



Human, canine and feline strongyloidiasis: beyond *Strongyloides stercoralis*

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Review Article

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Abstract

Strongyloides stercoralis has historically dominated research and control efforts for strongyloidiasis in both medical and veterinary fields. This has obscured the significance of other *Strongyloides* species infecting humans and their closest companions, dogs (*Canis lupus familiaris*) and cats (*Felis catus*). This review synthesized clinical and epidemiologic evidence on these neglected agents of human and companion animal strongyloidiasis and outlined priorities for future research. Our aim is to raise awareness of these understudied species and promote research to clarify their medical and veterinary public health significance. Targeted species-specific surveillance using molecular-genomic and advanced morphological tools is essential to uncover the true burden of these infections and inform strategies for their control and eventual elimination.

Introduction

Soil-transmitted nematodes of the genus *Strongyloides* infect a wide range of mammals, including humans (*Homo sapiens*) and their closest companion animals, dogs (*Canis lupus familiaris*) and cats (*Felis catus*) (Al-Jawabreh et al, 2024). *Strongyloides stercoralis* is the primary agent of human and canine strongyloidiasis and has historically been the focus of research and control efforts in both medical and veterinary contexts (Buonfrate et al, 2023; Al-Jawabreh et al, 2024). *Strongyloides fuelleborni* subsp. *fuelleborni*, historically considered a rare zoonosis acquired from non-human primates (NHPs) (Potters et al, 2020), has been identified at unexpectedly high prevalence in human populations in parts of Asia and Africa (Pampiglione and Ricciardi, 1972b; de Ree et al, 2024). Emerging reports of this species from Papua New Guinea (PNG) (Zhao et al, 2025), along with mounting evidence of human-to-human transmission (Hira and Patel, 1980; Hasegawa et al, 2016), suggest that *S. f. fuelleborni* is likely underreported globally (Buonfrate et al, 2022). A third agent of human strongyloidiasis, *Strongyloides fuelleborni* subsp. *kellyi*, is endemic to the island of New Guinea where it has been associated with a severe, often fatal protein-losing enteropathy in infants, known as ‘swollen belly syndrome’ (SBS) (Ashford et al, 1992; Bradbury, 2021). Recent molecular evidence suggests that *S. f. kellyi* may be synonymous with the Asian-Pacific clade of *S. f. fuelleborni* (Zhao et al, 2025).

Strongyloides infections in dogs and cats remain relatively underexplored. In addition to *S. stercoralis*, 3 other *Strongyloides* species have been identified in cats (Chandler AC, 1925; Rogers, 1939; Price and Dikmans, 1941); however, their veterinary clinical significance and public health relevance remain poorly understood (Zhao and Bradbury, 2024). There is ongoing debate about the existence of a dog-infecting *Strongyloides* sp. that is taxonomically distinct from *S. stercoralis* (Jaleta et al, 2017; Barratt et al, 2019; Bradbury et al, 2021; Bradbury and Streit, 2024), referred to by early researchers as ‘*Strongyloides canis*’ (Brumpt, 1922). This discussion has gained renewed relevance with the recent identification of a dog-specific *S. stercoralis* lineage (*cox1* lineage B) (Jaleta et al, 2017; Nagayasu et al, 2017; Barratt et al, 2019). Furthermore, cryptic genospecies of dog-infecting *Strongyloides* have been identified in remote Australian communities (Beknarova et al, 2019).

Diagnosis of strongyloidiasis in both medical and veterinary contexts has traditionally relied on morphological identification of larvae (as in *S. stercoralis* and *Strongyloides felis*) or embryonated eggs (as in *S. fuelleborni* and *Strongyloides planiceps*) in faeces, a method with limited sensitivity due to intermittent larval shedding and low parasite burden (Buonfrate et al, 2022). Parasitic females are small and often embedded deep within the intestinal mucosa, making detection difficult by necropsy (Speare, 1986; Buonfrate et al, 2022). Molecular diagnostics such as real-time PCR (qPCR), though increasingly available, generally do not provide species-level resolution (Buonfrate et al, 2022, 2023). Accurate identification of non-*S. stercoralis* infections in humans and companion animals often requires advanced morphological analysis of cultured

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free-living adult stages or molecular genotyping, both of which demand substantial expertise and time. This may lead to underdiagnosis or misattribution to *S. stercoralis* due to its well-known medical and veterinary impact. A recently developed duplex qPCR assay can differentiate between *S. stercoralis* and *S. f. fuelleborni*, but its sensitivity is markedly lower than that of the most widely used genus-level assay (Cunningham et al, 2025), although higher than that of faecal conventional PCR-based genotyping approaches for *S. fuelleborni* identification (Barratt et al, 2019).

