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Epidemiology and diversity of gastrointestinal tract helminths of wild ruminants in sub-Saharan Africa: a review

Review Article

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Abstract

This review summarises studies on distribution, diversity, and prevalence of gastrointestinal helminth infections in wild ruminants in sub-Saharan Africa. The results showed that 109 gastrointestinal tract (GIT) helminth species or species complexes were recorded in 10 sub-Saharan African countries. South Africa reported the highest number of species because most studies were carried out in this country. Eighty-eight nematode species or species complexes were recorded from 30 wild ruminant species across eight countries. The genus *Trichostrongylus* recorded the highest number of species and utilised the highest number of wild ruminant species, and along *with Haemonchus* spp., was the most widely distributed geographically. Fifteen trematode species or species complexes were reported from seven countries. The genus *Paramphistomum* recorded the highest number of species, and *Calicophoron calicophoron* was the most commonly occurring species in sub-Saharan African countries and infected the highest number of hosts. Six cestode species or species complexes from one family were documented from 14 wild hosts in seven countries. *Moniezia* spp. were the most commonly distributed in terms of host range and geographically. Impala were infected by the highest number of nematodes, whilst Nyala were infected by the highest number of trematode species. Greater kudu and Impala harbored the largest number of cestodes. The prevalence amongst the three GIT helminths taxa ranged between 1.4% and 100% for nematodes, 0.8% and 100% for trematodes, and 1.4% and 50% for cestodes. There is still limited information on the distribution and diversity of GIT helminths in wild ruminants in most sub-Saharan African countries.

Introduction

Helminths are a diverse group of parasitic worms that infect both animals and humans (MacDonald *et al.,* 2002).

Infectious diseases caused by helminth infections are among the most significant global health concerns, impacting both human and animal populations (Lustigman *et al.*, 2012; Rehman & Abidi, 2022). These parasites play a critical role in both wildlife and domestic animals, regulating host populations in natural environments, and influencing survival, reproduction, and trophic equilibrium (Grenfell, 1992; Holmes, 1995; Hudson *et al.*, 1998; Tompkins & Begon, 1999; van Wyk & Boomker, 2011; Watson, 2013). Furthermore, they pose significant threats to conservation efforts, restricting the ranges of host species and endangering species of conservation concern (Dobson & Hudson, 1986; Laurenson *et al.*, 1998; Morgan *et al.*, 2005; Page, 2013), such as the African buffalo, Nile lechwe, Mountain reedbuck, Mountain gazelle, and Walia ibex that occur in sub-Saharan Africa but have been considered endangered, near threatened, or vulnerable, with slowly decreasing populations in the wild according to the International Union for Conservation of Nature Red List of Threatened species (https://www.iucnredlist.org/). In wildlife and at the livestock-wildlife interface, parasitic infections can have severe consequences, including acute clinical signs leading to production losses and mortality (Meurens *et al.*, 2021).

These parasites can cause a wide range of diseases and health problems, including gastrointestinal tract (GIT) disturbances in animals and humans (Slifko *et al.*, 2000; Góralska & Blaszkowska, 2015). It has been established that GIT helminths may lead to nutritional deficiencies and poor health in wildlife (Gillespie, 2006; Egbetade *et al.*, 2014). Wildlife serves as carriers or reservoirs of various economically important helminths, which can be transmitted to domestic ruminants (Ogunji *et al.*, 1984; Muriuki *et al.*, 1998; Oyeleke & Edungbola 2001; Karere & Munene, 2002; Moudgil & Singla 2013; Rose *et al.*, 2014; Modabbernia *et al.*, 2021; Barone *et al.*, 2020). Wild ruminants such as Impala, African buffalo, Blue wildebeest, Eland, Nyala, and Greater kudu inhabit a variety of habitats in the savannas, woodlands, and open grasslands, and have a wide geographic distribution, making it possible for them to harbour a wide variety of gastrointestinal helminths in sub-Saharan African regions such as South Africa, Nigeria, Tanzania, and Kenya (Fuentes, 2021). According to Sepulveda and Kinsella (2013), wild animals are susceptible to different types of gastrointestinal helminths, including "roundworms" (nematodes), "flukes" (trematodes), and "tapeworms" (cestodes). Despite these parasitic infections, both wild and domestic animals have developed natural immune responses, allowing them to coexist with parasites without significant harm to the host (Borkovcova & Kopřiva, 2005). Understanding the impact of these parasites and the potential for interspecies transmission requires robust parasitological research (Begon *et al*., 1999). Additionally, to mitigate the impact of parasites on population dynamics, it is crucial to assess the incidence and prevalence of parasitic infections (Morner, 2002; Williams *et al*., 2002; Junge & Louis, 2005).

Gregory (1997) classified the primary possible determinants of parasite distribution in a particular host population into three components: host population factors (abundance, range, and migration), host individual parameters (such as age, sex, body size, diet), and environmental factors (habitat and climate). Animal ecology is impacted by the changing environment and living conditions of the host, which also makes them more susceptible to helminth infections (Goossens *et al.,* 2005; Singh *et al.,* 2006). According to Body *et al.* (2011), the infection rates of parasites in the host population may rise directly or indirectly as a result of factors such as weather, the quantity and quality of feed, or the lack of major predators. Climatic variables may directly impact the survival of free-living larval stages of the parasites and indirectly affect vertebrate hosts by affecting the frequency and intensity in which helminths are spread, and their geographic expansion (Mas-Coma *et al.,* 2008). Temperature and moisture-related variables have more frequently been linked to the distribution and abundance of helminths (Mas-Coma *et al.,* 2008).

The population of wild animals is seriously threatened by parasitic infections and associated complications, which have the potential to cause extinction (Harvell *et al.,* 2002). Although wildlife populations might seem to have adjusted to the existence of parasites, they have not adapted to the detrimental consequences of parasitism (Bliss, 2009; Opara *et al.,* 2010). It is therefore critical to know the helminth infections in the wildlife of a given area (van Wyk & Boomker, 2011), and baseline measures of parasite richness, prevalence, and intensity in wild populations in conservation biology, so that the emergence of new parasites or changes in abundance or disease conditions associated with existing parasites can be determined (Hahn *et al.,* 2003; Brooks & Hoberg, 2006). Hence, the review collated existing scientific data highlighting the distribution, diversity, and prevalence of GIT helminths in wild ruminants in sub-Saharan Africa.

Methodology

Scoping review

The scoping review was designed to address the following questions: Which GIT helminth species of wild ruminants occur in sub-Saharan African countries? What is the distribution of GIT parasite infection in sub-Saharan Africa? What is the prevalence of GIT parasites in sub-Saharan Africa? To address these questions, published peer-reviewed articles from accredited journals explicitly reporting on the GIT helminths infections in wild ruminants in the sub-Saharan African region were identified and reviewed following the recommended standards (Munn *et al.,* 2018) and guidelines for reporting from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses. The scoping review followed the approach outlined by Arksey and O'Malley (2005), which included the (i) identification of research question(s); (ii) searching of relevant literature; (iii) selection of relevant literature; (iv) charting of data; and last (v) systematising, summarising, and reporting the results.

Search strategy

Three electronic databases, Google Scholar (https://scholar.google.com), Science Direct (https://www.sciencedirect.com/), and PubMed (http://www.ncbi.nlm.nih.gov/pubmed/), were searched for relevant literature. The following keywords and Boolean operators (AND, OR) were used in the search: GIT helminths OR Occurrences OR Distribution OR Prevalence AND "GIT nematodes OR roundworms" AND "GIT trematodes OR flukes OR rumen flukes OR conical flukes OR Platyhelminths" AND "GIT cestodes OR Tapeworms" AND wild ruminants in sub-Saharan Africa (Angola, Benin, Botswana, Burkina Faso, Burundi, Cape Verde, Cameroon, Comoros, Ivory Coast [Côte d'Ivoire], Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Equatorial Guinea, Kenya, Lesotho, Liberia, Madagascar, Malawi, Mali, Mauritius, Mauritania, Mozambique, Namibia, Niger, Nigeria, Uganda, Central African Republic, Democratic Republic of the Congo, Rwanda, Sao Tome, and Principe, Senegal, Seychelles, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Swaziland, Tanzania, Chad, Togo, Zambia, Zimbabwe). The scope of the literature search was limited to articles written and published in English between 1980 and 2022. Relevant articles were first identified by screening through their titles and abstracts. Reference lists of selected articles were also screened as potential leads for additional relevant studies for review. Zotaro reference manager version 6.0.26 was used to manage the full texts of the retrieved articles.

