



MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 68

THE CYPRINODONT FISHES OF
THE DEATH VALLEY SYSTEM
OF EASTERN CALIFORNIA
AND SOUTHWESTERN
NEVADA

BY
ROBERT R. MILLER

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS
APRIL 20, 1948

CONTENTS

	PAGE
INTRODUCTION	7
Acknowledgments	8
MATERIALS AND METHODS	8
Methods Used in Counting	9
Methods Used in Measuring	11
Character Index	14
Statistical Computations	14
DESCRIPTIVE PHYSIOGRAPHY AND RECENT HYDROGRAPHY	16
PLEISTOCENE HYDROGRAPHY	18
GENUS <i>Cyprinodon</i> LACÉPÈDE	20
<i>Cyprinodon macularius</i> Baird and Girard	22
<i>Cyprinodon nevadensis</i> Eigenmann and Eigenmann	22
<i>Cyprinodon nevadensis nevadensis</i> Eigenmann and Eigenmann	24
<i>Cyprinodon nevadensis amargosae</i> , new subspecies	28
<i>Cyprinodon nevadensis calidae</i> , new subspecies	36
<i>Cyprinodon nevadensis shoshone</i> , new subspecies	39
<i>Cyprinodon nevadensis mionectes</i> , new subspecies	44
Races of <i>Cyprinodon nevadensis mionectes</i>	48
<i>Cyprinodon nevadensis pectoralis</i> , New Subspecies	58
<i>Cyprinodon diabolis</i> Wales	83
<i>Cyprinodon salinus</i> Miller	86
<i>Cyprinodon radiosus</i> , New Species	87
GENUS <i>Eupetrichthys</i> GILBERT	99
<i>Eupetrichthys merriami</i> Gilbert	101
<i>Eupetrichthys latos</i> , New Species	101
<i>Eupetrichthys latos latos</i> , New Subspecies	103
<i>Eupetrichthys latos pahump</i> , New Subspecies	104
<i>Eupetrichthys latos concavus</i> , New Subspecies	105
EXPERIMENTAL WORK ON <i>Cyprinodon</i>	111
Description of Pools	112
Temperature	113
Food	113
Interspecific Crosses	113
Intraspecific Crosses	115
Constancy Experiments	116
Conclusions from Experimental Studies	122
CONSIDERATIONS OF GENERAL BIOLOGICAL SIGNIFICANCE	126
Size of Populations	126
Isolation	128
Relation of Characters to Environment	129
Temperature	130
Salinity	145
Stability of Experimentally Raised Pure Stocks	145
Rate of Speciation and Extent of Differentiation	148
SUMMARY	149
LITERATURE CITED	152

ILLUSTRATIONS

PLATES

(Plates I-XV follow page 155.)

PLATE

- I. *Cyprinodon nevadensis nevadensis* Eigenmann and Eigenmann.
Fig. 1. Adult male.
Fig. 2. Adult female.
- II. Enlarged scale center of *C. n. nevadensis*.
- III. *Cyprinodon nevadensis amargosae*, new subspecies.
Fig. 1. Adult male.
Fig. 2. Adult female.
- IV. *Cyprinodon nevadensis shoshone*, new subspecies.
Fig. 1. Adult male paratype.
Fig. 2. Adult female paratype.
- V. *Cyprinodon nevadensis mionectes*, new subspecies.
Fig. 1. Adult male.
Fig. 2. Adult female.
- VI. *Cyprinodon nevadensis pectoralis*, new subspecies.
Fig. 1. Adult male paratype.
Fig. 2. Adult female paratype.
- VII. *Cyprinodon diabolis* Wales.
Fig. 1. Adult male.
Fig. 2. Adult female.
- VIII. *Cyprinodon salinus* Miller.
Fig. 1. Adult male holotype.
Fig. 2. Adult female paratype.
- IX. *Cyprinodon radiosus*, new species.
Fig. 1. Adult male paratype.
Fig. 2. Adult female holotype.
- X. Two species of *Empetrichthys*.
Fig. 1. *E. merriami* Gilbert. Immature male.
Fig. 2. *E. latos*, new species. Immature male paratype.
- XI. Four forms of *Empetrichthys*. Top to bottom: *E. merriami* Gilbert; *E. latos concavus*, new subspecies; *E. latos pahrump*, new subspecies; *E. latos latos*, new subspecies.
- XII. Fig. 1. North Tecopa Hot Spring (right) and South Tecopa Hot Spring.
Fig. 2. Big Spring, Ash Meadows, Nye County, Nevada.
- XIII. Devil's Hole, Ash Meadows, Nye County, Nevada.
- XIV. Fig. 1. Fairbanks Spring, Ash Meadows, Nye County, Nevada.
Fig. 2. Concrete pools in Los Angeles used for experimental studies of *Cyprinodon*.
- XV. Salt Creek, Death Valley, Inyo County, California.

FIGURES IN THE TEXT

FIGURE

1. A. <i>Cyprinodon nevadensis nevadensis</i> , B. <i>Cyprinodon salinus</i>	10
2. Mandibular teeth of 3 species of <i>Cyprinodon</i> : A. <i>Cyprinodon macularius</i> , B. <i>Cyprinodon nevadensis</i> , C. <i>Cyprinodon salinus</i>	88
3. Correlation of body circumference scales with temperature in 2 species of <i>Cyprinodon</i>	131
4. Correlation of number of pelvic fin rays with temperature in 2 species of <i>Cyprinodon</i>	132
5. Correlation of body circumference scales in <i>Cyprinodon nevadensis</i> with the temperatures of spring sources and outlets	135

MAPS

(Maps 1-3 follow Plate XV.)

MAP

1. Maximum extent of the Pleistocene waters of the southern Great Basin and adjacent areas.
2. Recent hydrography of the southern Great Basin and adjacent areas.
3. Ash Meadows and vicinity.

THE CYPRINODONT FISHES OF THE DEATH VALLEY SYSTEM OF EASTERN CALIFORNIA AND SOUTHWESTERN NEVADA*

INTRODUCTION

THE fish fauna of the arid American West is characterized by relict populations limited in number of species but rich in material for the student of evolution. In order to understand the present distribution of this fauna it is necessary to study the Pleistocene geology of the region, for the Recent fish life reached the now widely separated springs and creeks when the desert was a well-watered land. In what is now one of the driest parts of the Great Basin, in eastern California and southwestern Nevada, several deep lakes and large streams existed, connecting the many isolated basins which now characterize this region (Maps 1 and 2). This former drainage basin has been named the Death Valley system (Miller, 1943b: 69). Its continuity is demonstrated not only by the physiographic evidence but also by a study of the relict fish populations scattered throughout the area. The segmentation which the drainage has undergone has resulted in the separation of these populations, and since the basins were cut off from each other at different times, the fishes have been isolated for varying periods, and all the minor systematic categories—races, subspecies, and species—are now represented among the remnant populations.

The present work has a dual purpose: first to classify the cyprinodont fishes of the Death Valley system and discuss their ecology, distribution, speciation, and probable relationships; and second, to correlate the Recent distribution of the fish fauna with the Pleistocene hydrography of the area. A detailed discussion of the Pleistocene connections and their zoogeographical significance has already been published (Miller, 1946), and only a brief summary is given herein. The fossil fish fauna has been treated separately (Miller, 1945).

Only 3 genera of cyprinodont fishes are represented in the Recent fauna of the interior and the Colorado River basins: *Cyprinodon*, *Empetrichthys*, and *Crenichthys*. Two species of *Fundulus* are known from the Pacific coast, and fossils referable to this genus have been found in the western Great Basin. The present study treats in detail the species, subspecies, and races of *Cyprinodon* and *Empetrichthys* inhabiting the Death Valley system. Two new species and 7 new subspecies are recognized. The remaining genus, *Crenichthys*, diagnosed by Hubbs (1932) and briefly re-

* A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan in 1944. The material presented here represents approximately two-thirds of the original.

viewed by Hubbs and Miller (1941: 1-2), remains to be analyzed for sub-specific and racial variation.

ACKNOWLEDGMENTS

During the course of this study, which extended over a period of 8 years, I have received financial aid, encouragement, and assistance from many individuals and institutions. The late Professor Joseph Grinnell and Professor Alden H. Miller, of the Museum of Vertebrate Zoology, Berkeley, California, encouraged the early work. Specimens were loaned from Stanford University by Professor George S. Myers and Miss Margaret Storey, and from the United States National Museum by Dr. Leonard P. Schultz. Beginning in 1939, financial support was given by the Museum of Zoology, University of Michigan, and in 1940 and 1942 by the Rackham School of Graduate Studies of this University. The late Miss Grace Eager, accomplished artist of the University of Michigan Museum of Zoology, made the accurate drawings, and Norman J. Wilimovsky served ably as research assistant in tracing the maps. Through the courtesy of Dr. Carl L. Hubbs, Miss Elizabeth Kampa made the excellent graphs (Figs. 3-5). I am also indebted to C. S. Scofield, Principal Agriculturist of the Rubidoux Laboratory of the United States Department of Agriculture at Riverside, California, for allowing me to publish the water analyses made by that laboratory. The United States National Park Service has extended the fullest co-operation in the field work in Death Valley National Monument. I am deeply grateful to Professor Carl L. Hubbs, formerly Curator of Fishes in the Museum of Zoology, University of Michigan, and now Professor of Biology at the Scripps Institution of Oceanography, for his generous aid, encouragement, and invaluable advice. I also owe a debt of gratitude to my father, Ralph G. Miller, who has not only constantly aided me in the field work, but has also made innumerable collecting trips into the desert solely for my benefit. To my wife, Frances H. Miller, much credit is due for aid in the statistical computations and for typing the many drafts of the manuscript. Publication of this study was made possible by a grant from the Horace H. Rackham School of Graduate Studies.

MATERIALS AND METHODS

This systematic study of desert fishes is based almost wholly on the collections deposited in the University of Michigan Museum of Zoology (U.M.M.Z.). Between 1936 and 1942 more than 10,000 specimens of *Cyprinodon* and *Empetrichthys* were collected during personal trips, expeditions from the University of Michigan, and by Ralph G. Miller. Specimens deposited in the United States National Museum (U.S.N.M.) and in the Stanford Natural History Museum (S.N.H.M.) have also been examined.

