Monogeneans of freshwater fishes from cenotes (sinkholes) of the Yucatan Peninsula, Mexico

Edgar F. Mendoza-Franco, Tomáš Scholz, Clara Vivas-Rodríguez and Joaquín Vargas-Vázquez

1Laboratory of Parasitology, Centre for Research and Advanced Studies, National Polytechnic Institute (CINVESTAV-IPN), Mérida, Yucatan, Mexico; 2Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic

Key words: Monogenea, Ancyrocephalinae, Gyrodactylidae, Cichlidae, Rhamdia, Astyanax, Gambusia, cenotes, zoogeography, Mexico

Abstract. During a survey of the parasites of freshwater fishes from cenotes (sinkholes) of the Yucatan Peninsula the following species of monogeneans were found on cichlid, pimelodid, characid and poeciliid fishes: Urocleidoides travassosi (Heckel), Cichlasoma urophthalmus (Regan), and Cichlasoma octofasciastum (Regan), and Cichlasoma synspilum Hubbs, all new host records; Sciadicleithrum meekii Mendoza-Franco, Scholz et Vidal-Martínez, 1997 from Cichlasoma meeki (Brind); Urocledioides travassosi (Price, 1938) and Urocledioides chavarrai (Price, 1938) from Rhamdia guatemalensis (Günter); Urocledioides costaricensis (Price et Bussing, 1967), Urocledioides heteroancistrium (Price et Bussing, 1968), Urocledioides anops Kritsky et Thatcher, 1974, Anacanthocotyle anacanthocotyle Kritsky et Fritts, 1970, and Gyrodactylus neotropicalis Kritsky et Fritts, 1970 from Astyanax fasciatus; and Gyrodactylus sp. from Gambusia yucatana Regan. Urocledioides chavarrai, U. travassosi, U. costaricensis, U. heteroancistrium, U. anops, Anacanthocotyle anacanthocotyle and Gyrodactylus neotropicalis are reported from North America (Mexico) for the first time. These findings support the idea about the dispersion of freshwater fishes and their monogenean parasites from South America through Central America to southeastern Mexico, following the emergence of the Panamanian isthmus between 2 and 5 million years ago.

In 1993-1995, a study on the parasites of freshwater fishes from cenotes (sinkholes) of the Yucatan Peninsula was carried out (Scholz et al. 1995a). Endoparasitic helminths found in 581 fishes of 15 species have already been treated in papers by Moravec et al. (1995a,b) and Scholz et al. (1995a,b, 1996). In the present paper, a survey of monogeneans found on fishes from cenotes is presented.

MATERIALS AND METHODS

Fishes were caught in 39 cenotes by hook and line or casting nets between September 1993 and January 1995 (see Scholz et al. 1995a for details about cenotes and the numbers of fish examined). A total of 581 fish of 15 species were examined. Monogeneans were found on fishes of the following species: Cichlasoma urophthalmus (Günter) (a total of 77 specimens examined), Cichlasoma friedrichshali (Heckel) (4), Cichlasoma octofasciastum (Regan) (5), Cichlasoma synspilum Hubbs (17), Cichlasoma meeki (Brind) (11) (Cichlidae); Rhamdia guatemalensis (Günter) (229) (Pimelodidae); Astyanax fasciatus (Cuvier) (124) (Characidae); and Gambusia yucatana Regan (20) (Poeciliidae).

