Gastrointestinal helminths of waterfowl (Anatidae: Anatinae) in the Lerma marshes of central Mexico: Some pathological aspects

Patricia Padilla-Aguilar [a], Evangelina Romero-Callejas [a], José Ramírez-Lezama [b], David Osorio-Sarabia [c], Luis García-Prieto [c], Carlos Manterola [d], Luis Jorge García-Márquez [e], Heliot Zarza [f,*]

[a] Laboratorio de Diagnóstico Parasitológico, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Mexico
[b] Departamento de Patología, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Mexico
[c] Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico
[d] Grupo Anima Efferus, CDMX, Mexico
[e] Laboratorio de Patología, Facultad de Medicina Veterinaria y Zootecnia, Universidad de Colima, Mexico
[f] Departamento de Ciencias Ambientales, CBS, Universidad Autónoma Metropolitana Unidad Lerma, Lerma de Villada, Mexico

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ABSTRACT

Gastrointestinal helminths of migratory waterfowl can cause several lesions that may affect the health and even the survival of their hosts. As part of an ongoing project that aims to inventory the helminth species that infect this group of birds, as well as the histopathologic lesion they cause, a total of 200 digestive tracts of nine species of anatid birds (*Spatula discors, S. cyanoptera, S. clypeata, Mareca strepera, M. americana, Anas crecca, A. acuta, A. platyrhynchos diazi,* and *Oxyura jamaicensis*) were collected in the Atarasquillo marsh of Lerma, in the State of Mexico. The present work had a twofold goal: to determine the taxonomic identity of the helminth species present in waterfowl as well as their infection levels and to describe the lesions caused by gastrointestinal parasites in migratory and resident anatids in Atarasquillo marsh, State of Mexico. The specimens were examined using routine helminthological and histopathological techniques. A total of 23 helminths were identified: six trematodes (*Zygocotyle lunata, Notocotylus triserialis, Notocotylus seineti, Psilochasmus oxyurus, Australapatemon burti* and *Cotylurus magniacetabulus*), four cestodes (*Cloacotaenia megalops, Fimbriaria fasciolaris, Gatrotaenia cygni* and *Diorchis* sp.), eleven nematodes (*Echinuria uncinata, Tetrameres* sp., *Tetrameres fissispina, Hystrichis* sp., *Streptocara* sp., *Amidostomum* sp., *Epomidiostomum uncinatum, Capillaria* sp., *Capillaria contorta, Ascaridia* sp. and *Heterakis* sp.) and two acanthocephalans (*Pseudocorynosoma constrictum* and *Filicollis* sp.). At the proventriculus level, *Echinuria uncinata* caused the most severe lesions; in the gizzard, *Amidostomum* sp. and *E. uncinatum* produced hemorrhages and necrosis. Finally, the main lesions found in the intestine (necrosis, heterophilic granulomas and the formation of lumps on the serosa) were caused by the implantation of the acanthocephalans' proboscis. Eleven species of gastrointestinal helminths found are new records for the Lerma marshes, as well as the first record in Mexico of the nematode *Capillaria contorta* and the acanthocephalan *Filicollis* sp.

1. Introduction

Waterfowl are considered one of the vertebrate groups with the greatest diversity of parasites (Barrera-Guzmán and Guillén-Hernández, 2008; Leung and Koprivnikar, 2016). This diversity may be explained due to the natural history of their bird hosts, the great diversity of feeding habits (Graves and Fedynich, 2013), migratory (Garvon et al., 2011) and seasonal patterns (Wallace and Pence, 1986), as well as the complexity of the digestive tract of waterfowl species (Poulin, 1995). Parasites can affect body condition (Souchay et al., 2013), behavior, reproductive performance (Amundson and Arnold, 2010), and survival of their hosts (Wobeser, 1997). Waterfowl host numerous helminth species: particularly, gastrointestinal helminths are amongst the most common parasites of this group of birds, including Platyhelminthes,

Nematoda, Acanthocephalan and Annelida (Poulin, 1995). The degree of damage, often dependent on the parasite load, can be local or systemic, with manifestations ranging from subclinical to severe, tin extreme cases lead to the death of the host (Behnke, 1990; Barrera-Guzmán and Guillén-Hernández, 2008).

Thousands of waterfowl migrate annually from Canada and the United States to the marshes of the Central Mexican Plateau en-route south (Barragán et al., 2002). These marshes have suffered a reduction in surface area since the middle of the last century, due mainly to anthropogenic activity. Presently, there are only a few remnants of these areas in the Basin of Mexico (e.g. Xochimilco, Chalco, Texcoco) and in the Lerma River Basin, including the Lerma marshes, in the State of Mexico. By the end of the 19th century, the Lerma marshes extension was over 27,000 ha (Martínez, 1993). Currently, only 3023 ha of the original surface remain, divided in three isolated water bodies: Atarasquillo (346 ha), Tultepec (2081 ha) and Almoloya del Río (596 ha). The Lerma marshes have a great biological diversity, with numerous endemic and endangered species (Ceballos, 2003). The waterfowl diversity is particularly noteworthy; more than 280 species arrive in this region during the winter season (Rappole et al., 1993). Because of this, it is considered an "Important Bird and Biodiversity Area" (Wilson and Meléndez-Herrada, 2000).