To enable others to use the measurements and enumerations of characters and to allow the accumulation of comparable data, the methods of counting and measuring which have been employed in the present study are stated in detail.

METHODS USED IN COUNTING

FIN RAYS.—The last ray of the dorsal and anal fins is always regarded as a double ray, divided to the base of the fin. In this respect, my counts for these fins of *Cyprinodon* are 1 less than those given by Wales (1930), who counted every element. All of the rays of both pectoral fins are counted, including the often minute rudiments along the lower edge of the fin; the lowermost ray is frequently joined to its neighbor and some dissection may be necessary to reveal it. Similarly, each ray of both pelvic fins is enumerated, with special caution to note the innermost one, which is rather frequently represented as a mere sliver of cartilage or a very minute stub. The count for the caudal fin is the number of principal rays, the branched rays plus 2 (1 unbranched ray on either side).

In samples from salty water or those including breeding males, removal of the surface mucous on the fins greatly aids in counting the rays. I have found that by keeping the fins wet and using reflected daylight very accurate results are obtained.

SCALES.—The scales in the lateral series are counted from the first 1 in contact with the shoulder girdle to the 1 at the structural base of the caudal fin. The first scale counted lies just above and a little behind the opercular angle (Fig. 1). The last 1 is determined by moving the tail back and forth and noting where the crease so formed is in contact with the scale. If the flexure lies near the middle of the scale or posteriorly, the scale is included in the count; otherwise it is excluded. Care should be exercised to note whether a scale is regenerated, for I have found in *Cyprinodon* that a single regenerated scale often occupies the space formerly covered by 2 scales. Counting such a scale results in a count that is too low.

In the cyprinodonts, which lack a definite lateral line, the dorsal to pelvic count is made from the scale (usually small) lying just in the angle of the pelvic fin to the 1 just beside (but not anterior to) the origin of the dorsal fin. The dorsal to anal count is made from the small scale (or scales) lying in the angle of the anal fin to this same scale (Fig. 1).

The predorsal count involves the scales which intersect a straight line along the back between the snout and the origin of the dorsal fin. The first scale (or, usually, a pair of 2 very small scales lying side by side and occasionally difficult to see) lies on the snout, the fourth scale (usually enlarged and nonimbricated) almost invariably lies partly over and partly behind the posterior rim of the orbit. All scales which definitely, unequivocally

cally overlap the mid-line of the back on their exposed surfaces are counted. If it is not certain that 2 closely approaching scales definitely overlap and hence cross the mid-line, they are not counted. Certain modifications are followed when necessary, such as shifting the mid-line when otherwise an obviously incorrect count (usually too high) would result.

The scale count around the body begins with the eighth scale of the lateral series (the seventh in *C. radiosus*), and is made in a zigzag fashion,

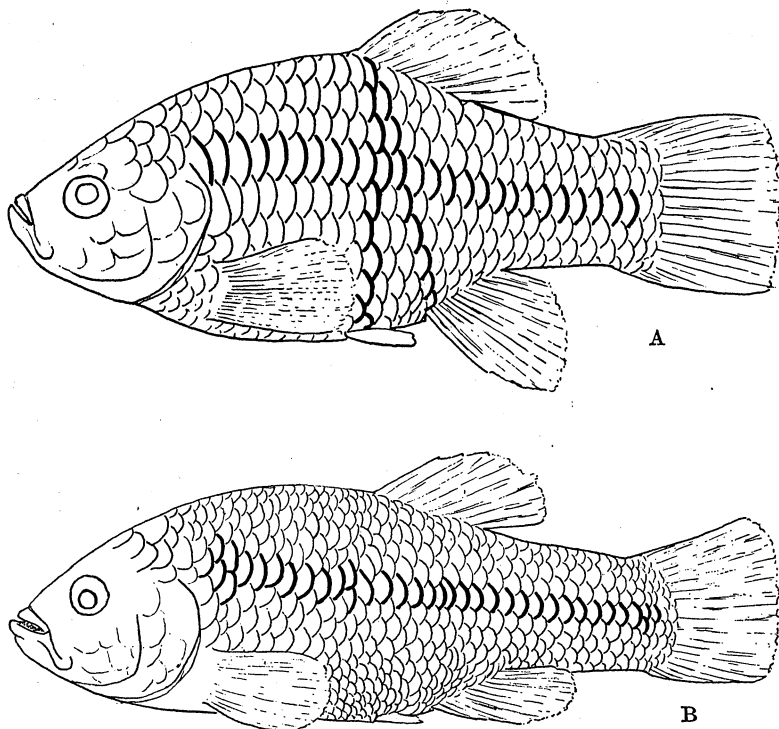


FIG. 1. Sketch of 2 species of *Cyprinodon*, to illustrate methods of counting scales in lateral, dorsal to pelvic, and dorsal to anal series. Drawn by Grace Eager. A. *Cyprinodon nevadensis nevadensis*: 26 lateral scales. B. *Cyprinodon salinus*: 33 lateral scales.

passing over the back about 1 scale row in front of the dorsal fin, and over the abdomen about 1 scale row in front of the pelvic fins.

The scales around the peduncle are counted according to the method followed for the count around the body; the count is started with about the sixth from the last scale in the lateral series.

SCALE RADII.—The scale radii are enumerated on the seventh to ninth scale of the lateral series on the right side, of adult specimens only. All

radii are counted, including the very minute ones. Injured or regenerated scales are not used.

GILL RAKERS.—The gill rakers of the first branchial arch are enumerated without a separate tabulation for the upper and lower limbs. All rudiments at either end of the arch are included in the count, even those that require high magnification and bright illumination to see.

HEAD PORES.—The lateral line system of pores on the head is of some taxonomic value in cyprinodonts. The preopercular pores are those lying along the lower and upper arms of the preopercle; the preorbital, those along the preorbital bone on the side of the snout; and the mandibular, those along the mandibles. The counts are recorded separately for each side, but are added together in the final presentation.

Reliability of Counts

All of the fin-ray counts are clear-cut, after due care is exercised in discerning the minute rays of the pectoral and pelvic fins. There may be some error in the counts for these 2 fins, but it is believed to be insignificant. The scale counts are generally precise, the least accurate being those of the predorsal and dorsal to anal series. The dorsal to anal count was mainly included as a basis for comparison of species of *Cyprinodon* with *C. diabolis*, which lacks pelvic fins. Only rarely is there some question of the number of scales in the lateral series in *Cyprinodon*, but this count is more difficult in *Empetrichthys*. Gill raker and scale radii counts offer no real difficulty if the precautions of proper light and sufficient magnification are exercised. The preopercular and preorbital pores are usually readily distinguishable when quickly dried by a jet of compressed air after the head of the fish has been dipped in liquid. The pores are best seen on larger individuals; fish smaller than 25 mm. in standard length were used only when necessary to fill the series. Rather uncommonly, it is difficult to tell whether a pore is open or not, and hence whether it should be counted.

The higher of 2 possible counts was always recorded, except in the predorsal scale count of *Cyprinodon*.

METHODS USED IN MEASURING

All measurements are made on the left side of the fish except the following: the preorbital margin to preopercular angle, eye margin to preopercular angle, upper jaw length, and mandible length, all of which were measured on the right side. On occasion it is necessary to measure a structure on the right side, for example, when the left pectoral is injured. The longer pelvic fin is measured.

The fish is not allowed to dry out, but is kept in good condition by occasionally immersing or spraying it with fluid. This practice is particularly

important with fin measurements. All fins are dipped in fluid just before they are measured. Good light is used, and the measurements are made, with very few exceptions, under a binocular microscope at a magnification which just includes the distance to be measured.

The calipers used are a precision instrument distributed by Glogau and Co. and record distances to 0.1 mm. Estimates to 0.01 are possible. Each fish measured is tagged. Considerable practice is required for accurate work, and all measurements on any particular genus should be made during one period. Thus, unconscious changes in techniques of measuring will be avoided.

STANDARD LENGTH.—The distance from the tip of the snout to the structural base of the caudal fin. The anterior limit of this measurement is the tip of the premaxillaries, in retracted position. Whenever the length is mentioned in this paper it refers to standard length.

PREDORSAL LENGTH.—Measured from the base of the first dorsal ray to the tip of the premaxillaries.

PREPELVIC LENGTH.—Measured from the inner base of the pelvic fin to the tip of the premaxillaries.

ANAL ORIGIN TO CAUDAL BASE.—The distance between the origin of the first anal ray and the structural base of the caudal fin on the mid-line of the body.

BODY, GREATEST DEPTH.—The greatest vertical distance between the back and the ventral surface of the abdomen, usually measured over the pelvics.

BODY, GREATEST WIDTH.—The greatest horizontal distance between the sides of the body, measured over the back usually just behind the head.

HEAD, LENGTH.—Measured from the posterior margin of the opercle (of the opercular flap when present) to the tip of the retracted premaxillaries.

HEAD, DEPTH.—The greatest vertical distance from the isthmus to the top of the head directly above the upper corner of the opercle.

HEAD, WIDTH.—The greatest horizontal distance across the opercles, measured from above.

CAUDAL PEDUNCLE, LENGTH.—The distance between the base of the last ray of the anal fin and the structural base of the caudal fin on the mid-line (in the fishes studied there is little or no membrane behind the last anal ray).

CAUDAL PEDUNCLE, LEAST DEPTH.—The vertical distance across the slenderest part of the caudal peduncle.

INTERORBITAL, LEAST BONY WIDTH.—The least distance between the bony rims of the orbits (in *Cyprinodon* and *Empetrichthys* the interorbital is narrowest between the middle of the pupils). The tips of the calipers are firmly pressed against the bony rim on each side.

PREORBITAL, LEAST WIDTH.—The least distance between the fleshy rim of the preorbital bone and the fleshy rim of the orbit.

PREORBITAL MARGIN TO PREOPERCULAR ANGLE.—Measured from a point on the preopercular margin about midway between the pore at the angle of the preopercle and the next one above, to the border of the preorbital at the corner of the mouth. A jet of air was used to remove the alcohol from this border just before measuring.

