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THE STATUS OF *CYPRINODON MACULARIUS* AND
CYPRINODON NEVADENSIS, TWO DESERT
FISHES OF WESTERN NORTH
AMERICA

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SINCE the account of the fishes of the Death Valley expedition was published by Gilbert (1893), members of the genus *Cyprinodon* throughout the arid Southwest have generally been assigned to a single species, *Cyprinodon macularius* Baird and Girard. Except for the local biometric study by Wales (1930), no careful comparison of the many isolated populations in this large area has been attempted, principally because adequate series have not been available. During the last five years, however, a large amount of material has been accumulated, which, with critical study, convinces me that the forms of the Death Valley and Colorado River systems should be recognized as distinct species. Criteria to support this view are presented in the pages which follow. The primary purpose of this paper is to clear up the existing confusion regarding the validity and range of *Cyprinodon nevadensis* Eigenmann and Eigenmann and to present diagnostic characters which will separate this species from its very close relative, *Cyprinodon macularius*. A comprehensive and detailed analysis of the cyprinodont fishes in Death Valley and adjacent regions is being prepared by me for a forthcoming paper.

HISTORICAL REVIEW.—With the advent of the Pacific Railroad surveys during the middle of the last century, the first serious study of the fauna of the American West began. Since this time the following species of *Cyprinodon* have been described from the Colorado River basin and the Death Valley region :

Cyprinodon macularius Baird and Girard (1853 : 389), from the Rio San Pedro, a tributary of the Rio Gila, Arizona.

Cyprinodon californiensis Girard (1859b : 157), from near San Diego [on the desert side], California.

Cyprinodon nevadensis Eigenmann and Eigenmann (1889 : 270), from Saratoga Springs in Death Valley, California.

Lucania [= *Cyprinodon*] *browni* Jordan and Richardson (1907 : 319), from a hot spring in northeastern Lower California.

Cyprinodon diabolis Wales (1930 : 68) from Devil's Hole, Ash Meadows, Nevada.

All of these species, with the exception of the last named, have been considered as synonyms of *C. macularius*. Jordan, Evermann, and Clark (1930 : 181) and Evermann and Clark (1931 : 56), however, list *C. nevadensis* as a valid species, but apparently restricted to Saratoga Springs. Schrenkeisen (1938 : 186) and Shapovalov (1941 : 444) provisionally recognize this species, pending further study. Only one recent writer, Cowles (1934 : 40), has questioned the currently accepted range of *C. macularius*, suggesting that this species is probably restricted to the lower Colorado River drainage basin (Salton Sea included). There can be no question that *C. californiensis* and *C. browni* (see Jordan, 1924 : 23; and Hubbs, 1926 : 6) are correctly placed as species in the synonymy of *C. macularius*. My father and I have recently collected thoroughly in the region from which these species have been recorded, and all of this material, as well as that contained in several earlier collections by others, is in complete agreement with the characters of *C. macularius* as herein defined.

ACKNOWLEDGMENTS.—For the loan of collections from important localities, and many other kindnesses, I am grateful to Professors John O. Snyder and George S. Myers, of Stanford University. I am further indebted to the late Dr. Joseph Grinnell and to Dr. Alden H. Miller, who greatly encouraged the work during its phase at the Museum of Vertebrate Zoology, University of California. Professor Carl L. Hubbs has critically read the manuscript and made valuable suggestions. The authorities of Death Valley National Monument have generously permitted collections from Death Valley. My father, Ralph G. Miller, has been of constant aid in the field work.

MATERIAL.—Because of the frequent difficulty of finding many of the isolated localities from which collections of *Cyprinodon* have been recorded, and in order that the reader may appreciate the quantity of material which forms the basis of this study, a complete list by localities of the specimens examined has been drawn up. During the last five years nearly all of this material, representing approximately 10,000 specimens (more than 6000 specimens of *C. macularius* and about 3500 of *C. nevadensis*), has been carefully studied. The abbreviations U.M.M.Z. and S.U. denote collections in the University of Michigan Museum of Zoology and Stanford University, respectively. The number of specimens is given in parentheses; this number represents the total for all collections whenever there is more than one collection from a single locality.

SPECIFIC COMPARISON.—All known populations of *Cyprinodon macularius* and *Cyprinodon nevadensis* may be distinguished by the set of characters listed in Table I. It must be stressed at the outset, however, that no single one of these features can be relied upon to separate all populations of the 2 species. If several of the characters are used in combination, however, recognition of the species is readily accomplished. The reliability of the proposed criteria is discussed in detail below.

1. The measurement of the distance between the tip of the premaxillaries (in retracted position) and the most posterior

TABLE I
DIAGNOSTIC DIFFERENCES BETWEEN TWO SPECIES OF *Cyprinodon*

Character	<i>C. macularius</i>	<i>C. nevadensis</i>
1. Prehumeral length stepped into predorsal length (see Table II)	1.3 to 1.7 (ave. 1.5)	1.6 to 2.0 (ave. 1.8)
2. Scales (see Pls. V-VII)		
Pattern	Scale surface without conspicuous reticulations; circuli with erect spinelike projections	Scale surface densely reticulate; circuli without conspicuous spinelike projections
Shape	Generally about as broad as deep; width usually 1.1 to 1.4 in length (ave. 1.3)	Usually much deeper than broad; width usually 1.4 to 1.6 in length (ave. 1.5)
Number of radii	Usually 12 to 18 (ave. 15)	Usually 18 to 24 (ave. 21)
3. Tricuspid teeth (see Fig. 1)	Central cusp broad, spatulate; outer cusps very much narrower, more pointed. Shaft constricted in basal part, where width is from $\frac{1}{3}$ to $\frac{1}{2}$ width at tip	Central cusp somewhat narrower, almost always truncate; outer cusps relatively broader, more rounded. Shaft gradually tapering to base where width is more than $\frac{1}{2}$ width at tip
4. Reach of longest pelvic ray*		
Males	Generally to or beyond base of anal fin; nearly always beyond vent	Generally about to vent, rarely beyond, and never to base of anal fin
Females	Almost always beyond vent	Very rarely beyond vent
5. Development of pelvic fins* (see Table III)	Only rarely reduced; never lacking on either side (in young or adults)	Typically reduced; one or both frequently absent (in adults as well as in young)
6. Male nuptial coloration†	Body intense light blue except over caudal peduncle and caudal fin, which are pale lemon-yellow to brilliant yellow-orange	Body intense deep blue throughout; never yellowish on caudal peduncle and caudal fin

TABLE I—(Concluded)

Character	<i>C. macularius</i>	<i>C. nevadensis</i>
7. Humeral process*.....	Generally larger and much thicker than adjacent scales	Usually scarcely larger or thicker than adjacent scales
8. Position of male dorsal fin*	With few exceptions, about equidistant between caudal base and tip of snout	With only rare exceptions, nearer caudal base than tip of snout
9. Vertical bars of females	Generally disrupted, forming a discontinuous lateral band along the mid-line	Generally continuous; no marked band; often very faint or absent

* See discussion of variability in text.

† In *C. macularius*, refers only to populations from Salton Sea Basin (California) and El Doctoro (Sonora, Mexico).

point on the margin of the humeral process, stepped into the predorsal length, generally provides a clear-cut specific distinction (Table II). This character was measured under the low power of the microscope using a pair of fine dividers, and does not apply to fish less than 20 mm. in standard length. Since the measurement involves a personal estimation (to the nearest tenth) and requires a certain skill and experience, it is perhaps less usable than some of the characters which follow.

