

Are Geckos Paratenic Hosts for Caribbean Island Acanthocephalans? Evidence from *Gonatodes antillensis* and a Global Review of Squamate Reptiles Acting as Transport Hosts

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ABSTRACT

It is well known that reptiles can act as paratenic hosts for parasites that use mammals as their definitive hosts. However, studies of potential paratenic hosts in the Caribbean have been temporally restricted to only diurnal species of lizards, thereby neglecting a dominant component of the nocturnal reptilian community: geckos. Many gecko species are human commensals with activity periods that overlap temporally with those of domestic cats, making them prime candidates as potential transport hosts for cat parasites. However, no studies have reported geckos as paratenic hosts for felid parasites on any Caribbean island. Here we report the first records of subcutaneous oligacanthorhynchid cystacanths on the Venezuelan Coastal Clawed Gecko (*Gonatodes antillensis*) based on specimens collected in Curaçao and Bonaire. The cysts were identified as belonging to the genus *Oncicola*, likely those of *Oncicola venezuelensis*. This study reports these geckos as a new host record for oligacanthorhynchid cystacanths, as well as Curaçao and Bonaire as new geographic locales for these acanthocephalan parasites. We additionally provide a review of saurian cystacanths, comparing the restricted taxonomic focus of transport hosts in Caribbean islands to the distribution of paratenic squamate hosts both in the Neotropics and globally. We find evidence that the ability of squamate reptiles to act as transport hosts is a pervasive feature across their Tree of Life, suggesting that these animals may serve as important vectors for transporting parasites between intermediate and definitive hosts.

KEYWORDS

Acanthocephala, intestinal helminths, cats, parasite, trophic transmission, mammals, birds, host–parasite interactions, vector species

Introduction

The transport of parasites by non-definitive transport, or paratenic, hosts creates an opportunity for parasitic organisms to utilize and potentially establish novel transmission pathways (Marcogliese 2007; Parker et al. 2015; Cable et al. 2017). Although it is well established that nonmammalian vertebrates often act as paratenic hosts for a variety of mammalian parasites (Bolt et al. 1993; Anderson 2000; Strube et al. 2013), baseline data

associating these species and the parasites they are transporting are uncommon across the Caribbean. This lack of data creates a knowledge gap that challenges our ability to accurately forecast the spread of internal parasites to both domestic animals and wildlife. In particular, despite the high potential of reptiles acting as paratenic hosts to the acanthocephalan parasites of cats and dogs, these potential transmission vectors have received little attention. To date, studies of lizards as paratenic hosts in the Caribbean have been restricted to

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TABLE 1. Institution and catalog numbers of *Gonatodes antillensis* specimens examined in this study. *Abbreviations*: CAS, California Academy of Sciences; LACM, Natural History Museum of Los Angeles County; MCZ, Museum of Comparative Zoology; NCMNS, North Carolina Museum of Natural Sciences; RMNH, Naturalis Biodiversity Center (former Rijksmuseum voor Natuurlijke Historie); UMMZ, University of Michigan Museum of Zoology; USNM, National Museum of Natural History, Smithsonian Institution; YPM HERR, Division of Vertebrate Zoology Herpetology Reptile Collection, Peabody Museum of Natural History, Yale University.

Institution code	Specimen numbers
CAS	113319–113345
LACM	126062–126078
MCZ	R-141593, R-141600, R-149268, R-149349, R-149351, R-149367, R-149369–R-149371, R-27548, R-60579, R-69577, R-69580, R-69581, R-69583, R-69584, R-69586, R-69587, R-69592, R-69596, R-69597, R-81514, R-82968, R-82969, R-82971, R-82973, R-82974, R-82976, R-82978, R-82979
NCMNS	89384–89387, 89390, 89392–89412, 89419–89443, 89445–89448, 89452, 89491
RMNH	13421, 14742A–B, 16682A–B, 18000, 18001A–C, 18002, 18004, 18008
UMMZ	57317–57345, 127795, 127796, 142675, 151501, 179309–179314
USNM	79231, 94980
YPM	YPM HERR 017579–017584, YPM HERR 018188–018199, YPM HERR 018438–018449, YPM HERR 018451–018460, YPM HERR 018603–018606, YPM HERR 018640–018644

diurnal species such as various species of *Anolis* or *Ameiva* (Dobson et al. 1992; Goldberg et al. 1998a; Nickol et al. 2006). This temporal bias neglects an important nocturnal component of Caribbean lizard communities: geckos.

With more than 1,600 species, geckos represent one of the most successful radiations of lizards and are common commensal organisms in urban and suburban landscapes worldwide (Gamble et al. 2012). Although several studies have found geckos to harbor cystacanths of acanthocephalans in Southeast Asia (Saehoong and Wongsawad 1997; Mahagedara and Rajakaruna 2015), Africa (Oluwafemi et al. 2017), Australia (Barton 2015), South America (Anjos et al. 2005), or Central America (Goldberg and Bursey 2004a; Bursey et al. 2007), no studies have investigated whether Caribbean island species act as paratenic hosts. Given both the spatial and temporal overlap of many Caribbean species with domestic and feral cats, geckos make likely paratenic host candidates. Ground-dwelling species may be particularly vulnerable to felid predation, making an assessment of their parasite transmission potential of high utility for veterinary and wildlife medicine. Herein we examine whether the ground-dwelling Venezuelan Coastal Clawed Gecko (*Gonatodes antillensis*; Lidth de Jude 1887) acts as paratenic host for acanthocephalan parasites by using a

combination of field-collected and museum specimens. To place our findings into a broader context, we provide a review of all known Caribbean island squamates as well a global survey of squamates that have been found to act as paratenic hosts for acanthocephalans.

Methods

As part of an ongoing study of the ecology and evolutionary biology of geckos on the southern Caribbean island of Curaçao (Dornburg et al. 2011, 2016; Lamb et al. 2017), we collected a total of 140 *Gonatodes antillensis* between 2011 and 2017 from 10 locales across Curaçao, which were deposited in the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA, and the North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA (Table 1). All specimens were visually inspected on collection, and those containing subcutaneous cysts were documented (Figure 1). To determine the historic prevalence of similar subcutaneous cysts, we were aided by collection staff who collectively visually inspected the specimen holdings of the Division of Vertebrate Zoology Herpetology Reptile Collection, Yale Peabody Museum of Natural History; the Museum of Comparative Zoology, Harvard University,

