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Review

TRICHINELLA AND TRICHINELLOSIS IN EUROPE

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Abstract

Background: Trichinellosis, the proper term for the human zoonotic disease is caused by nematodes of the genus *Trichinella*. These zoonotic parasites show a cosmopolitan distribution in all the continents but Antarctica. They circulate in nature by synanthropic-domestic and sylvatic cycles that are correlated with each other. Today, nine species and three genotypes are recognized in this genus, all of which infect mammals, including humans, while one species also infects birds, and two other species also infect reptiles.

Scope and Approach: To review the recent literature on these pathogens, which are unusual among the other nematodes in that the worm undergoes a complete developmental cycle, from larva to adult to larva, in the body of a single host, which has a profound influence on the epidemiology of trichinellosis as a zoonosis. When the cycle is complete, the muscles of the infected animal contain a reservoir of larvae capable of long-term survival. Humans and other hosts become infected by ingesting muscle tissues containing viable larvae.

Key Findings and Conclusions: The main source of human infection is raw or under-cooked meat products from pig, wild boar, bear, walrus, and horses, but meat products from other animals have been implicated. Both pre-slaughter prevention and post-slaughter control can be used to prevent *Trichinella* infections in animals. The first involves pig management control in high containment level farms as well as continuous surveillance programs. Meat inspection is a successful post-slaughter strategy. However, continuous consumer education is of great importance in countries where meat inspection is not mandatory.

Keywords: *Trichinella*, Epidemiology, Europe, Zoonosis, Prevention, Control

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INTRODUCTION

Trichinella spp. are nematode parasites which can only be transmitted through the foodborne route in carnivores, omnivores and scavengers (Gottstein et al., 2009). Vertical transmission was experimentally demonstrated in ferrets, guinea pigs, and mice, but not in foxes or pigs (Webster and Kapel, 2005). These pathogens show a cosmopolitan distribution in all the continents but Antarctica (Pozio and Zarlenga, 2013). Human trichinellosis has been documented in 55 (27.8%) countries around the world. In several of these countries, however, trichinellosis affects only ethnic minorities and sometimes tourists, because the native inhabitants do not consume uncooked meat or meat of some animal species. *Trichinella* spp. infection has been documented in domestic animals (mainly pigs) and in wildlife of 43 (21.9%) and 66 (33.3%) countries, respectively. Of the 198 countries of the world, approximately 40 (20%) are small islands far from the major continents, or are city-states where *Trichinella* spp. cannot circulate among animals for lack of local fauna (both domestic and wild). Finally, information on the occurrence of *Trichinella* spp. infection in domestic animals and/or wildlife is still lacking for 92 countries (Pozio, 2007).

Today, twelve taxa separated in two clades are recognized in this genus (Korhonen et al., 2016). One clade encompasses six species and three genotypes that encapsulate in host muscle tissues following muscle cell reprogramming, and the second clade encompasses three species that do not encapsulate (Pozio and Zarlenga, 2013). The six species (*T. spiralis*, *T. nativa*, *T. britovi*, *T. murrelli*, *T. nelsoni* and *T. patagoniensis*) and three genotypes (*Trichinella* T6, T8 and T9) of the first clade parasitize only mammals. Among the three species that comprise the second clade, one infects mammals and birds (*T. pseudospiralis*) and two parasitize mammals and reptiles (*T. papuae* and *T. zimbabwensis*) (Pozio and Zarlenga, 2013).

Trichinellosis, the proper term for the human zoonotic disease also known as trichinosis or trichiniasis, is caused in humans by *Trichinella* nematodes (Dupouy-Camet et al., 2002). Since infected animals do not show any clinical sign of the disease, it follows that the name of the disease, trichinellosis, can be used only for humans. For animals, the term '*Trichinella* infection' must be used. This zoonosis has had a long and eventful history of scientific investigation and discovery (Campbell, 1983).

The unraveling of the nature of trichinellosis may reach back to antiquity as suggested by historical references to diseases that bear striking similarities to clinical aspects of *Trichinella* infection. The earliest such case involved a young Egyptian living along the Nile about 1200 B.C. (Gould, 1970; Campbell, 1983). There is evidence of human infections even in prehistoric cultures (Owen et al., 2005). The modern history of trichinellosis, however, begins in 1835, with the discovery by microscopy of the larval stage of the parasite by James Paget and Richard Owen in London.

The epidemiological view of trichinellosis has, because of these new biological revelations, expanded from a primarily domestic cycle source to an increasingly sylvatic one. While the zoonosis is continuing to be brought under control in some regions (e.g., Europe and North America), its potential for rebounding, due to laxity in veterinary control, is great because of the parasite's ability to exploit new opportunities for transmission presented by changes in demography, agriculture and wildlife habitat (Djordevic et al., 2003; Pozio, 2014). The aims of this review are to describe these scientific advances and their practical impact on the control of these nematodes in domesticated and wild animals and humans.

