Zootaxa 5696 (4): 517–541
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5696.4.4
http://zoobank.org/urn:lsid:zoobank.org:pub:D13D3287-3865-4B88-A49F-5B8A067D8709

Helminths of the broad-tailed bat *Nyctinomops laticaudatus* (Geoffroy Saint-Hilaire) in Mexico, and description of a new species of nematode (Molineidae: Anoplostrongylinae)

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Abstract

Nyctinomops laticaudatus is an insectivorous bat distributed from Mexico to northern Argentina; however, it has few helminthological records. In the present study, we describe the helminth fauna of *N. laticaudatus* from the municipalities of Calcehtok and Homún in the state of Yucatán, Mexico. Helminths were identified using morphological techniques (clearing, staining, and scanning electron microscopy). We generated 28S rRNA and COI genetic sequence data for each of the taxa when possible. The helminth fauna of *N. laticaudatus* consisted of 17 taxa: seven trematodes, *Brachylecithum rileyi*, *Euparadistomum* sp., *Limatulum nanum*, Phaneropsolidae gen. sp., *Ochoterenatrema* sp., *Urotrema minuta*, and *Urotrema* sp.; two cestodes, *Vampirolepis* cf. *christensoni* and *Vampirolepis* cf. *phyllostomi*; six nematodes, *Aonchotheca pulchra*, *Anoplostrongylus allami* **sp. nov.** Panti-May & Digiani, *Physaloptera* sp., *Physocephalus sexalatus*, *Spirura mexicana*, and *Litomosoides* sp.; and two acanthocephalans, *Mediorhynchus* sp. and *Oncicola* sp. All these taxa, except for *Euparadistomum* sp., *Mediorhynchus* sp. and *Oncicola* sp., were recorded in both municipalities. The new species is distinguished from its only congener, *Anoplostrongylus paradoxus*, by the number of portions of the cephalic vesicle of males (two *vs*. three), the shape of the proximal half of the gubernaculum (asymmetric *vs*. symmetric) and, especially, by the marked sexual dimorphism in the ridge number and development. *Anoplostrongylus allami* had the highest prevalence and intensity values. This study adds new seven helminthological records for *N. laticaudatus* and four for Mexico,

Accepted by D. Vaughan: 1 Sept. 2025; published: 26 Sept. 2025

including the description of a new nematode species. This study also provides genetic sequences for most of the helminths found in *N. laticaudatus*, which will be useful in future studies, as few bat helminths have available genetic information.

Key words: Acanthocephala, Molossidae, Nematoda, Neotropical region, Platyhelminthes

Introduction

The broad-eared bat *Nyctinomops laticaudatus* (Geoffroy Saint-Hilaire) is an insectivorous species of free-tailed bat distributed from Mexico to northern Argentina (Velandia-Perilla & Garcés-Restrepo 2013). This species forms groups ranging from 150 to 1000 individuals. Hundreds of individuals can be observed in caves, while smaller groups are found under canopy of trees, hollows and crevices in abandoned buildings and bridges (Avila-Flores *et al.* 2002; Ortega *et al.* 2010). *Nyctinomops laticaudatus* feeds mainly on Lepidoptera (e.g., moths), which it captures during flight at high altitudes (up to thousands of meters above ground level), making it difficult to study using conventional techniques such as mist nets set at the understory level (Avila-Flores *et al.* 2002).

Despite its wide distribution, *N. laticaudatus* has few helminthological records, limited to Cuba, Paraguay, Brazil, and Mexico. These records include the trematodes *Brachylecithum rileyi* (Macy), *Limatulum limatulum* (Braun), *Limatulum gastroides* Macy, *Ochoterenatrema diminutum* (Chandler), *Ochoterenatrema* sp., *Paralecithodendrium aranhai* Lent, Freitas & Proença, *Urotrema scabridum* Braun, and *Urotrema minuta* Macy, the cestodes *Vampirolepis christensoni* (Macy), *Vampirolepis decipiens* (Diesing) and *Vampirolepis* sp., and the nematodes *Aonchotheca pulchra* (Freitas), *Anoplostrongylus paradoxus* (Travassos), *Anoplostrongylus* sp., *Molostrongylus acanthocolpos* Durette-Desset & Vaucher, *Physocephalus sexalatus* (Molin), *Tenoranema rivarolai* (Lent, Freitas & Proença), *Litomosoides chandleri* Esslinger, *Litomosoides guiterasi* Vigueras, and *Litomosoides* sp. (Lent *et al.* 1945, 1946; Rêgo 1962; Baruš & del Valle 1967; Silva-Taboada 1979; Rutkowska 1980; Martínez-Pérez 2021; Moguel-Chin *et al.* 2023, 2024).

In Mexico, two recent studies reported the first helminthological records of *N. laticaudatus*: five taxa in Oaxaca (Martínez-Pérez 2021) and seven taxa in Yucatán (Martínez-Pérez 2021; Moguel-Chin *et al.* 2023). However, these studies had limitations, such as the small sample size of bats (<15 specimens), the small number of collected helminths for some taxa (three specimens) or incomplete specimens. This latter point prevented specific identification of some helminths, such as *Ochoterenatrema* sp. and *Anoplostrongylus* sp. (Martínez-Pérez 2021; Moguel-Chin *et al.* 2023). Furthermore, only three helminth taxa from this bat have molecular information (28S rRNA gene), which is important for more accurate comprehensive identification when the material is limited (e.g., few specimens, incomplete specimens, and single sex specimens), as well as in molecular phylogeny studies.

Recent studies have shown that the helminth fauna of most Neotropical bat species remains poorly studied, and that bats may host a greater diversity of helminths than currently recognized (Fernandes *et al.* 2022). The present study provides a comprehensive list of helminths from two populations of *N. laticaudatus* in Yucatán, Mexico, and the description of a new species of Anoplostrongyline nematode. Where possible, genetic sequences of the studied taxa were obtained and published.

Materials and methods

Collection and examination of bats

From January to November 2024, 258 individuals of *N. laticaudatus* were collected in the state of Yucatán, Mexico: 130 from a cave (20°33′02.5″ N, 89°54′44.4″ W) located in the municipality of Calcehtok and 128 from a cave (20°44′48.1″ N, 89°17′48.9″ W) in the municipality of Homún (Figure 1). The two caves are separated by 68 km. The cave in Calcehtok is surrounded by low deciduous tropical forest and lies 1.4 km from the nearest rural community, whereas the cave of Homún is situated on the outskirts of a town, near hostels and farms. Collecting permit was obtained from the Ministry of Environment and Natural Resources of Mexico [SEMARNAT] (SPARN/DGVS/00788/24). The Bioethics Committee for Animal Use of the Faculty of Veterinary Medicine at the Universidad Autónoma de Yucatán approved the protocols used in this research (protocol number CB-CCBA-D-2023-003). All bats included in this study were captured using a mist net (6 m long × 2.5 m wide) positioned at the entrance of each cave. The captured bats were removed from the nets, placed in cloth bags and sexed. At the laboratory, animals were anesthetized and euthanized with isoflurane (Leary *et al.* 2020). Heart, lungs, esophagus, stomach, intestines, liver and mesenteries were collected from each bat. Tissues from some animals were immersed in 0.9% sodium chloride solution and examined under a stereomicroscope (Olympus SZ2-ILST), the rest of the tissues were preserved in 96% ethanol and examined afterwards. Helminths were collected, counted and separated into groups. Cestodes, trematodes, and acanthocephalans were placed in distilled water to allow relaxed death of the specimens, while nematodes were fixed with hot 70% ethanol (Gardner & Jiménez-Ruiz 2009). Helminths were collected, counted, and preserved in 70% ethanol or 10% formalin for light microscopy, 100% ethanol for DNA extraction, and 10% formalin for scanning electron microscopy (SEM).

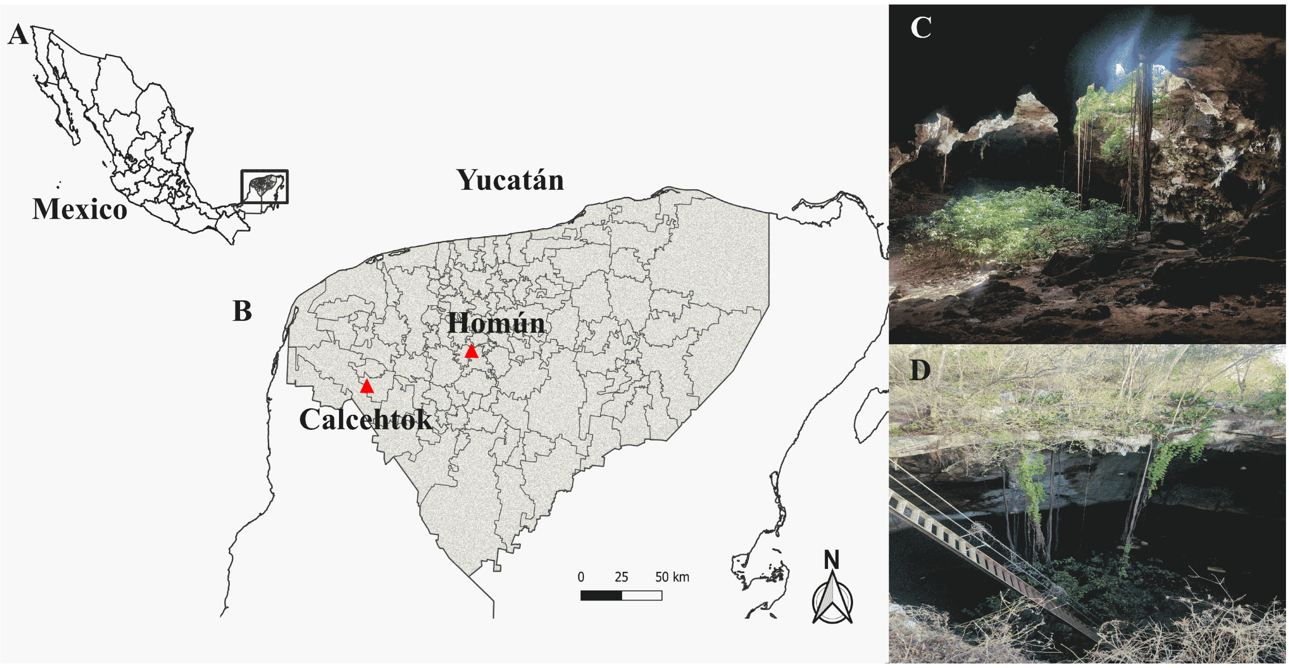

FIGURE 1. A. Geographic location of Mexico and the state of Yucatán (rectangle). B. Location of the study sites (red triangles) in the state of Yucatán. C. Cave entrance studied in Calcehtok. D. Cave entrance studied in Homún.

Nematodes and acanthocephalans were cleared and temporarily mounted in lactophenol. The synlophe of the new species of Anoplostrongyline nematode was studied through transverse sections of the body following the method of Durette-Desset (1985). Trematodes and cestodes were stained with Mayer's paracarmine, 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). All measurements are in micrometers (µm) unless otherwise stated. Measurements are provided as mean, standard deviation, and range (in parentheses). For taxa with fewer than five measured specimens, either the range is presented or, in the case of a single specimen, its individual measurements are given. In the description of the new species, the measurements of the holotype and allotype are presented first, followed by those of the paratypes.

For SEM, selected helminths were dehydrated using a graded ethanol series, critical-point dried with carbon dioxide, sputter-coated with a gold-palladium mixture, and examined at an accelerating voltage of 10 kV with a Hitachi SU1510 scanning electron microscope at the Laboratorio de Microscopía y Fotografía de la Biodiversidad, Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), Mexico City. Specimens were identified to the lowest level possible using keys for nematodes (Moravec 1982; Anderson *et al.* 2009), cestodes (Khalil *et al.* 1994), trematodes (Bray *et al.* 2008) and acanthocephalans (Schmidt 1972; Amin 1987), as well as original descriptions and redescriptions of bat helminths.

