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Review

Potential Hybridization of *Fasciola hepatica* and *F. gigantica* in Africa—A Scoping Review

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Abstract: The occurrence of *Fasciola gigantica* and *F. hepatica* in Africa is well documented; however, unlike in Asia, there is a paucity of information on the existence of hybrids or parthenogenetic species on the continent. Nonetheless, these hybrid species may have beneficial characteristics, such as increased host range and pathogenicity. This study provides evidence of the potential existence of *Fasciola* hybrids in Africa. A literature search of articles published between 1980 and 2022 was conducted in PubMed, Google Scholar, and Science Direct using a combination of search terms and Boolean operators. *Fasciola* species were documented in 26 African countries with *F. hepatica* being restricted to 12 countries, whilst *F. gigantica* occurred in 24 countries, identified based on morphological features of adult *Fasciola* specimens or eggs and molecular techniques. The co-occurrence of both species was reported in 11 countries. However, the occurrence of potential *Fasciola* hybrids was only confirmed in Egypt and Chad but is suspected in South Africa and Zimbabwe. These were identified based on liver fluke morphometrics, assessment of the sperms in the seminal vesicle, and molecular techniques. The occurrence of intermediate host snails *Galba truncatula* and *Radix natalensis* was reported in Ethiopia, Egypt, South Africa, Tanzania, and Uganda, where *F. hepatica* and *F. gigantica* co-occurrences were reported. The invasive *Pseudosuccinea columella* snails naturally infected with *F. gigantica* were documented in South Africa and Egypt. In Zimbabwe, *P. columella* was infected with a presumed parthenogenetic *Fasciola*. This suggests that the invasive species might also be contributing to the overlapping distributions of the two *Fasciola* species since it can transmit both species. Notwithstanding the limited studies in Africa, the potential existence of *Fasciola* hybrids in Africa is real and might mimic scenarios in Asia, where parthenogenetic *Fasciola* exist in most Asian countries. In South Africa, aspermic *F. hepatica* and *Fasciola* sp. have been reported already, and *Fasciola* hybrids have been reported? in Chad and Egypt. Thus, the authors recommend future surveys using molecular markers recommended to identify *Fasciola* spp. and their snail intermediate hosts to demarcate areas of overlapping distribution where *Fasciola* hybrids and/or parthenogenetic *Fasciola* may occur. Further studies should also be conducted to determine the presence and role of *P. columella* in the transmission of *Fasciola* spp. in these geographical overlaps to help prevent parasite spillbacks.

Keywords: *Fasciola hepatica*; *F. gigantica*; hybrids; parthenogenetic species; distribution; snail intermediate host; Africa



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1. Introduction

Fasciolosis is an important food and water-borne zoonotic infection of human, domestic, and wild animals mainly caused by the two liver flukes, *Fasciola hepatica* (Linnaeus, 1758) and *F. gigantica* (Cobbold, 1856) [1–3]. Of the two species, *F. hepatica* has been shown to have a cosmopolitan distribution occurring in five continents except for Antarctica [4,5], whilst *F. gigantica* is restricted to the tropical and subtropical regions of Asia and Africa [6]. According to [7], the distribution of both *Fasciola* species is associated with the availability and dispersal of viable snail vectors that act as - intermediate hosts (IHs) as well as climatic and ecological conditions suitable for the survival of these snails [8–10].

Previous data have suggested that *F. hepatica* originated from Eurasian ovicaprines, especially *Ovis* species [11]. This concept has been generally accepted due to the dispersion of its preferred IH snail, *Galba truncatula* (Müller, 1774), which is associated with areas with mild and cold climates [12], and very high altitudes [11]. Recent data elucidated that the ancestral fasciolids of *F. hepatica* and *F. gigantica* are speculated to have emerged in the lowlands of East Africa [13], followed by speciation of *F. hepatica* in the Eurasian Near East and *F. gigantica* in Africa [11]. *Fasciola hepatica* then spread from Eurasia to other parts of the world [11] where its main IH is *G. truncatula* [14,15]. In Africa, the cryptic species *Galba mweruensis* (Connolly, 1929) has been indicated as an IH of both *Fasciola* species [16,17] but has only been proven to transmit *F. hepatica* in Lesotho and Ethiopia [18,19].

Based on [11], the assumption that the emergence of Fasciolinae species and secondary colonization by *F. gigantica* and other *Fasciola* species in Africa was favored by a switch of IHs from planorbid to lymnaeid snails as stated by [20] does not fit the current knowledge. *Fasciola gigantica* is distributed throughout western, sub-Saharan, and eastern Africa following the wide distribution of the snail intermediate host species *Radix natalensis* (Krauss, 1848) that it adapted to [11]. Furthermore, this fasciolid species has adapted to ruminants from families Giraffidae, Reduncinae, and Alcelaphinae in sub-Saharan Africa as definitive hosts [11]. Following the movement of animals facilitated by humans and the subsequent introduction of intermediate host snail species into new areas, *F. gigantica* spread to other regions. In these regions, its main IHs are the *Radix* species of the “auricularia super-species” (Hubendick, 1951) *R. rubiginosa* (Minchin, 1831) in Asia, and *R. natalensis* in Africa [9,21].

