2016        |
| Wuhan         | Diarrhea children                | 170       | 0            | A (42); AII (4)  | All (4)             | Zhang S. X. et al., 2016        |
|               | Total                             | 23,098    | 197 (0.85%)  | A (51); B (23); C (16) | AI (8); All (43) |                                |

\(^a\) Not included in the G. duodenalis infection rate calculation.

\(^b\) Specimens from a cryptosporidiosis outbreak.

The average infection rate in cattle (including dairy cattle, beef cattle, and yaks) is 5.43% (693/12,753), with the highest rate observed in Shaanxi Province (18.87%, 70/371). However, use of different detection methods may contribute to the observed differences in prevalence.

There is a significant association between G. duodenalis infection and age in cattle. Most studies have reported that G. duodenalis infection rates are inversely associated with animal age in China (Liu et al., 2012; Huang et al., 2014; Wang et al., 2014b; Liu G. et al., 2015; Qi et al., 2015a; Li F. et al., 2016; Zhang et al., 2016b; Wang G. et al., 2017), except for a recent study from Xinjiang, which identified a higher prevalence in post-weaned calves (16.6%) compared with pre-weaned calves (9.7%; Qi et al., 2016b).

Cattle are dominantly infected with livestock-specific G. duodenalis assemblage E strains (Liu G. et al., 2015a; Li F. et al., 2016; Wang G. et al., 2017), with only a few reports of infection caused by assemblage A and/or B strains (Liu et al., 2012; Huang et al., 2014; Wang et al., 2014b; Zhang et al., 2016a). Moreover, sub-assemblies AI, AII, and AIII were identified by most studies conducted in China, with sub-assemblage AI found to be dominant (Wang et al., 2014b; Qi et al., 2016b; Wang X. T. et al., 2016). Mixed infections also appear to be common in cattle, especially those involving isolates
TABLE 2 | Giardia duodenalis infection rates and genotypes in non-human primates in China.

| Locations | Specimens | Positive (%) | Host species (no.) | Assemblage (no.) | Subassemblage (no.) | References |
|-----------|-----------|--------------|-------------------|-----------------|---------------------|------------|
| Henan     | 74        | 1 (1.35%)    | Rhesus macaque (1) | A (10)          | All (10)            | Zhao et al., 2011 |
| Guangxi   | 232       | 0            |                   |                 |                     | Zhao et al., 2011 |
| Sichuan   | 40        | 0            |                   |                 |                     | Zhao et al., 2011 |
| Guizhou   | 411       | 35 (8.52%)   | Rhesus macaque (10) | A (24)          |                     | Ye et al., 2012 |
|           |           |              | Rhesus macaque (24) |                 |                     | Ye et al., 2014 |
|           |           |              | Rhesus macaque / Cynomolgus monkey | B (24) |                     | Li J. et al., 2013 |
| Guangxi   | 784       | 4 (0.51%)    | Rhesus macaque (2) | A (2)           | All (2)             | Ye et al., 2014 |
|           |           |              | Rhesus macaque (3) |                 |                     | Li J. et al., 2013 |
| Beijing   | 72        | 16 (22.22%)  | Cynomolgus monkey (1) | A (1)           | All (1)             | Karim et al., 2014, 2015 |
|           |           |              | Ring-tailed lemur (6); Squirrel monkey (5); Golden monkey (3); Cynomolgus monkey (1) | B (15) | BIV (15) | |
| Hebei     | 89        | 10 (11.24%)  | Ring-tailed lemur (5); Rhesus macaque (4); Mona monkey (1) | B (10) | BIV (10) | Karim et al., 2014, 2015 |
| Henan     | 518       | 20 (3.86%)   | Rhesus macaque (14); Japanese macaque (3); Olive baboon (2); Assam macaque (1) | B (20) | BIV (20) | Karim et al., 2014, 2015 |
| Shanxi    | 66        | 9 (13.64%)   | Rhesus macaque (5); Yellow baboon (2); Northern white-cheeked gibbon (2) | B (9) | BIV (9) | Karim et al., 2014, 2015 |
| Shaanxi   | 197       | 4 (2.03%)    | Rhesus macaque (3); Samiri scireus (1) | E (4) |         | Du et al., 2015 |
| Shanghai  | 128       | 19 (14.84%)  | Green monkey (1) | A (1)           | AI (1)              | Karim et al., 2014, 2015 |
|           |           |              | Ring-tailed lemur (10); Golden monkey (2); Squirrel monkey (2); Cynomolgus monkey (2); King colobus (1); Mandril (1) | B (18) | BIV (18) | |
| Hubei     | 66        | 5 (7.58%)    | Pig-tailed macaque (4); Hamadryas baboon (1) | B (5) | BIV (5) | Karim et al., 2014, 2015 |
| Hunan     | 75        | 33 (44.00%)  | Ring-tailed lemur (2) | A (2)           | Al (1); All (1)     | Karim et al., 2014, 2015 |
|           |           |              | Pig-tailed macaque (8); Bornean orangutan (5); Hussar monkey (5); Ring-tailed lemur (3); Squirrel monkey (3); Cynomolgus monkey (3); Green monkey (2); Raffles monkey (1); Francois’ leaf monkey (1) | B (31) | BIV (31) | |
| Guangdong | 57        | 1 (1.75%)    | Cynomolgus monkey (1) | B (1)           | BIV (1)             | Karim et al., 2014, 2015 |
| Guangxi   | 363       | 9 (2.48%)    | Rhesus macaque (8); White-headed (1) | B (9) | BIV (9) | Karim et al., 2014, 2015 |
| Sichuan   | 304       | 0            |                   |                 |                     | Karim et al., 2014, 2015 |
| Yunnan    | 144       | 0            |                   |                 |                     | Karim et al., 2014, 2015 |
| Henan     | 2         | 1 (50.00%)   | Nomascus leucogenys (1) | B (1)           |         | Li J. et al., 2015 |
| Total     | 3,827     | 172 (4.49%)  |                   | A (16); B (146); E (4) | Al (2); All (13); AII (1); BIV (118) | |