The longstanding research focus on *S. stercoralis* has eclipsed the study of other *Strongyloides* spp. that are potentially relevant to human and animal health. This review summarises evidence on non-*S. stercoralis* aetiological agents of strongyloidiasis in humans, dogs and cats. Our aim is to raise awareness of these neglected and underexplored species and to promote research that will clarify their medical and veterinary public health significance.

Human strongyloidiasis

Strongyloides fuelleborni fuelleborni

Strongyloides fuelleborni fuelleborni is a common parasite of NHPs (Al-Jawabreh et al, 2024). Human infection with *S. f. fuelleborni* was first reported in 1932 in Zimbabwe, Southern Africa (Blackie, 1932). Wallace et al (1948) documented the first human case from Asia in 1948. Between 1968 and 1972, Pampiglione and Ricciardi (1972b) conducted a survey of *S. f. fuelleborni* infections in 4577 individuals across 13 nations, spanning the breadth of West to East Africa. Infection was detected in 13% (606/4577) of individuals, with prevalence by locality ranging from 0% to 78% (Pampiglione and Ricciardi, 1972b). Prevalence was higher in children compared to adults, and infection was endemic in tropical rainforest localities, but only sporadic in Savannah environments (Pampiglione and Ricciardi, 1972b). Subsequent examination of diagnostic specimens in two Zambian communities found *S. f. fuelleborni* prevalence of 10% (13/131) (Hira and Patel, 1977) and 31% (138/448) (Hira and Patel, 1980), respectively.

Since then, no active surveillance for *S. f. fuelleborni* in humans have been undertaken. However, over the past decade, human infections have been increasingly reported in sub-Saharan Africa (Hasegawa et al, 2010, 2016; Barratt et al, 2019; Potters et al, 2020), Southeast Asia (Labes et al, 2011; Thanchomnang et al, 2017; Janwan et al, 2020), and South Asia (Barratt et al, 2019; de Ree et al, 2024). While most reports involve isolated cases, a genotyping survey in Bangladesh identified *S. f. fuelleborni* infections in 3% (4/134) of people from four communities (de Ree et al, 2024). Most recently, *S. f. fuelleborni* was molecularly detected in 37% (7/19) of infant stool samples collected from the Eastern Highlands Province of PNG (Zhao et al, 2025). These findings suggest that *S. f. fuelleborni* may be far more prevalent and geographically widespread in human populations than currently recognized (Figure 1). Microscopy may misidentify *S. f. fuelleborni* eggs as morphologically similar embryonated hookworm eggs and hatched larvae are indistinguishable from those of *S. stercoralis* (Speare, 1986). Additionally, the lack of targeted control strategies for strongyloidiasis globally may contribute to sustained transmission (Lo et al, 2025). In regions where mass drug administration (MDA) with ivermectin, the most effective chemical against *S. stercoralis*, has been implemented for the control of onchocerciasis or lymphatic filariasis, *S. f. fuelleborni* prevalence may have been incidentally reduced, as has been observed for *S. stercoralis* (Stroffolini et al, 2023). Nonetheless, without targeted surveillance, the true

distribution and burden of *S. f. fuelleborni* remain unknown and likely underestimated.

There is limited understanding of the clinical presentation of *S. f. fuelleborni* infections. Most clinical insights come from a historical human experimental infection, which showed a broad spectrum of clinical signs, some resembling those seen in *S. stercoralis* infection (Pampiglione and Ricciardi, 1972a). These included localized dermatologic manifestations (such as urticaria and/or ground itch) at the onset, followed by transient, non-productive cough and gastrointestinal symptoms (epigastric burning, abdominal pain and diarrhea) in later stages. Marked eosinophilia (up to 48%) was observed 3–4 weeks post-infection (Pampiglione and Ricciardi, 1972a). It should be noted that this study used a human strain of *S. f. fuelleborni*, which had previously been inoculated into the same participant at a lower dose in a preliminary experiment (Pampiglione and Ricciardi, 1972a). Therefore, the observed symptoms may have been influenced by prior sensitization and/or immune response mounted to *S. f. fuelleborni* antigens. As this species is passed in the environment as eggs, it has been assumed that an internal autoinfective cycle does not occur (Centers for Disease Control and Prevention, 2019); however, this assumption has not been experimentally confirmed. It remains possible that small numbers of eggs could hatch in the gut or perianal folds and develop into filariform larvae and reinfect the host, although existing epidemiologic data do not support this hypothesis (Pampiglione and Ricciardi, 1972b).

