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NOTES ON THE CUTTHROAT AND RAINBOW TROUTS WITH THE DESCRIPTION OF A NEW SPECIES FROM THE GILA RIVER, NEW MEXICO

BY ROBERT RUSH MILLER

THE trouts of western North America have long provided recreation to the outdoorsman and perplexing problems to the systematic ichthyologist. The notorious variability of these fishes, in coloration as well as in body form and meristic characters, has led to the recognition of no less than 33 nominal species, many of them based on only 1 or a few specimens (Jordan, Evermann, and Clark, 1930: 56–59; Snyder, 1933, 1934, 1940). It is probable that the status of a number of these forms may never be securely clarified. The endless transplantation of stocks, with much interbreeding in hatcheries and in nature, has made it extremely difficult, often impossible, for the specialist to identify specimens with assurance. Many stocks have been either extirpated or greatly modified through alterations of the environment and through the widespread stocking of exotic forms, which often eliminate the native trout or hybridize with them. A few species seem to have been exterminated. The emerald trout of Pyramid Lake, Nevada (Map 1), *Salmo smaragdus* Snyder, rare even 35 years ago, is almost surely extinct. The royal silver trout, *Salmo regalis* Snyder, a species confined to the deep waters of Lake Tahoe, California and Nevada (Map 1), has not been taken for many years and is presumed to be extinct. Angling enthusiast Richard S. Croker, of the California Division of Fish and Game, has assured me that *Salmo evermanni* Jordan and Snyder, which once abounded above the falls of Santa Ana River in southern California (Map 1), disappeared about 1935, when he caught what may have been the last pure sample of this interesting species. Angler-artist Campbell Grant, of Carpinteria, California, has written that he fished exhaustively in this region in the fall of 1948, but caught only a few brown trout.

In addition to these supposedly distinct species, many subspecies and local races have been eliminated. Some have failed in competition with aggressive introduced stocks of rainbow trout, *Salmo gairdnerii* Richardson, cutthroat trout, *Salmo clarkii* Richardson, and lake trout, *Salvelinus namaycush* (Walbaum).[1] Others have been the victims of reckless fishing methods. Some have vanished because of the destruction of their pristine habitats by the "advance of civilization." Intraspecific interbreeding resulting from indiscriminate stocking has probably altered most of the many local subspecies and races to so great an extent that their original characteristics are difficult or impossible to determine. In addition, the rainbow trout has hybridized extensively with the native cutthroat trouts (subspecies of *S. clarkii*), where it has been introduced into intermountain and Rocky Mountain waters formerly inhabited only by cutthroats. Where cutthroat and rainbow naturally coexist, in coastal waters from northern California northward to Alaska, they evidently do not hybridize or do so only rarely. The close approach between coastal cutthroats and rainbows in a number of characters (Table II) may indicate, however, that hybridization has taken place, perhaps in the Pleistocene epoch.

Not only does the frequency of hybridization complicate trout identification, but it also poses a practical problem in

[1] There seems to be no valid reason for retaining *Cristivomer* at the generic level.

fishery management. Stocking programs should strive to avoid the cohabitation of rainbow and cutthroat trouts, particularly in interior waters where limited spawning sites force these species to engage in mass hybridization. Long ago Dymond (1928: 75) advised against the cohabitation of Kamloops and cutthroat trouts.

STATUS OF WESTERN TROUTS

The native salmonids of western North America belong to three major groups: the Pacific salmons (*Oncorhynchus*), the charrs (*Salvelinus,* including *Cristivomer*), and the trouts (*Salmo*). This paper is concerned only with the trouts. They are referable to the rainbow, *Salmo gairdnerii,* or the cutthroat, *Salmo clarkii,* or to species thought to have been derived from these 2 species groups.

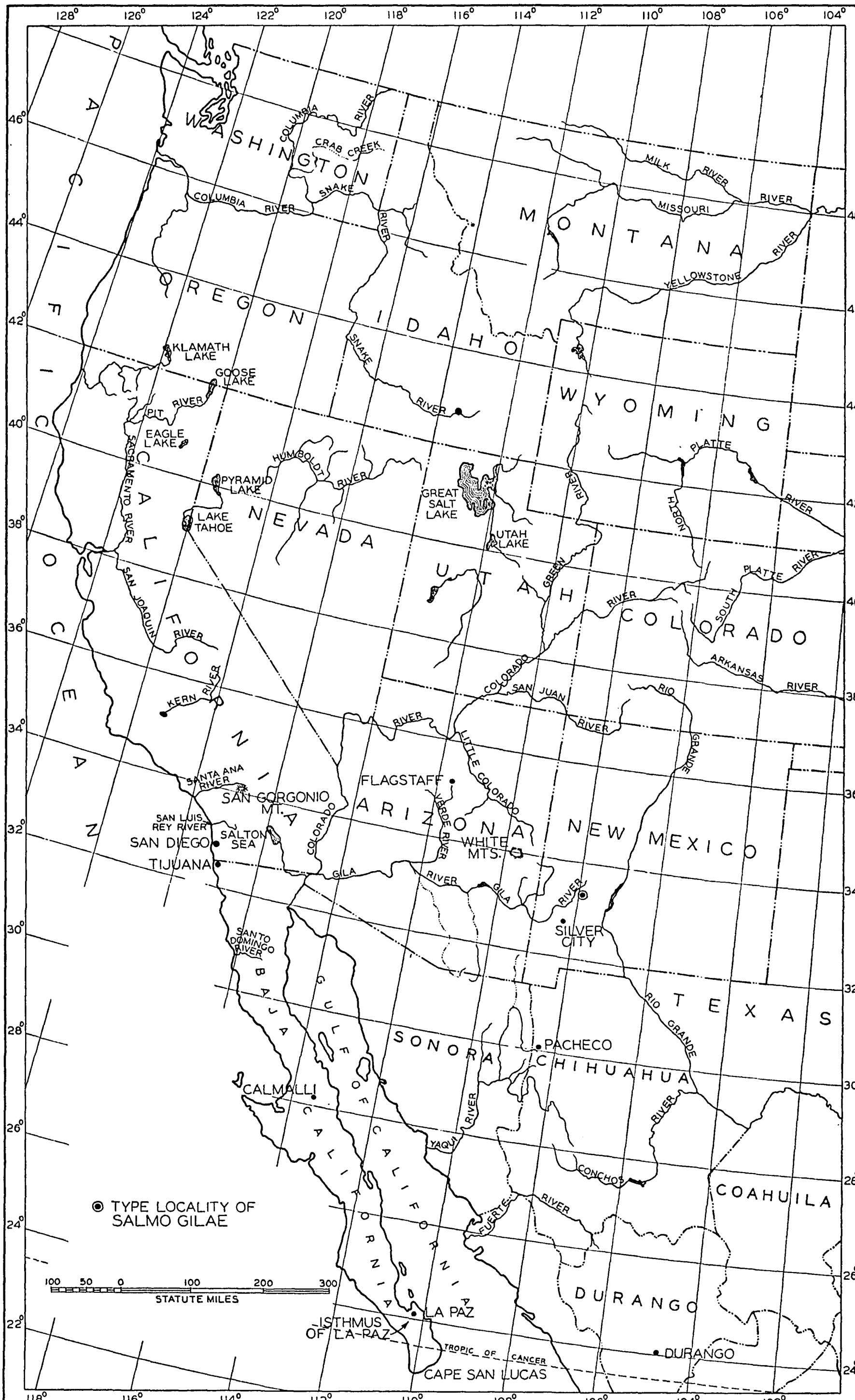
There have been sporadic attempts to investigate the systematics of these perplexing fishes, but such studies have been either too local in scope, too brief in duration, or have been based on insufficient material. Consequently, we still have a great deal to learn about the classification of the genus *Salmo.* Nor has the interpretation of this plastic group been rendered easier with the passage of time. Nevertheless, I feel that a reasonable solution is still possible. In my opinion such a solution will necessitate a long-time research program involving a 4-way attack: (1) critical examination of old museum collections for specimens secured prior to the major mixing and eradication of stocks; (2) thorough field work, including an exhaustive tagging program to determine, in particular, the status of migratory and nonmigratory forms; (3) careful and extensive experimental work designed to test the validity of systematic characters that have been used to distinguish trouts; and (4) detailed studies of collections of recent material from areas where introductions have not hopelessly confused the picture. It is expected that studies of comparative osteology would play an important role in determining relationships.