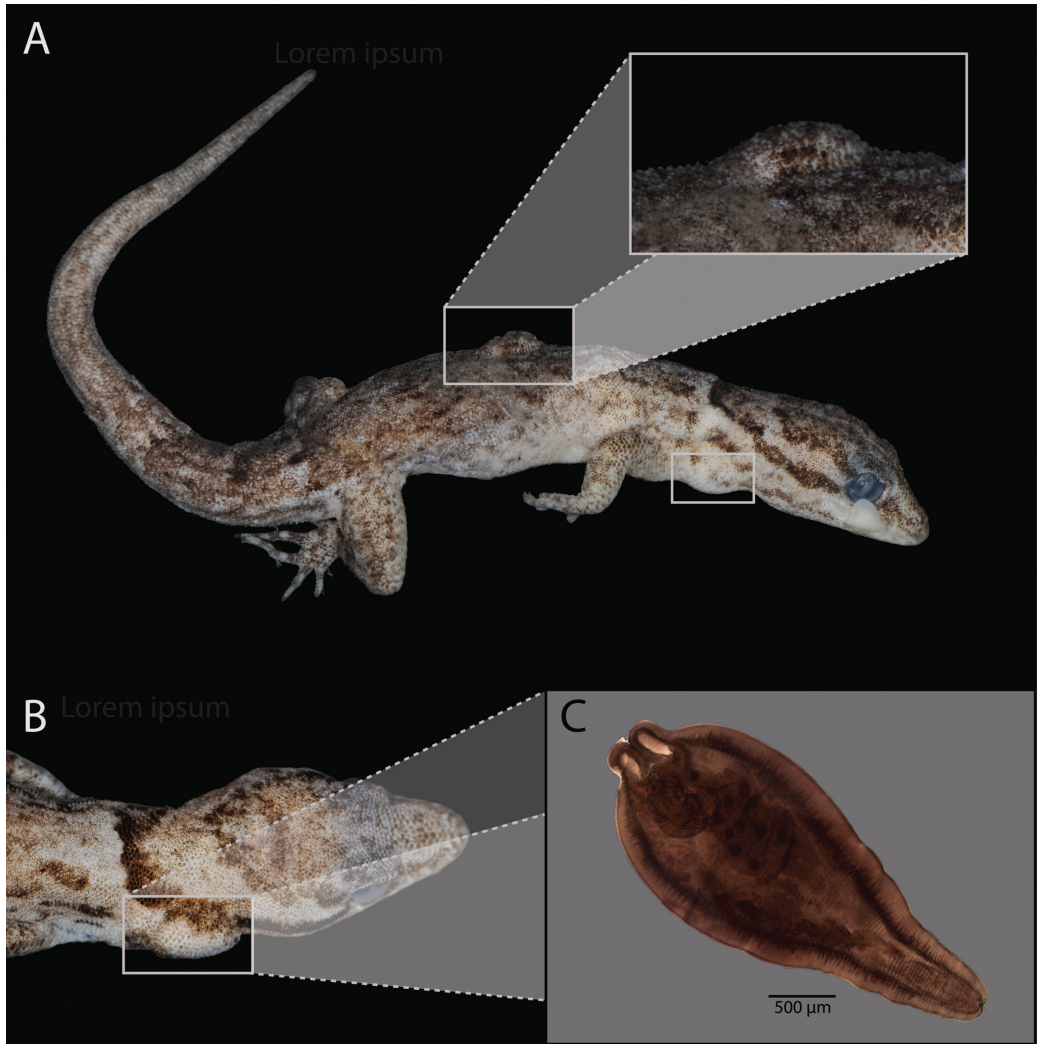


FIGURE 1. *Oncicola* cystacanths in *Gonatodes antillensis*. **A.** Individual *G. antillensis* with visible subcutaneous cystacanths highlighted. **B.** Dorsal view of *G. antillensis*. **C.** Slide of *Oncicola* cystacanth extracted from a cyst.

Cambridge, Massachusetts, USA; National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; the Natural History Museum of Los Angeles County, Los Angeles, California, USA; the Naturalis Biodiversity Center (former Rijksmuseum voor Natuurlijke Historie), Leiden, Netherlands; the California Academy of Sciences, San Francisco, California, USA; and the University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA, for specimens with similar subcutaneous cysts (Table 1). Subcutaneous cysts found in any samples were excised and sent to the parasitology laboratory at the College of Veterinary

Medicine at North Carolina State University, Raleigh, North Carolina, USA, for identification. Larval acanthocephalans (cystacanths) were extracted from cysts with the aid of a dissecting microscope. Cystacanths were stained with Semichon's carmine, dehydrated in an ethanol series, cleared in xylene and mounted in balsam for identification. Identifications were based on taxonomic keys and descriptions (Schmidt 1972, 1985; Nickol and Dunagan 1989; Smales 1997; Nickol et al. 2006; Santos et al. 2017). Comparative voucher specimens (HWML 48252, 48254, 48256, 48257, 48258, 49710) were borrowed from the Harold W. Manter Laboratory for

Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, USA (HWML).

To place our results into context, we compiled a list of all known paratenic saurian hosts for oligacanthorhynchid and centrorhynchid cystacanth across all Caribbean islands. These two groups represent two major radiations of acanthocephalans infecting terrestrial vertebrates that prey on squamates (mammals and birds; Petrochenko 1956), and would therefore be likely to co-opt squamates as transport hosts. Searches were conducted using Google Scholar and ISI Web of Knowledge using the following key terms: lizard, cystacanth, Caribbean, transport host, paratenic, saurian, gecko, *Anolis*, Iguanidae, snake, helminth, squamate, reptile, Acanthocephala, Oligacanthorhynchidae and *Centrorhynchus*. Additionally, references within each found document were checked for additional publications not captured by our key terms. Although additional key search terms are certainly possible, no additional terms we attempted yielded new reports. We further searched the Harold W. Manter Laboratory of Parasitology and the United States National Parasite Collection, National Museum of Natural History, Smithsonian Institution, for records not reported in the primary literature. This search was then expanded to compare Caribbean records to all records of these parasites in squamate reptiles globally.

Results

Across our survey of the 140 Venezuelan Coastal Clawed Geckos collected from Curaçao, only specimens (6 of 22) from one locale, Director's Bay, possessed subcutaneous cysts (Figure 2). Cysts were primarily located below the anterior surface of the neck and laterally along the main body, with several specimens also exhibiting cysts near the posterior insertion of the humerus with the scapula. Visual inspections of museum specimens for geckos that possessed subcutaneous cysts (Table 1) yielded only one specimen from the University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ 179309). That gecko had been collected in 1984 from Bonaire, Netherlands Antilles, and we found it to contain three previously undocumented subcutaneous cysts. Morphological characteristics (i.e., size, shape, proboscis hooks) of extracted cysta-

canths indicate inclusion in the family Oligacanthorhynchidae and the genus *Oncicola*. The long length of the lemnisci (Nickol et al. 2006) and the subcutaneous site of infection in Caribbean saurian hosts are suggestive of *Oncicola venezuelensis* (Marteau 1977). Unfortunately, the proboscis of our cystacanth specimens remained inverted, preventing a definitive species diagnosis. All cystacanth specimens were deposited in the Division of Invertebrate Zoology, Yale Peabody Museum of Natural History (YPM IZ 102933–102938).

