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Paratenic hosts of *Angiostrongylus cantonensis* and their relation to human neuroangiostrongyliasis globally

Helena C. Turck [a,b], Mark T. Fox [a], Robert H. Cowie [c,*]

[a] Royal Veterinary College, 4 Royal College St, London NW1 0TU, UK
[b] London School of Hygiene and Tropical Medicine, Keppel Street, London WC1E 7HT, UK
[c] Pacific Biosciences Research Center, University of Hawaii, 3050 Maile Way, Gilmore 408, Honolulu, HI 96822, USA

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A B S T R A C T

The nematode parasite *Angiostrongylus cantonensis* (rat lungworm) has a complex life cycle involving rats (definitive hosts) and gastropods (intermediate hosts), as well as various paratenic hosts. Humans become infected and develop rat lungworm disease (neuroangiostrongyliasis) when they consume intermediate or paratenic hosts containing the infective parasite larvae. This study synthesizes knowledge of paratenic hosts of *A. cantonensis* and investigates their role in causing human neuroangiostrongyliasis worldwide. A literature review was conducted by searching PubMed, JSTOR and Scopus, pooling additional information from sources accumulated over many years by RHC, and snowball searching. The review identified 138 relevant articles published between 1962 and 2022. Freshwater prawns/shrimp, crayfish, crabs, flatworms, fish, sea snakes, frogs, toads, newts, lizards, centipedes, cattle, pigs and snails were reported to act as paratenic hosts in various regions including South and Southeast Asia, Pacific islands, the USA and the Caribbean, as well as experimentally. Human cases of neuroangiostrongyliasis have been reported from the 1960s onwards, linked, sometimes speculatively, to consumption of freshwater prawns/shrimp, crabs, flatworms, fish, frogs, toads, lizards and centipedes. The potential of paratenic hosts to cause neuroangiostrongyliasis depends on whether they are eaten, how frequently they are consumed, the preparation method, including whether eaten raw or undercooked, and whether they are consumed intentionally or accidentally. It also depends on infection prevalence in the host populations and probably on how high the parasite load is in the consumed hosts. To prevent human infections, it is crucial to interrupt the transmission of rat lungworm to humans, from both intermediate hosts and frequently consumed paratenic hosts, by adhering to safe food preparation protocols. Educating the general public and the medical community about this largely neglected tropical/subtropical disease is key.

1. Introduction

The commonest cause of eosinophilic meningitis (EM) in humans globally is infection by the nematode parasite *Angiostrongylus cantonensis*, known commonly as the rat lungworm [1–3]. The resulting disease is known as neuroangiostrongyliasis because of the neurotropic behaviour of the infectious larvae. The most recently published global count of cases of human neuroangiostrongyliasis, as of 2012, is just over 3000 [4], although a more comprehensive screening of the literature, including grey literature indicates that approximately 7000 have in fact been recorded (S Lv, personal communication, 6 July 2021); the true number is surely higher because of underreporting and misdiagnosis [5,6].

To understand human infection with rat lungworm, one must understand the natural life cycle of the parasite, which involves slugs and snails (hereafter “snails”) as intermediate hosts and rats as definitive hosts [3,7–11]. First-stage larvae (L1) are passed by rats in their faeces, which are ingested by snails, in which the L1 develop into infective third-stage larvae (L3). Rats then consume infected snails, ingesting the L3, which migrate to the rat’s brain, develop into young adults and eventually return to the venous system and pulmonary arteries where they mature, mate and lay eggs that travel to the rat’s lungs and hatch. The emerging L1 then pass through the capillary/alveolar walls, ascend the respiratory tree, are coughed up, swallowed and passed in the faeces [12,13]. Other animals also play a significant role in transmission by serving as paratenic hosts, which become infected by consuming

* Corresponding author.
E-mail address: cowie@hawaii.edu (R.H. Cowie).

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intermediate hosts containing L3; however, they do not support larval development but act as substitute hosts, until eaten by a definitive host in which development of the dormant L3 continues to completion and reproduction [6,14].

Humans are accidental hosts of *A. cantonensis*. Infection occurs when people ingest infective L3 in raw or undercooked snails or paratenic hosts [15–18]. They are either ingested accidentally by consuming food such as salads and fresh produce containing infected hosts [19–21], or are deliberately eaten raw or undercooked as a delicacy [22], for medicinal, including aphrodisiac, purposes [23,24] or on a dare [25–28].

Disease is evoked as the L3 travel to the brain, but then primarily by the physical damage caused once they reach the brain, and an immune reaction that may be heightened when the parasites die. Patients often present initially with vomiting, nausea, weakness, fever, and tingling skin sensation, then neck stiffness, unremitting headache, bladder and bowel malfunction and other diverse signs and symptoms. Although the illness is often self-limiting, in severe cases it can lead to permanent neurological damage, coma and death [1,3,4,6,7,12,18,29,30].

During the 1940s, cases of EM occurred on several Pacific islands [19]; there may have been cases going back to 1915 [31]. Yet the disease was not linked to *A. cantonensis* until the early 1960s when cases caused by it were described in Hawaii [32,33]. However, the first known human case of neuroangiostrongyliasis was in 1944 in Taiwan [34], only realised retrospectively [35]. Various species known today to act as paratenic hosts were subsequently linked to cases of human disease that had occurred prior to full understanding of the aetiology [e.g. 19,31].

Since these early known and possible cases of EM, cases attributed to *A. cantonensis* have been reported increasingly in parts of Asia and certain Pacific islands [5] with the parasite found in numerous host species [3,11]. Cases of neuroangiostrongyliasis have occurred further afield, in Australia, the USA and the Caribbean (initially Cuba) since the 1970s and perhaps earlier [3,7,11,36–38]. More recently, *A. cantonensis* has been recorded in other areas, including additional Caribbean islands [20,39,40], Mallorca [41] and the Canary Islands [42]. It is now widely distributed across many tropical/subtropical regions globally [3,13,43], as well as a few more temperate localities [44–46].

Since many paratenic hosts, such as prawns, would have been eaten raw long before the first reported occurrence of EM in locations such as Tahiti, the parasite must have been imported more recently, probably by invasive rodents and snail species transported inadvertently via human activities [47–49]. The host range of rat lungworm is growing as these and other highly invasive alien species that carry it are introduced into new locations, where they not only threaten biodiversity [50] but also transmit rat lungworm to local animals [38,51,52]. Moreover, frequent travel to endemic regions including Latin America, the Pacific islands and parts of Asia have resulted in neuroangiostrongyliasis cases in non-endemic countries [3,53].

Although there are reports of paratenic hosts of *A. cantonensis* causing neuroangiostrongyliasis, the diversity of paratenic hosts globally has never been fully reviewed, unlike that of definitive and intermediate hosts [9,10]. Cases are reported haphazardly and there is no rigorous global understanding of the role paratenic hosts play in transmitting neuroangiostrongyliasis. Thus, there is a need to synthesize the scattered reports of species acting as paratenic hosts and whether and where they are involved in causing illness. With changing food habits and increased globalisation, it seems timely to address this need so as to improve understanding of epidemiological patterns and the dietary habits that may lead to clinical presentation of neuroangiostrongyliasis. This review was therefore undertaken to synthesize information on paratenic hosts of *A. cantonensis* from the literature, and assess their roles in causing human neuroangiostrongyliasis worldwide.

2. Methods

2.1. Search strategy

A literature review, with a partial systematic approach was undertaken. The databases searched (and view dates) were PubMed (13.V.2021), JSTOR (18.V.2021) and Scopus (19.V.2021), using keywords that were combined employing MeSH terms and Boolean operators. The key concepts "*Angiostrongylus cantonensis*", "paratenic hosts" and "human neuroangiostrongyliasis" constituted the foundation of the search. As the primary objective was to identify paratenic hosts reported in the literature, the concept of "human neuroangiostrongyliasis" was not incorporated into the search queries, since the disease is known by many names, which would have limited the results to only displaying paratenic hosts mentioned in combination with a specific name. Table 1 shows the key concepts and search queries used. The search term "parastrongylus" was also included, as *A. cantonensis* has in the past sometimes been placed in the genus *Parastrongylus*, although this is not widely accepted [54].

