New patterns of *Trichinella* infection

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**Abstract**

Human and animal trichinellosis should be considered as both an emerging and reemerging disease. The reemergence of the domestic cycle has been due to an increased prevalence of *Trichinella spiralis*, which has been primarily related to a breakdown of government veterinary services and state farms (e.g., in countries of the former USSR, Bulgaria, Romania), economic problems and war (e.g., in countries of the former Yugoslavia), resulting in a sharp increase in the occurrence of this infection in swine herds in the 1990s, with a prevalence of up to 50% in villages in Byelorussia, Croatia, Latvia, Lithuania, Romania, Russia, Serbia, and the Ukraine, among other countries. The prevalence has also increased following an increase in the number of small farms (Argentina, China, Mexico, etc.) and due to the general belief that trichinellosis was a problem only until the 1960s. The sylvatic cycle has been studied in depth at both the epidemiological and biological level, showing the existence of different etiological agents (*Trichinella nativa*, *Trichinella britovi*, *Trichinella murrelli*, *Trichinella nelsoni*) in different regions and the existence of “new” transmission patterns. Furthermore, the role of game animals as a source of infection for humans has greatly increased both in developed and developing countries (Bulgaria, Canada, Lithuania, some EU countries, Russia, USA, etc.). The new emerging patterns are related to non-encapsulated species of *Trichinella* (*Trichinella pseudospiralis*, *Trichinella papuae*, *Trichinella sp.*), infecting a wide spectrum of hosts (humans, mammals including marsupials, birds and crocodiles) and to encapsulated species (*T. spiralis*, *T. britovi*, and *T. murrelli*) infecting herbivores (mainly horses). The existence of non-encapsulated species infecting mammals, birds and crocodiles had probably remained unknown because of the difficulties in detecting larvae in muscle tissues and for the lack of knowledge on the role of birds and crocodiles as a reservoir of *Trichinella*. On the other hand, it is not known whether horse and crocodile infections existed in the past, and their occurrence has been related to improper human behavior in breeding. The problem of horse-meat trichinellosis is restricted to France and Italy, the only two countries where horse-meat is eaten raw, whereas mutton and beef have been found to be infected with *Trichinella* sp. only in China. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** *Trichinella* spp.; Sylvatic cycle; Domestic cycle; Human behavior; Carnivores; Game; Horses; Herbivores; Crocodiles; Birds
1. Introduction

Several foodborne parasitic infections are transmitted to humans because of improper animal breeding, food handling or both (Hui et al., 1994). With regard to *Trichinella*, for more than 100 years after its discovery in 1835, this parasite was considered to be transmitted only through the consumption of pork, and only in the last 50 years have different transmission patterns been documented (Campbell, 1988). These patterns range from those in which humans do not play any role to those in which improper human behavior is the only cause of transmission (Pozio, 1998; Casulli et al., 2001).

Most of the current knowledge on the transmission patterns of *Trichinella* parasites has been provided by studies adopting advanced techniques in biotechnology, which have been used to identify etiological agents, to trace the infection to the original source, and to identify the locality where transmission occurred (Murrell et al., 2000). Today, the genus *Trichinella* is considered to be composed of at least seven species (*Trichinella spiralis*, *Trichinella nativa*, *Trichinella britovi*, *Trichinella pseudospiralis*, *Trichinella murrelli*, *Trichinella Nelsoni*, and *Trichinella papuae*) and three additional genotypes (*Trichinella* T6, related to *T. nativa*, and *Trichinella* T8 and T9, related to *T. britovi*) (Pozio, 2000a). Although the cycle of *Trichinella* parasites is relatively simple compared to that of other parasites and despite the fact that in the past 15 years most questions regarding the transmission cycle have been answered, some transmission patterns are still not completely understood (e.g., trichinellosis in herbivores, birds, and crocodiles), and further epidemiological studies must be carried out to develop control strategies and to avoid transmission to humans.

The objective of this review is to illustrate the changes in the transmission patterns of *Trichinella* infections in different regions of the world, including recently discovered patterns, and the factors influencing these patterns. This review also includes suggestions for developing control strategies in both domestic animals and wildlife.

