

From wildlife to humans: The global distribution of *Trichinella* species and genotypes in wildlife and wildlife-associated human trichinellosis

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ARTICLE INFO

Keywords:

Epidemiology
Foodborne disease
Trichinella
Trichinellosis
Zoonotic disease

ABSTRACT

Zoonotic nematodes of the genus *Trichinella* are foodborne parasites that have a global distribution in wild carnivores and omnivores, with spillover and spillback into domestic livestock and people, with concomitant trade and health consequences. Historically, most human cases were linked to domestic pigs infected with *Trichinella spiralis*, but under current high biosecurity swine production in many countries, wildlife have become a more important source of human trichinellosis. The aim of this review is to update the global distribution of *Trichinella* species and genotypes reported in wildlife, as well as reported human outbreaks from the consumption of wildlife. Using several online databases and by “snowballing” references, hundreds of reports of *Trichinella* spp. in wildlife published between January 1991 and December 2023 provide an important update to the host and geographic range for each of the recognized 13 species/genotypes, grouped by continent. Surveillance effort was highest in Europe and North America, while Africa, Asia, Central and South America have had limited surveillance, in some instances with human cases serving as sentinels of transmission in a region. Dozens of human outbreaks are described, with wild boars (*Sus scrofa*) being the most frequently implicated wildlife species in human outbreaks globally. Bears are an important source of infection in North America, for wildlife tourism, and importation of bear meat has also been implicated in multicountry outbreaks. The largest study limitation was the dearth of molecular identification of larvae in both wildlife surveillance studies and human outbreaks, particularly in under-studied regions. We highlight the need for enhanced molecular epidemiological approaches to outbreaks of this important foodborne parasite, and emphasize the need for a One Health approach to manage *Trichinella* spp. which transmit among terrestrial and marine wildlife (including migratory birds), pigs, horses, and people, often across large geographic scales and borders.

1. Introduction

The nematode *Trichinella spiralis* was first described in 1835 by Richard Owen and James Paget (Owen 1835; Pozio 2021), initially based on the detection of muscle-dwelling larvae. For 137 years, it was believed that the genus *Trichinella* was monospecific, until 1972 when Britov and Boev first described two other encapsulated species (*T. nativa* and *T. nelsoni*) and Garkavi described the first non-encapsulated species (*T. pseudospiralis*) (Britov and Boev 1972; Garkavi 1972). With continuous additions to the taxonomy of *Trichinella*, the genus is currently comprised of 13 taxa: 10 named species [*T. spiralis* (T1), *T. nativa* (T2), *T. britovi* (T3), *T. pseudospiralis* (T4), *T. murrelli* (T5), *T. nelsoni* (T7), *T.*

papuae (T10), *T. zimbabwensis* (T11), *T. patagoniensis* (T12), *T. chanchalensis* (T13) and three unnamed genotypes (*Trichinella* T6, T8, and T9) (Pozio, 2021; Sharma et al., 2020). With the exception of Antarctica, *Trichinella* spp. have been reported from every continent; in wildlife from 66 countries and in humans from 55 countries (Pozio, 2007b). The most recent global prevalence estimates that 10–11 million humans may be currently infected from the consumption of both wild and domestic animal sources (Dupouy-Camet, 2000; Murrell and Pozio, 2011).

Historically most human cases of trichinellosis were linked to the consumption of infected domestic pigs; in the 1930s, nearly 1 in 6 humans tested in the United States had larvae in their musculature (Wright et al., 1943). With the implementation of high biosecurity

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<https://doi.org/10.1016/j.ijppaw.2024.100934>

Received 28 February 2024; Received in revised form 2 April 2024; Accepted 2 April 2024

Available online 7 April 2024

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production and testing of swine post-slaughter, human cases from pork consumption have drastically decreased in countries with well developed veterinary public health infrastructure (Gamble, 2022). As the frequency of human cases from pork consumption have decreased, reported cases of trichinellosis from consumption of meat from wildlife have become of greater importance (Crisostomo-Jorquera and Landaeta-Aqueveque, 2022).

Trophic transmission of *Trichinella* spp. relies on predation and scavenging to maintain the life cycle; thus wild carnivores and omnivores are perfect reservoirs. Indeed, *Trichinella* spp. have a greater biomass in wildlife than domestic animals, which makes eradication virtually impossible (Pozio, 2022). Humans are dead-end hosts and enter the life-cycle when they consume undercooked or raw meat from an infected animal (Fig. 1). Trichinellosis cases in many countries are predominantly reported among Indigenous and subsistence hunters, and tourists, which could be attributed to food consumption habits which may include eating meat raw or prepared using other methods insufficient to inactivate the larvae (Pozio, 2007b).

Human cases are often underdiagnosed due to lack of pathognomonic signs and difficulties in definitive diagnosis (Dupouy-Camet and Murrell, 2007). Muscle biopsies are invasive and of low sensitivity unless infection intensity in the patient is very high, making it difficult to acquire larvae for further investigation and genotyping (Dupouy-Camet and Murrell, 2007). Diagnosis in humans is most commonly made based on serology, which is unable to differentiate most species/genotypes, other than to distinguish encapsulated vs. non-encapsulated clades (Gomez-Morales et al., 2018; Gottstein et al., 2009; Yang et al., 2016).

The number of infections may also be underreported due to a lack of awareness among physicians along with no requirement for notification of health authorities, especially in non-endemic countries (Dupouy-Camet and Murrell, 2007; Gottstein et al., 2009). As well, source attribution is difficult, as the meat from infected animals suspected as the source of the outbreak is often unavailable. Treatment recommendations are the same regardless of species or genotype, which also disincentivizes molecular epidemiological investigation of human outbreaks (Centers for Disease Control and Prevention, 2020; Gottstein et al., 2009). This has created knowledge gaps in our understanding of the epidemiology, transmission patterns, and pathology of *Trichinella* species. Therefore, this narrative review comprehensively and rigorously addresses the role of wildlife as a source of human trichinellosis in diverse ecosystems around the world by including only genotyped reports in wildlife and humans with plausible source attribution in wildlife.

2. Methods

2.1. Literature search strategy

This narrative review is based on a literature search that was performed primarily, but not exclusively, in PubMed, Google Scholar, and Science Direct search engines. The following search terms and Boolean operators (AND, OR) were used: “*Trichinella*”, “*Trichin**”, “Trichinellosis OR Trichinosis OR Human infection”, “outbreak”, “wildlife”, “*Trichinella spiralis*” OR “T1”, “*Trichinella nativa*” OR “T2”, “*Trichinella britovi*” OR “T3”, “*Trichinella pseudospiralis*” OR “T4”, “*Trichinella murrelli*” OR “T5”, “*Trichinella nelsoni*” OR “T7”, “*Trichinella papuae*” OR “T10”, “*Trichinella zimbabwensis*” OR “T11”, “*Trichinella patagoniensis*” OR “T12”, “*Trichinella chanchalensis*” OR “T13”, “*Trichinella T6*”, “*Trichinella T8*”, and “*Trichinella T9*”, tailored to the targeted geographic regions (Europe, Asia, Africa, and the Americas). We also “snowballed” from references cited in the publications found using the search engines. We considered all peer-reviewed publications from 1991 to 2023 that described human or wildlife infections in which the species/genotype of *Trichinella* was molecularly identified. Publications that conducted surveillance in transcontinental countries were not subdivided; i.e. all data were included under the name of the country: Egypt (Africa), Turkey (Asia), Russia (Asia), Kazakhstan (Asia). We excluded studies where parasite taxa were not identified to species/genotype level, editorials, commentaries, conference abstracts, non-English publications, no full-text, and data from farmed wildlife.

3. Results

3.1. *Trichinella spiralis*

Trichinella spiralis was first described by Richard Owen in 1835 in London, England (Owen, 1835). *Trichinella spiralis* has a cosmopolitan distribution and is most often associated with farm ecosystems. It readily infects swine and rats, unlike most sylvatic encapsulating species (Kaplan and Gamble, 2000; Malakauskas et al., 2001; Pozio et al., 1992b). It appears that *T. spiralis* originated in Asia, with the European clade separating prior to the domestication of the pig, probably with the separation of the European and Asian clades of wild boar (Thompson et al., 2021). Thus, it has historically relied on a sylvatic cycle, probably involving wild boars (Thompson et al., 2021). *Trichinella spiralis* is considered a freeze-susceptible species, but limited freeze tolerance has been shown in horse tissue, -18°C for 4 weeks, and at -6.6°C for 106 h in pig tissue (Hill et al., 2007, 2009).

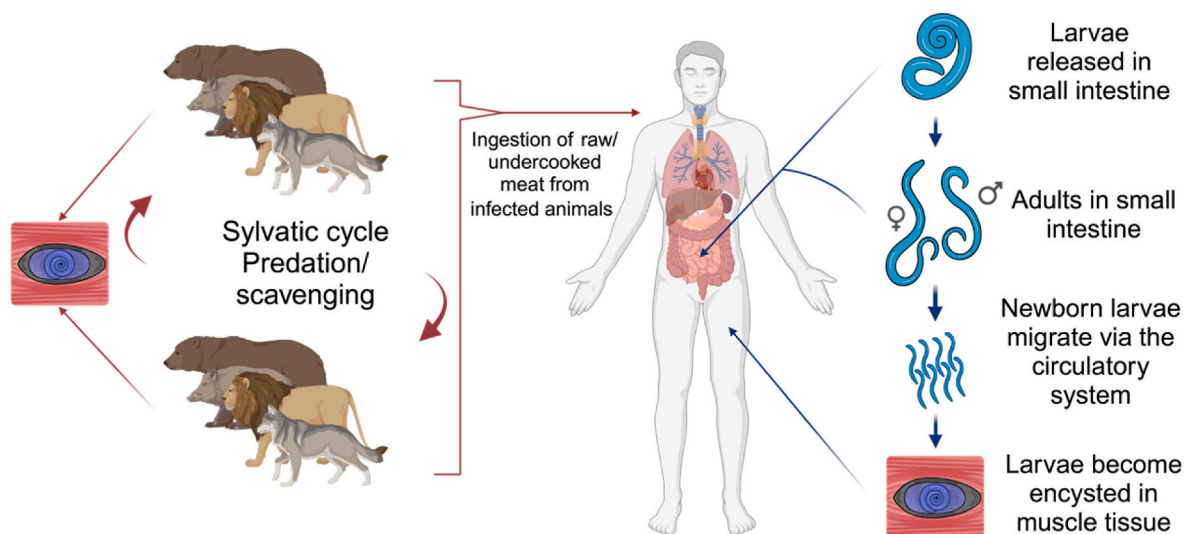


Fig. 1. Sylvatic life cycle and potential transmission routes of *Trichinella* spp. Created with BioRender.com.

3.1.1. *Trichinella spiralis* in Europe

Trichinella spiralis was the species most commonly associated with human trichinellosis historically, although a growing proportion of reported outbreaks are caused by sylvatic *Trichinella* species (Bruschi and Murrell, 2002). In Europe, *T. spiralis* is commonly found in wild boar, with several studies testing tens of thousands of samples or more, because of their omnipresence and their importance in consumption by humans (Table 1). *Trichinella spiralis* has also been shown to readily infect carnivores and omnivores (Table 1). In experimental infection of red foxes (*Vulpes vulpes*), *T. spiralis* led to a higher larval burden than equal infection doses of other species found in Europe (*T. britovi*, *T. nativa*, *T. pseudospiralis*), but when inoculated as a mixed infection with equal doses, *T. nativa* outcompeted *T. spiralis* (Webster and Kapel, 2005). As *T. spiralis* is not the most common species in sylvatic carnivores in Europe, it has been proposed that wild carnivores may not be an important reservoir for *T. spiralis* and cannot sustain the infection in the absence of other hosts (Pozio and Murrell, 2006; Pozio et al., 2009b). However, this hypothesis was challenged in the 2000s in Finland, as *T. spiralis* was found in ~15% of *Trichinella* isolates tested from wild carnivores and was found as far north as ~69° N in one red fox, despite no reports in domestic pigs in Finland over the same time period (Airas et al., 2010; Oivanen et al., 2002). However, in the following decade, *T. spiralis* prevalence in Finnish wild carnivores drastically decreased, indicating a delay in the disappearance from sylvatic cycle after the cessation of spill-over from the domestic cycle (Oksanen et al., 2018). *Trichinella spiralis* in Europe causes hundreds of cases of human trichinellosis each year in Europe, the vast majority from independently raised domestic pigs, but also from wild boar meat (EFSA & ECDC, 2021; Pozio, 2014) (Table 2) (Fig. 2).

3.1.2. *Trichinella spiralis* in Asia and Oceania

Trichinella spiralis has been reported in wildlife across Asia and Oceania, from Israel to Vietnam to New Zealand, in several carnivore species, as well as wild rats (*Rattus norvegicus*) and a northern Sea lion (*Eumetopias jubatus*) (Table 3). To date, there have been three reported human cases where the larvae were genotyped, all in South Korea, which is interesting as there have been no genotyped reports of *T. spiralis* directly from wildlife in South Korea (Table 4). Larvae of *Trichinella* spp. have been detected in wildlife throughout Asia, most of which were not genotyped; therefore, the true range of *T. spiralis* in wildlife in Asia is likely larger than currently described.

3.1.3. *Trichinella spiralis* in the Americas

Prior to modern methods of swine production and meat inspection, *Trichinella spiralis* in domestic swine commonly resulted in human infection in the Americas. This resulted in bans on the export of pigs or pork products from the United States to several European countries in the late 19th century and in part caused the 1880–1891 “pork war” (Snyder, 1945). While now virtually eradicated in commercial swine in the US and Canada, *T. spiralis* is reported, albeit rarely, in a range of wildlife hosts, including hosts of importance for human consumption such as bears and wild boar (Table 5). The vast majority of countries in the Caribbean, Central America, and South America have not reported *Trichinella* infections in humans, swine, or wildlife, but this is likely a dearth of investigation rather than absence from these regions. Reports of human infection with *T. spiralis* from wildlife in the New World are uncommon but have been reported in Canada and the United States (Table 6).

3.2. *Trichinella nativa*

Trichinella nativa was first described in 1972, although not recognized as a species until molecular methods evolved and the concept of sibling species became widely accepted (Britov and Boev, 1972; Pozio, 2021). *Trichinella nativa* is an encapsulated and freeze-tolerant species that has a holarctic distribution and is found in terrestrial and marine

carnivores/omnivores (Pozio, 2016a).

3.2.1. *Trichinella nativa* in Europe

The presence of *T. nativa* in Europe has been surveilled throughout Europe. *Trichinella nativa* has been found in many terrestrial carnivore hosts in Europe as well as a grey seal (*Halichoerus grypus*) off the coast of Finland (Table 7). *Trichinella nativa* is sympatric with *T. britovi* in northern, north-central, and eastern Europe (Fig. 3). One human outbreak in France was genotyped as *T. nativa* which originated from consumption of harvested black bear meat from Quebec, Canada (Ancelle et al., 2005; Public Health Agency of Canada, 2006) (Tables 8 and 11). The index cases were infected in Canada and then others were infected in France from the consumption of the illegally imported bear meat (Ancelle et al., 2005; Public Health Agency of Canada, 2006). As most human outbreaks of trichinellosis in Europe do not report *Trichinella* species, outbreaks with *T. nativa* have likely been underreported.

3.2.2. *Trichinella nativa* in Asia

The reported geographic range of *T. nativa* in wildlife in Asia has been limited to sporadic reports in terrestrial carnivores from Japan, Kazakhstan, and Russia, as well as in one northern sea lion from Russia (Table 9) (Goździk et al., 2017). There has been a dearth of surveillance studies in northern Asia that used molecular confirmation, which likely results in an underestimate of the true range of *T. nativa* and hosts in northern Asia. To date, there have been no reported human cases of genotyped *T. nativa* in Asia.

3.2.3. *Trichinella nativa* in the Americas

In the Americas, *T. nativa* is limited to a northern distribution in Canada, Alaska, and Greenland. The southern boundary of *T. nativa* has been identified as between the isotherms -5° to -4° C in January (Pozio, 2016a). This freeze-tolerant species can survive in the tissue of frozen carrion for months to years (Pozio, 2016a). *Trichinella nativa* has been found in terrestrial and marine mammals, some of significant food importance in northern North America, such as walrus (*Odobenus rosmarus*), polar bear (*Ursus maritimus*), and black bear (*Ursus americanus*) (Table 10). The distribution of *T. nativa* overlaps with Indigenous communities in northern Canada, Alaska, and Greenland that rely heavily on consumption of wildlife, and thus *T. nativa* infections in humans (including large scale outbreaks due to food sharing) are not uncommon (Fig. 3) (Table 11). Human cases of *Trichinella* spp. in Canada, Alaska, and Greenland, were reviewed by Jenkins et al., 2013, but only those that were genotyped are presented in Table 11.

3.3. *Trichinella britovi*

Trichinella britovi is an encapsulated and freeze-tolerant species that was first described in 1992 (Pozio et al., 1992a). *Trichinella britovi* has a temperate palearctic distribution spanning from Northwestern Africa through most of Europe and into central Asia (Pozio, 2016a). *Trichinella britovi* is predominantly found in sylvatic carnivores but also occasionally in domestic pigs (Gottstein et al., 2009).