Among the forms commonly recognized (Jordan and Evermann, 1898: 2819; Dymond, 1932; Schultz, 1935; Mottley, 1936; Snyder, 1940; Shapovalov, 1941; and others) in the rainbow trout and the cutthroat trout series, either as subspecies of *S. gairdnerii* or of *S. clarkii*, or as full species, are the following:

Rainbow Trout Series	Cutthroat Trout Series
S. gairdnerii gairdnerii Richardson Steelhead	*S. clarkii clarkii* Richardson Coastal cutthroat
S. gairdnerii irideus Gibbons Coast rainbow	*S. clarkii lewisi* (Girard) Yellowstone cutthroat
S. gairdnerii gilberti Jordan Kern rainbow	*S. clarkii alpestris* Dymond Mountain cutthroat
S. gairdnerii nelsoni Evermann Baja California rainbow	*S. clarkii utah* Suckley Utah cutthroat
S. gairdnerii kamloops (Jordan) Kamloops rainbow	*S. clarkii henshawi* Gill and Jordan Lahontan cutthroat
S. gairdnerii whitehousei Dymond Selkirk rainbow	*S. clarkii seleniris* Snyder Piute cutthroat
S. gairdnerii aquilarum Snyder Eagle Lake rainbow	*S. clarkii pleuriticus* Cope Colorado cutthroat
S. smaragdus Snyder Emerald trout	*S. clarkii stomias* Cope Platte cutthroat
S. regalis Snyder Royal silver trout	*S. clarkii macdonaldi* Jordan and Evermann Yellowfin cutthroat
S. agua-bonita Jordan South Fork golden trout	*S. clarkii virginalis* (Girard) Río Grande cutthroat
S. whitei Evermann Soda Creek golden trout	*S. clarkii eromogenes* Evermann and Nichols Crab Creek cutthroat
S. roosevelti Evermann Volcano Creek golden trout	*S. evermanni* Jordan and Grinnell San Gorgonio trout

Recent students of the genus *Salmo*, except Snyder (1940: 123), have accepted *gairdnerii* as the specific name of the rainbow trout. Whether Gairdner's specimen had coarse or fine scales cannot be determined from the original description. Kendall (1921: 196) insisted that the steelhead is coarse-scaled and he has been followed by almost all recent workers.

Map 1. Part of western North America showing localities mentioned in the text.



PACIFIC OCEAN
WASHINGTON
OREGON
CALIFORNIA
NEVADA
IDAHO
MONTANA
WYOMING
UTAH
COLORADO
ARIZONA
NEW MEXICO
TEXAS
SONORA
CHIHUAHUA
COAHUILA
DURANGO
BAJA CALIFORNIA
GULF OF CALIFORNIA
COLUMBIA RIVER
CRAB CREEK
SNAKE RIVER
MILK RIVER
MISSOURI RIVER
YELLOWSTONE RIVER
KLAMATH LAKE
GOOSE LAKE
PIT RIVER
EAGLE LAKE
SACRAMENTO RIVER
HUMBOLDT RIVER
PYRAMID LAKE
LAKE TAHOE
GREAT SALT LAKE
UTAH LAKE
GREEN RIVER
PLATTE RIVER
NORTH
SOUTH PLATTE RIVER
ARKANSAS RIVER
SAN JOAQUIN RIVER
KERN RIVER
COLORADO RIVER
SAN JUAN RIVER
RIO GRANDE
LITTLE COLORADO
FLAGSTAFF
VERDE RIVER
WHITE MTS.
SANTA ANA RIVER
SAN GORGONIO MT.
SAN LUIS REY RIVER
SAN DIEGO
SALTON SEA
TIJUANA
GILA RIVER
SILVER CITY
SANTO DOMINGO RIVER
PACHECO
YAQUI RIVER
CALMALLI
CONCHOS RIVER
FUERTE RIVER
LA PAZ
ISTHMUS OF LA PAZ
TROPIC OF CANCER
DURANGO
CAPE SAN LUCAS
TYPE LOCALITY OF SALMO GILAE
100 50 0 100 200 300
STATUTE MILES

The data given by Schultz (1935: 3779, 3782) would seem to indicate that Kendall was right, for *Salmo gairdnerii gairdnerii* is credited with having 120 to 138 scales, thus agreeing with Kendall's statement that the steelhead has "about 130" scales. The problem is complicated, however, by the existence of both fine-scaled and coarse-scaled steelheads in the lower Columbia River Basin and elsewhere (Jordan and Evermann, 1896: 498; Schultz, 1935: 3779). This parallels the situation in *Salmo clarkii,* which also has a fine-scaled and a coarse-scaled representative in the lower Columbia, although only one of these is believed to be anadromous (Schultz, 1936: 136, 137). Much more field work, and particularly experimental work such as that carried out recently by Neave (1944), is needed to clarify this long-standing problem. The term steelhead, if it is to be used, should be restricted to the sea-run rainbow. If we are going to apply the term to both the sea-run rainbow and the sea-run cutthroat (as was done by Snyder, 1940: 101), then it should be abandoned in favor of either the name anadromous trout or sea-run trout.

The recognition of subspecies in either the rainbow or the cutthroat series is necessarily provisional. In particular the status of *Salmo gairdnerii aquilarum,* the trout of Eagle Lake, Lassen County, California (Map 1), is uncertain. On the basis of an examination of the 2 types and an analysis of the original description by Snyder (1917: 77–78), Hubbs and Miller (1948: 38) regarded *aquilarum* as a probable hybrid between *S. gairdnerii* and *S. clarkii.* This interpretation, although logical, may be erroneous. A study of this trout is now under way by the California Division of Fish and Game, and this may lead to a confident decision on its status. If *aquilarum* is not a hybrid, specimens of this trout should show uniformity in counts, proportions, and life colors. If valid, *aquilarum* should probably be accorded only subspecific ranking in the rainbow series, as was suggested by Shapovalov (1941: 443).

Another questionable form is *S. gairdnerii nelsoni,* originally described as a full species because of a major error in scale count. It is doubtfully distinct from *S. g. irideus.* Hubbs (1946: 84–85) commented as follows on the status of this trout: "I find nothing in the published accounts of *S. nelsoni* to justify its separation even as a subspecies of the coarse-scaled rainbow trout (*S. gairdnerii irideus*) of coastal streams in California. Nor do specimens of the Baja California trout recently collected by Carl I. Johnson appear distinctive." It is likely, however, that even in this remote area, plantings of coast rainbow trout have affected the original characters of this trout (see discussion under the section on Relationships and Origin).

The Shasta rainbow of fish culture fame, *S. gairdnerii shasta* Jordan, is now regarded as inseparable from *S. g. irideus* (Hubbs and Follett, in Hubbs and Wallis, 1948: 134). Wales (1939: 282) suggested, after examining the types of *Salmo gairdnerii stonei* at Stanford University, that this subspecies might be the same as the steelhead. In 1945 Hubbs and Follett studied the same type specimens and confirmed the identification with *S. g. gairdnerii* (which name they apply to the fine-scaled form).

The Kamloops rainbow trout, *S. gairdnerii kamloops* (Jordan), is now generally regarded as a subspecies of *S. gairdnerii,* but Dymond (1947: 10, 11) retained the name *S. kamloops* for this fish. It seems to have been generally overlooked that this trout was evidently first described in the genus *Oncorhynchus.* This is a complex nomenclatorial problem and, to save others from the tedious task of tracing the history of this tangle, the case is presented in some detail. Jordan evidently submitted the manuscript, describing the Kamloops trout as a full species, to three different sources simultaneously: the Smithsonian Institution, *Forest and Stream,* and the California State Board of Fish Commissioners. The paper was not published by the Smithsonian Institution, although it was so credited by Jordan and Evermann (1896: 500). It did come out in the other 2 publications (Jordan, 1892 *a, b*) and the 2 accounts are almost identical. It seems clear that after he had submitted the manuscripts, Jordan decided that the reference to *Oncorhynchus* was an error, and when he received the proofs from the California State Board of Fish Commissioners, he changed the paper accordingly. Since he evidently never received proofs from *Forest and Stream,* the article came out in that publication unchanged. The issue of *Forest and Stream* containing Jordan's paper bears the date November 10, 1892, and since this serial was issued like a newspaper that is unquestionably the actual date of publication. I have not seen the article published by the California State Board of Fish Commissioners, but the original has been laboriously copied for me by W. I. Follett, who has also made every effort to determine the date of publication. Inquiries by Follett to the California Division of Fish and Game in the Ferry Building, San Francisco, to Dr. Carlton M. Herman, editor of the California Division of Fish and Game at Berkeley, to the California State Librarian at Sacramento, and to the California state printer at Sacramento failed to yield information on the date of publication of the report in question. At the main library of the University of California, however, he found that their copy of the *Biennial Report for 1891–1892* bore the date "DEC 5 1892," obviously the impression of a dating stamp. Since this appears to be the only evidence of the date of publication, I regard *Oncorhynchus kamloops* as having priority over *Salmo kamloops.* Follett concurs in this interpretation. The name *Salmo kamloops* actually first appeared as a *nomen nudum* (in Jordan, 1892*a:* 405) in a popular account of the trout by "G. B. C.," which immediately preceded Jordan's description of the fish as *Oncorhynchus kamloops.*

Although failing to mention that *S. clarkii seleniris* has hyoid teeth, Snyder (1933, 1934) clearly demonstrated that the Piute trout was derived from the Lahontan cutthroat (*Salmo clarkii henshawi*). A recent examination of specimens from Silver King Creek below Llewellyn Falls (U.M.M.Z. No. 157655) showed individuals that vary from almost unspotted to well spotted; the 2 forms thus intergrade in one of the most striking features thought to characterize *seleniris.*

As Miller and Alcorn (1946: 176) pointed out, *Salmo clarkii henshawi* of the Lahontan Basin in California, Nevada, and Oregon, is virtually extinct. *S. clarkii utah* of the comparable Bonneville Basin in Utah and Idaho, is believed to be extinct. *S. clarkii stomias,* described from the Platte River, has not been taken in recent years and *S. clarkii macdonaldi* of Twin Lakes, Colorado, in the basin of the Arkansas River, has been extinct for many years. The cutthroat indigenous to Crab Creek, Washington (Map 1), *S. clarkii eromogenes,* is also believed to have disappeared (Hubbs and Miller, 1948: 76).

