

Parsimony Analysis of Endemicity (PAE) of Mexican hydrological basins based on helminth parasites of freshwater fishes

Rogelio Aguilar-Aguilar^{1*}, Raúl Contreras-Medina² and Guillermo Salgado-Maldonado¹

¹Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, México and ²Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México

Abstract

Aim The distributional patterns of helminthological fauna of freshwater fishes were analysed to postulate a general hypothesis on the relationships of some Mexican hydrological systems.

Location Eight hydrological systems of central and eastern Mexico were studied and compared with records from Nicaragua.

Methods A Parsimony Analysis of Endemicity (PAE) was applied to the presence/absence of ninety-two helminth parasite taxa (Monogeneans, Digeneans, Cestodes, Acanthocephalans and Nematodes) of freshwater fishes, from eight Mexican hydrological systems, using the Hennig86 program.

Results The results represent the first attempt for a biogeographical analysis through application of the PAE method to the distributional patterns of helminth parasites of freshwater fishes in Mexico. A single most parsimonious cladogram was obtained, which grouped all the Neotropical systems in accordance with previous proposals based on other plant and animal taxa.

Main conclusions The most basal systems were Santiago and Lerma basins, which exhibited Nearctic affinities. The remaining areas of the cladogram showed Neotropical affinities. All the southeastern systems were grouped in a clade with the Nicaragua system, providing support for a 'Mesoamerican province' based on helminth parasites of cichlids. The cladogram also suggests that the treatment of the Lerma-Santiago basin as a single biogeographical unit is inaccurate and that they should be treated as separate systems.

Keywords

Biogeography, helminth parasites, freshwater fishes, hydrological basins, Mexico, parsimony.

INTRODUCTION

Recent research on the helminth parasites of freshwater fishes in the hydrological basins of Mexico has greatly increased the knowledge of the helminth fauna of these areas. In an effort to propose a general hypothesis on the

relationships between several Mexican hydrological basins, data set contained in these studies was used to create a data base for use in a Parsimony Analysis of Endemicity (PAE).

At least 375 freshwater fish species occur in Mexico, and this increases to over 500 species when those living in estuaries and coastal lagoons are included (Miller, 1982; Espinosa-Pérez *et al.*, 1998). Physical, climatic and ecological barriers of Mexico have affected the geographical distribution of its fish fauna (Álvarez & Lachica, 1974). Mexico also holds a unique place in the biogeography of the Americas because it straddles the transition between

*Correspondence: Rogelio Aguilar-Aguilar, Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, C.P. 04510, D.F., México.
E-mail: raguilar@mail.ibiologia.unam.mx

the Nearctic and Neotropical biogeographical regions. The Nearctic region includes almost all of North America, including the Mexican Highlands province, and its southern boundary lies along the Mexican Transvolcanic Belt (Halffter, 1976). The Neotropical region includes southern Mexico, Central and South America. Some authors place its northern limit in the Papaloapan basin, in the coastal plains of the state of Veracruz (Vidal-Martínez & Kennedy, 2000). Each region can be divided into subregions or provinces based on the congruence of the distribution patterns of the taxa inhabiting them (Morrone *et al.*, 1999). Using distributional data of different taxa, mainly vascular plants, arthropods and vertebrates, a revised regionalization of the Nearctic and Neotropic provinces in Mexico has been proposed (Morrone *et al.*, 1999; Morrone, 2001).

Of the wild animals used in biogeographical studies, helminth parasites have scarcely been used. The work by Vidal-Martínez & Kennedy (2000) on the helminth fauna of cichlid fishes is the unique previous study addressing some areas of Mexico. Based on helminth data, these authors claim a close similarity between Central America and southern Mexico, suggesting this area be regarded as a 'Mesoamerican province' of the Neotropics.

Recent surveys of the helminth parasites of freshwater fishes in several Mexican hydrological basins (Salgado-Maldonado *et al.*, 2001a,b, 2003a,b,c), indicate that the composition of helminth communities in different host species includes species with wide geographical distributions, and other species with more restricted distributions. This is especially the case in the Mexican Highland Plateau, where the Lerma-Santiago river basin is considered a centre of endemism (Salgado-Maldonado *et al.*, 2001b). Also, there are helminth species that exhibit a close ecological association to certain freshwater fish families throughout their distributional range, such as tropical cichlid and characid fishes (Salgado-Maldonado *et al.*, 2003a). This host specificity is determinant in helminth community composition in some tropical fishes, and can explain the distributional patterns of some helminth species.

Given these characteristics, the helminth parasites of freshwater fishes in Mexican hydrological basins offer an excellent opportunity to study distributional patterns, and to compare these patterns with those previously identified for other biological groups. However, the lack of cladistic analyses of the helminthological fauna of freshwater fishes, prevents any formal cladistic biogeographical analysis using comparison of taxon–area cladograms.