Due to the biological and avifaunal importance of the region, many studies have focused on estimating the richness of waterfowl populations. However, studies assessing the health status of these populations are limited. Therefore, our study had a twofold objective: 1) to determine the taxonomic identity of the helminth species present in waterfowl as well as their infection levels and, 2) to describe the lesions caused by gastrointestinal parasites in migratory and resident anatids in Atarasquillo marsh, State of Mexico.

2. Materials and methods

This study was conducted in the Wildlife Management Unit "San Antonio" (UMA San Antonio), located in the Atarasquillo marsh (19° 21′ 22.42″ N; 99° 30' 59.98″ W) in the Lerma marshes, municipality of Lerma, State of Mexico. The digestive tracts of 200 individuals belonging to nine Anatinae duck species (*Spatula discors, S. cyanoptera, S. clypeata, Mareca strepera, M. americana, Anas crecca, A. acuta, A. platyrhynchos diazi*, and *Oxyura jamaicensis*), were collected during the 2014/2015 and 2015/2016, November–February hunting seasons. Birds were identified using a field guide (Howell and Webb, 1995), following the taxonomic arrangement proposed by Clements et al. (2017). Ducks were obtained from hunter donations to UMA San Antonio. The entire gastrointestinal tract was removed from each specimen. Samples were placed in plastic bags with 0.85% saline solution (SS) and were frozen for later examination at the Laboratorio de Diagnóstico Parasitológico de la Facultad de Medicina, Veterinaria y Zootecnia (FMVZ) de la Universidad Nacional Autónoma de México (UNAM), in Mexico City.

A total of 200 digestive tracts were examined for helminths by placing them in Petri dishes with 0.85% SS. Each organ was analyzed (esophagus, gizzard, stomach, intestine, and cloaca) under a stereoscopic microscope. Parasites were collected, fixed in formalin, and processed (stained or cleared, and temporal or permanently mounted in Canada balsam) following routine helminthological techniques (Lamothe-Argumedo, 1997). All helminths were measured and schematized under an optical microscope with a drawing tube for identification, using the keys by Anderson et al. (2009), Czaplinzki and Vaucher (1994), Gibson et al. (2002), McDonald (1981, 1988), and Yamaguti (1971). Infection levels (prevalence and mean abundance) were determined using the ecological parameters proposed by Bush et al. (1997).

Of the 200 digestive tracts reviewed only 83 were parasitized by a helminth species and 21 showed an apparent macroscopic lesion and samples were collected and fixed with 10% formalin (pH 7.2). Subsequently, samples were cut and processed using standard histological procedures (Prophet et al., 1995). The staining techniques used standard

hematoxylin-eosin and Masson's trichrome. Voucher specimens of helminth taxa and histological sections were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biologia, UNAM in Mexico City.

3. Results

A total of one hundred eighty nine out of the 200 digestive tracts examined (94.5%) tested positive to at least one helminth species. Four hundred and nineteen adult helminths were collected and represented/identified in 23 taxa (14 identified at species level and 9 at genus level): six trematodes (*Zygocotyle lunata, Notocotylus triserialis, Notocotylus seineti, Psilochasmus oxyurus, Australapatemon burti* and *Cotylurus magniacetabulus*), four cestodes (*Cloacotaenia megalops, Fimbriaria fasciolaris, Gastrotaenia cygni* and *Diorchis* sp.), eleven nematodes (*Echinuria uncinata, Tetrameres* sp., *Tetrameres fissispina, Hystrichis* sp*., Streptocara* sp., *Amidostomum* sp., *Epomidiostomum uncinatum, Capillaria* sp., *Capillaria contorta, Ascaridia* sp. and *Heterakis* sp.) and two acanthocephalan: *Pseudocorynosoma constrictum* and *Filicollis* sp. (Table 1). Nematodes and trematodes represented 42.72% (n = 179) and 41.28% (n = 173) of total individuals found, respectively; followed by cestodes with 11.93% (n = 50), and less frequently by acanthocephalans with only 4.05% (n = 17). The nematode *E. uncinatum* had the widest distribution among hosts, found in nine duck species, followed by *Tetrameres* sp., *Amidostomum* sp. and the cestode *F. fasciolaris*, in eight waterfowl species each. The remaining helminth species were collected in one to seven duck hosts. The largest helminthological record was hosted by *O. jamaicensis* (18 helminth species), while the lowest by *A. acuta* (six species). On the other hand, *Tetrameres* sp., showed the highest value of prevalence among the 23 taxa of helminths as a parasite of *M. strepera* (40%), along with a group consisting of *F. fasciolaris, T. fissipina* and *E. uncinatum*, which exceeded 30% in *A. platyrhynchos diazi, M. americana* and *O. jamaicensis*, respectively. Overall, mean abundances for each helminth species in each waterfowl species were very low, averaging less than one individual per bird. Only *A. gracilis* and *E. uncinatum*, both in *O. jamaicensis*, slightly exceeded this value (Table 1). Macroscopic and microscopic analysis showed that 41.5% (n = 83) of the parasitized ducks had relevant alterations; histological examination of 21 subjects, found hemorrhages in one of 21 hosts, heterophilic infiltrates (2/21), eosinophilic infiltrates (1/21), mononuclear cells (6/21), necrosis (2/21), ulcers (2/21), lymphoid hyperplasia (6/21), glandular hyperplasia (3/21), formation of granulomas (7/21), proliferation of fibroblasts (3/21) and mucus (7/21) associated with the presence of helminths. The host species with the highest number of pathological lesions was *O. jamaicensis* with 32% (n = 64), whereas *A. acuta* had the lowest number with only 1% (n = 2). Lesions found in the gastrointestinal tracts studied were similar for all Anatidae species collected. Below, we described the lesions found in three of the seven parasitized organs and the associated helminth species (Table 1):

