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Prevalence and geographical distribution of amphistomes of African wild ruminants: A scoping review

Madeline Siyazisiwe Sibula^{a,b}, Ignore Nyagura^{a,*}, Mokgadi Pulane Malatji^a, Samson Mukaratirwa^{a,c}

^a School of Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, Durban, 4001, South Africa

^b National University of Science and Technology, P. Bag AC939, Ascot, Bulawayo, Zimbabwe

^c One Health Centre for Zoonoses and Tropical Veterinary Medicine, Ross University School of Veterinary Medicine, Basseterre, Saint Kitts and Nevis

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ABSTRACT

This review summarizes published records on the prevalence, species diversity, geographical distribution, mixed infections, co-infections with other trematodes and intermediate hosts (IHs) of amphistomes (rumen flukes) of wild ruminants in Africa. Literature search was conducted on Google Scholar, PubMed and JSTOR, using a combination of predetermined search terms and Boolean operators. Of the 54 African countries searched, results showed that occurrence of amphistome infections in wild ruminants have only been reported in 23 countries. A total of 38 amphistome species consisting of the following 11 genera were recorded, viz Bilatorchis, Calicophoron, Carmyerius, Choerecotyloides, Cotylophoron, Explanatum, Gastrothylax, Gigantocotyle, Leiperocotyle, Paramphistomum and Stephanopharynx. These were recorded in 39 wild ruminant species, belonging to the Bovidae family. The genus Carmyerius recorded the highest number of species (n = 13) across nine countries Africa. However, *Calicophoron* species (n = 9) were more widely distributed, occurring in 17 countries across all regions of Africa. Species of this genus collectively infected 27 wild ruminant species. However, at a species level, Cotylophoron cotylophorum infected the highest number of wild ruminant species. Prevalence of infection based on post-mortem examination ranged from 1.89% in African Buffalo to 100% in Defassa waterbuck from Egypt and Zambia, respectively. The most common mixed infections recorded were those between amphistomes of the same or different genus. Snail intermediate hosts (IHs) were described for 10/38 amphistome species, and these were predominantly species from Plarnobidae family. Despite the richness in diversity of amphistomes infecting wild ruminants in Africa, there is need to further confirm identity of snail IHs and the amphistome species using both morphological and molecular techniques. Furthermore, more studies are recommended to assess the burden of amphistomosis in commercially reared wildlife/game farming, mixed game and livestock farming systems in Africa.

1. Introduction

Intestinal amphistomosis, variously known as amphistomiasis (Pfukenyi and Mukaratirwa, 2018), paramphistomiasis (Lotfy et al., 2010; Horak, 1971) or paramphistomosis (Huson et al., 2017) is a neglected disease of domestic and wild ruminants (Pfukenyi and Mukaratirwa 2018). The disease is caused by conical flukes, commonly known as amphistomes (Sey, 1988), stomach or rumen flukes (Mitchell et al., 2021) due to their predilection site, and they are characterized by lack of the oral sucker and the positioning of the ventral sucker or the acetabulum at the posterior end of their body (Tandon et al., 2019). They belong to the superfamily Paramphistomoidea Fischoeder, 1901 (Lotfy et al., 2010), which is composed of hundreds of species belonging to 12 families (Jones 2005).

Amphistomes have a wide geographical distribution, with more than 70 species documented in diverse range of domestic and wild ruminant hosts (Ghatani et al., 2012; Ichikawa et al., 2013; Malik et al., 2017; Pfukenyi and Mukaratirwa, 2018; Mitchell et al., 2021). Studies have shown that the prevalence of infection in wild ruminants can be as high as 100% as recorded by Zieger et al. (1998) in *Kobus defassa* (Defassa waterbuck) in Zambia. Despite this, the disease remains understudied in wild ruminants which may act as reservoirs for domestic ruminants

* Corresponding author. *E-mail addresses:* nyaguraigy@gmail.com, 221119814@stu.ukzn.ac.za (I. Nyagura).

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(Niranjan et al., 2020), and consequently its burden is hugely underestimated particularly in the tropics and subtropics (Phiri et al., 2011; Huson et al., 2017) including Africa where focus on amphistomes infections have been on domestic ruminants (Pfukenyi et al., 2005; Mavenyengwa et al., 2008; Mavenyengwa et al., 2010; Lotfy et al., 2010; Dube et al., 2015; Laidemitt et al., 2017).

Although adult amphistomes have been collected from wild ruminants in recent years, few specimens have been characterized and identified to species level (Munyeme et al., 2010; Munang'andu et al., 2012) and were commonly designated as *Paramphistomum* spp. despite the vast diversity in amphistome genera in Africa (Pfukenyi and Mukaratirwa, 2018). As a result, losses due to amphistomosis in wildlife in Africa have not been quantified, despite the growing concern of cross-infection of amphistomes with domestic animals (Madzingira et al., 2002; Van Wyk and Boomker, 2011). As the domestic-wildlife interface increases due to scarcity of land for human settlement resulting in diminishing wildlife habitat, it becomes imperative to understand and determine distribution of parasitic fauna, especially amphistomes in wild ruminants (Brown et al., 2022).

Amphistomes have two hosts life cycle, with vertebrates serving as the definitive hosts and freshwater snails as intermediate hosts (Tandon et al., 2019). The geographical distribution and prevalence of amphistome infections is influenced by the availability and abundance of susceptible snail intermediate hosts (Eduardo, 1987) and susceptible definitive hosts (Pfukenyi and Mukaratirwa, 2018). Various freshwater gastropods belonging to the genera Bulinus Müller 1781, Biomphalaria Preston 1910, Ceratophallus Brown and Mandahl-Barth 1973 and Galba Müller 1774 have been implicated as the intermediate hosts of amphistome species in Africa (Dinnik, 1961; Dinnik, 1965; Wright et al., 1979b; Southgate et al., 1989; Pfukenyi et al., 2005). However, there are still gaps on the specificity of the incriminated snail IHs in the transmission of the documented amphistome species. Therefore, this review gathered data from peer-reviewed publications on the prevalence, species diversity, geographical distribution, mixed infections, co-infections with other trematodes and intermediate hosts (IHs) of amphistome infections in wild ruminants in Africa and identified research gaps for future studies.

2. Methodology

2.1. Scoping review

The scoping review aimed to answer the following questions on amphistomes of wild ruminants in Africa: (i) Which amphistome genera/species are currently circulating in wild ruminants in Africa? (ii) What is the geographical distribution of amphistome species of wild ruminants in Africa? (iii) What is the prevalence of infection recorded in Africa? (iv) What are the intermediate snail hosts implicated in the transmission of amphistomes in Africa? (v) Which other trematodes species co-infect with amphistomes in wild ruminants and their snail IHs in Africa? (vi) What are the predilection sites of the amphistomes in wild ruminants?