Helminth specimens were deposited in the Colección Nacional de Helmintos (CNHE), IB-UNAM, Mexico City, Mexico, and the Parasitic Worms Collection of the Natural History Museum (NHM), London, UK. Bats were deposited in the Colección Zoológica, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán (FMVZ-UADY 1727–1742) and the Mammal Collection of the Universidad Autónoma de Campeche

(CM-UAC 1058). A fragment of the cytochrome c oxidase subunit I (COI) gene of four isolates of *N. laticaudatus* were submitted to GenBank (PV426004–PV426007).

The prevalence and mean intensity of infection for each helminth taxon were estimated for every locality according to Bush *et al.* (1997). The 95% confidence intervals of these parasitological parameters were calculated following Rózsa *et al.* (2000).

DNA extraction and sequencing of helminths

Total genomic DNA of at least one specimen or fragment of each helminth taxon was extracted using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. A partial fragment (≈ 1,200 bp) of the 28S ribosomal RNA (28S) gene was targeted using the forward primer 391 5′-AGCGGAGGAAAAGAAACTAA-3′ (Stock *et al.* 2001) and the reverse primer 536 5′-CAGCTATCCTGAGGGAAAC-3′ (Stock *et al.* 2001). For nematodes identification, a fragment (≈ 600 bp) of COI was amplified using the primers forward NC01f1 5′-CCTACTATGATTGGTGGTTTTGGTAATTG-3′ and reverse NC01R2 5′-GTAGCAGCAGTAAAATAAGCAC-3′ (Kanzaki & Futai 2002). Polymerase chain reaction (PCR) amplifications were carried out using the conditions described by Hernández-Mena *et al.* (2017) and Kanzaki & Futai (2002). The PCR primers along with additional internal primer 503 5′-CCTTGGTCCGTGTTTCAAGACG-3′ (García-Varela & Nadler 2005), were used for sanger sequencing at Macrogen Inc. (Seoul, Korea). Contiguous sequences were assembled and edited using Geneious Pro 4.8.4 and submitted to GenBank®.

Results

A total of 258 bats of *N. laticaudatus* were examined (141 males and 117 females). Seventeen helminth taxa were identified: seven trematodes, two cestodes, six nematodes and two acanthocephalans. A commented list of the helminths of *N. laticaudatus* identified according to morphological and morphometric characteristics is provided.

List of helminths species

Phylum Platyhelminthes Gegenbaur

Class Trematoda Rudolphi

Order Plagiorchiida La Rue

Family Dicrocoeliidae Looss

***Brachylecithum* Shtrom**

***Brachylecithum rileyi* (Macy)**

Infection site: Liver, gallbladder and intestine

Localities: Calcehtok and Homún

Prevalence (%) and median intensity: Calcehtok 42.1 and 6.2 (4.9–8.1). Homún 14.1 and 9.5 (4.5–18.2)

Specimens deposited: CNHE-12306 and NHM 2025.8.13.1

GenBank accession numbers: PX232558–PX232560 (28S)

Comments: Based on 10 specimens. Elongated body, 2271 ± 577 (1400–3100) × 345 ± 93 (220–500). Oral sucker subterminal, 145 ± 23 (110–179) × 116 ± 19 (82–160). Ventral sucker 164 ± 14 (145–180) × 146 ± 22 (120–185) (Figures 2A, 3A). Oval pharynx 37.3 ± 7 (30–50) × 42 ± 7 (28–50). Testes oblique; anterior testis 200

± 45 (130–260) × 126 ± 34 (50–160), posterior testis 203 ± 71 (70–294) × 125 ± 36 (72–165). Ovary globular, posterior to the posterior testis, 95 ± 20 (60–120) × 120 ± 23 (88–155). Cirrus-sac and genital pore anterior to the oral sucker, 136 ± 25 (108–170) × 75 ± 11 (60–85). Vitellarium follicular, post-ovarian. Eggs 31 ± 0.9 (30–32) × 20 ± 0.8 (18–21).

The characteristics of the studied trematodes fit the recent redescription of *B. rileyi* collected from *N. laticaudatus* in Homún, Yucatán (Moguel-Chin *et al.* 2024). Other host recorded for this trematode in Mexico include *Tadarida brasiliensis* (Geoffroy Saint-Hilaire) in Durango, Morelos, Nuevo León, Puebla, Zacatecas (Guzmán-Cornejo *et al.* 2003; Caspeta-Mandujano *et al.* 2017; Martínez-Salazar *et al.* 2020).

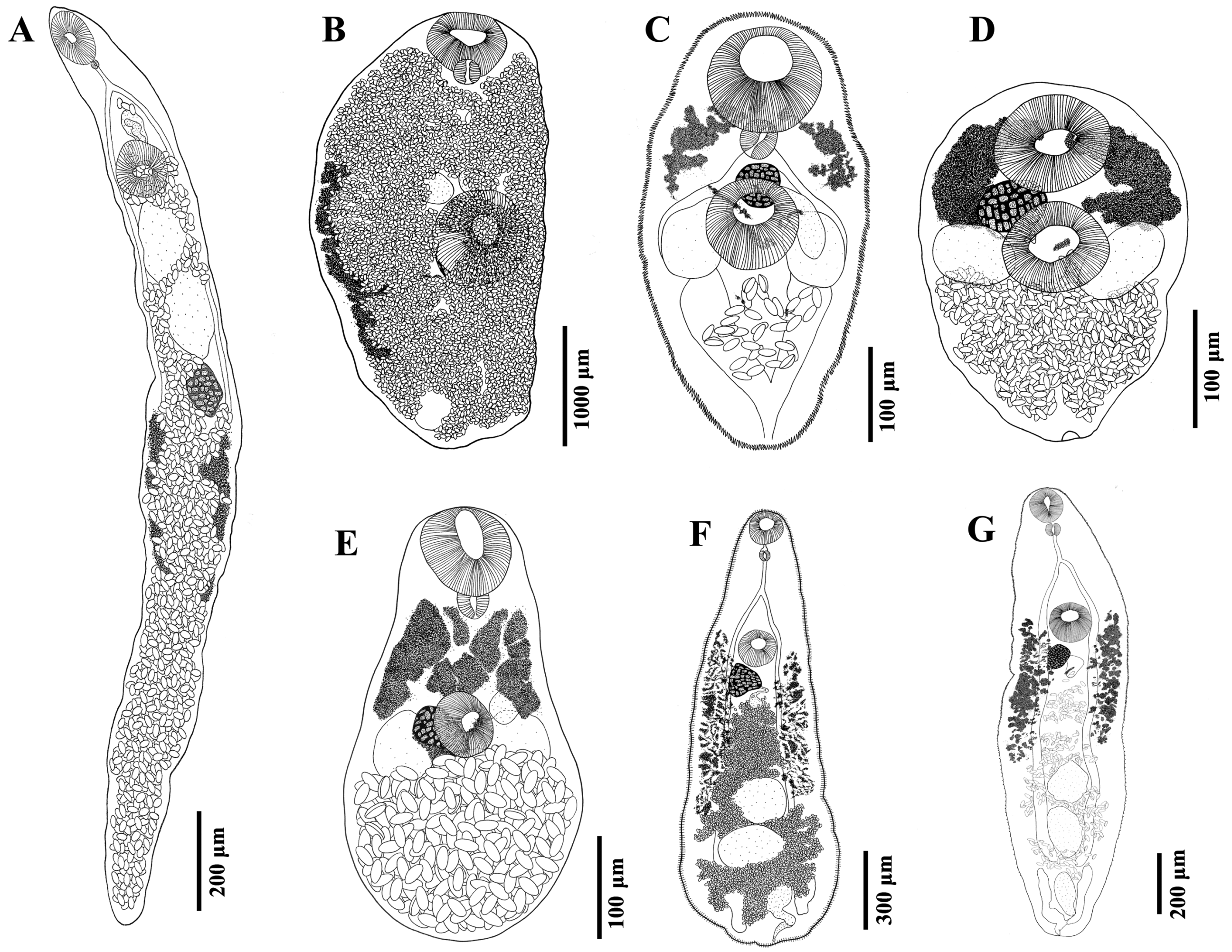

FIGURE 2. Trematodes of *N. laticaudatus*. A. Specimen of *B. rileyi*, ventral view. B. Dissected specimen of *Euparadistomum* sp., ventral view. C. Specimen of *L. nanum*, ventral view. D. Specimen of Phaneropsolidae gen. sp., ventral view. E. Specimen of *Ochoterenatrema* sp., ventral view. F. Specimen of *U. minuta*, ventral view. G. Specimen of *Urotrema* sp., ventral view.

Euparadistomum Tubangui

Euparadistomum sp.

Infection site: Gallbladder

Locality: Calcehtok

Prevalence (%) and median intensity: Calcehtok 1.6 and 1.5 (1–2)

Specimen deposited: CNHE-12307

GenBank accession number: PX232561 (28S)

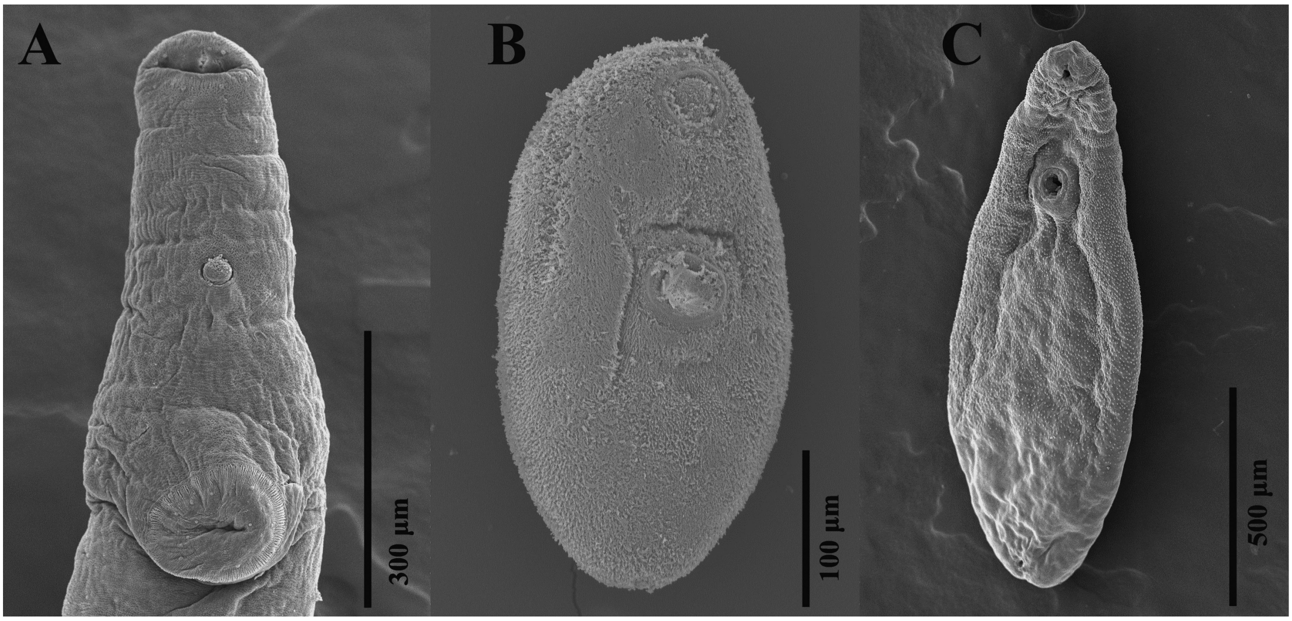

FIGURE 3. Scanning electron micrographs of trematodes of *N. laticaudatus*. A. Anterior part of *B. rileyi*, ventral view. B. Specimen of *L. nanum*, ventral view. C. Specimen of *Urotrema minuta*, ventral view.