In the original description of *S. evermanni,* it is stated that hyoid teeth are present and I have verified this on the 2 paratypes in the United States National Museum. Unfortunately, the presence or absence of a cutthroat mark on the San Gorgonio trout was not recorded. Richard S. Croker, however, wrote (December 8, 1949) that he observed no red cutthroat mark on the 2 San Gorgonio trout he caught on June 23, 1935. These specimens, 6 to 7 inches long, were a uniform dark brown (somewhat lighter on the belly) with very pronounced black spots. He felt that they were cutthroat derivatives and since *evermanni* agrees with the cutthroat series in all other characters, there seems to be no basis for considering this trout to be a rainbow derivative, as held by Jordan and Grinnell (1908), Evermann and Bryant (1919: 108–9), Snyder (1940: 99), and Shapovalov (1941: 443). *Salmo evermanni* might be regarded as a subspecies of *Salmo clarkii,* but its life colors are distinctive and it may have other attributes that warrant its retention as a full species.

The golden trouts may well represent only 1 or 2 species (Curtis, 1935 *a, b*), but critical studies of these forms in their native habitat are yet to be made in order to clarify their status. Until such studies are made and published I prefer not to shift from one problematical solution to another.

In the face of these difficulties and uncertainties concerning the classification of American trouts, the addition of another species to the system may well be questioned. A comparison of the 75 specimens on which the novelty here described is based, with type specimens of 13 nominal species of Western trouts in the United States National Museum, with topotypes of 4 other forms from the West, and with large series of rainbow and cutthroat trouts from the Pacific Coast (Washington to near Durango, Mexico, see Map 1), the Great Basin, and the southern Rocky Mountains, convinces me that the recognition of this trout is justified. The reasons for according the Gila trout full specific status are presented under the section on Relationships and Origin. Prior notice of this species has been given by Hubbs (1948: 463), who gave the initial clues to its determination and who concurs in the specific separation.

In the summer of 1939, at the request of Elliott S. Barker, State Game Warden of New Mexico, Dr. Hubbs asked me to obtain series of a trout which Mr. Barker and others felt sure was new to science. By prearranged plan, Superintendent Edwin Shelly of the Glenwood Fish Hatchery gave me 13 fine specimens from his brood stock and directed me to Diamond Creek, one of the last strongholds of this trout, where 62 additional specimens were seined. It is a pleasure to acknowledge the splendid co-operation offered by Mr. Barker and his staff, not only on this occasion but in later correspondence regarding this fish.

The few native trouts which yet survive in the intermountain and Rocky Mountain regions have been able to do so only in the more inaccessible areas, far removed from centers of population. The headwaters of the Gila River in New Mexico, where the trout described below has managed to persist, is such a remote region. Even today much of it is inaccessible except by rough trails. Although only a small fraction of its former range is now inhabited by the Gila trout, the commendable conservation policy of the New Mexico Department of Game and Fish in not stocking exotic species in certain tributaries has made possible the perpetuation of one of the few remaining native trouts of the American Southwest.

Salmo gilae, new species
Gila trout
(Pl. I)

TYPES.—The holotype, a mature male 204 mm. in standard length, University of Michigan Museum of Zoology No. 137088, was secured by R. R. Miller from brood stock at the Glenwood Fish Hatchery, Glenwood, Catron County, New Mexico, on July 17, 1939. The stock reared at this hatchery came from Diamond Creek, a tributary of Gila River, approximately 33 miles east-southeast of Beaverhead, Sierra County (Map 1). Twelve paratypes, U.M.M.Z. No. 137089, 110 to 225 mm. long, were obtained with the holotype. Sixty-two paratypes, 53 to 128 mm. long, U.M.M.Z. No. 137090, were seined from Diamond Creek on July 18, 1939, by R. R. Miller and J. Davis.

DIAGNOSIS.—An outstanding characteristic of this species is the extremely fine and profuse spotting on the dorsal and caudal fins. The body spots are mostly restricted to the region above the lateral line, and the adipose fin is unusually large and well spotted. In life, the body is deep golden yellow, with a yellowish "cutthroat" mark. The head is long and conical and the maxillary is long, extending far behind the eye. The moderate-sized scales number 133 to 151 along the side just above the lateral line. Pyloric caeca usually number 31 to 36. There are no hyoid teeth.

DESCRIPTION.—The shape of the body, the size of the adipose fin, and the diagnostic spotting are well portrayed on the holotype (Pl. I). Proportional measurements of 16 specimens are given in Table I.

The number of fin rays of 34 specimens vary as follows: dorsal, 10 to 12, usually 10 or 11 (mean 10.73); anal, 9 to 11, usually 10 or 11 (10.32); pectorals, 13 to 15, usually 14 (13.83); pelvics, 9 or 10, usually 10 (9.63); and caudal, in-

TABLE I

PROPORTIONAL MEASUREMENTS OF *Salmo gilae*

For each measurement, that for the holotype excepted, there is given the range and, in parenthesis, the mean. There is so little sexual dimorphism that the sexes are combined.

Measurement	Holotype (♂)	9 Paratypes from Hatchery	6 Paratypes from Diamond Creek
Standard length, mm.	204	152–225 (174)	72–126 (104)
In thousandths of the standard length:			
Dorsal origin to tip of snout	525	505–540 (521)	523–542 (534)
Pelvic origin to tip of snout	554	546–568 (559)	556–570 (565)
Occiput to tip of snout	189	183–200 (191)	199–223 (210)
Anal origin to caudal base	273	258–284 (269)	266–275 (271)
Body, greatest depth	246	226–251 (239)	256–284 (271)
Greatest width	112	117–130 (123)	127–153 (141)
Head, length	293	274–307 (293)	296–320 (306)
Depth	181	170–183 (179)	178–203 (192)
Width	132	126–145 (136)	124–153 (142)
Caudal peduncle, length	161	148–169 (156)	151–168 (162)
Least depth	110	106–116 (111)	113–121 (116)
Interorbital, least bony width	78	72– 79 (75)	67– 75 (70)
Preorbital, least width	9.3	8.3–11.6 (9.7)	7.9–9.8 (8.7)
Upper jaw, length	172	153–190 (168)	162–175 (169)
Snout, length	69	65– 76 (72)	66– 77 (71)
Eye, length	60	55– 66 (60)	69– 89 (78)
Adipose fin, depressed length	109	104–122 (110)	118–125 (122)
Dorsal fin, basal length	139	133–149 (139)	138–148 (142)
Depressed length	241	222–249 (235)	237–253 (243)
Anal fin, basal length	112	105–122 (112)	107–120 (113)
Depressed length	167	153–174 (164)	174–190 (180)
Middle caudal rays, length	143	128–156 (139)	141–162 (147)
Pectoral fin, length	178	166–188 (176)	187–211 (197)
Pelvic fin, length	142	137–162 (148)	151–164 (161)

variably 19. The last ray of the dorsal and anal fins, split to the base, was always regarded as a single ray; the first ray counted in these fins was the last unbranched ray, which was always preceded by several, progressively shorter, unbranched rays. All rays of both pectoral and pelvic fins were counted, and the number of caudal rays is that of the branched rays

plus 2 unbranched rays on either side. The number of scales along the side, counted 2 rows above the lateral line,[2] varies from 133 to 151 (141.24) in 25 specimens; those above the lateral line number 24 to 29 and those below vary from 23 to 27 in 16 specimens. The gill rakers on the first arch in 25 specimens, rudiments included, number 7 to 9 above the angle and 10 to 11 below, making a total variation of 18 to 20 (19.00), usually 19. In the same specimens the branchiostegals, recorded for both sides, vary from 9 to 11 (10.22), rarely 9; where there was a difference in count for the 2 sides, the left side always was the greater. The vertebrae number 59 to 62, usually 60 (60.20), in 20 specimens. The pyloric caeca in 10 specimens average 34.90 and number 31 to 36 in 9 specimens and 42 in 1.