3.3.1. *Trichinella britovi* in Europe

Trichinella britovi in wildlife from Europe has been extensively studied, especially in wild boar, the most consumed game meat source implicated in trichinellosis in Europe (Table 13). *Trichinella britovi* is most commonly reported in wild boar and red fox, but has also been reported in other canids, felids, mustelids, beavers (*Castor fiber*), brown bears (*Ursus arctos*), and rats (Table 12). In Northern and Northeastern Europe, *T. britovi* occurs sympatrically with *T. nativa* and mixed infections have been reported (Pozio, 2016a). Human infections with *T. britovi* occur frequently in Europe (Table 13).

3.3.2. *Trichinella britovi* in Asia

Reports of *T. britovi* in Asia confirmed by molecular characterization

Table 1
Published reports of *Trichinella spiralis* in wildlife in Europe (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. spiralis</i>	Reference
Austria	Not specified	Wild boar (<i>Sus scrofa</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Bulgaria	Gabrovo, Lovech	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	2	Lalkovski (2019)
Croatia	Dalmatia, Gorski Kotar, Lika	Wolf (<i>Canis lupus</i>)	Multiplex PCR	2/67 (3%)	Beck et al. (2009)
Croatia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	21/183,184 (0.01%)	Balic et al. (2020)
Czech Republic	Tovačov	Raccoon (<i>Procyon lotor</i>)	Multiplex PCR	6/22 (27%)	Cybulska et al. (2018)
Estonia	Not specified	Brown rat (<i>Rattus norvegicus</i>)	RAPD-PCR, PCR-RFLP, & Multiplex PCR	2/18 (11.1%)	Jarvis et al. (2001)
Estonia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	8/30,566 (0.03%)	Kärssin et al. (2021)
Estonia		Eurasian lynx (<i>Lynx lynx</i>)		5/90 (5.6%)	
Finland	Southern Finland	Red fox (<i>Vulpes vulpes</i>)	RAPD-PCR	1/19 (5.3%)	Oivanen et al. (2000)
Finland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/13 (7.7%)	Oivanen et al. (2002)
		Raccoon dog (<i>Nyctereutes procyonoides</i>)		5/22 (23%)	
		Brown rat (<i>R. norvegicus</i>)		28/29 (96.6%)	
Finland	South-western Finland	Brown rat (<i>R. norvegicus</i>)	Multiplex PCR	28/767 (3.7%)	Mikkonen et al. (2005)
Finland	Country-wide	Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	?/662 ^a	Airas et al. (2010)
		Red fox (<i>V. vulpes</i>)		?/1010 ^a	
		Eurasian lynx (<i>L. lynx</i>)		?/402 ^a	
		Wolf (<i>C. lupus</i>)		?/102 ^a	
Finland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/454 (0.4%)	Oksanen et al. (2018)
		Raccoon dog (<i>N. procyonoides</i>)		6/952 (0.6%)	
		Eurasian lynx (<i>L. lynx</i>)		4/1245 (0.3%)	
		Wolf (<i>C. lupus</i>)		4/85 (4.7%)	
France	Not specified	Wild boar (<i>S. scrofa</i>)	Allozyme analysis	1	La Rosa et al. (1992)
		Red fox (<i>V. vulpes</i>)		4	
France	Provence	Red fox (<i>V. vulpes</i>)	Isoenzymatic analysis	2/1912 (0.1%)	La Rosa et al. (1991)
France	Country-wide	Red fox (<i>V. vulpes</i>)	RAPD-PCR	7/5457 (0.1%)	Pozio et al. (1996)
Germany	Not specified	Red fox (<i>V. vulpes</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Germany	Country-wide	Red fox (<i>V. vulpes</i>)	RAPD-PCR	3/7103 (0.04%)	Wacker et al. (1999)
Germany	Usedom island	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1	Nockler et al. (2006)
Germany	Brandenburg	Raccoon dog (<i>N. procyonoides</i>)	PCR	24/1527 (1.6%)	Mayer-Scholl et al. (2016)
Germany	Country-wide	Raccoon (<i>P. lotor</i>)	Multiplex PCR	1/88 (1.1%)	Langner et al. (2022)
Hungary	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	4/2116 (0.2%)	Szell et al. (2008)
Hungary	Southern Hungary	Golden jackal (<i>Canis aureus</i>)	Multiplex PCR	1/11 (9.1%)	Szell et al. (2013)
Republic of Ireland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	4/454 (0.9%)	Rafter et al. (2005)
Northern Ireland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/443 (0.2%)	Zimmer et al. (2009)
Italy	Country-wide	Red fox (<i>V. vulpes</i>)	RAPD-PCR	1/3565 (0.03%)	Pozio et al. (1996)
Latvia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	5/129 (17.2%)	Malakauskas et al. (2007)
Latvia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex	1/3174 (0.03%)	Kirjusina et al. (2015)
Latvia	Country-wide	Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	2/394 (0.5%)	Deksne et al. (2016)
		Pine marten (<i>Martes martes</i>)		1/137 (0.7%)	
Lithuania	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	27/147 (18.4%)	Malakauskas et al. (2007)
		Raccoon dog (<i>N. procyonoides</i>)		4/23 (17.4%)	
		Wild boar (<i>S. scrofa</i>)		11/43 (25.6%)	
Netherlands	Not specified	Brown rat (<i>R. norvegicus</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Netherlands	Country-wide	Wild boar (<i>S. scrofa</i>)	RAPD-PCR	2/11 (18%)	Van Der Giessen et al. (2001)
Netherlands	Country-wide	Raccoon dog (<i>N. procyonoides</i>)	PCR & sequencing	1/9	Maas et al. (2016)
Poland	Not specified	Wild boar (<i>S. scrofa</i>)	Allozyme analysis	2	La Rosa et al. (1992)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	9/1634 (0.5%)	Chmurzynska et al. (2013)
Poland	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	10/833 (1.2%)	Moskwa et al. (2015)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	16/1447 (1.1%)	Cybulska et al. (2016)
Poland	Western Poland	Raccoon dog (<i>N. procyonoides</i>)	PCR	2/39 (5.1%)	Osten-Sacken and Solarczyk (2016)
Poland	Not specified	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	235	Bilska-Zajac et al. (2017)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	18/1740 (1.0%)	Bilska-Zajac et al. (2020)
Romania	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/71 (1.4%)	Blaga et al. (2009)
		Wild boar (<i>S. scrofa</i>)		2/5	
		Brown bear (<i>Ursus arctos</i>)		1/2	
Romania	Country-wide	Eurasian ermine (<i>Mustela erminea</i>)	Multiplex PCR & sequencing	1/3	Oltean et al. (2014)
		Polecat (<i>Mustela putorius</i>)		1/3	
Romania	Western Romania	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/121 (0.8%)	Imre et al. (2015)
Romania	Country-wide	Brown bear (<i>U. arctos</i>)	Multiplex PCR	9/147 (6.1%)	Nicorescu et al. (2015)
		Wild boar (<i>S. scrofa</i>)		45/5596 (0.8%)	
Romania	Northeast Romania	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	119/4189 (2.8%)	Iacob et al. (2022)

(continued on next page)

Table 1 (continued)

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. spiralis</i>	Reference
Serbia	Belgrade, Podunavlje, Branicevo, Zlatibor, and Piro	Brown bear (<i>U. arctos</i>)	Multiplex PCR	16/25 (64%)	Cvetkovic et al. (2011)
		Golden jackal (<i>C. aureus</i>)		3/3	
		European wild cat (<i>Felis silvestris</i>)		1/1	
Serbia	Branicevo district	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/4	Zivojinovic et al. (2013)
		Golden jackal (<i>C. aureus</i>)		5/13 (38.5%)	
		Red fox (<i>V. vulpes</i>)		6/57 (10.5%)	
Serbia	24 localities	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	2/94 (2.1%)	Cirovic et al. (2015)
		Golden jackal (<i>C. aureus</i>)		65/738 (8.8%)	
Serbia	12 localities across central Serbia	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/37 (5.4%)	Dmitric et al. (2017)
		Golden jackal (<i>C. aureus</i>)		5/13 (38%)	
Serbia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	8/296 (2.7%)	Klun et al. (2019)
		Wild cat (<i>F. silvestris</i>)		5/20 (25%)	
		Pine marten (<i>M. martes</i>)		1/12 (8.3%)	
Slovakia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/5270 (0.04%)	Hurnikova and Dubinsky (2009)
		Red fox (<i>V. vulpes</i>)		2/4669 (0.04%)	
Slovakia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	4/2295 (0.17%)	Miterpáková et al. (2009)
		Red fox (<i>V. vulpes</i>)		4/2295 (0.17%)	
Spain	Not specified	Wild boar (<i>S. scrofa</i>)	Allozyme analysis	6	La Rosa et al. (1992)
		Red fox (<i>V. vulpes</i>)		2	
		European wild cat (<i>F. silvestris</i>)		1	
Spain	Extremadura	Wild boar (<i>S. scrofa</i>)	RAPD-PCR	27/28,148 (0.1%)	Pozio et al. (1996)
		Red fox (<i>V. vulpes</i>)		1/213 (0.5%)	
Spain	Extremadura	Wild boar (<i>S. scrofa</i>)	RAPD-PCR	70/29,333 (0.2%)	Perez-Martin et al. (2000)
		Red fox (<i>V. vulpes</i>)		2/227 (0.9%)	
Spain	Province of Cáceres	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	1	Rodriguez et al. (2008)
		Wild boar (<i>S. scrofa</i>)		28/1278 (2.2%)	
Spain	Castilla y León and La Rioja	Wolf (<i>C. lupus</i>)	ISSR-PCR	1	Fonseca-Salamanca et al. (2009)
		Red fox (<i>V. vulpes</i>)		1/70 (1.4%)	
		Wild boar (<i>S. scrofa</i>)		17/2216 (0.8%)	
Spain	Southwest Spain	Wild boar (<i>S. scrofa</i>)	ISSR-PCR	225/692,678 (0.03%)	Garcia-Sanchez et al. (2009)
		Wild boar (<i>S. scrofa</i>)		225/692,678 (0.03%)	
Spain	Iberian peninsula	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	109/33,206 (0.3%)	Díaz et al. (2021)
		Wild boar (<i>S. scrofa</i>)		109/33,206 (0.3%)	
Sweden	Gällö	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/1800 (0.1%)	Pozio et al. (2004a)
		Red fox (<i>V. vulpes</i>)		2/1800 (0.1%)	
	Bräcke				

^a The proportion of *T. spiralis* amongst all animals tested was 13%, but the exact proportion per species was not reported.

Table 2

Human outbreaks of *Trichinella spiralis* from consumption of wildlife in Europe (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Belgium	Limburg and Antwerp	16	Wild boar (<i>Sus scrofa</i>)	Slowly roasted boar fillet, and/or boar stew	November–December 2014	Messiaen et al. (2016)
Bulgaria	Lovech Province	196	Wild boar (<i>S. scrofa</i>)	Homemade flat sausage	February 2000	Kurdova et al. (2004)
Croatia	Cities of Dakovo and Varaždin	26	Wild boar (<i>S. scrofa</i>)	Salami, bacon, and sausage	Early 2017	Balic et al. (2023)
Germany	Eastern Germany	14	Wild boar (<i>S. scrofa</i>)	Sausages	March 2013	Faber et al. (2015)
Poland	Koscian district	8	Wild boar (<i>S. scrofa</i>)	Cold smoked raw Polish sausage	December 2020	Rozycki et al. (2022)
Spain	Zaragoza	61	Wild boar (<i>S. scrofa</i>)	Sausage and cooked meat	1998	Perez-Perez et al. (2019)
		4			1999	
		7			2009	
		6			2011	

have become more common over the last decade. Recently, *T. britovi* was reported in several wildlife species from Armenia, including red fox, wolf (*Canis lupus campestris*), lynx (*Lynx dinniki*), Eurasian otter (*Lutra lutra*), and wild boar (Grigoryan et al., 2020). *Trichinella britovi* has also been reported in wildlife from Iran, Kazakhstan, Turkey, Russia, and Israel. (Table 14). To date, there have been no genotyped reports of human infection with *T. britovi* in Asia.

3.3.3. *Trichinella britovi* in Africa

Trichinella britovi has been reported in wildlife in the West African region with the first confirmed report from the Republic of Guinea in an African civet (*Viverra civetta*) and African palm civet (*Nandinia binotata*) (Pozio et al., 2005b) (Table 15). Pozio et al. (2005) speculates that

T. britovi reached the African continent as a result of colonization by carnivores from Europe and Eurasia (Kingdon, 1997; Savage, 1978). No other species of *Trichinella* have been confirmed in wildlife from the West African region.

3.4. *Trichinella pseudospiralis*

Trichinella pseudospiralis is a non-encapsulated and freeze-susceptible species first described in 1972 (Garkavi, 1972). *Trichinella pseudospiralis* has a cosmopolitan distribution and is commonly associated with domestic pigs, sylvatic mammals, and somewhat uniquely among the genus, birds.

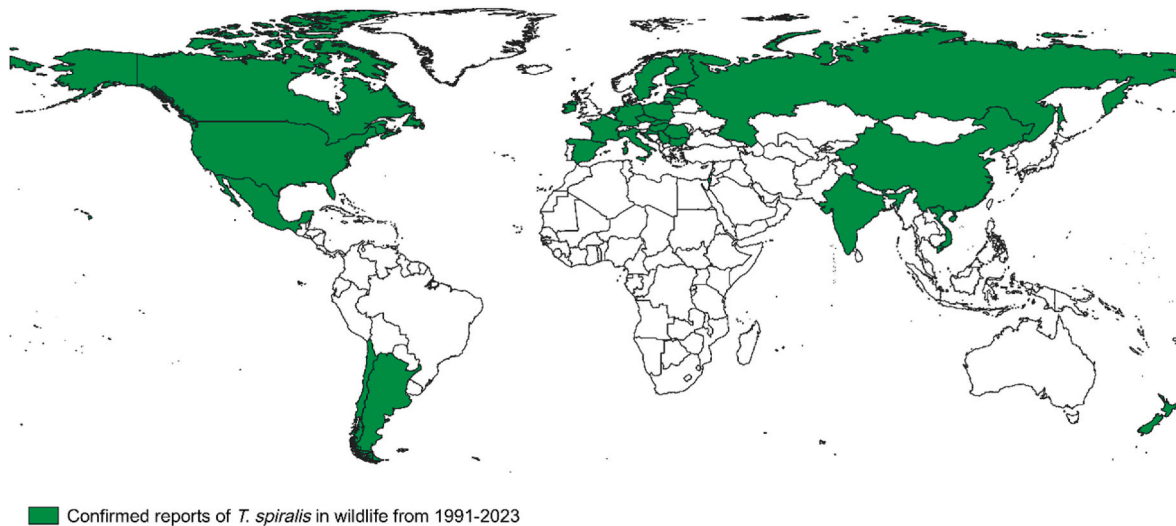


Fig. 2. Global distribution of *Trichinella spiralis* in wildlife reported in this review.

Table 3
Published reports of *Trichinella spiralis* in wildlife in Asia and Oceania (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. spiralis</i>	Reference
China	Tiandong, Guangxi	Civet cat (<i>Paguma larvata</i>)	PCR	1	Wang et al. (2012)
China	Shandong province	Wild rat (<i>Rattus norvegicus</i>)	Multiplex PCR & sequencing	2/102 (2%)	Zhang et al. (2022)
India	Dehradun, Uttarakhand	Leopard (not reported)	Multiplex PCR & sequencing	1	Nehra et al. (2020)
Israel	Northern and Central Israel	Golden jackal (<i>Canis aureus</i>) Wild boar (<i>Sus scrofa</i>) Red fox (<i>Vulpes vulpes</i>) Wolf (<i>Canis lupus</i>)	Multiplex PCR, Extended PCR	?/45 ^a ?/280 ^a ?/2 ^a ?/1 ^a	Erster et al. (2016)
New Zealand	Not specified	Brown rat (<i>R. norvegicus</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Russia	Russian Far East	Brown bear (<i>Ursus arctos</i>)	PCR	1	Odoevskaya and Spiridonov (2014)
	Yakutia & Chukotka	Polar bear (<i>Ursus maritimus</i>)		2	
	Chukotka	Arctic fox (<i>Vulpes lagopus</i>)		1	
	Yakutia	Wolverine (<i>Gulo gulo</i>)		1	
Russia	Chukotka Peninsula	Arctic fox (<i>V. lagopus</i>) Northern sea lion (<i>Eumetopias jubatus</i>)	Multiplex PCR & ISSR-PCR	2/3 1	Goździk et al. (2017)
Vietnam	Dien Bien and Son La	Wild boar (<i>S. scrofa</i>) Rat (not specified)	Multiplex PCR	2/62 (3.3%) 23/820 (2.8%)	Thi et al. (2014)

^a 58 isolates (10 from wild boar, 45 golden jackals, 2 red foxes and 1 wolf) were genotyped, 11 isolates were identified as *T. spiralis*, but the proportion infected per host species was not specified.

3.4.1. *Trichinella pseudospiralis* in Europe

Trichinella pseudospiralis has been reported in seven bird species and eight terrestrial mammals in 13 countries across Europe (Table 16). *Trichinella pseudospiralis* is commonly reported in wild boars which are the most common wildlife source of human trichinellosis in Europe (Tables 2, 13 and 16). One outbreak in humans was reported in 1999 in France, with undercooked wild boar meat as the source (Ranque et al., 2000) (Table 17).