Inclusion and exclusion criteria

Articles were considered if they had been published in ISI peer-reviewed accredited journals and specifically reported on the following: (i) occurrence or distribution of GIT helminths (nematodes, trematodes, and cestodes) in wild ruminants, (ii) prevalence of GIT helminths in wild ruminants, (iii) studies were conducted in the sub-Saharan African region; and (iv) studies were conducted and published from 1980 to 2022.

The review excluded studies reporting on (i) GIT parasites in non-ruminant wildlife; (ii) parasites that pass through the GIT during development but do not use the GIT as the predilection site of the adult parasite, e.g. *Fasciola* spp.; (iii) redescription of specimens collected before 1980; (iv) relevant studies but conducted in nations outside of the sub-Saharan African region, (v) GIT parasites other than helminths which fall outside of the three groups (nematodes, trematodes, and cestodes), and (vi) all reviews, books, dissertations and non-peer-reviewed reports.

Charting, collating, and summarising data

Data was extracted from articles with information that met the inclusion criteria after appraisal and contributed to answering the review questions. The aim or objectives of the study, the country in which the study was conducted, the outcomes of the study, and information relevant to the review questions were recorded on MS Word.

For this review, nomenclature updates for family/genus/species names were based on the following studies: Durette-Desset (1985), Durette-Desset *et al.* (1999), Boomker & Taylor (2004), Beveridge *et al.* (2013), Hosseinnezhad *et al.* (2021) and Hodda (2022) for nematodes; Eduardo (1982, 1985) and Pfukenyi and Mukaratirwa (2018) for trematodes (paramphistomes); and Mariaux *et al.* (2017) for cestodes (Anoplocephalidae).

Results

A literature search from the three databases yielded a total of 6164 hits, consisting of books, reviews, dissertations, unpublished reports, abstracts, and duplicate articles (Fig. 1). In addition, 12 articles were obtained through bibliographic searches from relevant articles. A total of 89 duplicating studies were removed, and a total of 6087 articles, books, reviews, and dissertations were deemed irrelevant and excluded after screening their titles and abstracts. The full text of 77 articles were downloaded and screened for eligibility, and 39 studies were deemed ineligible because they did not explicitly report on the GIT helminths found in wild ruminants and were not conducted in sub-Saharan countries. A total of 38 articles met the criteria and were included in the scoping review.

The distribution of the studies that fulfilled the inclusion criteria on a geographical scale and scope varied across the sub-Saharan Africa region. Of the 38 articles reviewed, 23 were from South Africa, four were from Zambia, two were from Kenya, two were from Nigeria, two from Sudan, one from Congo, one from Tanzania, one was from Rwanda, one from Ethiopia, and one study was conducted in both South Africa and Namibia. All the studies included in the scoping review were field studies or case reports. Most studies focused on the microscopic examination of faecal specimens using sedimentation and/or flotation methods, and the rest of the studies identified immature or adult specimens microscopically (Supplementary Table 1). Only one study (Ikeuchi *et al.*, 2022) used molecular methods; thus, some helminths could only be identified to genus level. The checklists were arranged according to taxa (i.e. nematodes, trematodes, and cestodes) (Tables 1–3).

Checklist and distribution of GIT nematodes in wild ruminants in sub-Saharan Africa from 1980 to 2022

The results showed that a total of 40 genera, 78 species, and 31 unidentified species complexes of GIT helminths were documented in 10 sub-Saharan African countries. Of these, 64 species and 24

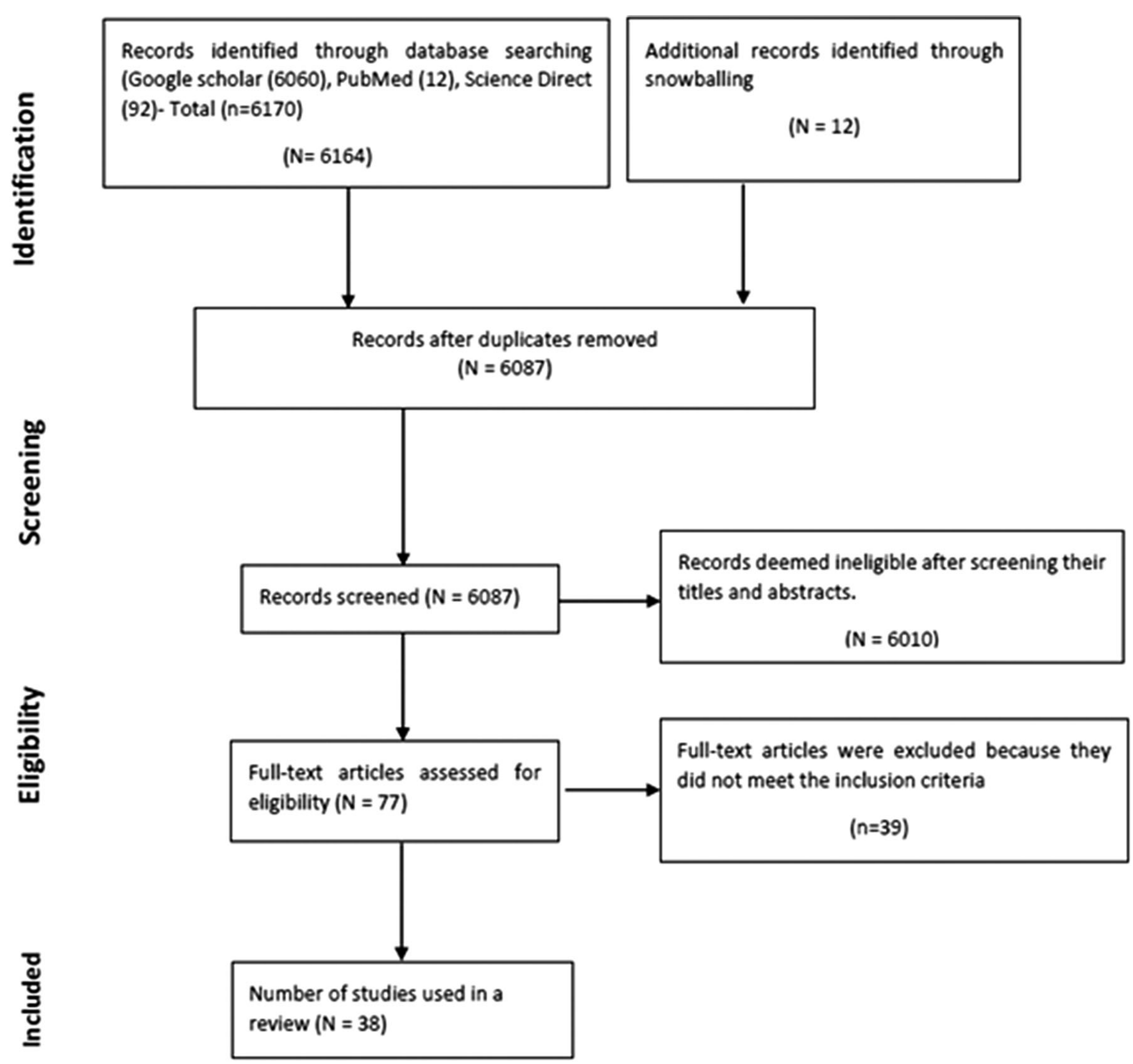

Figure 1. PRISMA diagram.

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Table 1. Checklist of GIT nematode species and their hosts reported in sub-Saharan Africa (1980-2022)

