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ORIGINAL ARTICLE

Endoparasites of *Crotalus tzabcan* (Serpentes: Viperidae), with a checklist in rattlesnakes

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Abstract The helminth and pentastomid fauna of 50 specimens of *Crotalus tzabcan* from the Yucatán Peninsula, Mexico is documented. The examination revealed the presence of three nematode species (*Hastospiculum onchocercum*, *Hexametra boddaertii*, and *Travassosascaris araujoi*), and one pentastomid (*Porocephalus crotali*). The threee nematode species had the same prevalence (2%), while the pentastomid had a higher prevalence (8%). The pentastomid *P. crotali* was the most abundant and intense parasite, although it was only found in four snake hosts. *Crotalus tzabcan* acts as definitive host for the adult helminths and pentastomids, with rodents as the probable intermediate hosts. This work represents the first systematic survey on the parasitic helminth and pentastomid fauna of *C. tzabcan*, and includes four new geographical records. Additionally, a checklist of helminths and pentastomids reported for *Crotalus* and *Sistrurus* is provided. To date, a total of 32 helminth and 7 pentastomid species have been recorded as parasites of rattlesnakes. Nematoda possessed the highest species richness. The genera with the highest number of host species were *Mesocestoides* and *Hexametra*, followed by *Kalicephalus*. The rattlesnake species with the highest number of reported parasites was *C. durissus* (18 nematodes and 2 pentastomids).

Keywords Acanthocephala · *Crotalus* · Nematoda · Pentastomida · Platyhelminthes · *Sistrurus* · Yucatán Peninsula

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Introduction

Rattlesnakes of the genera *Crotalus* Linnaeus, 1758 and *Sistrurus* Garman, 1884 are venomous snakes only distributed in the Western Hemisphere and contain 47 and 3 species, respectively (Campbell and Lamar 2004; Uetz et al. 2018). These snakes are hosts of a variety of parasites, particularly helminths (Acanthocephala, Nematoda and Platyhelminthes) and pentastomids (Klauber 1972; Campbell and Lamar 2004; Ernst and Ernst 2006). However, to date there has not been a detailed study addressing the parasites of the Tzabcan rattlesnake, *Crotalus tzabcan* Klauber, 1952, a secretive species endemic to the Yucatán Peninsula. There is only a lone report of *Porocephalus crotali* Humboldt, 1812 in a single specimen of *C. tzabcan* (González-Solís and Terán-Juárez 2013). The main goals of this work were to determine the endoparasitic fauna in *C. tzabcan* and to update the list of endoparasites (helminths and pentastomids) from rattlesnakes.

Materials and methods

Parasites were obtained from 20 freshly road-killed *C. tzabcan* collected between 2015 and 2017, and from 30 specimens from the herpetological collection of El Colegio de la Frontera Sur at Chetumal, Quintana Roo, deposited during 1992–2014. All examined snakes came from Campeche, Quintana Roo and Yucatán, Mexico. The snakes were stored in 70% ethanol and examined for parasites by performing a mid-ventral incision to analyze the viscera. Fixation and preservation of parasites were carried out according to Vidal-Martínez et al. (2001). Infection parameters (prevalence, mean abundance and average intensity) follow those of Bush et al. (1997). Parasites were

identified with the aid of specialized literature (e.g., Chitwood 1932; Sprent 1978; Riley and Self 1979; Bowman 1984) and deposited in the Parasite Collection at El Colegio de la Frontera Sur, Unidad Chetumal (ECOPA 108–113). Additionally, an exhaustive bibliographic review on the helminth and pentastomid parasites of rattlesnakes of the genera *Crotalus* and *Sistrurus* was carried out.

Results

Of the 50 specimens of *C. tzabcan* examined (32 males, 18 females, snout–vent length [SVL] = 255–1667 mm), 7 (overall prevalence = 14%) contained 59 individual parasites, belonging to 3 nematode species: *Hastospiculum onchocercum* Chitwood, 1932 (1 male, 2 females), *Hexametra boddaertii* (Baird, 1860) (8 gravid females), *Travassosascaris araujoi* (Schneider, 1866) (sex undetermined because the specimen was in poor condition); and 1 species of pentastomid: *Porocephalus crotali* (4 females, 43 males). Parasites were mostly found in lungs, but also occurred in body cavity, liver and stomach. The parasitized snakes ranged from 495 to 1541 mm SVL and were mostly adult females. The parasites were found in snakes from Campeche (*P. crotali*), Quintana Roo (*H. onchocercum*, *P. crotali* and *T. araujoi*) and Yucatán (*H. boddaertii*). The parasite with the highest prevalence, average abundance and intensity was *P. crotali*, while the 3 remaining helminth species showed similar and low values (Table 1).