Trichinella species circulating in Europe

Trichinella spiralis (Owen, 1835)

This was the first species discovered and has been the best characterized due to its importance as a cause of human disease and as a model for basic biological research investigations. This was due in large part to the relatively high prevalence of *T. spiralis* in domestic and sylvatic animals and to its high infectivity for laboratory animals. This species shows the highest infectivity and the longest survival time (more than three years; Pozio E., unpublished data) of larvae in muscles of domestic and wild swine, compared to the other species of the genus *Trichinella* (Pozio and Murrell, 2006). For these reasons, *T. spiralis* is the main etiological agent of trichinellosis in humans in Europe and worldwide (Murrell and Pozio, 2011). This species, originating in East Asia, was introduced to Europe by trade probably at the beginning of the second millennium; then it was spread into the American continent, New Zealand and Hawaii, during European colonization (Pozio and Zarlenga, 2013). Today, the distribution of *T. spiralis* is mainly linked to regions with high vocation for backyard and free-ranging pigs, generally corresponding to less developed regions (Figure 1)

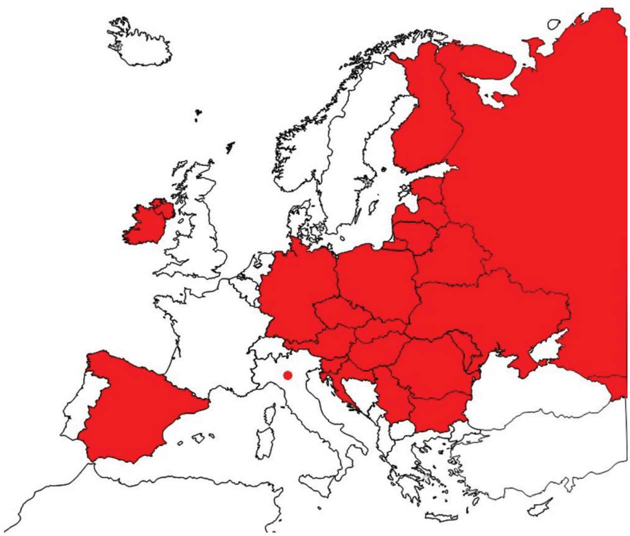

Figure 1. Distribution of *Trichinella spiralis* in Europe (red indicates countries with *Trichinella spiralis* in animals)

(Pozio, 2014). *T. spiralis* also circulates in wild animals, both omnivores and carnivores, which play important roles as reservoirs. Out of 2,810 isolates of *T. spiralis* from Europe, identified at the International *Trichinella* Reference Center (ITRC), Rome, Italy (https://trichinella.iss.it/), about 91% (2,553) originated from domestic pigs or wild boars, whereas, only 9% originate from carnivores (Table 1).

Table 1. *Trichinella* species detected in European animals and humans by host and country of origin, according to the database of the International Trichinella Reference Center, Rome, Italy (https://trichinella.iss.it/Trichinella).

Trichinella sp.	**Host**	**European Country**	**No. of isolates**
T. spiralis			2810
	Badger	Czech Rep.	1
	Black rat	Bulgaria	2
	Brown bear	Romania	18
	Brown rat	Bulgaria, Croatia, Finland, Hungary, Romania	31
	Domestic cat	Finland	2
	Domestic horse	Poland, Romania, Serbia	12
	Domestic pig	Bosnia-Herzegovina, Bulgaria, Croatia, Estonia, Finland, Germany, Hungary, Ireland[a], Lithuania, Poland, Romania, Russia, Serbia, Spain, Sweden	1044
	Field mouse	Bulgaria	2
	Golden jackal	Croatia, Hungary, Serbia	20
	Lynx	Estonia, Finland	8
	Man	France[b], Italy[b], Poland	3
	Raccoon dog	Finland, Germany, Poland	22
	Red fox	Croatia, Czech Republic, France[a], Germany, Hungary, Ireland, Italy, Poland, Romania, Slovakia, Serbia, Slovakia, Slovenia, Spain, Sweden, United Kingdom (North Ireland)	121
	Stray dog	Croatia, Serbia, Spain	7
	Wild boar	Austria, Bulgaria, Croatia, Czech Republic, Estonia, Finland, France[a], Germany, Hungary, Lithuania, Netherlands, Poland, Romania, Serbia, Spain, Sweden	1509
	Wild cat	Serbia	3
	Wolf	Germany, Serbia, Spain	5
T. nativa			1287
	Arctic fox	Norway	13
	Badger	Estonia, Finland	6
	Brown bear	Estonia, Finland, Sweden	29
	Lynx	Estonia, Finland, Latvia, Sweden	565
	Pine marten	Finland	7
	Polar bear	Iceland, Norway	6
	Raccoon dog	Estonia, Finland, Sweden	366
	Red fox	Estonia, Finland, Germany, Latvia, Norway, Poland, Sweden, Ukraine	147
	River otter	Finland	1
	Wild boar	Estonia, Finland, Latvia, Lithuania	8
	Wolf	Estonia, Finland, Latvia, Russia, Sweden	131

cont. Table 1.