Comments: Based on two specimens. Oval body, 3350–3560 × 1850–2170 (Figure 2B). Oral sucker 470–480 × 565–610. Ventral sucker 840 × 820. Oval pharynx 170 × 190–200. Testes small, in the anterior border to ventral sucker; right testis 230–270 × 190–240, left testis 240–280 × 260. Ovary postesticular, overlap on the posterior border to ventral sucker, 360–400 × 270–300. Uterus extending from pharynx to body end. Vitelline reservoir posterior to the ovary. Vitellarium in two bands extending laterally from testes level to the forebody. Eggs 44–45 × 25–26.

The morphological features fit with the description of *Euparadistomum* (Bray *et al.* 2008). This genus has been reported from a variety of host: reptiles, birds and mammals from New Guinea, Ivory Coast, Equatorial Guinea, Malaysia, Myanmar and Brazil (Betterton 1980; El-Dakhly *et al.* 2018; Emmerich *et al.* 2025). In bats, *Euparadistomum cerivoulae* Gogate has been reported in *Kerivoula picta* (Pallas) from Myanmar; however, studied specimens have some differences with this species, like bigger testes (*vs.* 163 ×134 and 167 ×145 in *E. cerivoulae*) (Gogate 1939). In the Americas, *Euparadistomum cisalpinai* Emmerich, Cenci de Aguiar & da Silva and *Euparadistomum paraense* (Jansen) have only been recorded from reptiles *Tropidurus torquatusand* (Wied-Neuwied) and *Tropidurus hispidus* (Spix) (Emmerich *et al.* 2025), respectively. However, these species differ from the specimens collected in Yucatán by having a higher oral sucker/ventral sucker ratio and by lacking cuticular papillae (Emmerich *et al.* 2025). These differences suggest that these trematodes may represent a species not described yet. This is the first record of *Euparadistomum* in bats from Mexico.

Family Phaneropsolidae Mehra

***Limatulum* Travassos**

***Limatulum nanum* Moguel-Chin, Panti-May, García-García & Hernández-Mena**

Infection site: Stomach and intestine

Localities: Calcehtok and Homún

Prevalence (%) and median intensity: Calcehtok 24.6 and 2 (1.4–2.7). Homún 13.3 and 1.5 (1.2–1.7)

Specimens deposited: CNHE-12308 and NHM 2025.8.13.2

GenBank accession number: PX232562 (28S)

Comments: Based on 10 specimens. Oval body, 575 ± 128 (460–860) × 338 ± 103 (210–550), completely covered with spines (Figures 2C, 3B). Oral sucker 130 ± 30 (84–180) × 140 ± 39 (80–190). Ventral sucker median, 124 ± 24 (96–160) × 127 ± 27 (91–170). Pharynx 47 ± 11 (35–70) × 42 ± 11 (30–65). Esophagus absent. Testes at level of mid-body; right testis 98 ± 20 (76–130) × 90 ± 16.3 (70–110), left testis 95 ± 14 (77–110) × 81 ± 27 (50–130). Ovary round, pretesticular, located at level of the ventral sucker, 75 ± 22 (42–105) × 79 ± 20 (45–100). Cirrus-sac sinistral 96 ± 21 (65–120) × 45 ± 10 (28–58). Eggs 19 ± 0.7 (18–20) × 10 ± 0.5 (9–10).

The morphological features agree with the description of *L. nanum* from *Eumops nanus* (Miller) in Campeche, Mexico (Moguel-Chin *et al.* 2024). This is the first record of *L. nanum* for *N. laticaudatus* and the first record for Yucatán.

Phaneropsolidae gen. sp.

Infection site: Stomach

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 1.6 and 1 (1). Homún 1.6 and 1 (1)

Specimen deposited: CNHE-12312

Comments: Based on two specimens. Body slightly oval, 310–490 × 222–320 (Figure 2D). Oral sucker subterminal, 80–150 × 100–180. Ventral sucker 75–120 × 90–125. Pharynx not observed. Genital pore in forebody. Testes post-ovarian at level of mid-body; right testis 48 × 70, left testis 45–90 × 80–128. Ovary pretesticular, 42–90 × 60–95. Vitellarium extending from oral sucker to anterior part of testes. The uterus covers the posterior third of body. Eggs 10–11 × 5–6.

The examined specimens have the main characteristics of Phaneropsolidae (Bray *et al.* 2008), namely, a genital pore sublateral, a pretesticular ovary, and the vitellarium in clusters. Due to the poor conditions of the specimens, some morphological characteristics (e.g., cirrus sac) could not be clearly observed; therefore, we prefer not to assign the trematodes to a specific level. This group of trematodes has been recorded in several bats belonging to the families Mormoopidae, Natalidae, Phyllostomidae, Molossidae, and Vespertilionidae from several countries in the Neotropics (see the complete references in Santos & Gibson 2015; Caspeta-Mandujano *et al.* 2017).

Family Lecithodendriidae Lühe

***Ochoterenatrema* Caballero**

***Ochoterenatrema* sp.**

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and median intensity: Calcehtok 25.4 and 12.7 (7.7–22.6). Homún 3.9 and 2.4 (1–4.4)

Specimens deposited: CNHE-12309 and NHM 2025.8.13.3

GenBank accession numbers: PX232563–PX232565 (28S)

Comments: Based on nine trematodes. Pear-shaped body, 348 ± 72 (260–470) × 223 ± 78 (150–400) (Figure 2E). Oral sucker subterminal, 72 ± 13 (55–85) × 76 ± 9 (70–90). Ventral sucker 62 ± 20 (32–89) × 59 ± 18 (48–98). Pharynx 30 ± 4 (26–35) × 28 ± 5 (20-32). Right testis 57 ± 10 (45–68) × 54 ± 10 (40–65). Left testis 53 ± 15 (42–80) × 61 ± 15 (38–78). Ovary at level of ventral sucker, overlapping to the right testis, 60 ± 7 (55–65) × 77 ± 3 (75–79). Vitellarium extending from the oral sucker to the anterior level of testes. Pseudocirrus sac at level of the ventral sucker, 62.8 ±15 (48–80) × 72 ± 20 (50–94). Eggs 20 ± 1 (18–21) × 10 ± 0.8 (8–10).

The newly collected specimens have morphological characteristics of the genus *Ochoterenatrema*, namely the presence of pseudogonotyl situated to the left of the ventral sucker, entire testes and median pseudocirrus sac (Fernandes *et al.* 2022). The material from Yucatán closely resembles *Ochoterenatrema piriforme* Tkach, Gasperetti, Fernandes, Carrión-Bonilla, Cook & Achatz for characteristics such as the position of the ovary and the vitellarium. However, the studied specimens have smaller structures than *O. piriforme*, such as ventral sucker and pseudocirrus sac (62 × 59 and 63 × 72 *vs*. 72 × 78 and 79 × 82, respectively) than *O. piriforme* (Tkach *et al.*

2024); thus, the specimens may represent a species not described yet. In Mexico, *Ochoterenatrema labda* Caballero has been reported from *Balantiopteryx plicata* (Peters), *T. brasiliensis*, *Pteronotus fulvus* (Thomas), *Mormoops megalophylla* (Peters), *Myotis velifer* (Allen), and *Natalus mexicanus* Miller in Morelos, Mexico City, Mexico State, Durango, Nuevo León, Puebla, Veracruz, and Zacatecas (Caspeta-Mandujano *et al.* 2017). In *N. laticaudatus*, an unidentified species of *Ochoterenatrema* has been reported in Oaxaca (Martínez-Pérez 2021). This is the first record of *Ochoterenatrema* for Yucatán.

Family Urotrematidae Poche

Urotrema Braun

Urotrema minuta Macy

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and median intensity: Calcehtok 29.4 and 2.7 (2–4.2). Homún 25 and 1.8 (1.5–2.3)

Specimens deposited: CNHE-12310 and NHM 2025.8.13.4

GenBank accession numbers: PX232566–PX232568 (28S)

Comments: Based on eight specimens. Body elongated, 1460 ± 249 (1070–1800) × 389 ± 115 (360–440). (Figures 2F, 3C). Tegument covered by spines up to a third of the body. Oral sucker subterminal, 107 ± 18 (80–135) × 103 ± 16 (82–125). Ventral sucker at intestinal bifurcation level, 125 ± 29 (105–150) × 116 ± 25 (89–150). Pharynx muscular, 40 ± 8 (30–50) × 38 ± 8 (28–47). Round testes, in tandem; anterior testis 170 ± 74 (100–320) × 131 ± 50 (68–185), posterior testis, 161 ± 62 (110–290) × 139 ± 64 (62–245). Ovary oval, pretesticular, 99 ± 34 (60–175) × 89 ± 39 (50–140). Vitellarium in forebody, extending from the posterior border of the oral sucker to the anterior/posterior border of the anterior testis. Cirrus-sac at posterior end of body, 157 ± 56 (100–230) × 82 ± 18 (60–100). Eggs 20 ± 0.5 (19–21) × 10 ± 0.5 (10–11).

The morphology of the specimens fits with the features of *U. minuta* described by Macy (1933). *Urotrema minuta* has been reported previously in *N. laticaudatus* from Yucatán and *E. nanus* from Campeche (Moguel-Chin *et al.* 2023).

Urotrema sp.

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and median intensity: Calcehtok 14.3 and 3.7 (2.2–6.6). Homún 8.6 and 2 (1.3–2.8)

Specimens deposited: CNHE-12311 and NHM 2025.8.13.5

Comments: Based on six specimens examined. Body 1945 ± 323 (1450–2450) × 665 ± 200 (400–860) (Figure 2G). Tegument covered by spines up to a third of the body. Oral sucker 129 ± 25 (105–160) × 125 ± 25 (86–152). Ventral sucker 169 ± 21 (134–200) × 162 ± 25 (128–198). Pharynx 60 ± 13 (40–70) × 50 ± 12 (40–70). Testes in tandem; anterior testis 167 ± 37 (122–235) × 207 ± 66 (131–300), posterior testis 178 ± 46 (130–252) × 218 ± 68 (110–300). Ovary oval, pretesticular, 141 ± 47 (86–210) × 131 ± 49 (65–200). Vitellarium in forebody, extending from the posterior border of the oral sucker to just anterior to the anterior testis. Cirrus-sac 159 ± 38 (128–225) × 77 ± 22 (48–110). Eggs 20 ± 0.4 (20–21) × 10 ± 0.8 (9–11).

These specimens closely resemble *U. minuta*. However, they in their body length (1945 *vs*. 1460) and vitellarium extension (ending before anterior testis level *vs*. reaching midlevel of anterior testis).

Class Cestoda Rudolphi

Order Cyclophyllidea Van Beneden in Braun

Family Hymenolepididae Perrier

***Vampirolepis* Spasskii**

***Vampirolepis* cf. *christensoni* (Macy)**

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 18.3 and 2.7 (1.7–4.4). Homún 6.2 and 1.6 (1–3)

Specimens deposited: CNHE-12314 and NHM 2025.8.13.6

GenBank accession number: PX232569 (28S)

Comments: Based on 31 immature or incomplete specimens. Rostellum armed with 49 ± 4 (39–58) hooks in a single row (Figure 4A). Hooks 29 ± 25 (24–34) long (Figure 4B). Suckers 86 ± 10 (70–110) in diameter.

We assigned our material to the species *V.* cf. *christensoni*, mainly because the number and size of rostellar hooks are similar to those originally reported by Macy (1931) from *Myotis lucifugus* Le Conte in Minnesota, USA and those reported by Zdzitowiecki & Rutkowska (1980) from *Pteronotus mesoamericanus* Smith and *Eptesicus fuscus* (Palisot de Beauvois) in Cuba. This cestode has been reported for *N. laticaudatus* in South America (Santos & Gibson 2015). This is the first record of *V.* cf. *christensoni* in bats from Mexico.

