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Review articles

Wildlife as an environmental reservoir of *Enterocytozoon bieneusi* (Microsporidia) – analyses of data based on molecular methods

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ABSTRACT. *Enterocytozoon bieneusi* is the most commonly identified Microsporidia in humans and has also been detected worldwide in a large group of wild living and domestic animals. The identification of *E. bieneusi* in wildlife has raised the question of the importance of animal reservoirs in the epidemiology of microsporidiosis and the implications of the infection with this pathogen in hosts. This review summarizes the available molecular data on the variety of *E. bieneusi* genotypes, both potentially zoonotic and host-specific isolated from wild living mammals and birds. In contrast to microsporidial infections of humans and domestic animals, wildlife deserves attention as a source of significant environmental reservoir of *E. bieneusi*.

Key words: *Enterocytozoon bieneusi*, microsporidia, genotype, zoonosis, wildlife, reservoir

Introduction

Microsporidia are a diverse group of obligate intracellular pathogens closely related to fungi [1]. *Enterocytozoon bieneusi*, the dominant member of the human pathogenic microsporidian species, is an unicellular organism that infects the enterocytes of the small intestine and causes diarrhea and enteric diseases in humans, and domestic and wild animals [1–3]. Clinical manifestations of microsporidiosis include enteritis, acalculous cholecystitis or unspecific symptoms in the case of disseminated infection [4,5]. In humans, it has been reported to cause self-limiting infections in immunocompetent individuals while life-threatening chronic diarrhea is caused in immunocompromised persons, particularly in AIDS patients and organ transplant recipients [1,4–10]. This species is estimated to be responsible for 90% of microsporidian infections [4,10] including a great number of asymptomatic ones [4].

Routes of transmission

Ingestion of spores with contaminated food or water offers the most likely route of transmission of *E. bieneusi* to humans [11,12]. Besides the oral route, it is possible that aspiration of air contaminated with spores led to infection in several cases [13].

There were described several risk factors associated with *E. bieneusi* infection: direct person-to-person transmission [14–18], drugs injection [18], living in rural areas with close contact with animals (i.e. cows, horses, poultry or insects) [16, 19], consumption of contaminated food, especially fruit and vegetables [20,21]. Spores were detected in retail fresh food produce (raspberries, lettuce and sprouts) [20] and were found to be the cause of a dangerous foodborne outbreak in Sweden [22]. Other described sources of outbreaks may be non-filtered water in recreational areas like pools, lakes, hot tubs [16,18] and insufficient hygiene (toilets, garbage, lack of running water) [21]. *E. bieneusi* can be transmitted to humans by anthroponotic or zoonotic transmission, after exposure to infected

individuals or animals, respectively [23]. Because of its public significance and a great potential threat to the public, according to National Institute of Allergy and Infectious Diseases, microsporidia are on the Priority Pathogens List and are considered Category B pathogens [24].

Molecular diagnostics

The identification of *E. bieneusi*, which is a complex species with multiple genotypes and diverse hosts range and pathogenicity, is based on the molecular methods [23]. Amplification of the internal transcribed spacer (ITS) of the rRNA gene, a hypervariable sequence with about 243 bp long, sequencing and then aligning of obtained PCR products with reference sequences, are the standard techniques used in genotyping *E. bieneusi* isolates from humans and animals [23]. The use of ITS as a single marker can identify *E. bieneusi* genotypes and can be helpful to explain its possible transmission routes [25,26]. Also other molecular method such as PCR-restriction fragment length polymorphism (RFLP) analysis can be employed [27,28]. To elucidate the precise genetic diversity and the route of transmission of *E. bieneusi*, the high-resolution multi-locus sequence typing (MLST) using as markers three microsatellites (MS1, MS3, and MS7) and one minisatellite (MS4) was developed [29] and it is widely used [25,26,30–34]. MLST is useful in identifying the sources of human *E. bieneusi* infections, especially those of the animal origin [23].

Genotypes' diversity

First, *E. bieneusi* was detected in pigs; then other domestic animals such as dogs, cats, horses, cattle, rabbits and sheep [35–42] have become identified as reservoirs of this microparasite. *E. bieneusi* has also been detected in a variety of wild living animals, including mammals and birds [2,35] – Tables 1 and 2.

Until now, the ITS of the rRNA gene has been used widely to genotype *E. bieneusi* isolates [23]. At present, over 240 *E. bieneusi* genotypes have been identified [24,43]. By ITS sequence analysis of *E. bieneusi* genotypes, nine different groups of all genotypes were established (groups 1 to 8 and the so called outlier in dog) [24]. A large cluster named as group 1 contains genotypes that are found both in humans and animals. Even though some genotypes are genetically similar to human-pathogenic ones, they have been found only in animals so far, suggesting their zoonotic potential [11]. The remaining groups (2–8 and the outlier in dog) are found mostly in specific hosts, including humans, and in wastewater [24,42].