The head is long and conical and the snout is pointed, like that of the cutthroat trout; the head length enters the standard length 3.15 to 3.7 (usually 3.3 to 3.5) times in 24 specimens (fingerling to adult). The upper jaw is long, its length entering that of the head 1.55 to 1.9 times in specimens varying from 99 to 224 mm. in standard length. The maxillary extends well beyond the large eye, as in *Salmo clarkii.*

No trace of hyoid teeth was found on 15 specimens of graded sizes examined for this character. The examination was made under magnification using a bright light, a jet of compressed air, and a delicate probe.

There is little variation at any given size in the shape of the caudal fin, which grades from weakly forked in the young to nearly emarginate in the large adults. The size of the pectoral fin appears to change very little with age; its length varies from 1.5 to 1.6 times that of the head length. The small axillary scale of the pelvic fin also varies little in size; its length (as measured from the insertion of the pelvic fin) is less than one-third that of the pelvic, less than one-fourth in some individuals.

COLORATION.—The life colors of *Salmo gilae* were carefully

[2] Following a method established by John O. Snyder. For a discussion of the methods of counting scales on salmonids see Neave (1943).

noted at the time of capture, both for the hatchery and for the wild stocks.

In the hatchery stock, in life, the fins are watery white on their posterior borders. The rays of the pectoral, pelvic, and anal fins vary from yellowish through yellowish orange to reddish orange, with the color most intense medially and fading posteriorly. The first rays of the dorsal are watery yellow to nearly white at the tips, and the posterior tips of the first rays of the pelvic and anal are milky white. Under the lower jaw there is a deep yellow to watery yellow "cutthroat" mark, which is unlike the intense blood-red streak characteristic of *Salmo clarkii.* Superintendent Shelly told me that the oldest fish have this mark best developed, but that it remains comparatively faint throughout life. The scales along the sides are golden yellow, fading to silvery above the lateral line, where they show bluish reflections. The yellow of the sides extends nearly to the belly; Mr. Shelly said that in 18-inch fish the entire belly is golden yellow. On some the belly is pinkish from the insertion of the pelvics nearly to the base of the pectorals. In nearly all of the younger fish the "rainbow" band on the side is evident, but it is very faint and has indistinct borders. On many of the larger fish it becomes almost wholly obsolete. The operculum is mostly golden, silvery on one specimen, with pinkish diffusion and turquoise reflections anteriorly.

The largest hatchery fish (a mature male and "truer to type than any other," according to Shelly) is deep golden yellow along the sides and belly, but this color fades rapidly above the lateral line, where the scales become silvery with a golden sheen and blue reflections. The faintly olive-yellow "cutthroat" mark of this individual extends to the tip of the jaw. Most of the lower rays of the anal fin are reddish orange; the remainder, deep yellowish orange. The pectorals and pelvics are deep yellowish orange and the caudal and dorsal are also yellowish. There is no "rainbow" band.

A sample of the wild stock seined at Diamond Creek, from which the hatchery brood stock was obtained, was described as follows. The dorsal and anal fins are watery yellow. The tips of the first 3 or 4 dorsal rays are yellowish orange to watery pink—almost milky white on the young; the first 5 or 6 rays of the anal fin are tipped with milky white, as are the outer rays of the pelvics; the rays of the pectorals are golden orange and the posterior margins of the paired fins and the anal are watery white. The adipose fin is deep yellow. The "cutthroat" mark is mustard yellow, varying to watery yellow, and is always quite faint; it is present on the young as well as on the adults and is barely visible externally when the jaws are closed. The belly varies from grayish white to orange and pinkish orange. In some specimens the area covered by such color is limited; in others, it extends from the base of the pectorals to the base of the anal, fading rapidly posterior to the base of the pelvics. The "rainbow" stripe along the side is rather well developed and varies from reddish pink to reddish orange. The scales are silvery, with a deep golden-yellow sheen along the sides, fading rapidly above the lateral line. The operculum is dull silvery, with a reddish-orange to bronze sheen and with turquoise reflections anterodorsally.

Differences in the sizes of the individuals and in the contrasting environmental conditions explain the slight differences in coloration between the two stocks described above. The largest fish in the stream collection is 128 mm. long, whereas the largest in the hatchery sample is 225 mm. long. Diamond Creek was well shaded and its waters were clear, whereas at the hatchery the brood stock was reared in open concrete pools containing brownish-white water.

The life colors of a trout, which almost surely was *Salmo gilae*, were described as follows in the field notes of the late F. M. Chamberlain, who made collections for the United States Bureau of Fisheries in southern Arizona in the spring of 1904 (these notes were kindly deposited by Isaac Ginsburg in the Division of Fishes of the National Museum). Between April 11 and 13, 1904, Chamberlain investigated "K. P. Creek," about 32 miles above the mouth of Blue Creek

(= Blue River), a tributary of San Francisco River of the Gila River system, in Greenlee County, Arizona. Only trout, the largest about 9 inches long, were secured by him in this creek. "They are golden on sides of head, body, and belly; pectorals golden, ventrals less so; ventrals and anal with white margin. About 10 roundish dark blotches [parr marks] on side, somewhat larger than eye; one or two supplementary rows of similar but smaller blotches all being below and independent of the regular black spots covering the upper parts, head, caudal, and dorsal fins. Rosy streak along side, along and under the lateral line about the breadth of the eye. The general golden color is said to increase with size, hence the larger ones are sometimes referred to as a different 'kind,' the 'yellow trout'." This description agrees very closely with the life colors and color pattern of the types of *S. gilae*. Although Chamberlain's large collection of southern Arizona fishes is now catalogued in the National Museum, these trout were unfortunately not found and are presumably lost. Hence the identity of the fish cannot be certain.

Spots and parr marks.—One of the outstanding characteristics of *Salmo gilae* is its distinctive spotting (Pl. I). The round to oval spots are particularly fine and dense on the dorsal and caudal fins, finer than in any other trout that I have seen. The largest of these spots, along the base of the dorsal fin, are only about two-thirds the diameter of the pupil; elsewhere on the dorsal and caudal fins they are usually uniformly small. Spots as large as half the diameter of the pupil occur on the dorsal fins of some of the fingerlings. The spotting of the caudal fin of the fingerlings is much less developed than it is on the adults. The spots are much larger on the top of the head, the anterior part of the back, and on the adipose fin. Those on the adipose are largest, of about the same size as those along the dorsal base. The number of spots on the adipose varies from 6 to 24. The anal fin and the paired fins are immaculate. Distinctive also is the usual lack or faint development of spots below the lateral line, especially in advance of the caudal peduncle. The sides of the head also largely lack spots. The number of spots, particularly on the caudal fin and on the top of the head, varies considerably, as does the size of the spots, especially those on the top of the head. The maxillary is usually unspotted.

Parr marks are still evident in hatchery specimens as large as 175 mm. standard length (about 8 inches total length), and a trace of these marks is still retained on a male 193 mm. long ($8\frac{3}{4}$ inches). Well-developed parr marks are retained on the 2 largest fish of the wild stock, males 125 and 128 mm. long (about 6 inches total length).

HABITAT AND ABUNDANCE.—Only a few remote upper tributaries of Gila River and San Francisco River, New Mexico, now support populations of *Salmo gilae*. Diamond Creek, the only stream from which we collected the species, lies about 33 miles east-southeast of Beaverhead, Sierra County (T. 11 S., R. 10 W.), in the Gila National Forest (Map 1; also see United States Forest Service map of Gila National Forest, New Mexico, 1946). The stream cuts through the heavily forested, rugged Black Range Primitive Area, approximately 8000 feet above sea level, and could be approached on July 18, 1939, only by a very rough road followed by a long hike from the canyon rim down to the stream bed. At the time of our visit there was very little water in the creek at "James Bros. Cabin," where we seined the trout. The water was sparkling and clear, with a temperature of 62.6° F. (air 64.4° F.) in late afternoon. The bottom consisted of coarse sand, gravel, boulders, and some silt, and the current varied from none to slight. Bordering Diamond Creek were stands of quaking aspen, alder, and yellow pine, but the only vegetation noted in the creek was a sparse growth of algae. The stream had a maximum width of about 9 feet and the water was up to $1\frac{1}{2}$ feet deep. The creek was rather well shaded. It had been closed to fishing for some time and logs had been placed across the stream to afford further cover for the trout.