EYE MARGIN TO PREOPERCULAR ANGLE.—The distance between the angle of the preopercle at the level of the angular pore to the nearest point on the fleshy orbital rim. Both this and the preceding measurement are made on the right side of the head.

OPERCLE, GREATEST LENGTH.—The greatest distance across the opercle from the preopercular rim, which is marked by the series of preopercular pores, to the edge of the membrane (when present). Usually measured near the upper angle of the opercle.

SNOUT, LENGTH.—The distance between the fleshy orbital rim and the retracted premaxillaries. This is one of the most difficult of all the measurements because the premaxillaries are so often out of position, and it is frequently difficult to estimate how far back they should be pressed.

ORBIT, LENGTH.—The greatest horizontal distance across the fleshy orbital rims. This is a very precise measurement.

MOUTH, WIDTH.—The greatest distance between the fleshy corners of the lips with the mouth closed and the premaxillaries in the retracted position.

UPPER JAW, LENGTH.—The distance between the distal end of the right maxillary and the tip of the retracted premaxillaries.

MANDIBLE, LENGTH.—The distance between the posterior end of the right mandible and the fleshy tip of the lower jaw.

DORSAL FIN AND ANAL FIN, BASAL LENGTH.—Measured forward to the structural base of the first ray. This point is determined by sliding the tip of the calipers anteriorly along the prolongation of the dorsal origin until they "hook" into the structural base.

DORSAL FIN AND ANAL FIN, LENGTH.—The length of the depressed fin from the structural base of the first ray to the tip of the longest ray or rays.

MIDDLE CAUDAL RAYS, LENGTH.—The distance between the structural base and the tips of the middle caudal rays.

PECTORAL, LENGTH OF LONGEST RAY.—The distance between the base of the pectoral fin and the longest ray or rays. To determine the basal starting point, the fin is bent forward, and the marked crease at the base is noted. The measurement is taken from this crease.

PELVIC, LENGTH OF LONGER FIN.—The distance between the structural base, determined by bending the fin forward and noting the crease, and the tip of the longest ray or rays. Unless it is obvious which fin is the longer, both are measured to determine this point.

Reliability of Measurements

Considerable practice was necessary before accurate results in measuring were obtained. When preliminary trials were made, checked, and re-checked over a short period, most of the measurements gave consistent values. Some of the most difficult of the measurements, in my experience, were the length of the snout, the width of the mouth, and the basal length of the dorsal and anal fins. When the disagreement in readings on these measurements was notable, I often made 3 readings and took the average for the result. It was only after 3 months of more or less continual measuring that I attempted to record the values for *Cyprinodon diabolis*, as in this dwarfed species the specimens measured averaged only 19 mm. in standard length. It was, for instance, difficult to measure the width of the preorbital on a fish of this size, for this distance is only about three-fourths of a millimeter.

CHARACTER INDEX

Because of the varying degree of differentiation undergone by certain populations of *Cyprinodon* and *Empetrichthys*, it is not always possible to distinguish the subspecies on the basis of single traits. Some forms differ significantly from others on the average for a number of characters, but each character alone is not sufficient to make certain their identity. The combinations of such characters lead to more precise determinations, and for this reason the character index is used.

In any combination of traits, whether they be counts or measurements or both, the total index is obtained by summing each particular value for each individual. Thus, a character index (Table X) based on the scale counts of 2 races of *Cyprinodon nevadensis shoshone* shows the relations between these 2 populations much more clearly than does any 1 of the meristic characters considered alone (Tables XXII-XXIV). This index greatly decreases the amount of overlap which occurs when only a single trait is considered, and, consequently, gives a truer picture of the actual differences which exist between these 2 races.

A historical review of the character index and a justification of its use was recently presented by Hubbs, Hubbs, and Johnson (1943: 4-6).

STATISTICAL COMPUTATIONS

The statistical computations used in the biometric analyses made in this study are given in Hubbs and Kuhne (1937). The formula for t is the conventional one,

$$t = \frac{M_1 - M_2}{\sqrt{(\sigma_{M_1})^2 + (\sigma_{M_2})^2}},$$

in which M_1 is the mean value of the particular character of one sample, and

M_2 that for the sample which is to be compared. This formula is adequate when the number in each sample is approximately equal ($N_1 = N_2$) and the standard deviations (σ) are similar, as has been recently pointed out by Hubbs and Perlmutter (1942:588-92). However, if the number of specimens in the samples to be compared differs markedly, and the standard deviations are dissimilar, the following formula, favored by Simpson and Roe (1939:192-94), is to be applied:

$$t = \frac{M_1 - M_2}{\sqrt{\frac{N_1}{N_2} \sigma_{M_1}^2 + \frac{N_2}{N_1} \sigma_{M_2}^2}}.$$

A t value of 2.5 is regarded as trustworthy, with the odds of significance 80 to 1. A value of 3.0 gives odds of significance of 369 to 1, and when the 6.0 level is reached there is only one chance in 500,000,000 that the result is due to chance alone (Hubbs and Perlmutter, 1942:586). The t values below 2.5 although less reliable, may be taken as evidence, valid to the degree indicated.

The calculation of the standard error of the mean ($\pm \sigma_M$) was not made for data which presented a markedly skewed or asymmetrical curve, since the derivation of this basic statistic assumes that the frequency curve is a "normal" one. Almost without exception, the pelvic fin rays in *Cyprinodon nevadensis* yielded frequencies which were asymmetrical (Table XVII). Hence, the standard error for these samples and the species as a whole was not computed. Such abnormal curves in biology might lead statisticians to view the systematic conclusions with suspicion, since, ordinarily, curves of this type indicate that one is dealing with combinations of different kinds of organisms or objects. There is, however, no reason to doubt that all of the fish analyzed in Table XVII belong to a single species. Moreover, that the frequency distributions as given are descriptive of each population is testified by the fact that repeated collections from the same locality give remarkably similar curves (Tables XLV-L).

On the evidence that these unusual curves are characteristic for these populations, one might justify the calculation of the standard error of the mean, if a formula for its computation could be devised, or if empirical tests should show that the observed fluctuation of the mean is consistent with expectations derived from a standard error computed by the standard formula. Wales (1930: 63-65) apparently considered such a computation permissible, and it is significant that his "P.E." (probable error of the mean) for the highly asymmetrical curve of pelvic rays at King's Spring (= Point of Rocks Spring), and the values I later obtained, are remarkably alike. My values lie within the error calculated by Wales (Table XLVII). The evidence of consistency, however, in periodic samples is not entirely

conclusive, because more samples are needed for statistical reliability. Therefore, I have thought it unwise to calculate the standard error of the mean for such types of curves.

DESCRIPTIVE PHYSIOGRAPHY AND RECENT HYDROGRAPHY

The parts of California and Nevada included within the hydrographic boundary of the Death Valley system lie in the Great Basin division of the Basin-and-Range Province. This system is bounded on the west by the rugged crest of the Sierra Nevada, on the north by the hydrographic rim of Pleistocene Lake Lahontan and smaller adjacent interior basins, and on the east by the Spring Mountains, New York Mountains, and other isolated mountain blocks near the California-Nevada line. To the south it is sharply separated from the coastal drainage by the east-west San Gabriel and San Bernardino ranges of southern California and indefinitely set off from the Colorado River system (Map 2).

This desert region, embracing an area of approximately 30,000 square miles, is made up of arid basins, separated by steep, parallel, fault-block ranges which trend in a north-south direction. The basins and ranges are largely bare and have very few surface waters. Elevations vary from 280 feet below sea level in Death Valley to 14,495 feet at the peak of Mount Whitney, the lowest and highest points, respectively, in the United States. Crests of the major desert ranges generally vary in elevation from 6,000 to 8,000 feet, and the basins range from below sea level in Death Valley to 4,000 feet in Owens Valley. The higher parts of the ranges support restricted stands of piñon and juniper, and so-called "forests" of the Joshua tree occur in favorable localities, generally between 2,500 and 3,500 feet. The creosote bush, usually in pure stands, covers great expanses of the broad desert basins and is the most widely distributed, and hence the most conspicuous, plant in the desert, ranging from below sea level to 5,500 feet. Other areas, usually in the lowest parts of closed basins, are entirely devoid of vegetation. These flat, bare stretches are the sites, after storms, of shallow ephemeral lakes and are generally referred to as playas, dry lakes, or alkali flats.

The climate is characterized by high summer temperatures but comparatively cold winters, low humidity, and low rainfall. Over the desert the average annual precipitation is about 6 inches, varying from 35 or 40 inches in the higher mountains to 1.5 inches in Death Valley. At Bagdad, on the central part of the Mohave Desert, 36 consecutive months without a trace of rain have been recorded (Thompson, 1929: 69). Most of the precipitation falls as rain during the winter and early spring, but summer thunderstorms occur on the Mohave Desert. A moderate snowfall is not

uncommon in the higher ranges, and snow occasionally falls on the higher slopes of the southern Mohave Desert proper.

The much restricted natural water supply of this desert expanse consists largely of 2 categories: permanent streams and perennial springs (Lee, 1906; Mendenhall, 1909; Waring, 1915, 1920; Thompson, 1929). There are 3 major, permanent streams in the Death Valley system (Map 2). Owens River, the largest of these, rises in snow-fed lakes 9,000 to 10,000 feet high along the eastern escarpment of the Sierra Nevada and receives many tributaries during the 130-mile course south to its sump, Owens Lake. Much of the water of this river is diverted into the Los Angeles aqueduct long before it reaches this lake, but under natural conditions Owens Lake was a larger body of saline water, without Recent outlet. The Mohave River rises on the northern slopes of the San Bernardino Range and follows a winding course northward on the desert for about 120 miles, where it finally sinks into the porous sands. In the headwater region, above 3,000 feet in the East Fork (Deep Creek), and 3,250 feet in the West Fork, its tributaries are generally permanent, but Mohave River becomes intermittent as soon as it debouches from the mountains onto the Mohave Desert. The third major stream, the Amargosa River, contains the smallest water supply, though its catchment area is greater than that of the Mohave. It rises above the old mining town of Beatty, in Nye County, southwestern Nevada, and its wash continues south for about 100 miles, where it makes an abrupt about face to terminate some 50 miles to the north in Death Valley. In the headwater region there is permanent water of good quality, but at the few other perennial flows of this "river," the water is of poor quality. The name Amargosa, meaning "bitter," is very appropriate for the middle and lower parts of this stream. At intervals, however, the Amargosa is fed by many large, warm springs, most notably in Ash Meadows, Nye County, Nevada (Map 3). These springs support many forms of life and provide a welcome water source for the thirsty desert traveler. The few clear streams and small springs in the higher mountain ranges contain no native fish life and are not important to this paper.