Although PAE is not considered an historical method (Humphries & Parenti, 1999), some authors (e.g. Morrone, 1994; Luna *et al.*, 1999; Morrone *et al.*, 1999; Cavieres *et al.*, 2002) propose its use for forwarding a preliminary hypothesis of relationships between analysed areas. This hypothesis can then be tested under a formal cladistic biogeographical protocol. Currently, this method has been applied to vascular plants, insects and vertebrates in different regions of the world, principally in Latin America (e.g. Luna *et al.*, 1999; Morrone *et al.*, 1999; Cavieres *et al.*, 2002). The objective of the present study is to propose a

general hypothesis on the relationships of Mexican hydrological systems, using a PAE based on the distributional patterns of their helminth parasites of freshwater fishes. The resulting relationships can then be used to test the concordance of these distributions with previously proposed biogeographical generalizations.

MATERIALS AND METHODS

Using published faunal surveys (Kritsky *et al.*, 1994; Moravec *et al.*, 1995, 2002a,b,c; Scholz *et al.*, 1995a,b, 1996, 2001; Moravec, 1998; Caspeta-Mandujano *et al.*, 1999, 2000, 2002; Mendoza-Franco *et al.*, 1999; Caspeta-Mandujano & Moravec, 2000; Choudhury & Pérez, 2001; Mendoza-Franco & Vidal-Martínez, 2001; Pérez, 2001; Salgado-Maldonado *et al.*, 2001a,b, 2004a,b,c; Scholz & Salgado-Maldonado, 2001; Moravec & Salgado-Maldonado, 2002, 2003; Aguilar-Aguilar *et al.*, 2003), a data matrix of the presence/absence was assembled containing data for ninety-two helminth parasites taxa (including monogeneans, digeneans, cestodes, acanthocephalans and nematodes) in freshwater fishes from Mexican hydrological basins and bodies of water in the state of Tabasco and the Yucatán Peninsula. We recognize that the bodies of water sampled in Tabasco (Salgado-Maldonado *et al.*, 2003c) do not conform a single basin, but rather correspond to the lower reaches of several large main drainages, mainly the Grijalva and Usumacinta river systems. Also, despite the lack of surface watercourses on the Yucatán Peninsula, and that the sinkholes and other water sources do not form a single drainage basin, they were grouped as a single basin in this analysis for the sake of clarity and data manageability. Additional data from authors' research recorded for helminths from the Papaloapan river basin were also included in the data base. All surveys used to build the data base were taxonomically validated to detect and updating synonyms.

The units of analysis were eight Mexican river basins (Fig. 1). For comparative purposes, helminthological records from Nicaragua (middle Central America) (Watson, 1976; Vidal-Martínez & Kennedy, 2000; Aguirre-Macedo *et al.*, 2001a,b; Vidal-Martínez *et al.*, 2001b) were also included in the analysis. Study units were delimited based on the Mexican hydrological basins map produced by the Comisión Nacional para el Conocimiento y uso de la Biodiversidad (CONABIO) (see de Alba & Reyes, 1998). To test the naturalness of Lerma-Santiago river basin as a single biogeographical unit, we treated the two drainages as two separate basins in this study. This was done because some studies about the fish or helminth fauna of fishes (Miller, 1986; Salgado-Maldonado *et al.*, 2001b), treated the Lerma-Santiago river basin as a unit, while other studies were carried out only in one of these basins (Díaz-Pardo *et al.*, 1993; Soto-Galera *et al.*, 1998).

The PAE, originally proposed by Rosen (1988), groups areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram. PAE data consist of an area-by-taxa matrices and the resulting cladograms represent nested sets of areas

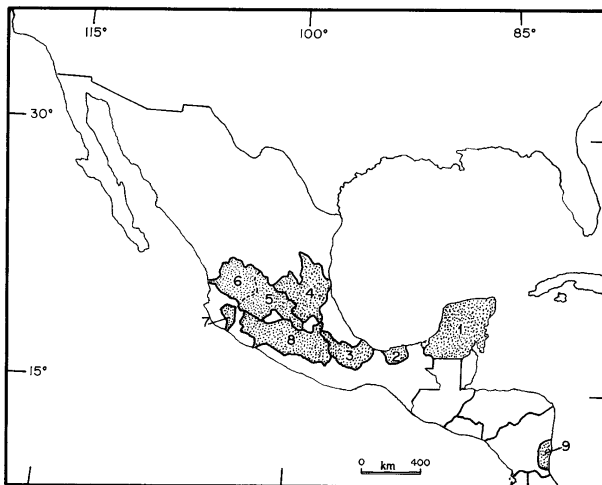


Figure 1 Mexican hydrological systems considered in the analysis. The areas displayed belong to the main basin. Main river inside each area are not shown. 1 = Yucatán hydrological system, 2 = Tabasco hydrological system, 3 = Papaloapan river basin, 4 = Pánuco river basin, 5 = Lerma river basin, 6 = Santiago river basin, 7 = Ayuquila river basin, 8 = Balsas river basin, 9 = Nicaragua hydrological system.