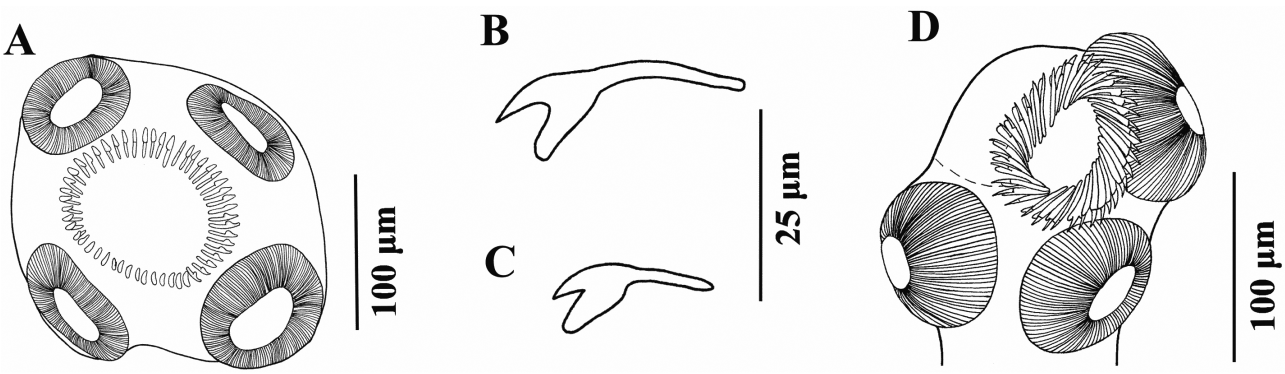

FIGURE 4. *Vampirolepis* cf. *christensoni* (A–B) and *Vampirolepis* cf. *phyllostomi* (C–D). A and D. Rostellum, apical view. B and C. Hook, lateral view.

***Vampirolepis* cf. *phyllostomi* (Vaucher)**

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 15.9 and 2.1 (1.6–3.2). Homún 10.2 and 1.6 (1.1–2.8)

Specimens deposited: CNHE-12313 and NHM 2025.8.13.7

GenBank accession numbers: PX232570, PX232571 (28S)

Comments: Based on 29 immature or incomplete specimens. Rostellum armed with 37 ± 3 (30–44) hooks in a single row (Figure 4D). Hooks 22 ± 1 (20–24) long (Figure 4B). Suckers 62.3 ± 4.1 (55–70) in diameter.

The material was identified as *Vampirolepis* cf. *phyllostomi* (Vaucher) because its characteristics agree with the description by Vaucher (1982) of cestodes from *Phyllostomus hastatus* (Pallas) in Peru, and the redescription by Vaucher (1986) from *Eumops bonariensis* (Peters) in Argentina. This species has been reported from *P. hastatus* in Peru and Bolivia (Vaucher 1982; Sawada & Harada 1986). This study expands the distribution of *V.* cf. *phyllostomi* to Mexico, and adds a new host, *N. laticaudatus*.

Phylum Nematoda Rudolphi

Class Adenophorea Chitwood

Orden Enoplida Baird

Family Capillariidae Railliet

***Aonchotheca* López-Neyra**

***Aonchotheca pulchra* (Freitas)**

Infection site: stomach and intestine

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 59.5 and 2.8 (2.4–3.4). Homún 41.4 and 2.1 (1.5–3.2)

Specimens deposited: CNHE-12315 and NHM 2025.8.13.8

GenBank accession number: PX232600 (28S)

Comments: Based on six males and seven females. Two wide lateral bacillary bands, composed of numerous hypodermal round cells. Stichocytes arranged in a single row and subdivided into several transverse annuli with large nuclei. Two mesenchymal cells observed at the esophago-intestinal junction. Male body length 13448 ± 1994 (10650–15720) and maximum body width 85 ± 12 (70–100). Total esophagus length 4833 ± 722 (4100–5740); muscular esophagus length 432 ± 93 (330–519), stichosome length 5095 ± 308 (4751–5332). Posterior body region 8520 ± 1443 (6550–10470) long. Ratio between anterior esophageal region and posterior intestinal region 0.6 ± 0.1 (0.5–0.6). Two caudal lateral alae, and a relatively small, caudal membrane supported by two lateral expansions (or rays), which end in papillae on posterior extremity of body. Ventrally, two digitiform expansions observed, each with two short projections arising from their base, ending in terminal papillae. Another pair of papillae on the sides of the cloaca, between the base of the caudal membrane and the posterior edge of the latero-caudal alae. Spicule indistinct due to little or no sclerotization. The rugged non-spiny spicular sheath generally protruded outside the body and curled (Figure 5A). Female body length 14090 ± 3165 (10105–18555) and maximum body width 173 ± 26 (140–207). Total esophagus length 4927 ± 1182 (3820–7108); muscular esophagus length 516 ± 94 (376–605), and stichosome length 4894 ± 1236 (4037–6732). Posterior body region 8842 ± 2711 (6285–13775) in length. Vulva at 3387 ± 1058 (2320–4350) from anterior extremity. Vulvar membranous appendage present (Figure 5B). Conical tail, slightly curved ventrally with subterminal anus. Eggs 44 ± 1 (42–45) × 26 ± 3 (24–30). Ratio between anterior esophageal region and posterior intestinal region 0.6 ± 0.1 (0.4–0.7).

The morphology and morphometric data of the Yucatán specimens fit the redescription of *A. pulchra* by Cardia *et al.* (2014). This is the first record of *A. pulchra* in Mexico.

Class Secernentea von Linstow

Order Strongylida Diesing

Family Molineidae Skrjabin & Schultz

***Anoplostrongylus* Boulenger**

***Anoplostrongylus allami* sp. nov. Panti-May & Digiani**

Infection site: Intestine

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 89.7 and 13.3 (11.4–16.6). Homún 90.6 and 13.5 (11.5–16.4)

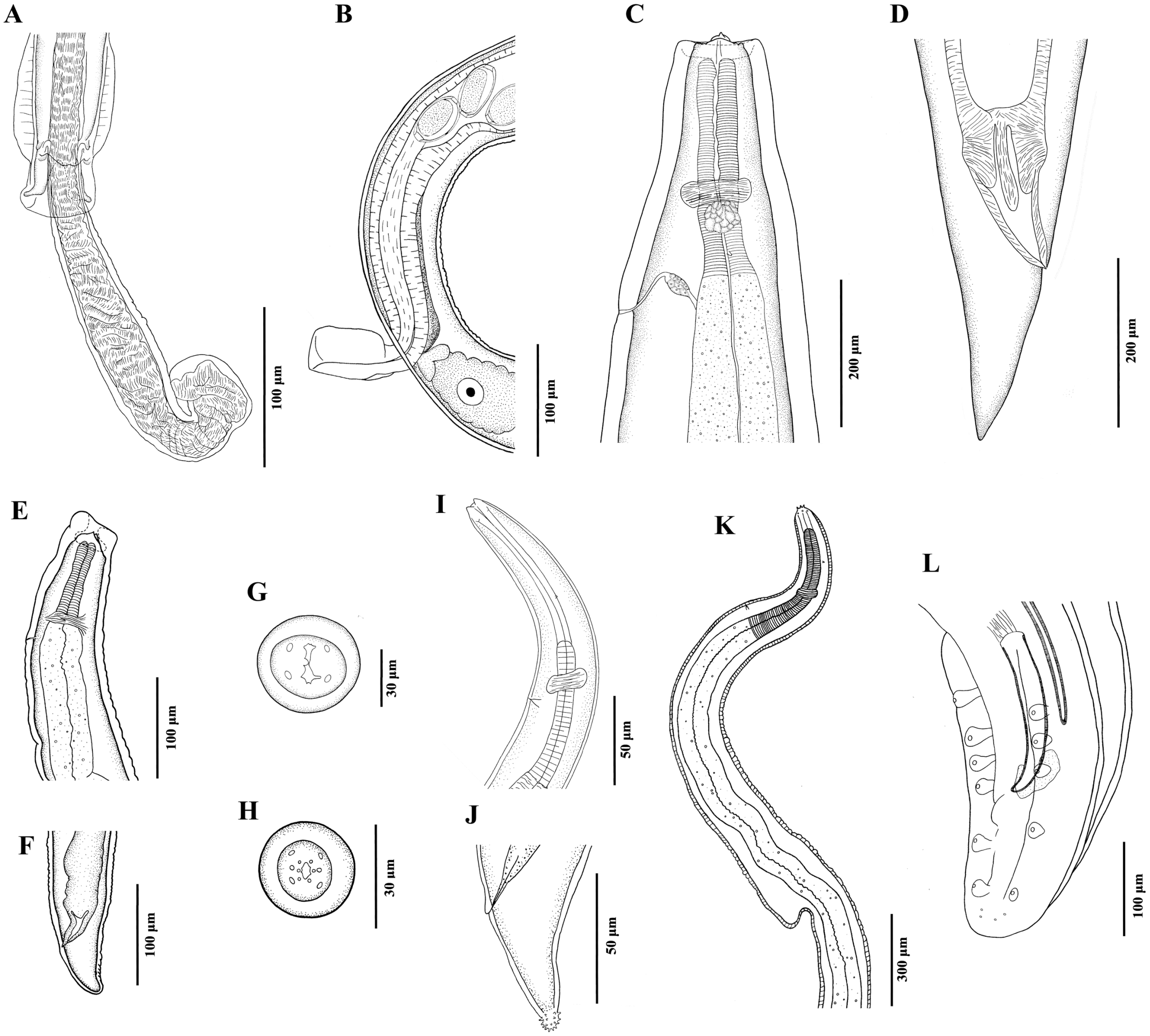

FIGURE 5. A. Male posterior extremity of *Aonchotheca pulchra*, ventral view. B. Esophagus-intestine juction and vulva of female *Aonchotheca pulchra*, lateral view. C. Female anterior extremity of adult *Physaloptera* sp., left lateral view. D. Female posterior extremity of adult *Physaloptera* sp., right lateral view. E. Anterior extremity of larva of *Physaloptera* sp., ventral view. F. Larvae posterior extremity of *Physaloptera* sp., lateral view. G. Cephalic region of larva of *Physaloptera* sp., apical view. H. Cephalic region of larva of *Physocephalus sexalatus*, apical view. I. Anterior extremity of larva of *Physocephalus sexalatus*, ventral view. J. Posterior extremity of larva of *Physocephalus sexalatus*, lateral view. K. Male anterior extremity of *Spirura mexicana*, ventral view. L. Male posterior extremity of *Spirura mexicana*, ventral view.

Specimens deposited: Holotype male (No. 12316), Calcehtok; allotype female (No. 12317), Calcehtok; and paratypes (No. 12318, 12319, 12320), Calcehtok and Homún, deposited at the CNHE. Paratypes from Calcehtok desposited at the NHM (2025.8.13.9–12)

GenBank accession numbers: PX232572–PX232574 (28S) and PX227565, PX227566 (COI)

ZooBank Life Science Identifier: 6949A151-EABB-475C-84CA-88537D612937

Etymology: This species is named in honor of the late Allam Tzab Pech (1992–2024), a friend, biologist, and passionate bat conservationist from Yucatán, who supported our fieldwork in Homún during the early stages of the project.

Description: General. Medium-sized nematodes. Sexually dimorphic, females larger than males. Oral opening circular with two amphids and six external labial papillae (Figure 7A–B). Dorsal esophageal tooth conspicuous

(Figure 7A). Nerve ring situated at middle of esophagus; excretory pore located posterior to nerve ring; deirids simple at about same level than excretory pore (Figure 6A–B).