Family	GIT nematode species	Country reported	Host species	Reference
Ancylostomatidae	*Ancylostoma* spp.	Nigeria	Waterbuck (*Kobus ellipsiprymnus*)	Atuman *et al.,* 2019
	Bunostomum spp.	South Africa, Tanzania, Nigeria	African buffalo (*Syncerus caffer*), Common reedbuck (*Redunca arundinum*), Eland (*Taurotragus oryx*)	Boomker *et al.,* 1984; Senyael *et al.,* 2013, Atuman *et al.,* 2019
	Gaigeria spp.	South Africa	Common reedbuck	Boomker *et al.,* 1989a
	Gaigeria pachyscelis	Zamiba, South Africa	Impala, Defassa waterbuck (*Antilope defassa*), Nyala (*Tragelaphus angasii*)	Anderson, 1983; Boomker *et al.,* 1989a, 1996; Zieger *et al.,* 1998
Ascarididae	*Ascaris* spp.	Ethiopia, Sudan	Bushbuck (*Tragelaphus sylvaticus*), Dikdik (*Madoqua kirkii),* Walia ibex (*Capra walie*)	Abuessailla *et al.* 2013, 2014; Bogale *et al.,* 2014
Cooperiidae	*Cooperia* spp.	South Africa, Kenya, Nigeria	African buffalo, Bushbuck, Greater kudu (*Tragelaphus strepsiceros*), Grey duiker (*Sylvicapra grimmia*), Impala, Thompson's gazelle (*Eudorcas thomsonii*), Waterbuck, Tsessebe (*Damaliscus lunatus*), Mountain reedbuck (*Redunca fulvorfula*), Walter's duiker (*Philantomba walteri*)	Boomker *et al.,* 1987, 1989a, 1989b; Reinecke *et al.,* 1988; Taylor *et al.,* 2005; van Wyk and Boomker, 2011; Budischak *et al.,* 2012; Gorsich *et al.,* 2014; Atuman *et al.,* 2019; Omonona *et al.,* 2019
	Cooperia fuelleborni	South Africa	African buffalo, Greater kudu, Tsessebe, Impala	Anderson, 1983; Reinecke *et al.,* 1988; Boomker *et al.,* 1989b; Penzhorn, 2000; van Wyk and Boomker, 2011; Taylor *et al.,* 2013
	Cooperia hungi	South Africa	African buffalo, Impala, Greater kudu, Tsessebe, Common reedbuck, Gemsbok (*Oryx gazella*), Nyala	Reinecke *et al.,* 1988; Boomker *et al.,* 1989a, 1989b, 1996; van Wyk and Boomker, 2011; Taylor *et al.,* 2013
	Cooperia acutispiculum	South Africa, Namibia	Greater kudu	Boomker *et al.,* 1988, 1989b
	Cooperia rotundispiculum	South Africa, Zambia	Blue duiker (*Philantomba monticola*), Eland, Greater kudu, Common reedbuck, Bushbuck, Red duiker (*Cephalophus natalensis*), Black wildebeest (*Connohaetes gnou*), Bontebok (*Damaliscus pygargus*), Nyala, Mountain reedbuck, Blesbok (*Damaliscus pygargus phillipsi*), Springbok (*Antidorcas marsupialis*)	Boomker *et al.,* 1984, 1991a, 1991b, 1991c, 1991d, 1996, 2000; Boomker, 1991; Zieger *et al.,* 1998; Taylor *et al.,* 2005
	Cooperia yoshidai	South Africa	Greater kudu, Tsessebe, Oribi (*Ourebia ourebi*), Mountain reedbuck, Gray rhebok (*Pelea capreolus*), Common reedbuck, Impala	Boomker *et al.,* 1984, 1989a, 1989b; Reinecke *et al.,* 1988; Taylor *et al.,* 2005
	Cooperia neitzi	Namibia, South Africa	Greater kudu	Boomker *et al.,* 1988, 1989b; van Wyk and Boomker, 2011
	Cooperia curticei	South Africa	Waterbuck	van Wyk and Boomker, 2011
	Cooperia connochaeti	South Africa	Blue wildebeest (*Connochaetes taurinus*)	van Wyk and Boomker, 2011
	Cooperia pigachei	South Africa	Mountain reedbuck	Boomker and Taylor, 2004; Taylor *et al.,* 2005
	Cooperioides spp.	Zambia	Impala	Zieger *et al.,* 1998
	Cooperioides hamiltoni	South Africa, Namibia, Zambia	Greater kudu, Impala	Anderson, 1983; Boomker *et al.,* 1988, 1989a; Anderson 1992; Zieger *et al.,* 1998; van Wyk and Boomker, 2011
	Cooperioides antidorca	South Africa	Springbock	Boomker *et al.,* 2000
	Paracooperia devossi	South Africa, Namibia	Greater kudu, Bushbuck	Boomker *et al.,* 1984, 1987, 1988, 1989b
	Paracooperia horaki	South Africa	Nyala	Boomker et al., 1991c, 1996
	Paracooperia serrata	South Affrica	Springbok	Boomker *et al.,* 2000

(*Continued*)

Table 1. (*Continued*)

Family	GIT nematode species	Country reported	Host species	Reference
	Paracooperioides peleae	South Africa	Mountain reedbuck, Gray rhebok	Taylor *et al.,* 2005
	Impalaia spp.	South Africa, Zambia, Namibia	Greater kudu, Tsessebe	Boomker *et al.,* 1988, 1989b; Reinecke *et al.,* 1988
	Impalaia tuberculata	South Africa,	Impala, Greater kudu, Tsessebe, Red duiker, Nyala	Anderson, 1983; Boomker *et al.,* 1988, 1989b, 1991b, 1996; Reinecke *et al.,* 1988; van Wyk and Boomker, 2011
	Impalaia nudicollis	South Africa, Namibia	Greater kudu, Mountain reedbuck	Boomker *et al.,* 1988; Taylor *et al.,* 2005
Chabertiidae	*Agriostomum gorgonis*	South Africa, Zambia	African buffalo, Greater kudu, Impala, Black wildebeest	Boomker *et al.,* 1989b; Zieger *et al.,* 1998; Penzhorn, 2000; van Wyk and Boomker, 2011
	Agriostomum spp.	South Africa, Namibia	Greater kudu, Impala	Boomker *et al.,* 1988, 1989a
	Agriostomum cursoni	Zambia	Tsessebe	Zieger *et al.,* 1998
	Agriostomum equidentatum	South Africa	Springbok	Boomker *et al.,* 2000
	Oesophagostomum spp.	South Africa, Nigeria, Tanzania, Zambia	African buffalo, Bushbuck, Eland, Dikdik, Impala, Grey duiker, Nyala	Boomker *et al.,* 1987, 1989a, 1991c, 1996; Zieger *et al.,* 1998; Senyael *et al.,* 2013; Abuessailla *et al.,* 2013, 2014; Atuman *et al.,* 2019
	Oesophagostomum columbianum	South Africa	Impala, Blue wildebeest, Tsessebe, Black wildebeest, Common reedbuck, Grey duiker	Anderson, 1983; Reinecke *et al.,* 1988; Boomker *et al.,* 1989a; van Wyk and Boomker, 2011; Mijele *et al.,* 2016
	Oesophagostomum radiatum	South Africa	African buffalo	Penzhorn, 2000
Gongylonematidae	*Gongylonema* spp.	South Africa	Blue duiker, Bushbuck, Red duiker (*Cephalophus natalensis*), Nyala, Common reedbuck	Boomker *et al.,* 1984, 1987, 1989a, 1991c, 1991d, 1996
	Gongylonema verrucosum	South Africa	Nyala	Boomker *et al.,* 1991c, 1996
Habronematidae	*Parabronema skrjabini*	South Africa	African buffalo	Penzhorn, 2000
	Parabronema spp.	South Africa	Greater kudu	Boomker *et al.,* 1989b
Haemonchidae	*Haemonchus* spp.	South Africa, Kenya, Nigeria, Sudan	African buffalo, Blue wildebeest, Walter's duiker, Eland, Greater kudu, Impala, Common reedbuck, Dikdik, Tsessebe, Mountain reedbuck, Nyala	Reinecke *et al.,* 1988; Boomker et al. (1989a, 1991a, 1991c); Taylor *et al.,* 2005; Jolles *et al.,* 2008; van Wyk and Boomker, 2011; Abuessailla *et al.,* 2013, 2014; Gorsich *et al.,* 2014; Atuman *et al.,* 2019; Omonona, *et al.,* 2019
	Haemonchus bedfordi	South Africa	African buffalo, Tsessebe, Impala, Mountain reedbuck, Springbok, Blue wildebeest, Black wildbeest	Anderson, 1983; Reinecke *et al.,* 1988; Penzhorn, 2000; Boomker *et al.,* 2000; van Wyk and Boomker, 2011
	Haemonchus contortus	South Africa, Zambia	African buffalo, Impala, Eland, Lichtenstein's hartebeest (*Alcelaphus lichhtensteinii*), Great kudu, Kafue lechwe (*Kobus leche kafuensis*), Tsessebe, Bushbuck, Moutain reedbuck, Gray rhebok, Bontebok, Common reedbuck	Anderson, 1983; Boomker *et al.* 1984, 1989a, 2000; Reinecke *et al.,* 1988; Zieger *et al.,* 1998; Penzhorn, 2000; Taylor *et al.,* 2005; van Wyk and Boomker, 2011
	Haemonchus krugeri	South Africa	Impala	van Wyk and Boomker, 2011
	Haemonchus vegliai	South Africa, Namibia	Greater kudu, Bushbuck, Nyala	Boomker *et al.,* 1987, 1988, 1989b, 1991c, 1996
	Haemonchus placei	Kenya	Black wildebeest	Mijele *et al.,* 2016
	Haemonchus mitchelli	South Africa	Eland	Boomker *et al.,* 2000
	Hyostrongylus rubidus	South Africa	Red duiker	Boomker *et al.,* 1991b
	Longistrongylus spp.	South Africa	Mountain reedbuck	Taylor *et al.,* 2005
	Longistrongylus sabie	South Africa	Impala, Mountain reedbuck	Anderson, 1983; van Wyk and Boomker, 2011