A great contribution to the knowledge on the diversity of *E. bieneusi* genotypes was the studies conducted in Peru on an HIV/AIDS persons [21,44]. During these researches 11 genotypes (Peru-1 to Peru-11) were identified. The most prevalent genotypes were Peru-1 (synonym of genotype A), Peru-2 (syn. Type IV) and Peru-9 (syn. genotype D). A great part of these genotypes was also detected in animals, including genotypes Peru-1, Peru-2, Peru-4 (syn. EbpC/E/WL13/WL17) and Peru-6 (syn. PtEb1/PtEbVII), Peru-7, Peru-9, Peru-10 and Peru-11 [14,21,27,35,37,39,42,45–49]. Humans have been predominantly affected with zoonotic group 1 genotypes: D, EbpC, Type IV and sporadically with the genotypes of other genetic groups (e.g. BEB4, BEB6, I, J, Nig3 to Nig5, etc.) [39,46].

A number of authors has reported that genotype D was commonly detected in immunocompetent persons; transplant recipients, HIV-positive and HIV-negative patients, diarrheal children etc. [9,14,44,46–48]. A wide range of animal reservoirs of this genotype includes, inter alia, wild and pet birds, livestock (cattle, sheep, goats, horses, pigs), cats, dogs and a great number of wildlife among different genera [36,49–51]. BEB6 has also been found in humans, cats, horses, non-human primates, and wastewater in China [24,25,31,52–54]. Contrastingly, some genotypes like B or C are considered as host specific because they were exclusively found in humans [23]. A vast majority of recent reports on *E. bieneusi* is focused on the prevalence and genotypes identification in pet animals or livestock; only a minor part of studies concern wildlife.

E. bieneusi in humans

The first case of *E. bieneusi* in humans was described in HIV-associated opportunistic intestinal infection in 1985 and was morphologically identified using electron microscopy [6]. The prevalence of *E. bieneusi* infections involving HIV-infected patients has been estimated beetwen 2% to 78% as documented by selected studies [7–10,13,16–19,21,23,55–63]. Although most of

Table 1. *E. bieneusi* genotypes detected in wild living and captured birds

Order	Species	Study location	*E. bieneusi* genotype	Prevalence (%)	References
Psittaciformes	*Agapornis roseicollis* (rosy-faced lovebird), *Agapornis personatus* (yellow-collared lovebird)	Czech Republic, Portugal	A (=Peru1)	12.5* 28.9*	[80] [83]
	Melopsittacus undulatus (budgerigar)	Czech Republic	A, EbpA (=F)		[80]
	Nymphicus hollandicus (cockatiel), *Myiopsitta monachus* (monk parakeet), *Alisterus scapularis* (Australian king parrot), *Polytelis swainsonii* (superb parrot), *Pyrrhura sp.* (parakeet), *Platycercus elegans* (crimson rosella), *Platycercus eximius* (eastern rosella),	Czech Republic	A		[80]
	Amazona aestiva (blue-fronted amazons)	Brazil	EbpA	5.6	[81]
	Amazona leucocephala (Cuban amazon), *Agapornis fischeri* (Fischer's lovebird), *Agapornis nigrigenis* (black-cheeked lovebird), *Agapornis cana* (lovebird), *Aratinga acuticaudata* (blue-crowned parakeet), *Aratinga mitrata* (mitred parakeet), *Aratinga auricapilla* (golden-capped parakeet), *Barnardius zonarius* (Australian ringneck), *Cyanoramphus novaezelandiae* (red-fronted parakeet), *Nandayus nenday* (nanday parakeet), *Neophema splendida* (scarlet-chested parrot), *Neophema pulchella* (turquoise parrot), *Polytelis alexandrae* (princess parrot), *Poicephalus senegalus* (Senegal parrot), *Platycercus caledonicus* (Tasmanian rosella)	Czech Republic	EbpA		[80]
	Psittacus erithacus (African grey parrot)	Czech Republic Portugal	EbpA PtEbII (=Peru6-var)		[80] [83]
Passeriformes	*Serinus canaria* (Atlantic canary), *Temenuchus pagodarum* (brahminy starling)	Czech Republic	A		[80]
	Corvus frugilegus (rook)	Poland	D (=Peru9), Peru6 (=PtEbI)	nd	[45]
	Sicalis flaveola (saffron finch)	Brazil	EbpA	nd	[81]
Columbiformes	*Columba livia* (pigeon)	Spain	nd Col01-06	9.7 nd	[38] [79]
		Brazil	EbpA	7.8	[81]
		Portugal	Peru6, Peru6var	43,2	[83]
		Iran	D, M, BEB1(=J)	42	[85]
		Netherland	nd	11	[86]
		Poland	nd	1.4	[87]
	Ocyphaps lophotes (crested pigeon)	Czech Republic	A		[80]
	Geopelia cuneata (diamond dove)	Czech Republic	EbpA		[80]
Falconiformes	*Falco* sp. (falcon)	United Arab Emirates	EbpA	25	[84]
Struthioniformes	*Struthio camelus* (ostrich)	Spain Brazil	Type IV(=Peru2) Type IV	nd 14.3	[81] [104]

