



Helminths of small rodents (Heteromyidae and Cricetidae) in the Yucatan Peninsula, Mexico: an integrative taxonomic approach to their inventory

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Abstract

In this survey, we inventoried the helminths of heteromyid and cricetid rodents captured in the Yucatan Peninsula from 2017 to 2019. Helminths were identified using morphological techniques (clearing, staining, and scanning electron microscopy). Also, the 28S rRNA gene of individuals from several helminth taxa was successfully amplified and sequenced. To confirm the identification at the generic level, and in some cases at the specific level, and the genealogical relationships of the parasites, phylogenetic analyses were performed with the new 28S sequences. We identified 22 species of helminths including three trematodes (Brachylaimidae, Dicrocoeliidae, and Microphallidae), five cestodes (Davaineidae, Hymenolepididae, and Taeniidae), and 14 nematodes (Trichuridae, Ancylostomatidae, Ornithostrongylidae, Heligmonellidae, and Oxyuridae) from *Heteromys gaumeri* (Heteromyidae), *Ototylomys phyllotis*, *Oligoryzomys fulvescens*, *Peromyscus yucatanicus*, *Sigmodon toltecus*, and *Reithrodontomys gracilis* (Cricetidae). The overall frequency of infection in small rodents was 84.1% (143/170); all specimens of *H. gaumeri*, *S. toltecus* and *Ol. fulvescens* were infected with helminths. In total, we provided 46 new sequences of the 28S gene from 17 species of helminths. Seven species are likely undescribed species, six are reported for the first time in rodents from Mexico, and 12 are new host records in the Americas. Before this study, 87 taxa of helminths had been reported from 35 cricetid and 12 heteromyid species in 21 Mexican states. Our findings increase to 93 the helminth taxa in these rodents, and to 36 the cricetid species parasitized by helminths. This large scale-survey is the first to use an integrative approach to inventory the helminths of wild small rodents in Mexico.

Key words: wild rodents, distribution, helminths, 28S gene, morphology

Introduction

The Yucatan Peninsula is a biogeographical province that comprises the Mexican states of Campeche, Quintana Roo and Yucatan, as well as northern Guatemala and northern Belize. In this province, large deforestation areas had been identified, such as central and southeastern Campeche, southern Yucatan and Quintana Roo and the northern

coastal regions of the peninsula (Ellis *et al.* 2020). Between 2001 and 2018, Campeche, Quintana Roo and Yucatan lost approximately 1.5 million hectares of tree cover mostly due to cattle production systems and agriculture (Global Forest Watch 2020). Deforestation and fragmentation have had a significant impact on the distribution and diversity of mammals in Mexico (Sánchez-Cordero *et al.* 2009), being increasingly threatened along with the helminths they harbor (Martínez-Salazar *et al.* 2016) and also changing the patterns of parasite infections (Bordes *et al.* 2015). Rodents account for approximately 39% of mammal species worldwide (Burgin *et al.* 2018). In Mexico, Rodentia consists of 233 species, of which 180 are small rodents (Ramírez-Pulido *et al.* 2014). In the Yucatan Peninsula there are records of 13 species of wild small rodents belonging to the families Heteromyidae and Cricetidae (Zaragoza-Quintana *et al.* 2016). *Heteromys gaumeri* Allen & Chapman, *Peromyscus yucatanicus* Allen & Chapman, and *Otonyctomys hattii* Anthony are endemic, and the first two are widely distributed. Despite the considerable information available on distribution, taxonomy, phylogeny, and parasitology of small rodents (Zaragoza-Quintana *et al.* 2016), little is known about their helminth fauna (Panti-May *et al.* 2018).

Studies on helminths parasitizing wild small rodents in Mexico began in the late 1930s (Chitwood 1938). Several decades later, numerous studies have investigated the helminths of small rodents throughout the country (see García-Prieto *et al.* 2012; Preisser & Falcón-Ordaz 2019). However, the reported list of helminth species of these rodents is incomplete due to the limited number of hosts examined and surveys conducted in some regions. The most recent checklist of the helminths of small rodents in Mexico reported 87 taxa of helminths in 47 of 190 cricetid and heteromyid rodent species from 21 Mexican states (Preisser & Falcón-Ordaz 2019). Particularly, in Yucatan, only 11 helminth taxa have been recorded in 4 of 13 heteromyid and cricetid rodent species: 3 in *H. gaumeri* (Panti-May & Robles 2016; Panti-May *et al.* 2018), 4 in *P. yucatanicus* (Panti-May *et al.* 2018), 3 in *Sigmodon toltecus* (de Saussure) (Panti-May *et al.* 2018) and 1 in *Ototylomys phyllotis* Merriam (Chitwood 1938). In Campeche and Quintana Roo, no helminths have been recorded in small rodents (Preisser & Falcón-Ordaz 2019). This clearly shows that the inventory of the helminths parasitizing wild small rodents is incomplete in the Yucatan Peninsula.

The aim of this study was to provide an inventory of the helminths of wild small rodents from the Yucatan Peninsula, Mexico, using morphological and molecular techniques.

Materials and methods

Collection and examination of rodents. This study was carried out in 14 sites in the Yucatan Peninsula, Mexico, 9 in Yucatan, 3 in Quintana Roo and 2 in Campeche (Figure 1), from March 2017 to September 2019 (Table 1). In each site, two quadrants were established with 120 Sherman traps each for three consecutive nights (720 night-traps in each site). Trapped rodents were anesthetized with isoflurane and euthanized with overdose of sodium pentobarbital. Rodents were identified following Reid (2009). When necessary, scientific names of hosts were updated following Ramírez-Pulido *et al.* (2014).

The bioethics committee for the use of animals in research from the Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán approved the protocols used in this study (protocol number CB-CCBA I-2018-001). The rodent trapping was conducted under license from the Mexican Ministry of Environment (SGPA/DGVS/01186/17, SGPA/DGVS/05995/19).

After euthanasia, the heart, lungs, stomach, small and large intestines, liver, pancreas, and mesenteries of each specimen were collected and stored in 96% ethanol. In the laboratory, all organs were placed in Petri dishes and examined under a stereomicroscope (Olympus SZ2-ILST). The helminths were removed, counted, and preserved in 70% ethanol. For morphological identification, nematodes were cleared and temporarily mounted in lactophenol; platyhelminths were stained with carmine acid or Gomori's trichrome, dehydrated through an ethanol series, cleared in methyl salicylate, and mounted permanently in Canada balsam. Specimens were studied and drawn with the aid of a light microscope (Leica DM500) with a drawing tube (Leica Microsystems). Some specimens were studied with the aid of a scanning electron microscope (SEM) at the Laboratorio de Microscopía y Fotografía de la Biodiversidad of the Instituto de Biología (IB), Universidad Nacional Autónoma de México (UNAM), Mexico. For SEM micrographs, specimens were dehydrated using a graded ethanol series and critical-point dried with carbon dioxide. Dry specimens were mounted on metal stubs, coated with a gold-palladium mixture, and examined with a SEM (Hitachi SU1510). All measurements are in micrometers unless otherwise stated. Morphological features were used to identify helminths at different taxonomic levels (i.e., order, family, genus, and species), using keys for nematodes

TABLE 1. Study sites in the Yucatan Peninsula (Mexico) where small rodents were trapped.

Site	Municipality, state	Trapping sites	Geographical coordinates	Collection date
Hobonil ranch	Tzucacab, Yucatan	Medium semi-deciduous tropical forest	20°01'10.4" N, 89°01'23.4" W	March 2017
Ich ha lol xaan ecological park	Hampolol, Campeche	Sub-evergreen medium tropical forest	19°56'47.3" N, 90°22'26.1" W	May 2017
Molas farm	Merida, Yucatan	Low deciduous tropical forest and pastures	20°47'54.5" N, 89°37'56.9" W	July 2017
Dzununcan farm	Merida, Yucatan	Low deciduous tropical forest	20°51'28.3" N, 89°38'34.4" W	August 2017
San Francisco cattle ranch	Panaba, Yucatan	Low deciduous tropical forest and pastures	21°21'50.3" N, 88°19'39.8" W	August 2017
Santa Cruz cattle ranch	Tizimin, Yucatan	Semi-deciduous tropical forest	21°08'54.4" N, 87°54'37.8" W	September 2018
Vallazoo	Valladolid, Yucatan	Secondary forest and zoo facilities	20°43'29.8" N, 88°12'26.4" W	September 2018
Aak ecological park	Merida, Yucatan	Low deciduous tropical forest	20°07'48.1" N, 89°37'16.5" W	November 2018
Papam ranch	Hunucma, Yucatan	Pastures and secondary forest	21°02'45.0" N, 89°53'18.9" W	January 2019
Kuncheil cattle ranch	Sotuta, Yucatan	Cultivated grasslands and secondary forest	20°39'14.7" N, 89°02'27.1" W	March 2019
Jolie Jungle eco-hotel	Puerto Morelos, Quintana Roo	Deciduous tropical forest	20°55'33.6" N, 87°07'39.4" W	August 2019
Balam Nah eco-hotel	Felipe Carrillo Puerto, Quintana Roo	Deciduous tropical forest	19°28'56.5" N, 88°03'52.6" W	September 2019
David Gustavo community	Bacalar, Quintana Roo	Cultivated grasslands and secondary forest	18°52'50.3" N, 88°41'25.5" W	September 2019
Zoh Laguna community	Calakmul, Campeche	Cultivated grasslands and secondary forest	18°35'21.9" N, 89° 25' 17.4" W	September 2019

(Anderson *et al.* 2009; Beveridge *et al.* 2013; Durette-Desset *et al.* 2017), cestodes (Khalil *et al.* 1994) and trematodes (Gibson *et al.* 2002; Jones *et al.* 2005; Bray *et al.* 2008), and original descriptions and redescrptions.

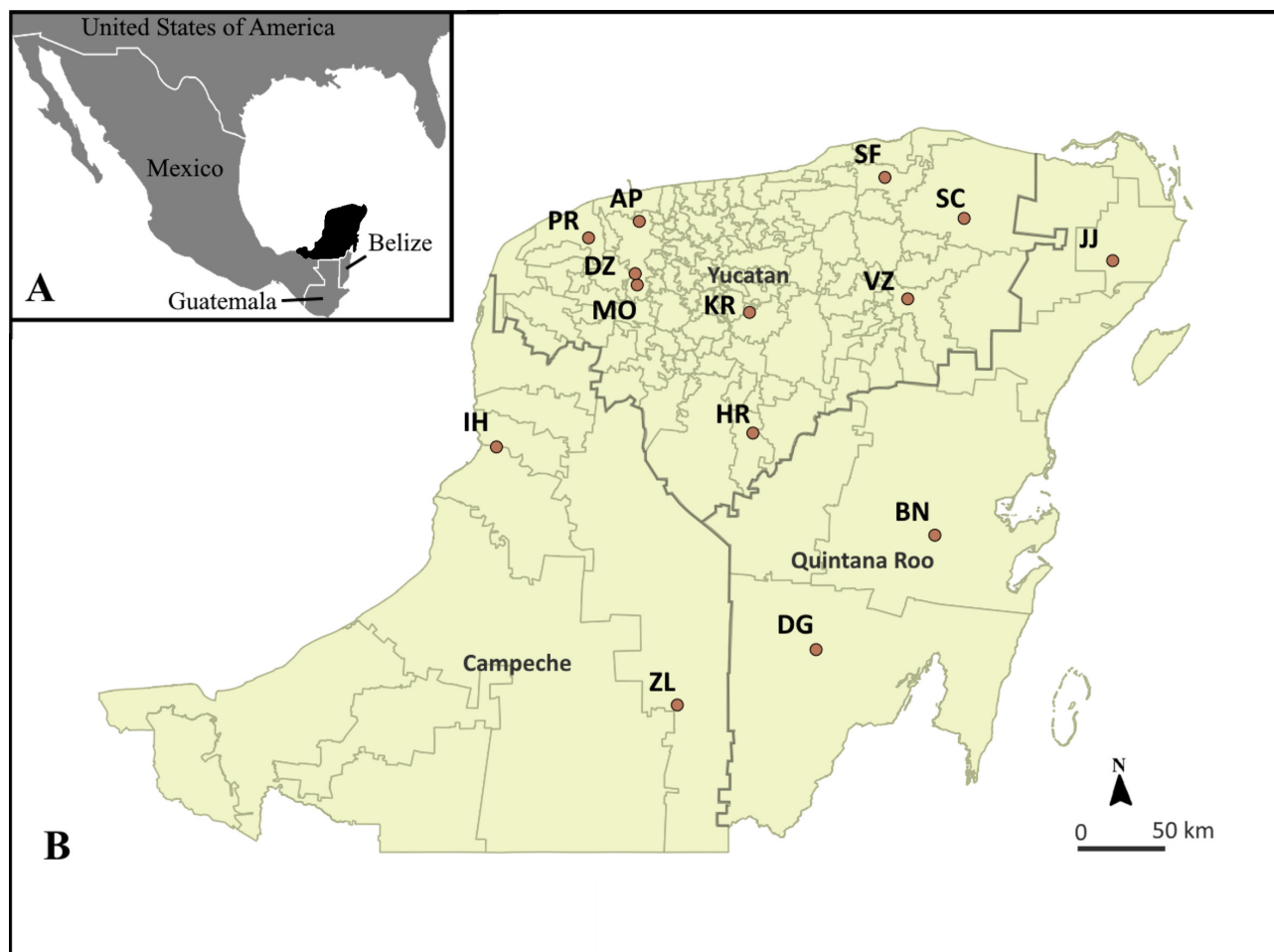


FIGURE 1. A. Geographic location of Mexico and the area covered by the Mexican states in the Yucatan Peninsula (black area). B. Location of the sites (red dots) where wild small rodents were captured in the states of Campeche, Yucatan and Quintana Roo, Yucatan Peninsula, Mexico. HR, Hobonil ranch; IH, Ich ha lol xaan ecological park; MO, Molas farm; DZ, Dzununcan farm; SF, San Francisco cattle ranch; SC, Santa Cruz cattle ranch; VZ, Vallazoo; AP, Aak ecological park; PR, Papam ranch; KR, Kuncheil cattle ranch; JJ, Jolie jungle eco-hotel; BN, Balam Nah eco-hotel; DG, David Gustavo community; ZL, Zoh Laguna community.

The nomenclature about the family group and terms for the Strongylida (Nematoda) followed Beveridge *et al.* (2013) while for the Trichuridae followed Robles *et al.* (2006). Vouchers of hosts were deposited in the Colección Mastozoológica (CM), Universidad Autónoma de Yucatán (Supplementary material, Table S1) and helminth specimens were deposited in the Colección Nacional de Helminfos (CNHE), IB-UNAM.

Prevalence (with the 95% confidence intervals) and intensity (mean and range) of infections were calculated following Bush *et al.* (1997), see Table 2.

DNA extraction and sequencing of helminths. Total genomic DNA from at least one specimen of each helminth taxon was extracted using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The 28S rRNA gene was amplified using a conventional PCR with the forward primer 391 5' –AGCGGAGGAAAAGAACTAA– 3' (Stock *et al.* 2001) and the reverse primer 536 5' –CAGCTATCCTGAGGAAAC– 3' (Stock *et al.* 2001) which amplify a fragment of 1400 base pairs (bp). These fragments were amplified using PCR protocols and thermal profiles previously described (Hernández-Mena *et al.* 2017).

