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Helminth Infracommunity Structure of *Leptodactylus melanonotus* (Anura) in Tres Palos, Guerrero, and Other Records for This Host Species in Mexico

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ABSTRACT: The amphibian genus *Leptodactylus* includes around 50 species, of which only 2 are distributed in Mexico; the helminth fauna of these 2 species is poorly known. As part of a research program on amphibian parasites in Mexico from 1997 to 2005, 281 sabinal frogs *Leptodactylus melanonotus* from 42 localities in 11 Mexican states were examined from a helminthological perspective. A total of 20 taxa of helminths—7 digeneans (5 adults, 2 larvae) and 13 nematodes (8 adults, 5 larvae)—was found to infect this amphibian host species. These data represent 105 new locality records, and 11 taxa are recorded in *L. melanonotus* for the first time. Infracommunity analyses of the sabinal frogs from Tres Palos indicated that these hosts are depauperate. The helminth community is dominated by specialist species, with *Cosmocerca podicipinus* the most common in almost 50% of the infracommunities. Percutaneous infection and predator-prey interactions were the 2 most common infection routes by helminths in frogs from Tres Palos, with 79% of the parasites recruited via skin penetration. Finally, our results show that the helminth fauna parasitizing *L. melanonotus* throughout Mexico has low similarity with the helminth fauna of leptodactylids studied comprehensively in South America, with only 2 digeneans and 3 nematodes being shared by hosts from both regions. As a result of our survey, the number of helminth species parasitizing *L. melanonotus* increased to 34. Considering its native distribution range, this number is now 36 with the inclusion of the nematodes *Oswaldocruzia costaricensis* and *Cruzia empera* in Costa Rica.

Leptodactylus includes approximately 50 species, of which only 2 are distributed in Mexico (Flores-Villela, 1993). *Leptodactylus melanonotus* (sabinal frog) occurs from Sonora and Tamaulipas in Mexico, throughout Central America, and into South America west of the Andes to Ecuador; they inhabit the edges of ponds or flooded pastures, at the base of tufts of grass, or within burrows in the mud (Lee, 1996). Despite the wide distribution of this species, little is known about their helminth fauna, to date constituted by 20 taxa (see Paredes-León et al., 2008).

As part of a research program on amphibian parasites in Mexico, specimens of *L. melanonotus* were examined for helminths in selected localities throughout the country. The aims of the present study were to describe the helminth infracommunity structure for this host species in Tres Palos, Guerrero, and increase the helminthological record of the sabinal frog along Mexico.

Specimens of *L. melanonotus* were collected from 42 localities in Mexico (Table I) from 1997 to 2005. Hosts were kept alive before necropsy, which was carried out within 24 hr of capture. Anurans were killed using an overdose of sodium pentobarbital and examined using standard procedures. Helminths were counted in situ. Helminth specimens were initially placed in saline (0.65%) and afterwards killed by sudden immersion in hot 70% ethanol. Trematodes were stained with Meyer's paracarmine or Gomori's trichrome, and whole-mounted in Canada balsam. Nematodes were cleared in lactophenol or glycerine, and examined on temporary slides. Voucher specimens were deposited on the Colección Nacional de Helmintos (CNHE), Instituto de Biología, UNAM, Mexico City. Ecological terminology follows Bush et al. (1997). Cumulative species richness curves were constructed for the sabinal frogs collected in the localities with the largest sample size: Tres Palos, Cerro de Oro, Champayán, and Teapa. Analyses of helminth infracommunity structure, irrespective of their site of infection, included measurements of mean number of helminths (abundance) and species of helminths (richness); mean diversity and evenness per frog (infected and uninfected) were calculated using Shannon's index with decimal logarithms (H′), and evenness (J′) as H′/H′ maximum. Numeric dominance was determined using the Berger-Parker dominance index. Quantitative and qualitative similarities were calculated for 1,512 pairs of infracommunities, using percent similarity and Jaccard's index, respectively (Magurran, 1988).

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A total of 2,005 specimens, representing 20 taxa of helminths—7 digeneans (5 adults, 2 larvae) and 13 nematodes (8 adults, 5 larvae)—was collected in 281 sabinal frogs from 42 localities distributed in 11 states of Mexico (Fig. 1). Nematodes were the most abundant group, totaling 1,806 specimens, while only 199 digeneans were found.