The bibliographic review showed that 31 rattlesnakes (28 *Crotalus*, 3 *Sistrurus*) have been found as host of 27 genera and 39 species of helminth and pentastomid taxa, including 47 records identified only to phylum (6), class (2), family (11) and genus (28). The majority of the helminth parasites were Nematoda (17 genera and 25 species; 65%), while Acanthocephala (1 genus, 1 species, and 11 unidentified taxa; 11%) was the least represented (Table 2). Most records belong to the genera *Kalicephalus* Molin, 1861 and *Mesocestoides* Vaillant, 1863 (12 species each), followed by *Hexametra* Travassos, 1920 (10), with *Hexametra boddaertii* and *Kalicephalus inermis* Molin, 1861 as the most common species (8 records each). Species of *Mesocestoides* and *Hexametra* parasitized 10 different rattlesnake species, while *Kalicephalus* only 8. The rattlesnake species with the highest number of helminth parasite records was *C. durissus* Linnaeus, 1758 with 18 (11 species and 6 unidentified nematodes). Geographically, most records (64) are from the United States of America, particularly Arizona (16). In Mexico there are records in Baja California Sur, Ciudad de México, Colima, Michoacán, Quintana Roo, and Yucatán (Table 2).

Concerning pentastomids, 11 *Crotalus* species have been recorded as host of 4 genera and 7 species of these parasites. The most common genus and species were *Porocephalus* Humboldt, 1812 and *P. crotali* with 11 and 9 records, respectively. The rattlesnake species with more pentastomid records are *C. adamanteus* Palisot de Beauvois, 1799, *C. basiliscus* (Cope, 1864), *C. durissus* and *C. tortugensis* van Denburgh et Slevin, 1921 (2 records each). Records for pentastomids came from the Argentina (1), Brazil (2), Mexico (9), United States of America (5) and Venezuela (1) (Table 2).

Discussion

This is the first systematic study of the parasitic fauna of the Tzabcan rattlesnake; therefore, the 3 nematode species represent new host and geographical records, while *P. crotali* has been previously reported in the same host and geographical region (see González-Solís and Terán-Juárez 2013). Despite not having a large sample of *C. tzabcan*, overall prevalence of 14% and 4 parasite species were obtained, unlike other studies with similar sample sizes, but lower overall prevalence and species richness (e.g., *C. enyo*

Table 1 Geographical records, infection site and parameters of infection of the parasites found in *Crotalus tzabcan* (n = 50)

Parasite	Snake (SVL in mm)	Locality	SI	# parasites	P	MA	MI
Hastospiculum onchocercum	Juvenile female-495	Chetumal, Q. Roo	ST	3	2	0.06 ± 0.42	3 ± 0
Hexametra boddaertii	Adult female-1450	Muchucuxab, Yuc.	BC	8	2	0.16 ± 1.13	8 ± 0
Travassosascaris araujoi	Juvenile female-533	Chetumal, Q. Roo	LV	1	2	0.02 ± 0.14	1 ± 0
Porocephalus crotali	Adult female-1325	Calakmul, Camp.	L	1	8	0.94 ± 6.07	11.7 ± 20.8
	Adult male-1470	Caobas, Q. Roo	L	43			
	Adult female-1515	Calakmul, Camp.	L	2			
	Adult male-1541	Chetumal, Q. Roo	L	1			

BC body cavity, *L* lung, *LV* liver, *MA* mean abundance, *MI* mean intensity, *P (%)* prevalence, *SI* site of infection, *ST* stomach, SVL Snout-vent length