Proventriculus. At a macroscopic level, gravid females of *Tetrameres* sp. and *T. fissispina* were observed within a firm and red nodule (1 × 1.5 cm) in the mucosa. Histological sections showed both species within the glands of the glandular epithelium lumen, surrounded by a capsule of fibrovascular connective tissue isolating the gland, as well as moderate lymphocytes, macrophages, and giant inflammatory cells (Fig. 1A and Fig. 2A). *Echinuria uncinata* was found in several nodules full of parasites within the proventriculus wall (Fig. 1D). All positive ducks presented ulcers; two *M. americana* had nodules of firm consistency and a size of 1.5 × 2 cm in diameter, and in one of them the nematode was observed penetrating the mucosa. At a histological level, nodules contained adults surrounded by two layers of fibrous connective tissue. Macroscopic inspection of the intestine of *O. jamaicensis* revealed the presence of an individual *Hystrichis* sp. adhered to the mucosa; due to its number, the specimen was used for taxonomic identification. The cestode species *Gastrotaenia cygni* was observed in the lumen of proventricular glands, producing ulcers, systemic necrosis and multiple inflammatory foci with

Table 1

Infection levels and histopathological lesions caused by the gastrointestinal helminths detected among waterfowl species from Atarasquillo marshes, Mexico.

Helminth species	Host species	Prevalence (%)	Mean abundance	Digestive tract studied for histopathology
TREMATODA				
Zygocotyle lunata (Diesing, 1836) Stunkard, 1916[C]	**A. acuta**	16.6	0.6	1
	A. crecca	30	0.36	0
	*O. jamaicensis***	13.6	0.18	0
	*S. cyanoptera***	4.5	0.09	0
	A. platyrhynchos diazi	10	0.15	0
Notocotylus triserialis Diesing, 1839[C]	*A. acuta*	11.1	0.21	0
	*A. crecca***	6.6	0.13	0
	*S. discors***	12	0.32	0
	S. clypeata*	18.1	0.18	1
	*O. jamaicensis***	9	0.18	0
	*M. strepera***	8	0.08	0
Notocotylus seineti Fuhrman, 1919[C]	*A. crecca*	6.6	0.5	0
	S. clypeata	18.1	0.95	1
	*O. jamaicensis***	9	0.27	0
Psilochasmus oxyurus (Creplin, 1825) Lühe, 1909[I]	*S. discors***	4	0.04	0
	*O. jamaicencis***	4.5	0.18	0
	*A. platyrhynchos diazi***	5	0.05	0
Australapatemon burti (Miller, 1923) Dubois, 1970[I]	*A. crecca*	16.6	0.46	0
	A. discors	15	0.12	0
	M. americana	16.6	0.27	1
	O. jamaicensis	27.2	1.72	0
	A. strepera	16	0.08	0
Cotylurus magniacetabulus Dubois & Angel, 1972[J]	**M. americana***	8.3	0.27	1
	*O. jamaicensis***	4.5	0.04	0
	*A. platyrhynchos diazi***	5	0.15	0
CESTODA				0
Fimbriaria fasciolaris (Pallas, 1781) Frölich, 1802[I]	*A. crecca***	13.3	0.13	0
	*S. discors***	4	0.04	0
	S. clypeata	4.5	0.04	1
	*S. cyanoptera***	16.6	0.04	0
	*M. americana***	27.2	0.05	0
	O. jamaicensis*	10	0.27	1
	A. platyrhynchos diazi	32	0.05	0
	*M. strepera***	12	0.04	0
Cloacotaenia megalops (Nitzch in Creplin, 1829) Wolffhügel, 1938[Cl]	*A. acuta*	11.1	0.07	0
	A. crecca	10	0.1	1
	S. clypeata	4.5	0.04	0
	*M. americana***	8.3	0.11	0
	*O. jamaicensis***	13.6	0.13	0
	A. platyrhynchos diazi	10	0.05	0
	M. strepera	24	0.04	0
Gastrotaenia cygni Wolffhugel, 1938[G,P]	*S. discors***	8	0.16	0
	S. clypeata*	13.6	0.13	1
	M. americana*	25	0.55	1
	*O. jamaicencis***	4.5	0.04	0
	*S. cyanoptera***	9	0.13	0
	*M. strepera***	16	0.08	0
Diorchis sp.[I]	*S. clypeata***	4.5	0.04	0
	O. jamaicensis*	16	0.18	1
	*M. strepera***	8	0.04	0
NEMATODA				0
Echinuria uncinata (Rudolphi, 1819) Soloviev, 1912[G,P]	*S. discors***	4	0.08	0
	M. americana	25	0.11	1
	M. strepera	40	0.12	0
Tetrameres sp.[P]	*A. acuta***	22.2	33	0
	A. crecca	10	0.2	0
	S. discors	8	0.12	1
	S. clypeata*	13.6	0.45	2
	*M. americana***	16.6	0.33	0
	*O. jamaicensis***	18.8	0.18	0
	*S. cyanoptera***	18.8	0.27	0
	A. platyrhynchos diazi	20	0.15	0
	*M. strepera***	40	0.32	0
Tetrameres fissispina (Diesing, 1861) Travassos, 1914[P]	*M. americana***	33.3	0.27	0
	O. jamaicensis*	4.5	0.18	2
	*S. cyanoptera***	9	0.13	0
	*M. strepera***	16	0.16	0
Hystrichis sp.[P]	*S. discors***	4	0.04	0
	*O. jamaicensis***	4.5	0.04	0
	*M. strepera***	4	0.04	0