The transmission patterns of *S. f. fuelleborni* in human populations are similarly not fully understood. Both NHP-to-human (Sandground, 1925; Blackie, 1932; Freedman, 1991) and human-to-human (Pampiglione and Ricciardi, 1972a) transmissions have been experimentally demonstrated. Human infections have historically been considered a zoonosis from NHPs. This is supported by molecular evidence showing identical or closely clustered genotypes in worms isolated from humans and NHPs living in close proximity in Tanzania (Hasegawa et al, 2010), the Democratic Republic of the Congo (Potters et al, 2020) and Thailand (Thanchomnang et al, 2017; Janwan et al, 2020). However, growing evidence suggests that exclusively interhuman transmission is also possible. Hira and Patel (1980) found high prevalence in people from urban and peri-urban communities in Zambia, where contact with NHPs was unlikely. Likewise, Hasegawa et al (2016) observed marked genetic divergence at the *cox1* and *18S rRNA* HVR-IV loci in worms from humans ($n = 7$) and NHPs ($n = 18$) cohabiting the Dzanga-Sangha Protected Area of the Central African Republic. These findings, together with emerging evidence of human *S. f. fuelleborni* infections in PNG where NHPs are absent (Zhao et al, 2025), suggest that this parasite has adapted to sustained human-to-human transmission in some parts of the world. Brown and Girardeau (1977) noted the transmammmary passage of *Strongyloides* infective filariform larvae (iL3), suspected to be *S. f. fuelleborni*, from one of 26 African nursing mothers to her infant. This finding requires further confirmation, as only a single larva was morphometrically characterised and found to be relatively small (340 μm) (Brown and Girardeau, 1977), so the possibility of this being an autoinfective larva of *S. stercoralis* cannot be excluded based on the size and morphology alone.

Strongyloides fuelleborni kellyi

Strongyloides fuelleborni kellyi was first reported by Allen Kelly in 1971 during a stool microscopy survey in western PNG (Kelly and Voge, 1973). Due to its morphological similarity in adult stages to

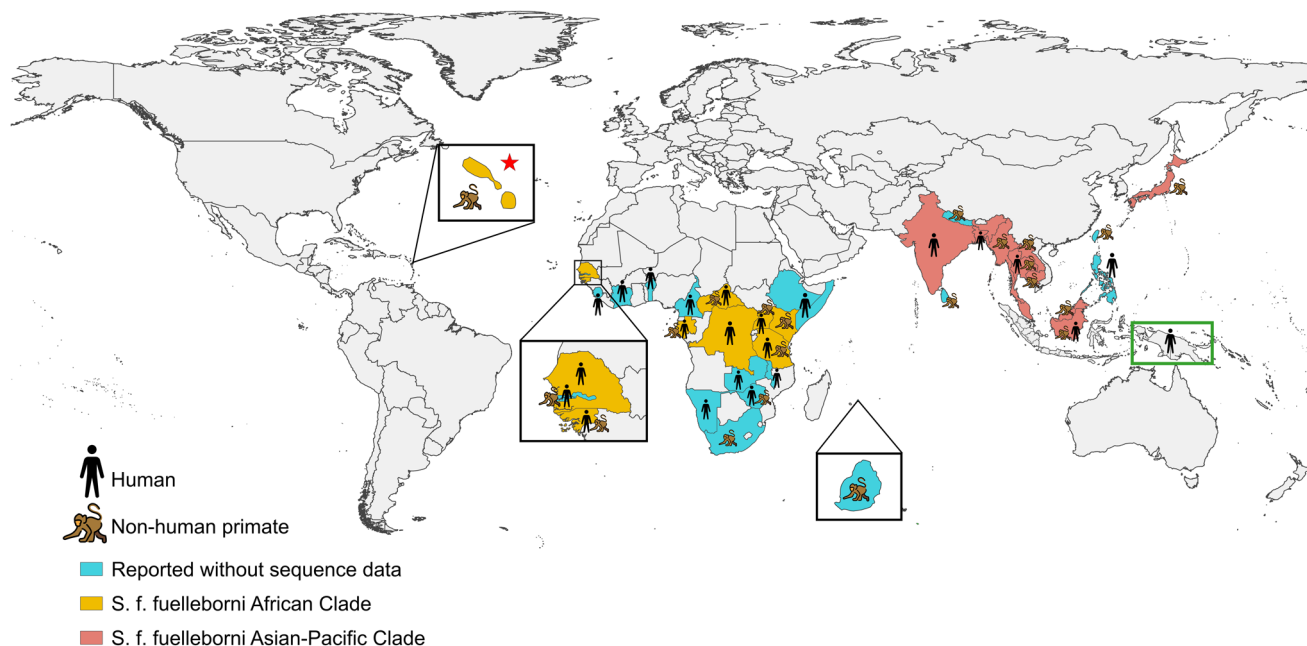


Figure 1. Global distribution of *Strongyloides fuelleborni fuelleborni* in humans and non-human primates (NHPs). African and Asian-Pacific clades of *S. f. fuelleborni*, inferred from available genbank sequences of *cox1*, *18S rRNA* HVR-IV and mitochondrial genome regions, are shown in yellow and pink, respectively. *Strongyloides f. fuelleborni* infecting St. Kitts vervet monkeys (*Chlorocebus aethiops sabaeus*), indicated by a red asterisk, were introduced from Africa in the 17th century (RICHINS et al., 2023). The distribution of *S. fuelleborni* on the Island of New Guinea, marked with a green box, remains unresolved (see Figure 2).

