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## Monophyly and Geography of the Río Pánuco Basin Swordtails (Genus *Xiphophorus*) with Descriptions of Four New Species

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### ABSTRACT

Four new species of the genus *Xiphophorus* (Cyprinodontiformes: Poeciliidae) from the Río Pánuco basin of eastern México are described. They, together with the four previously described swordtail species of this area and one recently described subspecies (herein treated as a full species), form a monophyletic group that is most closely related to one of the southern swordtails, *X. clemenciae*. The monophyly of the Río Pánuco (northern) swordtails is supported by four morphological and five electrophoretic characters. Relationships within the group are examined by means of parsimony analysis of morphological and electrophoretic characters. Three clades are described: (1) a *montezumae* clade with *X. montezumae* and *X. nezahualcoyotl* n. sp. as sister species, and *X. con-*

*tinens* n. sp. related to that pair; (2) a *cortezii* clade with *X. malinche* n. sp. and *X. birchmanni* as sister species, and *X. cortezii* related to that pair; and (3) a *pygmaeus* clade, with *X. nigrensis* and *X. multilineatus* n. sp. as sister species, and *X. pygmaeus* related to that pair. Among the three clades, the *cortezii* and *pygmaeus* groups are found to be most closely related.

The geographic distribution of this group is examined in detail. Sister taxa are allopatric with respect to each other with the exception of sympatry between *X. cortezii* and *X. birchmanni* and between *X. birchmanni* and *X. malinche*. This situation is discussed, and the relationship of the phylogenetic branching pattern to current distribution is explored for possible correlations with

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the geological history of the region. Both east-west and north-south dichotomies are recognized and related to uplift in particular regions of the Sierra

Madre Oriental and to the response of the major rivers to these uplifts.

## INTRODUCTION

Fishes of the genus *Xiphophorus* (Cyprinodontiformes: Poeciliidae) are commonly known as platyfishes and swordtails, and the 17 described species are found in freshwater streams of the Atlantic slopes of Mexico, Guatemala, Belize, and Honduras (Rosen and Bailey, 1963). These fishes have been studied extensively in many laboratories since 1927; perhaps more is known about this group than any other genus of teleost. Research has been concerned with its taxonomy, evolution, biogeography, genetics, endocrinology, behavior, embryology, and oncology, and good recent summaries can be found in Kallman (1984, 1989), Morizot and Siciliano (1984), Rosen (1979), and Vielkind and Vielkind (1982). Nevertheless, little is known about the details of the geographical distribution of the group, and several species have gone unrecognized for decades. The Río Pánuco basin of eastern Mexico, which drains the Sierra Madre Oriental and enters the Gulf of Mexico at Tampico, has a particularly diverse swordtail fauna, collectively known as the northern swordtails, consisting of five previously described forms and four more species described herein. This investigation examines in detail their phylogenetic relationships and geographical distribution.

In his 1960 review of the genus, Rosen (1960) recognized three species groups: the *maculatus* group (platyfishes), the *montezumae* group (northern swordtails), and the *helleri* group (southern swordtails). Subsequently, however, he rejected both the platyfish and northern swordtail species groups as "grade groups assembled largely on phenetic criteria of overall similarity and defined principally by means of primitive characters" (Rosen, 1979: 334). Indeed, the northern swordtails might easily have been defined as swordtails that lacked the advanced characters of the southern group, and Rosen (1979) presented evidence seeming to show that one clade of northern swordtails (*X. montezumae*–*X. cortezi*) was more closely related to the southern swordtails than to the other clade

of northern swordtails (*X. pygmaeus*–*X. nigrensis*).

Extensive collecting in the Río Pánuco basin has uncovered five new forms of northern swordtails. One of these (*X. birchmanni*) has recently been described as a subspecies of *X. montezumae* (Lechner and Radda, 1987); we recognize this form as a full species, closely related to *X. cortezi*. Following individual species accounts, we present an analysis of morphological, electrophoretic, pigmentary, and morphometric characters which unambiguously demonstrates that the northern swordtails are, in fact, a monophyletic group. Phylogenetic relationships within the group, relationships of the group to other members of the genus, the physical geography of the Pánuco area, and detailed patterns of distribution are also discussed.

## MATERIALS AND METHODS

Materials examined are recorded with each species account in which the number of specimens per lot is listed in parentheses after catalog number. Abbreviations for institutions and states are listed below, and names of rivers, which are quite idiosyncratic in this region of México, follow the synonymy given in figure 1, and are based on Carta Topográfica, Estados Unidos Mexicanos, Comisión de Estudios del Territorio Nacional, 1:50,000, 1972–1982.

Diagnoses and descriptions in the species accounts point out those characters used in the systematic analysis, in addition to autapomorphic features. Further general descriptive information is available in Rosen (1960, 1979).

Counts and measurements follow Miller (1948) except where noted. Illustrations of gonopodia are ink tracings of camera lucida drawings, using a Leitz dissecting microscope.

Character polarities were deduced using outgroup comparison and ontogenetic information. Parsimony analysis was facilitated

by PAUP (Vers. 2.4.0, D. Swofford), using the following options: BANDB, MISSING=9, ROOT=OUTGROUP, OPT=FARRIS. The MISSING=9 option was used in the PAUP analysis when character information (such as electrophoretic data for *X. malinche*) was unavailable or when characters (such as sword color in species without swords) were not applicable. The difference between these two conditions is indicated in the text.

Morphometric analyses were conducted using both multivariate and bivariate comparisons. Principal components analysis of the covariance matrix of log-transformed interlandmark truss distances (fig. 2) was performed for males, females, and juveniles of eight of the species (all except *X. malinche*), using the PC version of SAS (Vers. 6.02) run on an IBM-PC. Only the contrast of *X. montezumae* vs. *X. nezahualcoyotl* successfully described shape differences; these results are presented in the species description of *X. nezahualcoyotl*. Bivariate analysis investigated the relationship of standard length to sword length, producing a sword index. Sword indices are presented in table 1 and are discussed as part of the species accounts in which this character proved to be a useful discriminator.

Genetic variation at biochemical loci was investigated using the methods of Siciliano and Shaw (1976) and Morizot et al. (1977). Histochemical staining followed methods described in Siciliano and Shaw (1976) and Harris and Hopkinson (1977). Locus and protein nomenclature is that of Morizot and Siciliano (1984).

#### ABBREVIATIONS

##### *Institutions*

AMNH	American Museum of Natural History
SMF	Senckenberg-Museum, Frankfurt
SU	Stanford University
UMMZ	University of Michigan, Museum of Zoology

##### *States of México*

HID	Hidalgo
QUER	Querétaro
SLP	San Luis Potosí

TAMPS	Tamaulipas
VER	Veracruz

#### ACKNOWLEDGMENTS

This investigation is dedicated to the memory of Donn E. Rosen, who studied *Xiphophorus* from the time he was an undergraduate student and who was very much involved in the early part of this investigation.

Fieldwork in México has been supported by the New York Zoological Society, and permission to collect fishes was granted by a series of permits from the Mexican government, Dirección General de Regiones Pesqueras, Secretaría de Pesca (Permiso Nos. 1497, 1818, 3789, 130287-113-01, and 020987-113-03-1853 to K.D.K., and Nos. 242 2-0006/818, 340-346-204-2096, and 240184 333 04 31/414 to D.C.M.). This research was supported in part by grants from the National Institutes of Health, CA 289 09 and 397 29 (to D.C.M.) and GM 19934 (to K.D.K.), NSF BSR 16569 and USFWS contract 14-16-0002-85-920 (to D.C.M.). Preserved materials from these trips have been cataloged at the AMNH, and frozen material for electrophoresis was processed at the University of Texas System Cancer Center at Smithville. The live stocks have been maintained at the Osborn Laboratories of Marine Sciences of the New York Aquarium. We thank Dr. J. W. Atz, American Museum of Natural History, Dr. W. L. Minckley, Arizona State University, and Dr. R. R. Miller, University of Michigan, for critically reviewing the manuscript and for many valuable comments.

#### SPECIES ACCOUNTS

##### *Xiphophorus montezumae* Jordan and Snyder Montezuma Swordtail Figure 3

*Xiphophorus montezumae* Jordan and Snyder, 1900: 131-133 ("Río Verde" [Río Gallinas] near Rascón, SLP, México), holotype, SU 6145.

**DIAGNOSIS:** A swordtail with multiple zigzag lateral stripes, a well-developed reticulum, and a sword index averaging 1.0 (table 1).





**DESCRIPTION:** Long sword, ventrally edged with melanophores; well-formed hook on ray 5a of gonopodium; sword usually composed of unbranched rays, except when branched caudal-fin rays number 14 or more; grave spot (a pigment pattern of adult males, see p. 16) very well developed, not extending beyond the distal margin of the upper part of the caudal fin; distal dorsal sword pigment present; no polymorphic yellow carotenoid pigment patterns (see p. 18); sword upturned, at least when young, although fairly straight in larger males.

**REMARKS:** Males from populations other than that in the Río Gallinas have distinctive dorsal fin patterns. All males from Arroyo Ciénega Grande possess a basal row of macromelanophores and numerous macromelanophores throughout the fin above. Males of the Arroyo La Ciénega population also exhibit the basal row of melanophores as well as a second, more irregular row through the center of the fin; in a few males, however, this pattern is poorly developed and virtually absent. Fish from the Río Gallinas system are polymorphic for a macromelanophore pattern on the flank composed of irregular spots that extend onto the dorsal fin. Macromelanophore patterns are absent in the three other populations. The population near Tamasopo (Río Gallinas) may be polymorphic for the caudal blotch tail pattern, *Cb*, but a definite diagnosis was not possible from the preserved material. This micromelanophore pattern (see p. 15) is present in several northern swordtails. A few males of all the populations develop a deep bronze to red coloration. This pigmentation is produced by pterinophores, containing drosopterin, which are arranged in rows along each flank.

There are fixed electrophoretic differences between the Río Gallinas populations and those of the Arroyo Ciénega Grande and Arroyo La Ciénega, at the MP-4 (allele c), ES-2 (allele f), GAPD-2 (allele c), and MPI (allele a) loci. These are not yet thought to warrant

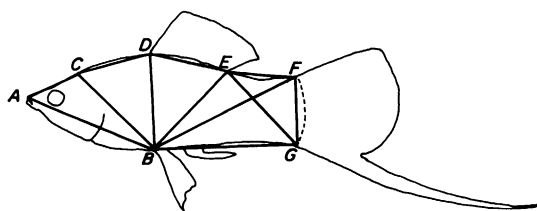


Fig. 2. Truss system for comparisons of shape. Fourteen interlandmark distances were measured: AB, snout to pelvic-fin insertion; AC, snout to occiput; CD, occiput to dorsal-fin origin; BD, pelvic-fin insertion to dorsal-fin origin; BE, pelvic-fin insertion to end of dorsal-fin base; BF, pelvic-fin insertion to dorsal edge of hypural plate; BG, pelvic-fin insertion to ventral edge of hypural plate; DE, dorsal-fin base length; EF, end of dorsal-fin base to dorsal edge of hypural plate (caudal peduncle length); EG, end of dorsal-fin base to ventral edge of hypural plate (caudal peduncle depth). Also measured were eye width (EW) and standard length (SL).

taxonomic distinction but the matter requires further study.

**DISTRIBUTION:** Mostly northern tributaries of Río Santa María, Río Pánuco drainage, SLP, except where noted: Río Gallinas system from Tamasopo and El Quince to Cascada Tamul, apparently absent from the Arroyo San Nicolás; Arroyo La Ciénega at Ojo Caliente and Arroyo Ciénega Grande; Arroyo Tanchanaquito, a southern tributary opposite Ojo Caliente. No *Xiphophorus* or any other fishes were found in an arroyo at La Jabonera, 5 km north of El Quince.

**MATERIAL:** All from SLP: Ojo Caliente—AMNH 75836(38), AMNH 75843(44), AMNH 45344(20), AMNH 76302(106); Arroyo Ciénega Grande—AMNH 75912(6), AMNH 75914(4), AMNH 75915(18); Río Gallinas at El Quince, Rascón—AMNH 75938(11), AMNH 75943(317); Río Gallinas at Tamasopo—AMNH 45286(6), AMNH 45287(2), AMNH 45288(1), AMNH

←

Calnali; ff. R. Conzintla; gg. R. Atlapexco; hh. R. El Encinal; ii. A. Soyatla; jj. R. Zontecomatlán. Synonymy notes: R. Tampaón is often called R. Tampoán or R. Tamuin; R. el Salto is often called R. Salto de Agua; R. Gallinas is often called R. Frio; R. Los Gatos is often called R. Mesillas; and A. La Playa is also referred to as A. La Flor.

TABLE 1  
Frequency Distribution of Sword Indices in *Xiphophorus montezumae* and *X. nezahualcoyotl*<sup>a</sup>

Species	Sword index						
	0-.2	.2-.4	.4-.6	.6-.8	.8-1.0	1.0-1.2	1.2-1.4
<i>X. montezumae</i>				8	35	31	12
<i>X. nezahualcoyotl</i>			31	11			

<sup>a</sup> Measurements taken on males 12 months after attaining sexual maturity. Data from laboratory-raised fish. Sword index = sword length/standard length.

45289(4), UMMZ 196697(40), UMMZ 203212(20), UMMZ 193511(20); Río Gallinas at Damian Carmona—AMNH 45307(30); laboratory descendants from Damian Carmona—AMNH 45308(9), AMNH 53939(2), AMNH 53940(8), AMNH 53941(1), AMNH 53942(1), AMNH 53943(1), AMNH 53944(1), AMNH 53945(8); laboratory descendants from Rascón—AMNH 76290(8), AMNH 76291(6), AMNH 76292(4), AMNH 76293(11), AMNH 76294(7), AMNH 76295(1), AMNH 76296(1); laboratory descendants from Ojo Caliente—AMNH 76297(1), AMNH 76298(2), AMNH 76299(1), AMNH 76300(1), AMNH 76301(1).

*Xiphophorus nezahualcoyotl*, new species  
Northern Mountain Swordtail  
Figure 4

*Xiphophorus montezumae montezumae*: Rosen, 1960: 92–96, 183–186, fig. 27.  
*Xiphophorus montezumae* ((Hamburg, 1964)): Lechner and Radda, 1987: 189, 191, 194–195, figs. 2, 3. Zander, 1967.  
*Xiphophorus*, sp. nov.: Zimmerer and Kallman, 1988: 299–307 (Río El Salto and Río Tamesí headwaters).

**DIAGNOSIS:** A swordtail species most closely related to *Xiphophorus montezumae*, with multiple zigzag lateral stripes and a well-developed reticulum; differing from that species in having a sword index averaging 0.56 (table 1), a relatively longer dorsal fin base, a more distinctly upturned sword, and smaller maximum adult size.

**TYPES:** The holotype, AMNH 88334, is a mature adult male, 43.0 mm SL, taken on April 6, 1985, by K. D. Kallman, D. C. Morizot, and M. Ryan, in the Arroyo Gallitos, 0.5 km west of Gallitos, an internal drainage, TAMPS, Mexico. Taken with the holotype

were the paratypes, AMNH 75845, consisting of 12 mature males, 18 females and juveniles. Other specimens referred to this species are listed under Material.

**DESCRIPTION:** Males with long sword, with dark ventral pigment; well-formed hook on ray 5a of gonopodium; many populations polymorphic for *Cb*; sword usually comprised of unbranched rays, except when branched caudal-fin rays number 14 or more; grave spot well developed, not extending beyond caudal margin; distal dorsal sword pigment present; polymorphic for a yellow xanthophore (carotenoid) pattern in the sword; sword distinctly upturned, although fairly straight in larger males.

**REMARKS:** The sword index is a useful discriminator between this species and its close relative, *X. montezumae* (table 1). Maximum size recorded from natural populations of *X. nezahualcoyotl* is 48 mm standard length versus 62 mm in *X. montezumae*. Multivariate analysis of the interlandmark distances of the truss system (fig. 2) shows that the dorsal fin base is relatively longer in *X. nezahualcoyotl* than in *X. montezumae*, extending further back along the caudal peduncle. Consequently, the caudal peduncle appears shorter, and the dorsal fin, when depressed, reaches the caudal fin. The caudal peduncle is also deeper in *X. nezahualcoyotl*, as seen by examining the variable loadings on the second principal component (table 2).

Some populations of *X. montezumae* and all of *X. nezahualcoyotl* are polymorphic for macromelanophore spotted pigment patterns on the flanks, but these are not identical. Only the pattern of *X. nezahualcoyotl* shows sex-linked inheritance (Kallman, 1983).

