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Role of rodents in the zoonotic transmission of giardiasis

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ABSTRACT

Four species of *Giardia* out of nine have been identified in rodents based on molecular data: *G. muris*, *G. microti*, *G. cricetidarum*, and *G. duodenalis*. A total of seven *G. duodenalis* assemblages (A, B, C, D, E, F, G) have been identified in rodents to date. The zoonotic assemblages A and B are responsible for 74.88% (480/641) of the total identified genotypes in rodents by statistic. For sub-assemblage A in humans, AII is responsible for 71.02% (1397/1967) of the identified sub-assemblages, followed by AI with 26.39% (519/1967) and AIII with 1.17% (23/1967), indicating a significantly greater zoonotic potential for *G. duodenalis* infections in humans originating from animals. For sub-assemblages of type A in rodents, AI was identified in 86.89% (53/61), and AII in 4.92% (3/61). For assemblage B, 60.84% (390/641) were identified in rodents as having zoonotic potential to humans. In environmental samples, the zoonotic assemblages A and B were responsible for 83.81% (533/636) in water samples, 86.96% (140/161) in fresh produce samples, and 100% (8/8) in soil samples. The same zoonotic potential assemblage A or B simultaneously identified in humans, rodents, and environment samples had potential zoonotic transmission between humans and animals via a synanthropic environment. The infections and zoonotic potential for *G. duodenalis* were higher in farmed rodents and pet rodents than that in zoo, lab, and wild rodents. In conclusion, the role of rodents in zoonotic transmission of giardiasis should be noticed. In addition to rodents, dogs, cats, wild animals, and livestock could be involved in the zoonotic transmission cycle. This study aims to explore the current situation of giardiasis in rodents and seeks to delineate the role of rodents in the zoonotic transmission of giardiasis from the One Health perspective.

1. Introduction

Giardia spp. are important zoonotic protozoan pathogens that infect the intestines of a wide range of vertebrate hosts, including humans [1,2]. *Giardia* spp. are diplomonad flagellates found in a broad range of vertebrates. There are currently nine validated species (*G. duodenalis*, *G. microti*, *G. muris*, *G. agilis*, *G. ardeae*, *G. psittaci*, *G. varani*, *G. peramelis*, and *G. cricetidarum*) that have been identified based on the combination of cysts, trophozoite morphology, and host specificity [2]. Among these, *G. duodenalis* (synonyms *G. lamblia* and *G. intestinalis*) is commonly identified in humans and a wide range of livestock, wildlife, and companion animals [3,4].

Although asymptomatic infections can often occur, the main symptom for giardiasis (caused by *G. duodenalis*) is self-limiting diarrhea. It has also been associated with arthritis and irritable bowel syndrome in humans [2,3]. *G. duodenalis* is one of the most prevalent enteric parasites globally, with a high prevalence in both developing and developed countries [4]. *G. duodenalis* is known as a multispecies complex [5], with a total of eight genetically distinct assemblages (A–H). The zoonotic assemblages A and B are found in both humans and animals; host-adapted assemblages C and D occur primarily in dogs, E in ruminants, F in cats, G in rodents, and H in seals [2]. These assemblages likely represent different *Giardia* species, and this is supported by the apparent host specificity and distinct genetic polymorphism [5,6].

The *ssu rRNA* locus is a common marker for *Giardia* species differentiation; the conserved nature of that locus, however, makes genotyping results of *G. duodenalis* less reliable [6,7]. In addition to the *ssu rRNA* gene, β-giardin (*bg*), triosephosphate isomerase (*tpi*), elongation factor 1 alpha (*ef1α*), and glutamate dehydrogenase (*gdh*) genes are common markers for species differentiation and genotyping and subtyping of *G. duodenalis* [4,6], and even for whole-genome sequencing (WGS) applied to identification [8]. This generally involves sequence

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Table 1
The infections of *Giardia duodenalis* in different human populations.

Populations	Locations	Total No.	Positive no.	Infection (%)	No. of genotyped	Assemblages	Sub-assemblage
Humans							
Common humans	Brazil, Canada, Egypt, Ethiopia, Iran, Italy, Jamaica, Malaysia, New Zealand, Poland, Romania, Uganda, United Arab Emirates	13,822	680	4.92%	502	A (311), B (175), E (2); F (1), A/B (12), B/E (1)	AI (63), AII (94)
Hospital patients	Bangladesh, Belgium, China, Turkey	7661	425	5.55%	349	A (64), B (266), A/B (19)	AI (8), AII (36), AI/AII (1), AII/AIII (8)
Diarrheal patients	Canada, Egypt, Nepal, Netherlands, Spain, Vietnam	4907	308	6.28%	239	A (66), B (142), B/E (9), A/B (22)	AI (7), AII (37)
Community							
Communities and households peoples [1]	Argentina, Brazil, Ethiopia, Malaysia, Mongolia, Peru, South Africa, Thailand	2230	329	14.75%	136	A (52), B (73), C (1), A/B (3), A/C or A/D (7)	AII (18), AII/AIII (1)
Poor communities people [2]	Australia, Bangladesh, Brazil, India, Thailand, Uganda,	6434	1172	18.22%	791	A (317), B (393), A/B (61), D (4), C (3), A/C or A/D (13)	AI (45), AII (124), AIII (21), AII/AIII (10)
Children in Community							
Common children [3]	Australia, Brazil, China, Cuba, Guinea-Bissau, Italy, Peru, Malaysia, Mexico, Mozambique, Sahrawi, Saudi Arabia, Spain, Tanzania, Thai-Myanmar border, Uganda	7818	791	10.12%	347	A (160), B (154), E (15), A/B (17), F (1)	AI (31), AII (77)
Children in poor communities [4]	Brazil, Slovakia, Thailand, Uganda	1578	235	14.89%	146	A (66), B (75), A/B (5)	AI (1), AII (44)
Children							
Asymptomatic children	Mozambique, Portugal, Spain	4764	1341	28.15%	156	A (20), B (132), A/B (4)	AI (1), AII (14), AII/AIII (6)
Symptomatic children [5]	Albania, China, Egypt, Ethiopia, Gabon, Mexico, Mozambique, Slovakia, Sweden	2321	518	23.06%	163	A (55), B (100), A/B (9)	AI (1), AII (27), AII/AIII (1)
Peoples frequently connected with animals [6]	Côte d'Ivoire, Egypt, Germany, Ghana, Spain	719	110	15.30%	89	A (75), B (7), A/B (7)	AI (60), AII (12)
Cases							
Sporadic and outbreaks cases [7]	Africa, Argentina, Australia, Brazil, Canada, China, Côte d'Ivoire, Egypt, Ethiopia, Europe, France, India, Iran, Japan, Italy, Mexico, Nicaragua, New Zealand, Norway, Peru, Qatar, Turkey, Netherlands, Norway, Portugal, South Korea, Spain, Sweden, Uganda, United Kingdom, United States				4703	A (1887), B (2666), A/B (81), C (3); D (4); E (37), F (5), A/F (7);	
Total		**52,254**	**5909**	**11.31%**	**7621**	**A (3072), B (4174), A/B (263), E (54), D (8), C (7), F (6), B/E (10), A/F (7), A/C or A/D (20)**	**AI (519), AII (1397), AIII (23), AI/AII (1), AII/AIII (27)**