2. The domestic cycle

The term “domestic cycle” refers to the transmission pattern occurring in a swine herd for the following reasons: the consumption of uncooked pork scraps from dining rooms, kitchens, restaurants, and slaughterhouses; the consumption of garbage (i.e., garbage-fed pigs); direct pig–pig transmission due to tail or ear bites or to eating swine carcasses that are not promptly removed from the herd; and transmission through synanthropic animals living near the swine herd (e.g., rats, mustelides, and foxes). With regard to this last point, the role played by rats in the transmission of trichinellosis to pigs has been a topic of debate for more than 100 years and definitive conclusions have yet to be reached (Madsen, 1974; Schad et al., 1987; Murrell et al., 1987; Leiby et al., 1988, 1990; Pozio, 2000a). However, it has been shown that transmission in a swine herd is stopped when a microbiological barrier against rodents and other synanthropic and domestic animals in the pigsty and in the food-silos is introduced together with other control measures, specifically: the use of food of animal origin to feed swine only if it is cooked (an internal temperature of 60°C for 1 min is enough to inactivate *Trichinella* larvae) and the introduction of new animals in a swine herd only after performing quarantine and serological controls for *Trichinella* (Pozio, 1998).
With regard to the geographic distribution of the domestic cycle of *Trichinella*, there have been no reports of infections on industrialized farms in western Europe since World War II, and the domestic cycle has only been reported among small swine herds of southern Finland and of certain regions in Spain where control measures were not adopted (Pozio, 1998). In several countries of central-eastern Europe (Tables 1 and 2), the breakdown of government veterinary services and state farms, in addition to economic problems and war, have resulted

Table 1
Different *Trichinella* cycles in the world. Data from the literature and from the International *Trichinella* Reference Center, Rome, Italy. There is no information from countries which are not reported in the table

<table>
<thead>
<tr>
<th>Countries</th>
<th>Domestic cycle T. spiralis</th>
<th>Sylvatic cycle with only T. spiralis</th>
<th>Sylvatic cycle with also T. spiralis</th>
<th>Sylvatic cycle without T. spiralis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Argentina, Chile, South Korea, Uruguay</td>
<td>Yes</td>
<td>Yes</td>
<td>?</td>
<td>–</td>
</tr>
<tr>
<td>New Zealand</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Bolivia, Burma, Cambodia, Cameroon, Egypt, Indonesia, Laos, Lebanon, Malaysia, Mexico</td>
<td>Yes</td>
<td>?</td>
<td>?</td>
<td>–</td>
</tr>
<tr>
<td>Armenia, Azerbaijan, Bulgaria, Byelorussia, China, Croatia, Finland, Georgia, Hungary, Latvia, Lithuania, Poland, Republic of Moldova, Romania, Russia, Serbia, Slovak Republic, Spain, Thailand, Ukraine</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>–</td>
</tr>
<tr>
<td>Austria, Bosnia and Herzegovina, Canada, Estonia, France, Germany, Iran, Sweden, The Netherlands, USA</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>–</td>
</tr>
<tr>
<td>Albania, Algeria, Australia, Czech Republic, Ethiopia, Greece, Greenland, India</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Austria, Belgium, Cuba, Denmark, Ireland, Iceland, Luxembourg, UK</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>

* T. britovi.

* T. nativa.

* T. nativa, T. britovi, and T. pseudospiralis.

* T. pseudospiralis.

* T. nativa, and T. britovi.

* T. pseudospiralis, T. murrelli, and *Trichinella* T6.

* Species unknown.

* T. nelsoni.

* Trichinella T8.

* T. papuae.

* Trichinella T9.
Table 2
Trichinella infection in humans of some countries where epidemiological data have been more or less routinely collected

<table>
<thead>
<tr>
<th>Country</th>
<th>Average infections per year</th>
<th>No. of infections per 100,000 inhabitants</th>
<th>Source of infection</th>
<th>Trichinella speciesb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Argentina</td>
<td>621c</td>
<td>1.7</td>
<td>Pig, game</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>892d</td>
<td>11.4</td>
<td>Pig, game</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Byelorussia</td>
<td>33d</td>
<td>0.3</td>
<td>Pig, game</td>
<td>NDf</td>
</tr>
<tr>
<td>Canada</td>
<td>18</td>
<td>0.06</td>
<td>Polar bear, walrus</td>
<td>T. nativa</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>wild boar</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Chile</td>
<td>63</td>
<td>0.4</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>China</td>
<td>541c,e</td>
<td>0.04</td>
<td>Pig, dog, mutton, game</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Croatia</td>
<td>290</td>
<td>6.7</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>France</td>
<td>125</td>
<td>0.2</td>
<td>Horse, game</td>
<td>T. spiralis, T. britovi, T. pseudospiralis</td>
</tr>
<tr>
<td>Germany</td>
<td>9</td>
<td>0.01</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Italy</td>
<td>18</td>
<td>0.03</td>
<td>Horse, pig, game</td>
<td>T. spiralis, T. britovi</td>
</tr>
<tr>
<td>Latvia</td>
<td>57c</td>
<td>2.4</td>
<td>Pig, game</td>
<td>ND</td>
</tr>
<tr>
<td>Lithuania</td>
<td>184c</td>
<td>5.1</td>
<td>Pig, game</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Mexico</td>
<td>4c</td>
<td>0.004</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Poland</td>
<td>59</td>
<td>0.2</td>
<td>Pig, game</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Romania</td>
<td>1744c</td>
<td>7.8</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Russia</td>
<td>630c</td>
<td>0.4</td>
<td>Pig, game</td>
<td>T. spiralis, T. pseudospiralis</td>
</tr>
<tr>
<td>Serbia</td>
<td>473</td>
<td>4.7</td>
<td>Pig</td>
<td>T. spiralis</td>
</tr>
<tr>
<td>Slovakia</td>
<td>75</td>
<td>1.4</td>
<td>Pig, dog, game</td>
<td>T. britovi, T. spiralis</td>
</tr>
<tr>
<td>Spain</td>
<td>48</td>
<td>0.1</td>
<td>Pig, game</td>
<td>T. spiralis, T. britovi</td>
</tr>
<tr>
<td>Thailand</td>
<td>181c</td>
<td>0.3</td>
<td>Pig, game</td>
<td>T. spiralis, T. pseudospiralis</td>
</tr>
<tr>
<td>United States</td>
<td>30</td>
<td>0.01</td>
<td>Pig, game</td>
<td>T. spiralis, T. murrelli, Trichinella T6</td>
</tr>
</tbody>
</table>