3.4.2. *Trichinella pseudospiralis* in Asia and Oceania

In Asia and Oceania, there has only been two genotyped reports of *T. pseudospiralis* in wildlife, in a ringed seal (*Pusa hispida*) in the Russian far-east and in a tiger quoll (*Dasyurus maculatus*) from Tasmania (Table 18) (Goździk et al., 2017; La Rosa et al., 1992). However, in Thailand and Australia/New Zealand, there have been two reports of human infections with *T. pseudospiralis* from game meat consumption, indicating endemicity of *T. pseudospiralis* (Table 19). The dearth of

Table 4
Human outbreaks of *Trichinella spiralis* from consumption of wildlife in Asia (1991–2023).

Country	Sampling location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
South Korea	Kochang-gun, Kyongsangnam-do	3	Badger (<i>Meles meles melanogenys</i>)	Raw liver, spleen, blood, and muscle	December 1997	(Sohn et al., 2000, 2003) ^a
South Korea	Gangwon-do	5	Wild boar (<i>Sus scrofa</i>)	Not specified	February 2001	Rhee et al. (2011)
South Korea	Gangwon-do	4	Wild boar (<i>S. scrofa</i>)	Not specified	February 2002	(Kim et al., 2003; Rhee et al., 2011)

^a *Trichinella* species were identified using molecular methods a few years after outbreak.

Table 5
Published reports of *Trichinella spiralis* in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. spiralis</i>	Reference
Argentina	Patagonian steppe	House mouse (<i>Mus musculus</i>)	Multiplex PCR	1/26 (3.8%)	Larrieu et al. (2004)
Argentina	Buenos Aires Province	Big hairy armadillo (<i>Chaetophractus villosus</i>)	Multiplex PCR	2/11 (18.2%)	Krivokapich et al. (2006)
Argentina	Entre Ríos Province	Wild boar (<i>Sus scrofa</i>)	Multiplex PCR	3/112 (2.7%)	Cohen et al. (2010)
Argentina	Córdoba, Río Negro, Chubut, Neuquén, and Buenos Aires	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	2/12 (16.7%)	Ribicich et al. (2010)
Argentina	Buenos Aires Province	Rat (<i>Rattus norvegicus</i>)		1/66 (1.5%)	
Argentina	Catamarca	Cougar (<i>Puma concolor</i>)	Multiplex PCR	1/4	Krivokapich et al. (2012)
Argentina	Buenos Aires Province	White-eared opossum (<i>Didelphis albiventris</i>)	Multiplex PCR	3/41 (7.3%)	Castaño Zubieta et al. (2014)
		Big lutrine opossum (<i>Lutreolina crassicaudata</i>)		1/20 (5%)	
Argentina	Río Negro	Sea lion (<i>Otaria flavescens</i>)	Multiplex PCR	1/4	Pasqualetti et al. (2018)
Canada	Yukon Territory	Wolverine (<i>Gulo gulo</i>)	Multiplex PCR & PCR-RFLP	1/338 (0.3%)	Sharma et al. (2021)
Chile	Biobío Region	Cougar (<i>P. concolor</i>)	Multiplex PCR	1	Landaeta-Aqueveque et al. (2015)
Chile	La Araucanía & Los Ríos	Wild boar (<i>S. scrofa</i>)	ISSR-PCR	5/278 (1.8%)	Hidalgo et al. (2019)
Chile	Ñuble region	Kodkod/Guinea (<i>Leopardus guigna</i>)	Multiplex PCR	1	Echeverry et al. (2021a)
Chile	Ñuble region	Cougar (<i>P. concolor</i>)	PCR	1	Echeverry et al. (2021b)
Chile	Los Ríos	American mink (<i>Neovison vison</i>)	Multiplex PCR	7/100 (7%)	Espinoza-Rojas et al. (2021)
United States	Montana	Bobcat (<i>Lynx rufus</i>)	Allozyme analysis	1	La Rosa et al. (1992)
United States	Pennsylvania	Black bear (<i>Ursus americanus</i>)		1	
United States	Arizona	Black bear (<i>U. americanus</i>)	Multiplex PCR	1	Pozio et al. (2001c)
United States	Florida	Florida panther (<i>Puma concolor coryi</i>)	Multiplex PCR	3/112 (2.7%)	Reichard et al. (2015)
United States	Alaska	Bear (<i>Ursus</i> spp.)	Multiplex qPCR	1/3	Almeida et al. (2018)
	California			4/8 ^a	
	Minnesota	Wild boar (<i>S. scrofa</i>)	Multiplex qPCR	2/2	
	Missouri			2/2 ^b	
	California			1/1	

^a 1 sample from a sausage containing a mixture of bear and deer meat.

^b 1 sample from a sausage containing a mixture of boar and deer meat.

Table 6
Human outbreaks of *Trichinella spiralis* from consumption of wildlife in the Americas (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (if specified)	Date of outbreak	Reference
Canada	Ontario	24	Wild boar (<i>Sus scrofa</i>)	Uncooked	1993/1994	Greenbloom et al. (1997)
United States	Iowa	2	Wild boar (<i>S. scrofa</i>)	Boar roast	2011	Holzbauer et al. (2014)

reports on *T. pseudospiralis* in Asia and Oceania could be attributed to the lack of surveillance. Further surveillance is warranted, especially regarding the role of migratory birds in the epidemiology and global transmission of *T. pseudospiralis*.

3.4.3. *Trichinella pseudospiralis* in the Americas

Trichinella pseudospiralis was first reported in wildlife in the Americas in 1995 in Alabama, United States (Lindsay et al., 1995). Since then, it has been reported elsewhere in the southern United States as well as on Vancouver Island, British Columbia in Canada in 2010 and the Northwest Territories in 2019 (Table 20) (Gajadhar and Forbes, 2010; Sharma et al., 2019). *Trichinella pseudospiralis* is a freeze-susceptible species which typically limits the northern geographic extent, but it has been reported in the subarctic of Canada in the Northwest Territories, possibly adventitiously introduced through migratory birds (Sharma et al., 2019). To date, there have been no reports of human infections attributed to *T. pseudospiralis* in the Americas, and it is the only species currently known to infect both mammals and birds in the Americas (Gottstein et al., 2009; Pozio, 2016b).

3.5. *Trichinella murrelli*

Trichinella murrelli was first identified as a possible subspecies of *Trichinella spiralis* in 1987 by Dame et al., but was not fully described until 2000 (Dame et al., 1987; Pozio and La Rosa, 2000). To date, *T. murrelli* has only been reported in southern Canada and the United States (Feidas et al., 2014). The northern extent of *T. murrelli* may be limited by freeze susceptibility (Gottstein et al., 2009). *Trichinella murrelli* primarily circulates among terrestrial omnivores and carnivores.

3.5.1. *Trichinella murrelli* in the Americas

The known distribution of *T. murrelli* is limited to the continental United States, from coast to coast, and the southern portions of two Canadian provinces (Ontario and British Columbia) (Table 21). *Trichinella murrelli* does not develop in swine and thus poses low to no risk to people via consumption of pork products (Gottstein et al., 2009). Only one human outbreak associated with *T. murrelli* has been reported in the Americas, from the consumption of black bear meat in Northern California (Table 22).

Table 7
Published reports of *Trichinella nativa* in wildlife in Europe (1991–2023).

Country	Location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. nativa</i>	Reference
Estonia	Jarvarmaa	Raccoon dog (<i>Nyctereutes procyonoides</i>)	RAPD-PCR	3	Pozio et al. (1995)
Estonia	Põlva	Wild boar (<i>Sus scrofa</i>)		1	
Estonia	Country-wide	Brown bear (<i>Ursus arctos</i>)	RAPD-PCR	2/13 (15.4%)	Pozio et al. (1998)
		Eurasian lynx (<i>Lynx lynx</i>)		3/13 (23.1%)	
		Raccoon dog (<i>N. procyonoides</i>)		3/19 (15.8%)	
		Red fox (<i>Vulpes vulpes</i>)		3/18 (16.7%)	
		Wild boar (<i>S. scrofa</i>)		2/667 (0.30%)	
		Wolf (<i>Canis lupus</i>)		5/24 (20.8%)	
Estonia	Not specified	Wolf (<i>C. lupus</i>)	RAPD-PCR, PCR-RFLP, & Multiplex PCR	27/34 (79.4%) ^b	Jarvis et al. (2001)
		Raccoon dog (<i>N. procyonoides</i>)		11/22 (50%) ^b	
		Eurasian lynx (<i>L. lynx</i>)		9/19 (47.4%) ^b	
		Red fox (<i>V. vulpes</i>)		8/19 (42.1%) ^b	
		Wild boar (<i>S. scrofa</i>)		7/695 (1%) ^b	
		Brown bear (<i>U. arctos</i>)		5/17 (29.4%)	
		Badger (<i>Meles meles</i>)		1/2	
Estonia	Country-wide	Wolf (<i>C. lupus</i>)	RAPD-PCR	13/26 ^a (50%)	Moks et al. (2006)
Estonia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	74/446 (16.6%)	Malakauskas et al. (2007)
		Raccoon dog (<i>N. procyonoides</i>)		25/157 (15.9%)	
Estonia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	27/87 (31.0%)	Kärssin et al. (2017)
		Raccoon dog (<i>N. procyonoides</i>)		36/113 (31.9%)	
Estonia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	20/30,566 (0.06%)	Kärssin et al. (2021)
		Brown bear (<i>U. arctos</i>)		25/429 (5.8%)	
		Eurasian Lynx (<i>L. lynx</i>)		19/90 (21.1%)	
Finland	Southern Finland	Red fox (<i>V. vulpes</i>)	RAPD-PCR	12/19 (63.2%)	Oivanen et al. (2000)
Finland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	12/158 (7.6%)	Oivanen et al. (2002)
		Raccoon dog (<i>N. procyonoides</i>)		11/199 (5.5%)	
		Brown bear (<i>U. arctos</i>)		3/150 (2%)	
		Eurasian lynx (<i>L. lynx</i>)		3/96 (3.1%)	
		Wolf (<i>C. lupus</i>)		2/18 (11.1%)	
Finland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	?/1010 ^c	Airas et al. (2010)
		Raccoon dog (<i>N. procyonoides</i>)		?/662 ^c	
		Eurasian lynx (<i>L. lynx</i>)		?/402 ^c	
		Brown bear (<i>U. arctos</i>)		?/5 ^c	
		Wolf (<i>C. lupus</i>)		?/102 ^c	
		Eurasian otter (<i>Lutra lutra</i>)		1/31 (3.2%)	
Finland	Baltic sea coast of Finland	Grey seal (<i>Halichoerus grypus</i>)	Multiplex PCR	1/171 (0.6%)	Isomursu and Kunnasranta (2011)
Finland	Country-wide	Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR	453/1245 (36.4%)	Oksanen et al. (2018)
		Raccoon dog (<i>N. procyonoides</i>)		245/952 (25.7%)	
		Red fox (<i>V. vulpes</i>)		79/454 (17.4%)	
		Wolf (<i>C. lupus</i>)		23/85 (27.1%)	
		Brown bear (<i>U. arctos</i>)		2/162 (1.2%)	
		Pine marten (<i>Martes martes</i>)		6/69 (8.7%)	
		European badger (<i>M. meles</i>)		2/40 (5.0%)	
		Wolverine (<i>Gulo gulo</i>)		1/4	
Germany	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/3154 (0.1%)	Chmurzynska et al. (2013)
Iceland	Middle North, Northeast, and Westfjords	Polar bear (<i>Ursus maritimus</i>)	PCR	1/5	Skírnisson and Jouet (2023)
Latvia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	24/1112 (2.2%)	Malakauskas et al. (2007)
Latvia	Vidzeme, Zemgale, Latgale, and Kurzeme	Red fox (<i>V. vulpes</i>)	Multiplex PCR & 5S rDNA PCR	2/35 (5.7%)	Franssen et al. (2014)
Latvia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	4/3174 (0.1%)	Kirjusina et al. (2015)
		Red fox (<i>V. vulpes</i>)		3	
		Wolf (<i>C. lupus</i>)		4	
Latvia	Country-wide	Wolf (<i>C. lupus</i>)	Multiplex PCR	3/23 (13.0%)	Deksne et al. (2016)
		Raccoon dog (<i>N. procyonoides</i>)		11/394 (2.8%)	
		Red fox (<i>V. vulpes</i>)		10/668 (1.5%)	
		Eurasian lynx (<i>L. lynx</i>)		1/34 (2.9%)	
		Pine marten (<i>M. martes</i>)		4/137 (2.9%)	
		Golden jackal (<i>Canis aureus</i>)		1/4	
Lithuania	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	5/567 (0.9%)	Malakauskas et al. (2007)
		Raccoon dog (<i>N. procyonoides</i>)		2/83 (2.4%)	
		Wild boar (<i>S. scrofa</i>)		1/9088 (0.01%)	
Norway	Svalbard	Polar bear (<i>U. maritimus</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Norway	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR & Sequencing	18/393 (4.6%)	Davidson et al. (2006)
Norway	Svalbard	Arctic fox (<i>Vulpes lagopus</i>)	Multiplex PCR	11/370 (3%)	Åsbakk et al. (2015)
		Polar bear (<i>U. maritimus</i>)		1	
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/1634 (0.06%)	Chmurzynska et al. (2013)
Poland	Varmian Masurian Province	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1	Bilska-Zajac et al. (2017)
Poland	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/1389865 (0.00007%)	Bilska-Zajac et al. (2020)
		Red fox (<i>V. vulpes</i>)		1/1740 (0.06%)	
Sweden	Stockholm, Västervik, Östersund, and Färgelanda	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/1800 (0.1%)	Pozio et al. (2004a)

- ^a *T. nativa* and *T. britovi* were genotyped but the number of positives for each host species were not reported.
^b Proportion of animals positive for *Trichinella* spp. detected were reported, but not the amount of animals positive with each species.
^c The proportion of *T. nativa* among all animals tested was 74%, but the exact proportion per host species was not reported.

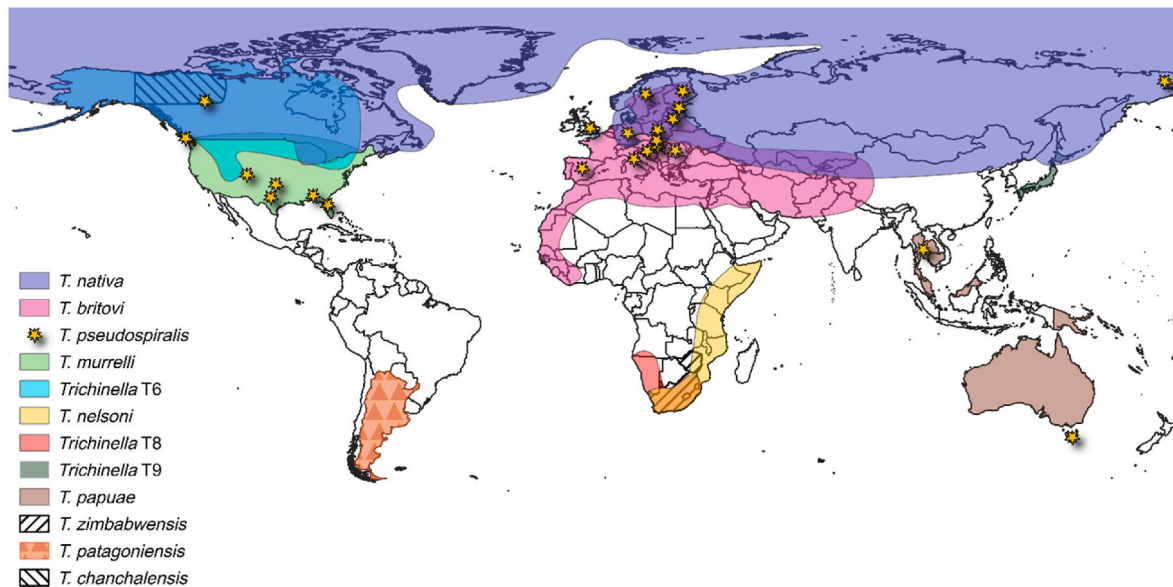


Fig. 3. Global distribution of sylvatic *Trichinella* species and genotypes adapted from Pozio (2016); Gottstein et al. (2009).

Table 8

Human outbreaks of *Trichinella nativa* from consumption of wildlife in Europe (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
France/ Canada	Orléans & Narbonne	9 ^a	Black bear (<i>Ursus americanus</i>)	Stew, undercooked steaks, or raw	September 2005	(Ancelle et al., 2005; Public Health Agency of Canada, 2006)

^a 8 French hunters were infected in Quebec, Canada and 9 more were infected in France from consuming meat illegally imported, see Table 11.

3.6. *Trichinella T6*

Trichinella T6 is a freeze-tolerant genotype first identified as a new phenotype with unknown taxonomic status in 1992 (Pozio et al., 1992a). Today, *Trichinella T6* remains an unnamed but recognized genotype. *Trichinella T6* has a Nearctic distribution and has so far only been reported in terrestrial carnivores from Canada and the United States.

3.6.1. *Trichinella T6* in North America

Reports of *Trichinella T6* have largely been from northern Canada, but it has also been reported in the United States as far east as Pennsylvania and as far south as California. *Trichinella T6* has been found in many species of terrestrial carnivores and omnivores, including several important food species consumed by humans, such as black bears, grizzly bears, cougars (*Puma concolor*), and lynx (*Lynx canadensis*) (Table 23). *Trichinella T6* has not been found in swine (domestic or wild boars) and experimental infections have shown that swine are not suitable hosts for *Trichinella T6* (Hill et al., 2009; Kapel and Gamble, 2000). Two human outbreaks with T6 have been reported, both from the United States: one in 1996 in Idaho associated with cougar jerky and the second in Ohio with undercooked black bear meat hunted from Ontario, Canada (Table 24).

