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Rapid Communication

Rapid spread of the invasive pentastome *Raillietiella orientalis* (Hett, 1915) in 14 new Florida counties and in pet trade snakes

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Abstract

Raillietiella orientalis is an invasive pulmonary parasite that is native to Southeast Asia and Africa and is rapidly spreading throughout Florida since its initial identification in South Florida in 2012. This obligate parasite utilizes invertebrates, anurans, and lizards as intermediate hosts and most often infects snakes as definitive hosts. While parasitism causes minimal fitness consequences to snakes in the native range of *R. orientalis*, in the introduced range it can cause severe infections in native snake species, sometimes leading to mortality. Through collaborative and opportunistic sampling, we examined snakes in the southeastern United States for *R. orientalis* infection. We documented 14 new Florida county records of *R. orientalis* infection in snakes sampled from August 2022 through October 2024. These new localities fill gaps in the known geographic range of *R. orientalis* in Florida and extend the parasite's range 435 km northwest into the Florida panhandle. We also document *R. orientalis* infections in four wild-caught snakes from South Florida that entered the pet trade. Human-aided dispersal of intermediate hosts and snakes, including those in the pet trade, is likely to rapidly increase the geographic range and conservation threat of this invasive parasite. Our results highlight the importance of monitoring biological invasions of parasites to clarify impacts on novel host species.

Key words: emerging infectious disease, geographic range, introduced, pentastome, reptile, spillover

Introduction

Raillietiellid pentastomes, especially *Raillietiella* spp., are highly invasive parasites of anurans (Kelehear et al. 2012), lizards (Pence and Selcer 1988), and snakes (Kelehear et al. 2014; Miller et al. 2020). These crustacean parasites

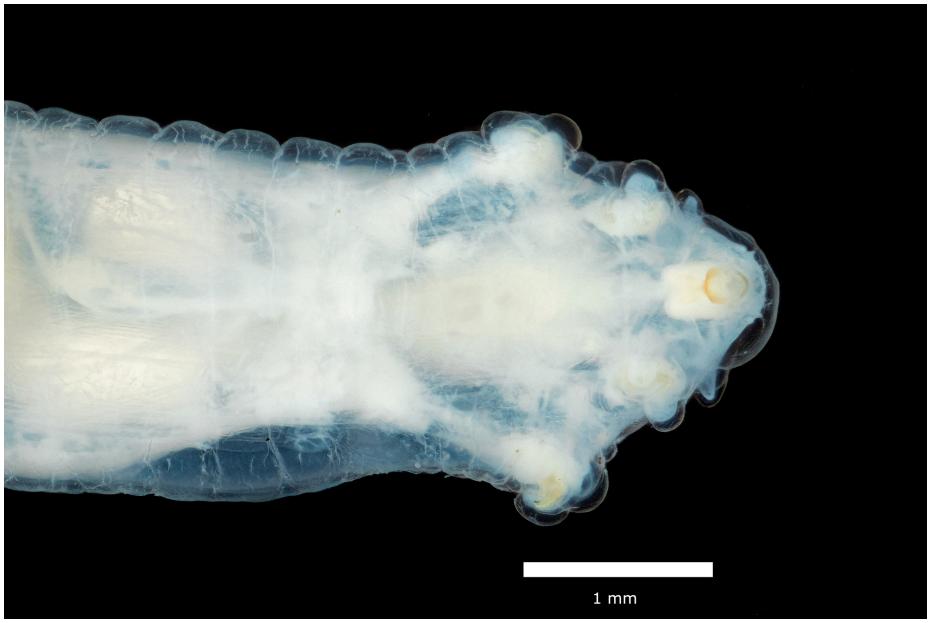

Figure 1. An anterior view of a *Raillietiella orientalis* adult with the four characteristic hooks and buccal cadre. *Raillietiella orientalis* has a flattened, triangular head with two small anterior hooks and two larger posterior hooks.