*overall prevalence estimated for different birds' species in studies [80] and [83]; nd – not determined

the reported cases concerned adults suffering from immunodeficiency due to HIV infection, *E. bieneusi* was also detected in HIV-negative patients who were immunocompromised due to cancers or different types of diseases or therapeutic immunosuppression when undergoing organ transplantation [8,10,64–69]. Furthermore, a few cases of infections in immunocompetent and healthy persons were reported and mostly classified as a traveler's diarrhea in Europe [70]; single cases were also reported in Africa [71,72]. Microsporidiosis generally, as opportunistic

Table 2. *Enterocytozoon bieneusi* genotypes in wild living and captive mammals

Order	Family	Species	Study location	*E. bieneusi* genotype	Prevalence (%)	References
Rodents	Sciuridae	*Sciurus carolinensis* (eastern gray squirrel)	USA	type IV, WL4, WW6, PtEbV, WL21	32.4	[42]
		Tamias striatus (eastern chipmunk)	USA	type IV, WL4, WL23	71.4	[42]
		Marmota monax (woodchuck)	USA	type IV, WL20, WL4, WL22, WW6	100	[42]
		Callosciurus erythraeus (red-bellied tree squirrel)	China	D, EbpC, SC02, CE01, CE02	16.7	[32]
	Castoridae	*Castor canadensis* (beaver)	USA	D, EpbC, WL7, WL8, WL9, WL12, WL13, WL15	15.3	[37]
	Cricetidae	*Peromyscus* sp. (deer mouse)	USA	WL4, WL23, WL25	23	[42]
		Myodes gapperi (borreal red-backed vole)	USA	WL20, WL21	20	[42]
		Myodes glareolus (bank vole)	Poland	WR2, WR6, WR10	39.1	[96]
		Microtus pennsylvanicus (meadow vole)	USA	Peru11, type IV, WL21	30	[42]
		*Ondartini zibethicu*s (muskrat)	USA	unknown, WL4, WL5, WL6, WL8, WL10, WL13, WL14, WL15, WL16	8.4	[37], [42]
	Leporidae	*Sylvilagus sp.* (cottontail)	USA	WL4, Peru11	25	[42]
	Muridae	*Apodemus agrarius* (striped field mouse)	Poland	D, WR5, WR7, WR8, gorilla1	42.9	[96]
		Apodemus flavicollis (yellow-necked mouse)	Poland	D, WR1, WR4, WR6, WR9	30	[96]
		Mus m. musculus (house mouse)	Czech Republic	EpbA, D, PigEBITS5, C, H	11	[40]
			Poland	WR3	28.6	[96]
		Mus m. domesticus (house mouse)	Czech Republic	CZ3, PigEBITS5, D, C, S6, Peru8	10.5	[40]
Carnivora	Mustelidae	*Mustela erminea* (ermine)	USA	WL4	100	[42]
		Lontra canadensis (river otter)	USA	D, EpbC, WL2, WL4, WL12, WL13	25.9-62.5	[37], [42]
	Procyonidae	*Procyon lotor* (raccoon)	USA	EpbC, Peru11, WL2, WL3, WL4, WL15, WL16, WL24, WL26, WW6,	27.3-81.8	[37], [42]
			Poland	NCF2	4	[96]
			China	D, SC02	2	[110]
	Canidae	*Vulpes vulpe*s (red fox)	USA	D, EpbC, WL8, WL11, WL13, WL15	13.5	[37]
			Spain	D	14.3	[104]
		Vulpes lagopus (arctic fox)	China	D, EpbC, CHN-F1, Peru8, CHN-DC1, Type IV, NCF1-NCF7	nd	[105], [106]
		Nyctereutes procyonoides (raccoon dog)	China	D, CHN-F1, CHN-R1, CHN-DC1, NCF2, WildBoar3, NCR1, NCR2	nd	[105], [106], [109]
	Ursidae	*Ursus americanus* (black bear)	USA	type IV, WL4	40	[42]
		Ursus thibetanus (asiatic black bear)	China	CHB1, SC01, SC02, horse2, ABB1, ABB2	1-27.4	[110], [111]
		Ursus arctos (brown bear)	China	CHB1	1	[110]
		Ursus arctos pruinosus (tibetian blue bear)	China	CHB1, SC02	2	[110]
		Helarctos malayanus (malayan sun bear)	China	CHB1,SC02	2	[110]
		Ailuropoda melanoleuca (giant panda)	China	Peru6	1	[110]
	Felidae	*Panthera leo* (african lion)	China	D	2	[110]
		Catopuma temminckii (asiatic golden cat)	China	D	1	[110]

Table 2. *Enterocytozoon bieneusi* genotypes in wild living and captive mammals cd.

