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The invasive giant African land snail, *Achatina fulica* (Gastropoda: Pulmonata): global geographical distribution of this species as host of nematodes of medical and veterinary importance

G. M. Silva[1,2], S. C. Thiengo[2], V. L. Sierpe Jeraldo[1,3], M. I. F. Rego[2], A. B. P. Silva[2], P. S. Rodrigues[2] and S. R. Gomes[2]

[1]Tiradentes University – UNIT, Graduate Program in Health and the Environment, Avenida Murilo Dantas, 300, Bairro Farolândia, 49032-490 Aracaju, SE, Brazil; [2]National Reference Laboratory for Schistosomiasis-Malacology: Oswaldo Cruz Institute – FIOCRUZ, Avenida Brazil 4365, Manguinhos, Rio de Janeiro 21.040-900, RJ, Brazil and [3]Laboratory of Infecious and Parasitic Diseases, Institute for Technology and Research – ITP, Avenida Murilo Dantas, 300, Prédio do ITP, Bairro Farolândia, 49032-490 Aracaju, SE, Brazil

Review Paper

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Author for correspondence:
S.C. Thiengo,
E-mail: scarvalhothiengo@gmail.com

Abstract

The giant African land snail, *Achatina fulica*, is an important invasive species in many countries, where it causes losses in biodiversity and agriculture, as well as impacting the health of both humans and animals, as the intermediate host of medically important nematodes. The present study is based on a comprehensive review of the literature on the nematodes that have been found in association with *A. fulica*, worldwide. We searched a number of different databases and used the findings to investigate the methods used to extract and identify the nematodes, their larval stages, and environment and collecting procedures of the infected molluscs. Between 1965 and 2021, 11 nematode species were recorded in association with *A. fulica* in 21 countries. Most of the studies recorded associations between *A. fulica* and *Angiostrongylus cantonensis*, which causes cerebral angiostrongyliasis in humans and *Aelurostrongylus abstrusus*, which provokes pneumonia in felines. The nematodes were extracted primarily by artificial digestion with hydrochloric acid or pepsin, and identified based on their morphology or through experimental infection to obtain the adult. In most cases, the nematodes were at larval stage L_3, and the infected *A. fulica* were collected from anthropogenic environments. The results demonstrate the importance of *A. fulica* as a host of nematodes of medical and veterinary importance, as well the contribution of anthropogenic environments to the occurrence of the parasites, and give information about the different methods used to collect and identify the nematodes found associated with this species.

Introduction

The giant African land snail, *Achatina* (*Lissachatina*) *fulica* Bowdich, 1822, is an invasive species of terrestrial gastropod native to East Africa. Vijayan *et al.* (2020), provide a brief history of the worldwide invasion of *A. fulica*, which shows that this species began to disperse from the African continent in around 1800, primarily through human activities, first reaching the islands of Mauritius or Madagascar, and from there, the Comoros, Seychelles and Reunion archipelagos. In around 1847, the species was introduced from Mauritius to India, where it spread subsequently throughout the Asian continent during the first half of the twentieth century, in particular during the Second World War, when it reached many Asian countries and several islands in the Pacific and Indian Oceans (Vijayan *et al.,* 2020). *Achatina fulica* arrived in South America in the 1980s, being first recorded in Brazil (Darrigran *et al.*, 2020). During this same period, the species was also recorded in the West Indies (Fontanilla *et al.*, 2014), and there are two records of its introduction into the United States, in Hawai'i in 1936 (Mead, 1961) and Florida in 1966 (Roda *et al.*, 2016). *Achatina fulica* is now present in Africa, the Americas, East and South Asia and Oceania (Thiengo *et al.*, 2007), with records from 52 countries around the world (Vijayan *et al.*, 2020).

Achatina fulica is considered to be a synanthropic species, that is, an organism found typically in environments modified by humans (Simião & Fischer, 2004; Fischer & Colley, 2005; Silva *et al.*, 2020), although it can also occur in tropical forests, where it competes for food and space with the endemic fauna (Raut & Barker, 2002; Simião & Fischer, 2004). In urban zones, *A. fulica* is found primarily in humid and shaded environments that lack adequate sanitation, often in direct contact with trash and sewage outlets, which are also conditions that favours the ocurrence of synanthropic rodents (Silva *et al.,* 2022). These are anthropogenic conditions,

which are invariably found observed in urban areas, and favourthe proliferation of *A. fulica* (Silva *et al.*, 2020, 2022).

Given its accelerated population growth, self-fecundation and high rates of dispersion, *A. fulica* is capable of colonizing many novel types of environments (Dickens *et al.*, 2018; Lima *et al.*, 2020). This snail is also resistant to warmer and drier periods, and is most active during cooler, rainy days, especially at night (Eston *et al.*, 2006; Almeida *et al.*, 2016). In fact, the active presence of *A. fulica* in the environment is related directly to rainy days and more humid conditions (Silva *et al.*, 2020). This snail also has an extremely diverse diet that includes approximately 500 different plant species, which may reduce the availability of resources for the native fauna, as well as impacting agricultural crops (Thiengo *et al.*, 2007; Fischer & Costa, 2010).

Grewal *et al.* (2003) reported that terrestrial molluscs, including *A. fulica*, are associated with many different species of nematodes, generally acting as the intermediate host, with part of the life cycle of the parasite being completed in the snail or slug. In other cases, the mollusc may be the definitive host, with the juvenile nematode developing in the body cavity or tissue of the foot muscle, and the adults living freely. Some nematodes may even complete their life cycle in the mollusc, which in some cases may lead to the death of the host (Grewal *et al.*, 2003). The molluscs may even act as paratenic hosts, transporting a larval stage from one host to the next without undergoing any type of development (Anderson, 2000).

Given the current global distribution of *A. fulica*, and the threats that the presence of this snail pose to public health, local biodiversity, and agriculture, we carried out a comprehensive literature review to identify the nematode species that have been found in association with *A. fulica* in different countries around the world. We also summarize the principal methods used to extract and to identify these species of nematodes, the larval stages of the nematodes found in *A. fulica*, as well as the type of environment occupied by this molluck and the specimen collection methods.

Material and methods

The present study was based on a comprehensive and integrated literature search, which was descriptive, exploratory and qualitative. This approach permits the systematic analysis of the data available on a specific topic based on the summarization of the results of previous studies (Soares *et al.*, 2014). The present study focused on the following question: 'Worldwide, which nematodes of interest to public health or veterinary medicine have been found parasitizing *A. fulica*?'.

The papers were selected according to specific criteria of both inclusion and exclusion. The inclusion criteria were full scientific papers that describe nematodes found infecting *A. fulica* naturally anywhere in the world, and include the key words presented below. The exclusion criteria included personal communications, abstracts of congresses and other events, reviews and studies that did not focus specifically on the themes or topics proposed for this review.

The literature search focused on five online databases: Scientific Electronic Library Online (SciELO); Scopus (Elsevier); LILACS (Latin American and Caribbean Life Sciences Literature); PubMed; and Google Scholar. The search was based on the following key words (in Portuguese and English): (a) *Achatina fulica* AND nematode OR zoonosis; (b) *Achatina fulica* AND nematode; (c) *Achatina fulica* AND Nematoda; (d) *Achatina fulica* AND parasite; and (d) *Achatina fulica* AND parasitosis. The Boolean operator AND was used to recuperate papers that contained both key words, while OR was used to amplify the search and guarantee the inclusion of the different key words selected for the study. The literature search was conducted between March and June 2021.

Once the papers were identified, the primary studies were selected based on the proposed research question and the inclusion criteria defined above. The papers were initially analysed according to the search criteria, being identified by the contents of their titles and abstracts, as defined in each database. The papers were then processed manually to eliminate duplicates, before being read in full to determine their eligibility and the data they contained. This identified the papers that would make up the final (analytical) sample. A set of information was extracted from each study and standardized for analysis, being presented in tables. This information included the locality from which the *A. fulica* specimens were collected, the procedure used to extract the nematodes from the mollusc, the method used to identify the nematode species (morphology, histology and molecular biology), the nematode development stage (larva/adult), the type of environment in which the molluscs were found (anthropogenic or sylvatic) and the method used to capture the specimens.

