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ZOOGONETICUS TEQUILA, A NEW GOODEID FISH
(CYPRINODONTIFORMES) FROM THE AMECA DRAINAGE OF
MEXICO, AND A REDIAGNOSIS OF THE GENUS

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ABSTRACT.—*Webb, S. A., and R. R. Miller: Zoogoneticus tequila, a new goodeid fish (Cyprinodontiformes) from the Ameca drainage of Mexico, and a rediagnosis of the genus. Occ. Pap. Mus. Zool. Univ. Michigan 725:1–23, 5 figs. Zoogoneticus tequila n.sp. is described from the Río Teuchitlán, an upper tributary to the Ameca drainage, Jalisco, México. The new species can be distinguished from its congener, Z. quitzeoensis, by adult males having a broad, red-orange band of pigment subterminally in the caudal fin, with melanization in the caudal fin restricted to a proximal, paddle-shaped region. The dorsal and anal fins of adult males possess narrow terminal bands of light yellow color. The laterocaudal pigment bars in both sexes are much less intense and fade at a younger age. The genus Zoogoneticus is diagnosed by the presence of a membrane attaching the sixth pelvic ray to the ventral midline of the body, pigment patches on the posteroventral part of the body, two basicaudal spots that may coalesce, dorsal and anal fins of adult males with narrow terminal bands of red-orange or yellow pigment, with melanization basally, and trophotaeniae with 9 to 14 termini.*

Key words: *Zoogoneticus*, *tequila*, *Goodeidae*, *systematics*, *Mexico*.

INTRODUCTION

The Mesa Central of México (West, 1964) contains a depauperate fauna of freshwater fishes which includes several endemic groups. The most

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diverse component of this system is the Goodeidae. Goodeids (*sensu* Parenti, 1981) comprise approximately 40 to 45 species, four of these are oviparous empetrichthyines of the Great Basin of the United States, and the remaining are viviparous goodeines of the Mexican high plateau and its periphery. Goodeine diversity appears to have resulted from vicariance events associated with volcanism and orogenic uplift during the Pliocene and Pleistocene (Barbour, 1973; Clements, 1963; Smith *et al.*, 1975). *Tapatia occidentalis*, the oldest known fossil of the group, establishes the minimum age of the Goodeinae as late Miocene (Miller and Smith, 1986). The previously mentioned geologic forces associated with this active-margin setting produced a wide range of aquatic environments throughout several drainage systems, and furnished repeated watershed communication and isolation cycles over the last several million years (Barbour, 1973). Goodeids fill many different ecological roles and possess unique and varied morphological and life-history specializations as a result.

When the genus *Zoogoneticus* Meek (1902) was described, goodeines (14 species) were included in the Poeciliidae, which also comprised what are now members of the Profundulidae, Fundulidae, Rivulidae, Cyprinodontidae, and Anablepidae (*sensu* Parenti, 1981). *Zoogoneticus* included four goodeines, as well as oviparous fishes currently recognized as Profundulidae. The revision by Hubbs and Turner (1939) restricted the genus to include only *Z. quitzeoensis*, removing other taxa to what are presently three different genera of goodeines (*Allotoca*, *Allophorus*, and *Allodontichthys*).

This paper is a contribution to knowledge of the diversity of Mexican Goodeidae. The genus *Zoogoneticus* is diagnosed, a new species from the Río Ameca, Jalisco, México is described, and descriptive data for four populations of *Z. quitzeoensis* are presented.

MATERIALS AND METHODS

Material of the new species is catalogued in the University of Michigan Museum of Zoology (UMMZ) and at the British Museum of Natural History (BMNH 1997.12.2.1). Pre-1939 synonymies of the genus *Zoogoneticus* and the species *Zoogoneticus quitzeoensis* were taken from Hubbs and Turner (1939). Diagnostic features were taken from part of a larger analysis of goodeid phylogenetic systematics based upon mitochondrial DNA sequence (cytochrome c oxidase subunit I) and morphology including osteology, karyology, and allozyme data (Webb, MS).

Cephalic sensory canal pores were counted according to Gosline (1949). All other counts were made as described by Miller (1948), except that all ray elements of the dorsal and anal fins were counted, including the first vestigial anal-fin ray. All gill rakers of the first arch were counted, with no distinction made of number on the upper and lower branchial elements. Measurements were made to the nearest 0.1 mm using Sylvac digital calipers. Specimens were cleared-and-stained according to the protocol of Taylor and Van Dyke (1985). For meristic data the condition of the holotype is indicated with boldface and the number of specimens in each category is included within parentheses. Discrepancies exist in the sample sizes of meristic characters due to data availability and damage to specimens.

Additional materials can be viewed at the web site of the UMMZ.

MONOPHYLY OF *Zoogoneticus* MEEK

Zoogoneticus. Meek, 1902:76, 89, 91, 126 (in part; original description; compared with *Fundulus*). Meek, 1904:xlix, 99, 109–110 (in part; distribution; description; key to species). Regan, 1907:85 (description; synopsis). Eigenmann, 1910:454 (in part; species listed; type properly designated). Regan, 1911:325 (listed). Hubbs, 1924:4 (classification). Hubbs, 1926:17 (in part; characters; relationships). Jordan, Evermann, and Clark, 1930:182 (species listed). Hubbs, 1932a:68–69 (in part; discussion). Hubbs, 1932b:2 (dentition). Turner, 1933a:93 (structures related to viviparity). Turner, 1933b:208–219 (distribution; classification). Turner, 1937:496, 508–509, 513, 520–521 (trophotaenial structure; relationships). Hubbs and Turner, 1939:7, 10, 11, table I, table II, 18–19, 48 (description; classification; reproductive structures). DeBuen, 1942:341–342 (in part; discussion). Alvarez, 1959:13 (in part; discussion). Turner, Mendoza, and Reiter, 1962:577, 579 (gonopodial morphology). Smith, 1980:table 1, 117 (comparisons; classification). Fitzsimons, 1981:4, 8 (sensory canals). Uyeno, Miller, and Fitzsimons, 1983:fig. 1, 507 (map; listed). Grudzien, White, and Turner, 1992:801, table 1, 810 (listed; relationships). Heironimus, 1995:8–9, figs. 1 and 3, table 6, 36, 161 (relationships).

