Review Article

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Anthelmintic resistance in gastrointestinal nematodes of sheep and goats: A systematic review

Ali Saidu[1], Bura Thlama Paul[1,2,3*], Faez Firdaus Abdullah Jesse[4], Juriah Kamaludeen[1], Suhaili Mustafa[1], Masnindah Malahubban[1], Ali Hanafiah Hakim[1], Jashilagari Stephen[5]

[1]Department of Animal Science and Fisheries, Faculty of Agricultural and Forestry Sciences, Universiti Putra Malaysia Bintulu Sarawak Campus, Nyabau Road, 97008 Bintulu, Sarawak, Malaysia.
[2]Veterinary Teaching Hospital, Faculty of Veterinary Medicine, University of Maiduguri, 600230 Bama Road Maiduguri, Borno Nigeria.
[3]Faculty of Agriculture, Salaam University, Wadnaha Street, Hodan District, Mogadishu, Somalia.
[4]Department of Veterinary Clinical Studies, Faculty of Veterinary Medicine, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia.
[5]Department of Theriogenology, Faculty of Veterinary medicine, University of Maiduguri, 600230 Maiduguri, Nigeria.

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*Correspondence:

Corresponding author: Bura Thlama Paul
E-mail address: burapaul@upm.edu.my

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ABSTRACT

Helminthosis caused by various parasitic nematodes, cestodes, and trematodes is especially important in small ruminant production due to loss of productivity and health challenges caused by infestations. The control of helminthosis in ruminants depends on various types of benzimidazole, macrocyclic lactone, and imidazothiazole anthelmintics. Unfortunately, prolonged indiscriminate use of these drugs has led to anthelmintic resistance (AR) in gastrointestinal nematodes (GINs) of ruminants. AR is a heritable loss of sensitivity of a parasite population to a previously effective anthelmintic. Understanding the mechanisms underlying AR is crucial for sustainable parasite management. This systematic review was conducted to answer the research question: "What is the prevalence, distribution, diagnosis, and molecular basis for anthelmintic resistance in gastrointestinal nematodes of small ruminants?" This paper attempts to present current knowledge on the occurrence, mechanisms, global situation, and diagnosis of anthelmintic resistance in *Trichostrongyle* nematodes of sheep and goats with reference to the situation in Malaysia. Eligible original research articles published between January 1, 1990, and April 30, 2024, from the Scopus and PubMed databases were retrieved and analyzed based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA). The results of the study showed that benzimidazole, macrocyclic lactone, and imidazothiazole resistance is rampant in 9 different species of gastrointestinal nematodes globally. *Haemonchus*, *Trichostrongylus*, and *Teladorsagia* are the most widely reported anthelmintic-resistant *Trichostrongyle*s in small ruminants globally. *In vivo* FECRT is still the most widely used method for detecting anthelmintic resistance in sheep and goats. Key resistance markers include mutations in the β-tubulin gene for benzimidazole resistance, the acr-8 gene for imidazothiazole resistance, and increased P-glycoprotein (P-gp) expression for macrocyclic lactone resistance. Despite current research efforts, data is lacking on the molecular markers for resistance in many gastrointestinal nematode species and the resistance status of hydropyrimidines, requiring further studies in this area. Therefore, future studies need to focus on developing standardized molecular diagnostics for detecting resistance in prevalent pathogenic *Trichostrongyle*s for more efficient tracking of resistance. Sustainable control using proper dosing of anthelmintics, rotation of anthelmintics, the refugia principle, and combination therapy can slow down the emergence of resistance in nematode populations.

Introduction

Small ruminants are known to play important roles in rural economies through the provision of animal protein and income in pastoral communities (Devendra, 2010) which experience low agricultural productivity due to frequent droughts and scarcity of resources (Pulina *et al.*, 2017). Parasitic gastroenteritis (PGE) is an endemic problem in pastured sheep and goat populations globally (Calvete *et al.*, 2014; Mpofu *et al.*, 2022), and their infections causes negative health and production outcomes (Paul *et al.*, 2020). *Haemonchus contortus*, *Trichostrongylus colubriformis*, and *Teladorsagia circumcincta* are the most prevalent species of *Trichostrongyle*s affecting sheep and goats (Bishop and Morris, 2007; Julienne *et al.*, 2021), but *H. contortus* and *T. circumcincta* are the most pathogenic species causing PGE (Mbaya *et al.*, 2010; Mpofu *et al.*, 2020), which is associated with severe diarrhoea, anaemia, reduced weight gain, retarded growth, decreased productivity, and mortality in sheep and goats (Paul *et al.*, 2020). The distribution of *Trichostrongyle*s in small ruminants populations varies widely across different geographies due to differences in local ecological conditions (Dorny *et al.*, 1995; Sharma and Ganguly, 2016; Paul *et al.*, 2020). The prevalence of *Trichostrongyle*s among small ruminants in the tropics is associated with grazing under the semi-intensive management system of livestock production (Chandrawathani *et al.*, 1999; Thongsahuan *et al.*, 2014; Zainalabidin *et al.*, 2015; Mohammed *et al.*, 2016; Paul *et al.*, 2020) and a favourable humid tropical climate, which ensures the success of the environmental stages of the parasites (Ikeme *et al.*, 1987; Chandrawathani *et al.*, 1999).

Chemical control of PGE traditionally relies on the use of anthelmintic drugs (Mickiewicz *et al.*, 2021). Modern anthelmintic control in grazing animals still employs regular deworming with anthelmintics to reduce the density of infective larvae on pasture (Coles *et al.*, 1992, 2006). The Benzimidazoles such as Albendazole; Imidazothiazoles such as Levamisole; Macrocyclic Lactones such as Ivermectin; and Pyrimidines such as Pyrantel are the four main groups of broad-spectrum anthelmintics used for deworming in grazing animals to control gastrointestinal nematodes globally (Coles *et al.*, 2006; Sonibare *et al.*, 2016; Kotze *et al.*, 2020; Mickiewicz *et al.*, 2021). Although, these drugs and their analogues were used effectively to control the pathogenic gastrointestinal nematodes and increase the productivity of grazing ruminants in the past (Sonibare *et al.*, 2016), the emergence of multiple anthelmintic resistance has become a significant concern globally, compromising the effectiveness of these drugs and limiting treatment options for farmers (Waller, 1997, 2006; Sissay *et al.*, 2006; Charlier *et al.*, 2014). Anthelmintic resistance (AR) can be defined as a transmissible loss of sensitivity of a parasite population to an anthelmintic that was previously effective against the same helminth (Fissiha and Kinde, 2021). Anthelmintic resistance has been recognized as a severe crisis in areas with resistance to multiple anthelmintic drugs (Waller, 1997). In small ruminants, the development of anthelmintic resistance is evident in *Cooperia* spp., *Haemonchus* spp., *Oesophagostomum*