Order	Family	Species	Study location	*E. bieneusi* genotype	Prevalence (%)	References
Artiodactyla	Suidae	*Sus scrofa* (wild boar)	China	WildBoar 7–11, EbpC, F, CHG19, CHC5, PigEBITS5, D, RWSH4, SC02, D	41.2	[118]
			Austria	Henan-I, EbpC	11.4	[119]
			Czech Republic	D, EbpA, WildBoar3-4, G	6.9	[119]
			Poland	EbpA, EbpC, WildBoar2-3, WildBoar5-6	7.7	[119]
			Slovak Republic	D, WildBoar1	3.6	[119]
	Cervidae	*Odocoileus virginianus* (white-tailed deer)	USA	WL4, WL18, WL19, I, J, WL1, DeerEb1-13	12.2	[2], [42], [115]
		Cervus elaphus (sika deer)	China	BEB6, HLJD-I- IV, J, EbpC, CHN-DC1, KIN-1, JLD-1- 3, COS-I, EbpA, D, JLD-I- XIV, HND-I-IV	32.6	[110], [113], [114], [117]
		Axis porcinus (hog deer)	China	BEB6, CHS9	3	[110]
		Cervus nippon (red deer)	China	BEB6, JLD-IV, JLD-XIII, HLJD-V	20	[113], [115]
		Elaphurus davidianus (Pere David's deer)	China	type IV, EbpC, EbpA, BEB6, COS-I	32	[116]
		Rangifer tarandus (reindeer)	China	COS-II	16.8	[122]
NHPs (non-human primates)	Cercopithecidae	*Macaca mulatta* (rhesus macaque)	China	BEB6, D, O, EpbC, CM1, CM8, SC02, SCM01	1.7- 33	[25], [31]
		Macaca fascicularis (cynomolgus monkey)	China	BEB6, EpbC, CM12, CM13	27.8	[25]
		Macaca nemestrina (pig-tailed macaque)	China	O, EpbC, PigEBITS5, CM14	25	[25]
		Macaca nigra (celebes crested macaque)	China	O	50	[25]
		Erythrocebus patas (hussar monkey)	China	D, O, EpbC	50	[25]
		Trachypithecus francoisi (Francois' leaf monkey)	China	EpbA, CM15, CM4	30	[25]
		Cercopithecus kandti (golden monkey)	China	D	31	[25]
		Colobus polykomos (king colobus)	China	D	14.3	[25]
		Chlorocebus sabaeus (green monkey)	China	D, Type IV, CS-1, CM4	66.7	[25]
		Mandrillus sphinx (mandrill)	China	CM4	4.4	[25]
		Papio hamadryas (hamadryas baboon)	China	D, Peru8, EpbC, Henan-IV, CM4	28.6	[25]
		Rhinopithecus roxellanae (snub-nosed monkey)	China	D, J, CHG1, CHG14, CM19, CM20, CM21	26.7- 69.4	[93]
		Papio sp. (baboon)	Kenya	A, D, Peru7, Peru11, KB1-KB6	12.3	[95]
		Papio anubis (olive baboon)	China	D, CM4	40	[25]
	Cebidae	*Cebus apella* (black-capped capuchin)	China	O, EpbA, EpbD, BEB4, CM16	27.3	[25]
		Cebus olivaceus (weeper capuchin)	China	O, EpbC, EpbA	75	[25]
		Cebus albifrons (white-fronted capuchin)	China	O	20	[25]
		Samiri sp. (squirrel monkey)	China	O, EpbC, EpbA, CM16, CM4	39.5	[25]
		Callithrix sp. (marmoset)	China	CM4	60	[25]