S. fuelleborni von Linstow, 1905, but the absence of a NHP reservoir in New Guinea, it was designated a subspecies of *S. fuelleborni* and named *S. f. kellyi* (Viney et al, 1991). A separate isoenzyme electrophoretic analysis grouped African and most PNG *S. fuelleborni* isolates together; however, 4 PNG isolates clustered with *Strongyloides ransomi* from local pigs (Viney and Ashford, 1990). Viney and Ashford (1990) speculated that these findings might represent artifact from participants submitting pig faeces in substitution for human samples. Subsequently, phylogenetic analysis of a 330 bp *18S rRNA* fragment from a formalin-fixed human isolate from PNG by Dorris et al (2002) placed the parasite within a clade containing *Strongyloides venezuelensis* and *S. ransomi*, but separate from *S. f. fuelleborni*. This placement was supported by a recent genotyping analysis of *18S rRNA* HVR-IV (252–259 bp) and HVR-I (432 bp) loci. Most importantly, this study demonstrated the co-occurrence, in one of 19 infants, of the genospecies identified by Dorris et al (2002) alongside the Asian clade of *S. f. fuelleborni* in PNG (Zhao et al, 2025).

The co-endemicity of two genetically distinct non-*S. stercoralis* human-infecting *Strongyloides* nematodes in PNG necessitates a reassessment of historical data previously attributed to *S. f. kellyi* (Figure 2). The parasite described by Viney et al (1991) and designated *S. f. kellyi* may represent the Asian-Pacific clade of *S. f. fuelleborni*, whereas the genospecies identified by Dorris et al (2002) and Zhao et al (2025) may represent an undescribed *Strongyloides* sp., potentially of animal origin. As there exists no morphological studies of *S. f. fuelleborni* from Asia, further comparative morphologic and genomic analyses of adult isolates from Africa, Asia and New Guinea are needed to resolve this taxonomic confusion.

Historical epidemiologic and clinical data on *S. f. kellyi*, generated prior to the molecular era, also warrant re-evaluation (Speare, 1986; Viney et al, 1991). Faecal microscopy surveys conducted

between 1976 and 1997 in PNG reported *S. f. kellyi* prevalence ranging from 20% to 93% in children and 5% to 20% in adults (Ashford and Babona, 1980; Ashford et al, 1979; Barnish and Ashford, 1989a, b; Barnish and Harari, 1989; Kelly et al, 1976; King and Mascie-Taylor, 2004; Shield et al, 1987; Shield and Kow, 2013). Infections were detected in children as young as 18 days, with prevalence peaking between 30 and 60 months of age and declining after 5 years (Ashford et al, 1992; Barnish and Ashford, 1989a, 1989b). Faecal egg count could reach up to 100 000 egg in late infancy (Barnish and Ashford, 1989a). Human infections have also been reported in Deiyai Regency, in the Indonesian province of Central Papua (Muller et al, 1987). No faecal surveys for *Strongyloides* have been conducted in New Guinea since 1997. However, two community-based serosurveys reported *Strongyloides* seroprevalence of 22.5% (27/120) (Scott et al, 2022) in Western Province by a *S. stercoralis* L3 crude antigen ELISA, and 68% (192/283) in Madang Province by a dual NIE and SsIR recombinant antigen ELISA (Tobon Ramos et al, 2025). In the absence of cross-reactivity data for these assays, the proportion of seropositivity attributable to *S. f. kellyi* remains unknown.

Uncertainty also surrounds the transmission pattern of *S. f. kellyi*. Ashford et al (1992) postulated that heavy infections in infancy may result from repeated exposure to iL3 within soiled straw bags (bilums) used to carry infants. Transmammary transmission has also been suspected; however, a survey of breastmilk from lactating women in a PNG community did not detect any larvae, although the infection status of the mothers and their infants was not assessed (Barnish and Ashford, 1989a). No zoonotic reservoir has been identified, despite investigations into local pigs, chickens and dogs (Kelly and Voge, 1973; Viney and Ashford, 1990).