As *A. cantonensis* and the disease caused by it have been reported in various countries, no language filter was applied when searching the databases. Further, since the objective was to identify all paratenic hosts reported in the literature up to April 2022, no start date was set. Also, reports mentioning paratenic hosts of *A. cantonensis* accumulated on an ad hoc basis by RHC during research between 1991 and 2022 were included. A manual snowball search was undertaken to find additional literature.

2.2. Data collection and eligibility criteria

Diverse literature types, not only traditional research articles, were considered admissible and often provided key information. For example, case reports were frequently the primary publications connecting ingestion of a paratenic host to cases of neuroangiostrongyliasis; grey literature such as agency technical reports were sometimes the first reports of both *A. cantonensis* in paratenic hosts and cases of neuroangiostrongyliasis; and review papers and book chapters provided access to additional primary literature via snowball searching. No literature type was explicitly excluded.

All records were assessed for relevance and eligibility between April 2021 and April 2022. After excluding duplicates (articles identified in more than one search), records identified from the database searches as well as those accumulated by RHC were screened by title and abstract for references to the key concept "*Angiostrongylus cantonensis*" in combination with "paratenic hosts" and/or "human neuroangiostrongyliasis". The same steps were applied when examining full-text articles, and for snowball searching. Since relevant publications were of diverse kinds, no standard quality appraisal was conducted, although a single item containing multiple errors was excluded.

Table 1
Database search strategy consisting of key concepts and search queries.

Key concepts	• *Angiostrongylus cantonensis* • Paratenic hosts • Human neuroangiostrongyliasis
PubMed search query	((*angiostrongylus cantonensis*) OR (a. cantonensis) OR (parastrongylus cantonensis) OR (rat lungworm) OR (rat-lungworm) OR (rat lung-worm)) AND ((paratenic host*) OR (carrier host*) OR (transport host*) OR (transfer host*))
JSTOR search query	("*angiostrongylus cantonensis*" OR "a. cantonensis" OR "parastrongylus cantonensis" OR "rat lungworm" OR "rat-lungworm" OR "rat lung-worm") AND ("paratenic host*" OR "carrier host*" OR "transport host*" OR "transfer host*")
Scopus search query	ALL (("*angiostrongylus cantonensis*" OR "a. cantonensis" OR "parastrongylus cantonensis" OR "rat lungworm" OR "rat-lungworm" OR "rat lung-worm")) AND ALL (("paratenic host*" OR "carrier host*" OR "transport host*" OR "transfer host*"))

The data extracted from the literature consisted of reported paratenic hosts of *A. cantonensis*, in particular (a) whether they were experimentally or naturally confirmed or merely assumed to act as paratenic hosts; (b) their relationship to human neuroangiostrongyliasis, including diagnostic techniques confirming infection; (c) the known or assumed food source associated with cases; and (d) where infected paratenic hosts and/or neuroangiostrongyliasis cases associated with paratenic hosts were reported. As some hosts were reported using scientific names that have since changed (e.g. different genus placement, species synonymised with another species), the current names, in authoritative taxonomic databases (Table 2), are used throughout, while noting the previous name, at least when first mentioned.

If insufficient information was available or the species name of a paratenic host was not given (e.g. if reference was only to "frogs"), snowball searching sometimes permitted pinpointing the missing data from the sources cited. Reports were considered "primary" if they were the first reports of a particular paratenic host, in a particular location or associated with a case of neuroangiostrongyliasis; "secondary" reports were those that simply cited primary reports or other secondary reports that cited the primary reports, and so on. Sometimes the chain of secondary reports leading to identification of specific hosts was long and complex, and lists of secondary reports tracking back to a primary report may not be comprehensive. In a few instances citation was unclear. For example if three consecutive sentences were followed by a single citation, it may not have been clear whether that citation referred only to the last sentence or to all three. In such cases we used our judgement regarding the authors' intentions.

3. Results

In total, 293 articles were relevant to our objectives: 61 from PubMed, 20 from JSTOR, 141 from Scopus, 89 from RHC and 27 through snowball searching. The flow diagram (Fig. 1) outlines the process for assessing eligibility and excluding articles, with the numbers excluded at each step. Overall, 138 publications were included in the search results.

3.1. Paratenic hosts of Angiostrongylus cantonensis

Twenty-three paratenic host species were reported under natural circumstances; nine additional species were recognised only experimentally; and one species was assumed to be a host in nature with no confirmation. Table 3 lists all primary and secondary reports. Table 4 lists reports only mentioning broad groups (e.g. "frogs") and for which tracking citations, if possible, did not permit identifying the specific taxon in question; almost all are secondary reports. In the following, confirmed paratenic hosts of *A. cantonensis* are reviewed, including those reported in nature and/or experimentally, as well as potential or assumed paratenic hosts. Some experimentally infected hosts seemed unlikely to be important in *A. cantonensis* transmission; these are discussed briefly below. Fig. 2 shows the global distribution of confirmed and assumed paratenic hosts.

3.1.1. Freshwater prawns/shrimp and crayfish

Some of the most frequently mentioned paratenic hosts of rat lungworm are freshwater prawns/shrimp (the terms were used interchangeably in the literature reviewed), notably of the genus *Macrobrachium* (Table 3). Rat lungworm larvae were first recovered from prawns, identified only as *Macrobrachium* sp., in Tahiti in 1962 [15]. Their role as paratenic hosts was ascertained via experimental infection of rats with *A. cantonensis* larvae from the prawns; young adult worms were subsequently found in the brain and pulmonary arteries of the rats. Subsequently in the 1960s, *Macrobrachium lar* was shown experimentally to act as a paratenic host [57], and in prawns examined across several Pacific islands, including Tahiti and other French Polynesian islands [15,19,56], Pohnpei, Saipan and Guam [67] and Rarotonga [66], infection prevalence ranged from 3% to 10%. However, in American Samoa larvae were found in 18/42 (43%) *Macrobrachium lar* individuals [58]. Prawns are known scavengers of snails and slugs and presumably acquired their infection via these intermediate rat lungworm hosts [15,19]. Nonetheless, in Hawaii, all 44 *Macrobrachium lar* collected in the wild, as well as all 390 *M. rosenbergii* from prawn farms, tested negative for *A. cantonensis* [60], yet given the American Samoa finding, *M. lar* could possibly act as a paratenic host in Hawaii; *M. rosenbergii* has not been reported specifically as a paratenic host and is not listed in Table 3.

Crayfish of the genus *Cambarus* in the USA have been successfully infected experimentally with *A. cantonensis* [76]. In *Cambarus clarkii*, L3 larvae were found up to seven days after experimental infection [44,104] and in *Cambarus* sp. specifically in the muscle tissue of the tails after five days [76,106]. However, all 35 *C. clarkii* screened in Hawaii tested negative [60].

3.1.2. Crabs

Infection was detected in the wild in two land crab species from Saipan (Mariana Islands, Micronesia), *Tuerkayana hirtipes* (as "*Cardisoma*" *hirtipes*) and *Birgus latro* (coconut crab), with an infection prevalence of 4.5% and 12%, respectively [19,67]. Included in the *T. hirtipes* data were 40 crabs previously referred tentatively to the genus *Ocypode* [69]. Wallace & Rosen [57] infected *Ocypode ceratophthalma* collected in Hawaii with L3 and found that the numbers of L3 remaining in them declined greatly within hours of infection, suggesting that they would be poor paratenic hosts if at all (see also Ash [59]); thus, this species is not included in Table 3. Coconut crabs (*Birgus latro*) and hermit crabs (*Coenobita perlatus*) consume the flesh of the giant African snail (*Lissachatina fulica*), a major intermediate host of rat lungworm in Micronesia; however, although coconut crabs have been found naturally infected and so could act as paratenic hosts, the hermit crabs investigated were not infected [67]. It remains possible that hermit crabs could act as paratenic hosts but there is no evidence of this and they are not included in Table 3. Also in Micronesia, the mangrove crab (*Scylla serrata*) has been assumed to serve as a paratenic host, in Pohnpei, but this remains unconfirmed [67]. Puthiyakunnon and Chen [4] listed land crabs (as "*Pleocyemata* spp.") as paratenic hosts but without additional information or citation (Pleocyemata is not a genus but a suborder of crustaceans that includes crabs and several other groups.)