belonging to assemblages A and E (Wang et al., 2014b; Liu G. et al., 2015).

Several studies using MLG have suggested the possibility of geographical distribution differentiation among assemblage E isolates in cattle (Wang et al., 2014b; Qi et al., 2016b; Wang X. T. et al., 2016; Zhang et al., 2016a). A MLG subtype AII isolate identical to human-derived isolates from Italy, Sweden, and China was identified in dairy cattle from Henan Province, raising the possibility of it being an important zoonotic multilocus genotype (Wang et al., 2014b).

Limited information is available on the prevalence and assemblage distribution of G. duodenalis in yaks, despite confirmed cases of infection in Qinghai, Gansu, Sichuan, and Henan Provinces, as well as in Tibet (Ma et al., 2014; Qi et al., 2015a; Song et al., 2016; Wang et al., 2016a,b; Wang G. et al., 2017). Thus far, only assemblage E isolates have been identified in yaks in China.

G. DUODENALIS IN SHEEP AND GOATS

Reports of G. duodenalis infections in sheep and goats in recent years have presented variable results (Table 4). The average infection rate in sheep and goats is 6.07% (418/6,890), with the highest infection rate recorded in goats from Chongqing city (27.78%, 5/18). Except for one study that identified two assemblage B-type isolates in sheep in Heilongjiang (Zhang et al., 2012c), all reports of G. duodenalis infections in sheep and goats in China were caused by assemblage E and A strains, with assemblage E being significantly dominant (Gu et al., 2014; Peng et al., 2016; Wang H. et al., 2016).
### TABLE 3 | Giardia duodenalis infection rates and genotypes in cattle in China.