The spread of both *Fasciola* species led to overlapping distributions in areas where climatic conditions allow the IHs of both species to survive and co-exist, particularly in tropical regions of Africa and Asia [11,22]. In South Africa, the invasive snail *Pseudosuccinea columella* (Say, 1817) has been suspected to be the vector snail responsible for possibly transmitting both *Fasciola* species, thus contributing towards the overlap [23], following an observed increase in infection rates of both *Fasciola* species coinciding with the introduction of the invasive snail species in the country [24]. *Pseudosuccinea columella* has been reported to be responsible for the secondary transmission of *F. hepatica* in South America and the Caribbean region [9,25], and it has been proven to naturally transmit *F. gigantica* in Africa [23,26]. Therefore, it can be hypothesized that *P. columella* may potentially be transmitting *F. hepatica* in Africa, supported by successful experimental infections of the Egyptian *P. columella* population with *F. hepatica* [27] and natural infections with an unknown yet suspected *Fasciola* hybrid in South Africa [23] and Zimbabwe [28], thus facilitating the overlapping geographical distribution of *Fasciola* species in some African countries as reported in Egypt [29] and South Africa [30].

In areas of geographical overlap, hybridization between *F. hepatica* and *F. gigantica* has been reported, resulting in *Fasciola* hybrid species consisting of admixed/introgressive genotypes due to interspecific mating [31,32]. According to [13], this hybridization may have occurred about 2000 years ago in China, resulting in parthenogenetic populations which were then spread across multiple Asian countries where they co-exist with *F. gigantica*. However, due to a lack of standardized methods for identifying these populations, the parthenogenetic *Fasciola* in Japanese populations was initially misidentified as *F. hepatica* [33]. Moreover, parthenogenetic *Fasciola* was previously called aspermic *Fasciola* but the discovery of few aspermic triploid individuals that produced and stored mature sperms in their seminal

vesicles led to this term being disregarded. Thus, parthenogenetic *Fasciola* can be distinguished from other *Fasciola* hybrids by its ability to reproduce and maintain successive generations [13].

Although [13] suggests that the parthenogenetic *Fasciola* populations have not been reported outside of Asia, other forms of *Fasciola* hybrid populations have been suspected in some African countries, as evidenced by the recent reports of aspermic *F. hepatica* and unidentified *Fasciola* sp. [23,28,30]. However, they could have been missed outside Asia due to the paucity of research on the occurrence of *Fasciola* hybrids in the areas of geographical overlap [30,34]. Moreover, African studies have not applied nuclear phosphoenolpyruvate carboxykinase (PEPCK) and DNA polymerase delta (POLD) markers which are recommended as suitable markers to identify parthenogenetic *Fasciola* [13]. Nonetheless, knowledge of the occurrence of *Fasciola* hybrids is significant since hybrid forms may have increased in their geographic and host expansion [2]. Hence, this review aimed to assess the possible hybridization of *F. hepatica* and *F. gigantica* resulting in parthenogenetic *Fasciola* in Africa as presented in published literature, and the role of *P. columella* in driving the convergence of the two *Fasciola* spp., allowing hybridization in the process.

2. Materials and Methods

The scoping review was conceptualized to address the following review questions: (1) What is the distribution of *Fasciola* species in Africa? (2) Which African countries have co-occurrences/overlapping geographical distribution of *F. hepatica* and *F. gigantica*? (3) Which intermediate snail hosts are implicated in these overlapping distributions? (4) Has the hybridization of *F. hepatica* and *F. gigantica* occurred in Africa? (5) If no, are there signs that hybridization is in the process or potentially occurring in Africa but under-documented? (6) If yes, is it occurring in the same way as in China, where two pure parental *Fasciola* species are hybridizing or other Asian countries where pure maternal *F. gigantica* is hybridizing with parthenogenetic species? To answer these questions, articles published in peer-reviewed journals reporting on the distribution of *F. hepatica*, *F. gigantica*, snail IHs, and the occurrence of *Fasciola* hybrids/parthenogenetic *Fasciola* populations in Africa were retrieved and appraised. Guidelines from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) were followed using the approaches for scoping review described by [35].

2.1. Search Strategy

A literature search was conducted on Google Scholar, PubMed, and Science Direct electronic databases. The search was completed using a combination of Boolean operators (OR, AND) and the following search terms: *F. hepatica* AND *F. gigantica* AND co-occurrence, *Fasciola* spp. AND intermediate hosts, *Fasciola* species AND hybridization, *Fasciola* hybrids OR Intermediate forms of *Fasciola* OR Parthenogenetic *Fasciola* in Africa (Algeria OR Angola OR Benin OR Botswana OR Burkina Faso OR Burundi OR Cameroon OR Cape Verde OR Central African Republic OR Chad OR Comoros OR Congo OR Côte d'Ivoire OR Djibouti OR DR Congo OR Egypt OR Equatorial Guinea OR Eritrea OR Ethiopia OR Gabon OR The Gambia OR Ghana OR Guinea OR Guinea-Bissau OR Kenya OR Lesotho OR Liberia OR Libya OR Madagascar OR Malawi OR Mali OR Mauritania OR Mauritius OR Morocco OR Mozambique OR Namibia OR Niger OR Nigeria OR Réunion OR Rwanda OR Sao Tome and Principe OR Senegal OR Seychelles OR Sierra Leone OR Somalia OR South Africa OR South Sudan OR Sudan OR Swaziland OR Tanzania OR Togo OR Tunisia OR Uganda OR Western Sahara OR Zambia OR Zimbabwe). Articles with relevant information were identified by screening titles and abstracts to obtain relevant articles. Full texts of relevant articles were retrieved and managed using EndNote reference manager version X9 (Clarivate Analytics, Philadelphia, PA, USA).

2.2. Inclusion and Exclusion Criteria

Articles were included in the study if they were published in peer-reviewed journals and they: (1) precisely reported on the occurrences and co-occurrences of *F. hepatica* and *F. gigantica* and their snail intermediate hosts in Africa; (2) reported on the occurrences of *Fasciola* hybrids or parthenogenetic *Fasciola* in Africa; (3) identified eggs or adult flukes up to species level using molecular techniques or morphological features; and (4) were conducted in Africa and published between January 1980 and February 2022.