3.1.3. Land planarians (flatworms)

Several authors have reported land planarians as paratenic hosts of *A. cantonensis*. *Endeavouria septemlineata* (as "*Geoplana*" *septemlineata*) feed on snails and slugs [75]. Natural infection of this species with L3 was first reported in Hawaii and, after feeding infected individuals to laboratory rats, L1 were found in the rats' faeces some weeks later [111]. L3 were also found in this species in Tahiti [111], with their role as paratenic hosts confirmed when developing worms were detected in the brains of experimentally infected rats [15]. Infected flatworms have been reported in the Cook Islands [66] and in New Caledonia and Vanuatu [145]. All these planarians, except those from Hawaii, were unidentified, with between 12 and 100% (including those from Hawaii) positive for *A. cantonensis* [19]. All were referred subsequently to *E. septemlineata* [47]. However, infected flatworms in New Caledonia

Table 2
Taxonomic databases used to confirm species names of paratenic hosts.

Amphibians	• Amphibian Species of the World 6.1 (https://amphibiansoftheworld.amnh.org/)
Reptiles	• The Reptile Database (https://reptile-database.reptarium.cz)
Molluscs	• MolluscaBase (https://www.molluscabase.org)
Fish	• World Register of Marine Species (https://www.marinespecies.org)
Crustaceans	• Animal Diversity Web (https://animaldiversity.org)
Land planarians	• Global Biodiversity Information Facility (https://www.gbif.org)

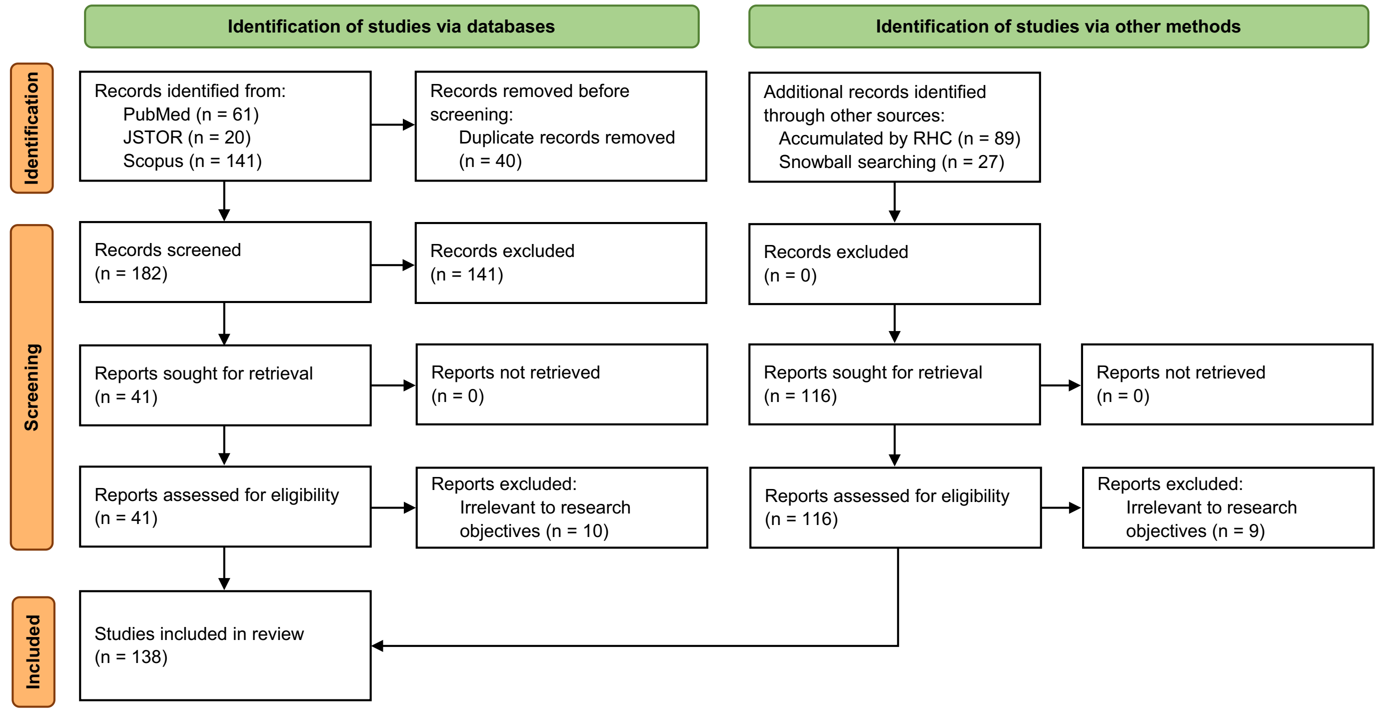

Fig. 1. Flow diagram illustrating the literature search protocol and the numbers of reports identified and excluded at each step (modified from reference [55]).

were identified later as *Kontikia forsterorum* (as "*Geoplana*" *forsterorum*) [110]. Whether both species occur on Pacific islands, particularly New Caledonia, or whether one or other represents a misidentification and in fact only one species was involved in these reports, is unclear.

Flatworms in the genus *Platydemus* are also predators of snails and slugs [157] and can also carry infective larvae of *A. cantonensis* [12,51]. Specifically, a 14.1% prevalence in *Platydemus manokwari* was reported in Okinawa, Japan [14]. In Hawaii, 8/12 flatworms tested positive, although only one was definitively identified as *P. manokwari* [112].

3.1.4. Fish and sea snakes

Fish have been infected experimentally with *A. cantonensis* but remain unconfirmed as paratenic hosts in nature. Only two fish species have been investigated [114]. *Oreochromis mossambicus* (as "*Tilapia mossambica*"), commonly known as "tilapia", a freshwater fish, can harbour infective larvae for up to four weeks; and *Selar crumenophthalmus* (as "*Trachurops*" *crumenophthalmus*), known in Tahiti as "ature", a marine fish, also proved to be a possible paratenic host.

In experimentally infected sea snakes (*Laticauda colubrina*), prevalent in New Caledonia, the larvae survived and remained infective for rats at least a month after infection [59].

3.1.5. Amphibians

Six frog species, formerly in the genus *Rana*, in addition to the common tree frog (among other common names), formerly known as *Rhacophorus leucomystax*, have been reported as hosts from Japan (Ryukyu Islands) and Taiwan [44,77,87,104,115,120,126] (Table 3). Their taxonomy has been revised significantly since the 1970s and all except *Rana chensinensis* are now in different genera [145], as followed here. The relevant publications are confusingly inter-related, as follows. Otsuru [44,104] and Otsuru et al. [126] reiterated the data presented by Otsuru et al. [120] (a meeting abstract). The data of Otsuru et al. [120] appear to represent a dataset incorporating (1) preliminary data of Asato et al. [124] (also a meeting abstract), which Otsuru [104] cited, and (2) data of "Asato & Kishimoto, 1976", which is neither of the two 1976 publications (again meeting abstracts) by these authors cited by Otsuru [104]. Asato et al. [77] reiterated the same data but noted that only four *R. leucomystax* (now in *Polypedates*) had been examined, not 15 as listed, probably in error, by Otsuru [104]. Otsuru [104] cited Asato et al. [124] as showing that L3 were alive >70 days after experimental infection, but Asato et al. [124] only stated that experiments were underway. It thus seems that among these publications those of Asato et al. [124], Otsuru et al. [120] and Otsuru [104] combined constitute the primary records of these species as paratenic hosts of *A. cantonensis*, with the proviso that the unknown "Asato & Kishimoto, 1976" may pre-empt Otsuru [104]. The other publications [44,77,126] are entirely derivative in this regard.

