

## Three New Pupfish Species, *Cyprinodon* (Teleostei, Cyprinodontidae), from Chihuahua, México, and Arizona, USA

W. L. MINCKLEY, ROBERT RUSH MILLER, AND STEVEN MARK NORRIS

Three new species of *Cyprinodon* (Teleostei, Cyprinodontidae) are described, each long recognized as distinct. *Cyprinodon pisteri* occupies a variety of systems and habitats in the Lago de Guzmán complex basin in northern Chihuahua, México. It is distinguished by its dusky to black dorsal fin and narrow or inconspicuous terminal bar on the caudal fin in mature males. *Cyprinodon albivelis* is distributed largely in relatively high elevation sites in the upper Río Papigochic (Río Yaqui basin), with a single occurrence in the Río Santa María basin. It is distinguished most notably by the striking white dorsal and anal fins displayed by breeding males. *Cyprinodon arcuatus* is a distinctive form most similar to *Cyprinodon macularius* and *Cyprinodon eremus* and is restricted to the upper Santa Cruz River basin in southern Arizona and Northern Sonora. It is distinguished in having a sharply convex dorsal body profile from the head to dorsal fin origin and in lacking yellow or orange pigmentation on the part of nuptial males. Extensive and careless human alterations to this system drove *C. arcuatus* to extinction, with the last natural population perishing in Monkey Spring (Santa Cruz County, Arizona), devoured by introduced sport fish. Where appropriate, biogeography and conservation issues are discussed with regard to these species.

NEARLY 80 years ago, while on the staff of the Field Museum of Natural History, Carl L. Hubbs recognized as new two of the three pupfishes described here, designating as types an abundance of preserved material from the Lago de Guzmán and Río Yaqui basins of northern Chihuahua, México. A third species from the Gila River drainage (Colorado River basin) of southeastern Arizona, and likely also in northern Sonora, México, was also known to Hubbs, who referred it to *Cyprinodon macularius* (e.g., Hubbs and Miller, 1941). The two senior authors have collected and studied these fishes over their respective geographic ranges for many years and offer their formal descriptions below.

### MATERIALS AND METHODS

Morphometric measures (listed in Tables 1–2), meristic counts (listed in Table 3) and descriptions of pupfish scale morphology follow Miller (1943, 1948). Professor Hubbs' notes and data on these pupfishes (and others) were given to RRM in the 1950s and proved invaluable for their descriptions. Vertebral counts taken from radiographs, with urostyle counted as one. CS indicates cleared-and-stained specimens. Abbreviations for depositories are from Leviton et al. (1985). Note variable authorship of species described in this report.

*Cyprinodon pisteri* Miller and Minckley, n. sp.  
Cachorrito de Guzmán, Guzman Pupfish  
Figures 1–2

*Cyprinodon eximius* (misident.): Bean, 1898:168; Evermann and Goldsborough, 1902:149; Meek, 1904:xxxii–xxxiii, 125 (in part); Fowler, 1916:430; de Buen, 1947:277 (from Evermann and Goldsborough, 1902); Contreras-Balderas, 1969:297.

*Cyprinodon elegans* (misident.): Garman, 1895: 23–24; Meek, 1902:97–98 (in part); de Buen, 1940:31 (in part).

*Cyprinodon bovinus* (misident.): Regan, 1907:83–84 (in part); Fowler, 1916:429–430.

*Cyprinodon bovinus bovinus* (misident.): de Buen, 1947:277 (in part).

*Cyprinodon* sp. or “sp. nov.”: Koster, 1957:83 (in part); Minckley and Arnold, 1969:225; Anascavage, 1973 (as “Ascencion [sic] pupfish”; det. by RRM as UMMZ 211153); Contreras et al, 1976:table 3 (Río del Carmen); Turner and Liu, 1977:fig. 1, no. 32 (in part); Echelle and Echelle, 1978:572; Miller and Chernoff, 1980:79–80; Gehlbach, 1981:270 (Palomas); Miller, 1981:fig. 2 [17, 19], p. 74; Minckley and Brown, 1983 (reprinted 1994), table 32, p. 234 (as “Casas Grandes pupfish”); Miller, 1986:table 1; Smith and Miller, 1986:table 13.1, p. 469 (as “Palomas pupfish”); Williams et al., 1989:10 (as “whitefin pupfish/cachorrito de Palomas”); Sublette et al., 1990:351; Minckley et al., 1991:table 15–1, p. 253 (as

TABLE 1. SELECTED MORPHOMETRIC FEATURES FOR *Cyprinodon pisteri* (UMMZ 162629, 162630) AND *Cyprinodon albivelis* (UMMZ 211582, 235040). Presented in 1000s of standard length, which is in millimeters. Mean is followed by 1 SD, range in parentheses;  $n = 11$  for male columns (including holotypes),  $n = 10$  for female columns.

	<i>Cyprinodon pisteri</i>			<i>Cyprinodon albivelis</i>		
	Holotype	Males	Females	Holotype	Males	Females
Standard length (mm)	41.5	41.6 ± 5.1 (33.7–49.0)	39.2 ± 5.8 (29.5–49.3)	36.8	40.8 ± 6.6 (34.4–53.1)	38.1 ± 1.7 (36.1–40.7)
Predorsal fin length	598	592 ± 11.2 (577–606)	595 ± 13.3 (572–609)	587	588 ± 21.4 (562–627)	592 ± 11.9 (577–615)
Prepelvic fin length	571	557 ± 12.6 (538–576)	555 ± 24.1 (524–610)	560	555 ± 16.6 (529–580)	566 ± 6.2 (551–572)
Preanal fin length	684	678 ± 11.9 (657–696)	673 ± 8.4 (661–686)	679	669 ± 16.2 (641–697)	684 ± 13.8 (659–701)
Anal origin to caudal fin base	383	391 ± 13.0 (373–416)	363 ± 4.4 (358–373)	397	398 ± 12.4 (383–429)	372 ± 15.6 (344–401)
Body depth	402	396 ± 19.4 (366–434)	363 ± 27.6 (310–398)	418	424 ± 37.2 (370–508)	363 ± 14.7 (337–385)
Body width	255	234 ± 15.0 (204–255)	229 ± 18.4 (193–252)	242	229 ± 13.2 (206–245)	246 ± 11.3 (232–266)
Head length	311	309 ± 8.8 (294–318)	311 ± 11.5 (295–330)	321	333 ± 14.7 (301–356)	318 ± 8.8 (306–332)
Caudal–peduncle length	289	285 ± 16.8 (248–311)	269 ± 15.6 (242–290)	280	293 ± 11.5 (271–313)	282 ± 1.30 (261–301)
Caudal–peduncle depth	214	206 ± 7.7 (190–216)	191 ± 6.0 (183–201)	215	216 ± 12.5 (189–237)	184 ± 6.1 (174–193)
Interorbital width	118	118 ± 10.0 (103–134)	117 ± 6.2 (106–128)	125	123 ± 12.1 (107–151)	114 ± 4.8 (106–121)
Snout length	104	103 ± 5.9 (94–113)	101 ± 8.5 (86–115)	106	110 ± 9.8 (92–126)	106 ± 10.2 (89 ± 127)
Orbital length	75	81 ± 4.9 (75–89)	81 ± 5.9 (75–92)	87	87 ± 6.0 (77–98)	85 ± 4.6 (80–93)
Mouth width	106	98 ± 9.4 (83–124)	97.2 ± 11.4 (75–111)	109	103 ± 7.9 (88–113)	103 ± 6.0 (97–116)
Mandible length	65	63 ± 5.4 (50–71)	64 ± 8.7 (47–78)	73	64 ± 5.6 (57–73)	69 ± 5.0 (64–78)
Dorsal-fin length	258	257 ± 13.9 (228–279)	239 ± 9.1 (225–249)	304	290 ± 21.8 (251–328)	245 ± 12.1 (229–271)
Anal fin length	207	221 ± 13.2 (202–244)	187 ± 19.1 (162–230)	245	235 ± 14.7 (218–256)	197 ± 11.1 (117–211)
Caudal fin length	222	226 ± 13.1 (204–247)	220 ± 16.2 (202–244)	236	237 ± 13.8 (215–271)	220 ± 10.5 (201–237)
Pectoral fin length	214	226 ± 12.9 (206–241)	220 ± 13.2 (196–234)	239	235 ± 14.1 (205–252)	221 ± 12.0 (202–233)
Pelvic fin length	108	124 ± 9.4 (108–140)	109 ± 9.7 (92–121)	130	118 ± 6.7 (108–130)	109 ± 7.3 (96–120)

“Guzmán pupfish”), p. 254 (as “Palomas pupfish”); Propst and Stefferud, 1994:233–234; Echelle and Dowling, 1992:200–201; Echelle and Echelle, 1993:276.

*Holotype*.—UMMZ 162629, male, 41.5 mm SL; México: Chihuahua, Ojo de Palomas Viejo (now dry), 5.2 km S Las Palomas, 31°45'N, 107°40'W; R. R. Miller and H. E. Winn (M50–8), 9 March 1950.