Helminths were collected from 6 sites within the hosts, with the intestine being the most common (12 taxa). *Spiroxys* sp., and *Cosmocerca podicipinus* were the only species found at more than 1 site (3 and 2, respectively).

From a geographic perspective, the most widely distributed species were *C. podicipinus* collected in 37 of the 42 sampled localities, and *Oswaldocruzia subauricularis* and *Rauschiella poncedeleoni* from 11 and 10 localities, respectively. *Aplectana incerta*, *Clinostomum* sp., *Cosmocerca parva*, *Eustrongylides* sp., and *Kalicephalus* sp., were collected in 1 locality exclusively. The number of helminth species among localities varied from 1 to 7; however, the mean richness recorded in sabinal frogs, considering all the 42 sampled localities, was 2.4. Hosts from Teapa and Armería had the greatest richness, with 7 helminth taxa each; in contrast, 1 or 2 helminth taxa were found in 55% of the sampled localities. There were 105 new locality records, and 11 taxa are recorded from *L. melanonotus* for the first time (see Table I).

Nine of the 20 taxa recorded as parasites of *L. melanonotus* could not be identified to specific level for several reasons, e.g., 6 of them because they were larval forms and 2 others, *Aplectana* sp. and *Rhabdias* sp., represent new species, which will be described elsewhere. Finally, *Oswaldocruzia* sp. could not be classified to the species level because we collected only female specimens (Table I).

Prevalence and mean abundance in all 42 localities varied from 2% to 100%, and from 0.04 to 34, respectively. However, sample size was heterogeneous, since in 14 localities only 1 individual host was collected, and in the other 20, the number of sabinal frogs sampled was <10 individuals. In the remaining 8 localities, sample size varied between 12 and 56. *Cosmocerca podicipinus* reached the highest levels of prevalence and abundance in 27 sampled sites and was the only species collected in sabinal frogs from other 11. This result agrees with that reported by Campiao et al. (2012), who considered this nematode as a "core" species for the *Leptodactylus podicipinus* helminth fauna; likewise, this nematode species has been recorded in 12 of the 19 studied species of *Leptodactylus* in the Neotropics with high prevalences (Bursey and Brooks, 2010 and references cited herein; Campiao et al., 2012). Two other species, *O. subauricularis* and *R. poncedeleoni,* occurred in relatively high levels of infection in the 11 and 10 localities where they were found, respectively.