The widely scattered springs of this desert region are the most important source of refuge for wild life, and they have saved the life of many an old prospector. Long before the advent of the white man they marked the camp sites of Indians and the watering places for the desert bighorn sheep. The lowland springs, largely on or near fault lines, are warm or hot, varying from 20° to 42° C. (Table XLI), but fish do not permanently inhabit those having a temperature much above 34° C. The temperature of each spring is remarkably constant. The springs vary from 1 foot to 50 feet in diameter and from a few to 30 or more feet in depth. None of them is bottomless and none contains blind fish—popular desert myths. Some have no

visible inlet or outlet, but nevertheless maintain a relatively steady flow and water level. Nearly all of the springs abound in plant and animal life, and most of them (at least 30) support fish populations. Those which do not are too hot, too saline, or too alkaline to contain fish, or they are above the level covered by Pleistocene waters and hence were never populated, or they lie in mountain canyons subject to irresistible floods.

PLEISTOCENE HYDROGRAPHY

During the latter part of Pleistocene time there existed in this desert region an integrated river system (Map 1) named the Death Valley system because Death Valley formed the sump for this drainage. The physiographic evidence for this river system is unmistakable, but the detailed history of the drainage appears to have been very complicated, and much of the story remains to be deciphered. The present knowledge of this past hydrography has been presented in detail elsewhere (Miller, 1946), and the present account is a condensed review.

The streams, rivers, and lakes portrayed on Map 1 were not all contemporaneous. At least 2 stages were represented, which Blackwelder (1933; 1941) has tentatively correlated with the Tahoe and Tioga stages of glaciation in the near-by Sierra Nevada. These stages in turn are thought to have been nearly coincidental with the earliest and latest stages of the Wisconsin or last continental glaciation of eastern North America (Blackwelder, 1931: 918). Still earlier phases were almost surely represented, but it is seldom possible to do more than speculate on conditions which may have existed during middle or early Pleistocene times.

Gale (1914) and Blackwelder (1933) have established that Owens River formerly overflowed its present sump, Owens Lake, and filled successive basins southward and eastward until it entered Lake Manly, the former body of water that covered most of Death Valley (Map 1). At the same time, Death Valley probably received the discharge of both the Amargosa and Mohave rivers, whose conjoined waters entered from the south. Lake Manly was about 100 miles long and 600 feet deep (Noble, 1926: 69-70; Blackwelder, 1933).

At this period, which Blackwelder has tentatively correlated with the Tahoe glacial stage, a continuous waterway probably connected Owens Valley with the Amargosa and Mohave river basins. It was, therefore, possible for fish life to move between these now isolated basins. Whether the lake in Pahrump Valley, in southern Nye County, Nevada, was also connected with this drainage is not known, although Free (1914: 43-44) claimed that this valley was tributary to Amargosa River during the existence of Pleistocene Lake Lahontan. The presence of the genus *Empetrichthys* in Pahrump

Valley and in Ash Meadows (of the Amargosa drainage) testifies to a connection at some time.

During the succeeding Tioga glacial stage, Blackwelder believed that Owens River was no longer tributary to Death Valley, and no doubt the flow from both the Mohave and Amargosa rivers had greatly diminished. It is even questionable if Mohave River then reached Death Valley at more than infrequent intervals. As a result, Lake Manly rapidly disappeared.

Fish life in the Mohave and Amargosa drainages was isolated from that in Owens Valley long before isolation was effective between and within those drainages. Within historic time, Mohave River has not overflowed its extreme sump basin, Silver Lake, but in January, 1916, a great flood filled that playa with 10 feet of water and raised its level to within 30 feet of overflowing through the old outlet of Lake Mohave (Thompson, 1929: 494, 564). It is obvious that a slight increase in rainfall would make it possible for the Mohave River to reach Death Valley again.

A hydrographic connection between Death Valley and the Colorado River has been suggested by geologists (Blackwelder, 1933; Blackwelder and Ellsworth, 1936). A series of troughs, which contained Pleistocene lakes (Map 1), extends south and east from Death Valley and may represent the route along which such a connection once existed. There is, however, no clear-cut physiographic evidence that these structural troughs were in the course of such a hydrographic connection, but there is good indirect evidence that a waterway once connected Death Valley and the Colorado River or its antecedent. The genus *Cyprinodon* is elsewhere known in the West only from the lower Colorado River basin, and the species of that drainage (*C. macularius*) was obviously derived from relatives to the east, where the genus reaches its maximum development. A fossil *Cyprinodon* (Miller, 1945) from late Pliocene or early Pleistocene beds in Death Valley indicates that the genus entered the valley from the lower Colorado River or its antecedent at an early time. When it is realized that the Grand Canyon probably has been cut since mid-Pleistocene time, it is not difficult to understand how the physiographic evidence for such a connection might have been erased. The occurrence of *Cyprinodon* in the Death Valley system demands a connection with the basin of the Colorado River.

There is also some direct and indirect evidence to indicate that the Death Valley system was united, for a time at least, with the basin of Lake Lahontan to the north by way of the Mono basin. Although Russell (1889: 300-301) found no evidence that the Mono and Lahontan basins were connected during the existence of Pleistocene Lake Mono, it seems quite likely that a waterway united the 2 basins during pre-Pluvial time by way of what are now the East Fork of the Walker River and Aurora Valley. After fish life entered the Mono basin, a connection was probably established, prior

to the formation of the Mono Craters, with the Owens River in Adobe Valley, and the species spread southward. W. C. Putnam, of the University of California at Los Angeles, who has studied this area, wrote (personal letter) that there is good physiographic evidence for such a connection. The presence of the cyprinid genus *Siphateles* in Owens Valley strengthens such a view, for this genus (also present in Mohave River) is unknown from the Colorado River basin, but is abundantly represented in the Lahontan basin and other systems to the north and west. In explanation for its presence in the Death Valley system it must be assumed that the Lahontan and Death Valley systems were once united.

Physiographic evidence for a stream capture between the Amargosa River basin and the upper part of Las Vegas Creek, a flood tributary to the Colorado River, has been described by Gilluly (1929: 682). An area of about 150 square miles between Charleston and Point of Rocks in Nevada (see United States Geological Survey, Las Vegas and Furnace Creek quadrangles) was formerly tributary to Indian Springs Valley, a northwestern extension of the Las Vegas trough, but has been captured by a tributary of Amargosa River. Minnows of the genus *Rhinichthys* inhabit both Las Vegas Creek and Amargosa River, and it is very possible that the ancestral Amargosa stock came from the Colorado River basin rather than from Owens Valley, the only other drainage in the Death Valley system in which this genus occurs. Owens River almost surely received its stock from the Lahontan basin. That *Cyprinodon* also entered the Death Valley system by the Las Vegas-Amargosa transfer is most unlikely, for this genus is not adapted for life in the current and never seeks the higher tributaries.

GENUS *CYPRINODON* LACÉPÈDE

Cyprinodon Lacépède, 1803: 486. Type, *Cyprinodon variegatus* Lacépède.

Lebia (Cuvier) Oken, 1817: 1182. Type, *Cyprinodon variegatus* Lacépède.

Trifarcus Poey, 1860: 306. Type, *Trifarcus riverendi* Poey.

The following generic diagnosis of *Cyprinodon* has been compiled after a study of nearly all of the known species and of the literature.

DIAGNOSIS.—Teeth tricuspid, incisor-like, in a single series in each jaw. Scales large, 20 to 34 from angle of opercle to caudal base, usually 25 or 26. Humeral scale slightly to greatly enlarged. Preorbital area below the level of the nostrils usually scaly, except in *rubrofluvialis*, *salinus*, *diabolis*, and some populations of *nevadensis*. Free edges of the preorbital scales directed upward. Anterior edge of squamation of top of snout formed of several scales which are usually somewhat irregular, leaving a variable (often rather narrow) naked strip between them and the premaxillary groove. Scaly flap separating pelvic fins usually short and somewhat irregular, composed of 1 or 2 distal scales and 2 to 5 basal scales (exceptions in *radiosus*), all of which

TABLE XXXI
HEAD-PORE AND GILL-RAKER COUNTS IN FOUR SPECIES OF *Cyprinodon* FROM THE
DEATH VALLEY SYSTEM

Species	Preopercular Pores											No.	$M \pm \sigma_M$	
	7	8	9	10	11	12	13	14	15	16	17			
<i>nevadensis</i> ...	1	1	1	15	42	1,065	380	283	22	7	1	1,818	12.53 \pm .02	
<i>diabolis</i>	5	66	35	16	1	123	14.53 \pm .07	
<i>salinus</i>	2	4	60	22	9	2	99	14.38 \pm .09	
<i>radiosus</i>	1	8	43	55	36	7	150	14.92 \pm .08	
	Preorbital Pores													
	0	1	2	3	4	5	6	7	8	9				
	74	9	46	34	130	216	1,128	125	25	1,787			5.40
	3	87	25	5	1	121			6.29 \pm .06
	1	2	14	63	16	4	100			6.02 \pm .08
<i>radiosus</i>	31	5	19	7	25	23	26	9	5	150	3.59		
	Gill Rakers													
	14	15	16	17	18	19	20	21	22					
	1	11	46	93	155	109	61	20	6	502	18.19 \pm .06			
	2	11	8	1	22	16.36 \pm .15			
	1	12	24	12	1	50	20.00 \pm .11			
<i>radiosus</i>	1	12	28	24	8	1	74	17.39 \pm .11			

GENUS *EMPETRICHTHYS* GILBERT

Empetrichthys Gilbert, 1893: 233-34. Type, *Empetrichthys merriami* Gilbert.

