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Describing Parasite Biodiversity: The Case of the Helminth Fauna of Wildlife Vertebrates in Mexico

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1. Introduction

Parasites are extremely abundant and diverse in nature, representing a substantial portion of global biodiversity. At least 50% of the species living on earth are parasites of some form, considering all viruses and some bacteria, and the eukaryotic species most commonly associated with parasitology, including agents of diseases affecting not only humans, but also livestock, crops, and wildlife (Brooks & Hoberg, 2006). Interestingly, only a small fraction of the existing species are of medical or veterinary importance (Price, 1980; Poulin & Morand, 2004). There are many reasons to include parasites in any biodiversity survey, and indeed to study parasite diversity on its own. For example, parasites have been mentioned several times as elegant and sophisticated biological markers and as contemporary probes of biodiversity (Gardner & Campbell, 1992). Additionally, parasite diversity provides insights into the history and biogeography of other organisms, into the structure of ecosystems, and into the processes behind the diversification of life (Brooks & Hoberg, 2000; Poulin & Morand, 2000, 2004). In this context, parasites have, according to Brooks & Hoberg (2006), a dual and conflicting significance because they may regulate host populations, playing a central role in maintenance of genetic diversity and structuring host communities and, at the same time, they represent treats to human health, agriculture, natural systems, conservation practices, and the global economy (see Horwitz & Wilcox, 2005). For a comprehensive overview of the role that parasites play in research programs on biodiversity, the reader should refer to Brooks and Hoberg (2000) and to Poulin and Morand (2000, 2004). On the other hand, even though parasites have been proposed as indicators of ecosystem stress (e.g., Marcogliese & Cone, 1997), more recently, based on new methodological approaches, some authors have emphasized the role of parasites as indicators of environmental changes, probably as a result of a renewed interest in the impacts of climate change on earth. For instance, Vidal-Martínez et al., (2010) reviewed the usefulness of parasites as bioindicators of environmental impact, and their meta-analysis showed significant effects and interactions between parasite levels and the presence and concentration of various pollulants and/or environmental stressors. Meanwhile, Palm et al. (2011) demonstrated that fish parasites are useful bioindicators to monitor long-term change in Indonesian grouper mariculture, and that groupers can be used to monitor environmental change in the wild.

1.1 Parasitic worms

Among eukaryotic metazoan parasites, helminths are represented by conspicuous and soft-bodied worm-shaped organisms that are commonly found living in virtually any habitat of the vertebrate host, as adults or as larval forms. In the later case, and depending on the habitat occupied by such larvae in the vertebrate´s body, the damage to the host my result in mortality, or at least, in a serious disease. According with Hugot et al. (2001) the term 'helminth' was originally used for worms living in the digestive tract of humans and animals, and thus was allied with the general concept of parasitism. Parasitism as a way of life evolved from free-living counterparts several times during the evolutionary history of life on earth. Helminths, as parasites in general, do not represent a monophyletic assemblage since under that term, members of phylogenetically not related phyla are included, i.e., Platyhelminthes ("flatworms"), Nematoda ("roundworms"), Acanthocephala ("thorny-headed worms), and Hirudinea ("leeches") (Fig. 1). Members of these groups are characterized as macroparasitic metazoans with a vermiform appearance, even though they represent independent evolutionary lineages. Some species have medical importance, e.g., *Taenia solium* and *Ascaris lumbricoides*, the first one causing diseases referred as teniosis (and cisticercosis when the larval form is the causal agent), and the second one causing ascariosis. Most helminth species possess a complex life cycle that involves one or more intermediate host, although some exhibit a direct life cycle (e.g., monogeneans).

Platyhelminths are characterized as dorsoventrally flattened acelomates with bilateral symmetry, and most of them are hermaphrodites. Among flatworms, free-living species are found, however, parasitic platyhelminths are included in three major groups, digeneans, monogeneans, and cestodes (Fig. 1) (Roberts & Janovy, 2005). Nematodes also contain free-living and parasite species; these are pseudocoelomate roundworms, with sexual dimorphism. The entire phylum Acanthocephala is represented by parasite species that infect, as adults, the digestive tract of vertebrates. Acanthocephalans are also pseudocoelomate worms diagnosed by possessing a particular attachment organ (proboscis) armed with hooks. Finally, hirudineans, commonly referred to as leeches (blood-sucking ectoparasites on a variety of hosts), belong into the phylum Annelida and are characterized as metameric celomate organisms, with some of the body segments at both extremities modified to form suckers (Bush et al., 2001).

According to estimates made by several authors, the number of known species of helminths infecting vertebrates varies between 23,670 and 52,000, with approximately 13,570 to >40,000 platyhelminths, 8,400 to >10,500 parasitic nematodes, 1,141 to >1,200 acanthocephalans, and >400 hirudineans (see Hugot et al., 2001; Poulin and Morand, 2004), however, quite possible, this biodiversity is underestimated since new helminth species are described in every volume of the major parasitological journals over the world on regular basis, and, as recently argued, the use of molecular tools is allowing a more accurate description of biodiversity by establishing a more robust species delimitation criteria, and parasites in general do not represent an exception to this trend (Nadler & Pérez-Ponce de León, 2011). Parasitologists are deeply aware that the inventory of the metazoan parasites of wildlife vertebrates on earth is far from complete. Particularly in Mexico, there is a long tradition in the taxonomic study of the helminth parasites of wildlife vertebrates, and they have been studied for more than 80 years. Due to this long tradition, a large amount of information has

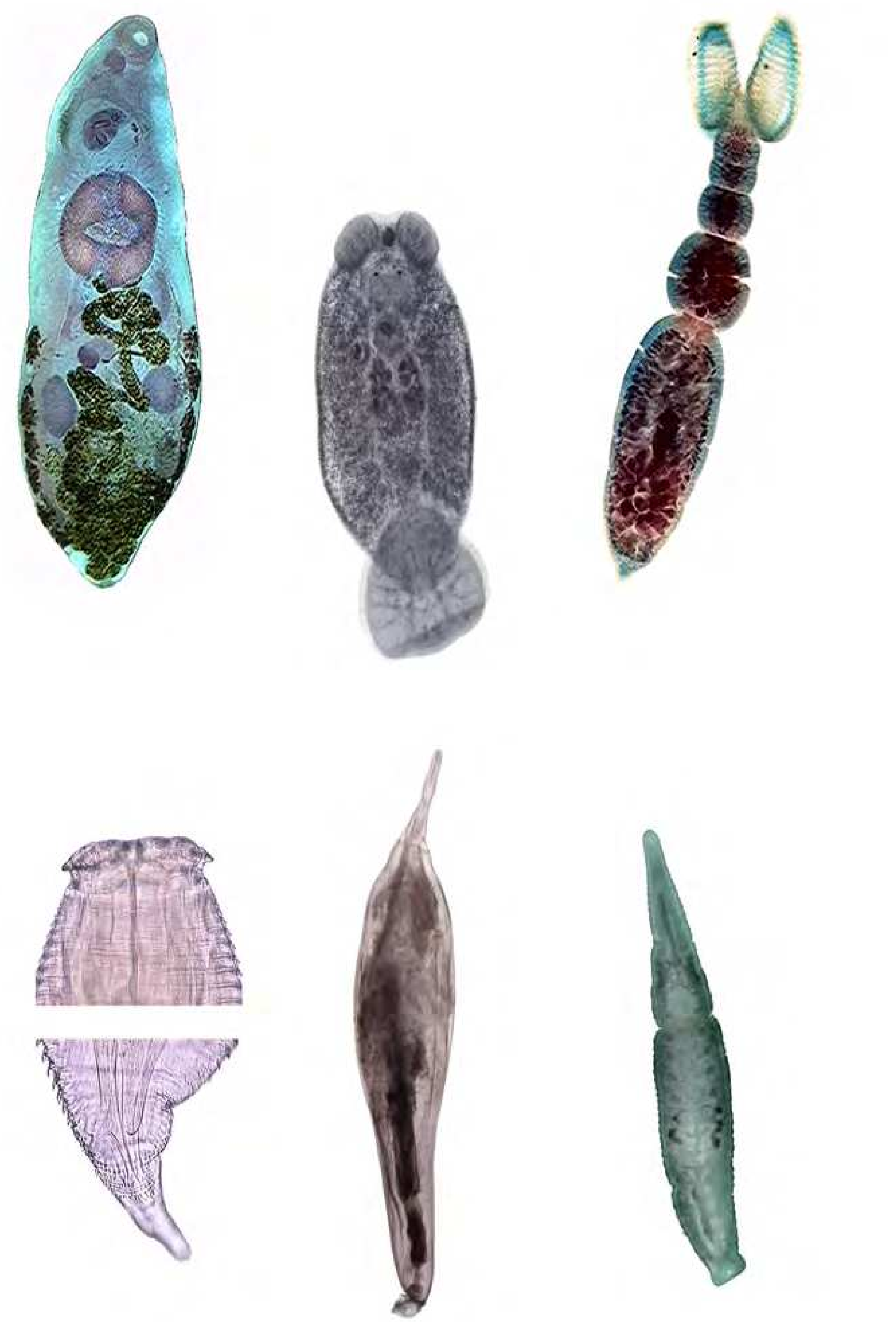

Fig. 1. Representatives of the major groups of parasitic helminths. Top line, from left to rigth, Digenean, Monogenean, Cestode. Bottom line, from left to rigth, Nematode, Acanthocephalan, Hirudinean.