Other frog species have also been reported as paratenic hosts of *A. cantonensis*. Guenther's frog, *Sylvirana guentheri* (then placed in *Hylarana*), has been reported in China [89], the golden bell frog, *Ranoidea aurea* (then in *Hyla*), in New Caledonia [59], the American green tree frog, *Dryophytes cinereus* (as "*Hylidae* [not a genus-group name] *cinereus*"), in Louisiana, USA [26], and two species of *Eleutherodactylus* in Hawaii [38]. While 21.4% of *Pelophylax plancyi* (then in *Rana*) and 21.4% of "*Hylarana*" *latouchii* (then in *Rana* and spelled incorrectly as "*latouchi*"; current generic placement provisional [145]) tested positive for rat lungworm in Taiwan ([120], etc.), a higher prevalence was observed in *R. aurea* in New Caledonia (53%) [59], and in Hawaii, infective larvae were detected in 21/24 (88%) coqui frogs, *Eleutherodactylus coqui*, and all four screened greenhouse frogs, *E. planirostris* [38]. In preliminary investigation of Cuban tree frogs (*Osteopilus septentrionalis*) in Florida, encysted L3 were confirmed by DNA analysis to be *A. cantonensis*, suggesting that they could act as paratenic hosts [122]. In *Lithobates catesbeiana* and *E. coqui*, remnants of slugs and snails known to serve as intermediate hosts for *A. cantonensis* were found in the stomachs [38,77]. Tadpoles of *Rana chensinensis* may be able to act as intermediate hosts, as L2 were found 12 and 16 days after experimental infection with L1; however, there is no evidence that this species can act as a paratenic host [115].

Three toad species are known to carry L3 in nature. Infected *Bufo gargarizans* were reported in Miyako (Ryukyu Islands, Japan) [123], and another study found the parasite in 42% and 10% of *B. gargarizans* in Miyako and Kitadaito (also in the Ryukyu Islands), respectively, with two publications presenting the same data [77,120]. In Taiwan, 8.3% of *Duttaphrynus melanostictus* individuals were infected [44,104,120]; and

Table 3
Paratenic hosts of *A. cantonensis*, with recorded location, whether confirmed (naturally or experimentally) or assumed as paratenic host, and primary and secondary references.

Host	Location	Confirmed or assumed	References
Freshwater prawns/ shrimp			
Macrobrachium australe	Tahiti	Naturally	**Primary:** [56] **Secondary:** [23,53]
Macrobrachium lar	French Polynesia, American Samoa	Naturally and experimentally	**Primary:** [56–58] **Secondary:** [20,23,53,59–65]
Macrobrachium spp.	French Polynesia, Pohnpei, Saipan, Guam, Rarotonga, Dominican Republic	Naturally and experimentally	**Primary:** [15,66,67] **Secondary:** [2–8,11,12,17,19,23,41,45,47,51,53,62,65,67–103]
Crayfish			
Cambarus clarkii	Japan	Experimentally	**Primary:** [104] **Secondary:** [44]
Cambarus sp.	USA	Experimentally	**Primary:** [76] **Secondary:** [105,106]
Crabs			
Birgus latro (coconut crab)	Saipan	Experimentally	**Primary:** [67] **Secondary:** [3,4,7,17,47,51,75,77,102,103,107,108]
Tuerkayana hirtipes (as "*Cardisoma*" *hirtipes* or *Ocypode* spp.) (land crab)	Saipan	Naturally	**Primary:** [67,69] **Secondary:** [3,6,7,17,19,23,51,53,59,61–63,71,74–77,92,103,108,109]
Scylla serrata (mangrove crab)	Pohnpei	Assumed	**Primary:** [67] **Secondary:** [3,7,17,19,47,51,71,77,103]
Land planarians (flatworms)			
Kontikia forsterorum (as "*Geoplana*" *forsterorum*)	New Caledonia	Naturally	**Primary:** [110] **Secondary:** [6,17,20,23,61,62,103,107,108]
Endeavouria septemlineata (as "*Geoplana*" *septemlineata*)	Tahiti, Hawaii, Pacific	Naturally and experimentally	**Primary:** [60,111] **Secondary:** [5,6,15,17,19,23,41,59,62–65,70,72,74,75–77,103,109]
Platydemus manokwari (New Guinea flatworm)	Hawaii, Japan, Thailand	Naturally	**Primary:** [14,112] **Secondary:** [3,4,6,17,51,52,101,103,113]
Platydemus sp.(p).		Naturally	**Primary:** [12] **Secondary:** [8,11,38,43,51,91,102]
Fish			
Oreochromis mossambicus (as "*Tilapia mossambica*")	Saipan, Tahiti	Experimentally	**Primary:** [114] **Secondary:** [7,8,17,18,20,23,53,59,61,62,64,65,74,75,77,79,87,102,110,115–117]
Selar crumenophthalmus (as "*Trachurops*" *crumenophthalmus*)	Tahiti	Experimentally	**Primary:** [114] **Secondary:** [3,7,8,17,18,20,23,53,59,61,62,64,65,71,74,75,77,79,87,102,110,115–117]
Sea snakes			
Laticauda colubrina	New Caledonia	Experimentally	**Primary:** [59] **Secondary:** [74,75,77,79,115]
Frogs			
Dryophytes cinereus (as "*Hylidae cinerea*") (American green tree frog)	Louisiana, USA	Naturally	**Primary:** [26] **Secondary:** [8,12,86,91,101,108]
Eleutherodactylus coqui (Puerto Rican coqui frog)	Hawaii	Naturally	**Primary:** [38]
Eleutherodactylus planirostris (Cuban greenhouse frog)	Hawaii	Naturally	**Primary:** [38]
Ranoidea aurea (as "*Hyla aurea*") (golden bell frog)		Naturally	**Primary:** [59] **Secondary:** [2–6,11,12,16,17,20,23,41,44,51,53,61,65,74–77,87,90–92,94,95,100–102,104,108,109,115,117–119]
Sylvirana guentheri (as *Hylarana guentheri*) (Guenther's frog)	China	Naturally	**Primary:** [89] **Secondary:** [4,8]
Polypedates leucomystax (as "*Rhacophorus*" *leucomystax*) (common tree frog)	Japan	Naturally	**Primary:** "Asato & Kishimoto, 1976" as cited by [104] **Secondary:** [2–4,14,16,17,23,44,53,77,100,115,118,126]
Lithobates catesbeianus (as "*Rana catesbeiana*") (American bullfrog)	Japan, Taiwan	Naturally and experimentally	**Primary:** "Asato & Kishimoto, 1976" as cited by [104] **Secondary:** [2–4,6,14,16–18,23,41,44,51,53,71,87,90,91,94,100,102,115,117–119,126]
"*Hylarana latouchii*" (generic placement uncertain; Frost, 2021) (as "*Rana latouchi*")	Taiwan	Naturally	**Primary:** [120] **Secondary:** [3,6,17,18,41,44,51,53,71,87,90,94,100,102,104,117,119,126]

(*continued on next page*)

Table 3 (*continued*)

Host	Location	Confirmed or assumed	References
Fejervarya limnocharis (as "*Rana limnocharis*") (Asian grass frog)	Japan, China	Naturally	**Primary:** "Asato & Kishimoto, 1976" as cited by [104]; [89] **Secondary:** [2–4,8,14,16,17,23,41,44,51,53,77,91,100,102,115,118,126]
Pelophylax plancyi (as "*Rana plancyi*")	Japan, Taiwan, China	Naturally	**Primary:** [23,87,89,120] **Secondary:** [4,6,8,17,18,41,44,53,64,90,94,100,102,104,117,119,121,126]
Hoplobatrachus tigerinus (as "*Rana tigrina*")	Japan, Taiwan	Naturally	**Primary:** [120] **Secondary:** [6,17,18,41,44,53,87,90,94,100,102,104,117,119,121,126]
Osteopilus septentrionalis (Cuban tree frog)	Florida, USA	Naturally	**Primary:** [122]
Toads			
Bufo gargarizans (as "*Bufo asiaticus*" by all except Kinjo et al., 1975)	Japan	Naturally	**Primary:** "Asato & Kishimoto, 1976" as cited by [104]; [123,124] **Secondary:** [2–4,6,14,16,17,23,44,53,71,77,87,91,101,102,104,108,115,117–119,125,126]
Duttaphrynus melanostictus (as "*Bufo melanostictus*")	Japan	Naturally	**Primary:** [89,120,126] **Secondary:** [4,6,8,44,71,87,104,117,119]
Rhinella marina (cane toad)	Hawaii	Naturally	**Primary:** [38]
Lizards			
Varanus bengalensis / nebulosus (Bengal monitor / yellow tree monitor – see text for taxonomy)	Sri Lanka, India, Thailand, Laos	Naturally and experimentally	**Primary:** [16,24,85,127–132] **Secondary:** [2–4,6,8,11,12,17,18,38,43,53,63–65,86,90,91,93–95,100–103,108,112,118,119,133,134]
Centipedes			
Scolopendra subspinipes (Chinese red-headed centipede)	China, Hawaii	Naturally	**Primary:** [18,38] **Secondary:** [6]
Cattle and pigs			
Bos taurus (domestic cattle)	Hawaii	Experimentally	**Primary:** [72,135,136] **Secondary:** [6,17,19,47,59,74,75,77,81,115]
Sus scrofa (domestic pig)	Hawaii	Experimentally	**Primary:** [72,135–137] **Secondary:** [6,17,19,47,59,67,74,75,77,115]
Snails			
Euglandina rosea	New Orleans, USA	Experimentally	**Primary:** [138]
Lymnaea palustris		Experimentally	**Primary:** [76]