Communities and households peoples [1]: Communities, Municipalities, Households, Asymptomatic immigrants.
Poor communities people [2]: Poor communities people: Asymptomatic Indigenous People, Rural communities, Villages communities, Poor communities, Valley communities, Rural villages community, Amazonas communities.
Children [3]: Children, kindergarten children, School children, Community children.
Children in poor communities [4]: School children in rural community, Low-income families children, School children in villages; Children and adolescents in villages.
Symptomatic children [5]: Children with acute gastroenteritis, Symptomatic children, Children with flatulence, Children with diarrhea, Symptomatic young children, Symptomatic school children.
Peoples frequently connected with animals [6]: Animals owners, Farmers connected with animals, Zookeepers, Zookeepers and veterinarians.
Sporadic and outbreaks positive cases [7]: Only with the positive samples identification. Cases.

analysis of PCR products from these targets. Apparent host adaptation has been observed among the three classical sub-assemblages within assemblage A; sub-assemblage AI is mainly found in animals, sub-assemblage AII is mostly found in humans, while sub-assemblage AIII has been almost exclusively found in wild ruminants, especially deer [4,6]. Assemblage B is more polymorphic than assemblage A, with the generation of numerous subtypes at each of the three common genotyping loci. In contrast, the initial identification of sub-assemblages BIII and BIV based on the results of allozyme electrophoretic analysis is not supported by phylogenetic analysis [7,9]. Sequence polymorphism is apparently also present among assemblages C, D, and E isolates, although the utility of subtyping of these pathogens has not been demonstrated [10–13]. Whole-genome sequencing and comparative genomics analysis have been used for high-resolution tracking of infection and contamination sources in giardiasis outbreaks [8,14]. Results of these comparative genomics analyses have confirmed the zoonotic transmission of assemblage B and sub-assemblage AI [14].

The life cycle of *G. duodenalis* comprises rapidly multiplying trophozoites and environmentally hardy cysts that are released in the feces and spread through the fecal-oral route [15]. The trophozoite is the vegetative form and replicates in the small intestine of the host, and the cyst is the environmentally stable stage of the parasite life cycle that facilitates the zoonotic transmission of cysts passed in the feces of one host into the environment to be ingested by the subsequent host, leading to waterborne or foodborne outbreaks [16–19]. Several drugs have been approved for the treatment of giardiasis in humans; however, treatment failures are common with giardiasis and no vaccines are available [3,19–21].

Rodents are the most abundant and diversified order of mammals [22]. Since the Middle Ages, it has been recognized that rodents can contribute to human disease [22–25]. In modern times, rodents are also recognized as carriers of many human pathogens with public health

