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Artículo Científico

Helminths of the false herring, *Harengula clupei* (Cuvier) (Dorosomatidae) in Puerto Progreso, Yucatán

Helminths of the sardinita carapachona, *Harengula clupei* (Cuvier) (Dorosomatidae), in Puerto Progreso, Yucatán



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**Helminths of the false herring, *Harengula clupei* (Cuvier) (Dorosomatidae)
in Puerto Progreso, Yucatán**

**Helmintos de la sardinita carapachona, *Harengula clupei* (Cuvier) (Dorosomatidae),
en Puerto Progreso, Yucatán**

► **ABSTRACT**

The false herring, *Harengula clupei* Cuvier, is distributed across the subtropical zone of the Western Atlantic coast. The species possesses a low commercial value and is captured mostly as bait. To date, 14 helminth species have been recorded for the false herring, including nine trematodes, three monogeneans, and two nematodes. However, information about the helminth fauna of *H. clupei* in the Yucatán Peninsula, Mexico is null. The aim of the present study was to determine the species composition of the helminth fauna of *H. clupei* from Puerto Progreso, Yucatán, sampled throughout a year using molecular and morphological data, and to estimate infection parameters. In total, 1,623 helminth specimens were recovered from *H. clupei* representing 14 taxa (two monogeneans, seven trematodes, two cestodes, and three nematodes). Ten helminth taxa are reported for the first time, including five trematodes, *Bucephalus margaritae*, *Saccularina* sp., *Tergestia* sp., Renicolidae gen. sp., and *Allopoistholecithum magaliae*; the monogenean *Pseudanthocotyloides* sp.; two nematodes, *Contracaecum rudolphii* and *Pseudoterranova* sp.; and the cestodes, *Anthobothrium* sp. and *Callitetrarhynchus gracilis*. This raises the number to 24 taxa. *Pseudobacciger manteri* and *Cribomazocraes travassosi* are sequenced for the first time. The information generated in this study will also be useful for further studies of parasites as bioindicators of ecosystem health and of the role of parasites in marine food webs.

Keywords: Parasite, Biodiversity, Mexico, Gulf of Mexico, DNA, Taxonomy



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► RESUMEN

La sardinita carapachona, *Harengula clupeiola* Cuvier se distribuye en la zona subtropical de la costa del Atlántico occidental; tiene escaso valor comercial, pues se captura principalmente como carnada. Hasta ahora se han identificado 14 especies de helmintos en *H. clupeiola*, incluidas nueve trematodos, tres monogeneos y dos nematodos. Sin embargo, no existe información disponible sobre la helmintofauna de *H. clupeiola* en la península de Yucatán, México. El objetivo del presente estudio fue analizar ejemplares de *H. clupeiola* en Puerto Progreso, Yucatán, colectados durante un año, para determinar la helmintofauna utilizando datos moleculares y morfológicos y estimar parámetros ecológicos de las infecciones. En total se recolectaron 1,623 ejemplares de helmintos de *H. clupeiola* en Progreso, Yucatán, México, representando 14 taxa, incluyendo dos monogeneos, siete trematodos, dos cestodos y tres nematodos. Se reportan 10 taxa por primera vez, con cinco trematodos, *Bucephalus margaritae*, *Saccularina* sp., *Tergestia* sp., *Renicolidae* gen. sp., y *Alloopistholecithum magaliae*; el monogeneo *Pseudanthocotyloides* sp.; dos nematodos, *Contracaecum rudolphii* y *Pseudoterranova* sp.; y los cestodos, *Anthobothrium* sp., y *Callitetrarhynchus gracilis*, incrementando el número a 24. *Pseudobacciger manteri* y *Cribomazocraes travassosi* se secuencian por primera vez. La información resultará útil para futuros estudios sobre los parásitos como bioindicadores de la salud del ecosistema, y sobre el papel de los parásitos en las redes tróficas de los ambientes marinos.