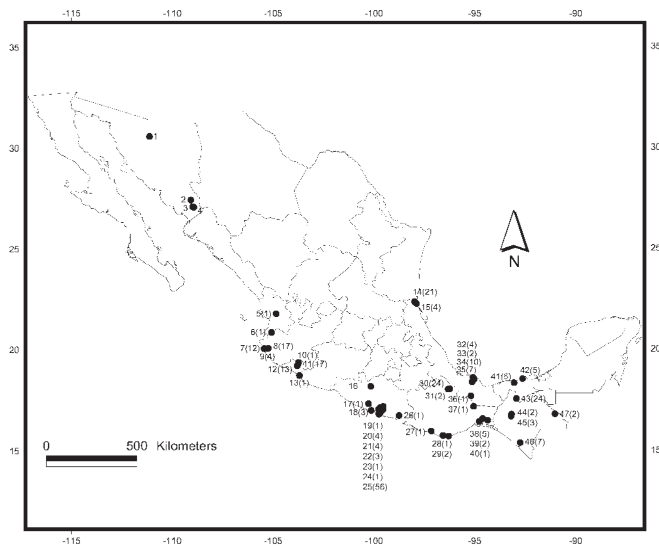

FIGURE 1. Map showing the localities studied in the present work. Sample size in parentheses. (1) Santa Ana. (2) Aduana. (3) Guiricoba. (4) Alamos. (5) Tepic-Aguamilpa (road). (6) El Tule. (7) Vallarta-Las Palmas (road). (8) Tomatlán. (9) Las Palmas. (10) Ticuizitan. (11) Armeria (river). (12) Coquimatlán. (13) México 200 (road). (14) Champayán (lagoon). (15) Chairel (lagoon). (16) Arcelia. (17) San Vicente Benitez (road). (18) El Carrizal. (19) Tierra Colorada. (20) Los Mayos. (21) El Pinito. (22) La Sabana (river). (23) Acapulco-Airport (road). (24) San Juan del Reparo. (25) Tres Palos (lagoon). (26) Marquelia-San Luis Acatlán (road). (27) Km. 125 México 200 (road). (28) San Antonio (river). (29) Progreso-México 185 (road). (30) Cerro de Oro (dam). (31) Paso Canoa. (32) Los Tuxtlas. (33) Escondida (lagoon). (34) Sontecomapan. (35) La Victoria (Catemaco). (36) Puente Los Amates. (37) Bajos de Coyula. (38) San Dionisio-Chicapa (road). (39) Puente Niltepec. (40) Puente Zanatepec. (41) Benito Juárez. (42) Pomposú. (43) Teapa (fish farm). (44) Madre Vieja. (45) El Chorro. (46) Rizo de Oro. (47) Ocosingo.

Cumulative species richness curves constructed for hosts collected in the 4 localities with higher sample sizes indicated that the number of examined hosts was sufficient to represent the helminth infracommunities only in Tres Palos ($n = 56$) (100% of the helminth species were recovered from only 8 specimens). At the other 3 sites, the curves did not stabilize, indicating that host sample size was insufficient, even though from 21 to 24 frogs were collected.

Considering all the studied sites in the present work, the best represented helminth group were the nematodes (13 taxa), followed by digeneans (7 species). In Tres Palos, the taxonomic composition was homogeneous, with 3 taxa for each group. The mean richness and abundance recorded in the sabinal frogs from all localities were 2.4 and 6.4, respectively; however, in hosts from Tres Palos, mean richness was slightly smaller (1.96), while abundance was greater (10.17), due to *C. podicipinus* dominating almost 50% of the infracommunities. The relative abundance of all species in the sabinal frogs from this locality is more or less homogeneous, which is why evenness values were moderate (0.54). Diversity was low (0.21) because 32% of the infracommunities were free of infection or parasitized by only 1 helminth species.

Prior to the present study, the helminth fauna of *L. melanonotus* in Mexico included 20 taxa (see Paredes-León et al., 2008). As a result of our survey, this number increased to 34. Considering its native distribution range, this number is now 36 with the inclusion of the nematodes *Oswaldocruzia costaricensis* and *Cruzia empera* in Costa Rica (Bursey and Brooks, 2010). The only helminth species shared by sabinal frogs from Mexico and Costa Rica are the digeneans *Catadiscus propinquus* and *R. poncedeleoni*, and the nematodes *Aplectana itzocanensis* and *C. podicipinus* (Brooks et al., 2006; Bursey and Brooks, 2010). However, the total number of helminth taxa parasitizing *L. melanonotus* may still be inaccurate. According to Razo-Mendivil et al. (2004), specimens of *Glypthelmins facioi* identified by Goldberg, Bursey, Salgado-Maldonado, et al. (2002), may be *Glypthelmins tuxtlasensis*. Likewise, it is possible that *Rhabdias elegans* is not distributed in Mexico and specimens collected from *L. melanonotus* represent a different species (see Martínez-Salazar and León-Règagnon, 2007). Unfortunately, the Mexican specimens of both species are not available for re-examination (Goldberg, Bursey, Salgado-Maldonado, et al., 2002).