Sanger sequencing (GENEWIZ, Inc.) of the 28S PCR products were performed with the previously used primers (391 and 536) and the following internal primers: 503 5' -CCTTGGTCCGTGTTTCAAGACG-3' (García-Varela & Nadler 2005) and 504 5' -CGTCTTGAAACACGGACTAAGG- 3' (Stock *et al.* 2001). The resulting sequences

were analyzed and edited in Geneious Pro 4.8.4 software (Biomatters Ltd., Auckland, New Zealand). The sequences generated in this study were submitted to GenBank (National Center for Biotechnology Information).

Phylogenetic analysis. To confirm the identification at the generic level, and in some cases at the specific level, and genealogical relationships of the parasites, phylogenetic analyses were performed with the new 28S sequences and those deposited in GenBank. The alignment of the sequences was generated with ClustalW (<http://www.genome.jp/tools/clustalw/>) using the approach “SLOW/ACCURATE” and weight matrix “CLUSTALW (for DNA)” (Thompson *et al.* 1994). The nucleotide substitution model was estimated for each data set with jModelTest v2. (Darriba *et al.* 2012). Akaike’s information criterion was used to select the best-fit model of nucleotide substitution. The phylogenetic analyses were performed with the Maximum Likelihood method (ML) in RAxML v. 7.0.4, and executed with 1,000 Bootstrap repetitions to obtain the best phylogenetic tree of each data set (Stamatakis 2006). The trees were visualized and edited in FigTree v.1.4.4. The molecular variation of 28S data sets was calculated using p-distances with the software MEGA v 6.0 (Tamura *et al.* 2013).

Results

170 wild small rodents belonging to 6 species were collected and examined for helminths, including 71 *H. gaumeri* (Heteromyidae), 36 *P. yucatanicus*, 35 *O. phyllotis*, 24 *S. toltecus*, 3 *Reithrodontomys gracilis* Allen & Chapman, and 1 *Oligoryzomys fulvescens* (Saussure) (Cricetidae). Twenty-two helminth species were identified, including three trematodes (Brachylaimidae, Dicrocoeliidae and Microphallidae), five cestodes (Davaineidae, Hymenolepididae and Taeniidae), and 14 nematodes (Trichuridae, Ancylostomatidae, Ornithostrongylidae, Heligmonellidae, and Oxyuridae). The overall frequency of infection in small rodents was 84.1% (143/170); all specimens of *H. gaumeri*, *S. toltecus* and *Ol. fulvescens* were infected with helminths.

List of species of helminths

Phylum Platyhelminthes Gegenbaur

Class Trematoda Rudolphi

Subclass Digenea Carus

Superfamily Brachylaimoidea Joyeux & Foley

Family Brachylaimidae Joyeux & Foley

Subfamily Ityogoniminae Yamaguti

Scaphiostomum Braun

Scaphiostomum sp.

Site of infection: Small intestine

Host species: *Heteromys gaumeri* and *Sigmodon toltecus*

Localities: Hobonil ranch, Santa Cruz cattle ranch (Yucatan) and Zoh Laguna community (Campeche)

Specimens deposited: CNHE 10973, 11954–6

GenBank accession number: OR271636

Comments: The collected specimens have morphological features that allowed us to identify them as a species of the genus *Scaphiostomum* (Mas-Coma *et al.* 1986), i.e., body filiform with tegument unspined; suckers slightly spaced; pharynx small; testes and ovary in tandem (ovary inter-testicular), close to each other, inter-caecal; cirrus-sac small; genital pore anterior to anterior testis; vitellarium not reaching at the level of ventral sucker and termi-

nating posteriorly at level of anterior testis; uterus very long, forming numerous loosely arranged coils, anteriorly very close to ventral sucker. Our specimens had suckers nearly equal in size; prepharynx absent; esophagus absent; anterior testis bilobed; and vitellarium slightly separated from the posterior region of the ventral sucker (Figure 2A). The main measurements of our specimens were: body length 5250–9625, maximum width 912.5–1225; oral sucker 262.5–375 long by 250–375 wide; ventral sucker 250–312.5 long by 237.5–325 wide; eggs 29.5–31.5 long by 19.5–20 wide. Two species of *Scaphiostomum* have been reported in American rodents (Mas-Coma *et al.* 1986), *Scaphiostomum microti* (Kruidenier & Gallicchio) and *Scaphiostomum pancreaticum* McIntosh. However, these species can be differentiated from our specimens by having a longer body (9710–12750 in *Sc. pancreaticum*), smaller oral sucker (128–220 in *Sc. microti* and 235 in *Sc. pancreaticum*), ventral sucker (150–220 in *Sc. microti* and 240 *Sc. pancreaticum*), and larger eggs (32–38 in *Sc. microti* and 35 in *Sc. pancreaticum*). In Belize, Bersot (2001) reported *Sc. pancreaticum* in *H. gaumeri* and *O. phyllotis*, however, he also stated that the identity of this trematode should be confirmed. Considering that the brief morphological description of Bersot' (2001) specimens is closer to our specimens than that of *Sc. pancreaticum*, it is likely that the trematode from the Yucatan Peninsula represent a new, undescribed *Scaphiostomum* species.

This is the first record of the genus *Scaphiostomum* in Mexico and for *S. toltecus*.

Superfamily Gorgoderioidea Looss

Family Dicrocoeliidae Looss

Subfamily Leiptrematinae Yamaguti

Skrjabinus Bhalerao

Skrjabinus sp.

Site of infection: Bile ducts

Host species: *Heteromys gaumeri*

Locality: Hobonil ranch (Yucatan)

Specimens deposited: CNHE 11957

GenBank accession number: OR271635

Comments: The morphology observed in the specimens of this study agrees with the characteristics established for the genus *Skrjabinus* (Pojmańska 2008), i.e., body elongate and fusiform, tegument unspined with acetabulum in anterior third of body, larger than the oral sucker; pharynx well developed and esophagus short, intestinal bifurcation anterior to ventral sucker and caeca reaching the posterior region of the hind body. Testes postero-lateral to ventral sucker. Cirrus-sac extends beyond intestinal bifurcation. Genital pore posterior to the pharynx but anterior to intestinal bifurcation. Ovary rounded, submedian, post-testicular, separated from testes by uterine coils. Uterus intercaecal, occupying entire hind body. Vitelline follicles fine, begin from the middle or from the posterior margin of the ventral sucker and reach the final region of the second third of the body. The main measurements of our specimens were: body length 2825–3725 and maximum width 875–1475; oral sucker 300–350 long by 275–362.5 wide; pharynx 125–162.5 long by 137.5–175 wide; ventral sucker 425–537.5 long by 437.5–500 wide; oral sucker/ventral sucker ratio 1.3–1.8; and eggs 32.5–37.5 long by 20–22.5 wide. The most similar species to our specimens is *Skrjabinus delectans* (Braun), parasite of *Nothura maculosa* (Temminck) from Argentina; however, *Sk. delectans* exhibits some morphological differences (Sutton & Lunaschi 1987), such as a shorter oral sucker (vs 160–200), shorter pharynx (vs 60–80), lower oral sucker/ventral sucker ratio (vs 1.6–2.8) and vitellarium not distributed to the last posterior third of the body (Figure 2B and C). For this reason, we consider that our specimens may represent a species not described yet.

This is the first record of the genus *Skrjabinus* in Mexico and for *H. gaumeri*.

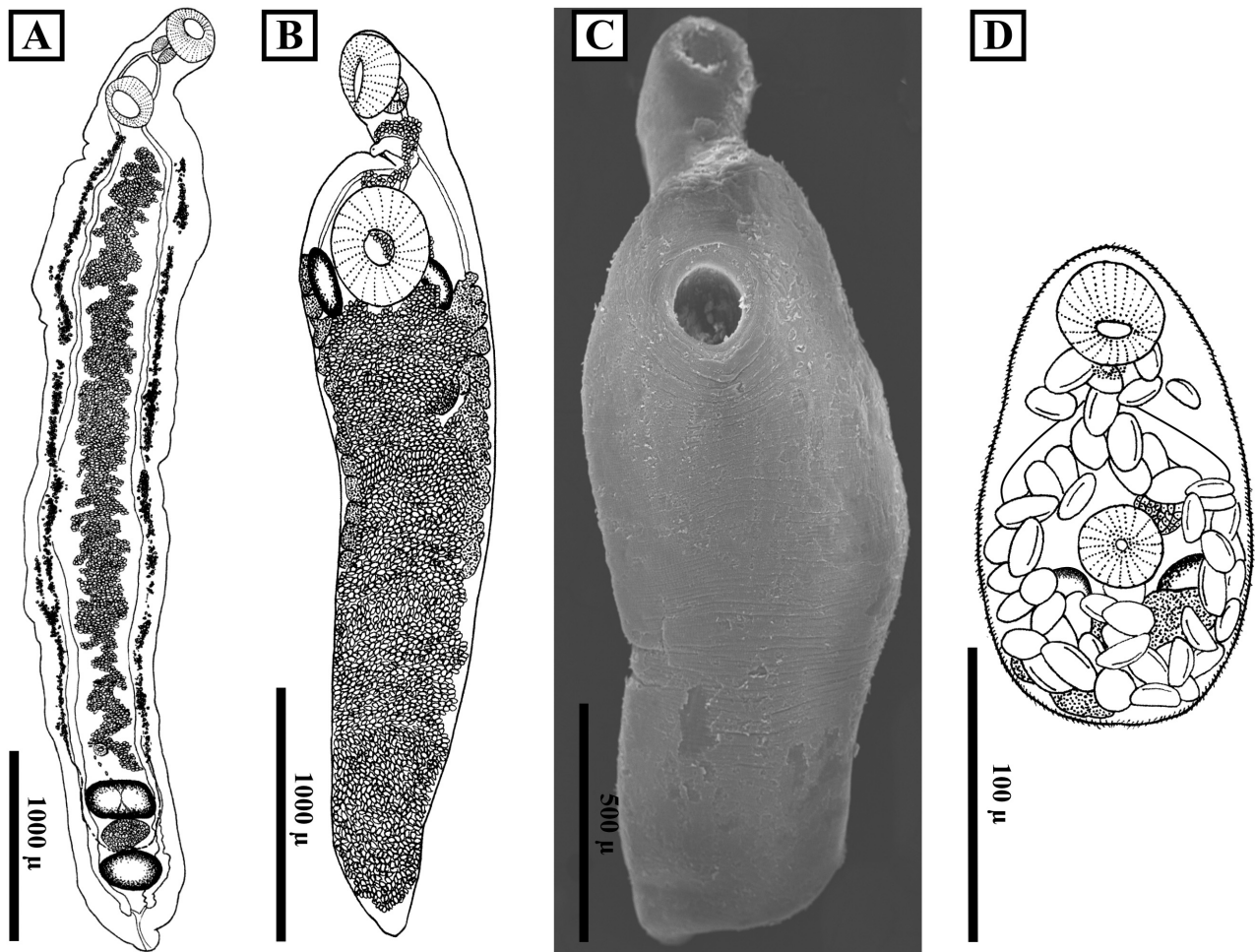


FIGURE 2. A. Adult specimen of *Scaphiostomum* sp. from *Heteromys gaumeri*, ventral view. B. Adult specimen of *Skrjabinus* sp. from *Heteromys gaumeri*, ventral view. C. SEM micrograph of *Skrjabinus* sp. from *Heteromys gaumeri* showing the ventral surface and the acetabulum, ventral view. D. Adult specimen of Microphallidae gen. sp. from *Peromyscus yucatanicus*, ventral view.

Superfamily Microphalloidea Ward

Family Microphallidae Ward

Microphallidae gen. sp.

Site of infection: Small intestine

Host species: *Peromyscus yucatanicus*

Locality: Molas farm and Aak ecological park (Yucatan)

Specimens deposited: CNHE 11958

Comments: The trematodes found in *P. yucatanicus* presented characteristics of Microphallidae (Deblock 2008), i.e., tiny adults, 500±300; body flattened dorsoventrally; tegument spinous; two medium-sized suckers, well separated; oral sucker subterminal and ventral sucker post-equatorial; pharynx present; caeca widely divergent, not extending beyond ventral sucker; two testes, lateral, symmetrical, and post-ovarian; male terminal genitalia inter-caecal, anterior to ventral sucker; ovary post-caecal, pretesticular, aporal at the level of ventral sucker and submedian; vitellarium follicular, in two symmetrical clusters post-caecal; eggs numerous unembryonated in utero. The specimens found in Yucatan had a body pyriform; suckers almost the same size; prepharynx absent; genital pore dextral to ventral sucker; and uterus extending to oral sucker. The main measurements of our specimens were: body

length 171.25 and maximum width 97.5; oral sucker 37.5 long by 40 wide; pharynx 16.25 long by 15 wide; ventral sucker 23.75 long by 25 wide; and eggs 21.25 long by 12.5 wide. The male and female genitalia and esophagus could not be clearly observed due to the large number of eggs present in the uterus (Figure 2D), which did not allow us to identify the specimens at the genus level.

This is the first record of Microphallidae in mammals from Mexico and for *P. yucatanicus*.

Class Cestoda Rudolphi

Subclass Eucestoda Southwell

Order Cyclophyllidea Van Beneden in Braun

Family Davaineidae Braun

Raillietina Fuhrmann

Raillietina sp. (1)

Site of infection: Small intestine

Host species: *Heteromys gaumeri*, *Ototylomys phyllotis*, *Peromyscus yucatanicus*, and *Sigmodon toltecus*

Localities: Hobonil ranch, Santa Cruz cattle ranch, Aak ecological park, Kuncheil cattle ranch (Yucatan), Ich ha lol xaan ecological park, Zoh Laguna community (Campeche), Jolie Jungle eco-hotel, and Balam Nah eco-hotel (Quintana Roo)

Specimens deposited: CNHE 10968, 10969, 10972, 11959, 11960–11971

GenBank accession numbers: OR271637–OR271648

Comments: The morphological characteristics observed in our specimens agreed with those established for the genus *Raillietina*, i.e., rostellum with double crowns of alternating hooks; armed suckers; craspedote proglottids; single reproductive organs; unilateral genital pores; small cirrus-sac, not reaching or just crossing the osmoregulatory canals; numerous testes; ovary median; and several eggs per capsule (Khalil *et al.* 1994). Our specimens had 72–80 rostellar hooks; suckers 65–135 long by 74–137 wide (Figure 3A); anterior hooks 16–20 long, posterior hooks 19–22.5 long; 14–17 testes; 34–105 egg capsules; and 1–4 eggs per capsule. In North America, two species of *Raillietina* have been described in rodents, *Raillietina bakeri* Chandler from *Sciurus niger rufiventer* Geoffroy and *Raillietina sigmodontis* Smith from *Sigmodon hispidus texianus* (Audubon & Bockman). *Raillietina bakeri* and *Ra. sigmodontis* were described with the same number (66) and length (20–22) of rostellar hooks but differences in the number of testes (30–40 vs 15–19) and egg capsules (80–90 vs 30–35) and eggs per capsule (6–10 vs 15–25) were observed (Chandler 1942; Smith 1954). In the original descriptions of *Ra. sigmodontis*, Smith (1954) mentioned that no morphological variations had been reported for *Ra. bakeri* and concluded that *Ra. sigmodontis* represented a new species. However, Baylis (1945) reported variations in the number (88–97) and length (25–30) of rostellar hooks for *Ra. bakeri* collected from *Sigmodon hispidus* Say & Ord, differences that could be related to its occurrence in a different host species. In *Ra. sigmodontis* collected from *S. toltecus* (originally reported as *S. hispidus*), *H. gaumeri* and *O. phyllotis* in Belize, Bersot (2001) also reported variations in the number (84) and length (25.6) of rostellar hooks and number (21–26) of testes, compared with the original description of this species. Considering these wide variations in the reported morphology of both *Raillietina* species and that our specimens shared traits with them, we cannot assign *Raillietina* to the species level. Indeed, Cameron & Reesal (1951) mentioned that substantial variation in dimensions and numbers of the characters used for the parasite diagnosis such as hooks, testes and egg capsules even within the cestodes from the same host can be observed in *Raillietina*.