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spp., *Teladorsagia* spp. and *Trichostrongylus* spp. (Baudinette *et al*., 2022), but the prevalence is highest in *H. contortus*, making it the most economically important gastrointestinal nematode in small ruminants (Fleming *et al*., 2006). The mechanisms underlying AR are multifaceted, involving genetic changes in the parasites that affect drug uptake, metabolism, and target site sensitivity (Shalaby, 2013). Anthelmintic resistance mechanisms include mutation or deletion of one or more amino acids in the target genes, reduction in the number of receptors, decreased affinity of receptors for drugs, and absence of bioactivating enzymes (Abongwa *et al*., 2017).

There are widespread reports on the prevalence and impact of anthelmintic resistance in gastrointestinal nematode parasites of small ruminants globally (Chartier *et al*., 2001; Mortensen *et al*., 2003; Fleming *et al*., 2006; Chandrawathani *et al*., 2013; Ramünke *et al*., 2016; Hinney *et al*., 2020; Amaral *et al*., 2021; Untersweg *et al*., 2021; Dyary and Banaz, 2021; Fissiha and Kinde, 2021; Batista *et al*., 2023; Devos *et al*., 2024). Although anthelmintic resistance is well documented in West Malaysia (Dorny *et al*., 1994; Chandrawathani *et al*., 1999, 2004; Chandrawathani, 2004; Khadijah *et al*., 2006; Basripuzi *et al*., 2012; Chandrawathani *et al*., 2013; Premaalatha *et al*., 2014; Khadijah *et al*., 2018; Wong and Sargison, 2018), the anthelmintic resistance status of gastrointestinal nematodes of sheep and goat flocks is unknown in Sarawak. This systematic review was conducted to answer the research question: "What is the prevalence, distribution, diagnosis, and molecular basis for anthelmintic resistance in gastrointestinal nematodes of small ruminants?" This review presents current knowledge on the occurrence, mechanisms, global situation, and diagnosis of anthelmintic resistance in *Trichostrongyle* nematodes of sheep and goats with reference to the situation in Malaysia.

Materials and methods

Study design

This study was designed based on the updated Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guideline for reporting systematic reviews in 2020 (Page *et al*., 2021). A total of 224 Scopus records of original peer-reviewed research articles written in the English Language reporting anthelmintic resistance in sheep and goats were considered eligible for this systematic review. The scope of review covers all epidemiological studies based on the standard phenotypic (*In vivo* faecal egg count reduction test - FECRT) or molecular methods (PCR or sequencing-based tests) for detecting anthelmintic resistance in small ruminant livestock (Coles *et al*., 2006). The *In vivo* FECRT is currently recognised by the World Association for the Advancement of Veterinary Parasitology (WAAVP) as the gold standard method for detecting anthelmintic resistance for all classes of anthelmintics (Coles *et al*., 1992, 2006; Sabatini *et al*., 2023). The FECRT assumes that faecal egg counts reflect the population of adult worms in the host and estimates efficacy by comparing pre-treatment and post-treatment faecal egg counts to determine the percentage reduction (Demeler *et al*., 2010).

Literature search and data quality control

A comprehensive literature search was conducted in the SCOPUS database using the Condition, Context, and Population (CoCoPop) search terms (Munn *et al*., 2015, 2018). Our search term combined the following keywords: "prevalence" AND "anthelmintic" AND "resistance" AND "mechanisms" AND "nematodes" AND "ruminants" AND "sheep" AND "goats". Based on this search, studies on anthelmintic resistance among sheep and goat flocks published from January 1, 1990, to December 31, 2024, were considered. In this review, we defined anthelmintic resistance as "the heritable reduction in the sensitivity of nematode population to the action of an anthelmintic in sheep and goat population based on the result of the phenotypic or genotypic test". Overall, there were 903 research articles matching the search criteria. These were initially streamlined using the SCOPUS automation tools to filter for only articles in Veterinary Sciences AND Agricultural and Biological Sciences (n=341 records were excluded). The remaining 562 records were further filtered to include only full-length research articles published in English (n=338 were excluded). The remaining 224 records were thoroughly screened by assessing the titles, abstracts, and whole papers for completeness of contents against the set eligibility criteria following the WAAVP guidelines for testing anthelmintic resistance in ruminants (n=193 were excluded). Furthermore, all studies that didn't report the nematode species or the specific anthelmintic used were excluded (n=6). Two investigators screened and selected research articles to minimize selection bias. Information extracted by the first investigator was further scrutinized for data entry errors, and all discrepancies in entries were resolved following a consensus between the two investigators.

Data extraction and processing

The literature synthesis was done narratively since none of the articles included in our study had comparable numerical values to permit quantitative analysis. The required information, such as the country, the method of detecting anthelmintic resistance, class of anthelmintic, and nematode species, was extracted from eligible papers and stored in a Microsoft Excel® spreadsheet Program 2024. Summarized data on the global status of anthelmintic resistance among sheep and goats was presented descriptively as proportions in tables. The global distribution of anthelmintic resistance was presented on a point distribution map constructed using Maptive®, an open-source web-based mapping software.

Results

Characteristics of the eligible studies

A total of 42 research articles were included in this systematic review comprising 32 epidemiological studies reporting the occurrence of anthelmintic resistance in sheep and goats based on the results of faecal egg count reduction test (FECRT), egg hatch assay (EHA), or molecular methods based on PCR or sequence analysis, and 10 studies based on the molecular mechanisms of nematode resistance to anthelmintics in sheep and goats. As shown below, these studies were carefully selected based on the predetermined inclusion criteria (Figure 1).