Table 1 (*continued*)

Helminth species	Host species	Prevalence (%)	Mean abundance	Digestive tract studied for histopathology
Streptocara sp.[G]	*A. crecca***	4.5	0.1	0
	S. discors	8	0.08	0
	*S. clypeata***	8	0.04	0
	*M. strepera***	4	0.12	0
Amidostomum sp.[G]	*A. crecca*	3.33	0.13	0
	*S. discors***	24	0.96	0
	S. clypeata	4.5	0.54	0
	M. americana*	8.3	0.2	1
	*O. jamaicensis***	9	0.27	0
	*S. cyanoptera***	22.7	0.27	0
	A. platyrhynchos diazi	5	0.4	0
	*M. strepera***	40	0.16	0
Epomidiostomum uncinatum (Lundahl 1841) Seurat 1918[G]	***A. acuta****	11.1	0.21	1
	*A. crecca***	3.3	0.1	0
	S. discors	20	0.8	0
	*S. clypeata***	4.5	0.18	0
	M. americana*	8.3	0.16	1
	*O. jamaicensis***	31.8	1.40	0
	*S. cyanoptera***	9	0.22	0
	A. platyrhynchos diazi	10	0.3	0
	*M. strepera***	10	0.2	0
Capillaria sp.[I]	*S. clypeata***	9	0.90	0
	*M. americana***	16.6	0.16	0
	*O. jamaicensis***	4.5	0.45	0
Capillaria contorta (Creplin, 1839) Travassos, 1915[M]*	*M. americana***	8.3	0.27	0
	*O. jamaicensis***	4.5	0.45	0
	*M. strepera***	4	0.11	0
Ascaridia sp.[I]	*O. jamaicensis***	4.5	0.09	0
Heterakis sp.[C]	*M. americana***	16.6	0.22	0
ACANTHOCEPHALA				0
*Pseudocorynosoma constrictum (*Van Cleave, 1918) Aznar, Pérez-Ponce de León and Raga, 2006[I]	*A. acuta*	20	0.14	0
	S. discors	20	0.2	0
	S. clypeata	22.2	0.40	0
	A. platyrhynchos diazi	10	0.15	0
Filicollis sp.[I,*]	***A. crecca****	3.3	0.06	1

[C]= Cecum; [I]= Intestine; [J] = Jejunum; [Cl]= Cloaca; [G] = Gizzard; [P]= Proventriculus; [M] = Maw; * = First record in Mexico; ** = New host record. Sample size for each waterfowl: *Spatula discors* (n = 25); *Anas crecca* (n = 30); *Mareca americana* (n = 18); *Anas acuta* (n = 14); *Spatula clypeata* (n = 22); *Oxyura jamaicensis* (n = 22); *Spatula cyanoptera* (n = 22); *Mareca strepera* (n = 25); *Anas platyrhynchos diazi* (n = 20). Histopathologically studied duck species are highlighted in bold.

lymphocytes and few eosinophils in the mucosa.

Gizzard. The lesions in this organ were caused by two nematode species: *Amidostomum* sp. and *E. uncinatum*, and the cestode *G. cygni*. In both nematode infections, the corneal layer or keratinized epithelium broke off easily due to a moderate parasitic load (2–3 parasites). Hemorrhages with different size were also observed in the mucosa (Fig. 1C). At a microscopic level, nematodes embedded in the keratinized epithelium were found without causing inflammatory reaction. In some cases, these parasites did not produce an inflammatory response, while in others there was a moderate presence of macrophages and lymphocytes in the basal epithelium, and a diffuse discrete lymphoid hyperplasia. In many cases, the helminths were surrounded by mucus (Fig. 2C–D). The cestode species *Gastrotaenia cygni* caused a lesion of 2 × 1 cm in diameter in the keratinized epithelium with severe necrosis, a granular appearance and lacking a corneal layer.