Table 2. *Enterocytozoon bieneusi* genotypes in wild living and captive mammals

Order	Family	Species	Study location	*E. bieneusi* genotype	Prevalence (%)	References
	Aotidae	*Aotus* sp. (night monkey)	China	CM4	75	[25]
	Lemuridae	*Lemur catta* (ring-tailed lemur)	China	Type IV, EbpA, O, CM10, CM11, CM16, CM18	24.4	[25]
		Varecia variegata (black-and-white ruffed lemur)	China	EpbC, O, CM4	100	[25]
	Hylobatidae	*Nomascus leucogenys* (northern white-cheeked gibbon)	China	Henan-IV, D, O, PigEBITS7	35.7- 66.7	[25], [31]
		Hylobates moloch (silvery gibbon)	China	EpbC, CM4	100	[25]
		Hylobates lar (white-handed gibbon)	China	EpbC, EbpA, BEB4, CM17	62.5	[25]
	Hominidae	*Pongo* sp. (orangutan)	Indonesia	D, Pongo2	2	[90]
		Pongo pygmaeus (bornean orangutan)	China	D, CM4	17.4	[25]
		Pan troglotydes (common chimpanzee)	China	CM4, CM9	14.3	[25]
		Gorilla beringei beringei (mountain gorilla)	Rwanda	EbpA, D, C, gorilla2, gorilla5-8	18	[91]
		Gorilla gorilla gorilla (western lowland gorilla)	Central African Republic	D, gorilla1-3	4	[92]

nd – not determined

infection, affects more often children and elderly due to their deficient immunological status [23]. For example, a study performed in Spain revealed that 8 out of 47 (17%) geriatric persons with diarrhea were infected with *E. bieneusi* [73]. DNA of this microsporidium was diagnosed in stool samples from African children with infection rates from 2.6% (Nigeria) to 76.9% (Uganda) [46,47,72,74], orphans from Asia (1.3–27.2%) (Thailand) [14,15,75,76], Australian children (1.4–30%) [77] and also among child-care workers [75]. Matos et al. [23] summarize the genotypes that have been found in human hosts; some of the potentially zoonotic ones have been detected more often in humans than others and correspond to: A, D, CAF1, EbpC, EbpA, Peru-6, Peru-7, Peru-10, Peru-11, Peru-16, Type IV, WL11, O, PigEBITS7, WL15, I, J, BEB4, PigITS5, BFRmr2, CHN1, CHN3 and CHN4, PtEbII [1,2,12,23,36–38,42]. All these data were gathered in varied populations from different geographic regions, involving all continents.

E. bieneusi in wild living birds

Since bird microsporidiosis caused by *E. bieneusi* was firstly described in chickens in Germany [78], many other bird species, including pigeons, falcons, rooks, cranes, ducks, geese, pet birds, and other exotic birds, have been found as reservoirs of *E. bieneusi* for human infection [38,45,79–87]. It is interesting that some birds, especially parrots (parakeets, love birds, budgies) are naturally infected with *E. bieneusi* spores and other microsporidian species such as *Encephalitozoon hellem* [4]. So far, a number of studies has been carried out on microsporosis in breeding birds such as poultry [78,83,88,89]. Table 1 summarizes the genotype data obtained during surverys carried out on wild living birds.

Based on literature data, the most studied wild living urban species is pigeon (*Columba livia*) with microsporidia infection rates ranging from 1.4% in Poland [87] to 42.3% in Portugal [83]. In feral pigeons, genotypes such as D, Peru-6, Peru 6-like and EbpA have been identified so far [81,83,85,86]. In other urban species such as rooks (*Corvus frugilegus*) zoonotic genotype D and Peru 6 was noted [45]. Urban rooks, pigeons and waterfowls can be of significant concern for public health, as *E. bieneusi* spores can be aerosolized from disturbed excrements of birds and then may potentially be inhaled by humans as airborne particles. Furthermore, viable spores of *E. bieneusi* may persist in air, water and pigeon guano serving as a persistent source of air- and waterborne pollution and contamination [89].

Surveys such as those conducted on captive falcons (*Falco* sp.*)* in Abu Dhabi, showed that *E. bieneusi* genotype D was detected in 25% of analysed falcon samples [84]. In the study developed by Lobo et al. [83], *E. bieneusi* was identified by PCR in 28.9% of the examined bird specimens. Most infected birds were apparently healthy and might serve as asymptomatic carriers of microsporidian species. Sequence analysis revealed that in birds from Psittaciformes order, i.e. a lovebird (*Agapornis* sp.), a cockatiel (*Nymphicus hollandicus)* and African gray parrot (*Psittacus erithacus)* Peru-6, Peru-6 variant and novel, non-determined *E. bieneusi* genotypes were detected. In droppings collected from a star finch (*Bathilda ruficauda*) from Passeriformes order the same genotypes were found [83].

