The Rainbow and Cutthroat Trouts of North America

by

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THE RAINBOW AND CUTTHROAT TROUTS OF NORTH AMERICA

Introduction

This paper represents a continuation and expansion of the work reported by Needham and Gard (1959) on the rainbow trout, Salmo gairdnerii Richardson, of Mexico and California. Behnke (1960, unpublished M.A. thesis) studied the cutthroat, Salmo clarkii Richardson, of the Great Basin, and his findings are included here.

This report is based on examination of ~~more than~~ approximately 2,000 specimens from 120 localities. The goals of the study were to establish the systematic status of the many described species and subspecies in the rainbow and cutthroat series, and to examine the variability and validity of the characters used in trout taxonomy, and to explain the sequence of events which led to the distribution and speciation of the present forms of these two species.

The problems of Salmo taxonomy were stated by Günther (1866), who said:

> "There is no group of fishes which offers so many difficulties to the ichthyologist, with regard to the distinction of species -- as this genus. Moreover, by far the greater portion of the voluminous literature on these fishes consists of descriptions giving trivial or general characters only, frequently confounding 2 or 3 species, or representing as species what are, in fact, merely variations of age, sex, etc., so that the task of giving an account of all the species noticed

has not been an easy one, and their history (in its present form) must form one of the most unsatisfactory portions of ichthyology".

The problem is aggravated by the activities of man, especially fish cultural practices which have promiscuously introduced exotics. In addition, the alteration of original environments has contributed to the elimination of native populations. In some areas ~~we will never know what~~ the native trout ~~were like for they~~ became extinct or hybridized before collections were made.

~~In addition to the~~ Thirty one 31 species of western North American *Salmo* were recognized by Jordan, Evermann and Clark (1930). In addition to these. The following have been considered Dymond (1928) ~~recognized~~ *Salmo kamloops* (Jordan) and as a species a described a new subspecies *S. kamloops whitehousei*. Dymond (1931), also *Salmo clarki*, *alpestris* was described by Dymond (1931). ~~from British Columbia.~~ *Salmo gilae* Miller (1950) and *Salmo chrysogaster* Needham and Gard (1964) are based on populations that have many intermediate characters between rainbow and cutthroat trout.

Miller (1950) and Needham and Gard (1959) have made the most recent attempts at a survey of western *Salmo*. Miller examined specimens and consulted the available literature to arrive at a list of 12 species or subspecies referred to the cutthroat series and 12 species or subspecies in the rainbow series.

Acknowledgements

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salmonids. The Max C. Fleischmann Foundation of Nevada contributed two grants for facilities at the Sagehen Creek Experimental Wildlife and Fisheries Project, a portion of which was utilized in the present study. We extend our sincere thanks to each of these groups.

Grateful acknowledgement is made to the many other persons who provided assistance during this study. Dr. George S. M~~e~~yers and the late Margaret ~~E.~~ H. Storey of Stanford University aided materially through loan of specimens, as did Dr. R. R. Miller of Michigan and Dr. Leonard P. Schultz of the U.S. National Museum. Mr. Joe H. Wales of Oregon State University provided both field notes and specimens. Dr. Arden Gaufin of the University of Utah and Dr. Vasco M. Tanner of Brigham Young University kindly permitted examination of specimens. Mr. Tom Trelease, Mr. William Nisbet and others with the Nevada Fish and Game Commission assisted by furnishing specimens and in suggesting areas in which to collect specimens in Nevada. We owe thanks to many other persons, both colleagues and students. Personnel of the Fish and Wildlife Service in Alaska were especially helpful in directing us to suitable collecting sites as well as in providing airplane transport to remote waters. Personnel of the California Department of Fish and Game were especially helpful in pointing out choice collecting areas and, in many instances, in actually helping us to collect specimens.

The following students rendered much aid: Dr. Warren Freihofer, Mr. John D. Hopkirk, Mr. James Gaffney, Mr. Kenneth Middleton, Mr. Francis M. Reid and Mr. Charles M. Seeley. We are indebted to Mrs. Emily Reid who drew the figures.

Materials and Methods

Field collections were made by angling, seining and electric shocking. Specimens were photographed in color and field notes were taken at the time of collection. Specimens were fixed in 10 percent formalin and later transferred to 40 percent isopropyl alcohol. A major collecting trip was undertaken by the authors in July and August, 1957, covering Oregon, Washington, British Columbia, Alberta, Yukon Territory and Alaska. Shorter trips were made from 1958 through 1963 in California, Nevada and Utah. Specimens were borrowed from the collections of the California Academy of Sciences, the University of Michigan Museum of Zoology, Stanford University and the U. S. National Museum.

Linear and Meristic Characters Used

Counts and measurements were made on the left side of the fish and, unless otherwise noted, were made according to Hubbs and Lagler(1949). All linear measurements were converted to thousandths of the standard length. A total of 32 linear and meristic characters were used with varying degrees of thoroughness. Ranges, means and standard deviations were plotted and graphed to observe the efficacy of the various characters for taxonomic purposes. In general, most linear characters proved to be of little taxonomic value for this study, not only because of the great degree of overlap, but also because most linear characters are readily affected by allometry and the environment. No attempt will be made to present the entire voluminous data, ~~all of which has been microfilmed and is on file in the University of California Library (Call No.).~~

Scale Counts

The lateral series and the lateral line scale counts have the same demarcation points. They begin with the first scale in contact with the pectoral girdle and terminate at the structural base of the caudal, found by flexing the tail and observing the crease. This crease is the posterior limit of the standard length measurement. Lateral series scale counts ~~were~~ ~~are~~ were made two rows above the lateral line. Much confusion exists in the literature concerning the lateral series count, not only because it is difficult to make with accuracy, but because most authors do not state precisely how their counts ~~were~~ ~~are~~ were made. Most European workers count to the last scale on the body (in contact with the caudal rays). Scale counts were made after the epidermis was scraped off by a scalpel and a malachite green stain applied and dried with a jet of air. A binocular microscope was used for magnification.