As has been established previously for helminth communities of amphibians, the infracommunities recorded for *L. melanonotus* from Tres Palos, are depauperate and highly variable. Aho (1990) attributed these conditions to the reduced amphibian vagility (that restrict their exposure to many helminth species), and the low energetic demands of poikilothermy (causing low consumption of potential intermediate hosts). Our results also agree with Aho's (1990) prediction related with the dominance of nematodes in the community composition, since 4 of the 6 species found belong to this group; *C. podicipinus* was the dominant species in almost 50% of the infracommunities of sabinal frogs, and the only species in 4 more hosts. Likewise, even when the number of helminth species that parasitize *L. melanonotus* by percutaneous infection (*C. podicipinus*, *O. subauricularis*, and *Rhabdias* sp.) and ingestion (ascaridid gen. sp., *R. poncedeleoni*, and *Rauschiella tineri*) is the same (see Yamaguti, 1975; Anderson, 2000), the number of individuals recruited via skin penetration is greater, since they represent 79% of the abundance of the infracommunities. This feature is in agreement with Bolek and Coggins (2003), who stated that the development of helminth communities in terrestrial frog (as *L. melanonotus*) is more related to direct life cycle strategies than to food web dynamics. If we consider the 42 sampled sites for the sabinal frogs, the composition pattern observed in helminth infracommunities of Tres Palos is similar, since in all these localities we found 7 digenean and 13 nematode species. However, the most frequent mode of parasite transmission in frogs from all these sites was related to predator-prey interaction (70% of the species were recruited through the food web) (Yamaguti, 1975; Anderson, 2000). It is probable that the ephemeral condition of ponds around Tres Palos where sabinal frogs were collected is related to greater recruitment of helminth species through skin penetration, as well as a reduced number of aquatic prey that could serve as intermediate hosts. In a more stable aquatic environment, e.g., Teapa (a fish farm), ingestion of prey had a more significant role in helminth transmission.

On the other hand, in the helminth infracommunities analyzed in the present study, the taxonomic composition was dominated by amphibian specialist species (83%). This is also a common trait observed in almost all the localities where the sabinal frogs were sampled in this study; the only generalist species recorded were metacercariae of *Clinostomum* sp., a strigeid, *Eustrongylides* sp., and *Spiroxys* sp., which often use fish as intermediate hosts (Yamaguti, 1975; Anderson, 2000). Likewise, in 10 of the 19 neotropical species of *Leptodactylus* studied to date, the taxonomic composition was dominated by nematode species specialists for amphibians (Bursey et al., 2001; Goldberg and Bursey, 2002; Goldberg, Bursey, Salgado-Maldonado, et al., 2002; Goldberg, Bursey, Trujillo, and Kaiser, 2002). This pattern contradicts the one reported by Bolek and Coggins (2003) in terrestrial frogs; they asserted that generalist species are dominant in the helminth fauna of their host group.

Quantitative and qualitative similarity indices among helminth infracommunities analyzed were very low, i.e., only 33.9 and 33.1% of the compared pairs had values greater than 0.50, respectively; this indicates a large disparity in abundance and composition of species across infracommunities, supporting the idea that stochastic events may be important in the assembly of parasite communities (see Poulin, 2003). In the same way, in many pairs of helminth infracommunities, *C. podicipinus* was responsible for the similarity levels obtained; the remaining species had lower infection levels, and, consequently, a predictable pattern was not observed. Similar results have been obtained for *L. podicipinus* from several ponds in the Pantanal wetlands, Brazil (Campiao et al., 2012). However, in spite of unequal sample size of sabinal frogs for each

TABLE I. Helminths of the Sabinal frog *Leptodactylus melanonotus* in Mexico.