been accumulated thanks to the dedicated work of national and foreign helminthologists that have contributed to the inventory of that parasite fauna. Based on the data gathered up to early 2011, in this book chapter we explore some general patterns of diversity of such parasitic group in the wildlife vertebrate fauna occurring within the Mexican territory, and we analyze these patterns in terms of host associations and geographical distribution, being aware that the inventory is not complete yet, and that unequal sampling effort may obscure some general patterns.

1.2 Mexico, a megadiverse country

The analysis we present here covers the entire country. Mexico is considered to be a Megadiverse country and, in this context, it occupies the 4th place worldwide in terms of species diversity. This is mainly the result of its position between the Nearctic and the Neotropical biogeographical zones; in addition to that, almost all the climates of the planet are found in Mexico, and it possesses a complex topography resulting from an intense geologic history (Sarukhán et al. 2009). As we recognized above, the inventory of the helminth parasite fauna is not complete yet of course, but we have gathered enough information thus far to start analyzing patterns and processes of parasite diversity and distribution, in an attempt to adjust such descriptive effort to modern taxonomic and biogeographic procedures (e.g., DNA-based taxonomy, niche modeling distribution, etc.), and to provide more accurate and realistic sampling strategies to try to complete the inventory in a timely manner, before the deterioration of some ecosystems produces the extinction of some species, or the particular habitats where they occur. Some efforts have been made to account for such patterns in the last decade; however, in this book chapter a general overview of the entire helminth fauna in wildlife vertebrates is presented for the first time, since previous analyses considered either a particular group of helminth, e.g., digeneans, or certain group of hosts, e.g. amphibians and reptiles (see Pérez-Ponce de León, 2001; Pérez-Ponce de León et al., 2002, 2007; Garrido-Olvera et al., 2006; Paredes-León et al., 2008; García-Prieto et al., 2010; Pérez-Ponce de León & Choudhury, 2010). Helminth parasites in humans as well as in domesticated (cattle, sheep, goats, swine, poultry) and companion (cats, dogs) animals are not considered in this review.

2. Gathering the data

The data on the helminth parasite fauna of wildlife vertebrates was obtained mostly from the database of the Colección Nacional de Helmintos (CNHE). The CNHE, hosted by the Biology Institute of the National Autonomous University of Mexico, is the national depository of helminth parasites in Mexico. In addition, information was also retrieved from foreign collections such as the U.S. National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A., the H. W. Manter Laboratory of Parasitology, University of Nebraska-Lincoln, U.S.A. (HWML), and the British Museum of Natural History (BMNH), Great Britain, where Mexican specimens were deposited in the past. After conducting an extensive bibliographical search using databases such as CAB Abstracts, ISI Web of Knowledge, and Biological Abstracts, we retrieved all published accounts where helminth parasites in wildlife vertebrates in Mexico were reported. All the specimen data was subjected to taxonomic confirmation and the nomeclature of both, helminths and vertebrates, was updated following particular taxonomic treatments. All the data were entered into a database on Access platform and most data are available from the web site of the Unidad de

Bioinformática de la Biodiversidad (UNIBIO- Instituto de Biología, UNAM) (http://unibio.unam.mx/collections/specimens/urn/IBUNAM: CNHE). The analyses we present here considers helminth species richness in terms of two variables, the major taxa of hosts where helminths have been found, as well as the geographical distribution. The major emphasis is made on species richness, and only in some particular cases, helminth species composition is taken into account. The analysis of major taxa of hosts considers a traditional classification of the vertebrates, i.e., 5 major groups such as fish, amphibians, reptiles, birds and mammals, even though we acknowledge some of them do not represent natural groups. Geographical distribution data are presented in terms of the division of the Mexican territory into 32 states based on geopolitical boundaries, not representing biogeographical units; however, a brief discussion on the transitional role of Mexico because of its latitudinal position between the Neotropical and Nearctic biogeographical regions is presented.

3. Species richness patterns

The knowledge accumulated thus far on the Mexican helminth fauna is asymmetrical in terms of geographical distribution, host taxa analyzed, and sampling effort. All the 32 states of the Mexican Republic have been surveyed for vertebrates and their associated helminth fauna, however sampling size in terms of individual hosts as well as host species is unequal. Another feature of the asymmetrical sampling effort is that, in every state of the Mexican Republic, intensive samplings have been made in particular localities but some regions within the state still remain unexplored. The effect of sampling size in establishing an accurate parasite inventory has been widely discussed (see Poulin & Morand 2004). Inequality in sampling effort (number of studies and number of hosts examined) can influence species occurrences and richness estimates, and consequently the patterns generated from any database. Generally, parasite species are recorded from their presence in hosts and as a consequence, the effort put in sampling hosts will determine how complete the parasite inventory is. Clearly, sampling is an issue and even in detailed surveys some parasite species go undetected because an insufficient number of hosts are examined. Cumulative parasite species richness curves as a function of sample size have been proposed as an alternative method to estimate the number of living species for certain group. These curves are based on the premise that for each independent host sample, the number of known species in the parasite assemblage increases asymptotically toward the true richness value as more individual hosts are examined (Poulin & Morand, 2004). Few attempts have been made to obtain cumulative species curves for the Mexican helminth parasite fauna. For example, Pérez-Ponce de León et al. (2007) plotted the cumulative number of species of digeneans described (or recorded for the first time) against time, and this curve, for the most well-know group of helminths in Mexico, has clearly not reached the asymptote. In a previous analysis, Pérez-Ponce de León (2001) estimated that the digenean species richness in Mexico ranged from 5,300 to 8,000. Even though this number may reflect an overestimation of the size of the fauna, it indicates that the inventory of this particular group of parasitic worms is far from complete, considering we only have documented less than 650 species.

3.1 The size of the fauna

Up to January 2011, at least 1,145 vertebrates had been studied for helminth parasites, and each of these vertebrates contained at least one helminth species, although, needles to say, most parasite surveys have been conducted only in a particular site, not covering other localities along the distribution range of the hosts; likewise, many of these studies do not report uninfected host species so the real number of analyzed hosts might be slightly higher. In addition, many vertebrate species analyzed have only once been recorded as hosts of helminth species, e.g., 52% in the case of tapeworms. In the 1,145 studied vertebrates, a total of 1,900 helminth species have been recorded, 603 of which were described as new species (referred to as holotypes). Helminths are represented by six major groups, including members of the Phylum Platyhelminthes: digeneans (634 species), aspidogastreans (5), monogeneans (331), and cestodes (271), Phylum Acanthocephala (87), Phylum Nematoda (538), and Phylum Annelida: hirudineans (34) (Fig. 2). Interestingly, a large number of species were described for the first time from some species of Mexican vertebrate. Figure 2 also shows the number of holotypes for each helminth group. It is noteworthy that the percentage of new species with respect to the total number of recorded species per helminth group varies between 14.7 (in hirudineans) and 46.2% in monogeneans. Even though two groups have received more attention in terms of the number of papers dealing with the alpha-taxonomy (digeneans and nematodes), there seems to be a correlation between the number of species recorded per helminth group and the overall diversity of each group, i.e., more species of digeneans and nematodes have been recorded, and these two as groups are the most diverse within helminths.