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Table 1. (*Continued*)

Family	GIT nematode species	Country reported	Host species	Reference
	Longistrongylus namaquensis	South Africa	Mountain reedbuck, Springbok, Bontebok	Boomker *et al.,* 2000; Taylor *et al.,* 2005
	Longistrongylus albifrontis	South Africa	Springbok	Boomker *et al.,* 2000
	Longistrongylus curvispiculum	South Africa	Springbok, Gemsbok, Bontebok	Boomker *et al.,* 2000
	Longistrongylus schrenki	South Africa	Common reedbuck, Mountain reedbuck, Impala, Grey duiker	Boomker *et al.,* 1984, 1989a; Taylor *et al.,* 2005
	Ostertagia spp.	South Africa, Tanzania	Grey duiker, African buffalo, Mountain reedbuck, Gray rhebok, Eland, Springbok, Bontebok, Impala	Boomker *et al.,* 1987, 1989, 1991b, 1996, 2000; Taylor *et al.,* 2005; Senyael, *et al.,* 2013
	Ostertagia harrisi	South Africa	Bushbuck, Red duiker, Nyala	Boomker *et al.,* 1984, 1987, 1991b, 1991c, 1996
	Ostertagia ostertagi	South Africa	Greater kudu, Gemsbok, Common reedbuck, Springbok	Boomker *et al.,* 1989a, 1991a, 2000
	Teladorsagia circumcincta	South Africa	Tsessebe, Red duiker	Reinecke *et al.,* 1988, 1991b
	Teladorsagia trifurcata	South Africa	Nyala	Boomker *et al.,* 1991c, 1996
Molineidae	*Nematodirus spathiger*	South Africa	Mountain reedbuck, Red hartebeest (*Alcelaphus buselaphus caama*), Springbok, Gray rhebok, Blesbok	Boomker *et al.,* 2000; Taylor *et al.,* 2005
	Nematodirus helvetianus	South Africa	Greater Kudu	Boomker *et al.,* 1991a
Oxyuridae	*Skrjabinema* spp.	Kenya, South Africa	Thompson's gazelle, Tsessebe, Mountain reedbuck, Eland	Reinecke *et al.,* 1988; Boomker *et al.,* 1989a, 2000; Taylor *et al.,* 2005; Vander Waal *et al.,* 2014
Protostrongylidae	*Protostrongylus* spp.	Nigeria, Ethiopia	Walter's duiker, Walia ibex	Bogale *et al.,* 2014; Omonona *et al.,* 2019
	Muellerius spp.	Ethiopia	Walia ibex	Bogale *et al.,* 2014
Onchocercidae	*Setaria* spp.	South Africa	Blue duiker, Greater kudu, Red duiker, Nyala, Mountain reedbuck, Gray rhebok, Common reedbuck, Tsessebe	Boomker *et al.,* 1984, 1989a, 1989b, 1991c, 1991d, 1996; Reinecke *et al.,* 1988; Taylor *et al.,* 2005
	Setaria africana	South Africa	Bushbuck, Nyala	Boomker *et al.,* 1984, 1987, 1991c, 1996
	Setaria caelum	South Africa	Grey duiker	Boomker *et al.,* 1987
	Setaria scalprum	South Africa	Red duiker, Grey duiker	Boomker *et al.,* 1984, 1987, 1991b
	Setaria bicoronata	South Africa	Common reedbuck	Boomker *et al.,* 1989a
	Setaria boulengeri	South Africa	Common reedbuck	Boomker *et al.,* 1989a
	Setaria hornbyi	South Africa	Common reedbuck, Gemsbok, Grey duiker	Boomker *et al.,* 1987, 1989a; van Wyk and Boomker, 2011
	Setaria yorkei	South Africa	Bushbuck	Boomker *et al.,* 1987
	Setaria labiatopapillosa	South Africa	Common reedbuck, Nyala	Boomker *et al.,* 1989a, 1991c, 1996
Strongyloididae	*Strongyloides* spp.	Nigeria, Kenya, Ethiopia, Sudan	Eland, Lichtenstein's hartebeest, Impala, Thomspon's gazelle, Walia ibex, Walter's duiker, African buffalo	Budischak *et al.,* 2012; Bogale *et al.,* 2014; Vander Waal *et al.,* 2014; Atuman *et al.,* 2019; Omonona *et al.,* 2019
	Strongyloides papillosus	South Africa	Impala, Red duiker, Common reedbuck, Nyala	Anderson, 1983; Boomker *et al.,* 1989a, 1991b, 1996
Strongylidae	*Strongylus* spp.	Tanzania, South Africa, Ethiopia	African buffalo, Walia ibex	Jolles *et al.,* 2008; Buischak *et al.,* 2012; Senyael *et al.,* 2013; Bogale *et al.,* 2014
Trichostrongylidae	*Trichostrongylus* spp.	South Africa, Nigeria, Kenya, Tanzania, Namibia, Sudan	African buffalo, Greater kudu, Bushbuck, Walter's duiker, Eland, Lichtenstein's hartebeest, Impala, Thompson's gazelle, Common reedbuck, Dikdik, Waterbuck, Oribi, Red duiker	Boomker *et al.,* 1984, 1987, 1988, 1989a; Abuessailla *et al.,* 2013, 2014; Senyael *et al.,* 2013; Vander Waal *et al.,* 2014; Omonona, *et al.,* 2019

(*Continued*)

Table 1. (*Continued*)

Family	GIT nematode species	Country reported	Host species	Reference
	Trichostrongylus deflexus	South Africa	African buffalo, Impala, Blue wildebeest, Greater kudu, Mountain reedbuck, Springbok, Gemsbok, Nyala, Impala	Boomker *et al.,* 1989a, 1989b, 1996, 2000; Penzhorn, 2000; Taylor *et al.,* 2005; van Wyk and Boomker, 2011; Taylor *et al.,* 2013
	Trichostrongylus axei	South Africa	African buffalo, Grey duiker, Impala, Bontebok, Red duiker	Anderson, 1983; Boomker *et al.,* 1987, 1991b, 2000; Penzhorn, 2000
	Trichostrongylus colubriformis	South Africa	Impala, Oribi, Common reedbuck, Tsessebe	Anderson, 1983; Boomker *et al.,* 1984, 1989a; Reinecke *et al.,* 1988; van Wyk and Boomker, 2011
	Trichostrongylus angistris	South Africa	Blue duiker, Red duiker, Impala	Boomker *et al.,* 1989a, 1991b, 1991d
	Trichostrongylus falculatus	South Africa, Namibia	Blue duiker, Greater kudu, Oribi, Common reedbuck, Mountain reedbuck, Eland, Gemsbok, Nyala, Springbok, Tsessebe, Impala	Anderson, 1983; Boomker *et al.,* 1984, 1988, 1989a, 1989b, 1991c, 1991d., 1996, 2000; Reinecke *et al.,* 1988; Taylor *et al.,* 2005
	Trichostrongylus rugatus	South Africa	Blue duiker, Gemsbok	Boomker *et al.,* 1991d; Boomker *et al.,* 2000
	Trichostrongylus anomalus	South Africa	Blue duiker, Red duiker	Boomker *et al.,* 1991b, 1991d
	Trichostrongylus capricola	South Africa	Red duiker	Boomker *et al.,* 1984
	Trichostrongylus vitrinus	South Africa	Red duiker	Boomker *et al.,* 1984
	Trichostrongylus thomasi	South Africa	Bontebok, Gemsbok, Red duiker, Impala, Tsessebe, Greater kudu	Reinecke *et al.,* 1988; Boomker *et al.,* 1988, 1989a, 1991b, 2000
	Trichostrongylus pietersei	South Africa	Gemsbok	Boomker *et al.,* 2000
Trichuridae	*Trichuris* spp.	South Africa, Nigeria, Kenya, Ethiopia	Greater kudu, Grey duiker, Eland, Jackson's hartebeest (*Alcelaphus buselaphus lelwel*), Thompson's gazelle, Walia ibex, Red duiker, Common reedbuck, Waterbuck, African buffalo	Boomker *et al.,* 1987, 1989a, 1989b, 1991b; van Wyk and Boomker, 2011; Budischak *et al.,* 2012; Bogale *et al.,* 2014; Vander Waal *et al.,* 2014; Atuman *et al.,* 2019
	Trichuris globulosa	South Africa	African buffalo, Impala	Anderson, 1983; Penzhorn, 2000
Trichonematidae	*Trichonema* spp.	Nigeria	Eland	Atuman *et al.,* 2019
Toxocaridae	*Toxocara* spp.	Nigeria, Tanzania	Walter's duiker, African buffalo	Senyael *et al.,* 2013; Omonona, *et al.,* 2019

unidentified species or species complexes were nematodes belonging to 29 genera from 17 nematode families (Ancylostomatidae, Ascarididae, Chabertiidae, Cooperiidae, Gongylonematidae, Habronematidae, Haemonchidae, Molineidae, Onchocercidae, Oxyuridae, Protostrongylidae, Strongylidae, Strongyloididae, Trichostrongylidae, Trichuridae, Trichonematidae, and Toxocaridae), and these were documented across Ethiopia, Kenya, Namibia, Nigeria, South Africa, Sudan, Tanzania and Zambia (Table 1, Supplementary Table 1). These nematode species infected approximately 30 species of wild ruminants.