Palabras clave: Parásitos, Biodiversidad, México, Golfo de México, ADN, Taxonomía



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► INTRODUCTION

The false herring, *Harengula clupeiola* (Cuvier, 1829), is a clupeiform of the family Dorosomatidae, and its distribution spans across the subtropical zone of the Western Atlantic coast, from southeastern Florida in the USA to northern Brazil (Froese and Pauly, 2026). This species feeds primarily on small crustaceans such as calanoid copepods (e.g.,

Calanus finmarchicus), other small crustaceans, krill (euphausiids), and fish larvae. The false herring possesses a relatively low commercial value since it is not highly appreciated by local consumers and is captured mostly as bait for fishing larger fish (Froese and Pauly, 2026). Some studies have addressed the helminth parasite fauna of *H. clupeiola* across its distributional range. A few isolated records were published in the Gulf of Mexico and the Caribbean Sea (Linton, 1910; Manter, 1934; 1947; Nahhas and Cable, 1964; Overstreet et al., 2009). However, most records of the parasites of the false herring were reported in Brazil (Kohn and Fernandes, 2016; Santos et al., 2016; Luque et al., 2000; Pantoja and Kudlai, 2022). To date, 14 helminth species have been found infecting the false herring, including nine trematodes, three monogeneans, and two nematodes (**Table I**). However, information on the helminth fauna of *H. clupeiola* in the Yucatán Peninsula, Mexico is lacking. The aim of the present study was to study specimens of *H. clupeiola* from the northern coast of the Yucatán Peninsula, in Puerto Progreso, Yucatán, to determine the species composition of the helminth fauna by using a combination of molecular and morphological data, and to estimate the prevalence and mean intensity of infection for each parasite species.

Table I. Helminths reported in *Harengula clupeiola* across its distributional range. GoM= Gulf of Mexico

Taxa	Locality	Reference
Trematoda		
<i>Brachyphallus parvus</i> (Manter, 1947) Skrjabin & Guschanskaja, 1955	GoM	Manter, 1947
<i>Dinosoma clupeiola</i> Fernandes & Goulart, 1989	Brazil	Fernandes and Goulart, 1989
<i>Ectenurus virgula</i> Linton, 1910	GoM	Linton, 1910; Overstreet et al., 2009
<i>Lecithochirium floridense</i> (Manter, 1934) Crowcroft, 1946	GoM	Manter, 1934
<i>Myosaccium ecaude</i> Montgomery, 1957	Brazil	Luque et al., 2000
<i>Myosaccium opisthonemae</i> (Siddiqi & Cable, 1960) Overstreet, 1969	Brazil	Kohn, et al., 2007; Amato, 1983; Kohn and Fernandes, 2016
<i>Parahemiurus merus</i> (Linton, 1910) Manter, 1940	GoM; Brazil	Linton, 1910; Luque et al., 2000; Pantoja and Kudlai, 2022; Kohn and Fernandes, 2016; Overstreet et al., 2009
<i>Pseudobacciger manteri</i> Nahhas & Cable, 1964	Canadá, Jamaica, Curazao	Nahhas and Cable, 1964; Manter, 1947; Margolis and Ching, 1965
<i>Pseudobacciger harengulae</i> (Yamaguti, 1938) Nahhas & Cable, 1964	GoM; Panama	Sogandares-Bernal, 1959; Overstreet et al., 2009

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Monogenea

(Polypoisthycotylea)

Cribromazocraes travassosi
Santos & Kohn, 1992

Brazil

Luque et al., 2000

Mazocraeoides georgei Prince
1936

Brazil

Luque et al., 2000

Mazocraeoides opisthonema
Hargis, 1955

Brazil

Luque et al., 2000; Kohn and Santos, 1988

Nematoda

Hysterothylacium fortalezae
(Klein, 1973) Deardorff &
Overstreet, 1981

Brazil;
GoM

Santos et al., 2016

Ichthyascaris vicentei (Santos,
1970) Bruce, 1990

Brazil

Santos et al., 2016; Luque et al. 2000

► MATERIALS AND METHODS

Host and parasite collection

Seventy-one specimens of *H. clupeiola* (TL= 4-15.3 cm) were sampled in Puerto Progreso, Yucatán (21°17'16.86"N; 89°39'56.88"W) between September 2023 and June 2024. Specimens of false herrings were obtained from commercial capture; local fishermen use a trawl net to catch false herrings to be used as bait for pelagic fishes in the locality. Individual false herring were kept alive until necropsied. Fish were identified following Gallardo-Torres et al. (2014) and euthanized by spinal severance (pithing), a procedure accepted by the American Veterinary Medical Association (AVMA, 2020). The parasitological survey included the examination of the external surface. The internal organs were then removed from the body cavity, separated in Petri dishes with 0.85% saline, and examined under a stereomicroscope. All recovered helminths were fixed in nearly boiling 0.85% saline solution and transferred to vials with 100% ethanol.