*Paratypes*.—All Chihuahua, México: UMMZ 162630, 103 ex., 15 CS, 2 dry skeletons, 19–53 mm SL, taken with the holotype; UMMZ 136126, 50 ex., 12–37 mm SL, Pozo de las Delicias, Río del Carmen basin 3.2 km W Ahumada, S. B. Benson, 16 May 1937; UMMZ 181124, 17 ex., 13–44 mm SL, spring near Lago de Guzmán, J. M. Legler, 2 Sept. 1950; UMMZ 162616, 181 ex., spring-fed pond 0.9 km SE Las Palomas, R. R. Miller and H. E. Winn (M50–4), 7 March

1950; UMMZ 182395, 305 ex., 10 CS, 10–46 mm SL, Laguna Bustillos, R. R. Miller and family (M64–8), 20 June 1964; UMMZ 182399, 2 ex., 21, 24 mm SL, Río del Carmen, R. R. Miller and family (M64–9), 21 June 1964; UMMZ 203017, 206 ex., 11–45 mm SL, Rancho la Nariz R. R. Miller et al. (M78–11), 27 May 1978; UMMZ 203024, 306 ex. (6 CS), 13–41 mm SL, Ojo Caliente WNW Janos, R. R. Miller et al. (M78–14), 29 May 1978; UMMZ 208225, 2 ex., 35, 42 mm SL, Laguna Bustillos, B. Chernoff and M. L. Smith (BC79–15), 27 May 1978; UMMZ 208230, 7 ex., 16–20 mm SL, Río Santa María at Bachiniva, B. Chernoff and M. L. Smith (BC79–16), 29 May 1979; UMMZ 208235, 1 ex., 28 mm SL, Río Santa María at Santa Ana de Bavícora, B. Chernoff and M. L. Smith (BC79–17), 29 May 1979; UMMZ 208241, 21 ex., Ignacio Zaragoza, B. Chernoff and M. L. Smith (BC79–20), 30 May 1979; UMMZ 209017, 57 ex., 13–38 mm SL, trib. Laguna Bustillos, R. R. Miller and M. L. Smith (M80–2), 23 April 1980; UMMZ 209021, 99 ex., 13–41 mm SL, Río Santa Clara, trib. Río del Carmen, R. R. Miller and M. L. Smith (M80–3), 24 April 1980; UMMZ 211147, 51 ex., 18–38 mm SL, Ojo Caliente, E. Zaragoza, R. R. and F. H. Miller (M82–81), 3 April 1982; UMMZ 211153, 102 ex., 16–40 mm SL, Ojo de San Juan ESE Ascención, R. R. and F. H. Miller (M82–84), 5 April 1982; UMMZ 211625, 104 ex., 13–35 mm SL, Ojo Vareleño W Nuevas Casas Grandes, R. R. and F. H. Miller, K. Bowman (M78–45), 21 June 1978; UMMZ 212314, 45 ex., 10–37 mm SL, Lago de Guzmán, C. Lowe and Todd (UAZ75–70), 28 April 1975; ASU 9258, 88 ex., 10–44 mm SL; UANL 15048 (ex-UMMZ 203024); UNAM 12922 (ex-UMMZ 203024).

*Diagnosis.*—A species of *Cyprinodon* distinguished from congeners by the following combination of characters: in breeding males dorsal fin dusky to black, not yellow or orange; band on caudal fin narrow (narrower than eye-diameter) and often diffuse or absent; first dorsal fin ray thickened and spikelike; ocellus usually well developed in dorsal fin of females, no anal fin ocellus; breast fully scaled; modally 10 dorsal and anal fin rays; 7 pelvic fin rays, 25–28 (mode 26) scales in lateral line, and modally 26 vertebrae.

*Description.*—Morphometric data presented in Table 1; meristic data presented in Table 3. Maximum size observed 53 mm SL. General morphology typical of genus. Dorsal fin origin positioned at midbody or slightly nearer tip of snout; eye small, lower jaw small, neither robust nor strongly upturned; mouth nearly terminal,

its cleft only slightly oblique when closed. Body shape and proportions variable among populations (Figs. 2–3). Some populations deeper bodied, some with upper body contour more evenly rounded than others, some have larger fins (especially dorsal fins of males, as in Río del Carmen basin).

First dorsal fin ray broad, spinelike; pectoral fin long, ovoid, extending beyond pelvic base in nuptial males; pelvic fin also long, in males often extending beyond anus; outer caudal rays in males often longer than central ones, resulting in weakly trapezoidal outline.

Venter and breast fully scaled; scale margins entire or irregular, not crenate; scales between pelvic fins and anus well developed; those between pelvics thick, free distally, and covering inner pelvic fin rays; body scales lack conspicuous surface reticulations (i.e., circuli lack erect, spinelike projections or lepidonts; similar to Miller, 1943: pl. 5, fig. 2; pl. 7, fig. 1); scale radii numerous, body scales deep; cleithral scale enlarged, 1.5–2.0 times as wide as those following; cleithral process extending posteriorly beyond pectoral fin base.

As with congeners, *C. pisteri* shows notable sexual dimorphism and dichromatism (Miller and Fuiman, 1987; also compare males with females in Figs. 2–3). Pigmentation differences noted below. Adult males tend to develop longer dorsal and anal fins than females. Sexually mature males more robust in many body measures, particularly becoming more compressed and deep-bodied. Predorsal profile slightly convex in females, nearly straight in males, sometimes with dorsal crest. Adult characters of form and color often develop in unusually small males (23–25 mm SL), although not to extent as in larger ones.

*Coloration.*—Life colors of nuptial males observed at various times from early April to July. Back and upper sides brilliant, deep metallic-blue, paler (becoming silvery to chalky-blue) on lower sides, whitish on belly. Opercles, cheeks, and branchiostegal areas suffused with yellow over blue. Sides with 7–8 dark vertical bars, sometimes coalescing just before distal part of caudal peduncle. In life, caudal peduncle distal third lighter and scarcely (but often obviously) suffused with yellow (but never as bright as in *C. macularius*). Dorsal fin dusky to black or dusky near base with broad, black margin. Anal fin slate-gray, overlain by chalky- to turquoise-blue at base, yellow medially, with intensely blackened distal border. Pectoral and pelvic fins milky- or chalky-blue to yellow or orange, with rays and distal margin blackened. Caudal fin

TABLE 2. SELECTED MORPHOMETRIC FEATURES FOR *Cyprinodon arcuatus* [UMMZ 162700, 162701,  $n = 12$  FOR MALES (INCLUDING HOLOTYPE) AND 10 FOR FEMALES] AND TWO REGIONAL CONGENERS *Cyprinodon macularius* ( $n = 10$ , EACH COLUMN) AND *Cyprinodon eremus*. Mean is followed by 1 SD, range in parentheses (data for *C. eremus* from Miller and Fuiman, 1987, UMMZ 162661, 162662,  $n = 15$ , each gender, standard deviation for these values not available).

	Holotype	<i>Cyprinodon arcuatus</i>		<i>Cyprinodon macularius</i>		<i>Cyprinodon eremus</i>	
		Males	Females	Males	Females	Males	Females
Standard length (mm)	39.3	37.25 ± 2.9 (31.8–42)	31.1 ± 3.7 (26.7–39.3)	33.7 ± 1.9 (30.5–36.0)	34.1 ± 2.8 (29.5–37.8)	35.5 (29.5–41.5)	34.9 (27.9–39.0)
Predorsal fin length	539	564 ± 11.1 (547–579)	557 ± 10.6 (546–573)	559 ± 10.5 (534–571)	569 ± 9.7 (553–582)	584 (554–604)	583 (552–602)
Prepelvic fin length	519	528 ± 8.6 (512–543)	530 ± 12.3 (509–544)	550 ± 11.6 (532–574)	565 ± 12.6 (547–591)	573 (557–588)	579 (545–602)
Precanal fin length	628	648 ± 12.6 (627–666)	652 ± 13.0 (633–668)	660 ± 16.4 (623–683)	682 ± 4.0 (675–687)	693 (676–704)	699 (667–728)
Anal origin to caudal fin base	415	420 ± 12.3 (400–437)	400 ± 16.2 (375–418)	432 ± 18.0 (389–450)	376 ± 15.3 (349–400)	386 (366–407)	359 (340–377)
Body depth	402	404 ± 20.5 (364–428)	358 ± 22.0 (329–394)	420 ± 18.1 (383–445)	399 ± 8.8 (388–414)	441 (393–449)	396 (369–421)
Body width	211	207 ± 7.6 (194–217)	209 ± 10.0 (192–228)	221 ± 9.9 (203–237)	244 ± 8.2 (233–258)	262 (235–285)	263 (239–292)
Head length	313	316 ± 10.3 (294–330)	309 ± 13.1 (281–325)	323 ± 13.8 (302–354)	308 ± 8.0 (299–321)	336 (322–353)	325 (310–339)
Caudal peduncle length	300	301 ± 16.7 (267–321)	290 ± 18.7 (259–417)	290 ± 14.7 (269–315)	269 ± 10.9 (254–291)	257 (231–275)	252 (235–268)
Caudal peduncle depth	206	202 ± 8.5 (191–215)	189 ± 11.1 (177–211)	201 ± 6.4 (190–209)	179 ± 3.8 (174–185)	205 (190–217)	186 (172–203)
Interorbital width	130	120 ± 2.3 (115–123)	116 ± 11.2 (91–134)	119 ± 4.6 (114–127)	112 ± 3.6 (107–117)	123 (115–140)	123 (115–129)
Snout length	104	99 ± 5.9 (88–108)	86 ± 13.6 (62–104)	104 ± 5.1 (97–111)	98 ± 4.8 (91–107)	100 (85–111)	95 (86–103)
Orbital length	87	91 ± 3.1 (86–94)	97 ± 4.5 (89–105)	87 ± 3.8 (81–93)	82 ± 3.5 (74–86)	85 (78–94)	81 (74–86)
Mouth width	107	100 ± 7.7 (86–108)	105 ± 11.8 (90–135)	91 ± 3.8 (82–95)	91 ± 2.5 (87–96)	122 (115–131)	113 (101–126)
Mandible length	66	65 ± 3.4 (60–71)	57 ± 5.6 (47–65)	65 ± 4.5 (59–75)	59 ± 5.3 (53–68)	102 (81–111)	101 (82–109)
Dorsal-fin length	282	288 ± 14.6 (265–309)	257 ± 20.4 (208–287)	307 ± 25.4 (255–344)	278 ± 9.1 (260–288)	305 (289–330)	252 (227–279)

TABLE 2. CONTINUED.

	<i>Cyprinodon arcuatus</i>			<i>Cyprinodon macularius</i>			<i>Cyprinodon eremus</i>		
	Holotype	Males		Males		Males		Males	
			Females	Females	Females	Females	Females	Females	
Anal fin length	260	239 ± 35.9 (204-298)	289 ± 12.2 (270-311)	228 ± 10.4 (214-241)	254 (235-274)	196 (181-208)			
Caudal fin length	239	251 ± 19.2 (232-296)	260 ± 17.6 (239-301)	225 ± 9.6 (209-235)	235 (221-251)	215 (193-239)			
Pectoral fin length	244	247 ± 11.9 (230-260)	231 ± 10.5 (220-252)	212 ± 10.7 (197-228)	254 (234-276)	230 (203-249)			
Pelvic fin length	140	149 ± 8.4 (131-162)	138 ± 21.1 (121-194)	125 ± 8.4 (112-136)	115 (99-126)	101 (92-107)			

gray washed with yellow, with narrow black border that may be weak to very nearly absent (conspicuous in males from Laguna Bustillos basin; Fig. 2). Other major variants include fish from Río del Carmen at Santa Clara (Fig. 2), where caudal peduncle of males have bronze to brassy sheen, caudal fins deep-orange in advance of a black terminal border, and Arroyo Nopabeche (Laguna Bustillos) where male abdomens orange-yellow from pelvic origins onto throat and lower sides to above upper base of pectoral fin.