E. bieneusi in wild mammals

Several recent studies have focused on *E. bieneusi* in non-human primates (NHPs) in China and some African countries, with 43 *E. bieneusi* ITS genotypes reported from various NHP species [25,31,90–94]. Research on this group of mammals has been mostly carried out in zoological gardens [25,31,93]. However, wild living populations of NHPs inhabiting tropical forests and nature reserves have been also studied, especially in China, which is a major supplier of primates for biomedical research [25]. Data from China and Kenya have shown infection rates from 3.5% to 67.7% in studied NHPs species [25,31,93–95]. Zhong et al. [31] described three known genotypes (D, PigEBITS7, and SC02) and a novel genotype (SCM01). Additionally, zoonotic *E. bieneusi* genotypes found in NHPs are: Type IV, D, I, PigEBITS7, EbpC, Peru-11, Peru-8, and Henan V [31]. Some of the genotypes in NHPs have a zoonotic potential, like a new genotype SCM01 from rhesus macaques; there were five nucleotide differences compared to Peru3 genotype isolated from patients from Peru [44]. SCM01 and SC02 were both found in rhesus macaque [25,31]. The result of the research conducted in Indonesia on the orangutan (*Pongo* spp.) showed the presence of *E. bieneusi* genotype D and novel genotype Pongo 2 in 2.0% of examined individuals [90]. In Rwanda, in the population of mountain gorillas (*Gorilla*

beringei beringei), *E. bieneusi* was the most frequently detected parasite and was found in 18% of samples including genotypes EbpA, D, C, gorilla 2 and five novel ones such as gorilla 4–8 [91]. In turn, in Central African Republic, the prevalence of this microsporidian species in western lowland gorillas (*Gorilla gorilla gorilla*) was estimated as 4% [92]. To understand better the genetic variety and the public health potential of parasites isolated from these animals, research should be continued. Therefore, a possibility of interspecies transmission of *E. bieneusi* among humans, NHPs, and other animals may be observed in this area in the near future [31].

There have been few epidemiological studies related to *E. bieneusi* in wild living rodents because of the rodents' low economic importance and also because of the difficulty in conducting such a type of studies [32,40,42,96]. The studies on the host specificity of *E. bieneusi* genotypes from the watershed of New York City's water source revealed that the prevalence of this pathogen among rodents ranged from 20% to 30% and was detected in the following species: deer mice (*Peromyscus* sp), the boreal red-backed vole (*Myodes gapperi*) and the meadow vole (*Microtus pennsylvanicus*) [42]. However, the highest infection rate was recorded for the squirrel family (Sciuridae) – 43%. In the examined rodents, both host-specific and zoonotic *E. bieneusi* genotypes have been found: Type IV, WL4, WW6, PtEbV, WL20, WL21, WL22, WL23, WL25, Peru-11. In addition, eight known genotypes including human pathogenic and an unknown one of the *E. bieneusi* genotype were identified in this group of rodents. The research conducted by Perec-Matysiak et al. [96] demonstrates *E. bienuesi* occurrence in wild living rodents in Poland with prevalence over 38% in three studied species of hosts: the striped field mouse (*Apodemus agrarius*), the yellow-necked mouse (*Apodemus flavicollis*) and the bank vole (*Myodes glareolus*). The sequencing of ITS region of rRNA gene made it possible to identify genotype D, gorilla genotype 1 and ten novel genotypes (WR1-WR10), wherein WR1-WR4 were genetically related to genotypes identified in humans and animals, so are potentially zoonotic and belong to group 1 [96]. Therefore, there were determined new genotypes WR5 and WR6 closely related to genotypes from group 2. Studies carried out on the Czech-German border showed that 11% of fecal samples from *Mus musculus* were positive by PCR for *E. bieneusi* [40]. Additionally, during this study, eight different known genotypes of this pathogen, previously reported in pigs, cattle, and humans, were also identified (D, C, H, EbpA, PigEBITS5, Peru-8, S6, CZ3). In China, the overall infection rate of *E. bieneusi* 16.7% (24/144) was observed in red-bellied tree squirrels (*Callosciurus erythraeus*) [99]. Altogether five genotypes of *E. bieneusi* were identified: three known genotypes- D, EbpC, SC02 (clustered into group 1 with the zoonotic potential) and two novel genotypes CE01, CE02 (clustered into group 6) [32]. These results indicate that red-bellied tree squirrels may play a potential role in the transmission of *E. bieneusi* to humans. Semiaquatic small mammals, for example, the beaver (*Castor canadensis*), inhabiting surface waters, can become a direct source of *Enterocytozoon* spores and participate in pathogen distribution also on land. Studies focused on beavers in the USA revealed the presence of D, EpbC, WL7, WL8, WL9, WL12, WL13, WL15 genotypes [37]. The fact that numerous identified genotypes belong to group 1 or are related to human pathogenic ones emphasizes the role of wild living rodents as a source of environmental contamination with genotypes being potentially hazardous for animal and human health.