(Morrone, 1994; Morrone & Crisci, 1995). The matrix for this study was prepared by coding taxa for the absence (0) or presence (1) in each area (Appendix 1). Taxa found in a single area (equivalent to autapomorphies) are not useful in assessing biogeographical relationships, and so were excluded from the matrix. *Posthodiplostomum minimum* (MacCallum, 1921) and *Contracaecum* sp. were also excluded from the analysis, because they were shared by all analysed hydrological basins.

Biogeographical analysis was carried out with the Hennig86 program (Farris, 1989) applying the ie* option, which calculates all possible most parsimonious trees. The cladogram was rooted using a hypothetical area coded with all zeros.

RESULTS

The PAE yielded a single most parsimonious area cladogram, with 153 steps, consistency index of 0.60, and retention index of 0.64 (Fig. 2; species diagnosing the nodes in the cladogram are detailed in Tables 1 and 2). Seven nested monophyletic groups were distinguished within the cladogram. The most basal areas, indicating Nearctic affinities, were occupied by the Lerma and Santiago river basins. The remaining areas showed Neotropical affinities. The Neotropical clade includes Ayuquila, Balsas, Pánuco, Papaloapan, Tabasco, Yucatán, and Nicaragua hydrological basins. The Tabasco, Yucatán, Papaloapan and Nicaragua basins formed a clade. There were a total of 120 helminth taxa restricted to a single analysed hydrological basins, which represent autapomorphies (see Appendix 2), and that were thus excluded from the matrix.

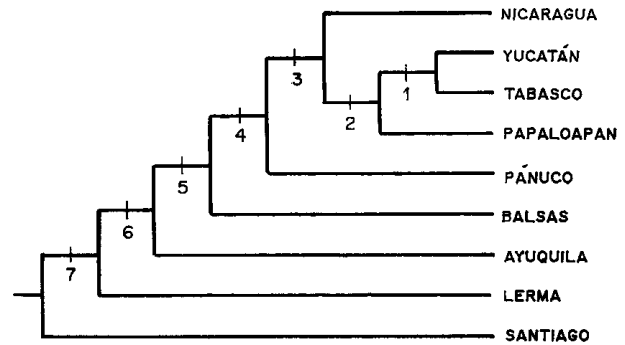


Figure 2 Area cladogram obtained by Parsimony Analysis of Endemicity. Species diagnostic for each node are given in Table 1.

DISCUSSION

The most parsimonious tree obtained represents a hypothesis of relationships between different hydrological basins in Mexico. In the cladogram, resultant clades group areas involving different biogeographical provinces and regions.

Relationships on the area cladogram are based on a data base from all available published records. At present there is a reasonable data set for helminth parasites of cichlids in southeastern Mexico (Salgado-Maldonado *et al.*, 1997; Vidal-Martínez & Kennedy, 2000; Vidal-Martínez *et al.*, 2001a); however, the data base for the helminths of other freshwater fishes is incomplete because each hydrological system has only been partially explored. Consequently, no information exists on the occurrence of helminth parasites in a large number of fish species, meaning that these results can be modified or supported by new data in the future; also, there may be a considerable number of helminth species not detected in one area because sampling effort was not sufficient, then some of the zero values in the presence/absence matrix may not be true absences. Despite these limitations, to date the data base used in this study is the most complete reference of helminthological records in each Mexican hydrological basin.

Anthropogenic movement of fish species has led to the introduction of exotic helminth species including *Actinocleidus fergusonii*, *Bothriocephalus acheilognathi*, *Centrocestrus formosanus* and *Pseudocapillaria tomentosa* among others (see Scholz & Salgado-Maldonado, 2000; Moravec *et al.*, 2001; Aguilar-Aguilar *et al.*, 2003; Salgado-Maldonado & Pineda-López, 2003), into the hydrological basins included in the data base. None of the clades were supported by these introduced species, and thus it was concluded that these helminths have no influence on the relationships proposed in the cladogram.

The Lerma and Santiago river systems located in the Mexican Plateau biogeographical province, have traditionally been treated as a single hydrological system, namely the Lerma-Santiago basin (see Miller, 1986; de Alba & Reyes, 1998). This proposal has been used in some helminthological studies carried out in this area (Salgado-Maldonado *et al.*,

Table 1 Data matrix of helminth taxa. Consecutive numbers refer to Appendix 1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Root	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaragua	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1
Yucatán	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	1
Tabasco	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	1
Santiago	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Pánuco	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	1	0
Balsas	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	1	1	1
Ayuquila	1	0	1	0	0	0	1	1	1	1	0	0	0	1	1	0	1	0	0	0	1	1	0
Lerma	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0
Papaloapan	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	1	1	1	0	1	1	1
Root	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Nicaragua	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Yucatán	1	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	1	1
Tabasco	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	1
Santiago	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pánuco	1	1	0	1	1	1	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	1	0
Balsas	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ayuquila	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Lerma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Papaloapan	1	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	1	1	0
Root	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Nicaragua	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yucatán	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0
Tabasco	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Santiago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pánuco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Balsas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ayuquila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lerma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Papaloapan	1	0	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	1	1	1
Root	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
Nicaragua	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Yucatán	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
Tabasco	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
Santiago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pánuco	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Balsas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ayuquila	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lerma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Papaloapan	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1	0

2001b). The present analysis results contrast with this hypothesis, because both Lerma and Santiago river basins are located in different positions in the cladogram, suggesting that their faunas actually represent different assemblages. Different fish species composition records from these two basins support this separation. However, the Lerma basin has been more extensively studied for its helminths than the Santiago basin, which could produce significant bias in these results.