In Mexico, *Raillietina baeri* Meggitt & Subramanian was recorded from *Heteromys irroratus* (Gray) in Hidalgo (Carmona-Huerta 1994), and *Raillietina celebensis* (Janicki) from *Oryzomys* sp. in Oaxaca (Flores-Barroeta & Hidalgo-Escalante 1960). In addition, unidentified species of *Raillietina* have been reported from *Heteromys pictus* Thomas in Durango (García-Prieto *et al.* 2012), *Dipodomys phillipsi* Gray in Puebla and Veracruz (García-Prieto *et al.* 2012), *Oryzomys couesi* (Alston) and *Oryzomys melanotis* Thomas in San Luis Potosí (Underwood *et al.* 1986),

H. irroratus in Tlaxcala (García-Prieto *et al.* 2012), *Chaetodipus* sp. in Zacatecas (Martínez-Salazar *et al.* 2016), and *S. toltecus* in Yucatan (Panti-May *et al.* 2018). Our finding extends the geographical distribution of the genus *Raillietina* including the states of Campeche and Quintana Roo in Mexico. In addition, this cestode genus is reported for the first time in *P. yucatanicus*. Further morphological and molecular studies on *Raillietina* species infecting small rodents in North America are needed to clarify their identity.

***Raillietina* sp. (2)**

Site of infection: Small intestine

Host species: *Heteromys gaumeri* and *Sigmodon toltecus*

Localities: Vallazoo, Kuncheil cattle ranch (Yucatan), Ich ha lol xaan ecological park and Zoh Laguna community (Campeche)

Specimens deposited: CNHE 10970, 10971, 11972–11974

GenBank accession numbers: OR271649– OR271651

Comments: The specimens were identified as *Raillietina* by the morphological features mentioned above. *Raillietina* sp. (2) differs from *Raillietina* sp. (1) as to the number (91–93 vs 72–80) and length (21–25 vs 16–20 anterior and 24–30 vs 19–22.5 posterior) of rostellar hooks. Because most specimens were immature and large sections of the strobila (mature and gravid proglottids) from mature specimens were in poor condition, detailed measurements of the reproductive structures could not be taken. Nevertheless, the characteristics of the hooks, and genetic distances and phylogeny (see results below) indicate that two species of *Raillietina* parasitize small rodents in the Yucatan Peninsula.

Family Hymenolepididae Pierrier

***Hymenolepis* Weinland**

***Hymenolepis* sp.**

Site of infection: Small intestine

Host species: *Heteromys gaumeri*

Locality: Hobonil ranch (Yucatan)

Specimens deposited: CNHE 11975

GenBank accession numbers: OR271652– OR271654

Comments: The morphological characteristics observed in our specimens agreed with those established for the genus *Hymenolepis* (*sensu stricto*) (Czapliski & Vaucher 1994), i.e., scolex with unarmed rostellum (Figure 3B); three testes separated in two groups by female gonads; ovary wide, median, lobed, fan shaped, and ventral to male genital organs; vitelline gland compact and median; cirrus-sac short, not reaching middle of proglottid; uterus labyrinthine. In North America, 11 species of *Hymenolepis* occur in sciurid, arvicoline, geomyid, and neotomine rodents (Rowan *et al.* 2023): *Hymenolepis diminuta* (Rudolphi), *Hymenolepis citelli* (McLeod), *Hymenolepis scalopi* Schultz, *Hymenolepis pitymi* Yarinsky, *Hymenolepis tualatinensis* Gardner, *Hymenolepis weldensis* Gardner & Schmidt, *Hymenolepis geomydis* Gardner & Schmidt, *Hymenolepis robertrauschi* Gardner, Luedders & Duszynski, *Hymenolepis folkertsi* Makarikov, Nims, Galbreath & Hoberg, *Hymenolepis crateogeomyos* Gardner, Dursahinan, Campbell & Rácz, and *Hymenolepis ackerti* Rowan, Hope & Jiménez. The species found in *H. gaumeri* has a scolex with rostrum-like projection, which allows us to differentiate it from *Hy. diminuta*, *Hy. citelli*, *Hy. crateogeomyos*, *Hy. ackerti*, *Hy. weldensis*, *Hy. geomydis*, *Hy. scalopi*, and *Hy. robertrauschi*. Our specimens can be differentiated from the other three species that posse a scolex with rostrum-like projection, *Hy. tualatinensis*, *Hy. folkertsi* and *Hy. pitymi*, by several characteristics, such as a wider scolex (255–330 vs 92–167 in *Hy. tualatinensis*, 168 in *Hy. folkertsi*, and 159 in *Hy. pitymi*), a longer rostellar pouch (70–115 vs 51–61 in *Hy. tualatinensis* and 67 in *Hy. folkertsi*), and larger suckers (120–140 x 90–130 vs 93–102 x 70–86 in *Hy. folkertsi* and 66–92 x 37–45 in *Hy. pitymi*). Moreover, *Hy. tualatinensi* and *Hy. pitymi* parasitize geomyid and cricetid rodents, respectively. Phylogenetic analysis

showed that *Hymenolepis* from *H. gaumeri* and *Hy. folkertsi* were sister species (see results below). Considering the above mentioned, the specimens found in *H. gaumeri* likely represent a new, undescribed *Hymenolepis* species.

In Mexico, unidentified species of *Hymenolepis* have been reported from other heteromyid rodents such as *H. irroratus* in Puebla and Queretaro (García-Prieto *et al.* 2012) and *Dipodomys merriami* Mearns in Zacatecas (Martínez-Salazar *et al.* 2016). This is the first record of *Hymenolepis* in *H. gaumeri*.

Family Taeniidae Ludwig

Hydatigera Lamarck

Hydatigera taeniaeformis (Batsch)

(= *Taenia taeniaeformis* Batsch; = *Taenia infantis* Bacigalupo)

Site of infection: Liver

Host species: *Sigmodon toltecus*

Locality: Zoh Laguna community (Campeche)

Specimens deposited: CNHE 11976

GenBank accession number: OR271655

Comments: Each cyst contained one metacestode (strobilocercus). All the specimens collected in this study showed characteristics that agreed with descriptions given by Jones & Pybus (2001) and Panti-May *et al.* (2018) from *Rattus rattus* Linnaeus and *S. toltecus*, i.e., scolex with four suckers, 303.9 long by 274.4 wide, and rostellum with 2 crowns of 18 hooks each, different in size (Figure 3C), longer hooks 360–400 in length and smaller hooks 230 in length (Figure 3D).

In Mexico, *Hyd. taeniaeformis* has been reported from commensal rodents *Mus musculus* Linnaeus, *Rat. rattus* and *Rattus norvegicus* (Berkenhout) in several states (see Panti-May *et al.* 2021). In wild rodents, this cestode has been reported from *S. hispidus* in Nuevo León (Gutiérrez-González 1980) and *S. toltecus* and *Sciurus yucatanensis* Allen in Yucatan (Panti-May *et al.* 2018, 2019). This is the first record of *Hyd. taeniaeformis* in Campeche.

Taenia rileyi Loewen

(= *Taenia lyncis* Skinker)

Site of infection: Liver

Host species: *Sigmodon toltecus*

Locality: Kuncheil ranch (Yucatan)

Specimens deposited: CNHE 11977

Comments: Each cyst contained one small, poorly developed metacestode 1.5–2.8 mm long (without bladder). The metacestodes examined in this study showed characters which agreed with descriptions given by Mollhagen (1979) from *S. hispidus*, Rausch (1981) from *Myodes rutilus* (Pallas) and *Tamiasciurus hudsonicus* (Erleben), and the updated revision of the genus *Taenia* (Loos-Frank 2000), i.e., invaginated scolex with four suckers 140 long by 160 wide and rostellum with 2 crowns of 19–20 hooks each (Figure 3E), longer hooks 240 in length and smaller hooks 190–205 in length (Figure 3F).

While some studies have reported strobilocercus larvae for *T. rileyi* (Grundmann 1958; Mollhagen 1979), other studies refer to it as cysticercus (Mahrt & Soo-Jeet 1972; Mollhagen 1978). There is considerable confusion on the form of larval *T. rileyi* due to the different levels of development of the strobilization. Since strobilization might easily interpret an evaginated cysticercus of *T. rileyi*, Mollhagen (1979) suggested not considering it as the sole diagnostic criterion. In Mexico, metacestodes of *Hyd. taeniaeformis* have also been reported in the liver of cricetid and murid rodents (Preisser & Falcón-Ordaz 2019; Panti-May *et al.* 2021). However, the length of large hooks of *Hyd. taeniaeformis* is larger than those of *T. rileyi*.

The only record of *T. rileyi* in Mexico was reported by Flores-Barroeta (1966) in *Canis familiaris* Linnaeus from Mexico City. Our study reports *T. rileyi* for the first time in rodents from Mexico.

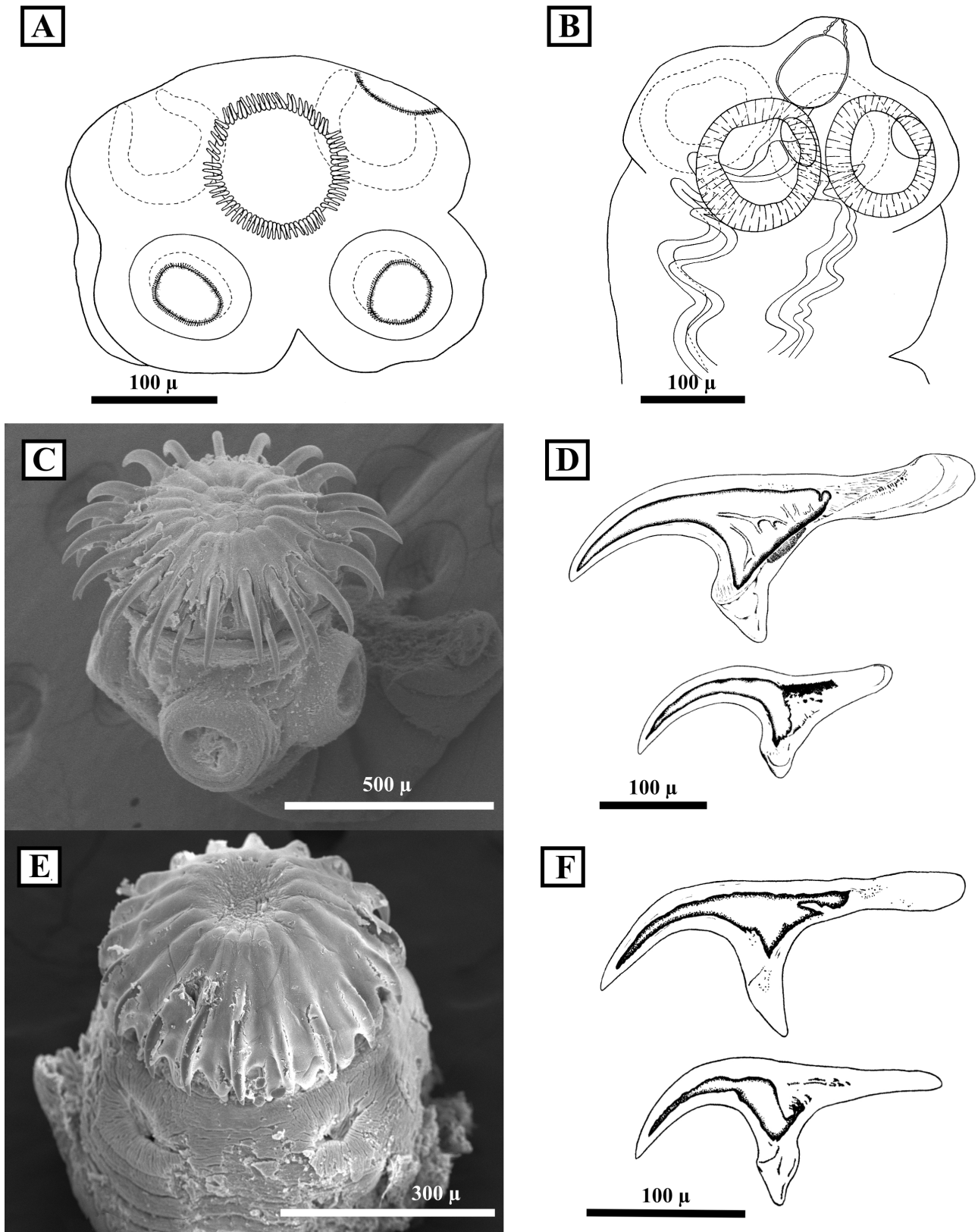


FIGURE 3. A. Scolex of *Raillietina* sp. (1) from *Sigmodon toltecus*, apical view. B. Scolex of *Hymenolepis* sp. from *Heteromys gaumeri*, dorsoventral view. C. SEM micrograph of scolex of the metacestode of *Hydatigera taeniaeformis* from *Sigmodon toltecus*, apical view. D. Large and small rostellar hooks of the metacestode of *Hydatigera taeniaeformis* from *Sigmodon toltecus*, lateral view. E. SEM micrograph of scolex of the metacestode of *Taenia rileyi* from *Sigmodon toltecus*, apical view. F. Large and small rostellar hooks of the metacestode of *Taenia rileyi* from *Sigmodon toltecus*, lateral view.

Phylum Nematoda Rudolphi

Class Adenophorea Chitwood

Order Enoplida Baird

Superfamily Trichinelloidea Ward

Family Trichuridae Ransom

***Trichuris* Roederer**

***Trichuris silviae* Panti-May & Robles**

Site of infection: Caecum

Host species: *Heteromys gaumeri*

Localities: Hobonil ranch, Molas farm, Dzununcan farm, San Francisco cattle ranch, Santa Cruz cattle ranch, Vallazoo, Aak ecological park, Papam ranch, Kuncheil cattle ranch (Yucatan), Ich ha lol xaan ecological park, Zoh Laguna community (Campeche), Jolie Jungle eco-hotel, and David Gustavo community (Quintana Roo)

Specimens deposited: CNHE 11978–11989

GenBank accession numbers: OR271656– OR271660

Comments: The specimens examined in this study had characteristics described by Panti-May & Robles (2016) of whipworms from *H. gaumeri*, i.e., males with spicular tube; spicule 1020–1762 long; proximal cloacal tube 850–1925 long, united laterally to a distal cloacal tube 412– 855 long; cylindrical (or slightly campanulate at apical end; Figure 4A) and spiny spicular sheath; females with non-protrusive vulva and eggs 52–60 long by 28–32 wide.