Local testimony indicated that the stream contained few trout of small size as compared with the size and abundance some years earlier. About 4 miles below where we seined, large pools were reported and these were said to contain the largest fish—as long as 1 foot. We were told that the stream was dry from about 1½ to 4 miles below James Cabin, the point where we collected, but that it was permanent for 7 miles above. At the point 4 miles below, the stream again became permanent and continued to flow on the surface for an unknown distance. The creek is normally dry for 10 to 15 miles, more or less, above its junction with Gila River. On July 18, 1939, Diamond Creek was dry at the crossing on the road between Beaverhead and Mimbres, about 7 miles above its mouth in Gila River. Information received locally and from state officials supports the view that Diamond Creek has never been stocked. Recent correspondence with Elliott S. Barker, New Mexico State Game Warden, and Fred A. Thompson, New Mexico Director of Fisheries, indicates that Spruce Creek is the only other stream now containing a sizeable, natural population of *Salmo gilae.* This creek lies about 10 to 12 miles east of Glenwood, and is tributary to San Francisco River. It is believed, however, that there are some remnant stocks of Gila trout in nearly all of the upper tributaries of Gila River. If this is true it seems safe to assume that these stocks have largely hybridized with the introduced rainbow trout. *Salmo gairdnerii irideus* is now being planted in almost all of the Gila and San Francisco tributaries except Diamond and Spruce creeks. The New Mexico Department of Game and Fish resorted to the stocking of rainbow trout because it was found that heavy fishing pressure and changing water conditions had brought about the decline of the native trout and because the department was unsuccessful in rearing *Salmo gilae* (see below).

Through the generous efforts of Fred A. Thompson in interviewing ''old-timers'' and others, valuable data dealing with the waning abundance of the Gila trout and with its original distribution and early stocking is available. In 1896

Salmo gilae ranged as far down Gila River as the mouth of the box canyon, which is about 7 miles northeast of Cliff. At that time there were no suckers or chubs in this section of the river, but now this area is alive with these fishes. "Speckled trout" were once so abundant in Gillita and Willow creeks (tributaries to the Middle Fork of the Gila) that it was possible to catch them at the rate of about 1 a minute. The usual weight of these fish varied from one-half to 1 pound and they averaged about 12 inches in length. On the West Fork, in contrast, these trout did not usually weigh more than one-fourth of a pound. Native trout fishing was good on South Diamond Creek and Black Canyon, just north and south, respectively, of the Sierra-Grant county line, but on certain parts of Mogollon Creek, particularly the West Fork (T. 2 S., R. 17 W.), there was an overpopulation of native trout and the fish were dwarfed. The largest fish caught by one "old-timer" in the early days weighed 2 pounds and was taken at the junction of the Middle and West Forks of the Gila, just west of the Gila Cliff Dwellings National Monument. In 1898 the Gila trout was found in all of the Gila headwaters and was generally referred to as "mountain trout." In later years these fish were found in Whitewater Creek, a tributary of San Francisco River near Glenwood. In 1915 trout were caught as far down the Gila as the mouth of Sapillo Creek (T. 14 S., R. 14 W.). At the present time the water is generally too warm in that section of Gila River for any species of trout.

Mr. Edwin Shelly, formerly superintendent of both the Jenks Cabin and Glenwood hatcheries, reported that his uncle caught "speckled trout" in the Gila as early as 1890. This common name is attributed to the fact that the early settlers, who originally came from the eastern United States, were familiar with no trout other than the eastern brook or "speckled" trout. The second generation of inhabitants in the Gila country customarily adopted "native trout" as the common name. According to testimony related to Mr. Shelly by an "old-timer," the San Francisco River was originally without native trout. In 1905 three men were hired by some prospectors and miners at Mogollon to pack fish from the Gila drainage to Big Dry Creek, Little Dry Creek, Little Whitewater Creek, Whitewater Creek, and Mineral Creek, tributaries of the San Francisco (or "Frisco") River. These fish were transported successfully across the divide in beer kegs carried on mules. The largest native trout seen by Mr. Shelly was $21\frac{3}{4}$ inches long. This fish, retained in the hatchery for 2 or 3 years, was then released and caught 2 years later in a neighboring stream (a distinctive scar received from an old injury confirmed the identity of the fish).

PROPAGATION.—From 1923 until 1947 the New Mexico Department of Game and Fish attempted to propagate this species with varying results. In 1923 a small hatchery, the Jenks Cabin Hatchery, was built in the heart of the Gila Wilderness Area, 18 miles by pack trip from the nearest road. It was located on the West Fork of the Gila River at its junction with White Creek (T. 12 S., R. 16 W.), a tributary rising on the eastern slopes of Mogollon Baldy Peak in south-central Catron County. It was possible to keep the trout in captivity, and some of the brood stock attained a length of 16 inches. In taking spawn from these fish, however, a very low percentage of fertilization resulted, perhaps because techniques were inadequate. The fish that were raised were planted as very small fingerlings because it was too expensive to transport food to the remote hatchery by pack animal. About 1935 this hatchery was abandoned since the low yield of fish did not justify the expense required to maintain it.

Another hatchery was constructed at Glenwood Springs, Catron County, but efforts to rear the Gila trout here also met with little success. It is assumed that the water temperature was too high for the adult trout, particularly for the successful development of the eggs after they were stripped and fertilized. Attempts to raise this trout at another hatchery, having a colder water supply, also failed, and the venture was finally abandoned about 1947.

According to reports from "old-timers" and those who have had the rare opportunity to fish for *Salmo gilae,* this trout possesses excellent game and fighting qualities. In the early 1900's, many people fished for this species and spoke highly of its sporting traits and also held it in high esteem as a table delicacy.

RELATIONSHIPS AND ORIGIN.—In attempting to determine the relationships of the Gila trout, I have tried to work out a set of characters (Table II) that will aid in distinguishing the rainbows from the cutthroats. This provisional comparison is based only on forms currently regarded as subspecies of *gairdnerii* or *clarkii* (see page 4) and does not represent an exhaustive study. The comparison brings together information that has been used to distinguish these species and its publication will, it is hoped, stimulate more thorough research on the systematics of these 2 complex species groups. I know of no single character that will invariably separate all forms of rainbow and cutthroat trout.

It seems desirable to enlarge upon the characters mentioned in the comparison (Table II).

Cutthroat mark: This is one of the most useful characters for distinguishing rainbow and cutthroat trouts, but its use is almost entirely limited to identifications of freshly caught specimens or of those accompanied by critical color notes. The mark fades very rapidly after the death of the fish and is reported to be obsolete in some sea-going cutthroats (Dymond, 1928: 72; Carl and Clemens, 1948: 42). Pure-blooded rainbows show no such mark or only a faint expression of it, but hybrids typically show color of intermediate intensity and development. The mark is much less developed in young and half-grown fish than it is in adults. It is particularly bright in breeding males.

Some confusion regarding this character has arisen from time to time. For example, Gilbert and Evermann (1894: 200–201) clearly had *Salmo gairdnerii* and *Salmo clarkii* badly confused in their account of *Salmo mykiss* (the name formerly used for the cutthroat trout). The conflicting statements regarding the presence or absence of the cutthroat

TABLE II

PROVISIONAL COMPARISON BETWEEN THE TROUTS OF THE RAINBOW AND CUTTHROAT SERIES

See text for discussion of characters.

Character	Rainbow (*Salmo gairdnerii*)	Cutthroat (*Salmo clarkii*)
Cutthroat mark	Absent; occasionally with an indistinct, pale yellowish or reddish dash	Usually a conspicuous blood-red dash, visible externally, varying from yellowish orange through reddish orange to salmon and strawberry; weaker in young fish and occasionally faint in adults*
Hyoid teeth	Absent	Present but frequently small and scattered and reportedly obsolete on old adults
Border on anal, pelvic, and dorsal fins	Conspicuously milky white, orange or yellowish in life; typically well defined	Typically not conspicuously light; red, rosy, dusky or plain in life; tips of fins occasionally light†
Red lateral band	Usually broad and well developed, with definite margins; red or pink in life	Usually weak or absent; sometimes with a reddish-pink or salmon-pink "band," but narrower than the "rainbow band" of *gairdnerii*
Length of upper jaw in adults‡	Usually noticeably shorter; 1.9 to 2.2, usually 2.0–2.1, in head	Usually conspicuously longer; 1.6 to 2.1, usually 1.7–1.9, in head
Number of scales	Generally fewer; usually less than 150 (116 to 165)	Generally more, usually 150 to 180 (143 to 230) but 120 to 140 in anadromous form from Puget Sound, Washington, and elsewhere
Shape of head	Shorter and blunter; rounded	Longer and more pointed; conical
Shape of body	Generally deeper and heavier-set	Generally more slender and more compressed
Spotting	Spots usually smaller, more irregular in size and shape and more diffuse	Spots usually larger, more regular in size and shape and more restricted (except in *S. c. clarkii*)
Pyloric caeca§	39 to 80	27 to 45

* Faint or absent in anadromous cutthroats, *fide* Dymond (1928 : 72) and Carl and Clemens (1948 : 42).