Results of our literature and database survey yielded 15 publications and 4 museum records containing information on paratenic saurian hosts on Caribbean islands (Table 2). *Anolis* was the most frequently represented genus, with 21 species reported as paratenic hosts. Of these, only three species were reported with oligacanthorhynchid cystacanths, whereas all 21 *Anolis* species as well as a species of *Ameiva* and the snake *Leimadophis reginae* were reported with centrorhynchid cystacanths (Table 2). No subcutaneous centrorhynchid infections were reported. In contrast, both our findings for *Gonatodes antillensis* and prior work in *Anolis cristatellus* and *Anolis stratulus* reported subcutaneous infections (Table 2).

The results of our search of paratenic hosts globally yielded 202 records that spanned 35 countries and 184 species (Appendix). The United States was the most represented country with 36 records, followed by Costa Rica with 33 (Appendix). We found records of 119 species possessing oligacanthorhynchid and 75 species possessing *Centrorhynchus* infections (Appendix). Infections in the body cavity (coelom) were most common in both oligacanthorhynchid and centrorhynchid infections, respectively representing 60% and 50% of the reported records. Ophidians were the most reported group of squamates (56%), followed by iguanians (19%) and lacertoids (13%). Only a single record of a centrorhynchid cyst was found for another *Gonatodes*, with *Hemidactylus* the most frequently represented (54%) gecko genus (Appendix).

Discussion

Understanding the transmission pathways that parasites can utilize to move between hosts at

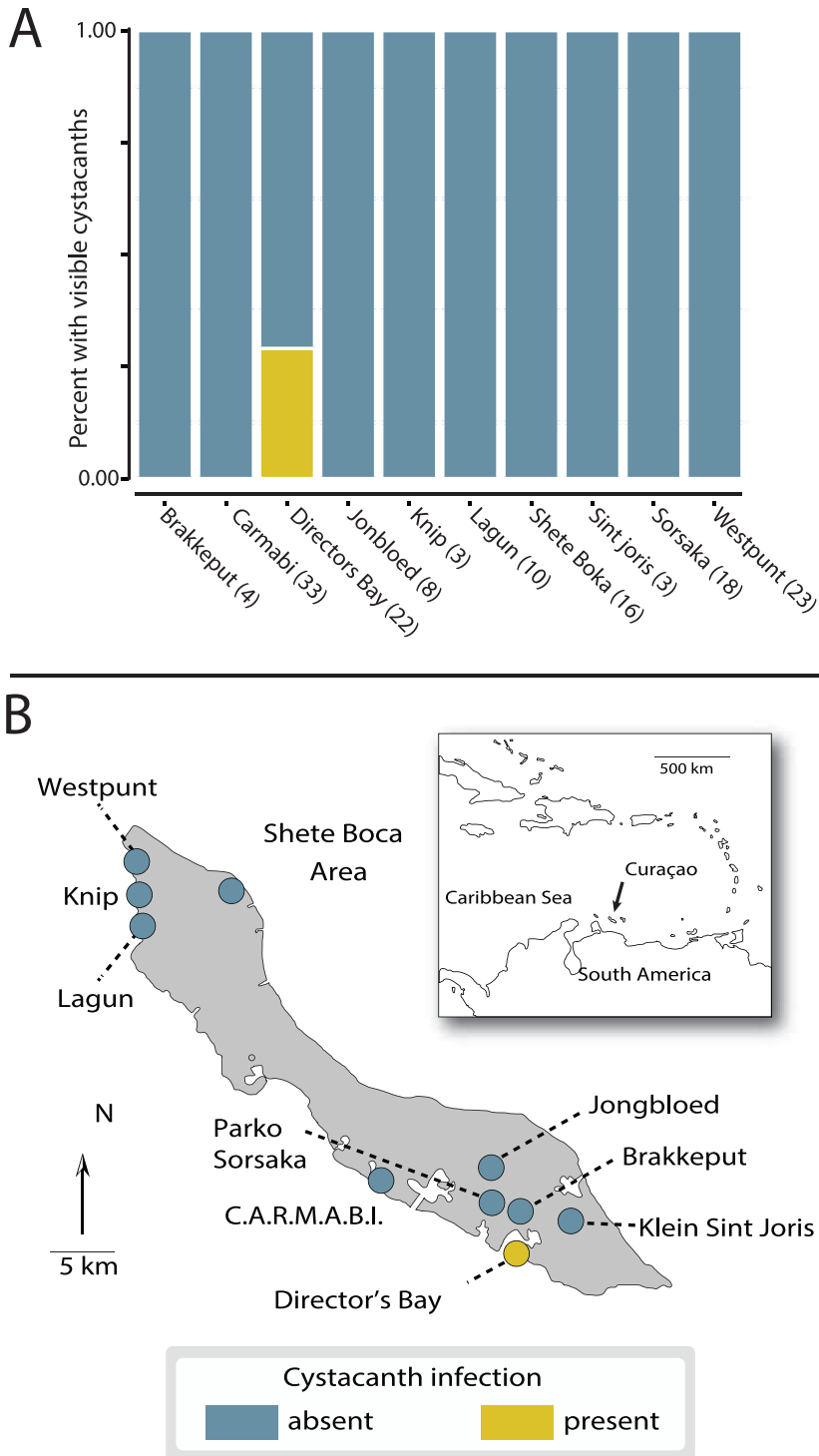


FIGURE 2. Frequency and spatial distribution of *Oncicola* cystacanths in Curaçao detected from our surveys and museum specimens. **A.** Frequency of cystacanths per site. **B.** Location of sites on the island. Blue indicates absence of cystacanths and yellow indicates presence of cystacanths. *Abbreviation:* CARMABI, Caribbean Research and Management of Biodiversity.

TABLE 2. Cystacanths found in squamate hosts on Caribbean islands. The abbreviations used indicate records from the Harold W. Manter Laboratory for Parasitology (HWMML) and United States National Parasite Collection (USNPM). Rows with boldface text indicate records from present study.