The helminthological fauna of Lerma and Santiago basins, apparently exhibit greater affinities with the Nearctic region, as about 90% of the taxa from both basins are also present in freshwater fishes of North America (see Hoffman, 1999).

These Nearctic affinities are also supported by the distribution of freshwater fishes (Álvarez & Lachica, 1974; Miller & Smith, 1986).

The analysis demonstrated the presence of a Neotropical clade, with a close relationship between Yucatán and Tabasco. Both Tabasco and Papaloapan, however, belong to the Mexican Gulf biogeographical province, while Yucatán is considered an independent province of the Neotropical region (Morrone, 2001). Nicaragua occupied the most basal position of this clade. In their analysis of the helminth fauna of the cichlid fishes in southeastern Mexico, Central America and South America, Vidal-Martínez & Kennedy (2000) suggested a close relationship between the helminth fauna of

Table 2 Detail of the taxa defining the nodes in the cladogram. Asterisks indicate species which support only partially the groups

Node	Taxa
1	<i>Ascocotyle chandleri</i> , <i>Ascocotyle leighi</i> , <i>Ascocotyle macrostoma</i> , <i>Ascocotyle numezae</i> , <i>Cichlasotrema ujati</i> , <i>Cichlidogyrus dossoui</i> , <i>Dendrouterina papillifera</i> , <i>Glossocercus caribaensis</i> , <i>Goezia</i> sp., <i>Haplorchis pumilio</i> , <i>Homalometron pallidum</i> , <i>Pelaezia loossi</i> , <i>Riberoia ondatrae</i> , <i>Sciadicleithrum splendidae</i> , <i>Tabascotrema veri</i> , <i>Valipora mutabilis</i> *
2	<i>Ameloblastella chavarriai</i> , <i>Aphanoblastella travassosi</i> , <i>Ascocotyle mcintosbi</i> *, <i>Ascocotyle megalcephala</i> *, <i>Crocodicicola pseudostoma</i> , <i>Drepanocephalus</i> sp.*, <i>Echinochasmus leopoldinae</i> , <i>Genarchella isabellae</i> , <i>Guavinella tropica</i> *, <i>Mexiconema cichlasomae</i> , <i>Neophilometroides caudata</i> *, <i>Octospiniferoides chandleri</i> , <i>Paracapillaria texeiraifreitasi</i> , <i>Urocleidoides</i> sp.
3	<i>Ascocotyle diminuta</i> , <i>Ascocotyle nana</i> , <i>Atrophecaecum astorquii</i> *, <i>Cladocystis trifolium</i> , <i>Falcaustra</i> sp., <i>Genarchella tropica</i> , <i>Oligogonotylus manteri</i> , <i>Perezitrema bychowskyi</i> *, <i>Procamallanus rebecae</i> , <i>Tylodelphis</i> sp., <i>Serpinema trispinosum</i> , <i>Sciadicleithrum meekii</i> *, <i>Sciadicleithrum mexicanum</i> *, <i>Stunkardiella minima</i>
4	<i>Apharyngostrigea</i> gen. sp., <i>Crassicutis cichlasomae</i> , <i>Genarchella astyanactis</i> *, <i>Procamallanus neocaballeroi</i> , <i>Sciadicleithrum bravohollisae</i>
5	<i>Diplostomum compactum</i> *, <i>Neoechinorhynchus golvani</i> *
6	<i>Ascocotyle tenuicollis</i> *, <i>Magnivittellinum simplex</i> *, <i>Rhabdochona kidderi</i> , <i>Saccocoelioides sogandaresi</i> , <i>Uvulifer amblopites</i>
7	<i>Clinostomum complanatum</i> , <i>Spiroxys</i> sp.

the Atlantic coastal drainages of Nicaragua and southeastern Mexico. Based on this, they proposed a Mesoamerican region within the Neotropics based on affinities between Central America and southeastern Mexico. The present analysis results support the findings of Vidal-Martínez & Kennedy (2000). The Neotropical clade produced by PAE in this study is consistent with the scheme of Morrone *et al.* (1999) for the biogeographical provinces of the Neotropical region.