The review was guided by the methodological approach described by Arkey and O'Malley (2005) which consisted of the following guidelines: (i) Identification of the research questions, (ii) Searching and identification of relevant articles, (iii) Selection of articles, (iv) Charting of data, collating, summarizing and reporting of the results. To address the questions raised, published peer-reviewed articles and reports reporting on amphistomes of wild ruminants and their snail IHs from Africa were identified and reviewed following guidelines for reporting from PRISMA (Moher et al., 2009).

2.2. Search strategy

The following electronic databases were searched: PubMed, JSTOR, Google scholar. Reference lists of relevant publications were searched as potential leads. Literature searches were carried out from a total of 54 African countries (Fig. 1). A thorough search was conducted using Boolean operators (AND, OR) and the following terms: Amphistome infection OR Amphistomosis AND wild ruminants OR intermediate hosts OR freshwater snails, Paramphistome infections OR Paramphistomosis AND wild ruminants OR intermediate hosts OR freshwater snails. Relevant articles were selected based on a preliminary screening of the titles and abstracts. All full text articles retrieved were managed in the EndNote reference manager.

2.3. Selection criteria

The literature search was not limited to articles in English but included articles in French and Afrikaans published from 1900 to 2022. Articles published in Afrikaans and French were translated using online Google translator. Included in this review were field or case studies explicitly reporting; (i) occurrence of amphistomes in wild ruminants in Africa; (ii) geographical distribution of amphistomes in wild ruminants in Africa; (iii) prevalence of amphistomes in wild ruminants in Africa; (iv) snail IH linked to the transmission of amphistomes in wild ruminants in Africa; (v) co-infection of amphistomes and other trematodes in wild ruminants and snail IHs; (vi) studies reporting postmortem and coprological examinations outcomes on amphistomes infections in wildlife in Africa. Furthermore, information on predilection site of amphistomes in wild ruminants were also extracted from the selected studies.

Excluded from this review were articles that reported on; (i) amphistome infections in non-ruminant wild animals; (ii) amphistome infections in domestic livestock; (iii) studies conducted outside Africa and (iv) did not identify the amphistomes (egg/larval/adult stage) to genus level.

2.4. Charting, collating, and summarizing the data

Data was extracted from articles that met the inclusion criteria after appraisal. Information of the authors, region and country, year of publication, intermediate and definitive host species, prevalence, and predilection site of amphistomes were extracted and tabulated.

3. Results

A total of 3287 records were obtained from the database search on Google scholar, JSTOR and PubMed, and this included peer reviewed articles, abstracts, reviews, books and duplicated articles (Fig. 1). Additional 32 articles were obtained through snowballing. Nine-hundred-and-ninety-three duplicated articles were excluded and the titles and abstracts of the remaining 2327 articles were screened of which 2204 articles were deemed ineligible and excluded. One-hundred-and-twenty-three full-text articles were appraised based on the predetermined inclusion criteria, and 69 articles did not meet the criteria and were excluded from the review. Fifty-four articles that met the inclusion criteria and were reviewed and were distributed across all Africa regions; Southern Africa (n = 25), East Africa (n = 18), Central Africa (n = 11), North Africa (n = 8) and West Africa (n = 6) (Fig. 2).

Of the 54 articles reviewed, 38 articles reported exclusively on amphistome infections in wild ruminants (Table 1), 15 reported on infections in the snail IHs (Table 4), and only one article reported on both the IHs and wild ruminant hosts. Thirty-five of the thirty-nine studies identified amphistomes up to species level, whilst 4/39 identify amphistomes up to genus level in the definitive hosts. Four articles reported on co-infection/mixed infection of amphistomes with other trematodes, or between amphistomes of similar or different genera in wild ruminants (Table 3). Fifteen articles reported on snail infections and identified amphistomes to species level with five records of mixed infections of amphistomes and other trematodes in snail intermediate hosts in Africa.

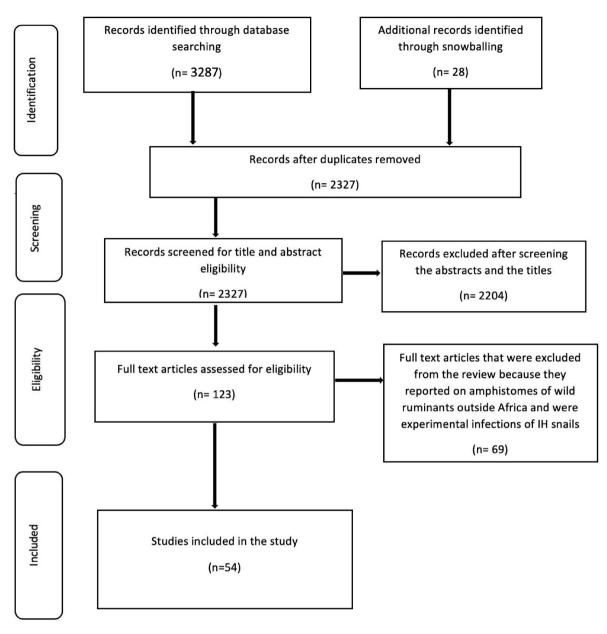


Fig. 1. Prisma diagram showing the search and selection process.

3.1. Checklist of amphistomes species and their wild ruminant host species in Africa (1900–2022)

A total of 38 amphistome records were documented in natural infections in wild ruminants in Africa (Table 1, Supplementary Table 1) and of these records, 36 records identified amphistomes up to species level. The recorded 39 wild ruminant species from the Bovidae family infected with amphistome species were viz. Impala (Aepyceros melampus), Red hartebeest (Alcephalus busephalus), Bongo (Alcelaphus boocerus eurycerus), Lichteinstein's hastebeest (Alcelaphus lichteinsteini), Lelwel hartebeest (Alcelaphus lelwel), Hartebeest (Alcelaphus spp.), Springbok (Antidorcas marsupialis), Blue wildesteest (Connochaete taurinus), Black wildebeest (Connochaete gnou), African Duiker (Cephalophus sp.), Black fronted duiker (Cephalophus nigrifrons), Topi (Damaliscus korrigum), Blesbuck (Damaliscus albifrons), Blesbok (Damaliscus dorcas), Common Tsessebe (Damaliscus lunatus), Thomson's gazelle (Gazella thomsoni), Roan Antelope (Hippotragus equinus, Sable (Hippotragus niger), Defassa waterbuck (Kobus defassa), Waterbuck (Kobus ellipsiprymnus), Kob (Kobus kob), Red lechwe (Kobus leche), Nile lechwe (Kobus megaceros), Puku (Kobus vardoni), Royal antelope (Neotragus pygmaeus), Klipspringer (Oreotragus oreotragus), Oribi (Ourebia oribi), Gemsbok (Oryx gazelle), East African oryx (Oryx beisa), Common reedbuck (Redunca arundinum), Bohor reedbuck (Redunca Redunca), Mountain reedbuck (Redunca fulvovufula), African buffalo (Syncerus caffer), Common duiker (Sylvicapra grimmia), Common eland (Taurotragus oryx), Nyala (Tragelaphus angasi), Sitatunga (Tragelaphus spekei), Bushbuck (Tragelaphus scriptus), Greater Kudu (Tragelaphus strepsiceros), Menelek's bushbuck (Tragelaphus scriptus meneliki), Mountain Nyala (Tragelaphus buxtoni).