Free-living terrestrial predators have recently been more often considered as a significant source of infectious diseases transmitted to humans [97–99]. Due to an increasing number of pathogens causing zoonoses in humans, the zoonotic potential of this group 1 is crucial [100]. Its high level of synanthropization manifested as the gradual colonization of suburban and urban areas may significantly increase the possibility of contact with humans and thus the probability of transfer of pathogenic agents onto both humans and domesticated animals [101]. Out of a relatively large percentage of the population of free-living carnivorous animals, several species such as e.g. the red fox, river otter, raccoon dog or raccoon, and bears were screened for *E. bieneusi* occurrence [102].

Fast increasing populations of red foxes (*Vulpes vulpes*), which have become synanthropic animals in many cases, have been spotted as a major problem throughout Europe [103]. *E. bieneusi* D genotype in wild foxes was noted in Spain [104] and the USA [37] and animal specific genotypes WL8, WL11, WL13 and WL15, were also identified [37]. Previous studies conducted on farmed foxes (*Vulpes lagopus*) revealed *E. bieneusi* genotypes of the

zoonotic potential such as genotypes D and EbpC and novel genotype named as CHN-F1 [105]. Recent evidence in China for the first time reported the presence of genotypes Peru-8, CHN-DC1 and Type IV, and seven novel genotypes (NCF1-NCF7) in farmed foxes [106].

The raccoon (*Procyon lotor*) is one of the most fast spreading alien species across Europe. Raccoons are now a permanent component of both the natural environment and urban areas (large and smaller cities) [107]. The importance of raccoons as a potential source of microparasites of animal origin such as *E. bieneusi* is still poorly understood. In 2016, the first survey concerning *E. bieneusi* in European raccoons showed that 4% of fecal samples of raccoons from Germany and Poland were *E. bieneusi* positive. During the phylogeny analysis, the detected genotype NCF2, clustered with other genotypes of group 1, suggesting its zoonotic potential [108]. This NCF2 genotype has so far been present only in farmed foxes and raccoon dogs in China [30,109]. Outside Europe, the raccoon, as introduced species, lives also in Asia with the most numerous wild living populations in Japan. Unfortunately, so far, there are no data on *E. bieneusi* occurrence in Japanese raccoons. Even so, in a Chinese zoo 2% of raccoons stool samples were positive for *E. bieneusi* with genotypes D and SC02 detected [110]. The previous studies undertaken by Guo et al. [42] showed that the infection rate of *E. bieneusi* in raccoons from a New York watershed area was as high as 82 %. The parasitofauna of the raccoon in its native American area may vary considerably from that of the introduction areas, but the prevalence of *E. bieneusi* was surprisingly high. This molecular studies revealed the presence of human pathogenic genotypes i.e., Peru-11, EbpC, WL15, and D genotypes. Additionally, in that investigation, a variety of the following raccoon-adapted genotypes was identified, i.e. WL1-3, WL13, WL15-17, WL24, WL26, and WW6 [37,42].

One of the most successful invasive carnivore species in Europe is the raccoon dog (*Nyctereutes procyonoides*). It may turn out to be an important link in the circulation and maintenance of microsporidian pathogens due to the coexistence in natural habitats with foxes, raccoons, wild boars and other predatory mammals. The presence of *E. bieneusi* in European raccoon dogs has not been determined yet. The only available data are from Asia. In China, in farmed raccoon dogs (*Nyctereutes procyonoides*), the following genotypes were described: D, genotypes CHN-F1, CHN-R1, CHN-DC1, NCF2, WildBoar3, NCR1 and NCR2 [105,106,109].

In 2014, Guo et al. [42] identified *E. bieneusi* Type IV and WL4 in black bear (*Ursus americanus*) in the New York area. Several Asiatic species of captive Ursidae were examined in Chinese zoos and the following genotypes were detected: CHB1, SC01, SC02 in the Asiatic black bear (*Ursus thibetanus*), CHB1 in the brown bear (*Ursus arctos),* CHB1, SC02 in the Tibetian blue bear (*Ursus arctos pruinosus*), Peru-6 in the giant panda (*Ailuropoda melanoleuca*) and CHB1 in the Malayan sun bear (*Helarctos malayanus*) [110]. Similar research conducted in 2017 revealed that the total of 29 out of the 106 fecal specimens from Asiatic black bears (27.4%) were found to be positive for *E. bieneusi* [111]. During this survey, five genotypes were identified, including three known genotypes (CHB1, SC02, and horse2) and two novel genotypes, named as ABB1 and ABB2. Genotype CHB1, which was identified in the largest number of *E. bieneusi*-positive specimens was the most prevalent genotype in all zoos included in the studies [111]. The observed differences in the infection rate of *E. bieneusi* among different zoos may be explained by geographical and climate changes, variations in feeding, density or a sample size [110].