Trematodes and monogeneans were stained with Mayer's paracarmine and mounted on permanent slides with Canada balsam. Nematodes were cleared with 50% glycerol in semi-permanent slides (Lamothe-Argumedo, 1997). Mounted specimens were examined under a bright-field Motic BA210 microscope (Motic, Kowloon, Hong Kong). Photomicrographs were taken using Motic Images Plus 3.1 microscope software (Motic). Voucher specimens were deposited at the Colección



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Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. Finally, the prevalence, mean intensity, and intensity range of the infection were estimated following Bush et al. (1997).

Molecular analysis

Twenty-one individual helminths were processed for molecular analyses to corroborate the morphological identification; in some cases, such as the larval cestodes, molecular data was used to accomplish the species identification. Genomic DNA was isolated following the protocol of Andrade-Gómez et al. (2023). The D1-D3 domains of the 28S rRNA were amplified by Polymerase Chain Reaction (PCR) using the primers 391 (5'-AGCGGAGGAAAAGAACTAA-3') and 536 (5'-CAGCTATCCT GAGGGAAAC-3') (García-Varela and Nadler, 2005). Amplification and sequencing protocols followed Andrade-Gómez et al. (2026). Sequences obtained in this study were deposited in GenBank. Molecular identification was initially tested through a BLAST search (Basic Local Alignment Search Tool) at NCBI (<https://www.ncbi.nlm.nih.gov/>).

To achieve species-level designation, we used an arbitrary sequence identity threshold of $\geq 99\%$ for the 28S rRNA gene. For helminth taxa not identified to species level based on the BLAST search, we built phylogenetic trees to determine their phylogenetic position relative to other members of their families. Five datasets were constructed separately; four corresponded to trematodes of the families Faustulidae Poche, 1926, Renicolidae Dollfus, 1939, Didymozoidae Monticelli, 1888, and Fellodistomidae Nicoll, 1909, and one corresponded to the monogenean Mazocreadidae. The jModel Test version 0.1.1 program (Posada, 2008) was used to calculate the best-fit model of molecular evolution for each dataset using the Akaike information criterion (AIC). The phylogenetic analyses were performed using maximum likelihood (ML) in IQ-TREE v. 2.4 with 10,000 bootstrap replicates (Minh et al., 2020). Trees were drawn using FigTree v.1.3.1 (Rambaut, 2012).



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► RESULTS

A total of 1,623 specimens of helminth parasites were recovered from *H. clupeola* in Puerto Progreso, Yucatán, Mexico. These specimens represented 14 taxa, including two monogeneans, seven trematodes, two cestodes, and three nematodes. Overall, the helminth fauna contained two ectoparasites and 12 endoparasites; for five of the 14 taxa, *H. clupeola* is the definitive host since they are adult worms, whereas for the remaining nine taxa, the host acts as their intermediate host because they are larval forms. Eight taxa were identified to species level using a combination of molecular and morphological data (Table II). The sequence of two species, i.e., *Pseudobacciger manteri* and *Cribomazocraes travassosi* is provided for the first time.

Table II. Helminth species of *Harengula clupeola* in Puerto Progreso, Yucatán; GB Accession; BLAST ID with GB identity as a percentage (%), Developmental Stage (DE), Infection Site. GB=GenBank. CNHE accession number.