| Animals            | Locations       | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References            |
|--------------------|-----------------|-----------|--------------|------------------|---------------------|-----------------------|
| Dairy cattle       | Guangdong       | 1         | Case report  | E (1)            |                     | Xiao et al., 2006     |
| Dairy cattle       | Heilongjiang    | 26        | Genotypes identified | B (10) |                     | Liu A. et al., 2014   |
| Dairy cattle       | Jilin           | 249       | 19 (7.63%)   | E (19)           |                     | Zhang J. et al., 2012 |
| Dairy cattle       | Heilongjiang    | 52        | 4 (7.69%)    | A (1)            | Al (1)              | Zhang J. et al., 2012 |
| Dairy cattle       | Heilongjiang    | 814       | 42 (5.16%)   | B (18)           | Bi (8); BII (1); BIV (2); BV (1); BVI (1); BVI (3); BX (1) | Liu et al., 2012 |
| Dairy cattle       | Heilongjiang    | 52        | 8 (15.38%)   | E (8)            |                     | Liu G. et al., 2015   |
| Dairy cattle       | Jilin           | 377       | 25 (6.63%)   | A (1)            | Al (1)              | Liu G. et al., 2015   |
| Dairy cattle       | Liaoning        | 226       | 19 (8.41%)   | E (18)           |                     | Liu G. et al., 2015   |
| Dairy cattle       | Beijing         | 822       | 14 (1.70%)   | E (14)           |                     | Li F. et al., 2016    |
| Dairy cattle       | Henan           | 1,777     | 128 (7.20%)  | A (21)           | Al (4); All (3); All III (1) | Wang et al., 2014b   |
| Dairy cattle       | Henan           | 622       | 21 (3.38%)   | E (18)           |                     | Wang et al., 2014a    |
| Dairy cattle       | Henan           | 507       | 48 (9.47%)   | E (48)           |                     | Wang C. et al., 2016  |
| Dairy cattle       | Henan           | 622       | 21 (3.38%)   | E (21)           |                     | Zhao et al., 2016     |
| Dairy cattle       | Xinjiang        | 514       | 69 (13.42%)  | A (5)            | Al (3); All (2)     | Qi et al., 2016b      |
| Dairy cattle       | Gansu           | 1,224     | 32 (2.61%)   | E (32)           |                     | Zhang et al., 2016a   |
| Dairy cattle       | Ningxia         | 1,366     | 29 (2.12%)   | B (4)            | BII (1); BII (3)    | Huang et al., 2014    |
| Dairy cattle       | Ningxia         | 1,614     | 74 (4.58%)   | E (73)           |                     | Zhang et al., 2016a   |
| Cattle             | Qinghai         | 47        | 3 (6.38%)    | A (8)            | Al (8)              | Ma et al., 2014       |
| Beef/dairy cattle  | Shaanxi         | 371       | 70 (18.87%)  | A (62)           |                     | Wang X. T. et al., 2016 |
| Yak                | Qinghai         | 57        | 7 (12.28%)   | A (8)            |                     | Ma et al., 2014       |
| Yak                | Henan           | 34        | 2 (5.88%)    | E (2)            |                     | Qi et al., 2015a      |
| Yak                | Gansu           | 117       | 4 (3.42%)    | E (4)            |                     | Qi et al., 2015a      |
| Yak                | Sichuan         | 146       | 4 (2.74%)    | E (4)            |                     | Qi et al., 2015a      |
| Yak                | Tibet           | 96        | 1 (1.04%)    | E (1)            |                     | Qi et al., 2015a      |
| Yak                | Qinghai         | 152       | 5 (3.29%)    | E (5)            |                     | Qi et al., 2015a      |
| Yak                | Qinghai         | 93        | 8 (8.60%)    | E (9)            |                     | Wang et al., 2016a    |
| Yak                | Qinghai         | 297       | 22 (7.41%)   | E (22)           |                     | Wang et al., 2016b    |
| Yak                | Gansu           | 208       | 4 (1.92%)    | E (4)            |                     | Song et al., 2016     |
| Yak                | Qinghai         | 297       | 10 (3.37%)   | E (10)           |                     | Wang G. et al., 2017  |

| Total              | 12,753          | 693 (5.43%)| E (571); A (37); B (32); A/E (4) | Al (17); All (5); All II (1); BI (7); BII (4); BIII (2); BIV (2); BVI (1); BVI (3); BVI (3); BX (1) |                      |

*Not included in the G. duodenalis infection rate calculation.

Mixed infections of assemblage A and E strains in sheep are commonly reported (Ye et al., 2015; Wang H. et al., 2016), while sub-assemblage AI was generally the dominant sub-genotype (Zhang et al., 2012c; Ma et al., 2014; Peng et al., 2016; Wang H. et al., 2016). A recent study from Henan Province using MLG yielded one new AI sub-assemblage with zoonotic potential, and six assemblage E MLGs (Wang H. et al., 2016).
### TABLE 4 | Giardia duodenalis infection rates and genotypes in sheep and goats in China.