The review excluded articles that (1) did not identify *Fasciola* species and their intermediate hosts up to species level; (2) reported on experimental infections; (3) did not contribute towards answering the research questions; and (4) were not conducted in Africa or were published outside the years indicated above and were not written in English.

2.3. Charting, Collating, and Summarising Data

Data were extracted from articles that met the inclusion criteria after appraisal. Data concerning the details of the authors and year of publication, the aim or objectives of the study, the country where the study was conducted, the outcomes of the study, and any information relevant to the main objectives of this review were extracted and recorded.

3. Results

The searches using Google Scholar, PubMed, and Science Direct electronic databases yielded 6721 records, and 23 additional records were identified through reference list screening (Figure 1). A total of 1023 duplicates were identified and removed. The titles and abstracts of 5698 records were screened for relevance and 5296 records were deemed irrelevant and excluded. Full-text articles of 402 records were extracted and assessed for eligibility, and 161 records were deemed ineligible and excluded because they did not contribute towards answering the review questions. A total of 241 records from 26 African countries were included in the scoping review (Tables S1 and 2).

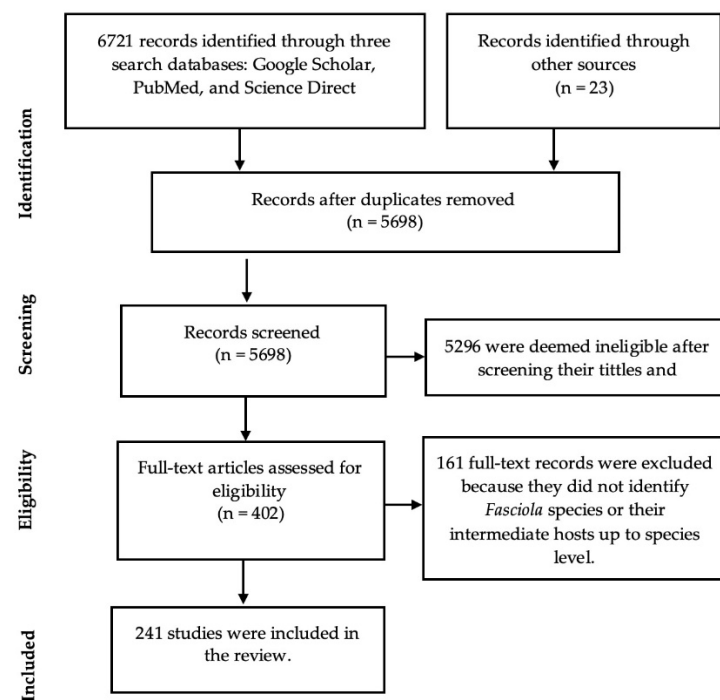


Figure 1. PRISMA diagram.

Results showed that *Fasciola* spp. were predominantly reported from cattle (*Bos taurus*) (Linnaeus, 1758) (n = 159), and also from other vertebrate hosts including sheep (*Ovis aries*) (Linnaeus, 1758) (n = 42), goat (*Capra hircus*) (Linnaeus, 1758) (n = 27), African buffalo

(*Syncerus caffer*) (Sparrman, 1779) (n = 9), donkey (*Equus africanus*) (Linnaeus, 1758) (n = 5), horse (*Equus ferus*) (Linnaeus, 1758) (n = 3), humans (*Homo sapiens*) (Linnaeus, 1758) (n = 3), antelope (*Hippotragus niger*) (Harris, 1838) (n = 2), pig (*Sus domesticus*) (Erxleben, 1777) (n = 2), mule (*Equus mulus*) (n = 1), camel (*Camelus dromedarius*) (Linnaeus, 1758) (n = 1), eland (*Taurotragus oryx*) (Pallas, 1766) (n = 1), duiker (*Sylvicapra grimmia*) (Linnaeus, 1758) (n = 1), impala (*Aepyceros melampus*) (Lichtenstein, 1812) (n = 1), Kafue lechwe (*Kobus leche*) (Gray, 1850) (n = 1), and kudu (*Tragelaphus strepsiceros*) (Pallas, 1766) (n = 1).

Most studies identified *Fasciola* specimens based on morphological features (n = 147), whilst 23 (n = 23) studies identified the parasites using molecular techniques. Other studies used egg morphology from coproscopy (n = 1), serology (n = 1), and 20 (n = 20) studies used a combination of more than one diagnostic technique (Table S1 and Figure 2).