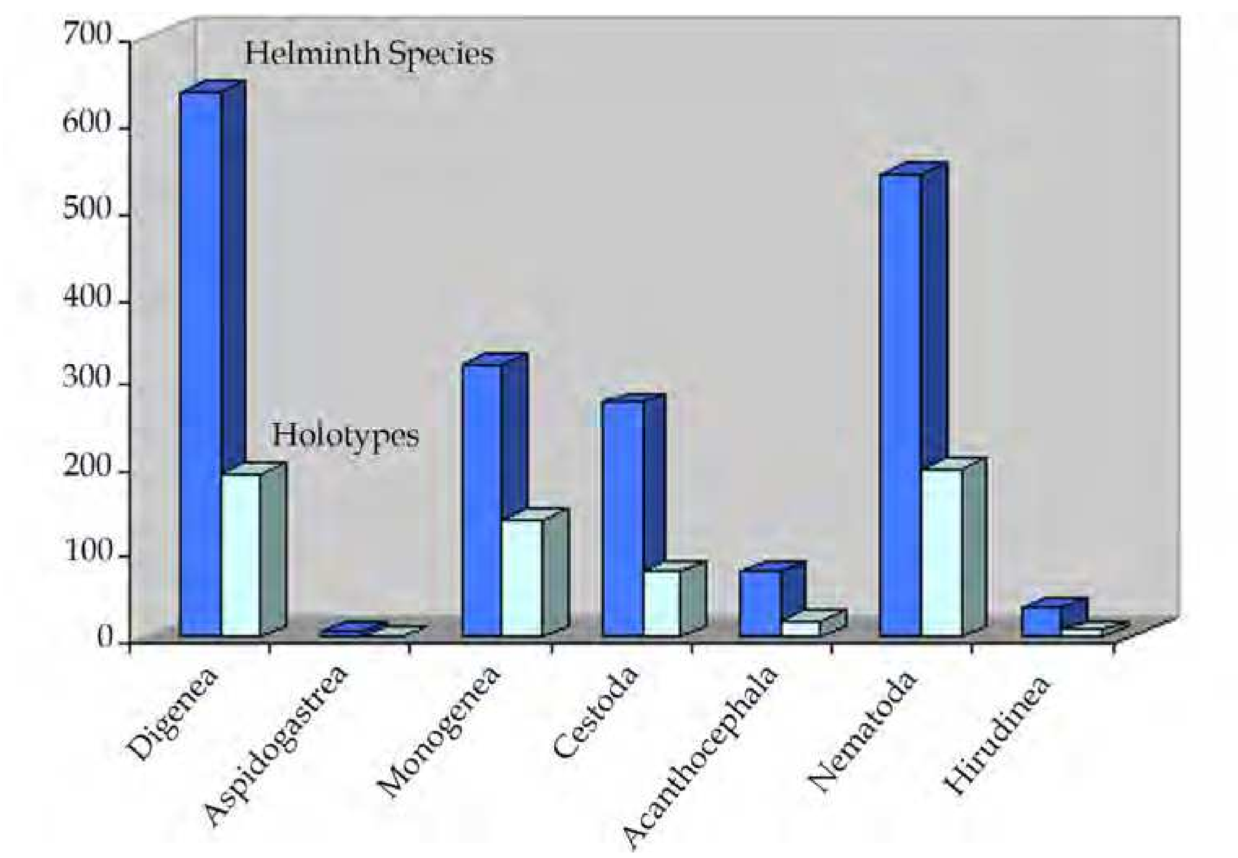

Fig. 2. Number of helminth species by parasitic group and the number of new species described for each helminth taxa.

The knowledge about the vertebrate helminth fauna in Mexico has been accumulated along eight decades, and various sampling strategies have been followed by parasitologists, both national and foreign. During the first six decades, parasitologists mainly focused their research to describe a parasite species from a particular host species and locality, a strategy that can be referred to as "parasite species approach" (see Pérez-Ponce de León & Choudhury, 2010). The last two decades, however, witnessed a shift of the focus of survey research programs from the traditional parasite species approach to a more comprehensive survey work attending a host group, a geographical area, or both. Surveys were designed to inventory, for example, the digeneans of freshwater fishes from the sinkholes of the Yucatan Peninsula (Scholz et al., 1995), or the helminth parasites of freshwater fishes of the Nazas River, in Northern Mexico (Pérez-Ponce de León et al., 2010). At the same time, checklists where the information about certain helminth group, or certain host group, were the main focus, were also published, and these papers contributed with the update and detailed revision of the taxonomic information. For instance, Paredes-León et al. (2008) published a checklist of the metazoan parasites of amphibians and reptiles of Mexico; meanwhile, Pérez-Ponce de León et al., (2007), and García-Prieto et al. (2010) published a checklist of the digeneans and acanthocephalans of wildlife vertebrates of Mexico, respectively. As a result, a great dealt of information has been synthesized and made available for further analysis, as the one we provide in this book chapter.

3.2 Vertebrate hosts

Among vertebrates, fish are clearly the most well-known host groups. When the number of helminth species is plotted against the vertebrate group it becomes evident that fish, in general, has received more attention from parasitologists than any other vertebrate. This reflects a genuine interest of the parasitologists for that particular group, with the commercial value implicit in discovering parasite species producing diseases in economically important fish, or because some parasites are transmitted to man by consuming uncooked or raw fish, but it also shows a dual situation; on the one hand, fish are more diverse among vertebrates and, on the other hand, they represent the most easy-to-handle and easy-to-obtain host group when compared with other more charismatic, and most probably, endangered and protected vertebrates. According to recent estimates, Mexican biodiversity includes about 5,488 described species of vertebrates of which 2,692 are fish, 361 are amphibians, 804 are reptiles, 1,096 are birds, and 535 are mammals (Sarukhán et al., 2009). Of these, up to the present, 1,145 vertebrates have been studied for helminth parasites, including 674 fish, 63 amphibians, 153 reptiles, 134 birds, and 121 mammals (Fig. 3).

Overall, about 21% of the wildlife vertebrate fauna of Mexico has been studied for helminths to some extent, with parasite loads that vary from 1 to 82 helminth species per analyzed host species; however, the percentage of the hosts studied for helminths is variable among vertebrate groups. For instance, 25% of the fish fauna (including marine, brackish and freshwater), 17.5% of amphibians, 19.0% of reptiles, 12.2% of birds, and 22.6% of mammals have been studied for helminths, and at least one species has been recorded (Table 1).

Of the total number of helminth species recorded in Mexican vertebrates, 1,064 are found parasitizing fish, followed by those found in mammals (332), birds (275), reptiles (242), and amphibians (156). This total count (2,069) does not correspond with the 1,900 species given above because some of them are recorded from two or more groups of vertebrates, corresponding with the larval stage, for example in fish, and the adult in birds. As a general rule, helminths tend to keep some fidelity for the host at a higher taxonomic level such as

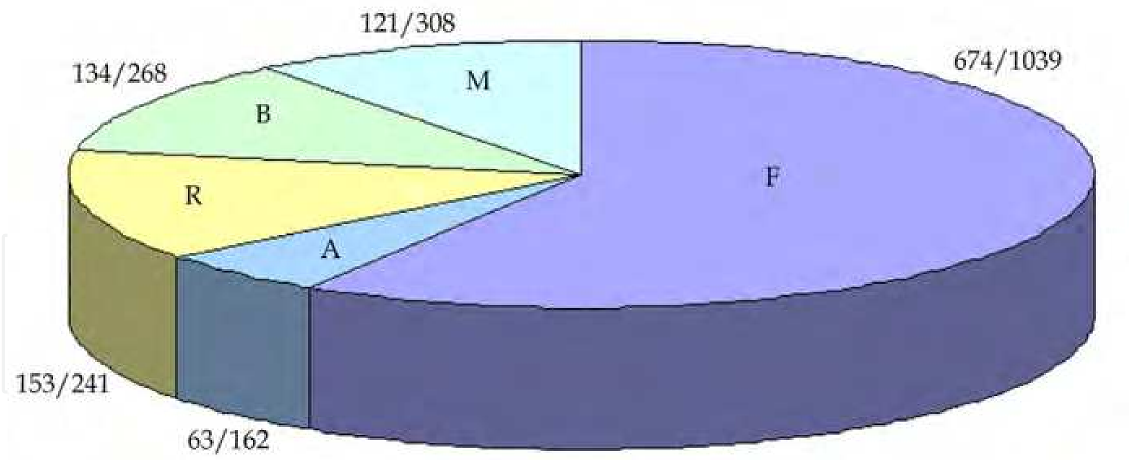

Fig. 3. Number of vertebrate species (per group) studied for helminths in Mexico, and number of helminth species reported. F = Fish, M = Mammals, B = Birds, R = Reptiles, A = Amphibians. Numbers outside the circle represent the number of studied species of hosts/ number of helminth species per group.