3.7. *Trichinella nelsoni*

Trichinella nelsoni is a freeze-susceptible species first described along with *T. nativa* by Britov and Boev (1972), and is considered one of the

most genetically divergent among the encapsulating *Trichinella* species (Pozio et al., 2005b). Despite being first described half a century ago, there are still few reports on the geographic and host range of *T. nelsoni*.

3.7.1. *Trichinella nelsoni* in Africa

Trichinella nelsoni has been confirmed in eight wildlife species from Tanzania, specifically from the Serengeti National Park (Pozio et al., 1997), a leopard (*Panthera pardus*) and lion (*Panthera leo*) from South Africa (Marucci et al., 2009; Mukaratirwa et al., 2017), and a spotted hyena (*Crocuta*) in Kenya (La Rosa et al., 1992) (Table 25). The current known geographical distribution is restricted to Eastern and Southern Africa. To date, there have been no reported human cases with *T. nelsoni*.

3.8. *Trichinella T8*

Trichinella T8 is an encapsulated and freeze-susceptible genotype first described in South Africa in spotted hyenas and lions, reported alongside *Trichinella T6* and *T. murrelli* (T5) in the 1992 taxonomic revisions by Pozio et al. (1992). *Trichinella T8*, like *T. nelsoni* is another under surveilled species/genotype in Africa having only a few genotyped reports over the last three decades.

3.8.1. *Trichinella T8* in Africa

To date, *Trichinella T8* has only been reported in wildlife from two countries, Namibia and South Africa in three species: the spotted hyena, lion, and leopard (Table 26) (La Rosa et al., 1992; Marucci et al., 2009; Pozio et al., 1994). *Trichinella T8* remains a recognized but unnamed genotype, as its relationship with *T. britovi* has not been fully elucidated.

Table 9
Published reports of *Trichinella nativa* in wildlife in the Asia (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. nativa</i>	Reference
Kazakhstan	Not specified	Red fox (<i>Vulpes vulpes</i>)	Allozyme analysis	1	La Rosa et al. (1992)
		Golden jackal (<i>Canis aureus</i>)		1	
Kazakhstan	Akmolinskaya, Karagandinskaya, Northern Kazakhstan, Ulytauskaya, Kostanaiskaya, Western Kazakhstan, Aktyubinskaya,	Eurasian badger (<i>Meles meles</i>)	Multiplex PCR	4/6 (66.7%)	Akibekov et al. (2023)
		Wolf (<i>Canis lupus</i>)		20/98 (20.4%)	
Kazakhstan	Kostanay, Akmola, South Kazakhstan, Pavlodar, Karaganda, East Kazakhstan, West Kazakhstan, Aktobe, Atyrau and Ulytau regions	Red fox (<i>V. vulpes</i>)	Multiplex PCR	7/26 (26.9%)	Uakhit et al. (2023)
		Eurasian lynx (<i>Lynx lynx</i>)		1/3	
		Wolf (<i>C. lupus</i>)		17/83 (20.5%)	
		Red fox (<i>V. vulpes</i>)		11/50 (22%)	
		Corsac fox (<i>Vulpes corsac</i>)		2/11 (18.2%)	
Japan	Otaru, Hokkaido	Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/43 (7%)	Yimam et al. (2001)
Japan	Otofuke, Hokkaido	Red fox (<i>V. vulpes</i>)	PCR	1/2	Kanai et al. (2006)
Japan	Hokkaido	Red fox (<i>V. vulpes</i>)	Multiplex PCR and PCR	1/28 (3.6%)	Kanai et al. (2007)
Russia	Primorsk region	Wolf (<i>C. lupus</i>)	Allozyme analysis	3	La Rosa et al. (1992)
		Raccoon dog (<i>Nyctereutes procyonoides</i>)		2	
		Leopard cat (<i>Felis euphilura</i>)		1	
Russia	Tvier and Smolensk regions (Northwestern Russia)	Tiger (<i>Panthera tigris</i>)	Multiplex PCR	1	Pozio et al. (2001a)
		Wolf (<i>C. lupus</i>)		79/82 (96.3%)	
		Red fox (<i>V. vulpes</i>)		14/29 (48.3%)	
		European polecat (<i>Mustela putorius</i>)		1/8	
		Unspecified mustelids		1/15 (6.7%)	
		Raccoon dog (<i>N. procyonoides</i>)		1/5	
Russia	Chukotka Peninsula & Arkhangelsk Oblast	Polar bear (<i>Ursus maritimus</i>)	Multiplex PCR & ISSR-PCR	1	Goździk et al. (2017)
		Wolverine (<i>Gulo</i>)		1	
		Arctic fox (<i>Vulpes lagopus</i>)		2/3	
		Northern sea lion (<i>Eumetopias jubatus</i>)		1	
		Brown bear (<i>Ursus arctos</i>)		1	

(Pozio et al., 2005b, 2009a; Pozio and Murrell, 2006). To date, there have been no reports of *Trichinella* T8 infections in humans.

3.9. *Trichinella* T9

Trichinella T9 is a freeze susceptible genotype first described by Nagano et al., 1999 in a raccoon dog (*Nyctereutes procyonoides viverrinus*) and a Japanese black bear (*Ursus thibetanus japonicus*) from Japan, which was originally genotyped as *T. britovi*, but later determined to be *Trichinella* T9 (Nagano et al., 1999). *Trichinella* T9 is currently the third recognized but unnamed genotype with an unresolved taxonomic status.

3.9.1. *Trichinella* T9 in Asia

Trichinella T9 has thus far only been reported in animals from Japan (Table 27). *Trichinella* T9 has been found in six different host species across Japan, primarily from Hokkaido, the northernmost of Japan's main islands, and from the northern regions of Honshu, Japan's main island. There has been one reported human outbreak of *Trichinella* T9 from wildlife, from consumption of undercooked brown bear meat (Tada et al., 2018) (Table 28).

3.10. *Trichinella papuae*

Trichinella papuae was first described in wild pigs (*S. scrofa*) from Papua New Guinea (Pozio et al., 1999b); it was the second

non-encapsulated species to be described. *Trichinella papuae* is a freeze-susceptible species that can infect mammals and reptiles, which at the time was a first within the genus that a species was able to infect homeotherms and poikilotherms (Pozio et al., 2004b). To date, *T. papuae* has only been found in Australia and Papua New Guinea in wild pigs and saltwater crocodiles (*Crocodylus porosus*) (Table 29).

3.10.1. *Trichinella papuae* in Asia and Oceania

Since the first description of *T. papuae* in 1999, it has been reported in wild pigs from Australia (Cuttell et al., 2012), as well as in saltwater crocodiles in Papua New Guinea (Pozio et al., 2004c, 2005a) (Table 29). In Papua New Guinea, antibodies to *Trichinella* spp. have been reported in humans (Owen et al., 2001), but clinical and genotyped cases have not been documented. Human infections linked to game meat consumption have occurred in Cambodia and Thailand despite there being no genotyped reports of *T. papuae* in wildlife from these countries (Table 30) (Caron et al., 2020; Khumjui et al., 2008; Kusolsuk et al., 2010). *Trichinella papuae* was misidentified as *T. spiralis* in a Thai patient (returned from Malaysia) in 2005 with a history of consuming wild boar meat (Chotmongkol et al., 2005), and was later correctly identified using PCR as *T. papuae*, which suggests circulation of *T. papuae* in wild boars in Malaysia (Intapan et al., 2011).

Table 10
Published reports of *Trichinella nativa* in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. nativa</i>	Reference	
Canada	Not specified Northern Canada	Wolf (<i>Canis lupus</i>)	Allozyme analysis	1	La Rosa et al. (1992)	
		Arctic fox (<i>Vulpes lagopus</i>)		1		
	Manitoba	Polar bear (<i>Ursus maritimus</i>)		1		
Canada	Nunavut	Wolverine (<i>Gulo gulo</i>)	Multiplex PCR	3/41 (7.3%)	Reichard et al. (2008)	
Canada	Northwest Territories	Wolverine (<i>G. gulo</i>)	Multiplex PCR	Proportion positive not specified per location, host species, and genotype	Gajadhar and Forbes (2010)	
		Black bear (<i>Ursus americanus</i>)				
		Polar bear (<i>U. maritimus</i>)				
		Wolf (<i>C. lupus</i>)				
	Nunavut	Walrus (<i>Odobenus rosmarus</i>)				
	British Columbia Mainland	Cougar (<i>Puma concolor</i>)				
	Saskatchewan	Black bear (<i>U. americanus</i>)				
	Quebec					
	Northwest Territories					
	British Columbia					
Canada	Northwest Territories	Black bear (<i>U. americanus</i>)	Multiplex PCR	4/120 (3.3%)	Larter et al. (2011)	
		Grizzly bear (<i>Ursus arctos</i>)		1/11 (9.1%)		
		Wolf (<i>C. lupus</i>)		6/27 (22.2%)		
Canada	Nunavik, Quebec	Walrus (<i>O. rosmarus</i>)	Multiplex PCR	20/694 (2.9%)	Larrat et al. (2012)	
Canada	Nunavik, Quebec	Red fox (<i>Vulpes vulpes</i>)	Multiplex PCR	14/39 (35.9%)	Nicholas et al. (2018)	
Canada	Québec	Arctic fox (<i>V. lagopus</i>)	Multiplex PCR & PCR RFLP	13/91 (14.3%)	Owsiacki et al. (2020)	
Canada	Yukon & Northwest Territories	Wolverine (<i>G. gulo</i>)	Multiplex PCR & PCR RFLP	29/42 (69%)	Sharma et al. (2020)	
		Wolf (<i>C. lupus</i>)				
	Newfoundland and Labrador & Northwest Territories	Walrus (<i>O. rosmarus</i>)		1		
		Raccoon (<i>Procyon lotor</i>)		1		
	Quebec	Red fox (<i>V. vulpes</i>)		19/19 (100%)		
	Quebec	Polar bear (<i>U. maritimus</i>)		3		
	Northwest Territories & Quebec	Cougar (<i>P. concolor</i>)		8/9		
	Northwest Territories & Quebec	Grizzly bear (<i>U. arctos</i>)		1		
	British Columbia & Alberta	Fisher (<i>Pekania pennanti</i>)		2		
	British Columbia	Coyote (<i>Canis latrans</i>)		1		
	British Columbia	Black bear (<i>U. americanus</i>)		1		
	Quebec	Bear (<i>Ursus</i> spp.)		1		
	Quebec	Arctic fox (<i>V. lagopus</i>)		6/6		
	Northwest Territories	Wolverine (<i>G. gulo</i>)		54/338 (16%)		
	Yukon		Multiplex PCR & PCR RFLP		Sharma et al. (2021)	
	Canada	Newfoundland Island	Coyote (<i>C. latrans</i>)	Multiplex PCR & Sanger sequencing	4/153 (2.6%)	Malone et al. (2023)
	Greenland	Not specified	Polar bear (<i>U. maritimus</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Greenland	Not specified	Arctic fox (<i>V. lagopus</i>)	RAPD-PCR	16/266 (6%)	Kapel et al. (1999)	
Greenland	Qaanaaq, Ilulissat, Sisimiut, and Ammassalik	Ringed seal (<i>Pusa hispida</i>)	Multiplex PCR	1/1706 (0.05%) ^a	Møller (2007)	
		Hooded seal (<i>Cystophora cristata</i>)		5/1706 (0.3%) ^a		
United States	Alaska	Polar bear (<i>U. maritimus</i>)	Allozyme analysis	1	La Rosa et al. (1992)	
United States	Alaska	Lynx (<i>Lynx canadensis</i>)	PCR	199/1065 (18.7%)	Zarnke et al. (1995)	
United States	Alaska	Bear (<i>Ursus</i> spp.)	qPCR	2/3	Almeida et al. (2018)	
	Alaska	Walrus (<i>O. rosmarus</i>)		4/12 (33%)		
	Wisconsin	Bear (<i>Ursus</i> spp.)		1		

^a Sample size of each species not reported.

3.11. *Trichinella zimbabwensis*

Trichinella zimbabwensis is a freeze-susceptible and non-encapsulated species first described by Pozio et al. (2002). *Trichinella zimbabwensis* is the third non-encapsulated species to be described and like *T. papuae* it is also able to infect homeotherms and poikilotherms. Genotyped reports of *T. zimbabwensis* have been limited to South Africa and Zimbabwe in reptiles as well as mammals.

3.11.1. *Trichinella zimbabwensis* in Africa

T. zimbabwensis has been reported in two poikilotherms, Nile crocodiles (*Crocodylus niloticus*) and Nile monitor lizards (*Varanus niloticus*) in South Africa and Zimbabwe (La Grange et al., 2009; Mukaratirwa et al., 2017; Pozio et al., 2002, 2007) and in four terrestrial mammals in South Africa (Table 31). The genotyped infections reported to date have been restricted to Eastern and Southern African regions, however a presumed, but ungenotyped case of *T. zimbabwensis* was reported in Ethiopia in a Nile crocodile (Pozio et al., 2007). A confirmed report of

Table 11Human outbreaks of *Trichinella nativa* from consumption of wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Canada	Nunavik, Québec	36	Walrus (<i>Odobenus rosmarus</i>)	Raw/undercooked	1997	Proulx et al. (2002)
Canada	Northern Saskatchewan	31	Black bear (<i>Ursus americanus</i>)	Inadequately cooked	2000	Schellenberg et al. (2003)
Canada/ France	Nunavik, Québec	8 ^a	Black bear (<i>U. americanus</i>)	Raw/undercooked	2005	(Ancelle et al., 2005; Public Health Agency of Canada, 2006)
Canada	Vancouver Island, British Columbia	26 probable, 14 confirmed	Black bear (<i>U. americanus</i>)	Barbecued, fried, and stewed	2005	McIntyre et al. (2007)
Canada	Northern Ontario	10	Black bear (<i>U. americanus</i>)	Jerky	2016	Dalcin et al. (2017)
Canada	Northern Saskatchewan	1	Black bear (<i>U. americanus</i>)	Raw meat	2019	(Tso et al., 2021; Jenkins and Kafle, unpublished data)

^a 8 hunters from France consumed the meat in Quebec, Canada, but were diagnosed in France. Bear meat brought back to France infected an additional 9 people, see Table 8.

T. zimbabwensis was also reported from Mozambique in a farmed Nile crocodile which indicates that the geographic range of *T. zimbabwensis* is likely larger than currently known (Pozio et al., 2007). To date there have been no reported human infections with *T. zimbabwensis*.

3.12. *Trichinella patagoniensis*

Trichinella patagoniensis is an encapsulated species with mild freeze-tolerance first detected in 2008 in a cougar (*Puma concolor*), and fully described in 2012 in two more cougars from Argentina (Table 32) (Krivokapich et al., 2008, 2012). To date, *T. patagoniensis* has only been reported in cougars from Argentina.

3.12.1. *Trichinella patagoniensis* in the Americas

Trichinella patagoniensis has a mild freeze-tolerance, with larvae surviving in the tissue of an experimentally infected domestic cat (*Felis silvestris*) frozen at -5°C for 3 months, but did not survive freezing at -18°C for 1 week (Krivokapich et al., 2012). Domestic cats and, to a lesser extent, guinea pigs (*Cavia porcellus*) can be experimentally infected, while experimental infections in domestic pigs, wild boars, rats, mice (*Mus musculus*), and chickens (*Gallus gallus domesticus*) were relatively unsuccessful (Fariña et al., 2017; Krivokapich et al., 2012; Pasqualetti et al., 2014; Ribicich et al., 2013). *Trichinella patagoniensis* has only been detected in three cougars from Argentina thus far which highlights the need for further surveillance in Argentina and surrounding countries in South America. To date, there have been no reported human infections attributed to *T. patagoniensis*.

3.13. *Trichinella chanchalensis*

Trichinella chanchalensis is the most recent *Trichinella* species to be discovered, being first found in wolverines (*Gulo gulo*) from the Yukon and Northwest Territories, Canada (Sharma et al., 2020). It has since been found in one American marten (*Martes americana*) in the Northwest Territories (Lobanov et al., 2023) (Table 33). *Trichinella chanchalensis* is a freeze-tolerant encapsulated species so far only reported in the northern territories of western Canada.

3.13.1. *Trichinella chanchalensis* in the Americas

The true geographic range of the *T. chanchalensis* is likely underestimated, as the current gold-standard for genotyping *Trichinella* spp. (multiplex PCR) cannot differentiate between *T. nativa* and *T. chanchalensis* which requires subsequent sequencing or PCR-RFLP (Pozio and Zarlenga, 2019; Sharma et al., 2021). This is problematic as the two species occur in sympatry; thus, previous isolates genotyped as *T. nativa* by the multiplex PCR may actually be *T. chanchalensis*. *Trichinella chanchalensis* is the third freeze-tolerant species/genotype endemic in Canada, along with *T. nativa* and *Trichinella* T6 (Sharma

et al., 2020). The infectivity of *T. chanchalensis* to domestic pigs and mice is currently unknown. To date, there have been no reports of human infections attributed to *T. chanchalensis*, but it is possible that human cases have previously been incorrectly genotyped as *T. nativa*; thus the zoonotic potential of *T. chanchalensis* is currently unknown.