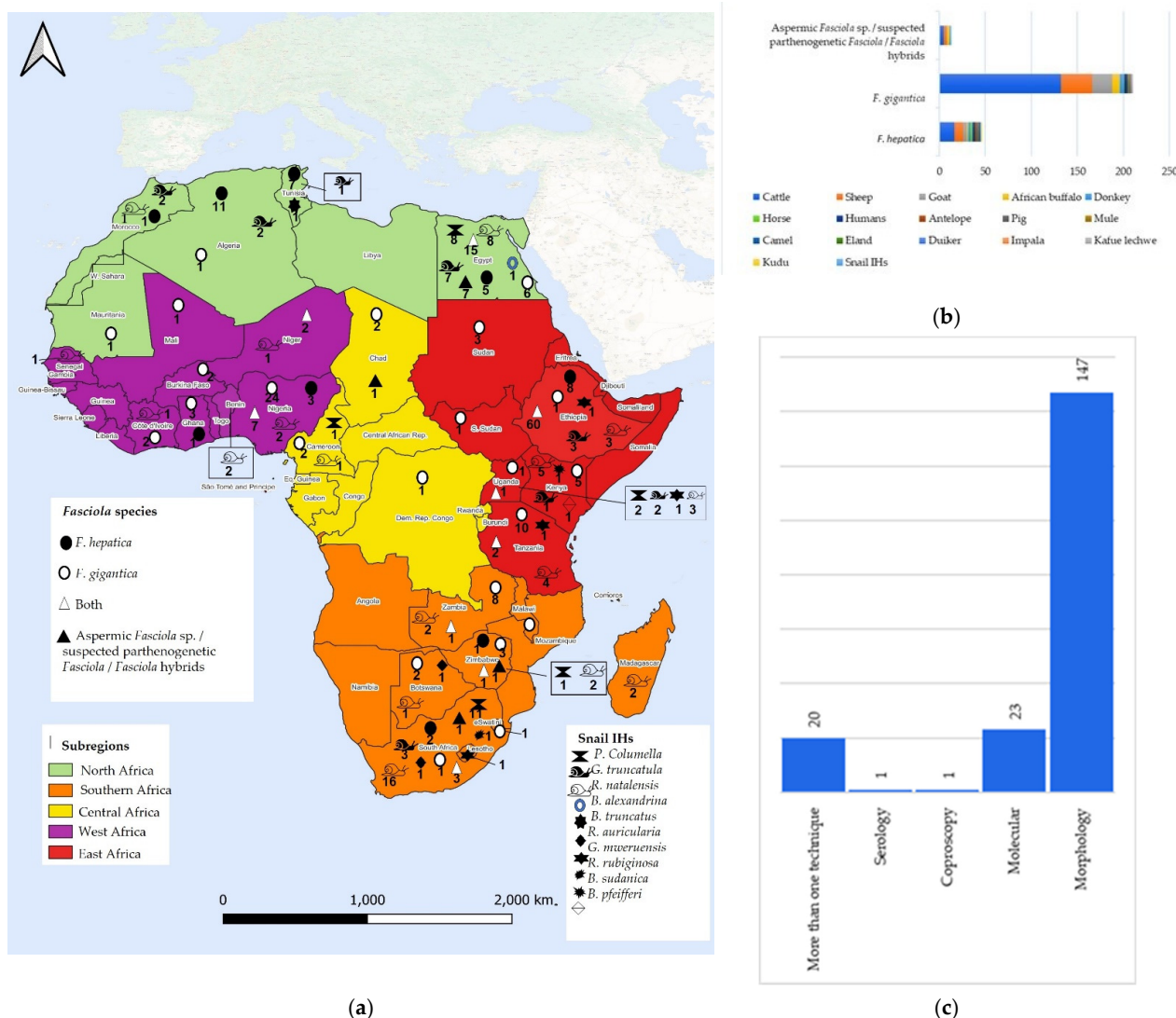


Figure 2. (a) A map showing the geographical distribution and occurrence of *Fasciola* spp. and their snail intermediate hosts in Africa based on records retrieved in the scoping review. The taxa reported are symbolized next to the number of studies in each country; (b) Reviewed studies that reported on *Fasciola* infection in various definitive hosts; (c) Techniques used in reviewed studies to identify *Fasciola* spp.

3.1. Geographical Distribution and Occurrence of *F. hepatica* and *F. gigantica* in Africa

Results show that *Fasciola* species occur in all five African subregions (Figure 2). In North Africa, both *F. hepatica* and *F. gigantica* have been reported in Egypt and Algeria,

whilst Morocco and Tunisia recorded the occurrence of *F. hepatica* only and *F. gigantica* was recorded in Sudan and South Sudan. In East Africa, both *Fasciola* species have been reported in Ethiopia, Uganda, and Tanzania, whilst Kenya and Malawi reported the occurrence of *F. gigantica* only. Reviewed studies further revealed that *F. gigantica* was the only fasciolid documented in Central African countries, viz., Cameroon, Chad, and the Democratic Republic of Congo. A total of five Southern African countries reported the occurrence of *Fasciola* species with Swaziland and Botswana recording *F. gigantica* only, whereas South Africa, Zambia, and Zimbabwe reported both *F. gigantica* and *F. hepatica*. In West Africa, Burkina Faso, Côte d'Ivoire, Mali, and Mauritania recorded the occurrence of only *F. gigantica*, whilst Ghana, Niger, and Nigeria recorded both *Fasciola* species (Table S2).

3.2. Checklist of Snail Intermediate Hosts of *F. hepatica* and *F. gigantica* in Africa

Evidence from the reviewed studies shows that both *G. truncatula* and *R. natalensis* snails occur in North, South, and East African subregions, whilst West and Central regions only documented the occurrence of *R. natalensis* (Table 1). Additionally [16], documented the presence of a cryptic *Galba* species, *G. mweruensis*, in Southern Africa (Lesotho) and East Africa (Ethiopia, Uganda, and Tanzania). In North Africa, both *R. natalensis* and *G. truncatula* were documented specifically in Egypt, whilst Algeria, Morocco, and Cameroon documented the presence of *G. truncatula* only. Reviewed studies further showed that *Fasciola* species in North Africa can infect other snail species with evidence of natural infections in *Biomphalaria alexandrina* (Ehrenberg, 1831) and *P. columella* by Egyptian *F. gigantica* and *Bulinus truncatus* (Audouin, 1827) by Tunisian *F. hepatica* (Table S3). In Central Africa, *R. natalensis* and *P. columella* were the only lymnaeid species documented in Cameroon. Southern African region showed the highest species diversity by documenting five lymnaeid species including *P. columella*, *R. natalensis*, *R. auricularia* (Linnaeus, 1758), *R. rubiginosa* (Michelin, 1831) and *G. truncatula*. South Africa documented all five lymnaeid species whilst Zimbabwe and Namibia recorded *R. natalensis* and *P. columella*. Zambia and Lesotho recorded *R. natalensis* and *G. truncatula*, respectively. Botswana recorded *R. natalensis* and *R. auricularia*. Evidence of natural infections in *P. columella* with *Fasciola* sp. was documented in Zimbabwe and South Africa. In West Africa, *R. natalensis* was the only lymnaeid species documented in Benin, Côte d'Ivoire, Niger, Nigeria, and Senegal. East African countries where *R. natalensis* and *G. truncatula* were documented include Ethiopia, Tanzania, and Uganda, whilst Kenya and Madagascar reported *R. natalensis* (Table 1). Results further showed evidence of infection of *Bio. pfeifferi* (Krauss, 1848) and *Bio. sudanica* (Martens, 1870) by *F. gigantica* in Kenya (Table S3).