	Hosts			Helminths	
	Species in Mexico	Species Studied	%	No. of Species	$\bar{X}$
FISH	2692	674	25.0	1039	1.5
AMPHIBIANS	361	63	17.5	162	2.4
REPTILES	804	153	19.0	241	1.6
BIRDS	1096	134	12.2	268	2
MAMMALS	535	121	22.6	308	2.5

Table 1. Host species studied for helminths in Mexico, with respect to the total number of each vertebrate group. The number of helminth species is presented, with the mean number of species per vertabrate examined.

class or order, reflecting some sort of higher level host-specificity, i.e., parasites of mammals are usually not found in birds, and viceversa, or those found in chiropterans are not found in caviomorphs, and viceversa. Some helminth genera may contain species that infect certain host group, while other species infect a different host group. For example, rhabdiasid nematodes are typical lung parasites of amphibians and reptiles; the genus *Rhabdias* is a species-rich group and it has been demonstrated that their species are host-specific and rarely are parasites of more than one host group (Martínez-Salazar, 2006, 2008; Martínez-Salazar et al., 2009); some infect amphibians, and some infect reptiles. In most cases, the presence of a helminth species in an unusual host may be described as an accidental infection, if the worms do not reach maturity and are able to reproduce, meanwhile in some others, it is a result of an experimental infection as in the digenean *Echinostoma revolutum*, a relatively common bird digenean (duck and goose) that was intentionally used to demonstrate this parasite may infect humans (Larios, 1940). One exception to the rule might be the presence of the nematode *Spiroxys contorta* in amphibians (*Lithobates dunni, Ambystoma dumerilii*), as well as in reptiles (*Terrapene ornata*) (Lamothe-Argumedo et al., 1997).

	D	A	M	C	Ac	Ne	H	Total	Loc/States
Fish									
Cichlasoma urophthalmus	44	0	3	7	9	18	1	82	(79/7)
Petenia splendida	34	0	5	1	4	15	1	60	(42/7)
Rhamdia quelen	18	0	4	9	5	21	3	60	(61/6
Amphibians									
Rhinella marina	11	0	0	3	5	30	1	50	(39/9)
Lithobates vaillanti	15	0	0	0	3	16	0	34	(8/4)
Lithobates montezumae	22	0	0	3	0	7	0	32	(5/3)
Reptiles									
Sceloporus jarrovi	0	0	0	2	1	14	0	17	(17/16)
Kinosternon hirtipes	3	0	2	0	1	8	1	15	(16/8)
Tamnophis melanogaster	4	0	0	3	1	7	0	15	(6/3)
Birds									
Anas platyrhynchos	7	0	0	12	2	11	0	32	(8/4)
Ardea alba	18	0	0	3	2	6	0	29	(25/9)
Phalacrocorax brasilianus	12	0	0	5	1	7	0	25	(26/10)
Mammals									
Didelphis virginiana	6	0	0	2	4	16	0	28	(58/14)
*Equus caballus**	0	0	0	1	0	27	0	28	(2/1)
Philander opossum	7	0	0	1	2	6	0	16	(18/5)

Table 2. Species of vertebrates with the highest helminth species richness in Mexico. Only the top three species are listed. D = Digeneans, A = Aspidogastreans, M = Monogeneans, C = Cestodes, Ac = Acanthocephalans, N = Nematodes, H = Hirudineans, * = Wild horses.

Each host species is parasitized by a variable number of helminth species, even though this may depend upon sampling effort (considering the number of hosts analyzed and the number of localities along its distribution range). Table 2 lists the top three host species (per vertebrate group) with the highest helminth species richness. Among vertebrates, fishes (in this case three freshwater representatives) harbor a more diverse helminth fauna than any other group, however, as shown in Table 1, when data are presented as an average of the number of helminth species with respect to the number of analyzed hosts within each group, mammals and amphibians reach the highest species richness with 2.5 and 2.4, respectively. In absolute numbers, the Mayan cichlid, *Cichlasoma urophthalmus,* is the host species with the highest helminth species richness (82 species, with samples from 79 localities along seven states of the Mexican Republic) (Table 2). This fish is originally distributed in fresh and brackish waters of the Atlantic slope of Neotropical America, from the Coatzacoalcos River basin in the Gulf of Mexico southward to the Prinzapolka River, Nicaragua, including the sinkholes of the Yucatan Peninsula. Most of these 82 helminth species have been found in other species of cichlids occurring in Mexican freshwaters (about 50 species, see Miller et al., 2005), and some of these species have been found in other fish families inhabiting Mexican freshwaters. At the vertebrate group level, helminths maintain fidelity to infect a particular host group, i.e., fish parasites are only find in fish, and not in any other vertebrate, probably with the sole exception of the Asian tapeworm (*Bothriocephalus acheilognathi*), a species that was introduced to Mexico along with common carps (*Cyprinus carpio*) from China with aquacultural purposes, and that has been found parasitizing now not only introduced but also native fish species, and even some amphibians and reptiles (Rojas-Sánchez and García-Prieto, 2008), but this is just the result of the dispersal capability of this invasive species of tapeworm. However, among the whole helminth fauna, some species exhibit a narrow host-specificity to parasitize cichlids as a group (family), a pattern that has been described as the biogeographical core helminth fauna (see Pérez-Ponce de León & Choudhury, 2005). Compared to *Cichlasoma urophthalmus,* a host species studied for helminths in 79 localities along seven states of Mexico, where 82 helminth species have been recorded, the oppossum *Didelphis virginiana*, is parasitized by 28 species of helminths, even though this mammal has been studied in 58 localities throughout a larger distributional range in Mexico that includes 14 states of the Mexican Republic, while the toad *Rhinella marina*, is parasitized by 50 worm species along its distributional range in 39 localities from 9 states, where its helminth fauna has been recorded.

3.2.1 The freshwater fish helminth fauna as a case study

Undoubtly, freshwater fish helminth parasites are the most well-known group among vertebrate parasites in Mexico. The helminth fauna consisted (up to September 2009) of 258 species in total, including 37 adult and 43 larval (metacertcariae) species of digeneans, 62 monogeneans, 15 adult and 18 larval (metacestodes) cestodes, 6 adult and 4 larval (cysthacanth) acanthocephalans, and 54 adult and 15 larval (L3) nematodes. Actually, Luque and Poulin (2007) suggested that Mexico stands out as a hotspot of parasite diversity in freshwater fishes. Based on that premise, the extent of the freshwater fish helminth parasite inventory of Mexico was evaluated using cumulative species curves by Pérez-Ponce de León and Choudhury (2010). These authors hypothesized that the inventory, as conventionally understood, is nearing completion for most helminth groups, excepting for monogeneans, where the cumulative species curve shows no tendency to reach the asymptote, indicating that further sampling and detailed alpha-taxonomy work is needed and the slope of the curve indicates more species of monogeneans will be described (Fig. 4). Interestingly, even though only 50.6% of the freshwater fish fauna in the country had been surveyed for helminths in a 80-yr period, the hypothesis is supported by empirical data and by the fact that the more species-rich groups of the native Mexican freshwater fish fauna, i.e., Cyprinidae, Cichlidae, Poeciliidae, Goodeidae, Aterinopsidae, and Ictaluridae, which overall account for 77% of the ichthyofauna, have been sampled intensively. Survey work we are conducting in areas of northern Mexico where these fish families are common, confirm this fact. In addition, in terms of geographical distribution, most of the major river drainages of Mexico such as the Lerma-Santiago and Balsas on the Pacific slope, and the Grijalva-Usumacinta, Panuco, and Papaloapan, as well as the sinkholes characteristic of the entire Yucatan Peninsula in southeastern Mexico, have been sampled to some appreciable extent. This does not mean that we will not find more species if we keep collecting data. We probably will, but it just means a slowdown in the rate of discovery of not previously recorded species of helminths.