In females, dorsal ocellus prominent in some populations, weak in others. Tending to be disrupted or lost in old (large) fish, apparently absent in very large adults (Fig. 2). Live females generally olive-brown dorsally with bronze to yellowish sides that often become reticulate. Both vertical and paired fins often yellowish. Most fish from Ojo de Las Palomas Viejo (e.g., UMMZ 162630; 28-42 mm SL) with vertical bars (as many as 15, Fig. 1) disrupted ventrally, while some with at least one bar continuous across belly. In life, females from Ojo Caliente (UMMZ 211147) with yellow streak along entire dorsal midline. Young of both sexes similar in pigmentation to females, as usual in pupfishes, with ~8 lateral bars of generally uniform width and usually prominent dorsal fin ocellus.

*Comparisons.*—*Cyprinodon pisteri* belongs to a clade of western pupfishes that also includes the Death Valley species (*C. diabolis*, *C. nevadensis*, *C. radiosus*, *C. salinus*), Colorado River basin forms [*C. macularius*, *C. eremus*, and presumably *C. arcuatus* (see below)], and other Guzman and Río Yaqui basin forms (*C. albivelis*, *C. fontinalis*). Relationships among the southern (Guzman/Yaqui basins) forms are yet unresolved (phylogenetics characterized using molecular data, Echelle and Dowling, 1992; Echelle and Echelle, 1993), and additional undescribed species exist in the Guzman Basin (S. Contreras-Balderas, pers. comm.). All three described Guzman Basin pupfishes show a frequent (approximately 40%) lack of mandibular pores (Table 3; Smith and Miller, 1980); a trait not observed in any of the three Colorado River forms.

*Distribution and habitat.*—*Cyprinodon pisteri* is restricted to the Lago de Guzmán basin of northern Chihuahua, México, and possibly southwestern New Mexico, USA and its former connective, Laguna Bustillos, Chihuahua (Fig. 3; Smith and Miller, 1986:fig. 13.1, nos. 8-12). In the Pleistocene and earlier, this vast endorheic region (pluvial Lago de Guzmán system of Smith and Miller, 1986:fig. 13.3) supported a

TABLE 3. FREQUENCY DISTRIBUTIONS OF SELECTED MERISTIC FEATURES FOR *Cyprinodon pisteri*, *Cyprinodon albivellus*, *Cyprinodon arcuatus*, *Cyprinodon macularius* (UMMZ 162680), AND *Cyprinodon eremus* (FROM MILLER AND FUIMAN, 1987); VALUES FOR HOLOTYPE (WHERE KNOWN) INDICATED BY AN ASTERISK (\*).

	Dorsal fin rays							Anal fin rays							Pectoral fin rays								
	7	8	9	10	11	n	Mean ± 1 SD	6	7	8	9	10	11	n	Mean ± 1 SD	12	13	14	15	16	17	n	Mean ± 1 SD
<i>C. pisteri</i>	—	1	71*	146	15	233	9.8 ± 0.6	—	—	—	21	177*	31	229	10.0 ± 0.5	—	—	23	132*	66	10	231	15.3 ± 0.7
<i>C. albivellus</i>	5	12	15*	6	—	38	8.6 ± 0.9	1	—	7	25	7*	—	40	8.9 ± 0.8	—	2	22	33*	2	—	59	14.6 ± 0.6
<i>C. arcuatus</i>	—	—	5	15*	—	20	9.8 ± 0.4	—	—	—	2	17*	1	20	9.9 ± 0.4	1	—	11*	7	1	—	20	14.3 ± 0.8
<i>C. macularius</i>	—	—	8	11	—	19	9.6 ± 0.5	—	—	—	1	17	2	20	10.1 ± 0.4	—	—	5	14	1	—	20	14.8 ± 0.5
<i>C. eremus</i>	—	—	4	20	6	30	10.1 ± 0.6	—	—	—	—	25	5	30	10.2 ± 0.4	—	—	—	17	37	6	60	15.8 ± 0.6

TABLE 3. CONTINUED

	Pectoral fin rays							Lateral line scales							Scales from dorsal fin origin to pelvic fin insertion							
	4	5	6	7	8	n	Mean ± 1 SD	24	25	26	27	28	29	n	Mean ± 1 SD	9	10	11	12	13	n	Mean ± 1 SD
<i>C. pisteri</i>	—	—	2	17*	1	20	7.0 ± 0.4	—	4	11	4*	1	—	20	26.1 ± 0.8	5	10	6*	—	—	21	10.0 ± 0.7
<i>C. albivellus</i>	1	2	18	39*	—	60	6.6 ± 0.6	—	—	7	25*	5	2	37	27.1 ± 0.7	—	9	17*	14	1	41	11.2 ± 0.8
<i>C. arcuatus</i>	—	1*	4	16	—	21	6.7 ± 0.6	1*	7	8	5	—	—	21	25.9 ± 0.8	—	16	5	—	—	21	10.2 ± 0.4
<i>C. macularius</i>	—	12	8	—	—	20	6.5 ± 0.5	2	13	4	—	1	—	20	26.3 ± 0.9	—	6	14	—	—	20	10.7 ± 0.5
<i>C. eremus</i>	—	1	—	58	1	60	7.0 ± 0.3	—	18	12	—	—	—	30	25.4 ± 0.5	—	—	—	—	no data	—	—

TABLE 3. CONTINUED

	Circumferential scales												Predorsal scales												Mean ± 1 SD	n		
	24	25	26	27	28	29	30	31	32	33	34	35	36	n	Mean ± 1 SD	14	15	16	17	18	19	20	21	22			23	24
<i>C. pisteri</i>	2	4	1	6	2	4*	1	—	—	—	—	—	—	20	27.0 ± 1.8	—	—	—	5	5	3	4	—	—	—	—	17	18.4 ± 1.2
<i>C. albivels</i>	—	—	1	8	10	7*	8	3	1	—	—	—	—	38	28.7 ± 1.4	—	—	1	1	1	2	2	6	4	1	1	19	20.4 ± 2.0
<i>C. arcuatus</i>	1	5*	4	5	2	3	—	—	—	—	—	—	—	20	26.6 ± 1.5	—	—	—	1	3	5*	1	1	—	—	—	11	18.6 ± 0.8
<i>C. macularius</i>	—	—	—	1	—	9	3	4	1	2	—	—	—	20	29.8 ± 1.4	3	8	6	2	—	—	—	—	—	—	—	19	15.4 ± 0.9
<i>C. eremus</i>	—	—	—	—	—	—	3	2	12	2	10	—	1	30	32.6 ± 1.5	—	—	—	—	—	—	—	no data	—	—	—	—	—

TABLE 3. CONTINUED

	Mandibular pores										Preorbital pores										Preopercular pores										Mean ± 1 SD	n
	0	1	2	3	4	5	n	Mean ± 1 SD	2	3	4	5	n	Mean ± 1 SD	5	6	7	8	9	10	n	Mean ± 1 SD	5	6	7	8	9	10	n			
<i>C. pisteri</i>	84	2	215*	1	1	—	303	1.4 ± 0.9	—	1	19*	—	20	4.0 ± 0.2	—	21	180*	—	2	—	203	6.9 ± 0.4	—	—	—	—	—	—	—			
<i>C. albivels</i>	99	3	239*	1	1	—	343	1.4 ± 0.9	—	4	55*	1	60	4.0 ± 0.3	—	28	207*	4	2	2	243	6.9 ± 0.5	—	—	—	—	—	—	—			
<i>C. arcuatus</i>	—	—	20*	—	—	—	20	2.0	1	2	17*	—	20	3.8 ± 0.5	1	17	2*	—	—	—	20	6.0 ± 0.4	—	—	—	—	—	—	—			
<i>C. macularius</i>	1	1	17	—	—	1	20	2.0 ± 0.9	—	2	16	2	20	4.0 ± 0.5	—	—	6	13	1	—	20	7.8 ± 0.6	—	—	—	—	—	—	—			
<i>C. eremus</i>	1	—	59	—	—	—	60	2.0 ± 0.3	1	10	49	—	60	3.8 ± 0.4	—	1	54	5	—	—	60	7.1 ± 0.3	—	—	—	—	—	—	—			



TABLE 3. CONTINUED

	Total vertebrae					<i>n</i>	Mean $\pm$ 1 SD
	25	26	27	28	29		
<i>C. pisteri</i>	8	36	16	—	—	60	26.1 $\pm$ 0.6
<i>C. albivelis</i>	—	—	6	42	12	60	28.1 $\pm$ 0.5
<i>C. arcuatus</i>	8	20	5	—	—	30	25.9 $\pm$ 0.7
<i>C. macularius</i>	1	25	24	—	—	50	26.5 $\pm$ 0.6
<i>C. eremus</i>	1	25	4	—	—	30	26.1 $\pm$ 0.4

complex of lakes, streams, and springs (Miller, 1981:fig. 3, nos. 5–7; fig. 4, no. 3). Former tributaries remain clearly identified within a now-disrupted array of desiccated intermontane basins by distributions of at least eleven native fishes in remnant aquatic habitats (Smith and Miller, 1986; Propst and Stefferud, 1994).