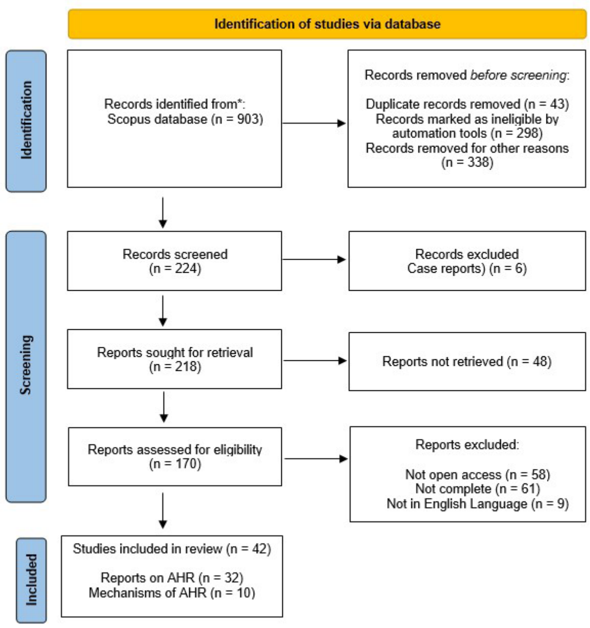

Figure 1. Flow diagram of inclusion criteria and selection of studies in the review

Global distribution of anthelmintic-resistant nematodes in small ruminants

Among the 9 different nematode genera associated with anthelmintic resistance in sheep and goats globally, *Haemonchus* spp. (42%) is the most frequently reported, followed by *Trichostrongylus* spp. (20%), *Teladorsagia* spp. (17%), and *Oesophagostomum* spp. (7%). While *Cooperia* spp., *Ostertagia* spp., *Bunostomum* spp., *Nematodirus* spp., and *Trichuris* spp. were rarely associated with resistance in small ruminants (Figure 2).

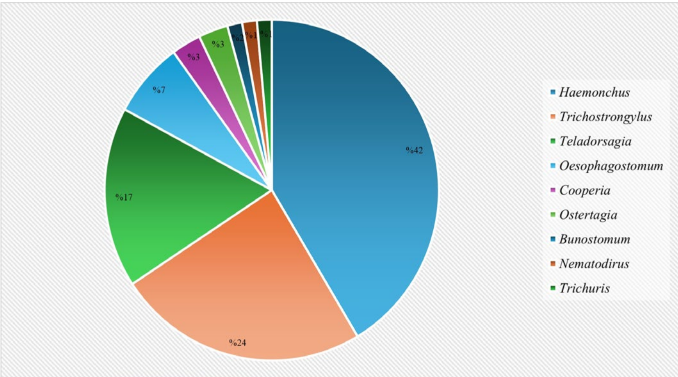

Figure 2. Frequency of anthelmintic-resistant nematode genera in sheep and goats.

Frequency distribution of resistance associated with various chemical classes of anthelmintics

Among the 4 major classes of anthelmintics used for controlling PGE in small ruminants, the BZ group (84.4%) is the most frequently associated with resistance among nematodes of sheep and goats, followed by ML (43.8%) and IMZ (21.9%), while HPD (15.6%) is the least frequently associated with resistance in literature (Figure 3).

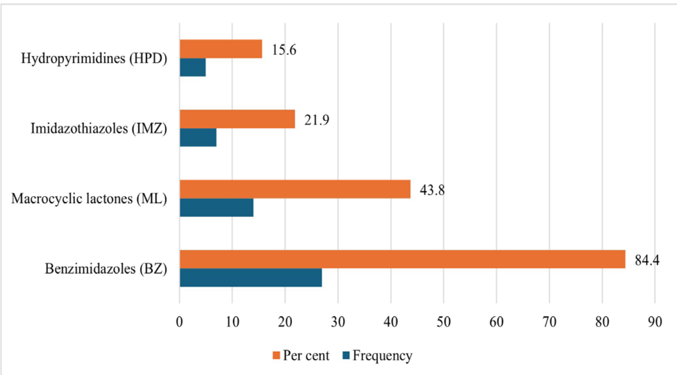

Figure 3. Frequency of reported resistance to major anthelmintics in sheep and goats

Global prevalence distribution of anthelmintic resistance in small ruminants

Anthelmintic resistance is currently reported in 21 countries from 5 continents. Europe had the highest frequency, involving 11 (52.4%) countries, followed by Asia with 6 (28.6%) countries, America with 2 (9.5%) countries, and Africa with 2 (9.5%) countries that reported anthelmintic resistance in sheep and goats during 1990-2024 (Figure 4).

Distribution of anthelmintic resistance in different states of Malaysia

In Malaysia, there are currently11 published reports from 6 different states on the occurrence of anthelmintic resistance involving *Trichostrongylus* spp., *Oesophagostomum* spp., and *Bunostomum* spp. Resistance of *H. contortus* to Benzimidazoles was first reported in the early 1990s. Since then, there has been a rapid emergence of resistance involving mainly Benzimidazoles and Macrocyclic lactones with low frequencies of resistance to Imidazothiazoles and Hydropyrimidines (Figure 5).

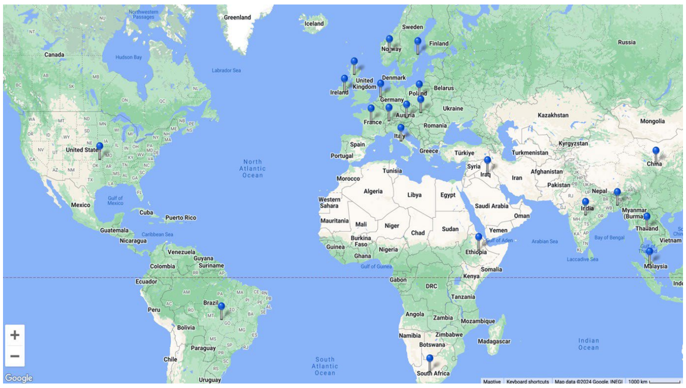

Figure 4. Point distribution map of anthelmintic resistance in nematodes of sheep and goats globally

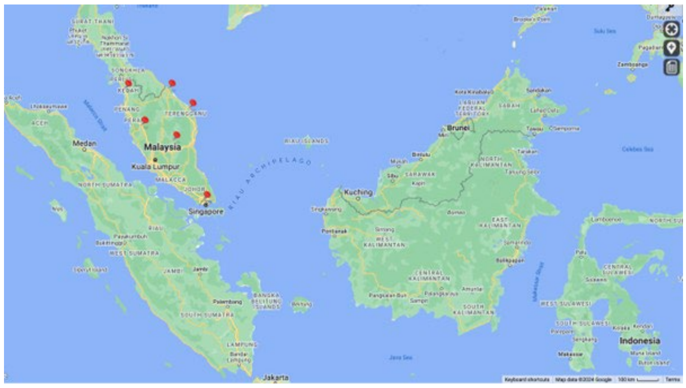

Figure 5. Point distribution map of anthelmintic resistance in nematodes of sheep and goats in Malaysia.

