Nonrandom variation in *Poecilia marcellinoi* n. sp. and *P. salvatoris* Regan, 1907 in El Salvador (Pisces, Poeciliidae)

Fred. N. Poeser
Institute for Systematics and Population Biology, Department of Ichthyology, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands

Abstract

A new species of the genus *Poecilia* Bloch & Schneider, 1801 is recorded from El Salvador. Morphological and meristic data of *P. marcellinoi* n. sp. and of the sympatric *P. salvatoris* Regan, 1907 are analysed. Intra- and interspecific variation are compared and correlated with environmental and interspecific influences. A high degree of character displacement is observed in populations from stable freshwater habitats. In habitats with presumed marine influences, this character displacement is counteracted by ecological stress. Based on the evidence presented, subspecific separation of observed ecotypes from literature is rejected.

Résumé

Une nouvelle espèce du genre *Poecilia* Bloch & Schneider, 1801 est décrite du El Salvador. Sont analysées les données morphologiques et méristiques de *P. marcellinoi* n. sp. et de l'espèce sympatrique *P. salvatoris* Regan, 1907. On compare leur variabilité intra- et interspécifique, celles-ci étant corrélées avec les influences interspécifiques et avec celles du milieu. Dans des populations d'habitats dulcicoles stables on observe un haut degré de déplacement des caractères, tandis que dans des habitats subissant apparemment des influences marines ce déplacement de caractères est contrecarré par le stress écologique. Les résultats présentés permettent de rejeter la séparation subspécifique des écotypes observés, telle qu'elle a été proposée dans la littérature.

Introduction

Rosen & Bailey (1963) published a monograph on poeciliid fishes that includes a revision of the genus *Poecilia* Bloch & Schneider, 1801, in which they provisionally attached 32 species and subspecies as synonyms of *P. sphenops* Valenciennes, 1846.

Several of these species have subsequently been reestablished. Miller (1983) published a checklist with 12 Mexican species of the genus *Poecilia* and included a key to these species (: 820–822). One species formerly considered synonymous with *P. sphenops* is *P. salvatoris* Regan, 1907, which is sympatric in El Salvador with *P. marcellinoi* n. sp. In their area of distribution, they show ecomorphological variation. During the development of poeciliid fishes, size, morphometric, and meristic characters are generally influenced by ecological factors (Hubbs, 1922, 1924, 1926). The variations observed in these studies are caused by a shift in their life history: in warmer and/or fresher water somatic growth is reduced, whereas meristic differentiation is enhanced (Hubbs, 1926). These two conditions result in smaller specimens, with lesser body depth and a more anterior position of the dorsal and anal fins. It also results in a lower number of vertebrae and scales, and more fin rays in the unpaired fins (with a possible exception of the dorsal fin in *P. reticulata* (cf. Schmidt, 1919)).

Another mechanism that influences characters in poeciliid fishes is character displacement. Several morphometric and meristic characters in sympatric populations of ecologically competitive species (Rivas, 1982) show variation; this results in greater differences between specimens in sympatric populations versus specimens in allopatric populations. This was found also by Menzel & Darnell (1973) in *P. mexicana* Steindachner, 1863, for populations where this species was sympatric with *P. sphenops* Valenciennes, 1846.
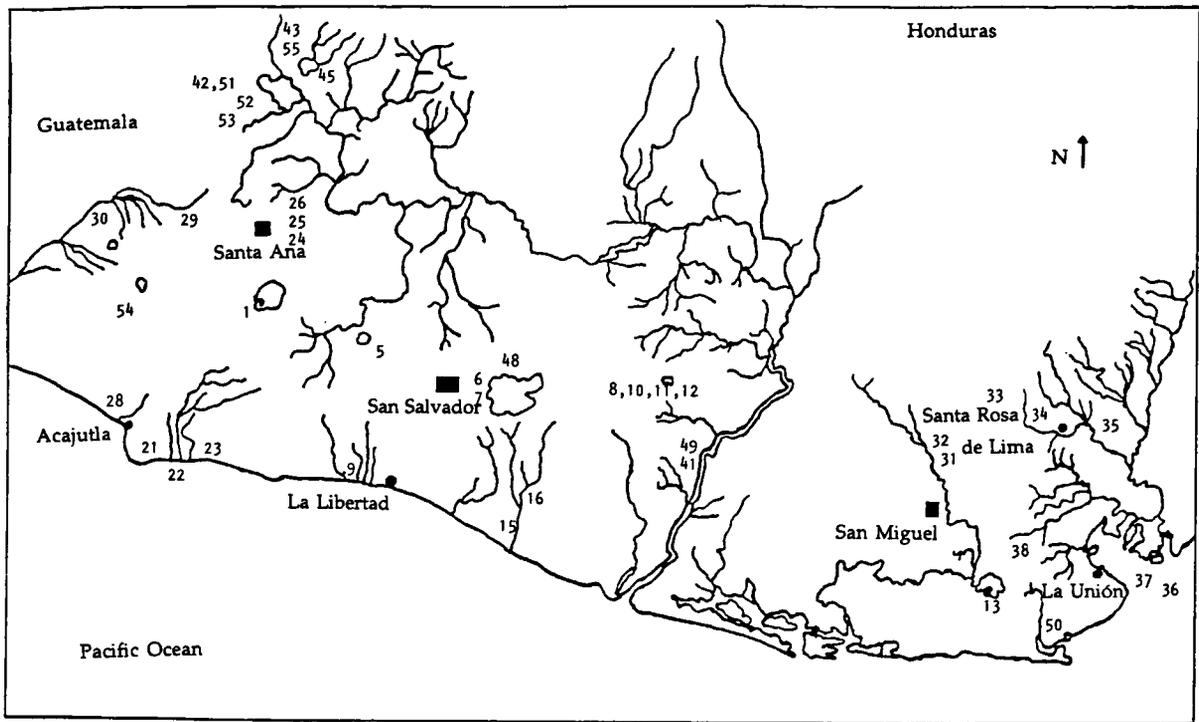
Fig. 1. Map of El Salvador, with localities numbered according to Boeseman (1956). Region 1 consists of the following station numbers: 24−26, 41−43, 45, 49, 51−53, 55, region 2: 1, 5−8, 10−12, 30, 48, 54, region 3: 9, 15, 16, 21−23, 28, region 4: 13, 31−38, 50.

The present paper records the variation in samples of *Poecilia* collected in El Salvador by Boeseman in 1953 (Boeseman, 1956). The material contains two species, *P. salvatoris* and *P. marcellinoi.* These species occur sympatrically in two categories of biotopes: (1) fresh water (large river systems, like the Río Lempa and river systems in the eastern part of the country, and the mountain lakes in the western part of the country), and (2) downstream localities with marine influences (relatively small rivers running from the mountain range to the Pacific Ocean) (Fig. 1).

Material and methods

Measurements were made by vernier callipers reading to 0.1 mm. From the type locality of *P. marcellinoi*, morphometric and meristic data are recorded from both *P. marcellinoi* and *P. salvatoris*, following Miller (1975) (Tables I & II). Specimens were examined from 35 localities in El Salvador.

Fig. 1 shows the localities for the material examined. The collection numbers (in parentheses) represent the localities mentioned by Boeseman (1956): (1) Lago de Coatepeque, (4) Río Opulujapa, (5) Laguna Chanmico, (6, 7, 7a, 48) Lago de Ilopango, (8, 10) Laguna de Apastepeque, (9) Río Majagual, (11) Riachuelo cerca de la Laguna de Apastepeque, (12) Riachuelo tributario del Río Acelhuate, (13) Laguna Olomega, (15) Río Comalapa, (16) Río Jiboa, (21) Río Chimalapa, (22) Río Banderas, (23) Río Mandinga, (24) Río Zarco, (25) Río Amayo al oeste del Río Agua Caliente, (26) Río Amayo cerca del Río Agua Caliente, (28) Río Coyol, (29) Laguna de Chalchuapa, (30) Laguna Del Llano, (31) Río Grande de San Miguel, (32) Río Las Marias, (33) Río cerca de las Lomas de la Coyotera, (34) Río Agua Caliente, (35) Río Sirama, (36) Paso de Conchagua, (37) Río Las Maderas, (38) Río El Carmen, (41) Poza Los Tres Amates, (42, 51, 52, 53) Lago de Guija, (43, 55) Laguna de Metapán, (45) Charco pequeño cerca Metapán, (49) Riachuelo en selva al sur de la Carretera Panamericana, km 80−81 este, (50) Laguna Managuara, (54) Laguna Verde.