	Wolverine	Finland, Sweden	8
T. britovi			2900
	Badger	Bulgaria, Czech Rep., Germany, Italy,	10
	Black rat	Bulgaria, Italy	2
	Brown bear	Bulgaria, Estonia, Italy, Romania, Slovakia, Slovenia	61
	Brown rat	Estonia, Italy, Romania	7
	Domestic cat	Italy, Latvia	4
	Domestic dog	France, Latvia, Romania, Russia, Slovakia	5
	Domestic horse	Poland	1
	Domestic pig	Bulgaria, Estonia, France, Greece, Italy, Latvia, Lithuania, Poland, Republic of North Macedonia, Romania, Serbia, Spain, Ukraine	279
	European beaver	Latvia	1
	Golden jackal	Bulgaria, Hungary, Latvia, Romania, Serbia,	18
	Lynx	Estonia, Finland, Latvia, Romania, Sweden, Switzerland	158
	Man	France, Greece, Italy	5
	Pine marten	Latvia, Ukraine	2
	Raccoon dog	Estonia, Finland, Germany, Latvia	103
	Red fox	Austria, Bulgaria, Croatia, Czech Rep., Estonia, Finland, France, Germany, Greece, Hungary, Italy, Latvia, Lithuania, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine,	810
	Stone marten	Italy	6
	Stray dog	Italy, Romania	6
	Wild boar	Belarus, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Rep., Estonia, France, Germany, Hungary, Italy, Latvia, Lithuania, Poland, Portugal, Romania, Serbia, Slovakia, Spain, Sweden,	1177
	Wild cat	Bulgaria, Italy, Romania	8
	Wolf	Bulgaria, Estonia, Finland, France, Germany, Italy, Latvia, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Ukraine	237
T. pseudospiralis			90
	American mink	Denmark	1
	Badger	Bulgaria	1
	Brown rat	Finland, Slovakia	2
	Domestic cat	Slovakia	1
	Domestic pig	Bosnia-Herzegovina, Croatia, Romania, Slovakia, Spain	8
	Lynx	Finland, Sweden	7
	Raccoon	Russia	1
	Raccoon dog	Finland, Germany, Russia	15
	Red fox	Bulgaria, Czech Rep., Finland, Germany Hungary, Italy, United Kingdom	7
	Wild boar	Bulgaria, Croatia, Czech Rep., Estonia, France, Germany, Hungary, Italy, Netherland, Poland, Sweden,	47

[a] *Trichinella* isolates collected before 1960; [b] imported from North America or Eastern Europe.

Trichinella nativa Britov and Boev, 1972

This species parasitizes prevalently wild carnivores present in arctic and subarctic regions of Asia, Europe and North America. In Europe, *T. nativa* has been detected in wild carnivores of the Scandinavian peninsula, Russia, Estonia, Latvia, Lithuania, Belorussia, Ukraine and in isolated foci in Poland and Germany (Figure 2). The southern distribution boundary has been identified between the isotherms -5 °C to -4 °C in January (Pozio and Murrell, 2006). This species does not infect swine; however, sometimes, *T. nativa*-infected wild boars were detected in Estonia, Latvia and Lithuania, suggesting that starvation, infections and stress can reduce the immunity of this species favoring the development of *T. nativa*. In Europe in the last twenty years, human infections caused by this species were documented only in persons who consumed uncooked bear meat imported from North America or consumed bear meat in North America and developed the disease when they come back to Europe (Ancelle et al., 2005; Dupouy-Camet et al., 2017). Out of 1,287 isolates of *T. nativa* from Europe identified at the ITRC, only 8 (0.6%) originated from wild boars, whereas, 99.4% originate from wild carnivores (Table 1). The main biological feature of *T. nativa* is the high resistance of larvae to freezing in carnivore muscles (up to 5 years) (Pozio and Murrell, 2006).

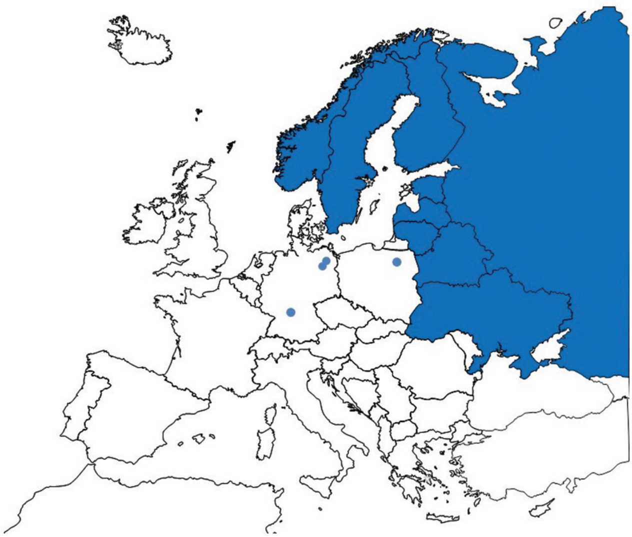

Figure 2. Distribution of *Trichinella nativa* in Europe (blue indicates countries with *Trichinella nativa* in animals)