† In *S. clarkii clarkii,* fin tips may be bright—even brighter than in most rainbows.

‡ There is considerable sexual dimorphism in this character, particularly in breeding fish. According to Stokell and Stokell (1937 : 367), the maxillary becomes attenuate in old rainbows, extending far beyond the eye.

§ Based on data given by Townsend (1944 : 54), Shapovalov (1947 : 190), and by Stokell and Stokell (1937 : 371–72). The latter recorded one rainbow with 91 caeca.

mark in their material are explainable on the grounds that their description of the cutthroat applies in part to the coarse-scaled, sea-run rainbow (Newaukum River at Chehalis), in part to the fine-scaled type of rainbow currently called *S. g. kamloops* (Wood River), and in part to intergrades between *S. g. gairdnerii* and *S. g. kamloops* (Umatilla, Natchess, and Pataha rivers).

Hyoid teeth: This is an important and helpful character but in looking for these teeth, special caution should be used. The presence or absence of hyoid teeth often can be determined only by extremely careful examination. I use adequate magnification, a bright blue light, a jet of compressed air, and an exceedingly fine dissecting needle that will not break off the teeth. I have found from 2 to 20 (usually about 4 to 8) hyoid teeth in the cutthroat trout examined,[3] but frequently it has been necessary to search many minutes before locating them, as they are often hidden by the mucous covering on the tongue and are easily scraped or broken off. A jet of compressed air is often more useful than probing, for shrinkage of the mucus by desiccation brings the teeth into relief. Trout having hyoid teeth are not necessarily cutthroats, for hybrids may have as many as 6 such teeth. Conversely, trout lacking hyoid teeth are not always rainbows, for hybrids may, and usually do, have no hyoid teeth. These teeth vary in number and development in the various forms of *S. clarkii*. A statistical study of this variation would reward the investigator for his painstaking work.

Coloration of fins: This character, like that of the cutthroat mark, is more useful in field identifications than it is after the specimens have been preserved for a long time. The pale edgings, however, usually are retained long after the cutthroat mark fades. Hybrids typically show an intermediate development of the light borders on the anal, pelvic, and dorsal fins. The character breaks down in the coastal

[3] Most but not all of this material is from the Rocky Mountain region and the Great Basin. Dymond (1928: 72) stated that these teeth are sometimes entirely lacking in *S. clarkii*.

cutthroat, *S. c. clarkii,* in which the fin tips may be as bright as, or even brighter than, those in most rainbows (as noted by C. L. Hubbs in the Tacoma Public Aquarium, Tacoma, Washington, in June, 1949).

Red lateral band: The statement that there is a more definite and intense band in the rainbow than there is in the cutthroat is based largely on the literature.

Length of upper jaw: It is believed that if the comparison is made between individuals of like age, identical sex, and similar sexual development, the difference stated is valid. If one compares breeding male rainbows with female cutthroats, the measurements given will not hold. The figures given for the length of the upper jaw in these 2 species are perhaps not as constant as indicated, but nevertheless they serve as an average difference to supplement other characters used for distinguishing the 2 species.

Number of scales: This character is of general value only, since it breaks down completely for several forms of the 2 species. For example, there is no significant difference in scale counts along the side between the rainbow and the anadromous cutthroat of the lower Columbia River (Schultz, 1936: 136, 137). I am unable to substantiate the count of 180 oblique rows of scales given for the California steelhead by Shapovalov (1947: 190).

Shape of head and body: The literature abounds with statements that the cutthroat trout has a more slender and more pointed head than the rainbow. The entire body of *S. clarkii* also seems to be slenderer; at comparable lengths, rainbows outweigh cutthroats.

Spotting: This is generally a very useful character that is difficult to express in words. The spotting on most cutthroats and rainbows looks very different. With experience, one learns to appreciate these differences. In cutthroat trouts of the intermountain region, and probably elsewhere too, there is a very distinctive round or oval dark spot behind the eye on the preoperculum. Jordan (1891: 13) claimed that this spot was characteristic of all forms of cutthroat trout, but the mark is not restricted to this species. In most of the cutthroat-rainbow hybrids that I have examined, this spot is evident though often weak, and it also occurs sporadically in *S. gairdnerii.*

Pyloric caeca: Counts of pyloric caeca on large series of specimens from many localities are necessary before this character can be accepted as a reliable criterion for aiding in the identification of rainbow and cutthroat trout. The figures presented are very suggestive, even if they are based on an examination of only a very few specimens.

On comparing the Gila trout with the rainbow and cutthroat trouts, it is seen that *S. gilae* resembles the rainbows in some characters and the cutthroats in others, but that it is entirely distinctive in its spotting and life colors. For this reason, I recognize the Gila trout as a full species. If forced to use a trinomial I would refer *gilae* to the rainbow series. *S. gilae* resembles *S. clarkii* in having a distinct (though not blood-red) cutthroat mark, a weak "rainbow" band, a long upper jaw, a long, pointed head, and few pyloric caeca. It resembles *S. gairdnerii* in lacking hyoid teeth, in the pale borders of the anal, pelvic, and dorsal fins, in the number of scales, in lacking a well-defined spot behind the eye, and generally in the body shape. The diagnostic spotting, the very large adipose fin, and the life colors distinguish the Gila trout from any rainbow or cutthroat trout that I have seen.

The resemblances of *S. gilae* to both *S. gairdnerii* and *S. clarkii,* and the capacity of those species to cross freely, suggest the possibility that the Gila trout may have resulted from hybridization between cutthroat and rainbow trouts, followed by a long period of inbreeding. If so, one of the parental forms probably would have been an introduced rainbow trout (*S. gairdnerii irideus* or a related subspecies) and the other a cutthroat trout (*S. clarkii lewisi,* the Yellowstone cutthroat, introduced, or *S. clarkii pleuriticus,* the Colorado River cutthroat, evidently not native, or another subspecies of *S. clarkii*). Both *S. c. lewisi* and *S. c. pleuriticus* were reared by the United States Bureau of Fisheries shortly after the turn of the century, and one or both were stocked in Arizona streams. According to published records, which are often incomplete and inaccurate, ''black-spotted trout,'' of undesignated subspecies, were first planted in the Gila River system in 1907, in Gila River at Silver City, New Mexico (U. S. Bur. Fish., 1907: 31); in 1908 they were stocked in streams near Flagstaff and Jerome, Arizona, also in the Gila River drainage (U. S. Bur. Fish., 1909: 32). According to the records of the New Mexico Department of Game and Fish, 35,000 trout (presumably cutthroats) were planted in the Gila drainage in 1906. The officials of this organization are positive that the cutthroat trout was never native to the Gila drainage. An examination of all rainbow-cutthroat hybrids (125 specimens) in the Museum of Zoology, University of Michigan, and of many in the United States National Museum, representing several subspecific combinations of *S. gairdnerii* with *S. clarkii,* has failed to reveal a specimen which approaches the diagnostic characters of *S. gilae.* Moreover, a native trout has been known in the upper Gila River Basin at least since 1885 (Bryan, 1925: 342), well before any organized plantings of either rainbow or cutthroat trout had been made in regions so remote. Since Diamond Creek, the stream from which the types of *S. gilae* came, is normally dry in its lower course, it is highly improbable that trout planted in other waters have made their way into this creek. Mr. Elliott S. Barker and others feel sure that no exotic trout have ever been stocked in Diamond Creek. Evidence against a hybrid origin for *S. gilae* may be summarized as follows: (1) the Gila trout does not look like any known hybrid between *S. clarkii* and *S. gairdnerii;* (2) it is well established that fish hybrids are more or less intermediate between their parental species, but *S. gilae* is like either *S. gairdnerii* or *S. clarkii* in most respects, is distinctive in some characters, and is intermediate in none, with the possible exception of the cutthroat mark; (3) a native trout was present in the upper Gila long before exotic species were introduced; (4) it would be necessary to assume that rainbow-cutthroat hybrids are fertile, but, to my knowledge, no conclusive evidence has been published to substantiate this assumption; and (5) elsewhere in the West, where the rainbow has been introduced into waters formerly inhabited only by the cutthroat, *S. gairdnerii* has either eliminated *S. clarkii* or reduced it to a remnant, through hybridization and competition. Unfortunately, no trout collected prior to introductions are available from the upper Gila watershed, but nevertheless there seems to be no valid reason to regard *Salmo gilae* as other than the indigenous trout of the Gila Basin.

