



Ancylostoma ceylanicum and other zoonotic canine hookworms: neglected public and animal health risks in the Asia–Pacific region

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Abstract

Zoonotic hookworm infections remain a significant public health problem, causing nearly 500 million cases globally and approximately four million disability-adjusted life years lost annually. More than one-fifth of these cases are attributed to *Ancylostoma ceylanicum*, an emerging zoonotic health issue in the Asia-Pacific region. This review presents key research gaps regarding the epidemiology, diagnosis, control, prevention and elimination of *A. ceylanicum* and other canine zoonotic hookworms as neglected health threats. *A. ceylanicum* is the second most prevalent human hookworm in the region; it is the most common hookworm among dogs and cats-reservoirs of zoonotic infections. Previous population genetic and phylogenetic analyses revealed that *A. ceylanicum* has three possible transmission dynamics: zoonotic, animal-only, and human-only pathways. The actual burden of zoonotic ancylostomiasis in most endemic countries remains unknown due to the use of parasitological techniques (e.g., Kato-Katz thick smear and floatation techniques) that have reduced diagnostic performance and do not allow accurate species identification in helminth surveys. The emergence of benzimidazole resistance in soil-transmitted helminths (STHs), including hookworms, is a concern due to the protracted implementation of mass drug administration (MDA). Resistance is conferred by single nucleotide polymorphisms (SNPs) that occur in the β -tubulin isotype 1 gene. These mutations have been reported in drug-resistant *A. caninum* but have not been found in *A. ceylanicum* in the field. *A. ceylanicum* remains understudied in the Asia-Pacific region. The zoonotic nature of the parasite warrants investigation of its occurrence in human and animal reservoir hosts to understand the dynamics of zoonotic transmission in different endemic foci. The detection of benzimidazole resistance-associated SNPs in zoonotic hookworms from Asia-Pacific countries has yet to be thoroughly explored. Considering the high level of hookworm endemicity in the region, the circulation of resistant isolates between humans and animals potentially presents a significant One Health threat that can undermine current MDA and proposed animal deworming-based control efforts.

Keywords Soil-transmitted helminths, Neglected tropical diseases, Mass drug administration, Deworming, Veterinary public health

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Introduction

Soil-transmitted helminths (STHs), including hookworms, roundworms, and whipworms, remain a significant global public concern because they are known to be the most prevalent of the 20 Neglected Tropical Diseases (NTDs) (Folahan 2023; Montresor et al. 2020). Hookworm infections cause a substantial disease burden worldwide. They are estimated to cause the loss of 800,000 to 4 million disability-adjusted life years (DALYs) (Jourdan et al. 2018; Kyu et al. 2018). Zoonotic ancylostomiasis (i.e., hookworm infection that can be transmitted from animals to humans) is estimated to cause 229 million to 500 million cases globally each year (James et al. 2018; Stracke et al. 2020). Moreover, *A. ceylanicum* has been posited to cause almost 100 million cases in Southeast Asia and the Pacific region (Traub et al. 2021; Traub 2013; Colella et al. 2021a). The economic burden of hookworm disease is estimated to be 139 billion US dollars annually (Albonico and Savioli 2017; Loukas et al. 2016). The true global burden of hookworm infections remains poorly understood due to the routine use of insensitive diagnostic tests in epidemiological studies and the general neglect attributed to diseases that disproportionately affect people in resource-lacking areas.

Ancylostoma ceylanicum is known to be highly endemic in the Asia-Pacific region (Colella et al. 2021a). In this region, it is the second most prevalent human hookworm (Inpankaew et al. 2014a, b; Bui et al. 2021). Moreover, it is the most common hookworm among dogs and cats and serves as a reservoir for zoonotic infections (Inpankaew et al. 2014a, b). It is commonly known as a canid hookworm, but it was originally described from a civet cat in Ceylon (present-day Sri Lanka) by Looss in 1905 (Kladkempetch et al. 2020; Looss 1905). It closely resembles *A. braziliense*, which makes morphological identification difficult. However, the lateral bursal rays of male *A. ceylanicum* worms have distinct conformations compared to those of *A. braziliense*: mediolateral and posteriolateral rays are parallel in the former, while all three rays are widely separated at their tips in the latter (Traub 2013). In addition to *A. ceylanicum*, other canine hookworms may cause human infections. These include *A. caninum*, *A. braziliense*, and *Uncinaria stenocephala*. *Ancylostoma tubaeforme* of cats is also of zoonotic importance (Bowman et al. 2010). Altogether, these hookworms cause various pathologies, ranging from cutaneous larva migrans (i.e., creeping eruptions) and eosinophilic enteritis to protein deficiency and iron deficiency anemia (Jourdan et al. 2018; Loukas et al. 2016).

The main objective of this narrative review is to highlight *A. ceylanicum* and other zoonotic canid hookworms as neglected health issues in the Asia-Pacific region. The life cycle, pathology, and treatment of this parasite are

reviewed herein. This review presents key research gaps regarding the epidemiology, diagnosis, control, prevention, and elimination of *A. ceylanicum* and other canine zoonotic hookworms as health threats to inhabitants in the region. The emergence of benzimidazole resistance among zoonotic hookworms and how it may undermine current STH control programs are also discussed. Research gaps and future research directions are likewise provided herein. Finally, this paper aims to contribute to eliminating zoonotic hookworms, which are prevalent in resource-lacking communities in the Global South.