Carmyerius was the genus with the most diverse species, with 13 species documented in in 20 wild ruminants, namely, Carmyerius bulbalis (Car. bubalis), Car. chabaudi, Car. endopapillatus, Car. exosporus, Car. graberi, Car. gregarius, Car. mancupatus/dollfusi, Car. multivitellarius, Car. papillatus, Car. parvipapillatus, Car. spatiosus, Car. schoutedeni and Car. wenyoni (Table 1, Supplementary Table 1). The Calicophoron genus was the second most diverse genus, with ten species namely, Calicophoron spp., Calicophoron bothriophoron (Cal. bothriophoron), Cal. calicophorum, Cal. clavula, Cal. daubneyi, Cal. microbothrium, Cal. phillerouxi, Cal.

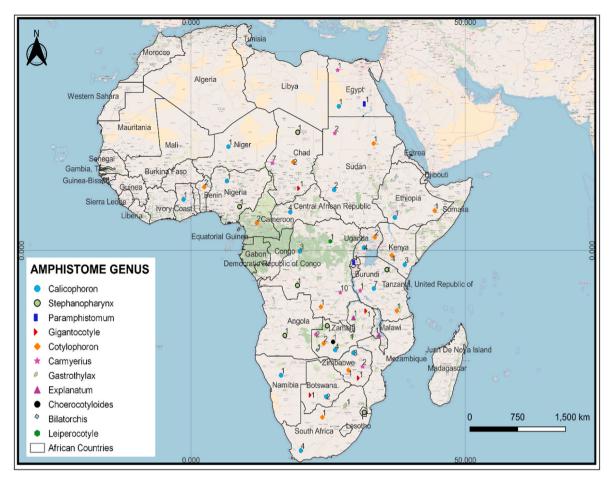


Fig. 2. Map showing geographical distribution of amphistomes in wild ruminants in Africa (1900-2022).

sukari, Cal. sukumum and Cal. raja. This genus, although ranks second in diversity, infected the highest number (n = 27) of wild ruminant host species when compared to other genera. Cotylophoron species such as Cotylophoron cotylophoron (Cot. cotylophorum), Cot. fuelleborni, Cot. macrosphinctris, Cot. jacksoni), and Paramphistomum species (Paramphistomum spp., Paramphistomum cephalophi (Par. cephalophi), Par. cervi, Par. gotoi) were reported in four wild ruminants species. However, Cotylophoron species utilized more host species (n = 23), followed by Calicophoron spp., and Paramphistomum spp. were only reported in six wild ruminants. The following were reported as the only species within their genera; Bilatoschis papillogenitalis (Bil. papillogenitalis), Explanatum explanatum (E. explanatum), Gigantocotyle symmeri (G. symmeri), Gastrothylax crumenifer (Gast. crumenifer), Leiperocotyle gretillati (Lei. gretillati), Stephanopharynx compactus (Ste. compactus) and Choerocotyloides onotragi (Cho. onotragi). Of these species, Ste. compactus infected more wild ruminant species (n = 2) comparatively.

Further results showed that the African buffalo (*Syncerus caffer*) was more susceptible to amphistomes infection, and recorded the highest number of amphistome species (n = 21). This included seven *Carmyerius* spp. (*Car. mancupatus, Car. gregarius, Car. exoporus, Car. endopapillatus, Car. spatiosus, Car. schoutedeni, Car graberi*), six *Calicophoron* spp. (*Cal. calicophorum, Cal. raja, Cal. clavula, Cal. sukari, Cal. phillerouxi, Cal. microbothrium*), three *Cotylophoron* spp. (*Cot. macrosphrinctris, Cot. cotylophorum, Cot. fuelleborni*), *Gig. symmeri, Ste. compactus, Lei. gretillati, Par. gotoi and Par cervi. Oryx beisa* infected with *Cal. daubneyi, Tragelaphus scriptus meneliki* with *Cot. cotylophorum, Tragelaphus buxtoni* with *Cot. cotylophorum, Antidorcas marsupialis* with *Cal. calicophorum* had the least (n = 1) number of amphistome species infection. 3.2. Geographic distribution of amphistomes of wild ruminants in Africa (1900–2022)

Results showed that amphistomes have been recorded in 39 wild ruminant species are distributed across 23 countries in Africa (Angola, Benin, Botswana, Cameroon, Central African Republic, Chad, DRC, Egypt, Ethiopia, Ghana, Kenya, Malawi, Namibia, Nigeria, Republic of Niger, Rwanda, South Africa, Sudan, Swaziland, Tanzania, Uganda, Zambia, Zimbabwe) as shown (Table 1, Fig. 2). Calicophoron species were the most distributed, occurring in 17 of 23 reviewed countries, but most commonly reported in the southern and eastern African countries. Calicophoron microbothrium was overall the most distributed amphistome species, recorded in 56.5% (13/23) of the reviewed countries (Table 1). Although majority of Calicophoron species reported in multiple countries, 40% (4/10) of species from this genus were however reported only in one country, i.e., Calicophoron spp. in Zambia, Cal. daubneyi in Ethiopia, Cal. sukumum and Cal. sukari in Tanzania. Carmyerius species were reported in nine countries across all regions except West Africa. Results showed that seven species were reported in more than two countries, and six species (Car. bubalis, Car. chabaudi, Car. graberi, Car. multivitellarius, Car schoutedeni and Car. wenyoni) documented in one country each. Cotylophoron species have recorded in 13 countries across all regions, but shown to occur mostly in the East African countries. Cotylophoron cotylophorum is the second most distributed amphistome species following Cal. microbothrium, reported in 12 of 23 reviewed countries. Results showed only Egypt recorded more than one Paramphistomum species (Par. cervi and Par. gotoi), whereas other Paramphistomum spp. and Par. cephalophi were reported in South Africa and Rwanda respectively. Reviewed results further showed that Bil. papillogenitalis and Cho. onotragi were documented in Zambia, and Lei.