Table 2 List of rattlesnakes and their respective endoparasites

Host	Parasite	Locality	References
Crotalus adamanteus	*Kiricephalus coarctatus* (Diesing, 1850)	Florida-US	Hill (1935)
	Porocephalus crotali	Florida-US	Leidy (1884), Hett (1924), Riley and Self (1979)
	Ascaris nuda Leidy, 1856	Captivity	Leidy (1856)
	Hexametra boddaertii	Captivity-Washington Zoo-US	Sprent (1978)
Crotalus atrox	*Porocephalus crotali*	Nuevo León-MX; Oklahoma, Texas-US	Hett (1924), Penn (1942), Riley and Self (1979), Peláez and Julia (1983)
	Pachysentis canicola Meyer, 1931	Texas-US	Bolette (1997b)
	Pachysentis sp.	Texas-US	Bolette (1997b)
	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona, New Mexico-US	Goldberg et al. (2002b)
	Hexametra boddaertii	Captive, San Diego Zoo, NY Zoo, New Mexico-US	Sprent (1978), Goldberg et al. (2002b)
	Kalicephalus inermis	New Mexico-US	Goldberg et al. (2002b)
	Physaloptera sp.	New Mexico-US	Goldberg et al. (2002b)
	Physocephalus sexalatus (Molin, 1860)	Texas-US	McAllister et al. (2004)
	Physocephalus sp.	New Mexico-US	Goldberg et al. (2002b)
	Unidentified nematode	Arizona-US	Klauber (1972)
	Mesocestoides sp.	Arizona, New Mexico, Texas-US	Bolette (1997b), Goldberg et al. (2002b)
	Oochoristica gracewileyae Loewen, 1940	Texas-US	Loewen (1940)
	Oochoristica osheroffi Meggitt, 1934	New Mexico-US	Goldberg et al. (2002b)
	Proteocephalus perspicua (LaRue, 1911)	Hidalgo-MX	Flores-Barroeta et al. (1961)
	Unidentified cestode	Oklahoma-US	Stephenson and Pisani (1991)
	Ochetosoma kansense (Crow, 1913)	Oklahoma-US	Ernst and Ernst (2006)
	Unidentifed trematode	Oklahoma-US	Stephenson and Pisani (1991)
Crotalus basiliscus	*Porocephalus basiliscus* Riley et Self, 1979	Colima-MX	Riley and Self (1979), Paredes-León et al. (2008)
	Porocephalus crotali	Captive-Philadelphia Zoo-US	Peláez and Julia (1983), Paredes-León et al. (2008)
	Oligacanthorhynchidae gen. sp. (cystacanth)	Michoacán-MX	Goldberg et al. (2006)
	Hexametra boddaertii	Sinaloa-MX	Goldberg et al. (2006)
	Macdonaldius oschei Chabaud et Frank, 1961	Colima-MX	Telford (1965)
	Oochoristica sp.	Colima-MX	Paredes-León et al. (2008)
Crotalus catalinensis Cliff, 1954	*Porocephalus crotali*	Santa Catalina Island-BCS-MX	Goldberg et al. (2003b)
Crotalus cerastes	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona-US	Goldberg and Bursey (2002)
	Hexametra boddaertii	California-US	Bursey et al. (1995)
	Thubunaea cnemidophorus	Nevada-US	Babero and Emmerson (1974)
	Oochoristica osheroffi	California-US	Alexander and Alexander (1957)
Crotalus cerberus (Coues, 1875)	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona-US	Goldberg and Bursey (2004)
	Mesocestoides sp.	Arizona-US	Goldberg and Bursey (2004)

Table 2 continued

Host	Parasite	Locality	References
Crotalus culminatus	*Porocephalus crotali*	Guerrero-MX	Peláez and Julia (1983), Paredes-León et al. (2008)
Crotalus durissus	*Cephalobaena tetrapoda* Heymons, 1922	Sao Paulo-BR	Motta (1963), Rego (1983)
	Porocephalus crotali	AR; VE	Humboldt (1812), Penn (1942), Riley and Self (1979), Martínez et al. (1999)
	Ascaridia flexuosa (Schneider, 1866)	BR	Vicente et al. (1993)
	Capillaria crotali	BR	Vicente et al. (1993)
	Hastospiculum onchocercum	Pernambuco-BR	Vicente et al. (1993)
	Hastospiculum sp.	Pará-BR	Pinto et al. (2010)
	Hexametra boddaertii	Paraná, Sao Paulo, Rio de Janeiro-BR	Sprent (1978), Pinto et al. (2010)
	Kalicephalus costatus (Rudolphi, 1819)	BR	Schad (1962), Vicente et al. (1993)
	Kalicephalus inermis inermis	BR	Schad (1962), Vicente et al. (1993)
	Kalicephalus inermis macrovulvus	Mato Grosso-BR	Pinto et al. (2010)
	Kalicephalus sp.	Captivity, Minas Gerais, Mato Grosso-BR	Araújo et al. (1999), Pinto et al. (2010)
	Ophidascaris ardnti	Paraná, Río de Janeiro, Minas Gerais-BR	Freitas (1968), Pinto et al. (2010)
	Ophidascaris durissus Panizzutti, Santos,Vicente, Muniz-Pereira et Pinto, 2003	Paraná-BR	Martins-Panizzutti et al. (2003)
	Ophidascaris sicki Freitas, 1951	Paraná-BR	Pinto et al. (2010)
	Ophidascaris sp.	Captivity, Minas Gerais, Paraná, Río de Janeiro, Minas Gerais-BR	Araújo et al. (1999), Pinto et al. (2010)
	Ophidascaris tuberculatum Siqueira, Panizzutti, Muniz-Pereira et Pinto, 2005	Minas Geiras-BR	Pinto et al. (2010)
	Oxyuris sp.	Captivity, Minas Gerais-BR	Araújo et al. (1999)
	Physaloptera sp.	Paraná-BR	Pinto et al. (2010)
	Rhabdias sp.	Captivity, Minas Gerais, Sao Paulo-BR	Araújo et al. (1999), Silva et al. (2001, 2007), Santos et al. (2008)
	Travassosascaris araujoi	Rio de Janeiro-BR	Araujo (1969a, b), Sprent (1978), Pinto et al. (2010)
Crotalus enyo Cope, 1861	Oligacanthorhynchidae gen. sp. (cystacanth)	Baja California Sur-MX	Goldberg et al. (2003a)
	Mesocestoides sp.	Baja California Sur-MX	Goldberg et al. (2003a)
Crotalus horridus Linnaeus, 1758	*Porocephalus crotali*	Captive-Washington Zoo; Oklahoma-US	Riley and Self (1979)
	Capillaria colubra Pence, 1970	North Carolina-US	Davis et al. (2016)
	Capillaria hepatica (Bancroft, 1893)	Virginia-US	Solomon (1974)
	Capillaria sp.	Virginia-US	Solomon (1974), Ernst and Ernst (2006)
	Hexametra leidyi Bowman, 1984	Louisiana-US	Bowman (1984)
	Kalicephalus costatus	North Carolina-US	Davis et al. (2016)
	Unidentified nematode	North Carolina-US	Davis et al. (2016)
	Ochetosoma kansense	US	Ernst and Ernst (2006)