Life cycle and transmission dynamics

The life cycle of *A. ceylanicum* is direct and does not require any intermediate hosts (Fig. 1). Dogs, cats and humans serve as the primary definitive hosts where the hookworms reach maturity and lay eggs in the small intestines. Eggs are liberated into the environment *via* defecation. Eggs can hatch into 1st-stage rhabditoid larvae after two to seven days and reach the third-stage filariform larvae after four to eight days (Eteawa et al. 2016). Several factors affect the development of hookworm larvae in the environment. A temperature between 20°C and 30°C is considered the optimal for development (Eteawa et al. 2016). Moreover, adequate moisture, sandy soil with abundant organic matter, and being away from direct sunlight are conducive for hatched larvae to develop into the infective stage (Irisarri-Gutiérrez et al. 2016). Infection is acquired through percutaneous penetration of 3rd-stage filariform larvae, which are found in the environment. Bare skin contact with the soil, which imparts temperature and moisture changes in the immediate environment, triggers the ability of infective stage larvae to penetrate the host's skin (Loukas et al. 2016). These larvae enter the bloodstream, find their way into the respiratory system, undergo tracheal migration, and are swallowed toward the digestive tract. These events occur approximately seven days postinfection (Colella et al. 2021a). After approximately 14 days in dogs or 18 to 35 days in humans (i.e., approximately 20 days on average), the hookworms mature to adulthood, copulate, and become patent infections (Colella et al. 2021a). The 60 × 20 μm eggs are liberated into the environment, embryonate, hatch, undergo two moltings, and become infective 3rd-stage larvae within two to 10 days (Jourdan et al. 2018; Traub 2013).

To assess the transmission dynamics of *A. ceylanicum*, studies have used phylogenetic and population genetic approaches to assess the mitochondrial *cox1* gene (Fig. 1). Phylogenetic analysis in Cambodia and Thailand revealed two clades (Fig. 1B): the prevalent zoonotic clade and the human-specific clade (Inpankaew et al. 2014a, b; Phoo-sangwalthong et al. 2023; Wongwigkan and Inpankaew

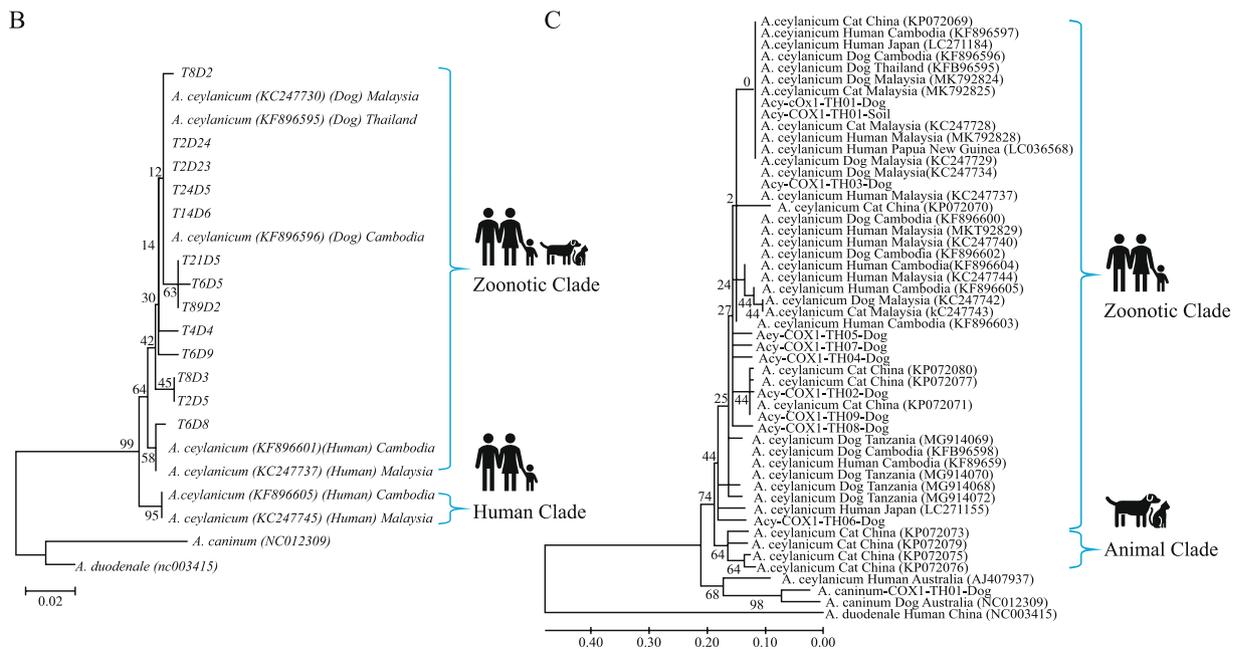
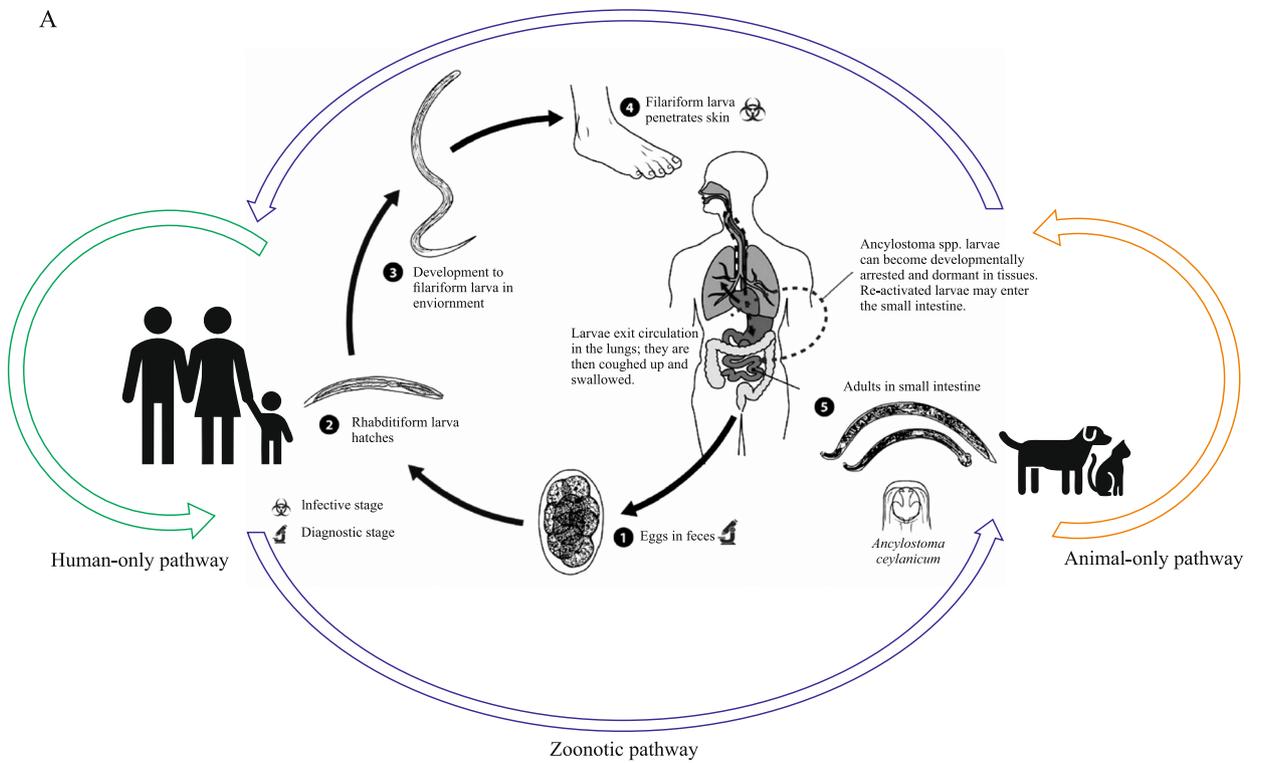