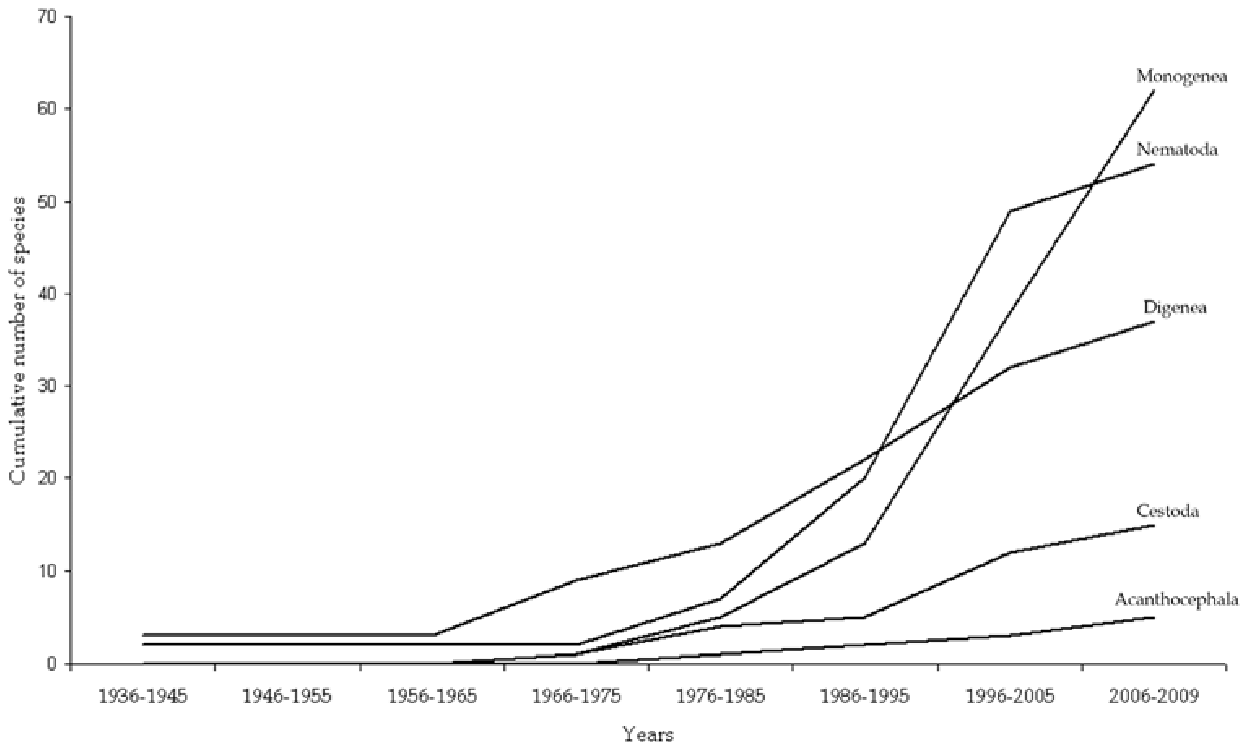

Fig. 4. Cumulative species curves for the helminth parasite fauna of freshwater fishes in Mexico. (Modified from Pérez-Ponce de León & Choudhury, 2010).

After analyzing their data, these authors contended that future survey work aimed at enhancing the biodiversity inventory of freshwater fish helminths in Mexico, should be strategic, and should combine the need to target missing components of the host spectrum with the choice of appropriate drainages based on biogeographic, faunistic, and hydrologic data. Additionally, Pérez-Ponce de León and Choudhury (2010) pointed out that the hypothesis that the inventory of this group of parasitic worms in freshwater fishes is nearing completion could be falsified if a closer look at the species delimitation criteria was made, by using molecular taxonomic methods instead of morphology-based approaches. Actually, they argue that this approach may indeed show that the helminth diversity has been seriously underestimated. At least three emblematic examples were recently published where the sequencing of various molecular markers allowed authors to demonstrate the presence of parasite cryptic species in what it was once thought to be only one species, including an acanthocephalan and a digenean infecting cichlids (Martínez-Aquino et al., 2009; Razo-Mendivil et al., 2010), and a digenean parasitizing ictalurid catfishes (Rosas-Valdez et al., 2011).

3.3 Geographic distribution

In terms of geographic distribution, sampling size is equally asymmetrical, considering the 32 states of the Mexican Republic. Figure 5 shows the number of helminth species that have been recorded in each of these 32 states, irrespective of the host group, the number of analyzed hosts, and the helminth group recorded. The states with the highest helminth species richness are Veracruz, in the Gulf of Mexico slope, with 377 species, and Jalisco, in the Pacific slope, with 285 (Fig. 5). Two states, the smallest, possess the poorer helminth fauna, Tlaxcala, with five species, followed by Aguascalientes, with 19, both in central

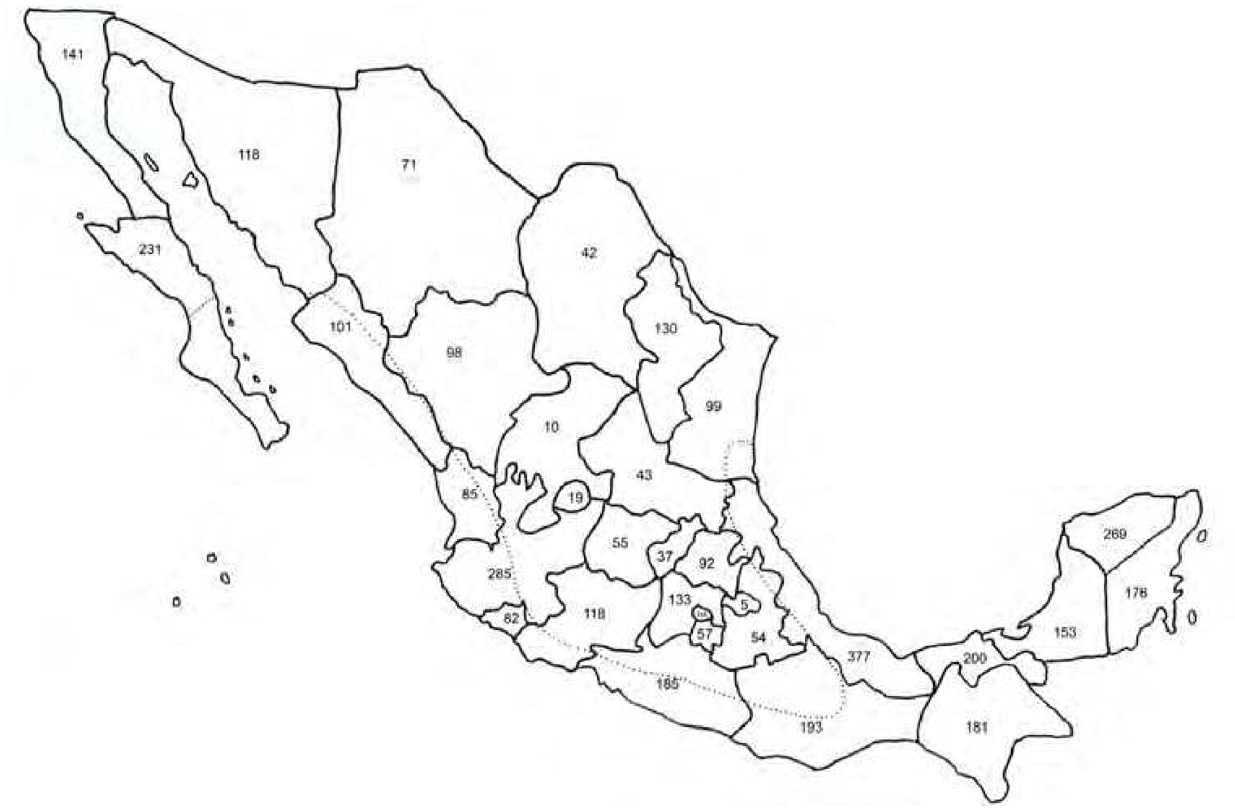

Fig. 5. Map of the Mexican Republic showing the number of helminth species in each of the 32 states. Dotted line represents the boundary between the Nearctic and the Neotropical biogeographical regions.