The nematode families Cooperidae and Haemonchidae were the most diverse. Both families recorded five genera, with the Cooperidae family represented by 17 defined species and three undefined species complexes, whereas Haemonchidae represented recorded 16 defined species and three unidentified species complexes. However, the genus *Trichostrongylus* recorded the highest number of species. Furthermore, the genera *Haemonchus* and *Trichostrongylus* were the most distributed, reported in seven countries each (Table 1). Furthermore, the results showed that the *Trichostrongylus* genus infected the highest number of wild ruminants (n = 22), followed by *Haemonchus contortus* (n = 12). Impala were more susceptible and were infected by the highest number of nematode species, followed by the African buffalo and the Greater kudu.

Checklist and distribution of GIT trematodes in wild ruminants in sub-Saharan Africa from 1980 to 2022

Eleven (n = 11) trematode species (*Calicophoron raja*, *Cal. calicophorum*, *Cal. microbothrium*, *Cotylophoron cotylophorum*, *Cot. jacksoni*, *Paramphistomum cephalophi*, *Leiperocotyle gretillati*, *Leiperocotyle congolense*, *Stephanopharynx compactus*, *Bilatorchis papillogenitalis,* and *Schistosoma mattheei*) and four species complexes (*Calicophoron* spp., *Fischoederius* spp., *Gastrothylax* spp., and *Paramphistomum* spp.) belonging to the families Gastrothylacidae, Paramphistomidae, and Schistosomatidae were identified. These were recorded from 17 species of wild ruminants and were distributed across Congo, Kenya, Nigeria, Rwanda South Africa, Tanzania, and Zambia (Table 2, Supplementary Table 1). The results also showed that *Paramphistomum* was the most widely distributed genus geographically, but species from the genus *Calicophoron* infected the most number of wild ruminants. Nyala were more susceptible to trematode infection and were infected by the

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Table 2. Checklist of GIT trematodes species and their hosts reported in sub-Saharan Africa (1980-2022)

Family	GIT trematode species	Country reported	Host species	References
Gastrothylacidae	*Gastrothylax* spp.	Tanzania	African buffalo	Senyael *et al.,* 2013
Paramphistomatidae	*Fischoederius* spp.	Tanzania	African buffalo	Senyael, *et al.,* 2013
	Calicophoron spp.	Zambia, South Africa	Impala, Sable antelope *(Hippotragus niger)*, Kafue lechwe, Tsessebe, Defassa waterbuck, Mountain reedbuck	Zieger *et al.,* 1998; Taylor *et al.,* 2005
	Calicophoron raja	Kenya, South Africa	Black wildebeest, Waterbuck	Mijele *et al.,* 2016; Ikeuchi *et al.,* 2022
	Calicophoron calicophorum	South Africa, Zambia	Water buffalo *(Bubaluxs bubalus)*, Nyala	Eduardo, 1983; Boomker *et al.,* 1991c, 1996
	Calicophoron microbothrium	South Africa	Nyala	Boomker *et al.,* 1991c, 1996
	Cotylophoron cotylophorum	South Africa	Impala, Nyala	Anderson, 1983; Boomker *et al.,* 1991c, 1996
	Cotylophoron jacksoni	South Africa	Nyala	Boomker *et al.,* 1991c, 1996
	Paramphistomum spp.	Nigeria, Kenya, Tanzania, South Africa	Waterbuck, Eland, Blue wildebeest, Tsessebe, Common reedbuck, Walter's duiker, Grey duiker	Boomker *et al.,* 1987; Reinecke *et al.,* 1988; Senyael, *et al.,* 2013; Vander Waal *et al.,* 2014; Atuman *et al.,* 2019; Omonona *et al.,* 2019
	Paramphistomum cephalophi	Rwanda	Black–fronted duiker *(Cephalophus nigrifrons)*	Eduardo, 1982
	Leiperocotyle gretillati	Congo	African buffalo	Eduardo, 1985
	Leiperocotyle congolense	Congo	African buffalo	Eduardo, 1985
	Stephanopharynx compactus	Zambia	Blue wildebeest	Eduardo, 1986
	Bilatorchis papillogenitalis	Zambia	Red lechwe *(Kobus leche)*	Eduardo, 1980
Schistosomatidae	*Schistosoma mattheei*	South Africa	Nyala	Boomker *et al.,* 1991c, 1996

Table 3. Checklist of GIT cestodes species and their hosts reported in sub-Saharan Africa (1980-2022)

Family	GIT cestode species	Country reported	Host species	References
Anoplocephalidae	*Avitellina* spp.	South Africa	Greater kudu, Waterbuck	Boomker *et al.,* 1989b; van Wyk and Boomker, 2011
	Avitellina centripunctata	Zambia	Tsessebe	Zieger *et al.,* 1998
	Moniezia spp.	South Africa, Nigeria, Ethiopia, Sudan	Waterbuck, Dikdik, Eland, Walia ibex, Mountain reedbuck, African buffalo	Taylor *et al.,* 2005; van Wyk and Boomker, 2011; Budischak *et al.,* 2012; Abuessailla *et al.,* 2013, 2014; Bogale *et al.,* 2014; Atuman *et al.,* 2019
	Moniezia benedeni	South Africa, Zambia	Greater kudu, Impala, Eland, Red duiker, Common reedbuck, Blue wildebeest, Black wildebeest, Nyala	Boomker *et al.,* 1989a, 1989b, 1991b, 1996, 2000; Zieger *et al.,* 1998; van Wyk and Boomker, 2011
	Moniezia expansa	Namibia, Kenya, South Africa	Greater kudu, Black wildebeest, Blue duiker, Impala, Grey duiker	Anderson., 1983; Boomker *et al.,* 1987, 1988, 1991d; van Wyk and Boomker, 2011; Mijele *et al.,* 2016
	Thysaniezia spp.	South Africa, Namibia	Tsessebe, Nyala	Reinecke *et al.,* 1988; Boomker *et al.,* 1996