Lechner and Radda (1987) reviewed the “*Xiphophorus montezumae/cortezii* complex,” listing four subspecies of *X. montezumae*: *X. m. montezumae*, *X. m. cortezii*, *X.*

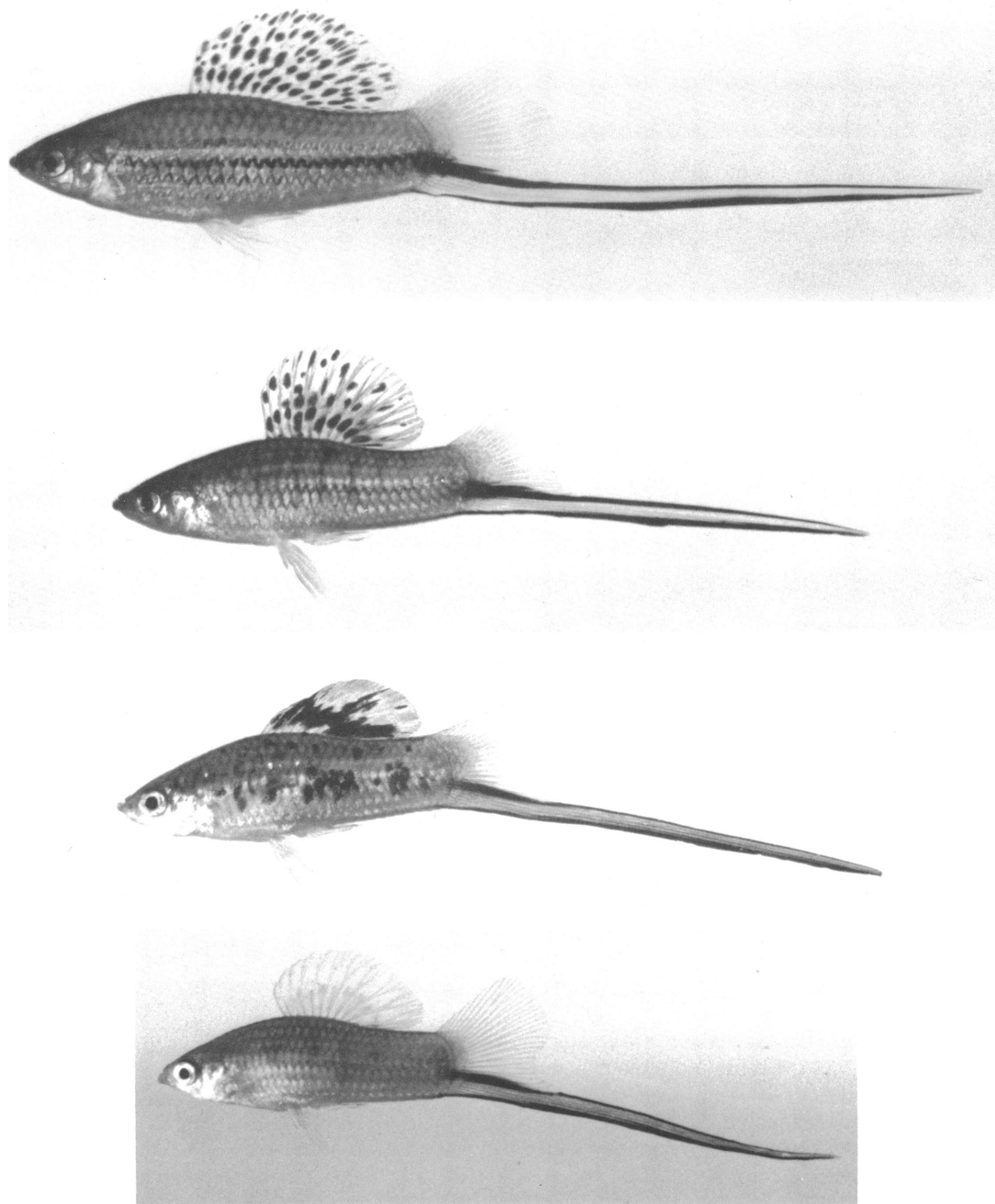


Fig. 3. *Xiphophorus montezumae*. **From top down:** Male, 50 mm SL, Ciénega Grande stock; male, 42 mm SL, La Ciénega stock; male, 42 mm SL, with polymorphic spotting pattern, Río Gallinas stock; male, 39 mm SL, wild-type, Río Gallinas stock. Only the males of the La Ciénega and Ciénega Grande (and Tanchanaquito) populations develop dorsal fin spotting which is a secondary sex character that develops at the time of sexual maturation. It can be induced in females by administration of androgenic hormone. Macromelanophore pattern in Río Gallinas stock is controlled by a single autosomal factor and can be inherited by both sexes. Pattern develops in males and females before sexual maturation; expression is stronger in males. Spotting on flank and dorsal fin are inherited together. Most individuals of the Río Gallinas population are wild-type. All four males were laboratory reared.

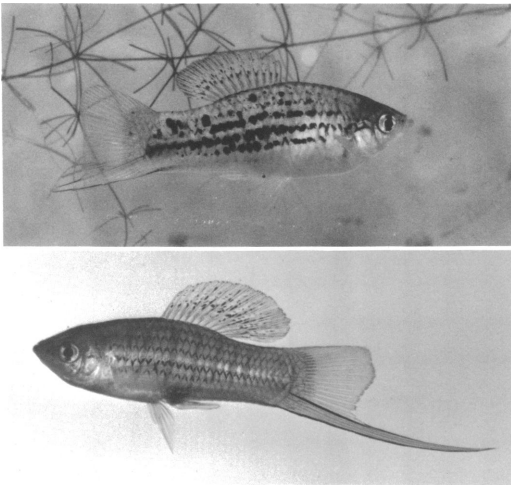


Fig. 4. *Xiphophorus nezahualcoyotl*. **Top:** Male, 41 mm SL, approaching sexual maturation and developing sword. Note that melanophore pigmentation along dorsal margin of sword develops first distally. Male also has macromelanophore pattern controlled by a y-linked factor, Río El Salto stock, laboratory reared. **Bottom:** Mature male, 44 mm SL, wild-type, with fully formed sword, laboratory reared, Río Santa María de Guadalupe stock.

*m. birchmanni*, and an undescribed form, *X. m.* ((Hamburg, 1964)). The first three we recognize as full species. The last, while not described, corresponds to *X. nezahualcoyotl* according to the distribution they give. The International Code of Zoological Nomenclature (1985), Article 1.b.6, declares that names proposed “as a means of temporary reference and not for formal taxonomic use as scientific names in zoological nomenclature” are excluded from the provisions of the code, and we believe that “*Xiphophorus montezumae* ((Hamburg, 1964))” is just such a temporary reference. Moreover, it would not be an available name for this species, because it was not “accompanied by a description or definition that states in words characters that are purported to differentiate the taxon” (Art. 13.a.i). Furthermore, “a name must be spelled out in Latin letters [no numbers or diacritical marks] and used as scientific name by the author when published” (Art. 11.b).

ETYMOLOGY: As the sister species of *X. montezumae*, we felt it appropriate to name this species for Nezahualcoyotl, the poet-phi-

TABLE 2  
Factor Pattern of PC1 and PC2 in an Analysis of Adult Males of *X. montezumae* (N = 80) and *X. nezahualcoyotl* (N = 80)

Variable <sup>a</sup>	PC1	PC2
AB .23 -.03		
AC	.19	.05
BC	.25	-.07
CD	.24	-.18
BD	.28	-.13
BE	.29	-.20
BF	.28	.06
BG	.28	.10
DE	.34	-.24
EF	.26	.75
EG	.29	.30
FG	.32	-.38
EW	.20	.15
SL	.25	.02

<sup>a</sup> Variable names refer to truss segments; see figure 2.

losopher emperor of Tezcoco (Texcoco), considered to be coequal with Montezuma, monarch of the Aztecs in the Aztec Triple Alliance (Prescott, 1843).

DISTRIBUTION: Río Tamesí drainage, TAMPS: extreme headwaters of Río Sabinas and Arroyo el Zarco but not Arroyo el Encino; extreme headwaters of Río Frío; springs in the vicinity of La Muralla and Ocampo and west of Santa María de Guadalupe. These springs flow into the Río Tamesí in the rainy season but are intermittent in the dry season, often disappearing underground for some stretches.

Internal drainages not connected by surface streams to any river in the Pánuco basin, TAMPS: Arroyo Gallitos at 1000 m elevation; spring at Callejones; unnamed stream at Ricardo Flores Magón.

Río Tampaón tributaries, SLP: Río Valles system (Río los Gatos and Río el Salto, at least as far downstream as the pools below the falls at Micos and the warm springs at El Jacube) and Río Tanchachín. The following stations are separated from the Río el Salto by long stretches of dry riverbed except during the rainy season: Arroyo el Caballote, west and south of Minas Viejas, elevation 500 m; Arroyo Hondo at Francia Chica, elevation 1220 m; Arroyo La Barranca, elevation 1150 m, at Santa Barbarita.

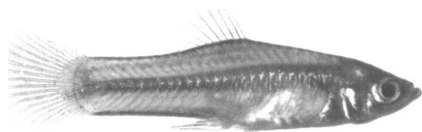


Fig. 5. *Xiphophorus continens*. Male, 22 mm SL. Laboratory reared.

No *Xiphophorus* population was found in the valley of Río Gallos Grandes (TAMPS) and Arroyo el Abrevadero (SLP), elevation 900–1000 m, which are connected to the source of the Río el Salto by the Arroyo el Tinajeno; nor in an internal drainage south of Santa Barbarita in Arroyo Milpillars at Diaz Gutiérrez and Arroyo Los Sabinas at Papagayos. All reports in the past to experimental work with *X. montezumae* actually refer to *X. nezahualcoyotl*.

**MATERIAL:** From SLP: Río el Salto—AMNH 75763(4); Minas Viejas—AMNH 75892(8), AMNH 75895(59); Francia Chica—AMNH 76790(211); Río Tanchachín—AMNH 75809(92); laboratory descendants from Río el Salto—AMNH 76287(1), AMNH 76288(1), AMNH 76289(3); El Sabinito—AMNH 45259(9); Santa Barbarita—AMNH 45260(61). From TAMPS: Arroyo Gallitos—AMNH 75845(30), AMNH 75843(31); Callejones—AMNH 75847(75); Ricardo Flores Magón—AMNH 75851(16); Arroyo el Zarco—AMNH 75900(20), AMNH 75905(129), AMNH 45283(271); Río los Gatos—AMNH 45262(30), AMNH 45261(7); Arroyo La Playa—AMNH 45339(5), AMNH 45343(3); laboratory descendants from Santa María de Guadalupe—AMNH 76285(1), AMNH 76286(4).

***Xiphophorus continens*, new species**  
El Quince Swordtail

Figure 5

*Xiphophorus*, sp. nov.: Zimmerer and Kallman, 1988: 299–307 (Río Ojo Frio).

**DIAGNOSIS:** A small slender species, with a slender caudal peduncle and with a midlateral stripe, composed of zigzags as well as one or two less prominent zigzag stripes above

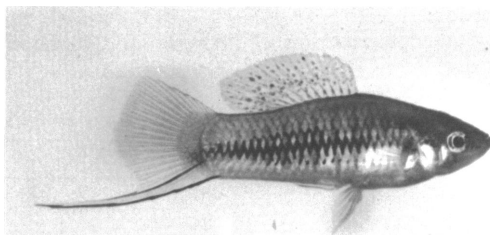


Fig. 6. *Xiphophorus cortezi*. Male (38 mm SL) of laboratory stock derived from Arroyo Seco (Río Axtla system). Ventral edge of caudal fin and sword are edged by melanophores. Grave spot is well developed and extends as far as the distal margin of the caudal fin where it meets the pigmentation along the dorsal edge of the sword.

the midlateral stripe. Males do not develop a sword greater than 1 mm.

**TYPES:** The holotype, AMNH 88335, is a mature adult male, 20.0 mm SL, taken on April 27, 1984, by K. D. Kallman and D. C. Morizot, in the nacimiento of the Río Ojo Frio at El Quince, north of Rascón, Río Gallinas—Río Pánuco drainage, SLP, Mexico. Taken with the holotype were the paratypes, AMNH 75942, consisting of 5 mature males, 19 females and juveniles. Other specimens referred to this species are listed under Material.

**DESCRIPTION:** Well-formed hook on ray 5a of gonopodium; distal serrae of ray 4p not reduced; no *Cb*; grave spot, when present, poorly expressed and only visible under 10× magnification; no xanthophore or pterinophore pigment patterns.

**REMARKS:** The habitus of this species (small, with slender caudal peduncle) is most reminiscent of the other diminutive fish of the group, *X. pygmaeus*; it has been referred to as “an undescribed species of pygmy swordtail from the Río Ojo Frio” in another publication (Zimmerer and Kallman, 1988). Based on general similarity, it had been assumed that *X. continens* was closely related to *X. pygmaeus*. However, *X. continens* appears to share more derived characters with the *montezuma-nezahualcoyotl* group (see discussion of relationships, p. 21).

**ETYMOLOGY:** From the Greek *conto-*, meaning short, and the Latin *ensis*, meaning sword, in reference to the very small sword developed in males of this species.

TABLE 3  
Frequency Distribution of Number of Branched  
Caudal-Fin Rays in Northern Swordtails

Species	Number of branched caudal-fin rays								
	10	11	12	13	14	15	16	17	
<i>X. montezumae</i>			7	78	3				
<i>X. nezahualcoyotl</i>	15	62	49	9					
<i>X. continens</i>	3	18	6						
<i>X. cortezi</i>	2	30	139	20	1				
<i>X. malinche</i>				4	13	27			
<i>X. birchmanni</i>					5	56	59	19	
<i>X. pygmaeus</i>	10	24	11						
<i>X. nigrensis</i>	4	22	62	36					
<i>X. multilineatus</i>	3	14	80	24					

DISTRIBUTION: Headwaters of the Río Ojo Frío, north of Damian Carmona, Río Pánuco drainage, SLP.

MATERIAL: All from SLP: Río Ojo Frío at El Quince—AMNH 75937(3), AMNH 75942(24); Río Ojo Frío north of Damian Carmona—AMNH 45306(44), AMNH 45305(26); laboratory descendants from Damian Carmona—AMNH 76270(1), AMNH 76271(1), AMNH 76272(1).

*Xiphophorus cortezi* Rosen  
Cortes Swordtail

Figure 6

*Xiphophorus montezumae cortezi* Rosen, 1960: 96 (Río Moctezuma, Río Pánuco basin, SLP, Mexico) holotype, UMMZ 177302.

DIAGNOSIS: A swordtail species with a single zigzag horizontal stripe; polymorphic for three unlinked macromelanophore patterns, Spotted caudal (*Sc*), Carbomaculatus (*Cam*), and Atromaculatus (*At*); a well-developed reticulum; males with swords; vertical bars, when present, long and narrow; branched caudal-fin rays 12–15 (table 3).

DESCRIPTION: Sword with dark ventral melanophore pigment; well-formed hook on ray 5a of gonopodium; most populations polymorphic for *Cb*; sword usually composed of unbranched rays, except when branched caudal-fin rays number 14; grave spot well developed, not extending beyond the upper caudal margin; distal dorsal sword pigment present, but faint in smaller males; polymorphic for yellow carotenoid pigment patterns; sword distinctly upturned.

REMARKS: Males often have a series of nar-

row vertical bars on the flanks. These rarely appear on females, but, when present, are also narrow. See Remarks section of the account of *X. malinche* (p. 10) for a discussion of characters that distinguish *X. cortezi*, *X. malinche*, and *X. birchmanni*.

DISTRIBUTION: South of the Río Tampaón, SLP (except where noted): Arroyo La Calera, Arroyo San José, independent tributaries to the Río Tampaón; tributaries to Río Coy and Río Moctezuma throughout Sierra Potosina; all tributaries to Río Coy from Sierra Madre, but absent from Río Coy; all tributaries to Río Axtla system including the headwaters of the Río Tancuilín at Río Verdito (QUER), elevation 1160 m (water temp. 13°C), and the rockpools of the arroyos Xilitilla and La Conchita, Xilitla, between 600 and 900 m elevation, relatively uncommon in Río Huichihuayán; Arroyos Palitla and Ameca, tributaries to Río Moctezuma; all streams in the Sierra San Martín, tributaries to Río Moctezuma and Río San Pedro (HID); lower parts of Río Claro drainage (HID); Río Tecoloco, including Arroyos Caimantla and Tecacalax (HID), independent tributary of Río Los Hules, Río Pánuco basin. Not explored are the Río Moctezuma and Río Amajac drainages upstream from Tamazunchale. No fishes were found in the Río San Miguel, an internal drainage 6 km south of San José el Viejo.

MATERIAL: All from SLP: Río Axtla system—AMNH 75769(2), AMNH 75813(100), AMNH 75818(28), AMNH 75841(60), AMNH 45300(32), AMNH 45280(10), AMNH 45297(2), AMNH 45301(12), AMNH 45303(16), AMNH 45325(3), AMNH 45269(43), AMNH 45311(1); San Martín—AMNH 75776(100), AMNH 75797(10); Río San Pedro—AMNH 75782(41), AMNH 75830(2); Río Coy system—AMNH 45294(61), AMNH 45290(35), AMNH 45291(13), AMNH 45292(7), AMNH 45293(10), AMNH 45321(1), AMNH 45274(10), AMNH 45276(8); Río Moctezuma—AMNH 45315(1).

*Xiphophorus malinche*, new species  
Highland Swordtail

Figure 7

DIAGNOSIS: A species closely related to *X. cortezi* and *X. birchmanni*, with one zigzag horizontal stripe; *Cam*; a well-developed re-

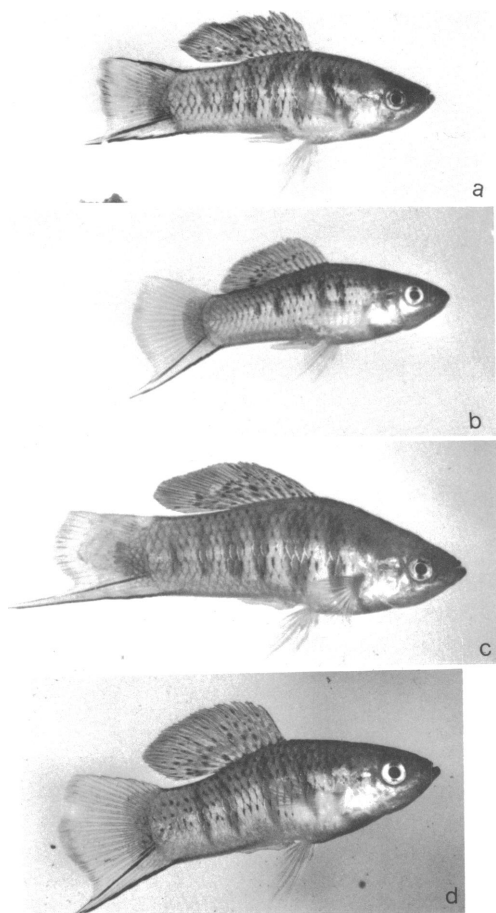


Fig. 7. *Xiphophorus malinche*. a: Male (43 mm SL) from Río Claro; c and d: Males (51 and 48 mm SL) collected in Río Calnali; b: Male (42 mm SL) of laboratory stock derived from Río Claro. Note the irregular broad vertical bars along the flank. Melanophore spotting at the nodes of the reticulum is well developed. Grave spot is very well expressed and merges with the melanophore pigmentation along the dorsal edge of the short sword. Pigmentation along the ventral margin of the caudal fin is strongly expressed. Wild-caught males were photographed 17 months after capture.

ticulum; males with swords; males with prominent bump on head; branched caudal-fin rays 13–15 (table 3); distinctive vertical bar pattern (see below); middorsal spotting.

**TYPES:** The holotype, AMNH 88336, is a mature adult male, 46.0 mm SL, taken on February 18, 1988, by K. D. Kallman, D. C. Morizot, M. Rauchenberger, and A. Basolo in the Río Claro at Tlatzintla, Río Pánuco

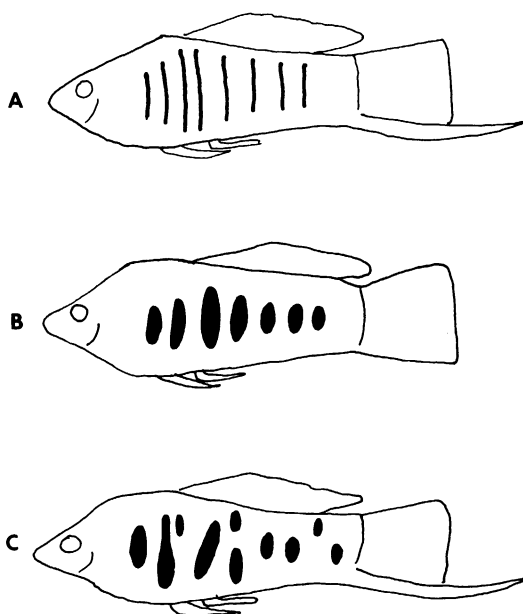


Fig. 8. Vertical bar patterns of adult males in the *cortezi* clade. A. *Xiphophorus cortezi*. B. *Xiphophorus birchmanni*. C. *Xiphophorus malinche*.

drainage, HID, Mexico. Taken with the holotype were the paratypes, AMNH 88338, consisting of 16 mature males, 250 females and juveniles. Other specimens referred to this species are listed under Material.