Although certainly less abundant now than in the recent past (Fig. 3), *C. pisteri* still enjoys a wide geographic range including much of the Lago de Guzmán basin. Greatest reductions in

range are at lower elevations, where springs and other surface waters are disappearing with human development (see below). The species once occurred in the United States in artificial ponds near Columbus, Luna County, New Mexico (MSB 949, 38 specimens collected in 1951), where it was apparently introduced from Mexican sources for mosquito suppression (pers. comm., W. J. Koster to RRM, 1978). This population is no longer extant, and Prof. Koster further reported that springs supporting the spe-

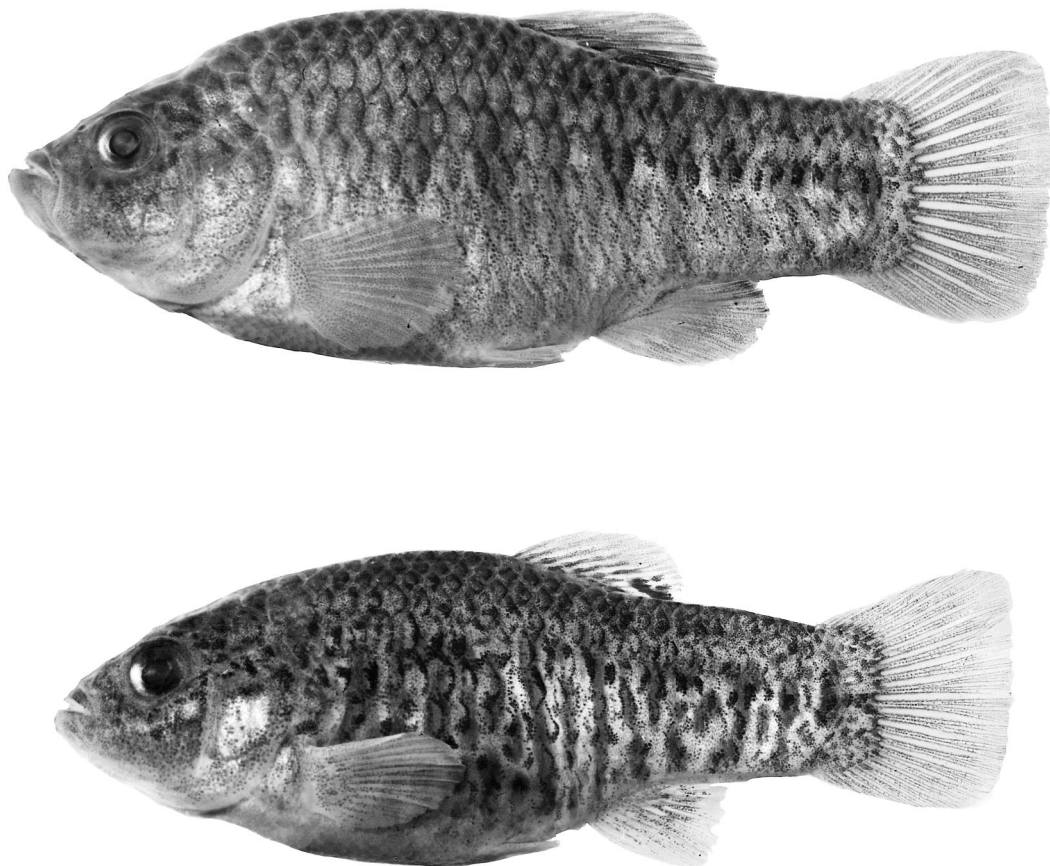


Fig. 1. *Cyprindon pisteri*, holotype (above), UMMZ 162629, 42 mm SL, male; paratype (below), UMMZ 162630, 37 mm female, México: Chihuahua, Palomas Spring (Ojo de Palomas Viejo; now dry).





Fig. 2. *Cyprinodon pisteri*, from top to bottom (paratypes): UMMZ 209017, male (35.8 mm SL) and female (34.8.9 mm SL), México: Chihuahua, Laguna Bustillos; UMMZ 209021, male (37.3 mm SL) and female (40.9 mm SL), México: Río Santa Clara at Santa Clara (Río del Carmen basin).

cies in México immediately south of Pancho Villa State Park, New Mexico dried in the 1940s.

The species is catholic in habitat, occupying springs, ciénegas, shorelines and cutoff channels of rivers and creeks, even colonizing ephemeral canals and ditches along roadsides (RRM and WLM, field obs.). When first visited by RRM in 1950, the type locality was a partially impounded water body perhaps 1.5 ha in surface area, with spring inflows along its north and west sides and old, shallow, ciénega-lined natural channels draining southward to apparently end in a desiccated salina or playa of unknown extent. Conditions were similar in 1968 (WLM, pers. obs.), but water was muddied by livestock and humans, and surroundings were severely denuded by grazing cattle, goats, and horses. Shorelines that were sufficiently boggy to exclude livestock were vegetated by dense stands of sedges (*Scirpus obnyi*, *Scirpus americanus*), with an undergrowth of *Eleocharis* sp. bor-

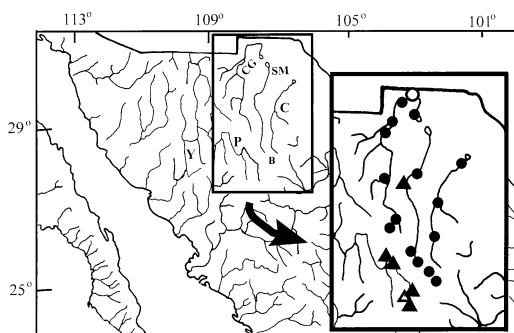


Fig. 3. Distributions of *Cyprinodon pisteri* (circles) and *Cyprinodon albivelis* (triangles), n. spp., in Chihuahua, México. Some symbols cover multiple, closely adjacent sites; type localities = open figures. B = Laguna Bustillos; C = Río del Carmen; CG = Río Casas Grandes; P = Río Papigóchic; SM = Río Santa María; Y = Río Yaqui.

dered upslope by sparse Bermuda grass (*Cynodon dactylon*) and a few shrubby mesquite (*Prosopis glandulosa*) and acacia (*Acacia greggii*). Isolated stands of cattail (*Typha angustifolia*) were in the pool. A thick, spongy mat of sedges occupied the shallow, natural outflow that passed east-southeast from the spring, although most outflow was through a newly dug canal leading eastward to agricultural fields.

The pupfish was abundant at the type locality in situations where it occurred largely in the absence of other fishes along pool margins and in outflow channels and ciénegas. It was rare to absent in open, deeper areas (to > 1.0 m) that were coinhabited mostly by *Pimephales promelas* (native) and *Cyprinella formosa* (native), and *Ameiurus melas* (nonnative). *Gambusia affinis* (nonnative) was not yet present but had become common by 1972, when the pupfish still remained abundant. The system at the type locality was dried by about 1975, presumably because of groundwater mining in both México and adjacent USA.

*Status*.—The Lago de Guzmán complex of northern Chihuahua, including in the past waters of pluvial Lago de Palomas, the now-independent Laguna Bustillos basin, and lesser lakes (Fig. 3), is composed of four major subbasins west-to-east: (1) Río Casas Grandes, originating in Madrean pine-oak forests along the Sierra Madre Occidental crest, with a historic terminus in Lago de Guzmán; (2) Río Santa María, collecting water from the Sierra Madre and Mesa del Norte west of Ciudad Chihuahua and ending in Lago de Santa María; (3) Río del Carmen (also called Río Santa Clara), beginning just east of the Sierra crest and terminating in Lago

de los Patos north of Villa Ahumada (see Brand, 1937: pl. 8c); and (4) Laguna Bustillos south of the Río del Carmen basin

In keenly perceptive observations in 1929–1931 and 1935–1936, Brand (1937:72–74) recorded the onset of major environmental degradation in this region. He noted that none of its three rivers “. . . has flowed constantly throughout a year and continuously from source to terminal lake since 1924.” During his period of observation, none of the streams was dammed, although several diversions took water from them. “The increasing use of spring and river water for irrigation in the haciendas and colonias of the region has contributed markedly to the lessened flow of the rivers in their lower courses. Many of the abundant springs that fed this system ~80 years ago have failed” (Brand, 1937:21).

In the recent past, contributions of water flow from New Mexico by Arroyo de Palomas and Mimbres River (see U.S. Geol. Surv. Map, El Paso, 1:250,000, NH 13–1, AMS Series V502, 1953) seems to have had only minor influences. Arroyo de Palomas crosses from the USA into México near Columbus, New Mexico and Palomas, Chihuahua as subsurface flow that may have fed springs near Palomas. One major spring was near the International Boundary (Gehlbach, 1981) and another (type locality for *C. pisteri*) was about 5.0 km south of the present village of Palomas Vieja. A small barrial lake locally called “Lago de los Patos” or “Lago de Palomas” (not to be confused with a larger, pluvial basin further south in Chihuahua), bordered by inflow channels and ciénegas on the north and west and low sand dunes on the northeast, was fed directly by the lower (larger) spring(s). During major floods, overflow from this depression may have reached the Río Casas Grandes, only about 15 km further south. These lagunas were visited in 1892 by Mearns (1907: 10; “Lake Palomas in the Mimbres Valley”), who described “Lakes Guzman and Palomas” as “considerable sheets of shallow, alkaline water. The sand wastes surrounding them are covered with a white deposit intolerable to the eye.”

Although Mearns (1907: 28) noted surface flow of the Mimbres River crossing the International Boundary in 1892, “flowing south into the Palomas Lakes, toward Lake Guzman in Chihuahua,” today’s extreme freshets rarely reach the Boundary. Only a faint channel can be traced toward Lago de Tiuldio about 30 km further south of the village of Arena, Chihuahua, approximately 22 km east of Palomas Vieja. Careful study of maps suggests surface water from the Mimbres River seldom reached the

Río Casas Grandes but likely ended most recently in Bolsón de los Muertos, another basin supporting *Cyprinodon fontinalis* and *Cyprinella bocagrande* (Smith and Miller, 1980; Chernoff and Miller, 1982; Mayden and Hillis, 1990). The Mimbres River evidently united with other drainages of the Lago de Guzmán complex in the recent past only during highest stages of pluvial Lake Palomas.

The direct or indirect human role in changing the hydrography and ecology of aquatic habitats in the Chihuahuan Desert may be summarized as follows. First, settlement and agricultural development led to channel incision (arroyo cutting) through sills protecting alluvial plains above them, with resulting reductions in base level of each succeeding basin. Although perhaps in part attributable to climate change (Hastings and Turner, 1966), this regional event (Cooke and Reeves, 1976) must have commenced shortly after 1640 as a likely result of watershed damage from extensive timbering, agriculture, and grazing by innumerable herds of domestic livestock originating with Spanish, Mexican, and Mormon settlers. Since the 1920s, several streams, the lower ríos Casas Grandes, Santa María, and del Carmen, and arroyos near Ascención, have incised 6 m or more below their original floodplains. Second, building of diversions, dams, and other structures to divert water from natural channels for agricultural and domestic use dried some reaches and changed patterns of flow in others. Third, groundwater mining (water extraction in excess of natural recharge) with the advent of electric pumps contributed to drying of springs and smaller channels, reducing reliability of base-flow in essentially all systems. Last, the transfer and naturalization of nonnative fishes (e.g., ictalurids, centrarchids) or interdrainage translocations of regionally indigenous forms (e.g., *Gambusia affinis*, etc.) forces new and sometimes fatal predation and competition on the indigenous fauna.