A few papers were added manually, including full articles that identified the infection of *A. fulica* by some nematodes but were not found during our previous search (table 1 – online supplementary appendix table S2). The remaining papers were not complete, but as they presented reports of *A. fulica* being infected by *Angiostrongylus cantonensis* in countries not identified in our search, they were included in the production of the map (countries in which *A. fulica* specimens infected naturally with nematodes have been collected), but not in table 1 or online supplementary appendix table S2.

The selected papers for analysis were read and evaluated independently by two different groups of reviewers, in order to better select the most appropriate studies for inclusion in the analysis and to better evaluate information obtained from them.

The data were analysed in the Statistical Package for the Social Sciences (SPSS) 22.0, with the results being summarized as absolute and relative frequencies. The variation in the frequency of studies (a) using the different methods for the detection of the nematodes, (b) capturing snails during the daylight or nighttime periods, and (c) reporting different nematode species was evaluated using Pearson's Chi-square, with a $P < 0.05$ significance level being considered in all cases.

Results

Characteristics of the studies

The literature search identified a total of 20,690 papers based on the data analysed, with a subsample of 168 files selected for further analysis after analysis of all titles and abstracts. One hundered of these papers were read in full, of which, five were manually included. After that, thrity papers were excluded because they did not satisfy the inclusion criteria, that is, they did not provide an adequate approach to the primary question raised in the present study. This left 70 papers, which were analysed completely, according to the inclusion criteria (fig. 1). The earliest paper was published in 1965, and the most recent, in 2021, with a progressive increase in the number of papers published after 2010, reaching a peak ($n = 8$) in 2019. The studies identified in this search were concentrated in Southeast Asia, the Americas and the basins of the Pacific and Indian Oceans (Robinson, 2000),

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Table 1. Methods used to extract and identify the nematode larvae released from *Achatina fulica* in the papers surveyed.

Country (Brazilian state)[a]	Method used to obtain the nematodes from *A. fulica*	Nematode identified (Brazilian state)[a]	Larvae identification method	Larval stage	Reference and year
Malaysia	artificial digestion with hydrochloric acid (HCl)	*Angiostrongylus cantonensis*	morphological and experimental infection	–	Lim & Heyneman (1965)
*United States – Hawai'i	artificial digestion with HCl	*A. cantonensis*	morphological and experimental infection	L_3	*Wallace & Rosen (1969)
*Malaysia	fragment of the body in 0.85% saline	*Angiostrongylus malaysiensis*	experimental infection	L_3	*Lim *et al.* (1976)
Papua New Guinea	–	*A. cantonensis*	experimental infection	–	Scrimgeour & Welch (1984)
Japan	artificial digestion with HCl–1% pepsin	*A. cantonensis*	–	L_3	Matayoshi *et al.*, (1987)
Japan	artificial digestion with HCl–1% pepsin	*A. cantonensis*	morphological and experimental infection	L_3	Noda *et al.* (1987)
Brazil (ES)	artificial digestion with 0.7% HCl	*A. cantonensis*	morphological, experimental infection and molecular polymerase chain reaction–restriction fragment length polymorphism (internal transcribed spacer 2)	L_2 and L_3	Caldeira *et al.* (2007)
Brazil (RJ, ES, GO, MT, SP, SE, MG)	artificial digestion with HCl – pepsin	*Aelurostrongylus abstrusus* (RJ/ES/GO/MT/SP/SE/MG)	morphological	L_2 and L_3	Thiengo *et al.* (2008)
		Strongyluris sp. (RJ/ES/GO)			
Brazil (RJ)	observation of the mantle	*Strongyluris* sp.	morphological	–	Franco-Acuña *et al.* (2009)
China	artificial digestion with 0.7% HCl – 0.2% pepsin	*A. cantonensis*	morphological and experimental infection	L_3	Lv *et al.* (2009)
Brazil (RJ/SC)	artificial digestion with 0.7% HCl	*A. cantonensis* (RJ/SC)	morphological and experimental infection	L_3	Maldonado *et al.* (2010)
		Strongyluris sp. (RJ)			
		Rhabditis sp. (RJ/SC)			
Brazil (GO)	artificial digestion with 0.7% HCl	*A. abstrusus*, *Rhabditis* sp. *Strongyluris* sp.	morphological	–	Oliveira *et al.* (2010)
Brazil (SP)	morphological (pepsin)	*A. abstrusus*	morphological	L_3 and L_2	Ohlweiler *et al.* (2010)
United States – Hawai'i	morphological (pepsin)	*A. cantonensis*	molecular polymerase chain reaction (internal transcribed spacer 1)	L_3	Qvarnstrom *et al.* (2010)
Brazil (PE)	artificial digestion with 0.7% HCl	*A. cantonensis*	morphological, experimental infection and molecular polymerase chain reaction (internal transcribed spacer 2)	L_3 and L_1	Thiengo *et al.* (2010)
Brazil (RJ)	artificial digestion with 0.7% HCl	*Rhabditis* sp., *Strongyluris* sp.	morphological	adult and L_3	Zanol *et al.* (2010)
China	artificial digestion with 0.7% HCl – 0.2% pepsin	*A. cantonensis*	morphological	L_3	Hu *et al.* (2011)
Thailand	artificial digestion with 0.7% HCl – 1% pepsin	*A. cantonensis*	morphological	L_3	Vitta *et al.* (2011)
Brazil (AM)	drowning	*A. abstrusus*	morphological	L_3	Andrade-porto *et al.* (2012)
Brazil (BA/RJ/PR/SC)	artificial digestion with 0.7% HCl	*A. cantonensis*	molecular polymerase chain reaction– restriction fragment length polymorphism (internal transcribed spacer 2/ClaI enzyme)	–	Carvalho *et al.* (2012)

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Table 1. (*Continued.*)

Country (Brazilian state)[a]	Method used to obtain the nematodes from *A. fulica*	Nematode identified (Brazilian state)[a]	Larvae identification method	Larval stage	Reference and year
China	fragment of the mantle in 0.85% saline	*A. cantonensis*	morphological	L_3	Deng *et al.* (2012)
French Polynesia	artificial digestion with 0.5% HCl – 0.7% pepsin	*A. cantonensis*	molecular–polymerase chain reaction (PCR) (small subunit ribosomal ribonucleic acid (SSU rRNA))	L_3	Fontanilla & Wade (2012)
*Japan	artificial digestion**	*A. cantonensis*	molecular–PCR (SSU rRNA)	L_3	*Tokiwa *et al.* (2012)
China	–	*A. cantonensis*	morphological	L_3	Yang *et al.* (2012)
United States – Hawai'i	fabric shredding	*A. cantonensis*	molecular – real time PCR	–	Kwon *et al.* (2013)
Brazil (PA)	artificial digestion with 0.7% HCl	*A. cantonensis*	morphological, experimental infection and molecular PCR (cytochrome c oxidase subunit I (COI))	L_3	Moreira *et al.* (2013)
Venezuela	mucus and faeces (Kato's direct method)	*Trichures* sp., *Ascaris* sp., *Strongyloides stercoralis*	morphological	–	Amaya *et al.* (2014)
Philippines	artificial digestion with 0.7% HCl – 0.5% pepsin	*A. cantonensis*, *Ancylostoma caninum*	molecular PCR (small subunit recombinant DNA (SSU rDna))	–	Constantino-Santos *et al.* (2014a)
Philippines	artificial digestion with 0.7% HCl – 0.5% pepsin	*Oslerus osleri*, *A. cantonensis*	molecular PCR (SSU rDna)	–	Constantino-Santos *et al.* (2014b)
United States – Hawai'i	artificial digestion with 0.7% HCl– 0.3% Pepsin	*A. cantonensis*	molecular–PCR (18S–internal transcribed spacer 1)	–	Kim *et al.* (2014)
Venezuela	Kato–Katz and mucus	Ascaridida Trichuroidea Ancylostomatidae Toxocaridae *Toxascaris* spp. Rabdithida	morphological	eggs	Morocoima *et al.* (2014)
United States – Florida	extraction of DNA (foot tissue)	*A. cantonensis*	molecular – quantitative polymerase chain reaction (qPCR) (internal transcribed spacer 1 (ITS1))	–	Iwanowicz *et al.* (2015)
Brazil (RJ)	artificial digestion with 0.7% HCl	*A. cantonensis* *Rhabditis* sp.	morphological and experimental infection	L_3	Oliveira *et al.* (2015)
United States – Florida	maceration	*A. cantonensis*	morphometry and molecular qPCR (ITS1)	L_1, L_2 and L_3	Smith *et al.* (2015)
Cuba	fragment of the mantle in 0.85% saline with sedimentation in Baermann's culture	*A. cantonensis*	morphological and experimental infection	L_3	Vázquez & Sánchez (2015)
*Nigeria	saline flotation	*S. stercolaris* *A. cantonensis*	–	–	*Igbinosa *et al.* (2016)
Ecuador	moist examination (stool samples)	*Strongyloides* sp. *Ascaris* sp.	morphological	L_1	Cuasapaz-Sarabia (2016)
Mayotte Island (France)	–	*A. cantonensis*	molecular – reverse transcription polymerase chain reaction (ITS1)	–	Epelboin *et al.* (2016)
Philippines	artificial digestion with 0.5% HCl – 0.7% pepsin	*A. cantonensis*	experimental infection and molecular PCR (SSU)	L_3	Tujan *et al.* (2016)
Argentina	distilled water with methanol – capture	*Strongyluris* sp.	morphological	L_3	Valente *et al.* (2016)
Thailand	0.7% pepsin	*A. cantonensis*	morphological and molecular PCR (COI)	L_3	Vitta *et al.* (2016)