Table 4. Prevalence of GIT nematode infections in wild ruminants in sub-Saharan Africa (1980-2022)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
South Africa	African buffalo	Worms	28	20	71.4	*Cooperia fuelleborni*	Microscopy	Taylor *et al.*, 2013
		Worms	28	2	7.1	*Cooperia hungi*	Microscopy	Taylor *et al.*, 2013
		Worms	28	9	32.1	*Trichostrongylus deflexus*	Microscopy	Taylor *et al.*, 2013
	Impala	Worms	10	1	10.0	*Cooperia fuelleborni*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	9	90.0	*Cooperia hungi*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	1	10.0	*Cooperia* spp.	Microscopy	van Wyk and Boomker, 2011
		Worms	10	2	20.0	*Cooperioides hamiltoni*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	2	20.0	*Haemonchus krugeri*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	2	20.0	*Haemonchus* spp.	Microscopy	van Wyk and Boomker, 2011
		Worms	10	5	50.0	*Impalaia tuberculata*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	1	10.0	*Impalaia* spp.	Microscopy	van Wyk and Boomker, 2011
		Worms	10	1	10.0	*Longistrongylus sabie*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	5	50.0	*Oesophagostomum columbianum*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	1	10.0	*Oesophagostomum* spp.	Microscopy	van Wyk and Boomker, 2011
		Worms	10	2	20.0	*Trichostrongylus colubriformis*	Microscopy	van Wyk and Boomker, 2011
		Worms	10	4	40.0	*Trichostrongylus deflexus*	Microscopy	van Wyk and Boomker, 2011
	Blue wildebeest	Worms	4	3	75.0	*Cooperia connochaet*	Microscopy	van Wyk and Boomker, 2011
		Worms	4	1	25.0	*Haemonchus bedfordi*	Microscopy	van Wyk and Boomker, 2011
		Worms	4	3	75.0	*Haemonchus contortus*	Microscopy	van Wyk and Boomker, 2011
		Worms	4	1	25.0	*Oesophagostomum columbianum*	Microscopy	van Wyk and Boomker, 2011
		Worms	4	2	50.0	*Trichostrongylus deflexus*	Microscopy	van Wyk and Boomker, 2011
	Gray rhebok	Worms	4	2	50.0	*Haemonchus contortus*	Microscopy	Taylor *et al.*, 2005
		Worms	4	3	75.0	*Ostertagia* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	4	4	100.0	*Cooperia yoshidai*	Microscopy	Taylor *et al.*, 2005
		Worms	4	2	50.0	*Paracooperioides peleae*	Microscopy	Taylor *et al.*, 2005
	Mountain reedbuck	Worms	66	21	32.0	*Haemonchus* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	66	62	94.0	*Haemonchus contortus*	Microscopy	Taylor *et al.*, 2005
		Worms	66	29	44.0	*Longistrongylus* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	66	1	2.0	*Longistrongylus namaquensis*	Microscopy	Taylor *et al.*, 2005
		Worms	66	1	2.0	*Ostertagia* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	66	44	66.0	*Cooperia* spp.	Microscopy	Taylor *et al.*, 2005

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Table 4. (*Continued*)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
		Worms	66	66	100.0	*Cooperia yoshidai*	Microscopy	Taylor *et al.*, 2005
		Worms	66	1	2.0	*Cooperia pigachei*	Microscopy	Taylor *et al.*, 2005
		Worms	66	28	43.0	*Trichostrongylus falculatus*	Microscopy	Taylor *et al.*, 2005
		Worms	66	1	2.0	*Trichostrongylus deflexus*	Microscopy	Taylor *et al.*, 2005
		Worms	66	7	10.0	*Impalaia nudicollis*	Microscopy	Taylor *et al.*, 2005
		Worms	66	1	2.0	*Paracooperioides peleae*	Microscopy	Taylor *et al.*, 2005
		Worms	66	28	43.0	*Skrjabinema* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	66	3	4.0	*Setaria* spp.	Microscopy	Taylor *et al.*, 2005
		Worms	66	5	8.0	*Longistrongylus albifrontis*	Microscopy	Taylor *et al.*, 2005
		Worms	66	38	58.0	*Nematodirus spathiger*	Microscopy	Taylor *et al.*, 2005
		Worms	66	20	31.0	*Cooperia rotundispiculum*	Microscopy	Taylor *et al.*, 2005
	Greater kudu	Worms	25	11	44.0	*Cooperia rotundispiculum*	Microscopy	Boomker *et al.*, 1991a
		Worms	25	1	40.0	*Haemonchus* spp.	Microscopy	Boomker *et al.*, 1991a
		Worms	25	1	4.0	*Nematodirus helvetianus*	Microscopy	Boomker *et al.*, 1991a
		Worms	25	2	8.0	*Ostertagia ostertagi*	Microscopy	Boomker *et al.*, 1991a
	Red duiker	Worms	25	22	88.0	*Cooperia rotundispiculum*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	2	8.0	*Cooperia yoshidai*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	10	40.0	*Haemonchus contortus*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	19	76.0	*Hyostrongylus rubidus*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	5	20.0	*Impalaia tuberculata*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	14	56.0	*Ostertagia harrisi*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	2	8.0	*Teladorsagia circumcincta*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	2	8.0	*Setaria scalprum*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	2	8.0	*Setaria* spp.	Microscopy	Boomker *et al.*, 1991b
		Worms	25	2	8.0	*Strongyoides papillosus*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	20	80.0	*Trichostrongylus angistris*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	15	60.0	*Trichostrongylus anomalus*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	1	4.0	*Trichostrongylus axei*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	1	4.0	*Trichostrongylus thomasi*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	5	20.0	*Trichuris* spp.	Microscopy	Boomker *et al.*, 1991b
		Worms	25	1	4.0	*Ostertagia spp.*	Microscopy	Boomker *et al.*, 1991b
		Worms	25	1	4.0	*Impalaia spp.*	Microscopy	Boomker *et al.*, 1991b
	Nyala	Worms	74	35	47.3	*Cooperia rotundispiculum*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	3	4.1	*Gongylonema spp.*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	14	18.9	*Haemonchus vegliai*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	1	1.4	*Impalaia spp.*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	1	1.4	*Oesophagostomum* spp.	Microscopy	Boomker *et al.*, 1991c
		Worms	74	72	97.3	*Ostertagia harrisi*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	38	51.3	*Paracooperia horaki*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	5	6.8	*Trichostrongylus falculatus*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	16	21.6	*Setaria* spp.	Microscopy	Boomker *et al.*, 1991c
		Worms	74	6	8.1	*Trichostrongylus deflexus*	Microscopy	Boomker *et al.*, 1991c
		Worms	74	1	1.4	*Impalaia tuberculata*	Microscopy	Boomker *et al.*, 1991c

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Table 4. (*Continued*)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
	Common reedbuck	Worms	57	48	84.2	*Cooperia yoshidai*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	3	5.3	*Gaigeria* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	57	21	36.8	*Haemonchus contotus*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	3	5.3	*Ostertagia ostertagi*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	20	35.1	*Setaria bicoronata*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	1	1.8	*Setaria labiatopapillosa*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	3	5.3	*Trichostrongylus falculatus*	Microscopy	Boomker *et al.*, 1989a
		Worms	57	2	3.5	*Trichuris* spp.	Microscopy	Boomker *et al.*, 1989a
	Impala	Worms	5	1	20.0	*Agriostomum* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Cooperia fuelleborni*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Cooperia hungi*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Cooperia yoshidai*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Cooperia* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Cooperioides hamiltoni*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	1	20.0	*Gaigeria pachyscelis*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	1	20.0	*Haemonchus contortus*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Impalaia tuberculata*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Oesophagostomum* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	5	2	40.0	*Ostertagia* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	5	1	20.0	*Strongyloides papillosus*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	4	80.0	*Trichostrongylus* spp.	Microscopy	Boomker *et al.*, 1989a
		Worms	5	1	20.0	*Trichostrongylus angistris*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	3	60.0	*Trichostrongylus thomasi*	Microscopy	Boomker *et al.*, 1989a
		Worms	5	1	20.0	*Trichostrongylus deflexus*	Microscopy	Boomker *et al.*, 1989a
Nigeria	Walter's duiker	Faecal	40	5	12.5	*Trichostrongylus* spp.	Microscopy	Omonona *et al.*, 2019
	Waterbuck	Faecal	11	2	18.2	*Ancylostoma* spp.	Microscopy	Atuman *et al.*, 2019
		Faecal	11	1	9.1	*Cooperia* spp.	Microscopy	Atuman *et al.*, 2019
	Eland	Faecal	24	3	12.5	*Haemonchus* spp.	Microscopy	Atuman *et al.*, 2019
		Faecal	24	3	12.5	*Strongyloides* spp.	Microscopy	Atuman *et al.*, 2019
	Wildebeest	Faecal	12	2	16.7	*Haemonchus* spp.	Microscopy	Atuman *et al.*, 2019
Tanzania	African buffalo	Faecal	123	12	20.3	*Trichostrongylus* spp.	Microscopy	Senyael *et al.*, 2013
		Faecal	123	9	7.3	*Oesophagostomum* spp.	Microscopy	Senyael *et al.*, 2013
		Faecal	123	5	4.1	*Strongylus* spp.	Microscopy	Senyael *et al.*, 2013
		Faecal	123	5	4.1	*Bunostomum* spp.	Microscopy	Senyael *et al.*, 2013
		Faecal	123	4	3.3	*Ostertegia* spp.	Microscopy	Senyael *et al.*, 2013
		Faecal	123	3	2.4	*Toxocara* spp.	Microscopy	Senyael *et al.*, 2013
Zambia	Impala	Worms	12	1	8.3	*Cooperioides hamiltoni*	Microscopy	Zieger *et al.*, 1998
		Worms	12	3	25.0	*Cooperioides* spp.	Microscopy	Zieger *et al.*, 1998
		Worms	12	1	8.3	*Gaigeria pachyscelis*	Microscopy	Zieger *et al.*, 1998
		Worms	12	1	8.3	*Haemonchus contortus*	Microscopy	Zieger *et al.*, 1998
	Tsessebe	Worms	3	1	33.3	*Agriostomum cursoni*	Microscopy	Zieger *et al.*, 1998
		Worms	3	1	33.3	*Gaigeria pachyscetis*	Microscopy	Zieger *et al.*, 1998
		Worms	3	1	33.3	*Impalaia* spp.	Microscopy	Zieger *et al.*, 1998