Table 4
Paratenic hosts of *A. cantonensis* not identified to species or genus and that could not be tracked back to specific species or genera, with recorded location, if given, and references (all secondary except references [66, 144] for land planarians); probably not comprehensive.

Host	Location	References
Shrimp/prawns	Not stated	[43,107,108]
Crabs	Not stated	[2,4,5,6,8,11,12,43,53,82,83,86,89,91,92,96,97,101,107,108]
Land planarians	New Caledonia, Vanuatu, Rarotonga, Taiwan	[5,7,42,47,53,66,75,79,80,83,84,96,112,121,139,144]
Fish	Not stated	[43,63,79,85,96,97,99,112,115,130,140,141]
Frogs	Not stated	[2,5,7,18,42,43,79,82–86,92,96–99,125]
Toads	Not stated	[2,59,82,83,86,102]
Amphibians	Not stated	[63,96,99,112,142,143]
Monitor lizards	Not stated	[42,85,97]
Reptiles	Not stated	[99,143]

L3 were also found in *Rhinella marina* (cane toad) in Hawaii [38].

Asato et al. [124] infected the Japanese fire-belly newt, *Cynops pyrrhogaster*, experimentally but the larvae only remained alive for a maximum of four days *post* infection. Otsuru [104], attributing the finding to himself, considered the newt of little importance as a paratenic host since *A. cantonensis* had not been found in newts in nature. Table 3 does not include newts.

3.1.6. Lizards

Monitor lizards, of a single species complex, are paratenic hosts of *A. cantonensis*. Taxonomy in this complex is confused [146] and two names appear in the literature reviewed here: *Varanus bengalensis* (Bengal monitor) and *V. nebulosus* (yellow tree monitor). We refer all instances to *V. bengalensis*, without an opinion regarding the true taxonomy. These lizards are widespread across Southeast Asia, and reported as paratenic hosts in Sri Lanka [130], India [131,133,134], Thailand [16,127,128,131] and Laos [24]. Of 22 individuals from five provinces in Thailand, 21 were infected [16].

No other lizard species are known as paratenic hosts. However, a falcon in a California zoo was diagnosed with neuroangiostrongyliasis, with the possible source of infection surmised to have been geckos imported from Southeast Asia and fed to the bird; but this was not confirmed [147]. Geckos are not included among paratenic hosts here.

3.1.7. Centipedes

The Chinese red-headed centipede, *Scolopendra subspinipes*, has recently been discovered and confirmed experimentally as a paratenic host of rat lungworm, in China [18] and Hawaii [6].

3.1.8. Pigs, cattle and chickens

Several experimental studies of infection in domestic pigs, cattle and chickens were undertaken in Hawaii in the 1960s. In pigs, L3 were recovered from the stomachs, livers, lungs and spleens, but not the musculature, two weeks after infection [135], yet in subsequent

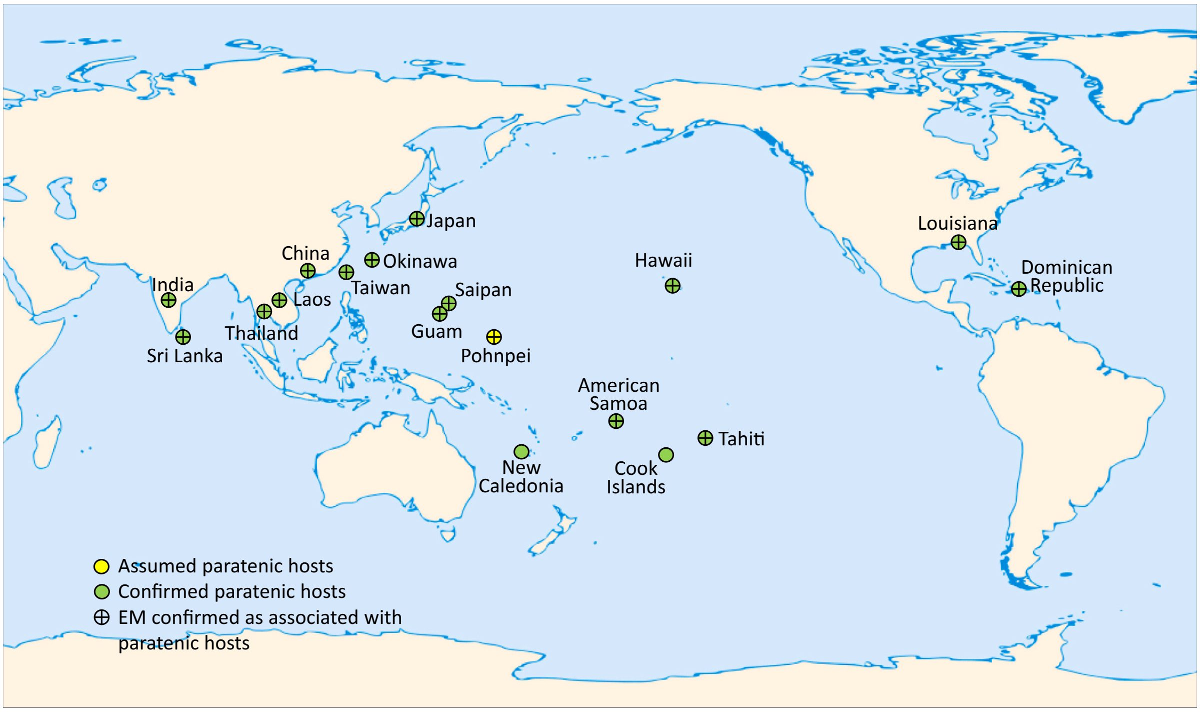

Fig. 2. Global distribution of assumed and confirmed paratenic hosts of *A. cantonensis* and of confirmed associations of paratenic hosts and EM. Okinawa is an island of Japan; Saipan is part of the United States Commonwealth of the Northern Mariana Islands; Guam is an unincorporated territory of the United States; Pohnpei (formerly "Ponape") is one of the Federated States of Micronesia.

experiments the larvae survived only a few days [72], or died just hours after infection [137]. In cattle, larvae were detected in the viscera up to two weeks after infection [135]. Experimentally administered larvae recovered from a pig and a calf and used to infect rats were later found in the rats' brains, confirming the capability of both as paratenic hosts [72]. Nevertheless, pigs and cattle have not been reported to serve as paratenic hosts naturally. Although chickens could be infected experimentally, no larvae were found after 15 days in one study [68], and only a very small number were found up to 2–3 days after infection and none subsequently in another [137], suggesting that they are unlikely to act as paratenic hosts; chickens are not listed in Table 3.

3.1.9. Snails

Although snails are intermediate hosts of *A. cantonensis*, some species that prey on other snails might also act as paratenic hosts [75]. The land snail *Euglandina rosea* (in fact a species complex [148]) feeds on other gastropods and, experimentally, *A. cantonensis* larvae from an ingested infected gastropod migrated into the tails of this species [138]. In the freshwater snail *Lymnaea palustris* fed previously infected crushed conspecifics, L3 were detected in 64% of the surviving snails and were infective for rats [76].