This remarkable genus of cyprinodont fishes is confined to the Death Valley system. It is represented by the type species, *Empetrichthys merriami*, in Ash Meadows of the Amargosa River drainage, and by *Empetrichthys latos*, described herein, in Pahrump Valley. These localities, both in southern Nye County, Nevada, are isolated by a low alluvial divide. The genus has been recorded erroneously from "Death Valley, California" (Jordan and Evermann, 1896: 667; Jordan, Evermann, and Clark, 1930: 182; and Evermann and Clark, 1931: 56).

The following diagnosis of *Empetrichthys* is based on published accounts and on the results of the present study.

DIAGNOSIS.—A funduline cyprinodont with molar, tuberculate, pharyngeal teeth. Jaw teeth conical, biserial or weakly triserial, a few of the outer teeth enlarged. Upper and lower pharyngeal bones greatly enlarged, the lower pharyngeals completely united. Intestine short, about $1\frac{1}{2}$ times the length of the body, forming a sigmoid curve. Scales cycloid, large, imbricated or nonimbricated, rather irregularly arranged, 29 to 33 in lateral series; those of nuptial males with 1 to 3 ctenii or contact organs. Pre-

maxillaries protractile. Jaws unequal, the lower one projecting. Borders of oviduct swollen, but not forming a distinct pouch about the anal fin (as in *Fundulus*). Dorsal and anal fins placed far back on the body, the anal inserted directly under or slightly behind the dorsal. Dorsal with 9 to 13 rays; anal with 10 to 15. Pectorals set low, but with 2 vertical bases; with 15 to 20 rays. Pelvic fins absent. Caudal fin truncate or rounded, with 16 to 23 principal rays. Preopercular pores usually 14 (13 to 16), pre-orbital pores 8 (7 to 9), and mandibular pores 8 (6 to 8) (Tables XXXIV-XXXVI).

The tubercular-shaped molar teeth and the greatly enlarged upper and lower pharyngeal bones (Gilbert, 1893: Pl. 5) are the most distinctive characters of the genus. The lack of pelvic fins is not diagnostic of *Empetrichthys*, for a related genus, *Crenichthys*, as well as other cyprinodonts (*Orestias*, *Cyprinodon diabolis*, and *Tellia*), has independently lost these fins.

RELATIONSHIPS.—During the course of its classification, this singular genus has been assigned to 3 different families by various authors. In his original description, Gilbert (1893: 233-34) correctly placed *Empetrichthys* in the Cyprinodontidae. Garman (1895: 19, 116) retained *Empetrichthys* in this family, concluding that it is "allied to *Fundulus* through the more compressed species." Jordan and Evermann (1896: 631, 667), following Gill (1894: 115), still put all of the cyprinodonts in 1 family, but used the name Poeciliidae. Later, Jordan (1923: 158), following Eigenmann (1920), regarded *Empetrichthys* and *Orestias* (a superficially similar genus of the High Andes) as the only members of a distinct family, the Orestiidae. Recently, Jordan, Evermann, and Clark (1930: 182) even erected a separate family, the Empetrichthyidae, for the sole reception of *Empetrichthys*. Myers (1931: 10) placed *Empetrichthys* in the subfamily Fundulinae of the family Cyprinodontidae, concluding that *Empetrichthys* "... appears to have nothing to do with *Orestias*."

Empetrichthys probably originated from *Fundulus*, as was suggested by Garman. The fossil evidence also supports this view for the Death Valley species, *Fundulus curryi* (Miller, 1945: 316-19, Fig. 1), appears to have been strikingly like *Empetrichthys*.

The nearest living relative of *Empetrichthys* is *Crenichthys* of Railroad Valley (Hubbs, 1932) and the White River basin in eastern Nevada (Hubbs and Miller, 1941). Each of these genera retains primitive features along with specializations. Both probably arose from an ancestral stock which differed from *Fundulus* primarily in the lack of pelvic fins.

HABITAT.—Desert warm springs, frequenting the deeper holes; usually uncommon in shallow spring-fed ditches or marshy areas.

TYPE SPECIMEN.—After my work on this genus was completed I examined the 6 specimens of *Empetrichthys merriami* in the United States

National Museum and found that the type (= holotype) was not so labeled. Jordan and Evermann (1896: 667) incorrectly designated the type as U.S.N.M. No. 46101. This jar contains 3 specimens, 41 to 58 mm. in standard length, none of which is the type; that specimen was figured and so labeled by Gilbert (1893: Pl. 5, Fig. 1). In the jar containing U.S.N.M. No. 46102, however, I found the specimen figured by Gilbert and removed it from the other 2 specimens in this jar. The type may now be correctly designated as U.S.N.M. No. 131151, a large female, 67 mm. in standard length.

Empetrichthys merriami Gilbert

(Pls. X and XI)

This species is present only in Ash Meadows (Map 3) of the Amargosa River drainage, where it is rare. Over the 6-year period (1936-42) during which we collected in this region, only 22 specimens have been taken, although we made special efforts to obtain greater numbers. Myers and Wales collected 3 in 1930. Over the same 6-year period, 3861 specimens of *Cyprinodon nevadensis* and 515 of the cyprinid *Rhinichthys osculus nevadensis* Gilbert were secured in Ash Meadows.

The 22 specimens of *E. merriami* were collected from 5 separated springs in the Meadows, namely Deep Spring, Eagle Spring, Point of Rocks Spring (Kings Spring), Forest Spring, and Hidden Spring (Map 3). According to Shapovalov (1941: 445), the type locality is Kings Spring. The largest number taken from a single spring, 13, came from Deep Spring, where neither *Cyprinodon* nor *Rhinichthys* is particularly common. *E. merriami* prefers the deeper springs, where it dwells near the bottom. A description of the habitat of these springs has been given under the account of *Cyprinodon nevadensis mionectes* (pp. 48-52, 56).

The systematic characters of *merriami* are discussed in detail in connection with the description of the new species, *latos*.

DIAGNOSIS.—A deep-bodied, heavy-set species of *Empetrichthys* with a broadly arched predorsal profile, a large, deep head, a rather narrow mouth, a strong mandible, and 29 or 30 scales in the lateral series. The sides are marked by a rather irregular lateral band (Pls. X and XI). The anal rays usually number 14.

There may be some local differentiation in the populations of the different springs, but the material now available is insufficient to determine whether the observed variations are significant.

Empetrichthys latos, new species

(Pls. X and XI)

To date *Empetrichthys* has been regarded as a monotypic genus. Gilbert (1893: 234) had at his disposal only 6 specimens from Ash Meadows and 1

from Pahrump Valley. It is not surprising that he referred that single specimen to *merriami*. A study of the many specimens of *Empetrichthys* which have been taken in recent years from Pahrump Valley convinces me that this isolated basin contains a species distinct from that of Ash Meadows.

The 3 springs from which we have collected *Empetrichthys* in Pahrump Valley are well isolated although only 7 miles apart, and their remnant populations are regarded as comprising 3 distinct subspecies. Several important characters, shared by all 3, distinguish each of these populations from *merriami*. Subspecific rank is assigned the 3 forms because the differences between them appear to be in the average only.

TYPES.—The holotype of the typical form, *E. latos latos*, is an adult female, 43 mm. long, seized by Robert R. and Frances H. Miller on October 5, 1942, from the main spring pool on Manse Ranch, Pahrump Valley, Nye County, Nevada (U. S. Geological Survey, Las Vegas Quadrangle); U.M.M.Z. No. 141855. The type specimens of each subspecies are designated in the subspecific descriptions.

DIAGNOSIS.—A rather slender species of *Empetrichthys* with a gently sloping to convex predorsal profile, a relatively short and slender head, a comparatively broad mouth, a weak mandible, and usually 31 or 32 scales in the lateral series. The sides are marked by a narrow axial streak (Pls. X and XI), which is faint to obsolescent in *E. l. concavus*. The anal rays usually number 12 or 13.

COMPARISON.—*Empetrichthys latos* differs from *E. merriami*, the only other known species of the genus, principally in mouth structure, body shape, and color pattern (Pls. X and XI). In *merriami* the head constricts abruptly in the preorbital region so that the 2 sides of the snout slope markedly toward the tip of the mandible. As a result of this constriction the mouth is narrower. In *latos* the sides of the head are almost parallel all the way to the tip of the mandible, and the mouth is consequently broader. When the mouth is forced open, as with a pair of forceps, the horizontal gape is definitely evident in *merriami*, but is almost eliminated in *latos*. The bones of the premaxillaries and mandible are much weaker and less firmly connected in *latos*.

In *merriami* the predorsal region is broadly convex. The change in slope of the predorsal profile takes place farther forward so that the head is deeper than it is in *latos*. The body is also thicker in *merriami*. The differences in color pattern between the 2 species are well shown in Plate X. In particular the narrow axial streak of *latos* contrasts with the disrupted lateral band of *merriami*.

The large difference in head depth and opercle length between *merriami* and *latos* can be expressed by a character index in which these measurements, expressed in thousandths of the standard length, are added together (Table XXXII).

TABLE XXXII

CHARACTER INDEX FOR HEAD DEPTH AND OPERCLE LENGTH IN
TWO SPECIES OF *Empetrichthys*

The index was derived by adding together the depth of the head and the length of the opercle, expressed in thousandths of the standard length. The sexes are combined.

Locality and Form	Character Index	
	Range (Ave.)	No.
Pahrump Valley		
<i>E. l. latos</i>	372-426 (391)	21
<i>E. l. pahrump</i>	382-413 (396)	20
<i>E. l. concavus</i>	383-421 (402)	19
Total	372-426 (398)	60
Ash Meadows		
<i>E. merriami</i>	414-449 (431)	13

SUBSPECIES AND ECOLOGY.—The 3 subspecies of *Empetrichthys latos* are discussed in order from south to north. The main spring pool on Manse Ranch was selected as the type locality because the population of *E. latos* is larger there and the natural conditions of that spring appear least likely to be seriously altered by man. *Empetrichthys* is the only fish native to Pahrump Valley. Its comparative abundance there may be largely due to lack of competition.

ETYMOLOGY.—The name *latos*, from *latus* and *os*, refers to the wide mouth of the new species.

