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Review

Taenia tapeworms: their biology, evolution and socioeconomic significance

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Abstract

A biological context for understanding human pathogens and parasites emanates from evolutionary studies among tapeworms of the genus *Taenia*. Human taeniasis and cysticercosis represent archaic associations and remain significant challenges for socioeconomic development, public health and food safety, and a continuing threat to animal production on a global basis. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Biology and systematics for species of *Taenia*

Cyclophyllidean tapeworms are among the crown groups of the eucestodes and encompass nearly all taxa that are parasites in terrestrial vertebrates. Among this diverse assemblage are the Taeniidae, highly characteristic tapeworms in the subfamilies Taeniinae and Echinococcinae that occur as adults in the intestine of carnivorous and omnivorous mammals, including humans, throughout the world. Taeniids, represented by *Taenia* Linnaeus, 1758 and *Echinococcus* Rudolphi, 1801, are globally of considerable medical and veterinary significance as causative agents of morbidity and mortality in humans and production losses to domestic food animals [1]. Individuals of various species of *Taenia* are generally large and conspicuous as adults, often exceeding several meters in length, with a distinctly segmented ribbon-like strobila and a characteristic arrangement of rostellar hooks on the scolex or holdfast; the metacestode is a cysticercus or a modification of such bladderworms [2].

Species of *Taenia* were among the earliest recognized helminths in humans, with written records of these parasites extending into antiquity. Notably, the first complex life cycles for any tapeworms, with the linkage of larval and adult morphology and ontogeny in conjunction with recognition of the ecological basis for transmission between intermediate and definitive host, were demonstrated for species of this group nearly 150 years ago [2]. Over the last century, the taxonomy and systematics, life history, epidemiology and ecology of species of *Taenia* have received exhaustive attention, such that members of this genus are now among the best known of the tapeworms [2,3].

Although the genus has received considerable scrutiny, a variety of opinions have led to a proliferation of generic-level taxa and have often resulted in differing conclusions about taxonomy, diversity and proposed relationships among species [4]. For example, prior to the elucidation of life history patterns for taeniids, the adults and larvae of single species were often listed under different generic names (among others: *Taenia saginata* Goeze, 1782 = *Cysticercus bovis* Cobbold, 1866; *T. solium* Linnaeus, 1758 = *C. cellulosae* Gmelin, 1789; *T. multiceps* Leske, 1780 = *Coenurus cerebralis* Batsch, 1786; *T. taeniaeformis* (Batsch, 1786) = *Hydatigera taeniaeformis* and *Strobilocercus fasciolaris* Rudolphi, 1808). More recently, a number of generic names have continued to be applied to putative species-groups of *Taenia* (e.g., *Multiceps* Goeze, 1782, *Hydatigera* Lamarck, 1816, *Fimbriotaenia* Korniushin and Sharpilo, 1986), based primarily on differences in larval morphology. In their adult stage, however, all species of *Taenia* are rather morphologically homogenous, and this has led to the current taxonomy, which subsumes a diversity of generic names within the genus [3,4]. The concept for *Taenia* as a cohesive monophyletic taxon received corroboration from recent phylogenetic studies indicating that larval

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diversity has been acquired secondarily, and that the recognized modifications of the cysticercus do not diagnose inclusive evolutionary groups within the genus [4].

The genus *Taenia* is speciose, and since the 1700s, nearly 100 nominal taxa have been proposed or described based on either adult or larval forms. The group has been large and unwieldy, with the actual number of valid species now appearing to be closer to 40 (and four subspecies), with 33 based on adults and metacestodes, five based only on adults and two species based only on metacestodes [3]. Thus, unlike other tapeworm groups, the life cycles have been elucidated for a substantial number of *Taenia* spp., 33 of 40, that have been described based on adult strobilate specimens [3,4]. This knowledge is significant because it allows us to develop a deeper understanding of the patterns of distribution and the evolutionary history for species of this diverse genus.