	GB Accession 28S	BLAST ID	GB Identity	%	DE	Infection Site	CNHE
Trematoda							
<i>Bucephalus margaritae</i>	PZ670799	<i>B. margaritae</i>	KT273395	99.6	Metacercariae	Mesentery	
<i>Allopoisthocythum magaliae</i>	PZ670800-01	<i>Allopoisthocythum magaliae</i>	PX648549	99.8	Adult	Intestine	12632
<i>Parahemisturus merus</i>	PZ670802-03	<i>P. merus</i>	PP919653	100	Adult	Intestine	12633
<i>Pseudobacciger manteri</i>	PZ670804-05	<i>Bacciger bacciger</i>	KJ648919	98.5	Adult	Intestine	12634
Renicolidae gen. sp.	PZ670806-07	Renicolidae sp.	AF184249	93.2	Metacercariae	Mesentery	
<i>Saccularina</i> sp.	PZ670808-09	<i>Saccularina</i> sp.	PP666254	95.4	Metacercariae	Mesentery	
<i>Tergestia</i> sp.	PZ670810-11	<i>T. henryi</i>	MF155628	98.7	Metacercariae	Mesentery	
Monogenea							
<i>Pseudanthocotylodes</i> sp.	PZ670812-13	<i>Pseudanthocotylodes mamaevi</i>	LC860879	98.7	Adult	Gills	12635
<i>Cribomazocraes travassosi</i>	PZ670814	<i>Kuhnia scombr</i>	MT508780	89.1	Adult	Gills	12636
Cestoda							
<i>Anthobothrium</i> sp.	PZ670815	<i>Anthobothrium</i> sp.	GQ470164	99.5	Larvae	Mesentery	12637
<i>Callitetrarhynchus gracilis</i>	PZ670816	<i>C. gracilis</i>	PQ227150	100	Larvae	Mesentery	12638
Nematoda							
<i>Contracaecum rudolphii</i>	PZ670817	<i>C. rudolphii</i> A	AF226585	99.9	Larvae	Mesentery	
<i>Hysterothylacium fortalezae</i>	PZ670818	<i>H. fortalezae</i>	KX098564	100	Larvae	Mesentery	12639
<i>Pseudoterranova</i> sp.	PZ670819	<i>Pseudoterranova</i> sp.	JQ951961	100	Larvae	Mesentery	

For five taxa, since the BLAST search was not conclusive, and no morphological traits were observed to achieve the species identification, phylogenetic trees were built (Figures 1 and 2). Figure 1 depicts the phylogenetic relationships among members of the families Renicolidae, Didymozoidae, and Fellodistomidae. The two newly sequenced individuals of Renicolidae gen. sp. were identical and formed an independent clade with strong nodal support; these sequences did not correspond to any identified species of the family for which sequences are available; however, these new sequences were yielded as the sister



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group of Renicolidae sp. (AF184249), which represents a sequence obtained from a cercariae released by the snail *Cerithium vulgatum* in the Mediterranean Sea (**Figure 1A**). Two identical sequences of the didymozoid *Saccularina* sp. were obtained and formed an independent clade with strong nodal support. The sequenced individuals were nested with *Saccularina* sp. (PP666254) reported as metacercariae from the scallop *Argopecten irradians* in North Carolina (**Figure 1B**). Finally, two identical sequences of the metacercariae of *Tergestia* sp. were also obtained and formed an independent clade with strong nodal support. These two new sequences were nested as the sister group of *Tergestia henryi* (MF155628) from the carangid *Pantolabus radiatus* in Australia (**Figure 1C**), although they do not correspond to that species because of the genetic divergence of 1.3% for the 28S rRNA gene (see **Table II**).