Empetrichthys latos latos, new subspecies

(Pl. XI)

TYPES.—The holotype has been designated in the description of the species. There are 143 paratypes, U.M.M.Z. No. 140489, 15 to 48 mm. long, taken with the holotype at Manse Ranch, and 34 paratypes, U.M.M.Z. No. 132915, 10 to 50 mm. long, collected by R. R. Miller and Alex J. Calhoun on July 16, 1938, from the outlet of the main spring pool.

DIAGNOSIS AND COMPARISONS.—A subspecies of *E. latos* characterized by a relatively short distance between anal origin and caudal base. In this character the males of *E. l. latos* show little or no overlap with the males of either *E. l. pahrump* or *E. l. concavus*; in the females the values show only slight overlap. The comparatively short distance between the anal origin and the caudal base appears to be influenced by the more posterior position and the short basal length of the anal fin. The head depth is less in the males, and the width of the preorbital is broader in both sexes than in those 2 subspecies, and the snout is longer than it is in *concavus*. The basal length of the anal fin is shorter, but overlaps the figures for the other 2 subspecies. The caudal fin of *latos* is much shorter than it is in

concavus (Pl. XI). On the average the mouth is broader and the dorsal fin more posterior in position than in either *pahrump* or *concavus* (Table XXXIII). The darker pigmentation of *latos* may be due, in part at least, to the darker habitat.

HABITAT.—The main spring pool at Manse Ranch is about 50 feet wide at the head, 10 feet wide at the outlet, and 60 feet long. It is 1 to 6 feet deep and has a silt bottom. The water is crystal clear and chalky blue in a deep hole near the center of the spring. On October 5, 1942, vegetation noted was thick water cress, *Chara*, green algae, and a fine-leaved *Potamogeton*. The shore is a low bank, bordered by cottonwood (*Populus Fremonti?*) and willow, which well shade the pool. The current is moderate in the pool and swift in the outlet. About 50 yards above is a much smaller spring which flows into the head of the pool just described; it contained no fish life.

The temperature of the main spring, as recorded by several investigators over a period of 26 years, is very constant, about 24° C. (23.3° C. to 24.0° C.).

Mr. Sawday, owner of the ranch at the time of our visit, kindly allowed us to collect specimens.

Empetrichthys latos pahrump, new subspecies

(Pl. XI)

TYPES.—The holotype, an adult female, 35 mm. long, was seined by R. R. and F. H. Miller from the marshy overflow of a spring-fed ditch on Pahrump Ranch, 6 miles northwest of Manse Ranch, in Pahrump Valley, Nye County, Nevada; U.M.M.Z. No. 141856. One hundred and forty-two paratypes, U.M.M.Z. No. 140490, 14 to 36 mm. long, were taken with the holotype.

DIAGNOSIS AND COMPARISONS.—A subspecies of *Empetrichthys latos* closely resembling *E. l. latos*, differing principally in the longer distance between anal origin and caudal base. From *concavus* it is readily separated by the much shorter and more nearly truncate caudal fin (Pl. XI). In the length of the anal and caudal fins *pahrump* is somewhat intermediate between *latos* and *concavus*. It also appears to be intermediate in color pattern, but the paleness is very probably influenced by the clay and silt bottom over which the sample was collected. The head is only very slightly concave.

HABITAT.—The 2 main springs on Pahrump Ranch, which rise about 200 yards east of the principal ranch houses, are used extensively for irrigation. Until recently the northern spring contained native fish life, but it was greatly altered by dredging in 1941, and only a few carp were observed there in 1942. The southern spring still harbored a few fish in 1942, but in October of that year most of the population of *pahrump* was in a marshy area about 200 yards from the source of the southern spring. As shown

by readings over a 26-year period, the temperature of the spring sources is constantly about 25° C. (24.7° C. to 25.0° C.); that of the outlets varies somewhat and is usually less than 25° C.

ETYMOLOGY.—This subspecies is named *pahrump* after the valley in which it is found, and more particularly for Pahrump Ranch, which is the more precise type locality.

Empetrichthys latos concavus, new subspecies

(Pl. XI)

TYPES.—The holotype is an adult female, U.M.M.Z. No. 141857, 39 mm. long. It was collected by R. R. and F. H. Miller on October 5, 1942, in a spring on the Raycraft Ranch, about one-half mile north of Pahrump Ranch, Pahrump Valley, Nye County, Nevada. This spring is named on a map (Pl. VIII) in Waring's report (1920). Twenty-six paratypes, U.M.M.Z. No. 140491, 17 to 40 mm. long, were collected with the holotype.

DIAGNOSIS AND COMPARISONS.—A subspecies of *Empetrichthys latos* most closely resembling *E. l. pahrump*, from which it differs chiefly in the much longer and more nearly rounded caudal fin. The rays along the upper and lower borders of this fin are definitely shorter than they are in either *pahrump* or *latos* (Pl. XI). The profile between snout and occiput is most strongly concave in this subspecies. The anal fin of *concavus* is longer than it is in *pahrump*, especially in the female, and much longer than the anal fin of *latos*. In the males the snout is shorter and the body is deeper than in the 2 other subspecies (Table XXXIII). The cheek is deeper than it is in either *pahrump* or *latos*. The axial streak is generally finer and much less conspicuous than it is in the other 2 subspecies, and in some specimens of *concavus* it is obsolescent.

HABITAT.—*E. latos concavus* was collected on Raycraft Ranch from the spring-fed pond, 5 to 25 feet wide and about 40 feet long, and its outlet ditch, 1 to 4 feet wide. The temperature of the spring on October 5, 1942, was 25.3° C., slightly warmer than were the springs on either Manse or Pahrump ranches. The water in the spring pond and outlet was clear but easily roiled because of a bottom of silt and trash. Vegetation noted in 1942 was water cress, *Typha*, and grass. The current in the spring was slight, but rather swift in the outlet. The depth of water was not over 1½ feet. The shore consisted of low banks, willows, and meadowland. According to Waring (1920: 76) this spring has a flow of about 10 gallons a minute. *Empetrichthys* was not common, perhaps because introduced carp were also present.

ETYMOLOGY.—The new subspecies is named *concavus* in reference to the marked concavity of the top of the head.

TABLE XXXIII

PROPORTIONAL MEASUREMENTS OF ADULTS OF TWO SPECIES OF *Empetrichthys*, EXPRESSED IN THOUSANDTHS OF THE STANDARD LENGTH

Locality and Form	Standard Length	Predorsal		Anal Origin to Caudal Base				Body, Greatest Depth		
				Males		Females				
	Range (Ave.)	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	
Pahrump Valley										
<i>l. latos</i>	26-47 (35)	669-693 (681)	20	332-356 (346)	10	310-344 (328)	10	274-332 (306)	20	
<i>l. pahrump</i>	28-42 (33)	658-687 (673)	20	355-382 (367)	10	338-358 (348)	10	281-333 (309)	20	
<i>l. concavus</i>	25-39 (32)	645-688 (663)	19	359-377 (366)	9	335-359 (350)	10	271-328 (293)	19	
Total	25-47 (33)	645-693 (672)	59	332-382 (359)	29	310-359 (342)	30	271-333 (303)	59	
Ash Meadows										
<i>merriami</i>	20-59 (35)	650-694 (675)	13	351-376 (362)	5	334-359 (342)	5	288-348 (314)	13	
Pahrump Valley	Body, Greatest Width		Head, Length		Head, Depth					
					Males		Females			
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.		
<i>l. latos</i>	185-225 (207)	20	306-337 (316)	20	252-277 (267)	10	271-302 (281)	10		
<i>l. pahrump</i>	194-219 (209)	16	294-326 (312)	20	269-290 (280)	10	272-287 (277)	10		
<i>l. concavus</i>	191-230 (205)	19	298-320 (310)	19	273-293 (284)	9	265-296 (276)	10		
Total	185-230 (207)	55	294-337 (313)	59	252-293 (277)	29	265-302 (278)	30		
Ash Meadows										
<i>merriami</i>	184-237 (204)	13	307-353 (329)	13	286-308 (298)	8	285-309 (299)	5		
Pahrump Valley	Head, Width				Caudal Peduncle, Length				Caudal Peduncle, Depth	
	Males		Females		Males		Females			
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
<i>l. latos</i>	210-218 (215)	10	219-239 (225)	10	188-212 (199)	10	187-218 (206)	10	143-164 (155)	20
<i>l. pahrump</i>	212-223 (217)	10	196-230 (214)	9	195-211 (206)	10	205-228 (217)	10	147-171 (157)	19
<i>l. concavus</i>	212-231 (219)	9	214-238 (222)	10	196-220 (209)	9	204-225 (214)	10	143-160 (153)	19
Total	210-231 (217)	29	196-239 (221)	29	188-220 (205)	29	187-228 (212)	30	143-171 (155)	58
Ash Meadows										
<i>merriami</i>	194-233 (212)	8	209-249 (227)	5	187-209 (196)	8	194-218 (207)	5	138-162 (149)	11

TABLE XXXIII (Cont.)