2. The nature of the scales (Pls. V–VII) affords a very dependable character for separating most populations of both species. Whereas the scales of *Cyprinodon nevadensis* from Amargosa River (particularly the Death Valley population) closely approach those of *Cyprinodon macularius*, in shape and number of radii, they can be readily distinguished by the more trenchant character of scale pattern. This is also true of some of the well-isolated populations of *macularius*, in which the scales are irregularly shaped (tending to be deeper than usual) and show an increase in the number of radii. This feature of scale structure appears to be the most reliable single criterion distinguishing the 2 species.

The circuli of *Cyprinodon macularius* bear erect (or sub-erect) spinelike projections which give a toothed appearance

TABLE II
 DISTANCE BETWEEN TIP OF SNOUT AND POSTERIOR MARGIN OF HUMERAL PROCESS STEPPED INTO PREDORSAL LENGTH

	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	No.	Ave.
<i>Cyprinodon macularius</i>										
Males	17	84	98	11	210	1.45
Females	1	33	139	36	2	211	1.50
<i>Cyprinodon nevadensis</i>										
Males	11	61	93	14	1	180	1.76
Females	1	36	100	37	1	175	1.80
TOTALS										
<i>Cyprinodon macularius</i>	18	117	237	47	2	421	1.48
<i>Cyprinodon nevadensis</i>	12	97	193	51	2	355	1.78

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to each circulus (Pl. VII, Fig. 1). These projections may point inward toward the focus or outward toward the distal margin of the scale. They are particularly well developed at and near the focus, generally diminishing distally. The interspaces separating successive circuli are without conspicuous reticulations, although near the exposed border of the scale a few may be present. Because of halation, the projections usually give a beaded appearance to the surface of each circulus (when the radii are in clear focus as shown in Pl. V). By adjusting both light and focus, the toothed nature of the circuli can be observed under sufficiently high power. In *Cyprinodon nevadensis* the circuli are without prominent erect processes, and the interspaces are densely reticulated (Pl. VI, and Pl. VII, Fig. 2). These striking reticulations are present in and about the focus as well as along the free margin of the scale. The structural markings ascribed to *C. nevadensis* appear to characterize all the forms of the Death Valley system, whereas the pattern described for *C. macularius* seems to be shared by related species to the south and east of the Colorado River basin.

The radii were counted and the proportionate measurements were made (with dividers) on the images of mounted scales, as magnified on a scale-reading machine.

Approximately 80 mounted scales of *C. macularius* and nearly 70 of *C. nevadensis* (from the entire range of both species) were studied. The number of radii overlaps widely in the 2 species (*C. macularius*, 10-21; *C. nevadensis*, 14-30), but the bulk of the counts show an overlap only at 18. Only 6 out of 66 specimens of *macularius* gave a count greater than 18, and only 8 out of 63 of *nevadensis* showed fewer than 18.

The greatest width of the scale stepped into its greatest length gave results which overlapped more widely, 1.0-1.6 in *C. macularius* and 1.3-1.9 in *C. nevadensis*. Of 80 scales of the former, 15 gave a ratio of 1.4 (and only 4 a higher value), and of 66 of the latter 13 had a ratio of 1.4 (and only 3 were 1.3). One other measurement was made: the distance between

the uppermost and the lowermost radius reaching the scale margin stepped into the greatest width of the scale. The results were: *C. macularius*, 1.0–2.0 (usually 1.0–1.5), average, 1.27; *C. nevadensis*, 0.7–1.2 (usually 0.8–1.0), average, 0.93.

The scales chosen for study were from the mid-line row; the eighth scale posterior to the upper angle of the shoulder girdle, generally on the right side of the body, was used, unless the scale structure was imperfect, in which case the seventh or ninth scale was used. All regenerated or injured scales were disregarded, as they gave unreliable results. In enumerating the radii all those developed are counted, including the

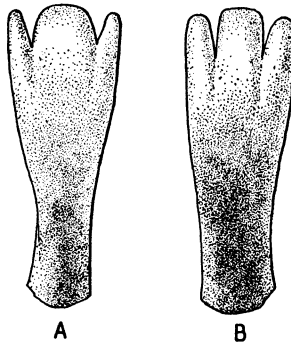


FIG. 1. Mandibular teeth of 2 species of *Cyprinodon*. Drawn by Grace Eager.

A. *Cyprinodon macularius*. Outer face of tooth from middle of lower jaw of female, 35 mm., from Wise Ranch, near Mecca, California. Length, 0.51 mm.

B. *Cyprinodon nevadensis*. Outer face of tooth from middle of lower jaw of female, 34 mm., from Saratoga Springs, Death Valley, California. Length, 0.56 mm.

small (often minute) upper and lower ones which can be seen only under high magnification. Fish less than 30 mm. in standard length were not used (with a few exceptions); scales taken from those between 32 and 38 mm. gave the most reliable results.

3. The teeth (Fig. 1), although subject to some variation, were generally found to provide very reliable characteristics. Those studied were taken from the middle of the lower jaw.

Since larger specimens show frequent injuries and evidence of wear, teeth were studied only in fish measuring less than 36 mm. in standard length.

4 and 5. The pelvic fins vary greatly not only in length but also in number of rays (Table III). All populations of *C. nevadensis* have a marked tendency toward degeneration of these fins, whereas only one population of *C. macularius* exhibits this trend to a noteworthy degree. It is the well-isolated and undoubtedly long-separated Mexican form (Pl. II, Figs. 3-4) inhabiting the Sonoyta River drainage basin, and is discussed separately below. With this exception Gilbert's statement (1893: 232), that the normal number of pelvic rays in *C. macularius* (including *C. nevadensis*) seems to be 6, is incorrect. Table III shows that 7 is the usual number in true *C. macularius*, and that the most frequent number in *C. nevadensis* is 6. There is a marked tendency in *nevadensis* toward a great or even complete loss of pelvic rays. Myers (1935: 303) stated that *macularius* often lacks pelvic fins, but he obviously referred to the Death Valley populations which are herein assigned to *nevadensis*. The only other species of *Cyprinodon* known to be characterized by reduced pelvics, with these fins occasionally totally lacking, are *C. diabolis* Wales (1930), which virtually never develops pelvic fins, and the recently described *Cyprinodon laciniatus* (Hubbs and Miller, 1942), from the Bahamas. A cyprinodont without pelvic fins, from Pahranaagat Valley, Nevada, was described by Gilbert (1893: 233) as *Cyprinodon macularius baileyi*, but this form is now known (Hubbs and Miller, 1941: 1-2) to represent a distinct species of a very different genus, *Crenichthys*. Great care must be taken in counting the number of pelvic rays, since the innermost ray is often represented by a mere remnant of cartilage. Good light and high magnification are necessary for an accurate count.