Fig. 1 Life cycle and transmission dynamics of *Ancylostoma ceylanicum*. The life cycle is direct and requires humans, dogs or cats as definitive hosts (A) As determined by population genetics and phylogenetic analyses, the transmission dynamics of *A. ceylanicum* can be divided into 3 routes (US Centers for Disease Control 2019) : the zoonotic (blue, B, C), human-only (green, B) (Wongwigkan and Inpankaew 2020), and animal-only (orange, C) pathways (Kladkempetch et al. 2020). Figures containing phylogenetic trees were modified with permission

2020). On the other hand, other studies in China and Thailand revealed that some *A. ceylanicum* populations may also be divided into zoonotic and cat-specific phylogenetic haplotypes (Kladkempetch et al. 2020; Hu et al. 2016) (Fig. 1C). These results indicate that there might be three possible transmission pathways exhibited by the zoonotic hookworm (Fig. 1A). The first is the zoonotic pathway, which circulates between humans and animal reservoir hosts in endemic areas. This seems to be the most prevalent and potentially the most dangerous, as canids and felids serve as primary reservoirs of human infections. The second and third are populations that seem to be distributed within their respective hosts: animal-specific and human-specific haplotypes. To date, few studies have investigated the population genetics and phylogeny of *A. ceylanicum* in the Asia-Pacific region. Hence, the distribution of these three populations with distinct transmission pathways remains unclear. Therefore, there is a need to evaluate the molecular epidemiology of this zoonotic parasite in most endemic countries.

Epidemiology of human infections

Ancylostoma ceylanicum is known to be the second most prevalent human hookworm in the Asia-Pacific region, next only to *Necator americanus* (Bui et al. 2021; Colella et al. 2021a, b; Stracke et al. 2020). A recent systematic review revealed that the pooled prevalence of

N. americanus was 67% in the region, while the pooled prevalence of *A. ceylanicum* and *A. duodenale* was 12% and 4%, respectively (Clements and Alene 2022). Hookworm infections have been reported to cause more than 800 thousand to four million DALYs to be lost (Jourdan et al. 2018; Kyu et al. 2018). Zoonotic ancylostomiasis has been estimated to cause at least 229 million to nearly 500 million annual cases globally (James et al. 2018; Stracke et al. 2020). Moreover, *A. ceylanicum* has been posited to cause almost 100 million cases in the Asia Pacific region (Traub et al. 2021; Traub 2013; Colella et al. 2021a, b). The disease burden attributed to hookworms is estimated to cause economic losses of approximately 139 billion US dollars (Albonico and Savioli 2017). Infections with *A. ceylanicum* have been noted in China, Cambodia, Japan, Thailand, India, Australia, Malaysia, Myanmar, Papua New Guinea, Vietnam, Bangladesh, Timor Leste, Sri Lanka, and the Philippines (Aula et al. 2020; Heo et al. 2022; Inpankaew et al. 2014a, b; Mallawarachchi and Samarasinghe 2020; Ngui et al. 2012; Stracke et al. 2020; Yoshikawa et al. 2018) (Table 1). Despite the recent increase in the number of papers reporting the occurrence of *A. ceylanicum* in the Asia-Pacific region, there are bottlenecks in the study of its epidemiology. Compared with novel molecular techniques, the diagnostic method recommended by the World Health Organization (2017; 2019) (i.e., the Kato-Katz thick smear