**DESCRIPTION:** Sword with dark ventral pigment; well-formed hook on ray 5a of gonopodium; *Cb* present; no *Sc*; sword composed solely of unbranched rays or with one branched ray; grave spot well developed, but not extending beyond caudal margin; distal dorsal sword pigment present; yellow carotenoid pigments; sword distinctly upturned.

**REMARKS:** In the Río Claro (the type locality), this species exhibited atypical behavior for swordtails of the *montezumae* or *cortezi* groups. In the other species of these groups, mature males are generally found darting among and underneath large rocks. Males (and females) of *X. malinche* were found in a shallow, sunny, sand-bottomed river under floating aquatic vegetation.

Vertical bar patterns for mature males of *X. cortezi*, *X. malinche*, and *X. birchmanni* are depicted in figure 8. In *X. cortezi*, the bars are long and narrow in males and generally absent in females. In *X. birchmanni*, vertical bars are present in most mature fish, and form wide, indistinct, deep-lying ovals. Males

TABLE 4  
Distinguishing Characteristics of *Xiphophorus cortezi*, *X. malinche*, and *X. birchmanni*

	<i>cortezi</i>	<i>malinche</i>	<i>birchmanni</i>
Sword	yes	yes	no
Oval bars, ♀	no	yes	yes
Disjunct bars, ♂	no	yes	no
Head bump	no	yes	yes
Middorsal spots	no	3–4 rows	1–2 rows
# BCFR <sup>1</sup>	11–15	13–15	15–17
Sc	yes	no	yes
Cb	yes	yes	no

<sup>1</sup> BCFR = Branched caudal-fin rays.

*Xiphophorus birchmanni* is characterized by one or two rows of middorsal spots, at the nodes of the reticulum, extending from the origin of the dorsal fin onto the caudal fin. Similar spots are also found in *X. malinche*; they rarely extend onto the caudal fin in this species, but more rows are accented, generally three to four.

Table 4 summarizes the characters that can be used to distinguish *X. cortezi*, *X. malinche*, and *X. birchmanni*.

ETYMOLOGY: In keeping with the allegorical use of important historical figures in the Spanish conquest of Mexico to suggest phylogenetic relationships of swordtails in the Pánuco basin, this species is named after Malinche (also called Marina or Dona Marina by the Spaniards), a linguistically gifted Indian slave who played a role in the Spanish conquest as the interpreter, secretary, and mistress of Hernando Cortes (Prescott, 1843).

DISTRIBUTION: Río Claro at 650 m, Río Moctezuma drainage, Río Pánuco basin, HID; Río Calnalí at 1000 m, and Río Conzintla at 1000 and 1140 m (water temp. 15°C), Río Atlapexco drainage, HID; and Arroyo Soyatla, HID, at 1280 m (water temp. 15°C), Río Calabozo drainage, Río Pánuco basin.

MATERIAL: All from HID: Río Claro—AMNH 88338(266); Río Atlapexco drainage—AMNH 88340(2), AMNH 88341(2), AMNH 88339(1).

*Xiphophorus birchmanni* Lechner and Radda  
Sheepshead Swordtail  
Figure 10

*Xiphophorus montezumae birchmanni* Lechner and Radda, 1987: 189–196 (Río Talol, headwater of

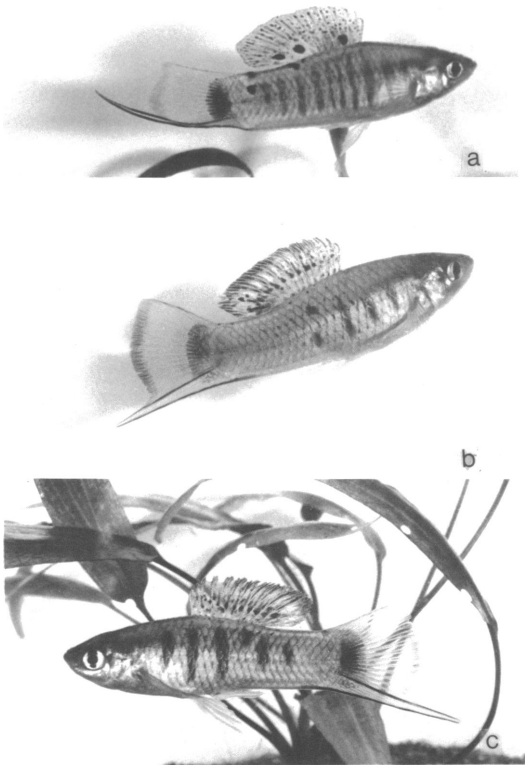


Fig. 9. (a) *Xiphophorus cortezi* and *X. malinche* from (b) Río Claro and (c) Río Calnalí photographed in community tank during social interaction to bring out the vertical bar pattern. *X. cortezi* has long, narrow, unbroken bars and a long, slender sword. Large black spots in dorsal fin and on flank constitute the Cam pattern. *X. malinche* specimens from both populations have broad, broken bars. Also note the short sword that tapers rapidly, and the developing spots (especially in b) in the nodes of the reticulum.

sometimes deviate from this pattern, either with fusion of the blotches or with narrower bars (never as narrow as those of *X. cortezi*). In *X. malinche*, females have oval blotches similar to those of *X. birchmanni*. Vertical bar patterns of *X. malinche* males, however, are very distinctive and irregular. Many of the bars are interrupted, and they may be of uneven thickness and sometimes slanted instead of vertical. This irregular pattern varies from fish to fish, and even from the right to left sides of the same specimen (fig. 9).



Río San Pedro, Río Tempoal, Río Pánuco system, HID, México) holotype, SMF 21154.  
*Xiphophorus*, sp. nov.: Zimmerer and Kallman, 1988: 299–307 (Río Calabozo).

**DIAGNOSIS:** A species closely related to *Xiphophorus cortezi* and *X. malinche*, with one zigzag horizontal stripe, *Sc* and *Cam* macro-melanophore patterns, a well-developed reticulum, and males with a prominent bump on the forehead; differing from those two species in that males are without a sword; branched caudal-fin ray count highest in genus, modally 15, range 14–17 (table 3); distinctive vertical bar pattern (see below); mid-dorsal spots located at nodes of reticulum.

**DESCRIPTION:** Well-formed hook on ray 5a of gonopodium; no *Cb*; grave spot either poorly expressed or absent; polymorphic for xanthophore patterns.

**REMARKS:** Males have along their flanks very broad vertical bars that often coalesce; in females, these are more indistinct and expressed as oval spots beneath the midlateral line. The nodes of the reticulum of the two most dorsal scale rows on the caudal peduncle are produced into distinct spots. On rare occasions, far less than one percent, a male may develop a short caudal appendage; this sword is unpigmented and is composed of unbranched caudal-fin rays.

Further study is needed to accurately describe the distributions of *X. cortezi*, *X. malinche*, and *X. birchmanni* in the Río San Pedro, Río Claro, Río Los Hules, and Río Calabozo systems. Sympatry occurs in some areas; as yet we have no good evidence of hybridization, but this is still being investigated. Distribution seems to be correlated with elevation. In the Río San Pedro drainage, *X. cortezi* is found at lower, *X. birchmanni* at higher, elevations. At the foot of the Sierra Madre, near Orizatlán, in the Arroyo Santa Cruz and in the Arroyo Xochititla (Río San Pedro drainage), both species were found together. A similar relationship seems to exist between *X. birchmanni* and *X. malinche* in the Río Atlapexco and Río Calabozo systems, this time with *X. malinche* at higher elevations and *X. birchmanni* downstream. Again, mixed samples were taken at midelevation sites in the Río Calnalí (Río Atlapexco drainage). (Water temperature at this site was measured at 18°C in Feb. 1988, 15°C in Feb. 1987.) Outside the abovementioned area, the

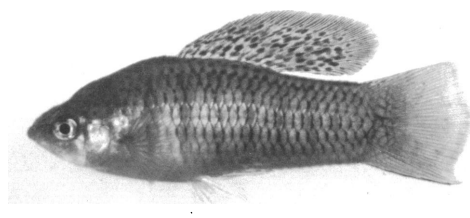


Fig. 10. *Xiphophorus birchmanni*. Male (51 mm SL) collected in Río Calnalí at Calnalí, photographed 17 months after capture. Note row of melanophore spotting at the nodes of the reticulum. Caudal appendage not more than 1 mm long. Melanophore pigmentation along ventral edge of caudal fin only moderately well developed. Grave spot is poorly developed and barely visible. Broad and oval vertical bars on flank are present but faded during photography.

three species are allopatric, with *X. malinche* in the upper Río Claro, *X. birchmanni* in the Río Tuxpan drainage, and *X. cortezi* in the Río Moctezuma, Río Axtla, and Río Coy drainages.

**DISTRIBUTION:** Throughout the Río La Candelaria and Río Axtlapexco drainages, except at higher elevations (HID), Río Los Hules system, Río Pánuco basin; Río Calabozo drainage (HID, VER) including the Hautla Plateau, absent for a small stretch of coastal plain, westsouthwest of San Sebastian (VER), and at all higher elevations; also present in Río Santa María, elevation 510 m, below Santa María (HID); headwater of Río San Pedro, Río Pánuco basin; and in the Río Tuxpan basin in headwaters of the Río Vinazco, near Llano Enmedio, VER; in Río Vinazco, 8 km southwest of Llano Enmedio; Río San Dionisio, tributary to Río Beltrán at Juntas Chicas, VER. Not found at higher elevation in Río Vinazco (1000 m), 5 km east of Huayacocotla, VER, or in Río Chiquito (1400 m), tributary to Río Vinazco, 13 km northwest of Huayacocotla (water temp. 13°C).

**MATERIAL:** From VER: Río Calabozo drainage—AMNH 78011(130), AMNH 77992(10), AMNH 77984(16), AMNH 75880(24), AMNH 78000(52), AMNH 75864(24), AMNH 45313(6), AMNH 45314(30), AMNH 45345(20); Río Tuxpan—AMNH 78015(1), AMNH 77989(4), AMNH 77994(22); from HID: Río Atlapex-

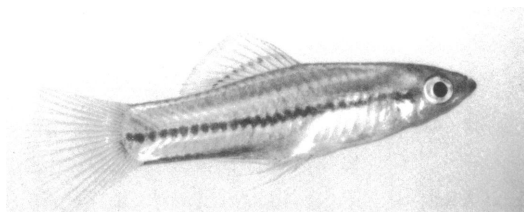


Fig. 11. *Xiphophorus pygmaeus*. Male, 24 mm SL, laboratory reared.

co drainage—AMNH 77976(25), AMNH 77970(26), AMNH 75873(35), AMNH 77969(89); Río Candelaria drainage—AMNH 77966(131), AMNH 77962(157), AMNH 75878(19).

*Xiphophorus pygmaeus* Hubbs and Gordon  
Slender Pygmy Swordtail  
Figure 11

*Xiphophorus pygmaeus* Hubbs and Gordon, 1943: 31–33 (Río Axtla, Río Pánuco basin, SLP, México) holotype, UMMZ 124365.

**DIAGNOSIS:** A small slender species in which most males are less than 24 mm in length, rarely to 38 mm; caudal appendage never greater than 8 mm (usually shorter than 2 mm, composed of unbranched caudal-fin rays); ventral edge of caudal fin and sword never pigmented by melanophores; with a single dense midlateral stripe formed of coalesced zigzags that appears solid and is present at birth, bordered above by a clear space; a long, slender, caudal peduncle; and reduced distal serrae on ray 4p of gonopodium.

**DESCRIPTION:** Well-formed hook on ray 5a of gonopodium, extending beyond the limit of the distal serrae on ray 4p due to reduction of distal serrae; *Cb* and grave spot absent; polymorphic for xanthophore patterns.

**REMARKS:** The dorsal fin in this species is short, both in height and base length, emphasizing the length of the caudal peduncle.

**DISTRIBUTION:** Río Axtla system, Río Pánuco drainage, SLP: abundant in Río Huichihuayán, less common in lower 9 km of Río Tancuilín and upper 5 km of Río Axtla; absent elsewhere.

**MATERIAL:** All from SLP: Río Axtla system—AMNH 45299(23), AMNH 45304(6), AMNH 45279(41), AMNH 45326(3).

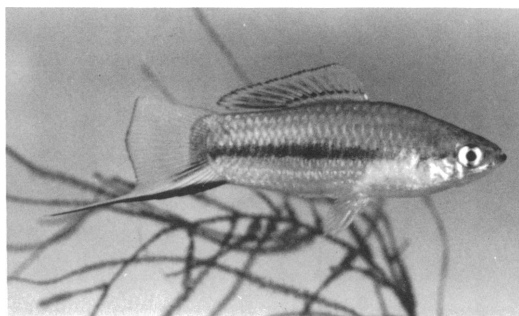


Fig. 12. *Xiphophorus nigrensis*. Male (37 mm SL) of laboratory stock from Río Choy. Black ventral margin of caudal fin and sword is well developed. Dorsal margin of sword is unpigmented. Grave spot is present but does not extend to distal margin of caudal fin.

*Xiphophorus nigrensis* Rosen  
El Abra Pygmy Swordtail  
Figure 12

*Xiphophorus pygmaeus nigrensis* Rosen, 1960: 100 (Río Choy, Río Pánuco basin, SLP, México) holotype, UMMZ 177301.

**DIAGNOSIS:** A swordtail similar to *X. pygmaeus*, with a single, dense midlateral stripe formed of coalesced zigzags that appears solid and is present at birth, bordered above by a clear space; reduced distal serrae on ray 4p of gonopodium; some males much larger (to 41 mm SL) and also deeper bodied as the result of allometric growth; caudal appendage also exhibits allometric growth.

**DESCRIPTION:** Sword exhibits allometric growth, rarely absent in a few small males; ventral edge of caudal fin and sword heavily pigmented by melanophores in males, missing in a few (2%) small males; well-formed hook on ray 5a of gonopodium, extending beyond limit of distal serrae of ray 4p due to reduction of distal serrae; polymorphic for *Cb*, well developed in large males, fainter in small males and females; sword composed of unbranched rays; grave spot well developed, but not extending beyond distal caudal margin; distal dorsal sword pigment usually not present, but appearing sporadically as an individual variation; polymorphic for xanthophore patterns; sword distinctly upturned, particularly when small.

**REMARKS:** Allometric growth in the sword

is exhibited only by this species and *X. multilineatus*; in other species, the sword index is constant. In small males, there is no correlation between the presence or absence of a short sword and the presence or absence of the black ventral edge of the caudal fin and/or sword. The genetic control of the size differences among males in this species and the following species, *X. multilineatus*, has been documented by Kallman (1989).

**DISTRIBUTION:** Río Choy, Río Pánuco drainage, SLP.

**MATERIAL:** All from SLP: Nacimiento (headspring) of Río Choy—AMNH 38478(7), AMNH 38490(17); Río Choy—AMNH 45344(10), AMNH 45337(43), AMNH 28621(10); lab descendants from Río Choy—AMNH 76134(1), AMNH 76135(2), AMNH 76072–76108(96).

***Xiphophorus multilineatus*, new species**  
High-Backed Pygmy Swordtail

Figure 13

*Xiphophorus nigrensis* Rosen, in part; referred to in discussion of *X. nigrensis* by Rosen, 1979: 357. Zander, 1967: 94.

**DIAGNOSIS:** A swordtail similar to *X. nigrensis*, with a single, dense midlateral stripe formed of coalesced zigzags that appear solid and is present at birth, bordered above by a clear space; reduced distal serrae on ray 4p of gonopodium; with some males much larger (to 42 mm SL) and deeper bodied due to allometric growth; caudal appendage exhibits allometric growth; numerous vertical bars along the flanks; a dark pigment spot above and behind the pectoral fin base, except in small males.

**TYPES:** The holotype, AMNH 88337, is a mature adult male, 25.0 mm SL, taken on February 17, 1979, by K. D. Kallman, D. C. Morizot, V. Borkoski, and G. Peters, in the Río Coy near its confluence with the Río Tapaón, Río Pánuco drainage, SLP, Mexico. Taken with the holotype were the paratypes, AMNH 45322, consisting of 7 mature males, 77 females and juveniles. Five mature males of this lot have been cleared and stained. Other specimens referred to the species are listed under Material.

**DESCRIPTION:** Sword exhibits allometric growth; in males, ventral margin of caudal

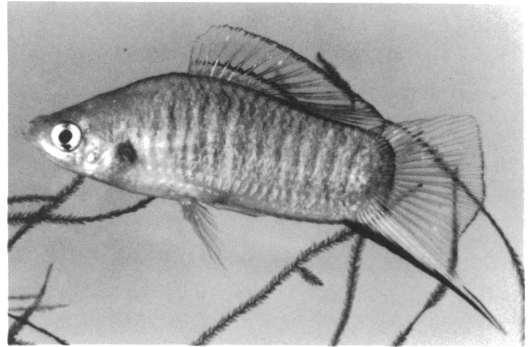


Fig. 13. *Xiphophorus multilineatus*. Male (40 mm SL) of laboratory stock derived from Río Coy. Male exhibits vertical barring and melanophore spot near insertion of pectoral fin. Ventral margin of caudal fin and sword are heavily edged with black. Grave spot moderately well developed in base of caudal fin. Note that the dorsal margin of the sword is edged by melanophores near its distal end. This trait is seen only in a few males of this species and in *X. nigrensis*.

fin and sword always heavily edged by melanophores; well-formed hook on ray 5a of gonopodium, extending beyond limit of distal serrae of ray 4p, due to reduction of distal serrae; polymorphic for *Cb*, well developed in large males, fainter in small males and females; sword composed of unbranched rays; grave spot well developed, not extending beyond distal caudal margin; distal dorsal sword pigment not usually present, but appearing sporadically as individual variation; polymorphic for xanthophore patterns; sword distinctly upturned, particularly when small.

**REMARKS:** These last two species are quite similar. However, in addition to the differences in pigmentation listed in the diagnosis, there are several electrophoretic differences between them (see p. 17). The inheritance of the vertical bars that distinguish *X. multilineatus* has been documented by Zimmerer and Kallman (1988), under *X. nigrensis*.