a Investigated period 1991–2000. For some countries, there is no information for all years of the investigated period. In this case, the total number of human infections refers to the number of investigated years. The average includes clinical infections and infections detected by serology, unless otherwise indicated.

b Trichinella species of larvae from human biopsies or from infected meat which was the source of infection for humans.

c The average infections refers to clinical cases only.

d The average infections refers to hospitalized individuals only.

e The official reports underestimate the prevalence of human trichinellosis at least for a coefficient of 10, as suggested by seroepidemiological investigations.

f Not determined.

in sharp increases in the occurrence of this infection among swine herds, with prevalence rates reaching 50% in some villages in the 1990s (Murrell and Pozio, 2000). However, in very recent years, gradual decreases in prevalence have been observed. In the United States and Canada, domestic trichinellosis has virtually disappeared, although sporadic foci do occur (Moorhead et al., 1999; Appleyard and Gajadhar, 2000).

In South and Central America, domestic trichinellosis is still endemic in Argentina, Bolivia, Chile, and Mexico. In Argentina, there has been a marked increase in prevalence among both humans and pigs in recent years (Tables 1 and 2) (Bolpe and Boñi, 2000).
Although most cases of infection have been reported in the provinces of Buenos Aires, Cordoba, Neuquen and Santa Fe, new foci have occurred in other provinces (e.g., Catamarca and San Luis, among others). In the period between 1990 and 1999, 5217 human infections were documented in Argentina; however, this may be an underestimate because many moderate infections may have been misdiagnosed. In the province of Buenos Aires, the number of human infections increased from 44 in 1991 to 543 in 1996, whereas the number of foci of porcine trichinellosis increased from 11 to 75 from 1992 to 1996. Infected animals generally originated from small farms where swine are slaughtered without any veterinary control. In Bolivia, a serological prevalence of 13.4% among domestic pigs slaughtered in the regions of Santa Cruz and Chuquisaca has been detected by ELISA using a soluble extract of *T. spiralis* (Brown et al., 1996). In Chile, in the past decade, the prevalence of domestic trichinellosis has decreased from 1 to 0.1% in pigs slaughtered under veterinary control; the prevalence of human infections has also decreased from 0.7% in 1989 to 0.3% in 1998 (Schenone et al., 2000). In Mexico, porcine trichinellosis is endemic in at least 15 federal districts; however, there are few actual data on the incidence among swine because inspections are only carried out in federal abattoirs, which are mostly supplied with pigs from industrialized farms (Ortega-Pierres et al., 2000). Serological surveys of backyard pigs in different areas of the country have revealed a seroprevalence ranging from 1 to 20%.

In east Asia, the domestic cycle occurs in China, where from 1964 to 1998 more than 25,000 human infections were documented in 10 of the country’s 34 provinces (Takahashi et al., 2000). By necropsy, the prevalence in hogs has been shown to range from 0.003 to 6.7% in 12 provinces, though in certain areas of these provinces it reaches 50% (Takahashi et al., 2000). By serology, the infection rate has been shown to be higher, reaching 10.4%, though the level of specificity of the serological test used is not known. A high prevalence of infection has been detected in dogs (up to 23.5 and 27.1% by necropsy in the Liaoning and Helongjiang provinces, respectively) (Takahashi et al., 2000) (Table 2). Foci of domestic trichinellosis involving swine and humans are also widespread in Thailand, and sporadic outbreaks have been documented in other countries of southeast Asia (Cambodia, Indonesia, Laos, Malaysia, and Myanmar) (Pozio, 2001). In Asia Minor, two human outbreaks of domestic trichinellosis were documented in Lebanon (Olaison and Ljungstrom, 1992; Haim et al., 1997). In Africa, domestic trichinellosis has been reported only in Egypt and only among pigs and dogs with free access to garbage (Azab et al., 1988; Mikhail et al., 1994).