Intestine. The strobili of the cestodes *F. fasciolaris* and *Diorchis* sp., in the intestinal lumen of the small and large intestine, as well as those of *C. megalops* in the cloaca, were covered by abundant mucus. The scolex of the three species, attached to the mucosa of the small intestine, was found surrounded by a few heterophiles and abundant lymphocytes. When the number of tapeworms was >2, slight congestion was observed. At a microscopic level, goblet cell proliferation and lymphoid hyperplasia were present while cestodes were surrounded by cellular detritus.

The presence of the trematode *Z. lunata* in the mucosa of the cecum of *A. acuta* did not produce pathological alterations, only a slight congestion, because only one parasite was involved in the infection. At a microscopic level, lymphoid hyperplasia and cellular debris surrounding

the flukes were the most common findings in this anatid species. *Notocotylus triserialis* and *N. seineti* also produced only a slight congestion when parasitic load was high (2–4 parasites). Microscopically, we observed lymphoid hyperplasia and a discrete amount of inflammatory cell (lymphocytes and macrophages) in the mucosa. Both trematode species were found covered by mucus and, in some cases, were delimited by giant cells.

Macroscopically, the acanthocephalans identified in the intestine, i. e., *Pseudocorynosoma constrictum* and *Filicollis* sp., caused white-colored nodulations in the intestinal serosa (Fig. 1A and E). At a histological level, the proboscis inserted into the subserosa led to the formation of granulomas, along with giant cells, epithelioid cells and heterophiles; the trunk, located in the intestinal lumen, was surrounded by mucus (Fig. 1B). In the intestinal mucosa of waterfowl such as *A. crecca*, *A. diazi,* and *S. clypeata*, the presence of acanthocephalans resulted in the observance of systemic necrotic areas.

4. Discussion

From a taxonomic perspective, this study increased the knowledge of the inventory of helminths associated to Mexican birds; this group of hosts has been neglected in Mexico, since only ≈12.2% of the birds distributed in the country have been studied (Pérez-Ponce de León et al., 2011). As a result of our research, the nematode *Capillaria contorta* and the acanthocephalan *Filicollis* sp., are registered for the first time in Mexico and another 11 taxa for the marshes of Lerma and central Mexico (see Pérez-Ponce de León et al., 2007; Mercado-Reyes et al., 2010; Martínez-Haro et al., 2012; García-Varela et al., 2013; Padilla-Aguilar
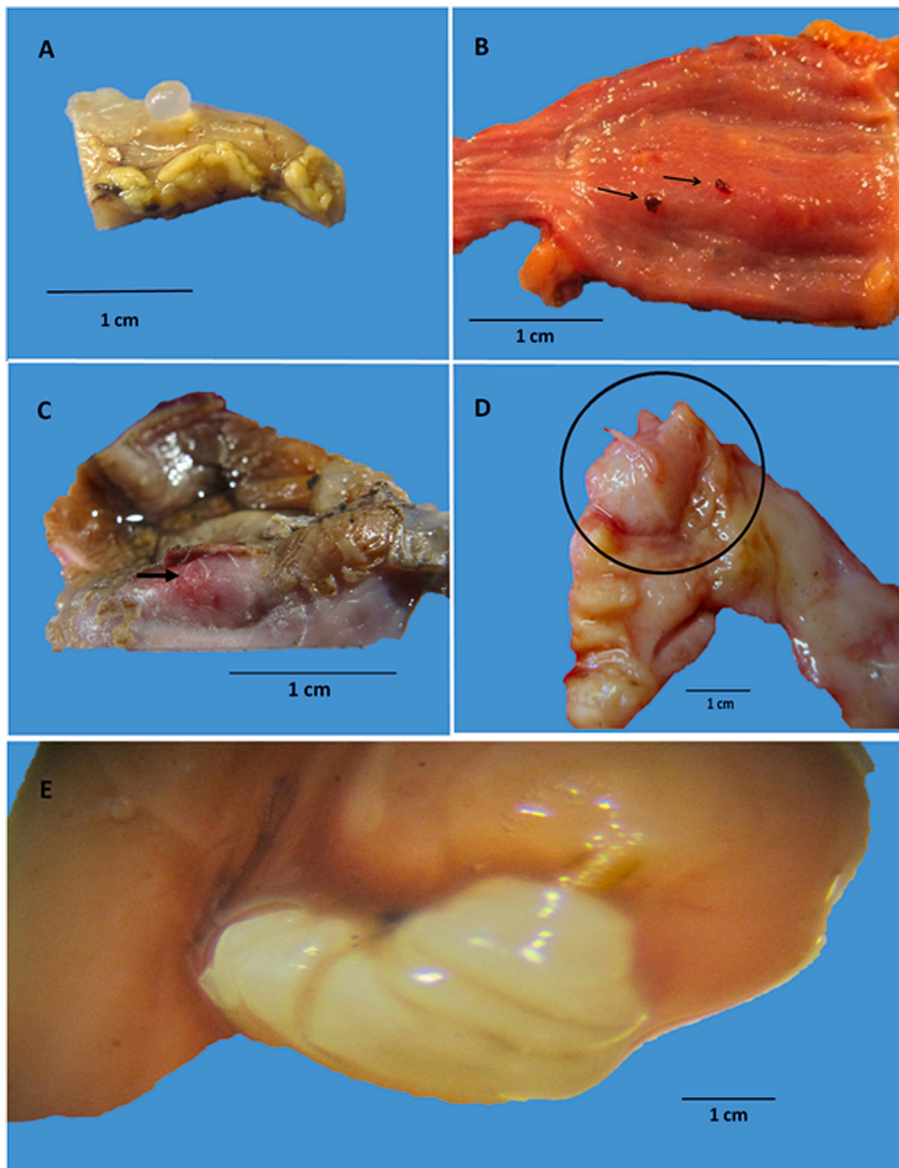
Fig. 1. A. Intestine of *Anas crecca* with a transparent nodule of 2 mm in diameter caused by *Pseudocorynosoma constrictum* penetrating the serosa. **B.** Proventriculus of *Spatula discors* with nodules (arrows): some of them whit *Tetrameres* sp. **C.** Gizzard of *Mareca americana* with hemorrhages (arrow) caused by the nematode *Amidostomum* spp. **D.** Gizzard of *Mareca americana* with a nodule of 1.5 × 2 cm in diameter and firm consistency, with the nematode *Echinuria uncinata*. **E.** Intestine of *Anas crecca* showing a nodule in the subserosa, containing the acanthocephalan *Filicollis* sp. in the intestinal lumen.