Life cycles for *Taenia* consistently involve two mammalian hosts, a carnivorous or omnivorous definitive host (e.g., canids, felids, viverrids, mustelids, hyaenids and humans) and a herbivorous intermediate host (principally artiodactyls, rodents and lagomorphs) [2,3]. The intermediate host is infected with cysticerci in the musculature, visceral organs or central nervous system, depending on the species of *Taenia*. The adult or strobilate tapeworm develops in the intestinal lumen of the definitive host following ingestion of the infective cysticerci, and the prepatent period varies according to species. Eggs or gravid proglottids containing oncospheres are passed in the feces and, when ingested by an appropriate herbivore, will complete development to the infective cysticercus stage.

In general, the taeniids are unique among the cyclophyllideans in having mammals as both definitive and intermediate hosts. Transmission is ecologically based, with life cycles linked to specific predator–prey associations [2–4]. During the evolution of these parasite–host assemblages, diversification or speciation of *Taenia* spp. appears to have been linked primarily to host-switching among carnivorous definitive hosts [4]. Thus, if we examine patterns of association between *Taenia* spp. and their definitive and intermediate hosts, it is apparent that parasite cospeciation with carnivores has been particularly limited. Patterns of host association appear consistent, with shifts between phylogenetically unrelated carnivores (e.g., among canids, felids and hyaenids) that have historically exploited common prey resources in what are regarded as foraging guilds linked to specific biogeographic zones [4]. The host distribution for most species of *Taenia* is a consequence of historical ecology and food habits of carnivorous hosts in contrast to coevolution.

Species of *Taenia* historically are characteristic of all continents except Australia and Antarctica, and there are no endemic species known from South America. The geographic distributions of some species, particularly those circulating in synanthropic cycles among dogs and domestic ruminants (e.g., *T. hydatigena* Pallas, 1766, *T. multiceps*, *T. ovis* (Cobbold, 1869)), among domestic canids or felids and rodents (*T. pisiformis* Bloch, 1780, *T. taeniaeformis*), and among humans and our primary food animals (*T. saginata* Goeze, 1782, *T. solium* Linnaeus, 1758, and potentially, *T. asiatica* Eom and Rim, 1993), have been extensively modified by global translocation coinciding with European exploration and colonization since the 1500s and by continuing globalization of agriculture and changing patterns of human immigration. These observations for evolution and biogeography are critical in developing an understanding of the occurrence and distribution of the three species of *Taenia* that are restricted to human definitive hosts.

2. Origins of human-*Taenia*

Phylogenetic information is the foundation for understanding the history of host association and geographic distribution of host–parasite assemblages and for making informed predictions about parasite behavior and biology. In this regard, the origins and relationships for the three species, *T. solium*, *T. saginata* and *T. asiatica*, that use human definitive hosts have, until recently, been unresolved. It has been well documented that the species of taeniids that are specific in human definitive hosts now have domestic ruminants as obligatory intermediate hosts [3]. How did this tight association arise, and what have been the driving mechanisms for the diversification of these economically and medically important tapeworms in humans?

Conventional wisdom has held that the origin of the association between humans and *Taenia* arose relatively recently, not more than 10,000 years in the past, coincidental with the domestication of major food animals including cattle and swine and the advent of agriculture. It was proposed that in these early times of animal husbandry, tapeworms circulating in synanthropic cycles between dogs and domesticated ruminants were the source of *Taenia* that first colonized and then diversified in humans [5]. A contrasting hypothesis had suggested that for one species, *T. solium*, the association with humans may have preceded the domestication of swine, and that the former was probably not closely related to *T. saginata* [6]. In the absence of a phylogenetic hypothesis for the parasites, it was not possible to critically evaluate these assumptions.

Phylogenetic studies of *Taenia* species have indicated that *T. saginata* and *T. asiatica* are sister-species, with both being distantly related to *T. solium* [4,7] (Fig. 1). Thus, the occurrence of *Taenia* in humans can be linked to a minimum of two independent host switches at some point in the past. Further analyses involving evaluation of phylogenetic, geographical, ecological and molecular divergence data (the latter for the sister-species *T. saginata* and *T. asiatica*) were compatible with an association between *Taenia* and hominids that developed prior to the origin of modern humans in Africa [8]. Remarkably, in the latter study, it was postulated that the origin of host–parasite assemblages involving *Taenia* and humans arose through direct predator–prey associations between hominids and bovids such as antelopes, or through the scavenging of bovids killed by carnivore predators, including those in a paleoguild of felids, canids and hyaenids on the savannahs of Sub-Saharan Africa during the Pleistocene or earlier. This is consistent with the following observations: (1) the sister-species of *T. solium* is *T. hyaenae* Baer, 1926, a taeniid that circulates among hyaenids and antelopes; and (2) the sister-species of *T. saginata* + *T. asiatica* is *T. simbae* Dinnik and Sachs, 1972, a typical parasite in lions and antelopes in Africa [8] (Fig. 1). An ecological and biogeographic context for the acquisition of *Taenia* by hominids is apparent, given that a shift in diet from herbivory to carnivory by our ancestors would have promoted the sharing of parasites within a guild of carnivores and their bovid prey.