spread rapidly, achieve high prevalence and intensity in novel host populations (Miller et al. 2020; Palmisano et al. 2022), and can have severe health consequences in infected hosts (*e.g.*, Pence and Selcer 1988). *Raillietiella orientalis* (Hett, 1915) is native to southeast Asia and Africa where it infects the lungs of native snakes, typically at low prevalence and intensity of infection (Christoffersen and De Assis 2013; Figure 1). In contrast, in its invasive ranges in Australia and North America, *R. orientalis* can cause severe infections in snakes, often with high population prevalence (Kelehear et al. 2014; Miller et al. 2020). The life cycle of *R. orientalis* is indirect, involving multiple intermediate hosts. Coprophagous invertebrates (*e.g.*, cockroaches) become infected by consuming egg-laden feces, and amphibians and lizards ingest these infected invertebrates. Infection experiments (Palmisano et al. 2022) indicate that once ingested, infective larvae from roaches encyst in vertebrate intermediate hosts, including southern toads (*Anaxyrus terrestris* (Bonnaterre, 1789)), southern leopard frogs (*Rana sphenocephala* (Cope, 1886)) and Cuban brown anoles (*Anolis sagrei* Dumeril and Bibron, 1837). The species that serve as intermediate hosts in the wild have not yet been documented. Snakes become infected by consuming infected intermediate hosts, and the pentastomes mature to their adult form in the respiratory tract of the snake. Although *R. orientalis* primarily utilizes snakes as a definitive host, recent reports have identified adult *R. orientalis* in two nonnative lizard species, tokay geckos (*Gekko gecko* (Linnaeus, 1758)) and the Argentine black and white tegu (*Salvator merianae* Dumeril and Bibron, 1839), in Florida (Fieldsend et al. 2021; Goetz et al. 2021).

First documented in Florida in 2012, *R. orientalis* appears to have spilled over from Burmese python (*Python bivittatus* Kuhl, 1820) in South Florida (Miller et al. 2018) and has since infiltrated Florida herpetofauna with sexually mature adults documented in at least 18 native snake species including members of *Agkistrodon*, *Coluber*, *Crotalus*, *Drymarchon*, *Farancia*, *Lampropeltis*, *Masticophis*, *Nerodia*, *Pantherophis*, *Sistrurus*, and *Thamnophis* (Metcalf et al. 2019; Miller et al. 2020; Bogan et al. 2022; Horvath et al. *in press*; *unpublished data*). The initial introduction of *R. orientalis* likely followed the "commodity" and "contaminant" pathways, as defined by Hulme et al. (2008), with escaped pythons from the pet trade acting as the primary vector. The potential spread of *R. orientalis* via "stowaway" pathways—such as the inadvertent transportation of infected hosts (cockroaches and small herpetofauna) in human-mediated transport like cargo ships, horticultural trade, and vehicular trafficking—offers additional invasion pathways (Hulme et al. 2008). *Raillietiella orientalis* infections appear to cause lethal pentastomiasis in several species of native snakes in Florida (Farrell et al. 2019; Bogan et al. 2022). For some susceptible species, particularly the pygmy rattlesnake (*Sistrurus miliarius* (Linnaeus, 1766)), the arrival of *R. orientalis* has been suggested to align temporally with population declines, though more published data are needed to substantiate this potential association (Farrell et al. 2019; *unpublished data*). *Raillietiella orientalis* presents an immediate conservation concern to native snake species throughout the southeastern United States and highlights that biological invasions can lead to significant disease threats to native species.

In May 2022, we created the Snake Lungworm Alliance and Monitoring (SLAM) to initiate a collaborative effort involving coordinated sampling of snakes throughout the southeastern United States and to document progression of the parasite's invasion into new regions and hosts. Here, we present SLAM data that documents the presence of *R. orientalis* in 14 Florida counties that represent range expansion 80 km to the northeast and 435 km to the northwest. We also document four cases of *R. orientalis* infection in wild-caught snakes collected in Florida for the pet trade, highlighting the potential for a human-aided dispersal pathway.