Methods for the detection of anthelmintic resistance

In this study 89.7% of published studies that reported anthelmintic resistance used mainly the FECRT as the primary method for detecting resistance in sheep and goat gastrointestinal nematodes. Although molecular methods offer a more sensitive alternative method for diagnosis of AHR, only 15% of published reports included in this review used molecular methods for detecting anthelmintic resistance in small ruminant gastrointestinal nematodes. Furthermore, only 10% of published studies included in this review have used *In vitro* method, specifically the egg hatch test (EHT), for detecting anthelmintic resistance (Table 1).

Mechanisms of anthelmintic resistance

At least one mechanism of AR has been described in the three major anthelmintics classes associated with resistance in gastrointestinal Nematodes of sheep and goats (Table 2).

Discussion

This review aimed to present current knowledge on the occurrence and mechanisms of anthelmintic resistance in pathogenic *Trichostrongyle* nematodes of small ruminants, its global spread, and diagnosis, with reference to the situation in Malaysia. The review was conducted to answer the research question: "What is the prevalence, distribution, diagnosis, and molecular basis for anthelmintic resistance in *Trichostrongyle* nematodes of small ruminants?" The results of study showed that Benzimidazole, Macrocyclic Lactone, and Imidazothiazole resistance is rampant in pathogenic *Trichostrongyle* nematodes of small ruminants in Africa, Asia, Europe, and the Americas. The results also revealed that 9 different species of PGE causing *Trichostrongyle* nematodes are associated with anthelmintic resistance in sheep and goats globally. This review has further revealed that Benzimidazoles, Macrocyclic Lactones, Imidazothiazoles, and Hydropyrimidines are the four groups of broad-spectrum anthelmintics that are currently used for treating grazing animals to control PGE caused by *Trichostrongyle* nematodes globally. The finding of *Haemonchus* with *Trichostrongylus*, and *Teladorsagia* as the most widely reported anthelmintic-resistant *Trichostrongyle*s in small ruminants in this review underscores their economic importance in small ruminant production globally (Fleming *et al*., 2006). Widespread reports suggesting high frequency of resistance to the BZ (84.4%) and ML (43.8%) in *Trichostrongyle* nematodes, especially *Haemonchus*, in small ruminants represents a significant threat to the chemical control of PGE and sustainability of small ruminant farming worldwide (Niciura *et al*., 2019) due to increased cost associated with treatment failure and limited effective treatment options (Kaplan and Vidyashankar, 2012), an increased burden caused by morbidity and mortality (Geurden *et al*., 2014). Moreover, *Haemonchus* is prevalent globally, have high pathogenicity and high biotic potentials, making it even more difficult to control (Soulsby, 1982; Roeber *et al*., 2013). Indiscriminate use of anthelmintic drugs is responsible for the emergence of resistance (Charlier *et al*., 2014). Frequent treatments, underdoses, genetics of the parasite, targets and poor timing of mass treatments are recognised as the main risk factors for anthelmintic resistance in ruminant livestock (Fissiha and Kinde, 2021).

In Africa, resistance to Albendazole, Levamisole, Tetramisole, and Ivermectin involving *Trichostrongylus*, *Teladorsagia*, and *Haemonchus* among sheep flocks was reported in Ethiopia (Mekonnen, 2007; Wondimu and Bayu, 2022). Additionally, resistance to Albendazole, Levamisole, and Ivermectin in *Haemonchus contortus* was also reported among sheep flocks in south Africa (Van Wyk *et al*., 1999). In the America's, resistant strains of *Trichostrongyle*s of sheep and goats were reported in North America (Waller *et al*., 1996). In southcentral United States, Albendazole and Ivermectin resistant strains of *H. contortus* were detected in small ruminant farms (Tsukahara *et al*., 2017). In Rio Grande do Sul, Brazil, the prevalence of resistance was 90% for Benzimidazole, 84% for Levamisole, 13% for Ivermectin, 73% for the combination, and 20% for Closantel anthelmintics and the primary resistant nematode species identified was *Haemonchus contortus* (Waller *et al*., 1996). Multi-drug resistance in-

Table 1. Summary of resistant nematode species and methods used for detecting anthelmintic resistance globally.