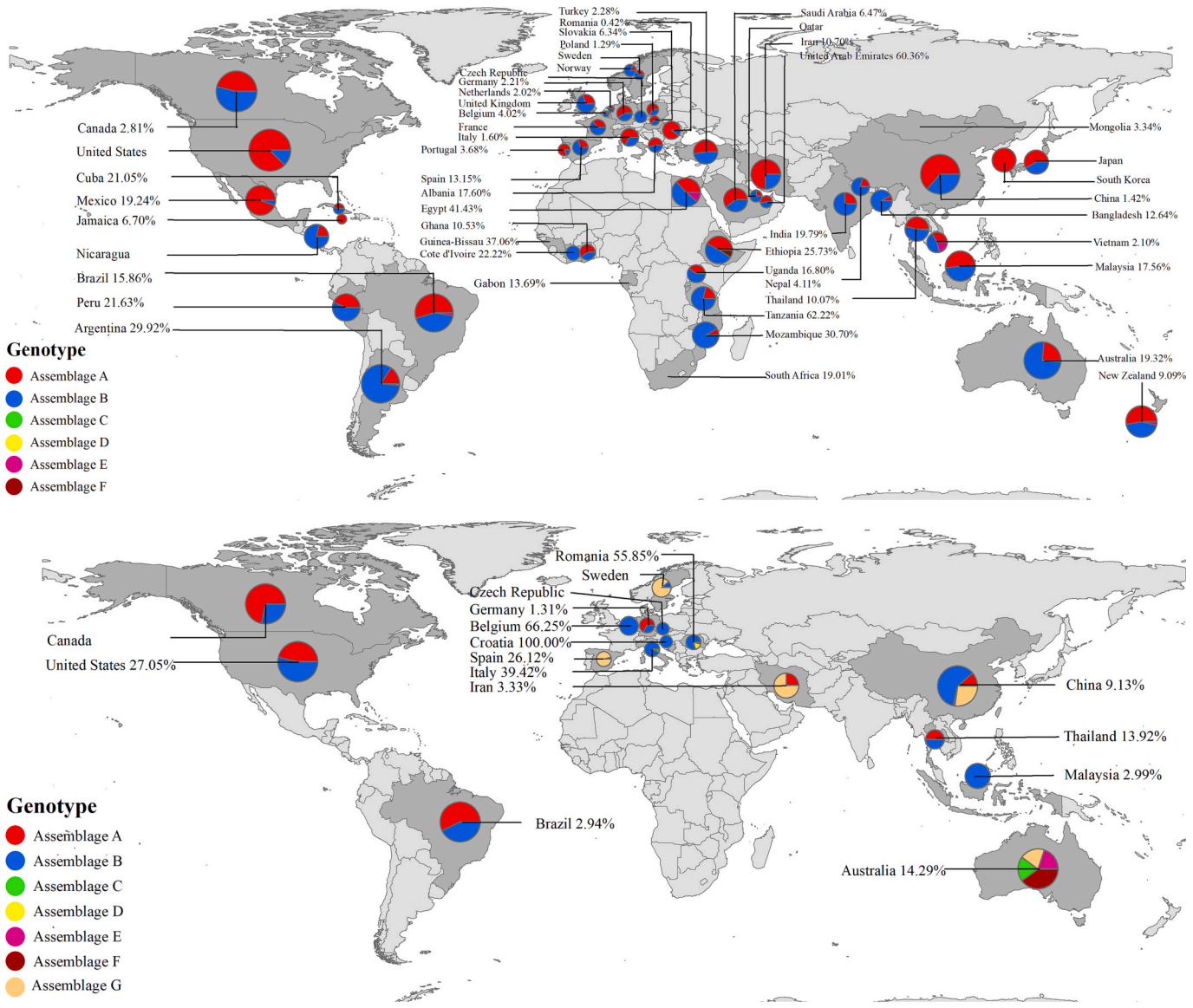

Fig. 1. The infections and assemblages distributions of *Giardia duodenalis* in humans (A) and rodents (B).

importance, and almost 10% of the global rodent population is either a carrier or a reservoir of pathogens with public health importance [24–26]. While much progress has been made in *Giardia* research, no retrospective analyses have been done on the epidemiology, diversity, or transmission routes of this parasite in rodents, and there has been no assessment of the potential risks posed to human and animal populations. This article aims to explore the current situation for giardiasis both in humans and rodents and attempts to examine the role of rodents in the zoonotic transmission of giardiasis from the One Health perspectives (human–animal–environment).

2. Search strategy and selection criteria

We searched PubMed, Web of Science, MEDLINE, ScienceDirect, China National Knowledge Infrastructure (CNKI), and WANGFANG DATA for publications written in both English and Chinese for epidemiology records of *Giardia* by using the search terms "*Giarida*" AND "Human," OR "*Giarida duodenalis*" AND "Human" for human populations; "*Giarida*" AND "Rodent," OR "*Giarida duodenalis*" AND "Rodent" for rodents populations; "*Giarida duodenalis*" AND "water," OR "*Giarida duodenalis*" AND "vegetable," OR "*Giarida duodenalis*" AND "soil" for environment samples. We restricted our search to updates published before October 10, 2022. The titles and abstracts of the literature were screened first, followed by the full articles, for inclusion in the epidemiology summary in this article. The literature from recent reviews was also used to find the original records. Additional key references were retrieved from the published personal databases of all coauthors. The raw data for occurrence and genotypes distributions of *Giarida* were showed in supplemental materials.

3. Molecular characteristics of *Giardia* in humans

Among the *Giardia* species, *G. duodenalis* is the only reported species that infects humans. There are many human populations that have been documented as having infections of *G. duodenalis* (Table 1). The pooled prevalence is 11.31% (5909/52254). For the locations, there were at least 53 countries that have reported *G. duodenalis* infections in humans, and the prevalence ranges from 0.42% (33/7805) [27] in humans in Romania to 62.22% (28/45) [28] for school children in Tanzania (Fig. 1).

The presence of diarrhea is a risk factor for *G. duodenalis* infections in previous investigations, as the pooled prevalence for diarrheal patients

Table 2
The infections of *Giardia duodenalis* in different rodents.