Table 1 Epidemiology of zoonotic hookworm infections in humans

Country	Zoonotic hookworm species	Key epidemiological findings	Reference
India	<i>Ancylostoma ceylanicum</i>	5% (2/41) of individuals were infected in tribal populations of Jawadhu Hills, Tamil Nadu	George et al. (2015)
Timor Leste	<i>Ancylostoma ceylanicum</i>	95.5% (21/22) of the samples assessed were positive using qPCR	Papaiakovou et al. (2017)
Bangladesh	<i>Ancylostoma ceylanicum</i>	3.8% (106/2799) of individuals tested harbored the infection	Benjamin-Chung et al. (2020)
Bangladesh	<i>Ancylostoma ceylanicum</i>	4.63% (30/648) of the individuals tested harbored the infection	Dunn et al. (2020)
Cambodia	<i>Ancylostoma ceylanicum</i>	46.0% (57/124) of the participants from Preah Vihear Province were infected	Inpankaew et al. (2014a, b)
Cambodia	<i>Ancylostoma ceylanicum</i>	12.67% (19/151) of the participants were infected	Colella et al. (2021b)
Philippines	<i>Ancylostoma ceylanicum</i>	26.6% (34/128) of the positive samples for <i>Ancylostoma</i> spp. were speciated	Aula et al. (2020)
Vietnam	<i>Ancylostoma ceylanicum</i>	52.1% (25/48) of the participants tested were infected	Bui et al. (2021)
Thailand	<i>Ancylostoma ceylanicum</i>	10% (3/30) of the cultured samples from the Northeast and Southern regions that tested were molecularly speciated	Phosuk et al. (2013)
Thailand	<i>Ancylostoma ceylanicum</i>	5.3% (97/1839) of the Burmese refugees that were assessed were infected	O'Connell et al. (2018)
Brazil	<i>Ancylostoma caninum</i>	1.9% (12/634) of the hookworm-positive samples were speciated	Furtado et al. (2020)
India	<i>Ancylostoma caninum</i>	16.8% (20/119) of hookworm-positive fecal samples were speciated	George et al. (2016)
Jamaica	<i>Ancylostoma caninum</i>	22.1% (17/77) of the human stool samples were infected	Lee et al. (2022)
South Africa	<i>Ancylostoma caninum</i>	6% (3/50) of the stool samples were determined to be infected using sequencing analysis	Ngcamphalala et al. (2019)
Lao PDR	<i>Ancylostoma caninum</i>	15% (3/20) of the hookworm positive samples that were sequenced were speciated	Sato et al. (2010)

technique) cannot distinguish hookworms to the species level, and it also has diminished sensitivity when used in settings of low endemicity (Benjamin-Chung et al. 2020; Levecke et al. 2011). Therefore, the actual epidemiological occurrence of human *A. ceylanicum* infections in endemic areas remains inconclusive and thus needs research attention.

In addition to *A. ceylanicum*, several canine hookworms have also been known to infect humans. Historically, canine hookworms, such as *A. caninum*, *A. braziliense*, and *Uncinaria stenocephala*, have been shown to cause dermatitis upon percutaneous infection similar to that caused by human hookworms and thereby have been noted to be zoonotic early on (Traversa 2012; White and Dove 1928). For instance, human *A. caninum* infections were reported to occur in Indonesia in 1925 and 1959, China in 1945, and South Korea in 2003 (Croese 1988; Kwon et al. 2003; Mao 1945). Recently, eosinophilic enteritis cases associated with *A. caninum* were reported in Egypt in 1999 and South Korea in 2020 (Bahgat et al. 1999; Jung et al. 2020; Khoshoo et al. 1995). Despite these many reports, immature canine hookworms that infect humans may fail to become patent either due to failure to reach maturity or single-sex infections (Traub 2013; Traub et al. 2021). In cases of eosinophilic enteritis where the clinical signs are acute and severe, infected *A. caninum* can be expelled as a result, thereby inhibiting the detection of adults or eggs, which complicates diagnosis (Procvic and Croese 1990). Indeed, historical and recent reports indicate that canine hookworm infections in humans are neglected public health concerns that continue to be relevant today. However, very little is known about its occurrence and current distribution. This is partly due to the difficulty of accurately identifying hookworms and the low probability of developing a patent infection. The development of molecular tools for the diagnosis of these hookworms may improve our understanding of these zoonoses. However, routine application of molecular tools may not be feasible at low-income loci where zoonotic hookworm transmission is most likely to occur. This necessitates the development of sensitive and specific tests that are economically feasible.

Epidemiology of companion animal infections

Reports on animal infections of *A. ceylanicum* have been gaining traction in the peer-reviewed literature (Table 2). A recent systematic review and meta-analysis revealed that the weighted prevalence of the zoonotic hookworm among canids in Asia is 35% (95% CI: 12 to 35%), with domesticated dogs having a 41% (95% CI: 29 to 53%) prevalence rate (Zibaei et al. 2020). Among other canine hookworms, *Uncinaria stenocephala* had the highest prevalence at 44% (95% CI: 18 to 55%), while *A. caninum*

and *A. ceylanicum* had prevalence rates of 27% (95% CI: 21 to 33%) and 24% (95% CI: 12 to 35), respectively (Zibaei et al. 2020). These results are echoed by recent surveys in different areas of the Asia-Pacific region. Taken together, the results shown in Table 2 imply that *A. ceylanicum* seems to be the most prevalent hookworm species that infects dogs and cats across Southeast Asia and in the greater Asia-Pacific region. However, the accurate identification of hookworm species that infect companion animals poses a problem in the study of the epidemiology of these helminths and their animal health implications. The zoonotic nature of the hookworm presents a potential One Health risk because it may undermine both public and veterinary health. Indeed, more research employing sensitive molecular techniques, perhaps combined with less expensive parasitological techniques, is needed to shed some light on these issues.