| Animals          | Locations          | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References              |
|------------------|--------------------|-----------|--------------|------------------|---------------------|-------------------------|
| Sheep            | Heilongjiang       | 21        | Genotypes identified | A (4) | E (17) | Liu A. et al., 2014 |
| Sheep/Goat      | Henan              | 880       | 16 (1.82%)   | A (4)            | A(3), AIV(1)        | Sui et al., 2015        |
| Sheep           | Heilongjiang       | 539       | 25 (4.64%)   | B (2)            | E (19)              | Zhang et al., 2012c     |
| Sheep           | Henan              | 162       | 3 (1.85%)    |                  |                     | Zhu et al., 2012        |
| Sheep           | Henan              | 1,028     | 58 (5.64%)   | A (5)            |                      | Li M. et al., 2013      |
| Sheep           | Henan              | 716       | 39 (5.45%)   |                  | A (9)               | Wang H. et al., 2016    |
| Sheep           | Jilin              | 48        | 0            |                  |                     | Li M. et al., 2013      |
| Sheep           | Liaoning           | 16        | 0            |                  |                     | Li M. et al., 2013      |
| Sheep           | Shandong           | 17        | 0            |                  |                     | Li M. et al., 2013      |
| Sheep           | Inner Mongolia     | 375       | 16 (4.27%)   | A (13)           | A/E (5)             | Ye et al., 2015         |
| Sheep           | Qinghai            | 61        | 8 (13.11%)   |                  |                     | Ma et al., 2014         |
| Goat            | Heilongjiang       | 139       | 4 (2.88%)    | E (4)            |                     | Zheng et al., 2012c     |
| Goat            | Henan              | 301       | 71 (23.59%)  |                  |                     | Chen et al., 2016       |
| Goat            | Henan              | 63        | 1 (1.59%)    |                  |                     | Li M. et al., 2012      |
| Goat            | Henan              | 844       | 48 (5.69%)   |                  |                     | Zhu et al., 2013        |
| Goat            | Anhui              | 80        | 7 (8.75%)    |                  |                     | Zhu et al., 2013        |
| Goat            | Chongqing          | 18        | 5 (27.78%)   |                  |                     | Zhu et al., 2013        |
| Goat            | Qinghai            | 50        | 0            |                  |                     | Zhu et al., 2013        |
| Goat            | Inner Mongolia     | 51        | 0            |                  |                     | Zhu et al., 2013        |
| Goat            | Anhui              | 506       | 32 (6.32%)   | E (32)           |                     | Gu et al., 2014         |
| Goat            | Qinghai            | 51        | 2 (3.92%)    |                  |                     | Ma et al., 2014         |
| Dairy goat      | Henan              | 316       | 3 (0.95%)    |                  |                     | Cao et al., 2015        |
| Dairy goat      | Shaanxi            | 170       | 11 (6.47%)   | E (11)           |                     | Peng et al., 2016       |
| Meat goat       | Henan              | 144       | 35 (24.31%)  | E (35)           |                     | Peng et al., 2016       |
| Cashmere goat   | Shaanxi            | 315       | 34 (10.79%)  | A (4)            | AV (4)              | Peng et al., 2016       |

Total 6,890 418 (6.07%) E (179); A (30); B (2); A/E (6) Al (16); AIV (13); All (1);

*Not included in the G. duodenalis infection rate calculation.

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**G. DUODENALIS IN DOGS AND CATS**

In recent decades, a large number of cases of *G. duodenalis* infection in dogs, and some in cats, have been documented in different regions of China ([Table 5](#)). The first report of *G. duodenalis* infection in dogs occurred in 2000 in Jilin Province (He et al., 2000). The average infection rate in dogs is 13.64% (757/5,549), with the highest rate in Shanghai City (26.19%, 127/485) (Xu et al., 2016), whereas the average rate in cats is 10.19% (32/314), with the highest rate of infection also observed in Shanghai (13.13%, 21/160) (Xu et al., 2016).

Scant information on the epidemiology or molecular characteristics of *G. duodenalis* in dogs and cats in China is currently available. *G. duodenalis* assemblages A, C, and D have been identified as the most common genotypes in dogs, with A and F most prevalent in cats. Occasionally, assemblage B and E isolates have been reported (e.g., in two studies on dogs; Gu et al., 2015; Li W. et al., 2015), while assemblage B, C, and D isolates have been reported in cats (Zheng et al., 2015; Xu et al., 2016).