Table 2 continued

Host	Parasite	Locality	References
Crotalus lepidus	Oligacanthorhynchidae gen. sp. (cystacanth)	Coahuila-MX	Goldberg and Bursey (1999)
	Abbreviata terrapenis	Arizona, New Mexico-US	Goldberg et al. (2002a)
	Physocephalus sexalatus	Texas-US	McAllister et al. (2004)
Crotalus molossus	*Kalicephalus inermis*	Ciudad de Mexico-MX	Prado-Vera (1971), Goldberg and Bursey (1999)
	Ophidascaris labiatopapillosa Walton, 1927	Durango-MX	Klauber (1972)
	Mesocestoides sp.	Arizona-US	Goldberg and Bursey (1999)
Crotalus oreganus	*Hexametra leidyi*	Captive, California-US	Sprent (1978), Bowman (1984)
	Physaloptera obtussima Molin, 1860	California-US	Morgan (1943)
	Mesocestoides sp.	California-US	Mankau and Widmer (1977)
	Mesocestoides variabilis Mueller, 1927	California-US	Mueller (1927), Voge (1953)
	Oochoristica osheroffi	California-US	Alexander and Alexander (1957)
Crotalus polystictus	*Ozolaimus ctenosauri*	Ciudad de Mexico-MX	Caballero (1939), Paredes-León et al. (2008)
	Unidentified nematode	NA	Klauber (1972)
Crotalus pricei	Unidentified nematode	Arizona-US	Klauber (1972)
	Mesocestoides sp.	Arizona-US	Goldberg and Bursey (1999)
Crotalus pusillus	*Kalicephalus inermis*	Michoacán-MX	Comroe (1948), Schad (1962)
Crotalus pyrrhus	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona, California-US	Goldberg and Bursey (2000a)
	Abbreviata terrapenis	Nevada-US	Goldberg et al. (2013)
	Physaloptera abjecta Leidy, 1856	California-US	Goldberg et al. (2013)
	Physocephalus sp.	Baja California-MX	Goldberg et al. (2013)
	Thubunaea cnemidophorus	California, Nevada-US	Babero and Emmerson (1974), Goldberg et al. (2013)
	Travassosascaris araujoi	California-US	Goldberg et al. (2013)
	Mesocestoides sp.	California-US	Goldberg and Bursey (2000a)
Crotalus ruber	*Raillietiella crotali* Ali, Riley et Self, 1984	Pond Island, BC-MX	Ali et al. (1984)
	Ophidascaris labiatopapillosa	California-US	Goldberg and Bursey (2000b)
	Mesocestoides sp.	California-US	Mankau and Widmer (1977)
Crotalus scutulatus	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona-US	Bolette (1997a)
	Kalicephalus inermis	NA	Ernst and Ernst (2006)
	Physocephalus sexalatus	Texas-US	McAllister et al. (2004)
	Thubunaea cnemidophorus	Nevada-US	Babero and Emmerson (1974)
Crotalus simus	*Capillaria crotali*	CR	Viquez (1933)
	Cosmocercoides variabilis (Harwood, 1930)	CR	Bursey and Brooks (2011)
	Hexametra boddaertii	CR	Bursey and Brooks (2011)
	Ophidascaris ardnti	CR	Bursey and Brooks (2011)
	Travassosascaris araujoi	Central America	Sprent (1978)
Crotalus tigris Kennicott, 1859	Oligacanthorhynchidae gen. sp. (cystacanth)	Arizona-US	Goldberg and Bursey (1999)
Crotalus tortugensis	*Raillietiella furcocercum* (Diesing, 1836)	Tortuga Island-BCS-MX	Klauber (1972), Ali et al. (1984)
	Porocephalus tortugensis Riley and Self, 1979	Tortuga Island-BCS-MX	Riley and Self (1979)