Country	Diagnostic method	Resistant species	Anthelmintic	References
Austria	Genotyping by sequencing	*H. contortus, Trichostrongylus colubriformis Trichostrongylus circumcincta*	Benzimidazole	(Hinney *et al*., 2020)
Austria	*In vivo* FECRT	*Haemonchus contortus*	Fenbendazole Albendazole Ivermectin Doramectin Moxidectin Monepantel	(Untersweg *et al*., 2021)
Bangladesh	*In vivo* FECRT *In vitro* EHA	*Haemonchus, Oesophagostomum Trichostrongylus*	Benzimidazole	(Dey *et al*., 2020)
Brazil	Genotyping by PCR and sequencing	*Haemonchus contortus*	Benzimidazole	(Amaral *et al*., 2021)
Brazil	*In vivo* FECRT	*Haemonchus, Trichostrongylus*	Ivermectin Albendazole	(Batista *et al*., 2023)
Colombia	*In vivo* FECRT	*Haemonchus, Trichostrongylus*	Albendazole Levamisole Ivermectin Moxidectin	(Chaparro *et al*., 2017)
Ethiopia	*In vivo* FECRT	*Haemonchus, Trichostrongylus*	Albendazole Levamisole Ivermectin	(Mekonnen, 2007)
Ethiopia	*In vivo* FECRT	*Trichostrongylus, Teladorsagia, Haemonchus*	Albendazole Tetramisole Ivermectin	(Wondimu and Bayu, 2022)
France	*In vivo* FECRT	*Teladorsagia, Trichostrongylus, Haemonchus*	Benzimidazole, Levamisole	(Chartier *et al*., 1998)
France	*In vivo* FECRT *In vitro* EHA	*Trichostrongylus colubriformis, Haemonchus contortus, Teladorsagia circumcincta*	Benzimidazole	(Chartier *et al*., 2001)
France	Genotyping by PCR and sequencing	*Trichostrongylus axei*	Benzimidazole	(Palcy *et al*., 2010)
France	*In vivo* FECRT	*Haemonchus contortus*	Eprinomectin	(Jouffroy *et al*., 2023)
Germany	*In vivo* FECRT	*Haemonchus contortus*	Benzimidazole Levamisole Ivermectin Moxidectin Monepantel	(Voigt *et al*., 2022)
Greece	*In vivo* FECRT	*Teladorsagia, Trichostrongylus, Haemonchus*	Benzimidazole Levamisole Ivermectin Moxidectin	(Geurden *et al*., 2014)
India	Genotyping by PCR-RFLP	*Haemonchus contortus*	Benzimidazole	(Nath *et al*., 2022)
Iraq	*In vivo* FECRT	*Trichostrongylus Nematodirus, Trichuris*	Ivermectin Levamisole	(Dyary and Banaz, 2021)
Ireland	*In vivo* FECRT	*Haemonchus Teladorsagia, Trichostrongylus*	Benzimidazole	(Ramünke *et al*., 2016)
Italy	*In vivo* FECRT	*Haemonchus Teladorsagia, Trichostrongylus*	Benzimidazole	(Ramünke *et al*., 2016)
Malaysia	*In vivo* FECRT	*Haemonchus contortus*	Benzimidazole	(Pandey and Sivaraj, 1994)
Malaysia	*In vivo* FECRT	*Haemonchus contortus*	Benzimidazole	(Dorny *et al*., 1994)
Malaysia	*In vivo* FECRT	*Haemonchus contortus*	Levamisole, Closantel, Ivermectin	(Chandrawathani *et al*., 1999)
Malaysia	*In vivo* FECRT	*Haemonchus contortus*	Benzimidazole Levamisole Ivermectin	(Chandrawathani *et al*., 2003)
Malaysia	*In vivo* FECRT	*Haemonchus, Trichostrongylus*	Benzimidazole, Closantel	(Nor-Azlina *et al*., 2011)
Malaysia	*In vivo* FECRT	*Haemonchus contortus, Trichostrongylus, Oesophagostomum*	Albendazole, Ivermectin	(Basripuzi *et al*., 2012)
Malaysia	*In vivo* FECRT	*Haemonchus contortus, Trichostrongylus*	benzimidazoles Ivermectin	(Chandrawathani *et al*., 2013)
Malaysia	*In vivo* FECRT	*Haemonchus contortus Trichostrongylus Oesophagostomum*	Benzimidazoles Levamisole Macrocyclic Lactones Closantel	(Premaalatha *et al*., 2014)
Malaysia	*In vivo* FECRT	*Haemonchus contortus Oesophagostomum, Bunostomum*	Benzimidazole	(Sabariah *et al*., 2017)

Table 1 (Continue). Summary of resistant nematode species and methods used for detecting anthelmintic resistance globally.

Country	Diagnostic method	Resistant species	Anthelmintic	References
Malaysia	*In vivo* FECRT	*Haemonchus contortus* *Trichostrongylus* *Oesophagostomum*	Benzimidazole Macrocyclic Lactones	(Premaalatha *et al*., 2019)
Malaysia	*In vivo* FECRT	*Haemonchus contortus*	Albendazole, Levamisole Fenbendazole Ivermectin	(Abd Majid *et al*., 2022)
Malaysia	*In vivo* FECRT Genotyping by PCR	*Haemonchus contortus*	Benzimidazole	(Khadijah *et al*., 2018)
Netherlands	*In vivo* FECRT	*Haemonchus contortus* *Trichostrongylus, Teladorsagia*	Oxfendazole Ivermectin, Moxidectin, Monepantel	(Ploeger and Everts, 2018)
Netherlands	*In vivo* FECRT	*Haemonchus contortus, Teladorsagia circumcincta, Trichostrongylus colubriformis*	Oxfendazole Ivermectin, Levamisole	(Borgsteede *et al*., 1997)
Norway	*In vivo* FECRT	*Teladorsagia* *Trichostrongylus* *Haemonchus*	Albendazole	(Domke *et al*., 2012)
Scotland	*In vitro* EHA	*Teladorsagia*	Benzimidazole	(Bartley *et al*., 2003)
Slovak Republic	*In vivo* FECRT	*Ostertagia, Trichostrongylus, Cooperia, Haemonchus*	Ivermectin, Albendazole	(Čerňanská *et al*., 2006)
South Africa	*In vivo* FECRT	*Haemonchus contortus*	Albendazole, Levamisole, Ivermectin	(Van Wyk *et al*., 1999)
Sweden	*In vivo* FECRT Genotyping by PCR and sequencing	*Haemonchus contortus*	Monepantel	(Höglund *et al*., 2020)
Switzerland	*In vivo* FECRT	*Haemonchus, Teladorsagia* *Trichostrongylus*	Benzimidazole	(Ramünke *et al*., 2016)
United States	*In vivo* FECRT *In vitro* EHT	*Haemonchus*	Albendazole, Eprinomectin Levamisole	(Tsukahara *et al*., 2017)

Table 2. Common mechanisms of anthelmintic resistance in *Trichostrongyle*s of sheep and goats.