Diagnosis.—The two species of *Zoogoneticus* share the following uniquely-derived features. The sixth pelvic ray lays in a plane dorsal to the remaining rays, between the preceding rays and the body wall, and is attached closely to the ventral midline of the body by a membrane. Two to five prominent patches of melanin are present on the posteroventral part of body from before birth, the anterior extending from the origin of the anal fin to the lateral midline, more-posterior patches are dispersed

relatively evenly, with the most posterior near the midpoint between the insertion of the anal fin and the ventral margin of the caudal fin. These spots sometimes fade in larger adults. A pair of caudal spots are present at the level of the hypural plate. These spots are typically well-formed in *Z. quitzeoensis*, less developed in the new species, and they may or may not fuse. The ribbon-type trophotaeniae possess 9–14 termini.

A phylogenetic analysis of goodeid interrelationships (Webb, MS) suggests that *Zoogoneticus* is also unambiguously diagnosed by the presence of a non-forked posttemporal bone (shared with *Characodon*, *Hubbsina*, *Girardinichthys*, and *Allotoca* except *A. meeki*), unicuspid teeth (shared with *Hubbsina*, *Girardinichthys multiradiatus*, *Allotoca*, and *Allophorus*), an antero-posteriorly compressed lacrimal bone (shared with *Allotoca*), and melanization in the dorsal fin of adult males that extends to a thin terminal band which lacks melanin but possesses red-orange or pale yellow pigment (shared with *Xenotoca variata* and *Ameca splendens*). Additionally, nine unambiguous third-codon-position nucleotide changes in the cytochrome c oxidase subunit I gene diagnose the genus.

Key to adults of species of *Zoogoneticus*

Features diagnostic of the genus *Zoogoneticus* are given above.

1a. Adult males with red-orange terminal bands in the dorsal and anal fins, melanization proximal to these bands concentrated between the fin rays; no red-orange subterminal band in the caudal fin of adult males, melanization ubiquitous; mottling in the region of the lateral scale series may coalesce to form a stripe; pigment stripe present on lateral surface of snout; posteroventral pigment patches prominent in large females, sometimes fading in adult males; modally 31 or 32 vertebrae; modally 30 or 31 scales in the lateral series

..... *Zoogoneticus quitzeoensis*

1b. Adult males with cream-colored terminal bands in the dorsal and anal fins, melanization proximal to these bands concentrated along the lengths of the fin rays; broad red-orange subterminal band present in the caudal fin of adult males, melanization restricted to a paddle-shaped region proximal to this band; mottling on the sides of the body does not coalesce to form a lateral stripe; pigment stripe not present on lateral surface of snout; posteroventral pigment patches tend to fade in large females and males; modally 30 vertebrae; modally 28 or 29 scales in the lateral series

..... *Zoogoneticus tequila*

Zoogoneticus tequila, new species

Figs. 1 and 2

Zoogoneticus sp. Lambert, 1990:26–27 (identification, behavior). Lambert and Lambert, 1994:no pag. (range, identification, behavior). Loiselle, 1991:3–4 (reproduction, behavior, discussion). Hieronimus, 1995:165 (remarks).

Holotype.—UMMZ 233655, adult male, 26.7 mm SL, R.R. Miller and J.T. Greenbank, 25 March, 1955, Río Teuchitlán (Río Ameca drainage), at east edge of Teuchitlán, Jalisco, México. Originally identified as *Z. quitzeoensis* (UMMZ 172224).

Paratypes.—UMMZ 233656, two immature females taken with the holotype, 25.4 and 28.0 mm SL. Aquarium-reared descendants of wild-caught fishes collected by M. Smith, C. Rodriguez, L. Butler, and D. Lambert, 26 February, 1990, Río Teuchitlán (Río Ameca drainage), Jalisco, México, includes four juveniles (UMMZ 233657), 19.6–27.0 mm SL, five adults (UMMZ 233658), 27.1–57.6 mm SL, and one adult (BMNH 1997.12.2.1), 41.3 mm SL.

Diagnosis.—A *Zoogoneticus* with cream-colored terminal bands in the dorsal and anal fins (sometimes pelvics) of adult males; subterminal melanization of the dorsal and anal fins of adult males concentrated primarily along the longitudinal axis of the rays; caudal fin of adult males (occasionally larger females) contains a prominent subterminal crescent-shaped band of red-orange, melanophores are restricted to a paddle-shaped area of the caudal fin proximal to this band, and the part of the caudal fin distal to the red-orange band lacks melanization and is transparent; adults tend to lose the large patches of melanin present on the posterior sides of the body and caudal peduncle; the lateral surface of the snout does not have a prominent stripe; modally 30 vertebrae and 28 or 29 scales in the lateral series (Table 1).

Cleared-and-stained aquarium-raised individuals of the new species (one male and one female, UMMZ 233658) lack interarcual cartilages, and all adult male aquarium specimens (four individuals) possess anterior keels on the first two proximal anal-fin pterygiophores. These features may be variable, or a result of successive generations of inbreeding in captivity.

Description.—Aspects of morphology and pigmentation can be observed in Fig. 1, morphometric data are given in Table 2 (comparative data for *Z. quitzeoensis* are given in Table 3), and the frequency distribution of vertebra and lateral-scale number is given in Table 1. The body is relatively deep and compressed laterally. The median fins are posterior of one-half of standard length, the dorsal-fin origin is slightly posterior to a

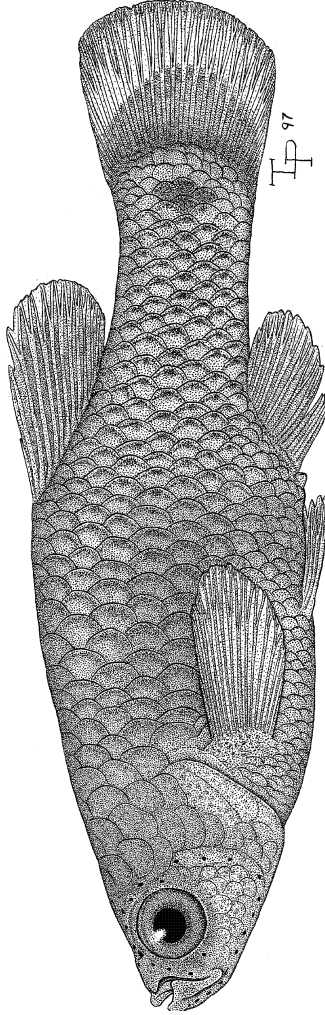


FIG. 1. Holotype of *Zoogoneticus tequila*, UMMZ 233655, adult male, 26.7 mm SL, Rio Teuchitlan, Jalisco, Mexico. Drawing by Teresa L. Petersen.