In PNG, *S. f. kellyi* infection has been uniquely associated with an acute, fatal infantile protein losing enteropathy known as SBS

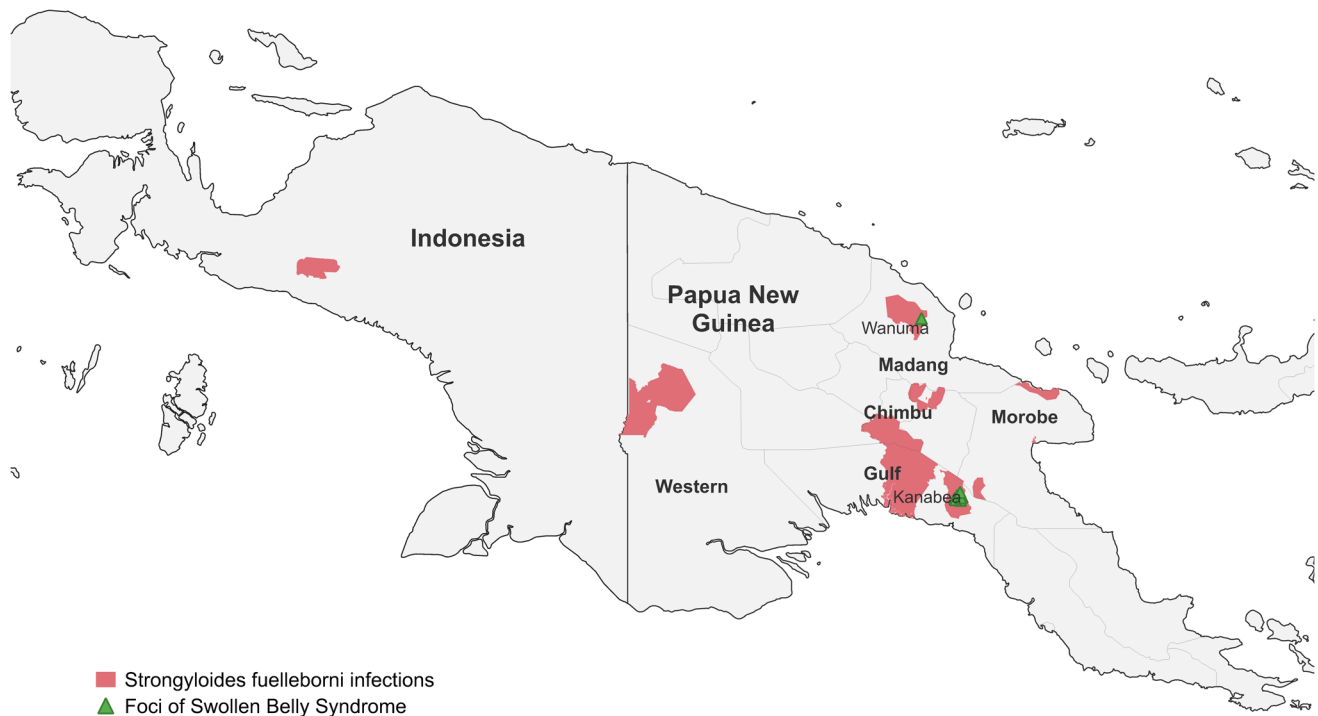


Figure 2. Human infections with *S. fülleborni* in New Guinea. The data presented may also include infections caused by an undescribed *strongyloides* sp. genetically distinct from *S. fülleborni*, as molecularly demonstrated by Dorris et al. (2002) and Zhao et al. (2025). Sites of confirmed SBS outbreaks are indicated by green triangles. Sporadic SBS cases have also been reported elsewhere in Papua New Guinea (data not shown).

(Ashford et al, 1992). Clinical features include hypoproteinemia, abdominal distension, respiratory distress, eosinophilia, diarrhea and peripheral oedema (Ashford et al, 1992). A remarkably similar syndrome, characterized by villus atrophy, malabsorption, hypoproteinaemia and sudden death, has been described in newborn piglets infected with *S. ransomi* (Enigk and Dey-Hazra, 1975). Between 1974 and 1983, SBS cases were predominantly reported from 2 regions of PNG, Kanabea in Gulf Province and Wanuma in Madang Province (Ashford et al, 1979; Vince et al, 2005). Elsewhere in the country, SBS was rare and sporadic (Ashford et al, 1992). In Kanabea, approximately 96 cases were recorded, accounting for 8% of infantile mortality (Ashford et al, 1979), although some high-intensity infections resulted in malnutrition without SBS (Barnish and Harari, 1989; King and Mascie-Taylor, 2004). A co-factor in the pathogenesis of SBS has been suggested (Ashford et al, 1992). Given renewed evidence on the co-endemicity of *S. f. fülleborni* (potentially synonymous with *S. f. kellyi*) and an undescribed genospecies closely related to *S. ransomi* in PNG (Zhao et al, 2025), it remains plausible that the latter may be the true aetiologic agent of SBS. This hypothesis is supported by clinical parallels to *S. ransomi*-induced disease in piglets. Future investigations into strongyloidiasis and SBS cases in PNG should employ species-specific molecular diagnostics and careful morphological characterization to accurately identify the causative agent and establish the epidemiologic link.