Cenotes in which monogeneans occurred were as follows: 1. Noc-chonchunex (20°48'53"N; 90°11'47"W); 2. Chaamanac (20°51'53"N; 90°09'18"W); 3. Dzaptün (20°51'19"N; 90°14'09"W); 4. San Gerardo (21°03'59"N; 89°41'30"W); 5. Dzibilchaltún (21°05'28"N; 89°38'55"W); 6. Dzonton Cervera (21°22'36"N; 88°49'59"W); 7. Cenote Azul (Puerto Aventuras) (18°38'47"N; 88°24'46"W); 8. Escondido (20°11'57"N; 87°27'57"W); 9. Cabañas (20°07'51"N; 87°27'57"W); 10. Dos Bocas (17°54'38"N; 88°51'20"W); 11. Los Cuates (17°55'00"N; 88°51'20"W); 12. Ixin-há (20°37'14"N; 88°06'40"W); 13. Hunucmá (21°00'03"N; 89°52'06"W); 14. Hubiku (20°49'79"N; 88°01'21"W); 15. Scan-Yui (20°40'20"N; 88°32'51"W); 16. Tixkanka (21°14'55"N; 88°58'45"W); 17. Xcanganchén (20°36'43"N; 89°05'32"W); 18. Homún (20°44'19"N; 89°17'49"W); 19. Gran Cenote (20°14'44"N; 87°27'54"W), and 20. Xumucuy (21°33'63"N; 88°59'50"W).

Monogeneans found were isolated and fixed with ammonium picrate–glycerin (Ergens 1969). All measurements are in micrometres (μm); the mean is followed by the range and the number (n) of specimens measured in parentheses.

Reference specimens were deposited in the Colección Nacional de Helminthos (CNHE), México; the United States National Parasite Collection, Beltsville, Maryland, USA (USNPC); the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic (IPCAS); the Natural History Museum, London, UK (NHBM); and the Parasitology Laboratory, CINVESTAV, Mérida, Mexico (CHCM).

Address for correspondence: E.F. Mendoza-Franco, Laboratorio de Parasitología, CINVESTAV-IPN Unidad Mérida, Carretera Antigua a Progreso Km. 6, A.P. 73 “Cordemex”, C.P. 97310 Mérida, Yucatán, México. Phone: ++52 99 812960; Fax: ++52 99 812917; E-mail: mfranco@kin.cieamer.conacyt.mx
Table 1. Measurements of *Sciadicleithrum mexicanum* from four *Cichlasoma* species. (In micrometres; mean with range in parentheses; n = number of specimens measured.)

<table>
<thead>
<tr>
<th></th>
<th><em>Cichlasoma urophthalmus</em></th>
<th>n</th>
<th></th>
<th></th>
<th><em>Cichlasoma friedrichstali</em></th>
<th>n</th>
<th></th>
<th></th>
<th><em>Cichlasoma octofasciatum</em></th>
<th>n</th>
<th></th>
<th></th>
<th><em>Cichlasoma synspilum</em></th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pharynx width</td>
<td>18 (13-20)</td>
<td>20</td>
<td>–</td>
<td>0</td>
<td>(17-26)</td>
<td>2</td>
<td>–</td>
<td>27 (22-30)</td>
<td>3</td>
<td>–</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ventral hamuli</td>
<td>33 (29-35)</td>
<td>22</td>
<td>30</td>
<td>(20-30)</td>
<td>4</td>
<td>32 (31-33)</td>
<td>7</td>
<td>31 (30-32)</td>
<td>6</td>
<td>–</td>
<td>32 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ventral hamuli width</td>
<td>16 (15-17)</td>
<td>17</td>
<td>(13-14)</td>
<td>2</td>
<td>15 (14-15)</td>
<td>7</td>
<td>15 (14-16)</td>
<td>6</td>
<td>–</td>
<td>16 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal hamuli</td>
<td>39 (35-41)</td>
<td>19</td>
<td>35</td>
<td>(34-36)</td>
<td>4</td>
<td>38 (38-39)</td>
<td>5</td>
<td>37 (35-38)</td>
<td>6</td>
<td>–</td>
<td>39 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal hamuli width</td>
<td>14 (13-16)</td>
<td>16</td>
<td>14</td>
<td>(13-14)</td>
<td>4</td>
<td>15 (14-17)</td>
<td>4</td>
<td>15 (14-15)</td>
<td>6</td>
<td>–</td>
<td>16 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ventral bar length</td>
<td>34 (30-37)</td>
<td>21</td>
<td>(32-36)</td>
<td>2</td>
<td>36 (35-38)</td>
<td>3</td>
<td>34 (34-35)</td>
<td>3</td>
<td>–</td>
<td>37 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal bar length</td>
<td>31 (29-33)</td>
<td>21</td>
<td>(31-32)</td>
<td>2</td>
<td>32 (31-32)</td>
<td>3</td>
<td>2 (31-32)</td>
<td>3</td>
<td>–</td>
<td>32 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hook length</td>
<td>15 (14-17)</td>
<td>71</td>
<td>15</td>
<td>(13-16)</td>
<td>3</td>
<td>15 (14-17)</td>
<td>16</td>
<td>15 (15-17)</td>
<td>7</td>
<td>15 (14-16)</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MCO² length</td>
<td>62 (53-68)</td>
<td>17</td>
<td>35</td>
<td>1</td>
<td>41 (40-49)</td>
<td>3</td>
<td>42 (40-46)</td>
<td>4</td>
<td>–</td>
<td>39 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accessory piece</td>
<td>45 (37-52)</td>
<td>12</td>
<td>(44-48)</td>
<td>2</td>
<td>0</td>
<td>48 (44-52)</td>
<td>3</td>
<td>–</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹ Original descriptions of *S. mexicanum* from Kritsky et al. (1994); ² Male copulatory organ.