3.2. Paratenic hosts and neuroangiostrongyliasis

Eleven of the above species, plus one or two unspecified fish species, were mentioned in association with human neuroangiostrongyliasis cases, in some cases based only on suggestive symptoms combined with a history of having ingested a species known to be a paratenic host (Table 5). Their roles in causing human neuroangiostrongyliasis are now reviewed. Other hosts mentioned above have not been reported as causing neuroangiostrongyliasis. Fig. 2 shows locations of reported neuroangiostrongyliasis cases associated with paratenic hosts.

3.2.1. Freshwater prawns/shrimp

Macrobrachium freshwater prawns have been associated frequently with human disease, mostly on Pacific islands. In an early 1960s case series in Tahiti, 28/30 EM cases were traced to consumption of either raw prawns or "taioro", a traditional Polynesian meal of grated coconut and raw prawn juice, prepared by grinding the stomach and other portions of the prawns in fresh water [15,19]. A comprehensive epidemiological study of 981 EM cases in Tahiti during 1957–1964 strongly implicated prawns or their juice ("taioro" and "mitihue") in many of them [56]. More recently, between 2000 and 2012, among 42 EM cases in Tahiti, 13 were caused by *A. cantonensis* infection, based on serological testing, and the remaining 29 were considered probable cases [97]. Among these patients, 16 had consumed taioro and six had eaten raw prawns. On Guam, three EM cases were attributed to eating "kelo-guen", also prepared with raw prawns and commonly eaten there [67]. Of nine EM patients in American Samoa, five were associated with eating raw prawns (*Macrobrachium lar*) six to fourteen days prior to onset of symptoms and four had shared a common meal [58]. However, although commonly consumed in Hawaii, no *Macrobrachium rosenbergii* screened were infected with *A. cantonensis* [60]. Reported in 2007, a traveller returning to Italy from the Dominican Republic, an endemic region for rat lungworm, was diagnosed with EM, possibly caused by *A. cantonensis* as he had eaten freshwater shrimp (whether raw or not was not stated) before onset of illness [88].

3.2.2. Crabs

Other crustaceans harbouring rat lungworm larvae and frequently eaten in many Pacific islands, including Pohnpei and Saipan, are crabs. During an EM outbreak in Pohnpei in 1947/1948 [31], before the connection between *A. cantonensis* and EM had been realised, the *Lissachatina fulica* (giant African snail) population was far more abundant than in 1964, correlating with the far fewer cases in 1963 [19]. Since mangrove crabs (*Scylla serrata*) may prey on *L. fulica* and are commonly eaten by Micronesians, a higher level of infection in the crabs in 1947/1948 may have been related to heavier predation on the abundant snails and led to the outbreak [19]. Correspondingly, two girls reported developing the disease "15 years previously" (i.e. around 1948) shortly

Table 5
Cases of human neuroangiostrongyliasis caused by ingestion of paratenic hosts, with location, date of case(s), clinical presentation, mode of diagnosis, food source (confirmed or presumed) and primary references (excluding cases of returning travellers, which were reviewed by Ansdell & Wattanagoon [53]).

Host	Location	Date	Clinical presentation	Mode of diagnosis	Food source	Reference
Freshwater prawns/shrimp						
Macrobrachium lar	American Samoa	1979	5 cases of eosinophilic meningitis	Blood smear, spinal tap, IHA, ELISA	Raw prawns	[58]
Macrobrachium spp.	Tahiti	1961	28 cases of parasitic meningoencephalitis 18 cases of parasitic meningoencephalitis	Unknown: "confirmed cases" Spinal tap, antigen test, clinical diagnosis	Raw prawns, taioro	[15]
	French Polynesia	2000–2012	42 cases of eosinophilic meningitis	Plasma and CSF serological tests and eosinophil counts, clinical diagnosis	Raw prawns, taioro	[97]
	Guam	1964–1965	3 cases of eosinophilic meningoencephalitis	Unknown	Raw prawns	[67]
Crabs						
Tuerkayana hirtipes (as *Ocypode* sp.).	Saipan	1958	7 cases of eosinophilic meningoencephalitis	Unknown	Raw land crabs	[19]
Scylla serrata (mangrove crab)	Pohnpei	c. 1948	2 cases of eosinophilic meningoencephalitis	Unknown	Raw mangrove crabs	[67]
Land planarians						
Endeavouria septemlineata (as "*Geoplana*" *septemlineata*)	Tahiti	1961–1962	Eosinophilic meningoencephalitis	Assumed	Planarians contained in lettuce	[15]
Platydemus manokwari (New Guinea flatworm)	Okinawa (Japan)	2000	Angiostrongyliasis	Assumed	Lettuce and cabbage contaminated with flatworms	[14]
Fish						
Not further specified	Tahiti	1996	Eosinophilic meningitis	Assumed	Raw fish	[141]
	Hawaii	1992	Eosinophilic meningitis	Assumed	Raw fish	[140]
Frogs						
Dryophytes cinereus (as "*Hylidae cinerea*")	Louisiana	2006	1 case of eosinophilic meningitis	CSF examination, clinical diagnosis	Raw frog legs	[26]
Pelophylax plancyi (as "*Rana plancyi*")	Taiwan	2006	1 case of eosinophilic meningitis	CSF examination, clinical diagnosis	Raw frog with soy sauce	[87]
	Taiwan	2009	1 case of encephalitis	ELISA, imaging, clinical diagnosis	Raw frogs with wine as health supplement	[23]
Toads						
Bufo gargarizans (as "*Bufo asiaticus*")	Okinawa (Japan)	1975	5 cases of eosinophilic meningitis	Unknown	Raw toad liver for medicinal purposes	[120]
Bufo gargarizans	Miyako (Japan)	1975	2 cases of eosinophilic meningitis and meningoencephalitis	Unknown	Fresh toad liver for medicinal purposes	[123]
Monitor lizards						
Varanus bengalensis (sometimes as "*Varanus nebulosus*" or "Yellow tree monitor") (Bengal monitor)	India	2012	1 case of eosinophilic meningoencephalitis	Blood and CSF cell counts and antigen testing, clinical presentation	Raw monitor lizard tongue, liver, gall bladder and testicles	[134]
	Sri Lanka	2005	1 case of eosinophilic meningitis	Blood and CSF cell counts, clinical presentation	Monitor lizard meat	[130]
	Thailand	1990	10 cases of eosinophilic meningitis	Unknown	Raw or partially cooked yellow tree monitors	[127]
	India	2000–2004	5 cases of eosinophilic meningitis	Blood and CSF cell counts, clinical presentation	Monitor lizard meat	[131]
	India	2012 or before	1 case of eosinophilic meningitis	Blood and CSF cell counts, clinical presentation	Raw monitor lizard meat for aphrodisiac properties	[132]
	Laos	2020	7 cases of angiostrongyliasis	PCR, case history, clinical presentation	Shared meal of wild raw monitor lizard	[24]
	Thailand	1998 or before	3 cases of eosinophilic meningoencephalitis	"clinical and laboratory confirmed"	Raw monitor lizard meat and liver	[129]
"Monitor lizard"	India	2004–2006	8 cases of eosinophilic meningoencephalitis	CSF cell counts	Raw monitor lizard flesh and liver	[85]
Centipedes						
Scolopendra subspinipes (Chinese red-headed centipede)	China	2012	2 cases of eosinophilic meningitis/ meningoencephalitis	CSF analysis, serum and CSF ELISA. clinical presentation	Raw centipedes	[18]

after eating raw mangrove crabs [67]. Nine additional EM cases were reported in Pohnpei; seven of the patients had consumed raw mangrove crabs [19]. On Saipan, two sisters presented with EM [149], reportedly having consumed raw land crabs (*Tuerkeyana hirtipes*) before the onset of illness [69].

3.2.3. Land planarians (flatworms)

Endeavouria septemlineata was associated with rat lungworm disease as early as 1962, in Tahiti, where EM cases were linked to *A. cantonensis* and planarians were confirmed as paratenic hosts [15]. The flatworms were on lettuce sold in the island's markets and human infection was suggested as resulting from accidentally ingesting them raw (as well as snails and slugs), hidden among the leaves.