Canine strongyloidiasis

Strongyloides stercoralis is currently recognized as the only *Strongyloides* sp. naturally infecting dogs (Speare, 1986; Thamsborg et al, 2017). In immunocompetent dogs, infection is often

asymptomatic or subclinical, though clinical signs such as diarrhoea, bronchopneumonia, emaciation and lethargy may occur, particularly in juvenile animals (Paradies et al, 2017; Thamsborg et al, 2017; Basso et al, 2019). Severe systemic disease has been documented in puppies and immunocompromised adult dogs, often with fatal outcomes (Paradies et al, 2017; Bourgoin et al, 2018; Alves et al, 2021; Unterköfler et al, 2022; Nosková et al, 2024).

Natural infection of dogs with *S. planiceps* has been suggested in two studies (Arizono, 1976; Horie et al, 1980). Horie et al (1980) experimentally infected cats with a *Strongyloides* sp. isolated from dogs and subsequently detected embryonated eggs in feline faeces, leading to the suspicion that the isolate was *S. planiceps*. Arizono (1976) described a strain identified as *S. planiceps*, reportedly isolated from a dog in Japan and serially maintained in puppies. However, neither study provided detailed morphological confirmation of the species, so it remains unclear whether dogs are indeed natural hosts of *S. planiceps*. Patent experimental infections of dogs with *S. f. fülleborni* (Sandground, 1925) and *Strongyloides procyonis* (Little, 1966) have been documented, but these are not the intended focus of this review.

Does '*Strongyloides canis*' exist?

Friedrich Fülleborn first reported natural *S. stercoralis* infection in dogs in 1911 (Fülleborn, 1914). In the years that followed, debate emerged over the taxonomic identity of this canine parasite. Despite being morphologically indistinguishable from human strains, Brumpt (1922) postulated that the dog-derived *S. stercoralis* may represent a separate species. This was based on observed differences in geographical distribution and some life cycle characteristics between human and canine strains, along with unfruitful experimental attempts to establish persistent infections in

dogs using human-derived worms (Braun, 1899; Brumpt, 1922; Sandground, 1925; Fülleborn, 1927). He proposed naming the canine parasite '*Strongyloides canis*' (Brumpt, 1922). However, this designation was largely disregarded in subsequent decades primarily due to the lack of morphological justification (Speare, 1986).

This debate has gained renewed attention in the molecular era. Population genetics studies based on partial regions of *cox1*, *18S rRNA* and whole-genome data support the existence of a dog-only lineage of *S. stercoralis* (*cox1* lineage B), alongside a dog-cat-primate shared lineage (*cox1* lineage A) (Jaleta et al, 2017; Nagayasu et al, 2017; Barratt et al, 2019). It has been hypothesized that human-infecting *S. stercoralis* may be a host-adapted variant of an ancestral canine parasite (Nagayasu et al, 2017; Liu et al, 2025). Several researchers suggested that this ancestral dog-restricted population, potentially *S. stercoralis cox1* lineage B, may represent '*S. canis*' as proposed by Brumpt (Jaleta et al, 2017; Barratt et al, 2019; Barratt and Sapp, 2020; Bradbury et al, 2021).

However, recent genomic analyses have revealed a more complex landscape. Liu et al (2025) demonstrated that *S. stercoralis* infecting humans and dogs in Asia consisted of 2 largely genomically separable but not reproductively isolated populations. This suggests that human and dog lineages may not be taxonomically distinct, as evidenced by occasional introgression between the two (Liu et al, 2025). Similarly, de Ree et al (2024) identified *S. stercoralis cox1* lineage B in a Bangladesh human. These findings do not rule out the existence of '*S. canis*', but caution against oversimplifying genotyping results based on single genes or short gene regions. Further whole-genome analysis of worms from a broader geographical range, coupled with detailed morphological analysis, is necessary to confirm or refute the hypothesis of '*S. canis*' as a distinct species or a subspecies of *S. stercoralis*.

Canine cryptic strongyloides species

In a faecal metabarcoding survey conducted in remote northern Australia, Beknazarova et al (2019) identified a *Strongyloides* sp. in 2 dog samples that clustered basally to all known *S. stercoralis* isolates on a 217 bp *cox1* region. One of these dogs also harboured unique *18S rRNA* HVR-I and HVR-IV haplotypes (genotype VIII/F) (Beknazarova et al, 2019). These findings suggest the possible existence of a novel, undescribed species, or a genetically distinct strain or subspecies of *S. stercoralis*, in Australian dogs. However, considering that coprophagy is very common in dogs, the possibility that the detected *Strongyloides* DNA originated from ingested material rather than true infection cannot be ruled out. Further morphological and long-read genetic sequencing analyses are needed to clarify its identity.

