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Review

State-of-the-art *Echinococcus* and *Taenia*: Phylogenetic taxonomy of human-pathogenic tapeworms and its application to molecular diagnosis

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ABSTRACT

The taxonomy of tapeworms belonging to the family Taeniidae has been controversial because of the paucity of adult phenotypic characters and the great plasticity of larvae in intermediate hosts. The family consists of the medically important two genera *Echinococcus* and *Taenia*, which are closely related to each other. Cladistic approaches using the molecular data of DNA and the numerical data of morphologic characters are clarifying phylogenetic relationships among the members of these genera. The nucleotide data of worldwide taeniid parasites accumulated in public DNA databases may provide a basis for the development of molecular diagnostic tools, and make it possible to identify the parasites, at least the human *Taenia* spp. by non-morphologists. Furthermore, the detection of intraspecific genetic variations prompts evolutionary and ecological studies to address fundamental questions of parasite distributional patterns. Here, we introduce the recent advances of taeniid phylogeny and its application to molecular diagnosis.

Contents

1. Introduction

The combination of morphological taxonomy, molecular genetics and evolutionary ecology is required to better understand the biodiversity of parasitic organisms. Fundamental information on their phenotypic and genotypic characteristics is especially important to control human and animal parasitic diseases. Moreover, regional and global phylogeographic surveys establish a basis of understanding for the evolutionary history of parasites. The species identification of pathogenic organisms is essential for the diagnosis and treatment of infectious diseases. Multicellular parasites have traditionally been classified by morphological taxonomists, who provide a prerequisite fund of knowledge to differentiate etiologic agents isolated from humans and animals. However, the delineation of sibling or cryptic species is a difficult issue in morphological taxonomy. In addition to identifying species, exploring intraspecific variations has become a scientific imperative to characterize the local populations of parasites. The knowledge of parasite diversity at intraspecific level is necessary to understand the difference of clinical manifestations, and become a basis for the development of vaccines and immunodiagnostic antigens.

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The classification of tapeworms belonging to the family Taeniidae has been controversial because of the paucity of adult phenotypic characters and the great plasticity of larvae developed in various intermediate hosts. Recent advances on biochemical tools for DNA amplification and sequencing have provided a basis for the development of molecular taxonomy. Database catalogs known as ‘‘DNA barcoding’’ (Hebert et al., 2003) make it possible to identify parasites by non-morphologists. A DNA-based approach to the identification of parasites has also prompted the fields of molecular epidemiology and ecology. In this review, we deal especially with the phylogenetic taxonomy of human taeniid tapeworms and summarize the molecular diagnosis of the parasites.

2. Basic knowledge of taeniid parasites

Table 1 shows a brief list of human-pathogenic taeniid species and their closest relatives. The family Taeniidae is a medically important group of tapeworms constituted of the two genera *Echinococcus* Rudolphi 1801 and *Taenia* Linnaeus 1758. Two mammalian hosts showing predator–prey relationships are necessary to maintain the life cycle of the parasites. Carnivores are mostly definitive hosts for hermaphroditic adults, and herbivorous mammals serve as intermediate hosts for bladder larvae. When the intermediate hosts are eaten by the definitive hosts, ingested scolices attach to the intestinal mucosa and develop into adult tapeworms consisting of a chain of proglottids with genital organs. The gravid proglottids containing embryonated eggs are released into external environment. The intermediate hosts orally ingest the eggs, and hatched oncospheres invade various tissues to develop into fluid-filled bladder larvae. The larvae of both hydatid (*Echinococcus* spp.) and coenurus (*Taenia* spp.) enlarge their sizes in connection with the asexual reproduction of scolices in the bladders, whereas cysticercus (*Taenia* spp.) containing an invaginated scolex is mostly regarded as a non-multiplying larva.