Table 1

Carmyerius bubalis

Car. chabaudi

Bongo

Thomson's gazelle

Zimbabwe

DRC

Table 1	Table 1 (continued)				
Checklist of amphis	stome species of wild	ruminants in Afric	a (1900–2022).	Amphistome spp.	Но
Amphistome spp.	Hosts	Countries	References	Car. gregarius	Afr
Bilatorchis papillogenitalis	Red lechwe	Zambia	Eduardo (1980)		Nil
Calicophoron sp.	Tsessebe, Red	Zambia	Zieger et al.		
1 1	lechwe, Defassa		(1998)		
	waterbuck				
Cal. bothriophoron	Defassa waterbuck	Tanzania, Kenya	Eduardo (1983)	Car. mancupatus/	Ree
Cal. calicophorum	African Buffalo,	South Africa,	Mettam (1932);	dollfusi	An
	Blesbuck, Black	Uganda, DRC,	Prudhoe (1957);		Ela
	wildebeest, Blue	Chad and Central	Ortlepp (1961);		Bui Wi
	Wildebeest, Impala, Lelwel's	African Republic	Graber et al. (1964)		Dei
	hartebeest, Red		(1904)		To
	hartebeest, iteu				gaz
	Springbok				Pul
Cal. clavula	African Buffalo,	Tanzania,	Stunkard (1929);		Co
	Bohor reedbuck,	Uganda, DRC,	Nasmark (1937);		Bol
	Common Eland,	CAR, Republic of	Prudhoe (1957);	Car.	The
	Defassa waterbuck,	Niger, Nigeria,	Dinnik et al.	multivitellarius	
	Impala, Oribi,	Sudan	(1963); Sey and	Car. schoutedeni	Afr
	Puku, Roan		Graber (1979a);		Bla
	antelope, Red		Eduardo (1983)	Car. wenyoni	dui Nil
	hartebeest, Sable		Dinnik et al. (1963)	Cotylophoron	Im
Cal. daubneyi	East African oryx	Ethiopia	Graber et al.	cotylophorum	Tse
Gui. uuubheyt	Last mircan oryx	Lunopia	(1980)	cotytophorum	Mo
Cal.	African Buffalo,	South Africa,	Maplestone		ree
microbothrium	Blesbok, Bohor	Zambia,	(1923); Baer		Sita
	reedbuck, Common	Zimbabwe,	(1923); Mettam		Ku
	Eland, Defassa	Tanzania, Kenya,	(1932); Myers		bus
	Waterbuck,	Uganda, Chad,	et al. (1960);		Mo
	Impala, Kob,	CAR, Ghana,	Ortlepp (1961);		Kli
	Lelwel hartebeest,	Sudan, Egypt,	Graber et al.		ant
	Red hartebeest,	Botswana	(1964); Sey		De: Afr
	Red lechwe, Roan		(1977); Eduardo		Co
	Antelope, Senegal hartebeest,		(1983); Halium et al. (2014)		Bus
	Waterbuck		ct al. (2014)		hai
Cal. phillerouxi	African Buffalo,	Zambia, Uganda,	Dinnik et al.		Ree
F	Bohor reedbuck,	Zimbabwe,	(1963); Sachs and		Wa
	Deffasa Waterbuck,	Tanzania, DRC,	Sachs, 1968; Sey		Ha
	Greater Kudu,	CAR	and Graber	Cot. jacksoni	Ree
	Impala, Kob, Topi,		(1979a); Eduardo		Sal
	Common Eland,		(1983);	Cot.	Afr
	Hartebeest,			macrosphinctris	
0-1	Thomson's gazelle	Courth A fuiles	0	Gastrothylax	Ree
Cal. raja	African Buffalo, Black wildebeest.	South Africa,	Sachs and Sachs,	crumenifer	Sita
	Blue wildebeest,	Botswana, Zambia,	1968; Eduardo (1983); Mijele	cruncinger	on
	Bohor reedbuck,	Zimbabwe,	et al. (2016);	Gigantocotyle	Afr
	Bushbuck, Deffasa	Namibia,	Ikeuchi et al.	symmeri	Ree
	waterbuck, Puku,	Tanzania, Kenya	(2022)		Gre
	Gemsbok, Greater				
	Kudu, Impala,			Leiperocotyle	Afr
	Puku, Red lechwe,			gretillati	
	Red hartebeest,			Paramphistomum	Ku
0.1 1	Thomson's gazelle		0 1 10 1	sp.	ree
Cal. sukumum	Blue Wildebeest, Deffasa Waterbuck,	Tanzania	Sachs and Sachs,		Tse dui
	Topi, African		1968; Eduardo (1983)		uu
	Buffalo, Kob,		(1963)	Par. cephalophi	Bla
	Thomson's gazelle,				dui
	Impala, Puku,			Par. gotoi	Afr
	Hartebeest,			Stephanopharynx	Afr
	Common eland			compactus	Blu
Cal. sukari	African Buffalo,	Tanzania	Sachs and Sachs,		Bol
	Kob, Blue		1968; Eduardo		Co
	Wildebeest,		(1983)		Dei
	Deffasa Waterbuck,				Im
	Topi, Thomson's				Mo ree
	gazelle, Impala, Puku, Hartebeest,				Ree
	Common eland,				An
Carmverius bubalis	Bongo	Zimbabwe	Sev (1983)		