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Table 4. (*Continued*)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
	Lichtenstein's hartebeest	Worms	1	1	100.0	*Haemonchus contortus*	Microscopy	Zieger *et al.*, 1998
	Eland	Worms	2	1	50.0	*Cooperia rotundispicutum*	Microscopy	Zieger *et al.*, 1998
		Worms	2	1	50.0	*Haemonchus contortus*	Microscopy	Zieger *et al.*, 1998
		Worms	2	1	50.0	*Oesophagostomum* spp.	Microscopy	Zieger *et al.*, 1998
	Greater kudu	Worms	4	1	25.0	*Agriostomum gorgonis*	Microscopy	Zieger *et al.*, 1998
		Worms	4	1	25.0	*Cooperia rotundispicutum*	Microscopy	Zieger *et al.*, 1998
		Worms	4	1	25.0	*Haemonchus contortus*	Microscopy	Zieger *et al.*, 1998
	Kafue lechwe	Worms	2	1	50.0	*Haemonchus contortus*	Microscopy	Zieger *et al.*, 1998
	Common reedbuck	Worms	1	1	100.0	*Cooperia rotundispicutum*	Microscopy	Zieger *et al.*, 1998
		Worms	1	1	100.0	*Setaria bicoronata*	Microscopy	Zieger *et al.*, 1998
Sudan	Bushbuck	Faecal	11	2	18.2	*Ascaris* spp.	Microscopy	Abuessailla *et al.*, 2013
	Dikdik	Faecal	101	1	0.9	*Ascaris* spp.	Microscopy	Abuessailla *et al.*, 2013

highest number of trematode species, followed by the African buffalo.

Checklist and distribution of GIT cestodes in wild ruminants in sub-Saharan Africa from 1980 to 2022

Cestodes were the least reported GIT parasites. Six cestode species or species complexes, belonging to one (n = 1) cestode family (Anoplocephalidae) were documented across seven countries (Ethiopia, Kenya, Namibia, Nigeria, South Africa, Sudan, and Zambia (Table 3, Supplementary Table 1). However, the results also showed that the majority of these species were recorded in South Africa. These infections were recorded in 14 species of wild ruminants. The results also showed that *Moniezia* was the most common cestode genus, reported in Namibia, Kenya, South Africa, Nigeria, Ethiopia, Sudan, and Zambia (Table 3). Furthermore, the results obtained showed that *Moniezia benedeni* infected the highest number of wild ruminant species (n = 7). The results also indicated that the Greater kudu and Impala were more susceptible to cestode infection as they haboured the greatest numbers of species.

Prevalence of gastrointestinal helminths in wild ruminants in the sub-Saharan African region from 1980 to 2022

The results showed that the prevalence of nematode infections ranged from 1.4% to 100% (Table 4). The lowest prevalence of 1.4% (1/74) was in Nyala that were infected with *Impalaia* spp. and *Oesophagostomum* spp. in South Africa (Boomker et al., 1991c). The highest prevalences of 100% were recorded in Gray rhebok (4/4) and Mountain reedbuck (66/66) infected with *Cooperia yoshidaii* in South Africa (Taylor et al., 2005). The following hosts also recorded high prevalences of nematode infection: 97.3% (72/74) of Nyala infected with *Ostertagia harrisi* (Boomker et al., 1991c), 94% (62/64) of Mountain reedbuck infected with *Haemonchus contortus* (Taylor et al., 2005), and 90% (9/10) of Impala infected with *Cooperia hungi* (Van Wyk and Boomker, 2011) in South Africa (Table 4).

The prevalence of trematode infections ranged from 0.8% to 100% (Table 5). The lowest prevalence was recorded in African buffalo infected with *Fischoederius* spp. (1/123, 0.8%) and *Gastrothylax* spp. (2/123, 1.6%) in Tanzania (Senyael *et al.*, 2013). The highest prevalence of 100% (6/6) was reported in the Defassa waterbuck in Zambia, infected with *Calicophoron* spp. (Zieger *et al.*, 1998). Reviewed studies showed that the lowest recorded cestode infections were reported in South Africa, with 1.4% (1/74) Nyala infected with *Thysaniezia* spp. (Boomker *et al.*, 2000, Table 6). The highest prevalence of 50.0% (1/2) was observed in an Eland in Zambia that was infected with *Moniezia benedeni* (Zieger *et al.*, 1998).

Discussion

The results of this study indicated that gastrointestinal helminth infections in wild ruminants in sub-Saharan Africa are common and diverse, with a total of 40 genera, 78 species, and 31 unidentified species or species complexes recorded from 31 species of wild ruminates across 10 countries. This rich diversity of GIT helminths is consistent with the wide diversity of wild animals in sub-Saharan Africa, which is also home to some of the world's most iconic species (Chapman *et al.*, 2022; O'Connell *et al.*, 2019). South Africa reported the highest diversity of both parasites and hosts, which is a reflection of the country's diverse fauna (Junker *et al.*, 2015). Additionally, South Africa's diverse climatic conditions, ranging from arid to temperate and subtropical regions provide a suitable environment for the survival and transmission of GIT helminths (Nalubamba *et al.*, 2015; Mosala, 2017). Thirty-one species complexes were not described to species level in the reviewed studies. Except for the study by Ikeuchi *et al.* (2022), molecular methods (DNA barcoding) were not used for species identification. Although microscopy is indispensable in the identification of helminth parasites (Halton, 2004), DNA barcoding allows for species identification and discovery, which is fundamental in assessing biodiversity (Mampang *et al.*, 2023). It is therefore likely that the diversity of parasites in wild ruminants reported in the reviewed studies in sub-Saharan African countries has been underestimated.

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Table 5. Prevalence of gastrointestinal tract trematode infections in wild ruminants in sub-Saharan African countries (1980-2022)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
South Africa	Mountain reedbuck	Worms	66	6	9.0	*Calicophoron* spp.	Microscopy	Taylor *et al.,* 2005
	Red duiker	Worms	25	8	32.0	*Paramphistomum* spp.	Microscopy	Boomker *et al.,* 1991
Nigeria	Waterbuck	Faecal	12	3	18.2	*Paramphistomum* spp.	Microscopy	Atuman, *et al.,* 2019
	Eland	Faecal	24	4	16.2	*Paramphistomum* spp.	Microscopy	Atuman, *et al.,* 2019
	Wildebeest	Faecal	12	1	8.3	*Paramphistomum* spp.	Microscopy	Atuman, *et al.,* 2019
Tanzania	African buffalo	Faecal	123	6	4.9	*Paramphistomum* spp.	Microscopy	Senyael *et al.,* 2013
		Faecal	123	2	1.6	*Gastrothylax* spp.	Microscopy	Senyael *et al.,* 2013
		Faecal	123	1	0.8	*Fischoederius* spp.	Microscopy	Senyael *et al.,* 2013
Zambia	Impala	Worms	12	1	8.3	*Calicophoron* spp.	Macroscopy	Zieger *et al.,* 1998
	Sable antelope	Worms	2	1	50.0	*Calicophoron* spp.	Macroscopy	Zieger *et al.,* 1998
	Defassa waterbuck	Worms	6	6	100.0	*Calicophoron* spp.	Macroscopy	Zieger *et al.,* 1998
	Kafue lechwe	Worms	2	1	50.0	*Calicophoron* spp.	Macroscopy	Zieger *et al.,* 1998

Table 6. Prevalence of cestode infections in sub-Saharan African wild ruminants (1980-2022)