The localities are sorted into four regions: (1) Río Lempa basin with mainly upstream localities, (2) mountain lakes with stable freshwater habitats, (3) rivers south of the mountain lakes, representing unstable downstream habitats, and (4) rivers in the eastern part of El Salvador.

Variation in meristic characters is recorded by counting dorsal and caudal fin rays following Hubbs & Lagler (1947). For the dorsal fin, position, depressed length, and basal length is

recorded in thousandths of the standard length. Least depth of caudal peduncle is measured instead of body depth, avoiding the variation prompted by pregnancy or feeding state of specimens.

The variation within samples in every region is given as the standard deviation (Tables III & IV). From RMNH 19811, the holotype and allotype of *P. marcellinoi* were selected, and were given other registration numbers (RMNH 31771 and RMNH 31772, respectively). Since they belong to the same population, they are recorded as one sample (RMNH 19811+).

Systematic section

Poecilia marcellinoi new species
(Tables I, III, IV; Figs. 2, 3, 6a)

Synonymy. – *Poecilia sphenops*; Hildebrand, 1925: 255, fig. 11 (non Valenciennes, 1846, in part); Boeseman, 1956: 83–84 (non Valenciennes, 1846, in part).

Material examined. – Mountain lakes west of the Río Lempa outlet: RMNH 31771, holotype (male, 59.0 mm SL), Lago de Ilopango (coll. Boeseman, sta. 6), 19-II-1953; RMNH 31772, allotype (female, 62.0 mm SL), same data as RMNH 31771; RMNH 19811, 9 paratypes, same data as RMNH 31771; RMNH 19813, 202 paratypes, Lago de Ilopango (sta. 7, 7a), 21-II-1953; RMNH 19816, 50 paratypes, Laguna Verde (sta. 54), 11-VI-1953; RMNH 31759, 2 paratypes, Laguna Chanmico (sta. 5), 18-II-1953.

Río Lempa drainage: RMNH 19815, 40 paratypes, Riachuelo en selva al sur de la Carretera Panamericana, km 80–81 este (sta. 49), 27/28-V-1953; RMNH 19821, 46 paratypes, Laguna de Metapán (sta. 55), 13-VI-1953; RMNH 19824, 10 paratypes, same data as RMNH 19821; RMNH 19830, 9 paratypes, Lago de Guija (sta. 51, 52, 53), 10/13-VI-1953; RMNH 19837, 59 paratypes, Poza Los Tres Amates (sta. 41), 21-IV-1953; RMNH 19854, 2 paratypes, Metapán (sta. 45), 12-V-1953; RMNH 31753, 4 paratypes, same data as RMNH 19830; RMNH 31754, 2 paratypes, same data as RMNH 19830; RMNH 31755, 10 paratypes, Río Amayo (sta. 26), 1-IV-1953; RMNH 31756, 1 paratype, Río Amayo (sta. 25), 1-IV-1953; RMNH 31757, 18 paratypes, Laguna de Metapán (sta. 55), 12-V-1953; RMNH 31758, 2 paratypes, Lago de Guija (sta. 42), 11-V-1953; RMNH 31773, 8 paratypes, Río Zarco (sta. 24), 1-IV-1953.

Rivers west of outlet of Río Lempa: RMNH 19847, 10 paratypes, Río Coyol (sta. 28), 8-IV-1953; RMNH 19858, 1 paratype, Río Banderas (sta. 22), 25-III-1953; RMNH 19832, 11 paratypes, Río Mandinga (sta. 23), 25-III-1953; RMNH 31760, 3 paratypes, Río Chimalapa (sta. 21), 15-III-1953.

Rivers east of Río Lempa: RMNH 31761, 9 paratypes, Río Las Marias (sta. 32), 16-IV-1953; RMNH 31762, 6 paratypes, same data as RMNH 31761; RMNH 31763, 6 paratypes, Río Las Maderas (sta. 37), 17-IV-1953; RMNH 31764, 2 paratypes, Río El Carmen (sta. 38), 18-IV-1953; RMNH 31765, 6 paratypes, Río Agua Caliente (sta. 34), 16-IV-1953; RMNH 31770, 13 paratypes, Río near las Lomas de Coyotera (sta. 33), 16-IV-1953.

Etymology. – This species is named for my friend Marcellino Rozemeyer, who has helped me throughout my studies.

Diagnosis and description. – *Poecilia marcellinoi* is a medium sized member of the *P. sphenops* complex (Rosen & Bailey, 1963; Schulz & Miller, 1971). Specimens from fresh water (Río Lempa drainage and mountain lakes) are usualy larger (50–60 mm SL) than specimens from downstream in brackish water (30–40 mm SL). Largest specimens examined: female: 62.0 mm SL, male: 59.0 mm SL.

The positions of the dorsal and anal fins are posterior of a point midway between the tip of the snout and the caudal fin base. The dorsal fin reaches halfway the caudal peduncle when depressed, with 8–10 (modally 9) rays. Anal fin with 9 rays, lateral scales 25–26 (Table I). The inner jaw teeth are tricuspid. Preorbital pores 1 and 2a present (Gosline, 1949).

The gonopodium is similar to that of *P. mexicana* (Miller, 1975: Fig. 3), with a membranous hook on ray 3, and with the 8–11 distal segments on rays 4A and 4P unserrated. Gonopodial ray 5P with a retrorse spine (Fig. 6a).

Body form and pigmentation are shown in Figs. 2 and 3. Table I records proportional body measurements and meristic characters of the holotype, the allotype, and three paratypes of each sex that come from the same locality. There is considerable variation in characters over their range (Tables III & IV).