When the difference in size of pelvics and in predorsal length in the 2 species is expressed by stepping the length of the longer fin into the latter distance, it is found that in *C. macularius* (Sonoyta River collections excepted) the range for

TABLE III
 VARIATION IN NUMBER OF PELVIC FIN-RAYS IN TWO SPECIES OF *Cyprinodon*

	0	1	2	3	4	5	6	7	8	No.	Ave.
<i>Cyprinodon macularius</i>											
Salton Sea basin, Colorado Desert, California*	2	13	161	406	10	592	6.69
Distributaries of Colorado R., Baja California, Mexico	4	38	151	7	200	6.81
Laguna Salada basin, Baja California, Mexico	3	1	2	45	142	7	200	6.72
Lerdo, lower Colorado R., Sonora, Mexico	1	1	40	77	1	120	6.62
El Doctoro, S. of Yuma, Sonora, Mexico	7	76	77	160	6.44
Sonoyta R. Valley, Sonora, Mexico	2	10	39	49	100	6.35
Santa Cruz R. basin, Gila R. system, Arizona	1	31	177	11	220	6.90
Salt R. near Phoenix, Gila R. system, Arizona	2	34	36	6.94
Gila R. below Dome, Gila R. system, Arizona	5	35	2	42	6.93
<i>Cyprinodon nevadensis</i>											
Amargosa R., Death Valley, California	8	1	1	2	28	145	14	1	200	5.64
Saratoga Sprs., Death Valley, California	2	1	9	65	211	12	300	5.71
Amargosa R., Tecopa, California	3	3	5	35	140	13	1	200	5.69
Spring-fed creek, Shoshone, California	20	1	1	2	23	145	8	200	5.27
Ash Meadows region, Nevada	75	1	1	8	60	176	414	29	764	5.02
TOTALS											
<i>Cyprinodon macularius</i>	1	3	5	38	437	1148	38	1670	6.70
<i>Cyprinodon nevadensis</i>	108	5	3	10	78	327	1055	76	2	1664	5.33

* Based on 5 separate populations in and about Salton Sea.

males is 3.6–5.3 (average, 4.1), whereas for males of *C. nevadensis* the range is 5.1–9.0 (only rarely less than 5.4). For females of typical *macularius*, the ratios are 3.9–6.3 (average, 4.7), and for females of *nevadensis*, 5.9–11.0 (only rarely less than 6.0). In the Sonoyta River populations of *macularius* this ratio is 4.5–6.5 (average, 5.2) for the males, and 5.1–7.0 (average, 6.0) for the females; these ratios only slightly approach those characteristic of most populations of *C. nevadensis*. Correlated with this reduction in size of the pelvics, this form also shows the lowest pelvic ray count (Table III) of any population of *C. macularius*. It further approaches *Cyprinodon nevadensis* in the more posterior position of the dorsal fin, as indicated below. In several major characters, however, especially the nature of the scales, teeth, humeral process, general body shape, and coloration of females, it agrees well with *Cyprinodon macularius*. With little doubt it represents a somewhat specialized derivative of that species.

In obtaining the ratios given above, 30 adults (15 of each sex) from every population were analyzed, except in collections of *C. macularius* from Rillito Creek, Gila River, and Salt River (all in Arizona), for which the analysis had to be based on fewer specimens; the results, however, fell well within the expected range.

6. The color of mature males during the breeding season (generally about April to September) presents a very striking character which distinguishes the 2 species at a glance. It is not known, however, whether all populations of *C. macularius* exhibit the color described. It is thus far known only for populations occurring in and about the Salton Sea (including a number of isolated springs and a western tributary), and the isolated spring at El Doctoro, Sonora, Mexico. The 4 populations from Lower California (from distributaries of the Colorado River and in Laguna Salada) were all taken in January and exhibited various shades of red in place of the yellowish nuptial color of individuals from the former regions. What significance this variation may have is not yet known. All breeding males of *C. nevadensis* are nearly uniform dark

blue throughout, showing no evidence of such strongly contrasting colors. These observations are based on living material, both in the field and the aquarium.

7. Generally speaking, the humeral process is larger and thicker in *macularius*, and its exposed portion is usually greater in area than are the exposed parts of adjacent scales. The lower border of this structure commonly juts out farther than does the corresponding region in *nevadensis*. The main overlying scale in *macularius* is generally only slightly larger than the bony process, rather than about twice this area. In *C. nevadensis* the process is commonly smaller and thinner, and the exposed portion is usually somewhat smaller than that of adjacent scales (as pointed out by Eigenmann and Eigenmann, 1889). Although there is a general trend toward reduction in size and thickness of this process in *nevadensis*, certain individuals of *macularius* show an almost equally reduced humeral, so that the value of this feature in distinguishing the species is limited.

8. As also indicated by Eigenmann and Eigenmann, the dorsal fin is more posterior in *C. nevadensis* than in *C. macularius*. Its position is best determined by using a pair of dividers. The distance between the caudal base and the origin of the dorsal fin is projected forward and the point reached is noted.

In males of *C. macularius* (Sonoyta River populations excepted), this point usually lies on or well in advance of the snout, although the position is quite variable (ranging from the posterior part of the pupil to slightly beyond the tip of the lower jaw). In males of the Sonoyta River form it usually varies from the anterior rim of the eye to the middle of the rostrum. In the females (all populations), the point usually fluctuates from near the pupil to the middle of the snout, varying from the posterior border of the pupil to the tip of the snout (uncommon).

In males of *C. nevadensis* the point reached is usually scarcely beyond the anterior rim of the eye, varying to well behind the eye. In about 20 per cent of the large males from

Amargosa River, Death Valley, however, it varies from the posterior margin of the rostrum to the rostral neuromasts; in the others, from the anterior to the posterior rim of the eye; in no individual examined did the tip of the dividers reach the tip of the snout. In the females, in all populations of *nevadensis*, the range is from well behind the eye to the anterior border of the pupil, usually near the posterior rim of the eye. This character was not measured on specimens less than 20 mm. in standard length.

9. The narrow vertical bars on the sides of the females (and immature) form a rather consistently different pattern in the 2 species. In *Cyprinodon macularius* these bars are characteristically interrupted (Pls. I-II), so that their upper and lower segments are mostly disconnected. This gives the impression, often quite striking, of an interrupted lateral band along the mid-line, a feature which has been pointed out by Mellen and Lanier (1935: 253). These disjointed markings are very prominent, due in part to the contrasting silvery background over which they lie. The specific name, meaning spotty, suggests the nature of this coloration.

In *Cyprinodon nevadensis* the pattern is much more variable, but the bars (when developed) are usually weaker and more nearly continuous (Pls. III-IV). They are commonly much less prominent because the background is usually brownish (occasionally lighter, but never bright silvery). Not uncommonly the bars are entirely absent; usually they are continuous throughout, connected only posteriorly, or partly (rarely completely) disconnected. In general, however, this feature will serve to distinguish the 2 species.

In addition to these major differences there are others which are less obvious. The body (Pls. I-IV) of *Cyprinodon macularius* is generally more slab-sided (less thick and rounded); the dorsal profile is more angular, not broadly arched; the head is somewhat longer, and the eye larger. Over most of its known range *C. macularius* has all the fins larger than those of *C. nevadensis*. As already pointed out, this is particularly true of the pelvic fins, but it is generally true also of the dorsal, anal, and caudal fins.

The number of pores of the lateral-line system of the head (counted on both sides) is another useful character. The 2 species show a good average difference, but overlap widely. In 656 specimens of *Cyprinodon macularius* (representing all populations), the average number of preopercular pores is 14.22 (usually 7 on each side of the head). A similar analysis of 651 specimens of *Cyprinodon nevadensis* gives an average of 12.71. The range of variability is much greater in *C. macularius* (9–19) than in *C. nevadensis* (10–16). The low counts for *macularius* were noted only for populations from well-isolated springs and creeks. A similar but less marked trend is exhibited by the number of lachrymal pores. Correlated with this reduction in pores, these relic populations also show reduced pelvics (both in size of fin and number of rays), a more posterior dorsal fin, and scale irregularities (as already mentioned). Such trends are found in well-isolated stocks of *Cyprinodon macularius*, but in no race examined have these trends evolved to the extent characteristic of *Cyprinodon nevadensis*.