Host animals	Scientific name	Rodent types	Locations	Total No.	Positive no.	Infection (%)	No. of genotyped	Genetic locus	Assemblages	Sub-assemblage
Giardia muris										
Hamsters		Farmed	USA				1	*SSU rDNA*		
Mouse	*Mus musculus*	Lab	Australia				3	*SSU rDNA*		
Rat	*Rattus* spp.	Wild	Sweden				2	*SSU rDNA*		
mouse	*Mus musculus*	Wild	Sweden				1	*SSU rDNA*		
Swiss albino mice		Lab	Turkey				1	*bg*		
Hamsters	*Phodopus sungorus*	Farmed	China	87	3	3.45%	3	*SSU rRN, bg, ef-1α*		
Berkenhout	*Rattus norvegicus*	Wild	China	23	4	17.39%	4	*SSU rRN, bg, ef-1α*		
Mice	*Apodemus spp*	Wild	Germany	93	31	33.33%	31	*SSU rDNA*		
Voles	*Microtus spp*	Wild	Germany	175	2	1.14%	2	*SSU rDNA*		
Voles	*Myodes spp*	Wild	Germany	301	3	1.00%	3	*SSU rDNA*		
Subtotal				**679**	**43**	**6.33%**	**51**			
Giardia microti										
Rats	*Rattus norvegicus*	Wild	US				1	*SSU rRNA*		
Deer mice	*Peromyscus maniculatus*	Wild	US				1	*SSU rRNA*		
Muskrat	*Ondatra zibethicus*	Wild	US				3	*SSU rRN, tpi*		
Mouse	*Mus musculus*	Wild	Sweden				1	*SSU rDNA*		
Günther's Voles	*Microtus guentheri*	Pet	Italy				2	*SSU rRNA*		
Milne Edwards	*Eothenomys melanogaster*	Wild	China	7	7	100%	7	*SSU rRNA*		
Mice	*Apodemus spp*	Wild	Germany	93	7	7.53%	7	*SU rRN, bg, gdh*		
Voles	*Microtus spp*	Wild	Germany	175	134	76.57%	134	*SU rRN, bg, gdh*		
Voles	*Myodes spp*	Wild	Germany	301	173	57.48%	173	*SU rRN, bg, gdh*		
Subtotal				**576**	**321**	**55.73%**	**329**			
Giardia cricetidarum										
Hamsters	*Phodopus campbelli*	Farmed	China	9	9	100%	9	*SSU rRN, bg, ef-1α*		
Hamsters	*Mesocricetus auratus*	Farmed	China	11	11	100%	11	*SSU rRN, bg, ef-1α*		
Hamsters	*Phodopus sungorus*	Farmed	China	87	36	41.38%	36	*SSU rRN, bg, ef-1α*		
Subtotal				**107**	**56**	**52.34%**	**56**			
Giardia doudenalis										
Alashan ground squirre	*Spermophilus alaschanicus*	Wild in the field	China	99	2	2.02%	2	*bg, gdh, tpi*	**B (2)**	
Asian house rats	*Rattus tanezumi*	Wild in the field	China	33	2	6.06%	2	*bg, gdh, tpi*	**G (2)**	
Bamboo rat	*Rhizomys sinensis*	Farmed	China	480	52	10.83%	52	*bg, gdh, tpi*	B (52)	
Beaver	*Castor canadensis*	Wild in the field	Canada, United States				32	*SSU rRNA, Tpi*	A (18); B (14)	AI (1)
Beaver	*Castor canadensis*	Zoo	United States	62	4	6.45%	4	*TPI, ssrRNA, bg*	B (4)	
Beaver	*Castor fiber*	Zoo	China	3	1	33.33%	1	*bg, gdh, tpi*	B (1)	
Berkenhout	*Rattus norvegicus*	Wild in the field	China	23	1	4.35%		*SSU rRN, bg, ef-1α*		
Black rats	*Rattus rattus*	Wild in the field	Iran	40	2	5.00%	2	*tpi*	B (1), G (1)	
Brown rats	*Rattus norvegicus*	Wild in the field	China , Iran	208	12	5.77%	12	*bg, gdh, tpi*	**G (12)**	
Brown rats	*Ruttus norvegicus*	Lab	China	355	33	9.30%	33	*bg, gdh, tpi*	**G (33)**	
Bush rat	*Rattus fuscipes*	Wild in the field	Australia	12	1	8.33%	1	*SSU rRNA, bg*	C/F (1)	
Chinchilla	*Chinchilla lanigera*	Farmed	Brazil, Romania, Italy, Europe	976	557	57.07%	236	*bg, tpi, gdh, SSU rRNA, ITS*	A (2); B (193); C (2), D (33), E (6)	AI (2)
Chinchilla	*Chinchilla lanigera*	Pet	Germany, Belgium, China, Czech Republic	220	91	41.36%	90	*bg, gdh, tpi*	A (13) B (62), C (14), E (1)	AI (8), AII (3), AI/AII (2)
Chipmunk	*Eutamias asiaticus*	Pet	China	279	24	8.60%	24	*bg, gdh, tpi*	A (13); G (11)	AI (13)

(*continued on next page*)

Table 2 (*continued*)

Host animals	Scientific name	Rodent types	Locations	Total No.	Positive no.	Infection (%)	No. of genotyped	Genetic locus	Assemblages	Sub-assemblage
Coypus	*Myocastor coypus*	Farmed	China	308	38	12.34%	38	*bg, gdh, tpi*	A (2); B (36)	AI (2)
Desmarest's hutia	*Capromys pilorides*	Pet	Europe				1	*bg, tpi, SSU rRNA, ITS*	B (1)	
Dolichotis	*Dolichotis patagonum*	Zoo	China	15	6	40.00%	6	*bg, gdh, tpi*	A (3); B (1), E (2)	AI (3)
Groundhog		Wild	Canada				2	*SSU rRNA*	A (2)	
Guinea pig	*Cavia porcellus*	Lab	Australia				3	*Allozymesb*	A (3)	AI (3)
Guinea pig	*Cavia porcellus*	Pet	Sweden				1	*bg, gdh, tpi*	B (1)	
Guinea pig	*Cavia porcellus*	Farmed	Europe	121	5	4.13%		*bg, tpi, SSU rRNA, ITS*		
Hamsters	*Phodopus sungorus*	Farmed	China	87	6	6.90%		*SSU rRN, bg, ef-1α*		
Himalayan marmot	*Marmota himalayana*	Wild in the field	China, Gansu	399	6	1.50%	6	*bg, gdh, tpi*	A (1); B (4), E (1)	
House mice	*Mus musculus*	Free living in community	China	31	1	3.23%	1	*bg, gdh, tpi*	G (1)	
House mice	*Mus musculus*	Wild in the field	Iran	40	1	2.50%	1	*tpi*	G (1)	
Mouse	*Pseudomys albocinereus*	Wild in the field	Australia	2	1	50.00%	1	*SSU rRNA, bg*	E (1)	
Mouse	*Apodemus* spp.	Wild in the field	Germany	82	1	1.22%	1	*SU rRNA, bg, gdh*	A (1)	
Mouse	*Mus musculus*	Wild in the field	Sweden				1	*bg, gdh, tpi*	A (1)	
Muskrat	*Ondatra zibethicus*	Wild in the field	United States				5	*SSU rRN, tpi*	B (5)	
Muskrat	*Ondatra zibethicus*	Wild in the field	Romania	1	1	100%	1	*gdh*	C (1)	
Norway rats	*Rattus norvegicus*	Free living in community	Spain	100	35	35.00%		*gdh, tpi*		
Prairie dogs	*Cynomys ludovicianus*	Lab	USA	60	29	48.33%	29	*bg, gdh, tpi*	A (19); B (6), A/B (4)	AI (16), AI/AII (3)
Prairie dogs	*Cynomys ludovicanus*	Pet	Thailand	79	11	13.92%	2	*ssu rRNA, tpi, gdh*	A (1); B (1)	AI (1)
Prairie dogs	*Cynomys ludovicanus*	Wild in the field	Canada				1	*SSU rRNA*	**A (1)**	
Patagonian cavy	*Docilchotis patagonum*	Zoo	Croatia	1	1	100%	1	*bg, tpi, gdh, SSU rRNA, ITS*	B (1)	
Prevost's squirrel	*Callosciurus prevosti*	Zoo	Croatia	1	1	100%	1	*bg, tpi*, SSU rRNA, *ITS*	**B (1)**	
Rat	*Rattus* spp.	Lab	Australia				2	*Allozymesb*	**G (2)**	
Rat	*Rattus* spp.	Wild in the field	Sweden				8	*bg, gdh, tpi*	**G (8)**	
Rat	*Rattus* spp.	Free living in community	Spain	64	9	14.06%	9	*bg, gdh, tpi*	**G (9)**	
Rodents	//	Wild in the field	Brazil	136	4	2.94%	4	*gdh, tpi*	A (4)	AI (4)
urban rodents	/	Free living in community	Malaysia	134	4	2.99%	1	*tpi*	B (1)	
Voles	*Myodes* spp.	Wild in the field	Germany	301	4	1.33%	4	*SU rRN, bg, gdh*	A (2), B (2)	
Wild rodent	//	Wild in the field	Spain	284	73	25.70%	20	*bg, gdh, tpi*	B (1); **G (19)**	
	Subtotal			**5306**	**1019**	**20.23%**	**641**		**A (86), B (390), G (99), D (33), C (17), E (11), A/B (4); C/F (1)**	**AI (53), AII (3), AI/AII (5)**