TABLE 1. Frequency distribution of vertebrae number and number of scales in the lateral series for *Zoogoneticus tequila* and *Z. quitzeoensis*. The total vertebrae number for *Z. quitzeoensis* includes collections from Tulane University (TU 30715, 30721, 30756, 30806, 30842, 31897, 31904, 31937, 31948, and 31996).

	Vertebrae						
	28	29	30	31	32	33	34
<i>Z. tequila</i>	1	2	8	3			
<i>Z. quitzeoensis</i> total		1	18	118	120	37	2
<i>Z. quitzeoensis</i> 172224 ¹		1	3	12	2		
<i>Z. quitzeoensis</i> 108651 ²				5	6	5	1
<i>Z. quitzeoensis</i> 189582 ³				10	8		
<i>Z. quitzeoensis</i> 192413 ⁴			1	9	9		

	Scales in lateral series						
	27	28	29	30	31	32	33
<i>Z. tequila</i>	3	4	4	1			
<i>Z. quitzeoensis</i> total		2	8	25	22	5	1
<i>Z. quitzeoensis</i> 172224		2	2	8	4	2	
<i>Z. quitzeoensis</i> 108651			1	2	5	2	1
<i>Z. quitzeoensis</i> 189582			4	5	6	1	
<i>Z. quitzeoensis</i> 192413			1	11	7		

¹Río Teuchitlán, Río Ameca drainage, Jalisco; ²Río Grande de Santiago, Jalisco; ³Ojo de Santiaguito, Río Turbio - Lerma drainage, Guanajuato; ⁴Canal NE Alvaro Obregón, Lago de Cuitzeo basin, Michoacan.

vertical from pelvic-fin insertion, and is well in advance of a vertical from anal-fin origin.

Meristic traits are as follows: scales in lateral series 27–30 (see Table 1, holotype **27**); dorsal fin rays 12 (specimen 1), **13** (2), 14 (10), 15 (1); anal fin rays 14 (1), **15** (10), 16 (3); caudal fin rays 17 (3), 18 (3), **19** (4), 20 (1), 21 (1); pectoral fin rays 15–14 (2), **15–15** (6), 16–15 (2), 16–16 (2), 16–17 (1); pelvic fin rays 6–0 (1), **6–6** (13); gill rakers 9 (1), 10 (5), 11 (4), **12** (3), 13 (1); total vertebrae 28–31 (see Table 1, holotype **30**); precaudal vertebrae 12 (3), **13** (7), 14 (4); caudal vertebrae 16 (4), **17** (8), 18 (2).

The jaw teeth are firmly attached, unicuspid, and those in the outer row are larger and size-graded, the largest occurring near the symphysis. The outer teeth of each of the upper and lower jaws total approximately 10 to 14, and are arranged in a single row. The inner teeth of each jaw total approximately 24 to 30. These teeth are arranged in a narrow band

TABLE 2. Proportional measurements of adults of *Zoogoneticus tequila* in thousandths of standard length. Specimens from UMMZ 233655 (holotype), 233656, 233657, and 233658.

Character	5 Males			7 Females	
	Holotype	Range	Mean	Range	Mean
Standard length (mm)	26.7	19.6–41.3	27.2	24.7–57.6	36.0
Predorsal length	622	586–622	606	583–616	603
Prepelvic length	547	542–595	558	532–554	544
Anal origin to caudal base	358	332–400	364	310–378	352
Body depth (maximum)	333	327–375	345	310–379	333
Body width (maximum)	162	163–185	171	166–192	178
Head length	316	300–330	315	262–324	299
Head depth	258	240–258	250	233–251	241
Head width (maximum)	184	174–209	188	168–202	187
Caudal peduncle length	258	251–274	263	251–296	273
Caudal peduncle depth	154	136–163	152	150–165	135
Interorbital width	116	103–119	113	102–117	109
Snout length	83	83–93	87	75–91	79
Orbit diameter	106	87–112	101	73–101	88
Mouth width	90	77–90	84	79–86	83
Mandible length	97	63–107	93	73–100	89
Dorsal-fin base length	181	177–189	183	157–175	167
Dorsal-fin total length	296	296–330	311	233–273	261
Anal-fin base length	124	102–130	119	90–114	105
Anal-fin total length	225	206–225	219	178–202	161
Caudal-fin length	209	209–255	230	209–247	226
Pectoral-fin length	232	221–251	235	201–223	206
Pelvic-fin length	154	151–160	155	134–166	147

posterior to the outer teeth, and barely emerge through the oral epithelium.

The acoustico-lateralis system of the head consists of mandibular, lacrimal, preopercular, and supraorbital canals and pores. The number of pores is as follows: mandibular 2–2 (1), 3–3 (1), 3–4 (1), ~~4–4~~ (8), 4–5 (1); lacrimal 3–5 (1), ~~4–4~~ (10); preopercular 7–7 (1), ~~8–8~~ (9), 8–9 (1), 9–7 (1). The supraorbital series is modally of the Type II designation of Gosline (1949), with canals between pores 1–2a, 2b–4a, 4b–7. However, eight fish (of 12) possess an additional break in the posterior canal segment on at least one side of the head, producing the 1–2a, 2b–4a, 4b–6a, 6b–7 condition. The holotype exhibits both conditions, with the additional break present on the right side of the head.

Karyology.—Gill epithelia of an adult male (UMMZ 233744) was karyotyped following the protocol of Uyeno and Fitzsimons (1969). *Zoogoneticus tequila* has a diploid complement of 46 chromosomes, 2 large metacentric, 2 submetacentric, and 42 subtelo-centric-telocentric.

TABLE 3. Proportional measurements of adults of *Zoogoneticus quitzeoensis* in thousandths of standard length. Each collection number comprises five males and five females. Values for dorsal and anal-fin lengths are determined from males only.