**ETYMOLOGY:** The name is derived from the Greek: *multi-*, many; *-lineatus*, line; in reference to the prominent vertical bars that distinguish this species from its close relatives.

**DISTRIBUTION:** Río Coy system, Río Pánuco drainage, SLP: throughout Río Coy, Arroyo Tambaque, and Arroyo Oxitipa as far as Octzen.

TABLE 5  
Micromelanophore Patterns and Caudal Appendage in Male Northern Swordtails<sup>1</sup>

	NEZ	MON	CON	COR	MAL	BIR	PYG	NIG	MUL
<i>Cb</i>	+	—	—	+	+	—	—	+	+
Vertical bars	+	+	—	+	+	+	—	—	+
Ventral edge of caudal fin (and sword) black	+	+	—	+	+	+ <sup>2</sup>	—	+	+
Grave spot	+	+	(—) <sup>3</sup>	+	+	(—) <sup>3</sup>	—	+	+
Sword <sup>4</sup>	+	+	—	+	+	(—)	—	+	+

<sup>1</sup> All traits are polygenic, except *Cb* which is an autosomal dominant; + present, (—) very poorly developed, — absent.

<sup>2</sup> Much weaker development than in the other species.

<sup>3</sup> Pattern can be recognized in some fish under 10× magnification.

<sup>4</sup> Even some males of *X. continens*, *X. pygmaeus*, and *X. birchmanni* exhibit a small projection of the ventral caudal-fin rays. We score a species as + when all males have a sword at least 3 mm long (except in *X. nigrensis* and *X. multilineatus*, in which it is an allometric trait).

MATERIAL: All from SLP: Arroyo Tam-  
baque, Río Coy system—AMNH 45296(2),  
AMNH 45320(22); Nacimiento of Río Coy—  
AMNH 45338(20); Río Coy—AMNH  
45336(8), AMNH 45332(84); laboratory de-  
scendants from Río Coy—AMNH 76109–  
76133(78).

PHYLOGENETIC RELATIONSHIPS

DISCUSSION OF CHARACTERS

Characters that Support Monophyly of  
Northern Swordtails:

1. Caudal blotch (*Cb*)—A micromelano-  
phore pattern controlled by a single domi-  
nant autosomal factor (Kallman and Atz,  
1966), expressed as an oval blot on the proxi-  
mal part of the caudal fin. Populations of *X.*  
*nezahualcoyotl*, *X. cortezi*, *X. malinche*, *X.*  
*nigrensis*, and *X. multilineatus* are polymor-  
phic for this pattern. The pattern is strongly  
displayed in dominant individuals. The distri-  
bution of this and other melanophore pat-  
terns is presented in table 5.

2. Sword consisting of unbranched rays—  
In southern swordtails, the sword always in-  
cludes at least one, sometimes two, branched  
caudal-fin rays; the longest ray is always  
branched, and the total branched caudal-fin  
ray count is usually 14 or greater. Northern  
swordtails that develop swords generally have  
13 or fewer branched caudal-fin rays, and the  
sword is composed entirely of unbranched  
rays. A few individuals with branched cau-  
dal-fin ray counts of 14 or 15 have a branched  
ray in the sword, but it is never the longest

one. In *X. birchmanni* and *X. pygmaeus*,  
species that do not normally develop swords,  
in those few individuals that do have swords  
(5 mm), the rays are unbranched. Swords of  
comparable lengths in platyfishes (*X. andersi*,  
*X. xiphidium*) have branched rays.

3. Distal dorsal sword pigment—The dor-  
sal pigment of the sword in this group is  
formed of two parts. The proximal part be-  
gins at the caudal-fin base and grows distally.  
This is considered to be a modification of the  
grave spot, described in both sexes of *X. sig-  
num* (Rosen and Kallman, 1969), but found  
only in mature males in some of the other  
species. In the southern swordtails, except *X.*  
*clemenciae*, this pattern extends distally to  
the end of the sword. In the Pánuco sword-  
tails, however, a separate pigment pattern be-  
gins near the distal dorsal end of the devel-  
oping sword and spreads proximally,  
eventually meeting the grave spot near the  
upper caudal-fin margin. The grave spot is  
present in all Pánuco swordtails except *X.*  
*pygmaeus* (albeit very poorly developed in  
*X. continens* and *X. birchmanni*), and never ex-  
tends beyond the distal margin of the caudal  
fin. The distal dorsal sword pigmentation is  
present consistently in *X. montezumae*, *X.*  
*nezahualcoyotl*, *X. cortezi*, and *X. malinche*,  
and sporadically in *X. nigrensis* and *X. mul-  
tilineatus*.

4. Upturned sword—The sword is decid-  
edly upturned in *X. cortezi*, *X. malinche*, and  
*X. nezahualcoyotl*. In *X. nigrensis*, *X. mul-  
tilineatus*, and some *X. montezumae*, the  
sword is upturned when short, but as it grows  
longer, it becomes straighter. In contrast, the

swords of the southern swordtails (except *X. clemenciae*) are straight at all stages of growth.

Note: *Xiphophorus malinche* has yet to be tested for most of the following loci, inasmuch as it was discovered after the present electrophoretic analysis had been completed. Thus, it is coded as MISSING=9 for these characters (5–16).

5. GAPD-1—A unique allele (*b*) is shared by all eight Pánuco swordtails tested, as compared with a different allele (*a*) found in platyfish and southern swordtails.

6. SOD-2—A unique allele (*b*) unites all eight Pánuco species tested, with a different allele (*a*) being present in both the platyfish and southern swordtail groups.

7. MP-1—All Pánuco species tested except *X. pygmaeus* share a unique allele (*c*); *X. pygmaeus* is autapomorphic for this trait (allele *d*); the *a* allele is common to southern swordtails and platyfish.

8. MDH-2—All eight species tested share a derived allele (*c*); the *a* allele is found in the outgroups.

9. MP-4—A unique allele (*b*) unites seven Pánuco species and *X. clemenciae*; *X. montezumae* is autapomorphic for this trait (allele *c*). Southern swordtails (*d*) and platyfish (*a*) exhibit different alleles. This character distribution is congruent with the hypothesis of monophyly for the northern swordtails, but a transformation series, not necessarily implying monophyly, represents a possible alternative for this character. However, the bulk of other evidence presented supports monophyly.

#### Characters Important for Determining Relationships Within the Pánuco Group:

10. MDH-1—*Xiphophorus montezumae*, *X. nezahualcoyotl*, and *X. continens* share a unique allele (*b*); allele *a* is common to other species in the genus.

11. GUK-1—*Xiphophorus pygmaeus*, *X. nigrensis*, and *X. multilineatus* share a unique allele (*g*); allele *a* is common to other species in the genus.

12. IDH-2—*Xiphophorus continens*, *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus* share a unique allele (*f*); other alleles (*a*, *b*, *e*) are widespread throughout the genus.

13. PEP-2—*Xiphophorus nigrensis* and *X.*

*multilineatus* share a unique allele (*h*); other alleles (*a*, *d*, *e*, *f*) are widespread throughout the genus.

14. PGM—*Xiphophorus nigrensis* and *X. multilineatus* share a unique allele (*c*); alleles *b*, *d*, and *e* are found elsewhere in the swordtails and allele *a* in the southern swordtails and platyfish.

15. Carbonic anhydrase—*Xiphophorus montezumae*, *X. nezahualcoyotl*, *X. continens*, and *X. multilineatus* possess an allele with a mobility of .8; that of *X. cortezi* and *X. birchmanni* is .9; and that of *X. pygmaeus* and *X. nigrensis* is 1.0, which is the common state for the rest of the genus. Although the 1.0 allele is unambiguously inferred to be the plesiomorphic state for this character, we are uncertain whether a transformation series (1.0 – .9 – .8) is justified or not. Consequently, this character has been run both ORDERED and UNORDERED, in separate analyses.

16. ADA—Although there are many alleles at this locus (about 22) and most species are highly polymorphic, *X. continens*, *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus* share an allele found nowhere else in the genus.

17. PEP-S—*Xiphophorus malinche* and *X. birchmanni* share an allele at this locus not found in *X. cortezi*. It was not tested in other species, however, so its polarity is unknown.

18. Drosopeterin—Drosopeterin is a common red pigment found throughout this genus. Many species are highly polymorphic for red patterns composed of pterinophores. For an individual to develop this pigmentation, it must possess an allele different from the wild-type one at the pterinophore (chromatophore) locus (e.g., sex-linked in *X. maculatus*) and in addition it must have autosomal genes that control the biochemical pathway leading to the synthesis of drosopeterin. Among the Pánuco basin swordtails, the bright reddish-bronze coloration of some of the males of *X. montezumae* and the reddish midlateral stripe that develops in some old males of *X. cortezi* are composed of pterinophores containing drosopeterin (Kallman, unpubl.). The red pattern reported for some *X. nezahualcoyotl* also appears to be composed of pterinophores (Zander, 1969). With respect to this trait, the information on *X. malinche* and *X. birchmanni* is limited. We have never seen any red or orange pigmen-

TABLE 6  
Polymorphic Xanthophore Patterns in Male Northern Swordtails<sup>1</sup>

	NEZ	MON	CON	COR	MAL	BIR	PYG	NIG	MUL
a. entire fish yellow	—	—	—	—	—	—	+	—	+
b. caudal fin yellow	—	—	—	+	2	+	+	+	+
c. sword yellow	+	—	3	+	+	3	3	+	+
d. dorsal and ventral margins of caudal fin yellow	—	—	—	+	2	+	—	+	+

<sup>1</sup> The traits listed show sex-linked inheritance with the following exception: trait b in *X. birchmanni* is autosomally inherited; traits c and d in *X. cortezi* and trait c in *X. malinche* were not tested.  
<sup>2</sup> Pattern not seen in our limited sample.  
<sup>3</sup> Trait does not pertain in this species; males have no caudal appendage.

tation in wild fish or in individuals of our colonies of *X. birchmanni* and *X. malinche*.

*Xiphophorus pygmaeus*, *X. nigrensis*, and *X. multilineatus* are known to lack drosopherin pigment, but they are polymorphic for numerous xanthophore (carotenoid) patterns showing sex-linked inheritance (see characters 19–21). When these factors are introduced, through introgressive hybridization into *X. maculatus* or *X. helleri*, they give rise to chromatophores containing both carotenoid pigment and drosopherin. Conversely, the sex-linked pterinophore factor of *X. maculatus*, when introduced into *X. pygmaeus* or *X. nigrensis*, gives rise to chromatophores with only carotenoid pigment (Zander, 1968, 1969).

*Xiphophorus continens* is uniformly wild type (monomorphic). When the allele for yellow caudal fin, *F1<sup>y</sup>*, of *X. multilineatus* is introduced through introgressive hybridization into *X. continens*, all the hybrids with *F1<sup>y</sup>* develop an orange pigment over much of their flanks. This pigmentation arises in pterinophores containing drosopherin. Therefore, *X. continens*, like *X. montezumae*, *X. nezahualcoyotl*, and *X. cortezi*, possesses the biochemical pathway essential for the synthesis of drosopherin. This pathway is absent in *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus*.

19. Yellow caudal fin—As mentioned under character 18, yellow pigment patterns occur in seven of the nine Pánuco swordtails, and most patterns—but not all—are known to be sex linked (table 6). Four separate polymorphic patterns are discernible: yellow caudal fin, yellow sword, yellow dorsal and ventral edges of caudal fin, and solid yellow body coloration, treated here as characters 19–22. Yellow caudal fin is found in *X. cortezi*, *X.*

*birchmanni*, *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus*. The apparent absence of this character in *X. malinche* may be due to our small sample size.

20. Males polymorphic for yellow swords are found in *X. nezahualcoyotl*, *X. cortezi*, *X. malinche*, *X. nigrensis*, and *X. multilineatus*.

21. Yellow dorsal and ventral edges of caudal fin is a polymorphic pattern found in males of *X. cortezi*, *X. birchmanni*, *X. nigrensis*, and *X. multilineatus*.

22. Solid yellow body coloration is a polymorphic pattern found in males of *X. pygmaeus* and *X. multilineatus*.

23. Distal serrae on ray 4p—In *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus*, the distal serrae are reduced as compared with those of the other species in this group and those of the platyfishes and southern swordtails (fig. 14). Therefore, the hook on ray 5a appears quite prominent, because it projects beyond the level of the distal serrae. In the other Pánuco basin swordtails, a well-formed hook is present on ray 5a, but because the distal serrae of ray 4p are not reduced in size, the hook does not project beyond them. This condition might be compared with that of the southern swordtails (except *X. clemenciae*), in which the 5a hook is quite well developed, and extends beyond the limit of the distal serrae, even though they are not reduced.

24. Growth rate—Differences in size and age at sexual maturation are controlled in many species of *Xiphophorus* by allelic variation at a sex-linked locus. In *X. nigrensis* and *X. multilineatus*, genetically late-maturing fish grow significantly faster than genetically early-maturing ones, whereas in all other species, immature fish of early and late genotypes grow at the same rate (Kallman, 1989).

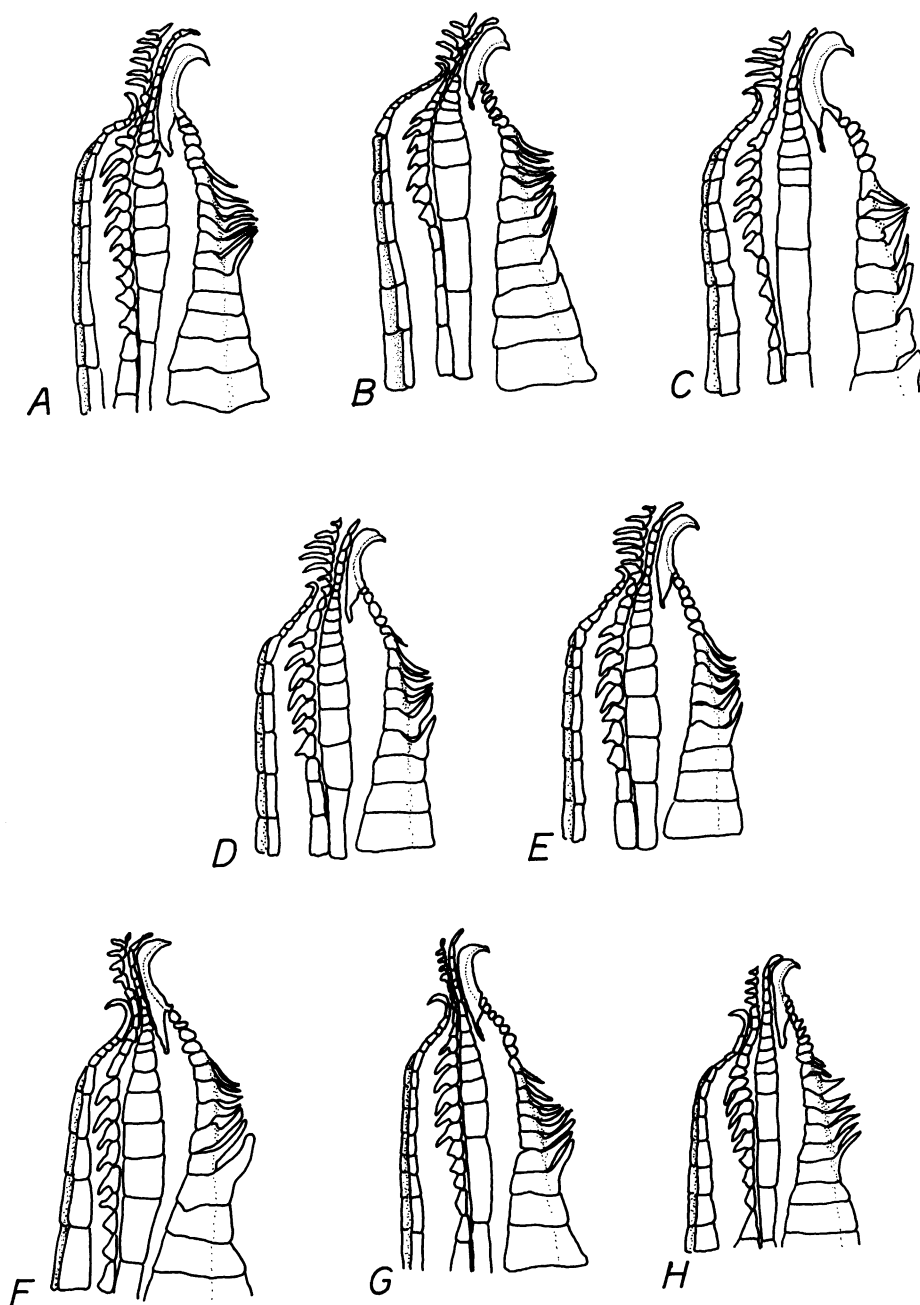


Fig. 14. Gonopodia of Río Pánuco basin swordtails. *Xiphophorus malinche* is not figured; its gonopodium is quite similar to those of *X. cortezi* and *X. birchmanni*. A. *Xiphophorus montezumae*; B. *Xiphophorus nezahualcoyotl*; C. *Xiphophorus continens*; D. *Xiphophorus cortezi*; E. *Xiphophorus birchmanni*; F. *Xiphophorus pygmaeus*; G. *Xiphophorus nigrensis*; H. *Xiphophorus multilineatus*.

25. Allometric growth of sword—In *X. montezumae*, *X. nezahualcoyotl*, *X. cortezi*, and the southern swordtails, the sword index (sword length/standard length) is constant for a given population or species. This is prob-

ably true for *X. malinche* as well, although our samples are not as extensive as for the other species. A constant sword index is also found in *X. andersi*, the only platyfish with a sword of appreciable length. In *X. nigrensis*

and *X. multilineatus*, however, the sword index depends on standard length.

26. Multiple lateral stripes—*Xiphophorus montezumae* and *X. nezahualcoyotl* have two or three zigzag lateral stripes; one midlateral stripe is the more common pattern for the genus. In *X. continens*, one or two zigzag lateral stripes are faintly visible above the prominent midlateral stripe. When this species is crossed with *X. multilineatus*, introducing a gene for large size, and then backcrossed twice, the results are large *X. continens*-like males, and in these fish, the multiple lateral stripes are readily apparent.

27. Solid midlateral stripe—In *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus*, the zigzags of the midlateral stripe are condensed, so as to appear as a solid band of pigment. It is present at birth, and has an unpigmented band just above it. The lateral stripes of the other species of *Xiphophorus* are not present at birth.