Helminths	Site of infection	Locality (CNHE accession number)	%‡	Ab§	Reference
Digenea					
Clinostomum sp.*†	Mesentery	Colima: Armeria (8123)	5.9	0.18	Present study
Catadiscus propinquus	Intestine	Veracruz: Los Tuxtlas	—	—	Brooks et al. (2006)
C. rodriguezi†	Intestine	Guerrero: La Sabana (8124)	3.7	0.04	Present study
		El Pinito (8125)	25	1	Present study
		Jalisco: Tomatlán (8126)	17.6	0.6	Present study
		Nayarit: Tepic-Aguamilpa (8127)	50	4	Present study
		Oaxaca: Progreso-México 185 (8128)	50	0.5	Present study
		Puente Los Amates (8129)	100	2	Present study
		Tabasco: Pomposú (8130)	100	15	Present study
		Teapa (8131)	26	7.8	Present study
Megalodiscus sp.	Intestine	Veracruz: Los Tuxtlas	4	3	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
M. temperatus	Intestine	Sonora: Alamos	3	2	Goldberg and Bursey (2002)
Glypthelmins facioi	Intestine	Veracruz: Los Tuxtlas	8	2.2	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
Gorgoderina attenuata	Urinary bladder	Chiapas: Ocosingo (8132)	100	8	Present study
		Colima: Coquimatlán (8133)	7.7	1	Present study
		Sonora: Cañón Estrella	3	2	Goldberg and Bursey (2002)
		Veracruz: Los Tuxtlas	10	1.4	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
G. festoni	Urinary bladder	Colima: Coquimatlán (5101)	8	1	Mata-López and León-Règagnon (2005)
		Armeria (5102, 5657)	2	1	Mata-López and León-Règagnon (2005)
		Guerrero: Arcelia (5100)	—	1	Mata-López and León-Règagnon (2005)
		El Pinito (8134)	25	1	Present study
Haematoloechus longiplexus	Lungs	Sonora: Cañón Estrella	3	2	Goldberg and Bursey (2002)
Rauschiella poncedeleoni	Intestine	Colima: Armeria (8135)	11.8	0.12	Present study
		Ticuizitán (8136)	100	1	Present study
		Guerrero: Acapulco airport (4065)	100	1	Present study
		Los Mayos (8137)	25	0.25	Present study
		San Juan del Reparo (8138)	100	1	Present study
		Tres Palos (3906, 4062, 4064)	7.9	—	Razo-Mendivil and León-Règagnon (2001)
		Jalisco: El Tule (8139)	100	1	Present study
		Vallarta-Las Palmas (8140)	8.3	0.08	Present study
		Oaxaca: Puente Los Amates (8141)	100	1	Present study
		Puente Zanatepec (8142)	100	2	Present study
		Sonora: Alamos	7	6	Goldberg and Bursey (2002)
		Tabasco: Benito Juárez (3733, 3738)	33.3	—	Razo-Mendívil and León-Règagnon (2001)
		Teapa (3737)	9.5	—	Razo-Mendívil and León-Règagnon (2001)
		Veracruz: Sontecomapan (3734, 3735)	25	—	Razo-Mendívil and León-Règagnon (2001)
		Escondida (3392)	12.5	—	Razo-Mendívil and León-Règagnon (2001)
R. tineri	Intestine	Guerrero: Tres Palos (4067–4069)	26.8	4.87	Razo-Mendivil et al. (2006)
		Acapulco airport (4070)	100	1	Present study
		Tabasco: Teapa (4072)	4.35	2	Present study
Strigeidae gen. sp.*†	Mesentery	Colima: Armeria (8143)	17.6	0.7	Present study
		Oaxaca: Paso Canoa (8144)	25	3	Present study
Cestoda					
Cylindrotaenia americana	Intestine	Sonora: Santa Ana	7	4.5	Goldberg and Bursey (2002)
Acanthocephala					
Centrorhynchus sp.*	Mesentery	Veracruz: Los Tuxtlas	13	1.3	Goldberg, Bursey, Salgado-Maldonado et al. (2002)

TABLE I. Continued.