Trichuris silviae has been reported from *H. gaumeri* in Merida, Tzucacab (Panti-May & Robles 2016) and Xkalakdzonot (Panti-May *et al.* 2018), Yucatan. These new records expand the geographical distribution of *Tr. silviae* to Campeche and Quintana Roo.

Class Secernentea Von Linstow

Order Strongylida Diesing

Suborder Ancylostomatina (Loss)

Superfamily Ancylostomatoidea (Looss)

Family Ancylostomatidae (Looss)

Subfamily Bunostominae (Railliet & Henry)

***Monodontus* Molin**

***Monodontus* sp.**

Site of infection: Small intestine

Host species: *Sigmodon toltecus*

Locality: Ich ha lol xaan ecological park and Balam Nah eco-hotel (Campeche)

Specimens deposited: CNHE 11990

GenBank accession number: OR271661

Comments: Infected rodents harbored only females. The characteristics of the mouth, i.e., buccal capsule well developed with two semilunar ventral cutting plates at oral margin (Figure 4B), a dorsal tooth terminating the

dorsal gutter, two irregular subventral teeth, and irregular toothlike serrations on lateral ridge, ventral teeth absent and dorsal inclination of anterior extremity pronounced, allows us to place the specimens in the genus *Monodontus* (Chitwood & Jordan 1965). The main measurements of our specimens were: body 5290–5560 long and 315–350 wide; esophagus 570–575 long; cervical papillae 250–365 from the anterior end; vulva 2430–2563 from the anterior end; and eggs 50–65 long by 30–40 wide. However, more specimens, particularly males, are necessary to identify this taxon at the species level.

This is the first record of *Monodontus* in Mexico.

Suborder Trichostrongylina Durette-Desest & Chabaud

Superfamily Heligmosomoidea Travassos

Family Ornithostrongylidae (Travassos)

Subfamily Ornithostrongylinae Travassos

Vexillata Travassos

Vexillata vexillata (Hall)

(= *Heligmosomum vexillatum* Hall)

Site of infection: Small intestine

Host species: *Heteromys gaumeri*

Localities: Hobonil ranch, Molas farm, Dzununcan farm, San Francisco cattle ranch, Santa Cruz cattle ranch, Vallazoo, Aak ecological park, Papam ranch, Kuncheil cattle ranch (Yucatan), Ich ha lol xaan ecological park, Zoh Laguna community (Campeche), Jolie Jungle eco-hotel, Balam Nah eco-hotel, and David Gustavo community (Quintana Roo)

Specimens deposited: CNHE 11991–12004

GenBank accession numbers: OR271662–OR271664, OR271674, OR271678, OR271681

Comments: The characteristics observed in all specimens examined from the Yucatan Peninsula were in accordance with the original description by Hall (1916) of parasites from *Thomomys talpoides fossor* (Allen), the redescriptions by Sanabria Espinosa *et al.* (1996) from *H. irroratus* and *Peromyscus difficilis* (Allen) and Durette-Desest (1978) from *Chaetodipus hispidus* (Baird), and a recent report by Panti-May *et al.* (2018) from *H. gaumeri*. All males had a synlophe with well-developed careen; 12 cuticular ridges in the synlophe at midbody (Figure 4C); subsymmetrical bursa with a pattern of type 2-2-1; dorsal ray with two small and asymmetric accessory branches starting about its mid-length; rays 8 arising from base of dorsal ray and similar in length to it; dorsal ray with bifid extremities (Figure 4D); simple genital cone; and simple spicules 300–425 long.

Vexillata vexillata has been reported from *H. pictus* in Chiapas (Caballero y Caballero 1958), *H. irroratus* and *P. difficilis* in Hidalgo (Sanabria Espinosa *et al.* 1996; Falcón-Ordaz & Sanabria Espinosa 1997), *H. irroratus* in Morelos (Ortiz 1999), and *H. gaumeri* in Yucatan (Panti-May *et al.* 2018). This is the first record of *V. vexillata* in Campeche and Quintana Roo, extending its geographical range.

Heligmosomoidea gen. sp. cf. *Vexillata*

Site of infection: Small intestine

Host species: *Ototylomys phyllotis*

Localities: Kuncheil cattle ranch, Papam ranch (Yucatan), Jolie Jungle eco-hotel, Balam Nah eco-hotel, and David Gustavo community (Quintana Roo)

Specimens deposited: CNHE 12005–12009

GenBank accession numbers: OR271665, OR271682

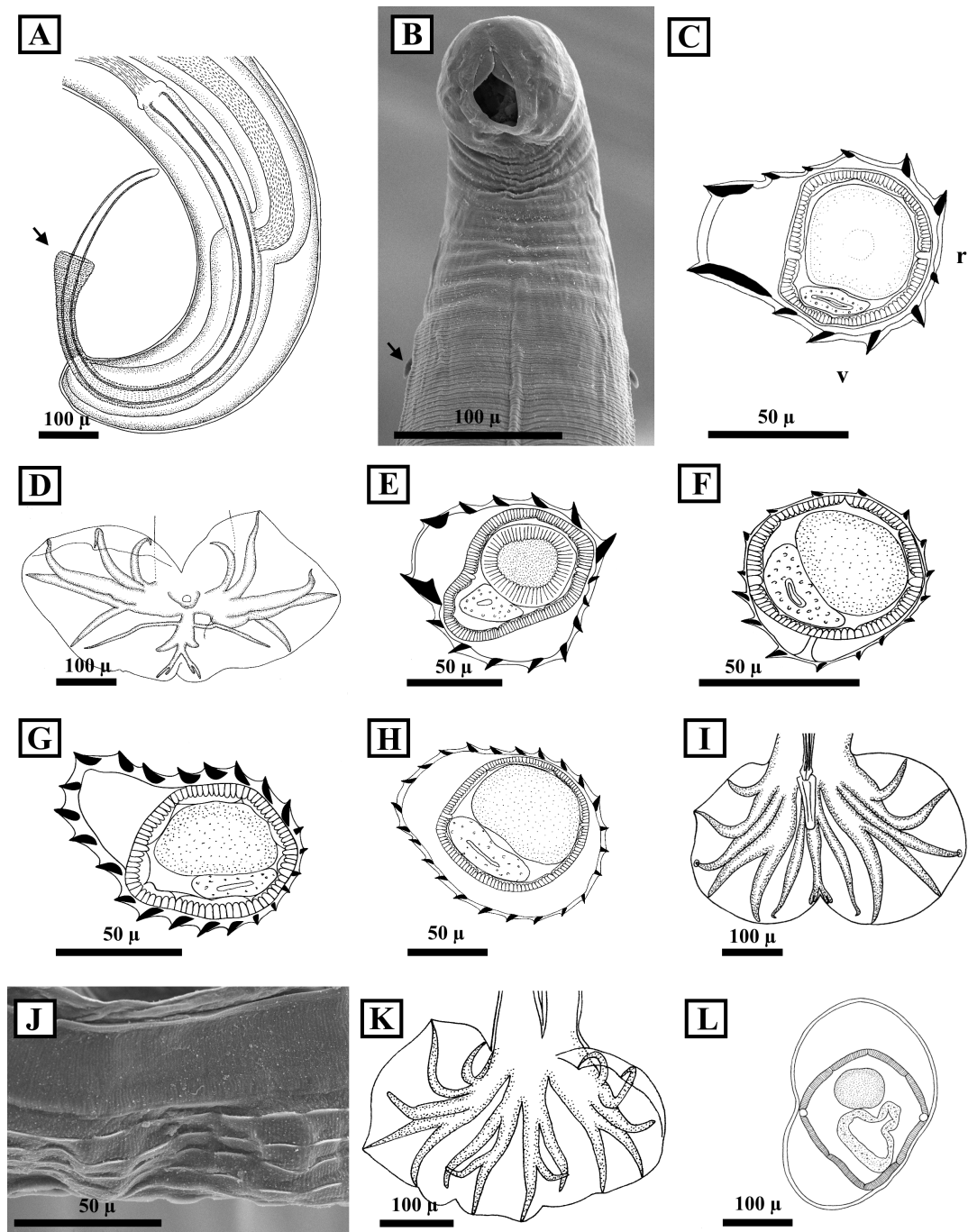


FIGURE 4. A. Posterior end of male specimen of *Trichuris sylviae* from *Heteromys gaumeri* showing the slightly campanulate spicular sheath (arrow), lateral view. B. SEM micrograph of the anterior extremity of *Monodontus* sp. from *Sigmodon toltecus* showing the mouth opening, paired cutting plates and cervical papillae (arrow), ventral view. C. Cross section at midbody showing features of the synlophe of female *Vexillata vexillata* from *Heteromys gaumeri*. D. Male caudal bursa of *Vexillata vexillata* from *Heteromys gaumeri*, ventral view. E. Cross section at midbody showing features of the synlophe of male Heligmosomoidea gen. sp. cf. *Vexillata* from *Ototylomys phyllotis*. F. Cross section at midbody showing features of the synlophe of female *Carolinensis* sp. from *Peromyscus yucatanicus*. G. Cross section at midbody showing features of the synlophe of male *Hassalstrongylus aduncus* from *Sigmodon toltecus*. H. Cross section at midbody showing features of the synlophe of female *Hassalstrongylus musculi* from *Oligoryzomys fulvescens*. I. Male caudal bursa of *Hassalstrongylus musculi* from *Ototylomys phyllotis*, dorsal view. J. SEM micrograph of female *Heligmostrongylus* sp. from *Peromyscus yucatanicus* showing the discontinuous ridges, lateral view. K. Male caudal bursa of *Heligmostrongylus* sp. from *Peromyscus yucatanicus*, ventral view. L. Cross section at midbody of female Heligmonellidae gen. sp. from *Sigmodon toltecus* showing the absence of synlophe. Abbreviations: r, right side; v, ventral side. All cross sections of the synlophe orientated as in figure C.

Comments: The specimens found in this study had a cephalic vesicle and a buccal capsule reduced to an annulus. Females were monodelphic and lack a caudal spine. The synlophe showed 15 ridges with struts, including a careen moderately developed composed of two stout ridges, an axis of orientation of the ridges oblique to subfrontal, and a slight decreasing gradient of the ridge size from right to left on the dorsal side (Figure 4E). Males possessed a subsymmetrical caudal bursa with a pattern of type 2-2-1, spicules filiform and a gubernaculum. In females, at the ovejector level, the synlophe was highly modified, with hypertrophy and loss of orientation of the ridges on the whole-body circumference.

The combination of the abovementioned characters allows us to place these specimens undoubtedly in the Heligmosomoidea excluding, among these, the families Herpetostrongylidae, Nicollinidae, Heligmosomidae and Viannaiidae (Beveridge *et al.* 2013). Particularly, the bursal pattern 2-2-1, the synlophe with careen, the ridges continuous and the presence of gubernaculum approach them to the Nippostrongylinae (Heligmonellidae) or, to a lesser degree, to species of *Vexillata* (Ornithostrongylidae), all parasites of rodents. The cosmopolitan Nippostrongylinae are typically parasites of cricetids, whereas species of the New World genus *Vexillata* have been reported from geomyids and heteromyids and from leporids of the genus *Sylvilagus* (Digiani *et al.* 2007). The only carenated Nippostrongylinae from the New World is, up to now, the monotypic genus *Mazzanema* Digiani, Notarnicola & Paulos, 2013, with a species parasitic in *Holochilus chacarius* from Argentina, characterized by a female synlophe of 19 ridges and a male bursal pattern 1-3-1 (Digiani *et al.* 2013). Attending to the main synlophial and bursal characters of the present specimens, plus the fact that the host is a cricetid, they could be assigned to a genus and species not yet described in the Nippostrongylinae. However, the phylogenetic analysis based on the 28S sequences recovered them as sister species of *V. vexillata*, and not of the other Nippostrongylinae comprised in the study. Morphological characters that approach these specimens to *Vexillata* are the careen made up of two ridges, the axis of orientation subfrontal, the bursal pattern 2-2-1, the bursal rays 8 filiform, and the distal division of the dorsal ray. However, the 14 known species of *Vexillata* are characterized by fewer ridges (9-12), ridges of the careen long and thin; usually lack modifications of the synlophe at the ovejector level and, up to now, have never been reported from cricetids. The taxonomic value of all these characters (morphology, genetics, host specificity) will be assessed with an integrative approach. By the moment the scenario is rather puzzling, and we prefer to consider these specimens from *O. phyllotis* as Heligmosomoidea gen. sp. cf. *Vexillata*.

This is the first record of the Heligmosomoidea for *O. phyllotis*.

Family Heligmonellidae Skrjabin & Schikobalova

Subfamily Nippostrongylinae Durette-Desset

Carolinensis Travassos

Carolinensis sp.

Site of infection: Small intestine

Host species: *Peromyscus yucatanicus*

Localities: Dzununcan farm, Aak ecological park, Papam ranch, Kuncheil cattle ranch (Yucatan) and Jolie Jungle eco-hotel (Quintana Roo)

Specimens deposited: CNHE 12010–12013

GenBank accession numbers: OR271666, OR271680

Comments: The morphological characters observed in the synlophe and the caudal bursa of the specimens agree with the description of the genus *Carolinensis* (Durette-Desset 2009). Our specimens had a synlophe with 16 ridges at midbody in both sexes (Figure 4F); subsymmetrical bursa with rays 8 arising from base of dorsal ray; bifid extremities of dorsal ray; and spicules 210–285 long, characters shared with *Carolinensis peromysci* (Durette-Desset). However, our specimens exhibit some differences, such as a pattern of type 1-4 t 1-3-1, the level of divergence of the dorsal ray (second half) and the spicule tips (curved). The latter two features are similar to those reported in *Carolinensis dikmansi* (Durette-Desset) but this species had a larger spicule (370) and a well-developed genital cone. Based on these differences, we cannot assign *Carolinensis* to the species level.

This finding expands the geographical distribution of *Carolinensis* to Quintana Roo.

Hassalstrongylus Durette-Dessete

Hassalstrongylus aduncus (Chandler)

(= *Longistriata adunca* Chandler; = *Longistriata norvegica* Dikmans)

Site of infection: Small intestine

Host species: *Sigmodon toltecus*

Localities: Hobonil ranch, Vallazoo, Kuncheil cattle ranch (Yucatan), Ich ha lol xaan ecological park, Zoh Laguna community (Campeche), and Balam Nah eco-hotel (Quintana Roo)

Specimens deposited: CNHE 12016–120221

GenBank accession numbers: OR271669, OR271677, OR271679

Comments: The specimens collected in the Yucatan Peninsula presented morphological characteristics in accordance with the original description given by Chandler (1932) for parasites of *S. hispidus* and the re-description by Durette-Desset (1972) from the same host, i.e., 23 cuticular ridges in the synophe at midbody (Figure 4G); sub-symmetrical bursa, with two well-developed lateral lobes and small dorsal lobe, bursal pattern type 1-4 with ray 2 well separated and divergent from the ray 3; dorsal ray with a thick trunk at the base and forking in the shape of an inverted U; and spicules 330–600 long with sigmoid tips.