28. *Sc*—*Xiphophorus cortezi* and *X. birchmanni* share a unique macromelanophore pigment pattern, Spotted caudal (Atz, 1962). An *Sc*-like pattern is also present in the Río Czones and Río Tuxpan populations of *X. variatus* (a platyfish); it is caused by a sex-linked gene that is not identical with *Sc* of these two species. There could be a *Sc* locus in *Xiphophorus* and the alleles for *Sc* in *cortezi*-*birchmanni* and *variatus* are not identical. Kallman and Atz (1966) cited evidence that *Sc* in *cortezi* is on a chromosome homologous with the sex chromosomes of the platyfishes.

29. *Cam*—Carbomaculatus, a macromelanophore pattern unique to *X. cortezi* and *X. birchmanni* (Kallman, 1971). Its absence in *X. malinche* could be the result of a sampling error. A third macromelanophore pattern, Atromaculatus (*At*), is unique to *X. cortezi*. Again, its absence from *X. malinche* could be due to small sample size. In *X. cortezi*, in which it has been tested, these three patterns (*Sc*, *Cam*, *At*) are controlled by unlinked loci (Kallman and Atz, 1966; Kallman, 1971).

30. Head bump—In mature males of *X. malinche* and *X. birchmanni*, a ridge of fatty tissue develops between the occiput and the dorsal fin origin, producing a pronounced "sheepshead" shape.

31. Broad, deep-lying vertical bars—Females of *X. malinche* and *X. birchmanni* have deep-lying broad blotches along the flanks, rather than the thin vertical bars found elsewhere in the Pánuco group. (*Xiphophorus pygmaeus* and *X. continens* lack vertical bars. Other species are polymorphic for them.) Males of *X. birchmanni* often have these spots, too, although many males of *X. birchmanni* and all males of *X. malinche* vary from this basic pattern.

32. Middorsal spots—In males of *X. malinche* and *X. birchmanni*, dark spots are formed at the nodes in the reticulum along the uppermost scale rows (1 or 2 rows in *X. birchmanni*, 3 or 4 rows in *X. malinche*). These begin at the level of the dorsal fin and extend onto the caudal fin.

Characters that Unite Northern and Southern Swordtails:

33. Grave spot—See discussion under character 3.

34. Ventral margin of caudal fin and sword densely edged by melanophores—Present in all species with well-developed swords. It is absent from *X. pygmaeus* and *X. continens* and some small males of *X. nigrensis*, and absent or poorly developed in *X. birchmanni*. This pattern is also found in *X. gordonii* (a platyfish).

35. Well-formed hook on ray 5a of gonopodium—Constant in all swordtails. It appears sporadically, as an individual variation, in some platyfishes (1%).

36. Sword—Unique to this genus among poeciliid fishes, but a difficult character to analyze. Some platyfishes develop small, unpigmented swords (*X. xiphidium*, *X. andersi*); others can be experimentally induced to produce swords (*X. maculatus*). Among the northern swordtails, interspecific variation of the sword index is very pronounced; in contrast, all four species of the southern swordtails have relatively long swords. One northern swordtail, *X. montezumae*, has the longest relative sword length in the genus; several others have a sword index half or less that of *X. montezumae*; three species have virtually no caudal appendage; and in two species the sword index is an allometric trait. Thus, both the northern and southern swordtail groups



TABLE 7  
Character Matrix Used for Parsimony Analysis<sup>1</sup>

Clemenciae	00110	00010	00000	09000	00000	00000	00
Montezumae	01111	11121	00002	09000	00000	20000	00
Nezahualcoyotl	11111	11111	00002	09000	00000	20000	00
Continens	0xxx1	11111	01002	1900x	0000x	10000	00
Cortezi	11111	11110	00001	00011	10000	00010	00
Malinche	01119	99999	99999	91091	90000	00091	11
Birchmanni	0xxx1	11110	00001	0101x	1000x	00111	11
Pygmaeus	0xxx1	12110	11000	1911x	0110x	01000	00
Nigrensis	11111	11110	11110	19111	10111	01000	00
Multilineatus	11111	11110	11112	19111	11111	01000	00

<sup>1</sup> Character numbering in text. 0 = absent; 1 = present; 9 = data not available; x = character not applicable. Character states listed here as x or 9 were coded as 9 = missing for PAUP analysis.

possess forms with long swords; however, details of the morphology of the sword (characters 2 and 3) differ between the two groups, and it is impossible, at this stage, to determine the states of these characters in the common ancestor of the northern and southern swordtail groups. The distribution of the character "long sword" is most parsimoniously interpreted as a synapomorphy uniting the two groups, particularly because of its congruence with other characters (33–35). It is possible, however, that the two forms of long sword evolved in parallel from a common ancestor with a gene pool that permitted the evolution of a long sword. Indeed, the ability to produce a sword may describe a larger group, probably the whole genus.

Within the northern swordtail group, the sword has become greatly elongated in some species and reduced in others. The loss of the caudal appendage has apparently occurred independently three times, inasmuch as each of the clades of northern swordtails contains one form with no sword. The alternative explanation, that in northern swordtails the sword evolved independently three times, is not only an unparsimonious interpretation of that character, but also unlikely because of the similarity of details of the pigmentation and structure of the sword (characters 2 and 3).

Considerable genetic change must have occurred in the pygmy swordtail lineage, because one species, *X. pygmaeus*, has no sword, and in *X. multilineatus* and *X. nigrensis* the sword has become an allometric trait. In this species pair, the caudal appendage is virtually absent in small males. Had the allele for large

size at the sex-linked locus been eliminated, then these species would consist of small fish only, similar to *X. continens* and *X. pygmaeus*. It would then have been impossible to determine whether the absence of a caudal appendage was genetically fixed and independent of size, or was the result of the fish being below the critical size at which a sword develops. The absence of swords in *X. continens* and *X. pygmaeus* is genetically fixed, because when the allele for large size (of *X. nigrensis* or *X. multilineatus*) is introduced into the above species through introgressive hybridization of several generations, no sword develops in the backcross hybrids, although they grow to a large size. The development of the sword, grave spot, and the pigmentation along the ventral edge of the caudal fin are well correlated with one another; it is remarkable that no trace of either pigmentation can be recognized in *X. pygmaeus*.

#### DISCUSSION OF RELATIONSHIPS

Parsimony analysis of the first 32 characters discussed above for the nine Pánuco species with *X. clemenciae* as an outgroup was conducted using the branch-and-bound procedure of PAUP (table 7). One tree resulted, with a length of 43 and a consistency index of .767; it is presented in figure 15. The same tree, but with a length of 41 and a consistency index of .805, resulted when the carbonic anhydrase character (15) was run as UNORDERED. The parsimony analysis was completed before it became known that *X. malinche* is polymorphic for *Cb*. Thus in table 7 the trait is recorded as being absent from

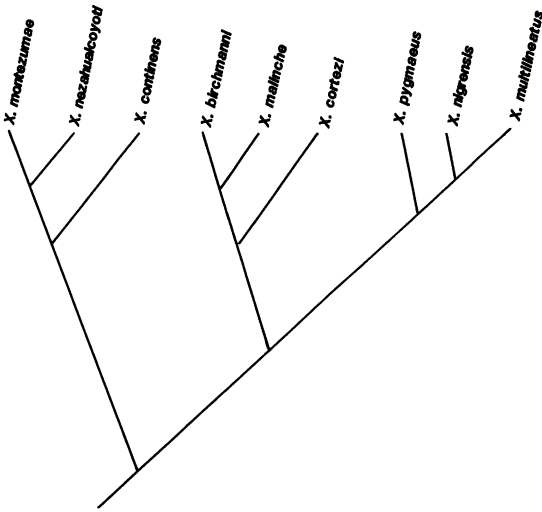


Fig. 15. Cladogram produced by parsimony analysis of character matrix presented in table 7; length = 43, C.I. = .767, produced when character 15 is run ORDERED; length = 41, C.I. = .805, when character 15 is run UNORDERED.

this species. Had the program been run with the trait coded as present, it would have raised the consistency index, but would not have changed the shape of the tree.

1. Northern swordtails, *X. clemenciae*, and the other southern swordtails are united by the general development of long, pigmented swords in males (36), although it is inferred that this character has been reduced or lost, apparently independently, in several northern swordtail species, and that the ability to produce a sword is a character possessed by a wider group, including some or all of the platyfishes. (It should be noted that we feel uncertain about the particular scenario regarding the evolution of the sword in these groups from a common ancestor—see discussion above.) The grave spot (33) is common to all swordtails except *X. pygmaeus* (inferred to be lost), although it is modified in the southern swordtails to extend the full length of the sword as the dorsal sword pigmentation. Ventral caudal fin (and sword) pigmentation (34) is common to all of these fishes, except those without swords (*X. pygmaeus*, *X. continens*, *X. birchmanni*) although, once again, this character might be of a wider generality, inasmuch as it is seen in a few platyfishes. Finally, all swordtails consistently have a hook on ray 5a of the

gonopodium, a character that appears only in very low frequency among platyfishes (35).

2. *Xiphophorus clemenciae* should probably be considered the sister group of the northern swordtails, as it shares a separate distal dorsal sword pigment pattern (3), an upturned sword, at least when young (4), and a derived allele for MP-4 (9) with the Pánuco swordtails. It has formerly been considered to be the most primitive member of the southern swordtails, based primarily on pigmentation characters. It also does not possess the advanced gonopodial characters of the southern swordtails.

3. The Pánuco swordtail species unambiguously form a monophyletic group. All the eight species that were tested share derived alleles for GAPD-1 (5), SOD (6), and MDH-2 (8); seven share a derived allozyme for MP-1 (7), with *X. pygmaeus* autapomorphic for this trait. *Cb* (1) fits best at this level of generality, although it requires three independent losses within the group.

4. Three monophyletic clades are recognized within the northern swordtail group: the *montezumae* clade, containing *X. montezumae*, *X. nezahualcoyotl*, and *X. continens*; the *cortezi* clade, containing *X. cortezi*, *X. malinche*, and *X. birchmanni*; and the *pygmaeus* clade, containing *X. pygmaeus*, *X. nigrensis*, and *X. multilineatus*. Among these three clades, the *cortezi* and *pygmaeus* clades are found to be sister groups, based largely on the xanthophore patterns polymorphic in males (19–22).

5. Within the *montezumae* clade, *Xiphophorus montezumae* and *X. nezahualcoyotl* are sister species, sharing distinct multiple lateral stripes (26). *Xiphophorus montezumae* is autapomorphic for MP-4 (9).

6. *Xiphophorus continens* is the sister taxon of the *montezumae-nezahualcoyotl* pair, sharing with them two derived alleles (10, 15; 15 being also shared with *X. multilineatus*, inferred to be homoplasious) and multiple lateral stripes (26), although the latter trait is not as distinctly expressed in *X. continens* as in the other two. *Xiphophorus continens* also shares two derived alleles with the *pygmaeus-nigrensis-multilineatus* clade (12, 16).

7. Within the *cortezi* clade, *Xiphophorus malinche* and *X. birchmanni* are sister species. They share the head bump in mature males (30), a distinctive vertical bar pattern (31),

and middorsal spotting (32). *Xiphophorus birchmanni* is inferred to have lost *Cb* (1). They also share an allele for PEP-S not found in *X. cortezi* (17), although that character has not been examined in the rest of the group. *Xiphophorus malinche* is inferred to have lost *Sc* (28) and *Cam* (29) (possibly a sampling error), and *X. birchmanni* to have lost the sword and its affiliated characters, perhaps related to its high number of branched caudal-fin rays.

8. *Xiphophorus cortezi* is the sister species of the *malinche-birchmanni* pair. *Xiphophorus cortezi* and *X. birchmanni* share two derived pigment patterns (28, 29) which are inferred to be lost or unsampled in *X. malinche*, and a unique allele for carbonic anhydrase (16—this has not been tested in *X. malinche*).

9. Within the *pygmaeus* clade, *Xiphophorus nigrensis* and *X. multilineatus* are sister species. They share two unique alleles at biochemical loci (13, 14), differential growth rates (24), and allometric growth of the sword (25). The two species differ in two pigment patterns (*X. multilineatus* has vertical bars and a pectoral spot), several electromorphs, including carbonic anhydrase (15), and the occurrence of males with a solid yellow body coloration in *X. multilineatus* (22).

10. *Xiphophorus pygmaeus* is the sister taxon of the *nigrensis-multilineatus* pair. These share one derived allele (11), a gonopodial feature (23), and a distinctive pigment pattern (27). Members of this group lack the biochemical pathway to produce drosoperin (18). These three species are also born at a relatively large size, but this character has not been studied in detail for other species. *Xiphophorus pygmaeus* is autapomorphic for MP-1 (7), and is inferred to have lost *Cb* (1). These three species are also united by derived alleles for ADA (16) and IDH-2 (12), which also occur in *X. continens*. Their occurrence in the pygmy swordtail clade and in *X. continens* is not congruent with the cladogram in figure 14. Their presence in *X. continens* is most parsimoniously explained as homoplasious, but the possibility cannot be ruled out that the ancestral form of the Pánuco basin swordtails was polymorphic for these alleles. In this case, the alleles would have been lost in the branches leading to the *montezumae-nezahualcoyotl* pair and to the *cortezi* clade.

## GEOGRAPHY AND DISTRIBUTIONS

Figure 16 depicts the major geological features of the Pánuco basin, and figures 17, 18, and 19 show the distributions of the nine northern swordtail species. (Consult fig. 1 for names of rivers and towns.) What follows here is a description of the physical geography of the area, and a discussion of the correlations between the species distributions and the geography in light of the proposed relationships of the taxa. Possible evolutionary scenarios resulting in the current distribution patterns are also discussed.

### PHYSICAL GEOGRAPHY

The central east-west axis of the Río Pánuco basin is formed by the Río Pánuco proper, which further upstream is known as the Río Tampaón (the section between the Río Gallinas and the Río Moctezuma), and eventually as the Río Santa María (upstream from Río Gallinas). It receives one major branch from the north, the Río Tamesí, and one from the south, the Río Moctezuma, which in turn has two major arms, Río Moctezuma and Río Tempoal. Only a few tributaries to these rivers penetrate the Mexican plateau (Arroyo Colonia at La Canoa, headwater of Río Tamasopo; Río Verde; Río Santa María; Río Moctezuma; and Río Amajac). All other tributaries originate on the eastern slope of the Sierra Madre.

In the northeast, the Río Pánuco basin is delimited by the Sierra Tamaulipas (east of the great bulge of the Río Guayalejo) and by several lower ridges of igneous rocks further east toward the Gulf of Mexico. In the north in front of the Sierra Madre, the Pánuco basin is bordered by basalt-topped mesas. Several tributaries of the Río Guayalejo penetrate a number of the arid, elevated interior valleys in the Sierra Madre (e.g., Jaumave, elev. 600–800 m) to the west and northwest from Llera where the river leaves the Sierra Madre through an axial depression of the front ranges. In the southeast, the Río Los Hules and Río Calabozo are deflected toward the northwest by the Sierra Otontepec, an isolated volcanic range, and by several lower ridges of Chicontepec sandstone that extend east of the river almost as far north as the town of Tempoal. Two series of volcanic plugs

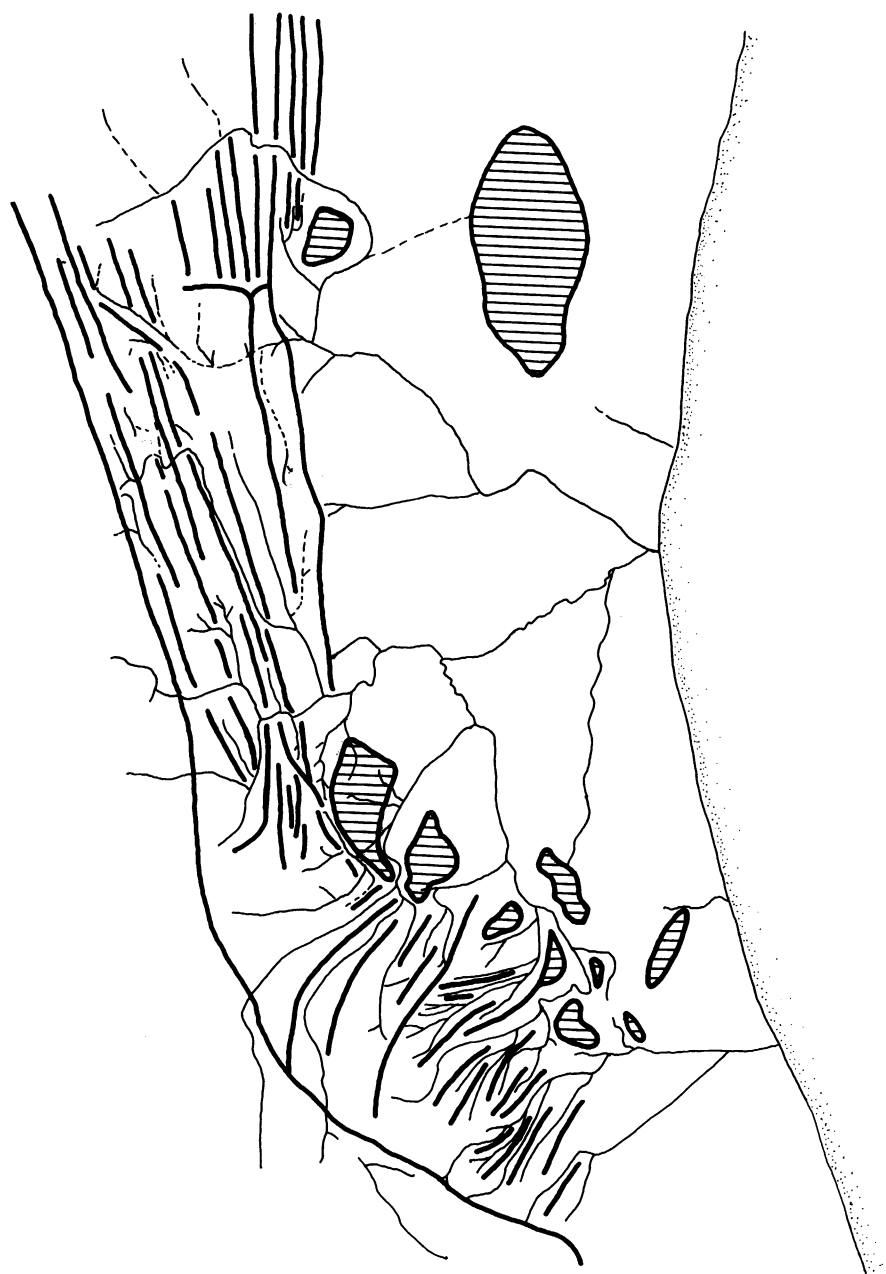


Fig. 16. Diagrammatic representation of some of the geological features of the Río Pánuco basin. Dark lines are mountain ranges of the Sierra Madre; cross-hatched areas are plateaus or mountains in front of the Sierra Madre front.

extending eastward from Chicontepec coincide roughly with the divide between the Río Pánuco and Río Tuxpan drainages.