Drug	Target	Molecular change	Resistant species	References
Benzimidazoles	β-tubulin gene SNPs at F200Y, E198A, E198L and F167Y	Mutations alter the binding site of Benzimidazoles, reducing drug efficacy.	*Haemonchus contortus* *Teladorsagia circumcincta* *Trichostrongylus*	(Silvestre and Humbert, 2002; Palcy *et al*., 2010; Beech *et al*., 2012; Morrison *et al*., 2014; Baltrušis *et al*., 2018, 2020; Kotze *et al*., 2020).
Macrocyclic Lactone	Mutation of the P-glycoprotein (P-gp) homologue	Increased expression of P-gap increases drug efflux and reduce drug concentration at target sites	*Haemonchus contortus*	(Xu *et al*., 1998; Beech *et al*., 2012; Urdaneta-Marquez *et al*., 2014; Maté *et al*., 2018; Antonopoulos *et al*., 2022, 2024; Luo *et al*., 2023).
Imidazothiazoles	S168T mutation in the acetylcholine receptor (acr-8) subunit gene	Reduces sensitivity to levamisole by decreasing the acetylcholine receptor, reducing drug binding affinity to the receptor, and decreasing drug effectiveness in paralyzing the parasite	*Haemonchus contortus*	(Antonopoulos *et al*., 2022, 2024)

volving Benzimidazoles, Imidazothiazoles, and Macrocyclic lactones in *H. contortus* and T. colubriformis was reported in sheep flock in Antioquia, Colombia (Chaparro *et al*., 2017). Moreover, resistance of *Haemonchus* and *Trichostrongylus* species to Benzimidazole and Ivermectin occurred in sheep flocks from Brazil (Amaral *et al*., 2021; Batista *et al*., 2023). In Europe, the resistance of *Trichostrongyle*s such as *H. contortus*, *Trichostrongylus* colubriformis, and *Teladorsagia* circumcincta to Benzimidazoles such as Fenbendazole and Albendazole (Hinney *et al*., 2020) and Macrocyclic Lactones such as Ivermectin, Doramectin, and Moxidectin (Untersweg *et al*., 2021) has been reported in small ruminant flocks in Austria. Resistance to Benzimidazole and Levamisole (Chartier *et al*., 1998, 2001; Palcy *et al*., 2010), and Eprinomectin (Jouffroy *et al*., 2023) were documented in *Teladorsagia*, *Trichostrongylus*, and *Haemonchus* species in sheep and goats in France. In The Netherlands, Benzimidazole-resistant strains of *H. contortus*, Cooperia spp., Ostertagia spp., *Trichostrongylus* spp. and *Teladorsagia* spp. were also reported in small ruminants (Borgsteede *et al*., 1997). In Sweden, Monepantel-resistant strains of *Haemonchus contortus* was reported in sheep (Höglund *et al*., 2020). Benzimidazole-resistant strains of *Haemonchus*, *Teladorsagia*, and *Trichostrongylus* species were reported among small ruminants in Switzerland (Ramünke *et al*., 2016), Norway (Domke *et al*., 2012), and Ireland (Ramünke *et al*., 2016), in addition to *Teladorsagia* species in Scotland (Bartley *et al*., 2003). In Greece, AR against LEV and BZ with multiple drug resistance (MDR) involving *Teladorsagia* sp., *Haemonchus* sp. and *Trichostrongylus* sp., was observed on sheep farms (Geurden *et al*., 2014). In Germany, AR against Benzimidazoles, Moxidectin, Monepantel, and Levamisole, and a combination of Closantel and Mebendazole involving *H. contortus* was observed in small ruminant flocks (Voigt *et al*., 2022).

Resistant strains of *H. contortus* have been reported in Australasia (Leathwick and Besier, 2014). Benzimidazole-resistant strains of *Haemonchus*, *Oesophagostomum*, and *Trichostrongylus* were reported in small ruminants in Bangladesh (Dey *et al*., 2020). Benzimidazole-resistant strains of *Haemonchus contortus* were also detected among sheep and goats in India (Nath *et al*., 2022). Multidrug resistance involving Ivermectin and Levamisole in *Trichostrongylus*, *Nematodirus* and *Trichuris* was also reported in Iraq (Dyary and Banaz, 2021). The broad spectrum of parasites that have developed resistant strains to most of the common anthelmintic compounds, especially BZ and ML, undermines the effectiveness of chemical control efforts, limiting treatment options for farmers, and threatening the productivity of grazing livestock globally (Waller, 1997, 2006; Sissay *et al*., 2006; Charlier *et al*., 2014). In Malaysia, the earliest report on anthelmintic resistance documented 34% Benzimidazole-resistant *Haemonchus contortus* from goat farms that frequently used anthelmintics (Dorny *et al*., 1994). Since then, the resistance of nematodes to multiple anthelmintics, including Benzimidazoles, Imidazothiazoles, Macrocyclic lactones, or combinations, was further documented all over West Malaysia (Chandrawathani *et al*., 1999). Currently, there is a significant body of published evidence documenting widespread anthelmintic failure involving the three major anthelmintics against pathogenetic nematodes such as *Haemonchus contortus*, *Trichostrongylus*, *Oesophagostomum*, and *Bunostomum* in Malaysia (Khadijah *et al*., 2006; Basripuzi *et al*., 2012; Premaalatha *et al*., 2014; Thongsahuan *et al*., 2014; Abubakar *et al*., 2015; Khadijah *et al*., 2018; Wong and Sargison, 2018; Baudinette *et al*., 2022). Thus, anthelmintic resistance has emerged as a significant threat to controlling gastrointestinal nematodes in small ruminant farms in West Malaysia. Although, anthelmintic resistance in *Trichostrongyle*s of small ruminant is rampant in Peninsular Malaysia, to the best of our knowledge, there is no record of the anthelmintic resistance profile of pathogenic nematodes to common anthelmintics used by farmers in Sarawak.

There are currently three methods for detecting anthelmintic resistance in strongyle nematodes, viz: *in vivo* methods such as egg count reduction test (FECRT) and controlled test; *in vitro* methods such as egg hatch test (EHT), larval paralysis, migration and motility tests, larval development tests (LDTs), adult development test; and molecular techniques. In the past, the controlled test was widely used in ruminants and laboratory animals to investigate anthelmintic resistance in nematode populations, but the method is no longer used because it is costly and cumbersome and subject to animal welfare concerns (Taylor *et al*., 2002). The FECRT uses a mean faecal egg count reduction of 90% or less as the reference for resistance to anthelmintics by nematode populations of sheep and goats (McKenna, 1994; Coles *et al*., 2006). Interestingly, 89.7% of the studies included in this review employed the *in vivo* faecal egg count reduction test (FECRT), making it the most popular method for diagnosis of anthelmintic resistance in *Trichostrongyle* Nematodes of sheep and goats. Although the *in vivo* FECRT is still the most widely used method for detecting anthelmintic resistance in sheep and goats, there are several limitations in terms of its accuracy and reliability (Coles *et al*., 2006). Firstly, faecal egg count generates variable results due to random distribution of eggs in faecal samples and differences in egg output among individual animals due to host factors such as the age, breed, and health status of the animals, as well as environmental conditions (Paul *et al*., 2014). Secondly, the sensitivity of FECRT is limited because it may not detect marginal reductions in egg counts and may produce false positives/negatives due to variations in the sensitivity and specificity of the methods used (Torgerson *et al*., 2012). Thirdly, thresholds of <95% reduction in egg count and a lower 95% confidence limit below 90% for determining resistance may not effectively distinguish between resistant and susceptible nematode populations in all cases (McKenna, 1994). Furthermore, conventional FECRT analysis using McMaster egg count does not account for the aggregated distribution of parasite eggs among hosts, which can affect the precision of resistance detection when advanced statistical models such as hierarchical Bayesian models are not used in the interpretation of results (Paul *et al*., 2014). Finaly, the accuracy of the FECRT results relies on the skill of the personnel performing the test, the process is also time-consuming, and the pharmacokinetics of the anthelmintic in the host may negatively influence the results (Coles *et al*., 2006).