et al., 2018). In addition, 69 new host records for the sampled waterfowl were reported (Table 1).

Parasitism is common in wild waterfowl (Atkinson et al., 2008). Forty three percent of the 200 digestive tracts examined in this study, belonging to nine anatid species, were positive to at least one helminth species. However, this percentage value is less than those recorded in previous studies with Mexican anatids, in which parasitism levels reached 83.3% (Mercado-Reyes et al., 2010), 75% (Padilla-Aguilar et al., 2018) and 70% reported by Farias and Canaris (1986), among others. The heterogeneity of our samplings, along geographical, age-related, and avian gender, could be determinants for the observed differences (see Bush, 1990). Likewise, the richness of helminth species in some of these studies [21 in Padilla-Aguilar et al. (2018), 25 in Farias and Canaris (1986), and 20 in Martínez-Haro et al., 2012)] is similar to our findings (23). These richness values are in accordance with the Fedynich and Pence (1994) statement, who pointed out that the taxonomic composition and infections of individual hosts are determined by the seasonality of the samples, as well as by the vagility of the birds, which promote the exchange of helminths along their migratory route. However, authors such as Gladden and Canaris (2009) suggest that the helminth fauna of waterfowl is removed during migration and replaced

at wintering sites, as has been observed in their study (where six species of helminths were found) and in that of Mercado-Reyes et al. (2010), who reported only eight species. Confirmation of both assumptions can only be done through more extensive studies on migratory waterfowl from wintering areas to understand their population dynamics.

Taxonomic composition of helminth fauna of Mexican waterfowl does not seem to follow a structured pattern; in our study, nematodes and trematodes were the best represented groups of helminths among anatids, with eleven and six species, respectively. Similar findings were reported by Padilla-Aguilar et al. (2018) (eight nematodes and seven trematodes) in the Altangatepec wetlands, in Central Mexico; on the contrary, Martinez-Haro et al. (2012) registered nine trematodes and eight cestodes in the Lerma marshes, also in Central Mexico. On the other hand, studies conducted in Northern Mexico revealed a higher presence of platyhelminths. Farias and Canaris (1986) found eleven cestodes and six trematodes in the Chihuahua dessert and Mercado-Reyes et al. (2010) found three trematodes and two nematodes in Zacatecas State. The only trait common to all five studies is the low number of acanthocephalans present, which do not exceed two species. According to Bush (1990), taxonomic variability among bird host populations could be attributed to environmental conditions, in which the
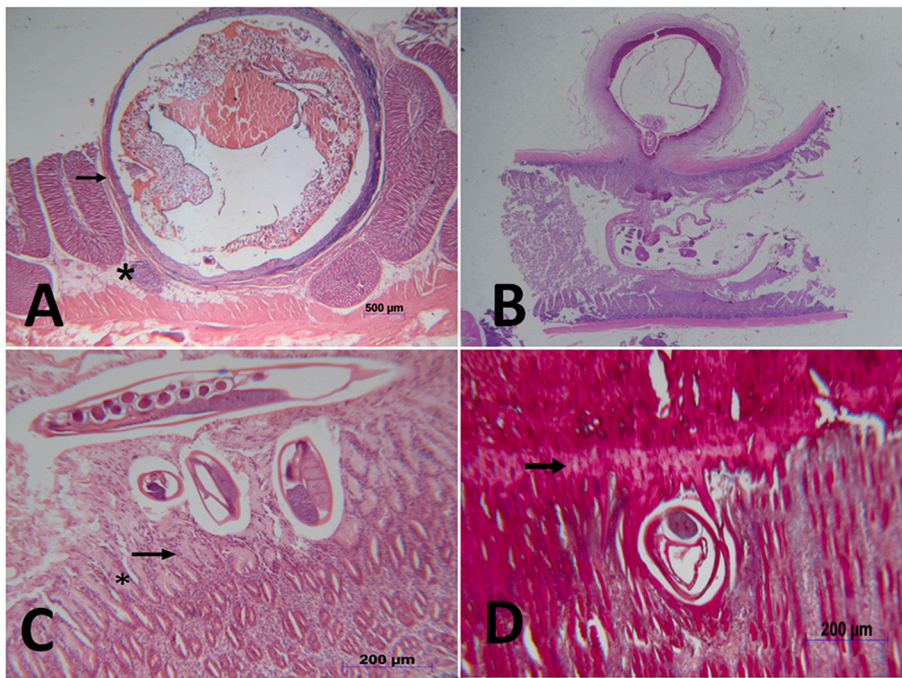
Fig. 2. A. Proventriculus section of *Oxyura jamaicensis* showing a *T. fissispina* gravid female in the lumen of the glandular epithelium, surrounded by some giant cells (asterisk), lymphocytes and wrapped by a fibrous vascular connective tissue capsule (arrow) that displaces the proventriculus glands. Stained with H-E. **B.** Proventriculus of *Mareca americana,* showing multiple inflammatory foci consisting of lymphocytes and a few eosinophils. The cestode *Gastrotaenia cygni* can be observed on the glands' lumen. Stained with H-E. **C.** *Anas acuta* gizzard, where the presence of abundant nematodes (*Epomidiostomun uncinatum* and *Amidostomum* spp.) can be observed below the keratinized epithelium, surrounded by an abundant amount of mucus (asterisk) and hyperplasia of the mucus-producing cells (arrow). Stained with H-E. **D.** Gizzard of *Anas crecca,* where nematodes of the genus *Amidostomum* can be observed below the keratinized epithelium surrounded by an abundant amount of mucus (arrow). Stained with Masson's trichromic.