### 3. The sylvatic cycle

The sylvatic cycle is that which occurs in nature among carnivores with cannibalistic and scavenger behavior (Campbell, 1988). This cycle occurs virtually throughout the world, and nearly all of the studies that have attempted to reveal its presence have succeeded in doing so, with few exceptions, as, e.g., studies conducted on islands located in temperate regions (Ireland, Great Britain, and the Mediterranean islands of Sardinia and Sicily) (Table 1). However, epidemiological surveys have been carried out only sporadically and there is no information on the sylvatic cycle in many countries.
The sylvatic cycle occurs mainly in natural ecosystems far from human settlements (Pozio et al., 1996) and involves the species *T. nativa*, *T. britovi*, *T. murrelli*, *T. nelsoni*, *T. pseudospiralis* and *T. papuae*. In those areas close to human settlements, the transmission of *Trichinella* is rare because the major food source consists of domestic animals and garbage, which the animals prefer to congener carcasses or carcasses of other carnivores. However, in these areas, sylvatic cycles of *T. spiralis* do occur, as a result of current or past transmission from the domestic environment (i.e., domestic animals infected with *T. spiralis* or garbage containing infected animal scraps) (Rossi et al., 1992; Pozio et al., 1996, 1997a; Pozio, 1998).

The human impact on the natural ecosystem can either favor or impede the sylvatic cycle. When hunters fail to properly dispose of game carcasses or use carcasses of sylvatic carnivores as bait for other carnivores, the prevalence of *Trichinella* infection increases (Casulli et al., 2001), whereas the sylvatic cycle is interrupted when carnivores rely on food sources other than cannibalistic and scavenger behavior, as reported above (Pozio, 1998).

### 3.1. *T. spiralis*

*T. spiralis* is present in sylvatic carnivores and omnivores of many countries of both temperate and tropical regions (Table 1), whereas in cold regions it is not transmitted or is only rarely transmitted among wildlife near human settlements, because muscle larvae do not survive in frozen host carcasses. Sylvatic animals infected with *T. spiralis* have been detected in Canada, USA, Argentina, Chile, and most European countries (Table 1), but not in Great Britain, Greece, Ireland, Italy, Norway, Portugal or Switzerland. In Asia, *T. spiralis* has been identified in sylvatic animals from Iran and Thailand (Shaikenov and Boev, 1983; Khamboonruang, 1991). In other Asian countries, many old reports refer to *T. spiralis* in sylvatic animals; however, in these reports, all of the isolated *Trichinella* larvae were considered to be *T. spiralis*, which was the only known species at the time. There are no reports from Africa (Pozio, 2000a), although *Trichinella* larvae isolated in North African carnivores were reported to be *T. spiralis*, which was, again, the only known species at the time (Fassbender and Meyer, 1974).

### 3.2. *T. nativa*

*T. nativa* is prevalent in sylvatic carnivores (wolf, *Canis lupus*; polar bear, *Ursus maritimus*; brown bear, *Ursus arctos arctos* and *U. arctos horribilis*; corsac fox, *Vulpes corsac*; arctic fox, *Alopex lagopus*; raccoon dog, *Nyctereutes procyonoides*; tiger, *Panthera tigris*; and several species of mustelides) in arctic and subarctic areas of North America (Alaska and Canada), northern Europe, and Asia. The genotype *Trichinella* T6 is prevalent in black bears (*Ursus americanus*) and grizzly bears (*U. a. horribilis*), wolves, mountain lions (*Felis concolor*), wolverines (*Gulo gulo*), fishers (*Martes pennanti*), and gray foxes (*Urocyon cinereoargenteus*) in the US states of Alaska, Idaho, Montana, Pennsylvania, and Wyoming and in Ontario, Canada. *T. nativa* has also been found in red foxes (*Vulpes vulpes*) of Europe (Estonia, Finland, Norway, Russia, and Sweden) and of Asia (Hokkaido island in Japan, Kazakhstan, Kirghizistan, Russia, and Tajikistan) (Shaikenov and Boev, 1983; Takahashi et al., 2000; International *Trichinella* Reference Center, Rome, Italy, www.trichi.)
iss.it). This *Trichinella* species has also been detected in two wild boars (*Sus scrofa*) from Estonia (Pozio and Kapel, 1999) and in domestic dogs and cats and in a pig from northern China (Gasser et al., 1998). The isotherm $-5^\circ C$ in January is the southern border of distribution in the Palearctic region (Shaikenov, 1992; Pozio et al., 1998a) and probably in the Nearctic region (Pozio and La Rosa, 2000). Larvae of *T. nativa* in frozen muscles of carnivores can survive for up to 5 years, whereas they lose their infectivity within a few weeks or months in non-carnivore muscles (Dick and Pozio, 2001).