Table 1. Checklist and distribution of snail intermediate hosts of *Fasciola* species reported in Africa based on studies conducted from 1980–2022.

Subregion	Country	Intermediate Host Species Recorded	References
North Africa	Algeria	<i>G. truncatula</i>	[36,37]
	Egypt	<i>P. columella</i> , <i>R. natalensis</i> , <i>G. truncatula</i> , <i>Bio. alexandrina</i>	[26,38–49]
	Morocco	<i>G. truncatula</i>	[16,50]
	Tunisia	<i>G. truncatula</i> , <i>Bulinus truncatus</i>	[51–53]
Central Africa	Cameroon	<i>R. natalensis</i> , <i>P. columella</i>	[54]

Table 1. Cont.

Subregion	Country	Intermediate Host Species Recorded	References
Southern Africa	Botswana	<i>R. auricularia</i> , <i>R. natalensis</i>	[55,56]
	Lesotho	<i>G. truncatula</i> , <i>G. mweruensis</i>	[16,57]
	Namibia	<i>R. natalensis</i> , <i>P. columella</i>	[58]
	South Africa	<i>P. columella</i> , <i>R. natalensis</i> , <i>R. auricularia</i> , <i>G. truncatula</i> , <i>R. rubiginosa</i>	[16,23,55,57,59–76]
	Zambia	<i>R. natalensis</i>	[77,78]
West Africa	Zimbabwe	<i>R. natalensis</i> , <i>P. columella</i>	[28,79–81]
	Benin	<i>R. natalensis</i>	[82,83]
	Côte d’Ivoire	<i>R. natalensis</i>	[84]
	Niger	<i>R. natalensis</i>	[85]
	Nigeria	<i>R. natalensis</i>	[86,87]
East Africa	Senegal	<i>R. natalensis</i>	[88]
	Ethiopia	<i>R. natalensis</i> , <i>G. truncatula</i> , <i>G. mweruensis</i>	[16,89–92]
	Madagascar	<i>R. natalensis</i>	[93,94]
	Kenya	<i>R. natalensis</i> , <i>Bio. pfeifferi</i> , <i>Bio. sudanica</i>	[16,95–99]
	Uganda	<i>R. natalensis</i> , <i>G. truncatula</i> , <i>G. mweruensis</i>	[16,100,101]
	Tanzania	<i>R. natalensis</i> , <i>Bio. pfeifferi</i> , <i>G. truncatula</i> , <i>G. mweruensis</i>	[16,98,102–104]

3.3. Occurrence and Identification of Fasciola Hybrids/Aspermic and Suspected Parthenogenetic Fasciola in Africa

Results show that *Fasciola* hybrids were confirmed in cattle from Egypt and Chad, and in buffalo and sheep from Egypt. These *Fasciola* hybrids were genetically identified by comparing the nucleotides of the ITS-1 and ITS-2 sequences and individuals displayed heterozygosity with the ITS-Fh/Fg genotype thus confirming mixed bases of both *Fasciola* types at the variable sites [1,2,29]. Furthermore, studies also compared the nuclear ITS gene sequences to the mitochondrial sequences of NADH dehydrogenase subunit I (NDI) and cytochrome c-oxidase subunit I (COI) regions. The hybrid individuals identified as one *Fasciola* species at ITS-1 and ITS-2, however, displayed sequences of the other species at NDI and/or COI (Table 2). Morphologically, the length/width ratio of *Fasciola* hybrid adult flukes (1.86–3.37 mm) significantly differed from those of *F. gigantica* (3.43–5.50 mm) and *F. hepatica* (1.65–2.76 mm) (Table 2). Hybrid species also showed variations in the size and position of the oral and ventral suckers, the structure of intestinal caeca, and the position and branches of testes from *F. hepatica* and *F. gigantica* (Table 2). Results also showed that some specimens which possessed morphometric characters of *F. hepatica* displayed a close genetical relation to *F. gigantica* based on the PCR-linked restriction fragment length polymorphism (PCR-RFLP) using the *AvaII* restriction enzymes [105].

Table 2. Summary of studies reporting on the occurrence of *Fasciola* hybrids/intermediate forms and suspected parthenogenetic forms in Africa based on morphological and molecular techniques.