Amphistome spp.	Hosts	Countries	References		
Car. gregarius	African buffalo, Nile lechwe	Sudan, Egypt, DRC	Myers et al. (1960); Dollfus (1963); Sey (1977); Sey (1983); Halium et al. (2014) Prudhoe (1957); Sachs and Sachs, 1968; Wright et al. (1979b)		
Car. mancupatus/ dollfusi	Red lechwe, Roan Antelope, Common Eland, African Buffalo, Kob, Blue Wildebeest, Deffasa Waterbuck, Topi, Thomson's gazelle, Impala, Puku, Hartebeest, Common eland, Bohor reedbuck	Zambia, DRC, Tanzania			
Car.	Thomson gazelle	DRC	Sey (1983)		
multivitellarius Car. schoutedeni	African Buffalo, Black fronted duiker	DRC	Sey (1983)		
Car. wenyoni Cotylophoron cotylophorum	Nile lechwe Impala, Common Tsessebe, Mountain reedbuck, Eland,	Sudan South Africa, Zambia, Zimbabwe, Ethiopia, DBC	Sey (1983) Maplestone (1923); Stunkard (1929); Le Roux		
	Sitatunga, Greater Kudu, Menelik bushbuck,	Ethiopia, DRC, Chad, CAR, Cameroon, Benin, Sudan,	(1932); Le Roux (1934); Nasmark (1937); Prudhoe (1957); Morel		
	Mountain Nyala, Klipspringer, Royal antelope, Puku, Defassa waterbuck, African Buffalo, Common eland, Bushbuck, Lelwel hartebeest, Kob, Red Hartebeest, Waterbuck, Hartebeest	Tanzania, Uganda	(1959); Ortlepp (1961); Mettrick (1962); Dinnik et al. (1963); Graber et al. (1964); Sachs and Sachs, 1968; Graber et al. (1980); Anderson (1983)		
Cot. jacksoni	Red hartebeest, Sable	Zambia, Uganda, Tanzania, Kenya	Nasmark (1937); Eduardo, 1985a		
Cot. macrosphinctris	African Buffalo	Uganda, CAR	Sey and Graber (1979b); Eduardo, 1985a		
Gastrothylax crumenifer	Red lechwe, Sitatunga	South Africa, Zambia	Le Roux (1932); Ortlepp (1961); Sey (1983)		
Gigantocotyle	African Buffalo,	Botswana,	Yeh (1957); Sey		
symmeri	Red lechwe, Greater Kudu	Zambia, Zimbabwe, CAR	and Graber (1979a); Eduardo (1984)		
Leiperocotyle gretillati	African buffalo	DRC	Eduardo (1985b)		
Paramphistomum sp.	Kudu, Common reedbuck, Tsessebe, Grey duiker	South Africa	Boomker et al. (1987); Reinecke et al. (1988); Boomker et al. (1989)		
Par. cephalophi	Black fronted duiker	Rwanda	Eduardo (1982)		
Par. gotoi Stephanopharynx compactus	African buffalo African Buffalo, Blue Wildebeest, Bohor reedbuck, Common Eland, Defassa waterbuck,	Egypt DRC, Chad, CAR, Zambia, Angola, Swaziland, Nigeria, Tanzania	Sey (1977) Ortlepp (1961); Sachs and Sachs, 1968; Wright et al. (1979b); Eduardo (1986)		
	Impala, Kob, Mountain reedbuck, Puku, Red lechwe, Roan Antelope, Topi		Euuatuo (1900)		

Cal. = Calicophoron; Car. = Carmyerius; Cot. = Cotylophoron; Ste. = Stephanopharynx; Par. = Paramphistomum.

Sey (1983)

Sey (1983)

Table 2

Prevalence of single infections of amphistomes as determined through post-mortem in wild ruminant species in Africa (1900-2022).

Region/ Country	Host species	No. examined	No. positive	Prevalence (%)	Amphistome species	Method of identification	References
Southern Africa							
South Africa	<i>Redunca arundinum</i> (Common reedbuck)	47	19	40.4%	^a Paramphistomum spp.	Fluke morphology	Boomker et al. (1989)
South Africa	Damaliscus lunatus lunatus (Tsessebe)	11	9	81%	^a Paramphistomum spp.	Histology	Reinecke et al. (1988)
South Africa	Sylvicapra grimmia (Grey duiker)	13	1	8%	^a Paramphistomum spp.	Fluke morphology	Boomker et al. (1987)
South Africa	Aeropyceros melampus (Impala)	46	41	89.1%	Cot. cotylophorum	N/A	Anderson (1983)
Zambia	Damaliscus lunatus lunatus (Tsessebe)	3	1	33.3%	^a Calicophoron spp.	N/A	Zieger et al. (1998)
Zambia	Kobus leche (Red lechwe)	2	1	50%	^a Calicophoron spp.	N/A	Zieger et al. (1998)
Zambia East Africa	Kobus defassa (Defassa waterbuck)	6	6	100%	^a Calicophoron spp.	N/A	Zieger et al. (1998)
Kenya	<i>Connochaetes taurinus</i> (Blue Wildebeest)	130	26	20%	Cal. raja	Fluke morphology	Mijele et al. (2016)
North Africa							
Egypt	Syncerus caffer (African Buffalo)	-	-	78%	Cal. microbothrium	Histology	Sey (1977)
Chad	Gazella rufifrons (Thomson Gazelle)	14	1	7.1%	Cal. microbothrium	Histology	Graber et al. (1964)

^a Identification was not to species level and might be mixed species, N/A - Not mentioned.

Table 3

Mixed amphistome species infections of species with other trematodes in wild ruminants (1900-2022).

References Co	Country	Host	Amphistome species	Mixed/co-infections		Prevalence of infection			Method of
				Other amphistomes species	Other trematodes	No. examined	No. infected	Prev. (%)	identification
Halium et al. (2014)	Egypt	Syncerus caffer	Cal. microbothrium	Car. gregarius, P. cervi	-	315	17	1.89	Fluke morphology
Zieger et al. (1998)	Zambia	Kobus defassa	Cal. calicophorum	-	Fasciola gigantica	ND	ND	ND	Fluke morphology
Lieger et al. (1998)	Zambia	Kobus lechwe	Calicophoron sp.	-	F. gigantica, Schistosoma sp.	ND	ND	ND	Fluke morphology
Wright et al., 1979	Zambia	Kobus lechwe	Car. spatiosus	Car. mancupatus, Ste. Compactus	-	ND	ND	ND	Fluke morphology
Pike and Condy (1966)	Zimbabwe	Tragelaphus spekei	Car. spatiosus	-	F. tragelaphi	ND	ND	ND	Fluke morphology
Graber et al. (1964)	Chad and CAR	Kobus defassa	Car. spatiosus	Cal. microbothrium, Car. parvipapillatus, Car. papillatus, Step. compactus	-	8	3	25	Fluke morphology
raber et al. (1964)	Chad and CAR	Alcelaphus lelwel	Cal. calicophorum	Cot. cotylophorum, Cal. microbothrium, Car. Spatiosus	-	11	3	18	Fluke morphology
(1964)	Chad and CAR	Syncerus caffer	Cal. microbothrium	Cot. cotylophorum, Car. endopapillatus, Car. spatiosus	-	5	3	60	Fluke morphology
Graber et al. (1964)	Chad and CAR	Damaliscus korrigum	Cal. microbothrium	Car. spatiosus, Car. exoporus, Car. parvipapillatus	-	8	1	14	Fluke morphology
raber et al. (1964)	Chad and CAR	Kobus kob	Cal. microbothrium	Ste. compactus, Car. spatiosus, Car. papillatus, Car. parvipapillatus	-	6	3	50	Fluke morphology
raber et al. (1964)	Chad and CAR	Redunca redunca	Cal. microbothrium	Ste. compactus, Car. spatiosus	-	2	1	50	Fluke morphology
Graber et al. (1964)	Chad and CAR	Hippotragus equinus	Cal. microbothrium	Ste. compactus, Car. spatiosus	-	9	2	22	Fluke morphology

ND = Not Determined; Cal. = Calicophoron; Car. = Carmyerius; Cot. = Cotylophoron; Ste. = Stephanopharynx.

gretillati was recorded in DRC. *Gastrothylax crumenifer* was reported in South Africa and Zambia, and *Gig. Symmeri* was documented in Botswana, Zambia, Zimbabwe and CAR. *Explanatum explanatum* was reported in Malawi and Zambia, whilst the presence of *Ste. compactus* infections in wild ruminants was documented in DRC, Chad and CAR, Zambia, Angola, Swaziland, Nigeria and Tanzania.