Both sexes have a conspicuous black blotch on the scales at the base of the caudal fin; the body of the males has four to six faint stripes. The sides of the body have a reticulate pattern with light brown dots. This pattern becomes darker dorsally. The fins have little pigment, not forming dark spots or blotches. Females have the same body pigmentation as males, with additionally four or five rows of spots along the body. In addition to the differences in pigmentation, the dorsal and anal fin (= gonopodium) are more anterior in males than in females. In the males the dorsal and pelvic fins are also longer and the body is deep compared to females.
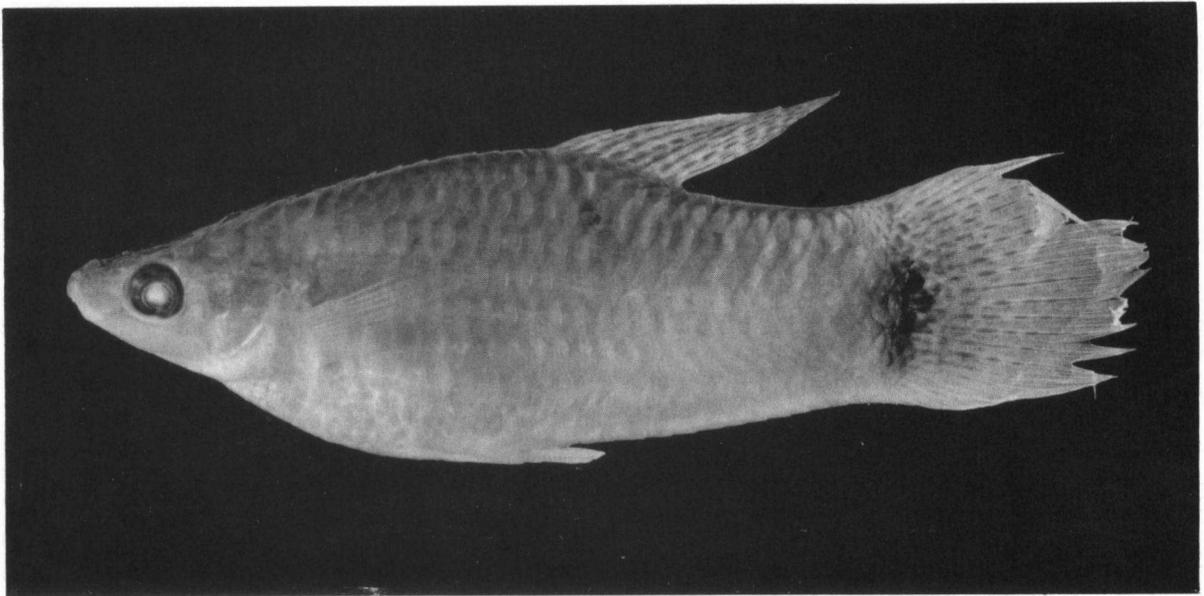
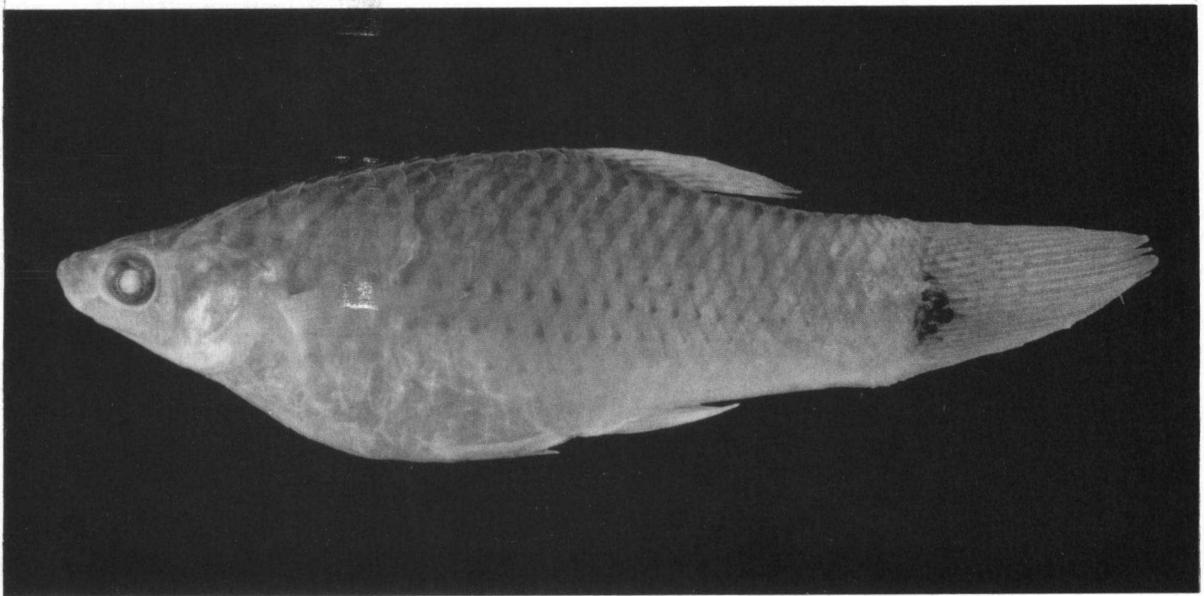Fig. 2a. Holotype of P. marcellinoi (photo: Louis van der Laan).

Fig. 2b. Allotype of P. marcellinoi (photo: Louis van der Laan).

Comparisons. – The shape of the inner jaw teeth has proven critical in the recognition of species (Schultz & Miller, 1971). *Poecilia marcellinoi* most resembles *P. sphenops*, another Central American species with tricuspid teeth (cf. Miller, 1983). Like this species, *P. marcellinoi* also has 9 anal fin rays and rows of spots along the sides of the females. *Poecilia marcellinoi* differs from *P. sphenops* in the number of scales around the caudal peduncle (modally 16). In *P. sphenops* (south of the Isthmus of Tehuantepec, Mexico) this is 18 (Schultz & Miller, 1971: 284). *Poecilia marcellinoi* possesses preorbi-
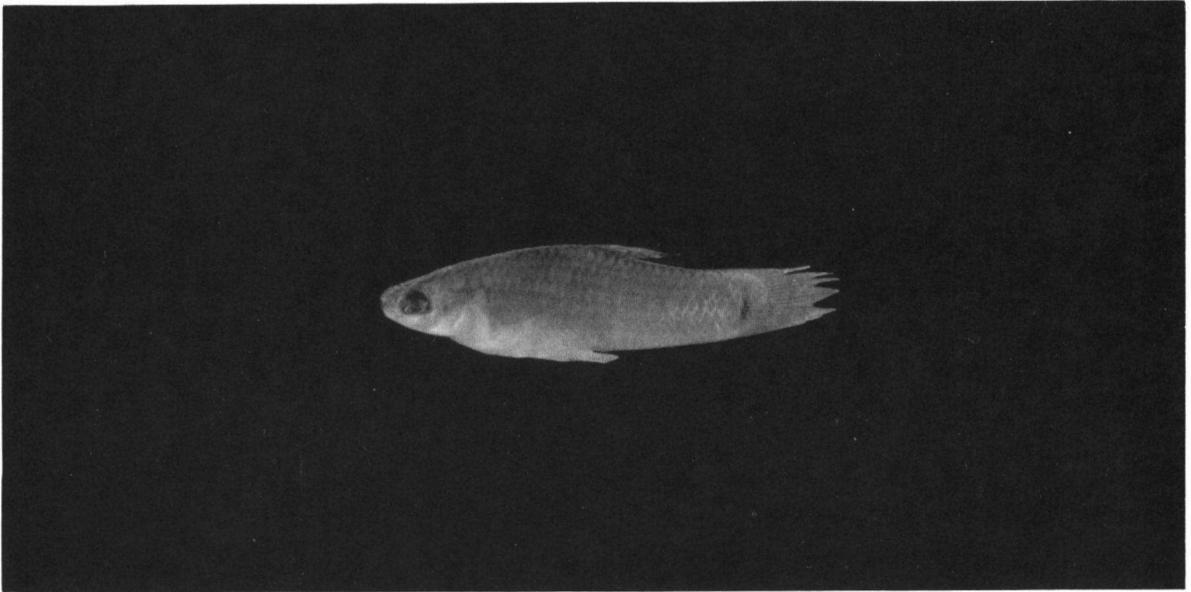
Fig. 3a. Male paratype of *P. marcellinoi* from a coastal region (same scale as Fig. 2; photo: Louis van der Laan).
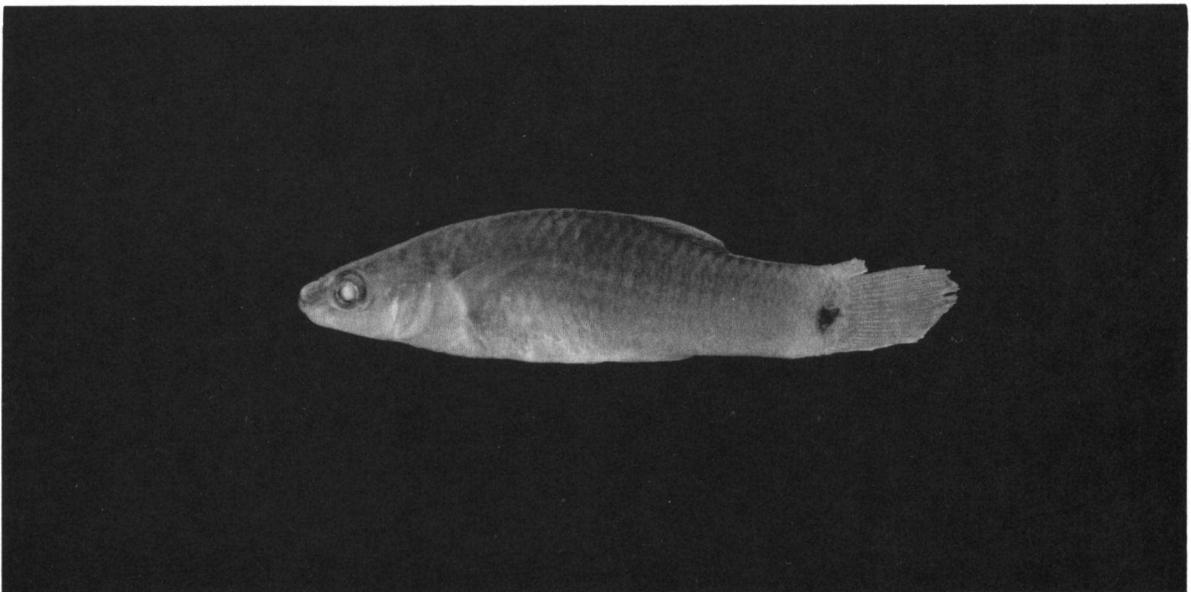