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Table 1. (*Continued.*)

Country (Brazilian state)[a]	Method used to obtain the nematodes from *A. fulica*	Nematode identified (Brazilian state)[a]	Larvae identification method	Larval stage	Reference and year
Colombia	crushing 1 × 1 cm molluscs and collecting in the mucus	*Angiostrongylus*, *Aelurostrongylus*, *Strongyluris* sp.	morphological	–	Córdoba-R *et al.*, (2017)
Guadeloupe Island (France)	–	*A. cantonensis*	molecular real time – PCR	–	Dard *et al.* (2017)
Brazil (SP)	artificial digestion with HCl	*A. cantonensis*	morphological, morphometry and molecular – PCR-RFLP (ITS2)	L_2 and L_3	Guerino *et al.* (2017)
China	artificial digestion with 0.7% HCl, pepsin	*A. cantonensis*	molecular PCR (cytochrome B)	L_3	Peng *et al.* (2017)
Argentina	artificial digestion with 0.7% HCl	*A. abstrusus*	morphological	L_3	Valente *et al.* (2017)
Brazil (RJ)	artificial digestion with 0.7% HCl	*A. cantonensis*	morphological and experimental infection	L_3	Bechara *et al.* (2018)
Colombia	Baermann's culture and method	*Caenorhabditis briggsae*	morphological and molecular PCR (ITS2)	adult	Guerrero *et al.* (2018)
Colombia	artificial digestion–pepsin	*Angiostrongylus vasorum*	molecular RT-PCR (ITS-2)	–	Lange *et al.* (2018)
Brazil (AC)	artificial digestion with HCl	*A. abstrusus*, *Strongyluris* sp., Rhabditiformes	morphological	–	Lima & Guilherme (2018)
Brazil (RJ)	cyst rupture	*Strongyluris* sp.	morphological	L_3	Oliveira & Santos (2018)
Brazil (SE)	artificial digestion with 0.7% HCl	*A. cantonensis* *Strongyluris* sp. *Caenorhabditis* sp.	morphological and molecular PCR-RFLP	L_3	Ramos-de-Souza *et al.* (2018)
Brazil (RJ)	artificial digestion with HCl	*A. cantonensis*	morphological and experimental infection	L_3	Tomaz *et al.* (2018)
Italy	stools and the Baermann's culture method	*Rhabditella axei*, *Rhabditis terricola*, *Cruznema* sp., *Pristionchus entomophagus*	morphological and molecular – PCR (ITS2)	–	d'Ovidio *et al.* (2019)
Thailand	artificial digestion with 0.7% pepsin	*A. cantonensis* *A. malaysiensis*	molecular – PCR (COI, ITS2, SSU rRNA, cytochrome B)	–	Dumidae *et al.* (2019)
Colombia	–	*A. cantonensis*	morphological and molecular – real time-PCR (ITS1)	–	Giraldo *et al.* (2019)
Cuba	observation of the pallial cavity and the application of 0.9% saline solution	*A. cantonensis*	morphological and movement	L_3	Meijides-Mejías & Robledo (2019)
Brazil (SP)	artificial digestion with HCl 0.7% – pepsin 0.4%	*A. cantonensis* *Ancylostoma caninum*	morphological and molecular PCR (ITS2)	L_3	Orico *et al.* (2019)
Colombia	artificial digestion with HCl – pepsin	*A. abstrusus*, *A. vasorum*, *Troglostrongylus brevior*, *Crenosoma vulpis*	morphological and molecular PCR (ITS2)	L_1	Penagos-Tabares *et al.* (2019)
Cuba	incision in the pallial cavity	*Strongylides* sp.	morphological	L_3	Pérez *et al.* (2019)
Ecuador	modified Lobato–Paraense method	*A. cantonensis*	morphological	L_3	Solórzano-Alava *et al.* (2019)
Brazil (AP)	artificial digestion with HCl 0.7%	*A. cantonensis*	molecular PCR (COI)	L_3	Barbosa *et al.* (2020)
Brazil (PR)	cyst rupture	*Strongyluris* sp.	morphological	L_3	Oda *et al.* (2020)

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Table 1. (*Continued.*)

Country (Brazilian state)[a]	Method used to obtain the nematodes from *A. fulica*	Nematode identified (Brazilian state)[a]	Larvae identification method	Larval stage	Reference and year
*Cameroon	organ maceration (flotation with granulated sugar)	*Protostrongylus* sp., *Angiostrongylus* sp., *S. stercoralis*, *Enteroubius vermiculares*	morphological	–	*Meffowoet *et al.* (2020)
Brazil (SE)	mucus and stools (spontaneous sedimentation)	*Rhabtidis* sp.	morphological and molecular PCR (RFLP)	–	Silva *et al.* (2020)
Brazil (MS)	artificial digestion	*A. abstrusus*, *Rhabtidis* sp.	morphological	L3	Oliveira *et al.* (2021)
Thailand	artificial digestion with 1% HCl – 1% Pepsin	*A. cantonensis*, *A. malaysiensis*	morphological and molecular (quantitative PCR; cytochrome B)	L_3	Jakkul *et al.* (2021)
Brazil (RJ)	artificial digestion with 0.7% HCl	*Cruzia tentaculata*	morphological and molecular PCR (18 s; COI)	L_3	Ramos-de-Souza *et al.* (2021)
United States – Hawai'i	artificial digestion**	*A. cantonensis*	molecular PCR (ITS1)	L_3	Rollins *et al.* (2021)
Brazil (BA)	artificial digestion with HCl	*A. cantonensis*	morphological and molecular PCR (RFLP)	–	Souza *et al.* (2021)

[a]AC = Acre; AM = Amazonas; AP = Amapá; BA = Bahia; ES = Espírito Santo; GO = Goiás; MG = Minas Gerais; MS = Mato Grosso do Sul; MT = Mato Grosso; PA = Pará; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; SC = Santa Catarina; SE = Sergipe; and SP = São Paulo.
*Articles and countries manually included.
**It was not specified whether it was artificial digestion by HCl or pepsin.

with the largest number of publications (25) being from Brazil (Caldeira *et al.*, 2007; Thiengo *et al.*, 2008; Barbosa *et al.*, 2020; Silva *et al.*, 2020; Ramos-de-Souza *et al.*, 2021) (table 1) fig. 2.