The number of scales and fin-rays in the 2 species is very similar, although many of the counts average slightly lower in *nevadensis* than in *macularius*.

Cyprinodon macularius Baird and Girard

Cyprinodon macularius.—Baird and Girard, 1853: 389 (original description; Rio Gila [Arizona]). Girard, 1859a: 68, Pl. 37, Figs. 8–11 (description, based on same material from “Rio San Pedro (Rio Gila)”). von Müller, 1865: 638 (record). Günther, 1866: 301 (Rio San Pedro). Jordan and Copeland, 1876: 141 (San Pedro River). Jordan, 1878: 432 (Rio Gila). Jordan and Gilbert, 1882: 330 (after Girard). Jordan, 1885: 835 (intermontane faunal region). Eigenmann, 1892: 129, 142 (Colorado Desert, in south-eastern California). Gilbert, 1893: 232–33 (in part; characters; coloration; habitat; food; synonymy; springs and wells throughout the desert region of southern California [Salton Sink], and Arizona; Lerdo, Sonora, Mexico, on the lower Colorado River). Evermann and Rutter, 1895: 475, 486 (in part; *Girardinus macularius*, misprinted for *Cyprinodon macularius*; not confined to the Colorado River basin; literature records). Garman, 1895: 24–25 (in part; characters; comparison; “Colorado River basin

to the Pacific Coast''). Jordan and Evermann, 1896: 314 (range, in part; Sonora). Jordan and Evermann, 1896-1900: 671, 674 (in part; characters in key; description after Gilbert; range). Gilbert and Scofield, 1898: 487-88, 498 (Colorado River and springs in the Colorado Desert, occurring only where natural drainage is toward Colorado River; spring-fed pond at Lerdo [Sonora], Mexico). Meek, 1904: 126 (literature records; description after Gilbert; Basin of the Rio Colorado). Regan, 1907: 83, 85 (characters in key; description; literature records; synonymy; in part; Colorado¹ to Sonora and Lower California). Snyder, 1915: 586 (color; habitat; Gila River at Gila City [= Gila Bend, Maricopa Co.] and Adonde Siding [= Adonde, Yuma Co.], Arizona; Sonoyta River [Sonora, Mexico]; spring near Sonoyta River). Evermann, 1916: 62-63 (habitat; ecology; toleration to high temperatures; in part; Figtree John Spring, 7 miles southwest of Mecca). Fowler, 1916: 432 (record; synonymy). Snyder, 1917: 202 (range, in part). Thompson, 1920: 84 (along shore of Salton Sea; Fish Springs). Thompson and Bryant, 1920: 62 (Salton Sea; Fish Spring; streams and springs of the desert throughout southern California and parts of Mexico). Coleman, 1929: 225, 226 (after Evermann; tolerance of salinity; breeding habitat; relationship with fish and bird predators; about Salton Sea from north shore to Fish Springs and Figtree John Spring). Clark, 1930: 553 (lower San Felipe Creek [western tributary to Salton Sea] and Salton Sea). Jordan, Evermann, and Clark, 1930: 181 (synonymy; in part; range after Jordan and Evermann, 1896-1900). Evermann and Clark, 1931: 43, 55-56 (literature records; synonymy; artesian well at Mecca [Southern Riverside Co.]; Fish Springs; Salton Sea). Blackwelder, 1933: 470 (range, in part; Colorado River basin). Cowles, 1934: 40 (ecology; breeding habits; probably confined to the lower Colorado River basin, including Salton Sea). Mellen and Lanier, 1935: 252-53 (color; size; breeding habits; temperature toleration; food; range). Ward, 1936: 137-38 (range, in part). Jaeger, 1938: 74 (in part; ''springs of the Salton Basin (Fish Springs, Dos Palms)''). Schrenkeisen, 1938: 186 (description; range, in part; comparisons). Dill and Shapovalov, 1939: 317-18, Fig. 115 (after Lanier; color; culture; Fig. 115, from Kennedy, 1916, is not *C. macularius*). Lanier, 1939: 190 (adaptation to high temperature; coloration; spawning temperature; isolated pools and springs in the desert regions of southern California, Arizona, and northern Mexico). Seale, 1940: 93 (Salton Sea; temperature toleration). Hubbs and Miller, 1941: 2-3 (Colorado River system). Shapovalov, 1941: 444 (provisionally listed from Cali-

¹ Meaning Colorado Desert (Hubbs and Miller, 1941: 3).

fornia). Dill and Woodhull, 1942: 171-72 (Salton Sink; eaten by *Elops affinis*). Miller and Miller, 1942: 96-7 (range; adaptability; coloration; notes on life history).

Cyprinodon californiensis.—Girard, 1859b: 157-58 (original description; neighborhood of San Diego, California [probably from salt springs in the desert, now Imperial County, according to Jordan, Evermann, and Clark, 1930: 181]). Günther, 1866: 301 (San Diego). Jordan and Copeland, 1876: 141 (San Diego). Jordan, 1878: 432 (San Diego). Jordan and Gilbert, 1881a: 457 (no locality); 1881b: 42 (San Diego). Jordan and Jouy, 1881: 13 (San Diego). Jordan and Gilbert, 1882: 330 (after Girard; San Diego). Jordan, 1885: 835 (questionably assigned to the California shore fauna; no locality given). Eigenmann and Eigenmann, 1888: 3-4 (re-description based on 4 specimens from Dos Palmas Spring [on the northwestern side of Salton Sea, Riverside County, California]). Garman, 1895: 24 (synonym of *C. macularius*). Jordan and Evermann, 1896-1900: 674 (synonym of *C. macularius*). Regan, 1907: 85 (synonym of *C. macularis*). Fowler, 1916: 432 (synonym of *C. macularius*). Jordan, Evermann, and Clark, 1930: 181 (synonym of *C. macularius*). Evermann and Clark, 1931: 55 (synonym of *C. macularius*).

Lucania browni.—Jordan and Richardson, 1907: 319, 1 fig. (original description; habitat; hot spring on eastern edge of the salt lake [= Laguna Salada] in northeastern Lower California). MacDougal, 1907: 18-19 (habitat; resistance to temperature and high salinity; same locality). Hogg, 1932: 29-30, 32-33, 1 fig. (habitat; 100 miles north of Elko, Nevada [undoubtedly erroneous]; Laguna Salada; [fig., page 31, is more likely of *C. nevadensis* from the Death Valley region]).

Cyprinodon browni.—Jordan, 1924: 23 (characters; comparison with *C. macularius* and *C. californiensis*; *Lucania browni* in synonymy; Thermal, and wells about Indio, California). Hubbs, 1926: 6 (genus).

MATERIAL EXAMINED

ARIZONA.—Gila River, 2 miles below Dome, U.M.M.Z. No. 94863 (21); C. L. Hubbs and L. P. Schultz, Sept. 10, 1926. Salt River, between Phoenix and Tempe, U.M.M.Z. No. 94869 (23); C. L. Hubbs and L. P. Schultz, Sept. 11, 1926. Rillito Creek, near Tucson, S.U. No. 21267 (18); U. S. Fish Commission. Monkey Spring, near Patagonia, Santa Cruz Co.,

U.M.M.Z. No. 125050 (229); C. L. Hubbs and family, Sept. 7, 1938.