The Pánuco, Balsas and Ayuquila river basins are located in Central Mexico. These three basins are included in the Neotropical region by Morrone (2001), although they belong to different biogeographical provinces. The Pánuco basin is located in the Mexican Gulf province, the Ayuquila basin in the Mexican Pacific Coast province, and the Balsas basin is its own province within the Neotropical region (see Morrone, 2001). Of these three basins, the Pánuco highlights a problem with the province assignment of basins in this area. The Mexican Gulf province includes the Pánuco, Papaloapan and Tabasco hydrological systems, but the present results indicate that these regions do not form a monophyletic group, suggesting that the Mexican Gulf province may not represent an accurate biogeographical unit. However, the helminth fauna of fish species from the Pánuco and Papaloapan basins show similarities, and significant similarities in the fish fauna of the Pánuco and some tropical regions have also been suggested (Miller & Smith, 1986). The position of the Pánuco basin in the cladogram can be explained by the low number of fish species examined from this basin compared with those for Papaloapan, Tabasco and Yucatán. For example, monogeneans represent a significant group supporting the relationships between Tabasco, Yucatán and Papaloapan, but there are no monogenean records from the Pánuco. Evidently, more taxonomic studies will be needed in the Pánuco to test its relationship with the other southeastern hydrological systems of Mexico.

The present study clearly demonstrates the utility of the helminth parasites of freshwater fish species in Mexico in contributing to general biogeographical theory aimed at detecting distributional patterns of Mexican biota. The data base assembled here is especially useful in proposing a general hypothesis of the relationships between several Mexican hydrological basins. These data formed into the nested sets in the area cladogram, indicating hypothetical relationships between the eight basins included in the study. These should be treated as preliminary results because they are based on a relatively small number of helminth taxa. A more accurate biogeographical analysis should be undertaken in the future by considering a larger data set, and incorporating more freshwater taxa, and other hydrological systems. The hypothetical relationships between Mexican basins proposed here can be tested through comparison of taxon–area cladograms of their taxa through an analysis of cladistic biogeography.

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BIOSKETCHES

Rogelio Aguilar-Aguilar is a PhD candidate at the Instituto de Biología, UNAM, México. He works in helminth parasites of freshwater fishes, especially in their biogeographical features and taxonomy of nematodes. He is professor of Systematics and Biogeography in the Facultad de Ciencias, UNAM.

Raúl Contreras-Medina is a PhD student and professor of Systematics, Biogeography and Plant Biology at the Facultad de Ciencias, UNAM, México. His research focuses on historical biogeography of Mexican biota.

Guillermo Salgado-Maldonado is a researcher at Instituto de Biología, UNAM, México. He is professor of Parasitology and Invertebrate Zoology at the Facultad de Ciencias, UNAM. His research interest focus on helminth parasites of freshwater fishes, taxonomy, surveys, ecology, community assembly, richness, exotic helminth parasite species introduced to Mexico, and biogeography. For further information see <http://www.ibiologia.unam.mx>

Appendix I List of taxa analysed

Number	Taxon
1	<i>Rhabdochona guerreroensis</i> Caspeta-Mandujano, Aguilar-Aguilar et Salgado-Maldonado, 2001
2	<i>Allocreadium mexicanum</i> Osorio-Sarabia, Pérez et Salgado-Maldonado, 1986
3	<i>Margotrema bravoae</i> Lamothe-Argumedo, 1970
4	<i>Phyllostomum lacustris</i> (Loewen, 1929)
5	Cryptogonimidae gen. sp.
6	<i>Proterodiplostomum</i> sp.
7	<i>Clinostomum complanatum</i> (Rudolphi, 1814)
8	<i>Diplostomum</i> sp.
9	<i>Centrocestus formosanus</i> (Nishigori, 1924)
10	<i>Bothriocephalus acheilognathi</i> Yamaguti, 1934
11	Proteocephalidea gen. sp.
12	<i>Valipora campylancristota</i> (Wedl, 1855)
13	<i>Dichelyne mexicanus</i> Caspeta-Mandujano, Moravec et Salgado-Maldonado, 1999
14	<i>Rhabdochona lichtenfelsi</i> Sánchez-Álvarez, García-Prieto et Pérez, 1998
15	<i>Eustrongylides</i> sp.
16	<i>Gnathostoma</i> sp.
17	<i>Spiroxys</i> sp.
18	<i>Polymorphus brevis</i> Van Cleave, 1916
19	<i>Gyrodactylus</i> sp.
20	<i>Urocleidoides costaricensis</i> (Price et Bussing, 1967)
21	<i>Saccocoelioides sogandaresi</i> Lumsden, 1961
22	<i>Magnivittellinum simplex</i> Kloss, 1966
23	<i>Diplostomum compactum</i> (Lutz, 1928)
24	<i>Uvulifer ambloplitis</i>
25	<i>Glossocercus auritus</i> (Rudolphi, 1819)
26	<i>Parvitaenia cochlearii</i> Coil, 1955
27	<i>Capillaria cyprinodonticola</i> Huffman et Bullock, 1973
28	<i>Rhabdochona canadensis</i> Moravec et Arai, 1971
29	<i>Rhabdochona kidderi</i> Pearse, 1936
30	<i>Rhabdochona mexicana</i> Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2000
31	Acuariidae gen. sp.
32	<i>Neoechinorhynchus golvani</i> Salgado-Maldonado, 1978
33	<i>Sciadicleithrum</i> sp.
34	<i>Valipora mutabilis</i> Linton, 1927
35	<i>Creptotrema agonostomi</i> Salgado-Maldonado, Cabañas-Carranza et Caspeta-Mandujano, 1998
36	<i>Ascocotyle tenuicollis</i> Price, 1935
37	<i>Spinitectus agonostomi</i> Moravec et Barus, 1971
38	<i>Polymorphus</i> sp.