Table 3
The infections of *Giardia duodenalis* in water sources, fresh produce, and soil.

Location	Environment factors	Total No.	Positive No.	Infection rate (%)	No. of samples genotyped	Genetic locus	Assemblages	
Philippines	Lake stations	36	6	16.67%	6	*SSU rRNA*	A (6)	
Philippines	Tributary rivers	69	26	37.68%	26	*SSU rRNA*	A (24), B (2)	
China	Sewer wastewater	386	319	82.64%	202	*tpi*	A (243), B (6), A/B (53)	AII (243)
Colombia	River Water	55	26	47.27%	26	*gdh*	A (19), B (7)	AII (2)
Pakistan	Water Bodies	600	160	26.67%	//	*SSU rRNA*		
Norway	Sewage	40	30	75.00%	30	*SSU rRNA, bg, gdh*	A (27), B (3)	AII (27)
Hungary	Raw, surface and sewage water	36	13	36.11%	12	*SSU rRNA, gdh*	A (7), B (1), A/B (4)	AI (1), AII (4)
China	Wastewater	40	32	80.00%	32	*bg, gdh, tpi*	A (31), B (1)	AII (31)
China	Combined sewer overflow	40	33	82.50%	33	*bg, gdh, tpi*	A (31), B (1), G (1)	AII (31)
Spain	Treated wastewater	96	12	12.50%	12	*SSU rRNA, bg*	A (5), A/E (7)	AI (2), AII (3)
Romania	Wastewater and Different Surface Water	76	22	28.95%	22	*gdh*	A (9), D (1); E (12)	AII (9)
France	Wastewater	36	25	69.44%	25	*tpi*	A (8), B (1), E (4), A/B (5), A/E (7)	
China	Raw urban wastewater	48	23	47.92%	23	*tpi*	A (17), B (5), A/B (1)	AII (17)
China	Recreational lakes	52	51	98.08%	5	*SSU rRNA*	A (3), B (1), D (1)	
Malaysia	Recreational lake water	9	7	77.78%	7	*SSU rRNA*	A (7)	
USA, Canada, New Zealand	Raw surface water				29	*tpi, WGS*	A (6), B (21), A/B (2)	AI (6)
Canada	Raw surface water				29	*SSU rRNA, bg, gdh, tpi, WGS*	A (4), B (25)	
Brazil	Water	10	3	30.00%	1	*SSU rRNA, gdh, tpi*	E (1)	
Egypt	Raw water	10	10	100.00%	//	*tpi, gdh*	A (10)	AII (10)
Bangladesh	Water samples	24	14	58.33%	5	*tpi, bg*	B (1), E (4)	
US	Sewage samples				1	*SSU rRNA*	A (1)	
	Subtotal	**1663**	**812**	**48.83%**	**636**		**A (458), B (75), A/B (12), A/E (14), D (2), E (21), G (1)**	AI (9), AII (377)
Italy	Ready-to-eat salads and berry fruits	324	25	7.72%	25	*bg*	A (6), B (18), E (1)	
Pakistan	Vegetables	200	16	8.00%	//	*SSU rRNA*		
Brazil	Vegetables	11	2	18.18%	2	*bg, gdh*	B (2)	
Brazil	Fresh Leafy Vegetables	128	16	12.50%	16	*gdh*	A (16)	AII (16)
Brazil	Vegetables	260	19	7.31%	11	*gdh*	A (9), B (1), E (1)	AI (9)
Brazil	Vegetables	62	16	25.81%	2	*SSU rRNA, gdh, tpi*	E (2)	
India	Fresh produce	284	13	4.58%	2	*SSU rRNA, tpi, gdh*	A (1), D (1)	
Italy	Ready-to-eat packaged salad	648	4	0.62%	4	*tpi*	A (4)	
Syria	Salad vegetables	128	17	13.28%	17	*bg*	B (17)	
Canada	Ready-to-eat packaged leafy greens	544	10	1.84%	9	*SSU rRNA*	A (2), B (7)	
Spain	Green leafy vegetables	129	30	23.26%	//	*qPCR*		
Morocco	Leafy green	152	4	2.63%	//	*qPCR*		
Iraq	Vegetables and fruits	230	4	1.74%	//	*SSU rRNA*		
China	Street markets vegetables	642	73	11.37%	73	*SSU rRNA*	B (72), E (1)	
Mozambique	Fresh Horticultural Products	321	12	3.74%	//	*bg*		
	Subtotal	**4063**	**261**	**6.42%**	**161**		**A (38), B (117), E (5), D (1)**	AI (9), AII (16)
Brazil	Soil	10	2	20.00%	//	*SSU rRNA, gdh, tpi*		
Pakistan	Soil	400	71	17.75%	//	*SSU rRNA*		
Colombia	Soil	50	8	16.00%	8	*gdh*	A (4), B (4)	AII (1)
	Subtotal	**460**	**81**	**17.61%**	**8**		**A (4) B (4)**	AII (1)

(6.28%, 308/4907) is significantly higher ($P < 0.001$) than that for common human populations (4.92%, 680/13822). Asymptomatic infections also seem common for *G. duodenalis*, as the pooled prevalence for the population of asymptomatic children (28.15%, 1342/4764) was higher than that for symptomatic children (23.06%, 518/2321) (Table 1).