Fig. 3b. Female paratype of *P. marcellinoi* from a coastal region (same scale as Fig. 2; photo: Louis van der Laan).

tal pores 1 and 2a, which are lacking in *P. sphenops*, and has a distinct blotch at the caudal base. Another tricuspid species occurring on the Pacific side of Mexico, *P. chica* Miller, 1975, is confined to southern Jalisco, Mexico and has only 8 anal fin rays.

Distribution. − *P. marcellinoi* is presently known only from El Salvador.

However, since it is distributed all over the country, it probably also occurs in neighbouring countries.

Table I. Mean proportional measurements (in thousandths of SL, SL in mm) and meristic data of *P. marcellinoi* from the type locality. In the measurement section, data of holotype and allotype are given in parentheses; in the meristic counts, the number of specimens counted is given in parentheses.

P. marcellinoi Measurements	Holotype	Average of three male paratypes	Allotype	Average of three female paratypes
Standard length	59.0	53.9	62.0	58.3
Predorsal length	592	618	616	639
Dorsal origin to caudal base	402	407	397	389
Anal origin to caudal base	508	477	360	387
Body depth	373	373	355	359
Head length	256	254	245	264
Head width	175	194	176	181
Caudal peduncle length	475	430	290	313
Caudal peduncle least depth	232	217	190	198
Interorbital least bony width	127	140	140	144
Mouth width	110	104	106	111
Snout length	47	52	71	63
Orbital length	66	62	60	63
Dorsal depressed length	356	327	258	240
Basal length	161	114	139	139
Anal depressed length	181	198	182	174
Basal length	–	–	89	82
Pectoral length	229	223	213	200
Pelvic length	186	165	142	139
Caudal length	319	305	289	285

Meristic counts	males, including holotype		females, including allotype	
Dorsal fin rays	9 ($n = 2$)		9 ($n = 4$)	
Anal fin rays	–		9 ($n = 3$)	
Pectoral fin rays	–		16 ($n = 2$), 17 ($n = 1$)	
Caudal fin rays	20 ($n = 1$), 22 ($n = 1$)		20 ($n = 1$), 21 ($n = 1$)	
Scales in a lateral series	25 ($n = 2$), 26 ($n = 1$)		24 ($n = 1$), 25 ($n = 1$), 26 ($n = 2$)	
Scales around caudal peduncle	16 ($n = 3$)		16 ($n = 3$), 17 ($n = 1$)	
Predorsal scales	12 ($n = 3$)		12 ($n = 1$), 13 ($n = 2$)	

Poecilia salvatoris Regan, 1907
(Tables II–IV, Figs. 4, 5, 6b)

Synonymy. – *Poecilia thermalis* Günther, 1866: 341. (Preoccupied; type locality: El Salvador, San Salvador, warm springs.)

   Poecilia salvatoris Regan, 1907: 104, plate 14 figs. 2–3 (replacement name for *P. thermalis* Günther, 1866); *Poecilia sphenops salvadoris*; Hubbs, 1935: 11.

   Mollienesia sphenops petersi Schindler, 1956: 1–4, fig. 1. (Type locality: Honduras, lake Yojoa.)

   Poecilia sphenops; Hildebrand, 1925: 255, fig. 11 (non Valenciennes, 1846, in part); Boeseman, 1956: 83–84 (non Valenciennes, 1846, in part); Rosen & Bailey, 1963: 49 (non Valenciennes, 1846, in part).

Material examined. – Mountain lakes west of the Río Lempa outlet: BMNH 1977.8.10.1–6, 1 syntype (of 6) of *P. salvatoris*,

El Salvador, San Salvador, warm springs; BMNH 1864.1. 26–191, 13 syntypes of *P. salvatoris*, same data as BMNH 1977.8.10.1–6; RMNH 19814, 21 specimens, Laguna Chanmico (sta. 5), 18-II-1953; RMNH 19820, 18 specimens, Lago de Coatepeque (sta. 1), 12-II-1953; RMNH 19823, 184 specimens, Laguna de Chalchuapa (sta. 29), 10-IV-1953; RMNH 19827, 81 specimens, Laguna Apastepeque (sta. 10), 1-III-1953; RMNH 19848, 1 specimen, Río Acelhuate (sta. 12), 7-III-1953; RMNH 19849, 25 specimens, Lago de Ilopango (sta. 48), 21-V-1953; RMNH 19850, 2 specimens, Laguna Del Llano (sta. 30), 10-IV-1953; RMNH 19851, 12 specimens, Laguna Apastepeque (sta. 8), 24-II-1953; RMNH 19856, 131 specimens, same data as RMNH 19814; RMNH 19857, 1 specimen, Laguna Apastepeque (sta. 11), 1-III-1953; RMNH 27675, 13 specimens, Lago de Ilopango (sta. 6), 19-II-1953; RMNH 31769, 1 specimen, Laguna Verde (sta. 54), 11-VI-1953.

   Río Lempa drainage: RMNH 19819, 10 specimens, Lago de Guija (sta. 51, 52, 53), 10/13-VI-1953; RMNH 19825, 44 speci-

Table II. Proportional measurements (in thousandths of SL, SL in mm) and meristic data of *P. salvatoris* from the type locality of *P. marcellinoi*; in the meristic counts, the number of specimens counted is given in parentheses.

P. salvatoris Measurements	Average of four males	Average of seven females
Standard length	50.0	62.9
Predorsal length	551	602
Dorsal origin to caudal base	444	414
Anal origin to caudal base	586	386
Body depth	353	346
Head length	221	219
Head width	178	199
Caudal peduncle length	557	325
Caudal peduncle least depth	214	177
Interorbital least bony width	123	133
Mouth width	97	105
Snout length	28	38
Orbital length	59	55
Dorsal depressed length	374	248
Basal length	146	139
Anal depressed length	220	173
Basal length	–	77
Pectoral length	236	231
Pelvic length	212	141
Caudal length	322	261

Meristic counts	males	females
Dorsal fin rays	10 (*n* = 4)	9 (*n* = 1), 10 (*n* = 6)
Anal fin rays	–	9 (*n* = 7)
Pectoral fin rays	–	15 (*n* = 1), 16 (*n* = 4), 17 (*n* = 1)
Caudal fin rays	19 (*n* = 1), 20 (*n* = 2)	19 (*n* = 1), 20 (*n* = 4)
Scales in a lateral series	26 (*n* = 3), 28 (*n* = 1)	25 (*n* = 2), 26 (*n* = 2), 27 (*n* = 2)
Scales around caudal peduncle	16 (*n* = 3)	15 (*n* = 2), 16 (*n* = 5)
Predorsal scales	12 (*n* = 1), 13 (*n* = 3)	12 (*n* = 1), 13 (*n* = 4), 14 (*n* = 2)

mens, same data as RMNH 31773; RMNH 19831, 2 specimens, Laguna de Metapán (sta. 55), 15-V-1953; RMNH 19836, 15 specimens, Río Amayo (sta. 26), 1-IV-1953; RMNH 19839, 19 specimens, Río Amayo (sta. 25), 1-IV-1953; RMNH 19844, 1 specimen, Laguna de Metapán (sta. 55), 12-V-1953; RMNH 19853, 2 specimens, Lago de Guija (sta. 42), 11-V-1953; RMNH 31767, 4 specimens, Laguna de Metapán (sta. 55), 13-VI-1953; RMNH 31768, 9 specimens, same data as RMNH 31767.

