



Molecular taxonomy, phylogeny and biogeography of nematodes belonging to the *Trichinella* genus

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ABSTRACT

Studying parasites of the genus *Trichinella* provides scientists of today many advantages. This is a group of zoonotic nematodes that circulates freely among wildlife hosts with one in particular, *Trichinella spiralis* that is exceptionally well adapted to domestic swine. Recent reports suggest that human infections from hunted animals are on the rise worldwide and numerous countries still experience problems with *T. spiralis* in their domestic food supplies. *Trichinella* is a genus whose members are easily propagated in the laboratories, have been used as models to investigate host–parasite relationships and parasitism among clade I organisms, and represent a poorly investigated link between the phylum Nematoda and other Metazoans. The importance of *T. spiralis* in better understanding the tree of life was so recognized that in 2004, its genome was carefully selected as one of only nine key non-mammalian organisms to be sequenced to completion. Since it was first discovered in 1835, this genus has expanded from being monospecific to eight species including four other genotypes of undetermined taxonomic rank. Inasmuch as discriminating morphological data have been scant, our understanding of the genus has been relegated to a compilation of molecular, biochemical and biological data. Herein, we provide a collection of information and up-to-date interpretations on the taxonomy, diagnostics, systematics, micro- and macroevolution, and the biogeographical and biohistorical reconstruction of the genus *Trichinella*.

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1. Introduction

Worms belonging to the genus *Trichinella* are unique among zoonotic nematodes. They are characterised by two generations in the same host and by infective first stage larvae (L1) rather than infective third stage larvae (L3) which typify most other nematode species (Pozio, 2007a). The only means of transmission is through the ingestion of infected, striated muscle tissue. The natural reservoirs of *Trichinella* species are wild carnivorous and omnivorous animals (Pozio, 2005). When humans fail to properly manage food animals or control the interface between wild and domestic animals, transmission of some species (i.e., *Trichinella spiralis*, *T. britovi* and *T. pseudospiralis*) can occur between these habitats. This transmission pattern inevitably involves pigs (Pozio and Murrell, 2006). Once an infection occurs in a population of domestic pigs, it can be perpetuated for many years within the neighbouring environment because of the scavenging and eating habits of these

animals. This problem is exacerbated when scraps from “home slaughtered”, infected pigs are scattered in local surroundings.

Trichinella parasites, which are widespread in all continents but Antarctica, are the etiological agents of a human disease, named trichinellosis (formerly known as trichiniasis or trichinosis), which can cause death in severe cases (Dupouy-Camet et al., 2002; Pozio and Murrell, 2006). If one considers all countries of the world, *Trichinella* spp. infections in domestic animals (mainly pigs) have been documented in 43 (21.9%) countries, whereas infections in wildlife have been documented in 66 (33.3%) countries (Pozio, 2007b). Human trichinellosis has been reported in 55 (27.8%) countries worldwide; however, the presence of *Trichinella* in wild and/or domestic animals is not always linked to human infection. Eating habits of the hosts play important roles in transmission (Pozio, 2007b). Given the ability of this parasite to infect nearly all mammals, its cosmopolitan distribution, and its ability to appear in the domestic food supply, it is important to understand the many species that make up this genus. In addition, having an appreciation for the biogeography and species level diversity among these parasites will provide a foundation for more detailed studies of population structure relevant to patterns of geographic and host distribution, and the future threat of human trichinellosis.

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2. Phylogeny and taxonomy

2.1. *Trichinella* and its historical context within Nematoda

Recent history depicts the phylum Nematoda being separated into two classes, the Adenophorea and Secernentea predominantly based upon morphological and some molecular characters (Maggenti, 1983). Classically, the genus *Trichinella* has been grouped with the Adenophorea; however, more recent molecular data have begun to question this classification scheme (Blaxter et al., 1998). In 1998, Blaxter et al. re-evaluated hierarchical relationships among terrestrial and economically-important nematodes predicated on small subunit ribosomal DNA (ssu rDNA) sequence data. They concluded that the prior separation of Adenophorea and Secernentea was insufficiently descriptive and did not adequately represent the high frequency of homoplasy relative to parasitism and other independently evolved biological characters. The studies of Voronov et al. (1998) mirrored these findings where they reported distinct patterns of embryonic development that were in good agreement with the divisions proposed by Blaxter et al. (1998). In this classification scheme, the genus *Trichinella* was partitioned with clade I plant, insect, and marine parasites along with some free-living nematodes. De Ley and Blaxter (2002) updated this phylogeny with morphological information to assist classification of organisms for which ssu rRNA information was not available. Holterman et al. (2006) performed more robust studies and concluded that the phylum would be best served if divided into 12 rather than five different clades as proposed by Blaxter et al. (1998). Most recently, Meldal et al. (2007) revised this phylogeny by including a large number of marine taxa that were severely underrepresented in previous analyses. They concluded that resolution at the base of the phylum was not sufficiently adequate to shed light on a marine ancestry for the group.