Nematodes found infecting A. fulica and their geographical distribution

Significant variation ($P = 0.001$) was found in the number of papers published on the different species of nematode found infecting *A. fulica*, with the largest number of papers referring to *A. cantonensis* (Chen, 1935), primarily in the countries of Asia ($n = 14$) and South America ($n = 15$). In Asia, *A. fulica* infected with *A. cantonensis* were recorded in Taiwan, Thailand, Japan, Malaysia, Indonesia, Philippines, China and Singapore (Lim & Heyneman, 1965; Bisseru, 1971; Stafford *et al.*, 1976; Lv *et al.*, 2009; Hu *et al.*, 2011; Deng *et al.*, 2012; Yang *et al.*, 2012; Constantino-Santos *et al.*, 2014a; Kim *et al.*, 2014; Song *et al.*, 2016; Peng *et al.*, 2017) while in South America, this nematode

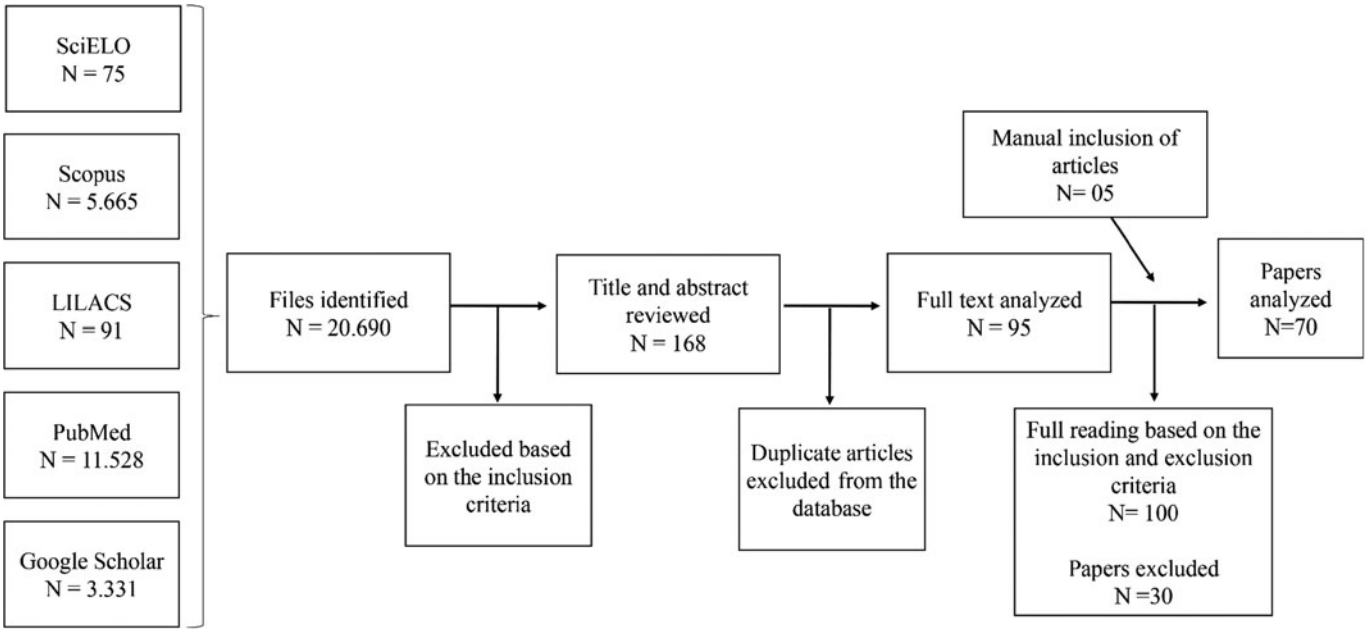

Fig. 1. Flowchart of the procedural steps of the present study.

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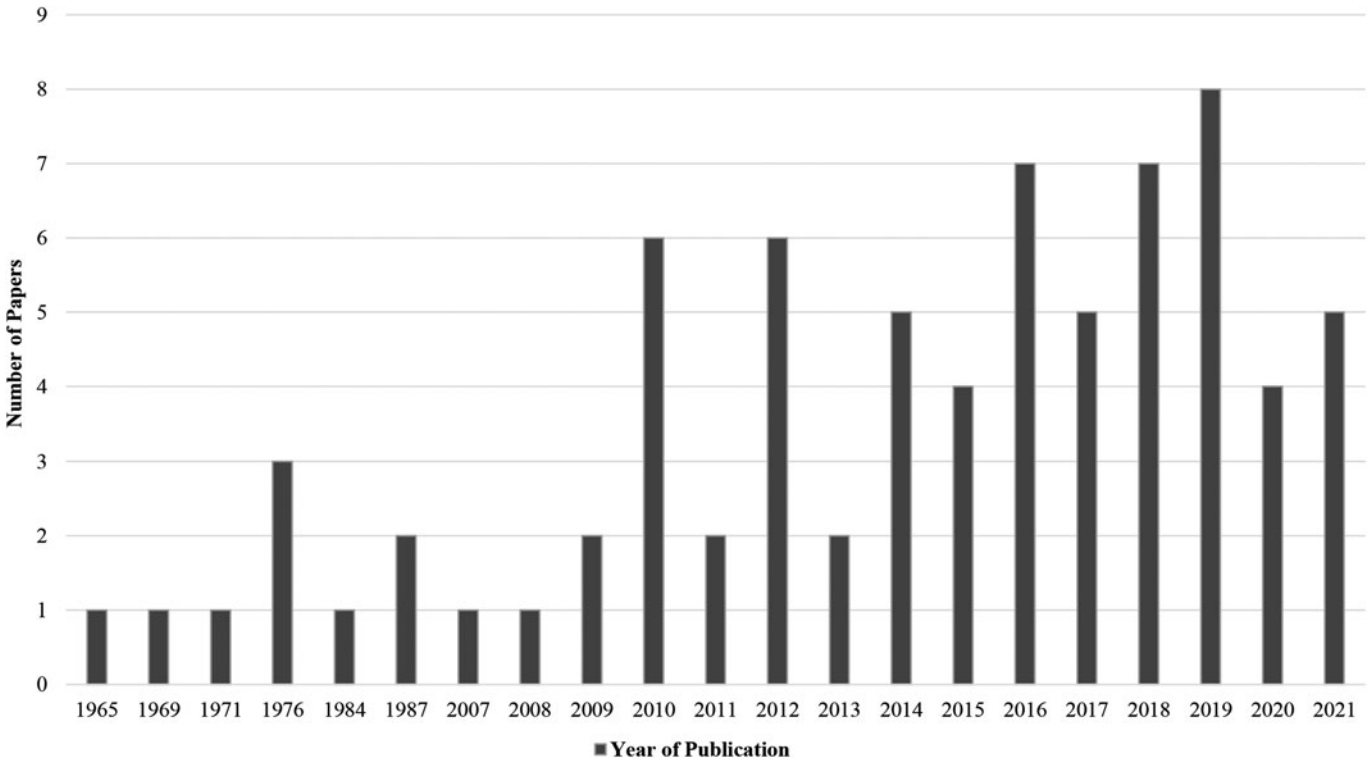

Fig. 2. Number of papers included in the present study.