Character	UMMZ 172224 ¹		UMMZ 108651 ²		UMMZ 189582 ³		UMMZ 192413 ⁴	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Standard length (mm)	30.4–39.8	35.1	35.7–55.9	43.3	26.1–35.5	29.5	26.5–54.6	42.6
Predorsal length	588–624	603	560–604	589	567–603	585	598–619	610
Prepelvic length	511–555	531	501–524	510	482–559	518	475–538	506
Anal origin to caudal base	296–377	334	338–370	355	319–370	344	341–407	364
Body depth (maximum)	323–391	346	302–363	335	261–347	304	324–383	363
Body width (maximum)	142–188	158	144–165	155	123–195	145	140–170	158
Head length	278–332	305	268–302	283	270–312	290	250–308	273
Head depth	212–250	236	208–243	223	196–227	212	168–224	204
Head width (maximum)	163–178	169	152–170	159	143–165	156	157–170	166
Caudal peduncle length	236–271	247	244–279	268	238–275	252	235–291	257
Caudal peduncle depth	155–166	159	144–170	159	130–154	143	150–177	163
Interorbital width	95–108	102	91–106	97	90–104	95	88–106	102
Snout length	72–86	78	70–84	75	62–77	69	63–73	69
Orbit diameter	81–96	89	73–88	81	93–105	99	73–98	83
Mouth width	70–85	80	62–81	74	62–84	69	64–84	71
Mandible length	70–82	76	66–81	73	61–80	74	65–86	74
Dorsal-fin base length	188–216	203	176–202	192	179–197	185	170–195	182
Dorsal-fin total length	293–322	305	307–322	316	298–316	307	271–308	291
Anal-fin base length	117–139	126	106–129	117	112–119	116	110–122	116
Anal-fin total length	190–214	203	197–222	208	205–225	214	203–230	217
Caudal-fin length	184–217	199	181–219	202	199–257	218	179–235	201
Pectoral-fin length	178–220	195	165–201	181	177–207	195	160–198	179
Pelvic-fin length	136–164	150	142–179	153	148–164	158	140–170	158

¹Río Teuchitlán, Río Ameca drainage, Jalisco; ²Río Grande de Santiago, Jalisco; ³Ojo de Santiguaito, Río Turbio - Lerma drainage, Guanajuato;

⁴Canal NE Alvaro Obregón, Lago de Cutitzo basin, Michoacan.

Reproductive biology.—The anterior part of the anal fin of adult males is modified in the manner diagnostic of Goodeinae (sensu Parenti, 1981). The first anal-fin ray is reduced to paired structures which are not externally visible (females also possess this feature, but the rudiments often meet and fuse at the midline). Anal-fin rays 2–7 are unbranched and reduced to approximately 60–70 percent of the length of the longest ray (ray 8 or 9). Rays 2–5 are crowded and slightly recurved. The first two proximal anal-fin pterygiophores of aquarium-reared descendants of wild-caught fish possess anterior keels. Mature males also possess a muscular urogenital organ, as described for *Characodon lateralis* and *Goodea atripinnis* by Nelson (1975), and a urogenital papilla that is wider than long.

The new species possesses the single, median ovary diagnostic of Goodeinae. Ovigerous tissue develops ubiquitously within the ovarian wall and septum. The septum is attached dorsally along the midline and does not branch. The septum rolls upon itself along the longitudinal axis of the ovary, owing to its large surface area, and irregularly-formed folds may be present.

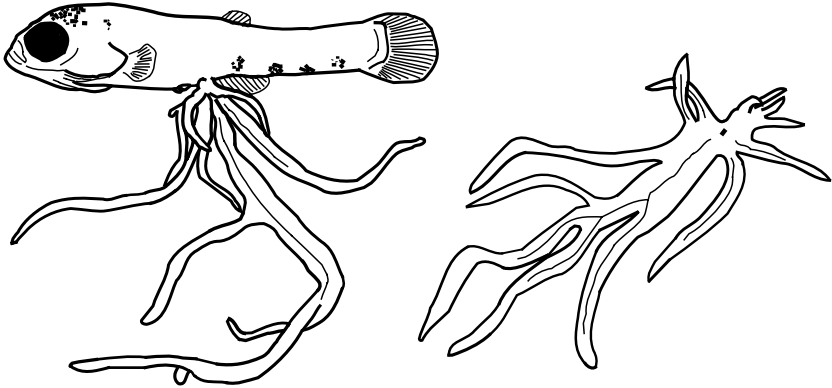


FIG. 2. Spontaneously aborted embryo of *Zoogoneticus tequila*, UMMZ 233658, 8.4 mm SL (left). Trophotaeniae of a mid-term embryo of *Z. tequila* from a different mother (right).

The trophotaeniae are embryonic structures responsible for nutrient uptake and gas exchange during gestation (Turner, 1937; Hollenberg and Wourms, 1994). Nineteen mid-eyed stage embryos (2.8–3.4 mm SL) of a female 51.6 mm SL (UMMZ 233658) possessed ribbon trophotaeniae (Turner, 1937) with 9–14 relatively pointed termini. The most prominent

trophotaenial projections are posteriorly-directed, with the largest typically longer than standard length (Fig. 2). A number of small projections extend from the margin anterior to the anus, and moderately-sized projections extend laterally.

Aquarium data (26–28 degrees C) suggest that males and females can become sexually mature by 6 and 10 weeks of age, respectively, and males can be identified within a few weeks of birth (Lambert, 1990; Loisel, 1991; Lambert and Lambert, 1994). However, since growth rate is correlated with temperature, natural populations on the high plateau could require substantially more time to reach maturity. Gestation requires approximately 6 to 8 weeks and reproduction occurs continuously during summer months. Broods have been recorded which number as many as 20 to 29 offspring (Lambert, 1990; Loisel, 1991; Langhammer, pers. comm.); however, females in their first year of reproduction typically have fewer than 10 offspring (Loisel, 1991). Interbrood intervals of between 28 and 32 days have been recorded (Loisel, 1991), but temperature is inversely correlated, and age of the female is positively correlated with interbrood interval (Langhammer, pers. comm.). Offspring are usually 10–12 mm SL at parturition (pers. obs.), and the trophotaeniae have been completely reabsorbed or sloughed off.