*Etymology.*—It is a distinct pleasure to honor our close, mutual friend, California biologist Edwin Philip Pister, with the patronym *pisteri*. For almost four decades, Phil Pister has unerringly and effectively performed the daunting task of preserving the integrity of natural aquatic habitats and biotas in North American deserts, along the way teaching others to do the same. His infectious and tireless persistence, enthusiasm, optimistic outlook, and unique capability to redirect conflicting views toward common goals have led to significant and enviable suc-

cesses in equating science and a strong environmental ethic with political reality.

*Cyprinodon albivelis* Minckley and Miller, n. sp.  
Cachorrito Aletas Blancas, Whitefin Pupfish  
Figure 4

*Cyprinodon* sp. or *Cyprinodon* sp. nov.—Minckley and Arnold, 1969:255; Hendrickson et al., 1981:78–79; Miller, 1981:fig. 2, no. 18, pp. 72–73 (as “whitefin pupfish”); Minckley and Brown, 1983 (republ. 1994):table 32, p. 234 (as “whitefin pupfish”); Minckley et al., 1991:254 (as “whitefin pupfish/cachorrito aleta blanco”); Rinne and Minckley, 1991:25–26, 44 (as “whitefin pupfish/cachorrito aleta blanco”); Echelle and Dowling, 1992:fig. 1); Echelle and Echelle, 1993:fig. 1.

*Holotype*.—UMMZ 235040, adult male 36.8 mm SL, México: Chihuahua, Río Papigóchic at Yepomera, 28°32'W, 107°29'N, 2048 m elevation; R. R. Miller, F. H. Miller, and R. L. Minckley, 19 June 1978.

*Paratypes*.—All Chihuahua, México: UMMZ 211597, 225 ex., 3–46 mm SL, collected with the holotype; UMMZ 211628, 237 ex., 8–43 mm SL, outlet of Ojo de Arrey (Array; Río Santa María basin) 4.8 km SSE Galeana, 30°02'N, 107°32'W, 22 June 1978, R. R. Miller and F. H. Miller (M78–46); ASU 806, 76 ex., 15–51 mm SL, outlet of Ojo de Galeana, SE Galeana, 28 May 1964, W. L. Minckley et al. (WLM 934–937); ASU 9524, 16 ex., 10–23 mm SL, Río Papigóchic at Rancho de San Pedro near Miñaca, 28°24'N, 107°26'W, 2100 m elevation, 16–17 June 1978, D. A. Hendrickson et al. (DAH 76–78); ASU 9938, 121 ex., 15–43 mm SL, El Ojo de Yepomera, 29°03'N 107°51'W, 1900 m elevation, 18 June 1978, D. A. Hendrickson et al.; UANL 15049, 30 ex. (ex-UMMZ 211597); UNAM 12923, 30 ex. (ex-UMMZ 211597).

*Diagnosis*.—A *Cyprinodon* distinguished from its congeners by the combination of a strikingly white, one-third or more of the dorsal and anal fin in nuptial males, when viewed in clear, shallow water as a brilliant, milky- to pearly-white flag with a proximal, blackened blotch on its posterior margin; terminal caudal bar strongly developed in adult males; first dorsal fin ray unmodified, narrower than or only as broad as the second; breast fully scaled; modally 9 dorsal and anal fin rays; 7 pelvic fin rays, 26–29 (mode 27) scales in lateral line; modally 28 total vertebrae.

*Description*.—Morphometric data presented in Table 1, meristic data in Table 3. Maximum observed size 54 mm SL. Body shape and form typical of pupfishes, compressed and deep (such more pronounced in males); both greatest body depth and dorsal fin origin are at mid-body; mouth is almost terminal; lower jaw not overly robust; predorsal profile nearly straight in males, tending toward convex in females.

First dorsal fin ray not sharply distinct from others; pectoral fin ovoid, reaching posteriorly to vertical from pelvic fin midpoint in males; pelvic fins also long in males, surpassing anus and sometimes anal fin origin. Outer, branched caudal rays of males distinctly longer on edges than in center, resulting in trapezoidal shape.

Scale margins entire; breast and venter fully scaled, with scales well developed between pelvic fins, their posterior margins free and covering inner pelvic rays; body scales lack conspicuous surface reticulations. Cleithral scale greatly enlarged, 2–4 times as wide as those following; cleithral process also expanded, extending beyond pectoral fin base.

*Coloration*.—Nuptial males with white, third or more of dorsal and anal fins. Body of males seined directly from breeding territories chalky-blue, darker to iridescent sky-blue on head and dorsum, grading to white below. Faint vertical bars (3–4) may extend ventrally from darker dorsal pigmentation to lower sides. Caudal fin, excepting distinct, black, terminal band, clear or only lightly dusted with melanophores on rays and interradiial membranes. Pelvic fins white, as on adjacent belly, may develop pearly-white cast as on anal fin. Pectoral fins clear to dusky, often with diffusely darkened, distal margins. In life, a few males with faint wash of light-yellow on pelvic and anal fin bases, which quickly disappears upon preservation.

Dorsal fin ocellus of females usually prominent. Speckled body pattern sometimes organized into diffuse, broken, vertical bars, especially on posterior third, which may sometimes consolidate into broken lateral band. Many females with an evident unpigmented area between last vertical bar on body and diffuse dark bar on caudal fin base, separated medially by diffuse lateral band. Other than dorsal ocellus and some pigmentation on basal rays of caudal and dorsal fins, fins of females clear or diffusely darkened by scattered melanophores, mostly associated with rays. Juvenile pigments resemble those of adult females.

*Comparisons*.—See discussion above for *C. pisteri*. *Cyprinodon albivelis* is unique among taxa ex-





Fig. 4. *Cyprinodon albivelis*, from top to bottom (holotype and paratypes): UMMZ 235040, male (36.8 mm SL, holotype) and UMMZ 211582, female (40.3 mm SL), México: Chihuahua, Río Papigóchic (Río Yaqui basin)

amined in having reduced dorsal and anal fin ray counts, and an elevated vertebral count (Table 3).

*Distribution and habitat.*—*Cyprinodon albivelis* is distributed mostly in the upper Río Papigóchic subbasin of the Pacific slope Río Yaqui drainage (Fig. 3), where it is exceptional among pupfishes in its consistent occurrence at relatively high elevations (1800–2300 m) (Hendrickson et al., 1981:fig. 19; Blasius, 1996). It also is known from a single, low-elevation (1430 m) spring complex, Ojo de Arrey, in the Río Santa María drainage (interior Lago de Guzmán Basin). This latter occurrence is enigmatic, and its nativity has been suspect. In 1972, a resident hesitantly reported to WLM that he thought the pupfish was translocated there from springs near Yepomera, Chihuahua (an unquestioned native population) to control mosquitoes. The fact that it was known only from one site in the Santa María basin, essentially surrounded by *C. pisteri* (Fig. 3), added credence to nonnativity, as did mtDNA and allozyme data. With regard to these, the Río Santa María populations are essentially identical to another sample of *C. albivelis* assayed from the Río Papigóchic (Echelle and Dowling, 1992; Echelle and Echelle, 1993).

It was also determined, however, that mtDNA of *C. albivelis* from both Ojo de Arrey and Río Papigóchic were essentially the same as *C. pisteri* (Echelle and Dowling, 1992), results tentatively attributed by Echelle and Echelle (1993) to replacement of *C. pisteri* mtDNA through introgressive hybridization from *C. albivelis*. Such an event surely cannot be attributed to a modern fish transfer, since replacement of such magnitude from one or a few introduced stocks of a species through myriad, disjunct populations of another must require far more time. Further, although similar in most meristic and morphologic features, considerable difference exists in number of gill rakers in specimens of *C. albivelis* from Ojo de Arrey (mean 17.2,  $n = 20$ ) versus Río Yaqui (mean 14.6,  $n = 80$ ), a degree of differentiation unlikely to be attained in a short time unless resulting from a severe bottleneck (not indicated by molecular data).

To our knowledge, *C. albivelis* and *C. pisteri* have not yet been collected in sympatry, but based on hydrographic history, Miller (1981:46) suggested that they and *C. fontinalis* (from the

adjacent Río del Carmen) must have been sympatric in the past. We anticipate that *C. albivelis* and *C. pisteri* are in contact near Ojo de Arrey and perhaps elsewhere in the Río Santa María system. Clearly, the assemblage of pupfishes in the Guzmán basin must as yet be considered poorly understood (also S. Contreras-Balderas, work in progress).

*Status.*—In 1978, Hendrickson et al. (1981) found *C. albivelis* widespread and locally abundant in the Río Papigóchic system. Although we expect local stocks to have disappeared because of increased human activities, we have no reason to believe the species is as yet in jeopardy. The population at Ojo de Arrey was intact in 1999 when visited by P. J. Unmack (pers. comm.).

*Etymology.*—The name *albivelis*, suggested by C. L. Hubbs, is from the Latin *albus* (white), and *velum* (a sail), alluding to pigmentation of the dorsal and anal fins in nuptial males.

*Cyprinodon arcuatus* Minckley and Miller, n. sp.  
Santa Cruz (Monkey Spring) Pupfish  
Figure 5

*Holotype.*—UMMZ 162700, adult male, 39.3 mm SL, USA, Arizona: Santa Cruz County, pond fed by Monkey Spring, trib. to Santa Cruz River (Gila River basin), 12 km north-northeast Patagonia, 27 April 1950, R. R. Miller et al. (M50-60).