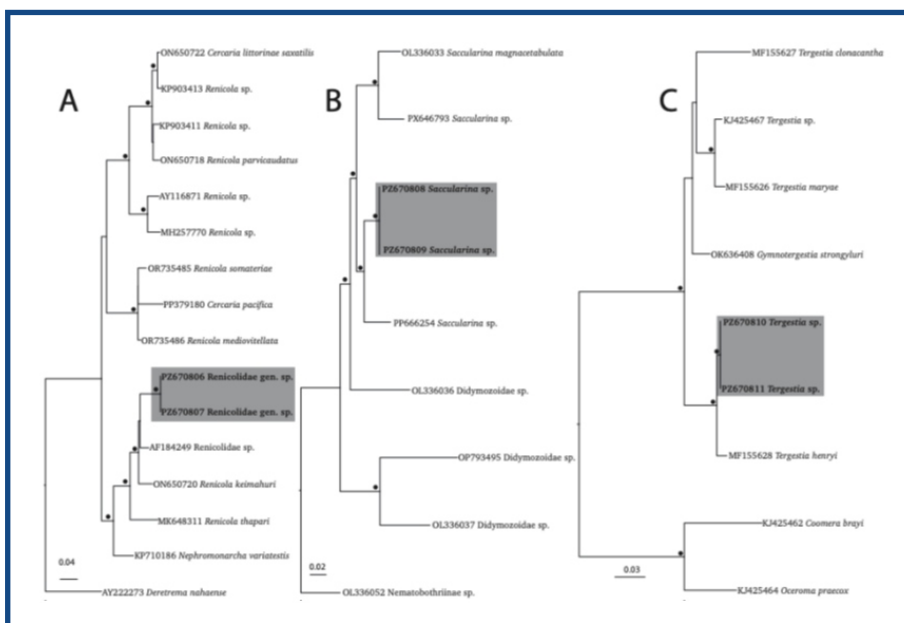


Figure 1. Maximum Likelihood trees showing the phylogenetic position of larval forms helminths of *H. clupeiola* from Puerto Progreso, Yucatán, Mexico. A) Renicolidae; B) Didymozoidae; C) Fellodistomidae inferred with 28S rDNA. Bootstrap support values >80 is indicated (*). Scale-bar= number of nucleotide substitutions per site.

In contrast, **Figure 2** depicts the phylogenetic position of two adult forms; the two new sequences of the member of the Faustulidae which was morphologically identified as *Pseudobaciger manteri*, were identical and nested as the sister species of a clade containing *Bacciger bacciger* (OQ438911) from the clam *Ruditapes philippinarum* in Korea



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+ *Pseudobacciger cheneyae* (KJ648919) from the pomacentrid *Chromis weberi* in Australia, with strong nodal support (**Figure 2A**). Finally, the three new sequences of the mazocreadoid monogeneans formed two independent clades (**Figure 2B**). One sequence corresponded morphologically to *Cribomazocraes travassosi* and nested as the sister species of a clade containing three species of *Mazocraeoides*, albeit with low nodal support values. The other two sequences, identified as belonging to *Pseudanthocotyloides* nested as the sister group of *Pseudanthocotyloides mamaevi* (LC860879) from the engraulid *Engraulis japonicus* from Japan, but with a genetic divergence of 1.3% for the 28S rRNA gene.

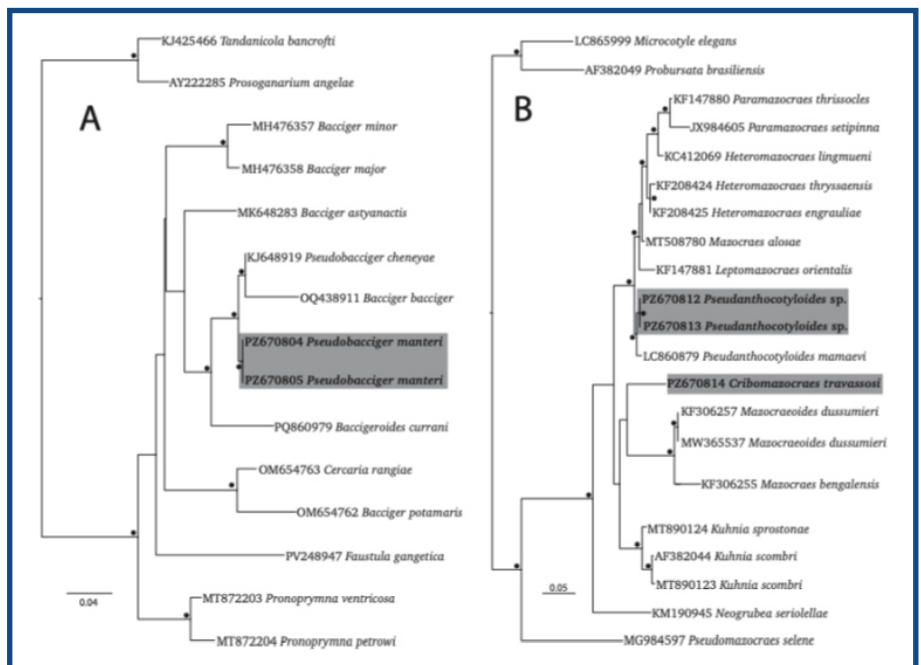


Figure 2. Maximum Likelihood trees showing the phylogenetic position of adult forms helminths of *H. clupeola* from Puerto Progreso, Yucatán, Mexico. A) Faustulidae; B) Mazocreadidae inferred with 28S rDNA. Bootstrap support values >80 is indicated (*). Scale-bar= number of nucleotide substitutions per site.