Poor sanitation and hygiene are other risk factors for *G. duodenalis* infections identified in previous investigations. Undoubtedly, the pooled prevalence for people in poor communities (18.22%, 1172/6434) is significantly higher ($P < 0.001$) than that for common communities and households (14.75%, 329/2230). As for the children and *G. duodenalis*, the rate of infection in children in poor communities (14.89%, 235/1578) was significantly higher ($P < 0.001$) than that for more affluent children (10.12%, 791/7818) (Table 1).

Contact with animals is another risk factor for *G. duodenalis* infections identified in some previous investigations. The pooled prevalence for people frequently in contact with animals (15.30%, 110/719) is significantly higher ($P < 0.001$) than that for the overall human population (4.92%, 680/13822) (Table 1).

The pooled prevalence for children is generally higher than that for

Table 4
Distributions of different *Giardia duodenalis* assemblages in humans and rodents.

Assemblages	No. of genotyped	Major hosts	Reports in humans	Reports in rodents (Positive no.)
Assemblage A	86	Humans, non-human primates, ruminants, pigs, horses, canines, felines, rodents, marsupials, other mammals	Numerous	Chinchilla (1), Beaver (12), Chinchilla (7), Guinea pig (3), Chinchilla (2), Beaver (6), Chinchilla (5), Prairie dogs (19), Mouse (1), Voles (2), Chipmunk (13), Rodents (4), Coypus (2), Prairie dogs (1), Himalayan marmot (1), Dolichotis (3), Mouse (1), Prairie dogs (1), Groundhog (2)
AI	66	Livestocks	Few	Chinchilla (1), Chinchilla (7), Guinea pig (3), Chinchilla (2), Beaver (6), Chinchilla (5), Prairie dogs (19), Chipmunk (13), Rodents (4), Coypus (2), Prairie dogs (1), Dolichotis (3)
AII	8	Humans	Numerous	Chinchilla (5), Prairie dogs (3)
Assemblage B	390	Humans, non-human primates, horses, rabbits, marsupials, chinchillas, beavers	Numerous	Beaver (7), Muskrat (5), Beaver (4), Guinea pig (1), Prevost's squirrel (1), Patagonian cavy (1), Chinchilla (10), Chinchilla (3), Chinchilla (29), Desmarest's hutia (1), Chinchilla (10), Wild rodent (1), Beaver (1), Beaver (7), Chinchilla (33), Prairie dogs (6), Chinchilla (151), Chinchilla (1), Voles (2), Bamboo rat (52), urban rodents (1), Chinchilla (18), Coypus (36), Black rats (1), Prairie dogs (1), Himalayan marmot (4), Alashan ground squirre (2), Dolichotis (1)
Assemblage C	17	Canines	Few	Chinchilla (16); Muskrat (1)
Assemblage D	33	Canines	Few	Chinchilla (33)
Assemblage E	11	Ruminants, pigs	Some	Mouse (1); Chinchilla (7); Himalayan marmot (1); Dolichotis (2)
Assemblage G	99	Mice, rats	None	Rat (2), Rat (8), Wild rodent (19), Brown rats (11), Asian house rats (2), House mice (1), Chipmunk (11), Brown rats (33), Rat (9), House mice (1), brown rats (1), Black rats (1)

other populations, indicating that the age group is a significant factor for *G. duodenalis* infections. Many factors, including specimen size, host immune status, and diagnostic techniques, may also be responsible for the differences in *G. duodenalis* prevalence in different geographic areas (Table 1).

Among the positive samples, a total of 7621 samples (including 4703 sporadic or outbreak positive cases) were successfully genotyped by *ssu rRNA* or by *bg*, *gdh* or *tpi* genes. For *G. duodenalis*, a total of six assemblages (A, B, C, D, E, and F) and some mixed assemblages have been identified. The *G. duodenalis* assemblage B is dominant (54.77%, 4174/7621), followed by assemblage A (40.31%, 3072/7621) and mixed infections of assemblage A and B (3.45%, 263/7621).

For *G. duodenalis* assemblage A, genotype AII is the most common sub-assemblage identified in humans at 71.02% (1397/1967). For other subtypes within assemblage A, sub-assemblage AI was identified in 26.39% of cases (519/1967), AIII in 1.17% (23/1967), and mixed infections (AI/AII or AII/AIII) comprised 1.42% (28/1967) in animals in previous investigations.

In addition to the zoonotic assemblages A and B, assemblage E (0.71%, 54/7621) has been identified in humans, followed by D (0.10%, 8/7621), C (0.09%, 7/7621), F (0.08%, 6/7621), and some mixed infections of B/E (0.13%, 10/7621), A/F (0.09%, 7/7621), and A/C or A/D mixed genotypes (0.26%, 20/7621).

Unquestionable, the assemblages A and B are the dominant genotypes in humans, being responsible for 98.53% (7509/7621) of the identified genotypes. It is worth noting that assemblage E, although it was considered as ruminant-specific previously, has the potential for zoonotic transmission between humans and animals.

4. Molecular characteristics of *Giardia* in rodents

4.1. Prevalence of Giardia in rodents

To date, among the nine valid *Giardia* species, four have been identified in rodents based on molecular data: *G. muris*, *G. microti*, *G. cricetidarum*, and *G. duodenalis* (Table 2). *G. microti* and *G. cricetidarum* were the most prevalent in rodents, being identified in 55.73% (321/576) and 52.34% (56/107), respectively. The pooled prevalence in rodents of *G. muris* was 6.33% (43/679), and *G. duodenalis* was 20.23% (1019/5306).

There were also other *Giardia* species identified in rodents based only on morphology, including the natural intestinal *G. muris* (9.3%, 19/204) in rodents in Iran [29] and 19.2% (10/52) in another study [30]; *Giardia* sp. was identified in captive rats (*Rattus norvegicus*) in Brazil zoos with 42.86% (3/7) [31]; *Giardia* sp. was identified in Syrian hamsters (*Mesocricetus auratus*) by morphology and histology of intestinal tissues [32].