Cystacanth	Host	Site of infection	Island	Reference	
Oligacanthorhynchid	<i>Anolis acutus</i>	Coelom	St. Croix, U.S. Virgin Islands	Goldberg et al. 1997a	
	<i>Anolis cristatellus</i>	Subcutaneous	St. Thomas and St. John, U.S. Virgin Islands	Fuller et al. 2003; Nickol et al. 2006	
		Peritoneum	British Virgin Islands	Goldberg et al. 1998a	
	<i>Anolis stratulus</i>	Subcutaneous	St. Thomas and St. John, U.S. Virgin Islands	Fuller et al. 2003; Nickol et al. 2006	
	<i>Gonatodes antillensis</i>	Subcutaneous	Curaçao	Present study	
	<i>Gonatodes antillensis</i>	Subcutaneous	Bonaire	Present study	
	Centrorhynchid	<i>Ameiva ameiva</i>		Trinidad, Bahamas	Everard 1975; HWMML 34618
		<i>Anolis acutus</i>	Coelom	St. Croix, U.S. Virgin Islands	Goldberg et al. 1997a
		<i>Anolis aeneus</i>	Coelom	Grenada	Goldberg et al. 1997b
		<i>Anolis armouri</i>	Coelom	Haiti	Goldberg, Bursley and Cheam 1996
<i>Anolis bahorucoensis</i>		Coelom	Dominican Republic	Goldberg, Bursley and Cheam 1996	
<i>Anolis bimaculatus</i>		Intestine	St. Eustatius	Dobson et al. 1992; Dobson and Pacala 1992	
<i>Anolis cristatellus</i>		Body cavity	Puerto Rico	Acholonu 1976	
		Peritoneum	British Virgin Islands	Goldberg et al. 1998a	
		Body cavity	Hispaniola	Goldberg et al. 1998b	
		Body cavity	Dominican Republic	USNPM 087547	
<i>Anolis etheridgei</i>		Body cavity	Hispaniola	Goldberg et al. 1998b	
		Coelom	Dominican Republic	USNPM 087349	
<i>Anolis eugenegrahami</i>		Body cavity	Hispaniola	Goldberg et al. 1998b	
<i>Anolis garmani</i>	Coelom	Jamaica	Bundy et al. 1987		
<i>Anolis gingivinus</i>	Coelom	Anguilla	Goldberg et al. 1997b		
<i>Anolis grahamsi</i>	Coelom	Jamaica	Bundy et al. 1987		
<i>Anolis leachii</i>	Intestine	Antigua	Dobson et al. 1992; Dobson and Pacala 1992		
<i>Anolis lineatopus</i>	Coelom	Jamaica	Bundy et al. 1987; Vogel and Bundy 1987		
<i>Anolis lividus</i>	Intestine	Montserrat	Dobson et al. 1992; Dobson and Pacala 1992		
<i>Anolis monticola</i>	Body cavity	Hispaniola	Goldberg et al. 1998b		
<i>Anolis oculatus</i>	Body cavity	Dominica	Goldberg and Bursley 1996; Goldberg et al. 1997b		
<i>Anolis richardii</i>	Coelom	Grenada	Goldberg et al. 1997b		

Continued

TABLE 2. CONTINUED.

Cystacanth	Host	Site of infection	Island	Reference
Centrorhynchid	<i>Anolis sagrei</i>	Coelom	Jamaica	Bundy et al. 1987
	<i>Anolis schwartzi</i>	Body cavity	Andros Island, Bahamas	Goldberg et al. 1994
	<i>Anolis valencienni</i>	Intestine	St. Eustatius	Dobson et al. 1992; Dobson and Pacala 1992
	<i>Anolis wattsi</i>	Coelom	Jamaica	Bundy et al. 1987
	<i>Leimadophis reginae</i>	Intestine	Antigua	Dobson et al. 1992; Dobson and Pacala 1992
			Trinidad and Tobago	HWML 33903

different life stages is a fundamental component of both veterinary and human medicine. Our study represents the first documentation of *Oncicola* in *Gonatodes antillensis* and the first record of a Caribbean island gecko acting as a paratenic host for acanthocephalans. While definitive hosts of *Oncicola* species include felids and birds, *Oncicola venezuelensis* is known only from felids, specifically domestic cats and ocelots (*Leopardus pardalis*) (Marteau 1977; Patton et al. 1986; Fuller and Nickol 2011; Santos et al. 2017). Rep (1975) reported *Oncicola* from cats in the Leeward Antilles, providing evidence that this parasite has likely been on the islands for at least four decades. Our finding of an additional *Oncicola* cystacanth from a specimen collected in 1984 from the island of Bonaire provides additional evidence that the Venezuelan Coastal Clawed Gecko has been acting as a paratenic host for nearly as long. However, this raises the question of the role *G. antillensis* plays in the life cycle of *Oncicola*.

Oncicola venezuelensis utilizes termites of the genus *Nasutitermes* as intermediate hosts, with transmission facilitated through the encounter of infected fecal matter (Fuller and Nickol 2011). Parasitized termites have been found to be more vulnerable to lizard predation (Fuller et al. 2003), and laboratory studies have demonstrated that ingestion of infected termites by lizards will result in transmission (Nickol et al. 2006). Unfortunately, the natural history of *Gonatodes antillensis* has received little attention outside of a few studies of basic ecology and reproductive biology (Bennett and Gorman 1979; Van Buurt 2005; Lamb et al. 2017), and resolution of the feeding ecology of *G. antillensis* is broadly classified as comprising small invertebrates (Van Buurt 2005). Although diets of *G. antillensis* have not been studied explicitly, termites of the genus *Nasutitermes* are considered native to Curaçao (Van Buurt and Debrot 2012) and species of *Gonatodes* for which diets are known have all been documented to eat termites (Quesnel 1957; Vitt et al. 2000; Miranda and Andrade 2003). This suggests that the feeding ecology of *G. antillensis* may predispose this species as a transmission vector for *O. venezuelensis*. Further studies of the feeding ecology of this gecko are needed to test this hypothesis.

Given that no native felid species occur in the Leeward Antilles, domestic cats likely represent the only definitive host of *Oncicola venezuelensis*

on these islands. This suggests a life cycle of *O. venezuelensis* beginning in a termite that has encountered infected fecal matter. Infected termites are then ingested by *Gonatodes antillensis*, which acts as a paratenic host, and the parasite is ultimately transmitted to domestic cats to restart the cycle. This intermediate termite to paratenic lizard to definitive cat host life cycle has been proposed for *Oncicola* on other Caribbean islands (Fuller and Nickol 2011), adding a veterinary health concern to the global conservation concern of predation by feral cats driving reptile extirpation (Gibbon et al. 2000; Medina et al. 2011). Although cat predation on *G. antillensis* has not been reported, many studies have described feral cat predation on geckos (Bonnaud et al. 2011; Kutt 2011), including other species of *Gonatodes* (Alonso et al. 2009). As such, the likelihood of at least some felid predation events is certainly not negligible. Additionally, we observed a high frequency of feral cats at the Director's Bay site where all cystacanth-containing *G. antillensis* specimens were collected. Although cat frequencies and habitat characteristics were not quantified, this was by far the most ecologically degraded site of all sampling locations, with large amounts of trash and debris scattered throughout. Large quantities of garbage are known to attract cats by providing food resources, thereby increasing the risk of pathogen infections (Plaza and Lambertucci 2017). The condition of this site could explain the high frequency of infection as the harsh arid conditions of the island might prevent aggregations of feral cats in nonurbanized settings. Further, *Nasutitermes* termites have repeatedly been found to be among the most common termites in highly disturbed or degraded habitats worldwide (de Souza and Brown 1994; Eggleton et al. 1995; Bandeira et al. 2003), suggesting that this site could constitute a perfect storm for acanthocephalan transmission potential.