These studies support the contention that the association between *Taenia* and humans is archaic, having resulted from ecological linkages established well in the past. Clearly, the occurrence of *Taenia* in humans pre-dates the domestication of major food animals and the global expansion of agriculture and animal husbandry [8]. Consequently, humans would have represented the source of taeniids that later became established in cycles now largely obligatory in cattle or swine as intermediate hosts. In this regard, acquisition of *Taenia* by domestic animals from humans has apparently occurred independently on three occasions, represented now by *T. saginata* in cattle, and the separate lineages *T. asiatica* and *T. solium* in swine. Significantly, ecological associations established by our ancestors have had consequences for the distribution of pathogens, parasites and parasite assemblages that continue to exert substantial medical and veterinary repercussions for contemporary humans.

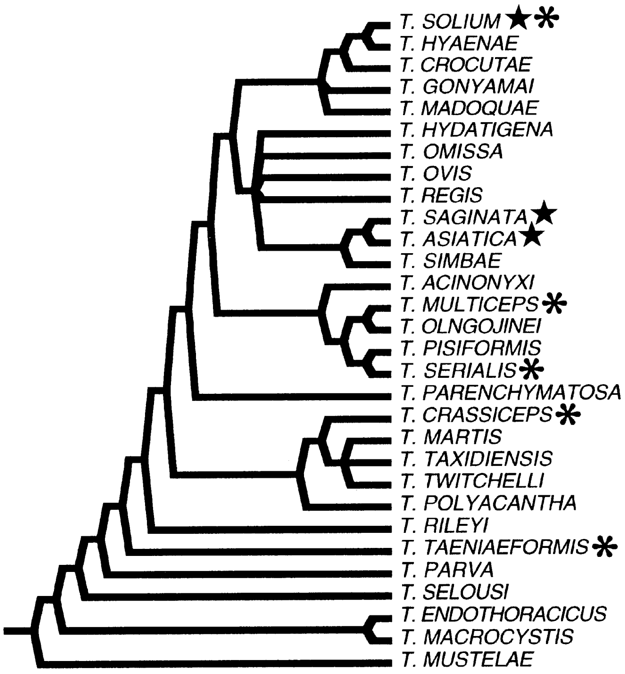

Fig. 1. Phylogenetic hypothesis for species of *Taenia* based on analyses among 30 species for which complete comparative morphological data for adults and metacestodes are available along with detailed life history information; tree is modified from Hoberg et al. [4]. Species of uncertain status, including *T. krepkogorski* (Shulz and Landa, 1934) and *T. retracta* von Linstow, 1903, are excluded. Shown are the relationships of those species that are host specific as strobilate adult worms in humans (stars), and those species known to cause cysticercosis or coenurosis in human hosts (asterisks). Only *T. solium* can cause both taeniasis and cysticercosis in human hosts.

3. Biology, distribution, impact and control of human-*Taenia*

The impact or socioeconomic significance of the three species of *Taenia* in humans varies according to patterns of distribution, biology and other specific characteristics of the host–parasite interface. *T. solium* remains the most significant because of its propensity for cysticercosis and neurocysticercosis (NCC) in humans [9–11]. Cysticercosis is currently considered the most common parasitic disease of the central nervous system [12] and continues as a major concern in endemic regions of Latin America, India, Asia, Eastern Europe and Africa.