### 3.3. *T. britovi*

*T. britovi* is the etiological agent of sylvatic trichinellosis in temperate regions of Eurasia. This species has been detected in wolves, foxes, brown bears, jackals (*Canis aureus*), raccoon dogs, mustelides, sylvatic and domestic swine (but with a lower prevalence than that of *T. spiralis*), brown rats (*Rattus norvegicus*) and horses (two times) in mainland Europe and in many countries of Asia (Azerbaijan, Iran, Kazakhstan, Tajikistan, Turkmenistan, and Uzbekistan), all the way to Honshu Island in Japan, where it is present with the genotype *Trichinella* T9 (Nagano et al., 1999; Pozio, 2000a). *T. britovi* is probably present in China, India and other Asian countries, but there are no reports supporting this hypothesis. The isotherm $-6^\circ C$ in January is the northern border of distribution in the Palearctic region (Shaikenov, 1992; Pozio et al., 1998a). *Trichinella* T8 has only been isolated three times, from sylvatic carnivores of South Africa (a lion, *Panthera leo*, a spotted hyena, *Crocuta crocuta*) and Namibia (a lion). It is believed that *Trichinella* T8 was introduced passively from Europe with domestic animals during the European colonization of South Africa in the 17th century (La Rosa and Pozio, 2000). Larvae of *T. britovi* in frozen muscles of carnivores (fox and wolf) can survive for up to 1 year, whereas they lose their infectivity within a few days or weeks in non-carnivore muscles (Pozio, 2000a).

### 3.4. *T. murrelli*

*T. murrelli* is the etiological agent of sylvatic trichinellosis in temperate regions of North America. This species has been detected in red foxes, raccoons (*Procyon lotor*), coyotes (*Canis latrans*), black bears, bobcats (*Lynx rufus*) and in one horse, in the states of Connecticut, Georgia, Illinois, Indiana, New Mexico, Pennsylvania, and Texas (Pozio and La Rosa, 2000; Pozio et al., 2001). This *Trichinella* species is unable to develop in pigs (Kapel and Gamble, 2000).

### 3.5. *T. nelsoni*

*T. nelsoni* is the etiological agent of sylvatic trichinellosis in Africa, south of the Sahara (Pozio et al., 1997a). This species is prevalent among carnivores ( striped jackal, *Canis adustus*; black-backed jackal, *Canis mesomelas*; spotted hyena, *Crocuta crocuta*; striped hyena, *Hyaena hyaena*; cheetah, *Acinonyx jubatus*; bat-eared-fox, *Otocyon megalotis*; lion, *P. leo*; leopard, *Panthera pardus*) and to a lesser degree among bush pigs (*Potamochoerus porcus*) and warthogs (*Phacochoerus aethiopicus*). The spotted hyena seems to be the most important reservoir of this species. To date, only *Trichinella* isolates from Kenya,
Tanzania and South Africa have been identified at the species level, whereas isolates from Ethiopia, Senegal and Zaire have not (Pozio et al., 1994a). Larvae of *T. nelsoni* in decaying host muscles are resistant to high temperatures, higher than those of the other species of *Trichinella* (Köller et al., 2001).

4. New cycles

4.1. *T. pseudospiralis*

After the discovery of *T. pseudospiralis* in a raccoon (*Procyon lotor*) (or in a raccoon dog, *Nyctereutes procyonoides*) in 1972 (Garkavi, 1972), this parasite was considered more as a scientific curiosity than as a human and animal pathogen because of the lack of a collagen capsule around the nurse cell–larva complex and because of its infectivity to both mammals and birds. However, this parasite has since been discovered in a corsac fox, a rook (*Corvus frugilegus*), and an eagle (*Aquila rapax*) of Kazakhstan, and in a mole rat (*Bandicota bengalensis*) of India (Shaikenov and Boev, 1983; Pozio et al., 1992). In Kamchatka, this parasite has been isolated from domestic pigs, brown rats and humans (Britov, 1997). In Thailand and France, meat from wild pigs infected with *T. pseudospiralis* was the source of human infections (Jongwutiwes et al., 1998; Ranque et al., 2000). *T. pseudospiralis* has been identified in a black vulture (*Coragypus atratus*) of Alabama (Lindsay et al., 1995) and in a tawny owl (*Strix aluco*) and a little owl (*Athene noctua*) of Italy (Pozio et al., 1999a). In Tasmania, a transmission pattern of *T. pseudospiralis* has been found among marsupials (tiger cat, *Dasyurus maculatus*; eastern Australian native cat, *Dasyurus viverrinus*; brush-tailed possum, *Trichosurus vulpecula*; Tasmanian devil, *Sarcophilus harrisii*) and birds (*Circus aeruginosus*; *Tyto novaehollandiae*) (Obendorf et al., 1990; Obendorf and Clarke, 1992). *T. pseudospiralis* larvae were detected in a biopsy conducted on a woman, who probably acquired the infection in Tasmania (Andrews et al., 1995). Recently, *T. pseudospiralis* was detected in raccoon dogs, in one wild boar and in one brown rat of Finland (Kapel et al., 2001).