Rivers west of outlet Río Lempa: RMNH 19817, 51 specimens, Río Chimalapa (sta. 21), 15-III-1953; RMNH 19838, 7 specimens, Río Comalapa (sta. 15), 15-III-1953; RMNH 19845, 2 specimens, Río Jiboa (sta. 16), 15-III-1953; RMNH 19855, 21 specimens, Río Majagual (sta. 9), 27-II-1953.

Rivers east of Río Lempa: RMNH 19812, 34 specimens, Río near las Lomas de Coyotera (sta. 33), 16-IV-1953; RMNH 19818, 46 specimens, Río Las Marias (sta. 32), 16-IV-1953; RMNH 19822, 56 specimens, Río Las Maderas (sta. 37), 17-IV-1953; RMNH 19826, 9 specimens, Río El Carmen (sta. 38), 18-IV-1953; RMNH 19828, 32 specimens, Paso de Con-chagua (sta. 36), 17-IV-1953; RMNH 19829, 1 specimen, Laguna Olomega (sta. 13), 4/7-III-1953; RMNH 19834, 30 specimens, Río Sirama (sta. 35), 17-IV-1953; RMNH 19835, 39 specimens, Río Agua Caliente (sta. 34), 16-IV-1953; RMNH 19841, 13 specimens, same data as RMNH 19818; RMNH 19846, 1 specimen, Río Grande de San Miguel (sta. 31), 16-IV-1953; RMNH 19852, 2 specimens, Laguna Managuara (sta. 50), 14-V-1953.

One locality is not indicated in Fig. 1: sta. 4 (RMNH 19842, 9 specimens of *P. salvatoris*), Río Opulujapa, which is probably a small river in the western part of the country.

Diagnosis. – This species is a member of the *P. sphenops* complex. Largest specimens examined: female: 92.1 mm SL, male 51.5 mm SL. The dorsal and anal fin have more or less the same position as in *P. marcellinoi*. Dorsal and caudal fin have pigmented spots, in the former these spots form one or
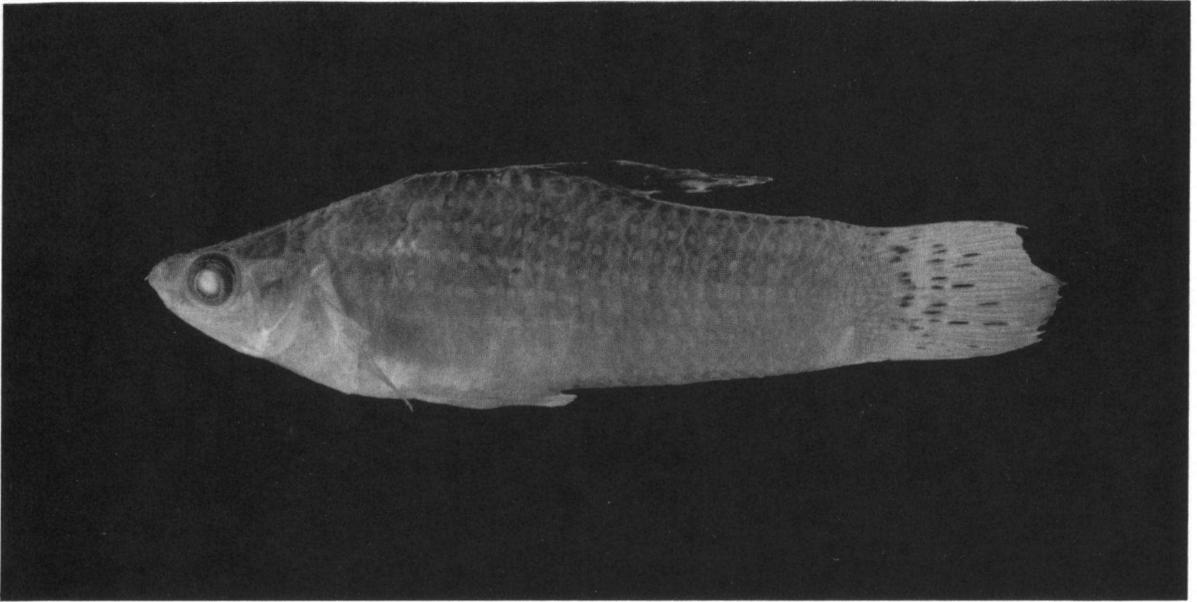
Fig. 4a. Male of P. salvatoris from the type locality of P. marcellinoi (same scale as Fig. 2; photo: Louis van der Laan).
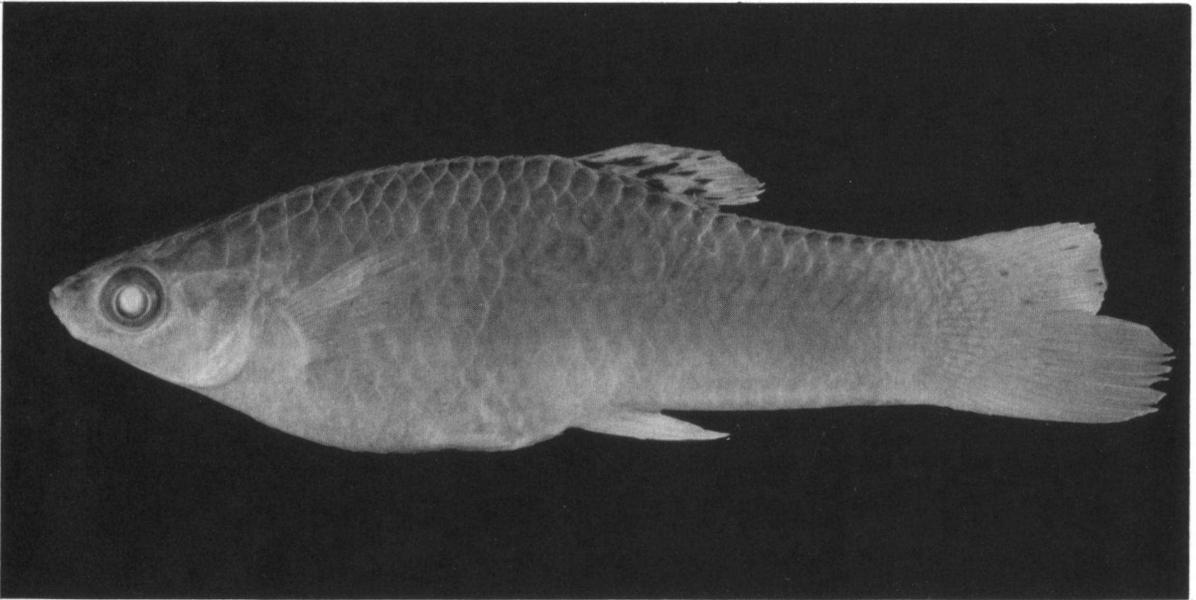

Fig. 4b. Female of P. salvatoris from the type locality of P. marcellinoi (same scale as Fig. 2; photo: Louis van der Laan).

two large blotches that are sometimes the size of the entire fin. Several specimens have four to seven conspicuous vertical stripes on the body (Figs. 4 & 5). Dorsal fin with 9–11 (modally 10) rays, anal fin with 9 rays, lateral scales 26–28 (Table II). Inner jaw dentition unicuspid. Preorbital pores 1 and 2a

are present. The gonopodium is similar to that in P. marcellinoi (Fig. 6b).