Paratenic Parasitism of Squamates and the Helminth Life Cycle

The results of our literature and database survey suggest squamates to represent an underappreciated component of the ecology and life cycle of acanthocephalans (Appendix). We found records from 184 species of squamates acting as potential transmission vectors in 35 countries (Appendix). These species span the squamate Tree of Life, fur-

ther suggesting that this mode of transmission may be a pervasive squamate-wide phenomenon. Of all squamate groups, snakes were the most frequently represented. However, this should not be taken to imply that snakes are particularly prone to acting as paratenic hosts, as a survey based on the combined pool of natural history notes and museum records cannot account for sampling biases (Dornburg et al. 2017). Further work is needed to discern geographic, taxonomic and life history-based biases in sampling efforts and complete a more robust understanding of patterns in paratenic parasitism in squamates globally. However, comparing the restricted taxonomic focus of transport hosts in Caribbean islands to the distribution of paratenic hosts both in the Neotropics and globally (Appendix) strongly suggests a significant knowledge gap in the region.

To date, our knowledge of squamates acting as paratenic hosts on Caribbean islands has been limited to records from *Anolis* and a single lacertoid and ophidian (Table 2). Our study expands the reservoir of potential Caribbean transport hosts to include geckos of the genus *Gonatodes*. Cystacanths of *Centrorhynchus* have previously been found in *Gonatodes albogularis* in Panama; however, our record is the first instance of *Oncicola*. Further, *G. albogularis* is diurnal whereas *G. antillensis* is nocturnal (Van Buurt 2005), thereby overlapping in diel activity with the other geckos found in our survey (Appendix). Of the other nocturnal geckos encountered in our survey, geckos of the genus *Hemidactylus* are of particular note as potential transmission vectors. *Hemidactylus* geckos have invaded tropical ecosystems worldwide and have been documented to prey on other geckos (Bolger and Case 1992; Dornburg et al. 2011, 2016), including *G. antillensis* in Curaçao (Dornburg et al. 2011), making this an additional prime candidate for investigation. More broadly, our survey of paratenic squamate hosts undoubtedly underestimates the extent to which squamates act as paratenic hosts.

The ability of acanthocephalan species to infect nondefinitive hosts while remaining transmittable offers a solution to the ecological problem of transitioning between different feeding guilds at different trophic levels between life stages. Many acanthocephalans such as *Oncicola* begin their life cycle in arthropod intermediate

hosts, yet require birds or mammals feeding at higher trophic levels for their adult stage (Schmidt 1985). The results of our survey and instances of paratenic parasitism by other parasites with similar complex life histories (e.g., Marcogliese 2002; Choisy et al. 2003; Cirtwill et al. 2017) reiterates a question: When do parasitic lineages evolve to co-opt pathways of energy flow across community food webs to reach their target definitive hosts? It should not be surprising that squamates are broadly used as transport hosts, as these often represent direct links between lower trophic level consumers (e.g., arthropods) and higher level vertebrate predators (Watkins-Colwell et al. 2006). Given that we found documented instances of squamate paratenic parasitism that span the globe, we suggest that investigating the ecology and evolution of paratenic parasitism in squamates represents a potentially rich area of research in the evolution of parasite transmission pathways of high importance to both wildlife and human medicine.

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Appendix

Oligacanthorhynchid, centrorthynchid and unknown cystacanths from paratenic squamate hosts outside of the Caribbean. A dagger (†) indicates reference listed in Schmidt (1985). The abbreviations used indicate records from the Harold W. Manter Laboratory for Parasitology (HWML) and United States National Parasite Collection (USNPM); HWML or USNPM with referenced studies indicate linked specimens.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
Unknown	Gekkota	<i>Hemidactylus frenatus</i> <i>Hemidactylus mabouia</i>	Intestine Intestine	Australia Tanzania	Barton 2015 Simonsen and Sarda 1985
	Iguania	<i>Sceloporus grammicus</i> <i>Sceloporus merriami</i> <i>Urosaurus auriculatus</i> <i>Uta stansburiana</i>	Muscle Small intestine Body cavity Body cavity	USA, Texas USA, Texas Mexico USA, California	Goldberg et al. 1995 Goldberg et al. 1995 Goldberg and Bursey 2012a Goldberg et al. 1999
	Lacertoidea	<i>Aspidoscelis dixoni</i> <i>Aspidoscelis gularis</i> <i>Aspidoscelis neomexicanus</i> <i>Aspidoscelis septemvittatus</i> <i>Aspidoscelis tigris</i> <i>Eremias pleskei</i>	Mesentery/muscle Body cavity Muscle fascia Muscle fascia Coelom	USA, Texas USA, Texas USA, New Mexico USA, Texas USA, Arizona Turkey	McAllister et al. 1991 McAllister 1990a McAllister 1990b McAllister et al. 1995 Benes 1985 Düßen et al. 2013
	Ophidia	<i>Bothrops moojeni</i> <i>Crotalus atrox</i> <i>Chironius quadricarinatus</i> <i>Erythrolamprus poecilogyrus</i> <i>Mimophis mahfalensis</i> <i>Pseudoboa nigra</i> <i>Thammodonastes hypoconia</i>	Small intestine Mesentery Small intestine Body cavity Mesenteries Small intestine Small intestine	Brazil USA, New Mexico Brazil Brazil Madagascar Brazil Brazil	Silva 2014 Goldberg et al. 2002 Silva 2014 Silva 2014 McAllister et al. 1993 Silva 2014 Silva 2014
	Scincomorpha	<i>Acontias kgalagadi</i> <i>Scincella lateralis</i> <i>Sphenomorphus simus</i>	Intestine	Southern Africa USA, Florida Papua New Guinea	Bursey and Goldberg 2007 Brooks 1972 Goldberg et al. 2009