3.3. Predilection sites for amphistomes of wild ruminants in Africa

The results from reviewed studies showed that the rumen, reticulum, abomasum and omasum are the most common predilection sites for amphistomes. Amphistome species from the *Cotylophoron* genus (*Cot. macrosphinctris*, *Cot. jacksoni*, *Cot. cotylophorum*, *Cot. fuelloborni*), *Cal.* clavula, Bil. papillogenitalis and Ste. compactus were reported to utilise the rumen as their predilection site (Eduardo, 1983, 1984, 1986). Authors also showed that other species, predominantly those from *Calicophoron* genus (*Cal. microbothrium, Cal. phillerouxi, Cal. clavula, Cal. daubneyi, Cal. sukumum, Cal. sukari, Cal. calicophorum, Cal. bothriophoron*) were found in the rumen and reticulum (Eduardo, 1983; Eduardo, 1985a; Eduardo, 1986, Sey and Graber, 1979). Results also showed that *Car. spatiosus, Car. mancupatus, Cal. raja* and *Gig. symmeri* were found in the rumen, reticulum, omasum and/or the abomasum. *Paramphistomum cephalophi* was found in the small intestines (Eduardo, 1982), *Lei. gretillatti* the intestine (Eduardo, 1985a), and *Cho. onatragi* utilizes the caecum (Prudhoe et al., 1964) as their predilection.

Table 4

Checklist of intermediate host snails involved in the transmission of Amphistomes of wild ruminants in Africa (1900–2022).

Amphistome species	IH snail species	Country	References		
Cal.	Bulinus tropicus	South Africa	Grobbelaar, 1922		
calicophorum					
Cal.	Bulinus tropicus	South Africa	Porter (1921)		
calicophorum					
Cal. clavula	Bul. abyssinicus	Somalia	Sobrero (1962)		
Cal. microbothrium	Bulinus tropicus	South Africa	Swart and Reinecke, 1962		
Cal.	Bulinus tropicus	South Africa	King and Van As		
microbothrium	•		(2001)		
Cal.	Bulinus tropicus	Zambia	Dinnik (1965)		
microbothrium					
Cal.	Bulinus tropicus	Kenya	Dinnik (1962)		
microbothrium					
Cal.	Bulinus (Physopsis)	Zambia	Dinnik (1965)		
microbothrium	globosus	Lambia			
Cal.	Bulinus (Physopsis)	Kenya	Dinnik (1965)		
microbothrium	nasutus	Renya	Dillik (1903)		
Cal.	Bulinus senegalensis	Gambia	Wright, et al. (1979a)		
microbothrium	Duunus seneguiensis	Gallibia	Wilgin, et al. (1979a)		
Cal.	Bulinus tropicus	Kenya	Southgate et al.		
microbothrium	Buunus u opicus	Kellya	(1985)		
Cal.	Delinera tuoniaria	Varra			
	Bulinus tropicus	Kenya	Southgate et al.		
microbothrium	Delin (Lenner)	17	(1989) Dissib (10(0)		
Cal. daubneyi	Radix (Lymnaea)	Kenya	Dinnik (1962)		
0-1	truncatula Balinan (analarii	Transis	Dis. 11 (10(1)		
Cal. phillerouxi	Bulinus forskalii	Tanzania,	Dinnik (1961)		
01.1.11	n /: 1 ·	Zambia	D: 11 (10(1))		
Cal. phillerouxi	Bulinus senegalensis	Gambia	Dinnik (1961)		
Cal. sukari	Biomphalaria pfeifferii	Ethiopia	Graber and Daynees,		
			1974		
Cal. sukari	Biomphalaria pfeifferii	Kenya	Dinnik (1965)		
Car. exosporus	Anisus natalensis	Kenya	Dinnik (1964)		
Car. exosporus	Anisus natalensis	Kenya,	Dinnik (1965)		
		Zambia			
Car. mancupatus	Anisus	Zambia,	Dinnik (1965);		
	(Ceratophallus)	Kenya	Laidemitt et al.		
	natalensis		(2017)		
Car. mancupatus	Bulinus mairei	Zambia	Gretillat (1960)		
Car. mancupatus	Bulinus liratus	Zambia	Gretillat (1960)		
Car.	Bulinus (Physopsis)	Zambia	Dinnik (1965)		
parvipapillatus	globosus				
Ste. compactus	Bulinus forskalii	Zambia	Dinnik (1965)		

Cal. = Calicophoron; Car. = Carmyerius; Ste. = Stephanopharynx.

3.4. Prevalence of amphistome species in wild ruminants in Africa (1900–2022)

Prevalence of amphistomes infections in wild ruminants ranged from 7.1% to 100% (Table 2). The lowest prevalence was recorded in in *Gazella rufifrons* (7.1%) in Chad which was infected with *Cal. microbothrium* (Graber et al., 1964), followed by Grey duiker (8%) infected with *Paramphistomum* spp. in South Africa (Boomker et al., 1987). The highest prevalence was in Zambian *Kobus defassa* (100%) infected with *Calicophoron* sp. (Zieger et al., 1998), followed by *Cot. cotylophorum* infections in South African *Aeropyceros melampus* (89.1%) (Anderson, 1983), and *Paramphistomum* spp. also in South African *Damaliscus lunatus* (81%) (Reinecke et al., 1988).

3.5. Mixed Infection of amphistomes species and co-infection with other trematodes in the animal host species (1900–2022)

Co-infection of amphistomes with other trematode species in the same animal host were reported in *Kobus defassa* with *Cal. calicophorum* + *Fasciola gigantica*, and Kobus lechwe with *Calicophoron* spp. + *F. gigantica* + *Schistosoma* sp. in Zambia (Zieger et al., 1998). In Zimbabwe, *Tragelaphus spekei* was found co-infected with *Car. spatiosus* + *F. tragelaphi* (Pike and Condy, 1966) (Table 3). Mixed infections with

multiple amphistome species in the same host were common in Chad and Central African Republic (CAR). The lowest prevalence (17/315, 1.89%) was recorded in *Syncerus caffer* which was infected with *Cal. microbothrium* + *Car. gregarius* + *P. cervi* in Egypt (Halium et al., 2014) and the highest prevalence of 60% (3/5) was recorded in *Syncerus caffer* mixed infected with *Cal. microbothrium* + *Car. endopapillatus* + *Car. spatiosus* + *Cot. cotylophorum* in Chad and RCA (Graber et al., 1964).