CALIFORNIA.—Salton Sea, U.M.M.Z. No. 64212 (24); W. F. Thompson, Jan. 31, 1920. Salton Sea at Date Palm Beach, 8 miles south of Mecca, Riverside Co., U.M.M.Z. Nos. 131745 and 133169 (441); R. R. and R. G. Miller, May 25, 1939, and July 29, 1940. Knoll Spring,² about 4 miles southwest of Dos Palmas Spring, Riverside Co., U.M.M.Z. No. 132916 (41); R. R. and R. G. Miller, Dec. 28, 1938. Spring-fed tank, southeast of Dos Palmas Spring, Riverside Co., U.M.M.Z. Nos. 132917 and 133168 (397); R. R. and R. G. Miller, May 23, 1937, and May 24, 1939. Shoreline Spring,² just east of Dos Palmas Spring, Riverside Co., U.M.M.Z. Nos. 132918–19 (39); R. R. and R. G. Miller, May 22, 1937, and Dec. 29, 1938. Carrizo Creek, just above junction with San Felipe Creek, Imperial Co., U.M.M.Z. No. 132920 (179); R. R. Miller, June 18, 1938. Wash below Harper Well, about 5 miles west of Kane Springs, Imperial Co., U.M.M.Z. Nos. 132922–24 (360); R. R. Miller and S. B. Ward, June 5, 1938; R. R. Miller, June 18, 1938; and R. G. Miller, June 18, 1938. San Felipe Creek, just above junction with Carrizo Creek, Imperial Co., U.M.M.Z. No. 132927 (200); R. R. and R. G. Miller, Dec. 27, 1938. San Felipe Creek, at mouth of wash below Harper Well, Imperial Co., U.M.M.Z. No. 132928 (150); R. R. Miller, June 19, 1938. Salton Sea, east of Kane Springs, Imperial Co., U.M.M.Z. No. 133029 (30); R. B. Cowles, June 24, 1934. Sink pool 12 miles north-northeast of Westmoreland, Imperial Co., U.M.M.Z. No. 133143 (964); R. G. Miller, Jan. 30, 1940. Artesian-fed reservoir on Wise Ranch, about 3 miles south of Mecca, Riverside Co., U.M.M.Z. No. 133172 (320); R. R. and R. G. Miller, May 25, 1939. Desert Wells, San Diego [= Colorado Desert], S.U. No. 1039 (25); C. R. Orcutt. Fish Springs, Colorado Desert, Imperial Co., S.U. (90); Stoddard and Hyatt.

MEXICO.—Pozo del Tule, along northwestern edge of Laguna Salada, about 23 miles west-southwest of Mexicali, Lower California, U.M.M.Z. No. 133074 (266); R. G. Miller, Jan. 7, 1940.

² So named by me. Not indicated on maps.

Pozo del Cerro Prieto, about 34 miles south of Mexicali, Lower California, U.M.M.Z. No. 133075 (423); R. G. Miller, Jan. 8, 1940. Rancho Agua Caliente (not the town of the same name), 3 miles southeast of Cerro Prieto, Lower California, U.M.M.Z. No. 133140 (1340); R. G. Miller, Jan. 29, 1940. Laguna about 5 road miles east of Rancho Agua Caliente, Lower California, U.M.M.Z. No. 133141 (423); R. G. Miller, Jan. 29, 1940. Pool 2 miles south and $3\frac{1}{2}$ miles east of Rancho Agua Caliente, Lower California, U.M.M.Z. No. 133142 (1020); R. G. Miller, Jan. 29, 1940. Sonoyta River Valley, 15 miles west of Sonoyta, Sonora, U.M.M.Z. No. 133243 (109); P. M. Blossom, April 26, 1933. La Salada, Sonoyta River Valley, 21 miles west of Sonoyta, Sonora, U.M.M.Z. No. 138918 (57); Seth B. Benson, Jan. 6, 1937. El Doctoro, Sonora, about 66 miles south of Yuma, Arizona, U.M.M.Z. No. 138919 (167); R. G. Miller, March 7, 1940. Lerdo, on the lower Colorado River, Sonora, S.U. Nos. 3831 and 5344 (90); C. H. Gilbert.

RANGE

The basin of the lower Colorado and Gila rivers and the Salton Sea, from southern Arizona to southeastern California and eastern Lower California, and the Sonoyta River of northern Sonora, Mexico.

Cyprinodon nevadensis Eigenmann and Eigenmann

Cyprinodon nevadensis.—Eigenmann and Eigenmann, 1889: 270 (original description; "Saratoga Spring," in the south arm of Death Valley, Inyo County [=San Bernardino Co.], California). Jordan, 1924: 23 (regarded as probably not distinct from *C. macularius*). Jordan, Evermann, and Clark, 1930: 181 (Death Valley; literature record). Evermann and Clark, 1931: 21, 56 ("probably not different from *Cyprinodon macularius*," but listed as a valid species; synonymy; Saratoga Springs, Death Valley). Schrenk-eisen, 1938: 186 (questionably distinct from *C. macularius*). Shapovalov, 1941: 444 (provisionally recognized).

Cyprinodon macularius (misidentification).—Gilbert, 1893: 232-33 (in part; characters; coloration; habitat; food; Saratoga Springs in Death Valley, Amargosa Creek, Medbury Spring [=spring-fed creek at Shoshone, Inyo Co.], and Amargosa Desert—all in California,

and Ash Meadows in Amargosa Desert, Nevada). Evermann and Rutter, 1895: 475-86 (in part). Garman, 1895: 24-25 (in part; description; range). Jordan and Evermann, 1896: 314 (range, in part; southern Nevada). Jordan and Evermann, 1896-1900: 671, 674 (in part; characters; description; southern Nevada). Regan, 1907: 83, 85 (in part; Nevada record only). Waring, 1915: 137 (Saratoga Springs, Death Valley). Evermann, 1916: 62-63 (in part; Saratoga Springs). Snyder, 1917: 202 (range, in part). Thompson, 1929: 60 (Saratoga Springs). Jordan, Evermann, and Clark, 1930: 181 (range, in part). Wales, 1930: 62, 69-70 (after Gilbert; Ash Meadows, Nevada; stream near Shoshone, and Saratoga Springs, California; comparison with *Cyprinodon diabolis*). Hogg,³ 1932: 30, 32, 2 figs. (habitat; comparison; "Saratoga Spring"). Blackwelder, 1933: 469, 470 (range, in part; relic waters of the Death Valley region). Anonymous, 1935: 17 (in part; Saratoga Springs). Ward, 1936: 135-42, 1 fig. (habitat; life colors; habits; aquarium use; origin of Death Valley population; in part; Saratoga Springs). Jaeger, 1938: 74 (in part; Mohave Desert, in and near Death Valley). Mac Donagh, 1938: 83-84 (after Ward). Miller, 1938: 147 (association with *Apocope* [= *Rhinichthys*] *nevadensis*; Amargosa River system from Ash Meadows, Nevada, to Tecopa and Amargosa River, California). Schrenkeisen, 1938: 186 (range, in part). Sumner and Sargent, 1940: 46 (springs of eastern California and neighboring parts of Nevada). Curry, 1942: 105 (range, in part; Death Valley).

*Cyprinodon macularius baileyi*⁴ (misidentification).—Hogg, 1932: 29, 31-32, 2 figs. (comparison; Tecopa Hot Spring⁵ [Inyo Co.], California).