In New Caledonia, land planarians (again identified as *E. septemlineata*) among salad greens were implicated in transmission, especially among inhabitants of French origin who customarily consumed raw green salad, unlike native people who rarely did; land planarians were also found in fruit such as ripe strawberries and fallen ripe mangos and figs [19,47]. Infected *Kontikia forsterorum* associated primarily with green salad were suggested as perhaps the most important source of human infection in New Caledonia [110]. Whether these reports from New Caledonia refer to just a single species is unclear, as noted above.

Lettuce and cabbage contaminated with infective *Platydemus manokwari* were assumed to be the main source of infection in an outbreak of cases in Okinawa in 2000 [14].

3.2.4. Fish

Although two fish species have been shown experimentally to act as paratenic hosts, none has been reported as definitively associated with neuroangiostrongyliasis. Nonetheless, Alto [7] suggested that *Oreochromis mossambicus* ("tilapia") may have caused the infection in a patient on Saipan. A confirmed EM case was reported in a traveller returning from Tahiti to France who had eaten raw fish during her visit, suggesting a connection between the fish and neuroangiostrongyliasis [141]. Raw fish was also the presumed source of infection in a patient who developed EM on return to the continental U.S. after visiting Hawaii [140].

3.2.5. Frogs and toads

In some traditional Chinese and Japanese medicine, consuming raw frogs and toads is thought to provide health benefits. For instance, raw liver is prescribed for improvement of bone health, asthma, cough and fever among other benefits and has been linked to several instances of EM [44,77,87,120,123,125]. Two EM cases probably resulting from swallowing fresh liver of the toad *Bufo gargarizans* were reported in the Ryukyu Islands (Japan) [123]. In Taiwan, one month after eating the raw muscles and bones of a frog (*Pelophylax plancyi*) seasoned with soy sauce, a patient developed EM [87]. Also in Taiwan [23], a patient presented with EM approximately three weeks after ingesting raw frogs (also *P. plancyi*) with wine as a health supplement; infection with *A. cantonensis* was later confirmed. In Taiwan, *Lithobates catesbeiana* and *Hoplobatrachus tigerinus* are also customarily eaten and could be involved in transmission [44]. In 2006, a patient in Louisiana, USA, was admitted to the hospital for muscle, back and neck aches, as well as hypersensitivity to touch and was later diagnosed with EM [26]; nine days before onset of symptoms he had eaten raw legs from a green tree frog, *Dryophytes cinereus*, on a dare.

3.2.6. Lizards

Monitor lizards (*Varanus* species) have been frequently associated with neuroangiostrongyliasis. In several Asian countries, raw *Varanus* meat, specifically the tongue and liver but also gall bladder and testicles, is believed to have aphrodisiac properties [132,134]. Cases of EM have been attributed to consumption of raw *V. bengalensis* meat since the early 1990s, in Sri Lanka [130], southern India, notably the adjacent states of Kerala [85,131] and Karnataka [132,134], Thailand, in both Bangkok and Khon Khaen [118,127–129], and Laos [24]. One case linked to consumption of raw or partially cooked liver of a monitor lizard in Bangkok in 1990 proved fatal [127]. A literature search [24] for cases of neuroangiostrongyliasis associated with eating raw monitor lizard, identified 36 cases, 20 with clinical details available; 19 of the 20 were male.

3.2.7. Centipedes

Scolopendra subspinipes was linked to two EM cases in 2012 in Guangzhou, China [18]. Both patients had ingested raw centipedes before developing multiple symptoms including headache, neck stiffness and cognitive impairment over several weeks. They later tested positive for *A. cantonensis* antibodies in serum and cerebrospinal fluid. Rat lungworm infections have also been confirmed in the same centipede species in Hawaii, although people are not known to consume them there [6,38].

4. Discussion

We provide a comprehensive synthesis of reports of paratenic hosts of rat lungworm (Table 3), including their roles in causing human neuroangiostrongyliasis worldwide (Table 5). Three genera, namely *Macrobrachium* (prawns), *Cambarus* (crayfish) and *Platydemus* (flatworm), were mentioned in some publications without specifying species or citing references pointing to certain species; whether additional species in these genera, other than those mentioned in other publications, also act as paratenic hosts is unknown.

Whether these paratenic hosts play a significant role in causing human disease depends on several factors. These include (1) accidental versus intentional consumption for dietary or supposed medicinal reasons or even as a dare or bet; (2) whether frequently consumed by many people or only small groups in certain regions; (3) likelihood that infected hosts cause disease upon consumption, perhaps related to parasite load; and (4) prevalence of infection in paratenic host populations.

Macrobrachium prawns were reported as paratenic hosts particularly frequently (Table 3). They occur across many regions in the Pacific and Caribbean and are a common food source among various ethnic groups, in parasite-endemic and non-endemic regions. They play a significant role in causing neuroangiostrongyliasis (Table 5).

Several crab species also serve, or have been assumed to serve, as paratenic hosts on various Pacific islands (Table 3). Coconut crabs have been found to be infected with rat lungworm but have not been implicated in parasite transmission to humans. Mangrove crabs have only been shown experimentally to act as paratenic hosts but a land crab species has been confirmed as a host in the wild; ingestion of both has been implicated in EM (Table 5).

Cambarus crayfish also feed on freshwater snails and have been confirmed as possible paratenic hosts experimentally (Table 3). However, infected individuals have not been found in nature and crayfish should not be definitively linked to neuroangiostrongyliasis. The same applies to domestic pigs, cattle and chickens, all of which have been experimentally infected. In pigs, however, because larval survival time varied among studies from a few hours or days up to two weeks and because larvae were only found in the organs not the musculature, it seems unlikely that pigs would be a source of human infection. Nonetheless, in parts of Micronesia raw pig liver was eaten [135] and in Pohnpei specifically [67], raw or poorly cooked pork was eaten, with pigs allowed to run wild, easily able to ingest infected snails, and thereby possibly being a source of human infection. The results for cattle were similar to those for pigs [19,70,135] but they have not been suggested as involved in human transmission, while in chickens no larvae or extremely few larvae were found after infection and they were considered unable to act as paratenic hosts [68,137].

Fish in the genera *Oreochromis* and *Selar* are both consumed in Tahiti, but were confirmed as paratenic hosts in experimental settings only (Table 3). However, consuming raw fish was tentatively implicated as the cause of eosinophilic meningitis in a traveller returning from the island to France [141], and since fish are part of many diets and are often consumed raw in traditional dishes, such as sushi in Japan, infection via ingestion of fish might occur in certain locales. Nonetheless, fish have been implicated far less frequently than crustaceans in causing neuroangiostrongyliasis.

In contrast to crustaceans and fish, frogs and toads are consumed in fewer countries yet have been associated frequently with causing neuroangiostrongyliasis (Table 5). When cooked, they are a normal part of some diets but are often ingested raw for supposed medical benefit in various Asian countries, notably Taiwan, China and Japan [87,125]. In Taiwan, the invasive snails *Lissachatina fulica* and *Pomacea canaliculata*, important intermediate hosts of the parasite, are abundant [87] and presumably play a part in rat lungworm prevalence in frogs, reported there to be as high as 18% [121]. Human cases have been caused by eating raw frog legs on a dare [26]. No cases of *A. cantonensis* infection have been linked to frogs in Hawaii. However, prevalence was extremely high in coqui frogs (*Eleutherodactylus coqui*), a highly invasive species introduced from Puerto Rico, which has spread across the Pacific as far as Guam [38]. Remnants of the invasive *Parmarion martensi*, an important intermediate host in Hawaii [49,51], were found in coqui frog stomachs [38].

Similar to frogs and toads, in Sri Lanka, India, Thailand and Laos, monitor lizards are eaten not as part of regular diets but because they are believed to have health benefits, particularly as aphrodisiacs [2,24,118,130–132]. Ironically, eating raw or partially cooked lizard meat can be fatal [118].

Two cases of neuroangiostrongyliasis in China have recently been attributed to ingesting raw centipedes, and seven of 20 centipedes purchased in a market in the same city tested positive for the parasite [18]. But how widespread this practice is and whether the centipedes are eaten purely for nutrition or for other purposes are unknown. Nonetheless, their presence in markets suggests an established practice.