In terms of the host association, the results indicate that four helminth taxa, i.e., *Parahemiurus merus*, *Saccularina* sp., *Cribomazocraes travassosi* and *Pseudoacanthocotyloides* sp., were found parasitizing *H. clupeola* along the sampling period (**Table III**). In particular, the trematode *P. merus*, and the monogenean *Pseudoacanthocotyloides* sp. were the helminths most commonly found, since they reached the



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highest prevalence of infection values (74.6% and 47.9% throughout the sampling period, respectively). *Parahemiurus merus* exhibited mean intensity values 16.3 individuals per parasitized host, whereas *Pseudanthocotyloides* sp. reached mean intensity values 7.7 specimens per infected host. In contrast, *B. margaritae* and *Anthobothrium* sp. were the helminths with the lowest prevalence and mean intensity values (Table III).

Table III. Infection parameters of *Harengula clupeiola* sampled in Puerto Progreso, Yucatán, Mexico. Total host length mean = 8.9 cm.

	Prevalence (%)	Mean Intensity	Intensity range	No. of Parasites
Trematoda				
<i>Bucephalus margaritae</i>	1.4	3	3	3
<i>Allopoisthocythum magaliae</i>	18.3	1.9	1-3	25
<i>Parahemiurus merus</i>	74.6	16.3	1-51	869
<i>Pseudobacciger manteri</i>	25.4	16.2	2-78	293
Renicolidae gen. sp.	16.9	7	2-25	84
<i>Saccularina</i> sp.	23.9	2.1	1-4	38
<i>Tergestia</i> sp.	2.8	2.5	1-4	5
Monogenea				
<i>Pseudanthocotyloides</i> sp.	47.9	7.7	1-35	264
<i>Cribromazocraes travassosi</i>	11.3	1.25	1-2	10
Cestoda				
<i>Anthobothrium</i> sp.	1.4	3	3	3
<i>Callitetrarhynchus gracilis</i>	8.5	2	1-4	12
Nematoda				
<i>Contracaecum rudolphii</i>	4.2	2	1-3	6
<i>Hysterothylacium fortalezae</i>	4.2	2.6	1-5	8
<i>Pseudoterranova</i> sp.	7	1	1	5

DISCUSSION

Previous to this study, the checklist of the helminth parasites of the false herring (*H. clupeiola*) included 14 taxa across its distributional range (see **Table I**). In the present study, 14 taxa were also reported; however, only four of them coincide with previous records. In consequence, 10 helminth taxa are reported for the first time for the false herring, raising the number to 24. The new records reported in the present study comprise four larval trematodes, i.e., *Bucephalus margaritae*, *Saccularina* sp., *Tergestia* sp., and one identified up to family level, Renicolidae gen. sp., and one adult trematode, *Allopoisthocythum magaliae*; the monogenean *Pseudanthocotyloides* sp.; two larval nematodes, *Contracaecum rudolphii* and *Pseudoterranova* sp.; and



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finally, the larval tetraphyllidean *Anthobothrium* sp., and the larval lacistorhynchid *Callitetrarhynchus gracilis*. The first record of *A. magaliae* in a clupeiform in the Gulf of Mexico is interesting because it was described from the atherinopsid *Odontesthes bonariensis* in Argentina (Montes et al., 2026); even though this host is an inhabitant of freshwater and coastal lagoons in South America, the identity percentage through the 28S (99.8%) unequivocally shows they are conspecific; the distributional range of the species is increased in this study. We cannot currently explain the presence of this species in *H. clupeola*.