*Paratypes.*—All Arizona, USA: UMMZ 162701, 41 ex., 27–42 mm SL, same locality, date, and collectors as holotype; AMNH 232395 (ex-UMMZ 125050), 20 ex.; ASU 729, 82 ex. 24–45 mm SL; ASU 600, 96 ex., 15–46 mm SL; ASU 4672, 7 ex., 35–44 mm SL, same locality as holotype; CAS 18561, 2 ex., Sonoita Cr. at Patagonia, Santa Cruz County, Sept. 1927, J. Mailliard; CAS 214579 (ex-UMMZ 125050), 20 ex.; UMMZ 125050, 223 ex., 14–46 mm SL; USNM 130002, 54 ex.; USNM 21315, 2 ex., “Yuscon” (= Tucson, Pima County), undated, 1840s?, A. Schott; USNM 44096, 1 ad., “drainage of small lake or pond, Santa Cruz River,” in Tucson, Pima County, 1891, P. L. Jouy; USNM 45441, 2 ex., “Tucson, Santa Cruz River,” Pima County, coll. 1893, H. Brown.

←

at Yepomera; UMMZ 211628, male (37.9 mm SL), and female (39.3 mm SL), México: Chihuahua, Ojo del Arrey (Array), Río Santa María drainage (Lago de Guzmán basin).

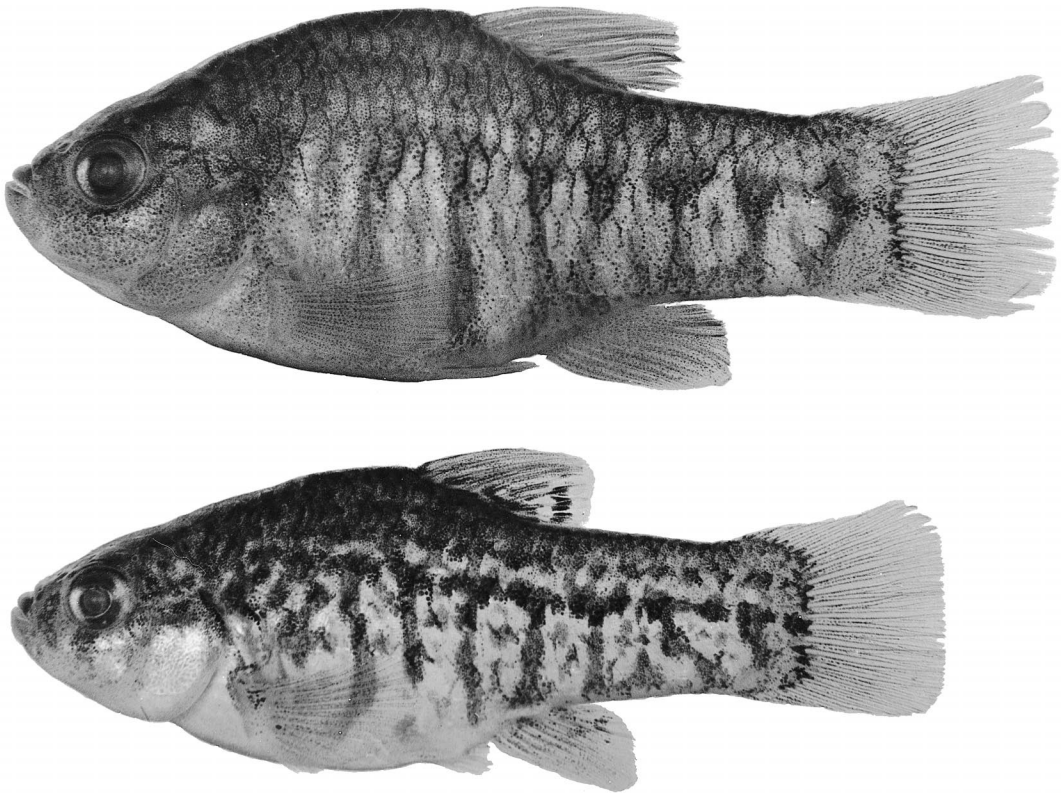


Fig. 5. *Cyprinodon arcuatus* (paratypes), UMMZ 125050, 38.0 mm SL, male (above); and 34.0 mm SL, female (below), USA: Arizona, Santa Cruz County, pond fed by Monkey Spring.

**Diagnosis.**—A species of *Cyprinodon* distinguished from congeners by the following combination of characters: a distinctive, dorsal-body surface, which is highly convex before the dorsal fin but changing abruptly at the dorsal origin into a deep, postdorsal concavity most developed in breeding males; absence in nuptial males of distinctive yellow or orange pigment on either the caudal fin or peduncle; weak development of lepidodonts, and modally six preopercular pores.

**Description.**—Morphometric data presented in Table 2, meristic data in Table 3. Maximum observed size 46 mm SL. Predorsal profile of mature animals with distinctive convex shape, otherwise, in general morphology, a typical member of *Cyprinodon*. First dorsal fin ray much like the others; pectoral fin oval, extending to at least pelvic fin midlength; pelvic fin reaching to anus; caudal fin square. Venter and breast fully scaled; body scales with weak surface reticulations or spines. Cleithral scale enlarged 1.5–2.0 times as wide as those following.

**Coloration.**—Notes by C. L. Hubbs and ourselves (WLM and RRM) concur in life colors of nuptial males. Dorsal pigmentation olivaceous to black, with scintillating surface coating of blue-green. Anal fin tended toward bluish-violet, becoming metallic blue in submarginal band. Hubbs noted both dorsal and anal fins with black margins and brilliant blue overcast; we also noted the former but observed only a tendency toward blue, sometimes chalky-blue, on fins. Most males with greenish gilt on sides, but otherwise brilliant, robin-egg blue laterally and anterodorsally, silvery below. No yellow or orange pigmentation on caudal fin or caudal peduncle, but bronze reflections on caudal fins of a few individuals inspected in full sunlight. Caudal fin brilliant silver-blue on base, olive on rays and chalky blue-gray on membranes. Pectoral fins clear or weakly olivaceous, pelvic fins whitened with light-blue cast. WLM noted adult males in winter (31 January) with opercles and cheeks white with apparent wash of blue, bases of pectoral and caudal fins with light yellow cast. Unfortunately, no one recorded life colors of



females in detail, except in winter dorsal ocellus was jet-black, delimited behind and sometimes surrounded by distinct, clear area; dorsal fin was otherwise darkened. Anal, caudal, pectoral, and pelvic fins clear. Lower two-thirds of sides strongly marked with continuous or broken vertical bars, more complete on posterior half of the body. Tendency for bar-forming pigmentation to widen into interrupted lateral band, then coalesce dorsally contributing to diffusely reticulate dorsum. Juveniles resembled females.

*Comparisons.*—Three pupfishes are native to southern Colorado River basin and closely associated Río Sonoyta drainage. *Cyprinodon macularius* was formerly widespread in the Gila River basin and lower Colorado River (it now persists largely in artificial or highly isolated habitats), with *C. eremus* (formerly *C. macularius eremus*; see Echelle et al. 2000) confined to Quitobaquito Springs and the adjacent Río Sonoyta and *C. arcuatus* to the Santa Cruz River system. These three species are similar enough that they were long confounded under *C. macularius*. *Cyprinodon macularius* and *C. eremus* are closely related, possibly sister taxa (Echelle et al., 2000). The phylogenetic position of *C. arcuatus* is unknown, but biogeographic considerations suggest that its affinities lie with *C. macularius* and *C. eremus* (or a common progenitor), likely having differentiated within its special and isolated habitat (see below), once separated from other populations.

*Distribution and habitat.*—Through most of the 1900s, this species was thought to be restricted to the immediate vicinity of Monkey Spring. A few records of native *Cyprinodon* in the Santa Cruz River basin outside this area [two specimens (CAS 18561) from Sonoita Creek in the town of Patagonia in 1927, 12 km downstream from Monkey Spring, and five others caught in and near Tucson in the 1800s (USNM 21315, 44096, 45441)] were consistently identified as *C. macularius* (Miller, 1961; Minckley, 1969, 1973). We reidentify all of them as *C. arcuatus*. Original distribution of the species was thus throughout the upper Santa Cruz River basin, Arizona-Sonora (Fig. 6).

Human alteration of the Santa Cruz River system has been extensive, based both on historic records (Hendrickson and Minckley, 1985) and evidence from prehistory (Haynes and Huckell, 1986). Even in the natural state, the stream was at most a flood tributary to the Gila River. It has a relatively small watershed (approximately 22,000 km<sup>2</sup> above the lower-most gauging station at Laveen, Arizona), and flows almost en-

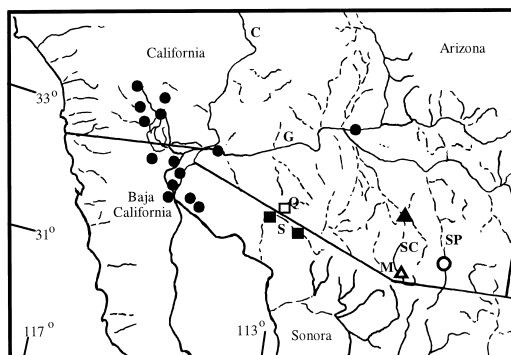


Fig. 6. Distributions of *Cyprinodon arcuatus*, n. sp. (triangles), *Cyprinodon macularius* (circles), and *Cyprinodon eremus* (squares) in Colorado River and Río Sonoyta drainages, Arizona, Sonora, and Baja California (modified from Miller and Fuiman, 1987: Fig. 2 and Echelle et al., 2000: Fig. 1). Some symbols cover multiple closely adjacent sites. Type localities are denoted by open figures. C = Colorado River; G = Gila River; M = Monkey Spring; Q = S = Río Sonoyta; SC = Santa Cruz River; SP = San Pedro River.

tirely across deeply alluviated intermontane basins with high floodplain infiltration. For example, in a flood on 12 September 1965, a  $9.7 \text{ m}^3 \times \text{sec}^{-1}$  peak was reduced 44% to  $5.4 \text{ m}^3 \times \text{sec}^{-1}$  on the 13th after flowing about 80 km, and 88% to only  $1.2 \text{ m}^3 \times \text{sec}^{-1}$  by the 14th 70 km further downstream (Conde de la Torre, 1970). More than 1.0% of the water was therefore lost for each 2.0 km of channel, mostly to infiltration. An additional 40% of the volume was estimated to be lost (reducing the peak to  $0.7 \text{ m}^3 \times \text{sec}^{-1}$ , approximately 7.0% of the original) over the remaining 46 km of channel leading into Tucson (Burkham, 1970).