3.6. Checklist of snail intermediate hosts implicated in the transmission of amphistomes species in Africa (1900–2022)

Results showed ten snail species documented as intermediate hosts of known amphistomes species across eight of 23 reviewed African countries. The species include nine Planorbidae Rafinesque 1815, viz, Bulinus (Physopsis) (Bul.) globosus, Bul. (Physopsis) nasutus, Bul. tropicus, Bul. forskalii, Bul. senegalensis, Bul. mairei, Bul. liratus, Biomphalaria (Bio.) pfeifferi, and Anisus (Ceratophallus) natalensis, and one Lymnaeidae Rafinesque 1815 species, Galba (Lymnaea) truncatula (Table 4). Bulinus tropicus was implicated in the transmission of Cal. calicophorum in South Africa (Porter, 1921; Grobbelaar, 1922). Calicophoron microbothrium was shown to use a variety of snail species as IH, ranging from Bul. tropicus in South Africa (Swart and Reinecke, 1962), Zambia (Dinnik, 1965) and Kenya (Dinnik, 1962), Bul. nasatus in Kenya (Dinnik, 1965) and Bul. globosus in Zambia (Dinnik, 1965). Calicophoron sukari has been reported to be transmitted by Bio. pfeifferii in Kenya (Dinnik, 1965) and Ethiopia (Graber and Daynees, 1974), whereas Cal. phillerouxi infections were documented in Bul. forskalii in Zambia and Tanzania, and Bul. senegalensis in Gambia (Dinnik, 1961). Calicophoron daubneyi reported in Kenya was the only amphistomes infection recorded in a Lymnaeidae species; Radix (Lymnaea truncatula) (Dinnik, 1962). Carmyerius exosporus was reported solely in Anisus natalensis (A. natalensis) in Zambia and Kenya (Dinnik, 1964; 1965), whereas Car. mancupatus was reported in several hosts such as Bul. mairei (Gretillat, 1960) and Bul. liratus (Gretillat, 1960) in Zambia, and A. natalensis in Zambia (Dinnik, 1965) and Kenya (Laidemitt et al., 2017). Bul. (Phy.) globosus was reported to transmit Car. parvipapillatus whilst Bul. forskalii transmitted Ste. compactus in Zambia (Dinnik, 1965).

Occurrence of co-infections between two trematode species in intermediate hosts included co-infections of *Cal. microbothrium* and *Schistosoma bovis*. in *Bul. tropicus* from Kenya (Southgate et al., 1985, 1989), and *Carmyerius* spp. and *Schistosoma margrebowiei* in *Bul. forskalii* from Zambia (Wright et al., 1979).

4. Discussion

Over 70 amphistome species have been previously identified and documented around the world, and have been reported to parasitize a diverse spectrum of hosts (Ghatani et al., 2012), mainly domestic and wild ruminants. In this review, we report 38 amphistome species in wild ruminants (36 of which were identified up to species level) distributed in 23 of 54 African countries. Although the species were reported across 39 wild ruminant's species, previous reports have shown that majority of the amphistomes reported are shared with domestic ruminants, with exception to Bil. papillogenitalis, Car. bubalis and Cot. macrophinctris which have only been documented in wild ruminants in Africa (Pfukenyi and Mukaratirwa, 2018). Several authors (Muma et al., 2007; Munyeme et al., 2008) have suggested that this overlap of species between wild and domestic ruminants may have been attributed to the bi-modal transmission of parasites facilitated by contact between wild and domestic ruminants through shared grazing areas or sources of drinking water.

African buffalo was the most frequently infected wild ruminant across Africa, infected with 21 amphistome species from different genera which include *Calicophon, Carmyerius, Cotylophoron, Paramphistomum, Gigantocotyle, Leiperocotyle* and *Stephanopharynx*. A similar trend was observed in Asian countries (Bangladesh, China, India, Indonesia, Iraq, Iran, Japan, Malaysia, Nepal, Pakistan, Phillipines, Sri Lanka, Thailand, Turkey), where over 26 amphistome species belonging to the families Gastrothylacidae and Paramphistomoidea were reported in buffaloes (Tookhy et al., 2022). These infections in African buffalo are not surprising as these ruminants are widely distributed across sub-Saharan Africa, and is often considered an important reservoir for livestock diseases (Eygelaar et al., 2015). Furthermore, Saha et al. (2013) and Nath et al. (2016) have argued that infection of buffaloes with amphistomes may have been due to factors such as their wallowing habit, and bulk ingestion of grasses near the water source (habitats of snail IHs) which in turn increase exposure to ingestion of the metacercariae encysted on the lush grass on the edges of water bodies.

The review showed that at genus level, species from the genus *Calicophoron* were most common and widely distributed across 17 of the 23 reviewed African countries. However, results also showed that at a species level *Cal. microbothrium* was the most widely distributed species, followed by *Cot. cotypophorum* as compared to the other genera. This was not surprising as *Cal. microbothrium* is regarded the most common and significant cause of amphistomosis in Africa (Pfukenyi et al., 2005; Pfukenyi and Mukaratirwa, 2018). Furthermore, the wider distribution of both species may have also been attributed to their ability to infect and utilise a wider range and wild rumninat species as their hosts. Amongst least reported amphistomes species in were *Gas. crumenifer*, *Cal. daubneyi* and *Par. cervi*. These three amphistomes have been linked with cases of amphistomosis beyond Africa (Raza et al., 2009; Gordon et al., 2013; Tehrani et al., 2015; Jones et al., 2015; Jones et al., 2017; Rafiq et al., 2020).