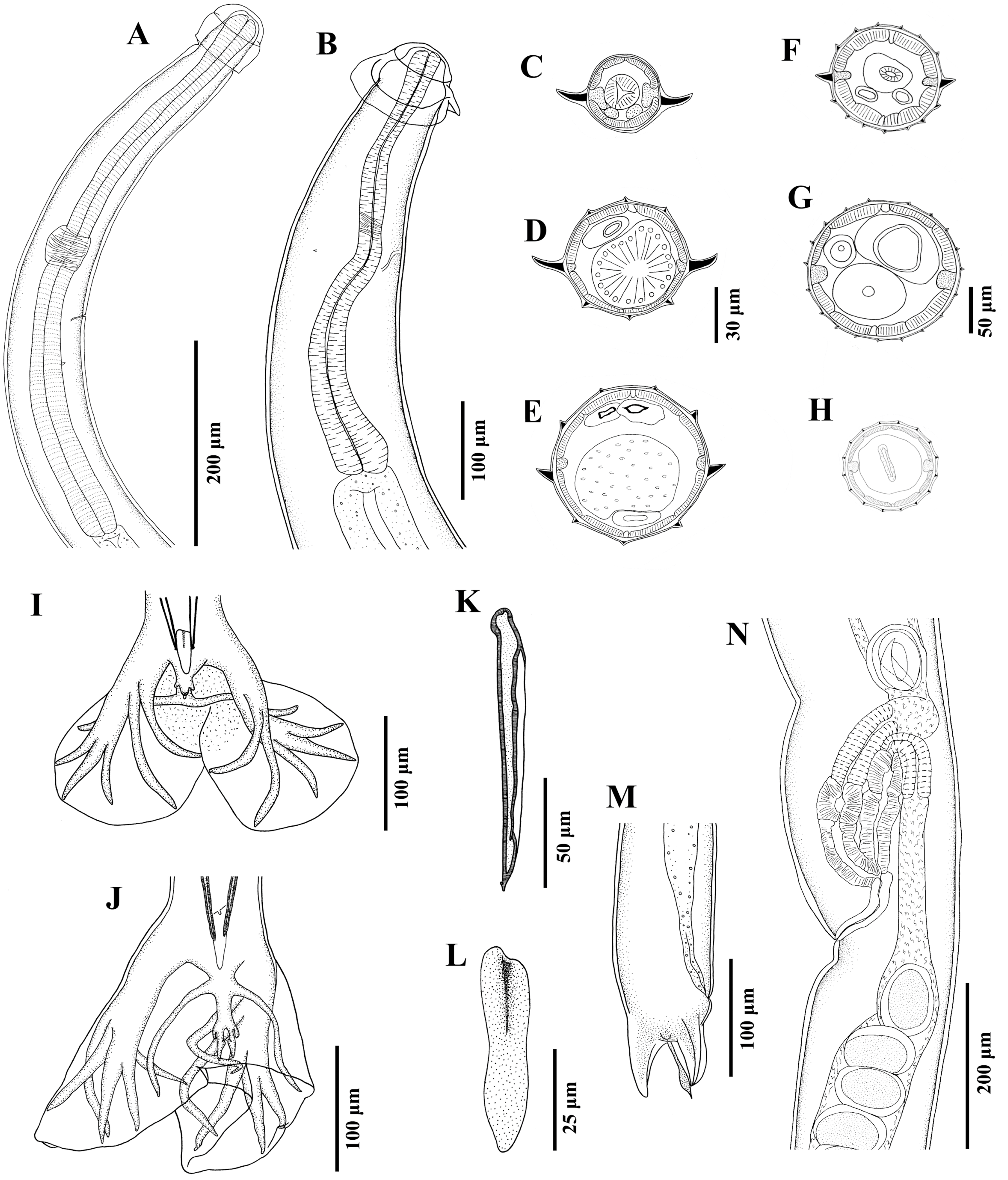

FIGURE 6. *Anoplostrongylus allami* sp. nov. A. Anterior part of male, right lateral view. B. Anterior part of female, right lateral view. C–E. Transverse sections of the body of male, at level of distal esophagus (C), mid-body (D), and proximal spicules (E); all sections share the scale bar. F–H. Transverse sections of the body of female, at level of distal esophagus (F), mid-body (G), and anterior to the tubercles (H); all sections share the scale bar. I. Male caudal bursa, ventral view. J. Male caudal bursa, dorsal view. K. Right spicule, ventral view. L. Gubernaculum, ventral view. M. Tail of female, right latero-ventral view. N. Vulvar region of female, left lateral view.

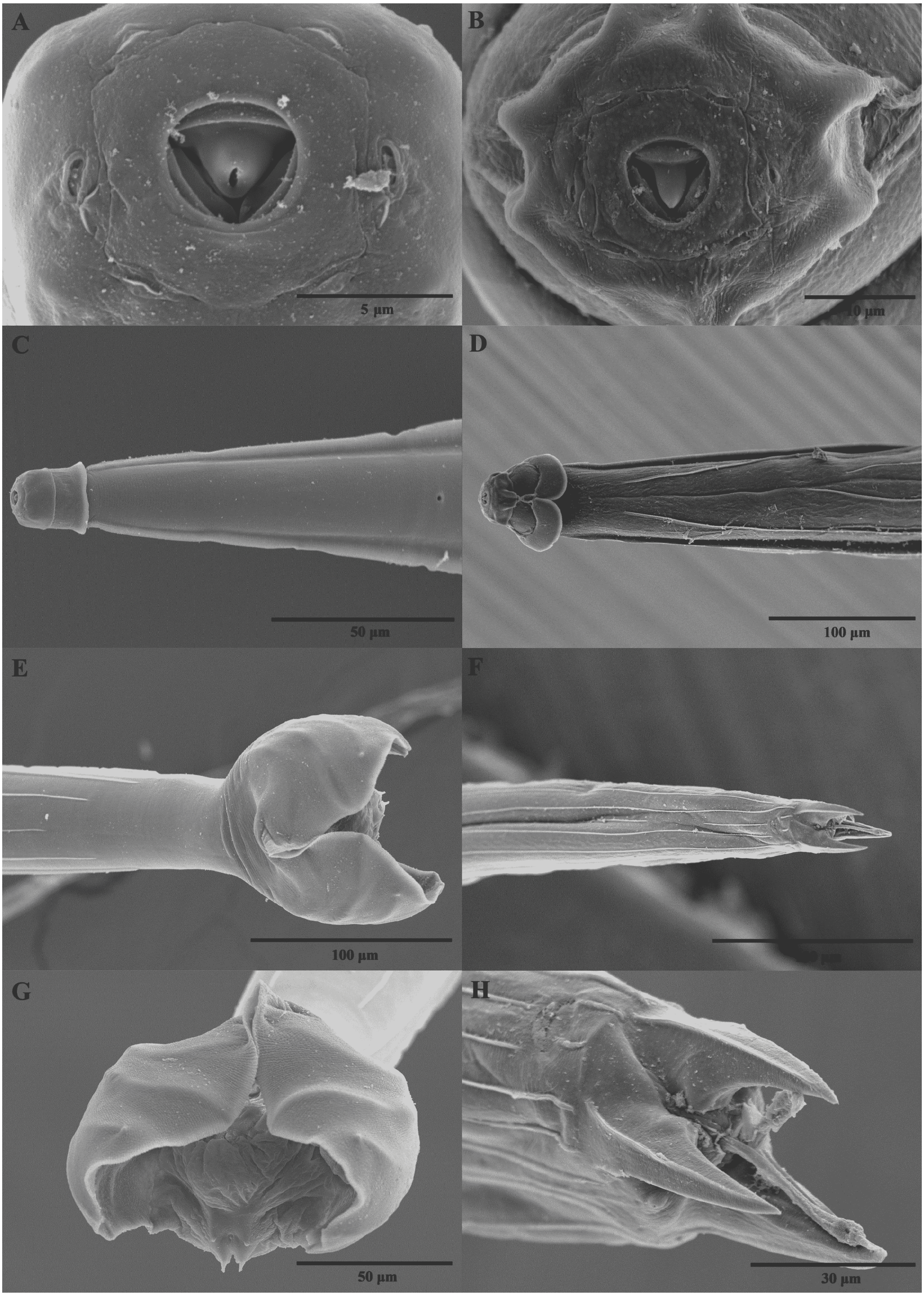

FIGURE 7. SEM micrographs of *Anoplostrongylus allami* sp. nov. A. Head of male, apical view. B. Head of female, apical view. C. Anterior part of male, ventral view. D. Anterior part of female, dorsal view. E. Posterior part of male, ventral view. F. Posterior part of female, ventral view. G. Male caudal bursa, ventral view. H. Tail of female, ventro-lateral view.

Cephalic vesicle: In males, campanulate with two distinct portions, posterior portion longer (Figures 6A, 7A). In females, umbelliform divided into three distinct portions: first one short, second longer, and third with dorsal and ventral notches (Figures 6B, 7B).

Synlophe (studied in two males and two females): Cuticle with longitudinally continuous ridges (Figures 7C–H); oriented ventral to dorsal. Ridges appearing posterior to cephalic vesicle (Figures 7C–D) and disappearing anterior to caudal bursa in males (Figure 7E, G) and anterior to cuticular tubercles in females (Figure 7F, H). Males: two ridges at level of distal esophagus, 8–9 at mid-body, and 9–10 at level of proximal portion of spicules (Figure 6C–E). In the anterior and middle region of the body, the two lateral ridges associated with lateral hypodermal cords widening to form alae; lateral alae are the only ridges present at esophageal level (Figure 7C), other ridges appearing posterior to esophagus. Females: 14–15 ridges at level of distal esophagus, 18–19 at mid-body, and 15–16 anterior to caudal tubercles (Figure 6F–H). In esophageal region, lateral ridges associated with lateral hypodermal cords also form alae; at midbody and at posterior part of body lateral ridges with same development as the remaining ridges.

Males (based on holotype and 11 paratypes): 3, 3 ± 0.3 (3–4) mm long and 88, 76 ± 13 (60–100) wide at mid-body. Cephalic vesicle 30, 27 ± 3 (22–30) × 25, 28 ± 3 (22–32). Nerve ring, excretory pore, and deirids situated at 155, 157 ± 12 (140–175), 195, 184 ± 20 (158–230), and 202, 195 ± 19 (175–240) from apex, respectively. Esophagus 320, 309 ± 26 (275–368) long. Bursa bell-shaped, with dorsal lobe poorly developed and accessory internal membrane (Figure 7E, G). Bursal pattern of type 2–3. Rays 2 and 3 longest, with short common trunk; rays 2 strongly curved toward median line, papillae 2 close to each other. Rays 4–6 with common trunk, rays 4 barely shorter, diverging first and slightly isolated from rays 5 and 6. Rays 8 long, arising symmetrically from proximal third of dorsal ray. Dorsal ray short, divided at distal third into two branches, each one bifurcated at proximal third into two sub-branches, rays 9 (external) and rays 10 (internal). Rays are 9 shorter than rays 10, arising at same level of dorsal ray bifurcation. Rays 10 bearing each a small internal projection (Figures 6I–J), probably phasmids. Genital cone small 40, 26 ± 5 (20–35) long and 40, 33 ± 6 (22–45) wide at base, with dorsal lip tapering distally and bearing two ventral papillae and a distal protuberance in form of lappet (Figure 6I). Spicules subequal, with a minute salient subterminal hook (Figure 6K). Spicules length 115, 129 ± 6 (120–142), representing 4, 5 ± 0.5 (4–5) % of body length. Gubernaculum 50, 43 ± 6 (32–50) long and 12, 11 ± 2 (8–15) wide, tapering at distal part (Figure 6L).