Table 2 continued

Host	Parasite	Locality	References
Crotalus totonacus	*Porocephalus crotali*	Tamaulipas-MX	Peláez and Julia (1983), Paredes-León et al. (2008)
	Ascarididae gen. sp.	Tamaulipas-MX	Armstrong and Murphy (1979)
Crotalus transversus	*Kalicephalus costatus*	México-MX	Goldberg et al. (2003c)
Crotalus tzabcan	*Porocephalus crotali*	Campeche, Quintana Roo-MX	González-Solís and Terán-Juárez (2013), This study
	Hastospiculum onchocercum	Quintana Roo-MX	This study
	Hexametra boddaertii	Yucatan-MX	This study
	Travassosascaris araujoi	Quintana Roo-MX	This study
Crotalus viridis Rafinesque, 1818	Unidentified acantocephalan	South Dakota-US	Bolette (1998)
	Kalicephalus inermis	Colorado; New Mexico-US	Widmer (1967), Pfaffenberger et al. (1989)
	Physaloptera retusa (Rudolphi, 1819)	New Mexico-US	Pfaffenberger et al. (1989)
	Physaloptera sp.	Colorado, South Dakota-US	Widmer (1967), Bolette (1998)
	Rhabdias sp.	Colorado-US	Widmer (1967)
	Unidentified nematode	Arizona-US	Klauber (1972)
	Mesocestoides corti Hoeppli, 1925	Captive	Hoeppli (1925), Hanson (1976), Hanson and Widmer (1985), Markoski et al. (2003)
	Mesocestoides sp.	South Dakota-US	Bolette (1998)
	Oochoristica osheroffi	Colorado, New Mexico-US	Widmer (1967), Widmer and Olsen (1967), Pfaffenberger et al. (1989)
	Manodistomum sp.	South Dakota-US	Bolette (1998)
Crotalus willardi Meek, 1905	Oligacanthorhynchidae gen. sp. (cystacanth)	New Mexico-US	Goldberg and Bursey (2000a)
	Mesocestoides sp.	Arizona-US	Goldberg and Bursey (2000a)
Crotalus sp.	*Proteocephalus* sp.	Arizona-US	Klauber (1972), Ernst and Ernst (2006)
Sistrurus miliarius	*Ochetosoma kansense*	Texas, Florida-US	Harwood (1932), Byrd and Denton (1938)
Sistrurus tergeminus	*Hexametra boddaertii*	New Mexico-US	Goldberg et al. (2001)
	Physaloptera sp.	New Mexico-US	Goldberg et al. (2001)
	Physocephalus sp.	New Mexico-US	Goldberg et al. (2001)
Sistrurus sp.	*Kalicephalus inermis*	NA	Schad (1962)
	Ochetosoma kansense	NA	Franz (1974)

4% overall prevalence, 52 analyzed specimens, 2 parasite species, Goldberg et al. 2003c; *C. lepidus* 5%, 55, 1, Goldberg and Bursey 1999).

However, in most studies that address wild rattlesnake parasites, the overall prevalence and parasite richness were highly variable, both within and among species, and seem not to be directly related to sample size (e.g., *C. atrox*; 72% overall prevalence, 112 specimens analyzed, 7 parasite species, Goldberg et al. 2002b; 67%, 6, 3, see Bolette 1997b; *C. lepidus* 16%, 267, 1, Goldberg et al. 2002a; *C. molossus* 2%, 129, 1, Goldberg and Bursey 1999). In addition, there are several parasitological studies where only 1 or 2 rattlesnake host specimens were analyzed and few species of parasites were found (e.g., Comroe 1948; Flores-Barroeta et al. 1961; Goldberg et al. 2003b, c; Martins-Panizzutti et al. 2003). Therefore, this lack of an evident pattern may be due to the developmental status of the host specimens, the diet of each rattlesnake species, the availability of intermediate hosts, as well as the conditions of each particular habitat, and deserves additional attention.