4. Discussion

4.1. Human trichinellosis of wildlife origin

Trichinella species have been reported on every continent—except Antarctica—and have been found in myriad wildlife species, terrestrial and marine. Many of these wildlife species pose a risk for human infection (for example, wild boar, bears, and walrus) if consumed as undercooked or raw meat intentionally or unintentionally, as freezing is often not effective against sylvatic taxa of *Trichinella* in temperate and northern regions. Although many wild carnivores and omnivores that host *Trichinella* spp. are not commonly consumed by humans, they may be consumed by animals of food importance, and serve as sentinels of trophic transmission—often infected at high prevalence and intensity compared to food species.

The average annual incidence of human trichinellosis is estimated to be 1.23 cases per million people per year, with a mortality rate of 0.2% (Pozio, 2007b), although per capita incidence is much higher in some regions, such as in parts of the Canadian North, with an incidence of 42 cases per million per year, all of which originate from consumption of wildlife (Gilbert et al., 2010). Prevalence of human trichinellosis of wildlife origin is likely both underdiagnosed and underreported, especially in low-middle income countries and in remote regions of developed countries because of the lack of diagnostic capacity and access to healthcare services (Chavez-Ruvalcaba et al., 2021), along with non-specific symptoms, lack of physician awareness, and lack of symptoms at low infection doses (Pozio, 2007a). It is interesting to note that in several cases described above, a particular species of *Trichinella* was detected in a geographic region where humans were infected from consumption of endemic wildlife (humans serving as sentinels), but there were no reports from wildlife directly, thus highlighting the lack of wildlife studies in many regions of the world (Chotmongkol et al., 2005; Intapan et al., 2011; Kim et al., 2003; Rhee et al., 2011; Sohn et al., 2000).

This study reveals many wildlife and human cases; however, there are still many reports where larvae are not identified to species or genotype level, rendering distribution maps incomplete. For example, in northern Canada, larvae detected in walrus are usually assumed to be *T. nativa*, but genotyping is rarely performed, limiting detection of other species/genotypes. We continue to discover cryptic species of *Trichinella* in wildlife, such as *T. patagoniensis* and *T. chanchalensis*, further emphasizing the need for thorough surveys using appropriate molecular

Table 12
Published reports of *Trichinella britovi* in wildlife in Europe (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Austria	Carinthia, Salzburg, Styria, Tyrols, and Vorarlberg	Red fox (<i>Vulpes vulpes</i>)	PCR	24/1546 (1.6%)	Krois et al. (2005)
Belgium	Mettet Municipality	Wild boar (<i>Sus scrofa</i>)	Multiplex PCR, sequencing, conventional PCR	1/20 (5%)	Schynts et al. (2006)
Bosnia and Herzegovina	Eastern part of the country	Wolf (<i>Canis lupus</i>)	Multiplex PCR	1/3	Teodorovic et al. (2014)
Bulgaria	Stara Zagora and Pazardjik Regions	Red fox (<i>V. vulpes</i>) Golden jackal (<i>Canis aureus</i>) Stone/Beech marten (<i>Martes foina</i>) European wild cat (<i>Felis silvestris</i>)	Multiplex PCR	25 20 8 7	Kurdova et al. (2004)
Bulgaria	Country-wide	Wild boar (<i>S. scrofa</i>) Wild boar (<i>S. scrofa</i>) Red fox (<i>V. vulpes</i>) Golden jackal (<i>C. Aureus</i>) European wild cat (<i>F. silvestris</i>) Stone/Beech marten (<i>M. foina</i>) Badger (<i>Meles meles</i>) Rat ^a Wolf (<i>C. lupus</i>) Brown bear (<i>Ursus arctos</i>) Eurasian otter (<i>Lutra lutra</i>)	Multiplex PCR and sequencing	2 5 1 5 1 2 2 3 2 2 1	Dilcheva and Petkova (2018)
Bulgaria	Country-wide	Wild boar (<i>S. scrofa</i>) Golden jackal (<i>C. aureus</i>) Red fox (<i>V. vulpes</i>) European badger (<i>M. meles</i>) Wolf (<i>C. lupus</i>) Brown bear (<i>U. arctos</i>)	Multiplex PCR	90 3 5 3 3 1	Lalkovski (2019)
Croatia	Country-wide	Wolf (<i>C. lupus</i>)	Multiplex PCR	20/67 (29.9%)	Beck et al. (2009)
Croatia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	15/183,184 (0.008%)	Balic et al. (2020)
Estonia	Jävarmaa district	Raccoon dog (<i>Nyctereutes procyonoides</i>) Red fox (<i>V. vulpes</i>)	RAPD-PCR	1/3 1	Pozio et al. (1995)
Estonia	Saaremaa island Country-wide	Wild boar (<i>S. scrofa</i>) Eurasian lynx (<i>Lynx lynx</i>) Raccoon dog (<i>N. procyonoides</i>) Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>) Wolf (<i>C. lupus</i>)	RAPD-PCR	1 2/13 (15.4%) 7/19 (36.8%) 6/18 (33.3%) 2/667 (0.3%) 11/24 (45.8%)	Pozio et al. (1998)
Estonia	Not specified	Wolf (<i>C. lupus</i>) Raccoon dog (<i>N. procyonoides</i>) Eurasian lynx (<i>L. lynx</i>) Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>) Wolf (<i>C. lupus</i>)	RAPD-PCR, PCR-RFLP, & Multiplex PCR	27/34 ^b (79.4%) 11/22 ^b (50%) 9/19 ^b (47.4%) 8/19 ^b (42.1%) 7/695 ^b (1%) 13/26 ^c (50%)	Jarvis et al. (2001)
Estonia	Country-wide	Wolf (<i>C. lupus</i>)	RAPD-PCR	13/26 ^c (50%)	Moks et al. (2006)
Estonia	Country-wide	Red fox (<i>V. vulpes</i>) Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	60/446 (13.5%) 25/157 (15.9%)	Malakauskas et al. (2007)
Estonia	Country-wide	Raccoon dog (<i>N. procyonoides</i>) Red fox (<i>V. vulpes</i>)	Multiplex PCR	28/113 (24.8%) 31/87 (35.6%)	Kärssin et al. (2017)
Estonia	Country-wide	Wild boar (<i>S. scrofa</i>) Brown bear (<i>U. arctos</i>) European badger (<i>M. meles</i>) Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR	223/30,566 (0.7%) 32/429 (7.5%) 2/5 43/90 (47.8%)	Kärssin et al. (2021)
Finland	Country-wide	Brown bear (<i>U. arctos</i>)	Multiplex PCR	5/17 (29.4%)	Oivanen et al. (2002)
Finland	Country-wide	Raccoon dog (<i>N. procyonoides</i>) Eurasian lynx (<i>L. lynx</i>) Red fox (<i>V. vulpes</i>)	Multiplex PCR	?/662 ^d ?/402 ^d ?/1010 ^d	Airas et al. (2010)

(continued on next page)

Table 12 (continued)

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Finland	Country-wide	Wolf (<i>C. lupus</i>)	Multiplex PCR	?/102 ^d	Oksanen et al. (2018)
		Eurasian lynx (<i>L. lynx</i>)		39/1245 (3.1%)	
		Raccoon dog (<i>N. procyonoides</i>)		24/952 (2.5%)	
France	Lozère & Haute Marne	Red fox (<i>V. vulpes</i>)	Isoenzymatic analysis	9/454 (2%)	La Rosa et al. (1991)
		Wolf (<i>C. lupus</i>)		2/85 (2.4%)	
France	Not specified	Red fox (<i>V. vulpes</i>)	Allozyme analysis	2	La Rosa et al. (1992)
France	Southwest and Southeastern Finland	Badger (<i>M. meles</i>)	RAPD-PCR	1/2	Pozio et al. (1996)
		Wild boar (<i>S. scrofa</i>)		1/330,000 (0.0003%)	
France	Haut-Var area	Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/108 (2.8%)	Aoun et al. (2012)
France	Corsica, Isère, Provence, Haute Savoie, Marne, Var, Ariège, and Alpes Maritimes	Red fox (<i>V. vulpes</i>)	Multiplex PCR	9	La Rosa et al. (2018)
		Wolf (<i>C. lupus</i>)		3	
		Wild boar (<i>S. scrofa</i>)		3	
Germany	Not specified	Red fox (<i>V. vulpes</i>)	PCR & PCR-RFLP	1/2	Pozio et al. (2000)
Germany	Baden-Württemberg, Berlin, Brandenburg, Hesse, Mecklenburg-Western Pommerania, and Thuringia states	Red fox (<i>V. vulpes</i>)	Multiplex PCR	9/3154 (0.3%)	Chmurzynska et al. (2013)
Germany	Brandenburg	Raccoon dog (<i>N. procyonoides</i>)	PCR & PCR-RFLP	1/1527 (0.07%)	Mayer-Scholl et al. (2016)
Hungary	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/100 (3%)	Sréter et al. (2003)
Hungary	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	30/2116 (1.4%)	Szell et al. (2008)
Hungary	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	11/220,000 (0.005%)	Szell et al. (2012)
Hungary	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	60/3304 (1.8%)	Tolnai et al. (2014)
		Wild boar (<i>S. scrofa</i>)		32/290,000 (0.01%)	
Italy	Not specified	Red fox (<i>V. vulpes</i>)	Allozyme analysis	30	La Rosa et al. (1992)
		Brown rat (<i>R. norvegicus</i>)		5	
		Black rat (<i>R. rattus</i>)		1	
		Marsican brown bear (<i>Ursus arctos marsicanus</i>)		1	
		Wolf (<i>C. lupus</i>)		3	
		Wild boar (<i>S. scrofa</i>)		2	
Italy	Country-wide	Red fox (<i>V. vulpes</i>)	RAPD-PCR	50/3565 (1.4%)	Pozio et al. (1996)
		Wolf (<i>C. lupus</i>)		12/81 (14.8%)	
		European badger (<i>M. meles</i>)		3/34 (8.8%)	
		Stone/Beech marten (<i>M. foina</i>)		2/5	
		Brown bear (<i>U. arctos</i>)		1	
		Wild boar (<i>S. scrofa</i>)		5/370,000 (0.001%)	
		Brown rat (<i>Rattus norvegicus</i>)		5/267 (1.9%)	
		Black rat (<i>Rattus rattus</i>)		1/159 (0.6%)	
		Wild boar (<i>S. scrofa</i>)		1/680 (0.1%)	
		Red fox (<i>V. vulpes</i>)		8/227 (3.5%)	
Italy	Aosta Valley region	Stone/Beech marten (<i>M. foina</i>)	PCR	3/38 (7.9%)	Riccardo et al. (2002)
		European badger (<i>M. meles</i>)		1/53 (1.9%)	
Italy	Sardinia	Red fox (<i>V. vulpes</i>)	Multiplex PCR	13/153 (8.5%)	Bandino et al. (2015)
Italy	Abruzzi region	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	3/8646 (0.03%)	Badagliacca et al. (2016)
		Wolf (<i>C. lupus</i>)		59/218 (27.1%)	
		Red fox (<i>V. vulpes</i>)		24/480 (5%)	
		Wild boar (<i>S. scrofa</i>)		3/16,323 (0.02%)	
		Stone/Beech marten (<i>M. foina</i>)		2/27 (7.4%)	
		European pine marten (<i>M. martes</i>)		2/6	
Italy	Sardinia, Emilia Romagna, Apulia, Marche, Abruzzo, and Molise	European wild cat (<i>F. silvestris</i>)	Multiplex PCR	1/8	La Rosa et al. (2018)
		Red fox (<i>V. vulpes</i>)		12	
		Wolf (<i>C. lupus</i>)		5	
Italy	Abruzzi region	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	3	Badagliacca et al. (2021)
		Wolf (<i>C. lupus</i>)		59/213 (27.7%)	
		Red fox (<i>V. vulpes</i>)		32/418 (7.7%)	
		European badger (<i>M. meles</i>)		1/149 (0.7%)	
		Stone/Beech marten (<i>M. foina</i>)		1/23 (4.3%)	

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Table 12 (continued)

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
		Wild boar (<i>S. scrofa</i>)		16/52,814 (0.03%)	
Italy	Abruzzi and Molise regions	Italian wolf (<i>Canis lupus italicus</i>) Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>)	Multiplex PCR	77/350 (22%) 42/668 (6.3%) 26/62,660 (0.04%)	Ricchiuti et al. (2021)
Italy	Sardinia	Unspecified mustelids Wild boar (<i>S. scrofa</i>) Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/264 (1.1%) 6/17,786 (0.03%) 6/141 (4.3%)	Bandino et al. (2023)
Italy	Western Alps	Wolf (<i>C. lupus</i>)	Multiplex PCR	9/130 (6.9%)	Martínez-Carrasco et al. (2023)
Italy	Province of Rieti	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/554 (0.18%)	Piccinini et al. (2023)
Italy	Emilia-Romagna Region	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	2/208,241 (0.001%)	Rossi et al. (2023)
Italy	Southern Italy	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	14/139,160 (0.01%)	Sgroi et al. (2023)
Latvia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	114/1112 (10.3%) 2/17 (11.8%)	Malakauskas et al. (2007)
Latvia	Vidzeme, Zemgale, Latgale, and Kurzeme	Raccoon dog (<i>N. procyonoides</i>) Red fox (<i>V. vulpes</i>)	Multiplex PCR & 5S rDNA PCR	28/35 (80%)	Franssen et al. (2014)
Latvia	Country-wide	Wild boar (<i>S. scrofa</i>) Red fox (<i>V. vulpes</i>) Eurasian lynx (<i>L. lynx</i>) Raccoon dog (<i>N. procyonoides</i>) Wolf (<i>C. lupus</i>) European pine marten (<i>M. martes</i>)	Multiplex PCR	73/3174 (2.3%) 51 43 43 35 1	Kirjusina et al. (2015)
Latvia	Country-wide	European beaver (<i>Castor fiber</i>)	Multiplex PCR	1/182 (0.5%)	Seglina et al. (2015)
Latvia	Country-wide	European badger (<i>M. meles</i>) European pine marten (<i>M. martes</i>) Stone/Beech marten (<i>M. foina</i>) Golden jackal (<i>C. aureus</i>) Wolf (<i>C. lupus</i>) Raccoon dog (<i>N. procyonoides</i>) Red fox (<i>V. vulpes</i>) Eurasian lynx (<i>L. lynx</i>) European pine marten (<i>M. martes</i>)	Multiplex PCR	2/2 61/137 (44.5%) 11/24 (45.8%) 3/4 22/23 (95.7%) 138/394 (35%) 273/668 (40.9%) 32/34 (94.1%) 5/13 (38.5%)	Deksne et al. (2016)
Latvia	Latgale region	European pine marten (<i>M. martes</i>)	Multiplex PCR	5/13 (38.5%)	Kirjusina et al. (2016)
Lithuania	Not specified	Wild boar (<i>S. scrofa</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Lithuania	Country-wide	Red fox (<i>V. vulpes</i>) Raccoon dog (<i>N. procyonoides</i>) Wild boar (<i>S. scrofa</i>) European pine marten (<i>M. martes</i>)	Multiplex PCR	132/567 (23.3%) 21/83 (25.3%) 35/9088 (0.4%) 3/15 (20%)	Malakauskas et al. (2007)
Netherlands	Border region, Veluwe region, and the coastal region	Red fox (<i>V. vulpes</i>)	RAPD-PCR	22/429 (5.1%)	(Van der Giessen et al., 1998; Van Der Giessen et al., 2001)
North Macedonia	Northern region	Wolf (<i>C. lupus</i>)	Multiplex PCR	1/8	Teodorovic et al. (2014)
Norway	Country-wide	Red fox (<i>V. vulpes</i>)	PCR	1/393 (0.3%)	Davidson et al. (2006)
Poland	Northeastern Poland	European pine marten (<i>M. martes</i>) European badger (<i>M. meles</i>)	Multiplex PCR	2/3 1/7	Moskwa et al. (2012)
Poland	Country-wide	Wild boar (<i>S. scrofa</i>)	Modified multiplex PCR	105	Bilska-Zajac et al. (2013)
Poland	Not specified	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	58	Bilska-Zajac et al. (2017)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	32/1634 (2%)	Chmurzynska et al. (2013)
Poland	Nowy Targ region	Red fox (<i>V. vulpes</i>)	Multiplex PCR	3/24 (12.5%)	Moskwa et al. (2013)
Poland	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	6/833 (0.7%)	Moskwa et al. (2015)
Poland	Bieszczady Mountains and Augustowska Forest	Wolf (<i>C. lupus</i>)	Multiplex PCR	12/21 (57.1%)	Bien et al. (2016)
Poland	West Pomeranian Province	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	16/16,737 (0.1%)	Bilska-Zajac et al. (2016)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	104/1447 (7.2%)	Cybulska et al. (2016)
Poland	Northeastern and northwestern Poland	American mink (<i>Neovison vison</i>)	Multiplex PCR	17/812 (2.1%)	Hurnikova et al. (2016)

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Table 12 (continued)