Mexico. There is no significant correlation between the size of the state and the number of helminth species reported, and clearly it also represents a biass of parasitologists to sample more intensively some localities within particular states. Veracruz and Jalisco states are the ones where the largest number of vertebrate hosts have been studied for helminths, 181 and 163, respectively (Table 3).

Figure 5 also shows a broad limit between the Nearctic and Neotropical biogeographic zones. If the two regions are considered, from a biogeographical point of view, helminth species richness is higher in the Neotropics than in the Nearctic region. The helminth species richness in vertebrates in the Neotropical part of Mexico doubles the species number in vertebrates in the Nearctic. This corresponds with general diversity patterns along a latitudinal gradient, however, due to sampling limitations, our results have to be taken with caution. As previously mentioned, this might be the result of a sampling artifact because the number of papers related with the helminth fauna of vertebrates ocurring in the neotropical part of Mexico are more than those in the Nearctic; additionally, a wider variety and number of vertebrate hosts have been studied in the entire region. In terms of helminth species composition, central Mexico represents a transitional biogeographic zone because a mixture of Nearctic and Neotropical elements are found, albeit a characteristic host association is made between the vertebrates whose origin is in the Nearctic or the Neotropics, and the helminth species that are found in them, i.e., the pattern of host fidelity is maintained. This might be established as a general pattern, and empirical data on helminth parasites of two vertebrate groups, freshwater fishes and amphibians, corroborate that observation (Pérez-Ponce de León et al., 2000; Pérez-Ponce de León & Choudhury, 2005). In these two groups of vertebrates, it was shown that the helminth fauna possess a Nearctic or Neotropical connection, closely linked with the biogeographical origin of their corresponding hosts. For instance, helminth parasites of ictalurid, catostomid, and centrarchid freshwater fishes (typical components of the Nearctic region), harbor characteristic species of helminths that are also found in the same hosts along its distributional range extending from Canada downwards to its most southern distribution limit in central Mexico. In the case of amphibians, the same pattern is repeated and parasite biogeographic affinities coincide with host affinities, showing some degree of evolutionary association. For example, the mexican species of leopard frogs examined for parasites (*Lithobates berlandieri*, *L. brownorum*, *L. dunni*, *L. forreri*, *L. megapoda, L. magnaocularis*, *L. montezumae*, *L. neovolcanica*, and *L. spectabilis*), show a parasite fauna with 50% of the adult species (26 out of 52) having Nearctic affinities, following the origins of the host group (Hillis & Wilcox, 2005); while a minority of the parasite fauna of this group of frogs (19 %) has Neotropical affinities, particularly those found in the transitional areas (Paredes-León et al., 2008).

	Helminth Species								Analyzed Hosts
State	D	A	M	C	Ac	N	H	Total	Total
Aguascalientes	6	0	0	9	2	2	0	19	3
Baja California Norte	52	0	26	39	2	21	1	141	106
Baja California Sur	95	0	44	50	11	30	1	231	145
Campeche	53	0	44	10	10	35	1	153	60
Chiapas	35	0	7	15	5	116	3	181	115
Chihuahua	10	0	0	26	4	31	0	71	25
Coahuila	10	0	6	5	2	16	3	42	20
Colima	36	0	10	7	6	23	0	82	61
Distrito Federal	33	0	5	19	2	58	1	118	63
Durango	27	0	17	23	8	23	0	98	44
Guanajuato	13	0	10	13	1	17	1	55	26
Guerrero	58	0	33	16	9	68	1	185	91
Hidalgo	14	0	7	16	2	53	0	92	58
Jalisco	125	1	56	26	13	61	3	285	163
México	63	0	5	19	2	43	1	133	64
Michoacán	36	0	4	20	5	51	2	118	83
Morelia	10	0	7	5	3	31	1	57	38
Nayarit	28	1	20	6	6	24	0	85	71
Nuevo León	45	0	10	18	4	50	3	130	52
Oaxaca	73	0	28	23	6	62	1	193	143
Puebla	12	0	1	6	3	30	2	54	39
Querétaro	5	0	2	2	1	27	0	37	22
Quintana Roo	79	2	32	7	9	47	0	176	79
San Luis Potosi	12	0	2	4	1	24	0	43	24
Sinaloa	42	0	31	0	9	19	0	101	72
Sonora	27	0	26	22	3	40	0	118	78
Tabasco	105	1	36	13	11	32	2	200	106
Tamaulipas	32	1	21	10	6	25	4	99	47
Tlaxcala	1	0	0	2	0	2	0	5	7
Veracruz	127	3	68	35	29	114	1	377	181
Yucatán	106	2	37	26	12	83	3	269	92
Zacatecas	2	0	1	3	0	4	0	10	5

Table 3. Helminth species richness of wildlife vertebrates in each of the 32 states of the Mexican Republic. D = Digeneans, A = Aspidogastreans, M = Monogeneans, C = Cestodes, Ac = Acanthocephalans, N = Nematodes, H = Hirudineans.

3.3.1 The state of Veracruz as a case study

To illustrate the effect of sampling size, we analyzed separately the vertebrate helminth fauna of the most species-rich state in the Mexican Republic (Veracruz) in terms of the distribution of the helminth fauna. In Veracruz state, 377 helminth species have been recorded, most of them, as parasites of fishes, with 203 (53.8%). Table 3 shows the number of helminth species per helminth group and clearly, more digeneans and nematodes have been recorded in Veracruz than any other parasitic helminths, albeit this trend is also true for the other states. Interestingly, even though Veracruz is the state with the largest number of papers published, including isolated reports as well as parasite surveys, not the entire state, and of course not all the vertebrate fauna, has been equally sampled. Figure 6 shows how the distribution of the known helminth fauna is concentrated to particular areas within the state, where at least 46 helminth species have been recorded in a region of the north (in the Tamiahua lagoon and surrounding areas), and 152 and 224 species have been recorded from central Veracruz, in the regions of Alvarado lagoon, and Los Tuxtlas tropical rain forest, respectively. More species of helminths have been recorded from Los Tuxtlas, than any other region within the state of Veracruz, and that include helminth parasites of fishes (105), amphibians (54), reptiles (15), birds (13) and mammals (37). Wide areas along the state have not been sampled for vertebrates and their helminth parasites yet (Fig. 6).