Appendix I *continued*

Number	Taxon
39	Dactylogyridae gen. sp.
40	<i>Urocleidooides</i> sp.
41	Apharyngostrigea gen. sp.
42	<i>Crassicutis cichlasomae</i> Manter, 1936
43	Tetrabothridae gen. sp.
44	<i>Procamallanus neocaballeroi</i> (Caballero-Deloya, 1977)
45	<i>Perezitrema bychowskyi</i> (Caballero y Caballero et Caballero-Deloya, 1975)
46	<i>Cichlasotrema ujati</i> Pineda-López et Andrade-Salas, 1989
47	<i>Oligogonotylus manteri</i> Watson, 1976
48	<i>Tabascotrema veri</i> Lamothe-Argumedo et Pineda-López, 1990
49	<i>Genarchella isabellae</i> (Lamothe-Argumedo, 1977)
50	<i>Genarchella tropica</i> (Manter, 1936)
51	<i>Homalometron pallidum</i> Stafford, 1905
52	<i>Atrophecaecum astorquii</i> (Watson, 1976)
53	<i>Pelaezia loossi</i> (Pérez Viguera, 1955)
54	<i>Stunkardiella minima</i> (Stunkard, 1938)
55	<i>Ribeiroia ondatrae</i> (Price, 1931)
56	<i>Drepanocephalus</i> sp.
57	<i>Echinochasmus leopoldinae</i> Scholz, Ditrich et Vargas Vázquez, 1996
58	<i>Ascocotyle leighi</i> Burton, 1936
59	<i>Ascocotyle chandleri</i> Lumsden, 1963
60	<i>Ascocotyle mcintoshi</i> Price, 1936
61	<i>Ascocotyle nunezae</i> Scholz, Vargas-Vázquez, Vidal-Martínez et Aguirre-Macedo, 1997
62	<i>Ascocotyle diminuta</i> Stunkard et Haviland, 1924
63	<i>Ascocotyle macrostoma</i> (Robinson, 1956)
64	<i>Ascocotyle mollienicola</i> Sogandares-Bernal et Bridgman, 1960
65	<i>Ascocotyle nana</i> Ransom, 1920
66	<i>Haplorchis pumilio</i> (Looss, 1896)
67	<i>Cladocystis trifolium</i> (Braun, 1901)
68	<i>Crocodicicola pseudostoma</i> (Willemoes-Suhm, 1870)
69	<i>Thylodelphis</i> sp.
70	<i>Ameloblastella chavarraii</i> (Price, 1938)
71	<i>Aphanoblastella travassosi</i> (Price, 1938)
72	<i>Cichlidogyrus dossauri</i> Paperna, 1960
73	<i>Cichlidogyrus sclerosus</i> Paperna et Thurston, 1969
74	<i>Guavinella tropica</i> Mendoza-Franco, Scholz et Cabañas-Carranza, 2003
75	<i>Sciadicleithrum bravohollisae</i> Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994
76	<i>Sciadicleithrum meekii</i> Mendoza-Franco, Scholz et Vidal-Martínez, 1997
77	<i>Sciadicleithrum mexicanum</i> Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994
78	<i>Sciadicleithrum splendidae</i> Kritsky, Vidal-Martínez et Rodríguez-Canul, 1994
79	<i>Urocleidooides strombicirrus</i> (Price et Bussing, 1967)
80	<i>Dendrouterina papillifera</i> Fuhrmann, 1908
81	<i>Glossocercus caribaensis</i> Rysavy et Macko, 1973
82	<i>Octospiniferoides chandleri</i> Bullock, 1957
83	<i>Procamallanus rebecca</i> Andrade-Salas, Pineda-López et García-Magaña, 1994
84	<i>Paracapillaria teixeirafreitasi</i> (Caballero-Rodríguez, 1971)
85	<i>Mexiconema cichlasomae</i> Moravec, Vidal-Martínez et Salgado-Maldonado, 1992
86	<i>Goezia</i> sp.
87	<i>Serpinema trispinosum</i> (Leidy, 1852)
88	<i>Falcaustra</i> sp.
89	<i>Genarchella astyanactis</i> (Watson, 1976)
90	<i>Neophilometroides caudata</i> (Moravec, Scholz et Vivas-Rodríguez, 1995)
91	<i>Ascocotyle megalcephala</i> Price, 1932
92	<i>Prosthenhystera obesa</i> (Diesing, 1850)