A glance at the map of the Río Pánuco basin readily reveals the existence of many more streams in the south than further north. This can be attributed to (1) an increase in

rainfall with decreasing latitude; (2) a higher altitude of the elevated rim of the Mesa Central in the south resulting in increased rainfall; (3) a more southeasterly trend of the Sierra Madre south of the Río Moctezuma, resulting in a blockage of the northeasterly trade winds accompanied by more frequent

rainfall, in contrast to the north where the ranges run in a south-southeasterly direction; and (4) the composition of many of the front ranges south of the Río Moctezuma, which are of shales or hard sandstone, often capped by basalt, whereas to the north they are composed of highly porous limestone. Here, even in regions of localized heavy rainfall due to adiabatic cooling as the warm moist air masses from the Gulf of Mexico rise over the Xilitla overthrust (elev. 2900 m) above the Aquismón-Matlapa valley (elev. 100 m) or over the Carabanchel plateau (elev. 2100 m) above the source of the Río Sabinas (elev. 180 m), the mountains are virtually without permanent streams. In the Xilitla area, there is but a single small stream, Arroyo La Conchita, that precipitously descends from 900 to 300 m over a distance of 6 km.

Southeast of the Río San Pedro, the front ranges run toward the north or northeast, roughly at right angles to the Mesa Central. This region constitutes an old, eastward sloping plateau (the Hidalgo Anticline) which begins at an elevation of 2100 m, just east of the barrier range. Folding and elevation were largely completed by early Oligocene (Palmer, 1925). It is indeed a striking sight to stand on some of the isolated, higher peaks and see dozens of flat-topped front ranges, all running in the same direction and all having the same slope and height. North of the Río Moctezuma, the front ranges run parallel to the plateau, trending in a north-northwest to south-southeast direction (fig. 16). Several low mountain ranges lie in front of the Sierra Madre. The Sierra Potosina (sandstone, Chicontepec formation, max. elev. 800 m) is located between the Río Moctezuma to the east and the Río Huichihuayán and Río Coy drainage to the west. The steep western slope of the Sierra Potosina, broken only by the Río Axtla, forms the eastern wall of the Aquismón-Matlapa valley. All streams of the Sierra Potosina drain in an easterly and northerly direction into the Río Moctezuma or Río Coy. A similar range of Chicontepec sandstone, the Sierra San Martín (max. elev. 540 m) separates the Río Moctezuma from the Río San Pedro, and similar ranges are found throughout the southeast. A narrow ridge (Hautla plateau, max. elev. 500 m) topped by basalt, running north, separates the Río Los Hules and Río Calabozo for 22 km.

The major tributaries to the Río Claro, Río Los Hules, Río Calabozo, and Río Tuxpan (in the states of Hidalgo and Veracruz) have cut deep, narrow valleys which end blindly, often at elevations around 1000 m, and then numerous small streams ascend rapidly several hundred to well over a thousand meters. Some of them have their origin in the moist pine oak forest. These streams are fed by countless small springs that collect runoff from cloud condensation and rainfall. These streams seem to have been rejuvenated by recent uplift (Palmer, 1925). The western, drier slope of the barrier range in Hidalgo feeds in part an internal drainage (Río Venados and Río San Agustín) that has cut a canyon into the plateau which deepens toward the northwest. It ends blindly in the dry Lake Metztlán, now intensively cultivated. A resurgence beyond the barrier range and below the level of Lake Metztlán undoubtedly is its underground outlet; it forms the source of the Río Almolón which joins the Río Amajac (Río Moctezuma drainage). It seems probable that the Río Amajac will eventually capture the Río Venados system.

North of the Aquismón-Matlapa valley, a series of synclinal valleys and anticlinal ranges runs parallel to one another and, in general, each successive syncline to the west is at a somewhat higher elevation than the one preceding it. For this reason, the base of each range is at a higher elevation on its western than on its eastern side. The eastern slopes of these ranges are usually very steep. Each valley dips gently toward the Río Tapaón or Río Santa María. The first three valleys have poorly marked surface divides about 10 m high that cause their northern parts to drain into the Río Tamesí. The first three series of synclines and anticlines are spaced widely apart, but farther west (toward the Plateau) they become more irregular and follow one another in rapid succession. Note that the easternmost front range, Sierra de El Abra, ends at the Río Tapaón. The second range, Sierra de Nicolás Pérez, dips under 28 km north of the Río Tapaón at Chantol. Consequently, the first two valleys, Valle de Antiguo Morelos between the first and second range, and Valle de Nuevo Morelos between the second and third range, Sierra La Colmena, become contiguous north of the Río Tapaón, and the third range now becomes

the front range that borders the coastal plain where the Río Tropaón leaves the Sierra Madre (elev. 55 m). From here to the Gulf Coast it is 138 km.

The third valley, Valle de El Naranjo, and its extension to the south, Valle de Tanchachín, runs west of the Sierra La Colmena for 122 km, from west of Ocampo to the Río Tropaón, and for most of its distance it is drained by the Río Salto de Agua (Río Valles) system. A fourth major valley, Valle de Rascón, begins 25 km north of Rascón and runs south for 38 km. It is drained by the Río Gallinas system and it parallels the southern part of the Valle de El Naranjo. A fifth valley, drained by the Arroyo Ciénega Grande, begins 6 km west of the southern end of the Valle de Rascón, and runs south for 31 km, as far as the Río Santa María.

The anticlinal ranges consist of highly porous limestone (El Abra formation) which does not support surface streams, whereas the synclines are covered by an impervious layer of shale (Méndez formation) flanked by flaggy limestone (San Felipe formation) on the lower slopes of the ranges (Mitchell et al., 1977). The Méndez formation lies above the San Felipe, and both have been stripped by erosion from the ranges. Exceptions are: (1) the southern part of the Sierra de Nicolás Pérez; (2) the pass at Tampemoche, 10 km north of Aquismón, on the trail from Tanchanaco to El Sabinal where the Sierra La Colmena, here known locally as the Sierra Las Anonas, dips under the Sierra Sacerdote coming from the northwest; and (3) the region around Xilitla. At Tampemoche, one arroyo (La Garita) arises that descends east toward the Río Coy and a second one that flows northwest into the valley of El Sabinal to join the Arroyo La Calera. All these areas are covered by the San Felipe formation. The presence of a synclinal valley with its stream on the steep slope near Xilitla is due to an overthrust (Heim, 1940).

In the north, virtually all rivers arise from nacimientos, the resurgences of large streams that have traveled underground for considerable distances, through large conduits collecting rainfall that percolates through the porous limestone rocks of the anticlinal ranges (figs. 20, 21). Such conduits are well illustrated in Mitchell et al. (1977) and can be seen in cross section in the walls of canyons cut through the ranges (e.g., those of the Río

Boquilla and Río Tropaón). Nacimientos are usually located along the eastern, lower bases of the ranges. At the foot of the Sierra de El Abra, two large nacimientos give rise to the Río Choy (elev. 34 m) and Río Mante (elev. 80 m). About 45 km north of the Río Mante, the Sierra de El Abra joins the Carabanchel plateau. South of Gómez Farias, three large springs at the base of the plateau give rise to the Río Frío, and 19 km farther north, in the La Flor valley, between the plateau and the Sierra Prieto (elev. 1240 m) to the east, there is a large nacimiento which forms the source of the Río Sabinas. This Sierra consists of several closely folded ranges, and where they dip under the coastal plain 3 km northwest of Encino, two small springs feed rockpools, the source of the Arroyo el Zarco. South of the Río Tropaón, a large nacimiento at the foot of an isolated limestone dome, "Salsipuedes," 6 km east of the front range, is the major source of the Río Coy. It also receives water from smaller nacimientos upstream, those of the Arroyo Tambaque, Arroyo Tanute, and Arroyo Campo Santo, all along the foot of the front range north of Aquismón. Farther south in the Aquismón-Matlapa valley, a large nacimiento 2 km southwest of Huichihuayán and three smaller ones, 2 and 8 km northwest of the village, respectively, feed the Río Huichihuayán (fig. 21). The Río Tancuilín, which enters the southern part of the valley, arises deep inside the Sierra from a large rockpool fed by underground springs in a narrow gorge, 1.5 km west of Neblinas at 550 m elevation, just before its streambed ascends rapidly to Río Verdito (elev. 1200 m) over a distance of 6 km, where additional springs are found. The headwater of the Arroyo Matlapa, Arroyo Atlamaxatl, which also arises in a narrow gorge inside the Sierra, enters the extreme southeastern tip of the valley. Except during the rainy season, the Arroyo Atlamaxatl goes underground 3 km before it reaches the valley, just after it spills over two large falls. Additional springs are present at Matlapa in the valley, and from here on the arroyo is permanent.

Other rivers that arise from large springs or nacimientos north of the Río Moctezuma are (in the Río Valles system): Río el Salto, 6 km west of the upper of two large falls (El Salto); Arroyo La Toma, 5 km upstream from above nacimiento; Río Gallos Grande at Ga-

llos Grande (elev. 980 m); Río Minas Viejo, 24 km south of El Salto; and Río El Gato, 8 km northwest of Nuevo Morelos (the springs of the last two arise in the middle of a valley, away from any obvious ridges). Nacimientos in the Río Gallinas system are those of the Río Tamasopo at the entrance to the Tamasopo canyon, a short distance upstream from "Puente del Dios"; the two sources of the Río Ojo Frío at El Quince north of Damian Carmona; and the Río San Nicolas at San Nicolas de los Montes. (Several other tributaries of this river have not been visited by us.) Several smaller streams that run into the Ríos Santa María and Tampaón and originate from nacimientos or large springs are those of Arroyo Ciénega Grande at Capuchin (several smaller springs also feed the Ciénega Grande), Arroyo La Ciénega at Ojo Caliente, Arroyo Tanchanaquito opposite Ojo Caliente, Arroyo La Calera, and Río Tanchachín. The latter is remarkable, inasmuch as it is one of the few examples of a nacimiento that is located on the western or elevated base of a range. Farther north, the Río Gallitos arises from several large springs located in an elevated valley between 1000 and 1100 m, and a small nacimiento is located at the base of the escarpment to the east at 480 m near Callejones. An isolated drainage arises from large springs west of Ricardo Flores Magón, remarkable in that the source is located somewhat above the base of the range. The Río Santa María de Guadalupe originates west of Nicolas Bravo from several small springs in a steep-sided valley at an elevation between 460 and 500 m. The permanent source of the Río Guayalejo is a large nacimiento (elev. 580 m) at the northern tip of the Sierra Los Nogales, 11 km northeast of Jaumave, just inside the gorge that cuts through the front ranges. The waters from a second, smaller nacimiento (elev. 900 m), located 8 km southwest of Jaumave where the gorge from Palmillas opens into the Jaumave valley, have been largely diverted for irrigation purposes.

There are several instances where a river passes through the immediate anticline to the east and enters the valley in front of it; large waterfalls have been formed, and these are barriers to fish movement. There are two such series along the Río Salto de Agua, one where it enters the valley of El Naranjo west of the

Sierra La Colmena, and a second one near Micos where the river breaks through the Sierra La Colmena. In the canyon that the Río Boquilla has cut through the Sierra de Nicolás Pérez, there is a series of falls 20–30 m high. At Cascada Tamul, where the Río Gallinas joins the Río Tampaón, there is a sheer drop of 105 m (fig. 22).

Often the layers of the Méndez and San Felipe formations have been removed through erosion near the escarpments where the gradient of the streambed steepens and the river now disappears (permanently or only in the dry season) into the exposed porous limestone (e.g., Río Gallitos, Río Santa María de Guadalupe, Arroyo Hondo, Arroyo El Sabinito, Río Minas Viejo, Arroyo Matlapa, Arroyo La Garita, Arroyo La Conchita). This has also been the fate of the Arroyo Ciénega Grande just before it joins the Río Santa María at La Boquilla. The Río Tancuilín, which cuts across numerous anticlines in rapid succession, goes underground in many places only to reappear a short distance beyond.

The main folding and uplift of the front ranges is considered to be post-Eocene and early Oligocene, but may have continued sporadically until recent times. In this karst region north of the Río Moctezuma, many watercourses probably last for only a limited time before, aided by uplift, new subterranean solution conduits arise and divert the water, resulting in nacimientos going dry or in greatly reduced discharge that significantly changes stream ecology. Large cave openings located well above the base of the steep slopes of these ranges may represent former nacimientos. Mitchell et al. (1977) suggested that such a fate may be in store for the Río Choy and Río Mante that drain the Sierra de El Abra. Their nacimientos are located at elevations of 34 and 80.5 m, respectively. The volume of discharge into the Río Mante is more than twice that into the Río Choy, and the subterranean divide was provisionally located by Mitchell et al. (1977) about 18 km north of the Río Choy, or 66 km south of the Río Mante. Progressive solution eventually will bring the underground drainage of the Río Mante into contact with the conduits of the Río Choy, into which this drainage will be diverted. The higher elevation of the base of the Sierra de El Abra at the nacimiento of the Río Mante was attributed to recent dif-

ferential uplift. Support for such a view is provided by a Pleistocene cap of lacustrine limestone on a small hill, Cerrito del Campo Santo (elev. 220 m), south of the Río Mante at Quintero and immediately in front of the Sierra de El Abra (Heim, 1940; Mitchell et al., 1977), and by the dissection of the basalt-capped mesas to the north near the Río Guayalejo, which are now 200–250 m above the surrounding plain. The age of the basalt is estimated to be late Pleistocene (Heim, 1940). In the southeast, Pleistocene gravel deposits are located on top of hills between the Río Pánuco and Río Tuxpan drainages and on the upper slopes (400 m above the plain below) of the approaches to the volcanic plugs (Muir, 1936; Palmer, 1925).

The Río Santa María de Guadalupe–Río Comandante system has cut across the Sierra de Nicolás Pérez (La Boquilla canyon) and the Sierra de El Abra. The walls of the La Boquilla canyon tower more than 300 m above the river bed. However, only a slight rise of about 10 m prevents this river from flowing south through the long valley of Nuevo Morelos. The canyons through both sierras are aligned with each other and also roughly with a gap in the next range to the west at Nicolas Bravo. This suggests that the river was already in place before the two ranges to the east arose, and agrees with the view that the ranges toward the west and the Mexican Plateau are considerably older.

Farther south, the relationship between the Sierra La Colmena and Río Salto de Agua is different. The Sierra must have been in place, because the river turns sharply south for 55 km before turning east and breaking through the Sierra at Micos. There is now a dry gap through the Sierra de El Abra east of Ciudad Valles (the route of Mex. Hwy. 70), which is roughly aligned with the break at Micos. Mitchell et al. (1977) have identified it as the old stream bed of the Río el Salto (also known as the Río Valles downstream from the falls at Micos) before it was pirated south toward the Río Tampaón. Again, this suggests that the Río el Salto was in place before the Sierra de El Abra was formed.

#### DISTRIBUTIONS

Northern swordtails are Sierra Madre fishes. They occur from the base of the foothills

upstream to an elevation between 1200 and 1300 m, roughly in a belt 300 km long and 55 to 60 km wide. It should be noted that the tributaries of main rivers in this area are of exceptional clarity.

*Xiphophorus nigrensis* and *X. multilineatus* have allopatric distributions in northern (*X. nigrensis*, Río Choy) and southern (*X. multilineatus*, Río Coy) tributaries of the Río Tampaón (fig. 17). Both rivers arise east of the Sierra Madre; they are fast-flowing streams with sandy to muddy bottoms and extensive stands of submerged aquatic vegetation and generally steep banks. Rocky habitats are restricted to the immediate areas of nacimientos. Both forms occur in these rivers as far as the Río Tampaón. *Xiphophorus multilineatus* also ranges upstream from the nacimiento in the Arroyo Oxitipa as far as Ocizen, and in the Arroyo Tambaque almost as far as its nacimiento. It is absent from all other headwaters and tributaries of the Río Coy system.

*Xiphophorus pygmaeus* occurs abundantly throughout the Río Huichihuayán, in the lower 6 km of the Río Tancuilín, and in the Río Axtla, about halfway toward the Río Moctezuma. It is absent from other tributaries of the Río Axtla system, including the numerous small rills and brooks that flow for a few hundred meters from the lower slope of the Sierra Potosina into the Río Huichihuayán. Like the Río Coy and Río Choy, the Río Huichihuayán is a fast-flowing stream (in some years, however, current can hardly be detected during the dry season) with a sandy and gravel bottom, some mud, and extensive stands of aquatic vegetation. Rocky terrain is restricted to nacimientos and some riffle areas north of Huichihuayán. We cannot confirm Gordon's (1953) conclusion that this form is partial to the steep slope below overhanging banks. On the contrary, we have found it to be common in dense vegetation in water 0.5 m deep along otherwise shallow banks. The bed of the Río Tancuilín, which has its origin deep inside the Sierra Madre, is strewn with boulders and rocks, and here *X. pygmaeus* is restricted to its lower 6 km, primarily in deep pools along the edge of the main river bed. Rocky habitat is also found in the break through the Sierra Potosina, where the Río Axtla spills toward the floodplain of the Río Moctezuma. Beyond Villa





Fig. 17. Collection localities of (★) *X. pygmaeus*, (●) *X. nigrensis*, and (■) *X. multilineatus*.

Terrazas, the gradient of the river becomes so slight that current can hardly be detected and water quality deteriorates rapidly.

One of the headwaters of the Río Coy system, Arroyo Oxitipa, arises in the middle of a swampy meadow near the narrowest point of the Aquismón-Matlapa valley, and comes within 2.5 km of the northernmost naci-

miento of the Río Huichihuayán. Differences of not more than 3 m in altitude separate the two watersheds. (An unnamed arroyo that runs into the Río Huichihuayán comes even closer to the Arroyo Oxitipa.) In the past, the entire valley (or the Río Huichihuayán) could have drained toward the north into the Río Coy. Slight changes in pitch of the valley (the



Fig. 18. Collection localities of (■) *X. montezumae*, (●) *X. nezahualcoyotl*, and (★) *X. continens*.

elevation at Comola where the Río Axtla leaves the valley is about 70 m; the elevation at the nacimientos is just below 100 m) could have led to a separation of the Río Coy and Río Axtla drainages and split the ancestral pygmy swordtail into the *X. pygmaeus* and *X. nigrensis*–*X. multilineatus* lineages.