Certain highly invasive land planarians are snail predators. In contrast to the hosts discussed above, they are presumed to be consumed inadvertently by eating uncooked, especially leafy, vegetables in which they are hidden [14,17,112]. Also, during food preparation they may be inadvertently chopped, releasing L3 onto the produce [17,112]. Although planarians are not eaten intentionally, their potential to cause disease has been implicated in several neuroangiostrongyliasis cases in Tahiti, New Caledonia and Okinawa (Table 5).

In particular, in addition to causing human disease, the New Guinea flatworm, *Platydemus manokwari*, is a threat to terrestrial biodiversity [150] and was recognised as among 100 of the world's worst invasive alien species [151]. It therefore should not be underestimated in rat lungworm transmission and global spread [152]. This species was detected in Thailand in 2010 and is now widespread, with infected individuals found in three locations [52]. However, the parasites were identified based on DNA sequencing as *Angiostrongylus malaysiensis* [52], which is widespread in Malaysia [153,154] and Thailand [155]. Neuroangiostrongyliasis cases have been attributed to *A. malaysiensis*, to the extent that it has been considered the only aetiological agent in Malaysia [154]. However, there is no convincing evidence that *A. malaysiensis* is zoonotic [11]. The difficulty of distinguishing *A. malaysiensis* from *A. cantonensis* may mean that both can cause neuroangiostrongyliasis, perhaps with different clinical presentations, or the attribution of neuroangiostrongyliasis cases to *A. malaysiensis* is incorrect, based on misidentification of the parasites. Nonetheless, co-infection with the two species in patients in Thailand after eating raw snails, a few of which were also co-infected, has been reported [156]. Further research on the potential for *A. malaysiensis* to cause neuroangiostrongyliasis is warranted.

Sea snakes and newts have been infected with *A. cantonensis* experimentally only and have not been observed to function as paratenic hosts in nature (Table 3). Moreover, they are not known to be consumed by humans and would presumably be low risk regarding human disease.

Snails are regularly consumed in various regions across the world but are generally cooked. Many species are intermediate hosts. However, some predatory snails, especially *Euglandina rosea* [138] but also *Lymnaea palustris* [76], have been confirmed experimentally to act as paratenic hosts of rat lungworm. *Euglandina rosea* may be an exclusive snail predator [157] and might not feed on rat faeces; it may yet act as an intermediate host if its snail prey contain L1 or L2 (which could develop to L3) and as a paratenic host when its prey already contain L3. Whether the role of *L. palustris* and other species that prey on or scavenge other snails is predominantly as intermediate or paratenic hosts in nature is unclear, as their diets are largely unknown. Nevertheless, the presence of infection in such species might act as a proxy for infection in other more important paratenic hosts such as prawns and crabs, and therefore should be monitored regularly.

Whilst cases of neuroangiostrongyliasis have been documented in travellers returning to Europe, especially, and to various other regions [53], most cases have been reported in Southeast Asia and the Pacific, areas now endemic for the parasite (Table 5). Similarly, most species identified as paratenic hosts of *A. cantonensis* were reported in Southeast Asia and the Pacific (Table 3). Other animal species could also be serving as paratenic hosts in these areas, though not yet recorded as such. For example, one (or two) monitor lizard species are known paratenic hosts, so other monitor lizard species might also act as paratenic hosts. Furthermore, some animals such as *Macrobrachium* prawns, which are paratenic hosts in several locations, notably French Polynesia, are widely distributed across all continents except Europe and Antarctica [158] and therefore may have the potential to serve as paratenic hosts in regions where this has not been reported. Nevertheless, even if these hosts were to harbour infective-stage rat lungworm larvae in other areas, the risk of transmission would depend on local eating habits. For example, monitor lizards as paratenic hosts in Sri Lanka, India and Thailand cause neuroangiostrongyliasis in humans regularly, whereas if other lizards became infected, for instance in North America, Europe and Australia, they would constitute a lesser risk because they are not commonly consumed, especially raw.

Although some of the identified paratenic hosts have only been infected with rat lungworm experimentally and/or are not known to be consumed by humans, they may still play an as yet unknown role in the parasite's life cycle in nature. Hence, it is important to monitor their global distributions, just as it is to monitor those of known or potential intermediate and definitive hosts, in order to develop a strategy to prevent further expansion of the parasite's range and of human infections.

Not only are clinical cases of neuroangiostrongyliasis steadily increasing [86], but recent studies have recorded *A. cantonensis* in areas where it was previously unknown [3,41,42,45,46,152]. This spread is facilitated by increasing globalisation leading to the further introduction of infected rats and other invasive host species, e.g. *Platydemus manokwari* [50,52] and *Lissachatina fulica* [96,159–161]. In addition to increased human mobility and global commerce leading to dispersal of the parasite and its hosts, climate change has a significant impact on the ecology of the zoonosis and is linked directly to host abundance and to changes in parasite distribution, transmission pathways and parasite load in intermediate and paratenic hosts [119,161–163]. Travellers going to *A. cantonensis*-endemic countries should be aware that local food items, such as raw prawns or crabs, may be infected with the parasite. The same applies to physicians working in non-endemic areas who should be aware of the risks their patients expose themselves to when travelling to parasite-endemic areas.

4.1. Study limitations

Various literature types were included in the review but no dedicated grey literature search was conducted (see Methods), although some important grey publications were unearthed. The comprehensive literature search strategy limited the risk of missing key publications, and papers in languages other than English were included when found. However, while the primary literature reporting new paratenic hosts and new human cases of neuroangiostrongyliasis was relatively manageable and most of these publications were probably captured, the secondary literature, citing these reports or just mentioning paratenic hosts in passing, has grown dramatically and some secondary publications were probably missed. Furthermore, human neuroangiostrongyliasis cases have certainly been underreported or misdiagnosed because of the non-specific nature of symptoms and the often self-limiting nature of the disease. Some paratenic hosts that were linked with neuroangiostrongyliasis have also never been definitively confirmed as such.

5. Conclusions

Overall, increased international trade, travel to disease-endemic regions, changes in dietary habits and global warming, are collectively expected to facilitate further range expansion of *A. cantonensis* [2,98]. More knowledge of species serving as paratenic hosts and methods of human infection are needed. The prevalence of neuroangiostrongyliasis in wildlife and companion animals is as much an indication of the distribution of the disease and possibly the parasite as is prevalence in humans [11,164,165] and should be tracked by public health authorities as sentinels to better estimate human infection risk. Although cases of neuroangiostrongyliasis have been reported from the Caribbean [20,39,40,88], South America [166,167], Australia [3] and the USA [37], there is a strong need for further investigation to confirm the presence of rat lungworm in local animal species, in particular to identify indigenous species acting as hosts in regions newly invaded by *A. cantonensis* (e.g. Walden et al. [46]).

Furthermore, a definitive diagnosis of neuroangiostrongyliasis can be made only when worms are detected in the CSF or the eye of a patient, both of which are uncommon [30]. Usually, the condition is diagnosed holistically based on presenting symptoms, exposure history including visiting a parasite-endemic region and eating potentially infected hosts, and eosinophilic pleocytosis in the CNS. In disease-endemic areas, there is a need for simpler protocols and more sensitive and specific techniques for diagnosis. Since it is difficult to eradicate rat lungworm from the environment, reduction in infection can only be achieved by hindering transmission. Following good hygiene and washing protocols for fresh produce [168] and implementation of rat and mollusc control [48] are necessary to interrupt transmission. In many regions, awareness of rat lungworm is low, not only in the general community but also among physicians and public health authorities. Educating medical professionals as well as lay people should therefore be a priority. The dangers of eating uncooked or partially cooked paratenic hosts should be a key part of such educational programmes, though changing such practices may be difficult where they are firmly established.

Author credit statement

Helena C. Turck: conceptualisation, methodology, investigation, data curation, writing - original draft. Mark T. Fox: supervision, writing - reviewing and editing, project administration, funding acquisition. Robert H. Cowie: conceptualisation, methodology, resources, supervision, writing - reviewing and editing, project administration. All authors read and approved the final version of the manuscript.

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Data statement

All data (references) and methods are provided within the body of this paper.

Declaration of Competing Interest

All authors declare no conflicts of interest.

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