The only other native trout known from the Colorado River system is the Colorado cutthroat, *Salmo clarkii pleuriticus*. It was formerly abundant in the basin of the upper Colorado, and the same or a closely related form may have once inhabited streams draining into the Little Colorado River on the northern slope of the White Mountains, Arizona (Cope and Yarrow, 1875: 694–95). Below this I know of no populations of native trout, past or present. The records of this cutthroat from the Salton Sea region, California (Dill, 1944: 149, and references cited), were almost certainly based on rainbow trout which had been washed into the basin from some stocked stream in Arizona. *Salmo gairdnerii* was planted in Oak Creek, near Flagstaff, Arizona, at least as early as 1898 (Ravenel, 1899: cxi), well before the first "records" of cutthroat trout from Salton Sea. Dr. Margaret Storey, of Stanford University, has kindly checked the collections of the Natural History Museum and reports that there are no California specimens of *S. c. pleuriticus*. Dr. W. M. Chapman found none in the collections of the California Academy of Sciences. It would appear, therefore, that the California records (insofar as they have not been merely repeated from the literature) were based on field observations only, rather than on a careful comparison of specimens. For these reasons I seriously doubt their validity.

There is evidence that prior to the introduction of the rainbow into Oak Creek, Arizona, a native trout inhabited the upper Verde River, a stream that still provides a fine habitat for trout. Mr. Alec Lucy, an "old-timer" living at Prescott, Arizona, has written that Jeff Howard caught trout in 1883 near Flagstaff (presumably from Oak Creek) and sold them in that town. Another "old-timer," Mr. W. J. Satathight, who lives at Yava (west of Prescott), told me in 1947 that there were native "speckled trout" about 45 years ago in Oak Creek. Both of these men had lived over 50 years in this section of Arizona. Their assertions are supported by specimens of trout from Oak Creek in the United States National Museum (Nos. 39577–79, 41568, and 144278) collected about a decade before and after the turn of the century. Some of these were recorded by Snyder (1915: 585) as *Salmo irideus*. He concluded that the fish were apparently "... introduced from some California stream." After a careful examination of these specimens, I concluded that they show some admixture of rainbow blood and are not the pure stock of the trout (presumably *S. gilae*) which originally inhabited this stream. The scale counts in 9 specimens vary from 126 to 145 which I interpret, along with other evidence, as an indication of hybridization with *S. gairdnerii*. Snyder (1915: 585) wrote: "Specimens of this same trout with 116 to 120 scales in the lateral line and measuring about fifteen inches are recorded by Doctor Mearns from Clear Creek." Clear Creek (= West Clear Creek) is also a tributary of the Verde River. The larger scales of this sample (140 in an Oak Creek specimen counted by Snyder) suggest that introduced rainbow trout were established in the upper Verde prior to 1900. The National Museum specimens from Oak Creek (particularly U.S.N.M. No. 144278) contrast sharply with the types of *Salmo gilæ* in having a shorter and more rounded head and a shorter maxillary. They still retain much of the diagnostic spotting and general appearance of the Gila trout, and I feel certain that the rainbow admixture had only recently been effected.

The Gila trout evidently still persisted in Arizona as late as the spring of 1904, for F. M. Chamberlain collected a trout closely resembling this species in the Blue River Basin along the Arizona–New Mexico boundary (see discussion under Coloration), and Bryan (1925: 342) mentioned that trout were present in this basin in 1885. *Salmo gilae* evidently was once widespread in all suitable tributaries of the Gila River, in Arizona as well as in New Mexico. Possibly it once occurred in the Yaqui River Basin of Mexico and it may still occur in a few remote areas of Arizona or Mexico, though widespread introductions of rainbow, and formerly of cutthroat, trout argue against this possibility.

Salmo gilae differs sharply from *S. clarkii pleuriticus,* the native trout of the Colorado River proper. It is most easily distinguished from that cutthroat by the size of the scales which, according to my counts, vary from 133 to 151 rather than from 180 to 205.

The Gila trout is evidently derived from the rainbow rather than from the cutthroat trout. It is perhaps closest to the rainbow trout from Santo Domingo River in northern Baja California, which may represent a distinct subspecies, *Salmo gairdnerii nelsoni* (Evermann, 1908: Snyder, 1926; Needham, 1938; Hubbs, 1946 and 1948). That trout (as represented by the types in the United States National Museum) also has a large eye, a large, spotted adipose fin, and a rather long head (for a rainbow)—characters that are shared with, or that closely approach, those of *S. gilae.* The Baja California trout further resembles *S. gilae* in having the spots largely restricted to the region above the lateral line. However, the details of spotting (especially the coarsely spotted fins), the number of scales (about 128 to 135, in the types examined by me, not 170 as reported by Evermann), and the life colors of this trout are very different from those of the Gila trout.

For at least 64 years trout have been known to inhabit certain streams on the mainland of Mexico (Meek, 1904: 96–97; Evermann, 1908), but the status of these fish is uncertain. As usual the picture has become confused through the introduction of rainbow trout, which took place at least as early as 1888 (Bean, 1891). The record by Meek (1904: 96) of *Salmo irideus* from the Yaqui River was referred by Regan (1906–8: 176–77) to *Salmo clarkii pleuriticus.* Recently de Buen (1947: 262, 323) identified the Yaqui trout with *Salmo clarkii virginalis,* the Río Grande cutthroat. This is logical, though unproved, for the fish fauna of the upper portion of Yaqui River has a high percentage of Río Grande types. These were transferred when the Yaqui cut back to capture a former tributary of the Río Grande (Meek, 1904: xxxviii). Otherwise there is no evidence that a cutthroat trout inhabited any Pacific drainage south of the middle portion of the Colorado River (above Grand Canyon). Two trout (U.M.M.Z. No. 167081) collected in August, 1948, by A. Starker Leopold on an upper tributary of Yaqui River, 7 miles southwest of Pacheco, Chihuahua (Map 1), appear to represent a rainbow type somewhat approaching *S. gilae.* The scales number about 140 and 152 and the head is unusually long and pointed for a rainbow. Unfortunately, the sample is too small to permit a positive identification, beyond the probable reference to *Salmo gairdnerii.* It is possible that *Salmo gilae* once inhabited upper tributaries of Yaqui River and was subsequently mixed with, or supplanted by, introduced rainbows. According to Stilwell (1948: 135), trout were introduced into northwestern Mexico by English immigrants as early as the eighteen eighties. The 2 specimens collected by Leopold could thus represent hybrids beteen *S. gilae* and *S. gairdnerii,* or they might have some admixture of blood from *Salmo clarkii virginalis.*

Salmo gilae differs from the golden trouts of the Kern River region, California (Evermann, 1906), most notably in having much larger scales, very different spotting, and different life colors. In the deep yellow belly and retention of parr marks, however, it approaches the golden trouts. The new species differs from *Salmo clarkii seleniris* Snyder and *Salmo evermanni* Jordan and Grinnell in the same characters which distinguish it from *Salmo clarkii,* for the Piute and San Gorgonio trouts are cutthroat derivatives (pages 8–9).

During Pleistocene time, when valley glaciers existed as far south as Mount San Gorgonio in southern California (Map 1), trout as well as many other boreal animals were forced far to the south of their present ranges (Kendall, 1921: 189–92; 1935: 15; Mottley, 1935). We may assume, for example, that cutthroat trout then ranged in coastal waters as far south as the Santa Ana River (Map 1). This is 660 miles by water route south of the present habitat of this species in Mad River, northern California. There is ample evidence, however, that *Salmo clarkii* occurred within historic time as far south as the Sacramento River Basin. Jordan (Jordan and Henshaw, 1878: 197) described a trout with 184 scales collected by Livingston Stone in McCloud River, an upper tributary of the Sacramento. He referred this fish to *Salmo henshawi,* the Lahontan cutthroat (now called *S. clarkii henshawi*). On the same page Jordan listed, under the name *Salmo tsuppitch,* a trout from a tributary of Pit River, Modoc County, California, which may have been a cutthroat. Jordan (1905: 102) wrote that "Large sea-run individuals analogous to the steelheads are sometimes found in the mouth of the Sacramento." Snyder (1908: 78) recorded *Salmo clarkii* from Goose Lake and its tributaries, along the California–Oregon boundary, and from Pit River near Alturas and Burney Creek (tributary to Pit River) at Burney. Evermann and Bryant (1919: 108) listed Pit River in the range of the cutthroat, but Hubbs and Miller (1948: 70) concluded that the cutthroat trout was presumably extinct in the Goose Lake Basin (upper Pit), and it is now evidently extremely rare or extinct throughout the Sacramento Basin.

Most writers have assumed that the rainbow trout of Baja California reached Santo Domingo River during the glacial epoch. The known southern limit of other land-locked rainbow trout in coastal streams today appears to be San Luis Rey River, 180 miles to the north (Map 1). Sea-run rainbows, however, are found in the ocean as far south as Tijuana River, along the California–Mexico boundary (Hubbs, 1946: 83–84). Furthermore, Jordan (1905: 98) stated that "streams above Tia Juana in Lower California" represented the southernmost locality from which he had obtained rainbow trout. Since ocean temperatures are cooler in northwestern Baja California than they are in the San Diego region (Hubbs, 1948: 460), it is very possible that steelheads even today penetrate as far south as Santo Domingo River. Consequently, the view that the origin of the Baja California trout dates back to the Pleistocene seems to find little support, particularly since this trout is at most only subspecifically distinct from *S. gairdnerii irideus*.