Taxon	Hydrological Basin
<i>Ancyrocephalus</i> sp.	Ayuquila
<i>Dendrorchis</i> sp.	Ayuquila
Microcotylidae gen. sp.	Ayuquila
<i>Procamallanus jalisciensis</i> Moravec, Salgado-Maldonado et Caspeta-Mandujano, 1999	Ayuquila
<i>Atractis bravoe</i> (Osorio-Sarabia, 1984)	Balsas
<i>Goezia nonipapillata</i> Osorio-Sarabia, 1982	Balsas
<i>Hysterothylacium</i> sp.	Balsas
<i>Parvitaenia macropeos</i> (Wedl, 1855)	Balsas
<i>Rhabdochona salgadoi</i> Caspeta-Mandujano et Moravec, 2000	Balsas
<i>Spinitectus humbertoi</i> Caspeta-Mandujano et Moravec, 2000	Balsas
<i>Valipora minuta</i> (Coil, 1950)	Balsas
Caryophyllidea gen. sp.	Lerma
<i>Crepidostomum cooperi</i> Hopkins, 1931	Lerma
Cyclophyllidea gen. sp.	Lerma
<i>Cyclustera ralli</i> (Underwood et Dronen, 1986)	Lerma
<i>Diplostomum</i> (<i>Tylodelphys</i>) sp.	Lerma
<i>Gyrodactylus elegans</i> Nordmann, 1832	Lerma
<i>Ligula intestinalis</i> (Linnaeus, 1758)	Lerma
<i>Margotrema guillerminae</i> Pérez, 2001	Lerma
<i>Octomacrum mexicanum</i> Lamothe-Argumedo, 1981	Lerma
<i>Ochetosoma</i> sp.	Lerma
<i>Paradilepis caballeroi</i> Rysavy et Macko, 1973	Lerma
<i>Paradilepis</i> sp.	Lerma
<i>Paradilepis urceus</i> (Wedl, 1855)	Lerma
Philometridae gen. sp.	Lerma
<i>Proteocephalus pusillus</i> Ward, 1910	Lerma
<i>Pseudocapillaria tomentosa</i> (Dujardin, 1843)	Lerma
<i>Spinitectus osorioi</i> Choudhury et Pérez, 2001	Lerma
<i>Acanthostomum gnerii</i> Szidat, 1954	Nicaragua
Allocreadiidae gen. sp.	Nicaragua
<i>Brevimulticaecum</i> sp.	Nicaragua
<i>Clinostomum</i> sp.	Nicaragua
<i>Gussevia heterotilapiae</i> Vidal-Martínez, Scholz et Aguirre-Macedo, 2001	Nicaragua
<i>Neochasmus ackerti</i> Watson, 1976	Nicaragua
<i>Saccocoelioides</i> sp.	Nicaragua
<i>Sciadicleithrum bicuense</i> Vidal-Martínez, Scholz et Aguirre-Macedo, 2001	Nicaragua
<i>Sciadicleithrum maculicaudae</i> Vidal-Martínez, Scholz et Aguirre-Macedo, 2001	Nicaragua
<i>Sciadicleithrum nicaraguense</i> Vidal-Martínez, Scholz et Aguirre-Macedo, 2001	Nicaragua
<i>Actinocleidus fergusonii</i> Mizelle, 1938	Pánuco
<i>Paracryptotrematina aguirrepequenoii</i> (Jiménez-Guzmán, 1973)	Pánuco
Pharingonidae gen. sp.	Pánuco
<i>Rhabdochona xiphophori</i> Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2001	Pánuco
<i>Ascocotyle longa</i> Ransom, 1920	Papaloapan
<i>Cucullanus caballeroi</i> Petter, 1977	Papaloapan
<i>Cucullanus mexicanus</i> Caspeta-Mandujano, Moravec et Aguilar-Aguilar, 2000	Papaloapan
<i>Cyclustera ibisae</i> (Schmidt et Bush, 1972)	Papaloapan
<i>Choanoscolex lamothei</i> García-Prieto, 1990	Papaloapan
<i>Echeneiobothrium</i> sp.	Papaloapan
<i>Gibsonnema ophisterni</i> (Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002)	Papaloapan
<i>Monticellia ophisterni</i> Scholz, de Chambrier et Salgado-Maldonado, 2001	Papaloapan