Females (based on allotype and 11 paratypes): 7, 8 ± 1 (6–10) mm long and 210, 185 ± 35 (150–250) wide at mid-body. Cephalic vesicle, 60, 66 ± 12 (50–95) × 110, 95 ± 10 (80–110). Nerve ring, excretory pore, and deirids at 190, 240 ± 30 (190–280), 220, 280 ± 38 (212–330), and 240, 309 ± 43 (235–360) from apex, respectively. Esophagus 455, 483 ± 42 (400–542) long. Didelphic, amphidelphic. Branches of ovejector divergent or both directed anteriorly then curving posteriorly (Figure 6N). Vulva at 5, 6 ± 1 (4–8) mm from anterior extremity, representing 73%, 74 ± 1 (72–76) of body length. Vagina vera 100, 92 ± 26 (65–160) long. Ovejector with posterior branch of vestibule slightly longer than anterior one; anterior branch 95, 72± 12 (65–95) long, posterior branch 100, 97 ± 15 (75–125) long. Anterior sphincter and infundibulum 50, 48 ± 8 (40–68) and 105, 95 ± 13 (75–120) long, respectively; posterior sphincter and infundibulum 52, 46 ± 9 (40–65) and 100, 83 ± 17 (50–110) long, respectively. Most gravid females with 17, 13 ± 16 (2–59) eggs in different embryonic development stages; eggs containing juvenile stage observed only in two females. Segmented eggs, 76 ± 8 (62–90) × 47 ± 6 (35–55) (based on 20 eggs measured from 11 paratypes). Eggs with juvenile stage, 72 ± 6 (68–80) × 52 ± 5 (45–55) (based on four eggs measured from allotype and one paratype). Anus 80, 82 ± 5 (70–90) from posterior extremity. Tail with three conical, sharp tubercles (two latero-ventral and one dorsal), and one thin, ventral spine 40, 44 ± 4 (38–50) long with a subterminal swelling (Figures 6M, 7H). A small papilla (probably phasmid) behind each latero-ventral tubercle (Figure 7H).

Remarks: The monotypic genus *Anoplostrongylus* was created to accommodate the species *Histiostrongylus paradoxus* Travassos described from *N. laticaudatus* in Brazil. This species was characterized by the absence of spines in the cephalic vesicle, the presence of three tubercles and a terminal spine on the female tail, and spicules with barbed distal extremities (Boulenger 1926). Later, Travassos (1937) expanded the generic definition to include the marked difference in size between males and females, the umbelliform cephalic vesicle of females; the postequatorial vulvar opening located within a depression; the bursa with reduced dorsal lobe, lateral rays decreasing in length from anterior to posterior, rays 8 arising from base of dorsal ray and dorsal ray forking distally, and the elongated gubernaculum.

Anoplostrongylus paradoxus was redescribed in detail by Lent *et al.* (1946) based on the type material and newly collected specimens; the synlophe of the species in transverse sections was described by Durette-Desset & Pinto (1977), also using the Brazilian type material.

Anoplostrongylus allami sp. nov. shares most of the morphological characters (e.g., sexual dimorphism in size, cephalic vesicle and synlophe; pattern of bursal rays; female tail) and biometrics (e.g., body length, spicules length, distance from vulva to anus). However, *A. allami* differs from *A. paradoxus* by the number of portions of the cephalic vesicle of males (two *vs*. three), the shape of the proximal half of the gubernaculum (asymmetric *vs*. symmetric) and, especially, by the marked sexual dimorphism in the ridge number and development. Durette-Desset & Pinto (1977) specified for *A. paradoxus* the same synlophe in both sexes at mid-body (19 ridges with similar development), but, at the anterior part of body the number and development of ridges differed in males and females: males with seven ridges of which the two lateral are developed forming lateral alae; and females with 18 ridges of which the two lateral ones are barely more developed than the other ones. In *A. allami*, males and females differ in their synlophe not only at the esophageal region but also at midbody. At level of distal esophagus, females possess 14–15 ridges of which the two lateral form the lateral alae; and males possess only the two ridges forming the lateral alae. At mid-body, males possess 8–9 ridges and the lateral alae are preserved, whereas females possess 18–19 ridges and the lateral alae disappear.

Anoplostrongylus allami and *A. paradoxus* share the same type of dimorphism on the cephalic vesicle. This structure in females shows dorsal and ventral notches whereas that of the male does not. That is why we consider that the generic definition of *Anoplostrongylus* should be further expanded to incorporate the sexual dimorphism of both the cephalic vesicle and the synlophe as important features.

Sexual synlophial dimorphism has been documented not only in *Anoplostrongylus* but also in other genera of Anoplostrongylinae parasitic in New World bats. In *Molostrongylus mbopi* Durette-Desset & Vaucher, a parasite of *Molossops* sp. from Paraguay, males possess a maximum of four ridges (lateral alae plus two other ridges) between the esophago-intestinal junction and the caudal bursa, whereas in females the number of ridges increases progressively with body length from four ridges at the esophago-intestinal junction (including the two lateral alae) to 24 ridges behind the vulva (Durette-Desset & Vaucher 1999). A case of extreme sexual dimorphism of the synlophe is found in *Macuahuitloides inexpectans* Jiménez, Peralta-Rodríguez, Caspeta-Mandujano & Ramírez-Díaz a parasite of *M. megalophylla* in Mexico in which males exhibit at mid-body 12 ridges, oriented ventral to dorsal, whereas females lack a synlophe. This latter species is also characterized by sexual dimorphism of the anterior part of the body. Males exhibit a simple, cap-like cephalic vesicle, whereas in females this structure is smooth and not prominent and is followed by a series of minute spines arranged in spiral rings covering the first quarter of body length (Jiménez *et al.* 2014).

Comments: Specimens of *A. allami* had been already isolated from *N. laticaudatus* in the same two sites sampled in the present study, and were treated provisionally as *Anoplostrongylus* sp. in Moguel-Chin *et al.* (2023).

Order Spirurida Chitwood

Family Physalopteridae Railliet

Physaloptera Rudolphi

Physaloptera sp.

Infection site: Stomach

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 3.2 and 3.2 (1–7). Homún 3.9 and 2.2 (1–4.2)

Specimens deposited: CNHE-12321 and NHM 2025.8.13.13

GenBank accession number: PX232575 (28S)

Comments: Based on an adult female and 10 larvae. Mouth laterally flattened with two pseudolabia, each pseudolabia with two cephalic papillae (Figure 5G); amphids not observed by light microscopy. Cephalic region with a cuticular dilatation at the base of the pseudolabia, forming a small collarette (Figures 5C, E). Conical tail (Figures 5D, F). Buccal capsule present. Body total length 8690 and width 420. Total esophagus length 2610: muscular esophagus 300 long, and glandular esophagus 2310 long. Anus 210 from posterior extremity. Larva 1451 ± 214 (1140–1890) in total length and 120 ± 16 (100–150) in body width. Larval esophagus 660 ± 52 (600–720) long: muscular esophagus 106 ± 38 (65–140) long and glandular esophagus 148 ± 52 (488–580) long. Anus 67 ± 12 (50–75) long.

In Mexico, larvae of the genus *Physaloptera* have been reported in *M. megalophylla* from Morelos (Caspeta-Mandujano *et al.* 2017). This is the first record of *Physaloptera* for *N. laticaudatus*.

Family Spirocercidae Chitwood & Wehr

***Physocephalus* Diesing**

***Physocephalus sexalatus* (Molin)**

Infection site: Stomach and intestine

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 4.8 and 1.5 (1–1.6). Homún 3.1 and 1.7 (1–2.5)

Specimens deposited: CNHE-12322 and NHM 2025.8.13.14

GenBank accession number: PX232576 (28S)

Comments: Based on eight encysted larvae. Cephalic region with two (ventral and dorsal) conical projections (Figure 5I). Head papillae well-defined, composed of six internal labial papillae and four cephalic papillae (Figure 5H). The funnel-shaped oral cavity passes into a narrow pharynx. Tail short, terminating in a small knob bearing spike-like projections (Figure 5J). Body, 1075 ± 229.3 (848–1500) × 65 ± 9 (60–80). Esophagus length 577 ± 139 (430–760): muscular esophagus 186 ± 74 (80–285) long and glandular esophagus 391 ± 108 (205–550) long. Tail 47 ± 6 (42–60) long.

The morphology and measurements of the specimens correspond to the third-stage larvae of *P. sexalatus* (Kirillov & Yu Kirillova 2021). This species has been recorded in *P. mesoamericanus*, *P. fulvus*, *B. plicata*, *Glossophaga mutica* Merriam and *Micronycteris microtis* Miller from Morelos (see complete references in Jiménez *et al.* 2017). This is the first record of *P. sexalatus* from bats in Yucatán.

Family Spiruridae Oerley

***Spirura* Blanchard**

***Spirura mexicana* Peralta-Rodríguez, Caspeta-Mandujano & Guerrero**

Site infection: Esophagus

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok 4.8 and 1.5 (1–2). Homún 3.9 and 2.2 (1–4.2)

Specimens deposited: CNHE-12323 and NHM 2025.8.13.15

GenBank accession numbers: PX232577 (28S) PX227569 (COI)

Comments: Based on two males and four females. Cuticle thick, with transverse striae (Figure 8A) and prominent ventral hump or protuberance in first third of body (Figure 5K). Oral aperture dorsoventrally elongated with four external labial papillae (Figure 8B). Two pseudolabia, symmetrical, each consisting of narrow bulge flanked by cheilorhabdion or cuticular expansions. Three pairs of teeth, with one larger central pair and two smaller lateral pairs (Figure 8B). Male body length 6800–9300 and 350 wide. Muscular esophagus 390–460 long; glandular esophagus 2360–3140 long. Ventral hump located at 1600 from apex. Posterior end with caudal ventral alae supported by pedunculated papillae: seven preanal (three on left side and four on right side), three pairs postanal, and one pair of small phasmids at distal end of tail (Figure 5L). Two unequal spicules, right spicule smaller, 158–175 long, left spicule 540–565 long. Female body, 6780–9210 × 340–450. Muscular esophagus 380–460 long; glandular esophagus 1250–3060. Ventral hump located at 1410–2000 from apex. Vulva situated 2900–3960 from apex. Embryonated eggs, 42–50 × 22–27. Anal opening 140–155 from posterior end.

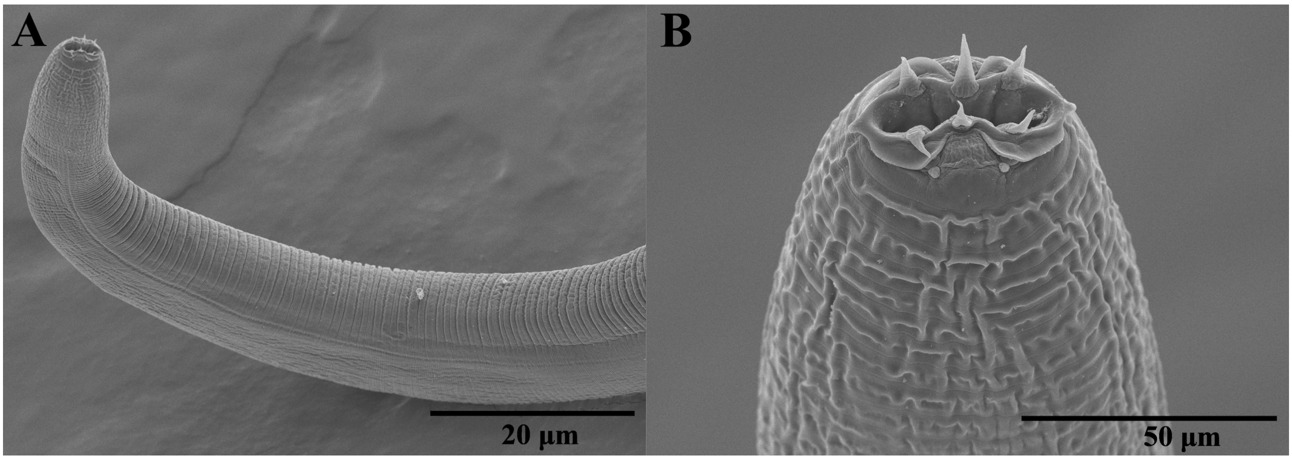

FIGURE 8. SEM micrographs of *Spirura mexicana*. A. Male anterior extremity, right lateral view. B. Male cephalic region, right lateral view.