Continued

APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
Oligacanthorhynchid	Anguimorpha	<i>Mesaspis monticola</i> <i>Pseudopus apodus</i>	Coelom	Costa Rica Azerbaijan	Bursev and Goldberg 2006 †Farzaliev and Petrochenko 1980
	Iguania	<i>Anolis acutus</i> <i>Anolis auratus</i> <i>Anolis carolinensis</i> <i>Anolis cristatellus</i> <i>Anolis humilis</i> <i>Anolis tropidogaster</i> <i>Anolis tropidolepis</i> <i>Chamaeleo namaquensis</i>	Coelom Cysts in body cavity Subcutaneous Body cavity Cysts in body cavity Cysts in body cavity Coelom Body wall, attached to various organs	St. Croix Panama Louisiana U.S. Virgin Islands Costa Rica Panama Costa Rica Southern Africa	USNPM 086637 Bursev et al. 2012 USNPM 090331 USNPM 087542 Bursev et al. 2012 Bursev et al. 2012 USNPM 093528 Prudhoe and Harris 1971
		<i>Enyalius bilineatus</i> <i>Gambelia wislizenii</i>	Coelom, encapsulated in thoracic and abdominal integument and musculature	Brazil USA, Texas	Vrcibradic et al. 2007 McAllister and Bursev 2007
		<i>Norops tropidolepis</i> <i>Paralaudakia caucasia</i> <i>Paralaudakia caucasia</i>	Body cavity	Costa Rica Azerbaijan Georgia	Bursev et al. 2004 †Farzaliev and Petrochenko 1980 Sharpilo 1976; Murvanidze et al. 2008
		<i>Paralaudakia lehmanni</i> <i>Phrynosoma ditmarsii</i> <i>Saara hardwickii</i> <i>Stellagama stellio</i> <i>Trapelus sanguinolentus</i> <i>Tropidurus hispidus</i> <i>Tropidurus semitaeniatus</i>		Kazakhstan Mexico Afghanistan Egypt Kazakhstan Brazil Brazil	Andrushko and Markov 1956 Goldberg and Bursev 2000a †Barus and Tenora 1976 USNPM 063106 Andrushko and Markov 1956 Brito et al. 2014 Brito et al. 2014

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Tropidurus torquatus</i>	Body cavity	Brazil	USNPM 089091
		<i>Urosaurus nigricaudus</i>	Body cavity	Mexico	Goldberg, Burse and Beaman 2003
		<i>Uta stansburiana</i>	Body cavity	USA, California	USNPM 087283
	Gekkota	<i>Hemidactylus frenatus</i>		Thailand	Saehong and Wongsawad 1997
		<i>Hemidactylus platyurus</i>		Thailand	Saehong and Wongsawad 1997
		<i>Hemidactylus turcicus</i>	Subcutaneous	USA, Louisiana	Criscione and Font 2001
		<i>Hemidactylus turcicus</i>	Body cavity	Turkey	Yildirimhan et al. 2008
		<i>Lepidoblepharis xanthostigma</i>	Stomach	Costa Rica	Goldberg and Burse 2004a
	Lacertoidea	<i>Acanthodactylus beershebenis</i>	Body cavity	Israel	USNPM 108056
		<i>Ameiva ameiva</i>		Paraguay	Ávila and Silva 2010; Smales 2007
		<i>Ameiva bifrontata</i>	Small intestine	Peru	Ávila and Silva 2010; Smales 2007; Goldberg and Burse 2012b
		<i>Ameiva festiva</i>	Coelom	Nicaragua	Burse et al. 2006
		<i>Ameiva leptophrys</i>	Body Cavity	Costa Rica	Goldberg and Burse 2011
		<i>Ameiva undulata</i>		Costa Rica	Goldberg and Burse 2009a
		<i>Aspidoscelis tigris</i>	Intestine	USA, Arizona	Goldberg et al. 1997c
		<i>Chernidophorus septemvittatus</i>		USA, Texas	USNPM 083365
		<i>Eremias pleskei</i>		Azerbaijan	†Farzaliev and Petrochenko 1980
		<i>Holcosus leptophrys</i>	Body cavity	Costa Rica	USNPM 103863
		<i>Holcosus undulatus</i>	Body cavity	Costa Rica	USNPM 101074
		<i>Lacerta strigata</i>		Azerbaijan	†Farzaliev and Petrochenko 1980
		<i>Lacerta strigata</i>		Georgia	Sharpilo 1976; Murvanidze et al. 2008
	Ophidia	<i>Agkistrodon bilineatus</i>		Mexico	USNPM 102286
		<i>Agkistrodon contortrix</i>		USA, North Carolina	Davis et al. 2016
		<i>Agkistrodon piscivorus</i>		USA, Louisiana	Elkins and Nickol 1983
		<i>Boa constrictor</i>		Brazil	Travassos 1917

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Bothrops jararaca</i>		Brazil	Travassos 1917
		<i>Bothrops neuwiedi</i>		Brazil	Travassos 1917
		<i>Cerastes vipera</i>	Body cavity	Egypt	HWML 35414
		<i>Chilomeniscus stramineus</i>	Body cavity	Mexico	USNPM 106939
		<i>Chironius carinatus</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Chironius exoletus</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Chironius fuscus</i>	Mesenteries	Brazil	USNPM 095379
		<i>Chironius grandisquamis</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Clelia clelia</i>		Brazil	Travassos 1917
		<i>Coluber constrictor</i>	Mesenteries	USA, Pennsylvania	Bolette 1998a
		<i>Coluber mentovarius</i>		Mexico	Goldberg and Burse 2004c
		<i>Coniophanes fissidens</i>	Coelom	Costa Rica	Goldberg and Burse 2007
		<i>Conopsis lineata</i>		Mexico	Goldberg and Burse 2004d
		<i>Crotalus atrox</i>	Subcutaneous	USA, Arizona	USNPM 096557
		<i>Crotalus atrox</i>	Mesenteries	USA, Texas	Bolette 1997a
		<i>Crotalus basiliscus</i>	Body cavity	Mexico	USNPM 095372
		<i>Crotalus cerastes</i>		USA, Arizona	USNPM 091080
		<i>Crotalus cerberus</i>	Body cavity	USA, Arizona	USNPM 094152
		<i>Crotalus enyo</i>	Mesenteries	Mexico	USNPM 092196
		<i>Crotalus lepidus</i>		Mexico	Goldberg and Burse 1999 (USNPM 087642)
		<i>Crotalus lepidus</i>		USA, Texas	McAllister et al. 2004 (USNPM 92421)
		<i>Crotalus mitchellii</i>		USA, California	USNPM 088617
		<i>Crotalus scutulatus</i>	Subcutaneous	USA, Arizona	Bolette 1997b
		<i>Crotalus tigris</i>		USA, Arizona	Goldberg and Burse 1999 (USNPM 087643)
		<i>Crotalus viridis</i>	Subcutaneous	USA, South Dakota	Bolette 1998b
		<i>Crotalus willardi</i>		Mexico	Goldberg and Burse 2000b