Author	Aim/Objective	Country	Host	No. of Specimen	Diagnostic Technique	Characteristics
[1]	To identify the phenotypic features and genetic characterization of adult fasciolids infecting buffaloes that were studied in Aswan, Egypt.	Egypt	Sheep	3	Morphology and molecular	<ul style="list-style-type: none"> - Intermediate <i>Fasciola</i> species had Body length (BL), Cone length (CL), Cone width (CW), ventral sucker diameter, and Pharynx width (PhW) measurements that overlapped between those of <i>F. hepatica</i> and <i>F. gigantica</i>. - Nucleotide bases varied from those of <i>F. gigantica</i> and <i>F. hepatica</i> at variable positions 1 and 3.
[2]	To molecularly characterize <i>Fasciola</i> flukes using the ITS-1 and 2 nuclear markers to confirm species and any hybrid forms.	Chad	Cattle	1	Molecular	<ul style="list-style-type: none"> - <i>Fasciola</i> hybrid showed heterozygosity at all variable sites. - Cloning and sequencing of both alleles confirmed the presence of one allele each for <i>F. hepatica</i> and <i>F. gigantica</i>.
[23]	Confirming whether <i>P. columella</i> was transmitting <i>F. gigantica</i> and/or <i>F. hepatica</i> in selected locations of KwaZulu-Natal and Eastern Cape provinces of South Africa.	South Africa	Snail IHs	1	Molecular	<ul style="list-style-type: none"> - <i>Pseudosuccinea columella</i> was found infected with <i>F. gigantica</i>, <i>Fasciola</i> sp., and <i>Echinostoma</i> sp. - <i>Fasciola</i> sp. showed a close affinity with <i>F. gigantica</i> on BLAST and genetic distance but formed its own haplotype and clade different from <i>F. gigantica</i> and <i>F. hepatica</i> based on the ITS-1 marker.
[28]	Assessed the prevalence of <i>Fasciola</i> sp. infections in the gastropod populations.	Zimbabwe	Snail IHs	3	Molecular	<ul style="list-style-type: none"> - Phylogenetic analyses showed a close affinity between suspected <i>Fasciola</i> sp. with <i>F. hepatica</i> and <i>F. gigantica</i> based on the ITS marker.
[29]	Molecularly ascertain the nature of <i>Fasciola</i> population derived from different hosts and different geographic locations in Egypt.	Egypt	Buffalo	2	Molecular	<ul style="list-style-type: none"> - Intermediate <i>Fasciola</i> forms had the ITS-2-Fh/Fg with mixed bases of both <i>Fasciola</i> types at all variable sites and nucleotide peaks of <i>F. hepatica</i> and <i>F. gigantica</i> overlapping at the 6 variable sites. - One isolate proved <i>F. gigantica</i> lineage at both NDI and COI markers, while the other worm was identified as <i>F. hepatica</i>.

Table 2. Cont.

Author	Aim/Objective	Country	Host	No. of Specimen	Diagnostic Technique	Characteristics
[30]	Morphological and molecular characterization of <i>Fasciola</i> spp. collected from cattle slaughtered at abattoirs located in the two provinces of South Africa, where two species are endemic.	South Africa	Cattle	17	Morphology	<ul style="list-style-type: none"> - Flukes that had no sperm in their seminal vesicles or had “very scanty sperm” were found and deemed “aspermic”. - Specimens were grouped into <i>F. hepatica</i>, <i>F. gigantica</i>, and <i>Fasciola</i> sp. based on the body length/width/ratio measurements. - The average length/width and corresponding standard deviations of <i>F. hepatica</i>, <i>F. gigantica</i> and <i>Fasciola</i> sp. were $21.16 \pm 4.29/10.53 \pm 1.80$ mm, $39.61 \pm 1.09/10.44 \pm 1.59$ mm and $28.87 \pm 5.12/9.32 \pm 1.72$ mm, respectively.
[105]	To differentiate between the three fasciolid worms encountered in sheep and cattle in Sohag, Egypt, through a simple and rapid PCR-restriction fragment length polymorphism (RFLP) assay, using the common restriction enzymes <i>Ava</i> II based on a 618-bp-long sequence of the 28S rRNA gene.	Egypt	Sheep, cattle	-	Morphology and molecular	<ul style="list-style-type: none"> - Intermediate forms possessed morphometric characters from <i>F. hepatica</i> (length and pattern of uterine coils) however the species was genetically more related to <i>F. gigantica</i>.
[106]	To determine the occurrence rate of <i>Fasciola</i> spp. in sheep as measured by post-mortem examination of slaughtered animals at abattoirs.	Egypt	Buffalo	2	Molecular	<ul style="list-style-type: none"> - Two introgressed <i>Fasciola</i> forms had ITS-1 sequences identical to <i>F. hepatica</i> and mitochondrial NDI sequences identical to <i>F. gigantica</i>.
[107]	To determine the prevalence of fascioliasis in cattle, and to describe the histopathological changes in the liver and lungs.	Egypt	Cattle	35	Morphology	<ul style="list-style-type: none"> - <i>Fasciola hepatica</i> possessed an oral sucker equal in size to the ventral sucker, at the conical anterior end and rudimentary inner intestinal branches. <i>F. gigantica</i> had an oral sucker that was larger than the ventral sucker at the anterior end and T- and Y-shaped intestinal caeca branches. The intermediate form had “few” of these morphological features from both <i>F. hepatica</i> and <i>F. gigantica</i>.

Table 2. Cont.

Author	Aim/Objective	Country	Host	No. of Specimen	Diagnostic Technique	Characteristics
[108]	To use sequence analysis of the ITS-2 region of rDNA and highly repetitive DNA sequences to determine the identity and heterogeneity among <i>Fasciola</i> isolated from buffalo, cow, and sheep hosts.	Egypt	Sheep	1	Molecular	- Intermediate <i>Fasciola</i> isolate had sequence variation in several sites from both <i>F. hepatica</i> and <i>F. gigantica</i> .
[109]	Analyzed the morphometric characteristics of fasciolid adults infecting the main livestock species present in the Nile Delta human endemic area.	Egypt	Cattle, buffalo	126	Morphology	- Body roundness (BR), Body length/Body width (BL/BW) and the distance between the ventral sucker and the posterior end of the body (VS-P) measurements of intermediate <i>Fasciola</i> overlapped between <i>F. hepatica</i> and <i>F. gigantica</i> measurements.