Zoogoneticus tequila and its congener, *Z. quitzeensis*, failed to produce offspring when individuals of opposite sexes were housed in a common aquarium (Loisel, pers. comm.). These two species were never observed to exhibit courtship behaviors toward their congeners, but readily entered displays once housed with conspecifics of the opposite sex (Loisel, pers. comm.).

Sexual dimorphism and coloration.—Adults of *Zoogoneticus tequila* are readily sexed due to characteristic differences in the dorsal and anal fins. All adult male goodeines possess modifications of the anterior part of the anal-fin (Turner *et al.*, 1962) which facilitate copulation by assisting in the alignment of the urogenital orifices (Nelson, 1975). The modified part of the anal fin of *Z. tequila* consists of seven reduced rays which are unbranched. Additionally, the dorsal and anal-fin base lengths and total (depressed) fin lengths are greater in males than females; however, no differences in ray number occur, as reported for some other goodeid fishes (Smith and Miller, 1986). The prepelvic length of males is slightly longer than that of females.

The sexes of the new species can also be distinguished by coloration. In life the sides, back, nape, and top of the head of adult males are dark olivaceous. Mottling is present on the side of the body, which often has a greenish hue. Many of the lateral scales are reflective, producing iridescence. Color fades to pale yellow below the lateral scale series on

the belly and below the eye. There is a pair of spots, which usually coalesce, at the base of the caudal fin. The mottling and the basicaudal spots may not be visible during breeding condition, when the body is its darkest. The unpaired fins are dark, fading towards the margins, with pigmentation concentrated along the lengths of the rays. The greenish cast of the body can occasionally be seen in the dorsal and anal fins. The borders of the dorsal and anal fins have a thin cream-colored band. The caudal fin has a broad subterminal red-orange band, and the region proximal to this band is heavily melanized. Quantity of carotenoids in the diet may influence the intensity of the subterminal band (Langhammer, pers. comm.). The pelvic fins occasionally show some terminal cream coloring, but the pectoral fins are unpigmented.

Preservation in ethyl alcohol blanches the nonmelanin pigments. The iridescence as well as the green, cream and red-orange colors are lost. The pale-yellow venter becomes buff in color. Melanization of the fins and body is retained, mottling may intensify, and the basicaudal spot persists.

In life adult females are olivaceous. The sides, back, nape, and top of the head are dark, and display mottling, while the belly below the lateral series and the area below the eye are pale yellow. Two to four large spots are found on the ventral half of the caudal peduncle. These spots occasionally fade in older individuals. A pair of basicaudal spots, which typically coalesce, are visible in most specimens. The unpaired fins may be dusky, but are not dark, and do not possess the cream-colored margins that males display. Occasionally large females show a thin subterminal band of red-orange in the caudal fin, but it is less intense than seen in males. The paired fins are unpigmented.

Preservation in ethyl alcohol diminishes the pale yellow on the belly and head to a buff color, and the red-orange band in the caudal fin, if present, disappears. The basicaudal spots and mottling persist. The unpaired fins retain a dusky appearance.

Juveniles exhibit coloration nearly identical to juvenile *Z. quitzeoensis*. The base color of the body is much lighter than in adults, but mottling is more evident. Posteroventral and basicaudal spots are present from before birth.

Habitat and associates.—The holotype was taken in the Río Teuchitlán, a headwater tributary to the Río Ameca (Pacific drainage, Figs. 3 and 4). This locality at the east edge of Teuchitlán is at an elevation of 1311 m (4300 ft, 20° 38' N, 103° 45' W). The stream expands into a rather shallow and open lake-like habitat approximately 8 meters wide and 1.3 meters deep. Fishes were generally captured in less than 1 meter of water. The water at this locality was almost continuously turbid due to the presence



FIG. 3. Type locality of *Zoogoneticus tequila*, Rio Teuchitlan, Jalisco, Mexico (25 March 1955).

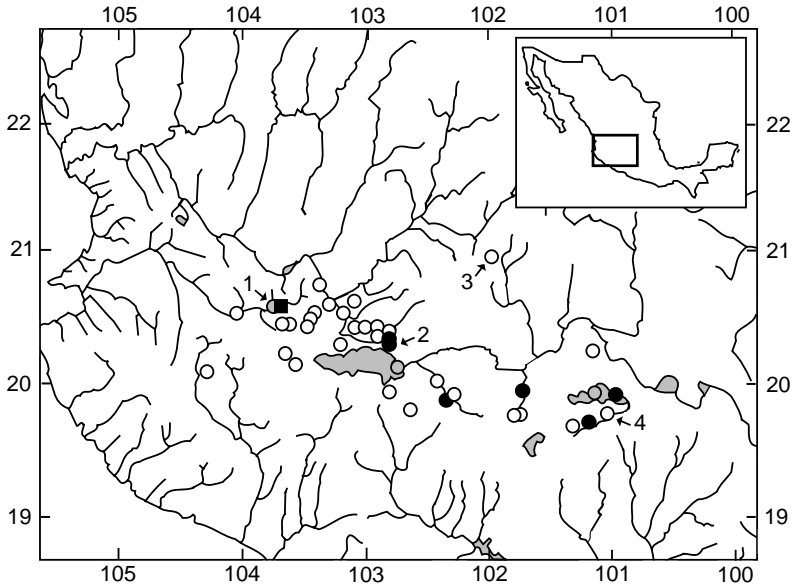


FIG. 4. Map of a portion of central Mexico showing the distribution of *Zoogoneticus tequila* (square) and *Z. quitzeensis* (open circles represent single collections, lightly-shaded circles two collections, and darkened circles three collections). Numbers correspond to localities of *Z. quitzeensis* in Table 1.

of cattle, pigs, and horses. The bottom was mostly mud, but some sand and rocks were present. Silt was abundant and current was absent to moderate. Aquatic macrophytes at the locality included broad-leaved *Potamogeton*, *Eichornia*, and another hyacinth-like plant. The water and air temperatures were 26° C.