In Mexico, *Ha. aduncus* has been reported from *S. hispidus* in Hidalgo and Jalisco (García-Prieto *et al.* 2012) and from *S. toltecus* and *Rat. rattus* in Yucatan (Panti-May *et al.* 2018). This is the first record of *Ha. aduncus* in Campeche and Quintana Roo. This finding extends the geographical range of *Ha. aduncus* in the Yucatan Peninsula.

Hassalstrongylus musculi (Dikmans)

(= *Longistriata musculi* Dikmans)

Site of infection: Small intestine

Host species: *Ototylomys phyllotis* and *Oligolyzomys fulvescens*

Localities: Ich ha lol xaan ecological park (Campeche)

Specimens deposited: CNHE 12014, 12015

GenBank accession numbers: OR271667, OR271668

Comments: The characteristics observed in our material agreed with those described by Dikmans (1935), the re-description by Durette-Desset (1974) and by Panti-May *et al.* (2018) of parasites from *M. musculus*, i.e., 24 cuticular ridges in the synophe at midbody (Figure 4H); slightly dissymmetrical bursa with right lobe larger than left, with pattern of type 1-3-1; rays 8 stout and longer than the dorsal ray; dorsal ray divided in its second third (Figure 4I); spicules 400–430 long with typical foot shaped tips; and gubernaculum absent.

In Mexico, *Ha. musculi* has been recorded from *Ol. fulvescens*, *Or. couesi*, and *Handleyomys melanotis* Thomas in San Luis Potosí (Underwood *et al.* 1986) and *M. musculus* in Yucatan (Panti-May *et al.* 2018, 2021). *Hassalstrongylus musculi* is reported for the first time in Campeche and for *O. phyllotis*.

Subfamily Pudicinae Skrjabin & Schikhobalova

Heligmostrongylus Travassos

(= *Heligmodendrium* Travassos; = *Squamastrongylus* Travassos)

Heligmostrongylus sp.

Site of infection: Small intestine

Host species: *Peromyscus yucatanicus* and *Ototylomys phyllotis*

Locality: Santa Cruz cattle ranch, Vallazoo (Yucatan) and Balam Nah eco-hotel (Quintana Roo)

Specimens deposited: CNHE 12022

GenBank accession numbers: OR271675, OR271676

Comments: The specimens found in the Yucatan Peninsula belong to the genus *Heligmostrongylus* according to the features described by Durette-Desset *et al.* (2017), i.e., synlophe with 10–14 ridges; careen made up of two large continuous ridges and other ridges discontinuous or scalloped; single axis of orientation subfrontal; bursal pattern of type 2-2-1; dorsal ray dividing generally within proximal half; gubernaculum absent; spicules ending in a single sharp tip. Our specimens had a synlophe with 13 ridges; a well-developed careen made up of two ridges plus 11 interrupted, scalloped ridges, arranged in linear series (five dorsal and six ventral) (Figure 4J), single axis of orientation subfrontal; bursal pattern of type 2-2-1, dorsal ray dividing within proximal third, rays 9 long, slightly hook-shaped, crossing over rays 8 ventrally, gubernaculum absent (Figure 4K); and spicules 570–620 long.

Following the keys of Durette-Desset *et al.* (2017) the genus *Heligmostrongylus* includes nine species reported from the Cuniculidae, Echimyidae and Dasyproctidae in South America: *Heligmostrongylus almeidai* (Durette-Desset & Tchérakoff) in Brazil, *Heligmostrongylus chiarae* Durette-Desset, Deharo, Santiváñez-Galarza & Chabaud in Bolivia, *Heligmostrongylus crucifer* (Travassos) in Brazil, *Heligmostrongylus differens* Lent & Freitas in Brazil, *Heligmostrongylus echimyos* Diaw in French Guiana, *Heligmostrongylus elegans* (Travassos) in Brazil, *Heligmostrongylus proechimysi* Durette-Desset in Colombia, *Heligmostrongylus sedecimradiatus* (Linstow) in Brazil, and *Heligmostrongylus squamastrongylus* (Travassos) in Brazil. Our specimens differ from *He. almeidai*, *He. chiarae*, *He. elegans*, *He. echimyos*, *He. proechimysi*, *He. sedecimradiatus*, and *He. squamastrongylus* by having rays 9 crossing over rays 8 (in these seven species rays 9 do not touch rays 8). In the case of *He. differens* and *He. crucifer*, differences in the pattern of rays 9 can be observed. *Heligmostrongylus crucifer* has rays 9 oriented to the dorsal lobe of bursa and *He. differens* has rays 9 smaller than rays 10, whereas our specimens have slightly curved rays 9, oriented to the lateral lobes and as long as rays 10. In addition, *He. crucifer* has 12 ridges in both sexes and *He. differens* possesses spicular alae developed. Based on these differences, the specimens from Mexico may represent a species not described yet.

This is the first record of *Heligmostrongylus* in North American rodents and for representatives of the Cricetidae.

Heligmonellidae gen. sp.

Site of infection: Mesentery

Host species: *Sigmodon toltecus*

Localities: Vallazoo (Yucatan)

Specimens deposited: CNHE 12023

GenBank accession numbers: OR271670

Comments: Only two female specimens were collected from the mesentery of *S. toltecus*. They exhibited characteristics of the family Heligmonellidae, such as presence of cephalic vesicle; monodelphy, and absence of caudal spine. However, the synlophe was absent (Figure 4L). Among heligmonellid nematodes of rodents, a strong reduction or even absence of synlophe is observed in species of the genus *Hypocristata* Durette-Desset. Three species of this genus have been described from sigmodontine rodents in Northern South America, including *Sigmodon hirsutus* (Burmeister) (originally described as *S. hispidus*) in Venezuela (Durette-Desset 1971; Durette-Desset & Guerrero 2006). The present specimens are very probably related to *Hypocristata* but the scarcity and condition of specimens and especially the lack of males prevent a more accurate identification.

Order Oxyurida Chabaud

Superfamily Oxyuroidea Cobbold

Family Oxyuridae Cobbold

Subfamily Syphaciinae Railliet

Syphacia Seurat

Syphacia peromysci Harkema

Site of infection: Caecum and large intestine

Host species: *Peromyscus yucatanicus*

Localities: Aak ecological park and Kuncheil cattle ranch (Yucatan)

Specimens deposited: CNHE 12024, 12025

Comments: The specimens examined from Yucatan had characteristics described by Kruidenier *et al.* (1961), Quentin & Kinsella (1972) and Panti-May *et al.* (2018), i.e., cephalic plate rounded (males) or laterally-elongated (females) (Figure 5A); cervical alae present in both males and females (Figure 5B); deirids in females, not observed in males; males with three mamelons (Figure 5C), spicule 57 long, gubernaculum 27 long, accessory hook with ornamentation, three pairs of caudal papillae surrounding the cloacal region, and tail 60 long (Figure 5D); some females with slightly prominent vulva; eggs 93.5–95.9 long by 27.1 wide (Figure 5E), and tail 441–509.6 long.

In Mexico, *Sy. peromysci* has been recorded from *Peromyscus* sp., *Peromyscus boylii* (Baird), *Peromyscus maniculatus* (Wagner), *Peromyscus melanotis* Allen & Chapman in Chihuahua (Preisser & Falcón-Ordaz 2019), *P. maniculatus* in Hidalgo (Pulido-Flores *et al.* 2005), *P. difficilis* in Veracruz (Falcón-Ordaz *et al.* 2016), and *P. yucatanicus* in Yucatan (Panti-May *et al.* 2018). Our study adds two new locality records in Yucatan.

Syphacia sp. (1)

Site of infection: Caecum and large intestine

Host species: *Heteromys gaumeri*

Localities: Hobonil ranch, Kuncheil cattle ranch (Yucatan) and Zoh Laguna community (Campeche)

Specimens deposited: CNHE 12026–12028

GenBank accession numbers: OR271671, OR271672

Comments: The genus *Syphacia* is characterized by short and stout body; cephalic papillae near amphids; well defined esophagus bulb; and females with long tail, and elliptical eggs flattened at one side (Anderson *et al.* 2009). In the Americas, 20 species of *Syphacia* have been reported from native rodents (Robles 2010; Robles *et al.* 2014): *Syphacia alata* Quentin, *Syphacia artica* Tiner & Rausch, *Syphacia carlitosi* Robles & Navone, *Syphacia criceti* Quentin, *Syphacia evaginata* Hugot & Quentin, *Syphacia hodarae* Rojas Herrera, Miño, Notarnicola & Robles, *Syphacia kinsellai* Robles & Navone, *Syphacia hugoti* Robles, Panisse & Navone, *Syphacia megadeiros*, Quentin, *Syphacia nigeriana* Baylis, *Syphacia obvelata* (Rudolphi), *Syphacia odilbaine* Hugot & Quentin, *Syphacia oryzomyos* Quentin & Kinsella, *Syphacia peromysci* Harkema, *Syphacia petrusewiczii rauschi* Quentin, *Syphacia phyllotios* Quentin, *Syphacia quentini* Robles & Navone, *Syphacia samorodini* Erickson, *Syphacia sigmodoni* Quentin & Kinsella, and *Syphacia venteli* Travassos. Of these species, 18 were described in cricetids and 2 in murids. The specimens found in *H. gaumeri* had a cuticle with fine transverse striations, fields between transverse striations with shallow longitudinal depressions in females; a cephalic plate laterally-elongated in females (Figure 5F); cervical and lateral alae absent in both males and females; deirids well developed in females; male spicule 80–110 long; female tail 580–620; some females with slightly prominent vulva; and eggs 82–90 long by 25–30 wide (Figure 5G). Our specimens share a common feature (i.e., absence of cervical alae) with the following species: *Sy. venteli*, *Sy. quentini*, *Sy. criceti*, *Sy. nigeriana*, *Sy. artica*, *Sy. megadeiros*, *Sy. oryzomyos*, *Sy. phyllotios*, *Sy. evaginata*, *Sy. odilbainea*, *Sy. kinsellai*, and *Sy. hugoti*. However, the specimens from *H. gaumeri* differ from all the above species by having a longer (350–480 in *Sy. quentini* and 500 in *Sy. kinsellai*) or shorter tail in females (750 in *Sy. criceti*, 850–950 in *Sy. nigeriana*, 900–1010 in *Sy. artica*, 740 in *Sy. megadeiros*, 630 in *Sy. oryzomyos*, 940 in *Sy. phyllotios*, 750 in *Sy. evaginata*, and 625–975 in *Sy. hugoti*). In addition, *Sy. venteli* has a quadrangular cephalic plate and *Sy. odilbaine* has longer eggs (115), which allows us to differentiate them from our specimens. These differences suggest that our specimens may represent a species not described yet.

In Mexico, unidentified species of the genus *Syphacia* have been recorded in heteromyid species such as *Perognathus flavus* Baird in Chihuahua (Rendón-Franco *et al.* 2014), *H. irroratus* in Morelos (García-Prieto *et al.* 2012) and *H. gaumeri* in Yucatan (Panti-May *et al.* 2018). This is the first record of *Syphacia* in Campeche.

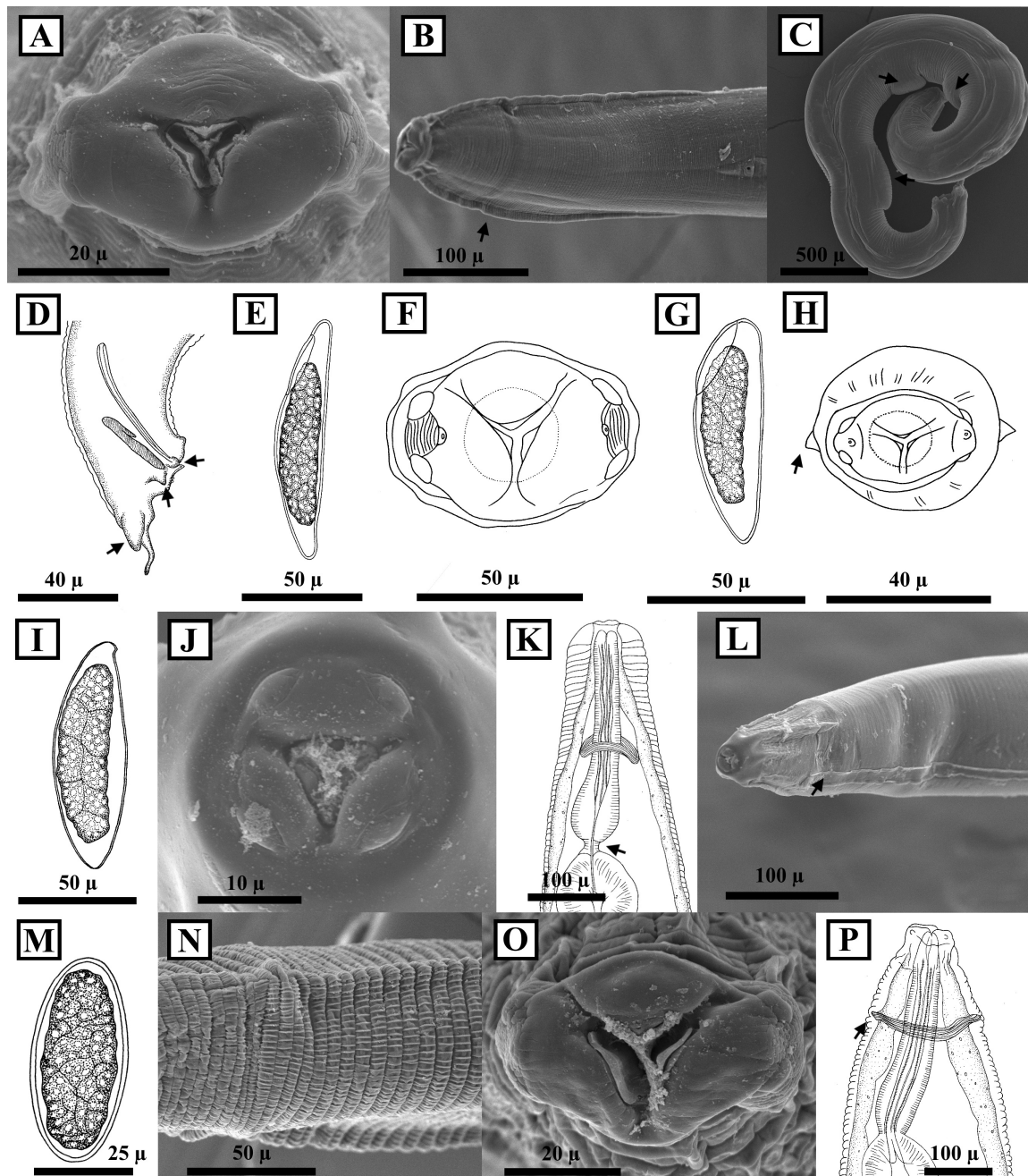


FIGURE 5. A. SEM micrograph of cephalic plate of female *Syphacia peromysci* from *Peromyscus yucatanicus*, apical view. B. SEM micrograph of anterior extremity of female *Syphacia peromysci* from *Peromyscus yucatanicus* showing the cervical alae (arrow), ventral view. C. SEM micrograph of complete male of *Syphacia peromysci* from *Peromyscus yucatanicus* showing the mamelons (arrows), lateral view. D. Caudal extremity of male *Syphacia peromysci* from *Peromyscus yucatanicus* showing the caudal papillae (arrows), lateral view. E. Egg of *Syphacia peromysci* from *Peromyscus yucatanicus*, lateral view. F. Cephalic plate of female *Syphacia* sp. (1) from *Heteromys gaumeri*, apical view. G. Egg of *Syphacia* sp. (1) from *Heteromys gaumeri*, lateral view. Cephalic plate of female *Syphacia* sp. (2) from *Reithrodontomys gracilis* showing the cervical alae (arrow), apical view. I. Egg of *Syphacia* sp. (2) from *Reithrodontomys gracilis*, lateral view. J. SEM micrograph of cephalic plate of female *Syphacia* sp. (3) from *Ototylomys phyllotis*, apical view. K. Anterior extremity of female *Syphacia* sp. (3) from *Ototylomys phyllotis* showing the isthmus (arrow), ventral view. L. SEM micrograph of anterior extremity of *Syphacia* sp. (3) from *Ototylomys phyllotis* showing the lateral folds (arrow), lateral view. M. Egg of *Syphacia* sp. (3) from *Ototylomys phyllotis*, lateral view. N. SEM micrograph of the anterior section of female *Syphacia* sp. (4) from *Ototylomys phyllotis* showing the cuticle with transverse striations and shallow longitudinal depressions, lateral view. O. SEM micrograph of cephalic plate of female *Syphacia* sp. (4) from *Ototylomys phyllotis*, apical view. P. Anterior extremity of female *Syphacia* sp. (4) from *Ototylomys phyllotis* showing the deirids (arrow), ventral view.