Eight of the 14 helminths recorded in the present study were identified at species level using an integrative taxonomy approach (see **Table II**). Six of the eight species were identified to species level through the BLAST analyses, including four larval stages, i.e., *B. margaritae*, *C. gracilis*, *C. rudolphii*, and *H. fortalezae*. This remarks the importance of the use of molecular data in the identification of larval forms of helminths by increasing the possibility to link these forms with adults previously identified to species level and sequenced for some molecular marker, although this tool is also useful also for adults as previous studies have recently addressed (Grano-Maldonado et al., 2023; Espínola-Novelo et al., 2023, 2025; Andrade-Gómez et al., 2026).

Furthermore, two of the 14 species, the adult worms, *P. manteri* and *C. travassosi*, were identified using morphological as well as host association and distribution characteristics because the BLAST analyses were not conclusive and showed a moderate to low identity percentage with *Bacciger bacciger* (98.5%) and *Kuhnia scombri* (89.1%), respectively. For instance, the faustulid trematode *P. manteri* was described from *H. clupeola* in the Caribbean (Jamaica) by Nahhas and Cable (1964) and also reported in the same host by Manter (1947) in Florida. Morphologically, our specimens are very similar. Moreover, the monogenean *C. travassosi* was also described from *H. clupeola* and was first found off Rio de Janeiro, Brazil by Santos and Kohn (1992), but later reported in the engraulid *Cetengraulis edentulus* in the same locality and in the dorosomatid *Opisthonema libertate* in the Gulf of California, although it was reported as *Cribomazocraes* cf. *travassosi* (López-Moreno et al., 2023). The record of *C. travassosi* from the Gulf of

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California, on the northeast Pacific coast of Mexico is doubtful and requires further verification and ideally, gathering sequence data for comparison. The individuals identified as *P. manteri* and *C. travassosi* closely resemble morphologically with the original descriptions of these species and they were sampled from the same host species, within an overall similar geographical region on the western Atlantic coast. The 28S DNA sequences of *P. manteri* and *C. travassosi* are reported herein for the first time.

One of the adults recovered from the false herring was the mazocraeidid monogenean *Pseudanthocotyloides* sp., although it was not identified to species level. The phylogenetic tree unequivocally showed that the newly generated sequence was nested as the sister species of *P. mamaevi* (LC860879) from the engraulid *Engraulis japonicus* in Japan (Nitta, 2026). The genus *Pseudanthocotyloides* currently contains four species apparently specific to clupeiform fishes (Nitta, 2026). The remaining three species are *P. heterocotyle* (Van Beneden, 1871) reported in two clupeiforms from the Mediterranean and also from off the coast of Brazil (Euzet and Prost, 1969; Kohn et al., 1992); *P. banghami* Price, 1958 from the freshwater dorosomatid *Dorosoma cepedianum* in USA (Price, 1958); and *P. dossae* Caballero & Bravo-Hollis, 1965 from the engraulid *Anchoa hepsetus* in the Gulf of Mexico (Caballero & Bravo-Hollis, 1965). Based on these data, our specimens could be conspecific with *P. dossae* because both species parasitize clupeiform fishes in the Gulf of Mexico. However, *P. dossae* is morphologically readily distinguished from the specimens sampled from *H. clupeola* in the present study; for example, the haptor in the newly sampled specimens is smaller than that of *P. dossae* (Caballero and Bravo-Hollis, 1965). Most likely, the specimens of *Pseudanthocotyloides* herein reported may represent an undescribed species; unfortunately, the quality of the collected material prevents further detailed taxonomic work.

One of the adults characterized molecularly and morphologically was the trematode *Parahemiurus merus*. The sequence is identical to that reported by Espínola-Novelo et al. (2025) from a fundulid in coastal lagoons of Yucatán. This species apparently possesses a global

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distribution and has been reported from more than 150 host species according to WoRMS (2026a). Linton (1910) described it from a clupeiform (*Chupanodon pseudohispanicus* = *Sardinella aurita*) from Tortugas, Florida, in the Gulf of Mexico. It might be assumed to be a common parasite of clupeiformes, but current data on host association and distribution do not support that conclusion. A detailed genetic study across its geographic range is needed to determine whether this represents a single species or a species complex. However, only a few studies have reported sequence data of *P. merus* (Pantoja and Kudlai, 2022; Espínola-Novelo et al., 2025). The fact that this was the species most commonly found and most abundant in *H. clupeola* in Yucatán (see Table III) indicates a close association between the trematode and this clupeiform species.