*Xiphophorus montezumae* and *X. nezahualcoyotl* have allopatric distributions, and with one minor exception they are found north of the Río Tampaón–Río Santa María axis (fig. 18). *Xiphophorus montezumae* occurs throughout most of the Río Gallinas system, but is apparently absent from the Río

San Nicolás. This species is absent from the two springs of an internal drainage that flows into a huge limestone sink, Laguna Grande, 15 km north of Tamasopo. This species is also not present above the Tamasopo canyon, at the edge of the plateau. It occupies a stream, Arroyo Ciénega Grande, in a north-south running valley southwest of the Río Gallinas, and Arroyo La Ciénega at Ojo Caliente, just southwest of the southern terminus of the above valley. The population opposite Ojo Caliente in the Arroyo Tanchanaquito represents the only instance of the *X. montezumae*-*X. nezahualcoyotl* pair found south of the Río Tropaón-Río Santa María axis.

In the Río Pánuco system, *X. nezahualcoyotl* is present throughout the Río el Salto (Río Valles) system, from small springs at 1200 m at the edge of the plateau in the valley of Papagayos (northern part only, Arroyo La Barranca near Santa Barbarita and Arroyo Hondo at Francia Chica) to the large pools below the falls at Micos. At Santa Barbarita, these fish are even present in wells dug into the steep hillsides. The Río Valles drainage is by far the most extensive one occupied by this species. The only other tributary of the Río Tropaón inhabited by it is the Río Tanchachín, which is only 18 km long and which is located just west of the front range through which the Río Tropaón breaks into the coastal plain. The specimens of UMMZ 124436, collected in an arroyo "near Valles" and described as *X. cortezi* (Rosen, 1960), have been, upon reexamination, properly referred to *X. nezahualcoyotl*.

The valley of Papagayos runs northwest-southeast and dips from 1400 to 1000 m. The Arroyo Hondo, in the north, turns abruptly east at Santa Barbarita and breaks through a gap in the anticlines eventually to join the nacimiento of the Río el Salto, but in the wet season only. Two kilometers beyond Santa Barbarita, the drainage of the valley of Papagayos continues toward the southeast, and eventually ends blindly in temporary lakes. *Xiphophorus nezahualcoyotl* is absent from this internal drainage.

To the north in the Río Tamesí drainage, this species is commonly found in the few relatively short watercourses of interior valleys, including several that now have no surface connection with either the Río Tamesí

or Río Tropaón. There is a series of springs around the town of Ocampo, and each one is inhabited by this species. No representative of this species has been collected in the valley of Antiguo Morelos. In two rivers that arise from the base of the easternmost front range, *X. nezahualcoyotl* is restricted to the headwaters. It is common in the nacimiento of the Río Sabinas and further upstream in the springs and rockpools of the boulder-filled Arroyo La Playa (fig. 23). It becomes exceedingly rare downstream, and no specimen has been taken more than 7 km below the nacimiento. In one of the tributaries of the Río Sabinas, Arroyo el Zarco, this species is common and restricted to two headwater rockpools, which in the dry season are not more than 50 m in length and 3 m wide. *Xiphophorus nezahualcoyotl* occurs here sympatrically with *X. variatus*, with which it hybridizes sparingly. No specimen of *X. nezahualcoyotl* has been taken further downstream in this arroyo (where, in the dry season, it consists of stagnant pools fed by small underground springs), although the arroyo has been extensively sampled since 1950, with more than 5000 *X. variatus* specimens collected (Borowsky, 1984; Darnell, 1962). Similarly, in the Río Frío, *X. nezahualcoyotl* has only been collected within the 4 km below the nacimientos.

Several populations of both *X. montezumae* and *X. nezahualcoyotl* live above significant barriers, suggesting that these fish already occupied this region before the series of valleys and ranges arose (figs. 22, 23). The presence of *X. nezahualcoyotl* in the Río Tamesí drainage suggests a former connection with the Río Valles system in the Ocampo region. There are no significant barriers in the two valleys that extend south from Ocampo on both sides of the Sierra La Colmena toward the Río Tropaón. Numerous swamps are located in the poorly drained area between the Río Boquilla canyon and the source of the Río Los Gatos, 22 km to the south.

Until historical times, the Río Gallitos between 1100 and 900 m spilled over a 400 m high escarpment (Cascada El Contadero) into the very head of the valley of El Naranjo (the valley west of the Sierra La Colmena) at 470 m. From there it ran south for 6 km along the western side of a steeply plunging anti-

cline. At its southern tip (elev. 440 m), the stream could have turned sharply north and passed through a narrow gap to join the Río Santa María de Guadalupe at Nicolás Bravo (elev. 440 m). However, no trace of such a watercourse can now be seen. Alternatively, the Río Gallitos could have continued south and joined with the stream at Ricardo Flores Magón, 21 km to the south, where the altitude of the valley drops to 380 m. From there it is 20 km south to the Río el Salto (elev. 300 m). At the present time the two rivers are kept separate by a rise of only 10 m in the valley floor. Even before the Río Gallitos went underground on top of the escarpment, its passage south would have become blocked by the lava flow of Cerro Partido, 7 km northwest of Ricardo Flores Magón. Heim (1940) has suggested that this lava may have flowed in historical times, perhaps as recently as 2000 years ago. At the present time, the old dry bed of Río Gallitos heads south-southeast into the lava bed, where it disappears.

East of Ricardo Flores Magón, the Sierra La Colmena dips under for 11 km. There is a broad opening to the valley of Nuevo Morelos to the east, where the elevation drops gently 60 m. This path also could have been taken by the above streams that would then have joined the Río Los Gatos. If this was indeed the case, the passage would also have become blocked by the lava flow. The stream at Ricardo Flores Magón now closely follows the southern edge of the lava field, until it ends in a swamp with no outlet. The lava flow itself moved east into the Valle de Nuevo Morelos. There the flow divided. One arm passed through the Río Boquilla canyon in the Sierra de Nicolás Pérez and the other passed south in the Valle de Nuevo Morelos as far as Rancho El Jacube, 28 km northwest of Ciudad Valles. Obviously, at the time of the eruption, the slope toward the east was steeper than the one south into the Valle de El Naranjo toward the Río el Salto, just as it is today.

The vicariant event responsible for the split between the *X. montezumae*-*X. nezahualcoyotl* pair could have involved a shift in the course of the Río Gallinas. The Río Gallinas and its tributary to the north, the Río Ojo Frío, run parallel to the Río el Salto and one of its tributaries, Arroyo Los Sabinos, 4.5 to

10 km to the east. At Micos, the Río el Salto (elev. 210 m) turns east and breaks through the Sierra La Colmena. The two river systems are separated from each other by the Sierra El Corita (max. elev. 740 m), but several passages through it could have provided former connections between the two systems. One of the passages is located at the northern terminus of the valley of Rascón (see discussion under *X. continens* below). The other two passages run from Rascón (elev. 300 m) toward Micos. They begin jointly at Rascón; one of them soon turns sharply north and follows for most of its course the arroyo "Los Sabinos" (also paralleled by the Mexican National Railroad) before turning east toward Micos. This arroyo is inhabited by *X. nezahualcoyotl*. The highest elevation of this pass is 350 m. The second passage continues northeast for another 5 km and after rising to an elevation of 320 m, it descends rapidly to the 230 m level before turning sharply north just in front of the Sierra La Colmena. The perfectly level section of the northward passage is extensively covered by swamps. We suggest that the Río Gallinas might have followed either one of these passages, before it was pirated by a stream to the south. Such an event would also explain the youthfulness of the Cascada Tamul (fig. 22), where, in contrast to the many other waterfalls of the Pánuco basin, there is no evidence that the river has yet begun to cut back into the rock. Once the river changed its course, the fish populations in the Río Gallinas and Río el Salto became separate. The valley of Tanchachín is only indistinctly delimited from the Micos area, and the second one of the above suggested passages of the Río Gallinas passes within 3 km of the nacimiento of the Río Tanchachín (elev. 200 m). An arroyo, La Pagua, arises in the Sierra La Colmena northeast of the Río Tanchachín and flows toward the northwest before it is swallowed by a cave near the point at which the second of the above passages turns north. This arroyo is the only watercourse in this region that is inhabited neither by *X. montezumae* nor *X. nezahualcoyotl*, perhaps because it lacks flowing water during the dry season.

Further south, only a low, rather short and broken ridge is located between the Río Gallinas (elev. 250) and La Ciénega Grande, a 24

km<sup>2</sup> swamp (elev. 280 m), 6.5 km to the west. At the present time, the lowest pass between these two bodies of water is 350 m, and a former connection cannot be ruled out. The present, 15 km long outlet of La Ciénega Grande to the south is paralleled on the east by a 300 m high ridge from Tamul to La Boquilla, which also forms the western wall of the gorge of the Río Santa María which runs north. Most of the drop in altitude between Ciénega Grande and La Boquilla occurs in the last 5 km.

*Xiphophorus continens* is restricted to the Río Ojo Frío north of Damian Carmona, where it is sympatric with *X. montezumae*. This is a deep, fast-flowing stream, with numerous rockpools, boulders, and dense stands of submerged aquatic vegetation. This species is abundant in the large spring pool which feeds one branch of the Río Ojo Frío, 1 km northeast of El Quince, but relatively uncommon in a second branch which arises from several large springs inside a canyon 1 km north of the village.

An interesting geological feature at Damian Carmona may provide a clue to the evolution of *X. continens*. Just north of the town, the long valley of Rascón abruptly rises by 100 m and the Río Ojo Frío descends from the elevated northern part of the valley over a distance of 4–5 km. In the past, the descent could have been steeper and could have involved waterfalls that acted as barriers to fish movement. Thus, *X. continens* may have evolved in isolation in the Río Ojo Frío. *Xiphophorus montezumae* may not have reached the river until this barrier was removed by erosion. Access to the northern part of the valley could also have been provided by a gap through the mountain range to the east that leads toward the Río el Salto. At the present time, an arroyo (not inhabited by fishes) at La Jabonera at the northern tip of the valley drains through this gap during the rainy season instead of south toward the Río Ojo Frío.

The *X. cortezi*–*X. birchmanni*–*X. malinche* alliance is found in the Río Pánuco basin south of the Río Tapaón (fig. 19). *Xiphophorus cortezi* is the only member of this group that occurs between the Río Tapaón and the Río Moctezuma; toward the southeast, *X. cortezi* and *X. birchmanni* interdigitate in

complex ways at low elevations in the Río San Pedro and Río Candelaria drainages. Further toward the southeast at low and intermediate elevations in the Río Atlapexco and Calabozo drainages and the adjacent Río Tuxpan system, *X. birchmanni* is the only member of this group. The distribution of *X. malinche* is poorly known; it has been found at high elevation in the Río Calabozo and Atlapexco drainages and in the Río Claro.

*Xiphophorus cortezi* favors streams with boulders and other rocky habitats. It is present in all streams of the Sierras Potosina and San Martín which arise from small springs and runoff near the height of land. This species disappears from these streams as they enter the coastal plain, where rocky habitats are nonexistent. In the Río Coy drainage, *X. cortezi* is abundant in every one of the small rocky tributary streams, but absent from the Río Coy itself, which has a bottom of sand and fine gravel. (Between the nacimiento and the Río Tapaón, 2901 *X. multilineatus* specimens were taken but no *X. cortezi*.) *Xiphophorus cortezi* and *X. multilineatus* were sympatric only at two sites, both rocky locations: the Arroyo Oxitipa at Octzen (86 *X. multilineatus*, 62 *X. cortezi*), and 300 m downstream from the nacimiento of the Arroyo Tambaque (5 *X. multilineatus*, 24 *X. cortezi*). Both areas represent the upstream limit of *X. multilineatus* and the downstream limit of *X. cortezi* distribution.

A similar situation exists in the Río Axtla system. In its northern branch, the Río Huichihuayán, which is fed by several nacimientos, rocky habitat is largely absent and *X. pygmaeus* is 17 times more common than *X. cortezi* (104 *X. cortezi*, 1792 *X. pygmaeus*, a summary of many collections). However, in all the small rocky tributaries, *X. cortezi* is a common denizen, but *X. pygmaeus* has not been taken in any of them. In the Río Tancuilín, which is the boulder-filled southern branch of the Río Axtla drainage, *X. cortezi* is abundant throughout, while *X. pygmaeus* is restricted to the lower 6 km, primarily in the deeper pools along the main channel (260 *X. cortezi*, 88 *X. pygmaeus*).

Like *X. nezahualcoyotl*, *X. cortezi* occurs above major barriers, waterfalls more than 10–50 m in height (Arroyo La Conchita, Arroyo Atlamaxatl, Río Verdito). The highest

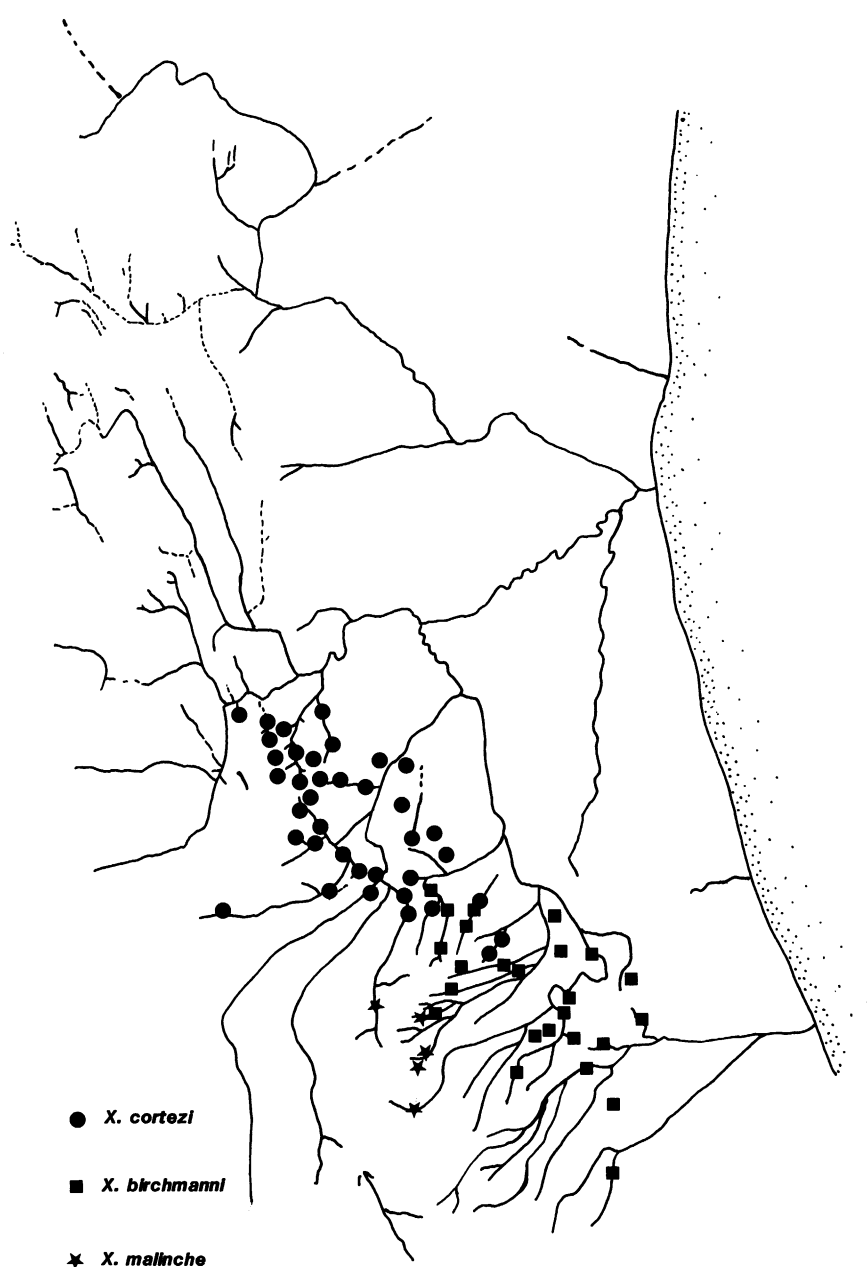


Fig. 19. Collection localities of (●) *X. cortezi*, (★) *X. malinche*, and (■) *X. birchmanni*.

elevation at which *X. cortezi* has been taken in the Xilitla areas is 840 m and at Río Verdito at 1200 m.

The Río Tampaón is clearly the barrier between the *montezumae* and *cortezi* groups, and an interesting geographic puzzle is posed by the distribution of *X. cortezi* in the two narrow valleys just south of the Río Tam-

paón. The valley of El Sabinal, drained by the Arroyo La Calera, is the more easterly of the two. It actually represents a southward extension of the valley of Tanchachín across the Río Tampaón, which is inhabited by *X. nezahualcoyotl*. *Xiphophorus cortezi* may have lived in this region before these two valleys arose; otherwise, one would have to



Fig. 20. Nacimiento del Río Choy, New York Zoological Society photograph taken in 1940. *Xiphophorus nigrensis* is common around the rocks in front of the cave. Around 1950, a series of steps was constructed that leads into the cave from the left.

assume that *X. cortezi* entered the Río Tampaón, migrated upstream through its gorge in the Sierra La Colmena, and, while doing so, overcame a 100 m long underground passage (the river goes underground in the gorge), and then turned south and entered the Arroyo La Calera, and also continued further upstream, bypassing the Río Tanchachín which comes in from the north, eventually to reach and ascend the Arroyo San José on the second valley which comes in from the south. If one or both of the tributaries south or north of the Río Tampaón had been unoccupied by *Xiphophorus*, one might expect that the first species to arrive would colonize the tributaries on both sides of the river. This obviously occurred deep inside the Sierra Madre at Ojo Caliente. Perhaps several 3 m high falls over which the Río Tanchachín spills

into the Río Tampaón could have kept *X. cortezi* out, but the descent of the two arroyos from the south is also very precipitous. Conceivably, *X. cortezi* could have occupied the Arroyo La Calera by ascending the Arroyo Garita from the Arroyo Oxitipa to the height of land at Tampemoche (400 m) and then descending a nearby stream to the Arroyo La Calera. But, this does not explain why this arroyo has remained uncolonized by *X. nezhualcoyotl*. No such explanation can account for the presence of *X. cortezi* in the adjacent valley to the west, that of San José el Viejo, which is separated from the Arroyo La Calera by a 340 m high ridge (Sierra el Botadero, max. elev. 500 m). The Arroyo San José joins the Río Tampaón 2 km east of Cascada Tamul.

With regard to the split between the *mon-*



Fig. 21. **Top:** Arroyo La Ciénega at Ojo Caliente 200 m downstream from spring pool. Tree islands stand in the middle of the stream. Further downstream the channel narrows and the current increases until after 2 km the stream cascades into the Río Santa Maria 10 m below. The name Ojo Caliente (the warm eye) derives from the small, round spring pool with a water temperature of 28°C considerably warmer than other springs (23°C) in the region. Note the clear water. *Xiphophorus montezumae* specimens were collected beneath the logs in the foreground. **Bottom:** The main source of the Río Huichihuayán after two days of heavy rain. *Xiphophorus pygmaeus* often pick at algae on the rocks to the left.