Comparison. — Poecilia salvatoris resembles P. mexicana, but differs in some meristic characters. Mature P. mexicana females have several rows of
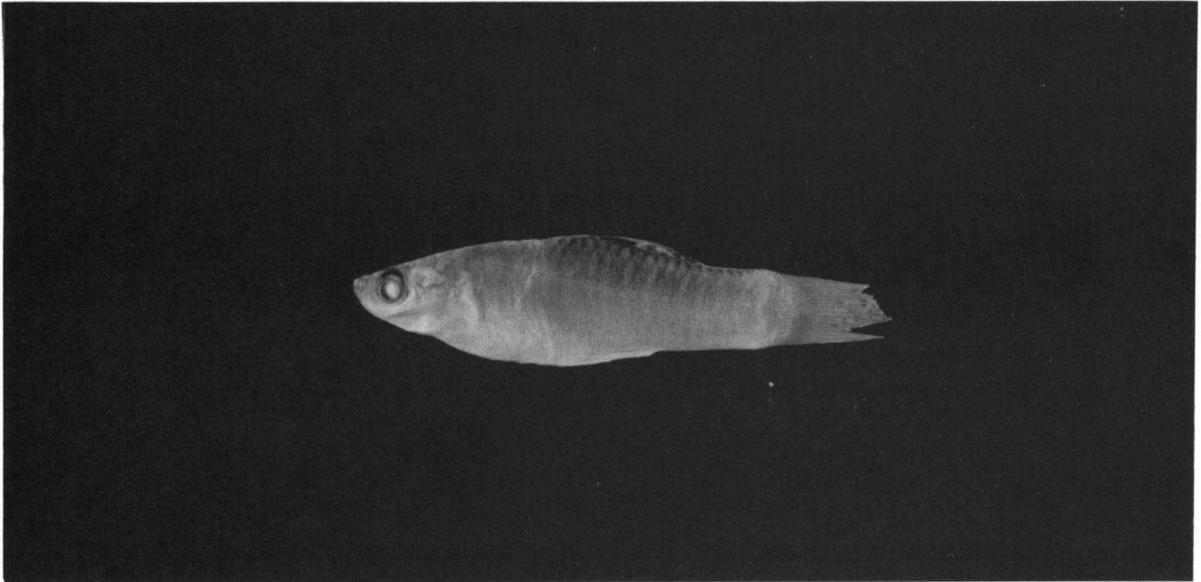
Fig. 5a. Male of *P. salvatoris* from a coastal region (same scale as Fig. 2; photo: Louis van der Laan).
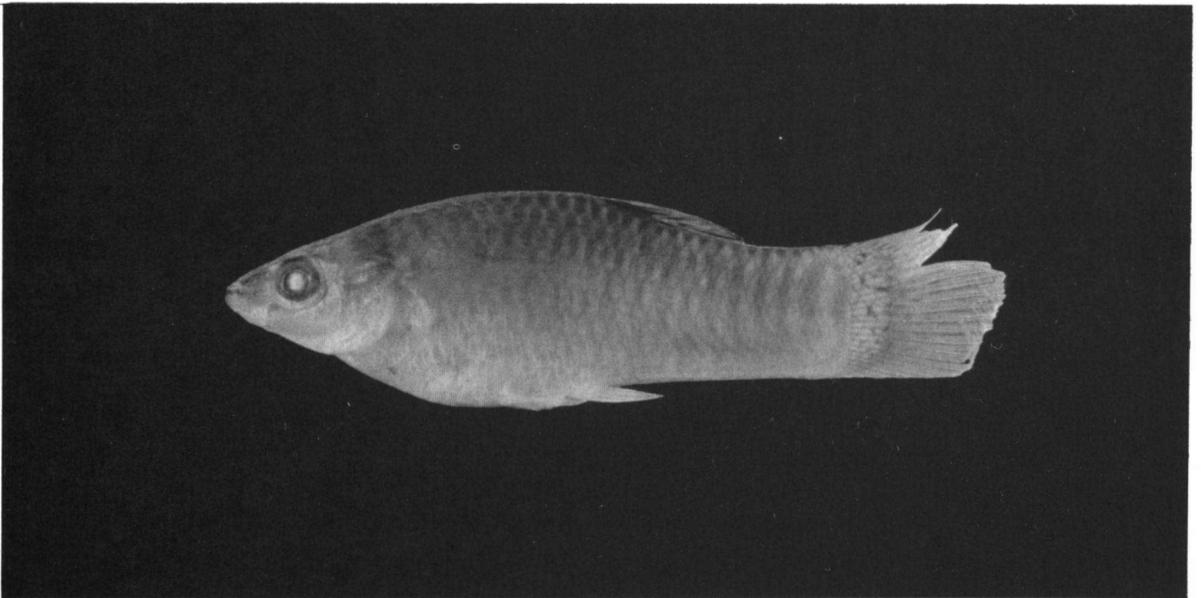

Fig. 5b. Female of *P. salvatoris* from a coastal region (same scale as Fig. 2; photo: Louis van der Laan).

black spots on their sides, lacking in *P. salvatoris*. The high degree of agreement in characters with *P. mexicana* indicates close relationship.

In El Salvador, *P. marcellinoi* and *P. salvatoris* occur largely sympatrically. The two El Salvadorian species have many similarities, like the variabili-

ty of body sizes (Figs. 2–5). However, *P. marcellinoi* has tricuspid teeth and pigmented scales covering the base of the caudal fin, forming a caudal blotch, whereas *P. salvatoris* has unicuspid teeth and a blotch on the anterior basal part of the dorsal fin, sometimes extending over most of the fin. All
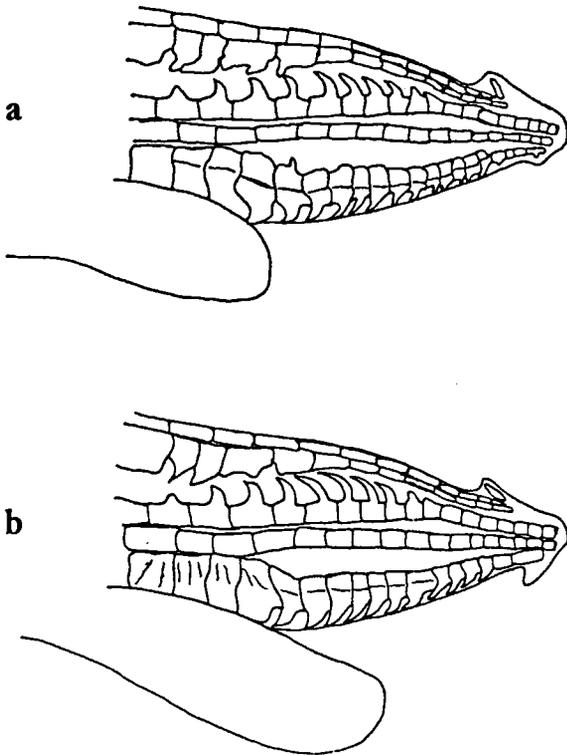
Fig. 6. Gonopodial tips: a, *P. marcellinoi* (holotype, RMNH 31771); b, *P. salvatoris* (largest male, RMNH 27675).

other characters vary in degree rather than in kind, in sympatric freshwater populations more than in brackish water populations (Tables I–IV). The position of the dorsal fin is more posterior in *P. marcellinoi*, with fewer rays (modally 9 versus 10 in *P. salvatoris*). *Poecilia salvatoris* has a deeper body and a longer head than *P. marcellinoi*. Furthermore, there is a slight difference in the number of scales: *P. salvatoris* has more scales in a lateral series and more predorsal scales than *P. marcellinoi* (respectively 26–28 scales versus 25–26 scales, and 13 (modally) versus 12 (modally)). However, *P. marcellinoi* has more scales around the caudal peduncle (16 versus 15–16 in *P. salvatoris*).