Other zoonotic and host-specific genotypes were found in several wild living Carnivora species such as the river otter (*Lontra canadensis*) which is equally versatile in the water and on land. There have been several *E. bieneusi* genotypes: D, EpbC, WL2, WL4, WL12, WL13 detected in this animal [37,42]. Instances of otters eating small mammals, such as mice and squirrels, and occasionally birds have been reported as well and it creates an opportunity for a successful interspecies microsporidia transmission.

The Artiodactyla are ungulates that include, among others, pigs, whales, camels, llamas, alpacas, deer, giraffes, sheep, goats, and cattle [112]. Wild living Artiodactyla with a different geographical distribution like deer and wild boars, as game animals, may be a potential source of zoonoses including microsporidiosis. Several studies were focused on boars and deer as the environmental reservoirs of *E. bieneusi*. Research has been conducted on the white-tailed deer (*Odocoileus virginianus*), the sika deer (*Cervus elaphus*), the red deer (*Cervus nippon*), and the Pere David's deer

(*Elaphurus davidianus*) [42,113-118]. Recent evidence confirmed that genotypes I, J, WL4, WL18, WL19, LW1, and DeerEb1 to DeerEb13 were detected in the USA in the white-tailed deer (*Odocoileus virginianus*) and genotypes BEB6, Type IV, EbpC, EbpA, J, CHS9, COS-I, COS-II, CHN-DC1, KIN-1, JLD-1 to JLD-3, and HLJD-I to HLJD-V were found in China in the hog deer (*Axis porcinus*), the red deer, and the sika deer [42,110,113–118]. Huang et al. [113] in newly published studies identified 25 ITS genotypes, including seven known genotypes (BEB6, EbpC, EbpA, D, HLJDI, HLJD-IV, and COS-I) and 18 novel genotypes (designated JLD-I to JLD-XIV, HND-I to HND-IV) in the sika deer and red deer. Among these, BEB6 (59.3%) was the predominant genotype [113]. Nevertheless, the information concerning *E. bieneusi* infections in cervids in the world, especially in Europe, is still limited. Although many *E. bieneusi* genotypes were found in breeding pigs, only single cases of *E. bieneusi* infection have been reported in captive wild boars (*Sus scrofa*) [118,119]. Within *E. bieneusi*-positive DNA isolates, 14 *E. bieneusi* genotypes comprising five novel genotypes (WildBoar 7–11) and eight known genotypes (EbpC, F, CHG19, CHC5, PigEBITS5, D, RWSH4, and SC02) were identified by ITS sequencing analysis [118,119]. The novel WildBoar genotypes identified in Chinese boars may indicate that *E. bieneusi* in wild boars has a relatively higher genetic variability. Several of WildBoar genotypes have been identified in other animal hosts such as the raccoon dog in China and it seems they are not host specific [118]. The genotypes EbpC, D, and PigEBITS5 previously identified in domestic pigs were also detected in wild boars subjected to these analyses [120]. The results of European studies confirmed 4 of 11 *E. bieneusi* genotypes (D, EbpA, EbpC, and G) which were previously detected in domestic pigs. Interestingly, the first three of these genotypes were the most frequent in both domestic pigs and wild boars [118, 120]. Additionally, six novel genotypes, WildBoar1–6, were reported in wild boars from Central Europe [119]. The most frequent genotype in this study was zoonotic EbpC, which in turn suggests that boars might be a potential source of human microsporidiosis. Several findings suggest that wild boars, exactly like domestic pigs, could be a natural source of zoonotic *E. bieneusi* genotypes e.g. Henan-I genotype, which was previously detected in humans [121]. Wild reindeer (*Rangifer tarandus*) from the northeast forest region of Great Hinggan Mountains of China were examined by Liu et al. [122]. Five genotypes of *E. bieneusi* were identified: Peru6 and four novel genotypes named as CHN-RD1-4. In phylogenetic analysis, all the novel genotypes together with the known genotype Peru6 were clustered into group 1 suggesting the possibility of *E. bieneusi* transmission from reindeer to humans [122].

In conclusion, *E. bieneusi* appears to be common in wild living mammals and birds and these hosts should be considered as important reservoirs for environmental contamination and maintenance of this pathogen. The detection of zoonotic genotypes from *E. bieneusi* group 1 among various animals highlights the potential for zoonotic transmission to humans. Nevertheless, so far, there is no evidence to suggest the potential role of captive-bred wildlife in the transmission of *E. bieneusi*-associated human microsporidiosis. Thus, methods for controlling this transmission are needed. Novel techniques like multi-locus genotyping analyses are now widely used in molecular epidemiology research and they are a great facilitator. More precise methods and richer groups of surveyed hosts will help to expand the knowledge of *E. bieneusi* in the future.

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