Pathology of zoonotic hookworm infections in humans and dogs

Zoonotic hookworm infections in humans and canids present a myriad of clinical signs that range from dermal conditions to gastrointestinal involvement and hematological disturbances. Cutaneous larva migrans (CLM) is widely recognized, with more than 300 cases reported annually in the peer-reviewed literature (Rodriguez-Morales et al. 2021). This skin condition is caused by the percutaneous entry of the infective larvae and their subsequent migration within the epidermis without penetration of the basement membrane (Traub 2013). Hookworms that normally infect humans (i.e., *A. duodenale* and *N. americanus*) and zoonotic canine hookworms (i.e., *A. caninum*, *A. ceylanicum*, *U. stenocephala* and *A. tubaeforme*) are known to cause CLM (Bowman et al. 2010). However, the more severe “creeping eruptions” are attributed to *A. braziliense*; this condition is characterized by pruritic, erythematous, and serpiginous eruptions (Jourdan et al. 2018; Traub et al. 2021). It has been noted that these dermatological lesions predominate among those who live in impoverished areas during rainy seasons and tourists from developed countries who visit such resource-lacking foci (Heukelbach and Feldmeier 2008; Rodriguez-Morales et al. 2021). Recently, CLMs have also been reported in nontropical areas, such as in the United States, where cases are commonly caused by *N. americanus* and *A. braziliense* (Johanis et al. 2023). The parasitism of *A. caninum* in the intestinal tract triggers an adverse condition known as eosinophilic enteritis. Patients with eosinophilic enteritis suffer from abdominal pain that resembles appendicitis, diarrhea, and melena due to eosinophilic infiltration of the intestinal mucosa and increased IgE levels (Procvic and Croese 1990; Walker et al. 1995). Parasitic infections, such as

Table 2 Epidemiology of zoonotic hookworm infections in companion animals

Country	Zoonotic hookworm species	Host species	Key epidemiological findings	Reference
Thailand	<i>Ancylostoma ceylanicum</i>	Dogs	96.5% (56/58) of the infected canine samples from Northern Thailand were speciated	Kladkempetch et al. (2020)
	<i>Ancylostoma caninum</i>		3.45% (2/58) of the infected canine samples from Northern Thailand were speciated	
Thailand	<i>Ancylostoma ceylanicum</i>	Dogs	67.7% (21/31) of the hookworm-positive samples from Bangkok were speciated	Wongwigkan and Inpankaew (2020)
	<i>Ancylostoma caninum</i>		32.3% (10/31) of the hookworm-positive samples from Bangkok were speciated	
China	<i>Ancylostoma ceylanicum</i>	Dogs	33.1% (47/142) of canine hookworm-positive samples were identified	Fu et al. (2019)
	<i>Ancylostoma ceylanicum</i>	Cats	51.1% (24/47) of feline hookworm-positive samples were identified	
	<i>Ancylostoma caninum</i>	Dogs	59.9% (85/142) of the canine hookworm-positive samples were identified	
	<i>Ancylostoma tubaeforme</i>	Cats	48.9% (23/47) of the feline hookworm-positive samples were identified	
Malaysia	<i>Ancylostoma ceylanicum</i>	Dogs	52.4% (43/82) of the of the canine hookworm-positive samples were identified	Mahdy et al. (2012)
	<i>Ancylostoma caninum</i>		47.6% (39/82) of the of the canine hookworm-positive samples were identified	
Malaysia	<i>Ancylostoma ceylanicum</i>	Dogs and cats	12 samples from dogs and 2 from cats were molecularly speciated	Ngui et al. (2013)
Philippines	<i>Ancylostoma ceylanicum</i>	Dogs	36.4% (12/33) of the hookworm-positive canine stool samples from Samar Province were identified	Aula et al. (2020)
Cambodia	<i>Ancylostoma ceylanicum</i>	Dogs	15.2% (68/447) of the hookworm-positive canine stool samples were speciated	Zendejas-Heredia et al. (2023)
	<i>Ancylostoma caninum</i>		13.9% (61/447) of the hookworm-positive canine stool samples were speciated	
	<i>Ancylostoma braziliense</i>		4.3% (19/447) of the hookworm-positive canine stool samples were speciated	
West Indies	<i>Ancylostoma ceylanicum</i>	Dogs	4.7% (10/211) of hookworm-positive canine stool were identified	Zendejas-Heredia et al. (2022)
	<i>Ancylostoma caninum</i>		27.5% (58/211) 4.7% (10/211) of hookworm-positive canine stool were identified	
	Mixed infection		8.5% (18/211) of the hookworm-positive canine stool carried mixed infections	

those caused by canine hookworms, should be included as a differential diagnosis for cases of human eosinophilic gastroenteritis (Sunkara et al. 2019). Additionally, larval migration of immature worms through the respiratory tract may result in Loeffler syndrome, a form of eosinophilic pneumonia associated with cough, dyspnea, and hemoptysis (Jourdan et al. 2018; Loukas et al. 2016; Ng et al. 2021).

The most notorious consequence of hookworm infections in humans and animals is iron deficiency anemia, which is deleterious to developing children and puppies and to females of reproductive age (Bowman et al. 2017; Owada et al. 2019; 2017). *A. ceylanicum* has been noted to consume 4 to 14 μ L of blood per worm per day (Traub 2013). In dogs, acute heavy infections have been posited

to cause blood loss of more than 500 mL within the first fortnight of infection (Rep et al. 1971). In cases of severe infections in humans, blood loss may be significant and results in the depletion of patient erythrocytes, iron, and hemoproteins, leading to severe anemia (Jourdan et al. 2018). *Ancylostoma* spp. infections have been noted to cause severe anemia in 37% of affected individuals, while *Necator americanus* was found to cause <1% to 14% severe anemia (Clements and Alene 2022). Moreover, both low- and high-intensity hookworm infections have been reported to be associated with reduced hemoglobin levels (Byrne et al. 2021). Additionally, recent case studies of infection among patients in endemic countries have shown that marked increases in eosinophil counts are associated with *A. ceylanicum* infections: counts of 1,570

to 20,470 cells/ μL and up to about 50% of leukocytes (Brunet et al. 2015; Yoshikawa et al. 2018). These adverse pathological consequences of infection are particularly harmful to preschool-aged and school-aged children. Hookworm infections, together with infections caused by other STH species, have been noted to impair the cognitive and motor development of children, potentially leading to life-long deleterious effects (Owada et al. 2019; 2017; Pabalan et al. 2018).