Appendix 2 List of taxa found in a single area

Appendix 2 continued

Taxon	Hydrological Basin
<i>Philometra ophisterni</i> Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002	Papaloapan
<i>Proteocephalus brooksi</i> García-Prieto, Rodríguez et Pérez, 1996	Papaloapan
<i>Pseudocapillaria ophisterni</i> Moravec, Salgado-Maldonado et Jiménez-García, 2000	Papaloapan
<i>Pygidiopsis pindoramensis</i> (Travassos, 1929)	Papaloapan
<i>Spinitectus mexicanus</i> Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2000	Papaloapan
<i>Beaninema nayaritense</i> Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2001	Santiago
<i>Amphimerus</i> sp.	Tabasco
<i>Amphoteromorphus</i> sp.	Tabasco
<i>Bucephalopsis</i> sp.	Tabasco
<i>Caballerorhynchus lamothei</i> Salgado-Maldonado, 1977	Tabasco
<i>Cichlidogyrus tilapiae</i> Paperna, 1960	Tabasco
<i>Cotylogaster</i> sp.	Tabasco
<i>Cruzia</i> sp.	Tabasco
<i>Cucullanus</i> sp.	Tabasco
<i>Cystoopsis attractostei</i> Moravec et Salgado-Maldonado, 2003	Tabasco
<i>Diplectanocotyla</i> sp.	Tabasco
<i>Encotyllabe</i> sp.	Tabasco
<i>Enterogyrus niloticus</i> Eid et Negm, 1987	Tabasco
<i>Gyrodactylus niloticus</i> Cone, Arthur et Bondad-Reantaso, 1995	Tabasco
<i>Haplorchoides</i> sp.	Tabasco
<i>Ligictaluridus mirabilis</i> (Mueller, 1937)	Tabasco
<i>Mazocraeoides</i> sp.	Tabasco
<i>Microcotyle</i> sp.	Tabasco
<i>Neochasmus olmecus</i> Lamothe-Argumedo, Pineda-López et Andrade-Salas, 1989	Tabasco
<i>Neodiplectanum</i> sp.	Tabasco
<i>Olmeca laurae</i> Lamothe-Argumedo et Pineda-López, 1990	Tabasco
<i>Palaeocryptogonimus</i> sp.	Tabasco
<i>Palombitrema heteroancistrum</i> Price et Bussing, 1968	Tabasco
Phyllobothriidae gen. sp.	Tabasco
<i>Phyllobothrium</i> sp.	Tabasco
<i>Polymorphus mutabilis</i> (Rudolphi, 1819)	Tabasco
<i>Procamallanus</i> sp.	Tabasco
<i>Proteocephalus singularis</i> La Rue, 1911	Tabasco
<i>Pseudoacanthostomum</i> sp.	Tabasco
<i>Pseudoacancicola batallae</i> Lamothe, Salgado-Maldonado et Pineda-López, 1991	Tabasco
<i>Pseudohaliotrematoides</i> sp.	Tabasco
<i>Raillietnema kritscheri</i> Moravec, Salgado-Maldonado et Pineda-López, 1993	Tabasco
<i>Salsuginus seculus</i> (Mizelle et Arcadi, 1945)	Tabasco
<i>Scutogyrus longicornis</i> (Paperna et Thurston, 1969)	Tabasco
<i>Spinitectus tabascoensis</i> Moravec, García-Magaña et Salgado-Maldonado, 2002	Tabasco
<i>Thynnascaris</i> sp.	Tabasco
<i>Urocleidoides reticulatus</i> Mizelle et Price, 1964	Tabasco
<i>Anacanthocotyle anacanthocotyle</i> Kritsky et Fritts, 1970	Yucatán
<i>Ascocotyle ampullacea</i> Miller et Harkema	Yucatán
<i>Ascocotyle gemina</i> Font, Overstreet et Heard, 1984	Yucatán
<i>Ascocotyle</i> sp.	Yucatán
<i>Bothriocephalus pearsei</i> Scholz, Vargas-Vázquez et Moravec, 1996	Yucatán
<i>Capillaria cichlasomae</i> Moravec, Scholz et Mendoza-Franco, 1995	Yucatán
<i>Capillostrongyloides</i> sp.	Yucatán
<i>Cyclusteria capito</i> (Rudolphi, 1819)	Yucatán
<i>Dendroterina pilherodiae</i> Mahon, 1956	Yucatán
<i>Dollfusentis chandleri</i> Golvan, 1969	Yucatán

Taxon	Hydrological Basin
<i>Echinochasmus</i> sp.	Yucatán
Echinorhynchidae gen. sp.	Yucatán
Echinostomatinae gen. sp.	Yucatán
<i>Euhaplorchis californiensis</i>	Yucatán
<i>Gyrodactylus neotropicalis</i> Kritsky et Fritts, 1970	Yucatán
Heterophyidae gen. sp.	Yucatán
<i>Hysterothylacium cenotae</i> (Pearse, 1936)	Yucatán
<i>Nomimoscolex</i> sp.	Yucatán
<i>Paracapillaria rhamdiae</i> Moravec, González-Solís et Vargas-Vázquez, 1995	Yucatán
<i>Phocitrema ovale</i> Martin, 1950	Yucatán
<i>Physocephalus sexalatus</i> (Molin, 1860)	Yucatán
<i>Porrocaecum</i> sp.	Yucatán
<i>Pseudocapillaria yucatanensis</i> Moravec, Scholz et Vivas-Rodríguez, 1995	Yucatán
<i>Pseudoterranova</i> sp.	Yucatán
<i>Salsuginus neotropicalis</i> Mendoza-Franco et Vidal-Martínez, 2001	Yucatán
<i>Southwellina hispida</i> (Van Cleave, 1925)	Yucatán
<i>Urocleidoides annops</i> Kritsky et Thatcher, 1974	Yucatán
<i>Urocleidoides heteroancistrum</i> (Price et Bussing, 1968)	Yucatán