Locality and Form	Interorbital, Least Bony Width		Preorbital, Least Width		Preorbital Margin to Preopercular Angle		Eye Margin to Preopercular Angle			
							Males		Females	
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
Pahrump Valley										
<i>l. latos</i>	100-118 (107)	20	24- 33 (29)	20	147-167 (155)	20	80- 92 (86)	10	84-110 (94)	10
<i>l. pahrump</i>	103-116 (109)	20	20- 28 (24)	20	144-156 (147)	19	80- 91 (85)	10	76- 97 (88)	10
<i>l. concavus</i>	102-115 (107)	19	19- 28 (24)	19	143-158 (151)	19	78- 90 (84)	9	81- 90 (85)	10
Total	100-118 (108)	59	19- 33 (26)	59	143-167 (151)	58	78- 92 (85)	29	76-110 (89)	30
Ash Meadows										
<i>merriami</i>	98-125 (114)	13	24- 36 (28)	13	130-159 (147)	13	81-101 (87)	8	85- 99 (92)	5
Pahrump Valley	Greatest Length Opercle,		Snout, Length		Orbit, Length				Mouth, Width	
					Males		Females			
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
Pahrump Valley										
<i>l. latos</i>	107-128 (117)	20	78- 89 (83)	20	69- 95 (81)	10	70- 89 (76)	10	104-125 (113)	20
<i>l. pahrump</i>	108-124 (118)	20	71- 87 (79)	20	75- 84 (80)	10	69- 83 (77)	10	102-113 (105)	19
<i>l. concavus</i>	115-129 (122)	19	66- 79 (73)	19	77- 93 (86)	9	70- 84 (76)	10	102-114 (106)	19
Total	107-129 (119)	59	66- 89 (78)	59	69- 95 (82)	29	69- 89 (76)	30	102-125 (108)	58
Ash Meadows										
<i>merriami</i>	123-140 (132)	13	73- 88 (80)	13	65-104 (84)	8	61- 91 (74)	5	82-107 (97)	13
Pahrump Valley	Upper Jaw, Length		Mandible, Length				Dorsal Fin, Basal Length			
			Males		Females		Males		Females	
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
Pahrump Valley										
<i>l. latos</i>	96-112 (103)	20	95-104 (99)	10	93-110 (101)	10	147-171 (159)	10	136-152 (145)	10
<i>l. pahrump</i>	95-105 (101)	20	94-108 (97)	10	89-102 (95)	10	148-165 (158)	10	127-152 (142)	10
<i>l. concavus</i>	92-106 (100)	19	78- 93 (87)	9	93-103 (98)	10	146-165 (157)	9	132-146 (139)	10
Total	92-112 (101)	59	78-108 (95)	29	89-110 (98)	30	146-171 (158)	29	127-152 (142)	30
Ash Meadows										
<i>merriami</i>	89-107 (98)	13	88-105 (97)	8	93-110 (100)	5	138-173 (150)	8	120-145 (136)	5

TABLE XXXIII (Cont.)

Locality and Form	Dorsal Fin, Length				Anal Fin, Basal Length			
	Males		Females		Males		Females	
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
Pahrump Valley								
<i>l. latos</i>	230-257 (242)	10	216-247 (227)	10	130-153 (139)	10	112-131 (123)	10
<i>l. pahrump</i>	229-259 (244)	10	203-236 (224)	10	151-167 (158)	10	123-143 (133)	10
<i>l. concavus</i>	241-257 (251)	9	217-233 (227)	10	142-165 (155)	9	127-142 (134)	10
Total	220-259 (245)	29	203-247 (226)	30	130-167 (151)	29	112-143 (130)	30
Ash Meadows								
<i>merriami</i>	208-233 (222)	8	195-218 (209)	5	151-179 (160)	8	124-147 (134)	5
	Anal Fin, Length				Middle Caudal Rays, Length			
	Males		Females		Males		Females	
	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.	Range (Ave.)	No.
Pahrump Valley								
<i>l. latos</i>	214-239 (223)	10	181-210 (199)	10	199-221 (211)	10	194-227 (210)	10
<i>l. pahrump</i>	225-251 (239)	10	195-218 (207)	10	215-228 (221)	10	205-224 (214)	8
<i>l. concavus</i>	236-263 (247)	9	213-226 (221)	10	221-246 (232)	9	220-241 (228)	10
Total	214-263 (236)	29	181-226 (209)	30	199-246 (221)	29	194-241 (218)	28
Ash Meadows								
<i>merriami</i>	216-240 (230)	8	191-213 (204)	5	181-215 (197)	6	179-191 (184)	4
	Pectoral, Length Longest Ray							
	Males		Females					
	Range (Ave.)	No.	Range (Ave.)	No.				
Pahrump Valley								
<i>l. latos</i>	165-182 (173)	10	163-187 (171)	10				
<i>l. pahrump</i>	165-178 (170)	10	154-168 (162)	9				
<i>l. concavus</i>	170-186 (179)	9	165-186 (173)	10				
Total	165-186 (174)	29	154-187 (169)	29				
Ash Meadows								
<i>merriami</i>	156-189 (174)	7	153-174 (162)	5				

TABLE XXXIV

FIN-RAY COUNTS IN *Empetrichthys latos* AND *E. merriami*

Locality and Form	Dorsal Rays					No.	$M \pm \sigma_M$			
	9	10	11	12	13					
Pahrump Valley										
<i>l. latos</i>	6	60	44	3	113	11.39 \pm .06			
<i>l. pahrump</i>	7	46	19	4	76	11.26 \pm .08			
<i>l. concavus</i>	1	18	7	26	11.23 \pm .10			
Total	14	124	70	7	215	11.33 \pm .04			
Ash Meadows										
<i>merriami</i>	1	4	15	6	26	11.00 \pm .14			
	Anal Rays									
	10	11	12	13	14	15				
Pahrump Valley										
<i>l. latos</i>	1	10	61	38	3	113	12.28 \pm .07		
<i>l. pahrump</i>	8	37	29	2	76	12.33 \pm .08		
<i>l. concavus</i>	5	20	1	26	12.85 \pm .09		
Total	1	18	103	87	6	215	12.37 \pm .05		
Ash Meadows										
<i>merriami</i>	2	7	15	6	30	13.83 \pm .15		
	Pectoral Rays									
	15	16	17	18	19	20				
Pahrump Valley										
<i>l. latos</i>	17	106	70	7	1	201	17.35 \pm .05		
<i>l. pahrump</i>	1	32	88	16	137	16.87 \pm .05		
<i>l. concavus</i>	28	22	2	52	16.50 \pm .08		
Total	1	77	216	88	7	1	390	17.07 \pm .04		
Ash Meadows										
<i>merriami</i>	1	10	15	12	38	17.00 \pm .13		
	Caudal Rays									
	16	17	18	19	20	21	22	23		
Pahrump Valley										
<i>l. latos</i>	4	24	30	31	9	2	100	19.23 \pm .11
<i>l. pahrump</i>	1	1	14	16	25	5	1	1	64	19.36 \pm .15
<i>l. concavus</i>	1	5	7	11	24	19.17 \pm .18
Total	1	6	43	53	67	14	3	1	188	19.27 \pm .08
Ash Meadows										
<i>merriami</i>	1	3	6	7	17	19.12 \pm .22

TABLE XXXV
SCALE COUNTS IN *Empetrichthys latos* AND *E. merriami*

Locality and Form	Lateral Series Scales					No.	$M \pm \sigma_M$							
	29	30	31	32	33									
Pahrump Valley														
<i>l. latos</i>	5	45	41	5	96	31.48 \pm .07							
<i>l. pahrump</i>	1	14	41	15	2	73	31.04 \pm .09							
<i>l. concavus</i>	4	13	7	24	31.13 \pm .14							
Total	1	23	99	63	7	193	31.27 \pm .05							
Ash Meadows														
<i>merriami</i>	10	9	19	29.47 \pm .11							
Dorsal to Anal Scales														
	12	13	14	15	16									
Pahrump Valley														
<i>l. latos</i>	25	30	19	16	3	93	13.38 \pm .12							
<i>l. pahrump</i>	2	18	32	12	1	65	13.88 \pm .10							
<i>l. concavus</i>	1	13	9	2	25	13.48 \pm .14							
Total	28	61	60	30	4	183	13.57 \pm .07							
Ash Meadows														
<i>merriami</i>	7	9	3	19	13.79 \pm .16							
Predorsal Scales														
	23	24	25	26	27	28	29	30	31					
Pahrump Valley														
<i>l. latos</i>	9	17	29	26	9	1	91	26.13 \pm .12			
<i>l. pahrump</i>	4	9	15	17	12	3	1	1	62	25.69 \pm .19			
<i>l. concavus</i>	3	3	9	5	3	1	24	26.25 \pm .28			
Total	4	21	35	55	43	15	2	1	1	177	25.99 \pm .10			
Ash Meadows														
<i>merriami</i>	2	3	5	6	1	2	19	26.63 \pm .36			
Circumference of Peduncle Scales														
	16	17	18	19	20	21	22	23	24					
Pahrump Valley														
<i>l. latos</i>	9	14	19	5	37	3	6	93	18.86			
<i>l. pahrump</i>	2	11	7	44	1	65	19.46			
<i>l. concavus</i>	3	18	1	2	1	25	20.12			
Total	11	14	33	12	99	4	9	1	183	19.25			
Ash Meadows														
<i>merriami</i>	1	6	4	7	1	19	19.00			
Circumference of Body Scales														
	27	28	29	30	31	32	33	34	35	36	37	38		
Pahrump Valley														
<i>l. latos</i>	1	2	8	15	12	13	12	7	8	6	5	4	93	32.47 \pm .28
<i>l. pahrump</i>	1	2	2	4	9	13	12	11	7	1	1	63	33.44 \pm .25
<i>l. concavus</i>	2	5	7	4	3	2	1	24	31.50 \pm .34
Total	1	3	12	22	23	26	28	21	19	14	6	5	180	32.68 \pm .18
Ash Meadows														
<i>merriami</i>	1	2	2	4	4	5	1	19	32.42 \pm .36

TABLE XXXVI
HEAD-PORE COUNTS IN *Empetrichthys latos* AND *E. merriami*

Locality and Form	Preopercular Pores				No.	$M \pm \sigma_M$
	13	14	15	16		
Pahrump Valley						
<i>l. latos</i>	1	86	9	3	99	14.14 \pm .05
<i>l. pahrump</i>	6	59	1	1	67	13.95 \pm .05
<i>l. concavus</i>	1	25	26	13.96 \pm .04
Total	8	170	10	4	192	14.05 \pm .03
Ash Meadows						
<i>merriami</i>	1	9	2	12	14.08 \pm .14
Preorbital Pores						
	7	8	9			
Pahrump Valley						
<i>l. latos</i>	5	91	3		99	7.98 \pm .03
<i>l. pahrump</i>	1	66		67	7.99 \pm .01
<i>l. concavus</i>	26		26	8.00
Total	6	183	3		192	7.98 \pm .01
Ash Meadows						
<i>merriami</i>	13		13	8.00
Mandibular Pores						
	6	7	8			
Pahrump Valley						
<i>l. latos</i>	4	95		99	7.96 \pm .02
<i>l. pahrump</i>	2	3	62		67	7.89 \pm .04
<i>l. concavus</i>	1	25		26	7.96 \pm .04
Total	2	8	182		192	7.94 \pm .02
Ash Meadows						
<i>merriami</i>	1	11		12	7.92 \pm .08

EXPERIMENTAL WORK ON *CYPRINODON*

The experimental work on the genus *Cyprinodon* was begun by myself and my father, Ralph G. Miller, in August, 1940, and with my supervision has been carried on by him since that time. During the field work in 1942, I checked the progress of the experiments. The results for the 3-year period ending in the fall of 1943 clearly indicate that we have only scratched the surface of several fields of investigation. At this time, therefore, only the broad outlines and general indications of the work can be briefly presented.