Syphacia sp. (2)

Site of infection: Caecum and large intestine

Host species: *Reithrodontomys gracilis*

Localities: Kuncheil cattle ranch (Yucatan)

Specimens deposited: CNHE 12029–30

Comments: The specimens found in *R. gracilis* had a cuticle with fine transverse striations, fields between transverse striations with shallow longitudinal depressions; a cephalic plate laterally-elongated in females; deirids present in females; cervical alae poorly developed (Figure 5H); lateral alae absent; male spicule 60 long; female tail 315–550 long; females with not prominent vulva; and eggs 85–108 long by 25–35 wide (Figure 5I). Among the eight species of *Syphacia* with cervical alae (*Sy. carlitosi*, *Sy. alata*, *Sy. obvelata*, *Sy. peromysci*, *Sy. samorodini*, *Sy. p. rauschi*, *Sy. sigmodoni*, and *Sy. hodarae*), our specimens can be differentiated from *Sy. carlitosi*, *Sy. alata*, *Sy. obvelata*, *Sy. samorodini*, and *Sy. hodarae* by having deirids. In addition, the species from *R. gracilis* has a longer spicule than that of *Sy. peromysci* (57–70), *Sy. p. rauschi* (56) and *Sy. sigmodoni* (64). Based on these findings, we consider that our specimens likely represent a new, undescribed *Syphacia* species.

This is the first helminthological record for *R. gracilis*.

Syphacia sp. (3)

Site of infection: Caecum and large intestine

Host species: *Ototylomys phyllotis*

Localities: Hobonil ranch, Vallazoo, and Kuncheil cattle ranch (Yucatan)

Specimens deposited: 12031–12033

Comments: We found only two males, but they were in poor condition to characterize and compare them with their congeners. Female specimens had a cuticle with fine transverse striations; a cephalic plate round (Figure 5J); esophageal isthmus present; deirids absent (Figure 5K); cervical alae absent; lateral alae absent but two folds occurs at the position where the former would be (Figure 5L), beginning at level of nerve ring extending posterior to the anus; body 3500–3630 long; tail 470 long; vulva not prominent; and eggs 58 long by 26 wide (Figure 5M). The presence of two lateral folds is a feature shared only with *Sy. phyllotios*, parasite of *Phyllotis darwini* in Chile. However, this species has several characteristics that differentiate it from our specimens, such as a cephalic plate laterally elongated, presence of deirids, and vulva slightly prominent. The characteristics exhibited by our specimens clearly distinguish them from the other *Syphacia* found in New World rodents. These specimens likely represent a new, undescribed *Syphacia* species, however, new material, mainly males, should be collected to describe this species.

In Yucatan, *Sy. obvelata* was reported from *O. phyllotis* by Chitwood (1938). However, this record was based on an immature female and no morphological description was provided. This study extends the geographical range of the genus *Syphacia* to Quintana Roo.

Syphacia sp. (4)

Site of infection: Caecum and large intestine

Host species: *Ototylomys phyllotis*

Localities: Ich ha lol xaan ecological park (Campeche) and Balam Nah eco-hotel (Quintana Roo)

Specimens deposited: CNHE 12034–12035

GenBank accession number: OR271673

Comments: Only non-gravid females were found. Collected specimens had a cuticle with fine transverse striations, fields between transverse striations with shallow longitudinal depressions (Figure 5N); a cephalic plate laterally elongated (Figure 5O); deirids present (Figure 5P); cervical alae absent; lateral alae absent but different cuticular morphology occurs at the place where the former would be, and vulva slightly prominent. Although all these features are shared only with *Syphacia* sp. (1), genetic differences and phylogeny of the 28S gene (see results below) show that *Syphacia* sp. (1) from *H. gaumeri* and *Syphacia* sp. (4) from *O. phyllotis* are sufficiently distant to be

considered two species. This suggests that specimens likely represent another new, undescribed *Syphacia* species, however, as mentioned above, new material, mainly males, should be collected to describe this species.

This finding extends the geographical range of the genus *Syphacia* to Campeche.

Phylogenetic analysis

In total, we provided 46 new sequences for the 28S gene of 17 helminth taxa. These new sequences were used to calculate genetic distances and perform phylogenetic analysis. Details of each dataset used to construct phylogenetic trees are given in Supplementary material (Table S2). Unfortunately, DNA samples of Microphallidea gen. sp., *T. rileyi*, *Sy. peromysci*, *Syphacia* sp. (2), and *Syphacia* sp. (3), were not successfully amplified or sequenced.

The results of the analyses based on 28S gene sequences confirmed that the sequence from the specimen identified morphologically as *Hy. taeniaeformis* was identical to the published sequence for this cestode from Yucatan (Panti-May *et al.* 2019) while the sequences of specimens of *Skrjabinus* sp., *Raillietina* sp. (1), *Raillietina* sp. (2), *Hymenolepis* sp., *Syphacia* sp. (1), and *Syphacia* sp. (4) helped us to confirm their generic identities. In addition, the obtained sequences of *Scaphiostomum* sp., *Tr. silviae*, *Monodontus* sp., *V. vexillata*, Heligmosomoidea gen. sp. cf. *Vexillata*, *Carolinensis* sp., *Ha. musculi*, *Ha. aduncus*, and *Heligmostrongylus* sp. represent the first available genetic data for these taxa.

The alignment of the Trematoda dataset comprised 32 sequences, including sequences of *Skrjabinus* sp. and *Scaphiostomum* sp. from the Yucatan Peninsula (Figure 6). The 28S sequence of *Skrjabinus* sp. was grouped with other sequences of the genera *Skrjabinus* and *Lyperosomum* from birds (Bootstrap = 58). The genetic differences between our sequence of *Skrjabinus* sp. and *Sk. delectans* and *Skrjabinus alveyi* (Martin & Gee) were 0.6% and 1.0%, respectively. On the other hand, the sequence of *Scaphiostomum* sp. was recorded as a sister species of *Postharmostomum commutatum* (Diesing) and *Pseudoleucochloridium ainohelicis* (Asakawa, Kamiya & Ohbayashi). The genetic differences between *Scaphiostomum* sp. and *Po. commutatum* and *Ps. ainohelicis* were 12.1% and 6.8%, respectively.

The phylogenetic tree of cestodes included the sequences of *Hymenolepis* sp., *Raillietina* sp. (1), *Raillietina* sp. (2), *Hy. taeniaeformis* and other 51 sequences of related cestodes (Figure 7). Our sequences of *Hymenolepis* were grouped with other species of this genus (Bootstrap = 100). These sequences were found to be as a sister species of *Hymenolepis folkertsi* Makarikov, Nims, Galbreath & Hoberg from *Peromyscus polionotus* (Wagner) and *Hymenolepis weldensis* Gardner & Schmidt from *Geomys bursarius* (Shaw) in North America. The genetic differences between our three sequences of *Hymenolepis* ranged from 0 to 0.1 % while comparing these sequences with *Hym. folkertsi* and *Hym. weldensis* variations were 2.1–2.5% and 2.2–2.6%, respectively. The phylogenetic analyses grouped the sequences of *Raillietina* sp. (1) and *Raillietina* sp. (2) with other davaineid (e.g., *Raillietina*) and anoplocephalid cestodes from several mammals and birds. Our *Raillietina* sequences were divided in two subclades (Bootstrap = 100), one containing *Raillietina* sp. (1) from *H. gaumeri*, *P. yucatanicus*, *O. phyllotis* and *S. toltecus* and the other one with *Raillietina* sp. (2) from *H. gaumeri* and *S. toltecus*. The genetic difference among sequences of *Raillietina* sp. (1) ranged from 0 to 0.2% while among *Raillietina* sp. (2) sequences variation was 0%. When comparing these two species of *Raillietina* they exhibit a genetic difference that ranged from 1.2 to 1.3%. The sequence of *Hyd. taeniaeformis* was grouped with other sequences of the same species and had a difference of 0% with another sequence of this cestode from *Sci. yucatanensis* collected in Yucatan.

The 28S sequences of nematodes were analyzed separately due to genetic divergences between trichinellids, strongylids, and *Syphacia*. The phylogenetic tree of strongylids was divided in two clades, one containing nematodes of the superfamily Heligmosomoidea and the other one with nematodes of the superfamily Ancylostomatoidea (Figure 8). At the family level, the sequences of *V. vexillata*, Heligmosomoidea gen. sp. cf. *Vexillata*, *Carolinensis* sp., *Ha. musculi*, *Ha. aduncus*, and Heligmonellidae gen. sp. were grouped in a subclade with other heligmonellid nematodes (Bootstrap = 77). The sequences of *Ha. aduncus* exhibit genetic differences that ranged from 0 to 0.1% and were grouped with *V. vexillata* and Heligmosomoidea gen. sp. cf. *Vexillata* (Bootstrap = 58). The genetic difference among our sequences of *V. vexillata* was 0%, and 0.6% when comparing with the sequence of Heligmosomoidea gen. sp. cf. *Vexillata*. Heligmonellidae gen. sp. and *Ha. musculi* were sister species (Bootstrap = 99); the genetic difference between these species was 0.4%. The sequences of *Ha. musculi* from *O. phyllotis* and *Ol. fulvescens* were identical. The genetic difference between the two sequences of *Heligmostrongylus* sp. was 0% and

they nested within the subclade formed with other heligmonellid and ornithostrongylid nematodes (Bootstrap = 42). Unfortunately, there were no 28S sequences available from other representatives of the Pudicinae which could have produced a better resolved phylogeny.

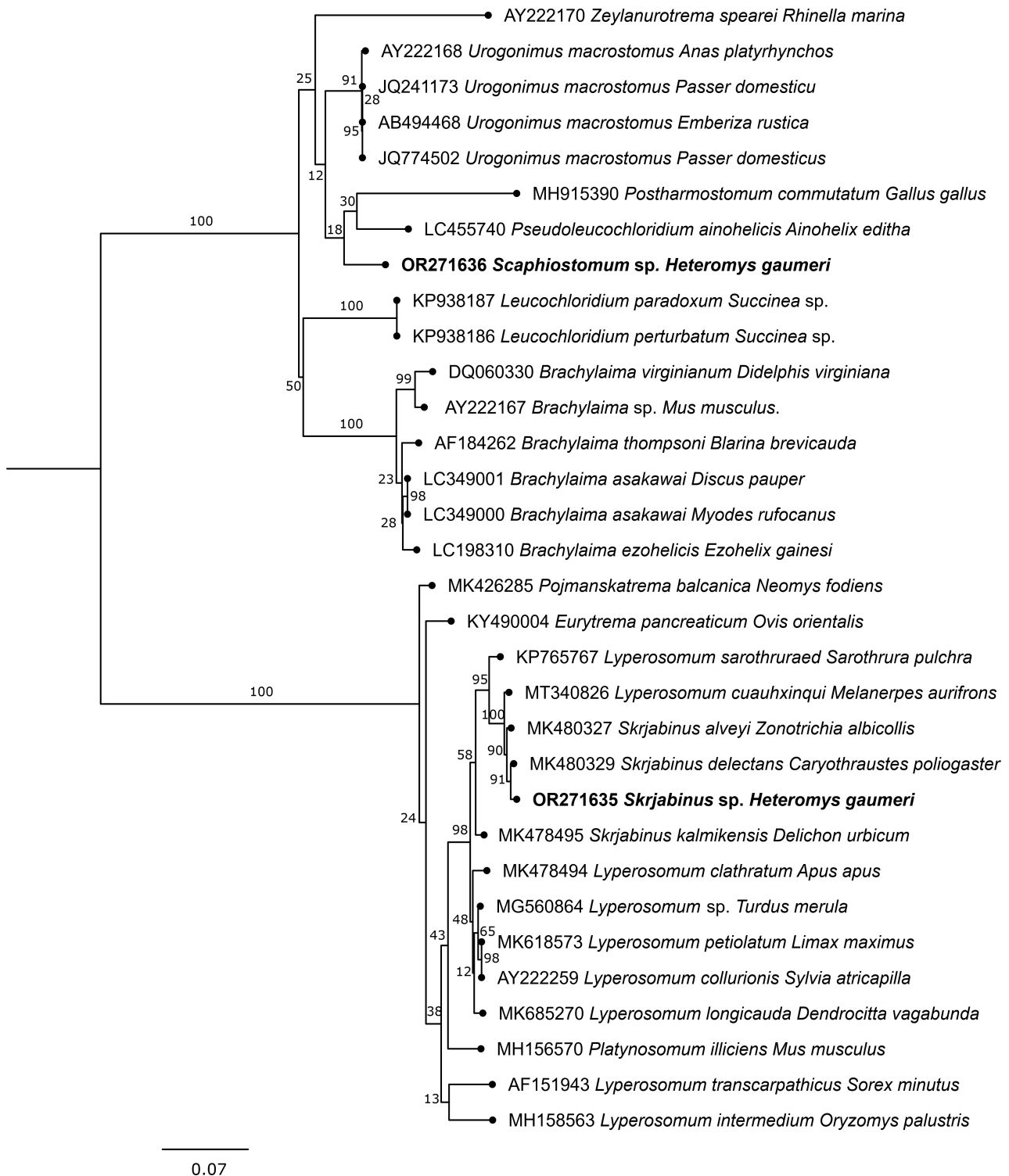


FIGURE 6. Phylogenetic tree based on the ML analysis constructed on partial large subunit ribosomal gene (28S) of trematodes from different hosts. Individual GenBank accession numbers precede species name, followed by host name. Bootstrap support values for ML are provided at the nodes. The new sequences of the present study are in bold.