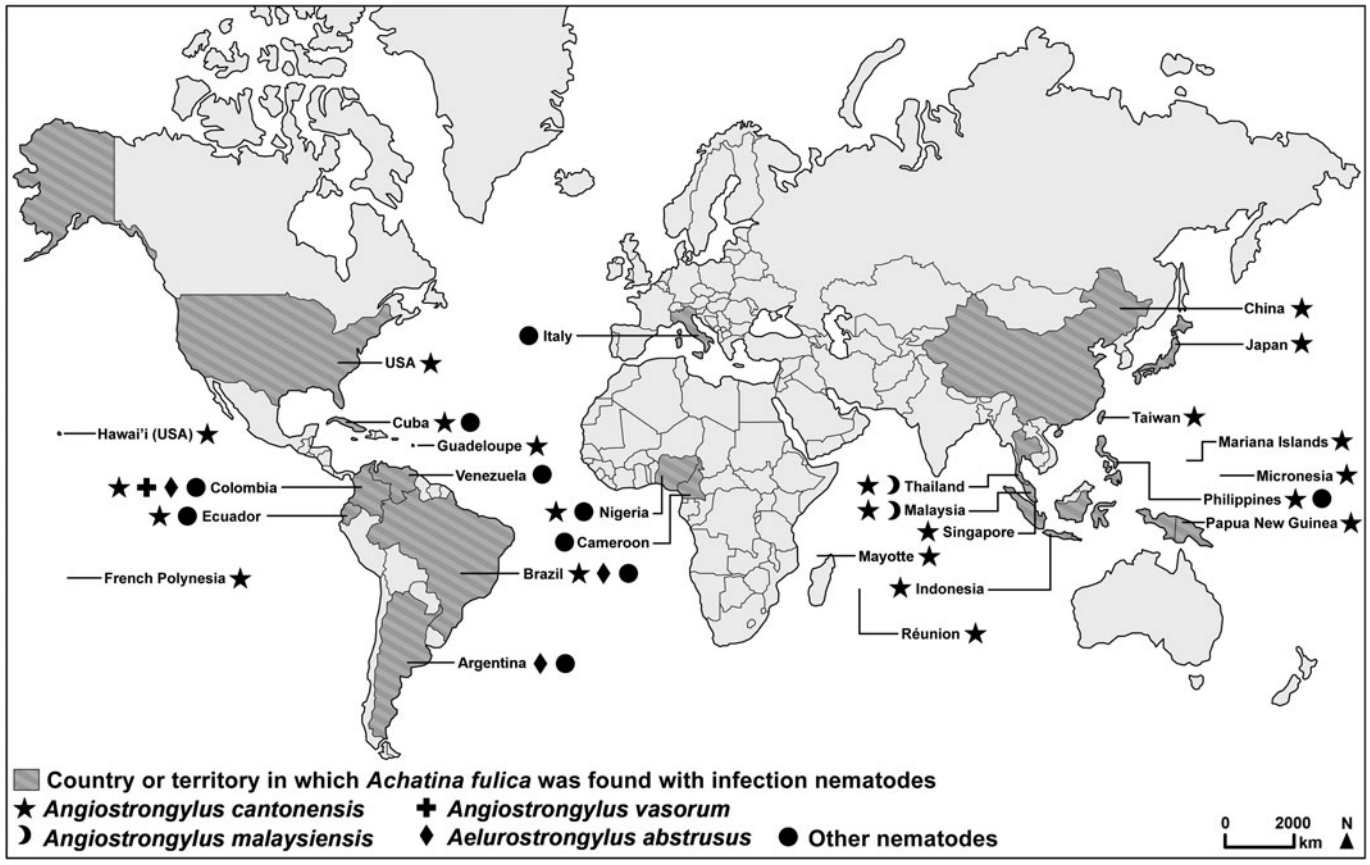

Fig. 3. The countries in which *Achatina fulica* specimens infected naturally with nematodes have been collected.
Note: Indonesia, Taiwan, the Mariana Islands (USA), Micronesia, the Ogasawara Islands and Okinawa are all mentioned in the appendix of Kim *et al.* (2014) and Réunion Island is mentioned by Picot *et al.* (1976).

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has been recorded in Brazil, Colombia and Ecuador (Thiengo *et al.*, 2010; Giraldo *et al.*, 2019; Solórzano-Alava *et al.*, 2019). *Angiostrongylus cantonensis* was also recorded in Cuba and Guadalupe ($n = 3$) in the Caribbean (Vázquez & Sanchez, 2015; Dard *et al.*, 2017), in Florida, ($n = 6$) in North America (Smith *et al.*, 2015) and in Hawai'i, in the Pacific Ocean ($n = 1$), and in the Mariana Islands (Wallace & Rosen, 1969; Kim *et al.*, 2014), Papua New Guinea (Scrimgeour & Welch, 1984), French Polynesia (Fontanilla & Wade, 2012) and Micronesia (Kim *et al.*, 2014) in Oceania. There were also four records from Africa – Nigeria, Cameroon, and the French island dependencies of Mayotte and Réunion (Picot *et al.*, 1976; Epelboin *et al.*, 2016; Igbinosa *et al.*, 2016; Meffowoet *et al.*, 2020) (fig. 3, table 1).

Other metastrongylid species were also recorded infesting *A. fulica*, including *Aelurostrongylus abstrusus* (Railliet, 1898), in Brazil, Argentina and Colombia ($n = 8$) (Thiengo *et al.*, 2008; Oliveira *et al.*, 2010; Andrade-Porto *et al.*, 2012; Valente *et al.*, 2017; Lima & Guilherme, 2018; Penagos-Tabares *et al.*, 2019), *Angiostrongylus vasorum* (Baillet, 1866) in two studies from Colombia (Lange *et al.*, 2018; Penagos-tabares *et al.*, 2019) and *Angiostrongylus malaysiensis* Bhaibulaya and Cross 1971 in two studies from Thailand and one in Malaysia (Lim *et al.*, 1976; Dumidae *et al.*, 2019; Jakkul *et al.*, 2021). No records of natural infection by *Angiostrongylus costaricensis* Morera and Céspedes, 1971 were found in any of the papers examined in the present study.

A number of other nematode species were found in association with *A. fulica* (fig. 3; table 1), such as *Cruzia tentaculata* (Rud, 1819), which was recorded in Brazil (Ramos-de-Souza *et al.*, 2021), *Ancylostoma caninum* (Ercolani, 1859), found in both the Philippines and Brazil (Constantino-Santos *et al.*, 2014a; Orico *et al.*, 2019) and *Strongyluris* sp., with 11 records in Brazil and Argentina (Franco-Acuña *et al.*, 2009; Maldonado *et al.*, 2010; Oliveira *et al.*, 2010; Lima & Guilherme, 2018; Oliveira & Santos, 2018; Ramos-de-Souza *et al.*, 2018; Oda *et al.*, 2020). In addition, some larvae were also reported in the faeces of *A. fulica*, not actually configuring mollusc infection. Some examples are: *Rhabditis* sp. found in faeces and mucus of *A. fulica* in five studies in Italy and Brazil (Oliveira *et al.*, 2015; d'Ovidio *et al.*, 2019; Silva *et al.*, 2020); *Trichuris* sp., eggs of *Ascaris* sp. ($n = 2$) and larvae of *Strongyloides stercoralis* Bavay, 1876 ($n = 02$) found in faeces of *A. fulica* in Venezuela (Amaya *et al.*, 2014; Meffowoet *et al.*, 2020); larvae of *Strongyloides* sp. recorded in faeces of *A. fulica* in Ecuador (Cuasapaz-Sarabia , 2016); and larvae of *Oslerus osleri* (Cobbold, 1879) in the Philippines (Constantino-Santos *et al.*, 2014b). In most cases ($n = 42$), the nematodes were present in larval stage L_3.

Methods used to collect and identify the nematodes

Artificial digestion was the method most used in 39 studies, making this method significantly ($P < 0.031$) more frequent than any other (table 1). This technique involves the digestion of the *A. fulica* tissue in a solution of hydrochloric acid (HCl), with the resulting liquid being sedimented in a Baermann funnel for the isolation of the nematode larvae (Lim & Heyneman, 1965; Maldonado *et al.*, 2010; Thiengo *et al.*, 2010; Zanol *et al.*, 2010; Rollins *et al.*, 2021; Souza *et al.*, 2021). Other methods were also used to extract the nematodes, including artificial digestion with pepsin ($n = 19$ studies), which was most frequent ($n = 14$) in Asia (Noda *et al.*, 1987; Tujan *et al.*, 2016; Lange *et al.*, 2018; Penagos-Tabares *et al.*, 2019; Jakkul *et al.*, 2021). These two techniques, in a solution of HCl or pepsin were also more frequently used in South America, being significantly more used ($P < 0.001$) when compared to other methods. However, it was observed that articles generally do not report the activity of HCl and pepsin, which prevents any reliable standardization and evaluation of the effectiveness of the digestive solution. The parasitological examination of the mucous and faeces was also used in three studies (Amaya *et al.*, 2014; Morocoima *et al.*, 2014; Silva *et al.*, 2020). The application of saline to the mantle (Deng *et al.*, 2012; Vázquez & Sánchez, 2015) was most used in North America ($n = 4$) and once in Malaysia (table 1).