MATERIAL EXAMINED

CALIFORNIA.—Saratoga Springs (main spring pool), Death Valley, San Bernardino Co., U.M.M.Z. Nos. 132934-35 and 133159 (340); R. R. and R. G. Miller, June 6, 1937; R. G. and L. B. Miller, March 20, 1937; and R. R. and R. G. Miller, May 16, 1939. Spring-fed creek at Shoshone, Inyo Co., U.M.M.Z. No. 132936 (657); R. R. and R. G. Miller, Jan. 8, 1939. Spring about $\frac{1}{4}$ mile north of Tecopa, Inyo Co., U.M.M.Z. No. 132938

³ This popular article contains much unauthentic information.

⁴ Described from Pahranaagat Valley, Nevada; = *Crenichthys baileyi* (see Hubbs and Miller, 1941: 3).

⁵ My father and I have visited this hot spring but have never seen fish in it. There are fish in the cooler outlet which flows into Amargosa River.

(14); R. R. Miller, June 6, 1937. Amargosa River, about 8 miles northwest of Saratoga Springs, San Bernardino Co., U.M.M.Z. Nos. 132939 and 133177 (1655); R. R. and R. G. Miller, April 8, 1939, and June 4, 1939. Amargosa River at Tecopa, Inyo Co., U.M.M.Z. No. 133160 (164); R. R. and R. G. Miller, May 16, 1939.

NEVADA (all in Ash Meadows, Nye Co.).—Isaac Ranch, U.M.M.Z. No. 132899 (22); R. R. and R. G. Miller, June 6, 1937. Big Spring, U.M.M.Z. No. 132900 (17); R. R. and R. G. Miller, June 5, 1937. Forest Pool, U.M.M.Z. Nos. 132902 and 132905 (203); R. R. and R. G. Miller, Jan. 8, 1939, and June 6, 1937. Spring on Tubb Ranch, U.M.M.Z. Nos. 132906 and 133153 (49); R. R. and R. G. Miller, Jan. 9, 1939; F. B. Sumner and M. C. Sargent, April 30–May 2, 1939. Spring and reservoir on Lovell Ranch, U.M.M.Z. Nos. 132908 and 133154 (310); R. R. and R. G. Miller, Jan. 9, 1939; F. B. Sumner and M. C. Sargent, May 1, 1939. King's Spring ("Point of Rocks Spring" locally), spring source and outlet ditches, U.M.M.Z. Nos. 132909–10 (533); R. R. and R. G. Miller, Jan. 10, 1939. Eastern Spring, U.M.M.Z. No. 133189 (24); R. R. Miller, May 17, 1939. "Ash Meadows, Nevada," S.U. No. 681 (8); T. S. Palmer, March 4, 1891.

RANGE

Springs and streams of the desert in the Amargosa River basin, from Ash Meadows, Nye County, Nevada, to Saratoga Springs and Amargosa River in the southeastern arm of Death Valley, San Bernardino County, California.

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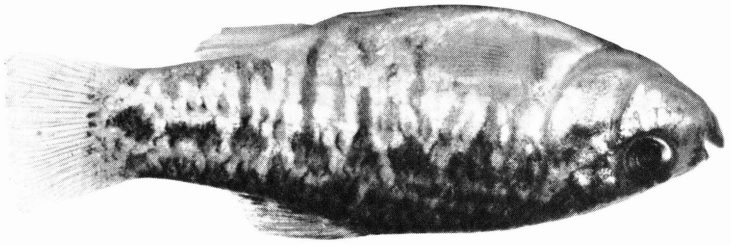
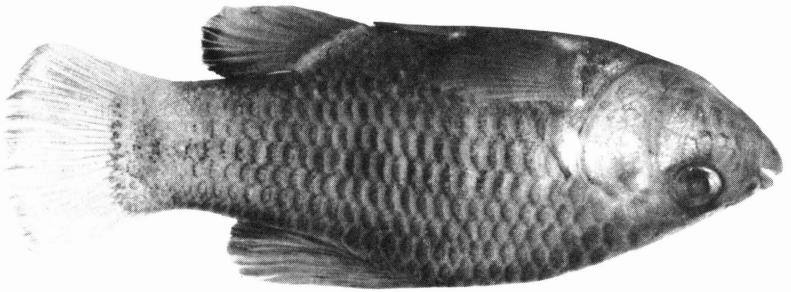
Robert R. Miller

PLATE I

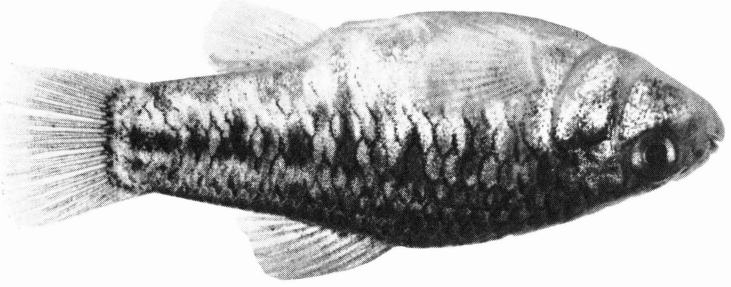
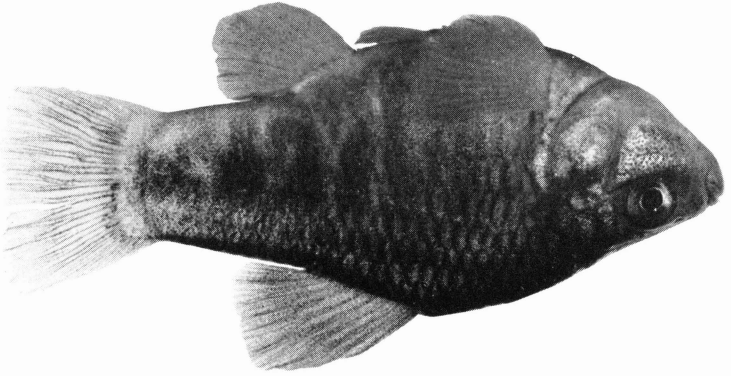
Cyprinodon macularius

Photographs by Clarence Flaten

- FIG. 1. Adult male, 39 mm. in standard length, from Salton Sea at Date Palm Beach, Riverside County, California.
- FIG. 2. Adult female, 38 mm., from same locality.
- FIG. 3. Adult male, 37 mm., from Pozo del Tule, Laguna Salada, Lower California, Mexico.
- FIG. 4. Adult female, 37 mm., from same locality.



FIGS. 1-2



FIGS. 3-4

Robert R. Miller

PLATE II

Cyprinodon macularius

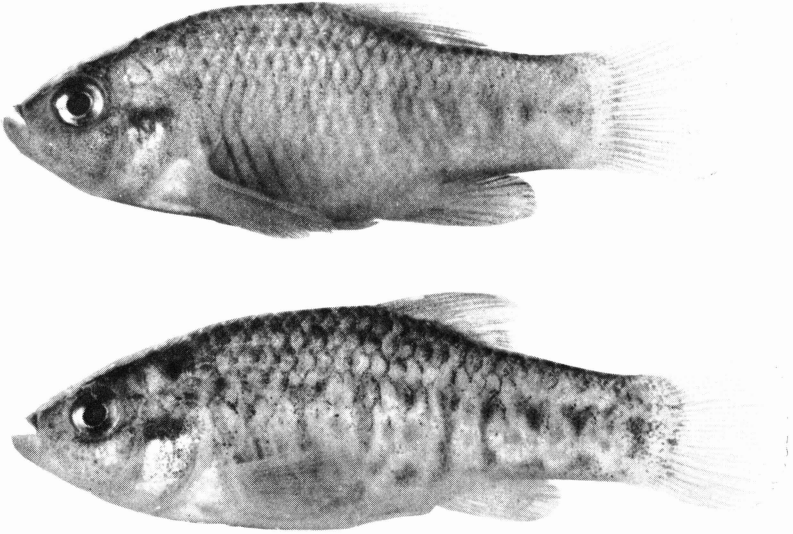
Photographs by Clarence Flaten

FIG. 1. Adult male, 32 mm., from Gila River below Dome, Yuma County, Arizona.