The occurrence of helminths and pentastomids in *C. tzabcan* showed an evident differentiation according to development status, since only adults and two juveniles were parasitized. Probably, older organisms have been exposed for longer time to infectious agents or the presence of the latter is strongly related to the feeding type of every age class. Adults of *C. tzabcan* feed on small and large rodent species, but newborns and juveniles do not consume larger prey species, due to limited gape (Carbajal-Márquez et al. 2018).

The nematodes found in this study showed a low prevalence, mean abundance and intensity values. A similar pattern was found in other studies that address these parasites in rattlesnakes, with the exception of *T. araujoi* in *C. pyrrhus* (Cope, 1866), with higher prevalence (25%) and mean intensity (5) (Goldberg et al. 2013). These patterns of low infection parameters of each species may indicate low snake predation on the intermediate host, and also may be related to sample size (e.g., Bursey et al. 1995; Goldberg et al. 2006; but see Goldberg et al. 2002b). However, the different pattern of *T. araujoi* in *C. pyrrhus* might be due to ecological differences in each region (e.g., xeric and temperate for *C. pyrrhus* and tropical for *C. tzabcan*), and this might influence prey type (intermediate hosts) and their availability (Campbell and Lamar 2004).

It seems that *H. onchocercum* rarely parasitizes rattlesnakes, since it has only been documented in *Crotalus durissus* (Vicente et al. 1993), a species closely related to *C. tzabcan*, and its geographic range includes Brazil, Costa Rica, Panama and Trinidad (Desportes 1941; Caballero 1947; Everard 1975; Bursey and Brooks 2011). Therefore, the specimens of *H. onchocercum* found in this study represent the first record of the genus in Mexico. The rarity of *H. onchocercum* in our survey might be related to the fact that this is probably the northern limit of its distribution.

Hexametra boddaertii has been reported in several rattlesnakes: *C. adamanteus* (Sprent 1978), *C. atrox* Baird et Girard, 1853 (Goldberg et al. 2002b), *C. basiliscus* (Goldberg et al. 2006), *C. cerastes* Hallowell, 1854 (Bursey et al. 1995), *C. durissus* (Sprent 1978), *C. simus* Latreille, 1801 (Bursey and Brooks 2011), *Sistrurus tergeminus* (Say, 1823), (Goldberg et al. 2001), and a "rattlesnake" (Bowman 1984). Therefore, our finding represents the second record of the species in Mexico. *Hexametra boddaertii* had not been previously reported in the Yucatán Peninsula, maybe because there have been few studies of snake parasites in the region (e.g., González-Solís and Terán-Juárez 2013; González-Solís et al. 2014). *Travassosascaris araujoi* has been documented in *C. durissus*, *C. pyrrhus* and *C. simus* (Sprent 1978; Bursey and Brooks 2011; Goldberg et al. 2013). Sprent (1978) suggested that *T. araujoi* appears to be restricted to rattlesnakes in Central and South America, but it also occurs in rattlesnakes from North America, and has been documented in colubrid and dipsadid snakes (Bursey and Brooks 2011; Goldberg et al. 2013). Therefore, *T. araujoi* found in Quintana Roo represent a new record for Mexico.

Porocephalus crotali was the parasite with the highest prevalence, mean abundance and intensity in *C. tzabcan*, as in other rattlesnakes (*C. adamanteus*, *C. atrox*, *C. basiliscus*, *C. culminatus* Klauber, 1952, *C. durissus* and *C. totonacus* Gloyd et Kauffeld, 1940) (Peláez and Julia 1983; Martínez et al. 1999; Yabsley et al. 2015). Female *P. crotali* produce eggs within the host that are discharged through nasal secretions or feces, and these remain viable in water or soil for several months. The nymphal stages can infect a variety of mammals (Paré 2008), many of which constitute prey species for co-occurring rattlesnakes.

All the *C. tzabcan* specimens parasitized by *P. crotali* found in this study appeared healthy. However, it has been documented that these parasites can heavily infect rattlesnakes, filling the lung cavity and eventually causing suffocation (see Fantham and Porter 1953; Peláez and Julia 1983). On the other hand, Riley (1986) mentions that there is little evidence that pentastomids are responsible for significant pathology in wild infected definitive hosts, although this does not necessarily apply to captive hosts. Self and Kuntz (1967) reported a wild and apparently healthy rattlesnake with 100 adults of *P. crotali* recovered from the lung, and they suggest this is evidence of host parasite co-evolution of pentastomids and their reptilian hosts which has resulted in a poorly exacerbated tissue and physiological reaction to the infection.