Between these two species, hybridization is suspected. In several lots, seemingly containing only one species, specimens are found with combined specific characters, indicating hybridization and therefore the presence of the other species within the habitat. In the eastern rivers of El Salvador,

P. salvatoris is abundant, whereas nearly no adults of *P. marcellinoi* are found. In most samples from mountain lakes, *P. salvatoris* is predominant, with two exceptions: Laguna Verde in the western part of the country, which is dominated by *P. marcellinoi*, and Lago Ilopango near San Salvador, where both species occur in approximately equal numbers.

Distribution. – *P. salvatoris* probably occurs from Guatemala to Nicaragua.

Results and discussion

Distribution of the species

The data from regions 1 and 2 in Tables III and IV, from upstream localities and freshwater lakes, are remarkably similar and are therefore considered characteristic of fresh water. They differ from the data from regions 3 and 4, the less stable habitats, which probably have marine influences.

In most samples from mountain lakes (region 2) *P. salvatoris* is dominant, with two exceptions: Laguna Verde in the western part of the country (where *P. marcellinoi* is dominant) and Lago Ilopango near San Salvador (both species in similar frequency) (Fig. 1, Tables III & IV). This suggests ecological preference and dominance of *P. salvatoris* in this situation.

Every river in region 3 has its own dominant species, like in the mountain lakes; the separation is not as strict as in region 2. Co-occurrence in larger river systems indicates that their niches are not identical.

Evaluation of the data

The data presented here are being subjected to further statistical analysis and will be presented more extensively in a subsequent paper.

Because of the small sample size of males (Table IV), the comparisons below are based on females. From the little evidence presented, however, it seems that males generally show the same pattern of differentiation, sometimes even more pronounced.

Table III. Comparison of means of meristic and proportional data (in thousandths of SL, SL in mm), with standard deviation (SD), in females of *P. salvatoris* and *P. marcellinoi*.

| *Poecilia salvatoris* ♀ ♀ | Region 1 18 | | Region 2 20 | | Region 3 8 | | Region 4 29 | |
n	average	SD	average	SD	average	SD	average	SD
Standard length	50.2	16.6	51.0	10.8	42.6	3.8	44.4	7.7
Dorsal fin rays	9.9	0.2	10.1	0.6	9.6	0.5	9.4	0.5
Caudal fin rays	18.7	0.8	18.5	0.8	19.5	0.5	19.3	0.8
Predorsal length	576	44	598	10	598	11	616	18
Least depth caudal peduncle	167	15	164	14	181	10	183	13
Depressed length dorsal fin	223	25	236	15	232	12	231	23
Dorsal fin basal length	129	16	134	9	131	7	131	18

| *Poecilia marcellinoi* ♀ ♀ | Region 1 27 | | Region 2 17 | | Region 3 7 | | Region 4 6 | |
n	average	SD	average	SD	average	SD	average	SD
Standard length	47.2	9.1	46.7	14.0	34.6	3.6	37.9	5.1
Dorsal fin rays	9.1	0.4	9.0	0.4	9.4	0.4	9.7	0.5
Caudal fin rays	18.2	0.8	19.4	1.4	18.4	0.9	18.3	1.3
Predorsal length	619	17	617	12	639	17	612	21
Least depth caudal peduncle	174	12	184	14	188	9	170	10
Depressed length dorsal fin	234	29	228	23	257	18	215	15
Dorsal fin basal length	128	10	120	11	137	22	126	13

Table IV. Comparison of means of meristic and proportional data (in thousandths of SL, SL in mm), with standard deviation (SD), in males of *P. salvatoris* and *P. marcellinoi*.

| *Poecilia salvatoris* ♂ ♂ | Region 1 3 | | Region 2 10 | | Region 3 2 | | Region 4 10 | |
n	average	SD	average	SD	average	SD	average	SD
Standard length	53.4	3.1	39	9.6	41.9	0.1	44.1	9.2
Dorsal fin rays	10	0	9.8	0.4	10	1.4	9.2	0.4
Caudal fin rays	18.7	0.6	18.9	0.9	20	0	19.3	0.8
Predorsal length	563	5.1	564	14.3	595	3.7	585	12.5
Least depth caudal peduncle	199	6.0	191	8.5	195	4.4	197	11.6
Depressed length dorsal fin	343	16.2	321	36.6	279	5.8	294	32.4
Dorsal fin basal length	167	5.0	154	18.0	138	3.8	140	17.1

| *Poecilia marcellinoi* ♂ ♂ | Region 1 9 | | Region 2 6 | | Region 3 1 | | Region 4 2 | |
n	average	SD	average	SD	average	SD	average	SD
Standard length	40.7	8.2	43.7	14.3	45.5	−	27.8	1.8
Dorsal fin rays	8.8	0.5	9	0	9	−	9.5	0.7
Caudal fin rays	18.1	1.2	19.7	1.6	18	−	19	1.4
Predorsal length	570	28.9	596	15.7	611	−	590	23.6
Least depth caudal peduncle	195	14.7	212	19.5	209	−	195	2.9
Depressed length dorsal fin	295	43.1	300	59.3	306	−	266	34.8
Dorsal fin basal length	137	8.5	141	25.4	143	−	135	1.0

This is most obvious in the development of the dorsal fin; in fresh waters there is strict differentiation and enlargement of the fin. This phenomenon is explained by sexual selection. In two similar species with female partner choice, the males show more differences in appearance than the females. This also explains the difference in pigmentation: *P. marcellinoi* has a pronounced caudal blotch, whereas *P. salvatoris* has a dorsal blotch.

Both species are larger in regions 1 and 2 (freshwater habitats) versus 3 or 4 (habitats with marine influences) (Table III). In regions 3 and 4 there is interspecific difference in size.

In freshwater habitats the size differences overlap (Table III). In general, *Poecilia salvatoris* is larger than *P. marcellinoi*. The trend in the size differences is similar in both species, in regions 1 and 2 both species are large compared to regions 3 and 4. This seems more evident in *P. marcellinoi* than in *P. salvatoris*.

Poecilia salvatoris has more dorsal fin rays than *P. marcellinoi*, except in regions 3 and 4, where their numbers overlap (Table III). Both species have a different number of dorsal fin rays between freshwater regions and brackish environments. Each species has 9 to 10 dorsal fin rays in regions 3 and 4, from which both differentiate differently, i.e., *P. salvatoris* has 10 (or more) dorsal fin rays in regions 1 and 2, where *P. marcellinoi* has modally 9 (or less) dorsal fin rays.

Both species have a variable number of caudal fin rays. Interspecific differences seem to exist in all regions (Table III). In most regions, *P. salvatoris* has 19−20 (modally 19) caudal fin rays, but 18−19 (modally 18) in region 2. In three regions, *P. marcellinoi* has 18−19 (modally 18) caudal fin rays, but 19−20 (modally 19) in region 2.

Poecilia salvatoris has the dorsal fin more anterior than *P. marcellinoi* (Table III). The variation is considerable; both the area and the presence of the other species seem to have an effect on the position of the dorsal fin.

The caudal peduncle of *P. salvatoris* is deeper in regions 3 and 4 in relation to regions 1 and 2, and equally deep in *P. marcellinoi* in all regions.

Both species have different lengths of dorsal fins

in separate regions. The differences are probably due to the relatively large fins of the small sample of *P. marcellinoi* in region 3.