Diagnosis

Hookworm infections can be diagnosed through various methods (Table 1). The recommended method for human epidemiological studies, surveillance and control programs, and monitoring of drug efficacy is the Kato-Katz thick smear technique (World Health Organization 2017; 2013; 2011). The technique involves sieving fecal samples, clearing them with glycerol, and mounting them with cellophane (Mbong Ngwese et al. 2020). Zoonotic hookworm infections that are likely to be non-pathogenic or of low intensity are possibly missed when using the Kato-Katz technique, and species identification is impossible (Benjamin-Chung et al. 2020; Traub et al. 2021). Using Kato-Katz, the intensity of infection can also be estimated: 1–1999 geometric mean egg counts per gram (GMEC) for light infections; 2000–3999 GMEC for moderate infections; and more than 4000 GMEC for heavy infections (World Health Organization 2017). An alternative to the Kato-Katz thick smear technique is the use of centrifugal or gravitational floatation-based methods. The McMaster technique involves the floatation of fecal samples suspended in a solution that has a specific gravity that is higher than that of STH eggs, usually more than 1.25 (Mbong Ngwese et al. 2020). These techniques are also widely used in the detection of hookworm infections in dogs in low-income endemic foci in Africa, South America, and Asia (Ayinmode et al. 2016; Rodríguez-Vivas et al. 2011; Urgel et al. 2019).

Molecular diagnostic techniques developed to detect hookworms have been designed to amplify the semi-conserved ITS-1, 5.8S, and ITS-2 regions of *Ancylostoma* and *Necator* ribosomal DNA (Traub et al. 2021; 2008). A popular technique utilizing the aforementioned gene is PCR followed by restriction fragment length polymorphism digestion using specific enzymes. For instance, canine hookworms can be identified by digesting amplicons of the *ITS-1*, *5.8S* and *ITS-2* genes using the EcoRII, BSTnI and BsuRI endonucleases (Liu et al. 2015; Traub et al. 2004). The same principle has also been adopted for the identification of human hookworms (Inpankaew et al. 2014a, b). PCR protocols that amplify sections of the aforementioned gene region that are specific to hookworm species have also been developed and

used in studies performed in China and Bangladesh (Fu et al. 2019; Liu et al. 2015; Singh et al. 2022). Moreover, molecular identification of hookworms has also been performed *via* PCR and subsequent sequencing of the *Ancylostoma* spp. ITS gene. This method relies on species-level differences in the ITS sequences between different hookworm species (Mahdy et al. 2012; Liu et al. 2015). Methods based on real-time PCR that use specific probes have also been developed for the identification of hookworms (Aula et al. 2020; Papaikovou et al. 2017). Table 3 summarizes the diagnostic performance, advantages, and disadvantages of the different techniques.

Treatment, control, and elimination

Clinical treatment of hookworm infections in humans and animals involves the administration of anthelmintic drugs to eliminate the parasites (Table 4). For humans, benzimidazole derivatives such as albendazole and mebendazole are recommended (Jourdan et al. 2018). Among animal reservoirs (i.e., dogs and cats), various deworming drugs are currently available for clinical treatment and prevention of further infections (TroC-CAP 2019a; 2019b). Current anthelmintic agents that are effective against canine and feline hookworm infections include drugs from numerous drug classes: pyrimidine derivatives, benzimidazoles, macrocyclic lactones, cyclic depsipeptides, and macrolides (Table 3). In veterinary medicine, it is not uncommon for these drugs to be packaged or utilized in combination to increase their efficacy and/or to broaden the spectrum of parasitic infections that can be cured by treatment (Dantas-Torres et al. 2020; Hess et al. 2019; Steagall et al. 2023).

Controlling hookworm infections in humans and animals is imperative to abate the risk of pathological consequences in their respective populations (Fig. 2). Human population-based control, prevention, and elimination of soil-transmitted helminths, including hookworms, have been advocated by the World Health Organization (2021; 2011). Strategies recommended include mass drug administration (MDA) in vulnerable groups, such as preschool-aged and school-aged children, women of reproductive age, and other immunocompromised populations (Mationg et al. 2021; World Health Organization 2011). BPA with benzimidazoles, albendazole at 400 mg, and mebendazole at 500 mg is recommended to be performed twice a year for areas with a prevalence of more than 50%, while it is recommended to be administered annually for those with an STH prevalence of less than 50% but higher than 20% (World Health Organization 2017). This strategy aims to lower the burden and occurrence of STHs, including hookworms (World Health Organization 2017). A recent study revealed that community-wide MDA and school-based MDA are equally