Obviously, such high infiltration leads also to dramatic, up-to-downstream reduction in competency of the stream to transport sediment, so stream-carried material is deposited in and along lower reaches. This was amplified regionally, through Holocene and perhaps before, by progressively increasing aridity, resulting in aggradation of "a broad, flat alluvial plain with intermittent channels" termed the "Santa Cruz Flats" (Woods et al., 1999). Flood flows spread over this deltalike area in a broad pattern of anastomosing distributaries. Except in the greatest floods that must have connected with the mainstem Gila River, infiltration, ponding, and evapotranspiration intercepted surface flows, impeding fish dispersal. This may well explain the vicariant event leading to pupfish speciation and help explain the historic absence of other Gila River stream fishes (*Gila robusta*, *Meda ful-*

*gida*, *Tiaroga cobitis*) from the Santa Cruz system (Minckley, 1973).

Sometime around 1890, human activity in both the upper and lower Santa Cruz basin began to influence surface discharges even more. Water depletion was caused by increasing aridity, groundwater pumping for irrigation, and flow diversion for domestic use. By the early 1900s (Woods et al., 1999), even the uppermost reaches had become intermittent, dry in summer and with occasional flows at other times of year associated only with heavy precipitation. Channel incision ("arroyo cutting"; summarized by Cooke and Reeves, 1976 and Hendrickson and Minckley, 1985) lowered water tables in the upper system, draining floodplain backwaters and ciénegas. Channelization downstream on the Santa Cruz Flats consolidated flows for a time in that area, until groundwater pumping lowered water tables so infiltration again absorbed any overland discharges that might occur.

Endemic Santa Cruz basin fishes persisted in only a single refugium. This special habitat, Monkey Spring (Santa Cruz County, Arizona), is perched on a terrace about 10 m above a small, ephemeral arroyo tributary to Sonoita Creek, in turn tributary to Santa Cruz River. Carbonate-rich water from the spring originally precipitated an extensive shield of tufa about 20.5 km downstream, protecting the arroyo wall from eroding and ultimately creating a steep, vertical to overhanging waterfall. Upstream tufa deposition, about 100 m below the spring source, accumulated further to form a natural dam impounding a marshy ciénega where fishes were isolated. Then, about a century ago, humans altered the system, deepening the ciénega into an open pond and diverting spring outflow into a canal, thereby beheading the system. Most fishes persisted downstream in a human-made impoundment.

Apparently, isolation of Monkey Spring, in addition to protecting and isolating the pupfish, had been sufficiently long and complete that a chub (*Gila* sp. cf. *intermedia*) and topminnow (*Poeciliopsis occidentalis*) both differentiated from other stocks. The topminnow persisting today is genetically unique, proposed as an evolutionarily significant unit for conservation purposes (Parker et al., 1999; Sheffer et al., 1999; Minckley, 1999b), and the chub, now extinct, was morphologically distinct from other known populations (DeMarais, 1986). Pupfish extinction and chub extirpation occurred during repair of the irrigation system. Attempts to maintain and repatriate both taxa failed because of erroneous assumptions and unexpected events (for full de-

tails, history, and broader context, see Minckley et al., 1991:261–264). Both were ultimately lost in 1971 when nonnative largemouth bass (*Micropterus salmoides*) became abundant and devoured them. The downstream part of the system today supports the bass, nonnative bluegill (*Lepomis macrochirus*), and a few native topminnow, which also survives in the headspring, too small to support the predatory exotics and remaining isolated by a precipitous outflow.

*Status*.—This species is described almost 150 years following its discovery and more than three decades after the last known population was destroyed. *Cyprinodon arcuatus* was first collected (and misidentified as *C. variegatus* Lacepède) from the Santa Cruz River in "Yucson" (= Tucson, Pima Co., Arizona), almost certainly in the late 1840s, during the U.S. and Mexican Boundary Survey (Emory, 1857). Three additional specimens (originally identified as *C. macularius*) were preserved from that same area in the later 1800s. F. W. Chamberlain, a biologist for the U.S. Bureau of Fisheries (Jennings, 1987; Minckley, 1999a), collected 54 specimens in April 1904 from a pond fed by Monkey Spring, where the species persisted until the late 1960s or early 1970s.

The fate of habitats in the Santa Cruz River system are intimately interlaced with that of *C. arcuatus* (as noted above). This species is extirpated in the wild, and unless an unknown remnant is in culture by a hobbyist, which is conceivable, it is extinct. Unfortunately (or fortunately in a case such as this, if such proves true), theft of a few individuals of an imperiled species for personal use is not unknown. Such an event was possible, even probable, because of popularity of pupfish with aquarists and vulnerability of *C. arcuatus* to theft while it was under culture by agency and university individuals attempting to perpetuate the species. If such a population exists, its keeper is urged to return it to the world ownership from which it came.

*Remarks*.—Minckley (1973:192–194) initially recognized this species as an undescribed taxon he called "Monkey Spring pupfish." Otherwise, it has been consistently referred to either *C. macularius*, "Monkey Spring pupfish," or "*Cyprinodon* sp." in systematic, biogeographic, and conservation-oriented works that have noted its existence and extinction (detailed in Minckley et al., 1991).

Marsh and Sada (1994) reported a nonnative *macularius*-like pupfish of questionable origin, illicitly stocked (but no longer present) to Bog-Hole Tank, an artificial pond in the extreme

Santa Cruz headwaters in San Rafael Valley, Arizona. A similarly questionable population still occupies a cattle tank on the private Research Ranch near Elgin, Arizona, in the adjacent San Pedro River basin (Marsh and Sada, 1994). Although within or just beyond the presumed original range of *C. arcuatus*, these stocked populations do not represent *C. arcuatus*.

*Etymology.*—The name is derived from the Latin *arcus* meaning arch or shaped or bent like a bow. This is in reference to the highly convex dorsal body profile.

*Additional material examined.*—*Cyprinodon arcuatus*: CU 18202, UAZ uncat., UAZ 95–79, UAZ 95–174; *C. albivelis*: UMMZ 182391, UMMZ 211607, UMMZ 211623; *C. eremus*: UMMZ 162661; *C. macularius*: UAZ 65–79, UMMZ 162680.

#### ACKNOWLEDGMENTS

This report was in near final form when Professor Minckley passed away unexpectedly on 22 June 2001. Because Professor Miller was no longer active because of advancing age, SMN (who had assisted in this research) was added as third author to complete the manuscript and arrange for its review, revision, and publication. A. A. Echelle (OSUS), P. J. Unmack (ASU), P. C. Marsh (ASU), and S. Contreras-Balderas (UANL) assisted in this. Figure 3 was prepared with the assistance of M. H. Gach, using Fishmap by P. A. Buckup. Photographs in Figure 2 were taken by E. Theriot (UMMZ), other photographs by unspecified UMMZ staff. Many of the Río Yaqui system specimens were collected under Permit 3618 issued by Departamento de Pesca, México. Minckley and Miller's original acknowledgments follow unaltered: We are indebted to C. L. Hubbs for sharing his insights and data on pupfishes, without which their descriptions would be far less detailed. We dedicate this paper to his memory. M. L. Smith also contributed information and data toward completion of the manuscript. S. M. Norris provided comparative measurements, counts, and other amenities. We especially thank T. Hunt of the Rail-X Ranch, Arizona, where Monkey Spring is located, the long-time manager (through a number of owners), for access and other courtesies over the years.

Note added in proof: *Cyprinodon pisteri* was discussed in an unpublished manuscript by C. L. Hubbs (circa 1935), in which Hubbs intended to name the species "*Cyprinodon artatus*." Al-

though never published, this name is well known in southwestern ichthyological circles, and it can be encountered in correspondence, unpublished materials, and museum collections.

#### LITERATURE CITED

- ANASCAVAGE, J. 1973. The Ascencion pupfish. *Adv. Aquar. Mag.* 47:3.
- BEAN, R. H. 1898. Notes on Mexican fishes obtained by Dr. Carl Lumholz. *Bull. Am. Mus. Nat. Hist.* 10: 168.
- BLASIUS, H. B. 1996. Biogeography of freshwater fishes of northwestern México. Unpubl. master's thesis, Arizona State Univ., Tempe.
- BRAND, D. D. 1937. The natural landscape of northwestern Chihuahua. *Univ. New Mexico Bull.* 316, *Geol. Ser.* 5:1–74.
- BURKHAM, D. E. 1970. Depletion of streamflow by infiltration in the main channel of the Tucson Basin, southeastern Arizona, p. 827–863. *In: Floods of 1965 in the United States.* U.S. Geological Survey Water-Supply Pap. 1939-B, Reston VA.
- CHERNOFF, B., AND R. R. MILLER. 1982. *Notropis bogrande*, a new cyprinid fish from Chihuahua, Mexico, with comments on *Notropis formosus*. *Copeia* 1982:514–533.
- CONDE DE LA TORRE, A. 1970. Streamflow in the upper Santa Cruz River Basin, Santa Cruz and Pima cos., Arizona. U.S. Geological Survey Water-supply Pap. 1939-A, Reston, VA.
- CONTRERAS-BALDERAS, S. 1969. Perspectivas de la ictiofauna de las zonas aridas del norte de México. *Internat. Cent. Arid-Semiarid Land Stud., Tex. Tech. Univ. Publ.* 3:293–304.
- , V. LANDA-SALINAS, T. VILLEGAS-GAYTÁN, AND G. RODRÍGUEZ-OLMOS. 1976. Peces, Piscicultura, Presas, Polución, Planificación Pesquera y Monitoreo en México, o la Danza de las P. *Memorias del Primer Simposio de Pesquerías en Aguas Continentales*, I:315–346. Secretaría de Industria y Comercio, Subsecretaría de Pesca, México.
- COOKE, R. U., AND R. W. REEVES. 1976. Arroyos and environmental change in the American Southwest. Clarendon Press, Oxford.
- DE BUEN, F. 1940. Lista de peces de agua dulce de México, en preparacion de su catalogo. *Estac. Limnol. Patzcuaro, Trab.*, 2:1–66 (mimeo.).
- . 1947. Investigaciones sobre ictiología mexicana. I. Catalogo de los peces de la region nearctica en suelo mexicano. *Ann. Inst. Biol. (México)* 18: 257–292.
- DEMARAIS, B. D., 1986. Morphological variation in *Gila* (Teleostei: Cyprinidae) and geologic history: Lower Colorado River Basin. Unpubl. master's thesis, Arizona State Univ., Tempe.
- ECHELLE, A. A. 1993. Allozyme perspective on mitochondrial DNA variation and evolution of the Death Valley pupfishes (Cyprinodontidae: *Cyprinodon*). *Copeia* 1993:275–287.
- , AND T. E. DOWLING. 1992. Mitochondrial DNA variation and evolution of the Death Valley pupfish-