Trichinella britovi Pozio et al., 1992

This species predominantly parasitizes wild carnivores of the entire European continent, Western Asia and North-Western Africa, excluding some islands (e.g., Great Britain and Ireland) and the far north of Europe (Figure 3). The northern geographic boundary appears to be determined by the isotherms -6 °C to -5 °C in January. In the

Palearctic region, this species is sympatric with *T. nativa* between the isotherms -4 °C and -6 °C (Pozio and Murrell, 2006), and there are many reports of mixed infections in the same host from Estonia, Finland, Latvia, Lithuania and Sweden. *T. britovi* larvae survive less than one year in swine muscles, whereas circulating IgG can be detected in swine sera for up to two years (Pozio E., unpublished data). The short survival time of *T. britovi* in swine explains why muscle larvae of this species are detected in a low percentage of wild boar, e.g., 0.02% in Italy and 2.5% in Latvia, even if the prevalence in wild carnivores can be up to 50% (Gómez-Morales et al., 2014; Kirjušina et al., 2015; Deksne et al., 2016). Out of 2,900 isolates of *T. britovi* from Europe identified at the ITRC, about 50% (1,456) originated from domestic pigs (279) or wild boars (1,177), and the other 50% originate from wild carnivores (Table 1) (Pozio et al., 2009). Muscle larvae of *T. britovi* survive in frozen swine muscles up to three weeks and up to 11 months in fox muscles (Pozio et al., 2006).

Figure 3. Distribution of *Trichinella britovi* in Europe (green indicates countries with *Trichinella britovi* in animals)

Trichinella pseudospiralis Garkavi, 1972

This species belonging to the non-encapsulating clade of the genus *Trichinella* is the only one infecting both mammals and birds (Pozio and Murrell, 2006). In Europe, *T. pseudospiralis* has been detected in almost all the countries (Figure 4) (Pozio, 2016a). However, since its prevalence in animals known to be reservoir hosts of encapsulated species is very low, the lack of reports of *T. pseudospiralis* in any one country could be purely coincidental. Since the number of mammals tested for *Trichinella* spp. by digestion was much higher than that of birds, the role played by birds in the epidemiology of *T. pseudospiralis* still needs to be elaborated in more detail. *T. pseudospiralis* larvae survive less than six months in swine muscles, whereas circulating IgG can be detected in swine sera for up to one year (Pozio E., unpublished data). In Europe, two outbreaks of human trichinellosis caused by *T. pseudospiralis* were documented in France in 2000 and in Italy in 2015 (Ranque et al., 2000; Gómez-Morales et al., 2015). Out of 90 isolates of *T. pseudospiralis* from Europe identified at the ITRC, about 61% (55) originated from domestic pigs or wild boars, and 39% originated from carnivores (Table 1).

Figure 4. Distribution of *Trichinella pseudospiralis* in Europe (yellow indicates countries with *Trichinella pseudospiralis* in animals)

Mixed infections

According to the ITRC database, of 7,296 *Trichinella* isolates identified so far, 209 (2.86%) mixed infections were detected in Europe. The most common mixed infection was *T. spiralis*/*T. britovi*, detected in 100 animals. *T. nativa*/*T. britovi* mixed infection was detected in 83 animals; *T. spiralis*/*T. nativa* in 10 animals; *T. spiralis*/*T. pseudospiralis* in 6 animals; *T. nativa*/*T. pseudospiralis* in 5 animals; *T. britovi*/*T. pseudospiralis* in 4 animals; and a triple infection *T. spiralis*/*T. nativa*/*T. britovi* in 1 animal (ITRC, https://trichinella.iss.it/).

Non-European *Trichinella* taxa detected in Europe

Of the eight *Trichinella* taxa not present in Europe (Pozio and Zarlenga, 2013; Korhonen et al., 2016), *T. murrelli* circulating among wild carnivores of North America, was the only species imported from the USA (Connecticut) into Europe (France) by a horse carcass in 1985, where it was the source of infection for 431 patients, two of whom died (Ancelle et al., 1988; Pozio, 2015).

Trichinella hosts

Three classes of vertebrates are known to act as hosts; mammals, birds and reptiles. Mammals are the most important hosts and all *Trichinella* species are able to develop in this vertebrate class. Natural infections with *Trichinella* have been described in more than 150 mammalian species belonging to 12 orders (i.e., Marsupialia, Insectivora, Edentata, Chiroptera, Lagomorpha, Rodentia, Cetacea, Carnivora, Perissodactyla, Artiodactyla, Tylopoda and Primates) (Pozio, 2005). The epidemiology of the infection greatly varies by species relative to characteristics, such as diet, life span, distribution, behavior, and relationships with humans. As reported above, the non-encapsulated species *T. pseudospiralis* is the only species of this genus infecting both mammals and birds. Two additional non-encapsulated species, *Trichinella papuae*, detected in wild pigs and saltwater crocodiles of Papua New Guinea, and *Trichinella zimbabwensis*, detected in farmed Nile crocodiles of Zimbabwe, can complete their life cycle in both mammals and reptiles. To the best of our knowledge, *T. papuae* and *T. zimbabwensis* are the only two parasites known to complete their entire life cycle independently of whether the host is warm-blooded or cold-blooded. This suggests that these two *Trichinella* species are capable of activating different physiological mechanisms, according to the specific vertebrate class hosting them (Pozio, 2005).