The reported information

As of June 2024, the SLAM network consists of 94 collaborators across the Carolinas, Georgia, Florida, and Alabama, with 71 individuals in Florida and 13 in Georgia. SLAM members opportunistically collected road-killed specimens and fecal samples from live snakes. Live snake sampling was conducted by collaborators who are actively researching other aspects of snake biology and already possess relevant permits. We dissected 384 snakes across the genera *Agkistrodon*, *Cemophora*, *Coluber*, *Crotalus*, *Diadophis*, *Farancia*, *Heterodon*, *Lampropeltis*, *Masticophis*, *Micrurus*, *Nerodia*,

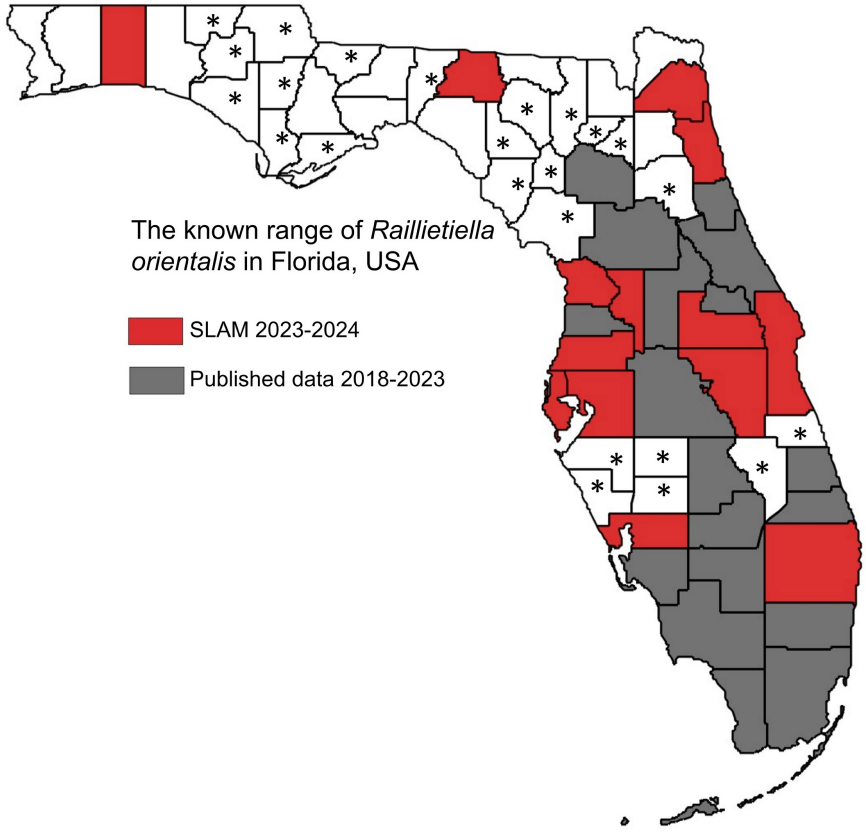

Figure 2. New (red) and previously (grey) documented localities for the pentastome *R. orientalis* in Florida snakes sampled from 2022 to 2024. The asterisks denote counties lacking samples. For details, see Supplementary material Table S1.

Opheodrys, *Pantherophis*, *Pituophis*, *Rhadinea*, *Sistrurus*, and *Thamnophis* to screen for the presence of adult *R. orientalis* and processed 220 fecal samples via wet mounts from *Agkistrodon*, *Coluber*, *Crotalus*, *Drymarchon*, *Heterodon*, *Liodytes*, *Masticophis*, *Nerodia*, *Pantherophis*, *Pituophis*, and *Sistrurus*. We detected 66 *R. orientalis* infections from 217 Florida snakes (~ 30%) and zero *R. orientalis* infections from 170 Georgia snakes following postmortem dissection. The infection intensity ranged from 1 to 107 adult parasites. *Raillietiella orientalis* infections were confirmed in snakes from 14 Florida counties not previously documented to be affected by the invasive parasite (Figure 2; Table 1). We identified the parasites as *Raillietiella orientalis* based on morphological characteristics of the anterior end of adult pentastomes, including head shape, hook morphology, copulatory spicules, and uterus structure (de Luna et al. 2022) and confirmed our identification using molecular methods. Given the lack of morphological data on pentastome eggs, we relied on molecular identification of eggs found upon inspection of the fecal samples via wet mounts and microscopy. All infections were examined post-dissection except for Sumter County, where infections were identified in five living *S. miliarius* via fecal sample examination using both microscopy and genetic analysis.