4.2. Molecular characteristics of G. duodenalis by rodents species

The pooled prevalence of *G. duodenalis* was 20.23% (1019/5306) in rodents by molecular identification. For the locations, there were at least 16 countries that reported rodent infections of *G. duodenalis*, and the infection rates ranged from 1.31% (5/383) [33,34] in chinchillas in Germany to 66.25% (53/80) [35] for chinchillas in Belgium, and 100% (2/2) [36] for squirrels in Croatia [37] (Fig. 1).

Among the *G. duodenalis*-positive samples identified in rodents, only 641 samples were successfully genotyped by *ssu rRNA*, *bg*, *gdh* or *tpi* genes. A total of seven assemblages were identified in rodents: A (86), B (390), G (99), D (33), C (17), E (11), A/B (4), and C/F (1). Assemblage B was predominant (60.84%, 390/641), followed by assemblage G (15.44%, 99/641), assemblage A (13.42%, 86/614), assemblage D (5.15%, 33/641), assemblage C (2.65%, 17/641), assemblage E (1.72%, 11/641), and some mixed infections (assemblage A/B (0.62%, 4/641) and assemblage C/F (0.16%, 1/641)).

For different rodent species, the prevalence of *G. duodenalis* varied from 1.00% (3/301) in voles (*Myodes* spp.) to 57.07% (557/976) in chinchillas (*Chinchilla lanigera*) (Table 2). Among the genotypes, the *G. duodenalis* zoonotic assemblages B ($n = 390$) were frequently identified in most rodent species, and the *G. duodenalis* zoonotic assemblages A ($n = 86$) and rodent host-specific G ($n = 99$) were both commonly identified in rodents (Table 2).

For subtypes of assemblage A in rodents, sub-genotype AI is the most common sub-assemblage, identified in 86.89% (53/61) in rodents. Sub-assemblage AII, previously identified in humans, was responsible for 4.92% (3/61), and mixed (AI/AII) infections are also common at 8.20% (5/61).

For the other assemblage distributions, assemblage C ($n = 17$) has been reported in chinchillas (*Chinchilla lanigera*) in Italy [38], and

Table 5
Distributions of *Giardia duodenalis* in rodents of different feeding types.

Rodents feeding types	Total No.	Positive no.	Infection (%)	No. of genotyped	Assemblages(no.)	Sub-assemblage A	Zoonotic potential (%)
Wild in the field	1660	111	6.69%	106	A (30); B (29); C (1); E (2); G (43), C/F (1)	AI (5)	53.15%
Free living in community	329	49	14.89%	11	B (1); G (10)	//	9.09%
Pet	578	126	21.80%	118	A (27); B (65); G (11), C (14), E (1)	AI (22), AII (3), AI/AII (2)	77.97%
Farm	1972	658	33.37%	326	A (4); B (281); C (2); D (33); E (6)	AI (4)	87.42%
Zoo	82	13	15.85%	13	A (3); B (8); E (2)	AI (3)	84.62%
Lab	415	62	14.94%	67	A (22); B (6); G (35); A/B (4)	AI (19), AI/AII (3)	41.79%
Total	**5036**	**1019**	**20.23%**	**641**	**A (86), B (390), A/B (4); G (99), C (17); D (33); E (11); C/F (1)**	**AI (53), AII (3), AI/AII (5)**	**74.26%**

muskrats (*Ondatra zibethicus*) in Romania [36]. Assemblage D ($n = 33$) was only reported in chinchillas in one study in Romania [39]. Assemblage E ($n = 11$) was reported in mice (*Pseudomys albocinereus*) in Australia [40], chinchillas (*Chinchilla lanigera*) in Romania [39], and Himalayan marmots (*Marmota himalayana*) and maras (*Dolichotis patagonum*) in China [41,42]. The mixed of assemblage C and F was identified in wild bush rats (*Rattus fuscipes*) in Australia [40].

5. Molecular characteristics of *G. duodenalis* in environmental samples

The environmental factors involved in the *G. duodenalis* transmission are cysts contaminating water, soil, or fresh produce (Table 3). For water samples, the pooled prevalence of *G. duodenalis* was 48.83% (812/1663), with the highest record in recreational lakes in China at 98.08% (51/52) [43] and 100% (10/10) in untreated water in Egypt [44]. Among the positive samples, only 636 were successfully genotyped by *ssu rRNA*, *bg*, *gdh*, or *tpi* genes. There were five kinds of *G. duodenalis* assemblages identified in water samples, namely A, B, D, E, and G, and some mixed infections A/B and A/E. The zoonotic assemblage A was dominant (72.01%, 458/636), followed by assemblage B (11.79%, 75/636), assemblage E (3.30%, 21/636), assemblage D (0.31%, 2/636), and mixed infections A/B (1.89%, 12/636) and A/E (2.20%, 14/636).

For the fresh produce, *G. duodenalis* was identified in green leafy vegetables, street market vegetables, ready-to-eat packaged leafy greens and fresh horticultural products, ready-to-eat salads, and fruits (Table 3). The pooled prevalence of *G. duodenalis* infection in fresh produce was 6.42% (261/4063). Among the positive samples, only 161 were successfully genotyped by *ssu rRNA*, *bg* or *gdh* genes, with assemblage A, B, D, and E being identified. Among these, the zoonotic assemblage B was dominant (72.67%, 117/161), followed by assemblage B (23.60%, 38/161), assemblage E (3.11%, 5/161), and assemblage D (0.62%, 1/161).

For the soil, only three studies have reported infections of *G. duodenalis* in soil samples. The pooled prevalence was 17.61% (81/460) [45–47]. Among the positive samples, only eight samples were successfully genotyped by *ssu rRNA* or *gdh* genes, including assemblage A (50.0%, 4/8) and B (50.0%, 4/8) [47]. There were also some other negative results reported for *G. duodenalis* infections in soil samples, such as in Brazil [48,49], Egypt [44], and Mongolia [50].

Both *G. duodenalis* sub-genotypes AI and AII were identified in environmental factors (Table 3). Sub-assemblage AI has mostly been seen in animals in previous investigations, and AII in humans.