Isolates of *T. pseudospiralis* collected from the Nearctic, Palearctic, and Australian regions showed molecular and biochemical differences among them (Zarlenga et al., 1996; La Rosa et al., 2001), suggesting a reproductive isolation among populations living in these regions, in spite of the potential role of raptorial birds in disseminating the parasite throughout the world. The presence of *T. pseudospiralis* in domestic pigs and brown rats of Kamchatka suggests that, in particular epidemiological situations, this parasite can be transmitted by a domestic cycle in the human environment. The low number of animals infected with this species in comparison to those infected with encapsulated species could suggest that the biomass is lower; this apparent low prevalence could also be due to the lack of a collagen capsule, which can prevent the larvae from being detected by trichinelloscopy, or to the fact that few birds have been examined. Since it is very difficult to detect *T. pseudospiralis* larvae in the muscle tissue of large animals by trichinelloscopy, this method can no longer be used for screening in slaughterhouses. Another issue that needs to be addressed is that despite the finding that the larvae of this non-encapsulated species are unable to survive in frozen muscles (Pozio et al., 1994b), a transmission cycle has been documented in frigid...
zones (Finland, Kamchatka), where the freezing-resistant encapsulated species *T. nativa* is present.

4.2. *T. papuae*

*T. papuae*, the second non-encapsulated species, was recently described (Pozio et al., 1999b). This parasite was discovered in domestic sows and wild pigs of a remote area of Papua New Guinea (PNG) in 1988 (Owen et al., 2000). The prevalence among the people living in this area was quite high (28%), and infection was due to eating raw or undercooked wild pig (Owen et al., 2001). Although domestic pigs from other districts of PNG and wild animals from the same areas where the infected wild pigs were found, were examined (Owen et al., 2000), the main reservoir is still unknown. The natural cycle and the epidemiology of this species in nature require further investigation.

5. *Trichinella* in marine mammals

*Trichinella* larvae have been detected in 2.4% (37/1529) of walruses (*Odobenus rosmarus*) killed in Alaska, Greenland, and the Chukchi peninsula of Russia, with a prevalence ranging from 0 to 9.4%. They have also been detected in 0.3% (3/876) of bearded seals (*Erignathus barbatus*) and in 0.1% (3/2743) of ringed seals (*Phoca hispida*) from Alaska and Greenland, in 0.2% (1/482) of beluga whales (*Delphinapterus leucas*) from Alaska, and in 0.4% (8/2177) of seals (not identified at the species level) from Alaska, Greenland, and Russia (Forbes, 2000). These data strongly suggest that only walruses act as a reservoir of *Trichinella* larvae, whereas seals and cetaceans seem to be only occasional hosts whose role is negligible in terms of maintaining this parasite in nature.

*Trichinella* larvae from walruses have been identified as *T. nativa*, a finding that is consistent with the distribution area of this parasite and with its presence in other carnivores living in circumpolar regions. Walrus meat represents an important source of infection for humans living in arctic regions, and outbreaks occur at an early age among Inuits. The polar bear is undoubtedly the main reservoir of *T. nativa* in the Arctic, with the prevalence exceeding 50%. However, the walrus cycle may exist separately from that of the polar bear (Madsen, 1961), given that the geographic areas of origin of infected polar bears and infected walruses do not overlap, whereas trichinellosis in sled dogs occurs in the same area as infected walruses. There probably exists a walrus–walrus cycle, favored by the predation of walruses upon other walruses and their cannibalistic behavior; furthermore, polar-bear and dog carcasses infected with *Trichinella* increase the biomass of the parasite ingested by walruses through their scavenger behavior.

6. Horse trichinellosis

As early as the late 19th century there have been reports of both experimental infections with *Trichinella* larvae in horses (in Germany and Austria) (Gerlach, 1873; Csokor, 1884) and a natural infection (OH, USA) (Thornbury, 1897); however, the potential role of horses in the transmission to humans had been ignored until 1975, when an outbreak of trichinellosis...
occurred among 89 persons in Italy who had eaten horse meat (Mantovani et al., 1980). In the same year, another outbreak occurred in France, prompting the European Union (EU) to examine thousands of horses for the presence of *Trichinella* larvae, adopting the method used to detect this infection in pigs (i.e., artificial digestion of 1.0 g of diaphragm pillars). No natural infections in horses were detected at that time. Since 1975, human trichinellosis has occurred in France (2296 persons in eight outbreaks) and Italy (1030 persons in six outbreaks), and each outbreak was attributed to the consumption of meat from single horses, imported from Canada, former Yugoslavia, Mexico, Poland, and USA. Routine examinations in the slaughterhouses had revealed infection in only one of the 14 horses involved in these outbreaks, though the meat from this horse was erroneously placed on the market (Pozio et al., 1998b). The failure to detect infection in the other 13 horses was mainly due to the fact that routine examinations had been conducted on small quantities of muscle tissue (i.e., 1.0 g). In fact, since larger quantities of muscle tissue (i.e., 5–100 g) have begun to be used, *Trichinella* larvae have been detected in 14 horses, all of which originated from Mexico, Poland, Romania, and Serbia.