varied habitats, determine the 'supply' of helminths that are available for colonization in each specific site.

Despite the fact that wild birds generally have moderate parasitic loads, which apparently do not cause problems for their hosts (Papini et al., 2012), knowing their helminth fauna, the levels at which they are infected and also the effect on its digestive tract is relevant, especially for game birds. This is due to several reasons: 1) the relatively scarce information on the lesions caused by helminths in this group of hosts, which also can make birds susceptible to secondary infections by enteric bacteria or fungi (Dunstand et al., 2019), causing malnutrition, loss of the feed conversion ratio, weight, and even bird death (Puttalakshmamma et al., 2008); 2) some of the species could be zoonotic [e. g., *Gnathostoma spinigerum*, recorded in ducks in Asia, see Bussaratid et al. (2005)] or 3) infect other animals by throwing eggs with their feces into the environment or when other hosts consume them, ending their biological cycle (Larki et al., 2018).

Fourteen of the 23 helminths found caused apparent lesions to at least six of the duck species studied (Table 1). The cestode *G. cygni* was found in proventriculus and gizzard, common sites where the parasite is housed (Willers and Olsen, 1969); its presence in the gizzard did not produce an inflammatory reaction, possibly due to the existence of a physical barrier (keratinized epithelium); however, in the proventriculus the inflammatory reaction was constituted of lymphocytes and eosinophils. Behm and Ovington (2000) pointed out that the presence of eosinophils is related to the destruction of large foreign bodies to be phagocytosed, as well as participating in tissue repair by fibrosis and releasing antigens; however, these cells did not appear in the rest of the infections, possibly due to the time of infection or because several of these species migrate to other organs during their development. Other species of cestodes, e.g., *Retinometra bulbocirrosus*, have been collected in the same organs (Oyarzún et al., 2019); however, authors do not report lesions in these parts of the digestive tract. Additionally, in our study, this cestode species along *F. fasciolaris, Diorchis* sp., and the acanthocephalans *P. constrictum* and *Filicollis* sp., caused systemic necrosis at the implantation site. Similar damage was reported by La Sala and Martorelli (2007) with *P. chagmasnathi* and Mahdi et al. (2018) with the tapeworms *Cotugnia* sp. in domestic chickens and by Gamra et al. (2015) with *Raillientina echinobothrida* and *Choanotaenia infundibulum* in *Coturnix coturnix*. The finding of necrosis at the implantation site in the mucosa is the product of the mechanical action of the worm's fixing organs (suckers, hooks and proboscis), as well as their body size, which prevents the passage of blood through of the mucosa, avoiding nutrition and oxygenation. This leads to the appearance of ischemia and systemic necrosis in the tissue. The 3 species of cestodes found in the waterfowl also caused, although less frequently, congestion, observed macroscopically in the mucosa of the intestine and the cecum, where the trematode *Z. lunata* was also found. Unlike our study, Mahdi et al. (2018) recorded the damage in the *lamina propia* and external layer of muscle. In general, congestion causes compression of the blood vessels avoiding the normal flow of blood. The inflammatory reaction caused by *Diorchis* sp. and *F. fasciolaris* presented lymphocytes, histiocytes and few heterophiles, and for both acanthocephalans giant cells and heterophiles. This variety of responses could be attributed to several causes: 1) the time that the parasites had been affecting the host, since heterophiles are the first line of attack against the parasite; 2) the extent of the lesion associated with the size of the entire parasite or fixation structures; 3) type of fixation structures, 4) group of parasite or 5) by bacteria or fungi inoculated in the cuticle during the process of fixation to the organ (Dunstand et al., 2019), which stimulate the appearance of heterophiles (Phillips et al., 1980). According to the classification of the lesions established by Silva et al. (2014), who studied the damage caused by the acanthocephalan *Corynosoma australe* in mammals, *P. constrictum* and *Filicollis* sp., the 2 species found in the waterfowl, could be located in the grade II, due to the presence of necrosis, destruction of villi and Lieberkühn crypts and by the low lymphocyte infiltration; the only differences with respect to the study by Silva et al. (2014), is the presence of heterophils and giant cells in our samples. This type of reaction suggests that the 2 species had been attached to the intestine for a long time, so the host's immune system developed this response, preventing the worms from causing more damage, or that the helminths stimulated the proliferation of fibroblasts around them to evade the immune system.