**SURVEY OF SPECIES**

*Sciadicleithrum mexicanum* Kritsky, Vidal-Martinez et Rodriguez-Canul, 1994 [Figs. 1, 2]

**Description:** measurements of specimens from different hosts are given in Table 1.

**Hosts and localities:** *Cichlasoma urophthalmus*:
- Dzonot Cervera (23 May 1994) – 8 fish infected of 10 examined; mean intensity of infection 78 worms per infected fish (range 6-252); *C. friedrichstali*: Dzaptun (8 November 1993) – 1/2; 16; Cenote Azul (Puerto Avencaturas) (24 February 1994) – 2/3; 21 (16-46); *C. octofasciatum*: Dzonot Cervera (23 May 1994) – 1/1; 50; Chaamac (21 September 1994) – 2/2; 12 (7-17); *C. synspilum*: Cabañas (23 May 1994) – 2/2; 4 (1-7).

**Site of infection:** gills.

**Remarks:** This species was described by Kritsky et al. (1994) on the basis of specimens from *C. urophthalmus*. The present study demonstrated that these authors did not mention the presence of filaments on shafts and point of ventral and dorsal hamuli (see Figs. 1, 2). In other features, the specimens from cenotes well correspond to those described by Kritsky et al. (1994). *Cichlasoma octofasciatum*, *C. friedrichstali* and *C. synspilum* represent new hosts. *Sciadicleithrum mexicanum* is, therefore, a species which exhibits a relatively wide host range within one fish family.

*Sciadicleithrum meekii* Mendoza-Franco, Scholz et Vidal-Martinez, 1997

**Description** (based on 4 specimens): Ventral hamuli 26 (24-28; n = 5) long; base width 14 (13-14; n = 6); dorsal hamuli 42 (40-44; n = 5) long; base width 15 (14-15; n = 6). Ventral bar 34 (29-36; n = 3) long; dorsal bar 33 (31-35; n = 3) long. Marginal hooks 14 (13-15; n = 5) total length. Length of first ring of copulatory organ 13 (10-15; n = 3). Accessory piece 16 (15-17; n = 3) long.

**Hosts and localities:** *Cichlasoma meeki*:
- Nohchconunchey (22 September 1993) – 5/6; 34 (6-60); Los Cuates (5 April 1994) – 1/1; 3; Cabañas (9 May 1994) – 1/3; 1.

**Site of infection:** gills.

**Remarks:** *Sciadicleithrum meekii* can easily be differentiated from congeners by having a dorsal hamulus with an enlarged superficial root and coiled tube comprising one ring of the vagina (see Mendoza-Franco et al. 1997).