6. Ecological significance from a one health perspective for giardiasis transmission

6.1. Possible waterborne or foodborne zoonotic transmission

Giardia duodenalis causes large numbers of gastrointestinal illnesses in humans, and there have been over 300 reported outbreaks of giardiasis in the world since 1954, most of which were related to contaminated water [16,17,51]. The largest drinking water outbreak of giardiasis was reported in Portland, Oregon, USA in 1955, with 50,000 infected individuals [17]. More recently, important waterborne giardiasis extensive outbreaks have been documented in Bergen, Norway, in 2004, with over 2500 individuals becoming infected (1500 patients were laboratory diagnosed) caused by drinking water contaminated with *Giardia* cysts in sewage pipes due to leakage from one particular septic tank [52,53].

In North America, there were two outbreaks (83 laboratory confirmed cases were documented in the first outbreak, and 124 laboratory confirmed cases were identified during the second outbreak) at five-year intervals that occurred in the same community with a population of 4200 in the mountains of British Columbia, Canada [54]. In November 1981, an outbreak of waterborne giardiasis occurred at a popular ski resort in Colorado, United States [55]. Many waterborne giardiasis outbreaks have been documented, and giardiasis outbreaks are usually associated with drinking water or recreational water exposure [16].

Very few foodborne outbreaks have been documented [17], and only 38 foodborne outbreaks of giardiasis have been reported [56]. In many of the outbreak investigations, the food type or source was frequently undetermined. However, a variety of foods have been implicated, with fresh produce the most common food type and infected food handlers the most common source [56].

For sporadic cases, numerous risk factors have been identified, including direct and indirect fecal contact, male–male sexual contact, and international travel; these factors have very high odds ratios, but on a population basis, additional risk factors with lower odds ratios are still important because of their high prevalence. These include daycare exposure, swimming in or drinking from natural water bodies, and even chronic gastrointestinal conditions or the use of antibiotics [19,57].

Numerous studies of the relative importance of genotypes A (usually AII) and B have been reported, but the results of these studies do not clearly identify a difference in epidemiology. In contrast, there is accumulating evidence that genotype AI is primarily a zoonotic infection [19]. These studies have also identified the common concurrence of both assemblages A and B in drinking water-associated outbreaks of giardiasis [7,14].

6.2. Zoonotic potential of G. duodenalis from rodents

From a One Health perspective, the human–animal–environment has been identified as being involved in the *G. duodenalis* transmission. For humans, the zoonotic assemblages A, B, and mixed infections have been identified in 98.53% (7509/7621) of the human samples. The animal host-specific C, D, E, F, and mixed infections were identified in 0.98% (75/7621) of cases, and the mixed genotypes were identified in 0.49% (37/7621).

For rodents, the zoonotic assemblages A, B and mixed infections were identified in 74.88% (480/641) of rodents samples. The rodent

host-specific assemblage G was identified in 15.44% (99/641); the dog host-specific assemblages C and D were identified in 7.80% (50/641); the ruminant host-specific assemblage E was identified in 1.72% (11/641), and one dog/cat host-specific assemblage C/F (0.16%, 1/641) was identified.

For the environmental samples, the zoonotic assemblages A, B, and mixed infections were identified in 85.69% (545/636) in water samples; the ruminant host-specific assemblage E was identified in 3.30% (21/636); the dog host-specific assemblage D was identified in 0.31% (2/636); the rodent host-specific assemblage G was identified in 0.16% (1/636), and there were 14 assemblage A/E mixed infections (2.20%, 14/636). The zoonotic assemblages A, B, and mixed infections were identified in 96.27% (155/161) in fresh produce samples; the ruminant host-specific assemblage E was identified in 3.11% (5/161); the dog host-specific assemblage D was identified in 0.62% (1/161). The zoonotic assemblages A ($n = 4$) and B (n = 4) were identified in 100% (8/8) of reported soil samples.

G. duodenalis assemblages A and B are the major zoonotic assemblages, and assemblage E has also been reported in humans; C and D are occasionally reported in humans, while G has not been reported in humans to date (Table 4). The animal host-specific assemblages C, D, E, and F identified in rodents indicated that the dogs, cats, wild animals, and some farm animals could be involved in the *G. duodenalis* zoonotic transmission cycle. The rodents could also serve as the reservoir for *G. duodenalis* transmission between different animals.

For rodents, there are six feeding types, namely wild in the field, free living in the community, pets, farmed, zoo, and lab (Table 5). The rodents of the farm feeding type had the highest prevalence of *G. duodenalis* infections with 33.37% (658/1972), followed by pet rodents with 21.80% (126/578), zoo rodents with 15.85% (13/82), lab rodents with 14.94% (62/415), free living in community rodents with 14.89% (49/329), and the lowest in wild rodents at 6.69% (111/1660).

For the zoonotic potential assemblages in the different rodent feeding types, the highest was in farm rodents (87.4%) followed by zoo rodents (84.6%), pet rodents (77.97%), wild in the field rodents (53.15%), lab rodents (41.79%), and the lowest in the free living in the community rodents (9.09%). In summary, the farmed rodents and pet rodents had a higher prevalence and potential for *G. duodenalis* zoonotic transmission between rodents and animals (Table 5).

There are also some biases for the published literature, as only studies with positive results or those reporting the highly zoonotic potential for *G. duodenalis* assemblages were easy to have published.

7. Conclusions

From the One Health perspective, *G. duodenalis* zoonotic assemblages (A and B) have been simultaneously identified in humans, animals, and environment factors involved in zoonotic transmission. The role of rodents in the zoonotic transmission of giardiasis should be taken into consideration from the One Health perspective owing to the fact that rodents are both in close contact with humans and different types of environments. Among the total of seven *G. duodenalis* assemblages identified in rodents, assemblages A and B were responsible for the majority of infections, indicating their higher zoonotic potential. Rodents played an essential role in the zoonotic transmission of giardiasis. In addition to rodents, dogs, cats, wild animals, and some farm animals could be involved in the zoonotic transmission cycle. Therefore, giardiasis can only be effectively controlled by implementing the One Health approach. Further studies are required to investigate *G. duodenalis* among the diverse human population, livestock, pet animals, and rodents in various ecosystems, and researchers should pursue a multidisciplinary One Health approach with contributions from zoologists, ecologists, veterinarians, and public health experts to understand rodent-related *G. duodenalis* and possible transmission routes.

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Declaration of Competing Interest

The authors declare no competing interests.

Data availability

The data that has been used is confidential.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.onehlt.2023.100500.

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