Epidemiology

Trichinella infection in humans

Humans acquire *Trichinella* infections by the consumption of raw meat or meat-derived products from domestic (pigs, dogs and horses) or wild (armadillo, badger, black bear, brown bear, polar bear, cougar, fox, horse, jackal, walrus, warthog, wild boar) animals (Murrell and Pozio, 2011). Most infections are caused by pork, followed by wild boar meat and derived products thereof. Soft-shelled turtles were suspected as source of *T. papuae* infections in humans in Eastern Asia (Lo et al., 2009; Lee et al., 2013; Jeong et al., 2015) and Nile crocodile meat in Zimbabwe (Mukaratirwa S., personal communication).

At the global level from 1986 through 2009, there were 65,818 cases and 42 deaths reported from 41 countries (Murrell and Pozio, 2011). Europe accounted for 86% of cases (56,912), of which 28,564 (50%) occurred in Romania, mainly during 1990-1999. Today, trichinellosis (formerly trichinosis) is a rare but serious human disease that is still present in the European Union. In the last 20 years, almost half of the European Union countries did not have any documented trichinellosis infections including Cyprus, Luxembourg, Malta and Portugal that have never reported any cases. In the last 16 years (2002-2017), 5,518 cases (range 101 in 2016 to 867 in 2007) of trichinellosis were documented in the European Union with a decreasing trend (EFSA, 2007, 2013, 2018).

The majority of human cases were reported from a few European countries mainly in Eastern Europe and were domestically-acquired. The trend of the occurrence of trichinellosis is greatly affected by the number and size of disease outbreaks. The number of cases and the European Union notification rate has, however, been steadily decreasing in recent years (EFSA, 2018). The decrease was mainly due to a markedly reduced number of trichinellosis cases reported over the same period from Bulgaria and Romania, which had experienced the majority of *Trichinella* outbreaks in previous years. The main reason for this reduction was the increased number of pigs raised under controlled housing conditions and the reduced number of pigs not raised under controlled housing conditions, farmer's education, and increased control at slaughter of pigs not raised under controlled housing conditions. These measures strongly reduced the parasite biomass in the domestic habitat and consequently the risk for humans to acquire the infection. Even though the numbers are reduced, Bulgaria and Romania still reported more than half of the confirmed cases and outbreaks in 2017. The recurring peak in trichinellosis cases in January and February reflects the consumption of various pork products during Christmas as well as the wild boar hunting season. On average, one-third of the confirmed human trichinellosis cases were hospitalized with no fatal outcomes.

***Trichinella* in domestic pigs**

When humans fail to properly manage domestic pigs and wildlife, *Trichinella* spp., particularly *T. spiralis*, are transmitted from the sylvatic to the domestic environment, triggering the onset of the domestic cycle. This cycle occurs where there are high-risk farming practices, such as the intentional feeding of food waste, which can contain pork scraps, or unintentionally through exposure to carcasses of dead swine or infected wildlife; unsecured, free-range pasturing is typically to blame (Pozio and Murrell, 2006). Farming practices at risk for *Trichinella* spp. transmission occur, in general, in disadvantaged and poor areas where veterinary services do not exist or are unable to control the myriad of small pig units. The domestic transmission cycle also includes pigs being allowed to scavenge in garbage dumps, feeding of pigs on wild game carcasses or scraps from hunting, and using carcasses of slaughtered fur animals as feed. The intersection of hunters, the manner in which they deal with wild game carcasses, and free-ranging and/or backyard pig farming practices combine to perpetuate infection with *Trichinella* spp. (Pozio, 2014).

Trichinella infection has been never documented in pigs raised under high containment levels, and the risk of infection is mainly related to the lack of compliance with rules on the treatment of animal waste. Pigs raised outdoors are at risk of contact with potentially *Trichinella*-infected wildlife (Pozio, 2014). In recent decades in countries of the European Union, investigations carried out to identify the source of *Trichinella* infections in domestic pigs identified direct (free-ranging pigs) or indirect (e.g. farmers who were also hunters) contacts with wild animals, which are reservoirs of these zoonotic nematodes (Pozio, 2014).

The international pig trade is one of the largest livestock markets in the world (Pozio, 2014). However, in the last 20 years, there have been only eight documented reports of pig meat illegally imported in personal baggage into another country where it was the source of trichinellosis in humans or it was, by chance, tested for *Trichinella* sp. larvae (Pozio, 2015). *Trichinella* sp. infected pigs have originated from countries where its prevalence was quite high in the pig population not reared under controlled management conditions at that time (Marinculić et al., 2001; Olteanu, 2001; Cuperlovic et al., 2005; Sofronic-Milosavljevic et al., 2013). There is no report on the detection of *Trichinella* sp. infected pigs originating from the international pig trade (Pozio, 2015).