The basal lengths of dorsal fins are generally random and are probably due to the difference in number of dorsal fin rays.

The variations of the data observed are not simply explained by the influence of salinity (cf. Hubbs, 1926), where less somatic growth and more meristic differentiation is expected in fresh water (i.e., smaller specimens with a larger number of rays in the unpaired fins). In the present study, both species from freshwater environments grow larger and have larger dorsal fins, and *P. marcellinoi* has a lower number of dorsal fin rays. The number of caudal fin rays seems random, which also does not agree with the proposed mechanism.

Also the proposed character displacement (Rivas, 1982) is not fully applicable. Only in regions 1 and 2, a complete interspecific separation of characters is demonstrated. In regions 3 and 4, nearly all characters show overlap and intraspecific variation exceeds interspecific variation (Table III).

To explain the variations found in the present paper, a combination of the two aforementioned mechanisms is presented.

Hubb's proposed shift of intraspecific characters is based on a "one species, two environments" situation. Rivas' proposed mechanism, on the other hand, is based on a "two species, one environment" situation.

This latter mechanism is confirmed in the freshwater region. In less stable, presumably brackish environments, a lesser degree of intraspecific character development is possible (according to Hubbs' arguments) and character displacement is less plausible. Indirectly, this would confirm Hubbs' theory.

The observed variations are thus explained in this "two species, two environments" situation. Character displacement causes an increase of size within sympatric populations. In the El Salvador situation, where both species are sympatric throughout the country, size only increases where differentiation is possible (in accordance with Hubbs' mechanism). The same holds true for the

amount of variation in the number of dorsal fin rays and dorsal fin size. In sympatric populations they differ, when possible.

The variation in the number of caudal fin rays seems randomly distributed, but the interspecific differences within a region are always contrary. For this attribute, therefore, character displacement is found in all regions.

The morphometric data, i.e., predorsal length and least depth of caudal peduncle, are not only correlated to species and/or area, but are also inter-related to body size. The variation in depth of the caudal peduncle of *P. salvatoris* is explained by eco-logical differences between freshwater and marine habitats, whereas the caudal peduncle of *P. marcel-linoi* is relatively deep in all regions. This tendency is probably caused by character displacement, counteracting the smaller size of *P. marcellinoi*. Therefore, the diverse distribution of morpho-metric variations cannot directly be attributed to either of the proposed mechanisms (Hubbs, 1926; Rivas, 1982), nor by the combination proposed in this paper. These data show that both mechanisms have a combined and sometimes complementary effect on the variation of characters.

The effective working of the mechanisms described here is largely ignored in traditional *Poecilia* taxonomy. Hubbs (1935, 1936) described three subspecies of *P. sphenops*, viz., *P. s. vanty-nei*, *P. s. macrura*, and *P. s. altissima*, based on morphological and meristic differences, which he had indicated ten years earlier (Hubbs, 1926) to be ecological modifications. His tables in the descrip-tion of *P. s. altissima* (Hubbs, 1936: 238–245) are illustrative of this variation. Miller (1983) placed these intraspecific taxa in the synonymy of *P. mex-icana*, without any remarks on their subspecific sta-tus. Variations in upstream and downstream popu-lations, corresponding to the results of Feltkamp & Kristensen (1969) in *P. vandepolli* Van Lidth de Jeude, 1887, have been recorded in *P. mexicana* by Menzel & Darnell (1973).

The ecomorphological variations noted here in *Poecilia* represent a shift in life history (Hubbs, 1926). However, rather than an observed trade-off between growth and reproduction (Reznick, 1983), there is also a trade-off between somatic growth

and meristic differentiation (Hubbs, 1926). Since intraspecific life history traits in poeciliid fishes have been shown to be genetic (Reznick, 1982), the claims that subspecies in *Poecilia* are genetically stable are, therefore, not convincing. Species, rang-ing over large areas and occurring in different habitats, commonly show genetic adaptations to different environmental demands (Hubbs, 1926). Because populations interbreed readily, and occa-sional (Menzel & Darnell, 1973) or seasonal (Felt-kamp & Kristensen, 1969) migration is common, genetic drift (and therefore the formation of subspecies) is prevented. Recognition of subspecies in *Poecilia* is therefore doubtful and taxonomically confusing.

Acknowledgements

References

Boeseman, M., 1956. Sobre una coleccion de peces de la republi-ca de El Salvador. Comun. Inst. trop. Invest. cient. San Sal-vador, 5 (2/3): 75–88.

Feltkamp, C.A. & I. Kristensen, 1969. Ecological and morpho-logical characters of different populations of Poecilia sphenops vandepolli (Cyprinodontidae). Stud. Fauna Cura-çao, 31: 102–130.

Gosline, W.A., 1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus Fundulus. Occ. Pap. Mus. zool. Univ. Mich., 519: 1–17.

Günther, A., 1866. Catalogue of the fishes in the British Muse-um, 6: i–xv, 1–386 (printed by the order of the Trustees, London).

Hildebrand, S.F., 1925. Fishes of the republic of El Salvador, Central America. U.S. Bull. Bur. Fish., Wash., 41 (985): 237–287.

Hubbs, C.L., 1922. Variations in the number of vertebrae and

other meristic characters of fishes correlated with the temperature of the water development. Am. Nat., 56: 360–372.

Hubbs, C.L., 1924. Seasonal variation in the number of vertebrae in fishes. Pap. Mich. Acad. Sci., 2: 207–214.

Hubbs, C.L., 1926. Structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. Am. Nat., 60: 57–81.

Hubbs, C.L., 1935. Fresh-water fishes collected in British Honduras and Guatemala. Misc. publs. Mus. Zool. Univ. Mich., 28: 1–22, pls. I–IV, 1 map.

Hubbs, C.L., 1936. Fishes of the Yucatan Peninsula. Publs. Carnegie Mus., 17 (457): 157–287.

Hubbs, C.L. & K.F. Lagler, 1947. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci., 26: i–ix, 1–186, pls. 1–18.

Menzel, B.W. & R.M. Darnell, 1973. Systematics of Poecilia mexicana in northern Mexico. Copeia, 1973 (2): 225–237.

Miller, R.R., 1975. Five new species of Mexican poeciliid fishes of the genera Poecilia, Gambusia, and Poeciliopsis. Occ. Pap. Mus. Zool. Univ. Mich., 672: 1–44.

Miller, R.R., 1983. Checklist and key to the mollies of Mexico (Pisces: Poeciliidae: Poecilia, subgenus Mollienesia). Copeia, 1983 (3): 817–822.

Regan, C.T., 1907, in: Regan, C.T., 1906–1908. Biologia Centrali-Americana. Pisces. Ser. III: 1–203, figs. 1–24.

Reznick, D., 1982. The impact of predation on the life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. Evolution, 36 (6): 1236–1250.

Reznick, D., 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology, 64 (4): 862–873.

Rivas, L.R., 1982. Character displacement and coexistence in two poeciliid fishes of the genus Poecilia (Mollienesia) from Hispaniola. Northeast Gulf Sci., 5 (2): 1–24.

Rosen, D.E. & R.M. Bailey, 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography and systematics. Bull. Am. Mus. nat. Hist., 126 (1): 1–176.

Schindler, O., 1956. Mollienesia sphenops petersi nov. subsp., eine neue Poeciliiden-Unterart aus Nordwest-Honduras (Pisces, Familie Poeciliidae). Opusc. zool., München, 31: 1–6.

Schmidt, J., 1919. Racial investigations. III. Experiments with Lebistes reticulatus (Peters) Regan. Compt.-rend. Trav. Lab. Carlsberg, 14 (5): 1–7.

Schultz, R.J. & R.R. Miller, 1971. Species of the Poecilia sphenops complex in Mexico. Copeia, 1971 (2): 282–290.