We extracted DNA from the adult parasites using Qiagen DNeasy kits following manufacturer protocols for tissue extraction (Qiagen, Hilden,

Table 1. New county records for *R. orientalis* in Florida with the first definitive host species found with infection.

County	Host	GenBank Accession Associated with Infection
Charlotte	*Thamnophis sirtalis*	PQ067964
Citrus	*Coluber constrictor*	PQ067963
Duval	*Coluber constrictor*	PQ067956
Hillsborough	*Coluber constrictor*	PQ067955
Lake	*Micrurus fulvius*	PQ067957
Madison	*Coluber constrictor*	PQ035031
Okaloosa	*Agkistrodon conanti*	Produced identical CO1 sequences to other samples
Orange	*Sistrurus miliarius*	PQ067954
Osceola	*Masticophis flagellum*	PQ067960
Palm Beach	*Lampropeltis getula*	PQ067959
Pasco	*Coluber constrictor*	PQ067958
Pinellas	*Sistrurus miliarius*	PQ067961
Sumter	*Sistrurus miliarius*	PQ067948, PQ067949, PQ067950
St. Johns	*Coluber constrictor*	PQ067962

Table 2. Records of *Raillietiella orientalis* in three captive snakes wild-caught in South Florida.

Host	GenBank Accession Associated with Infection
Thamnophis sirtalis 1	PQ067951
Thamnophis sirtalis 2	PQ067952
Lampropeltis elapsoides	PQ067953

Germany). We extracted DNA from the fecal samples using the extraction protocol from Ayana et al. (2019) without bead beating. We then ran a *Raillietiella orientalis* specific PCR targeting part of the CO1 gene and visualized product using gel electrophoresis. The fecal samples were assessed using a novel PCR assay (Palmisano et al. *in review*). All samples produced PCR bands of the expected size and seventeen were confirmed by Sanger sequencing. All sequences exhibited 100% nucleotide identity to *R. orientalis* sequences in the NCBI database (GenBank accession numbers provided in Tables 1 and 2). Molecular confirmation of *R. orientalis* infection in the Madison County black racer *(Coluber constrictor* Linnaeus, 1758*)* was achieved with PCR and subsequent Sanger sequencing targeting a portion of the 18S gene as described in Walden et al. (2020). The amplicon exhibited 100% nucleotide identity to previously accessioned *R. orientalis* 18S sequences (GenBank accession numbers in Table 1).

In the spring of 2023, we dissected three native snakes purchased from an individual reptile supplier in South Florida. These animals were sold and shipped by a commercial organization that advertised the snakes online. The snakes, two garter snakes (*Thamnophis sirtalis* (Linnaeus, 1766)) and scarlet king snake (*Lampropeltis elapsoides* (Holbrook, 1838)) were of unknown origin, but likely to have been wild-caught due to their size and apparent external lesions. These snakes exhibited emaciation, anorexia, and died within two months of being sold. Additionally, an eastern kingsnake (*Lampropeltis getula* (Linnaeus, 1766)), a native snake, was captured from the wild in southeast Florida in February 2024 and was kept as a pet by a private citizen. This snake exhibited anorexia and died within a month of captivity. Upon dissection, all four of these captive snakes were found to be

infected by adult *R. orientalis* (the *T. sirtalis* individuals had three and 36 pentastomes, the *L. elapsoides* had nine pentastomes, and the *L. getula* had three pentastomes).

Discussion

Our recent sampling indicates that *R. orientalis* continues to spread rapidly throughout Florida, and without clear barriers for continued spread, will likely soon appear in Georgia and/or other neighboring states in the southeastern U.S. The record in Madison County, FL indicates a 135 km expansion to the northwest from the prior northernmost location in Alachua County (Walden et al. 2020) and the record in Okaloosa County, FL involves an additional 350 km expansion to the west of the Madison record. The Duval County, FL record is the northern-most location along the Atlantic coastline and represents a northward expansion of 80 km from the nearest prior locality (Palmisano et al. 2023). The new county records presented within fill distributional gaps present in the previously documented range of *R. orientalis* (Palmisano et al. 2023). These new localities span peninsular Florida with four new counties located on the Atlantic coast, four counties located on the Gulf Coast, and one county bordering Georgia (Figure 2). *Raillietiella orientalis* has now been detected in all but six (Desoto, Hardee, Indian River, Manatee, Okeechobee, Sarasota) of the 24 counties in the southern half of peninsular Florida; however, as we have not actually examined snakes from those six counties, we suspect these distributional gaps are the result of a lack of sampling and not an actual absence of the parasite (Figure 2).