Table 3 Diagnostic tests used to assess zoonotic hookworm infections

Method	Diagnostic performance	Advantages and disadvantages	References
Kato-Katz (KK) Technique	Sensitivity in areas of high infection intensity: 74% to 95% Sensitivity in areas of low infection intensity: 41% to 56% Performance is dependent on the utilization of the technique. 3-sample KK had higher sensitivity than 1-slide preparations	<ol style="list-style-type: none"> 1. It is considered the gold standard for STH research. 2. It is easy to use in resource-lacking endemic areas. 3. It allows systematic determination of infection intensity. 4. The technique requires rapid examination of prepared slides when examining hookworms. 5. Accurate reading of the KK slides requires considerable staff training. 6. Species identification cannot be done using this technique. 	Nikolay et al. (2014); Mbong Ngwese et al. (2020)
McMaster Technique	It has higher sensitivity when compared to KK: 44% for McMaster vs. 36% for KK	<ol style="list-style-type: none"> 1. Easy to use in resource-lacking endemic areas <p>It is recommended as a robust (i.e., it has an accurate multiplication factor) and accurate (i.e., it provides reliable results) alternative to KK.</p> <ol style="list-style-type: none"> 2. Various floating solutions can (e.g., table salt, sugar, Sodium nitrate, or Zinc sulfate). 3. Species identification cannot be done using this technique. 	Inpankaew et al. (2014a,b); Zendejas-Heredia et al. (2021); Levecke et al. (2011)
ELISA (Enzyme-linked Immunosorbent Assay) Techniques	IgG-ELISA had a sensitivity of 93.75% and specificity of 98.39 in assessing <i>Ancylostoma caninum</i> cutaneous larva migrans in human patients	Better diagnostic performance compared to coprological techniques The techniques are easier to perform and require less sophisticated equipment compared to molecular techniques	Adam et al. (2023)
Molecular Techniques	qPCR had higher sensitivity than 2-slide KK preparations: 93% to 98% in qPCR vs. 32% to 34% in KK qPCR reported prevalences three times higher than those reported by KK: 21.4% in qPCR vs. 7.5% in KK	Molecular techniques have better diagnostic performance than KK These techniques can detect infections that KK misses These require expensive reagents, equipment, and staff training Species identification subsequent molecular analysis can be done using this technique	Benjamin-Chung et al. (2020); Mationg et al. (2017)

Table 4 Anthelmintic drugs, their recommended dose, and route of administration for the treatment of hookworms in humans and animals

Anthelmintic drug	Host	Dose	Route of administration	Reference
Albendazole	Human	500 mg	Single administration, Oral	Jourdan et al. (2018)
		400 mg	Once daily for 3 days to treat CLM	Blackwell and Vega-Lopez (2001)
Mebendazole		400 mg	Single administration, PO	Jourdan et al. (2018)
		100 mg	Taken twice daily for 3 days	Jourdan et al. (2018)
Thiabendazole		1.5 g	Once daily for 3 days to treat CLM	Blackwell and Vega-Lopez (2001)
Pyrantel pamoate	Dog	5 mg/kg	Oral	TroCCAP (2019a)
	Cat	20 mg/kg		TroCCAP (2019b)
Pyrantel embonate	Dog	14 mg/kg	Oral	TroCCAP (2019a)
	Cat	57.5 mg/kg		TroCCAP (2019b)
Emodepside	Dog	0.45 mg/kg	Oral	TroCCAP (2019a)
	Cat	3 mg/kg		TroCCAP (2019b)
Oxantel embonate	Dog	55 mg/kg	Oral	TroCCAP (2019a)
Milbemyacin oxime	Dog	0.5 mg/kg	Oral	TroCCAP (2019a)
	Cat	2 mg/kg		TroCCAP (2019b)
Moxidectin	Dog	2.5 mg/kg	Topical	TroCCAP (2019a)
	Cat	1 mg/kg		TroCCAP (2019b)
Ivermectin	Human	200 µg/kg	Single administration to treat CLM	Vanhaecke et al. (2014)
	Dog	0.20 mg/kg	Oral	TroCCAP (2019a)
	Cat	0.024 mg/kg		TroCCAP (2019b)
Selamectin	Dog and Cat	6 mg/kg	Topical	TroCCAP (2019b; 2019a)
Fenbendazole	Dog and Cat	50 mg/kg for 3 days	Oral	TroCCAP (2019b; 2019a)
Oxibendazole	Dog	10–20 mg/kg	Oral	TroCCAP (2019a)
Eprinomectin	Cat	0.5 mg/kg	Topical	TroCCAP (2019b)

effective at reducing hookworm infections among school-aged children in Vietnam (Dyer et al. 2023). In the same region of Vietnam, community-based and school-based MDA were found to cost approximately 0.27 USD and 0.43 USD per individual, respectively (Delos Trinos et al. 2023). In addition to MDA, community health education and improvement of water safety, sanitation, and hygiene (WASH) have also been used to supplement MDA programs (Mationg et al. 2021; World Health Organization 2023; 2017). Reducing environmental egg contamination by implementing efforts aimed at ending human open defecation practices and appropriate disposal of animal feces are also integral in ending soil-borne transmission in endemic areas (Mationg et al. 2021; Bowman et al. 2017; World Health Organization 2011).

From the veterinary perspective, the Tropical Council for Companion Animal Parasites (TroCCAP) (2019a) recommends that puppies should be dewormed at two weeks of age to prevent vertical transmission of hookworms. The treatment will continue fortnightly until the age of eight weeks. Similarly, kittens are also advised to be dewormed starting at two weeks of age, which should continue fortnightly until they

are 10 months old (TroCCAP 2019b). Thereafter, it is recommended that dogs and cats be dewormed every month (Dantas-Torres et al. 2020). Like the goal of preventive chemotherapy in humans, the routine deworming of companion animals aims to reduce the occurrence and burden of helminth infections and reduce the risk of environmental contamination with eggs, which may become a source of human infections (Dantas-Torres et al. 2020; TroCCAP 2019a; 2019b; Tull et al. 2022). This is of particular concern since companion animals from the tropics, where hookworms and other geohelminths are most likely to be endemic, are constantly exposed and thus at risk of acquiring infections even after treatment (Dantas-Torres et al. 2020). A recent modeling study revealed that human MDA with animal deworming of moderate coverage (20–50%) may reduce the human *A. ceylanicum* prevalence to less than 1% by 2030; increasing animal treatment coverage to at least 75% may result in transmission interruption (Walker et al. 2023). The results of Walker et al. (2023) indicate the importance of including animal reservoir hosts in control and preventive measures aimed at reducing the public health threat of zoonotic hookworms, such as *A. ceylanicum*.