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Poland	North-eastern and Southern Poland	Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR	2/11 (18.2%)	Kolodziej-Sobocinska et al. (2018)
Poland	Głęboki Bród Forest District	Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	45/113 (39.8%)	Cybulska et al. (2019)
Poland	Country-wide	Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>)	Multiplex PCR	59/1740 (3.4%) 322/1389865 (0.02%)	Bilska-Zajac et al. (2020)
Poland	Głęboki Bród Forest District	European pine marten (<i>M. martes</i>)	Multiplex PCR	5/12 (41.7%)	Cybulska et al. (2020)
Portugal	Northern Portugal	Red fox (<i>V. vulpes</i>)	Multiplex PCR	5/36 (13.9%)	Lopes et al. (2015)
Portugal	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/47 (2.1%)	Vieira-Pinto et al. (2021)
Romania	Tulcea	Golden jackal (<i>C.aureus</i>)	Multiplex PCR	1/857 (0.1%)	Blaga et al. (2008)
Romania	Country-wide	European wild cat (<i>F. silvestris</i>) Eurasian lynx (<i>L. lynx</i>) Golden jackal (<i>C. aureus</i>) Red fox (<i>V. vulpes</i>) Wolf (<i>C.lupus</i>) Wild boar (<i>S. scrofa</i>)	Multiplex PCR	4/28 (14.3%) 3/5 1 4/71 (5.6%) 9/35 (25.7%) 3/5	Blaga et al. (2009)
Serbia	Belgrade, Podunavlje, Branicevo, Zlatibor, and Pirot	Red fox (<i>V. vulpes</i>) Wolf (<i>C. lupus</i>)	Multiplex PCR	2/4 4/4	Cvetkovic et al. (2011)
Romania	Country-wide	Stone/Beech marten (<i>M. foina</i>) Eurasian ermine (<i>Mustela erminea</i>)	Multiplex PCR & sequencing	2/4 2/3	Oltean et al. (2014)
Romania	Western Romania	Red fox (<i>V. vulpes</i>)	Multiplex PCR	24/121 (19.8%)	Imre et al. (2015)
Romania	Country-wide	Wild boar (<i>S. scrofa</i>) Brown bear (<i>U. arctos</i>)	Multiplex PCR	43/5596 (0.8%) 7/147 (4.8%)	Nicorescu et al. (2015)
Romania	Country-wide	European badger (<i>M. meles</i>)	Multiplex PCR	1/61 (1.6%)	Boros et al. (2020)
Romania	North-eastern Romania	Wild boar (<i>S. scrofa</i>) Brown bear (<i>U. arctos</i>)	Multiplex PCR	37/10,695 (0.3%) 9/68 (13.2%)	Iacob et al. (2022)
Romania	Western Romania	European pine marten (<i>M. martes</i>)	Multiplex PCR	1/12 (8.3%)	Marin et al. (2023a)
Romania	Ialomita County	Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	1	Marin et al. (2023b)
Serbia	Branicevo district	Red fox (<i>V. vulpes</i>) Wolf (<i>C. lupus</i>) Golden jackal (<i>C.aureus</i>) Wild boar (<i>S. scrofa</i>)	Multiplex PCR	3/57 (5.3%) 3/3 2/13 (15.4%) 1/94 (1.1%)	Zivojinovic et al. (2013)
Serbia	Country-wide	Wolf (<i>C. lupus</i>)	Multiplex PCR	52/105 (49.5%)	Teodorovic et al. (2014)
Serbia	Northern and Eastern Serbia	Golden jackal (<i>C. aureus</i>)	Multiplex PCR	26/738 (3.5%)	Cirovic et al. (2015)
Serbia	Zlatibor, Moravica, Raska, Rasina, Nisava, and Jablanica district	Red fox (<i>V. vulpes</i>) Golden jackal (<i>C.aureus</i>)	Multiplex PCR	11/37 (29.7%) 3/13 (23.1%)	Dmitric et al. (2017)
Serbia	Country-wide	Red fox (<i>V. vulpes</i>) European wild cat (<i>F. silvestris</i>) Stone/Beech marten (<i>M. foina</i>)	Multiplex PCR	2/296 (0.7%) 1/20 (5%) 1/103 (1%)	Klun et al. (2019)
Slovakia	Tatras National Park	Red fox (<i>V. vulpes</i>) Stone/Beech marten (<i>M. foina</i>) European pine marten (<i>M. martes</i>) European polecat (<i>Mustela putorius</i>) Brown bear (<i>U. arctos</i>)	Multiplex PCR	15/76 (19.7%) 2/5 1/3 1/3 1/1	Hurníková et al. (2007)
Slovakia	Country-wide	Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>)	Multiplex PCR	?/5270 ^d ?/70,568 ^e	Hurnikova and Dubinsky (2009)
Slovakia	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	391/4669 (8.4%)	Miterpáková et al. (2009)
Slovakia	Country-wide	Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>) Brown bear (<i>U. arctos</i>)	Multiplex PCR	155/2295 (6.8%) ^g 43/155,643 (0.03%) ^h 2/178 (1.1%) ^g	Antolova et al. (2020)
Spain	Not specified	Red fox (<i>V. vulpes</i>) Wolf (<i>C. lupus</i>)	Allozyme analysis	1 1	La Rosa et al. (1992)
Spain	Extremadura	Wild boar (<i>S. scrofa</i>)	RAPD-PCR	13/28,148 (0.05%)	Pozio et al. (1996)
Spain	Extremadura	Red fox (<i>V. vulpes</i>) Wild boar (<i>S. scrofa</i>)	RAPD-PCR	3/213 (1.4%) 22/29,333 (0.08%)	Perez-Martin et al. (2000)
Spain	Northwestern Spain	Red fox (<i>V. vulpes</i>) Wolf (<i>C. lupus</i>)	RAPD-PCR	4/227 (1.8%) 1/47 (2.1%)	Segovia et al. (2001)

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Table 12 (continued)

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Spain	Province of Cáceres	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	1	Rodriguez et al. (2008)
Spain	Castilla y León and La Rioja	Wild boar (<i>S. scrofa</i>) Wolf (<i>C. lupus</i>) Red fox (<i>V. vulpes</i>) European wild cat (<i>F. silvestris</i>)	ISSR-PCR	40/1278 (3.1%) 3 15/70 (21.4%) 1	Fonseca-Salamanca et al. (2009)
Spain	Northeastern Spain	Red fox (<i>V. vulpes</i>)	Not specified ^b	2/1319 (0.2%)	Lopez-Olvera et al. (2011)
Spain	Iberian peninsula	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	114/692,678 (0.02%)	Zamora et al. (2015)
Spain	Extremadura, Aragon, and Castile and León	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	8	La Rosa et al. (2018)
Spain	Northeastern Spain	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	3/33,206 (0.009%)	Díaz et al. (2021)
Sweden	Not specified	Red fox (<i>V. vulpes</i>)	Allozyme analysis	1	La Rosa et al. (1992)
Sweden	Stockholm, Västervik, Östersund, and Färgelanda	Red fox (<i>V. vulpes</i>) Wolf (<i>C. lupus</i>)	Multiplex PCR	4/1800 (0.2%) 1/7	Pozio et al. (2004a)
Switzerland	Country-wide	Red fox (<i>V. vulpes</i>)	RAPD-PCR	1/452 (0.2%)	Gottstein et al. (1997)
Switzerland	Country-wide	Red fox (<i>V. vulpes</i>) Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR	21/1289 (1.6%) 8/55 (14.5%)	Frey et al. (2009)
Switzerland	Schwyz, Graubünden, Fribourg, and Bern	Golden jackal (<i>C. aureus</i>)	Multiplex PCR	1/4	Frey et al. (2022)

^a Rat species not specified.

^b Number of animals positive for each genotype/species not reported.

^c *T. nativa* and *T. britovi* were genotyped but the number of positives for each species not reported.

^d The proportion of *T. britovi* amongst all animals tested was 6%, but the exact proportion per species was not reported.

^e Animals were skinned in the field by hunters, and were thus not defined by species.

^f 43 wild boar and 608 red fox were positive for *Trichinella* spp., 417 isolates were genotyped, 99% of which were *T. britovi*.

^g 220/2295 red fox, 65/155,643, and 3/178 brown bears were positive for *Trichinella* spp., 205/288 were genotyped, of which 93.9% were identified as *T. britovi*, but genotyped results were not reported by host species.

^h Larvae were genotyped but the method was not described.

loci to completely understand the taxonomy and transmission of *Trichinella* spp. in wildlife around the globe. Non-encapsulated species in particular appear to have the ability to utilize avian and reptile hosts, which are no doubt greatly underrepresented compared to mammalian studies of parasite diversity.

4.2. Methodological considerations

Currently the main method for isolation of larvae of *Trichinella* spp. is the double separatory funnel method, and the gold standard for molecular identification is the multiplex PCR (ESV, ITS-1, and ITS-2) (Forbes and Gajadhar, 1999; Zarlenga et al., 1999). The multiplex PCR requires limited training for laboratory staff familiar with molecular methods, and basic laboratory infrastructure, both of which have allowed for global adoption in developed countries. The multiplex PCR currently differentiates the most epidemiologically significant species/genotypes, but cannot differentiate T8 or T9 from *T. britovi*, or *T. nativa* from *T. chanchalensis*; however, ancillary PCR-RFLP's can be used to differentiate these species (Pozio and Zarlenga, 2019; Sharma et al., 2020). This review also highlighted the widespread adoption and dominance of the multiplex PCR for the last two decades, which has resulted in many more genotyped reports, especially in low-middle income countries. However, the over reliance on the multiplex PCR may have contributed to unrecognized diversity within the genus.

In low-middle income countries, infrastructure limitations result in ungenotyped reports of *Trichinella* spp., and in all countries, lack of formal surveillance in wildlife limits capacity to define fine scale host and geographic assemblages of *Trichinella* spp. Even in regions where testing of game meats (boar, walrus) for hunter/harvesters is supported, this requires government collaboration and a system for hunter/harvesters to submit tissues for testing.

4.3. Terrestrial and marine food webs in transmission of *Trichinella* spp.

The sylvatic *Trichinella* spp. are overwhelmingly found in terrestrial carnivores and omnivores, but in the circumpolar Arctic, *Trichinella* spp.

have also been found in several marine mammals, primarily polar bear and walrus, with a few reports in bearded seals (*Erignathus barbatus*), ringed seals (*Phoca hispida*), beluga (*Delphinopterus leucus*), and an orca whale (*Orcinus orca*) (Appleyard and Gajadhar, 2000; Forbes, 2000; Nunavut Department of Health, 2022). *Trichinella* spp. prevalence and intensity in seals and whales is typically quite low, which likely become infected through the infrequent consumption of infected carcasses (Forbes, 2000). Prevalence in polar bear and walrus is typically higher because they exhibit active predation, carrion feeding, and cannibalism (Forbes, 2000). While not fully elucidated, the marine cycle likely involves terrestrial to marine, marine to marine, and marine to terrestrial transmission.

4.4. Issues and knowledge gaps identified: Europe

In Europe, four species of *Trichinella* have been reported: *T. spiralis*, *T. nativa*, *T. britovi*, and *T. pseudospiralis*, many of which are sympatric. *Trichinella spiralis* and *T. britovi* have been responsible for the vast majority of wildlife and human cases from the consumption of wildlife (Tables 2 and 13). Thousands of human infections with *Trichinella* spp. have occurred in Europe in the last couple decades, but very few of these result in genotyped larvae (EFSA & ECDC, 2021; Lupse et al., 2023; Pozio, 2014). In Europe, the vast majority of human infections occur from the consumption of non-inspected domestic pigs, with wild boars being the most significant wildlife source of infection. Bulgaria, Croatia, Poland, Romania, and Spain have historically seen the most cases of trichinellosis in Europe (EFSA & ECDC, 2021; Pozio, 2014). Surveillance in many parts of Western Europe has been thoroughly conducted on wildlife, but there is still room for improvement in regards to genotyping and clear reporting of proportions of animals infected with each genotype, as mixed infections are very common. Additional studies in the British Isles, Eastern, and Southeastern Europe with comprehensive genotyping results would help fill the minor knowledge gaps that currently exist in these regions, and facilitate molecular epidemiological tracing in outbreaks which may well occur across multiple countries within the European trade zone.

Table 13
Human outbreaks of *Trichinella britovi* from consumption of wildlife in Europe (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Bosnia and Herzegovina	Bijeljina Municipality	1	Wild boar (<i>Sus scrofa</i>)	Undercooked	February 2013	Santrac et al. (2015)
Bulgaria	Smoljan District	9	Wild boar (<i>Sus scrofa</i>)	Not specified	June 1999	Kurdova et al. (2004)
	Smoljan District	6		Not specified	October 2001	
	Plovdiv District	6		Not specified	November 2001	
	Pazardjik District	66		Homemade flat Sausage	January 2002	
	Sofia District	17		Homemade flat Sausage	January 2002	
France	Alpes-Maritimes	6	Wild boar (<i>S. scrofa</i>)	Meat was cooked Medium-rare	October 2003	Gari-Toussaint et al. (2005)
France	Northern Alps	6	Wild boar (<i>S. scrofa</i>)	Salted hind leg	Mid-February 2022	Peju et al. (2023)
Italy	Abruzzo	23	Wild boar (<i>S. scrofa</i>)	Not specified	1995	Pozio et al. (2001b)
	Abruzzo	10			1996	
Italy	Southwestern Alps	1	Wild boar (<i>S. scrofa</i>)	Salami and sausages	December 2008	Romano et al. (2011)
Italy	Lucca province	32	Wild boar (<i>S. scrofa</i>)	Raw sausages ^a	2012	Fichi et al. (2015)
Italy	Southern Italy	5	Wild boar (<i>S. scrofa</i>)	Raw dried sausages	Feb/Mar 2016	Turiac et al. (2017)
Italy	Northwest Italy	45	Wild boar (<i>S. scrofa</i>)	Raw sausages	2020	Stroffolini et al. (2022)
Romania	Zaragoza	13	Wild boar (<i>S. scrofa</i>)	Sausage	2007	Perez-Perez et al. (2019)
Serbia	Zlatibor district	114	Wild boar (<i>S. scrofa</i>)	Ham and dried sausages	January 2016	Dmitric et al. (2018)
Serbia	Zlatibor district	111	Wild boar (<i>S. scrofa</i>)	Ham and sausages	January–February 2016	Pavic et al. (2020)
Spain	Province of Teruel	38	Wild boar (<i>S. scrofa</i>)	Not specified	February 1994	Rodriguez et al. (1995)
Spain	Granada	38	Wild boar (<i>S. scrofa</i>)	Sausage ^b	April–May 2000	Gomez-Garcia et al. (2003)
Spain	Aragon region	140	Wild boar (<i>S. scrofa</i>)	Sausage	December 1998	Rodriguez-Osorio et al. (2003)
Spain	Castile, León, Basque Country, and the Balearic Islands	21	Wild boar (<i>S. scrofa</i>) ^c	Sausage	January 2007	Gallardo et al. (2007)
Sweden	Not specified					

^a Sausages were 70/30 mix with wild boar meat and store bought pork subject to meat inspection.

^b Uninspected wild boar meat mixed with inspected pork from a domestic pig.

^c Animal was hunted in Spain. Spanish student returned to Sweden with boar sausages and seven additional people were exposed.

4.5. Issues and knowledge gaps identified: Asia and Oceania

In Asia and Oceania, six species/genotypes have been reported, *T. spiralis*, *T. nativa*, *T. britovi*, *T. pseudospiralis*, *Trichinella* T9, and *T. papuae*. Asia and Oceania are vast areas which make adequate surveillance, especially in wildlife, extremely challenging. Many studies in the region lack molecular identification, which causes a large gap in understanding what *Trichinella* spp. are present, in what animals, and where. In some regions, for example Russia, shifting dietary preferences and swine husbandry practices have led to an increase in the proportion of human outbreaks of trichinellosis associated with consumption of wildlife, which was implicated in more than half of outbreaks between 1998 and 2002 (Ozeretskovskaya et al., 2005). More than half of the global population lives in Asia and Oceania, and it is one of the least surveyed regions for *Trichinella*. While this obviously is a large knowledge gap, it also presents a massive opportunity for further research in the region to provide informed risk based assessments for public health, and for scientific pursuits to further elucidate the diversity of *Trichinella* spp. in the region.