3.1. T. solium

The pork tapeworm, *T. solium*, has a global distribution but is most common in those regions where pork is consumed [1–3]. The strobilate adult occurs in the intestinal lumen of human hosts, and most infections involve a single parasite. Symptoms associated with taeniasis are often non-specific and include such manifestations as hunger pains, altered appetite, weight loss, abdominal pain, vomiting, diarrhea and constipation, or infections may be largely asymptomatic; the primary pathognomonic sign is the spontaneous release of proglottids [13]. Toxic effects from parasite metabolites have also been reported. Diagnosis of taeniasis attributable to *T. solium* continues to be challenging, although an array of methods for detection have been developed [1,13]. Luminal infections in humans, although readily treated, may remain undetected for an extended period of time. Basic information on the life history of *T. solium* has often been extrapolated from studies on *T. saginata*; the current understanding that these species are only distantly related suggests a new focus on the biology of the former species is warranted [14].

A broader understanding of the potential impact for NCC was established through application of computerized imaging and improved serodiagnostic capabilities. Diagnosis of NCC, however, remains challenging, and primary criteria should be based on neuroimaging, serology, clinical history and exposure [11]. Based on data for 1992, there were an estimated 50 million cases of human taeniasis/cysticercosis, with annual deaths attributed to NCC of 50,000. Accurate estimates of the true prevalence of infection in humans, however, are hindered because cysticercosis is not a reportable disease [10]. It may be possible, however, to derive an estimate of the prevalence of NCC based on neurological records. For example, in endemic areas, it has been shown that 50% of late onset epilepsy is attributable to NCC [15]. Thus, in California, where epileptic seizures are currently reportable, it is conceivable that a correlation between NCC and late onset epilepsy that is carefully validated could serve as an adjunct in developing a broader understanding of the distribution of human infection for other regions. Possible strain variation for *T. solium* that is geographically partitioned may result, however, in differing behavior, sites of predilection and pathology for cysticercosis. Currently, NCC appears to predominate in Latin America and Africa, whereas a combination of neural and subcutaneous cysticercosis is observed in Asia, and such patterns of distribution could complicate a clear interpretation of neurological records [16,17].

Most infected individuals are between 20 and 50 years of age, and debilitation from cysticercosis represents a multifaceted economic impact, with substantial human suffering. Attendant losses are seen in productivity, costs of treatment and hospitalization and an insurmountable challenge to medical resources that may be reflected in several billion dollars US on an annual basis. Across developing countries, this can constitute a substantial challenge for economic expansion [9,18]. Neurocysticercosis is of increasing concern, as this disease of poverty continues to emerge and be maintained in developing countries of Asia, Africa and Latin America [1]. Additionally, the globalization of taeniasis and cysticercosis through travel, commerce and increased immigration by a migrant workforce has led to re-emergence and heightened incidence of NCC in industrialized centers that border endemic regions, where otherwise the parasite had been previously eradicated [10–12,18,19].

The adult pork tapeworm can survive up to 25 years in its human host, enhancing the possibilities for dissemination of eggs to a parasite naive population via food contamination and other routes [18]. Extended longevity and high fecundity of the adult parasites, and eggs that are highly resistant to ambient environmental conditions, remaining viable for up to 8 months in warm and humid climates, exacerbate the challenge of breaking the cycle for transmission. Control of cysticercosis and NCC remains problematic and must rely on differing strategies for developing and industrialized regions. A predisposition for perpetuation of human cysticercosis attributable to *T. solium* is linked to well-recognized factors: (1) inadequate sanitation, or disposal of human sewage, particularly for agricultural workers; (2) free-ranging swine and absence of confinement rearing; (3) ineffective systems for meat inspection; and (4) ingestion of inadequately cooked pork that maintains the circulation of adult parasites (e.g., cooking in excess of 77 °C for 30 min is required) [9,10,20].

It has been proposed, however, that because *T. solium* has two primary obligate hosts, humans and swine, this parasite could be successfully eradicated by elimination of the reservoirs for infection [10]. Interruption of transmission in the US and Western Europe has been achieved by changes in animal husbandry and improved meat inspection and sanitation [11]; in such non-endemic areas, the primary need is surveillance and intervention leading to identification and treatment of those harboring adult tapeworms. In developing countries, broader measures may include: (1) massive and sustained chemotherapy for humans and swine (a difficult option to achieve); (2) education; (3) vaccination of swine [21]; (4) socioeconomic development as a basis for improved hygiene and capabilities for inspection; and (5) surveillance and intervention [9,12,18].