The EHT and the larval development test (LDT) are the two *in vitro* methods most commonly used for detecting anthelmintic resistance in *Trichostrongyle* nematodes of ruminants (Coles *et al*., 2006; Mickiewicz *et al*., 2021). The EHT is used mainly to detect benzimidazole (BZ) resistance by evaluating ovicidal activity of BZs at increasing dosages by measuring numbers of unhatched eggs (Coles *et al*., 2006; Tsukahara *et al*., 2017). In the EHT, nematode eggs are incubated at 26°C for 48 h in serial concentrations of BZ, and the number of eggs and hatched first stage larvae are counted to determine the ED50 or concentration of BZ producing 50% inhibition of hatching (Várady and Čorba, 1999; Babják *et al*., 2021). The LDT, which was developed for detecting anthelmintic resistance in sheep nematodes evaluates the ability of first-stage larvae (L1) to develop into infective third-stage larvae (L3) in the presence of various anthelmintic compounds (Taylor, 1990). The assay determines the minimum inhibitory concentration (MIC) required to halt larval development. A commercial LDT for the detection of resistance to Benzimidazoles and Imidazothiazoles in sheep and goat gastrointestinal nematodes is available as the DrenchRite® in Australia (Demeler *et al*., 2010). Both EHT and LDT have demonstrated comparable and reliable results for detecting BZ resistance and have an advantage over other techniques due to their higher sensitivity in identifying relatively small proportions (4%) of resistant worms in a population. The EHT and LDT are so far recognised as the most suitable *in vitro* methods for field screening of AR in small ruminant nematodes (Várady and Čorba, 1999). Although the EHT is a valuable tool for detecting resistance in nematode populations, its application is limited to Benzimidazoles. Moreover, while the LDT provides controlled conditions for assessing drug efficacy, it does not account for the host interactions such as immunity and pharmacokinetics, which can influence the *in vivo* activities of anthelmintics in different species. Other *in vitro* assays such as the larval paralysis assay with physostigmine and larval micro motility assay have been evaluated as potential methods for the detection of anthelmintic resistance in sheep and goats (Várady and Čorba, 1999), but the results are unreliable. Hence, the tests are rarely recommended for detecting anthelmintic resistance in *Trichostrongyle* nematodes of ruminants. The numerous limitations of *in vivo* and *in vitro* diagnostic tests and the quest for understanding the molecular basis of anthelmintic resistance stimulated the development of more precise and robust molecular diagnostics for the specific and early detection of anthelmintic resistance in *Trichostrongyle* nematodes.

Although only a small 15% of published reports included in this review used molecular methods for detecting anthelmintic resistance in small ruminant gastrointestinal nematodes, there is increasing interest in deploying molecular methods in detecting anthelmintic resistance to overcome the challenges associated with the use of *in vivo* and *in vitro* diagnostics in current use. A wide range of molecular testing platforms and assays such as diagnostic PCR, restriction enzyme digestion, direct sequencing, and pyrosequencing have been developed for detecting anthelmintic resistance in various species of *Trichostrongyle* nematodes of sheep and goats (Beech *et al*., 2012). Molecular tests focus on identifying genetic mutations associated with reduced drug susceptibility in parasitic nematodes (Kotze *et al*., 2020). Both conventional and real-time PCR assays have been developed to detect specific single nucleotide polymorphisms (SNPs) or mutations linked with resistance in various nematode species (Samson-Himmelstjerna, 2006). Polymerase chain reaction (PCR) techniques amplify DNA sequences containing known resistance-associated mutations (Beech *et al*., 2012). Currently, point mutations F200Y, E198A, E198L, and F167Y in the isotype 1 β-tubulin gene are the major determinants of resistance to Benzimidazoles and used as the primary targets of molecular diagnostics in many gastrointestinal nematodes of ruminants (Silvestre and Humbert, 2002; Palcy *et al*., 2010; Morrison *et al*., 2014; Baltrušis *et al*., 2018, 2020; Kotze *et al*., 2020). A specific q-PCR has been developed and is widely used to detect the expression pattern of P-glycoprotein (P-gp) homologue in *Haemonchus contortus* as a primary target for detecting anthelmintic resistance to Macrocyclic Lactone anthelmintics such as Ivermectin and Moxidectin (Luo *et al*., 2023). Allele specific PCR targeting mutation at the acr-8 sub-unit of the acetylcholine receptor (AChR) conferring a serine-to-threonine substitution (S168T) has been developed for the detection of AR to Imidazothiazole, Levamisole in *Haemonchus* (Antonopoulos *et al*., 2022). Currently, well-established molecular markers are available predominantly for benzimidazole resistance, with ongoing research aiming to identify reliable markers for other anthelmintic classes. While these molecular diagnostics offer the advantage of early and precise detection of resistance, their effectiveness is contingent upon a comprehensive understanding of the genetic mechanisms underlying resistance to each drug class. Consequently, the development and implementation of molecular tests for field use are anticipated to progress as our knowledge of these genetic markers expands.