Parthenogenetic *Fasciola* were suspected in the form of aspermic *Fasciola* species from cattle in South Africa. The aspermic *Fasciola* sp. (suspected parthenogenetic) were characterized as specimens with no sperms in their seminal vesicles or had “very scanty sperms” and mean length/width ratio measurements that significantly varied from those of *F. gigantica* and *F. hepatica* which were 2.02 ± 0.35 mm, 2.79 ± 0.48 mm and 4.41 ± 1.10 mm, respectively [30]. Unidentified *Fasciola* sp. isolated from *P. columella* were recorded in Zimbabwe and South Africa (Table S2 and Table 2). In Zimbabwe, the unidentified *Fasciola* sp. showed a close affinity to *F. gigantica* and *F. hepatica* on a phylogenetic tree based on the ITS marker [28]. In South Africa, the unidentified *Fasciola* sp. Showed a close affinity to *F. gigantica* on BLAST and genetic distance; however, they formed their own haplotype and clade different from that of *F. gigantica* and *F. hepatica* based on the ITS-1 marker [23].

4. Discussion

Previous studies have indicated that *F. hepatica* has a cosmopolitan distribution [4,5], whereas *F. gigantica* is restricted to parts of Asia and Africa [6]. Reviewed studies have confirmed that *F. gigantica* is more widespread in Africa as expected following the distribution of its IHs [100] and was reported in 24 African countries. In contrast, *F. hepatica* was more restricted in its distribution, corresponding to the restricted distribution of its IHs which occur in cooler parts of Africa [100]. *Fasciola hepatica* was reported in a few countries including Egypt and the Maghreb countries (Algeria, Morocco, and Tunisia) in North Africa; South Africa, Zimbabwe, and Zambia in Southern Africa; Nigeria and Niger in West Africa; and Tanzania, Uganda, and Ethiopia in East Africa, which corresponded to reports from previous studies [22,110–112]. The results also showed co-occurrences of the two *Fasciola* species in Algeria, Ghana, Ethiopia, Egypt, Nigeria, South Africa, Niger, Tanzania, Uganda, Zambia, and Zimbabwe.

Fasciola specimens were predominately collected from their “primary domestic definitive hosts” [113], i.e., cattle, sheep, and goats in all subregions. This is not surprising since these mammalian hosts easily consume *Fasciola* metacercariae from pastures [114] when grazing in areas near water bodies which are habitats of the snail IHs [115]. Results also showed that natural infections of *F. hepatica* in Africa occurred in cattle, African buffalo, sheep, goat, camel, humans, pig, horse, antelope, duiker, kudu, mule, and donkey, whilst *F. gigantica* infected cattle, sheep, goat, impala, Kafue lechwe, donkey, African buffalo, humans, antelope, horse, duiker, mule, and eland (Figure 2). The low number of studies reporting fasciolosis in wildlife supports a suggestion by [116–118] that infections might be accidental and a result of shared drinking water between wildlife and cattle since most wildlife animals are browsers and thus less likely to become infected through aquatic vegetation [22]. Moreover, a few reviewed studies reported infections in humans, thus highlighting that human fasciolosis is either occurring at a very low rate or neglected since humans can easily become infected by ingesting watercress or other edible raw plants contaminated with metacercariae, which form part of the regular diet in several countries [119–121], or through drinking water contaminated with metacercariae. Studies from North, East, and Southern Africa recorded infections in buffalo, donkey, horse, mule, camel, and pig. A few South, West, and East African studies reported infections in humans and wild animals including antelope, eland, duiker, impala, Kafue lechwe, and kudu.

Reviewed studies show that both *G. truncatula* and *R. natalensis* co-occur in Ethiopia, Egypt, South Africa, Tanzania, and Uganda, and these are the countries where both *F. hepatica* and *F. gigantica* have been documented. However, other countries such as Algeria, Ghana, Nigeria, Niger, Zambia, and Zimbabwe reported co-occurrence of both *F. hepatica* and *F. gigantica*, with only the presence of one IH being documented. According to [111], such outcomes can be attributable to livestock transhumance, or these species use other freshwater snails from other families and not Lymnaeidae or Raciadinae and we further add that limited or no effort has been made to look for the IH. However, altitude and topography have been reported to have an influence on the survival of the snail IHs,

thus contributing to the occurrence of *Fasciola* species [22,100,103]. No records on the occurrence of snail IHs of *Fasciola* species were retrieved for nine African countries (South Sudan, Sudan, Chad, DR Congo, Burkina Faso, Ghana, Mali, Mauritania, and Malawi), thus highlighting the paucity of research on snail IHs-*Fasciola* spp. in these African countries. Moreover, the presence of lymnaeid snail IHs were reported in Lesotho, Namibia, Benin, Senegal, and Madagascar, where there was no reviewed evidence of *Fasciola* spp. This raises concern about possible rapid transmission should the trematodes be introduced, and according to [122] it might be harmful to inhabitants should there be an introduction of the parasite by infected livestock near water bodies with IHs and accessed by humans during their anthropogenic activities.