In a majority of the studies (50 papers), the nematodes were identified based on the analysis of their external morphology (table 1), with 13 of these studies employing experimental infection (Lim & Heyneman, 1965; Thiengo *et al.*, 2010; Oliveira *et al.*, 2015; Tomaz *et al.*, 2018) and three, morphometry (Maldonado *et al.*, 2010; Smith *et al.*, 2015; Guerino *et al.*, 2017). Molecular methods (polymerase chain reaction (PCR) and the sequencing of molecular markers) were also used ($n = 29$ papers), in particular in Brazil (Caldeira *et al.*, 2007; Thiengo *et al.*, 2010; Carvalho *et al.*, 2012; Guerino *et al.*, 2017; Orico *et al.*, 2019; Barbosa *et al.*, 2020).

Habitats, methods and the period during which the A. fulica specimens were collected

The infected giant African land snails were collected principally in anthropogenic environments (both urban and rural), with specific characteristics, such as the front and back gardens of houses (peri-domestic environment), public parks, vacant lots and abandoned sites containing piles of trash and building rubble (Smith *et al.*, 2015; Vázquez & Sánchez, 2015; Epelboin *et al.*, 2016; Dard *et al.*, 2017; Meijides-Mejías & Robledo, 2019; Pérez *et al.*, 2019). Only a few studies ($n = 7$) refer to the capture of *A. fulica* specimens in the rural zone (Lim & Heyneman, 1965; Noda *et al.*, 1987; Lv *et al.*, 2009; Hu *et al.*, 2011; Andrade-Porto *et al.*, 2012; Tujan *et al.*, 2016; Oda *et al.*, 2020), where the snails were collected from plantations of rice (*Oryza* sp.), rubber trees (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.) (Lim & Heyneman, 1965), sugarcane (*Saccharum* sp.) (Noda *et al.*, 1987), cassava (*Manihot esculenta* Crantz) and papaya (*Carica papaya* L.) (Andrade-Porto *et al.*, 2012) (supplementary file table S2).

In most studies ($n = 58$), *A. fulica* was captured manually, with no detailed description being provided on the search time or the area surveyed. In a few cases ($n = 6$), the snails were captured manually in fixed plots (Lv *et al.*, 2009; Moreira *et al.*, 2013; Oliveira *et al.*, 2015; Vázquez & Sánchez, 2015; Córdoba-R *et al.*, 2017; Silva *et al.*, 2020) or capture rates were presented per unit of sampling effort ($n = 3$) (Cuasapaz-Sarabia, 2016; Solórzano-Alava *et al.*, 2019; Silva *et al.*, 2020) (online supplementary file table S2).

Significantly ($P = 0.007$) more studies were based on the collection of specimens during the daylight period ($n = 14$ papers), in particular in South America (Moreira *et al.*, 2013; Peng *et al.*, 2017; Bechara *et al.*, 2018; Ramos-de-Souza *et al.*, 2018; Silva *et al.*, 2020; Souza *et al.*, 2021), with only five surveys being conducted at night (Lim & Heyneman, 1965; Morocoima *et al.*, 2014; Cuasapaz-Sarabia, 2016; Peng *et al.*, 2017; Bechara *et al.*, 2018), and thirty-two studies did not specify the collection period (online supplementary file table S2). Five studies referred to the collection of specimens during the rainy season (Caldeira *et al.*, 2007; Vitta *et al.*, 2011; Andrade-Porto *et al.*, 2012; Cuasapaz-Sarabia, 2016).

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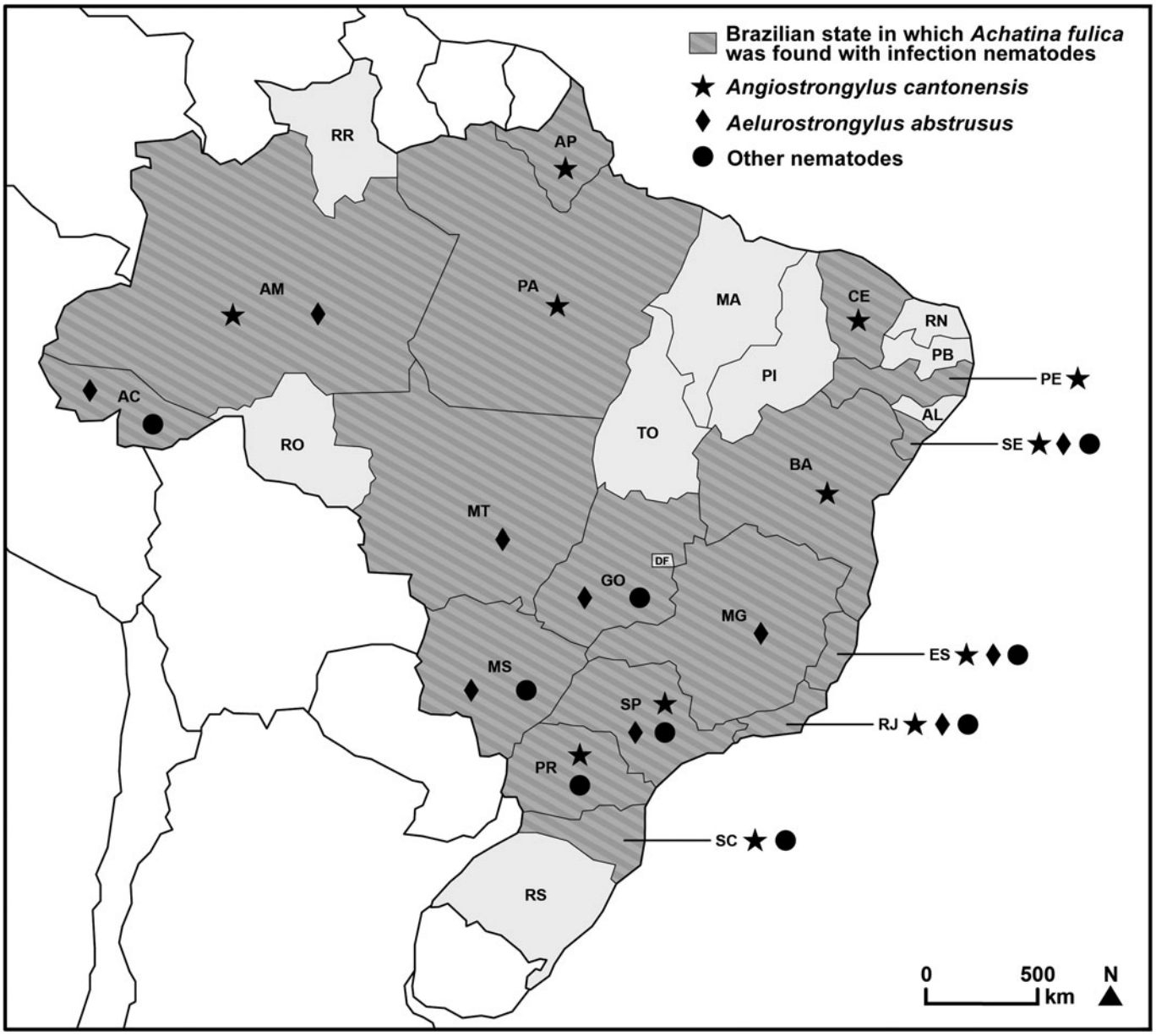

Fig. 4. Distribution of the nematodes associated with *Achatina fulica* in Brazil.