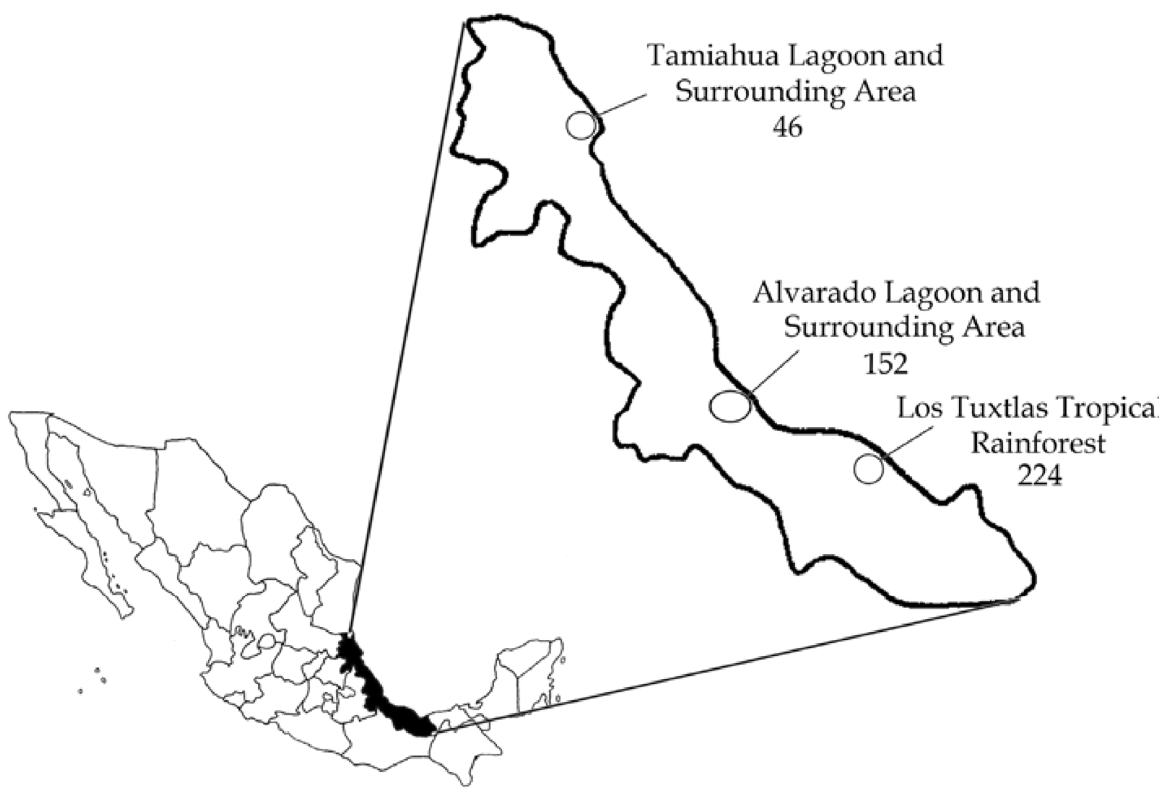

Fig. 6. Distribution of the vertebrate helminth parasite fauna in Veracruz, the state with the highest helminth species richness recorded thus far in Mexico.

4. Helminth parasite survey work: The future

After the recognition that good alpha taxonomy is central to biology, the last decade has witnessed a renaissance of the taxonomic practice. Taxonomists have recognized the importance of using multiple data sources to establish more robust criteria for species delimitation, and to produce inventories supported by well-defined and novel protocols designed to explore and understand biodiversity. Certainly, good alpha taxonomy is crucial to overcome the biodiversity crisis, both for assisting conservation programs and documenting diversity before it is lost (Schlick-Steiner et al., 2010). Authors such as Padial et al. (2010) recognized that taxonomy as a discipline is confronted with the challenge to fully incorporate new theory, methods and data from disciplines that study the origin, limits and evolution of species. The latter authors concluded that taxonomy needs to be pluralistic to improve species discovery and description, and to develop novel protocols to produce the much-needed inventory of life in a reasonable time. Two terms have been used more frequently in the taxonomic literature, *New Taxonomy*, and *Integrative Taxonomy*, for the framework that should be used by taxonomists nowadays to bring together all the conceptual and methodological developments within the discipline (Wheeler, 2008; Padial et al., 2010). Some of these developments include virtual access to museum specimens, DNA sequencing, computer tomography, geographical information systems, multiple functions of the internet, and also that fact that taxonomic information is increasingly digitized and made available through several global initiatives (see Padial et al., 2010 and references therein).

In Parasitology, it has been recently recognized the need to follow an integrative taxonomy approach in order to obtain a more accurate description and understanding of parasite diversity, following modern taxonomic procedures that incorporate, for instance the use of molecular markers (Nadler and Pérez-Ponce de León, 2011). According to these authors, molecular tools offer an unprecedented opportunity to include new components in our discovery and description of parasite biodiversity, for example, characterization of genetic variability, population genetic structure, genetic differentiation and phylogenetic relationships. The molecular assessment of parasite biodiversity, including testing for cryptic species, is a largely unexplored opportunity for parasitologists. Deciding what species are and how to find them in nature (species delimitation) are prerequisite to characterizing this biodiversity (Adams, 1998; Nadler, 2002). For parasitic organisms, particularly those infecting humans, correct identification is crucial to understanding epidemiology, designing control programs, effective drug treatment and prophylaxis and investigating the potential for gene flow of drug resistance genes among populations (Nadler and Pérez-Ponce de León, 2011). One of the results of using an integrative taxonomy approach in parasite taxonomy is the recognition of cryptic species (those morphologically similar but genetically distinct). Recognizing cryptic parasite species from all kinds of hosts will permit a more accurate understanding of parasite biodiversity, systematics, epidemiology, evolutionary biology and biogeography. In this context, molecular data can independently corroborate that species recognized by morphological criteria are separate genetic lineages or conversely, uncover evidence that individuals appearing to be morphologically indistinguishable belong to independent evolutionary lineages. Species complexes of parasites are being revealed by molecular data where it was once thought there was either a single phenotypically variable species or a single morphologically uniform species (see Pérez-Ponce de León and Nadler, 2010 and references therein).

Characters, other than molecular markers, will be equally important in our description of helminth faunal diversity. In recent years, microscopy tools have been used to describe some traits that cannot be identified by conventional (light) microscopy. Some techniques have been of great value in helminth taxonomy such as the scanning electron microscopy (SEM) and confocal microscopy (CM). Halton (2004) argued that parasite surfaces have understandably demanded most of the attention of microscopists, largely as a result of the pioneering studies using transmission electron microscopy. Among all techniques, SEM has become increasingly useful in describing the surface topography of helminth parasites (Fig. 7), and that is the reason we contend that future taxonomic work intended to describe helminth parasite biodiversity, should incorporate the description of body surface traits by means of SEM. Empirical studies have demonstrated the usefulness of this microscopy technique in discovering taxonomically important traits in helminths, such as sensory receptors (papillae number, shape, size and position along body surface in digeneans) (Mata-López and León-Règagnon, 2006), or the size and shape of cuticular spines in nematodes (Bertoni-Ruiz et al., 2005).

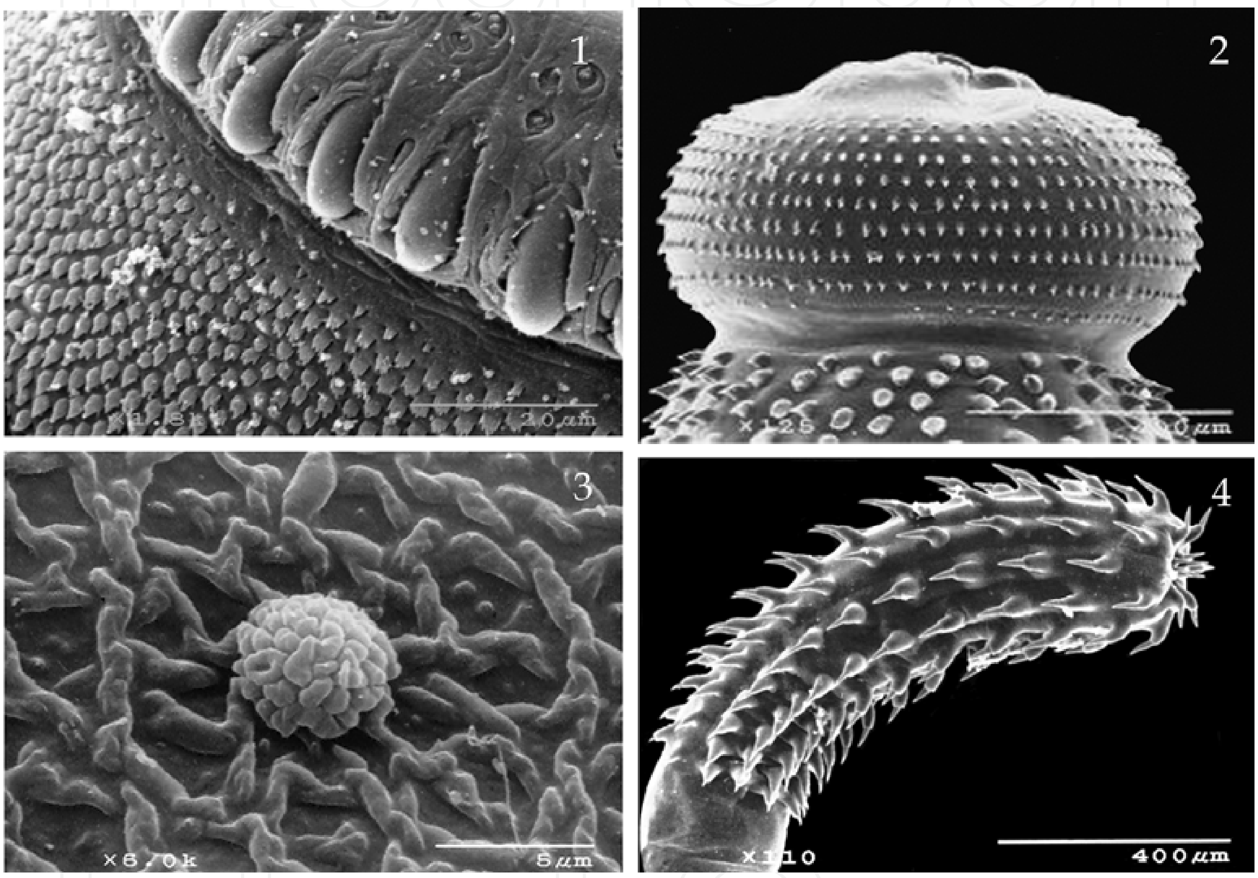

Fig. 7. SEM microphotographs of representative helminths, showing taxonomically important characters. 1 *Echinostoma* sp. (Digenea, anteriror end), 2 *Gnathostoma turgidum* (Nematoda, cephalic bulb) 3 *Phyllodistomum centropomi* (Digenea, papillae), 4 *Atactorhynchus duranguensis* (Acanthocephala, proboscis).