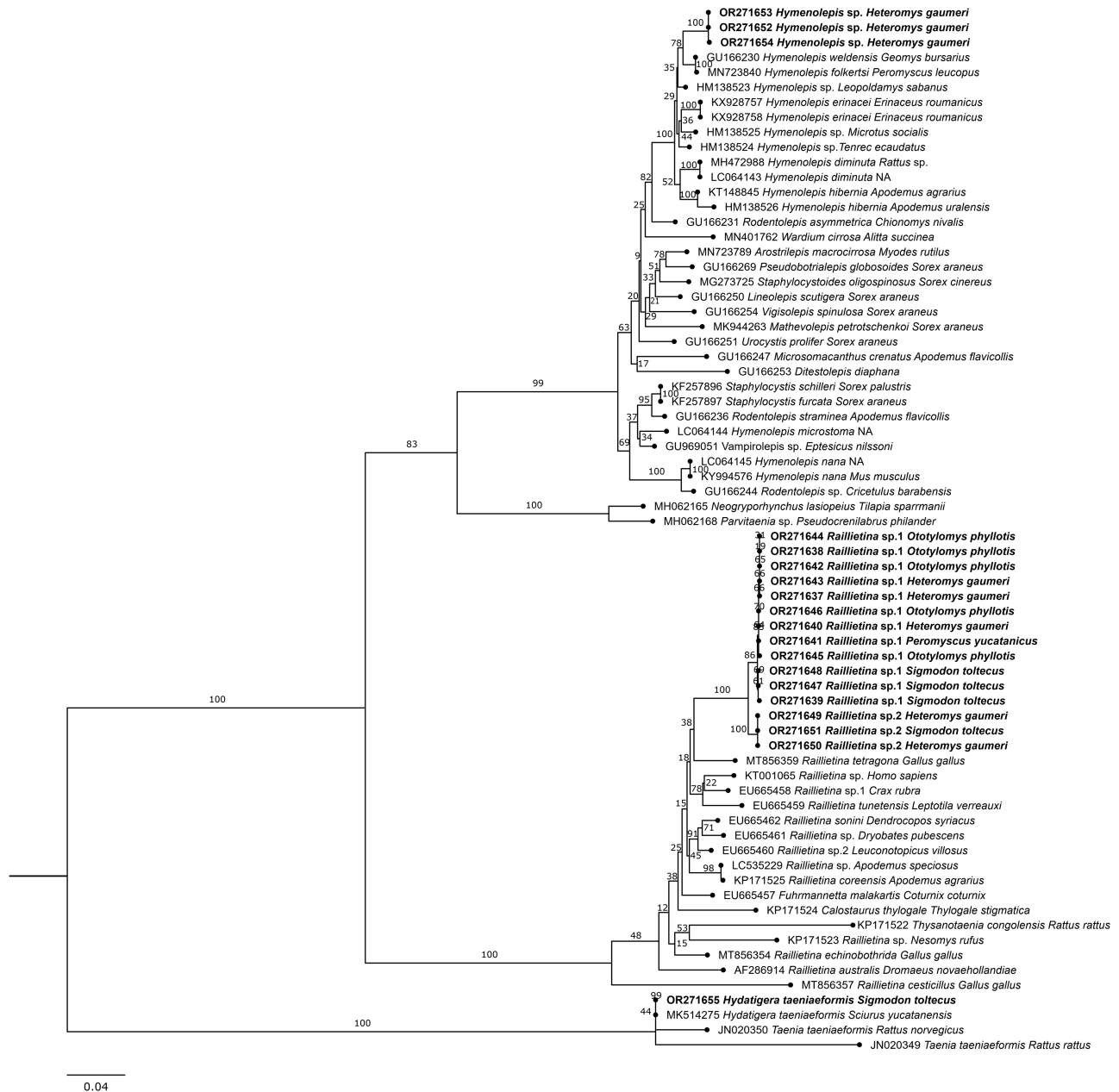


FIGURE 7. Phylogenetic tree based on the ML analysis constructed on partial large subunit ribosomal gene (28S) of cestodes from different hosts. Individual GenBank accession numbers precede species name, followed by host name. Bootstrap support values for ML are provided at the nodes. The new sequences of the present study are in bold.

The phylogenetic tree of *Syphacia* included 20 sequences of members of this genus (Figure 9). Our sequences of *Syphacia* were grouped in a clade with *Syphacia petruszewiczi* Bernard from *Myodes rutilus* (Pallas) in Japan (Bootstrap = 100). The genetic difference among sequences of *Syphacia* sp. (1) from *H. gaumeri* was 0.6% and among these sequences and *Syphacia* sp. (4) from *O. phyllotis* was 1.2%. Comparing the sequence of *Sy. petruszewiczi* with those from *H. gaumeri* and *O. phyllotis*, the genetic differences were 6.7–7.5% and 7%, respectively. On the other hand, the sequences of *Tr. silviae* were similar to *Trichinella spiralis* (Owen) and other trichinellid nematodes with similarity values that ranged from 83% to 92% but with poor coverage (36–41%). This implies that currently there are not 28S sequences closely related to *Tr. silviae*, which did not allow us to produce a resolved phylogeny.

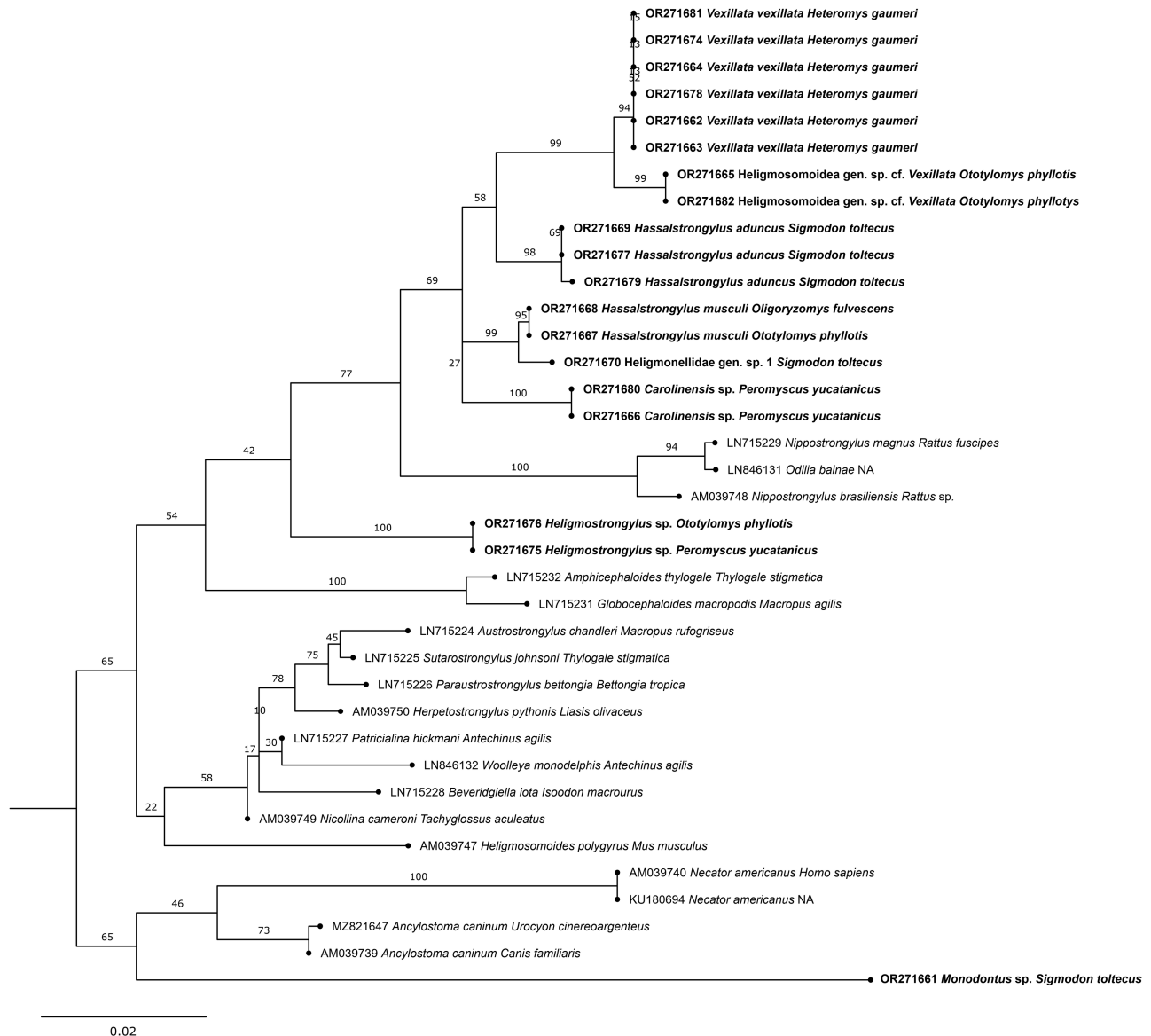


FIGURE 8. Phylogenetic tree based on the ML analysis constructed on partial large subunit ribosomal gene (28S) of strongylids from different hosts. Individual GenBank accession numbers precede species name, followed by host name. Bootstrap support values for ML are provided at the nodes. The new sequences of the present study are in bold.

Discussion

This large-scale survey is the first to use an integrative taxonomy approach (morphological characters and molecular phylogenetic analysis) to identify the helminth fauna of wild small rodents from Mexico. Although helminths of Mexican mammals have been extensively studied, their records are asymmetrical in terms of geographical distribution, host taxa analyzed, and sampling effort (Pérez-Ponce de León *et al.* 2011). In this sense, the Yucatan Peninsula is a region where the study of helminths of small rodents have been neglected (Panti-May *et al.* 2018). Consequently, most of the helminths parasitizing wild small rodents have not been characterized using morphological techniques (e.g., scanning electron microscopy) and genetic markers. In our study, we recorded 22 helminth species, 7 of which are likely undescribed species, 6 are reported for the first time in rodents from Mexico, and 12 are new host records in the Americas (see Table 2).

TABLE 2. Infection levels of the helminths of small rodents from the Yucatan Peninsula, Mexico. 95% confidence intervals (CI), Colección Nacional de Helmintos (CNHE).

Helminth species	Host species	Site	n	Prevalence (CI)	Mean intensity (range)	CNHE catalog number	GenBank accession number
TREMATODA							
Brachylaimidae							
<i>Scaphiostomum</i> sp. ^a	<i>H. gaumeri</i>	HR	23	13 (2.7–33.6)	1.7 (1–3)	10973	–
	<i>H. gaumeri</i>	SC	4	25 (0.6–80.6)	8 (8)	11954–5	OR271636
	<i>S. toltecus</i> ^b	ZL	4	25 (0.6–80.6)	1 (1)	11956	–
Dicrocoeliidae							
<i>Skrjabinus</i> sp. ^a	<i>H. gaumeri</i> ^b	HR	23	4.3 (1.1–21.9)	158 (158)	11957	OR271635
Microphallidae							
Microphallidae gen. sp. ^a	<i>P. yucatanicus</i> ^b	MO	1	100 (2.5–100)	4 (4)	11958	–
		AP	1	10 (0.2–44.5)	1 (1)	–	–
CESTODA							
Davaineidae							
<i>Raillietina</i> sp. (1)	<i>H. gaumeri</i>	HR	23	34.8 (16.4–57.3)	2.1 (1–6)	10968	OR271637
	<i>O. phyllotis</i>		2	50 (1.2–98.7)	2 (2)	11959	OR271638
	<i>O. phyllotis</i>	IH	4	50 (6.7–93.2)	3 (1–5)	10969	–
	<i>P. yucatanicus</i> ^b		4	25 (0.6–80.6)	1 (1)	11960	–
	<i>S. toltecus</i>		1	100 (2.5–100)	1 (1)	11961	OR271639
	<i>H. gaumeri</i>	SC	4	50 (6.7–93.2)	2.5 (1–4)	11962	OR271640
	<i>P. yucatanicus</i>		1	100 (2.5–100)	5 (5)	10972	OR271641
	<i>O. phyllotis</i>	AP	2	100 (15.8–100)	4 (2–6)	11963	OR271642
	<i>H. gaumeri</i>	KR	7	57.1 (18.4–90.1)	2.5 (1–3)	11964	OR271643
	<i>O. phyllotis</i>		3	66.7 (9.4–99.2)	10 (1–19)	11965	OR271644
	<i>P. yucatanicus</i>		9	11.1 (0.3–48.2)	1 (1)	11966	–
	<i>S. toltecus</i>		11	34.6 (10.9–69.2)	1.5 (1–3)	11967	–
	<i>O. phyllotis</i>	JJ	6	33.3 (4.3–77.7)	4 (2–6)	11968	OR271645
	<i>O. phyllotis</i>	BN	10	30 (6.7–65.3)	4 (1–10)	11969	OR271646
	<i>S. toltecus</i>		3	33.3 (0.8–90.6)	1 (1)	–	OR271647
	<i>H. gaumeri</i>	ZL	10	40 (12.2–73.8)	1.3 (1–2)	11970	–

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TABLE 2. (Continued)

Helminth species	Host species	Site	n	Prevalence (CI)	Mean intensity (range)	CNHE catalog number	GenBank accession number
<i>Raillietina</i> sp. (2)	<i>S. toltecus</i>		4	50 (6.8–93.3)	1.5 (1–2)	11971	OR271648
	<i>H. gaumeri</i>	IH	2	50 (1.2–98.7)	19 (19)	10970	OR271649
		ZL	10	10 (0.3–44.5)	2 (2)	11972	–
	<i>S. toltecus</i>	VZ	4	75 (19.4–99.4)	5.7 (1–9)	10971	OR271650
		KR	6	54.5 (23.4–83.3)	2.8 (1–6)	11973	OR271651
		ZL	4	50 (6.8–93.3)	11.5 (5–18)	11974	–
Hymenolepididae							
<i>Hymenolepis</i> sp.	<i>H. gaumeri</i> ^b	HR	23	30.4 (13.2–52.9)	3.6 (1–6)	11975	OR271652–4
Taeniidae							
<i>Hydatigera taeniaeformis</i>	<i>S. toltecus</i>	ZL	4	50 (6.8–93.3)	1.5 (1–2)	11976	OR271655
<i>Taenia rileyi</i> ^a	<i>S. toltecus</i> ^b	KR	12	18.2 (2.3–51.8)	24.5 (12–37)	11977	–
NEMATODA							
Trichuridae							
<i>Trichuris silviae</i>	<i>H. gaumeri</i>	HR	23	69.6 (47.1–86.8)	7.3 (1–18)	11978	OR271656
		IH	2	100 (15.8–100)	13.5 (2–25)	11979	OR271657
		MO	5	80 (28.3–99.5)	5.7 (1–17)	11980	–
		DZ	2	100 (15.8–100)	2.5 (2–3)	11981	–
		SF	7	57.1 (18.4–90.1)	7 (1–13)	11982	–
		SC	4	50 (6.7–93.2)	8 (6–10)	11983	–
		VZ	2	50 (1.2–98.7)	1 (1)	–	–
		AP	1	100 (2.5–100)	44 (44)	11984	–
		PR	1	100 (2.5–100)	6 (6)	11985	OR271658
		KR	7	57.1 (18.4–90.1)	10.7 (7–15)	11986	OR271659–60
		JJ	3	33.3 (0.8–90.6)	8 (8)	11987	–
		DG	3	100 (29.2–100)	7.3 (3–11)	11988	–
		ZL	10	90 (55.5–99.8)	6.1 (1–17)	11989	–
Ancylostomidae							
<i>Monodontus</i> sp. ^a	<i>S. toltecus</i> ^b	IH	1	100 (2.5–100)	1 (1)	–	OR271661