Discussion

The present study identified reports of the infection of *A. fulica* by nematodes between 1965 and 2021, which reflect, in part, the history of the progressive invasion and dispersion of the species in many parts of the world. The earliest studies that reported the association of *A. fulica* with nematodes were conducted in Asia and Oceania (Malaysia, Papua New Guinea and Japan) between 1965 and 1987, based on the experimental infection of the snail with *A. cantonensis*. In the Americas, where *A. fulica* was introduced in the late 1980s, the first study to confirm natural infection with a nematode was published only in 2007 in Brazil, and also involved *A. cantonensis*. This was also the first report of the occurrence of this nematode in Brazil, where it was also found in a number of terrestrial molluscs. This also coincides with the territorial expansion of *A. fulica* in Brazil (Thiengo *et al.,* 2007; Maldonado *et al.,* 2010), and the concomitant growth in the number of studies about this mollusc, especially in Brazil (25 papers), where publications peaked after 2019 ($n = 12$). Despite 11 nematode species have been recorded parasitizing *A. fulica*, a majority of the reports refer to *A. cantonensis*, throughout the world, that is, in Asia, the Americas, Africa and Oceania, and, principally, in Brazil (Caldeira *et al.,* 2007; Thiengo *et al.*, 2010) (fig. 4).

Achatina fulica is believed to have been introduced into Brazil on at least three independent occasions. Two, possibly intentional introductions are known to have occurred, one in Curitiba, in Paraná state, in 1989, and the other in 1998 in Santos, in São Paulo state, for the commercial production of the animals (Teles & Fontes, 2002; Fischer & Costa, 2010). There is also a less well documented case from 1975, when a resident of the city of Juiz de Fora, in Minas Gerais state, reported having bought *A. fulica* breeding stock from an open-air market in an undetermined foreign country (Zanol *et al.,* 2010). The large distribution of *A. cantonensis* in Brazil is probably a result of repeated

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introductions through rat vectors during the colonial period, given the intense trade between this country and both Africa and Asia during this period (Maldonado *et al.,* 2010). It seems likely that the tropical and subtropical climate of Brazil, together with the lack of any adequate intervention for the control of the spread of *A. fulica* have favoured its role as an intermediate host of nematodes (Maldonado *et al.,* 2010; Thiengo & Fernandez, 2016). This process would have been accelerated by socio-economic problems, in particular a lack of public sanitation environmental education, which results in the inadequate disposal of domestic residues and effluents.

Achatina fulica has now been recorded in all 26 of the Brazilian states and the Federal District, with the highest infestation rates being recorded in the states of Goiás, São Paulo, Paraná, Rio de Janeiro, Mato Grosso, Espírito Santo and Minas Gerais (Thiengo *et al.*, 2007). The species was only recently reported in Rio Grande do Sul (RS), where a juvenile specimen was found in the garden of a residential condominium in the city of Porto Alegre (Arruda & Santos, 2022). The dissemination de *A. cantonensis* in Brazil is a major public health problem due to the widespread occurrence of infected rats and snails (Thiengo *et al.,* 2013). In addition, this parasite is an aetiological agent of eosinophilic meningitis (EM) in humans (Zanol *et al.,* 2010), with the parasite being transmitted primarily through the ingestion of molluscs infected with L_3 larvae (Vitta *et al.,* 2016), which migrate to the brain, where they transform into stage L_4 and then die. The reaction to this process provokes serious neurological damage, which may result in coma and even death, in some cases (Graeff-Teixeira *et al.,* 2009; Thiengo *et al.,* 2013). Worldwide, more than 2800 human cases of EM caused by *A. cantonensis* have been reported from more than 30 countries (Wang *et al.*, 2008) since the first report, from Taiwan, in 1945 (Beaver & Rosen, 1964). Eosinophilic meningitis is considered to be an emerging disease in Brazil, with approximately 40 confirmed and 84 suspected cases between 2007 and 2020 (Morassutti *et al.,* 2014; Cunha, 2017; Barbosa *et al.,* 2020). In Brazil cases of the disease have been reported in the states of Pernambuco, Espírito Santo, Paraná, Rio de Janeiro, Rio Grande do Sul, São Paulo, Sergipe and Amapá (Caldeira *et al.,* 2007; Thiengo *et al.,* 2008, 2010; Lima *et al.,* 2009; Espírito-Santo *et al.,* 2013; Morassutti *et al.,* 2014; Cunha, 2017; Ramos-de-Souza *et al.,* 2018; Barbosa *et al.,* 2020).

Angiostrongylus cantonensis has also been found in association with *A. fulica* on islands, such as the Hawaiian archipelago (Kim *et al.,* 2014) and French Polynesia, in the Pacific Ocean (Fontanilla & Wade, 2012), Mayotte Island, in the Indian Ocean (Epelboin *et al.,* 2016) and the Ilha Grande in Brazil (Oliveira & Santos, 2018), in the Atlantic Ocean. This nematode has also been recorded in Ecuador (Solórzano-Alava *et al.,* 2019), Cuba (Meijides-Mejías & Robledo, 2019), Colombia (Giraldo *et al.,* 2019), the contiguous United States, in Florida (Kwon *et al.,* 2013; Rollins *et al.,* 2021), Thailand (Dumidae *et al.,* 2019; Jakkul *et al.,* 2021), China (Lv *et al.,* 2009), Japan (Matayoshi *et al.,* 1987; Noda *et al.,* 1987), Malaysia (Lim & Heyneman, 1965) and the Philippines (Tujan *et al.,* 2016). In Europe, the single record from Italy was obtained from a study of snails being raised as pets, which evaluated the potential for the transmission of parasites from the animals to humans, and found snails infected with *Rhabditis* sp. (d'Ovidio *et al.,* 2019).

Other studies of the nematodes associated with *A. fulica* have been conducted on oceanic islands that are French overseas territories, including Guadalupe (Dard *et al.,* 2017), Mayotte (Epelboin *et al.,* 2016), French Polynesia (Fontanilla & Wade, 2012) and Réunion (Picot *et al.*, 1976). *Achatina fulica* is believed to have played an important role in the introduction of parasites into all these different regions, as well as other areas of the Indian Ocean and many Pacific islands (Alicata, 1966; Robinson, 2000). The dispersal of *A. fulica* and synanthropic rodents around the world has also contributed to the propagation of *A. cantonensis* (Civeyrel & Simberloff, 1996; Espírito-Santo *et al.,* 2013). The explosive and uncontrolled expansion of *A. fulica* populations in Brazil and other parts of the world may have led to a major increase in the number of diseases that are potentially spread by this species (Thiengo *et al.*, 2010).

The present study was unable to verify any reports of the natural infection of *A. fulica* by *A. costaricensis*. This may be related to the reduced susceptibility of *A. fulica* to this nematode, given that experimental trials have found low infection rates and a reduced parasite load (Neuhauss *et al.,* 2007).

One other nematode that was reported frequently in association with the giant African land snail was *A. abstrusus*, with records from Brazil (Oliveira *et al.,* 2010), Colombia (Penagos-tabares *et al.,* 2019) and Argentina (Valente *et al.,* 2017). This parasite causes severe pneumonia in both wild and domestic felines (Thiengo *et al.,* 2008). Lima *et al.* (2020), recently reviewed the epidemiological evidence on *A. abstrusus* in Brazil, and identified nine studies that described an association between this nematode and molluscs which were, in all cases, *A. fulica*. According to Rodrigues *et al.* (2022), there is an intense association between this nematode and *A. fulica*, with 99% of the snails of this species collected from some municipalities of the state of Rio de Janeiro, Brazil, being infected with *A. abstrusus*.

Two papers recorded *A. malaysiensis*, which is also considered to be a source of EM, in association with *A. fulica* in Thailand (Dumidae *et al.,* 2019) and Malaysia (Lim *et al.,* 1976). This nematode was initially identified as a Malaysian strain of *A. cantonensis*, given the morphological similarities of their larval stages (Jakkul *et al.,* 2021), although diagnostic differences in their morphology are present in the adult phase (Bhaibulaya, 1979).