In European Union countries, most pigs are subject to official meat inspection at slaughter in accordance with Regulation (EC) No 2015/1375 (European Union, 2015); only pigs slaughtered for a farmer's own home consumption are not covered by the regulation. A total of 186 million pigs were tested for *Trichinella* in 2014, out of about 246 million reared pigs in the European Union (Marquer et al., 2014), with only 184 positive animals, i.e. 0.7 per million reared pigs.

After a peak at the beginning of the nineties of *Trichinella* infections in European domestic pigs and consequently also in wild animals, which fed on pork scraps and offal dispersed by humans in the environment, the prevalence was strongly reduced in the pig population, all originating from uncontrolled housing conditions, and has reached a plateau. The prevalence is an underestimation, since an amount of free-ranging and backyard pigs from remote areas of the European Union are not controlled by veterinary services. There is a vicious cycle between uneducated and low income people, remote areas, inadequacy of local veterinary services and the occurrence of *Trichinella* in domestic animals. The distribution of the pig population by size of the pig herds is a key factor indicating the circulation of *Trichinella* parasites among pigs. For example, in the European Union, the distribution of the pig population by size of the pig herds showed that 1.5% of pig farms have at least 400 fattening pigs and manage 75.7% of the pigs in the area (120 million animals) (Marquer, 2010; Eurostat, 2016). These figures conceal national differences; for example, only 21.6% of fattening pigs in Poland are kept under controlled conditions on farms as compared with 90% or more in nine other EU countries. However, pigs kept in units of less than 10 animals constitute a consistent part of the pig population in Bulgaria (34.8%), Lithuania (31.9%), and Romania (66.2%). These small units manage 5.3% of fattening pigs (approximately 8.5 million animals), but account for 85.8% of the pig farms (Marquer, 2010; Eurostat, 2016). In fact, the higher the number of small pig herds in a country, the higher the prevalence risk of *Trichinella* infections in pigs (Pozio, 2014). Furthermore, most of the *Trichinella* infections are in domestic pigs meant for the farmer's own home consumption, so these pigs at higher risk for this infection are not registered.

Trichinella in horses

From 1975 to 2005, when the first and the last outbreaks of trichinellosis caused by horse meat consumption were documented, 15 human outbreaks of trichinellosis have been documented in France (eight outbreaks, 2296 human infections with five deaths in 1985) and Italy (seven outbreaks, 1038 human infections) resulting from the consumption of horsemeat imported from Eastern European countries (Former Yugoslavia, Poland, Serbia, Romania) or from North America (Pozio, 2015). Between 1988 and 2008, *Trichinella* larvae (mostly *T. spiralis*) were detected in 12 horses imported to France and Italy from Eastern European countries (Poland, Romania, Serbia, Former Yugoslavia) out of about 250,000 tested horses per year (Pozio, 2015). Since 2006 in the European Union, it is mandatory to test fresh horsemeat produced in or imported to the EU according to the Commission Regulation 2075/2005 (European Union, 2005). In the last decade, only four horses tested positive in the EU (in 2008, 2010 and 2012) out of more than one million tested animals. In 2012, *T. murrelli* larvae were detected in a horse imported from the USA and slaughtered in Canada (Scandrett et al., 2018). This extremely low (<0.001%) prevalence could be related to the strong reduction of *Trichinella* infections in domestic pigs, since pig scraps and offal were the main source of infection for horses (Pozio, 2015).

Trichinella in wild animals

Wild mammals serve as the major reservoir hosts, and the role of wildlife is underscored by the biomass of the parasites, which is greater in wild than in domestic animals, unlike other nematode infections that involve both sylvatic and domestic animals (Pozio and Murrell, 2006). These zoonotic parasites circulate among wild animals in large parts of Europe, and only Cyprus, Luxembourg and Malta have never reported any findings (EFSA, 2016). The prevalence of *Trichinella* infections in wild animals is also influenced by human behavior and animal rearing practices, which favor the transmission of these pathogens from the domestic to the sylvatic habitat by the spread of pork and hunted animal scraps and offal. In the European Union in recent years, the prevalence of *Trichinella* infection has reduced by 3-fold (from 0.13% in 2012 to 0.04% in 2016) in the wild boar population and by 2-fold (from 2.43% in 2012 to 1.12% in 2016) in the red fox population (EFSA, 2017). Uncontrolled hunting activities play an important role in the spread of *Trichinella* by infected game carcasses and offal, which can be ingested by wild or domestic animals (Pozio and Murrell, 2006). The prevalence of *Trichinella* infection in wildlife other than wild boar was higher in bears, lynxes, raccoon dogs, and wolves, but the prevalence of infection is also influenced by environmental characteristics and human behavior. Carnivore mammals at the top of the food chain and with a life span longer than that of other animals are more likely to be infected (e.g. lynxes, wolves, bears); however, the population size and the distribution in Europe of these animals are generally limited. Red foxes, with a much larger and widespread population, can be considered as the main natural reservoirs for these pathogens through Europe. The lower prevalence of infection in red foxes (1.12%) than that detected in other carnivores is probably related to the spread of this mammal into populated areas where it feeds mainly on garbage resulting from human activities, where *Trichinella* spp. are not transmitted. It follows that only a percentage of tested foxes originate from regions where *Trichinella* spp. are circulating.