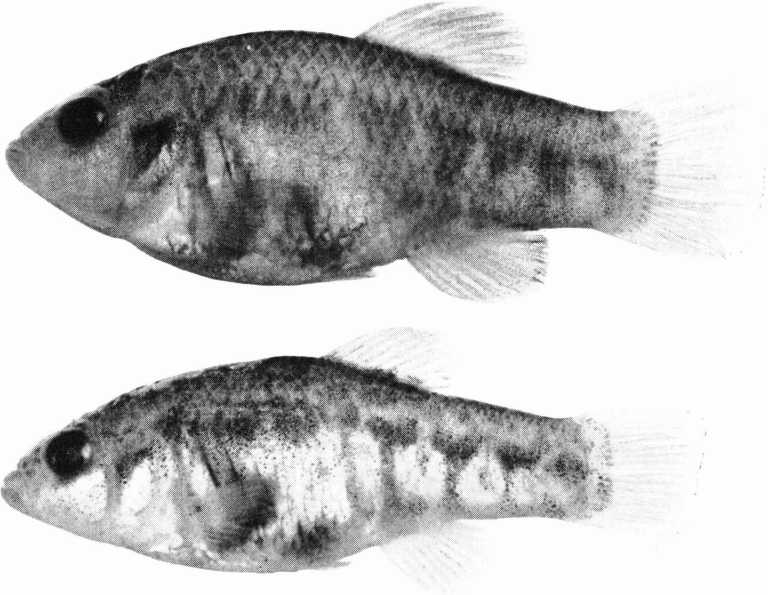
FIG. 2. Adult female, 34 mm., from same locality.

FIG. 3. Adult male, 37 mm., from La Salada, Sonoyta River Valley, Sonora, Mexico.

FIG. 4. Adult female, 35 mm., from same locality.



Figs. 1-2



Figs. 3-4

Robert R. Miller

PLATE III

Cyprinodon nevadensis

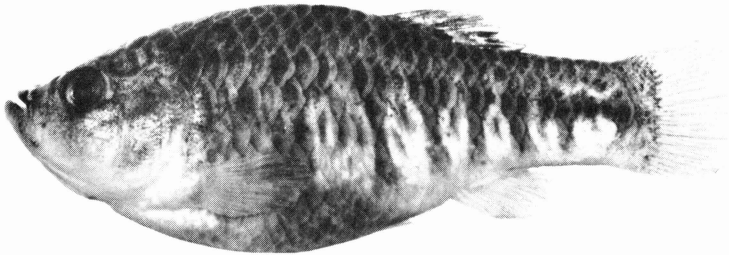
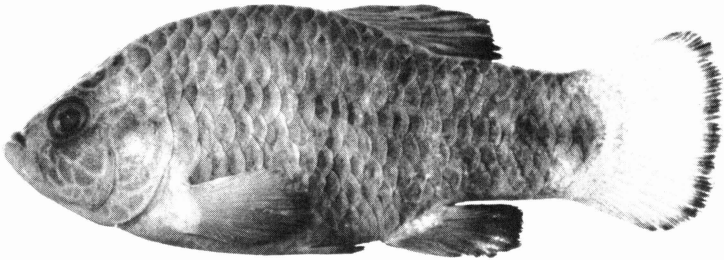
Photographs by Clarence Flaten

FIG. 1. Adult male, 38 mm., from Amargosa River in Death Valley, San Bernardino County, California.

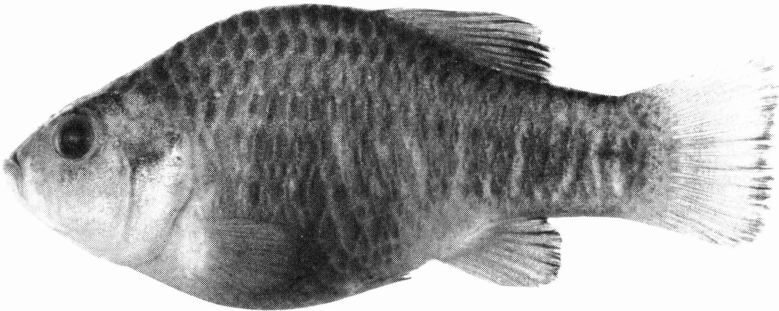
FIG. 2. Adult female, 39 mm., from same locality.

FIG. 3. Adult male, 43 mm., from Saratoga Springs in Death Valley, San Bernardino County, California.

FIG. 4. Adult female, 41 mm., from same locality.



FIGS. 1-2



FIGS. 3-4

Robert R. Miller

PLATE IV

Cyprinodon nevadensis

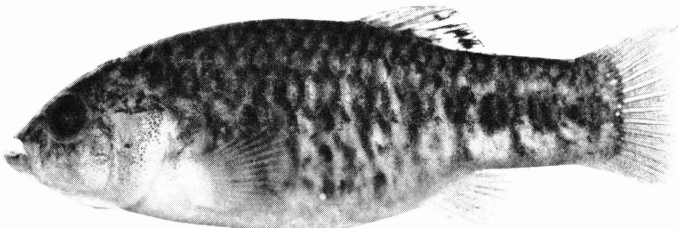
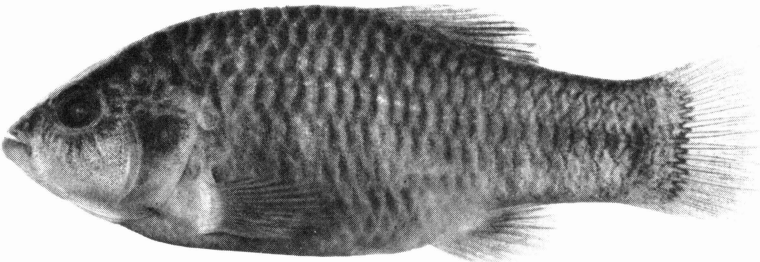
Photographs by Clarence Flaten

FIG. 1. Adult male, 42 mm., from spring-fed creek at Shoshone, Inyo County, California.

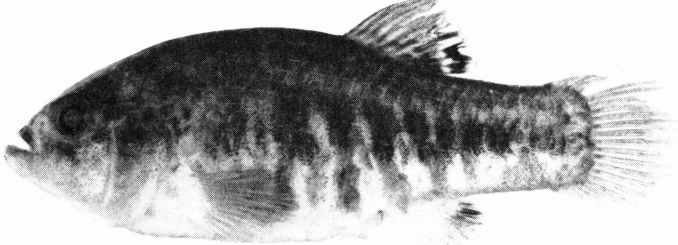
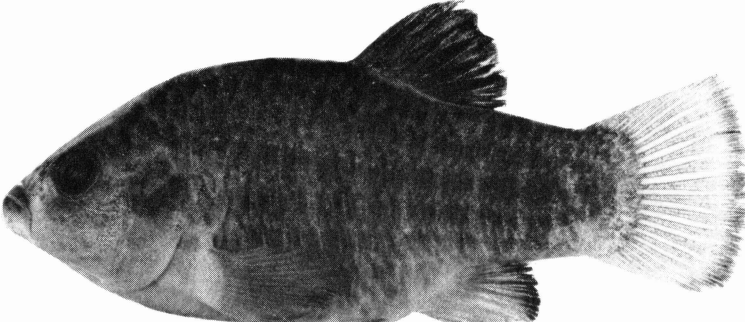
FIG. 2. Adult female, 38 mm., from same locality.