Feline strongyloidiasis

Strongyloides felis

Strongyloides felis was first described by Chandler (1925) in cats from India in 1925. Since then, only 3 studies have reported this species (Speare and Tinsley, 1986, 1987; Jitsamai, 2019). In two faecal (Baermann) surveys conducted in North Queensland, Australia, *S. felis* infection was morphologically confirmed in 41% (83/203) (Speare and Tinsley, 1986) and 33.5% (169/504) (Speare and Tinsley, 1987) of shelter cats, respectively. A third study in Thailand identified rhabditiform *Strongyloides* larvae in 1.7% (14/835) of feline faecal samples by PBS-ethyl acetate centrifugal sedimentation microscopy; adults cultured from 6 of these were

morphologically identified as *S. felis* (Jitsamai, 2019). However, this morphological identification is dubious, as it described a hexagonal stoma in the free-living female whereas this feature is characteristic of the parasitic female (Speare, 1986). Larvae in the remaining positive samples were not identified to species level (Jitsamai, 2019) and could represent *S. felis* or other feline *Strongyloides* spp.

No other reports of *S. felis* are available, and its true prevalence and distribution remain obscure. Given its substantial morphological similarity to *S. stercoralis* (Speare, 1986), *S. felis* is likely underdiagnosed. Both species characteristically shed larvae, rather than eggs, in faeces (Speare, 1986; Speare and Tinsley, 1986). Differentiation of these two species requires detailed morphological analysis of stomal and tail shape in the parasitic female and vulval morphology in the free-living female. *Strongyloides felis* is distinguished by a rectangular stoma shape and a more finely tapered tail in the parasitic female, and by the presence of post-vulval narrowing and posterior vulval rotation in the free-living female (Speare, 1986). Morphometrics alone cannot reliably differentiate most *Strongyloides* spp., including *S. stercoralis* and *S. felis* (Speare, 1986). Accurate identification currently relies on a very advanced level of parasitological expertise, skills which have been largely lost from the parasitology community (Bradbury et al, 2022). Therefore, the development of species-specific molecular tools is urgently needed to support future studies.

The clinical picture of *S. felis* infection in cats is not fully clear. This parasite is considered moderately pathogenic in cats, based on observations from both natural and experimental infections (Speare, 1986; Speare and Tinsley, 1986). Pathological changes include adenomatous metaplasia of the glandular epithelium in the intestinal crypts, where parasitic females reside. Larval migration may cause pulmonary inflammation, with frequent interstitial changes or focal haemorrhage. Watery diarrhoea has been noted in some high-burden infections, though it is not a consistent feature (Speare and Tinsley, 1986).

Strongyloides felis appears to infect adult cats more commonly than kittens. In the study by Speare and Tinsley (1986), prevalence of *S. felis* was found to be 56% (77/138) in adult cats compared to only 9% (6/65) in kittens. The infection tends to be long-lasting; experimentally infected cats maintained patent infections for over a year (Speare and Tinsley, 1986). These epidemiological features resemble those of *S. stercoralis* in humans and dogs, indicating the likelihood of autoinfection and potential lifelong infections (Buonfrate et al, 2023; Al-Jawabreh et al, 2024). Transmission of *S. felis* in cats is thought to occur predominantly via skin penetration by iL3 from the environment. In a survey of 65 kittens, no infection was found in those under 3 months of age, suggesting that transmammmary transmission is unlikely (Speare and Tinsley, 1986).

Strongyloides tumefaciens

Price and Dikmans (1941) first described *S. tumefaciens* in cats from the USA in 1941. During necropsy, multiple tumour-like lesions, some of which were haemorrhagic, were observed in the colonic wall of infected cats. Adult worms were found within the nodules but not in the colonic lumen. These pathological features were considered unique among feline *Strongyloides* spp. Based on these, and the apparent larger body length of *S. tumefaciens* (5000 µm) compared to other known feline *Strongyloides* spp. (<3330 µm) in the parasitic female, a new species was designated (Price and Dikmans, 1941).

Remarkably, another necropsy survey of cats from St. Kitts (Wulcan et al, 2019) observed similar colonic nodules in cats infected by *S. stercoralis*. The recovered adult worms were morphologically indistinguishable from *S. tumefaciens* as described by Price and Dikmans (1941); however, phylogenetic analysis of a 522 bp region of *cox1* placed them within the *S. stercoralis* lineage A (Wulcan et al, 2019). These findings challenged the taxonomic validity of *S. tumefaciens*.

Since its original description, *S. tumefaciens* has been reported in cats from the USA (Malone et al, 1977; Lindsay et al, 1987), Brazil (Moura et al, 2016) and India (Dubey and Å, 1964). In all instances, species identification was based solely on the presence of colonic nodules, which Wulcan et al (2019) indicated to be unreliable.