5. Conclusion

The main question that raises after presenting the analysis of the data we have gathered after studying helminth parasites of wildlife vertebrates in Mexico over a 80 yr period is: how far are we of completing the inventory? The short answer would be: far away of completing such inventory, considering that we have studied about 21% of the vertebrate fauna occurring within the Mexican territory. All biodiversity surveys are based on the premise that the harder you look, the most species you will find, i.e., if you spend more time searching, if you increase the size and the number of localities, and the number of collecting

trips, it is likely that you will find more species. The same argument is true for parasitic organisms but in this case we have to add the fact that the larger number of host you study, the larger number of helminth species you will find. Assuming the same rate of species discovery after studying one fifth of vertebrate hosts occurring in Mexico, this would mean that we will require at least another 320 years to complete the inventory. This kind of striking calculations parallels that made by Cribb (1998); this author estimated that to find just all trematode species in Australian vertebrates, about 160,000 hosts need to be killed and examined, taking up 30,000 days of work, not considering the time required to accomplish the species identification and description. In the case of the Mexican vertebrate helminth fauna, 1,900 helminth species have been recorded from 1,145 analyzed vertebrate hosts. Based on this data, the average number of helminths per vertebrate in Mexico is 1.66. At the same rate of species discovery, if all the vertebrates in Mexico are analyzed (5,488 species) the estimated number of helminth species to be recorded overpass 9,000, if the inventory could be completed in the next 320 years.
The result of all these species richness estimations, beyond a pesimistic view, is that survey work intended to describe biodiversity in not very well-known groups of organisms (such as helminths), lacks of a conceptual value. Part of the problem is that these calculations do not take into account some attributes of species distribution, and actually, are based on premises that are almost impossible to demonstrate. For example, we cannot assume that we will find different helminth species in each one of the vertebrate hosts we have not looked at, i.e., the assumption that the species discovery rate will be at the same pace, as more vertebrates are studied for helminths, is just wrong. The case of the aforementioned freshwater fish helminth parasite fauna illustrates this contention. No matter about 51% of the fish fauna in the freshwaters of country has been studied for helminths, we concluded that the inventory is nearing completion. Unfortunately, for the entire helminth fauna of Mexican vertebrates, based on inequality of sampling effort in terms of both, hosts, and geographic regions, cumulative species curves cannot be used. These curves, along with the use of non-parametric species richness estimators represent the best methodological approaches to estimate the number of species that would be described (Poulin and Morand, 2004). Values obtained thorough these methods allow for an strategic planning to keep working in biodiversity surveys aimed to complete the inventory of certain taxonomic group. In the case of the Mexican helminth fauna, it is unrealistic to try to complete the inventory in the near future, because clearly, a lot of work needs to be done, and some additional aspects need to be considered. One of the most important is the so-called taxonomic impediment. In recent years, the number of properly trained taxonomists has decreased dramatically, and this is not the exception for helminthology as a discipline. If the inventory work is going to be maintained, we have to be aware that more generations of well-trained taxonomists need to be produced. In addition, these new generations need to be able to use modern taxonomic methods, in addition to the expertise on the morphology of each group, and this implies the use of various molecular techniques to establish more robust species delimitation criteria, added to an appropriate knowledge of evolutionary and biogeographical methods, intended to complement molecules and morphology, to achieve a better understanding of the diversity of the helminth parasite fauna.
A second question that raises from the current analysis is: Why should be try to complete the inventory of the helminth parasite fauna of wildlife vertebrates in Mexico?. There are many reasons for such a task. Some of them are referred in the introductory section of this book chapter, but probably the most important is because parasites, in general, represent a

substantial portion of global biodiversity since at least 50% of the species living on earth are parasites of some form, considering all viruses and some bacteria, and the eukaryotic species most commonly associated with parasitology, including agents of diseases affecting not only humans, but also livestock, crops, and wildlife (Brooks & Hoberg, 2006). A second reason derives from the fact that some species of helminths that are commonly found in the wildlife, maybe become disease agents in human beings. The more we know about the diversity of this parasite fauna in the wildlife, the more we will understand about their life-cycles and the potential that some species may have in the context of emergent infectious diseases. Recently, while discussing the structure of helminth parasite faunas with respect to the invasive process in nature, Hoberg (2010) concluded that faunal baselines derived from arrays of biological specimens, integrated surveys and informatics are a permanent record of the biosphere when archived in museum collections. This author also mentioned that if we do not have comprehensive taxonomic inventories of parasites, our ability to recognize the introduction of non-indigenous parasites, and to document patterns of expansion for local faunas under a regime of environmental perturbation, would be limited.

In this book chapter we presented an overview of the general data on this parasitic group, we analyzed the information we have gathered thus far, and we presented an estimate of the number of helminth species that remain to be found if the inventory is completed. As a result, we propose here some sampling strategies in order to optimize time and resources and to contribute with valuable information on the diversity of this group of organisms. First, we contend that the inventory needs to be completed by approaching particular vertebrate groups. As for the freshwater fish parasite fauna, an approximation has to be taken with respect to other vertebrate groups. For instance, vertebrate groups have to be targeted by researchers and a sampling strategy needs to be established. After fish, mammals represent the vertebrates with a higher percentage of species studied for helminths. It is impossible to postulate that all the mammals occurring in Mexico would be studied for helminths, considering the entire distribution range for each species. Particular groups, such as caviomorph rodents, or chiropterans, or marsupials, need to be evaluated based on their diversity and geographical distribution, and then estimate the number of helminth species that would be found, based on proper sampling effort and an accurate description of the data that should include surveys that fail to find helminth parasites from a sample of hosts in a particular locality, i.e., even reporting uninfected hosts.

With no doubt, there remains much to be done and overall, the end is not yet in sight. However, a large amount of information has been produced and this analysis allow us to establish a strategic plan to address the inventory of the helminth parasite fauna of wildlife vertebrates in Mexico in the upcoming years, and more importantly, to recognize that such inventory work needs to be done under novel taxonomic procedures that guarantee the quality of the information. The inventory is not complete yet, but it is our responsability to set the better way to accomplish the task, and leave for future generations of parasitologists the task of advance in the accumulation of data with the hope that the diversity of the helminth fauna in Mexican vertebrates will be better understood, and that the generated data will be useful for other members of the scientific community.

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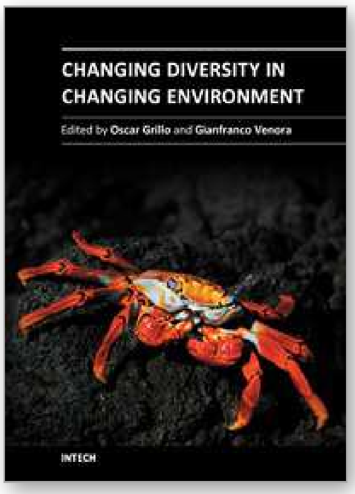

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As everybody knows, the dynamic interactions between biotic and abiotic factors, as well as the anthropic ones, considerably affect global climate changes and consequently biology, ecology and distribution of life forms of our planet. These important natural events affect all ecosystems, causing important changes on biodiversity. Systematic and phylogenetic studies, biogeographic distribution analysis and evaluations of diversity richness are focal topics of this book written by international experts, some even considering economical effects and future perspectives on the managing and conservation plans.

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