The morphology and morphometric data of specimens from *N. laticaudatus* fit with description of *S. mexicana* (Peralta-Rodríguez *et al.* 2012). This nematode has been reported from *P. mesoamericanus*, *Pteronotus personatus* (Wagner), *Macrotus waterhousii* Gray, *P. fulvus* and *M. megalophylla* (Peralta-Rodríguez *et al.* 2012) and *Antrozous pallidus* (Le Conte) in Puebla and *Molossus* sp. in Oaxaca (Martínez-Pérez 2021). This is the first record of *S. mexicana* for *N. laticaudatus*.

Family Onchocercidae Leiper

***Litomosoides* Chandler**

***Litomosoides* sp.**

Infection site: Mesentery and thoracic cavity

Localities: Calcehtok and Homún

Prevalence (%) and mean intensity: Calcehtok: 4.8 and 1 (1). Homún: 0.8 and 1 (1)

Specimens deposited: CNHE-12324 and NHM 2025.8.13.16

GenBank accession numbers: PX227567, PX227568 (COI)

Comments: Based on one male and four females (one complete and three incomplete). Anterior extremity rounded, dome-like (Figures 9A, B). Mouth oval. Large amphids, cephalic papillae not observed (Figure 10A, B). Buccal capsule slender; anterior segment transparent and posterior portion chitinous with slight thickenings; buccal cavity longer than wide (Figure 9A, B). Cuticle with lateral thickening on the anterior extremity and punctuations on the posterior extremity of the body in both sexes, most marked in females (Figure 10C–F). Esophagus not differentiated in muscular and glandular portions (Figure 9C). Male tail with three small pairs of papillae: two ad-cloacal and one postcloacal (Figures 10E). Area rugosa begins anterior to cloaca, composed of transverse ridges of small longitudinal crests (Figure 9D). Vulva close to the distal part of the esophagus (Figure 9C). Female tail with a terminal process (Figures 9E, 10F). Male body length 5850 and 100 wide. Buccal capsule 6 long and 5 wide. Male tail 50 long. Left spicule 224 long, right spicule 50 long. Female body length 9190 and 100–125 wide. Buccal capsule 8–12 long and 5–7 wide. Esophagus 208–385 long. Vulva situated 355–390 from apex. Tail 90 long.

Seventeen species of *Litomosoides* have been reported as parasites of bats (Oviedo *et al.* 2016). Females isolated from *N. laticaudatus* closely resemble *Litomosoides saltensis* Oviedo & Notarnicola by the body size (< 20 mm), presence of lateral cuticular punctuations, and the position of the vulva. However, the examined specimens have smaller buccal capsule, tail, and esophagus, and lack salient phasmids on the tail. On the other hand, the male found in *N. laticaudatus* has punctuations on the posterior extremity and a body length (< 9.7 mm) similar to *Litomosoides molossi* Esslinger and *Litomosoides chandleri* Esslinger. However, these species exhibit different cephalic (e.g., dorsal-caudal papillae, buccal capsule thick) and caudal (e.g., number of caudal papillae, tail length, and spicular ratio) characteristics than those observed in our specimen. These differences suggest that the specimens from Yucatán may represent a species not described yet.

In Mexico, five species of *Litomosoides* have been reported, *Litomosoides brasiliensis* Almeida, *Litomosoides chitwoodi* Bain, Guerrero, Rodríguez & Babayan, *L. guiterasi*, *Litomosoides hamletti* Sandground, *Litomosoides leonilavazquezae* Caballero in bats of Mormoopidae (e.g., *M. megalophylla*) and Phyllostomidae (*M. waterhousii*) (see the complete references in Caspeta-Mandujano *et al.* 2017). In *N. laticaudatus*, Martínez-Pérez (2021) reported an unidentified species of *Litomosoides* in the mesentery of *N. laticaudatus* from Uxmal, Yucatán.

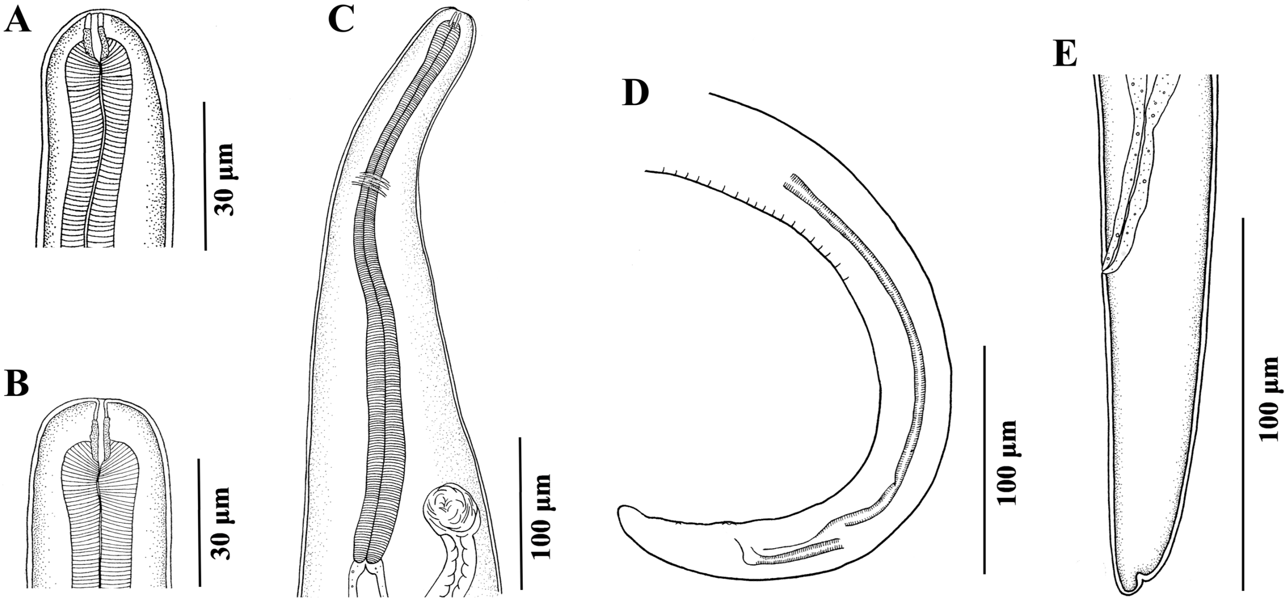

FIGURE 9. *Litomosoides* sp. A. Male head, median view. B. Female head, median view. C. Female anterior extremity, ventro-lateral view. D. Male posterior extremity, lateral view. E. Female posterior extremity, left lateral view.

Acanthocephala Koelreuter

Class Archiacanthocephala Meyer

Order Gigantorhynchida Southwell & Macfie

Family Gigantorhynchidae Hamann

Genus *Mediorhynchus* Van Cleave

***Mediorhynchus* sp.**

Infection site: Mesentery

Locality: Homún

Prevalence (%) and mean intensity: Homún: 0.8 and 1 (1)

Specimen deposited: CNHE-12326

Comments: Based on one encysted juvenile with partially everted proboscis (Figure 11A, B). Proboscis in two parts. Anterior proboscis slightly oval, 300 × 200, with *ca*. 20 irregularly arranged longitudinal rows, each with 14 hooks (Figure 11B). Hooks 23–25 long. Posterior proboscis partially retracted, longitudinal rows of spines not counted. Spines 12–14 long. Trunk smooth, cylindrical, slightly swollen at posterior end, 1650 in length and 650 in maximum width. Pseudo-segmentation, proboscis receptacle and reproductive organs are not observed.

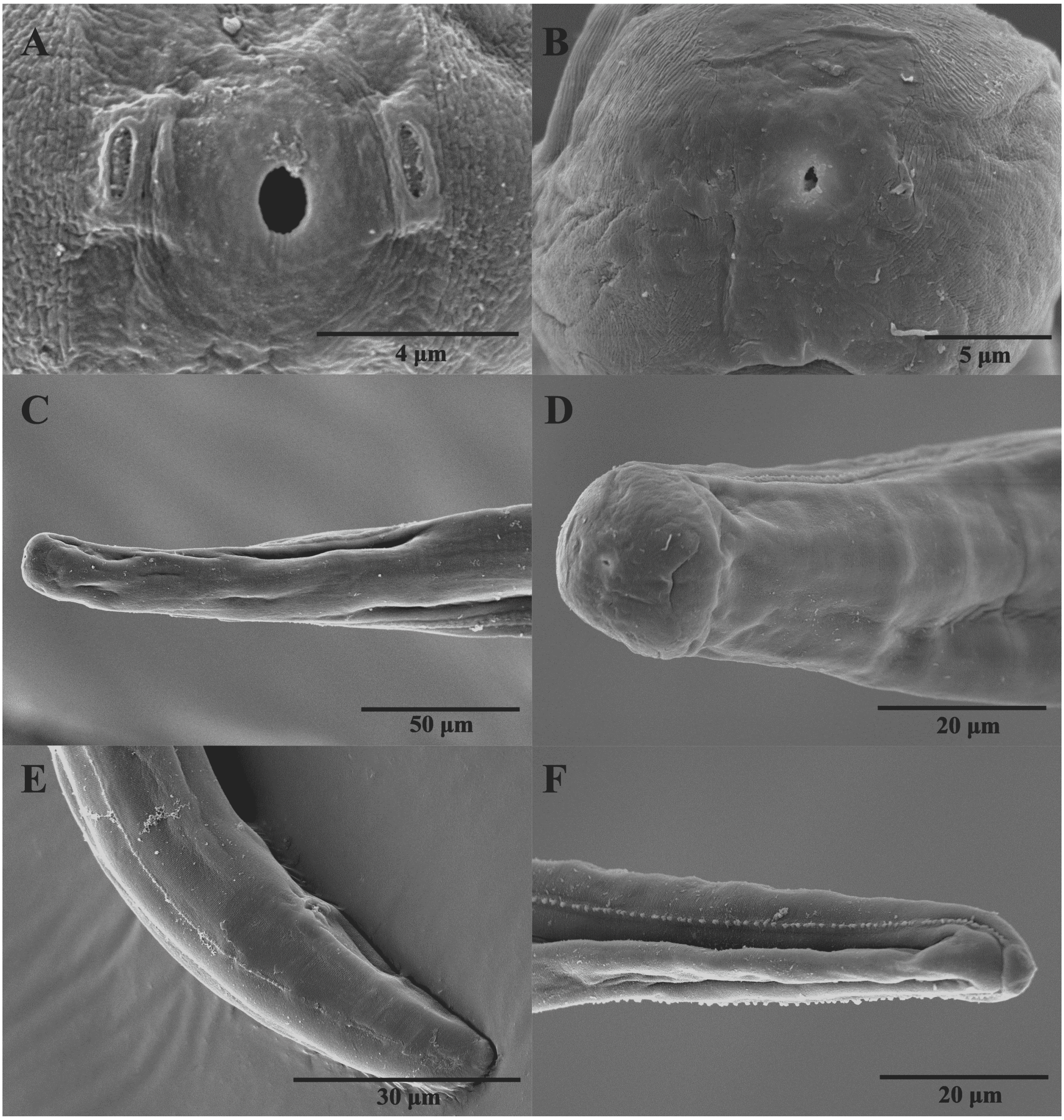

FIGURE 10. *Litomosoides* sp. A. Male head, apical view. B. Female head, apical view. C. Male anterior extremity, ventral view. D. Female anterior extremity, ventral view. E. Male posterior extremity, right lateral view. F. Female posterior extremity, dorso-lateral view.

The specimen was not alive and consequently its preparation for examination was not ideal. However, the morphological data observed in our specimen, particularly the irregularly arrangement of the longitudinal rows of hooks and the proboscis armature, fit with the genus *Mediorhychus* (Schmidt & Kuntz 1977). In Mexico, a juvenile stage of *Mediorhynchus* has been recorded from *M. waterhousii* in Michoacán (Luviano-Hernández *et al.* 2018). This is the first record of *Mediorhynchus* for *N. laticaudatus*.