Overall, the helminth species that reached the highest prevalence and mean intensity of infection in the sample were the trematodes *Parahemiurus merus*, *Pseudobacciger manteri*, and the monogenean *Pseudanthocotyloides* sp. (Table III). This is probably because these taxa are common parasites of clupeiformes. For example, the four species of *Pseudanthocotyloides* have only been recorded as parasites of clupeiformes (Nitta, 2026), whereas the species *Pseudobacciger manteri* is a parasite of the same host species (Manter, 1947; Nahhas and Cable, 1964).

Furthermore, nine of the 14 helminth species reported in this study are larval forms which indicate the role of this small-bodied fish in the food webs of the marine ecosystem. The larval forms infecting the false herring in Yucatán complete their life cycle when they are consumed by other vertebrates. Three trematodes (*B. margaritae*, *Saccularina* sp., and *Tergestia* sp.) and one nematode, *H. fortalezae* require a larger fish to complete their life cycle (Deardorff and Overstreet, 1980; Costa-Marchiori et al., 2010; Andres et al., 2016; Wee et al., 2017; Louvard et al., 2022), whereas the two cestodes (*Anthobothrium* sp., and *C. gracilis*) are parasites of elasmobranchs such as sharks and rays (Jensen and Bullard, 2010; Menezes et al., 2018). Particularly, *C. gracilis* has also been reported infecting the muscle of *Sardinella brasiliensis* in Brazil



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which is a member of the Dorosomatidae (Menezes et al., 2018). Apparently, there is a strong association of the lacistorhynchid *C. gracilis* with clupeiformes (Dorosomatidae) as intermediate hosts, and this tapeworm is widely distributed since it has been sampled as an adult or metacestode in several host species from the Mediterranean, Gulf of Mexico, and southwestern Atlantic (WoRMS, 2026b). The unidentified trematode of the family Renicolidae and the nematode *C. rudolphii* complete their life cycle when false herrings are eaten by fish-eating birds. For instance, *C. rudolphii* has been widely recorded in several fish-eating birds belonging to different families (Dziekońska-Rynko and Rokicki, 2007). This parasite uses a broad range of fish as intermediate hosts, including both commercial and non-commercial fish, as reported for the Gulf of Mexico by González-Morales et al. (2023). In general, renicolid trematodes complete their life cycle in fish-eating birds (Gibson, 2008).

As a side note, two species may have zoonotic importance: Raphidascarididae (*H. fortalezae*) and Anisakidae (*Pseudoterranova* sp.). Even though human infections with raphidascarids are rare, a few studies report accidental infections of humans with some *Hysterothylacium* species after eating raw or insufficiently cooked fish (e.g., Yagi et al., 1996; Valero et al., 2003). Likewise, the anisakid *Pseudoterranova* sp. has been recorded parasitizing humans (Mercado et al., 2001; Arizono et al., 2011). In our opinion, the chances of the human population becoming infected with these nematodes are very low because false herring are not commonly consumed and are mostly used as bait for pelagic fish and, if consumed, are not raw or undercooked.

Finally, this study increases knowledge of the parasite fauna of *H. clupeiola* along its distributional range on the Western Atlantic coast. As mentioned before, very few studies have been conducted describing the whole helminth parasite fauna of this host, but most of them have been in Brazil (Kohn and Portes-Santos, 1988; Luque et al., 2000); all the other reports are isolated records of the presence of a helminth species in a particular locality. This study also enhances the information on the parasites of clupeiform fishes in Mexican waters, and particularly in the

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Gulf of Mexico, since previous studies were conducted in clupeiforms of the Pacific coast, such as those on *Harengula thrissina* and *Opisthonema libertate* (Pérez-Ponce de León et al., 2000; López-Moreno et al., 2023). Clearly, the use of several sources of data, including molecular markers, is very useful to refine taxonomic hypotheses and to reveal more accurately the biodiversity of parasites in particular host species. In this context, the information generated in this study will also be useful in further studies of parasites as bioindicators of ecosystem health, and studies of the role of parasites in food webs in marine environments.

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