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Dendrophidion pericarinaratum</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Dendrophidion vinitior</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Diadophis punctatus</i>	Mesenteries	USA, Arizona	Goldberg and Burse 2004e (USNPM 092282)
		<i>Dolichophis jugularis</i>	Mesenteries around small intestine	Azerbaijan	†Farzaliev and Petrochenko 1980
		<i>Drymarchon couperi</i>	Coelom	USA, Florida	Foster et al. 2000
		<i>Drymobius margaritiferus</i>	Coelom	Costa Rica	Goldberg and Burse 2005 (USNPM 095055)
		<i>Elaphe quatuorlineata</i>		Europe	Travassos 1917
		<i>Erythrolampus aesculapii</i>		Brazil	Travassos 1917
		<i>Erythrolampus bizona</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Erythrolampus miliaris</i>	Peritoneum	Brazil	Pizzatto and Marques 2006; Travassos 1917
		<i>Hypsiglena torquata</i>	Body cavity	USA, Arizona	USNPM 090584
		<i>Imantodes cenchoa</i>	Body cavity	Costa Rica	USNPM 101519
		<i>Imantodes gemmistratus</i>	Body cavity	Costa Rica	Goldberg and Burse 2009b
		<i>Imantodes inornatus</i>	Body cavity	Costa Rica	USNPM 101522
		<i>Lampropeltis getula</i>	Mesenteries	USA, Louisiana	Elkins and Nickol 1983
		<i>Leptodeira maculata</i>		Mexico	Goldberg and Burse 2004b
		<i>Leptodeira septentrionalis</i>	Coelom	Costa Rica	USNPM 101174
		<i>Leptophis ahaetulla</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Erythrolamprus epinephelus</i>	Coelom	Costa Rica	Goldberg and Burse 2004b
		<i>Macrovipera lebetina</i>	Intestines	Uzbekistan	†Markov et al. 1967
		<i>Malpolon monspessulanus</i>		Egypt	HWML 35417
		<i>Mastigodryas bifossatus</i>		Brazil	Travassos 1917
		<i>Micruroides euryxanthus</i>	Mesenteries	USA, Arizona	Goldberg and Burse 2000c (USNPM 088779)
		<i>Micrurus corallinus</i>			Pizzatto and Madi 2002
		<i>Micrurus nigrocinctus</i>	Coelom	Costa Rica	Goldberg and Burse 2004b

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Naja oxiana</i>	Mesenteries	Turkmenistan and Tajikistan	†Markov et al. 1968
		<i>Nerodia cycloption</i>	Mesenteries	USA, Louisiana	Elkins and Nickol 1983
		<i>Nerodia fasciata</i>	Mesenteries	USA, Louisiana	Elkins and Nickol 1983
		<i>Oxybelis aeneus</i>	Coelom	Mexico	Goldberg and Bursley 2001
		<i>Oxybelis aeneus</i>	Coelom	Costa Rica	Goldberg and Bursley 2004b
		<i>Oxybelis fulgidus</i>	Coelom	Costa Rica	Goldberg and Bursley 2004b
		<i>Psammophis schokari</i>	Body cavity	Egypt	HWML 35427
		<i>Psammophis sibilans</i>	Body cavity	Egypt	HWML 35426
		<i>Philodryas olfersii</i>	Body cavity	Brazil	Travassos 1917
		<i>Philodryas patagoniensis</i>	Body cavity	Paraguay	Smales 2007
		<i>Pliocercus euryzonus</i>	Body cavity	Costa Rica	USNPM 099526
		<i>Pseustes poecilonotus</i>	Coelom	Costa Rica	Goldberg and Bursley 2004b
		<i>Ptyas mucosa</i>	Subcutaneous	India	Rengaraju and Das 1981
		<i>Rhinocheilus lecontei</i>	Subcutaneous	Mexico and USA, Arizona, California, Texas	Bolette 1997b; Goldberg, Bursley and Holshuh 1998
		<i>Salvadora grahamiae</i>	Abdominal integument	USA, Texas	McAllister et al. 2017
		<i>Salvadora mexicana</i>	Coelom	Mexico	Goldberg and Bursley 2004c
		<i>Tantilla yaquia</i>	Body cavity	USA, Arizona	Goldberg and Bursley 2004f
		<i>Thamnodynastes strigatus</i>	Coelom	Paraguay	Smales 2007
		<i>Trimorphodon tau</i>	Coelom	Mexico	Goldberg and Bursley 2004c
		<i>Urotheca euryzona</i>	Coelom	Costa Rica	Goldberg and Bursley 2007
		<i>Walterinnesia aegyptia</i>	Intestine	Egypt	HWML 35418
		<i>Xenodon histricus</i>	Coelom	Brazil	Travassos 1917
		<i>Xenodon merremii</i>	Coelom	Brazil	Travassos 1917
		<i>Xenodon rabadcephalus</i>	Coelom	Costa Rica	Goldberg and Bursley 2007
Scincomorpha		<i>Brasiliscincus agilis</i>	Body cavity	Brazil	USNPM 089079
		<i>Eumeces schneideri</i>	Body cavity	Azerbaijan	†Farzalliev and Petrochenko 1980
		<i>Plestiodon multivirgatus</i>	Body cavity	USA, New Mexico	Goldberg and Bursley 2012c
		<i>Scincella lateralis</i>	Body cavity	USA, Arizona	USNPM 106913

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
	Varanoidea	<i>Varanus bengalensis</i> <i>Varanus griseus</i>		Afghanistan Egypt	†Barus and Tenora 1976 USNPM 063105
Centrotrichinid	Gekkota	<i>Eublepharis macularius</i> <i>Gonatodes albogularis</i> <i>Hemidactylus agrisus</i> <i>Hemidactylus mabouia</i>	Body cavity, small intestine Stomach wall Body cavity Small intestine; stomach wall; intestinal wall, mesenteries	Pakistan Panama Brazil Brazil	Goldberg, Bursley and Telford 2003 Bursley et al. 2007 Anjos et al. 2011 Rodrigues 1970; Anjos et al. 2005
		<i>Phyllodactylus lanei</i>		Mexico	Mayén-Peña and Salgado- Maldonado 1998
		<i>Tarentola gomerensis</i>	Body cavity	Canary Islands	Roca et al. 1999
	Iguania	<i>Anolis auratus</i> <i>Anolis limifrons</i> <i>Anolis nebulosus</i>	Body cavity Body cavity	Panama Panama Mexico	Bursley et al. 2012 Bursley et al. 2012 Mayén-Peña and Salgado- Maldonado 1998
		<i>Anolis poecilopus</i> <i>Anolis tropidogaster</i> <i>Anolis uniformis</i>	Body cavity Body cavity	Panama Panama Mexico	Bursley et al. 2012 Bursley et al. 2012 Cabrera-Guzmán and Garrido- Olvera 2014
		<i>Ctenosaura pectinata</i>		Mexico	Mayén-Peña and Salgado- Maldonado 1998
		<i>Enyalius bilineatus</i> <i>Enyalius perditus</i> <i>Norops limifrons</i> <i>Norops tropidolepis</i> <i>Phrynocephalus interscapularis</i> <i>Sceloporus jarrovii</i>	Stomach wall Small intestine, stomach Small intestine Body cavity Coelom	Brazil Brazil Costa Rica Costa Rica Turkmenistan Mexico	Vrcibradic et al. 2007 Vrcibradic et al. 2008 Bursley and Goldberg 2003 Bursley et al. 2004 Velikanov 1989 Goldberg, Bursley and Bezy 1996