Two reports, both from Colombia, recorded an association between *A. fulica* and the nematode *A. vasorum* (Lange *et al.,* 2018; Penagos-Tabares *et al.*, 2019). Other papers, based on experimental infection, reported that *A. vasorum* is a parasite of the pulmonary arteries of wild and domestic canids (Pereira *et al.,* 2020). The reduced number of records of *A. vasorum* infecting *A. fulica* naturally may be related to the snail's phenoloxidase enzyme, which may inhibit infection by this nematode, although further research is needed to better define this defence mechanism (Coaglio *et al.,* 2016). *Angiostrongylus vasorum* has been found in other gastropods examined in urban environments (Hicklenton & Betson, 2019), based on PCR sequencing, which detected the presence of the DNA of this nematode in 4.1% (4/97) of the snails and 9.1% (4/44) of the slugs examined.

Geohelminths, such as *Caenorhabditis* sp. and *Rhabditis* sp., have also been reported to be associated naturally with *A. fulica* (Guerrero *et al.,* 2018; d'Ovidio *et al.,* 2019). These helminths may use *A. fulica* as a phoretic host, by attaching themselves to the snail's mucus to reach new environments or becoming attached accidentally when the snail secretes mucus as it moves. Given this, it is important to note the potential presence of ancylostomids or species of the genus *Strongyloides* when examining the mucus, faeces or even the digestive tract of molluscs. Protozoa, platyhelminths and bacteria mays also be detected during the examination of the mucus and faeces of these animals

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(Amaya *et al.,* 2014; Morocoima *et al.*, 2014), although the presence of nematodes is not considered to be a natural component of the ecological relationships of these organisms (Ferreira *et al.,* 2012). In most cases, the nematodes are free-living, and normally feed on decomposing organic matter, where they may be ingested accidentally by foraging molluscs. *Achatina fulica* is a generalist that may exploit any available food source, including fruit and other decomposing matter, in which nematodes are common (Silva *et al.,* 2020). The coprological technique may be appropriate for the extraction of some nematode species, but when the animal ingests the nematodes, irrespective of the developmental phase of the parasite, the extraction of these organisms from the faeces does not necessarily imply that the snail plays some role in the life cycle of the nematode, reinforcing the need to distinguish parasitism from phoresia (Ferreira *et al.,* 2012). Larvae in the L_3 stage are mentioned most often because of their more developed morphological structures, which are easier to visualize, allowing comparison with published references, but also because experimental infection and morphometry are possible at the L_3 stage.

The artificial digestion methods used to extract the nematodes in the papers identified in the present study can be divided into those that used pepsin and those that did not use this enzyme. When HCl is used on its own, the samples must be immersed in the solution for longer to ensure the rupture of the snail tissue to release the nematode larvae (Coaglio *et al.,* 2016). The use of pepsin guarantees the more rapid extraction of the larvae, as long as the process occurs at an ideal temperature for enzymatic activity, that is, 37°C (Thiengo *et al.,* 2008; Lv *et al.,* 2009). Under these conditions, while digestion with pepsin may release the larvae more rapidly, digestion in a 0.7% solution of HCl is effective at room temperature, even though this process takes much longer (Graeff-Teixeira & Morera, 1995). This procedure is also more cost-effective than methods that use pepsin. One other approach to the extraction of the nematodes was the use of saline solution, although this method is much less effective because it does not dissolve the mollusc tissue (Graeff-Teixeira & Morera, 1995). The adequate extraction of the larvae is essential for a reliable parasitological analysis of *A. fulica*, in order to determine the prevalence of the nematodes and the parasite load, as well as the identification of the nematode species. Despite the properties of the solutions used for artificial digestion, such as their acidity, the nematodes, in particular the gastrointestinal forms, are relatively more resistant than the mollusc tissue, and are often extracted alive with no structural damage (Carvalho *et al.,* 2012).

Most of the studies recorded here identified the nematodes based on their morphology (Lim & Heyneman, 1965; Guerino *et al.,* 2017), even though many of the larval characteristics used to diagnose the species are shared by most of the taxa of a given genus (Spratt, 2015), which hampers reliable identification. Some studies also used morphometric parameters and movement patterns to identify the nematodes (Meijides-Mejías & Robledo, 2019), as a complement to the morphological identification. In this case, an adequate diagnosis requires the analysis of both the males and the females (Oliveira *et al.,* 2010; Silva *et al.,* 2020), which may require the experimental infection (Bechara *et al.,* 2018) of the definitive host to obtain the largest possible number of diagnostic characteristics. However, it takes approximately 30 days to obtain the adult forms and, ideally, they should be identified by a taxonomic specialist (Carvalho *et al.,* 2012; Bechara *et al.,* 2018). The examination of cysts was also used in some cases (Oliveira & Santos, 2018), although this may not be adequate for the identification of species, given that some species of different genera may present similar characteristics in the intermediate host. According to many authors such as Valente *et al.* (2020), the morphological characteristics of the larvae of the genus *Angiostrongylus* are insufficient for the reliable identification of species. Molecular techniques were used in some studies to identify the nematode species found in *A. fulica*, using different markers, such as cytochrome c oxidase subunit I (Barbosa *et al.,* 2020), internal transcribed spacer 1, (Rollins *et al.,* 2021), internal transcribed spacer 2 (Thiengo *et al.,* 2010) and cytochrome B (Peng *et al.,* 2017). This approach is undoubtedly the most reliable for the identification of the larvae.

In most studies, *A. fulica* was found in anthropogenic environments, in particular in household gardens, vacant lots and sites with accumulated trash or debris, which favour the proliferation of the snail (Cuasapaz-Sarabia, 2016; Silva *et al.,* 2020). Overall, few of the papers identified in the present study referred to the standardization of collection procedures, such as the fixed plot method (Moreira *et al.,* 2013; Oliveira *et al.*, 2015; Córdoba-R *et al.*, 2017; Silva *et al.,* 2020) or capture per unit of effort (Cuasapaz-Sarabia, 2016; Solórzano-Alava *et al.,* 2019; Silva *et al.,* 2020). The standardization of sampling procedures is important to ensure the most effective possible evaluation of the impact of *A. fulica* in a given environment through the systematic comparison of different study sites using indices of abundance and diversity, and the evaluation of environmental parameters. In most cases, in addition, the paper did not specify the period or season of the specimen collection, although a small number did define daylight or nighttime collecting, or searches during the rainy season (Moreira *et al.,* 2013; Peng *et al.,* 2017).

In addition to being an intermediate host of nematodes that infect domestic animals, *A. fulica* may also be an intermediate host of the parasites of wild animals, which implies a threat to the local wildlife (Thiengo *et al.,* 2008). In particular, Ramos-de-Souza *et al.* (2021), reported the natural infection of *A. fulica* by *C. tentaculata*, a parasite of the opossums of the genus *Didelphis* Linnaeus, 1758.These authors also concluded that larvae of *Strongylus* sp., which were previously reported infecting terrestrial mollusks in Brazil are actually larvae of *C. tentaculata*.

Overall, then, the findings of the present study highlight the potentially significant role of the giant African land snail, *A. fulica*, in the transmission of parasites to both humans and animals, as well as the importance of understanding the relationship between this snail and the environment, its parasites, and their definitive hosts. The present study showed that these parameters are closely related, and should be considered carefully for the best possible diagnosis and control of areas that may be epidemiologically vulnerable, which is consistent with the 'One Health' concept, in which human and animal health are seen as interdependent and linked by the local environment (Lerner & Berg, 2015). The study also provides important insights for the diagnosis of the nematodes found in association with *A. fulica*, which is fundamentally important for the development of adequate measures for the control and prevention of zoonoses.

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Conflicts of interest. The authors declare that they have no conflict of interestrelated to the publication of this manuscript.

Ethical standards. This study fully satisfies the ethical criteria and norms.

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Authors' contributions. Guilherme Mota da Silva: substantial contribution to the concept and design of the study, data collection, data analysis and interpretation, manuscript preparation, contribution to critical revision and adding intellectual content. Silvana Carvalho Thiengo, Verônica L. S Jeraldo and Suzete R. Gomes: substantial contribution to the concept and design of the study, critical revision and adding intellectual content. Matheus I. F. Rego, Alexandre. B. P. Silva and Paulo S. Rodrigues: contribution to data collection, data analysis and interpretation, manuscript preparation, contribution to data analysis and interpretation. All the authors reviewed and approved the definitive version of the manuscript.

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