The natural dispersal of *R. orientalis* infected snakes and known intermediate hosts, such as lizards, anurans, and roaches (Palmisano et al. 2022), seems unlikely to account for the apparent rapid geographic range expansion of the parasite, and human activity is likely facilitating dispersal. The four cases of *R. orientalis*-infected snakes documented in captive animals with confirmed or presumed wild origins, along with a prior record of an infected banded water snake (*Nerodia fasciata* (Linnaeus, 1766)) purchased in Michigan (Farrell et al. 2023), suggest a dispersal pathway through the transport of host organisms as commodities. Intermediate and definitive host species of *R. orientalis* are often wild caught and sold both nationally and internationally from Florida (Enge 2005), either as potential pets, or in the case of *A. sagrei*, as food for captive animals (T. Farrell *personal observation*). Additionally, some known intermediate hosts of *R. orientalis* are regularly moved long distances through the horticulture industry (Glorioso et al. 2018) and vehicular rafting (Campbell 1996), which likely facilitates dispersal along the stowaway pathway (Hulme et al. 2008). These findings underscore the critical role of human-mediated dispersal in the rapid geographic expansion of *R. orientalis* and highlight the need for management strategies to mitigate its spread.

Given the high prevalence of *R. orientalis* in impacted areas (Miller et al. 2020) and the great diversity of snake species that have been found to be infected (Miller et al. 2020), as well as the severity of infection (Bogan et al. 2022) and the potential for population-level impacts (Farrell et al. 2019), this invasive pentastome represents a major conservation concern. Its rapid geographic spread further underscores the urgency of addressing this issue. *Raillietiella orientalis* will almost certainly continue to pervade Florida's herpetofaunal communities and spread to neighboring states due to the ecological similarity of the coastal plain of the southeastern United States to the northern half of peninsular Florida. Sustained monitoring of intermediate and definitive hosts remains essential, alongside research on disease mechanisms to comprehensively understand the threat posed to native snake species. Furthermore, strategic sampling for lizard and anuran-feeding snakes that are listed for protection (*e.g.*, southern hognose snake (*Heterodon simus* (Linnaeus, 1766)) and short-tailed kingsnake (*Lampropeltis extenuata* (Brown, 1890))) is needed as these species are rarely encountered during more opportunistic sampling (Crawford et al. 2020). The disease dynamics of *R. orientalis*, including its spread across regions, impact on host populations, and role in emerging infectious diseases, offer numerous avenues for research in invasion biology, conservation, and disease management. The discoveries and resources generated by SLAM advocate for a collaborative approach to tackling large-scale issues, thereby aiding in informed management decisions. Considering the widespread prevalence of *R. orientalis* infection in Florida, implementing biosecurity regulations for wild-caught definitive and intermediate hosts brought into captivity is imperative.

Authors' contribution

JNP, TMF, AES, MB, and AMD conceived the project. JNP, TMF, MB, AMD, RJO, JHK, TM, and HW performed dissections and collected and preserved pentastomes. JNP, RJO, HDSW, and AES conducted morphological and molecular confirmation of identification of pentastome species. JNP and TMF compiled the data. JNP, MB, AMD, ZL, BSS, EEL, ST, SLM, KT, and LM collected samples contributing to novel findings. ZL, BSS, ST, KT, and LM have facilitated widespread surveillance. All authors contributed to writing and editing the manuscript.

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Data availability

Data used in this work are available from the corresponding author upon reasonable request. All sequences have been uploaded to Genbank with the accession numbers listed in Table 1 and Table 2.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Geo-referenced records of *Raillietiella orientalis* in Florida.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2025/Supplements/BIR_2025_Palmisano_etal_SupplementaryMaterial.xlsx