Notably, it is possible for *T. solium* to be transferred to sylvatic intermediate hosts [22]. Human to bear transmission has been confirmed only recently, and such may have unknown consequences with respect to potential sylvatic sources of *T. solium* for human definitive hosts.

Compared to congeners, *T. solium* appears unusual with respect to the diverse array of intermediate hosts, among others including swine, canids, ursids and humans, in which cysticerci can develop successfully. Apart from *T. solium*, only *T. crassiceps* (Zeder, 1800), *T. hydatigena*, *T. pisiformis* and *T. serialis* (Gervais, 1847) are known to both infect a broad array of herbivores and also cause cysticercosis in their typical definitive hosts [2,3]. Phylogenetic studies in conjunction with comparative and functional genomics could be a useful approach for identifying possible intrinsic genetic and biochemical factors or pathways associated with the infective potential demonstrated for *T. solium* and these other species of *Taenia*.

In contrast to *T. solium*, there is currently no evidence that cysticerci of either *T. saginata* or *T. asiatica* can develop in humans [23]. From a predictive standpoint, relative to the phylogeny for *Taenia* spp. and, specifically, to the putative sister-species relationship for *T. saginata* and *T. asiatica* [4,8], human cysticercosis and NCC may not be expected for the latter species, although this potential requires further evaluation [23] (Fig. 1).

3.2. T. saginata

Similarly to *T. solium*, the beef tapeworm *T. saginata* has a cosmopolitan distribution and an obligate relationship with primary food animals for humans [2,3]. The strobilate adult occurs in the intestinal lumen and, though rarely fatal, can result in nausea, weight loss and abdominal pain and a range of symptoms similar to those documented for *T. solium* [13]. Luminal infections in humans may be of long duration, perhaps exceeding 20–25 years, in the absence of treatment. Cysticercosis in humans, however, is not attributable to this species, and thus, *T. saginata* does not have significant implications for public health in the realm of those attributed to *T. solium*.

Cysticercosis caused by *T. saginata* in cattle, however, is not benign and is the source of substantial production losses and subclinical infections that result in condemnation and exclusion of infected cattle from the human-food chain. Bovine cysticercosis causes in excess of US $2 billion in production losses annually and continues to constitute a major issue for food safety on a global scale, as summarized by Fan and Chung [24]. Infected carcasses imported to non-endemic regions can be the source of human infections, such as those associated with the increasing prevalence of taeniasis documented in Norway [25]. Human exposure can be controlled by freezing carcasses or meat for consumption at –10 °C for 10 d, or by heating above 60 °C; in cases where lesions are extensive, the carcass is condemned [26]. Substantial economic impacts accrue, however, through increasing labor costs of handling infected carcasses and processes that are required to render cysticerci non-viable.

Bovine cysticercosis and human taeniasis are perpetuated in agricultural environments. Often, infected agricultural workers are the source of contamination for cattle feed, and transmission cycles are driven by several mechanisms: (1) direct transmission through fecal contamination from agricultural workers; (2) application of untreated human sewage sludge onto pastures; (3) indirect contamination of food products or water for cattle; and (4) dissemination of parasite eggs by birds from sewage sources to feed bins, silage and cattle pens. Human hosts may release several segments daily, each containing thousands of eggs, and a single infected agricultural worker can be responsible for epizootic outbreaks in cattle [20]. Notably, eggs are resistant and may survive and remain infective for several months under suitable conditions. Measures for control of bovine cysticercosis are, in general, those for human taeniasis and rely on meat inspection, human sanitation, education, surveillance and treatment to break the transmission cycle.

3.3. T. asiatica

Although the biology and distribution of taeniasis in humans has been extensively documented over the past 150 years, recently, a third, apparently host-specific, species of *Taenia* was discovered and described [27,28]. Extensive epidemiological studies, in conjunction with molecular analyses and comparative morphology, were the foundation for the recognition of *T. asiatica*, an abundant and prevalent parasite in human populations across southern Asia [23,27–29]. Recent molecular evaluations and phylogenetic analyses have indicated the independent and specific status of *T. asiatica* [4,7,30], although others have suggested that it is a subspecies of *T. saginata* [3,31]. In endemic areas of Taiwan, Indonesia and Korea, it may occur in 21% of local human populations [32]. In northern Sumatra, it was demonstrated in 10% of humans and 23% of pigs examined by Murrell et al. [33]. Current data suggest that *T. asiatica* has a relatively limited geographic distribution in Southeast Asia, although the problematic nature of identification and its similarity in the strobilate stage to *T. saginata* suggest the potential for a wider range for the host–parasite assemblage [23]. The primary life cycle involves humans as definitive hosts and swine or wild boar as intermediate hosts.