In general, sub-assemblage A1 appears to be the dominant sub-genotype amongst isolates derived from dogs and cats in China (Li et al., 2012b; Li W. et al., 2013; Zheng et al., 2014, 2015), which agrees with findings from the limited number of reports from dogs and cats in Europe, USA, Brazil, Australia, and Japan (Vasilopoulos et al., 2007; Volotão et al., 2007; Sprong et al., 2009; Feng and Xiao, 2011). However, one study from Shanghai showed that amongst 25 assemblage A sequences obtained from dog and cat specimens, 23 canine sequences and one feline sequence were identified as subtype A1 (Xu et al., 2016).
| Animals | Locations | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References |
|---------|-----------|-----------|--------------|------------------|---------------------|------------|
| Dog     | Jilin     | 1<sup>a</sup> | Case report  |                  |                     | He et al., 2000 |
| Dog     | Jilin     | 1<sup>a</sup> | Case report  |                  |                     | He et al., 2002 |
| Dog     | Beijing   | 2<sup>a</sup> | Case reports |                  |                     | Gao et al., 2009 |
| Dog     | Guangdong | 1<sup>a</sup> | Case report  | A (1)            |                     | Zhu et al., 2011 |
| Dog     | Guangdong | 2<sup>a</sup> | Case reports | A (1)            | D (1)               | Zhang et al., 2011 |
| Dog     | Guangdong | 1<sup>a</sup> | Case report  | D (1)            |                     | Li et al., 2011 |
| Dog     | Guangdong | 1<sup>a</sup> | Case report  | D (1)            |                     | Li et al., 2012a |
| Dog     | Shaanxi   | 56<sup>a</sup> | Case statistics |                     |                     | Quan et al., 2016 |
| Dog     | Jinlin    | 242       | 61 (25.21%)  |                  |                     | He et al., 2001 |
| Dog     | Henan     | 404       | 15 (3.71%)   |                  |                     | Qi et al., 2010a |
| Dog     | Henan     | 531       | 72 (13.56%)  |                  |                     | Qi et al., 2011 |
| Dog     | Sichuan   | 146       | 46 (31.51%)  |                  |                     | Hu et al., 2011 |
| Dog     | Beijing   | 910       | 109 (11.98%) |                  |                     | Bi et al., 2011 |
| Dog     | Shaanxi   | 120       | 11 (9.17%)   |                  |                     | Wang et al., 2015 |
| Dog     | Henan     | 358       | 71 (19.83%)  |                  |                     | Dong et al., 2015 |
| Dog     | Guangdong | 209       | 23 (11.00%)  | A (6)            | D (23)              | Li et al., 2012b |
| Dog     | Liaoning  | 205       | 27 (13.17%)  | A (26)           |                     | Li W. et al., 2013 |
| Dog     | Guangdong | 216       | 21 (9.72%)   | A (7)            |                     | Zheng et al., 2014 |
|         |           |           |              | C (2)            |                     |              |
|         |           |           |              | D (1)            | A/C (2); A/D (7); C/D (2) |              |
| Dog     | Heilongjiang | 267   | 12 (4.49%)   | C (7)            |                     | Li W. et al., 2015 |
| Dog     | Henan     | 940       | 134 (14.26%) | C (57)           |                     | Qi et al., 2016a |
| Dog     | Shanghai  | 485       | 127 (26.19%) | A (23)           | All (23)           | Xu et al., 2016 |
|         |           |           |              | B (1)            |                     |              |
|         |           |           |              | C (26)           |                     |              |
|         |           |           |              | D (58)           |                     |              |
|         |           |           |              | A/C (2)          |                     |              |
|         |           |           |              | A/D (1)          |                     |              |
|         |           |           |              | C/D (10)         |                     |              |
| Dog     | Qinghai   | 31        | 2 (6.46%)    | A (1)            |                     | Ma et al., 2014 |
| Dog     | Qinghai   | 10        | 1 (10.00%)   |                  |                     | Wang G. et al., 2013 |
| Dog     | Taiwan    | 42        | 4 (9.52%)    | A (1)            |                     | Liang et al., 2012 |
| Dog     | Taiwan    | 118       | 11 (9.32%)   | C (7)            |                     | Tseng et al., 2014 |
|         |           |           |              | D (4)            |                     |              |
| Dog     | Anhui     | 215       | 10 (4.65%)   | B (6)            |                     | Gu et al., 2015 |
| Dog     | Zhejiang  | 100       | 0            |                  |                     | Gu et al., 2015 |
| **Subtotal** | 5,549      |            | 757 (13.64%) | D (137); C (81); A (63); B (7); E (5); C/D (12); A/D (8); A/C (4) | AI (38); All (23) |