Water in this locality was heavily utilized for irrigation, drinking, and washing, and heavy domestic and livestock pollution was also present. However, all species of fishes taken with the holotype (*Algansea tincella*, *Ictalurus dugesi*, *Poeciliopsis infans*, *Ameca splendens*, *Skiffia francesae*, *Xenotoca melanosoma*, and *Goodea atripinnis*) were numerous except *Notropis amecae* and *Yuriria alta*. Five species of goodeids (*Ameca splendens*, *Goodea atripinnis*, *Allophorus robustus*, *Xenotoca melanosoma*, and *Zoogoneticus quitzeoensis*) and two poeciliid species (*Poeciliopsis infans* and *Poecilia sphenops*) were taken in the Río Teuchitlán in 1978 and 1985, but the new species was not found (Meyer *et al.*, 1985). In 1990 the new species was taken with *Allotoca maculata*, but *Skiffia francesae* was no longer found (Lambert, pers. comm.). Several exotic species have been introduced at or near the type locality, causing declines in populations of many native fish species. Tilapia (*Tilapia aurea*, UMMZ 233596), platies (*Xiphophorus maculatus*) and bluegill sunfish (*Lepomis macrochirus*) have been recorded since 1977 (T77-22/23, D. Soltz field notes, UMMZ). Additionally, carp (*Cyprinus carpio*) have more recently been established in the headwaters of the Río Ameca.

Conservation status.—The abundance of *Zoogoneticus tequila* has declined since its discovery in 1990, and collection effort since 1992 has been unsuccessful (Lambert, pers. comm.). Intensive sampling in 1996, in fact, failed to reveal any goodeines at the type locality (Lambert, pers. comm.). *Z. tequila* appears to have been extirpated in the wild, but it is presently maintained in captivity by aquarists in North America and Europe.

Distribution and Relationships.—The new species is only known from the Río Teuchitlán of the Ameca drainage system. In that locality it is sympatric with its more widely distributed congener *Z. quitzeoensis*, which is found in the Río Lerma system and surrounding drainages (Fig. 4).

The pattern of distribution of these sister taxa is potentially indicative of vicariance associated with the historical loss of connection of the Río Ameca drainage and the Río Lerma system. This hydrological history is supported by geological evidence (Smith *et al.*, 1975), as well as the distribution of species pairs of other goodeines (*Skiffia multipunctata* and *S. francesae*, and *S. bilineata* and an undescribed species of *Skiffia*). The presence of *Z. quitzeoensis* in Río Ameca tributaries and the Río Unión de Tula of the Lerma drainage would then be interpreted a result of secondary dispersal.

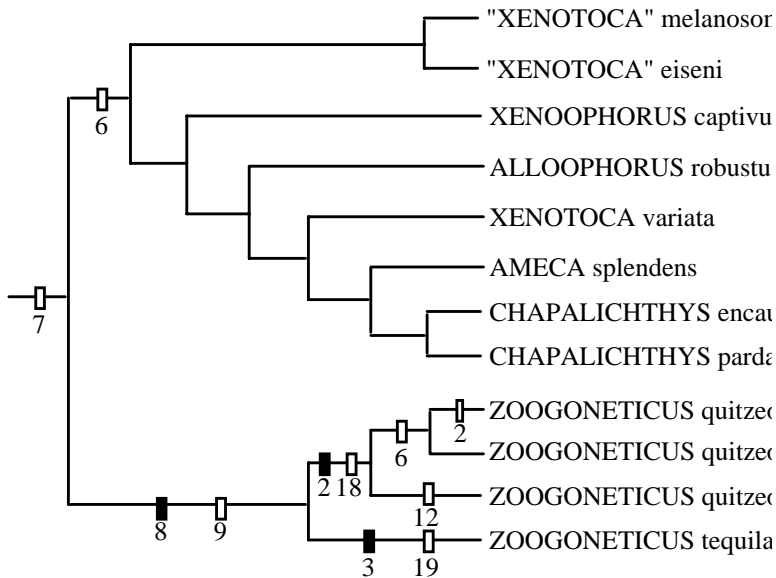


FIG. 5. Partial cladogram of goodeid relationships showing the phylogenetic position of *Zoogoneticus* (Webb, MS). Numbers below nodes indicate the number of unambiguous morphological (black boxes) and molecular (open boxes) changes for selected nodes. Support for other nodes given in Webb (MS).

Analysis of the mitochondrial cytochrome c oxidase subunit I gene of the two species of *Zoogoneticus* reveals a level of sequence divergence that exceeds most other species pairs of goodeine fishes (Fig. 5, Webb, MS). These changes, chromosomal differences, and the inability to interbreed, support species separation, but cannot imply the timing of divergence. No fossil material of the genus *Zoogoneticus* is known.

A parsimony analysis of goodeid relationships utilizing all available data suggests the genus *Zoogoneticus* is the sister taxon to a clade that includes *Ameca*, *Xenotoca variata*, *Chapalichthys*, *Alloophorus*, “*Xenotoca*” (*X. eiseni* and *X. melanosoma*), and *Xenoophorus* (Figure 5). One first codon position and six third codon-position changes in the cytochrome c oxidase subunit I gene support this relationship. The clade that includes *Ameca*, *Xenotoca variata*, *Chapalichthys*, *Alloophorus*, “*Xenotoca*,” and *Xenoophorus* is supported by six molecular characters. Monophyly of the genus *Zoogoneticus* is supported by eight morphological and nine molecular characters. Three morphological and 19 nucleotide characters diagnose *Z. tequila*, and the three examined individuals of *Z. quitzeoensis* share two

morphological and 18 nucleotide characters. The intraspecific molecular variation of *Z. quitzeensis* exceeds the level of variation between sister species of some other goodeid genera (Webb, MS).

A parsimony analysis of the allozyme dataset of Grudzien *et al.* (1992) alone supports an alternative relationship of *Zoogoneticus* to *Allotoca*. *Zoogoneticus* also shares several morphological traits with *Allotoca*: the presence of a straight, unforked posttemporal (found in *Characodon*, *Girardinichthys*, and *Hubbsina*); monofid teeth (found in *Allophorus*, *Girardinichthys*, and *Hubbsina*); and an antero-posteriorly compressed lacrimal bone (found in *Girardinichthys* and *Hubbsina*). However, these characters do not outweigh the molecular evidence.

Etymology.—The specific epithet, *tequila*, derives from the Volcan Tequila (2920 m), which looms north of the type locality. The name is used as a noun in apposition.