Worldwide, the prevalence of horse infection appears to be very low, with only 27 infections reported since 1975, 23 of which were detected in France and Italy (the remaining four were detected in Mexico). However, since France and Italy consume 71% of the horse-meat in the EU (39.4 and 77.0 × 1000 t per year, respectively) and they are the only two EU countries where horse-meat is eaten raw and where human infections for horse-meat consumption have occurred, controls for *Trichinella* are more thorough in these countries, which could in part explain why they are the only two EU countries where infected horses have been detected.

Since 1975, approximately six million horses have been consumed in the EU; thus the 23 infected animals represent an incidence of only 3.8/1 million slaughtered horses (Pozio, 2000b). However, this may be an underestimate, in that the controls conducted in EU countries other than France and Italy may be less thorough. Nonetheless, the true prevalence in other countries is probably similar to that detected in Italy and France, in that horses are imported from the same countries; in any case, even when taking into consideration a reasonable underestimate, the prevalence can still be considered as very low.

The fact that all of the infected horses were imported from countries with a high prevalence of trichinellosis in pigs and/or wildlife suggests that there exists a relation between the infection in these animals and horse infection. Specifically, four infected horses detected in 1998, 2000 and 2001, two of which were sources of human infections in France and three that were detected at the slaughterhouse in Italy and France, had been imported from Serbia, certain areas of which have a high prevalence of domestic trichinellosis. Five infected horses (four detected at a slaughterhouse in Mexico in 1994 and one that was a source of infection in France the same year) were from Mexico, which has a high prevalence of domestic trichinellosis (Arriaga et al., 1995; Dupouy-Camet, 1997). Two infected horses detected in Italy in 1996 and 2001 had been imported from Romania, which has a high prevalence of porcine trichinellosis (Pozio et al., 1997b).

Until 1991, testing for *Trichinella* larvae in local and imported horses was not mandatory in the EU. The mandatory testing of fresh horse-meat produced in or imported to the EU was established by Directive 91/497/EEC of the European Community Council. Specifically, this directive specifies that testing is to consist of the artificial digestion of 1 g of muscle
tissue, according to the procedures used to detect this infection in pigs (Council Directive 77/96/EEC). In 1994, the minimum weight of the meat sample to be tested was increased to 5 g (Council Directive 94/59/EEC). Indeed, *Trichinella* larvae in slaughtered horses have only been found when conducting artificial digestion on at least 5–10 g of muscles.

Serological diagnosis is not acceptable as an inspection tool in horses, since 5–6 months after experimental infection, circulating antibodies have been shown to disappear in sera, although there are still infective muscle larvae (Soulé et al., 1989; Pozio et al., 1997b). Furthermore, the examination of 5000 serum samples from Romanian horses by ELISA and Western blot using an excretory/secretory antigen revealed a prevalence of 3.5%, whereas all these positive sera resulted negative when they were examined by ELISA using a highly specific synthetic tyvelose glycan–BSA antigen (Sofronic-Milosavljevic et al., 2001), supporting the low prevalence of *Trichinella* infection in horses.

It has been demonstrated that the muscles from the head of the horse constitute the predilection site for *T. spiralis* larvae. In particular, the highest muscle burden in naturally infected animals has been found in *Musculus buccinator*, *Lingua*, *Musculus levator labii maxillaris*, and *Musculus masseter*. Compared to the diaphragm, the number of larvae per gram is 3.5–6.8 times higher in *Lingua*, 3.5–6.5 times higher in *M. levator labii maxillaris*, and 2.5–4.6 times higher in *M. buccinator*. The diaphragm, which is still the most common muscle used for detecting *Trichinella* in horses, never ranks higher than the sixth position among the predilection muscles for the diagnosis of this infection (Pozio et al., 1999c). Published data from experimental infection in horses confirm these results (Soulé et al., 1989; Gamble et al., 1996).

Epidemiological investigations of the four most recent human outbreaks have shown that they occurred because of inadequate veterinary controls at the slaughterhouse. Horse-meat outbreaks have important consequences on public health (a high number of infected persons, some of them with a very severe symptomatology, at times resulting in death). They also have a great impact on medical costs, on the horse-meat market (a collapse in sales of horse meat after each outbreak), and in legal and administrative terms (implementation of control measures at the national and international levels) (Ancelle, 1998).