**Cat**

| Animals | Locations | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References |
|---------|-----------|-----------|--------------|------------------|---------------------|------------|
| Cat     | Hebei     | 1<sup>a</sup> | Case report  |                  |                     | Cui et al., 2010 |
| Cat     | Guangdong | 1<sup>a</sup> | Case report  | F (1)            |                     | Zheng et al., 2013 |

(Continued)
G. DUODENALIS IN PIGS

G. duodenalis infections in pigs have been reported in Australia, Africa, Asia, Europe, and North America (Feng and Xiao, 2011). However, there are limited reports on the prevalence and genotypes of this organism in pigs in China, except in Sichuan Province, where the average infection rate was 3.51% (24/683, Table 6). Although assemblage E was the predominant genotype amongst these isolates from China, assemblage A is also frequently identified (Li W. et al., 2016; Li J. et al., 2017). In contrast, isolates belonging to assemblages A–F have been found in domestic pigs in other countries, with assemblage B and E isolates found in Canada (Budu-Amoako et al., 2012), assemblage C and F isolates in the UK (Minetti et al., 2014), assemblage A, D, and E isolates in Denmark (Petersen et al., 2015), and isolates belonging to assemblages A, E, and F identified in Australia (Armson et al., 2009). Thus far, the majority of the assemblage A strains from pigs in China belong to sub-assemblage AI (Li W. et al., 2016, 2017).

G. DUODENALIS IN RABBITS

G. duodenalis infections occur in rabbits in China at an average rate of 6.86% (271/3,746), and have mainly been documented in Henan and Heilongjiang Provinces (Table 6). Although assemblage E isolates are occasionally found (Qi et al., 2015b), assemblage B strains appear dominant in rabbits in China (Zhang et al., 2012b; Liu A. et al., 2014; Qi et al., 2015b), which agrees with reports from Europe (Pantchev et al., 2014) and the USA (Sulaiman et al., 2003).

G. DUODENALIS IN RODENTS

G. duodenalis infections have been reported in rodents in Norway (Robertson et al., 2007), Poland (Bajer, 2008), Latin America (Bueno et al., 2016), Europe (Pantchev et al., 2014), and Sweden (Lebbad et al., 2010). Currently, G. duodenalis infections in rodents in China have only been reported in Henan Province, where the average infection rate was 20.09% (213/1,060; Table 6). According to the limited number of genotyping studies on G. duodenalis in rodents in China, only assemblage A and B strains, which have zoonotic potential, and host-adapted assemblage G isolates have been identified (Qi et al., 2015c; Zhao Z. et al., 2015).

G. DUODENALIS IN OTHER MAMMALS

G. duodenalis infections have also been reported in beavers, Chinese leopards, Siberian tigers, golden takins, raccoon dogs, horses, deer, and donkeys (Table 7). Some of these infections have high prevalence rates, such as in donkeys in Shandong Province (18.27%, 19/104) (Zhang et al., 2017), raccoon dogs in Liaoning Province (15.28%, 11/72) (Zhang et al., 2016b), golden takins in Shaanxi Province (8.90%, 17/191) (Zhang G. H. et al., 2015), and Pika (9.09%, 1/11) and donkeys (7.69%, 1/13) in Qinghai Province (Ma et al., 2014). Certain G. duodenalis assemblages have been associated with host adaptation in specific animals, such as, assemblages C and D in raccoon dogs (Zhang et al., 2016b), assemblage E in golden takins (Zhao G. H. et al., 2015) and deer (unpublished data), and assemblage F in a Chinese leopard and Siberian tigers (Li J. et al., 2014). Zoonotic G. duodenalis isolates belonging to assemblages A and B were also identified in beavers (Li J. et al., 2015), golden takins (Zhao G. H. et al., 2015), and horses (Qi et al., 2015d). The number of zoonotic isolates found in wild animals is quite limited, an observation supported by a large survey of G. duodenalis in wild mammals from Croatia that revealed a low prevalence and limited zoonotic potential for the parasite (Beck et al., 2011). This suggests that wild animals are probably not a major reservoir for human infections.