The intermediate hosts of *P. crotali* in the Yucatán Peninsula are unknown. Known intermediate hosts include a shrew *Blarina carolinensis* (Bachman, 1837), rodents *Peromyscus gossypinus* (Le Conte, 1853), *P. maniculatus* (Wagner, 1845), *Sigmodon hispidus* Say et Ord, 1825, and the opossum *Didelphis virginiana* Kerr, 1792, with short-tailed shrews (*B. carolinensis*) with the highest prevalence (Layne 1967; Riley and Self 1979; Yabsley et al. 2015). In *C. tzabcan*, the shrew *Cryptotis mayensis* (Merriam, 1901) is consumed by juveniles, and *Sigmodon toltecus* (Saussure, 1860) is one of the main rodent prey species of adults (Carbajal-Márquez et al. 2018).

Crotalus tzabcan has been previously reported as host of *P. crotali* in Chetumal, Quintana Roo (González-Solís and Terán-Juárez 2013). The finding of *P. crotali* in Campeche is a new state record. *Porocephalus crotali* appears to be restricted to the subfamily Crotalinae in the New World, since it has not been documented in other snake subfamilies (Poore 2012; Christoffersen and De Assis 2013). Therefore, its distribution is associated with that of its hosts, with records from the United States of America to northern Argentina (Riley and Self 1979; Goldberg et al. 2003b). Recently, Bino-Sundar et al. (2015) documented *P. crotali* in the Indian rat snake, *Ptyas mucosa* (Linnaeus, 1758), but the record seems dubious because the head of the pentastomid is distinctly separated from the abdomen by a neck (the separation is indistinct in *Porocephalus*), the absence of external double hooks (present in *Porocephalus*), and atypical distribution (Riley and Self 1979). In fact, that record could be *Kiricephalus pattoni* (Stephens, 1908), which was previously reported in *P. mucosa* (Hett 1921; Riley and Self 1980).

Crotalus tzabcan acts as definitive host of pentastomids and helminths, all restricted to the New World, being typical of Neotropical snakes, and apparently with some degree of host specificity. Additionally, none of the specimens examined appeared to be affected by the presence of the parasites. Such parasites have been able to colonize several rattlesnake species, including those in the *Crotalus durissus* group (to which *C. tzabcan* belongs), like *Capillaria crotali* (Rudolphi, 1819), *H. onchocercum*, *H. boddaertii*, *K. inermis*, *Ophidascaris ardnti* Sprehn, 1929, *P. crotali* and *T. araujoi* (Peláez and Julia 1983; Goldberg and Bursey 1999; Goldberg et al. 2006; Pinto et al. 2010; Bursey and Brooks 2011).

In the checklist, nematodes were the best represented in terms of number of species followed by pentastomids, cestodes, trematodes and acanthocephalans. This pattern is not unusual in the case of helminths, since it has been documented that the nematodes and trematodes presented the highest species richness, and to a lesser degree acanthocephalans, while the pentastomids have been reported with low richness in amphibians and reptiles from Mexico, and is related with the environment inhabited by the host (Paredes-León et al. 2008).

Crotalus durissus harbors the highest number of parasite species, perhaps influenced by its wide distribution in South America. This broad range has favored studies of parasite fauna (e.g., Araújo et al. 1999; Martínez et al. 1999; Pinto et al. 2010). Viperids have a low number of parasites when compared with colubrids. This difference may be due to the type of environment inhabited by the hosts, as habitat conditions affect parasite diversity (Brandt 1936; Brooks 1976; Paredes-León et al. 2008; González-Solís et al. 2014). In general, snake hosts with semiaquatic habits, such as *Drymarchon melanurus* (Duméril, Bibron et Duméril 1854), *Nerodia rhombifer* (Hallowell, 1852), *N. sipedon* (Linnaeus, 1758), *Thamnophis eques* (Reuss, 1834) and *T. melanogaster* (Wiegmann, 1830) (Colubridae and Natricidae), have a more diverse helminth fauna than snakes that are strictly terrestrial (Pérez-Ponce de León and García-Prieto, 2001; Ernst and Ernst 2006; Paredes-León et al. 2008). Rattlesnakes tend to concentrate in the driest places in the habitats where they occur (Klauber 1972). These habits might account for the relatively depauperate parasite fauna of rattlesnakes.