Although there do not exist any epidemiological or scientific data on the modes of *Trichinella* transmission in horses, two hypothesis have been proposed: (1) grazing in pastures contaminated with infected rodent carcasses or pork scraps; (2) ingesting infected flesh from pigs and wild carnivores. This second hypothesis is supported by the practice of using the carcasses of carnivores bred in captivity or hunted for their fur for a mash to fatten the horse before slaughter. Indeed, the use of proteins of animal origin in breeding herbivorous animals is now a common practice in many countries. This is also confirmed by the identification of larvae as *T. britovi* and *T. murrelli* from patients who acquired trichinellosis in three horse-meat outbreaks in Italy and France. The presence of thin capsules around the larvae in muscle tissues of the horse slaughtered in January and the presence of thick capsules in the larvae from horses slaughtered in April and October seem to support the hypothesis that horses acquire this infection in late autumn or winter, either passively (i.e., by grazing in pastures contaminated with rodent carcasses or pork scraps) or actively (i.e., by fattening horses with infected swine meat). Additional field research is needed to determine the modes of transmission of trichinellosis from domestic animals and wildlife to horses, in order to establish new preventive strategies. The development of improved diagnostic
methods at the slaughterhouse or a new diagnostic method for detecting the infection in live horses will be of great importance if the occurrence of human outbreaks for horse-meat consumption is to be avoided.

7. Trichinellosis in other herbivorous mammals

Of particular interest is the role of mutton, which since 1982 has been implicated, though only on an epidemiological basis, as the source of infection for humans in 23 outbreaks in China (Takahashi et al., 2000). In China, mutton is used as stuffing for dumplings, which are boiled for 5–10 min, often resulting in an undercooked central portion. “Scoured” mutton (i.e., thin slices of meat boiled for not more than 1 min) is also a source of infection in China (Takahashi et al., 2000). However, there is no scientific evidence of natural infections with Trichinella in sheep and goats, though experimental infections have shown that both animals can be infected with T. spiralis (Theodoropoulos et al., 2000; Reina et al., 1996). It could be argued that sheep and goats acquire and retain Trichinella larvae in their muscles when they are bred in areas that are highly endemic for domestic trichinellosis. In China, a human outbreak of trichinellosis was attributed to beef consumption (Murrell, 1994); however, this isolated finding requires further investigation to clarify if beef can be a source of trichinellosis for humans. Experimental infection in cattle showed that these animals can acquire trichinellosis (Smith et al., 1990). Among wild herbivores, Trichinella infection was detected in a reindeer (Rangifer tarandus) of Russia (Bessonov, 1981) and in two roe deer (Capreolus capreolus) of Croatia (A. Marinculic, personal communication), suggesting that, in a particular epidemiological situation, this parasite can infect not only carnivores and omnivores but also herbivores. However, infections among wild herbivores can be considered more as a scientific curiosity than as a veterinary problem.

8. Reptiles

Reptiles and cold-blooded vertebrates in general are not considered as suitable hosts for Trichinella in nature. Trichinella larvae have never been detected in muscles of sylvatic reptiles. In laboratory conditions, Kapel et al. (1998) did not succeed in infecting caimans (Caiman sclerops) with eight serotypes of Trichinella, whereas some authors were able to reproduce, in laboratory conditions, the Trichinella cycle in reptiles (Texas horned lizard, Phrynosoma cornutum; European pond tortoise, Emys orbicularis; sand lizard, Lacerta agilis; Caucasian agama, Agama caucasia; and horned adder, Vipera ammodytes), yet only when maintained at temperatures (37–40°C) higher than those necessary for breeding these reptiles in captivity (25–30°C) (Jordan, 1964; Guevara Pozo and Contreras-Pena, 1966; Cristeau and Perian, 1999; Asatryan et al., 2000). For the first time in 1995–1996, non-encapsulated larvae of Trichinella sp. were detected in a cold-blooded vertebrate, specifically, in muscles of crocodiles (Crocodylus niloticus) of 11 farms in Zimbabwe (Foggin et al., 1997). These larvae were able to infect laboratory rats, baboons and domestic pigs (Mukaratirwa and Foggin, 1999). Because crocodile meat is sold for human consumption, the detection of Trichinella infection in this species represents a new potential zoonotic
problem. However, there was no information on the epidemiology of this outbreak and it is not known whether the crocodile is an important host. Furthermore, the parasite is still in the process of being identified at the biochemical and molecular level.

9. Conclusions

The increase in domestic trichinellosis which occurred in many countries of central and eastern Europe, South America, and Asia in the 1990s suggests that all measures for controlling this infection at the farm and slaughterhouse level must be routinely carried out, at least for pigs bred in ecological (organic) farms, even if epidemiological data suggest that the occurrence of infection has been decreasing recently in eastern European countries. In fact, the pressure of the parasite biomass present in sylvatic animals and improper human behavior in animal husbandry can easily favor the transmission of *Trichinella* from the wild to the domestic habitat. At the same time, routine controls for *Trichinella* infection in sylvatic animals and the proper disposal of offal from field-dressed animals are useful for the proper management of wildlife and for monitoring the prevalence of infection in order to prevent its transmission to domestic animals and humans.

References