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TABLE 2. (Continued)

Helminth species	Host species	Site	n	Prevalence (CI)	Mean intensity (range)	CNHE catalog number	GenBank accession number		
Ornithostrongylidae <i>Vexillata vexillata</i>	<i>H. gaumeri</i>	BN	3	33.3 (0.8–90.6)	3 (3)	11990	–		
		HR	23	100 (85.2–100)	79.3 (4–305)	11991	OR271662		
		IH	2	100 (15.8–100)	253.5 (214–303)	11992	OR271678		
		MO	5	100 (47.8–100)	78.2 (16–140)	11993	–		
		DZ	2	100 (15.8–100)	78.5 (35–122)	11994	–		
		SF	7	100 (59–100)	66 (2–239)	11995	OR271663		
		SC	4	100 (39.8–100)	281.5 (74–794)	11996	–		
		VZ	2	100 (15.8–100)	98.5 (83–114)	11997	–		
		AP	1	100 (2.5–100)	7 (7)	11998	–		
		PR	1	100 (2.5–100)	1 (1)	11999	–		
		KR	7	100 (59–100)	41.6 (14–102)	12000	OR271681		
		JJ	3	100 (29.2–100)	68.7 (30–115)	12001	–		
		BN	1	100 (2.5–100)	49 (49)	12002	OR271674		
		DG	3	100 (29.2–100)	90.3 (6–138)	12003	OR271664		
		ZL	10	100 (69.2–100)	163.3 (33–521)	12004	–		
		Heligmosomoidea gen. sp. cf. <i>Vexillata</i>	<i>O. phylotitis</i> ^b	KR	3	33.3 (0.8–90.6)	6 (6)	12005	–
				PR	3	100 (29.2–100)	67.7 (24–103)	12006	–
JJ	6			33.3 (4.3–77.7)	8 (1–15)	12007	OR271682		
BN	10			10 (0.3–44.5)	2 (2)	12008	–		
DG	2			50 (1.2–98.7)	79 (79)	12009	OR271665		
Heligmonellidae <i>Carolinensis</i> sp.	<i>P. yucatanicus</i>			AP	10	70 (34.7–93.3)	5.6 (1–21)	12010	–
				DZ	3	33.3 (0.8–90.6)	1 (1)	–	OR271666
		KR	9	77.8 (40.0–97.2)	37.3 (3–132)	12011	–		
		PR	2	100 (15.8–100)	2 (1–3)	12012	OR271680		
		JJ	5	20 (0.5–71.6)	15 (15)	12013	–		

.....continued on the next page

TABLE 2. (Continued)

Helminth species	Host species	Site	n	Prevalence (CI)	Mean intensity (range)	CNHE catalog number	GenBank accession number
<i>Hassastrongylus aduncus</i>	<i>S. toltectus</i>	HR	1	100 (2.5–100)	5 (5)	12016	OR271677
		IH	1	100 (2.5–100)	18 (18)	12017	OR271679
		VZ	4	100 (39.8–100)	69.5 (33–144)	12018	OR271669
		KR	11	100 (71.5–100)	50.9 (6–139)	12019	–
<i>Hassastrongylus musculi</i>	<i>O. phyllotis</i> ^b	BN	3	66.7 (9.4–99.2)	53 (52–54)	12020	–
		ZL	4	25 (0.6–80.6)	32 (32)	12021	–
		IH	4	50 (6.8–93.3)	2.5 (1–4)	12014	OR271667
		IH	1	100 (2.5–100)	9 (9)	12015	OR271668
<i>Heligmostrongylus</i> sp. ^a	<i>P. yucatanicus</i> ^b	SC	1	100 (2.5–100)	3 (3)	12022	OR271675
		VZ	1	100 (2.5–100)	2 (2)	–	–
		BN	10	20 (2.5–55.6)	2 (1–3)	–	OR271676
Heligmonellidae gen. sp.	<i>S. toltectus</i>	VZ	4	25 (0.6–80.6)	2 (2)	12023	OR271670
Oxyuridae							
<i>Syphacia peromysci</i>	<i>P. yucatanicus</i>	AP	10	10 (0.2–44.5)	17 (17)	12024	–
		KR	9	44.4 (13.7–78.8)	262 (21–948)	12025	–
<i>Syphacia</i> sp. (1)	<i>H. gaumeri</i>	HR	23	34.8 (16.4–57.3)	274.7 (2–630)	12026	OR271671
		KR	7	14.3 (0.4–57.9)	364 (364)	12027	OR271672
<i>Syphacia</i> sp. (2)	<i>R. gracilis</i> ^b	ZL	10	30 (6.7–65.3)	167.3 (29–393)	12028	–
		KR	1	100 (2.5–100)	103 (103)	12029–30	–
<i>Syphacia</i> sp. (3)	<i>O. phyllotis</i>	HR	2	50 (1.2–98.7)	1 (1)	12031	–
		VZ	1	100 (2.5–100)	23 (23)	12032	–
<i>Syphacia</i> sp. (4)	<i>O. phyllotis</i>	KR	3	33.3 (0.8–90.6)	21 (21)	12033	–
		IH	4	25 (0.6–80.6)	30 (30)	12034	OR271673
		BN	10	10 (0.3–44.5)	2 (2)	12035	–

HR, Hobonil ranch; IH, Ich ha lol xaan ecological park; MO, Molas farm; DZ, Dzununcan farm; SF, San Francisco cattle ranch; SC, Santa Cruz cattle ranch; VZ, Vallazoo; AP, Aak ecological park; PR, Papam ranch; KR, Kunchheil cattle ranch; JJ, Jolie Jungle eco-hotel; BN, Balam Nah eco-hotel; DG, David Gustavo community; ZL, Zoh Laguna community.

^aNew record in rodents from Mexico

^bNew host record

es may survive for long periods and be exposed to various definitive hosts. Notably cestodes of the genus *Raillietina* were recorded in the most abundant rodent species (i.e., *H. gaumeri*, *P. yucatanicus*, *O. phyllotis* and *S. toltecus*) and almost all the studied localities, with prevalence values usually greater than 30%. Members of this genus infect birds and mammals and use a wide range of arthropods as intermediate hosts, such as ants, beetles and cockroaches (Bartel 1965). This indicates that arthropods may be an important component in the diet of infected rodents. On the other hand, trematode infections were rare in rodents. However, we found *Scaphiostomum* and *Skrjabinus* infecting *H. gaumeri*, which could be related to the reported consumption of terrestrial snails (potential second intermediate hosts of trematodes) *Choanopoma largillierti*, *Choanopoma gaigei*, *Neocyclotus dysoni* and *Drymaeus shattucki*, by this rodent (Hernández-Betancourt et al. 2005).

The use of DNA sequences as genetic markers has proven to be useful for species identification, discovery of new species, cryptic species complexes and also for clarifying relationships between groups of organisms in systematic studies (Chan et al. 2021). In this sense, our phylogenetic analysis of the 28S gene showed that at the genetic level, *Raillietina* cestodes recovered from several rodent species from the Yucatan Peninsula, formed two subclades, supporting the morphological identification. Irrespective of the host or the site where the host were sampled, we consider that *Raillietina* cestodes whose specimens and DNA sequences were analyzed represent two species. The presence of *Ha. musculi* and the possible undescribed species of *Heligmostrongylus* in two rodent species was also confirmed through analysis of DNA sequences, notwithstanding that no male specimens were found in some hosts. Although only females of *Hassalstrongylus* were found in *O. phyllotis*, the sequence obtained from this host was identical to the sequence of *Ha. musculi* from *Ol. fulvescens*. Similarly, we found that the sequence of a female *Heligmostrongylus* from *O. phyllotis* in Quintana Roo was identical to the sequence of a male *Heligmostrongylus* from *P. yucatanicus* in Yucatan. In addition, the genetic differences and phylogeny of the 28S gene of *Syphacia* sp. (4) from *O. phyllotis* and *Syphacia* sp. (1) from *H. gaumeri* supported the conclusion that they represent two species.

Helminths are important component of biodiversity in any habitat (Marcogliese 2023). However, we still know only a small percentage of the helminths of vertebrates. It has been estimated that the 100,000–350,000 described species of helminths represent only 5–15% of the global diversity (Carlson et al. 2020). Given that almost 90% of helminth diversity is undescribed and closer to 95% is undescribed in Mexico (Carlson et al. 2020), our study contributes to document the helminth diversity of wild small rodents and the geographical patterns in host-parasite associations in a region with paucity information.

Before this study, 87 taxa of helminths had been reported from 35 cricetid and 12 heteromyid species in 21 Mexican states (Preisser & Falcón-Ordaz 2019). Our findings increase to 93 the helminth taxa in these rodents, and to 36 the cricetid species parasitized by helminths. Particularly, we added the first helminthological records in small rodents from the states of Campeche and Quintana Roo. At the province level, 15 taxa of helminths had been reported in the Yucatan Peninsula, 11 in the state of Yucatan (Chitwood 1938; Panti-May & Robles 2016; Panti-May et al. 2018) and 4 in Corozal District, Belize (Bersot 2001). With our new records, the number helminth taxa parasitizing wild small rodents from this region increases to at least 23 species. Nevertheless, further integrative studies are needed to complete the inventory of the helminths of wild small rodents at the country and province level.

Acknowledgements

We thank Erendira Martínez for her assistance in the Colección Mastozoológica at the Universidad Autónoma de Yucatán, B. Mendoza Garfias for SEM micrographs, and Guadalupe Isabel Pech Simá for the drawings of *Syphacia* species. Fieldwork was financed by the Project “Análisis y evaluación de los probables vectores y reservorios del virus del Ébola en México, CONACYT-251053, Proyecto Apoyado por el Fondo Sectorial de Investigación para la Educación”. The sequences of the 28S gene were financed by the grant CONACYT No. 201441 entitled “Plataformas de observación oceanográfica, línea base, modelos de simulación y escenarios de la capacidad natural de respuesta ante derrames de gran escala en el Golfo de México”.

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TABLE S1 Rodent hosts deposited in the Colección Mastozoológica, Universidad Autónoma de Yucatán, Mexico.

Study site/Host	Catalog number
Hobonil ranch	
<i>Heteromys gaumeri</i>	1097–1102, 1104–1107, 1109–1114, 1116–1121, 1123
<i>Otodylomys phyllotis</i>	1103, 1115
<i>Sigmodon toltecus</i>	1108
Ich ha lol xaan ecological park	
<i>Otodylomys phyllotis</i>	1144, 1145, 1148, 1149
<i>Peromyscus yucatanicus</i>	1147, 1150, 1151, 1154
<i>Heteromys gaumeri</i>	1152, 1153
<i>Sigmodon toltecus</i>	1143
<i>Oligoryzomys fulvescens</i>	1155
Molas farm	
<i>Heteromys gaumeri</i>	1184, 1185, 1187–1189
<i>Peromyscus yucatanicus</i>	1186
Dzununcan farm	
<i>Peromyscus yucatanicus</i>	1191–1193
<i>Heteromys gaumeri</i>	1190, 1194
<i>Otodylomys phyllotis</i>	1195
San Francisco cattle ranch	
<i>Heteromys gaumeri</i>	1197–1203
<i>Otodylomys phyllotis</i>	1196
Santa Cruz cattle ranch	
<i>Heteromys gaumeri</i>	1301–1304
<i>Peromyscus yucatanicus</i>	1300
Zoological garden	
<i>Sigmodon toltecus</i>	1306–1309
<i>Heteromys gaumeri</i>	1310, 1312
<i>Peromyscus yucatanicus</i>	1305
<i>Otodylomys phyllotis</i>	1311
Aak ecological park	
<i>Peromyscus yucatanicus</i>	1313–1321, 1323
<i>Otodylomys phyllotis</i>	1324, 1325
<i>Heteromys gaumeri</i>	1322
Papam ranch	
<i>Otodylomys phyllotis</i>	1400, 1404, 1406
<i>Peromyscus yucatanicus</i>	1399, 1401

.....continued on the next page

TABLE S1. (Continued)

Study site/Host	Catalog number
<i>Heteromys gaumeri</i>	1407
Kuncheil cattle ranch	
<i>Sigmodon toltecus</i>	1434–1438, 1452, 1454, 1456–1459
<i>Peromyscus yucatanicus</i>	1444–1448, 1453, 1455, 1461, 1462
<i>Heteromys gaumeri</i>	1439–1443, 1450, 1451
<i>Ototylomys phyllotis</i>	1431–1433
<i>Reithrodontomys gracilis</i>	1430
Jolie Jungle eco-hotel	
<i>Ototylomys phyllotis</i>	1483–1485, 1493–1495,
<i>Peromyscus yucatanicus</i>	1487, 1489, 1490, 1492, 1496
<i>Heteromys gaumeri</i>	1486, 1488, 1491,
<i>Reithrodontomys gracilis</i>	1497
Balam Nah eco-hotel	
<i>Ototylomys phyllotis</i>	1513, 1514, 1516–1520, 1522, 1523, 1526
<i>Sigmodon toltecus</i>	1515, 1524, 1525
<i>Heteromys gaumeri</i>	1521
David Gustavo community	
<i>Heteromys gaumeri</i>	1543, 1544, 1547
<i>Ototylomys phyllotis</i>	1545, 1546
Zoh Laguna community	
<i>Heteromys gaumeri</i>	1559, 1563, 1565–1568, 1571–1574
<i>Sigmodon toltecus</i>	1561, 1562, 1569, 1570,
<i>Reithrodontomys gracilis</i>	1560

TABLE S2. Description of each data set used for the phylogenetic analyses.

Tree	No. of sequences	Length of alignment	Proportion of pair bases	Substitution model	Value of ln
Trematoda	32	1166	A = 0.218 C = 0.213 G = 0.304 T = 0.265	GTR	-6543.844894
Cestoda	70	2117	A = 0.204 C = 0.231 G = 0.337 T = 0.228	GTR+CAT	-14010.250786
<i>Syphacia</i>	21	1226	A = 0.248 C = 0.209 G = 0.292 T = 0.251	GTR	-5760.558265
Strongylida	37	943	A = 0.255 C = 0.203 G = 0.296 T = 0.245	GTR	-3056.083831