G. DUODENALIS IN WASTEWATER

Cases of giardiasis associated with polluted recreational and potable waters have been documented for more than a century worldwide (Guy et al., 2003; Karanis et al., 2007; Moss, 2016). Although there have been no G. duodenalis outbreaks documented in China, a high prevalence of oocysts was identified
### TABLE 6 | *Giardia duodenalis* infection rates and genotypes in pigs, rabbits, and rodents in China.

| Animals       | Locations   | Specimens | Positive (%) | Assemblage (no.) | Subassemblage (no.) | References                          |
|---------------|-------------|-----------|--------------|------------------|---------------------|-------------------------------------|
| Wild boars    | Sichuan     | 308       | 11 (3.57%)   | A (1)            | Al (1)              | Li W. et al., 2016                  |
| Pig           | Sichuan     | 18        | 2 (11.11%)   | E (2)            |                     | Li W. et al., 2016                  |
| Wild boars    | Sichuan     | 357       | 11 (3.08%)   | A (2)            | Al (2)              | Li J. et al., 2017                  |
|               |             |           |              | E (9)            |                     |                                     |
| Rabbits       | Heilongjiang| 14^a      | Genotypes identified | B (14)     |                     | Liu A. et al., 2014                   |
| Rabbits       | Henan       | 1,027     | 80 (7.79%)   |                  |                     | Xi et al., 2011b                    |
| Rabbits       | Henan       | 1,081     | 57 (5.27%)   |                  |                     | Shi et al., 2010                    |
| Rabbits       | Henan       | 305       | 12 (3.93%)   |                  |                     | Xi et al., 2011a                    |
| Rabbits       | Heilongjiang| 378       | 28 (7.40%)   | B (28)           | BVI (26)            | Zhang et al., 2012b                 |
| Rabbits       | Henan       | 955       | 80 (8.38%)   | B (26)           | BIV (26)            | Qi et al., 2015b                    |
|               |             |           |              | E (2)            |                     |                                     |
|               |             |           |              | B/E (4)          |                     |                                     |
| Subtotal      |             | 683       | 24 (3.51%)   | E (21); A (3)    | Al (3)              | Liu A. et al., 2014                  |
| Rodent        | Henan       | 140       | 38 (27.14%)  | A (5)            | Al (5)              | Qi et al., 2015c                    |
| Rodent        | Henan       | 232       | 14 (6.03%)   | G (14)           | BIV (31)            | Zhao Z. et al., 2015                 |
| Rodent        | Henan       | 96        | 36 (37.50%)  |                  |                     | Lv et al., 2009b                    |
| Rodent        | Henan       | 439       | 91 (20.72%)  |                  |                     | Qi et al., 2010b                    |
| Rodent        | Henan       | 153       | 34 (22.22%)  |                  |                     | Lv et al., 2009a                    |
| Subtotal      |             | 3,746     | 257 (6.86%)  | B (68); E (2); B/E (4) | BVI (16); BII (4); BIII (3); BIV (27); BV (1); BVI (1) | Qi et al., 2015c                    |

^aNot included in the *G. duodenalis* infection rate calculation.

amongst samples from numerous municipal and domestic raw water sources in Shanghai (Zhang et al., 2010; Li N. et al., 2012), Guangzhou (Zhong et al., 2010; Sun et al., 2014), Wuhan (Li N. et al., 2012; Sun et al., 2014), Jiangsu (Sun et al., 2014), Harbin (Liu et al., 2012; Sun et al., 2014), Guiyang (Chen et al., 2009), Nanjing (Li N. et al., 2012), Qingdao (Li N. et al., 2012), Taiwan (Liang et al., 2012), and Qinghai (Ma et al., 2014), among others.

Assemblage A and B isolates, which have zoonotic potential, were identified in urban waste in China (Liu et al., 2011; Liang et al., 2012; Li N. et al., 2012), suggesting that this pathogen could be maintained and transmitted by water sources, with the attendant risk of disease outbreaks occurring. Similarly, zoonotic isolates were also identified in Iran (Mahmoudi et al., 2015), Australia (Nolan et al., 2013; Koehler et al., 2016), Malaysia (Lim et al., 2009a,b, and Portugal (Lobo et al., 2009), among others.

Isolates belonging to other assemblages, such as assemblage E, were also documented in wastewater in France (Bertrand and Schwartzbrod, 2007).