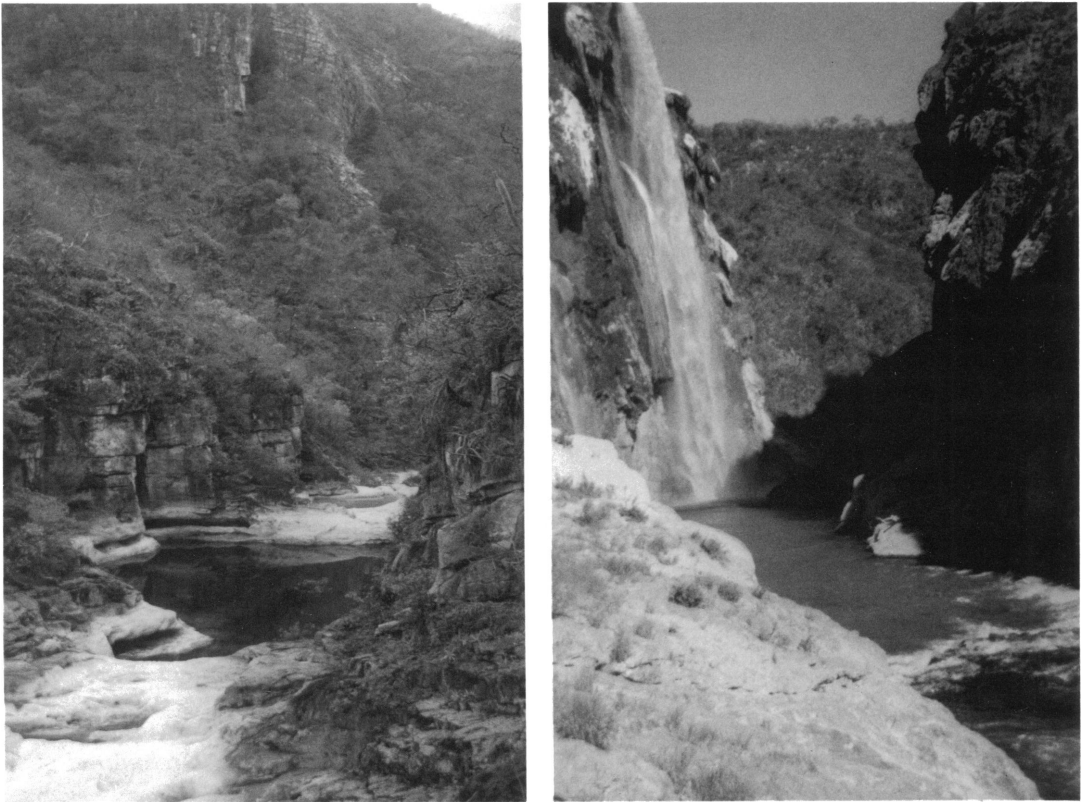


Fig. 22. **Right:** Cascada Tamul. The Río Gallinas spills into the gorge of the Río Santa Maria. The height of the fall is 105 m. **Left:** The canyon of the Río Boquilla through the Sierra de Nicolás Pérez. A series of 10–15 m high “steps” prevents upstream movement of fishes. Except during the rainy season when a torrent scours the canyon, permanent water is restricted to a few large rock pools.

*tezumae* and *cortezi* clades, one possibility is that an ancestral species was present in streams only on one side of the Río Tampaón. Presumably, a founder population eventually became established and isolated in a stream or river located on the opposite bank and subsequently evolved into a new species. Exactly such a process might also have been responsible for the *X. nigrensis*–*X. multilineatus* split. The ancestral species probably occupied the region south of the Río Tampaón, where streams are much more common than farther north. The new founder population would then have invaded some stream on the north side of the Río Tampaón, a good candidate being the Río Valles after it had changed its course from passing through the Sierra de El Abra to join the Río Tampaón, just a short distance east of the Sierra La Colmena.

*Xiphophorus birchmanni* and *X. malinche* are closely associated with the Hidalgo anticline. The westernmost population of *X. birchmanni* occupies the headwaters of the Río San Pedro, which is a short, rather precipitous watershed that drains the front of a high range capped by igneous extrusions. This species was collected at the foot of this range (Río Talol, Río Coahuilco) at San Felipe de Orizatlán (elev. 180 m) and farther upstream near Santa Maria (elev. 500 m). In the Arroyo Xochititla, 5 km west of Orizatlán, *X. cortezi* and *X. birchmanni* are sympatric. Two kilometers east of Orizatlán, the Arroyo Los Sabinos arises and it is occupied by *X. cortezi*. Seven kilometers farther east, both species occur sympatrically in the Arroyo Santa Cruz, preliminary evidence indicating that *X. birchmanni* is significantly more abundant upstream. The next river, Río Tecoloco (Río

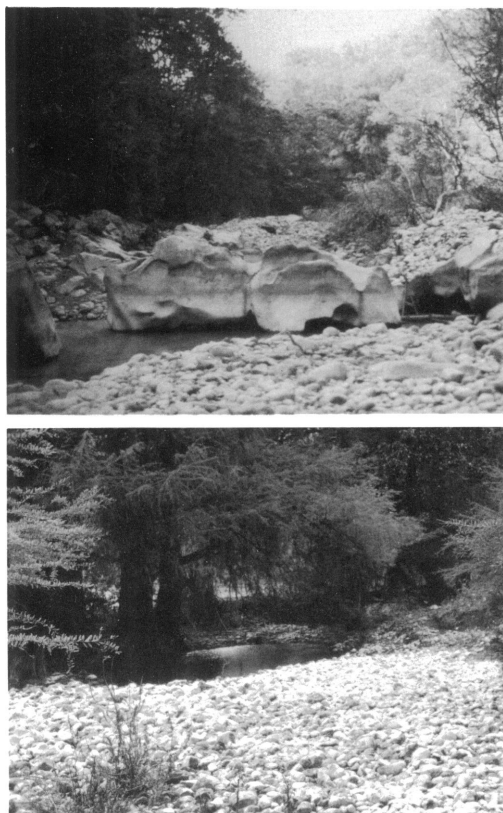


Fig. 23. **Top:** Large boulders in Arroyo La Playa, 150 m upstream from the Nacimiento del Río Sabinas. Boulders composed of El Abra limestone have been washed down from a narrow canyon, 8 km upstream. Note concavities on the boulders, the remnants of solution cavities characteristic for this limestone. Pools around the boulders are inhabited both by *X. nezahualcoyotl* and *X. variatus*. **Bottom:** Pool below bald cypress tree in Arroyo Gallitos (1000 m). During the dry season this stream flows only intermittently and *X. nezahualcoyotl* become concentrated in isolated pools fed by underground seepages. During the wet season level of stream rises to height of lower limbs.

Los Hules system), 5 km to the southeast, and its major tributary, the Río Caimantla, which joins it at Huejutla de Reyes, drains the shoulder of this mountain massif; only *X. cortezi* occurs here. From here on, all streams to the east and southeast in the Río Pánuco basin and in the adjacent Río Tuxpan drainage are occupied by *X. birchmanni*, but only at low and intermediate elevations. Like *X. cortezi*, *X. birchmanni* is partial to streams with rocks and boulders, and as the streams

enter the coastal plain, the species disappears from the collections. Indigenous people near Atlalco, Hidalgo, capture these fishes for food by scooping them up from beneath boulders with their hands or hats.

The presence of *X. malinche* at higher elevations in the headwaters of the Río Atlapexco and Río Calabozo drainages and across the major divide in the Río Claro strongly suggests a past connection in this geologically active region. Palmer (1925) has described several overthrusts in the region around Molango (HID) where the three watersheds come close to the divide. Significantly, this species is missing from the Río Tuxpan drainage, the headwaters of which are 30 km to the southeast of Molango.

We interpret the present distribution of *X. cortezi* and *X. birchmanni* in the foothills of the Sierra Madre between the Río Moctezuma (Tamazunchale) and the Río Candelaria drainages (Huejutla de Reyes) as being the result of secondary contact. *Xiphophorus cortezi* occupies mainly the Río Axtla and Río Coy drainages, the Sierra Potosina, and the Sierra San Martín; *X. birchmanni* occupies the Hidalgo anticline.

In the absence of detailed information on what forms live upstream in the Río Moctezuma and Río Amajac, it is difficult to pinpoint which geological event might have led to the splitting of the *cortezi* group. Conceivably, the ancestral form of *X. birchmanni* could have invaded the Río Atlapexco and Río Calabozo drainages from the Río Claro in the highlands through stream capture (see above) and then moved southeast into the Río Tuxpan basin and northwest along the foot of the Sierra Madre until it came into contact with *X. cortezi*. *Xiphophorus birchmanni* probably gained access to the Río Tuxpan drainage in the region south of Benito Juárez (VER), where the Río Zontecomatlán and Río Xilotla, tributaries to the Río Calabozo, turn sharply north, being blocked by the massif of Cerro Tzozocalco. But only a low, gently sloping ridge separates them from the Río Vinazco (Río Tuxpan drainage). Arroyos from both drainages (e.g., Arroyo Xocoyo, Pánuco; Arroyo Pilpuerta, Tuxpan) ascend this ridge and come to within as little as 2 km of each other. Both are inhabited by *X. birchmanni*.

No account of Pánuco basin *Xiphophorus* would be complete without some comments on a tenth species, *X. variatus*, which occurs in this region. *Xiphophorus variatus* (or the *X. variatus* clade) occurs in parts of the Pánuco basin and in rivers further south, as far as the Río Nautla, VER. *Xiphophorus variatus* belongs to the platyfish group, which ranges from Coahuila, Mexico, to Belize.

In the Río Pánuco basin, *X. variatus* occurs commonly in small streams throughout the coastal plain. Its northwesternmost outpost is represented by several populations in small springs and brooks (elev. 600–880 m) in the broad desertlike valley of Jaumave, west of the Carabanchel plateau. It inhabits the Arroyo Membral (at nacimiento, Canyon La Borrega), which drains the western slope of the Sierra de Tamaulipas toward the Río Guayalejo and the nacimientos of numerous small streams that originate from the eastern base of the Sierra de El Abra (Riachuelo, Santa Clara, Río Tantoán, Taninul). We have failed to take this species at the nacimientos de San Rafael de Los Castros, del Río Mante, and del Río Choy, although it is present in these rivers further downstream. Other stations for this species in this area have been listed by Rosen (1960). For the remaining area north of the Río Tampaón, *X. variatus* is found in the valley of Nuevo Morelos, but it has not penetrated any other front range. The report by Meek of *X. variatus* collected at Rascón must have been the result of an error. In the headwater of the Río Sabinas, Arroyo La Playa, and in the two spring pools at the head of the Arroyo el Zarco, this species occurs sympatrically with *X. nezahualcoyotl*. At the latter location, hybrids (complex backcrosses) between the two species have been found. Farther south, *X. variatus* is broadly sympatric with *X. cortezi*. It is common in all tributaries to the Río Coy and throughout the Aquismón–Matlapa valley. At two locations in the Río Coy drainage, three species of *Xiphophorus* (*X. variatus*, *X. cortezi*, and *X. multilineatus*) have been collected in the same seine haul (Arroyo Oxitipa, and downstream from the nacimiento of the Arroyo Tambaque). Between the Río Moctezuma and the Río Tampaón, *Xiphophorus variatus* is again absent from every stream inside the Sierra Madre. *Xiphophorus variatus* is also

found sympatrically with *X. cortezi* throughout the Sierra Potosina and Sierra San Martín. Further toward the southeast, *X. variatus* occurs together with *X. birchmanni*, and has penetrated the headwaters of the Río Calaboza and Río Los Hules drainages to an altitude of approximately 400 to 500 m (upper limit not precisely known yet). Across the Río Pánuco–Río Tuxpan divide, the populations of *X. variatus* are distinct (based on pigment patterns and biochemical loci) but the *X. birchmanni* populations are indistinguishable from one another.

Several geographical puzzles are posed by the distribution of *X. variatus*. How did the species gain access to the Jaumave valley? Why is it absent from any of the valleys inside the Sierra Madre north of the Río Moctezuma? This situation can be contrasted with the one found in the Río Czones and Río Tecolutla systems, farther south, where *X. variatus* (or its sister species *X. evelynae*) occurs above major barriers, at altitudes of 1000 m and higher.

## REFERENCES

- Atz, J. W.  
1962. Effects of hybridization on pigmentation in fishes of the genus *Xiphophorus*. *Zoologica* 47(4): 153–181.
- Borowsky, R.  
1984. The evolutionary genetics of *Xiphophorus*. In B. J. Turner (ed.), *Evolutionary genetics of fishes*, pp. 235–310. New York: Plenum Press.
- Darnell, R. M.  
1962. Fishes of the Río Tamesi and related coastal lagoons in east-central Mexico. *Publ. Inst. Mar. Sci. Port Aransas, Texas* 8: 299–365.
- Gordon, M.  
1953. The ecological niche of the pygmy swordtail, *Xiphophorus pygmaeus*. *Copeia* 1953(3): 148–150.
- Harris, H., and D. A. Hopkinson  
1977. *Handbook of enzyme electrophoresis in human genetics*. New York: American Elsevier.
- Heim, A.  
1940. The front ranges of the Sierra Madre Oriental, Mexico, from Ciudad Victoria to Tamazunchale. *Ecol. Geol. Helv.* 33: 313–352.
- Hubbs, C. L., and M. Gordon  
1943. *Studies of cyprinodont fishes*. XIX. *Xi-*

- xiphophorus pygmaeus*, new species from Mexico. *Copeia* 1943(1): 31–33.
- International Code of Zoological Nomenclature  
1985. Third edition; adopted by the twentieth General Assembly of the International Union of Biological Sciences, London.
- Jordan, D. S., and J. O. Snyder  
1900. Notes on a collection of fishes from the rivers of Mexico, with descriptions of twenty new species. *Bull. U.S. Fish Comm.* for 1899: 115–147.
- Kallman, K. D.  
1971. Inheritance of melanophore patterns and sex determination in the Montezuma swordtail, *Xiphophorus montezumae cortezi* Rosen. *Zoologica* 56(3): 77–94.  
1983. The sex-determining mechanism of the poeciliid fish *Xiphophorus montezumae* Jordan and Snyder and the genetic control of the sexual maturation process and adult size. *Copeia* 1983(3): 755–769.  
1984. A new look at sex determination in poeciliid fishes. In B. J. Turner (ed.), *Evolutionary genetics of fishes*, pp. 95–172. New York: Plenum Press.  
1989. Genetic control of size at maturity in *Xiphophorus*. In G. K. Meffe and F. S. Snelson, Jr. (eds.), *Ecology and evolution of livebearing fishes (Poeciliidae)*, pp. 163–184. Englewood Cliffs, N.J.: Prentice Hall.
- Kallman, K. D., and J. W. Atz  
1966. Gene and chromosome homology in fishes of the genus *Xiphophorus*. *Zoologica* 51(4): 107–135.
- Lechner, P., and A. C. Radda  
1987. Revision des *Xiphophorus montezumae/cortezi*—Komplexes und Neubeschreibung einer Subspezies. St. Gallen, Switzerland. *Aquaria* 34: 189–196.
- Miller, R. R.  
1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. *Misc. Publ. Mus. Zool. Univ. Michigan* 68: 1–155.
- Mitchell, R. W., W. H. Russell, and W. R. Elliot  
1977. Mexican eyeless characin fishes, genus *Astyanax*: environment, distribution, and evolution. *Mus. Texas Tech Univ., Spec. Publ.* 12: 89 pp.
- Morizot, D. C., and M. J. Siciliano  
1984. Gene mapping in fishes and other vertebrates. In B. J. Turner (ed.), *Evolutionary genetics of fishes*, pp. 173–234. New York: Plenum Press.
- Morizot, D. C., D. A. Wright, and M. J. Siciliano  
1977. A three point linkage of enzyme loci in fishes; implication in the evolution of vertebrate chromosomes. *Genetics* 86: 645–656.
- Muir, J. M.  
1936. Geology of the Tampico region, Mexico. *Am. Assoc. Petrol. Geol., Tulsa, Oklahoma*, 280 pp.
- Palmer, R. H.  
1925. Geology of eastern Hidalgo and adjacent parts of Veracruz, Mexico. *Bull. Am. Assoc. Petrol. Geol.* 11: 1173–1220.
- Prescott, W. H.  
1843. History of the conquest of Mexico. New York: Random House, Modern Library ed.
- Rosen, D. E.  
1960. Middle American poeciliid fishes of the genus *Xiphophorus*. *Bull. Florida State Mus., Biol. Sci.* 5(4): 57–242.  
1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bull. Am. Mus. Nat. Hist.* 162(5): 267–376.
- Rosen, D. E., and R. M. Bailey  
1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bull. Am. Mus. Nat. Hist.* 126(1): 1–176.
- Rosen, D. E., and K. D. Kallman  
1969. A new fish of the genus *Xiphophorus* from Guatemala, with remarks on the taxonomy of endemic forms. *Am. Mus. Novitates* 2379: 29 pp.
- Siciliano, M. J., and C. R. Shaw  
1976. Separation and visualization of enzymes on gels. In I. Smith (ed.), *Chromatographic and electrophoretic techniques*, 2 (4th ed), pp. 185–209. Chicago: Yearbook Medical Publ.
- Vielkind, J., and U. Vielkind  
1982. Melanoma formation in fish of the genus *Xiphophorus*: a genetically-based disorder in the determination and differentiation of a specific pigment cell. *Can. J. Genet. Cytol.* 24: 133–149.
- Zander, C. D.  
1967. Ökologische und morphologische Beiträge zur Systematik und geographischen Verbreitung der Gattung *Xiphophorus* (Pisces). *Mitt. Hamburg. Zool. Mus. Inst.* 64: 87–125.  
1968. Über die Vererbung von Y-gebundenen Farbgenen des *Xiphophorus pygmaeus nigrensis* Rosen. *Mol. Gen. Genet.* 101: 29–42.  
1969. Über die Entstehung und Veränderung von Farbmustern in der Gattung *Xiphophorus* (Pisces). I. Qualitative Ver-

änderungen nach Artkreuzung. Mitt.  
Hamburg. Zool. Mus. Inst. 66: 241–271.  
Zimmerer, E. J., and K. D. Kallman  
1988. The inheritance of vertical barring

(aggression and appeasement signals) in  
the pygmy swordtail, *Xiphophorus ni-*  
*grensis* (Poeciliidae, Teleostei). Copeia  
1988(2): 299–307.





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