In some cases, the biogeographic affinities of parasites coincided with those of their hosts, thus showing some degree of evolutionary association (e.g., *H. onchocercum* and snake hosts with Neotropical distribution). Therefore, some groups of parasites that are specific to a group of snakes have probably co-evolved, as is the case of 2 *Porocephalus* species that were described from 2 rattlesnakes host endemic to northwestern Mexico (*P. basiliscus* and *P. tortugensis*). Because many rattlesnake species have restricted distributions, it is necessary to include molecular and ecological evidence to obtain more insights on the identity of their parasites (Riley and Self 1979; León-Règagnon, 2003; Paredes-León et al. 2008).

Diet is a factor that mainly influences the presence of metazoan endoparasites in wild snakes, since most species infect their host through ingestion of eggs, larvae or intermediate hosts (Fontenot and Font 1996). Therefore, the most likely way in which free-living rattlesnakes become infected is when they feed on lizards and rodents. Some of the parasites documented in rattlesnakes could be secondarily ingested with the prey item, e.g., *Abbreviata terrapenis* (Hill, 1941) in wild *C. lepidus* Kennicott, 1861 (Goldberg et al. 2002a), *Thubunaea cnemidophorus* Babero and Matthias, 1967 in wild *C. cerastes*, *C. pyrrhus* and *C. scutulatus* (Babero and Emmerson 1974), or *Ozalaimus ctenosauri* Caballero, 1938 in a captive specimen of *C. polystictus* (Cope, 1865) (see Caballero, 1939; Moravec et al. 1996). In the first 2 cases, the definitive hosts are lizards commonly consumed by rattlesnakes in the wild; in the last, the captive *C. polystictus* probably had been fed an iguana *Ctenosaura acanthura* (Shaw, 1802), a known definitive host of *O. ctenosauri*. Additionally, many parasites have been documented from captive rattlesnakes. For these, it is unclear if the infections originated prior to collection from the wild or arose later through feeding while in captivity. It is widely known that captivity-induced stress can induce pathologies, mainly those related to parasites (Santos et al. 2008; Siqueira et al. 2009; Pinto et al. 2010).

Several errors in the nomenclature of reptile hosts were found in the literature and corrected in the checklist. These errors can arise in several ways. For example, researchers might lack expertise in the taxonomy of parasites or reptiles. Taxonomic arrangements in both groups periodically undergo modification confusion, as in the use of the names *C. confluentus* Duméril et Bibron, 1854 and *C. cinereous* Le Conte 1852, both of which are synonyms of *C. atrox* (see Flores-Barroeta et al. 1961; Sprent 1978; Baker 1987; Paredes-León et al. 2008). Other herpetological examples include the use of the name *C. durissus* on specimens from Central America and Mexico, which are currently placed in *C. simus* (see Sprent 1978; Peláez and Julia 1983; Bursey and Brooks 2011), and *C. triseriatus* Wagler, 1830 reported by Comroe (1948) that likely refers to *C. pusillus* Klauber, 1952. Christoffersen and De Assis (2013) list erroneously a *Sambonia wardi* (Sambon in Vaney et Sambon, 1910) as a parasite of *C. horridus* (in fact *C. durissus* based on distribution). These parasite species are exclusively associated with lizard hosts, as noted by Sambon in Vaney et Sambon (1910), and was misidentified by Diesing (1836) as *Pentastomum proboscideum* (Rudolphi, 1812; see Poore 2012)

now synonym of *P. crotali*, and therefore omitted in this study.

The presence of *P. crotali* represents an interesting finding, since it may cause visceral pentastomiasis when humans ingest ova from feces (Paré 2008; Tappe and Büttner 2009). Rattlesnakes are commonly consumed by humans in several regions (Fitzgerald et al. 2004; Gómez-Álvarez et al. 2007; Alves et al. 2008); therefore, it is important to monitor the occurrence of *P. crotali* to avoid possible infections in humans after consuming the meat of these snakes or when they are in captivity.

Only 33 (66%) of the total number of rattlesnake species currently recognized (47 *Crotalus* and 3 *Sistrurus*) (Uetz et al. 2018) have so far been surveyed for metazoan endoparasites. This suggests that our knowledge about parasites of rattlesnakes is far from complete. Increasing the investigations on the parasitic fauna of rattlesnakes will help to understand the parasite-host relationship, as well as trophic networks, which in turn can positively influence management plans and conservation strategies.

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Authors' contribution RACM designed the study. RACM and JRCV collected and dissected the snakes. RACM and DGS identified the parasites. The manuscript was written by the three authors.

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

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