### CONCLUSIONS AND PERSPECTIVES

In conclusion, *G. duodenalis* is widely distributed in humans and various other animals in China. Among the *G. duodenalis* assemblages, A and B are considered to have the broadest host specificities, and strains belonging to these assemblage types have zoonotic potential. Generally speaking, assemblage A isolates are more frequently found in humans, livestock, and companion animals, while assemblage B isolates are commonly isolated from humans, NHPs, and rabbits, with only a few reports of infections in sheep, goats, dogs, and cats in China. Cattle, sheep, goats, and pigs are predominantly infected with host-specific assemblage E isolates, while assemblage C and D isolates have been found in dogs, assemblage F is associated with cats, and rodents tend to be infected with assemblage G isolates. Within assemblage A, humans and NHPs are more commonly infected with subgroup AII isolates, while in other animals, sub-assemblage AI is predominant.

Most molecular investigations of *G. duodenalis* in China have only examined one or two loci, which cannot provide sufficient information on the transmission profile of this pathogen. However, the availability of the whole genome sequence of *G. duodenalis* has enhanced population genetics-based studies, and multi-locus sequence typing (MLST) tools are increasingly being used for characterizing *G. duodenalis* infections in humans and animals. Access to these methods is especially important for gaining a better understanding of some host-adapted assemblages (e.g., C, D, E, and F) that are pathogenic in humans, and for assessing the zoonotic assemblages (A and B) with infective potential. Therefore, a comprehensive and systematic study based on MLST analysis should be carried out to allow a full assessment of the burden of giardiasis of animal origin in humans.
TABLE 7 | Giardia duodenalis infection rates and genotypes in other mammals in China.

| Animals         | Locations | Specimens | Positive (%) | Assemblage (no.) | References          |
|-----------------|-----------|-----------|--------------|------------------|---------------------|
| Pika            | Qinghai   | 11        | 1 (9.09%)    |                  | Ma et al., 2014     |
| Chinese leopard | Henan     | 2         | 1 (60.00%)   | F (1)            | Li J. et al., 2015  |
| Beaver          | Henan     | 1         | 1 (100.00%)  | B (1)            | Li J. et al., 2015  |
| Siberian tiger  | Henan     | 6         | 2 (33.33%)   | F (2)            | Li J. et al., 2015  |
| Golden takins   | Shaanxi   | 191       | 17 (8.90%)   | B (3)            | Zhao G. H. et al., 2015 |
| Grazing horses  | Xinjiang  | 262       | 4 (1.50%)    |                  | Qi et al., 2015d    |
| Raccoon dog     | Jilin     | 110       | 7 (6.36%)    |                  | Zhang et al., 2016b |
| Raccoon dog     | Heilongjiang | 40   | 3 (7.50%)    | C (3)            | Zhang et al., 2016b |
| Raccoon dog     | Shandong  | 29        | 0            |                  | Zhang et al., 2016b |
| Raccoon dog     | Hebei     | 54        | 1 (1.85%)    | C (1)            | Zhang et al., 2016b |
| Raccoon dog     | Liaoning  | 72        | 11 (15.28%)  | C (10)           | Zhang et al., 2016b |
| Donkey          | Qinghai   | 13        | 1 (7.69%)    |                  | Ma et al., 2014     |
| Donkey          | Jilin     | 48        | 5 (10.42%)   | B (5)            | Zhang et al., 2017  |
| Donkey          | Shandong  | 104       | 19 (18.27%)  | B (19)           | Zhang et al., 2017  |
| Donkey          | Liaoningz | 29        | 4 (13.79%)   | B (4)            | Zhang et al., 2017  |
| Deer            | Henan     | 199       | 5 (2.51%)    | E (5)            | Unpublished         |
| Total           |           | 1,171     | 82 (7.00%)   | A (2); B (34); C (20); E (19); F (3); C/D (2) |                    |

AUTHOR CONTRIBUTIONS

LZ conceived the idea for the review and revised the manuscript. JL and HW wrote the manuscript, and JL, HW, and RW reviewed and abstracted the data from each selected article.

FUNDING

This study was supported in part by the Key Program of the National Natural Science Foundation of China (31330079), the National Science Foundation of Henan Province (162300410129), the Key National Science and Technology Specific Projects (2012ZX10004220-001), and the National Natural Science Foundation of China (U1404327).

ACKNOWLEDGMENTS

We thank Tamsin Sheen, Ph. D, from Liwen Bianji, Edanz Editing China (www.liwenbianji.cn/ac), for editing the English text of a draft of this manuscript.

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