Strongyloides planiceps

Strongyloides planiceps was initially reported by R.T. Leiper in rusty tiger cats (*Prionailurus rubiginosus*) from Malaysia and later described in domestic cats by Rogers (1939). A distinguishing feature of *S. planiceps* is that larvated eggs, rather than rhabditiform larvae, are shed in faeces (Rogers, 1939; Speare, 1986). Morphologically, the parasitic female of *S. planiceps* has spiralled ovaries and a bluntly rounded tail, contrasting with the straight ovaries and narrowly tapered tail of *S. stercoralis* and *S. felis* (Rogers, 1939; Speare, 1986). Unlike *S. stercoralis*, the life cycle of *S. planiceps* involves multiple free-living generations, up to 9, as demonstrated experimentally (Yamada et al, 1991).

Strongyloides planiceps is believed to primarily infect wild felids and only sporadically occur in domestic cats (Horie et al, 1981; Fukase et al, 1983; El-Seify et al, 2017). Reports of *S. planiceps* have almost exclusively come from Japan (Arizono, 1976; Horie et al, 1980, 1981; Fukase et al, 1983, 1985; Sato et al, 2006). Although numerous feline surveys from other countries have reported egg-shedding *Strongyloides* spp. in cat faeces, none identified the parasites to the species level, so it is unknown whether they represent *S. planiceps* (Abbas et al, 2022; Adams et al, 2008; Adhikari et al, 2023; Borkataki et al, 2013; de Sousa¹ et al, 2015; Heidt et al, 1988; Monteiro et al, 2016; Nyambura Njuguna et al, 2017; Solórzano-García et al, 2017; Susilowati, 1985). One study from Egypt found *S. planiceps* in one of 170 cat faecal samples, but the method for confirming species was not reported (El-Seify et al, 2017). It is likely that this helminth is significantly underreported in cats globally.

Feline cryptic Strongyloides species

Two studies reported molecular evidence of a *Strongyloides* sp. in cats (Jitsamai, 2019; Ko et al, 2020). Ko et al (2020) analysed partial *cox1* and protein-coding mitochondrial genome sequences of 70 *Strongyloides* isolates from 19 cats in Myanmar and found that they formed a sister taxon to *S. stercoralis*. A similar finding was reported by Jitsamai (2019) based on a 708 bp region of 18S rRNA. It has been suggested that the *Strongyloides* detected in both studies may represent *S. felis*, but without morphological confirmation, this remains speculative.

Conclusions and future directions

Beyond *S. stercoralis*, multiple other *Strongyloides* spp. infect humans and companion animals. Yet these remain grossly understudied due to diagnostic limitations, scarce morphological and molecular data and a historical research focus on *S. stercoralis*. This

review synthesized evidence on these neglected nematodes, aiming to raise awareness and encourage further research to clarify their significance in medical and veterinary public health. Below, we highlight key research gaps and propose priorities for future research:

a) Major gaps remain in the global burden and epidemiology of *S. f. fuelleborni* infections in humans. Mounting evidence of interhuman transmission suggests that this parasite may be more widely disseminated via human migration than currently understood. In parallel, the translocation of infected NHP may serve as a mobile zoonotic reservoir. Invasive NHP species have been reported in several Pacific regions, including New Guinea (Kemp and Carter, 2022). Transmission among introduced or imported NHP, as demonstrated by Richins et al (2023) and Juhasz et al (2023), may pose a risk to local humans. Large-scale, species-specific surveillance is needed to define the true prevalence, geographic range, and public health relevance of *S. f. fuelleborni*.

b) The taxonomic, epidemiologic, and clinical landscape of *S. f. kellyi* infection requires re-evaluation using species-discriminative molecular diagnostics. Comparative morphological analysis of adult isolates from Asia, Africa and New Guinea, combined with mitochondrial and whole-genome sequencing, is needed to determine whether *S. f. kellyi* is truly synonymous with the Asian-Pacific clade of *S. f. fuelleborni*. Molecular taxonomy based on 18S rRNA loci suggests the existence of an undescribed human-infecting *Strongyloides* sp. in PNG (Dorris et al, 2002; Zhao et al, 2025). This hypothesis requires validation through detailed morphological characterization of worms of all life stages combined with genomic analysis. Renewed surveillance for strongyloidiasis and SBS in New Guinea is needed to clarify the causative species and their respective public health significance.

c) The potential existence of a dog-specific population of *S. stercoralis*, historically referred to as '*S. canis*', remains unresolved. Whole-genome analysis of isolates from humans and dogs across diverse and sympatric settings will be essential to delineate host specificity and transmission dynamics. Additionally, cryptic *Strongyloides* genospecies identified in Australian dogs require further research to determine whether they represent true infections or reflect transient DNA passage or sequencing artefacts.

d) *Strongyloides* spp. infecting cats remain overall poorly understood. Species-specific surveillance globally using molecular and morphological tools, combined with veterinary clinical data, is needed to clarify their prevalence, distribution, veterinary impact and potential zoonotic relevance.

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