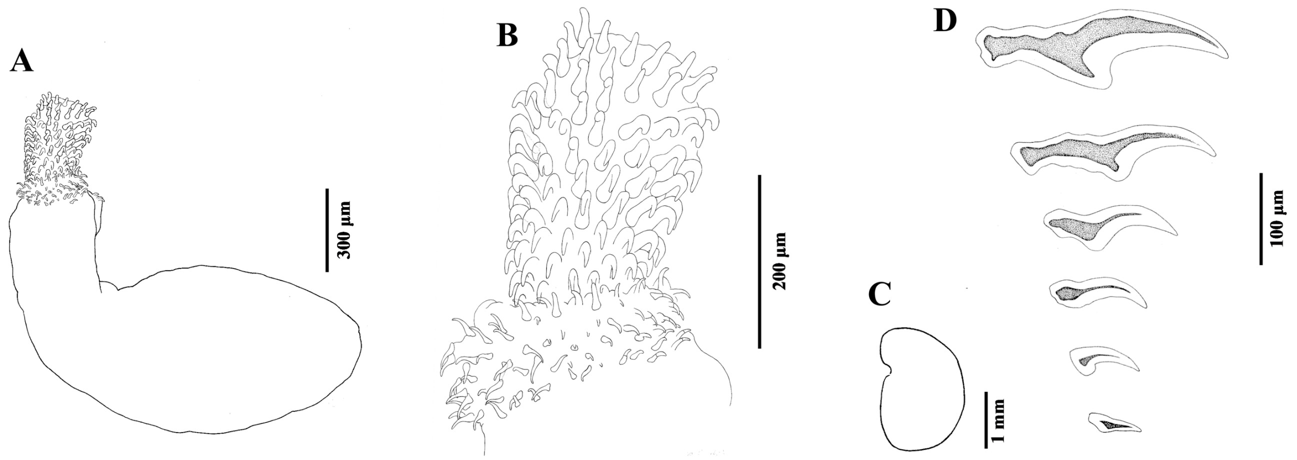

FIGURE 11. A. Juvenile specimen of *Mediorhynchus* sp., right lateral view. B. proboscis of *Mediorhynchus* sp., right lateral view. C. Juvenile specimen of *Oncicola* sp., left lateral view. D. Hooks of *Oncicola* sp., lateral view.

Order Oligacanthorhynchida Petrochenko

Family Oligacanthorhynchidae Southwell & Macfie

***Oncicola* Travassos**

***Oncicola* sp.**

Infection site: Surface of liver

Locality: Calcehtok

Prevalence (%) and mean intensity: Calcehtok: 0.8 and 1 (1).

Specimen deposited: CNHE-12325.

Comments: Based on one encysted juvenile with invaginated proboscis (Figure 11C). Proboscis slightly subspherical, with 36 hooks, organized in six alternative circles of six hooks each one. Hooks in anterior three circles robust, with roots much elongated anteriorly; roots of hook in circle four less elongated; roots of hooks in circles five and six slightly flat, platelike (Figure 11D). Trunk narrows anteriorly enlarging to widest point near posterior body end, 2000 × 600 (Figure 11C). Lemnisci, proboscis receptacle and reproductive organs are not observed.

The number of hooks observed in the proboscis (36) of the specimen fit with the number reported for members of *Oncicola*, *Macracanthorhynchus* and *Oligacanthorhynchus* (Schmidt 1972). However, the newly collected specimen is placed in *Oncicola* because hooks on the circle three are dramatically smaller than those in circles one and two (Figure 11D) (Richardson 2005). In addition, the specimen showed somewhat similar morphology to cystacanths of *Oncicola luehei* (Travassos) such as the size of the body and the presence of a subterminal genital pore (Sereno-Uribe *et al.* 2025). However, additional morphological and molecular data is clearly necessary to provide a reliable species identification of this acanthocephalan. This is the first record of *Oncicola* for *N. laticaudatus*.

Discussion

In this study, 17 helminth taxa were identified: *B. rileyi*, *Euparadistomum* sp., *L. nanum*, Phaneropsolidae gen. sp., *Ochoterenatrema* sp., *U. minuta*, *Urotrema* sp., *V.* cf. *christensoni*, *V.* cf. *phyllostomi*, *A. pulchra*, *A. allami*, *Physaloptera* sp., *P. sexalatus*, *S. mexicana*, *Litomosoides* sp., *Mediorhynchus* sp., and *Oncicola* sp. This study provides new records for *N. laticaudatus* (*Euparadistomum* sp., *L. nanum*, *V.* cf. *phyllostomi, Physaloptera* sp., *S. mexicana*, *Mediorhynchus* sp., and *Oncicola* sp.), new records for Mexican bats (*Euparadistomum* sp., *V.* cf. *christensoni*, *A. pulchra*, and *Oncicola* sp.), as well as the description of a new nematode species (*A. allami*). In

Mexico, previous records in *N. laticaudatus* include the trematodes, *B. rileyi*, *L. gastroides*, *Ochoterenatrema* sp., *U. minuta*, *U. scabridum* the cestode *Vampirolepis* sp. and the nematodes Capillariinae gen sp., *Anoplostrongylus* sp., *A. paradoxus*, *M. acanthocolpos*, and *Litomosoides* sp. (Martínez-Pérez 2021; Moguel-Chin *et al.* 2023). Thus, this study increases the number of helminth taxa recorded in *N. laticaudatus* from Mexico from 11 to 21.

The life cycles of bat helminths remain poorly known or, more frequently, are completely unknown. Most of the helminths found in *N. laticaudatus* have indirect life cycles that require the involvement of intermediate hosts. The insectivorous diet of bats of the genus *Nyctinomops* exposes them to various prey, including moths (Lepidoptera), beetles (Coleoptera), and leafhoppers (Homoptera) (Avila-Flores *et al.* 2002; Sparks & Valdez 2003), which may serve as potential intermediate hosts. The life cycle of trematodes found in *N. laticaudatus*, such as *Urotrema* spp. and *Limatulum* spp., is unknown. However, some authors, such as Bray *et al.* (2008) suggest that bats acquire these urotrematids by ingestion of insect intermediate hosts that harbor the metacercariae. In the case of cestodes, members of the family Hymenolepididae (e.g., *Vampirolepis*) use arthropods as intermediate hosts (Bush *et al.* 2001). Intermediate hosts of *Spirura* species include locusts, grasshoppers, crickets, cockroaches, and beetles, whereas for *Physaloptera*, beetles, earwigs, and cockroaches have been mentioned (Anderson 2000). The genus *Aonchotheca* includes species that are transmitted directly through the consumption of embryonated eggs, as well as species that require intermediate hosts such as earthworms (Anderson 2000). It is necessary to conduct future studies to identify the intermediate hosts that are part of the diet of *N. laticaudatus* to understand the life cycles of its helminths.

The new species *A. allami* had the highest prevalence and intensity values. This could be related with aspects of the life cycle of monoxenous trichostrongylines. The infective third-stage larva of trichostrongylines molts in the external environment and is transmitted between hosts by skin penetration or ingestion (Durette-Desset *et al.* 1994). Larvae of trichostrongylines can be very active at warm temperatures and in moist conditions (Anderson 2000), which prevail in the studied caves (data not shown).

In this study, three species found in *N. laticaudatus* represent accidental infections because they were only found in immature stages: the acanthocephalans *Mediorhynchus* sp. and *Oncicola* sp., and the nematode *P. sexalatus*. According to Gibson & Mccarthy (1987) there are no species-specific acanthocephalans of bats, these latter act as accidental hosts by consuming intermediate hosts of helminths that infect other vertebrates (e.g., birds). *Mediorhynchus* species are parasites that affect birds from different groups, like Accipitriformes, Bucerotiformes, Falconiformes, and Passeriformes, and they use cockroaches as their intermediate hosts (Rodríguez *et al.* 2022). Adult stages of *Oncicola* parasitize usually terrestrial mammals (e.g., carnivorous), whereas larval stages can be found in arthropods (intermediate hosts) and also in birds and amphibians (paratenic hosts) (Kennedy 2006; Fuller & Nickol 2011). *Physocephalus sexalatus* is a parasite of suids, tapirs, equines, cattle, and lagomorphs, with several genera of beetles acting as intermediate hosts (Anderson 2000).

Nematodes of the genus *Litomosoides* have been recorded in marsupials, rodents and bats. These nematodes use mites, usually dermanyssoid, as vectors where larvae develop up to the L3 stage. Bats become infected when vectors inject the larval stages during blood feeding (Rendón-Franco *et al.* 2019). Mites of Dermanyssoidea (e.g., *Chiroptonyssus* spp.) have been documented in *N. laticaudatus* (Avila-Flores *et al.* 2002) and may serve as vectors of *Litomosoides*.

In Mexico, helminthological studies on bats are scarce, and most of them are based on occasional, non-intensive sampling and lack coverage across different seasons. Studies on mormoopid bats such as that of Salinas-Ramos *et al.* (2017) in Jalisco, Mexico, have showed that the prevalence and occurrence of helminths may vary between seasons. Changes in temperature or humidity between seasons (e.g., rainy and dry seasons) can affect the survival of helminth stages (eggs and larvae) in the environment, the abundance of intermediate hosts, and consequently the helminth fauna of bats throughout the year (Lord *et al.* 2012; Salinas-Ramos *et al.* 2017). This highlights the importance of studies with a large sample size and sampling in different seasons to represent the entire helminth fauna (common and rare helminths) of bats.

Populations of *N. laticaudatus* from Calcehtok and Homún shared 14 of the 17 (82%) helminth taxa. Parasite communities of bats can change among localities due to several factors, such as human disturbance and abundance of intermediate hosts (Warburton *et al.* 2016). However, this can vary between different bats, especially for those that can fly long distances of up to 50 km, such as molossid bats during reproductive events (Wilkins 1989), which in turn may affect both gene flow and the spread of monoxenous nematodes.

Although none of the helminth species identified in this study are zoonotic, continued monitoring of the helminth fauna of bats is recommended, as some families, such as Lecithodendriidae, include species capable of parasitizing various mammals. For example, *Caprimolgorchis molenkampi* (Lie-Kian-Joe) has been reported in natural infections in humans, the rat *Rattus rattus* (Linnaeus), and the bats *Scotophilus kuhlii* Leach and *Taphozous melanopogon* Temminck from Laos (Manning & Lertprasert 1973).

The helminth fauna of Neotropical bats species is poorly known. In Mexico, recent studies have increased the diversity in helminths of bats, describing new species and genera of trematodes (Moguel-Chin *et al.* 2023; Ruiz-Torres *et al.* 2024; Tkach *et al.* 2024). Tkach *et al.* (2024) suggest that the numbers of some helminth groups may continue to increase if a greater diversity of bats continues to be examined, and the geographic ranges of the studies are expanded. The present study increases the helminth fauna of *N. laticaudatus*, a species widely distributed in the Americas, adding new helminth records for this bat species, for Mexico, as well as describing a new species of Anoplostrongyline nematode.

Acknowledgements

The authors would like to thank Berenit Mendoza Garfias for the SEM micrographs, María Rosa Chi López for the drawings, Juan Chable Santos and Oscar Retana Guiascón for their assistance in depositing the hosts in the zoological collections, and Iván Rodríguez Vivas, David Hernández Mena and Celia Selem Salas for the recommendations provided during the development of the first version of the protocol. We also thank Eliana Mendez Pino, Andrea España Medina, Lisette Chan González, Andrea Yam Lozada, and Claudia Carrillo Chan for their support in bat collection and examination of bat tissues. SECIHTI awarded WIMC with a doctoral scholarship (No. 001399). This study was partially founded by the Czech Science Foundation (project 23-05733S).

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