Country	Host species	Sample type	No. examined	No. infected	Prevalence (%)	Species of infection	Diagnostic tool	Reference
South Africa	Blue wildebeest	Worms	4	1	25.0	*Moniezia benedeni*	Microscopy	van Wyk and Boomker, 2011
	Mountain reedbuck	Worms	66	6	9.0	*Moniezia spp.*	Microscopy	Taylor *et al.,* 2005
	Eland	Worms	25	1	5.5	*Moniezia benedeni*	Microscopy	Boomker *et al.,* 2000
	Nyala	Worms	74	1	1.4	*Thysaniezia* spp.	Microscopy	Boomker *et al.,* 1991c
	Red duiker	Worms	25	5	20.0	*Moniezia benedeni*	Microscopy	Boomker *et al.,* 1991b
Nigeria	Eland	Faecal	24	2	8.3	*Moniezia* spp.	Microscopy	Atuman *et al.,* 2019
Zambia	Impala	Worms	12	2	16.7	*Moniezia benedeni*	Microscopy	Zieger *et al.,* 1998
	Tsessebe	Worms	3	1	33.1	*Avitellina centripunctata*	Microscopy	Zieger *et al.,* 1998
	Eland	Worms	2	1	50.0	*Moniezia benedeni*	Microscopy	Zieger *et al.,* 1998
Sudan	Dikdik	Faecal	101	7	6.90	*Moniezia* spp.	Microscopy	Abuessailla *et al.,* 2014
	Waterbuck	Faecal	22	2	9.10	*Moniezia* spp.	Microscopy	Abuessailla *et al.,* 2014

Nematodes were by far the most diverse and widely distributed (in host and geographic range) GIT species with 88 species or species or complexes from 17 distinct families, infecting 30 host species, recorded from nine sub-Saharan countries. Nematode infections are generally common in both domestic and wild animals across sub-Saharan Africa (Nalubamba *et al.,* 2015). They have a well-adapted life cycle that involves free-living stages in the environment (such as larvae in grass or soil), thereby exposing them to grazing animals (Morgan & van Dijk, 2012). This review therefore indicated that wild ungulates play an important role in the transmission of these parasites to livestock. The families Cooperidae and Haemonchidae were the most diverse nematode families. Some genera of these families, such as *Haemonchus*, *Ostertagia*, and *Cooperia*, are significant parasites of veterinary importance in endemic countries (Szewc *et al.,* 2021), and are among the most important GIT parasites in domestic ruminants globally (Santos *et al.*, 2019). According to Hoberg *et al.* (2001) and Barone *et al.* (2020), *Cooperia* spp. and *Haemonchus* spp. are most commonly found in the southern temperate and boreal zones, and have only rarely been recognised among sylvatic hosts at higher latitudes of the subarctic and arctic regions. Moreover, *Haemonchus* (including *H. contortus*) and *Trichostrongylus* species were the most commonly recorded in most countries and infected the greatest number of host species. This was not surprising as species from these genera have a global distribution and have been reported from different hosts (including roe deer, fallow deer, red deer, and mouflon) in Europe (Halvarsson *et al.,* 2022). In South Africa, Boomker *et al.* (1996) and van Wyk and Boomker (2011) noted that the subtropical regions of Limpopo and KwaZulu-Natal provinces,

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distinguished by elevated temperatures and humidity, provided favorable conditions for the presence and spread of *Haemonchus* species.

The results of this study indicated that browsers (Bushbuck, Greater kudu, Grey duiker, Eland, Red duiker, Eland, Gray rhebok, Springbok) harbored the highest number of nematode infections. Although it is expected that the prevalence of infection in these wild ruminants species would be low because of their feeding patterns as observed in Nyala (1.4%), which are predominantly browsers, Gray rhebok also recorded a 100% infection with *Cooperia yoshidai* in South Africa. The high prevalence of nematode infections recorded in Mountain reedbuck, Common reedbuck, and Lichtenstein's hartebeest infected with *Cooperia yoshidai*, and *Haemonchus contortus* respectively, may have been due to them feeding on vegetation close to the ground where free-living infective stages of nematodes may be abundant (Atuman *et al.,* 2019). Furthermore, the ability of the infective larvae of *Cooperia* spp. to resist desiccation and low temperatures, and their ability to survive winter on irrigated pastures increases their chance to infect browsers that graze during the dry season and reedbucks which are known to utilise irrigated pastures during winter (Boomker *et al*., 1989a).

The results of this review indicated that 17 species of wild ruminants, distributed across Congo, Kenya, Nigeria, Rwanda South Africa, Tanzania, and Zambia were infected by 15 trematode species or species complexes from three genera. Nyala and African buffalo were more susceptible to infection by trematode species. These infections in African buffalo are not surprising as they are widely distributed across sub-Saharan Africa and regarded as an important reservoir for livestock diseases (Eygelaar et al., 2015). However, the water dependency of Waterbucks and the wallowing habit of the African buffalo, and their subsequent grazing of grasses near water sources predispose them to metacercariae (Saha *et al.,* 2013; Nath *et al.,* 2016; Atuman *et al.,* 2019). This was corroborated by the observed high prevalence of 100% (6/6) *Calicophoron* spp. infection in the Zambian Defassa waterbuck (Zieger *et al.,* 1998). The lowest prevalence of *Fischoederius* spp. (1/123, 0.8%) in African buffalo in Tanzania (Senyael *et al.,* 2013) may have been due to *Fischoederius* spp. generally detected at low prevalence in ruminant infections (Buddhachat *et al.,* 2022).

Geographically, *Paramphistomum* was the most widely distributed trematode genus, however, *Calicophoron* species infected the highest number of hosts species. Reports from as early as the 1920s have shown that *Cal. microbothrium* is the most common paramphistome species in Africa (Pfukenyi *et al.,* 2005; Pfukenyi & Mukaratirwa, 2018), and this could have been factored by the ability of this species to infect a high number of both wild and domestic ruminants (Pfukenyi & Mukaratirwa, 2018; Sibula *et al.,* 2024). The current study corroborates this observation, suggesting that *Cal. calicophorum* is prevalent among wild ruminants across numerous sub-Saharan African countries. This species has been identified from Water buffalo and Sika deer in South Africa and Kenya (Eduardo, 1983; Boomker *et al*., 1991c) according to this review. Other studies have reported *Cal. calicophorum* from other wildlife such as the African buffalo, Blesbuck, Black wildebeest, Blue wildebeest, Impala, Lelwel's hartebeest, Red hartebeest, Springbok, and others in other parts of Africa (Pfukenyi & Mukaratirwa, 2018; Sibula et al., 2024) and from domestic ruminants in Angola, Kenya, Mozambique, South Africa, Zambia, and Zimbabwe (Pfukenyi & Mukaratirwa, 2018).

The results of this review showed that Greater kudu has shown to be highly susceptible to infection. High number of cestode infections in Greater kudu have been documented in Namibia and South Africa (Cilliers, 2019). However, the density of the Greater kudu population especially in South Africa where most infections by a wide diversity of GIT nematodes and cestodes have been recorded may have been the contributing factor (Müller *et al.,* 2022). The most diverse and widely distributed GIT cestode species was *Moniezia.* This could be expected because *Moniezia* species have a cosmopolitan distribution (Demiaszkiewicz *et al.,* 2020; Nagarajan *et al.,* 2022), with at least 12 species currently described in domestic and wild ruminants based on their morphological features (Ohtori *et al.,* 2015). Although they use both domestic and wild ruminants as their definitive hosts, infections of these tapeworms have also been documented in primates and angulates from the orders Artiodactyla and Perissodactyla. Their life cycle involves oribatid mites, which act as intermediate hosts (Nagarajan *et al*., 2022).

Despite the high prevalence of *Moniezia benedeni* (50.0%) observed in Zambian Elands (Zieger *et al.,* 1998), infection by *Moniezia* spp., including *Moniezia benedeni,* are typically common in domestic ruminants (Ohtori *et al.,* 2015). Monieziasis pathogeneicity is mild and is associated with moderate infection (Kumar & Kaur, 2023). However, heavy infections do occur and often lead to considerable economic losses associated with detrimental clinical manifestations such as pot-belly, poor growth rate, diarrhoea, anaemia, intestinal pathology, poor quality of wool, and even death of the ruminant host (Fagbemi & Dipeolu, 1983; Zhao *et al.,* 2009; Yan *et al.,* 2013).

Conclusion

This review has indicated that wild ruminants in sub-Saharan African are infected by a wide range of GIT species of conservation, economic and zoonotic importance, and act a reservoir hosts of helminths of domestic ruminants. Furthermore, this study has highlighted limitations in the studies reporting on GIT helminths, especially trematodes and cestodes, in sub-Saharan Africa, with data available for only 10 countries. Moreover, these are mostly case reports or involved a low sample size, which created bias in the prevalence of infection. Therefore, we recommend surveys in all sub-Saharan African countries, equally focusing on screening all GIT helminths in wild ruminants, targeting a larger number of animals and species, and using a combination of a wide variety of diagnostic and identification tools such as the traditional method (coprology), morphological identification of adult specimens, and molecular techniques to allow identification to species level. Furthermore, standardised and improved diagnostic tools such as next-generation sequencing should be used for identification and characterisation of infections to distinguish between species and further ensure proper identification to species level that will bridge the gap of misidentification of species.

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