A macroscopically circulatory lesion associated to the nematodes *Epomidiostomum* sp. and *Epomidiostomum uncinatum* was the irregular fragmentation of the keratinized layer of the mucosa of the gizzard, accompanied by hemorrhages. However, authors such as Lapage (1961), Soulsby (1982), Anisuzzaman et al. (2006) and Yousuf et al. (2009), have only reported the presence of petechiae in some anatidae gizzard due to the infection of the related *Amidostomum anseris* nematode; Islam

et al. (1988) only recorded the tissue erosion. The hemorrhages found in the mucosa of the gizzard of the studied waterfowl are due to the deep penetration of the parasites into the keratinized layer, which breaks the blood vessels; being between the layers, they generate its thickening and rupture.

The nematodes *T. fissipina* and *Tetrameres* sp., were found within small red nodules in the proventriculus; the histological sections of the nodules revealed the presence of both males and gravid females, aspect previously reported by Cvetajeva (1960) and Kamil et al. (2011). The damage these nematodes caused was the dilation of the proventricular glands. Upon close examination, the glands presented a flat epithelium with picnosis, karyorexis, and karyolysis, in addition to atrophy of the epithelial cells (cysts) associated with compression exerted by the parasite. Cysts were delimited by fibrous connective tissue and an inflammatory reaction (numerous lymphocytes and histiocytes). Similar lesions were reported by Colas et al. (2016) in infections by *Tetrameres americana* and by Kamil et al. (2011) in cases produced by *T. fissipina*. The lesion caused by these nematodes is specifically referred by Soulsby (1982) as inflammation, while Cvetajeva (1960), Nagy et al. (1978), Bergan et al. (1994) and Kamil et al. (2011), list the same type of components that those found in our work, adding the presence of eosinophils, which constitutes a normal response to parasitic infections (Campbell, 1994).

The most common macroscopic damage found in Atarasquillo waterfowl was the formation of granulomas, consisting of yellowish caseous material, which were confirmed through histopathologic studies. This tissue inflammatory reaction is associated with the nematodes *E. uncinatum* and *E. uncinata* in the proventriculus, the trematodes *N. triserialis* and *N. seineti* in the cecum and the acanthocephalans *P. constrictum* and *Filicollis* sp. in the small intestine. Previous studies also mention the development of granulomas with *E. uncinata* inside (Work et al., 2004); Da Silveira et al., 2006; Oyarzún et al. (2019) and Graczyk et al. (1993) associated them with *N. attenuatus*. Work et al. (2004) also pointed out that *E. uncinatum* caused dilation of the glands with flat epithelium, overproduction of mucus, ulcers and sporadically the formation of granulomas.

An uncommon damage found in the sampled birds was hyperplasia of the intestinal lymphoid tissue, which was observed during infections with *Amidiostomum* sp., *E. uncinatum*, and *C. megalops*. This lesion is triggered by the presence of the parasite and can intensify with the age of the host, its type of nutrition or the microenvironment (Liebler et al., 1988).

Finally, in infections with *N. triseralis*, *N. seineti*, *Amidiostomum* sp., *E. uncinatum*, *F. fasciolaris*, *Diorchis* sp. and C. *megalops*, hyperplasia of the goblet cells was identified, which generated abundant mucus in the intestine. Hyperplasia is a product of the constant irritation generated by the helminths on the mucosa, as a response of the host to avoid its fixation, also generating proteolytic enzymes to destroy it and facilitate the departure of the intestinal tract with the peristaltic movements (Malin et al., 2013).

Since parasitism is common among waterfowl, threats such as pollution and habitat loss (among others), can cause stress to the bird and consequently, debilitate their immune system making them more susceptible to diseases or amplifying co-evolutionary responses such as mild lesions, and even lead to massive deaths (Wobeser, 1997; Cordero del Campillo, 1999; Atkinson et al., 2008; Saif et al., 2008). Transversal and longitudinal studies are necessary to establish a baseline and understand the ecological dynamics in the host-parasite interaction and comprehend how they respond over time. The protection and conservation of migratory waterfowls in North America, as is the case of the community of birds that arrive during the winter season into the Central Mexican Highlands, requires a surveillance system focused on the etiological agents that can cause diseases and are damaging wild populations, while facilitating the detection of zoonotic agents that are of public health interest.

Declaration of competing interest

The authors declared that no conflicts of interest exist.

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