The origin of the Gila trout in southern Arizona, however, definitely calls for a Pleistocene timing, for this seems to be the only logical theory to explain the presence of this fish in a region now cut off from the Pacific coast by desert barriers and by semitropical and tropical waters. In a recent summary of the geology of Baja California, Beal (1948) concluded that there was a major submergence of the peninsula in Pleistocene time. Although the available data is not nearly as complete or conclusive as desired, there is a strong possibility that a marine corridor lay across the region about halfway down the peninsula, extending northward to just north of 28° N. latitude, near Calmalli (Map 1; Beal, 1948: 31). The presence of terraces and the finding of Recent sea shells up to an elevation of 1800 feet are cited by Beal as clear-cut evidence for a Pleistocene submergence of the peninsula to at least 1000 feet. The shells deserve more careful study, however, and the dating of the higher terraces as Pleistocene needs further confirmation. Schmidt (1922: 626) accepted as fact the submergence of the middle part of the peninsula in late Pleistocene time, with the supporting statement that ". . . marine fossils and beaches are found to a height of over 3,000 feet." He found that this hypothetical submergence correlated nicely with the origin and distribution of the reptiles and amphibians of the peninsula. Hubbs (1948: 463) pointed out that the occurrence of numbers of northern relicts in the upper part of the Gulf of California indicates a southward displacement of isotherms and faunas during Pleistocene time.

It is not necessary, however, to assume that the northern relicts in the upper Gulf had to cross the Baja California barrier via a marine corridor in the middle part of the peninsula. An alternative explanation involves the cooling of the ocean by glacial runoff and by lowered air temperatures, thereby making it possible for northern types to reach the Gulf of California by migrating around Cape San Lucas or, more plausibly, by crossing the peninsula via the Isthmus of La Paz (Map 1). That depression, which lies between La Paz and Todos Santos, near 24° N. latitude, is overlain by Recent and Pleistocene alluvium and provides the only major break in the mountain chain forming the backbone of the peninsula. The elevation in this region is nowhere greater than 600 feet and ancient shore lines indicate that at some stage of the Pleistocene the area was an isthmus (Beal, 1948: 19; Ives, 1949: 145).

The southward displacement of isotherms and faunas is strikingly illustrated by the presence of a Pacific salmon in Formosa, an island almost bisected by the Tropic of Cancer. *Oncorhynchus formosanum*[4] (Jordan and Oshima, 1919) is the only native salmonid known from this island, where it is confined to high mountain streams of the interior. Critical temperatures of the surrounding ocean approach 28° C. (82.4° F.) (Shapiro, 1948: Fig. 3), far too warm for even adult *Oncorhynchus* (Davidson and Hutchinson, 1938: 674). The distribution of such boreal species, far to the south of the range of the parental types, is believed to have taken place during glacial times, just as the destruction of coral reefs from world-wide elevation of sea level and chilling of the ocean has been correlated with events of late Pleistocene times. Recent studies by Oshima (1934), however, suggest that *Oncorhynchus* may have reached Formosa during postglacial time, for he reported that *O. formosanum,* formerly thought to be confined to Formosa, also occurs in southern Japan.

[4] The gender of *Oncorhynchus* is neuter. Therefore the species formerly called *O. formosanus* must be written *O. formosanum.*

It may be postulated, therefore, that at some time during the Pleistocene the ancestral stock of *Salmo gilae* either crossed the peninsula of Baja California by way of a marine corridor near 28° N. latitude, or at the Isthmus of La Paz, or, possibly, migrated around the tip of Cape San Lucas. Moving up the region occupied by what is now the Gulf of California, this trout entered the Gila River and subsequently differentiated, through geographic isolation, into the species now endemic to that basin. Changing water conditions and the effects of introductions of other trout by man have greatly restricted its distribution and the new species is now known only from a few remote tributaries of the Gila River in New Mexico.[5] There is no evidence that *Salmo gilae* penetrated the Colorado River. Its failure to do so may be related to the geological history of that river, for Blackwelder (1934) has proposed the hypothesis that the Colorado River was not a continuous drainage until after the beginning of the Pleistocene.

That the Colorado cutthroat also entered the Colorado River by migrating across Baja California seems extremely unlikely. *S. c. pleuriticus* was native only to the upper and middle portions of the river and is, or was, abundant only in the headwater region. It may be inferred from this distribution that *pleuriticus,* like other representatives of *S. clarkii* which entered the Platte, Arkansas, and Río Grande basins, gained access to the Colorado via headwater connections. Cutthroats are more boreal in their habitat predilections and distribution than are rainbows.

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[5] While this paper was in press, the author and his party collected a native trout, apparently referable to *S. gilae,* from the Salt River drainage high in the White Mountains in Arizona.

history, distribution, game qualities, and propagation. Carl L. Hubbs has critically read the manuscript and offered valuable advice. W. I. Follett generously spent many hours on the nomenclature of the Kamloops rainbow trout. Margaret Storey and W. M. Chapman helped in checking for certain specimens under their care and John Davis ably assisted in the field work. Richard S. Croker generously made available his valuable notes on the life colors of *Salmo evermanni* and on the disappearance of this species. William L. Cristanelli carefully drafted the map. To all of these people I am most grateful.

SUMMARY

Salmo gilae, a new species of trout from the headwater region of Gila River, New Mexico, is described and figured. Gila River, a flood tributary to the lower Colorado River, eventually drains into the Gulf of California. On comparison with the many forms of trout described from western North America, the new species is seen to resemble the rainbow trout (*Salmo gairdnerii*) in some characters, the cutthroat trout (*Salmo clarkii*) in others, and to be especially distinctive in its life colors and spotting. The status of the trouts of western North America is reviewed and suggestions are made for solving the complicated systematics of this plastic group. The effects of artificial plantings, interbreeding of hatchery stocks, natural hybridization, reckless fishing methods, and changes in environment are cited as causal factors in the decline, extermination, and fusion of species and subspecies. Hybridization between rainbow and cutthroat trouts, in particular, poses practical problems in the fishery management of western trout streams. It is therefore urged that administrators avoid the stocking of rainbow and cutthroat trouts in the same stream. A provisional comparison between the trouts of the rainbow and cutthroat series is presented and discussed.

The complicating circumstance of the presence of both fine-scaled and coarse-scaled steelheads (*Salmo gairdnerii* sub-

species) in western waters is pointed out. *S. g. stonei* is relegated to the synonymy of *S. g. gairdnerii* (in the sense of the fine-scaled steelhead). The Baja California trout, *S. g. nelsoni,* and the Eagle Lake trout, *S. g. aquilarum,* are dubiously given provisional status. The latter may be a cutthroat–rainbow hybrid and *nelsoni* is questionably distinct from *S. g. irideus.* It is pointed out that *S. g. kamloops* was first described in the genus *Oncorhynchus.* The Piute cutthroat, *S. c. seleniris,* is regarded as a subspecies of *clarkii* because of the discovery of intergrades between *seleniris* and *S. c. henshawi. Salmo evermanni,* regarded as a glacial relict, is aligned with the cutthroat rather than the rainbow series. *Cristivomer* is considered a generic synonym of *Salvelinus.*

The Gila trout is interpreted as having been widespread at one time in the Gila River drainage of Arizona and New Mexico, and it may have once inhabited the Río Yaqui of Mexico. It is now known only from a few, remote headwater tributaries of the Gila River in New Mexico and probably has been extinct throughout Arizona since the early part of the century (see footnote 5). A possible hybrid origin for *S. gilae* is discussed in detail and discounted. The testimony of ''old-timers'' in the upper Gila watershed strongly indicates that there never was a native cutthroat in the Gila River. The records of *S. c. pleuriticus* from Salton Sea, California, are interpreted as having been based upon rainbow trout washed into Salton Sea from Arizona.

The origin of *Salmo gilae* is believed to be correlated with events of late Pleistocene time, when the ocean was sufficiently cooler than now to allow for the migration of an ancestral trout down the outer coast of Baja California, across the peninsula via the Isthmus of La Paz, and up the Gulf of California into Gila River. Evidence for the southward displacement of isotherms and faunas is cited. The origin of *Salmo clarkii* in the Colorado River, however, is interpreted as the result of natural headwater transfer, since cutthroats are more boreal in their distribution and habitat requirements than are rainbows.

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PLATE I

Holotype of *Salmo gilae,* a male 204 mm. long. Photographed by G. I. Hightower and retouched by Mrs. Aime M. Awl (both of the Smithsonian Institution).

PLATE I