Zoogoneticus quitzeensis BEAN

Platypoecilus quitzeensis. Bean, 1898:540, 1 fig. (original description; Lake Quitzeo = Lago de Cuitzeo). Jordan and Evermann, 1898:2873 (description).

Zoogoneticus quitzeensis. Meek, 1902:91–92, 94 (description; LaBarca, Ocotlan). Meek, 1904:xl, 110–111; Fig. 29 (as *cuitzeensis*; description). Regan, 1904:257 (comparison). Regan 1907:85–86 (as *cuitzeensis*; description). Eigenmann, 1909:304 (as *cuitzeensis*, listed). Eigenmann, 1910:454 (as *cuitzeensis*; listed). Jordan, Evermann, and Clark, 1930:182 (listed). Hubbs, 1932a:69 (as *cuitzeensis*; listed). Turner, 1933a:94 (as *cuitzeensis*; structures related to viviparity). Turner 1933b:218–45; pl. 1, fig. 8, and pl. 5, figs. 22–23 (as *cuitzeensis*; structures related to viviparity). Turner, 1937:496, 508–510, 513, pl. 3, fig. 15 (trophotaeniae). Mendoza, 1937:97–98, 105, 108–111, pl. 1, figs. 1 and 4, pl. 3, fig. 2 (as *cuitzeensis*; trophotaeniae). Hubbs and Turner, 1939:table I, 13–14, 22, 28–29, 48, 73, pls. I and III (keys; description; classification; reproductive structures). Turner, 1940:277–278, figs. 10–11 (structures related to viviparity). Turner, Mendoza, and Reiter, 1962:577, table 1, pl. 1, fig. 4 (gonopodial morphology). Mendoza, 1965:305, pl. II fig. 11, 307, 313 (trophotaenial structure). Robins, Bailey, Bond, Brooker, Lachner, Lea, and Scott, 1990:87 (common name; distribution). Fitzsimons, 1981:table 1 (sensory pores). Uyeno, Miller, and Fitzsimons, 1983:499, table 1, fig. 4J, 507 (karyotype; material). Meyer, Wischnath, and Foerster, 1985:tables 1, 3, 5, 124–125 (description; distribution; habitat). Miller and Smith, 1986:table 14.2 (listed; distribution). Smith and Miller, 1987:610, 612, 615

(relationships; characters). Grudzien, White, and Turner 1992:table 2, figs. 2 and 3, 809 (relationships). Schindler and Hamlet, 1993:379, fig. 12 (embryotrophe; trophotaeniae). Hollenberg and Wourms, 1994:105–107, 115, 118–119, 121, 124–126, 128, figs. 1–3, 6, 10, 11 (trophotaenial cytology and function). Heironimus, 1995:tables 6 and 7, 8, 43, 51, 55–56, 161–165 (biology; description; habitat).

Diagnosis.—A *Zoogoneticus* (to 57 mm SL) with red terminal bands in the dorsal and anal fins of adult males, subterminal melanization of these fins is concentrated between the fin rays; the caudal fin of adult males lacks a subterminal crescent-shaped band of red-orange; melanization is not restricted to a paddle-shaped area of the caudal fin, but is ubiquitous, sometimes fading terminally; adults tend to retain the large patches of melanin present on the posterior sides of the body and caudal peduncle; a pigment stripe present on the lateral surface of the snout; modally 31 or 32 vertebrae and 30 or 31 scales in the lateral series.

Description.—Morphometric data are given in Table 3, and the frequency distributions of vertebrae and lateral-scale number are given in Table 1. The body is relatively deep and compressed laterally. The median fins are posterior of one half of standard length, the dorsal-fin origin is slightly posterior to a vertical from pelvic-fin insertion and is well in advance of a vertical from anal-fin origin.

Meristic traits are as follows: dorsal fin rays 12 (3), 13 (31), 14 (27), 15 (6); anal fin rays 14 (19), 15 (43), 16 (10), 17 (1); caudal fin rays 16 (1), 17 (7), 18 (11), 19 (17), 20 (10), 21 (9), 22 (3); pectoral fin rays 13–13 (1), 13–14 (5), 14–13 (5), 14–14 (15), 14–15 (2), 15–14 (3), 15–15 (20); pelvic fin rays 6–6 (51); gill rakers 9 (2), 10 (8), 11 (11), 12 (6), 13 (2), 15 (1); precaudal vertebrae 13 (5), 14 (38), 15 (12); caudal vertebrae 16 (6), 17 (35), 18 (13).

The jaw teeth are firmly attached, unicuspid, and those in the outer row are larger and size-graded, the largest occurring near the symphysis. The outer teeth of each of the upper and lower jaws total approximately 10 to 16, and are arranged in a single row. The inner teeth of each jaw total approximately 24 to 32, are arranged in a narrow band posterior to the outer teeth, and barely emerge through the oral epithelium.

The acoustico-lateralis system of the head consists of mandibular, lacrimal, preopercular, and supraorbital canals and pores. The number of pores is as follows: mandibular 2–0 (1), 2–2 (2), 2–3 (1), 2–4 (1), 3–2 (1), 3–3 (15), 3–4 (3), 4–3 (11), 4–4 (12), 5–4 (1); lacrimal 3–3 (1), 3–4 (1), 4–3 (1), 4–4 (46); preopercular 7–6 (1), 7–7 (1), 7–8 (1), 8–5 (1), 8–7 (1), 8–8 (21), 8–9 (1), 8–10 (1), 9–7 (1), 9–8 (5), 9–9 (10), 9–10 (1), 10–8 (1), 10–9 (1), 11–8 (1). The preopercular series of eight fish (of 48) had

a break near the angle of the canal on at least one side of the head. The supraorbital series is of the two forms seen in the new species, however, the majority of fish possess a break in the posterior canal segment on at least one side of the head.

Karyology.—*Zoogoneticus quitzeoensis* (UMMZ 189582) has a diploid complement of 28 chromosomes, 20 large metacentric, two small metacentric, and six subtelocentric-telocentric (Uyeno *et al.*, 1983).

Reproductive biology.—Aspects of reproductive biology are largely similar to those of *Zoogoneticus tequila*. Anal-fin, ovarian, and other urogenital modifications are as with the new species. The first two proximal anal-fin pterygiophores of adult males do not possess anteriorly-directed keels.