Helminths	Site of infection	Locality (CNHE accession number)	%‡	Ab§	Reference
Nematoda					
Ascarididae gen. sp.*†	Mesentery	Colima: Armeria (8145)	5.9	0.06	Present study
		Guerrero: El Carrizal (8146)	33.3	2	Present study
		Tres Palos (8147)	12.5	2.9	Present study
		Oaxaca: Cerro de Oro (8148)	8.3	1	Present study
		Tamaulipas: Champayán (8149)	4.8	2	Present study
Porrocaecum sp.*	Mesentery	Veracruz: Los Tuxtlas	8	1.5	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
Atractidae gen. sp.*†	Intestine	Oaxaca: Progreso-México 185 (8150)	59	2.7	Present study
Aplectana incerta†	Intestine	Tabasco: Benito Jáurez (5737)	10	1	Present study
A. itzocanensis	Intestine	Guerrero: Los Mayos (6976)	25	7	Present study
		Nayarit: Tepic-Aguamilpa (6970)	50	2	Present study
		Oaxaca: Bajos de Coyula (6967)	100	1	Present study
		Sonora: Guiricoba	7	2	Goldberg and Bursey (2002)
		Veracruz: Los Tuxtlas (8169)	50	2	Present study
Aplectana sp.†	Intestine	Chiapas: Ocosingo (6993)	100	16	Present study
		Guerrero: San Juan del Reparo (6981)	100	1	Present study
		Tabasco: Teapa (5749, 5752)	8.3	0.12	Present study
		Oaxaca: Cerro de Oro (8151)	12.5	0.25	Present study
Cosmocerca parva†	Intestine	Oaxaca: San Dionisio-Chicapa (6962)	40	2	Present study
C. podicipinus	Intestine	Chiapas: Madre Vieja (8152)	50	1	Present study
	Lungs	Ocosingo (6975)	50	7	Present study
		Rizo de Oro (6987)	86.7	8.5	Present study
		Colima: Coquimatlán (4608–10)	76.9	5.1	Present study
		Río Armeria (8153)	100	10	Present study
		Ticuizitan (8154)	100	13	Present study
		Guerrero: Acapulco airport (8155)	100	13	Present study
		El Carrizal (8156)	100	5	Present study
		Los Mayos (6982)	75	5.3	Present study
		Marquelia-Acatlán (6971)	100	5	Present study
		Papagayo-Xolapa (6965)	100	10	Present study
		El Pinito (6961, 6984, 6985)	75	10.7	Present study
		La Sabana (6977, 6979)	100	8.6	Present study
		Tres Palos (5748, 5759, 5780, 5762, 5764)	75	8.6	Present study
		Tierra Colorada (La Laguna) (8157)	100	22	Present study
		Jalisco: Las Palmas (8158)	100	5.2	Present study
		Tomatlán (8159)	35.3	0.9	Present study
		Vallarta-Las Palmas (8160)	75	2.2	Present study
		Michoacán: México 200 (6992, 6997)	100	3	Present study
		Oaxaca: Bajos de Coyula (6968)	100	12	Present study
		Cerro de Oro (7281)	62.5	6.2	Present study
		Km 125, México 200 (6972)	100	8	Present study
		Paso Canoa (7620)	100	11.7	Present study
		Progreso-México 185 (6978)	50	4	Present study
		Puente Los Amates (8161)	100	10	Present study
		Puente Niltepec (8162)	50	34	Present study
		Puente Zanatepec (8163)	100	8	Present study
		San Antonio (6969)	100	2	Present study
		San Dionisio-Chicapa (6964)	80	16.7	Present study
		Sonora: Aduana	97	7.6	Goldberg and Bursey (2002)
		Tabasco: Pomposú (5734, 5736)	80	4.8	Present study
		Benito Juárez (7621)	60	5.5	Present study
		Teapa (5750, 5754)	65.2	5.7	Present study
		Tamaulipas: Champayán (6988, 6998)	100	7.1	Present study

TABLE I. Continued.