All *Echinococcus* spp. are tiny tapeworms within several millimeters in length, but numerous tapeworms are parasitic on a canine definitive host because of the predation of infected animals containing many protoscolices. Medically important pathogens are the dog tapeworm *Echinococcus granulosus* sensu stricto (s. s.) and the fox tapeworm *Echinococcus multilocularis* (Eckert and Deplazes, 2004). Humans are vulnerable to the larval infestation through oral ingestion of eggs derived from feces of canine definitive hosts. Cystic echinococcosis caused by *E. granulosus* s. s. occurs worldwide, particularly in African, Asian and South American countries, whereas alveolar echinococcosis by *E. multilocularis* is restricted in the endemic areas of the Northern Hemisphere. Because sheep is a main intermediate host for *E. granulosus* s. s., a pastoral environment in which working dogs ingest the viscera of sheep is essential for maintaining the synanthropic cycle of the parasites. In human cystic echinococcosis, the liver and lungs are main target organs, and it takes many years to enlarge the spherical hydatid larvae. Alveolar echinococcosis caused by *E. multilocularis* exhibits a contrast to cystic echinococcosis. The parasite principally utilizes foxes as definitive hosts and voles as intermediate hosts, but humans are involved as an aberrant host. In humans, alveolar hydatid usually occurs in the liver, and minute vesicles proliferate slowly in the manner of exogenous budding. The invasive larval development is lethal to humans and animals. The disease is hyperendemic in the Tibetan communities of China (Schantz et al., 2003; Craig et al., 1992, 2008; Craig, 2006), but sporadically occurs even in industrialized European countries (Romig et al., 2006) and in Japan (Ito et al., 2003a).

Among the members of the genus *Taenia*, only *Taenia solium*, *Taenia saginata* and *Taenia asiatica* use humans as a definitive host. The latter species was formerly treated as a geographic race of *T.*

Table 1

Human-pathogenic species of the family Taeniidae and their closest relatives.

Species (genotype)[a]	Human infections[b]	Main hosts for		Distribution[c]
		Adult	Larva	
The genus *Echinococcus*				
E. granulosus (G1)	Common*	Dog	Sheep	Cosmopolitan
E. equinus (G4)	Unknown	Dog	Horse	PA
E. ortleppi (G5)	Rare*	Dog	Cattle	PA, ET and NT
E. canadensis (G6, G7)	Rare*	Dog	Camel, pig	PA, ET and NT
E. canadensis (G8, G10)	Rare*	Wolf	Cervid	PA and NA
E. felidis	Unknown	Lion	Warthog?	ET
E. multilocularis	Common*	Fox	Rodents	PA and NA
E. shiquicus	Unknown	Fox	Pika	PA (Tibet)
E. oligarthrus	Very rare*	Wild felids	Rodents	NT
E. vogeli	Not rare*	Bush dog	Rodents	NT
The genus *Taenia*				
T. saginata	Common#	Human	Cattle	Cosmopolitan
T. asiatica	Common#	Human	Pig	OR and PA (Asia)
T. solium	Common#,*	Human	Pig	Cosmopolitan
T. multiceps	Rare*	Canids	Ungulates	Cosmopolitan
T. serialis serialis	Rare*	Canids	Lagomorphs	Cosmopolitan
T. serialis brauni	Rare*	Canids	Lagomorphs	ET
T. crassiceps	Very rare*	Canids	Rodents	PA and NA
T. taeniaeformis	Very rare*	Felids	Rodents	Cosmopolitan
T. hyaenae	Unknown	Hyena	Ungulates	ET
T. crocutae	Unknown	Hyena	Ungulates	ET
T. simbae	Unknown	Felids	Ungulates	ET

[a] Data of each species are mainly taken from Verster (1969), Gasser et al. (1999), Loos-Frank (2000), Hoberg (2006), McManus and Thompson (2003), Xiao et al. (2005), Hüttner et al. (2008, 2009), Lavikainen et al. (2008), Moks et al. (2008), Saarma et al. (2009) and D'Alessandro and Rausch (2008). The genotypes G6 and G7 of *E. canadensis* were considered as a distinct species, namely *E. intermedius* (Thompson, 2008). The final taxonomic revision awaits the completion of ongoing studies.

[b] Asterisks indicate the accidental invasion of larvae into internal tissues, and hash marks denote the parasitism of adults in the small intestine. The categories of ‘‘very rare’’, ‘‘rare’’, ‘‘not rare’’ mean ‘‘few’’, ‘‘around 10 or more’’, and ‘‘around 100 or more’’ records have been reported, respectively.

[c] The areas are shown as zoogeographic regions; ET, Ethiopian; NA, Nearctic; NT, Neotropical; OR, Oriental; PA, Palearctic.