FIG. 3. Adult male, 38 mm., from Forest Pool, Ash Meadows, Nye County, Nevada.

FIG. 4. Adult female, 35 mm., from same locality.



FIGS. 1-2



FIGS. 3-4

Robert R. Miller

PLATE V

Scales of *Cyprinodon macularius* $\times 44.3$

Photographs by William C. Beckman

FIG. 1. From an adult male, 34 mm. in standard length, from Salton Sea at Date Palm Beach, Riverside County, California.

FIG. 2. From an adult male, 33 mm., from Wise Ranch, south of Mecca, Riverside County, California.

FIG. 3. From an adult male, 34 mm., from a laguna near Rancho Agua Caliente, about 35 miles south of Mexicali, Lower California, Mexico.

FIG. 4. From an adult female, 33 mm., from La Salada, Sonoyta River Valley, Sonora, Mexico.



FIG. 1

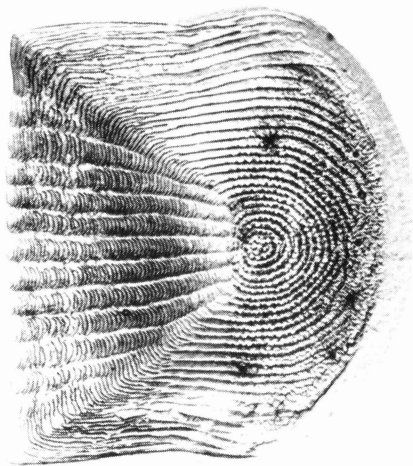


FIG. 2

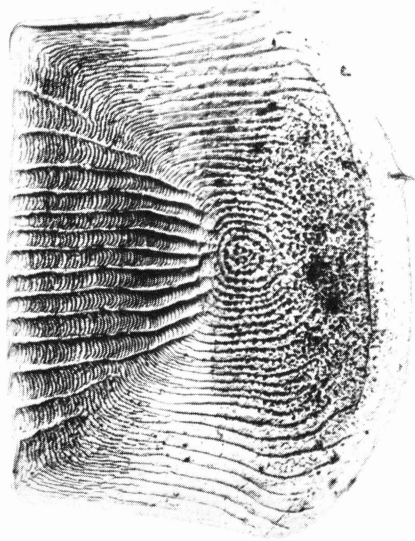


FIG. 3

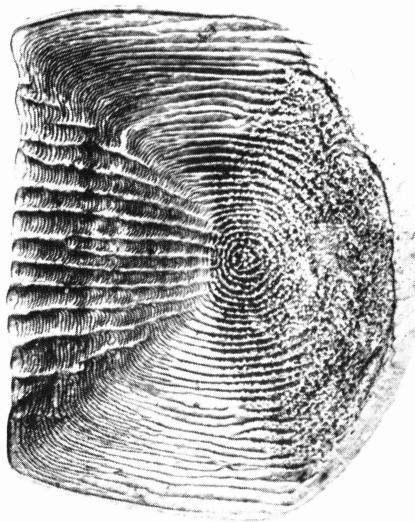


FIG. 4

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PLATE VI

Scales of *Cyprinodon nevadensis* $\times 44.3$

Photographs by William C. Beckman

FIG. 1. From an adult male, 41 mm., from Saratoga Springs in Death Valley, San Bernardino County, California.

FIG. 2. From an adult female, 30 mm., from Amargosa River at Tecopa, Inyo County, California.

FIG. 3. From an adult male, 34 mm., from spring-fed creek at Shoshone, Inyo County, California.

FIG. 4. From an adult male, 33 mm., from Lovell Ranch, Ash Meadows, Nye County, Nevada.

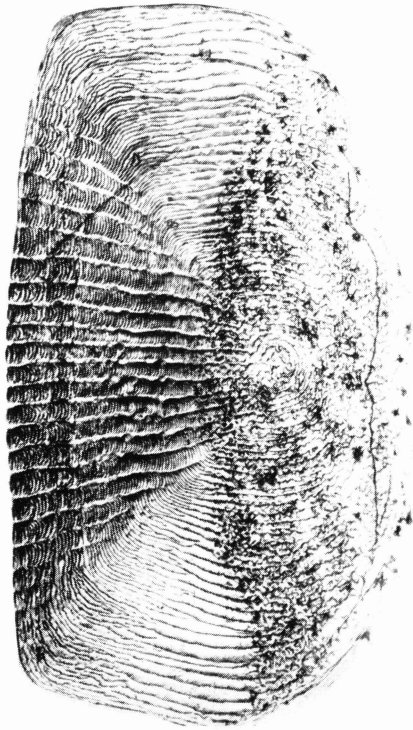


FIG. 1



FIG. 2



FIG. 3



FIG. 4

Robert R. Miller

PLATE VII

Enlargements of the central region of the scales
of two species of *Cyprinodon*

Photographs by William C. Beckman

- FIG. 1. *Cyprinodon macularius*. From the scale shown in Plate V,
Fig. 2. $\times 90$.
FIG. 2. *Cyprinodon nevadensis*. From the scale shown in Plate VI,
Fig. 3. $\times 90$.



FIG. 1

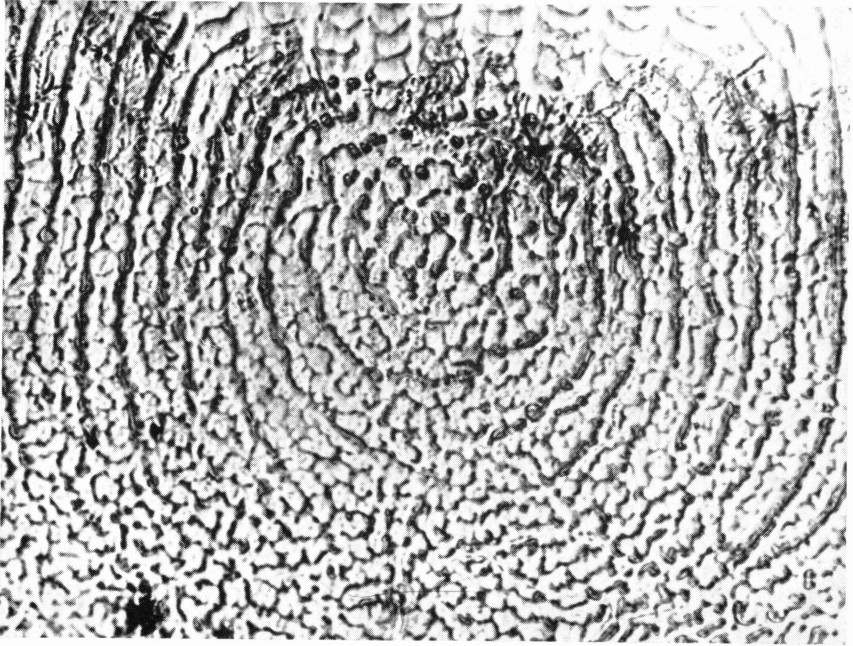


FIG. 2