The increasing number of wild boar and red foxes and the spread of the raccoon dog from eastern to western Europe and of the jackal from southern-eastern to northern-western Europe may increase the prevalence of *Trichinella* circulating among wild animals (Alban et al., 2011; Széll et al., 2013). Therefore, it is important to continue educating hunters and others eating wild game about the risk of eating undercooked game meat.

Trichinella parasites and environmental conditions

An important adaptation that facilitates the transmission of *Trichinella* spp. muscle larvae is the physiological mechanism to survive in decaying carcasses; the greater the persistence of larval viability, the higher the probability of being ingested by a scavenging host. In spite of the larva-induced angiogenic process that develops around the nurse cell after larval penetration of the muscle cell, larval metabolism is basically anaerobic (Despommier, 1990), which favors its survival in decaying tissues. In fact, *Trichinella* spp. of the encapsulate clade are dispersed in a way analogous to many nematodes that have hardy eggs or a free-living stage in water or soil. *Trichinella* spp. have a similar free-living stage, with populations of larvae in collagen capsules in a special biotope, the carcass (Pozio, 2016b). These populations are maintained in a way analogous to helminth egg populations. The persistence of larvae in putrefying flesh is also influenced by the environment: high humidity and low temperatures favor survival even when the muscle tissue is completely liquefied. This adaptive survival mechanism is a biological characteristic displayed by all taxa in the genus *Trichinella*; the survival in host carcasses is longer for the encapsulated than for the non-encapsulated species (Stewart et al., 1990; Owen and Reid, 2007). In the natural cycle of the parasite, the importance of the larvae survivability in animal carcasses is further proved by the resistance of muscle larvae in frozen muscles for one (*T. britovi*) or more years (*T. nativa*) (Pozio, 2016). The anaerobic metabolism favoring the survival in putrefying flesh, along with the ability of larvae of some species to survive freezing, are two separate mechanisms that strongly increase larval survival in nature. Survival is greatest at temperatures between 0° C and -20° C. At lower temperatures, the survival time is reduced, suggesting that the optimal temperature range for survival at freezing temperatures corresponds to the temperature under the snow (Pozio, 2016b; Rossi et al., 2019). This habitat has been termed the “subnivium”. The subnivium can be described as habitat below snow that provides environmental stability (Keppel and Wardell-Johnson, 2012). The warmer and more stable conditions within the subnivium are principally driven by snow duration, density, and depth (Rossi et al., 2019).

Prevention and control

The best way to prevent the transmission of these pathogens to domestic pigs is the improvement of pig rearing conditions. As reported above, epidemiological data clearly show that *Trichinella* nematodes are not transmitted in pig herds under high containment level (Pozio, 2014). This is not surprising because ingestion of infected flesh is necessary for the transmission of *Trichinella* parasites. It follows that transmission can be easily interrupted by the control of feedstuffs. However, testing of slaughtered pigs for *Trichinella* spp. is still the best way to prevent transmission of these zoonotic parasites among animals and to humans. Veterinary services should, therefore, carefully test all pigs, and the only condition under which the animals should escape testing is if they are, without a doubt, identified as having been reared under controlled management conditions. Regulation 2075/2005 and more recently the regulation 1375/2015 (European Union, 2005; 2015) list the main measures to be taken to prevent *Trichinella* transmission. These measures not only allow the control of *Trichinella* infection but also of a large number of other zoonotic and non-zoonotic pathogens that can cause high economic losses in pig farms. Standard biosecurity measures inherent in modern swine production facilitate the identification of *Trichinella*-free farms and herds (European Union, 2015). However, control of *Trichinella* infection in free-range pasturing and backyard rearing practices for organic pork and for traditional, ready-to-eat meat products bypassing conventional treatments to inactivate *Trichinella* larvae in meat can be more challenging. For these animals, the only way to avoid the occurrence of infections in humans and the spread of these parasites to other pigs and to wildlife is the systematic control using artificial digestion tests at the slaughterhouse for all pigs originating from uncontrolled housing (Gottstein et al., 2009). This test must be performed by trained analysts who participate in proficiency testing at least one per year (Marucci et al., 2016). To detect *Trichinella* infection in domestic or wild animals, samples of preferential muscles should be tested by artificial digestion (Nöckler and Kapel, 2007). The sensitivity of testing 1 g per carcass is about 3-5 larvae per gram (LPG) but it can reach 1 LPG when a sample of 5 g per carcass is tested. In field conditions, the compressorium method (trichinoscopy) can be used. This method shows a sensitivity of approximately 3 LPG when carried out properly by skilled personnel, but it usually misses *Trichinella* larvae belonging to non-encapsulated species. Once isolated from infected muscles, larvae can be identified to the species or genotype level by a molecular method (Pozio and La Rosa, 2010). Such identification of larvae is very useful for epidemiological and risk-based studies (Pozio, 2014). Once the species has been identified, there is the chance to trace the parasite back 'from fork to farm' using recently developed tests based on microsatellite DNA (La Rosa et al., 2018a; 2018b).