Data have recently surfaced suggesting that Trichinellidae and Trichuridae diverged from a common ancestor 250–300 million years ago (Ma) (Zarlenga et al., 2006). Estimates for the divergence of lineages leading to *Caenorhabditis* and *Trichinella* have been as high as 600 Ma (Mitreva and Jasmer, 2006). Research performed by Parkinson et al. (2004) and more recently by Mitreva et al. (2004, 2005) indicated as much similarity (45–50%) between *T. spiralis* (clade I) and *Caenorhabditis elegans* (clade V) as that shared between *T. spiralis* and the arthropod, *Drosophila melanogaster* based upon predicted consensus sequences from expressed-sequence tag (EST) clusters. This level of similarity is more related to sequence conservation within the broader context of metazoan evolution but clearly demonstrates the great genetic diversity among organisms in the phylum Nematoda. This finding was mirrored in the mtDNA sequence of *T. spiralis* which in many aspects was more similar to non-nematode metazoans than to nematodes or was intermediate between these groups (Lavrov and Brown, 2001).

2.2. *Trichinella* phylogeny and taxonomic structure: the earlier years

For nearly 150 years following the 19th century discovery of *T. spiralis* (Owen, 1835), the genus was considered to be monospecific (Table 1) (e.g., Pozio and Zarlenga, 2005). With the characterization of a handful of unique *Trichinella* isolates 30–35 years ago, the taxonomy of this genus became controversial (Pozio et al., 1992). Recent molecular epidemiological studies have served to validate the contributions of earlier work based on epidemiology (Rausch et al., 1956; Nelson, 1970; Rausch, 1970), cross-breeding (Britov and Boev, 1972), and biology and morphology (Garkavi, 1972). Thus, by the early 1970s, biological data had suggested that the genus comprised a complex of largely cryptic parasite species even though morphological characters among the group were equivocal (Lichtenfels et al., 1983). Indeed, the most telling character, the presence or absence of a host-derived, collagen sheath around the infected muscle cell led to the conclusion that the genus could be biologically delineated into 2 distinct groups: the encapsulated and non-encapsulated clades (Zarlenga et al., 2006). These groups received heightened interest from the genome sequencing community and in 2004, a major effort was launched to sequence the complete genome of *T. spiralis* as a representative clade 1, encapsulated nematode (Mitreva and Jasmer, 2008). Genome sequencing efforts have since expanded to include the non-encapsulated species, *T. pseudospiralis*, using “next generation” sequencing technologies (Zarlenga et al., 2009) and *T. spiralis* data for comparative sequence assignment.

Better resolution of taxonomic issues has occurred only in the last 25 years, facilitated by the adoption of biochemical and molecular techniques (Flockhart et al., 1982; Mydnyski and Dick, 1985; Fukumoto et al., 1987, 1988; Murrell et al., 1987; Pozio, 1987; La Rosa et al., 1992) which have been improved for both sensitivity and specificity (Chambers et al., 1986; Dame et al., 1987; Zarlenga and Barta, 1990; Zarlenga and Dame, 1992). Among the earliest dendrograms were those based upon distance algorithms of allozyme data from more than 150 field isolates obtained from different hosts and geographical origins (La Rosa et al., 1992). In their simplest forms, these trees biochemically delineated encapsulated and non-encapsulated species but broadly grouped the encapsulated genotypes with variable levels of resolution. Within this context, the allozyme data supported recognition of five species (*T. spiralis*, *T. nativa*, *T. britovi*, *T. pseudospiralis*, and *T. nelsoni*) and three additional genotypes (*Trichinella* T5, T6, and T8) whose taxonomic rank was unresolved (La Rosa et al., 1992; Pozio et al., 1992). This proposal constitutes the current paradigm where modification has resulted only from the addition of new species and genotypes (Tables 1 and 2) (Pozio and Zarlenga, 2005; Krivokapich et al., 2008).

The use of polymerase chain reaction (PCR)-derived methods has been instrumental in identifying *Trichinella* isolates and has

Table 1
The taxonomy of the *Trichinella* genus from the parasite discovery to today.

Year	Genus and species	Identification based on	Reference
1835	<i>Trichina spiralis</i>	Morphology	Owen, 1835
1892	<i>Trichinella spiralis</i>	Not applicable	Railliet, 1896
1972	<i>Trichinella nativa</i> , <i>T. nelsoni</i>	Cross-breeding, epidemiology, zoogeography	Britov and Boev, 1972
1972	<i>T. pseudospiralis</i>	Biology, morphology	Garkavi, 1972
1992	<i>T. britovi</i> , <i>T. nelsoni</i> s.s., <i>Trichinella</i> T5, T6, and T8	Allozymes, biology, epidemiology, zoogeography	Pozio et al., 1992
1999	<i>T. papuae</i>	Allozymes, molecular markers, biology, epidemiology, zoogeography	Pozio et al., 1999a
1999	<i>Trichinella</i> T9	Molecular markers	Nagano et al., 1999
2000	<i>T. murrelli</i>	Cross-breeding, biology, zoogeography	Pozio and La Rosa, 2000
2002	<i>T. zimbabwensis</i>	Allozymes, molecular markers, biology, cross-Breeding, epidemiology, zoogeography	Pozio et al., 2002
2008	<i>Trichinella</i> T12	Molecular markers, epidemiology, zoogeography	Krivokapich et al., 2008

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