Reviewed studies showed that apart from *G. truncatula*, *F. hepatica* has been observed to naturally infect *B. truncatus* in Tunisia [51]. Additionally, *G. mweruensis*, based on studies by [16], appears to be well established as a major IH of *F. hepatica* throughout the Sub-Saharan Africa region and has been reported in Lesotho, Ethiopia, Uganda, and Tanzania. This species is presumed to be the most predominant snail species in the highlands of Ethiopia and Lesotho [18,19] and is believed to be the main IH of both *F. hepatica* and *F. gigantica* [17], and potentially other trematode infections [18,19]. Natural infections with *F. gigantica* were also detected in *Bio. alexandrina* in Egypt based on molecular techniques [123], and *Bio. Pfeifferi* and *Bio. Sudanica* in Kenya [96], and *P. columella* in South Africa [23] and Egypt [26]. In South Africa [23] and Zimbabwe [28], *P. columella* has been found naturally infected with a suspected parthenogenetic *Fasciola* sp. Considering that this invasive snail species transmit *F. hepatica* in other parts of the world, it can be suggested that *P. columella* may be responsible for the overlapping distribution of both *F. hepatica* and *F. gigantica* and, hence, promote the occurrence of *Fasciola* hybrids playing a role in the overlap between the two species.

In Asia, the occurrence of *Fasciola* hybrids has been extensively studied and documented in China [123,124], Vietnam [125–128], Japan [129,130], Korea [131,132], Bangladesh [133], Nepal [134], and Myanmar [135]. A recent study by [12] highlighted the existence of a parthenogenetic *Fasciola* population originating from hybridization between “pure” *F. gigantica* and *F. hepatica* in China at least 2000 years ago, and these populations have spread to other Asian countries including Vietnam, India, the Philippines, Thailand, Myanmar, Bangladesh, and Nepal where it co-exists with *F. gigantica*, and these have not been reported to occur outside Asia. Results from this review highlighted that hybridization may have already occurred or is in the process in some African countries including Chad, Egypt, and South Africa. This is supported by the individual flukes which have been identified to have intermediate morphological characters of *F. gigantica* and *F. hepatica* in Egypt [1,105,109] and South Africa [30], and those presumed to be *F. hepatica* with little to no sperm in their seminal vesicle in South Africa [30]. Considering that the Asian parthenogenetic *Fasciola* which were aspermic and those identified as *F. hepatica* in Japan were later classified as parthenogenetic hybrids [13], it is possible that the “aspermic” populations found in South Africa might also be parthenogenetic *Fasciola*. Thus, the presence of parthenogenetic *Fasciola* in Africa could have been missed due to a lack of specific studies focusing on the detection of hybrid populations, or the use of inappropriate or non-specific markers to identify these populations, especially in areas with overlapping distributions of these two *Fasciola* species. Itagaki [13] recommended the use of a multiplex PCR based on the PEPCK and POLD markers, but recent studies have suggested that the fatty acid binding protein type I gene markers are more reliable compared to the PEPCK and POLD markers [136].

Fasciola hybrids from Egypt [105] that had morphometric characters of *F. hepatica* were genetically more related to *F. gigantica*. The results also showed that similar to other countries where *Fasciola* hybrids/parthenogenetic populations were reported, these specimens were also characterized by either the ITS-Fh/Fg mixed genotype or the possession of sequences of one *Fasciola* species at ITS-1 and ITS-2 but sequences of the other species at NDI and/or COI [1,2,29,106,108]. Furthermore, the populations found in *P. columella* in

South Africa [23] and Zimbabwe [28] were shown to be genetically closer to *F. gigantica* but formed their own clade on the phylogenetic tree based on the ITS-1 marker (genetic distances). Similar observations were reported by [13] that the Asian parthenogenetic *Fasciola* were genetically closer to *F. gigantica* than *F. hepatica* [137–139].

5. Conclusions

Fasciola gigantica and *F. hepatica* co-occur in Algeria, Ghana, Ethiopia, Egypt, Nigeria, South Africa, Niger, Tanzania, Uganda, Zambia, and Zimbabwe. However, the presence of *Fasciola* hybrids has only been confirmed in Egypt and Chad, and parthenogenetic populations are suspected in Zimbabwe and South Africa. *Galba truncatula* and *R. natalensis* are the main IH of *F. hepatica* and *F. gigantica*, respectively, in Africa. However, a cryptic *Galba* sp. (*G. mweruensis*) in Sub-Saharan Africa is worth investigating as it is claimed to be the major host of *F. hepatica* and might also be sustaining both *Fasciola* species in the continent. The role of *P. columella* in the transmission of *F. gigantica*, *F. hepatica*, and *Fasciola* sp. is not clear, and the current results suggest that the snail species might be responsible for *Fasciola* species overlaps as it was proven to transmit both *F. hepatica* and *F. gigantica* in other countries. Hence, the authors recommend that surveys should be conducted to assess if this is also the case in Africa and to detect hybrids in areas of geographical overlap using appropriate molecular and morphological techniques. Evidence suggests that *Fasciola* hybrids recorded in some African countries might be parthenogenetic *Fasciola* as reported in Asia. This calls for reliable molecular studies such as the concurrent use of ITS-1 and ITS-2 markers with the PEPCK, POLD, and ND1 markers combined with sperm observations for validation and identification of African *Fasciola* species to avoid misidentifications.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/pathogens11111303/s1>. Table S1: Summary of African studies reporting on the presence of *Fasciola* species recovered from various definitive hosts. Table S2: The distribution and occurrence of *Fasciola* species in Africa based on studies conducted from 1980–2022. Table S3: Summary of African studies reporting on the occurrence of *Fasciola* species in their snail intermediate hosts. Table S4: Summary of studies reporting on the occurrence of intermediate hosts of *Fasciola* spp. in Africa. References [140–317] are cited in the supplementary materials.

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