Figs. 1, 2. *Sciadicleithrum mexicanum* (1 – ventral hamulus; 2 – dorsal hamulus). Scale bar in µm.
**Urocleidoides costaricensis** (Price et Bussing, 1967)  
Figs. 3-12

**Description** (based on 4 specimens): Pharynx (23-33) wide. Ventral hamuli 34 (33-35; n = 5) long; base width 19 (18-19; n = 4). Dorsal hamuli 26 (25-27; n = 7) long; base width 14 (13-15; n = 6). Ventral bar 24 (22-27; n = 3) long; dorsal bar 25 (24-27; n = 4) long. Hooks 2, 3, 4, 6, 7: 19 (19-21; n = 4) total length; hook 1: 16 (n = 4) total length; hook 5: 10 (n = 4) total length. Male copulatory organ (27-37) long. Accessory piece (21-22) long.

**Host and localities:** *Astyanax fasciatus*: Nocchonunchey (21 September 1993 and 2 February 1994) – 5/7; 29 (15-42); 3/3; 12 (1-32); Chaamaac (21 September 1993) – 2/2; 7 (7-8); Dzaptun (2 February 1994) – 1/2; 5; Dzibilchaltun (13 May 1994) – 7/8; 9 (3-32); Gran Cenote (25 April 1994 and 9 May 1994) – 6/13; 8 (1-33); 2/3; 34 (26-43); Escondido (9 May 1994) – 1/6; 24; Cabanas (23 May 1994) – 3/5; 10 (3-22); Dos Bocas (5 April 1994) – 2/3; 1 (1-2).

**Site of infection:** gills.

**Specimens deposited:** CNHE (No. 2918); USNPC (No. 86887); NHBM (No. 1996.10.22.23); CHCM (No. 234).

**Remarks:** This species was originally described as *Cleidodiscus costaricensis* from *Astyanax fasciatus* from Costa Rica by Price and Bussing (1967). Subsequent taxonomic studies of this species from the same host from Costa Rica (Kritsky and Leiby 1972) revealed that *C. costaricensis* had some typical features of the genus *Urocleidoides* Mizelle et Price, 1964 and was transferred to it. Kritsky and Thatcher (1974) reported *U. costaricensis* from *A. fasciatus* from Colombia. Kritsky et al. (1986), revising species of *Urocleidoides*, excluded *U. costaricensis* from this genus and considered it to be a species *incertae sedis*. However, this taxon is provisionally maintained within *Urocleidoides* in this paper because no new generic assignment of *U. costaricensis* has been provided. Comparison of the present material with a voucher of *U. costaricensis* from *A. fasciatus* from the U.S. National Parasite Collection, Beltsville (No. 73614) did...
not reveal any differences, except for the presence of a sclerotised structure in the midventral position (see Fig. 7). Kritsky and Leiby (1972) did not mention this feature. The present findings represent a new zoogeographical record.

**Urocleidoides heteroancistrium** (Price et Bussing, 1968) Figs. 13-18

**Description** (based on 4 specimens): Ventral hamuli 19 (17-19; n = 12) long; base width 8 (7-9; n = 11); dorsal hamuli 28 (25-28; n = 12) long; base width 15 (12-20; n = 12). Ventral bar 22 (17-26; n = 6) long; dorsal bar 25 (22-28; n = 6) long. Hook 7: 28 (25-32; n = 12) total length; hooks 1, 6: 12 (10-12; n = 12) total length. Male copulatory organ 6 (4-8; n = 5) base. Length of copulatory organ 30 (29-31; n = 3).

**Host and localities:** *Astyanax fasciatus*: Noc-choncunchey (21 September 1993) – 5/7; 29 (15-42); San Gerardo (23 March 1994) – 1/1; 86.

**Site of infection:** gills.

**Specimens deposited:** CNHE (No. 2919); USNPC (No. 86885); CHCM (No. 235).

**Remarks:** In Noc-choncunchey cenote a simultaneous infection of *A. fasciatus* with three *Urocleidoides* species (*U. costaricensis*, *U. heteroancistrium*, and *U. anops*) was found. Since all worms could not be properly identified, the data on infection rate relate to all these species. *U. heteroancistrium* was reported by Kritsky and Leiby (1972), and Kritsky and Thatcher (1974) from *A. fasciatus* from Costa Rica and Colombia. Slight differences in the morphology of the superficial root on the dorsal hamuli between *U. heteroancistrium* and specimens from cenotes were found (see Fig. 18), but the worms are considered conspecific.