In contrast to *T. solium* and *T. saginata*, specific sociocultural factors and customs are the primary determinant of transmission for *T. asiatica* [32]. Transmission to humans occurs through the consumption of undercooked viscera or organs of swine and wild boar, particularly the liver; other wild mammals could be involved based on local customs. Clinical signs are limited, but may include nausea, dizziness, increased appetite, headache and other manifestations, and often, infection is revealed by the spontaneous release of gravid proglottids [13,32]. Across the region, annual losses in excess of US $35 million are attributed to medical intervention and associated economic impacts of taeniasis in Taiwan, Korea and Indonesia, with *T. asiatica* representing the dominant species [32].

4. Other *Taenia* as zoonotic parasites—coenurosis/cysticercosis

Taenia spp. have substantial zoonotic potential, resulting in what appear to be exceptional cases of cysticercosis and coenurosis in human hosts [34]. Human infections for a variety of metacestodes of *Taenia* spp., however, may be more common than currently documented, particularly if localization for larval parasites does not involve vital organs. Infections by metacestodes of *Taenia* in humans often involve those species associated with synanthropic cycles and otherwise circulate among companion animals such as dogs and cats as definitive hosts [2,3]. Excluding *T. solium*, metacestodes of four species, *T. crassiceps*, *T. multiceps*, *T. serialis* and *T. taeniaeformis*, have been documented in humans [2,3]. The ability of certain species of *Taenia* to infect humans as intermediate hosts does not appear to have a phylogenetic basis [4] (Fig. 1).

Coenurosis in humans is attributable to metacestodes of *T. multiceps* and *T. serialis* that respectively involve life cycles among sheep, goats and canines or among lagomorphs, rodents and canines and some felids [34]. These parasites have cosmopolitan distributions, and the former is abundant in all countries where sheep and goat herding remain important components of local economies. In contrast to cysticercosis linked to *T. solium*, most cases of coenurosis are observed in children. Worldwide, several hundred cases have been documented, with infections being most prevalent in Africa [34]. Cerebral coenurosis is generally considered to represent *T. multiceps*, whereas subcutaneous infections are attributed to *T. serialis*, although morphologically the metacestodes are nearly indistinguishable [2,34].

Other species of *Taenia* that circulate in sheep–dog cycles (*T. ovis* and *T. hydatigena*), or among dogs, wolves and semi-domestic stock such as reindeer and wild cervids, including caribou (*T. ovis krabbei*), have not been implicated in cysticercosis in humans. Although Abuladze [2] lists humans as an intermediate host for *T. hydatigena*, such records could not be confirmed.

Although cysticerci of *T. crassiceps* have been infrequently reported in humans, such infections are potentially serious because of the proliferative nature of the metacestodes [35]. Strobilate adults of this species occur in foxes and occasionally in dogs, and cysticerci occur in rodents and have also been reported in other carnivores [2,35]. Contributing factors to the distribution of cysticercosis in atypical intermediate hosts are large rodent and fox populations and free-ranging dogs. Subcutaneous cysticercosis may pose a limited clinical problem in humans, but localization in other organs, including the eye, may indicate the potential for serious disease [35]. Of particular concern may be the development of proliferative cysticercosis in patients with HIV-AIDS or otherwise impaired immune systems [36,37].

T. taeniaeformis is the only other species known to infect humans, but reports of characteristic strobilocercus-type larvae have been rare [38]. This taeniid is a characteristic parasite in felid definitive and rodent intermediate hosts, but interestingly, there are also uncommon reports of strobilate tapeworms in luminal infections of humans in Argentina, Japan and Sri Lanka [38,39].

Although infections of strobilate adult *Taenia* in humans are rare [2], it is not inconceivable that exposure to infection through ingestion of cysticerci or coenuri from a variety of wild game animals, including wild ruminants and lagomorphs used as a food resource, could result in taeniasis. The potential might be heightened for those individuals with impaired immune function, and suggests that health care professionals should be alert to this unexpected phenomenon.