The main purpose of this work is to determine whether differences which have been used to distinguish certain races, subspecies, and species of *Cyprinodon* are genetic or environmental, or both. Thus far no complete answer can be given to this important question, but a preliminary analysis of the data obtained strongly indicates that many of the characters are

PLATE X

Two species of *Empetrichthys*.

FIG. 1. *E. merriami* Gilbert. Immature male, U.M.M.Z. No. 140467, 20 mm. long, from Eagle Spring, Ash Meadows, Nye County, Nevada.

FIG. 2. *E. latos*, new species. Immature male paratype, U.M.M.Z. No. 140489, 20 mm. long, from main spring pool on Manse Ranch, Pahrump Valley, Nye County, Nevada.

Drawn by Grace Eager.

PLATE X

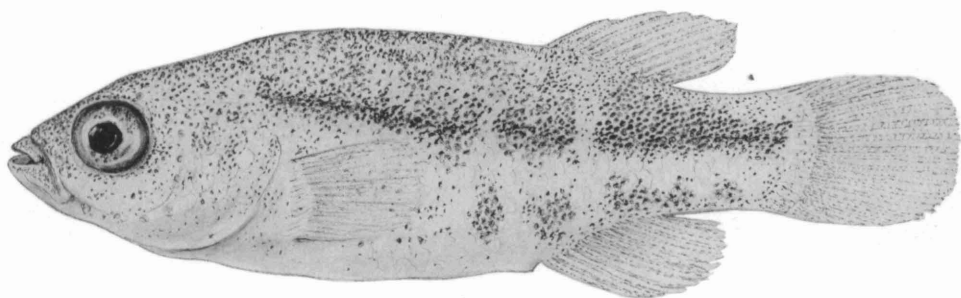


FIG. 1

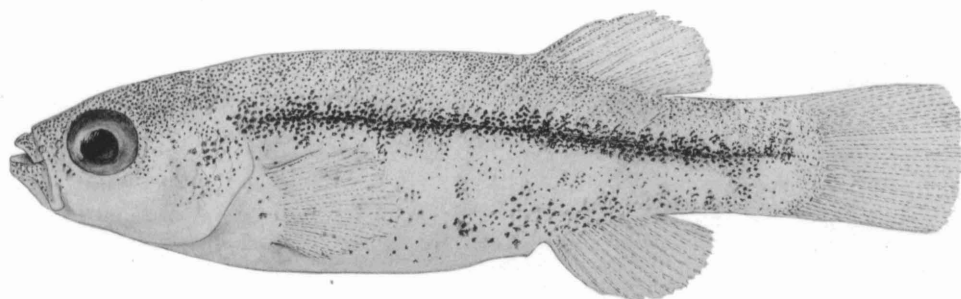


FIG. 2

PLATE XI

Four forms of *Empetrichthys*.

Top to bottom:

E. merriami Gilbert. Adult male, U.M.M.Z. No. 140467, 34 mm. long, from Eagle Spring, Ash Meadows, Nye County, Nevada.

E. latos concavus, new subspecies. Adult male paratype, U.M.M.Z. No. 140491, 34 mm. long, from spring on Raycraft Ranch, Pahrump Valley, Nye County, Nevada.

E. latos pahrump, new subspecies. Adult male paratype, U.M.M.Z. No. 140490, 32 mm. long, from spring-fed ditch on Pahrump Ranch, Pahrump Valley, Nye County, Nevada.

E. latos latos, new subspecies. Adult male paratype, U.M.M.Z. No. 140489, 34 mm. long, from main spring pool in Manse Ranch, Pahrump Valley, Nye County, Nevada.

Photographed by F. W. Ouradnik.

PLATE XI

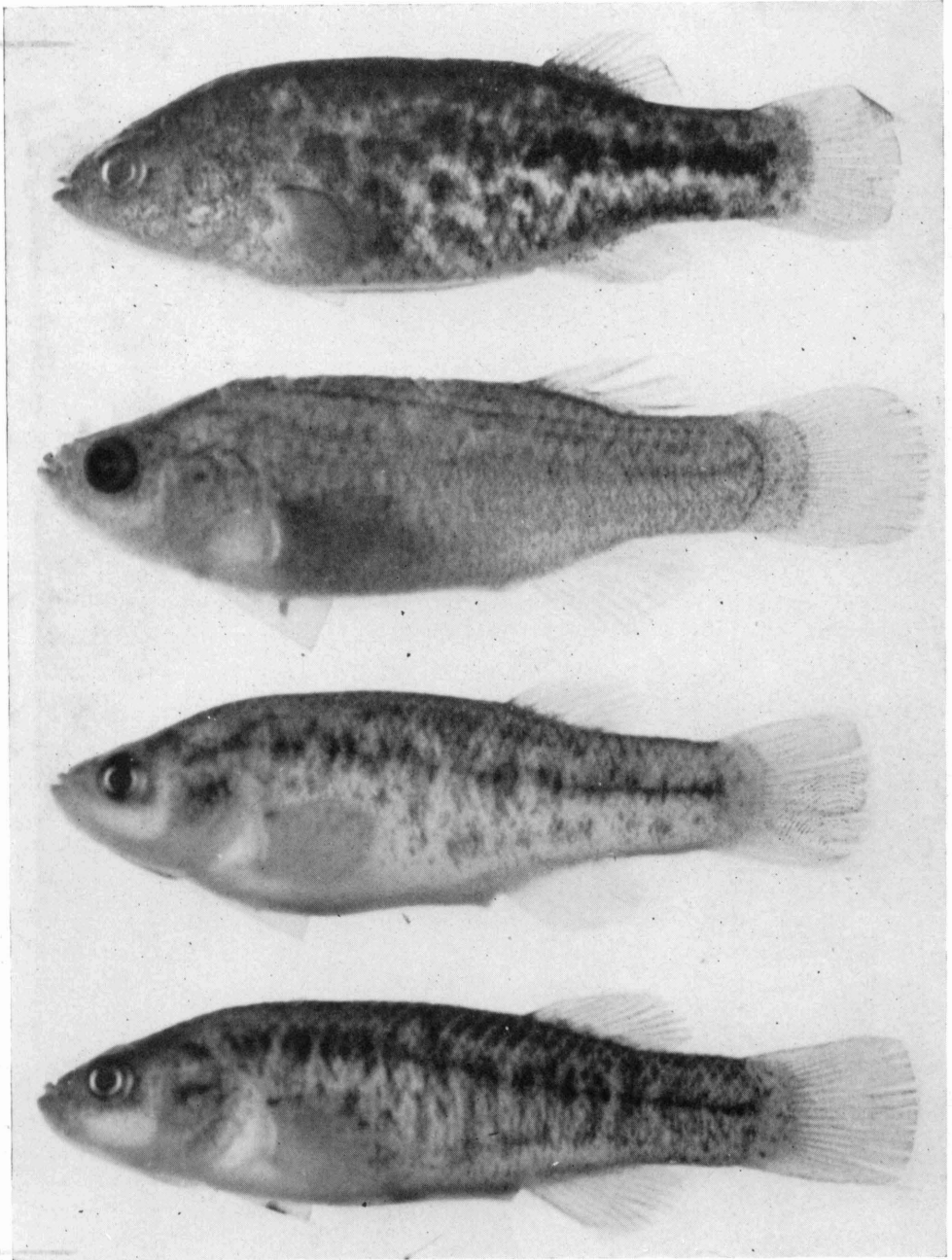


PLATE XII

FIG. 1. North Tecopa Hot Spring (right) and South Tecopa Hot Spring, looking west. Photographed September 26, 1942.

FIG. 2. Big Spring, Ash Meadows, Nye County, Nevada, looking north. In the left foreground is the outlet ditch. Photographed September 27, 1942.

PLATE XII

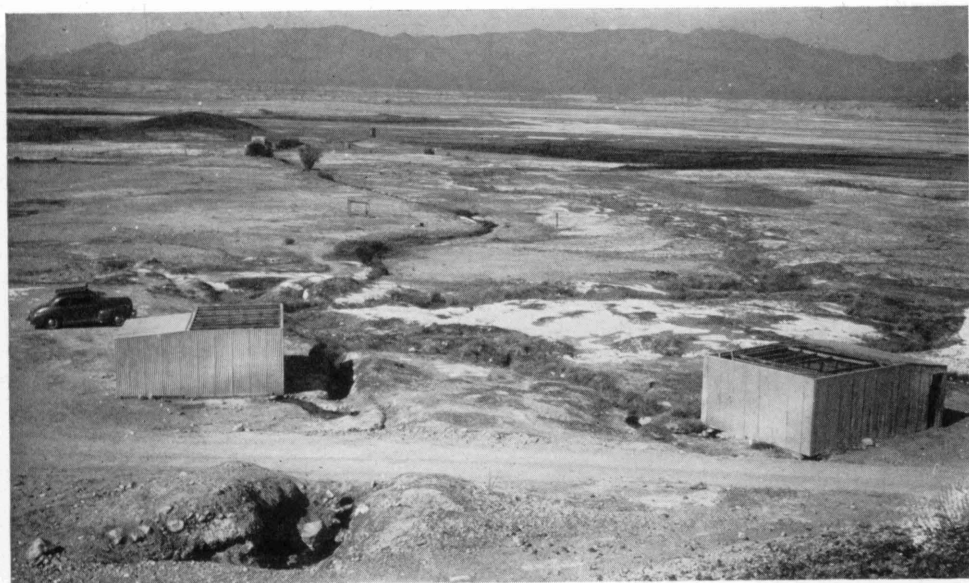


FIG. 1



FIG. 2