Kritsky et al. (1986) considered *U. heteroancistrium* to be a species *incertae sedis*. However, it is tentatively retained within the genus *Urocleidoides* until new generic assignation of this taxon is available. The present findings represent the first record of this parasite in North America.

**Urocleidoides anops** Kritsky et Thatcher, 1974 Figs. 19-23

**Description** (based on 3 specimens): Pharynx 31 (29-31; n = 3) wide. Ventral hamuli 33 (31-35; n = 6) long; base width 21 (19-24; n = 6); dorsal hamuli 28 (27-28; n = 4) long; base width 16 (14-17; n = 4). Ventral bar 29 (27-31; n = 3) long; dorsal bar 35 (34-35; n = 3) long. Hooks 2, 3, 4, 6, 7: 21 (20-21; n = 11) total length; hooks 1, 5: 14 (13-15; n = 8) total length. Vaginal sclerite 17 long. Accessory piece 26 long.

Site of infection: gills.

Specimens deposited: CNHE (No. 2917); USNPC (No. 86896); CHCM (No. 236).

Remarks: The specimens well fit into the diagnosis of *U. anops*, a species described by Kritsky and Thatcher (1974) from *Characidium caucanum* from the Río Pance, Colombia. This species is differentiated from *U. costaricensis* and *U. heteroancistrium* by the presence of a hook-shaped vaginal sclerite. The material from cenote fish represents new host and geographical records.

*Urocleidoides chavarriai* (Price, 1938)


Site of infection: gills.

Specimens deposited: CHCM (No. 313).

Remarks: The specimens found in *R. guatemalensis* correspond to those described by Price (1938) as *Cleidodiscus chavarriai*. This taxon was transferred to *Urocleidoides* by Molnár et al. (1974) but Kritsky et al. (1986) considered it a species *incertae sedis*. Generic assignation, together with the redescription of this taxon, will be presented in a separate paper (D. Kritsky – pers. comm.).

This species was found only in one locality, where it occurred simultaneously with *U. travassosi*. Since all specimens were not fixed and identified to the species level, values of infection rates refer to mixed infections with both *Urocleidoides* taxa.

*Urocleidoides travassosi* (Price, 1938)

Host and localities: *Rhamdia guatemalensis*: Ixin-há (see *U. chavarriai*); Hunucmá (8 November 1993) – 2/2; 14 (7-21); Hubiku (18 April 1994) – 7/16; 6 (1-13); Scan-Yui (25 January 1994) – 5/16; 1; Tixkanka (23 May 1994) – 7/9; 10 (1-7); Xcanganché (16 November 1993) – 1/3; 2; Homún (3 November 1993) – 1/1; 2; Xmucuy (16 November 1993) – 1/2; 1; (25 July 1994) – 11/14; 4 (1-8).

Site of infection: gills.

Specimens deposited: CHCM (No. 314).

Remarks: Similar to *U. chavarriai*, this taxon was originally described within the genus *Cleidodiscus* by Price (1938) and then transferred to *Urocleidoides* by Molnár et al. (1974). Kritsky et al. (1986) questioned its generic designation and placed it within taxa *incertae sedis*. This species will be redescribed in a paper dealing with the generic status of ancyrocephaline monogeneans from catfishes (D. Kritsky – pers. comm.).


*Anacanthocotyle anacanthocotyle* Kritsky et Fritts, 1970

Description (based on 2 specimens): Body 323 total length. Haptor (38-42) wide. Pharynx (16-20) wide by (16-36) long. Marginal hooks 18 (17-18; n = 4) total length; length of hook proper 4 (3-4; n = 4).

Host and locality: *Astyanax fasciatus*: Nohchoncunchey (21 September 1993) – 1/2; 3.

Site of infection: fins.

Specimens deposited: CNHE (No. 3719); CHCM (No. 237).

Remarks: This species was described by Kritsky and Fritts (1970) from *Astyanax fasciatus* from Costa Rica. The specimens found in cenote from Yucatan do not differ from those described by these authors and they represent a new geographical record.
**Gyrodactylus neotropicalis** Kritsky et Fritts, 1970 Figs. 27, 28

**Description** (based on 2 specimens): Body 543 total length. Haptor 64 wide. Hamuli (60-62) total length; (10-12) width.