4.6. Issues and knowledge gaps identified: the Americas

In the Americas, seven *Trichinella* species/genotypes (*T. spiralis*, *T. nativa*, *T. pseudospiralis*, *T. murrelli*, *Trichinella* T6, *T. patagoniensis*, and

T. chanchalensis) have been reported in wildlife (many in sympatry), along with human infection from consumption of infected wildlife with four of the seven (*T. spiralis*, *T. nativa*, *T. murrelli*, and genotype T6). Significant surveillance for *Trichinella* spp. in wildlife has occurred in Canada, Greenland, and the United States, and to a lesser extent Argentina and Chile; however, a large gap exists in the literature for Mexico, and most of central and South America, for which studies are needed to determine sero-prevalence in humans, *Trichinella* spp. diversity, and wildlife reservoirs. Black bear meat was the most common source of human infection in the Americas, but cougar, walrus, and wild boar meat were also implicated in trichinellosis outbreaks. The incidence of human infection in North America is much higher in the northern latitudes (>60 °N) than in the south, which could be attributed to the higher reliance on consumption of game meat in the North as well as the consumption of food prepared in traditional ways (raw, fermented, smoked, dried) that may be ineffective in inactivating the larvae. The incidence of human infections in northern Canada, particularly Nunavut and Nunavik (Northern Quebec), can be ~800x higher, 41.65 per million vs. 0.05 per million, than in the rest of Canada (Gilbert et al., 2010). The mean annual incidence in Alaska between 2008 and 2012 compared with the rest of the United States was 40x higher, 4.1 cases per million vs 0.1 per million (Wilson et al., 2015). There are no updated annual incidence rates of human trichinellosis in Canada or the US, where this condition is no longer notifiable to public health, but we

Table 14
Published reports of *Trichinella britovi* in wildlife in Asia (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Armenia	Artavan, Vayots Dzor	Fox (<i>Vulpes vulpes</i>)	Multiplex PCR	1/1	Grigoryan et al. (2020)
		Wolf (<i>Canis lupus campestris</i>)		1/1	
		Lynx (<i>Lynx lynx dinniki</i>)		1/1	
		Eurasian otter (<i>Lutra lutra</i>)		1/1	
		Wild boar (<i>Sus scrofa</i>)		1/1	
Iran	Ardabil Province (north western Iran)	Leopard (<i>Panthera pardus saxicolor</i>)	Multiplex PCR	1/1	Mowlavi et al. (2009)
Iran	Khuzestan Province (south-west Iran).	Golden jackal (<i>Canis aureus</i>)	PCR	2/18 (11.1%)	Mirjalali et al. (2014)
Iran	Mazandaran Province (Northern Iran)	Wild boar (<i>S. scrofa</i>)	PCR	2/35 (5.7%)	Rostami et al. (2017)
Iran	Northern Iran	Wild boar (<i>S. scrofa</i>)	PCR	3/79 (3.8%)	Rostami et al. (2018)
Iran	Khorasan-e-Razavi province (Northeastern Iran)	Golden jackal (<i>C. aureus</i>)	Multiplex PCR	1/12 (8.3%)	Shamsian et al. (2018)
Israel	Northern and Central Israel	Golden jackal (<i>C. aureus</i>)	Multiplex PCR, Extended PCR	?/45 ^a	Erster et al. (2016)
		Wild boar (<i>S. scrofa</i>)		?/280 ^a	
		Red fox (<i>V. vulpes</i>)		?/2 ^a	
		Wolf (<i>Canis lupus</i>)		?/1 ^a	
Kazakhstan	Not specified	Red fox (<i>V. vulpes</i>)	Allozyme analysis	1/1	La Rosa et al. (1992)
		Golden jackal (<i>C. aureus</i>)		2/2	
		European wild cat (<i>F. silvestris</i>)		1/1	
Kazakhstan	South Kazakhstan	Golden jackal (<i>C. aureus</i>)	Multiplex PCR	1/4 (25%)	Uakhit et al. (2023)
Turkey	Cankiri province	Wolf (<i>C. lupus</i>)	Multiplex PCR & Sanger sequencing	1/1	Erol et al. (2021)
Russia	Tvier and Smolensk regions	Wolf (<i>C. lupus</i>)	Multiplex PCR	1/82 (1.2%)	Pozio et al. (2001a)

^a 58 isolates (10 from wild boar, 45 golden jackals, 2 red foxes and 1 wolf) were genotyped, 11 isolates were identified as *T. spiralis*, but the proportion infected per host species was not specified.

Table 15
Published reports of *Trichinella britovi* in wildlife from the continent of Africa (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. britovi</i>	Reference
Republic of Guinea	Moyenne-Guinée	African civet (<i>Viverra civetta</i>)	Multiplex PCR	1/19 (5.3%)	Pozio et al. (2005b)
		African palm civet (<i>Nandinia binotata</i>)		2/45 (4.4%)	

can expect marked disparity in regional incidence because of differences in dietary norms.

4.7. Issues and knowledge gaps identified: Africa

On the African continent, five species/genotypes (*T. spiralis*, *T. britovi*, *Trichinella* T8, *T. nelsoni*, and *T. zimbabwensis*) are present, and all except for *T. spiralis* have been reported in wildlife. As with the Americas, some countries have greater surveillance effort than others, with South Africa being the most studied area to date for *Trichinella* spp. presence in wildlife. Consumption of game meat (bush meat) in Africa is a large industry; in sub-Saharan Africa, millions of tons of bushmeat, primarily wild mammals, are harvested annually (Kurpiers et al., 2016). This creates a tremendous gap in the literature as bush meat consumption is inextricably linked to food security for those populations (Nasi et al., 2011). Despite the large volume of bush meat consumed annually across the continent there has only been one genotyped report of a human infection from consumption of wildlife (golden jackal) occurring in Algeria (Nezri et al., 2006), however this publication was not in English and was not included in this review.

Surveillance studies are needed to determine the wildlife species involved in the circulation of *Trichinella* spp. in the diverse ecosystems of Africa. A substantial amount of reports of *Trichinella* spp. to date from Africa were not identified to a species level due to lack of equipment, infrastructure, human capacity, and competing priorities with other diseases/parasites among other factors. Without addressing these areas, it will be a challenge to achieve a comprehensive understanding of the diverse and complex sylvatic cycles of *Trichinella* spp. infecting wildlife in Africa and the subsequent public health risk.

4.8. Effects of climate change on ecology and transmission of *Trichinella* spp.

Trichinella species do not have an environmental or free-living stage, which is somewhat unusual compared with other nematodes. The ability of the larvae of encapsulating species to survive in the nurse cell in a frozen carcass or putrefying tissue has been described as the “free-living” or “pseudo free-living” stage for *Trichinella* spp. (Madsen, 1974; Pozio, 2022), which enables transmission through scavenging of carrion as well as predation (Pozio, 2022). The survival of the “free-living stage” (muscle dwelling larvae) is likely responsible for climate sensitivity of *Trichinella* spp. in the tissue of carcasses. For freeze-tolerant species (*T. nativa*, *T. britovi*, *Trichinella* T6, and *T. chanchalensis*), snow fall levels can influence subniveal (the area between the ground and the snowpack) temperatures, with ideal larva survival conditions of 0 °C to –20 °C compared to temperatures as low as –30 to –40 °C above the snowpack (Pozio, 2016a, 2022; Rossi et al., 2019). Effects of climate change on snow duration, density, and depth can therefore impact *Trichinella* spp. transmission, as seen in a Latvian study that found that more days of snow cover resulted in a higher incidence of *Trichinella* spp. in wild boars (Kirjusina et al., 2015; Pozio, 2022). In the Canadian North, warming can potentially limit extreme winter temperatures favouring *Trichinella* spp. transmission (Piffold et al., 2021). Climate change could potentially change geographic distributions of *Trichinella* spp. limited by thermic regions, such as northward expansion of freeze-susceptible species and a northward retreat of the freeze-tolerant

Table 16
Published reports of *Trichinella pseudospiralis* in wildlife in Europe (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. pseudospiralis</i>	Reference
Croatia	Country-wide	Wild boar (<i>Sus scrofa</i>)	Multiplex PCR	2/183,184 (0.001%)	Balic et al. (2020)
England	Near the village of Olveston	Red fox (<i>Vulpes vulpes</i>)	Multiplex PCR	1/6806 (0.01%)	Learnmount et al. (2015)
Estonia	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	6/30,566 (0.02%)	Kärssin et al. (2021)
Finland	Southern Finland	Raccoon dog (<i>Nyctereutes procyonoides</i>)	Multiplex PCR	4/199 (2%)	Oivanen et al. (2002)
		Brown rat (<i>Rattus norvegicus</i>)		1/29 (3%)	
Finland	Country-wide	Raccoon dog (<i>N. procyonoides</i>)	Multiplex PCR	3/662 (0.5%)	Airas et al. (2010)
		Red fox (<i>V. vulpes</i>)		1/1010 (0.1%)	
		Eurasian lynx (<i>Lynx lynx</i>)		3/402 (0.7%)	
Finland	Country-wide	Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR	1/1245 (0.08%)	Oksanen et al. (2018)
		Raccoon dog (<i>N. procyonoides</i>)		2/952 (0.2%)	
		Red fox (<i>V. vulpes</i>)		1/454 (0.2%)	
Germany	Usedom island	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/1	Nockler et al. (2006)
Germany	Baden-Württemberg, Berlin, Brandenburg, Hesse, Mecklenburg-Western Pomerania, and Thuringia states	Red fox (<i>V. vulpes</i>)	Multiplex PCR	2/3154 (0.06%)	Chmurzynska et al. (2013)
Germany	Brandenburg	Raccoon dog (<i>N. procyonoides</i>)	PCR	1/1527 (0.06%)	Mayer-Scholl et al. (2016)
Hungary	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/2116 (0.05%)	Szell et al. (2008)
Hungary	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/220,000 (0.0005%)	Szell et al. (2012)
Italy	Southern and Central Italy	Tawny owl (<i>Strix aluco</i>)	PCR	1/18 (5.5%)	Pozio et al. (1999a)
		Little owl (<i>Athene noctua</i>)		1/12 (8.3%)	
Italy	Emilia-Romagna region	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/1	Meriardi et al. (2011)
Italy	Basilicata region	Red kite (<i>Milvus milvus</i>)	Multiplex PCR	1/1	Marucci et al. (2021)
Italy	Abruzzi and Molise regions	Wolf (<i>Canis lupus</i>)	Multiplex PCR	1/350 (0.3%)	Ricchiuti et al. (2021)
Italy	Emilia-Romagna region	Western marsh harrier (<i>Circus aeruginosus</i>)	Multiplex PCR	1/9	Rugna et al. (2022)
Lithuania	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/567 (0.2%)	Malakauskas et al. (2007)
Poland	Nowy Targ region	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/24 (4.2%)	Moskwa et al. (2013)
Poland	West Pomeranian Province	Wild boar (<i>S. scrofa</i>)	Multiplex PCR & Sequencing	1/16,737 (0.006%)	Bilska-Zajac et al. (2016)
Poland	Country-wide	Red fox (<i>V. vulpes</i>)	Multiplex PCR	1/1447 (0.07%)	Cybulska et al. (2016)
Poland	Northern Poland	American mink (<i>Neovison vison</i>)	Multiplex PCR	1/812 (0.1%)	Hurnikova et al. (2016)
Poland	Western Poland	Raccoon (<i>Procyon lotor</i>)	Multiplex PCR & Sequencing	1/87 (1.1%)	Cybulska et al. (2018)
Poland	Country-wide	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	8/1389865 (0.0006%)	Bilska-Zajac et al. (2020)
Romania	Constanta County	Golden jackal (<i>Canis aureus</i>)	Multiplex PCR & Sanger sequencing	1/3	Marin et al. (2023c)
Slovakia	Eastern Slovakia	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/70,568 (0.001%)	Hurnikova and Dubinsky (2009)
		Red fox (<i>V. vulpes</i>)		1/5270 (0.02%)	
Slovakia	Eastern Slovakia	Golden eagle (<i>Aquila chrysaetos</i>)	Multiplex PCR	1/2	Hurnikova et al. (2021)
		Peregrine falcon (<i>Falco peregrinus</i>)		1/5	
		Common kestrel (<i>Falco tinnunculus</i>)		2/76 (2.6%)	
Slovakia	Budca, Žilina Region	Wild boar (<i>S. scrofa</i>)	Multiplex PCR	1/204,516 (0.0005%)	Antolova et al. (2020)
Spain	Iberian peninsula	Wild boar (<i>S. scrofa</i>)	Multiplex-PCR	1/155,643 (0.0006%)	Zamora et al. (2015)
		Wild boar (<i>S. scrofa</i>)		1/692,678 (0.0001%)	
Sweden	Frösö	Eurasian lynx (<i>L. lynx</i>)	Multiplex PCR & Sequencing	1/200 (0.5%)	Pozio et al. (2004a)
	Hölö	Wild boar (<i>S. scrofa</i>)		3/1800 (0.2%)	
Sweden	Southern Sweden	Tawny owl (<i>S. aluco</i>)	Multiplex PCR	2/38 (5.3%)	Hurníková et al. (2014)

Table 17
Human outbreaks of *Trichinella pseudospiralis* from consumption of wildlife in Europe (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (if specified)	Date of outbreak	Reference
France	Town of Miramas	4	Wild boar (<i>Sus scrofa</i>)	Undercooked barbecued meat	October 1999	Ranque et al. (2000)

Table 18
Published reports of *Trichinella pseudospiralis* in wildlife in Asia and Oceania (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. pseudospiralis</i>	Reference
Australia	Tasmania	Tiger quoll (<i>Dasyurus maculatus</i>)	Allozyme analysis	1/1	La Rosa et al. (1992)
Russia	Chukotka Peninsula	Ringed seal (<i>Pusa hispida</i>)	Multiplex PCR & ISSR-PCR	1/1	Goździk et al. (2017)

Table 19
Human outbreaks of *Trichinella pseudospiralis* from consumption of wildlife.

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Thailand	Ta Sae district of Chumphon Province	59	Wild pig	Raw	December 1994	Jongwutiwes et al. (1998)
New Zealand/ Australia ^a	Tasmania	1	Potentially wallaby (species not reported)	Not specified	1993	(Andrews et al., 1993, 1994, 1995)

^a Patient was diagnosed in home country of New Zealand, but infection may have occurred in Tasmania, Australia.

Table 20
Published reports of *Trichinella pseudospiralis* in wildlife in the Americas (1991–2023).

Country	Location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. pseudospiralis</i>	Reference
Canada	Vancouver Island	Cougar (<i>Puma concolor</i>)	Multiplex PCR	?/127 ^a	Gajadhar and Forbes (2010)
Canada	Northwest Territories	Wolverine (<i>Gulo</i>)	Multiplex PCR & Sanger sequencing	1/131 (0.8%)	Sharma et al. (2019)
United States	Alabama	Black vulture (<i>Coragyps atratus</i>)	Slot-blot analysis	1/1	Lindsay et al. (1995)
United States	Texas	Wild boar (<i>Sus scrofa</i>)	Multiplex PCR	1/1	Gamble et al. (2005)
United States	Florida	Florida panther (<i>Puma concolor coryi</i>)	Multiplex PCR	18/124 (14.5%)	Reichard et al. (2015)
United States	Colorado	Cougar (<i>P. concolor</i>)	Multiplex PCR	3/39 (7.7%)	Reichard et al. (2016)
United States	Oklahoma	Bobcat (<i>Lynx rufus</i>)	Multiplex PCR	1/306 (0.3%)	Reichard et al. (2021)

^a The exact proportion of animals infected with *T. pseudospiralis* was not reported.

Table 21
Published reports of *Trichinella murrelli* in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. murrelli</i>	Reference
Canada	British Columbia (Vancouver Island)	Cougar (<i>Puma concolor</i>)	Multiplex PCR	?/127 ^a	Gajadhar and Forbes (2010)
Canada	Southern Ontario	Red fox (<i>Vulpes vulpes</i>) Raccoon (<i>Procyon lotor</i>)	Multiplex PCR	1/1 1/1	(Scandrett et al., 2018; Scandrett unpublished)
United States	Illinois	Raccoon (<i>P. lotor</i>) Red fox (<i>V. vulpes</i>)	Slot blot, Southern blot, & allozyme analysis	5/323 (1.6%) 2/9	Snyder et al. (1993)
United States	Texas	Coyote (<i>Canis latrans</i>) Black bear (<i>Ursus americanus</i>)	Multiplex PCR	7/154 (4.5%) 1/9	Pozio et al. (2001c)
United States	Wisconsin	Raccoon (<i>P. lotor</i>) Coyote (<i>C. latrans</i>)	Multiplex PCR	11/59 (19%) 11/42 (26%)	Hill et al. (2008)
United States	Pennsylvania	Black bear (<i>U. americanus</i>)	Allozyme analysis	2/2	La Rosa et al. (1992)
United States	Oklahoma and North Texas	Coyote (<i>C. latrans</i>)	Multiplex PCR	4/77 (5.2%)	Reichard et al. (2011)
United States	Northern California	Black bear (<i>U. americanus</i>)	Multiplex PCR	1/1	Hall et al. (2012)
United States	Maryland	Black bear (<i>U. americanus</i>)	Multiplex PCR	2/389 (0.5%)	Dubey et al. (2013)
United States	Colorado	Cougar (<i>P. concolor</i>)	Multiplex PCR	5/39 (12.8%)	Reichard et al. (2016)
United States	California	Bear (<i>Ursus</i> spp.)	Multiplex qPCR	3/7 (42.9%)	Almeida et al. (2018)
United States	Oklahoma	Bobcat (<i>Lynx rufus</i>)	Multiplex PCR	17/306 (5.6%)	Reichard et al. (2021)

^a The exact proportion of animals infected with *T. murrelli* was not reported.