Helminths	Site of infection	Locality (CNHE accession number)	%‡	Ab§	Reference
		Chairel (6995)	100	3	Present study
		Veracruz: Sontecomapan (4607, 4611, 4612)	80	2.6	Present study
		La Victoria (Catemaco) (5761)	71.4	2.8	Present study
		Los Tuxtlas (8164)	75	3.6	Present study
		Los Tuxtlas	88	10.4	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
Eustrongylides sp.*	Mesentery	Chiapas: El Chorro (6991)	14.3	0.14	Present study
		Sonora: Alamos	23	2.6	Goldberg and Bursey (2002)
Spiroxys sp.*	Mesentery	Tabasco: Teapa (5760)	34.8	2.9	Present study
	Peritoneum	Tamaulipas: Champayán (6974, 6989)	4.8	0.05	Present study
	Stomach	Veracruz: Los Tuxtlas	15	6.6	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
Kalicephalus sp.*†	Intestine	Guerrero: San Vicente Benítez (6966)	100	1	Present study
Oswaldocruzia pipiens	Intestine	Sonora: Alamos	17	3.4	Goldberg and Bursey (2002)
Oswaldocruzia sp.	Intestine	Veracruz: Los Tuxtlas	36	2.5	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
		Chiapas: Ocosingo (6996)	50	2	Present study
		Guerrero: El Pinito (6980)	25	0.25	Present study
O. subauricularis†	Intestine	Colima: Coquimatlán (4618, 4619)	30.7	2.7	Present study
		Armeria (8165)	11.8	0.6	Present study
		Guerrero: Tres Palos (5746, 5758, 5763, 5779)	25	4.3	Present study
		Acapulco airport (8166)	100	3	Present study
		El Carrizal (8167)	33.3	5	Present study
		Jalisco: Vallarta-Las Palmas (8168)	58	2.3	Present study
		Oaxaca: San Antonio (6983)	11	2	Present study
		Tabasco: Benito Juárez (7664)	20	7.5	Present study
		Teapa (5753, 5755)	39.1	4.8	Present study
		Tamaulipas: Champayán (6986)	33.3	1.3	Present study
		Chairel (6994)	75	4.6	Present study
Subulascaris falcaustriformis	Intestine	Veracruz: Los Tuxtlas	6	2	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
Rhabdias elegans	Lungs	Veracruz: Los Tuxtlas	41	3.3	Goldberg, Bursey, Salgado-Maldonado et al. (2002)
R. ranae	Lungs	Sonora: Alamos	7	2	Goldberg and Bursey (2002)
Rhabdias sp.†	Lungs	Guerrero: El Carrizal (8170)	33	0.3	Present study
		Tres Palos (5747, 5757)	26.8	1.8	Present study
		Oaxaca: Paso Canoa (7662)	25	1	Present study
		Tabasco: Pomposú (5735)	60	6.3	Present study
		Benito Juárez (7663)	10	4	Present study
		Teapa (5756)	34.8	3	Present study
		Tamaulipas: Champayán (6963)	9.5	1	Present study
		Chairel (6990)	25	1	Present study
		Veracruz: Sontecomapan (4603)	40	3.2	Present study
Ascarops sp.*	Stomach	Veracruz: Los Tuxtlas	6	2.6	Goldberg, Bursey, Salgado-Maldonado et al. (2002)

* Larvae.
† New host record.
‡ Prevalence.
§ Mean abundance.

particular locality studied in Mexico, our results suggest that a suite of helminth species (*R. poncedeleoni*, *O. subauricularis,* and, particularly, *C. podicipinus*) could have a determinant role in the similarity among helminth communities of *L. melanonotus* populations.

Considering that *Leptodactylus* spp. is a predominantly Neotropical group, it should be expected that helminth fauna of this species would exhibit similarity with its congeners in the south even with *L. melanonotus* having the northernmost distribution. However, the only shared helminth species among some of the South American and Mexican leptodactylids are 2 digeneans (*C. propinquus* and *Haematoloechus longiplexus*), as well as 3 nematodes (*O. subauricularis, C. parva*, and *C. podicipinus*) (Vicente and Santos, 1976; Kleeman, 1981; Hamman et al., 2006; Campiao et al., 2012).

Instead, the helminth fauna of Mexican leptodactylids is composed of an important number of species endemic to Mexico or Central America (also found in other amphibian species), i.e., *Catadiscus rodriguezi, G. tuxtlasensis, Gorgoderina festoni, R. poncedeloni, R. tineri, A. incerta, A. itzocanensis, Aplectana* sp., and *Rhabdias* sp., as well as species commonly reported in other amphibians with Nearctic distribution, i.e., *Megalodiscus temperatus, Gorgoderina attenuata, H. longiplexus, Cylindrotaenia americana, Oswaldocruzia pipiens*, and *Rhabdias ranae*. Complementing the helminth fauna of Mexican leptodactylids, but in fewer number, there are species that have been reported in South American amphibians other than leptodactylids (*Subulascaris falcaustriformis* and *R. elegans*: but see Martínez-Salazar and León-Règagnon, 2007). The presence of *H. longiplexus* in leptodactylids in Sonora, Mexico (Goldberg and Bursey, 2002) and Argentina (Hamann et al., 2006) is probably the result of colonization after the introduction of bull frogs (Akmentins and Cardoso, 2010), the original host of this helminth species, in the same way that was documented for other parasites in local species of leopard frogs in the Yucatán peninsula and Costa Rica (León-Règagnon et al., 2005). The composition of the helminth fauna of leptodactylids in Mexico clearly shows that host-parasite systems are the result of complex evolutionary scenarios including coevolution, but, perhaps more frequently, parasite loss and new parasite colonization after host range expansion events, then followed by isolation periods as has been suggested by Hoberg and Brooks (2010) for other host-parasite systems.

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