Veterinary services should introduce a risk-based surveillance system for *Trichinella* spp. by documented control of management conditions according to the regulations established by the international agencies and institutions (OIE, 2013; European Union, 2015). Furthermore, veterinary services should make control of *Trichinella* spp.

compulsory for all pigs from herds kept in non-controlled management conditions, regardless of whether the animals are for the market or private consumption. In addition to veterinary services placing strict controls on pigs by testing them for *Trichinella* spp. and monitoring housing and feed conditions on pig farms, public health services should promote the education of consumers. *Trichinella* infection in humans is strongly associated with the consumption of raw or undercooked meat; thus, cultural factors such as traditional dishes based on raw or undercooked meat or meat-derived products play an important role in the transmission of these parasites to humans. Conversely, when a population exclusively consumes well-cooked meat, trichinellosis cases are lacking or very scarce despite persistent wildlife and domestic pig transmission (Gottstein et al., 2009). If the public health and veterinary services will not invest funds in the education of consumers, farmers, and hunters, *Trichinella* spp. will continue to circulate in disadvantaged regions of the world, causing human outbreaks.

CONCLUSIONS

Although trichinellosis has declined significantly as a zoonosis, due chiefly to a reduction of *Trichinella* infections in domestic pigs in developed countries, it remains a potential risk because of the continuing presence of most species of *Trichinella* as parasites of wild animals. Furthermore, the strong opportunism associated with this parasite, with its broad reservoir host range and diverse transmission features, creates potential for its re-emergence whenever the food safety barriers are weakened by socioeconomic events. Examples are seen in the equine *Trichinella* outbreaks in Europe, and the reemergence of porcine infections in countries undergoing major political and economic change (e.g. former Yugoslavia, Romania and Argentina). It behooves veterinary and public health agencies to become well acquainted with the causes of the re-emergence of *Trichinella* infections in countries where formerly successful control measures for this zoonosis have been placed in jeopardy or severely compromised by political, economic and agricultural changes. It is important then, that the systematics and ecology of all *Trichinella* species, including both the classical domestic *T. spiralis* and the sylvatic species, which increasingly are implicated as a cause of human trichinellosis or a significant risk, be well understood.

The emphasis placed in this review, therefore, is the knowledge gained in recent years on the basic biology, ecology, and biogeography of *Trichinella* spp. It should be apparent that our current knowledge of these aspects represents only the barest of essentials pertaining to these parasites. In a sense, we are only at the beginning of the journey to full knowledge, and certainly much more research will need to be carried out before the gaps are filled. Those interested in pursuing these questions can look forward to a demanding task, but they can also take comfort in having a good platform to build upon, the availability of molecular tools for genetic analysis, and a large, available collection of isolates and biogeographic knowledge residing in the International *Trichinella* Reference Centre.

Competing interests

The author declare that they have no competing interests.

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TRIHINELA I TRIHINELOZA U EVROPI

POZIO Edoardo

Kratak sadržaj

Uvod. Trihineloza je zoonotsko oboljenje ljudi prouzrokovano nematodama iz roda *Trichinella*. Ovi paraziti imaju kosmopolitsku rasprostranjenost na svim kontinentima, izuzev na Antarktiku. U prirodi kruže sinantropnim i silvatičnim ciklusom, koji su međusobno povezani. Danas je u ovom rodu utvrđeno 9 vrsta i tri genotipa, a svi imaju sposobnost infekcije sisara, uključujući i ljude, dok jedna vrsta inficira i ptice, a dve vrste i gmizavce.

Cilj i pristup. Uvidom u najnoviju literaturu u vezi sa ovim patogenim parazitima, drugačijim od ostalih nematodama, jer se kompletan ciklus razvoja od larve do odraslog oblika odvija u telu jednog domaćina, što ima veliki značaj u epidemiologiji trihineloze kao zoonoze. Kada je cikus završen, mišići inficirane životinje sadrže *rezervoar* larvi sposobnih za dugoročno preživljavanje. Čovek, kao i ostali domaćini inficiraju se konzumiranjem mišićnog tkiva/mesa koje sadrži larve ovog parazita.

Ključni nalazi i zaključak. Glavni izvor infekcije ljudi su sirovo i/ili nedovoljno termički obrađeno meso i proizvodi od mesa svinja, divljih svinja, medveda, morža i konja, ali i meso/proizvodi dobijeni od drugih životinja. Primena preventivnih mera pre klanja, kao i kontrola nakon klanja životinja su značajni za sprečavanje infekcija trihinelama kod životinja. Prvi uključuje kontrolu farme sa visokim nivoom zaštite i kontinuiranog nadzora, a drugi inspekciju mesa i trihinoskopski pregled mesa kao značajna post-mortem strategija. Takođe, kontinuirana edukacija potrošača je od velikog značaja u onim zemljama gde pregled mesa na prisustvo ovog parazita nije obavezan.

Ključne reči: trihinela, epidemiologija, Evropa, zoonoza, prevencija, kontrola