**Host and locality:** *Astyanax fasciatus*: Nocchoncunchey (21 September 1993) – 1/2; 3.

**Site of infection:** fins.

**Specimens deposited:** CNHE (No. 3718).

**Remarks:** *G. neotropicalis* was described by Kritsky and Fritts (1970) from *Astyanax fasciatus* from Costa Rica. The specimens studied were apparently conspecific with those found by these authors and they are reported from North America for the first time.

**Gyrodactylus sp.**

**Host and locality:** *Gambusia yucatana*: Homún (3 November 1993) – 1/1; 1.

**Site of infection:** fins.

**Remarks:** Poor quality of the only specimen found did not enable us to establish species identification.

**DISCUSSION**

The present study revealed that the fauna of monogeneans of fishes from cenotes of the Yucatan Peninsula included 10 species (7 dactylogyrids and 3 gyrodactylids). Rates of infection (values of prevalence and particularly intensity of infection) were fairly low compared to those of trematodes (10 species of adults and 21 of metacercariae with the prevalence up to 100% and intensity of infection up to hundreds or thousands of specimens – Scholz et al. 1995a,b) and nematodes (9 species of adults and 9 of larvae – Moravec et al. 1995a,b).

The monogeneans found in cenote fishes from the Yucatan Peninsula are undoubtedly Neotropical elements (zoogeographical affinity of a single specimen of *Gyrodactylus sp.* from *Gambusia yucatana* could not be assessed) and exhibit a close resemblance to Neotropical species of the same or related genera. From a zoogeographical point of view this resemblance seems to be related to the dispersion route followed by freshwater fishes and their parasites from South America through Central America to southeastern Mexico, following the emergence of the Panamanian isthmus between 2 and 5 million years ago (Rosen 1976, Briggs 1987).

Relatively poor fauna of monogeneans of cenote fishes appears to support the theory of Bussing (1985) about long isolation (until the Pleistocene) of southeastern Mexico from South America. Similarly, Kritsky et al. (1994) argued that Yucatan species of *Sciadicleithrum* are more closely related to each other than to their congener from South America as a result of speciation initiated since dispersal of a common ancestor to the area. This assumption is based on the presence of highly derived morphological traits (synapomorphies) in the Yucatan species as longitudinal lateral grooves on the shaft and point of the ventral and dorsal hamuli, the sheath-like accessory piece, slightly overlapping gonads, slightly appressed roots of the dorsal hamuli and thickened walls of the seminal vesicle. This is also valid for *S. meeki*, a species described recently from *C. meeki* from Yucatan (Mendoza-Franco et al. 1997).

Although the present study provided new data on host spectrum and distribution of several species, the information about the fauna of monogeneans in southeastern Mexico is still limited. This information, together with data on the occurrence of monogeneans in Central America, is necessary for better understanding the species composition and phylogeny of these parasites of freshwater fishes.

**Acknowledgements.** The authors are indebted to Dr. Delane C. Kritsky, Idaho State University, Pocatello, Idaho, USA, for identification of gyrodactylid species and valuable suggestions, to Raúl Simá-Alvarez, Jorge Güimez-Ricalde and Gregory Arjona-Torres for their help in collecting fish, to Drs. Victor M. Vidal-Martínez and Leopoldina Aguirre-Macedo for critical remarks on an early draft of the manuscript, to Esperanza Pérez-Díaz, Mirrella Hernández de Santillana and Victor Castillo-Escalante, all CINVESTAV-IPN Mérida, for help in identification of fishes. Thanks are due to Drs. J. Ralph Lichtenfels and Patricia Pilitt, U.S. National Parasite Collection, Beltsville, Maryland, USA, for lending the voucher of *Urocleidoides costaricensis*. This study was financially supported by the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO), Mexico (project No. PO 99).

**REFERENCES**


Received 20 November 1998 
Accepted 30 March 1999