The potential for cysticercosis or coenurosis in humans is a function of the following: (1) prevalence of the cestode in canid or felid definitive hosts; and (2) frequency of contact between humans and the definitive host and the possibility of contact with cestode eggs. Thus, for some species, domestic cats and dogs are potential sources of infections for humans. Emphasized here is the importance of synanthropic foci and an array of infected sylvatic intermediate hosts that may serve as reservoirs for infection [38]. Control is achieved by adequate and regular treatment of companion animals to reduce dissemination of infective oncospheres. The potential for infections by a number of *Taenia* spp. in humans and companion animals continues to drive the necessity for accurate and rapid methods for diagnosis.

5. Diagnostics and molecular markers

Identification of various species of *Taenia* is often problematic, given the great superficial similarity of morphological characters that are diagnostic, and the often overlapping distributions with respect to both intermediate and definitive hosts and geographic range [3]. The standard or classical foundation for diagnostics among most species remains comparative morphology based on the study of characteristic structural attributes of adult and gravid worms, and unique characters of larval parasites [2,3]. The presence, arrangement and structure of rostellar hooks are often diagnostic for both strobilate adults and metacestodes, although substantial overlap in meristic parameters may occur among some species [3]. Consequently, combined approaches using well-defined morphological characters in conjunction with molecular sequence analysis and comparison of molecular markers should now represent the baseline or standard for modern diagnostics, particularly when structural attributes are ambiguous [22,40].

Morphological homogeneity, particularly among cysticercus-type metacestodes, can confuse accurate identification. In issues related to food safety, particularly for *T. saginata*, *T. asiatica* and *T. solium*, it cannot always be assumed that the correct identification can be based on host occurrence; e.g., Van der Logt and Gottstein [40] demonstrated this problem with unidentified cysticerci presumed to be *T. saginata* in cattle from New Zealand and Switzerland. Additionally, it is often assumed that human cysticercosis, and neural infections, are attributable only to *T. solium*; however, such potential misdiagnosis can be avoided through detailed morphological and/or molecular analysis of metacestodes [41]. Significantly, such observations also suggest that the diversity and geographic distribution of *Taenia* spp. among food animals, and possibly human definitive hosts, has yet to be completely documented [23]. The critical priority in diagnostics for *Taenia*, however, continues to be differentiation of those species in humans and, particularly, rapid and unequivocal identification of human hosts for *T. solium*.

The utility of molecular markers derived from either mitochondrial or nuclear loci for the identification of human-*Taenia* has been amply demonstrated [29,30,42–45]. These studies, however, have focused on a limited number of species in the genus, and a more synoptic comparative approach seems warranted in order to define patterns of genetic diversity and interspecific variation for *Taenia* spp. and to further recognize and refine unequivocal diagnostic markers.

6. Conclusions

The association between humans and taeniid tapeworms is archaic, having resulted from ecological linkages established in Africa among our ancestors, carnivores and their bovid prey. Thus, the basis for contemporary human taeniasis has deep historical roots, and is not the result of relatively recent domestication of our major food animals, including cattle and swine, and acquisition of tapeworms circulating in a synanthropic assemblage. Domestication of ungulates and expansion of human agriculture throughout the world, however, served to secondarily create the conditions for a broad cosmopolitan distribution for *T. saginata* and *T. solium*.

Human taeniasis and cysticercosis remain significant challenges for public health and food safety, and a continuing threat to animal production on a global basis. Infections in humans and our food animals cause in excess of US $3–4 billion in annual losses that are sustained in measures for control and medical intervention, and through lost productivity. Although the problem is global in scale, the majority of such costs are incurred in the developing world, where their effects are particularly exacerbated by poverty and where economic impacts act to dampen socioeconomic development.

Ultimately, effective control of taeniasis and cysticercosis relies on epidemiological data and accurate identification of both adult and larval stages. There continues to be insufficient knowledge of the prevalence of infections for human taeniasis in both developing and industrialized countries and regions. This lack of knowledge has tended to mask the recognition of the depth and scope of economic and medical impacts associated with the emergence and re-emergence of human taeniasis and cysticercosis throughout the world.

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