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Sceloporus nelsoni</i>		Mexico	Mayén-Peña and Salgado-Maldonado 1998
		<i>Stenocercus guentheri</i>	Mesenteries	Ecuador	USNPM 103202
		<i>Tropidurus torquatus</i>	Stomach wall	Argentina	Vicente 1978; Ávila and Silva 2010; Lamas and Zaracho 2006
Lacertoidea		<i>Apathya cappadocica</i>	Stomach wall	Turkey	Birlik et al. 2015
		<i>Darevskia rudis</i>	Small intestine	Turkey	Birlik et al. 2018
		<i>Gallotia caesaris</i>	Body cavity	Canary Islands	Roca et al. 2012
		<i>Gymnophthalmus spectiosus</i>	Stomach wall	Panama	Bursey et al. 2007
		<i>Lacerta agilis</i>	Intestinal wall	Laboratory	Krasnoshchekov and Lisitsyna 2009
		<i>Lacerta agilis</i>		Ukraine	Sharpilo et al. 2001
		<i>Lacerta strigata</i>		Georgia	Sharpilo 1976; Murvanidze et al. 2008
		<i>Leposoma rugiceps</i>	Stomach wall	Panama	Bursey et al. 2007
Ophidia		<i>Podarcis lilfordi</i>	Body cavity	Spain, Balearic Islands	Roca 1995
		<i>Podarcis milensis</i>	Body cavity	Greece, Milos Island	Roca 1995
		<i>Podarcis pityusensis</i>	Body cavity	Spain, Balearic Islands	Roca 1995
		<i>Takydromus tachydromoides</i>		Japan	Telford 1997
		<i>Tupinambis teguixin</i>	Body cavity	Paraguay	Smales 2007
		<i>Agkistrodon piscivorus</i>		USA, North Carolina	Collins 1968, 1969
		<i>Amphisema stolatum</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
		<i>Coluber constrictor</i>	Coelom	USA, Oklahoma	McAllister et al. 2015
		<i>Coniophanes fissidens</i>	Coelom	Costa Rica	Goldberg and Bursey 2007
		<i>Drymarchon couperi</i>	Mesenteries around small intestine	USA, Florida	Foster et al. 2000
	<i>Deinagkistrodon acutus</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969	
	<i>Echinanthera undulata</i>	Body cavity	Brazil	Smales 2007	

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Echis carinatus</i>		Turkmenistan	Markov et al. 1970
		<i>Elaphe</i> sp.		China	USNPM 052195
		<i>Elaphe carinata</i>		China	USNPM 052197, 052198
		<i>Erythrolamprus viridis</i>		Brazil	Quirino et al. 2018
		<i>Helicops leopardinus</i>	Body cavity	Paraguay	Smales 2007
		<i>Leptophis ahaetulla</i>	Body cavity	Paraguay	Smales 2007
		<i>Liophis lineatus</i>	Body cavity	Paraguay	Smales 2007
		<i>Liophis poecilogyrus</i>	Body cavity	Paraguay	Smales 2007
		<i>Lycodon</i> sp.		India	†Das 1950
		<i>Lycodon semicarinatus</i>		China	USNPM 052221
		<i>Lycodon subcinctus</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
		<i>Malpolon monspessulanus</i>	Body cavity	Egypt	HWML 35428
		<i>Naja hannah</i>		USA, Washington, DC (Zoo)	USNPM 056852
		<i>Naja naja</i>		India	†Das 1950
		<i>Naja naja</i>		Pakistan	Heckmann et al. 2011
		<i>Nerodia erythrogaster</i>		USA, North Carolina	Collins 1968, 1969
		<i>Nerodia sipedon</i>	Intestinal wall	USA, Kentucky	Ward 1940
		<i>Nerodia sipedon</i>		USA, North Carolina	Collins 1968, 1969; Richardson and Nickol 1995
		<i>Nerodia taxispilota</i>		USA, North Carolina	Collins 1968, 1969
		<i>Philodryas patagoniensis</i>	Body cavity	Paraguay	Smales 2007
		<i>Platyceps najadum</i>		Georgia	Sharpilo 1962; Murvanidze et al. 2008
		<i>Protobothrops mucrosquamatus</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
		<i>Psammodynastes pulverulentus</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
		<i>Ptyas mucosa</i>		India	†Das 1950
		<i>Rhabdophis tigrinus</i>		China	USNPM 052199, 052200, 052206
		<i>Rhadinaea calligaster</i>	Coelom	Costa Rica	Goldberg and Burse 2007
		<i>Rhinocheilus lecontei</i>		USA, Arizona	Goldberg, Burse and Holshuh 1998 (USNPM 086194)

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APPENDIX CONTINUED.

Cystacanth	Clade	Host species	Site of infection	Location	Reference
		<i>Sinomatrix annularis</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
		<i>Trimeresurus steingeri</i>	Small intestine	Taiwan	†Schmidt and Kuntz 1969
	Scincomorpha	<i>Brasiliscincus agilis</i>	Stomach, intestine, lungs, liver	Brazil	Vrcibradic et al. 2002
		<i>Emoia caeruleocauda</i>	Body cavity	Northern Mariana Islands, Agrihan Island	USNPM 103499
		<i>Mochlus sundevalli</i>	Stomach wall	Kenya	USNPM 104678
		<i>Notomabuya frenata</i>	Stomach wall	Brazil	Anjos et al. 2005
		<i>Plestiodon latiscutatus</i>	Body cavity	Japan	Bursey et al. 2005
		<i>Psychosaura macrohyncha</i>	Stomach, intestine, lungs, liver	Brazil	Vrcibradic et al. 2002; Vrcibradic and Rocha 2005

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