Hubbs and Turner (1939) reported *Z. quitzeoensis* to have 10–12 very long, unsheathed, ribbon trophotaeniae. The most prominent projections are posteriorly-directed, and a number of small projections border the anterior margin. The trophotaeniae begin development by 1.2 mm, assume typical morphology by 3 mm embryo length, and are partially resorbed before birth (Turner, 1940).

Little is known of reproduction in the wild. Captures of young indicate reproduction occurs from January into April. The species was present in all size classes and pregnant females were noted in April in Lago Camécuaro, Jalisco (Kingston, 1979). Dissection of three gravid wild-caught females (47–48 mm SL, UMMZ 192413) revealed 15 and 16 near-term embryos approximately 10–12 mm SL, and 30 mid-term embryos approximately 7–8 mm SL, all with trophotaeniae attached and well developed.

Data collected by aquarists suggest that many aspects of reproductive biology are largely similar to *Z. tequila*. A brood size of 23 and first-brood sizes of between five and nine offspring have been recorded (Hartman, 1989; Langhammer, pers. comm.). Interbrood interval ranges between 4 and 6 weeks, and is dependent on female condition and water temperature.

Sexual dimorphism and coloration.—Adults males of *Zoogoneticus quitzeoensis* possess an anal fin modified in the typical goodeid fashion (Turner *et al.*, 1962). The dorsal and anal-fin base lengths and total (depressed) lengths are greater in males than females, but there are no differences in ray number.

In life adult males are dark and mottled, with the sides, back, nape, and top of the head olivaceous. Mottling in the region of the median lateral scale series may coalesce to form a lateral stripe. Antorbital pigmentation typically carries the lateral stripe onto the snout (also found in females). A series of four, typically large, posteroventral spots can be found in smaller adults. The size at which these spots fade varies. Body

color fades to pale yellow below the lateral scale series on the belly, and below the eye. A pair of spots, which may coalesce, lies at the caudal-fin base. The unpaired fins are dark, fading toward the margins, with pigmentation concentrated between the rays in the dorsal and anal fins. The borders of the dorsal and anal fins each have a thin red-orange band. Melanization is ubiquitous in the caudal fin, but typically fades somewhat terminally. A single male exhibited a slight amount of diffuse red-orange pigment in the caudal fin (Webb, pers. obs., Manantial Mintzita, Jalisco). The paired fins lack pigmentation.

Preservation in ethyl alcohol blanches the nonmelanin pigments. The body color dulls and the red-orange color disappears. The pale ventral surfaces of the head and body dull to a buff color. The pigmented regions of the fins and body remain dark, and the basicaudal spot persists. The pelvic fins often become dusky terminally.

In life adult females are olivaceous and mottled. The sides, back, nape, and top of the head are dark, while the belly below the lateral series and the area below the eye are pale yellow. Two to four large spots are found on the ventral half of the posterior part of the body. These spots do not fade with age, unlike in males. A pair of basicaudal spots, which may coalesce, are visible in most specimens. The unpaired fins are lightly pigmented, giving them a dusky appearance, and these fins do not possess the red-orange margins that males display. The paired fins are unpigmented.

Upon preservation in ethyl alcohol, the body color dulls and the pale venter becomes buff. Mottling of the body neither intensifies nor diminishes, and the posteroventral and basicaudal spots remain evident.

Juveniles exhibit coloration nearly identical to *Z. tequila* juveniles. The base color of the body is much lighter than in adults, but mottling is more evident. Posteroventral and basicaudal spots are present from before birth.

Distribution.—*Zoogoneticus quitzeoensis* is widely distributed in lakes and streams of the Mesa Central, presently or historically connected to the Río Lerma system (Fig. 4). The species can be found in the Río Grande de Santiago, Río Lerma, Lago de Chapala, Río Ameca, Río Unión de Tula (Río Armería drainage), and a number of endorheic basins including Lago Camécuaro, Laguna de Atotonilco, Laguna San Marcos, and Lago de Cuitzeo. *Z. quitzeoensis* appears to have arrived in the Río Unión de Tula (Armería drainage) by a stream capture to a tributary of the Río Atenguillo by the Río Ayutla west of Soyatlán.

Locality records.—**Jalisco:** Ocotlán (UMMZ 65216); Río Grande de Santiago (UMMZ 108651, 189678, 192281, 192288, 201583, 201588); roadside pond SW Guadalajara (UMMZ 154334); trib. Río Teuchitlán

ESE Teuchitlán (UMMZ 160915); irrigation ditch 3.3 km N and 0.8 km W Guadalajara (UMMZ 160924); Río Teuchitlán (UMMZ 172224); Lago de Chapala (UMMZ 173537); stream at Santa Ana, Acatlán de Juárez (UMMZ 173568); stream pond at Santa Cruz de las Flores (UMMZ 173575); pond behind dam at Lago Unión de Tula (UMMZ 173623); creek W side Guadalajara (UMMZ 179725); trib. Río Ameca W of Ameca (UMMZ 192186); Laguna de Atotonilco (UMMZ 192241); Laguna San Marcos (UMMZ 192245); Laguna Zacoalco (UMMZ 201566). **Michoacan:** Lago de Chapala (UMMZ 167681, 160932); Lago de Camécuaro (UMMZ 172171, 198828); Presa de Cointzio (UMMZ 172181); canal at Tarecuato (UMMZ 173632); Lago de Mintzita (UMMZ 189032); Río Duero (UMMZ 192435); Laguna de Cuitzeo (UMMZ 189043, 192362); canal de Queréndaro (UMMZ 191688); Lago de Balneario Cointzio (UMMZ 192390); canal NE Alvaro Obregón (UMMZ 192400, 192413); Laguna de Zacapu (UMMZ 192421); spring N Jaripo (UMMZ 192531); spring of Tangancícuaro (UMMZ 202419, 211025); Río Grande de Santiago (UMMZ 211011); Manantial Tanque Grande (UMMZ 211018); spring at Irancuátaro (UMMZ 211021). **Guanajuato:** Ojo de Agua de Santiaguito (UMMZ 189582).

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NOTE ADDED IN PROOF

- In synonymy of *Zoogoneticus quitzeoensis* (p. 17) add:

Hollenberg and Wourms, 1995:379-381, table 1, figs. 2-3, 7 (ovarian activity).