Table 22Human outbreaks of *Trichinella murrelli* from consumption of wildlife in the Americas (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
United States	Northern California	29	Black bear (<i>Ursus americanus</i>)	Raw/undercooked	October 2008	Hall et al. (2012)

Table 23Published reports of *Trichinella* T6 in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>Trichinella</i> T6	Reference
Canada	Nunavut	Wolverine (<i>Gulo gulo</i>)	Multiplex PCR	33/41 (80.5%)	Reichard et al. (2008)
Canada	Northwest Territories	Wolverine (<i>G. gulo</i>)	Multiplex PCR	Proportion positive not specified per location, host species, and genotype	Gajadhar and Forbes (2010)
	British Columbia	Cougar (<i>Puma concolor</i>), grizzly bear (<i>Ursus arctos</i>) & lynx (<i>Lynx canadensis</i>)			
	Nunavut	Lynx (<i>L. canadensis</i>)			
Canada	Northwest Territories	Black bear (<i>U. americanus</i>)	Multiplex PCR	2/120 (1.7%)	Larter et al. (2011)
		Grizzly bear (<i>U. arctos</i>)		7/11 (63.6%)	
		Wolf (<i>Canis lupus</i>)		5/27 (18.5%)	
Canada	Yukon	Wolverine (<i>G. gulo</i>)	Multiplex PCR	63/95 (66.3%)	Sharma et al. (2018)
Canada	Nunavut	Arctic fox (<i>Vulpes lagopus</i>)	Multiplex & PCR RFLP	1/91 (1.1%)	Owsiacki et al. (2020)
Canada	Northwest Territories & Yukon	Wolverine (<i>G. gulo</i>)	Multiplex PCR & PCR RFLP	6/42 (14.3%)	Sharma et al. (2020)
Canada	British Columbia & Alberta	Cougar (<i>P. concolor</i>)	Multiplex PCR & PCR RFLP	2/9	Sharma et al. (2020)
Canada	Yukon	Black bear (<i>U. americanus</i>)	Multiplex PCR	6/30 (20%)	Harms et al. (2021)
		Grizzly bear (<i>U. arctos</i>)		24/34 (71%)	
Canada	Yukon	Wolverine (<i>G. gulo</i>)	Multiplex PCR & PCR RFLP	231/262 (88%)	Sharma et al. (2021)
United States	Montana	Grizzly bear <i>U. arctos</i>)	Allozyme analysis	1/1	La Rosa et al. (1992)
		Wolverine (<i>G. gulo</i>)		1/1	
		Cougar (<i>P. concolor</i>)		1/1	
	Pennsylvania	Grey fox (<i>Urocyon cinereoargenteus</i>)		1/1	
United States	Idaho	Cougar (<i>P. concolor</i>)	PCR	1/1	Dworkin et al. (1996)
United States	Alaska	Wolf (<i>C. lupus</i>)	Multiplex PCR & Heteroduplex analysis	5/57 (8.8%)	La Rosa et al. (2003)
United States	Colorado	Cougar (<i>P. concolor</i>)	Multiplex PCR	1/39 (2.6%)	Reichard et al. (2016)
United States	Idaho	Cougar (<i>P. concolor</i>)	Multiplex qPCR	1/1	Almeida et al. (2018)
	California	Black bear (<i>U. americanus</i>) ^a		1/7	

^a From a sausage containing both black bear and deer meat.

Table 24Human outbreaks of *Trichinella* T6 from consumption of wildlife in the Americas (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
United States	Idaho	10	Cougar (<i>Puma concolor</i>)	Jerky	1996	Dworkin et al. (1996)
United States	Ohio	9	Black bear (<i>Ursus americanus</i>) (hunted in Ontario, Canada)	Undercooked ground meat and roast	1998	Nelson et al. (2003)

species (Pozio, 2016a). It is also possible that in the high Arctic, warming may cause conditions to become more favourable for the freeze-tolerant species; however, this is hampered by lack of data on thermal thresholds for all species of *Trichinella*, especially the more recently discovered species. High humidity is also necessary for larvae to survive long periods in carrion (Pozio, 2022) and therefore it is important to consider highly regional changes in precipitation, snowmelt, permafrost thaw, sea ice loss, and regional hydrology when predicting the net effects of climate change on transmission of *Trichinella* spp.

4.9. Challenges in managing sylvatic trichinellosis

Many recommendations made for controlling *Trichinella* spp. in

domestic cycles are simply impractical for wildlife. There is no formal meat inspection or testing in many regions for wildlife, nor can hunters easily destroy leftover portions of carcasses to prevent scavenging transmission. In the field and in some cultural contexts, fully cooking meat to an internal temperature of 165 °F (74 °C) prior to consumption may not be possible or desirable. For the circumpolar Inuit, game meat (country food) is of nutritional, cultural, and spiritual importance, often consumed in traditional ways such as raw, frozen, dried, or fermented, which may result in a higher risk of transmission of *Trichinella* spp. and zoonotic diseases in general (Campbell et al., 2022; Pufall et al., 2011). With the variable cuts and non-standard methods of preparing game meat such as cold smoking, hot smoking, fermenting, drying, among others, it is difficult to determine if meat is sufficiently cooked to

Table 25
Published reports of *Trichinella nelsoni* in wildlife from the continent of Africa (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. nelsoni</i>	Reference
Kenya	Not specified	Spotted hyena (<i>Crocuta crocuta</i>)	Allozyme analysis	1/1	La Rosa et al. (1992)
South Africa	Kruger National Park	Lion (<i>Panthera leo</i>)	Multiplex PCR & secondary PCR to differentiate <i>T. nelsoni</i> from T8	2/2	Marucci et al. (2009)
South Africa	Greater Kruger National Park	Leopard (<i>Panthera pardus</i>)	Multiplex PCR & Sanger sequencing	1/6	Mukaratirwa et al. (2017)
Tanzania	Not specified	Desert warthog (<i>Phacochoerus aethiopicus</i>)	Allozyme analysis	1/1	La Rosa et al. (1992)
Tanzania	Serengeti National park and surrounding area	Lion (<i>P. leo</i>)	PCR	3/3	Pozio et al. (1997)
		Spotted hyena (<i>C. crocuta</i>)		3/3	
		Striped hyena (<i>Hyena hyena</i>)		1/1	
		Leopard (<i>P. pardus</i>)		1/1	
		Cheetah (<i>Actinonyx jubatus</i>)		1/5	
		Serval (<i>Felis serval</i>)		1/1	
		Bat-eared fox (<i>Otocyon megalotis</i>)		1/6	
		Desert Warthog (<i>P. aethiopicus</i>)		1/1	

Table 26
Published reports of *Trichinella* T8 in wildlife from the continent of Africa (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. murrelli</i>	Reference
Namibia	Unknown	Spotted hyena (<i>Crocuta crocuta</i>)	?	1/1	(Pozio and Murrell, 2006; Pozio et al., 1994)
Namibia	Etosha National Park	Lion (<i>Panthera leo</i>)	RAPD-PCR	1	ITRC ^a
South Africa	Not specified	Lion (<i>P. leo</i>)	Allozyme analysis	1	La Rosa et al. (1992)
		Spotted hyena (<i>C. crocuta</i>)		1	
South Africa	Greater Kruger National Park	Lion (<i>P. leo</i>)	Multiplex PCR & secondary PCR to differentiate <i>T. nelsoni</i> from T8	2/4	Marucci et al. (2009)
South Africa	Greater Kruger National Park	Leopard (<i>Panthera pardus</i>)	Multiplex PCR & Sanger sequencing	1/6	Mukaratirwa et al. (2017)

^a International *Trichinella* Reference Centre.

Table 27
Published reports of *Trichinella* T9 in wildlife from Asia (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>Trichinella</i> T9	Reference
Japan	Not specified	Black bear (<i>Ursus thibetanus japonicus</i>)	PCR & PCR RFLP	1/1	Nagano et al. (1999)
		Raccoon dog (<i>Nyctereutes procyonoides viverrinus</i>)		1/1	
Japan	Sapporo, Hokkaido	Red fox (<i>Vulpes vulpus</i>)	PCR	1/2	Kanai et al. (2006)
Japan	Hokkaido	Red fox (<i>Vulpes vulpes japonica</i>)	Multiplex PCR & PCR	21/28 (75%)	Kanai et al. (2007)
		Brown bear (<i>Ursus arctos</i>)		4/28 (14.3%)	
		Raccoon dog (<i>N. procyonoides viverrinus</i>)		2/28 (7.1%)	
Japan	Hokkaido	Raccoon (<i>Procyon lotor</i>)	Multiplex PCR & PCR	5/648 (0.8%)	Kobayashi et al. (2011)
Japan	Iwate	Japanese black bear (<i>U. thibetanus japonicus</i>)	PCR	2/144 (1.4%)	Tominaga et al. (2021)
Japan	Hokkaido	Brown bear (<i>U. arctos</i>)	PCR	6/236 (2.5%)	Murakami et al. (2023)
	Aomori, Akita, and Iwate	Japanese black bear (<i>U. thibetanus japonicus</i>)		1/117 (0.9%)	

Table 28
Human outbreaks of *Trichinella* T9 from consumption of wildlife in Asia (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Japan	Mito	21	Brown bear (<i>Ursus arctos</i>)	Undercooked	2016	Tada et al. (2018)

inactivate *Trichinella* larvae. Wildlife tourism poses new risks, as evidenced by several international outbreaks where hunters from Europe becoming infected during hunting trips in North America and through importation of infected meat (Pozio, 2015), or pilots indulging in local

delicacies (such as polar bear in Greenland) (Dupouy-Camet et al., 2016).

Trichinella spp. in wildlife are an important One Health problem that requires multiple disciplines and stakeholders to come together for

Table 29
Published reports of *Trichinella papuae* in wildlife in Asia and Oceania (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>Trichinella T. papuae</i>	Reference
Australia	Torres Strait	Wild pig (<i>Sus scrofa</i>)	PCR	1/12 (8.3%)	Cuttell et al. (2012)
Papa New Guinea	Bula Plain	Wild pig (<i>S. scrofa</i>)	Sequencing	1/6	Pozio et al. (1999b)
Papua New Guinea	Country-wide	Saltwater crocodile (<i>Crocodylus porosus</i>)	PCR	16/72 (22.2%)	Pozio et al. (2004c)
Papua New Guinea	Lae, Morobe Bula Plain in the Bensbach river area and Kikori area	Saltwater crocodile (<i>C. porosus</i>) Wild pig (<i>S. scrofa</i> , considered to be hybrids between <i>Sus scrofa vittatus</i> and <i>Sus celebensis</i>)	PCR	47/160 (29.4%) 12/81 (14.8%)	Pozio et al. (2005a)

Table 30
Human outbreaks of *Trichinella papuae* from consumption of wildlife in Asia and Oceania (1991–2023).

Country	Location in Country	Number of humans infected (probable and confirmed)	Animal species implicated	How meat was prepared (If specified)	Date of outbreak	Reference
Cambodia	Chak Tav village, Mean Rith commune, Sandan District in Kampong Thom Province	33	Wild pig (<i>Sus scrofa</i>)	Raw	2017	Caron et al. (2020)
Thailand	Ban-rai district of Uthai Thani Province	28	Wild boar (<i>S. scrofa</i>)	Undercooked	2006	Khumjui et al. (2008)
Thailand	Uthai Thani Province	34	Wild boar (<i>S. scrofa</i>)	Undercooked	2006	Kusolsuk et al. (2010)
Thailand/ Malaysia ^a	Khon Kaen province	1	Wild boar (<i>S. scrofa</i>)	History of consuming raw boar meat	2005	(Chotmongkol et al., 2005; Intapan et al., 2011)

^a The patient was a Thai citizen who worked in Malaysia and consumed raw wild boar meat from Malaysia. The patient is believed to have been infected in Malaysia and diagnosed in Thailand.

Table 31
Published reports of *Trichinella zimbabwensis* in wildlife from the continent of Africa (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. zimbabwensis</i>	Reference
South Africa	Country-wide	Nile crocodile (<i>Crocodylus niloticus</i>)	Multiplex PCR	3/15 (20%)	La Grange et al. (2009)
South Africa	Kruger National Park	Lion (<i>Panthera leo</i>)	Multiplex PCR	1/1	La Grange et al. (2010)
South Africa	Kruger National Park	Nile crocodile (<i>C. niloticus</i>)	Not specified	11/16 (68.8%)	La Grange et al. (2013)
South Africa	Greater Kruger National Park	Lion (<i>P. leo</i>) Nile monitor lizard (<i>Varanus niloticus</i>) Spotted hyena (<i>Crocuta crocuta</i>) Leopard (<i>P. pardus</i>) Common genet (<i>Genetta genetta</i>)	Multiplex PCR & Sanger sequencing	3/13 (23.1%) 1/2 2/8 1/6 1/2	Mukaratirwa et al. (2017)
Zimbabwe	Country-wide	Nile monitor lizard (<i>V. niloticus</i>)	Multiplex PCR & Sequencing	1/28 (3.6%)	Pozio et al. (2007)

Table 32
Published reports of *Trichinella patagoniensis* in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. patagoniensis</i>	Reference
Argentina	Rio Negro Province	Cougar (<i>Puma concolor</i>)	Multiplex PCR & sequencing	1/1	Krivokapich et al. (2008)
Argentina	Santa Cruz and Catamarca Provinces	Cougar (<i>P. concolor</i>)	Multiplex PCR & sequencing	2/4	Krivokapich et al. (2012)

mitigation. Domestic species of *Trichinella* (*T. spiralis*) may be realistically eliminated from swine production through biosecurity and routine testing, but it is not possible (or desirable) to eradicate sylvatic strains from natural food webs involving wildlife. Indeed, *Trichinella* transmission is in many ways a positive indicator of intact trophic relationships within ecosystems. Therefore, human infection from consumption of game meat will always be possible, as the biomass of *Trichinella* spp. is greater in wild animals than in domestic animals (Pozio, 2014).

Unfortunately, this also means that sylvatic *Trichinella* spp. still can pose a risk to domestic swine production, especially in systems that involve free-range outdoor rearing (Murrell, 2016). There have been reported instances of spillover from wildlife into domestic swine and also spill-back from swine into wildlife; ecological manipulation and human encroachment have previously been responsible for the introduction of *T. spiralis* into wild animals (Murrell, 2001).

Table 33
Published reports of *Trichinella chanchalensis* in wildlife in the Americas (1991–2023).

Country	Sampling location in Country	Animal Host Species	Methodology	Proportion infected with <i>T. chanchalensis</i>	Reference
Canada	Northwest Territories and Yukon	Wolverine (<i>Gulo gulo</i>)	Multiplex PCR, PCR-RFLP, & Illumina MiSeq ^a	12/42 (28.6%)	Sharma et al. (2020)
Canada	Northwest Territories	American marten (<i>Martes americana</i>)	Illumina MiSeq & Multiplex PCR	1/1	Lobanov et al. (2023)

^a Only 1 isolate was run using whole genome sequencing on the Illumina MiSeq platform.

4.10. Current taxonomic status of *Trichinella* genotypes

The taxonomic status of *Trichinella* T6, T8, and T9 are yet to be fully elucidated. Many criteria are important for determining a new species: in particular, maintaining genetic isolation despite geographic sympatry (Britov, 1985). All three of the genotypes with unresolved taxonomic status share a geographic range with another species: T9 with *T. nativa* in Japan, T6 with *T. nativa* and *T. chanchalensis* in northern Canada, T6 with *T. spiralis* and *T. murrelli* in southern Canada and the USA, and finally T8 with *T. nelsoni* and *T. zimbabwensis* in Africa. Sharing of the same geographic range and co-infection within the same animal host raises the potential for hybridization, and indeed T8 and T9 have been experimentally interbred with *T. britovi*, and natural and experimental hybridization has been reported between T6 and *T. nativa* (La Rosa et al., 2003; Nagano et al., 1999; Pozio et al., 2009a). Wildlife studies (revealing natural hybridization) are critically needed to determine if the genotypes preferentially breed within their own lineages, and therefore meet criteria for species status.

5. Conclusion

This review provides an update on *Trichinella* species and genotypes reported in wildlife globally and associated human cases. The geographic distribution of *Trichinella* spp. is vast, reported on every continent (except Antarctica) and is capable of moving long distances along with natural movements of migratory wildlife, as well as human translocation of wildlife and their products. However, our understanding of host assemblages, geographic distribution, and diversity of *Trichinella* spp. are limited by the quality and comprehensiveness of surveillance conducted globally. This review highlights that many wildlife species are competent hosts for *Trichinella* spp., the majority being terrestrial mammals, but it is also imperative to recognize the importance of marine mammals in transmission of some encapsulated species of *Trichinella* and the importance of birds and reptiles in maintaining transmission of the non-encapsulated species. Understanding which animal species can be infected, which species are infected at high prevalence and intensity, and which species are important for human food security are important to create targeted and effective policy and advice to people most at risk, many of them vulnerable populations. The marine cycle of *Trichinella* has yet to be fully elucidated and neither has the role migratory birds may play in the transmission and possible range expansion of some species of *Trichinella*. There are still many regions, such as Latin America, most of Africa, and much of Asia that lack surveillance data on the prevalence and diversity of *Trichinella* spp. in wildlife. We encourage more wildlife surveillance, especially in these understudied regions, and molecular identification of larvae, which is increasingly accessible and powerful with new Next-generation sequencing approaches, and is key to determining spillover and spill-back between wild and domestic animal reservoirs (with concomitant trade significance). We also strongly encourage health care providers to genotype larvae from human muscle biopsies as well as suspected animal tissue whenever possible to enable molecular tracking and source attribution of outbreaks, as well as to reveal differences in zoonotic potential and pathogenicity among *Trichinella* species and genotypes.

6. Limitations

A systematized search strategy was not exclusively used for this review, which may have resulted in missed publications; conversely, many systematic reviews discard relevant publications due to narrow selection criteria, and our goal was to capture the state of the knowledge broadly. We did not capture reports of *Trichinella* infection in wildlife or humans prior to 1991, or ungenotyped reports, which under-represents true presence and prevalence in both wildlife and people. Geographic bias towards genotyped reports misses regions where the parasites are under-researched and underreported.

CRedit authorship contribution statement

Cody J. Malone: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Antti Oksanen:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Samson Mukaratirwa:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Rajnish Sharma:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Emily Jenkins:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors report no conflicts of interest.

Funding Acknowledgement

Authors C.J.M. and E.J. thankfully acknowledges the financial assistance provided by the Weston Family Foundation, One Health Against Pathogens (Natural Science and Engineering Research Council – NSERC-CREATE training grant), ArcticNet Network Centre for Excellence, Western College of Veterinary Medicine Wildlife Health Research Fund, and an NSERC Discovery grant. The author R.S. thankfully acknowledges the financial assistance provided by the National Agricultural Higher Education Project (IDP-NAHEP) of the Indian Council of Agricultural Research (ICAR) at Guru Angad Dev Veterinary and Animal Sciences University, India, to carry out the International Faculty Training program at the University of Saskatchewan, Canada.

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