This study has shown that at least one mechanism of AR has been described in the three major anthelmintics classes associated with resistance in gastrointestinal Nematodes of sheep and goats. There are generally multiple independent origins of resistance and mixing of alleles by recurrent mutations associated with animal movements (Skuce *et al*., 2010). Early studies on the molecular mechanism of anthelmintic resistance were primarily focused on the Benzimidazoles (Taylor *et al*., 2002), which are the first broad-spectrum anthelmintics. Thus, the mechanism of resistance to BZs is well documented (Kotze *et al*., 2020). *Haemonchus contortus*, which is the most prevalent gastrointestinal Nematode of sheep and goats, has evolved multiple sources of resistance through recurrent mutations. A major breakthrough in understanding BZ resistance in nematodes was the discovery that specific polymorphism (s) in the β-tubulin gene are linked to resistance (Roos *et al*., 1990), suggesting that Benzimidazole-resistant worm populations possess an altered, possibly reduced, complement of the β-tubulin genes (Taylor *et al*., 2002). Further studies reported a 1000-fold increase in resistance associated with all isotype 1 β-tubulin alleles, and a portion of isotype 2 alleles, which harboured a glutamate-to-alanine substitution at position E198A (Rufener *et al*., 2009). Currently, it is known that point mutations F200Y, E198A, E198L and F167Y in the isotype 1 β-tubulin gene are recognised as the major determinants of Benzimidazole resistance in *Haemonchus* and other *Trichostrongyle*s of ruminants (Silvestre and Humbert, 2002; Palcy *et al*., 2010; Morrison *et al*., 2014; Baltrušis *et al*., 2018, 2020; Kotze *et al*., 2020). Benzimidazoles act by blocking the polymerization of microtubules in nematode worms (Samson-Himmelstjerna, 2006; Rufener *et al*., 2009). The inhibition of microtubule formation via β-tubulin binding causes the disruption of essential cellular functions such as cell division, shape and motility or intracellular substrate transport in parasitic nematodes (Samson-Himmelstjerna, 2006).

Mutation reduces BZ binding affinity to the beta-tubulin transport protein, diminishing its effectiveness against the parasite by decreasing concentrations at the target sites (Baltrušis *et al*., 2020). Therefore, the effectiveness of BZs is threatened by the emergence of resistant parasites that carry point mutations in the β-tubulin gene (Beech *et al*., 1994).

The primary targets of Macrocyclic Lactones such as Ivermectin and Moxidectin in parasitic nematodes is the glutamate-gated and GABA-gated chloride ion channels. The binding of Macrocyclic Lactones increases chloride ion permeability, leading to hyperpolarization of neuronal and muscle cells, resulting in paralysis and expulsion of the parasite (Samson-Himmelstjerna, 2006). The P-glycoprotein (P-gp) is also known to mediate ivermectin resistance in *H. contortus*. A higher P-gp mRNA expression coinciding with alterations in the P-gp genomic locus was observed in ivermectin-selected strains (Xu *et al*., 1998). An increase in P-gp expression increased drug transport and prevent drug access to its site of action (Beech *et al*., 2012). Transcriptomic analysis has also revealed differential expression of genes associated with neuronal function and chloride homeostasis, suggesting an adaptive response to ivermectin-induced hyperpolarization of neuromuscular cells in *Haemonchus contortus*. Notably, the transcription factor gene *cky*-1 was consistently upregulated in resistant populations, indicating its potential role in resistance mechanisms. Additionally, sex-specific differences were observed, including the upregulation of pgp-11 in resistant males. These findings enhance the understanding of ivermectin resistance and may inform strategies for managing anthelmintic resistance in parasitic nematodes (Laing *et al*., 2022).

The primary source of resistance to Imidazothiazole, Levamisole in *Haemonchus* is a mutation at the acr-8 sub-unit of the acetylcholine receptor (AChR) conferring a serine-to-threonine substitution (S168T) (Antonopoulos *et al*., 2022). This alteration reduces sensitivity to levamisole by decreasing the acetylcholine receptor, reducing drug binding affinity to the receptor, and decreasing drug effectiveness in paralyzing the parasite (Antonopoulos *et al*., 2024). For Ivermectin a macrocyclic lactone, the P-glycoprotein (P-gp) homologue of *Haemonchus contortus* is thought to play a significant role in resistance (Luo *et al*., 2023). Increased expression of P-gap increases drug efflux and decreases drug concentration at target sites. Despite significant advances in our understanding of molecular mechanisms of resistance and the widespread application of novel molecular tools for detecting anthelmintic resistance (AR) in various gastrointestinal nematodes, reliable molecular markers that correlate well with AR are currently available only for the detection of benzimidazole resistance in *Haemonchus* and other *Trichostrongyle* nematodes (Beech *et al*., 2012).

Summary of findings and future directions

This review highlights the widespread prevalence of anthelmintic resistance in *Trichostrongyle* nematodes of small ruminants, with *Haemonchus contortus*, *Trichostrongylus*, and *Teladorsagia* being the most resistant species globally. High resistance of pathogenic nematodes to Benzimidazoles, Macrocyclic Lactones, and Imidazothiazoles limits treatment options and increase economic burdens for farmers. Benzimidazole and Macrocyclic Lactones resistance is widespread in *H. contortus*, *Trichostrongylus*, *Oesophagostomum*, and *Bunostomum* in West Malaysia. Although the FECRT is the most used diagnostic test for the direct detection of anthelmintic resistant nematode populations, its reliability, reproducibility, sensitivity and ease of interpretation are questionable. Molecular methods, including PCR-based detection of resistance-associated mutations, offer promising alternatives for early detection. Key resistance markers include mutations in the β-tubulin gene for Benzimidazole resistance, the acr-8 gene for Imidazothiazole resistance, and increased P-glycoprotein (P-gp) expression for Macrocyclic Lactone resistance. Despite these advances, molecular markers for detecting resistance in many species, other than the well-studied *Haemonchus contortus*, are unknown, requiring further advanced research in this area. Future studies should focus on developing standardized molecular diagnostics for all known pathogenic *Trichostrongyle*s and validating resistance markers for Macrocyclic Lactone and Imidazothiazoles for more efficient tracking of resistance. Additionally, integrated parasite management strategies, including targeted selective treatments (TST) and alternative sustainable non chemotherapeutic control methods, should be explored to reduce drug selection pressure and slow down the development of resistance. More epidemiological studies, particularly in underreported regions like Sarawak, are necessary to fully understand resistance patterns and guide sustainable treatment strategies for small ruminants in Malaysia.

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Conflict of interest

The authors declare no competing interests.

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