Fig. 2 Controlling and eliminating zoonotic hookworms. Mitigating the One Health risks and consequences of zoonotic hookworm infections may involve clinical treatment and preventive chemotherapy, improving sanitation, improving access to health institutions, advancing diagnostics, and expanding community health education efforts

Benzimidazole resistance in zoonotic hookworms

The emergence of resistant hookworms in companion animals has been regarded as a grave threat to One Health (Tinkler 2020). This concern echoes the growing apprehension surrounding the emergence of benzimidazole-resistant helminth infections in livestock, poultry and equids (Von Samson-Himmelstjerna et al. 2007; Whittaker et al. 2017). Single nucleotide polymorphisms (SNPs) associated with benzimidazole resistance were identified at codons 167 (TTC, TTT/phenylalanine → TAC, TAT/tyrosine), 198 (GAG, GAA/glutamic acid → GCG, GCA/alanine) and 200 (TTC/phenylalanine → TAC/tyrosine) (Diawara et al. 2013; Furtado et al. 2016). Interestingly, these SNPs have also been reported in canine hookworms. The F200Y mutation was first reported in the *A. caninum* population

from Brazil (Furtado et al. 2014). Recently, *A. caninum* from the Brazilian city of Santa Maria was observed to have a reduced egg reduction rate against fenbendazole (D'ambroso Fernandes et al. 2022). A high prevalence of the F167Y mutation was observed in multidrug-resistant canine hookworms originating from the USA (Jimenez Castro et al. 2019; Kitchen et al. 2019). Additionally, Q134H, a novel resistance-associated SNP, was discovered in Brazil (Venkatesan et al. 2023). Resistance-associated SNPs have also been detected in *A. caninum* and *U. stenocephala* populations from Australia and New Zealand (Stocker et al. 2023). Although single nucleotide polymorphisms (SNPs) causing benzimidazole resistance have not been identified in field isolates of *A. ceylanicum*, laboratory-induced resistance has been associated with SNPs at codon E198A (Medeiros et al. 2022). Additionally, a novel A200L mutation

was observed at a low frequency among laboratory-induced resistant isolates (Medeiros et al. 2022).

These results imply that resistance may therefore be possible in field isolates that are repeatedly exposed to benzimidazole dewormers. Benzimidazole resistance in canine hookworms potentially harms public health, as resistant isolates may cause zoonotic infections in humans. This is of particular concern since patent canine hookworms have also been increasingly found in humans (Furtado et al. 2020; Jung et al. 2020). To the best of the researchers' knowledge, no peer-reviewed literature has reported the detection of these resistance-associated SNPs among *A. ceylanicum* and other zoonotic hookworms from the Asia–Pacific region, except for the aforementioned study in Australia and New Zealand. Resistance to other drug classes, such as macrocyclic lactones (e.g., ivermectin) and tetrahydropyrimidine (e.g., Pyrantel), has also been documented in canine hookworms from many parts of the world (Kopp et al. 2007; Jimenez Castro et al. 2019). Benzimidazole resistance is of particular concern due to its potential public health implications. Comprehensive methods that can be employed to study benzimidazole resistance in the future may use genomic methodologies similar to those used for *Haemonchus contortus* (Doyle et al. 2022) or metabolomics methods to identify key metabolites involved in resistance, such as those reported for *Mycobacterium tuberculosis* (Chaiyachat et al. 2023). Efforts to control human STH infections also rely on benzimidazole drugs (e.g., albendazole and mebendazole). Hence, benzimidazole resistance may emerge from either human or animal populations and can circulate between them.

Conclusion and future directions

Ancylostoma ceylanicum remains understudied in the Asia-Pacific region. Determination of its epidemiology in humans and animals remains limited due to the need for expensive molecular identification techniques that may not be suitable for use in routine clinical diagnosis and epidemiological studies in low-income endemic areas. The zoonotic nature of *A. ceylanicum* warrants investigation of its occurrence in animal reservoir hosts (e.g., dogs and cats) to understand the dynamics of zoonotic transmission at different endemic foci. Understanding the transmission dynamics of *A. ceylanicum* requires assessments of its molecular epidemiology, perhaps through population genetic and phylogenetic analyses. Doing so is necessary because it has implications for the design and implementation of appropriate control and prevention programs. The occurrence of the zoonotic hookworm has only been confirmed in limited geographical areas in most endemic countries, and its epidemiology in humans

and animals on a national scale has yet to be clearly defined. Hence, it is not surprising that most, if not all, national STH control programs neglect the contributions of animal reservoirs in maintaining hookworm infections in endemic communities. As a result, infections persist in communities despite decades-long human-focused MDA and WASH programs. Moreover, control methods that are focused on environmental efforts that can reduce soil-borne infections are often not explicitly included in most programs. Therefore, true One Health programs that address hookworms and other zoonotic parasitoses from human, animal, and environmental perspectives are imperative in the Asia–Pacific region. The emergence of SNPs related to benzimidazole resistance in hookworms infecting dogs that have experienced extensive deworming is worrisome. Protracted human MDA programs coupled with excessive veterinary deworming may fast track the development of benzimidazole resistance in hookworms. The detection of these SNPs in Asia–Pacific countries, apart from Australia and New Zealand, has yet to be reported in the peer-reviewed literature. Considering the high level of hookworm endemicity in the region, the circulation of resistant isolates between humans and animals potentially presents a significant One Health threat that can undermine current MDA and deworming-based control efforts.

Abbreviations

STH	Soil-transmitted Helminths
MDA	Mass Drug Administration
NTD	Neglected Tropical Diseases
DALY	Disability-adjusted life years
CLM	Cutaneous Larva Migrans
PCR	Polymerase chain reaction
ITS	Internal transcribed spacer
Cox 1	Cytochrome C Oxidase Subunit 1
GMEC	Geometric mean egg counts per gram
qPCR	Real-time polymerase chain reaction
SNP	Single Nucleotide Polymorphism

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