- es (*Cyprinodon*, Cyprinodontidae). *Evolution* 46: 191–206.
- AND A. F. ECHELLE. 1978. The Pecos pupfish, *Cyprinodon pecosensis*, n. sp. (Cyprinodontidae), with comments on its evolutionary origin. *Copeia* 1978: 569–582.
- , R. A. VAN DEN BUSSCHE, T. P. MALLOY JR., M. L. HAYNIE, AND C. O. MINCKLEY. 2000. Mitochondrial DNA variation in pupfishes assigned to the species *Cyprinodon macularius* (Atherinomorpha: Cyprinodontidae): Taxonomic implications and conservation genetics. *Ibid.* 2000:353–364.
- EMORY, W. H. 1857. Chap. 1, Part II, General geological features of the country, p. 1–24. *In*: Report on the United States and Mexican boundary survey. W. H. Emory. Vol. 1. Sen. Exec. Doc. No. 108, 34th Congr., 1st Sess. A.O.P. Nicholson, Printer, Washington, DC.
- EVERMANN, B. W. AND E. L. GOLDSBOROUGH. 1902. A report on fishes collected in Mexico and Central America, with notes and descriptions of five new species. *Bull. U.S. Fish Comm.* 21:137–159.
- FOWLER, H. W. 1916. Notes on fishes of the orders Haplomi and Microcyprini. *Proc. Acad. Nat. Sci. Phila.* 68:415–439.
- GARMAN, S. 1895. The cyprinodonts. *Mem. Mus. Comp. Zool.* 19:1–179.
- GEHLBACH, F. R. 1981. Mountain islands and desert seas: a natural history of the U.S.-Mexican borderlands. Texas A&M Univ. Press, College Station.
- HASTINGS, J. C., AND R. M. TURNER. 1966. The changing mile: an ecological study with time in the lower mile of an arid and semiarid region. Univ. of Arizona Press, Tucson.
- HAYNES JR., C. V., AND B. B. HUCKELL. 1986. Sedimentary successions of the prehistoric Santa Cruz River, Tucson, Arizona. *Arizona Geol. Surv. Open-File Rept.* 86–15:1–47.
- HENDRICKSON, D. A., AND W. L. MINCKLEY. 1985. Cienegas: vanishing climax communities of the American Southwest. *Desert Plants (Boyce Thompson Arboretum, Superior, Arizona)* 6:131–175 + cover photos.
- , ———, R. R. MILLER, D. J. SIEBERT, AND P. H. MINCKLEY. 1981. Fishes of the Río Yaqui basin, México and United States. *J. Ariz.-Nev. Acad. Sci.* 15: 65–106.
- HUBBS, C. L., AND R. R. MILLER. 1941. Studies of the fishes of the order Cyprinodontes. XVII: genera and species of the Colorado River system. *Occ. Pap. Univ. Mich. Mus. Zool.*, 443:1–9.
- JENNINGS, M. 1987. Faces from the past: Frederic Morton Chamberlain (1867–1921), pioneer fisheries biologist of the American West. *Fisheries* 12:22–29.
- KOSTER, W. J. 1957. Handbook of the fishes of New Mexico. Univ. of New Mexico Press, Albuquerque.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part 2. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- MARSH, P. C., AND D. W. SADA. 1994. Desert pupfish, *Cyprinodon macularius*, recovery plan. U.S. Fish Wildlife Service, Albuquerque, NM.
- MAYDEN R. L., AND D. M. HILLIS. 1990. Natural history and systematics of the bigmouth shiner, *Cyprinella bocagrande* (Teleostei: Cypriniformes), with comments on conservation status. *Copeia* 1990:100–111.
- MEARNS, E. A. 1907. Mammals of the Mexican boundary of the United States: a descriptive catalogue of the species of mammals occurring in that regional; with a general summary of the natural history, and a list of trees. *Bull. U.S. Natl. Mus.* 56(Pt. 1):i–xv, 15–30.
- MEEK, S. E. 1902. A contribution to the ichthyology of Mexico. *Publ. Field Columbia Mus. (Zool. Ser.)* 3:63–128.
- . 1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec. *Ibid.* 5:i–lxii, 1–252.
- MILLER, R. R. 1943. The status of *Cyprinodon macularius* and *Cyprinodon nevadensis*, two desert fishes of western North America. *Occ. Pap. Mus. Zool., Univ. Mich.* 473:1–25.
- . 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. *Misc. Publ. Mus. Zool. Univ. Mich.* 68: 1B155.
- . 1961. Man and the changing fish fauna of the American Southwest. *Pap. Mich. Acad. Sci., Arts, Lett.* 46:365–404.
- . 1981. Coevolution of deserts and pupfishes (genus *Cyprinodon*) in the American Southwest, p. 39–94. *In*: Fishes in North American deserts. R. J. Naiman and D. L. Soltz (eds.). John Wiley and Sons, New York.
- . 1986. Composition and derivation of the freshwater fish fauna of Mexico. *An. Esc. Nac. Cienc. Biol., Méx.* 30:121–153.
- , AND B. CHERNOFF. 1980. Status of populations of endangered Chihuahuá chub, *Gila nigrescens*, in New Mexico and Mexico. *Proc. Desert. Fish. Council* 11:74–84.
- , AND L. A. FUIMAN. 1987. Description and conservation status of *Cyprinodon macularius eremus*, a new subspecies of pupfish from Organ Pipe Cactus National Monument, Arizona. *Copeia* 1987:593–609.
- MINCKLEY, W. L. 1969. Aquatic biota of the Sonoita Creek basin, Santa Cruz County, Arizona. *Ecol. Stud. Leaf. (Nat. Conserv.)* 15:1–8.
- . 1973. Fishes of Arizona. Arizona Game Fish Department, Phoenix.
- . 1999a. Fredric Morton Chamberlain's survey of Arizona fishes in 1904, with annotations. *J. Southwest* 41:177–237.
- . 1999b. Ecological review and management recommendations for recovery of the endangered Gila topminnow. *Great Basin Nat.* 59:230–244.
- , AND E. T. ARNOLD. 1969. "Pit digging," a behavioral feeding adaptation in pupfishes (genus *Cyprinodon*). *J. Arizona Acad. Sci.* 5:254–257.
- , AND D. E. BROWN. 1983. Part 6. Wetlands, p. 222–287, 333–351 + lit. cited. *In*: Biotic communities of the American Southwest—United States and Mexico. D. E. Brown (ed.). Desert Plants (Boyce Thompson Arboretum, Superior, AZ) 4.
- , G. K. MEFFE, AND D. L. SOLTZ. 1991. Conser-



- vation and management of short-lived fishes: examples from the cyprinodontoids, p. 247–282 + lit. cited. *In: Battle against extinction: native fish management in the American West.* W. L. Minckley and J. E. Deacon (eds.). Univ. of Arizona Press, Tucson.
- PARKER, K. M., R. J. SHEFFER, AND P. W. HEDRICK. 1999. Molecular variation and evolutionarily significant units in the endangered Gila topminnow. *Conserv. Biol.* 13:108–116.
- PROBST, D. E., AND J. A. STEFFERUD. 1994. Distribution and status of the Chihuahua chub (Teleostei: Cyprinidae: *Gila nigrescens*), with notes on its ecology and associated species. *Southwest. Nat.* 39:224–234.
- REGAN, C. T. 1907. Pisces. *Biologia Centrali-Americana* 8:33–160.
- RINNE, J. N., AND W. L. MINCKLEY. 1991. Native fishes of arid lands: a dwindling resource of the desert southwest. U.S. For. Ser. Gen. Tech. Rept. RM-206: 1–43 + covers, frontis.
- SHEFFER, R. J., P. W. HEDRICK, AND A. L. VELASCO. 1999. Testing for inbreeding and outbreeding depression in the endangered Gila topminnow. *Anim. Conserv.* 2:121–129.
- SMITH, M. L., AND R. R. MILLER. 1980. Systematics and variation of a new cyprinodontid fish, *Cyprinodon fontinalis*, from Chihuahua, Mexico. *Proc. Biol. Soc. Wash.* 93:405–416.
- , AND ———. 1986. The evolution of the Rio Grande basin as inferred from its fish fauna, p. 457–485. *In: Zoogeography of North American Fishes.* C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York.
- SUBLETTE, J. E., M. D. HATCH, AND M. SUBLETTE. 1990. *Fishes of New Mexico.* Univ. of New Mexico Press, Albuquerque.
- TURNER, B. J., AND R. L. LIU. 1977. Extensive interspecific genetic compatibility in the New World killifish genus *Cyprinodon*. *Copeia* 1977:259–269.
- WILLIAMS, J. E., J. E. JOHNSON, D. A. HENDRICKSON, S. CONTRERAS-BALDERAS, D. J. WILLIAMS, M. NAVARRO-MAEDA, D. E. MCALLISTER, AND J. E. DEACON. 1989. *Fishes of North America: endangered, threatened, or of special concern: 1989.* Fisheries 14:2–20.
- WOODS, M. L., P. K. HOUSE AND P. A. PEARTHREE. 1999. Historical geomorphology and hydrology of the Santa Cruz River. *Arizona Geol. Surv. Open-file Rept.* 99–13:1–92, maps.
- (WLM) DEPARTMENT OF BIOLOGY, ARIZONA STATE UNIVERSITY, TEMPE, ARIZONA; (RRM) FISH DIVISION, MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN 48109; AND (SMN) DEPARTMENT OF ZOOLOGY, MIAMI UNIVERSITY, OXFORD, OHIO 45056. PRESENT ADDRESS: (SMN) 1 UNIVERSITY DRIVE, CALIFORNIA STATE UNIVERSITY—CHANNEL ISLANDS, CAMARILLO, CALIFORNIA 93012. Send reprint requests to SMN. Submitted: 19 Nov. 2001. Accepted: 1 March 2002. Section editor: S. A. Schaefer.