According to Eduardo (1987), the establishment of an amphistome species in a particular region may be dependent more on the intermediate host as compared to the definitive host. Saito et al. (2023) stated that freshwater snails may be moved from one region to another through migratory birds, or through aquarium trades (Derraik, 2008; Work and Mills, 2013). Reviewed studies showed that certain amphistome species only utilise Planorbidae species as IHs. Our results showed that the distribution of the widely spread amphistomes genera Calicophoron in Africa were linked to the presence and distribution of Bul. tropicus; Bul. globosus; Bul. forskallii; Bul. nasutus; Bul. senegalensis and Bio. pfeifferii in (Gretillat, 1960; Dinnik, 1961; Swart and Reinecke, 1962; Dinnik, 1962; Dinnik, 1964; Dinnik, 1965; Graber and Daynees, 1974). Several authors indicated that Bulinus species are highly susceptible to infection and have a capacity to aestivate during the dry season (Dinnik, 1964; Dinnik, 1965; de Kock et al., 2002), which may explain the dispersion of Cal. microbothrium which was linked with Bul. tropicus, Bul. globosus, and Bul. nasutus (Dinnik, 1962; Swart and Reinecke, 1962; Dinnik, 1965). Calicophoron daubneyi was the only amphistomes species linked with Radix (Lymnea) trancatula in East Africa (Dinnik, 1962).

The lowest prevalence of amphistomes infection in in this review was recorded in Gazella rufifrons (7.1%) and the Sylvicapra grimmia (8%) infected with Cal. microbothrium from Chad based on histology and Paramphistomum spp. from South Africa based on fluke morphology, respectively. The low prevalence in Sylvicapra grimmia was not surprising as these species are predominantly browsers (Wilson and Clarke, 1962; Keymer, 1969; Boomker, 1981; Skinner and Smithers, 1990), and they feed on shrub leaves and buds, trees, forbs, bark, roots, flowers, fruits, seeds and cultivated crops (Wilson, 1996; Hofmann and Stewart, 1972; Dunbar, 1978; Skinner and Smithers, 1990), thereby limiting their exposure to infective stages of amphistomes (Condy, 1972; VanderWaal et al., 2014). Furthermore, low prevalence of other trematode infection patterns has been noted in browsers such as Sambar deers and Nilgai in Indian (Gupta et al., 2011) and in domestic ruminants in Ethiopia (Legesse et al., 2014) and India (Hassan et al., 2005). Gupta et al. (2008) indicated that snails and environmental factors play an integral role in the transmission of trematodiasis. This was observed in Agra region where low prevalence of amphistomosis and fasciolosis observed was due to harsh climatic conditions which were not conducive for the intermediate snail host. Nonetheless, the results also showed bias in the

prevalence rate attributed to the differences in number of research conducted across different countries.

The highest prevalence from this review were recorded in Zambian *Kobus defassa* infected with *Calicophoron* spp. (100%), followed by South African Impala infected with *Cot. cotylophorum*. These Bovidae species are predominantly grazers and the observed high prevalence may be due to their feeding behavior, which increases exposure to parasites (Phiri et al., 2011). Amoroso et al. (2019) argued that sharing of waterholes may potentially be a source of parasite exposure and subsequent high prevalence especially in the case of amphistomes. However, Zieger et al. (1998) suggested that transmission of parasites in wild ruminants may also be impacted by habitat type and stocking density. The higher the density of animals often lead to contamination of grazing and water source, and consequently lead to infections and re-infection of animals (Condy, 1972; Zieger et al., 1998). This was later supported by Singh et al. (2009), who mentioned that pasture contamination by parasites may result in a high incidence of parasites.

In general, results showed that Southern African countries recorded some of the highest prevalence rates of amphistomes infections, while East, North, and Central Africa have low to moderate rates. Regional differences in amphistome prevalence are likely due to factors like environmental conditions, ecology, host-parasite interaction, and collection season (Phiri et al., 2011; Tookhy et al., 2022). According to (Hajipour et al., 2021) this variation in prevalence of amphistomes may due to different climatic conditions, ecological and management systems. Gonzalez -Warleta et al. (2013) also confirms that climatic conditions may affect the life-cycle of the parasites resulting in regional differences of prevalence amphistomes. Furthermore, all prevalence cases were based on coprological and morphological techniques, which not only failed to identify to species level in most cases, but may have underestimated the true incidence of amphistomes species in Africa. This was supported by several authors who indicated the challenges associated with identifying various species of immature amphistomes based on morphology alone (Chaoudhary et al., 2015; Ikeuchi et al., 2022). Furthermore, Sargison et al. (2016) also highlighted that although coprological technique/faecal egg count is the only practical test that is validated for diagnosis and identification of rumen fluke infections in live animals, it also has the potential to underestimate infections as it can only diagnose patent infections.

Reviewed studies also documented the presence of mixed infections of amphistomes and other trematodes such as Fasciola spp. and Schistosoma spp. in both intermediate and definitive hosts. Similar coinfection of amphistomes with other trematodes have been documented outside Africa in Sambar deer, Chital, Neelgai, Gaur and buffalo in India (Gupta et al., 2008; Singh et al., 2009; Gupta et al., 2011; Saha et al., 2013; Swarnakar et al., 2014) and goats of Pakistan (Ayaz et al., 2013). Furthermore, 60.42% of Black Bengal goats were found harboring two or more species of amphistomes in India (Uddin et al., 2006), whilst in Pakistan 12,8% of buffaloes were also reported to harbor multiple species of amphistomes (Nazar et al., 2019). According to Alstedt et al. (2022), co-infection of amphistomes with other trematodes such as Fasciola spp. in the intermediate and definitive hosts is possibly due to the similar heteroxenous lifecycle of these trematodes and shared intermediate hosts. Furthermore, exposure to various sources of infection, vast habitats, (González-Warleta et al., 2013; Nazar et al., 2019; Amoroso et al., 2019) and the movement and foraging habits of wild ruminants (Mijele et al., 2016) are all factors that can result in co-infections in ruminants. Moreover, large wild ruminant populations and high stocking densities offer opportunities for parasite colonisation and transmission, which can result in the development of mixed or co-infections within a population (Amoroso et al., 2019; Schmid-Hempel, 2021).

5. Conclusion

Results from this review showed natural infection of 39 wild

ruminant species with 38 amphistome species occurred across 23 African countries. *Calicophoron microbothrium* and *Cot. cotylophorum* were the most distributed species. High prevalence of amphistome infections were documented in southern Africa compared to all the other regions. The low number of studies showed that there is still paucity of information on amphistome of wild ruminants and their intermediate snail hosts. Future study should focus on determining the geographical expansion and prevalence of amphistomes in their wildlife hosts. Furthermore, provide more information on the species of intermediate hosts involved in the distribution of amphistomes in Africa. Most importantly, there is need to adopt both morphological characterization and newer molecular tools not only to detect amphistomes in the larval stages for conservation of wildlife, but also study their taxonomy and genetic relationships.

Author's contributions

SM conceptualized the study. MSS and IN developed the concept note, conducted the search, selected studies and wrote the first draft of the manuscript under MPM's guidance. All author's contributed to the article, agreed on the final draft and approved the submitted version.

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Declaration of competing interest

The authors declare no conflict of interest.

Appendix A. Supplementary data

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