~~Closely related with the lateral series count is the scale count~~ Scale counts ~~made~~ above the lateral line, ~~i.e.~~ are made, beginning ~~from~~ with the first scale in front of the origin of the dorsal fin, counting down and back following an oblique row to the lateral line but not including the scale in the lateral line. ~~The scale count from the origin of the adipose fin to the lateral line is also generally correlated with the lateral series count.~~

Fin Ray Counts

Extensive counts were made only on the pelvic and pectoral fins. ~~All of the rays~~ Every element ~~were~~ was counted. Generally, all of the pectoral and pelvic rays are well developed and accurate counts are simple.

Vertebral Counts

Vertebral counts were made by x-raying the specimens and examining the negative. All of the centra in the vertebral column were counted, including the last three upturned centra which support the hypural plates. Every element with a definite separation was counted. Fused vertebrae were counted by their neural spines. The urostyle in salmonid fishes is a cartilaginous rod and was not counted.

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ПОПРОСИТЕ ЗОТОВА.

page 6

Basibranchial Teeth

Basibranchial teeth counts were made for all cutthroat specimens. The counts were made according to the technique described by Miller (1950:23). Most authors incorrectly call basibranchial teeth hyoid teeth. Basibranchial teeth are actually borne on a thin, flattened bony plate applied over the basibranchial bones and cartilage which lie in a median series forming the floor of the pharynx.

Branchiostegal Rays

Both the right and left branchiostegal rays were counted. The left side often has one more ray than the right side. ~~Each caecal element~~

Pyloric Caeca

Each caecal element was removed with a forceps under a binocular microscope. Every caecum, no matter how small, was counted.

Osteology

Cleared and stained specimens, skulls, chondrocrania and other skeletal material were prepared.

THE RAINBOW TROUT SERIES

— redo

Salmo gairdnerii Richardson, The Coast Rainbow

Salmo gairdnerii Richardson, Fauna Bor.-Amer., 3; 1836:221.

Columbia River at Ft. Vancouver.

Salmo iridia Gibbons, Proc. Calif. Acad. Nat. Sc., 1; 1855:35.

San Leandro Creek, Alameda Co., Calif.

Salmo rivularus Ayres, Proc. Calif. Acad. Nat. Sci., 1; 1855:42.

Martinez, California

Salmo gibbsii Suckley, Ann. Lyc. Nat. Hist. N.Y., 7; 1858:1.

Middle Columbia River system.

1

The Rainbow Trout, ~~Salmo~~ Salmo *gairdnerii* Richardson.

Salmo gairdnerii ranges from the Kuskokwim River, just to the south of the mouth of the Yukon River in Alaska, southward in a continuous distribution in coastal drainages to southern California. Both anadromous and non-anadromous populations occur throughout this range. Isolated, non-migratory populations occur in the Rio Santo Domingo system in Baja California and in the upper Rio del Presideo drainage at 24° north latitude, in the Province of Durango, Mexico. This appears to be the most southerly native occurrence of any salmonid. The only ~~native~~ indigenous populations of rainbow trout in non-Pacific Coast drainages occur in limited areas in the upper Mackenzie River system in Alberta and British Columbia, and in Eagle Lake, California, a disrupted part of the Lahontan basin. ~~The~~ Salmo *regalis* and *S. smaragdus* described from the Lahontan basin, were probably based on hatchery introductions.

The native distribution of *S. gairdnerii*, characterized by a lack of isolated, relict interior populations, suggests the species is of relatively recent origin and arrived on the scene in North America after the cutthroat ~~species~~ trout was established in interior waters. Based on ~~chromosome~~ the member and morphology of the chromosomes, Simon and Dollar (1963) believed the rainbow trout was derived from the cutthroat trout.

~~Compared with the cutthroat trout, the rainbow~~ *S. gairdnerii*, as a species, is less variable than *S. clarkii*. Many species and subspecies ~~of~~ have ~~some~~ been named ~~to~~ in the rainbow trout series, however. Jordan, Evermann and Clark (1930) recognized 16 species and Miller (1950) listed 12 species and subspecies referable to the rainbow series. At the other extreme, Needham and Gard (1959) recognized only *Salmo gairdnerii* with no subspecies.

This work considers *Salmo gairdnerii* to consist of four subspecies. These subspecies, however, do not form neat, discrete units; there is considerable intergradation and overlap in characters. There are (or were) populations ~~in~~ indigenous to desiccating basins in southern Oregon which are intermediate between *gairdnerii* and *clarkii*. The golden trout, *S. aguabonita* Jordan, ~~is~~ is closely related to the rainbow, but for reasons explained later, is considered a separate species.

The Coast Rainbow or Steelhead Trout, *Salmo gairdnerii gairdnerii* Richardson.

- synonymy

Salmo truncatus Suckley, Ann. Lyc. Nat. Hist. N.Y., 7; 1858:3.

Anadromous; Puget Sound.

Salmo masoni Suckley, Pac.R.R. Surv., 12, pt. 2; 1860:345.

Small tributaries of Columbia River

Salmo mendocino Gibbons, Proc. Calif. Acad. Sci., ser. 1, 4; 1876:142-144.

Streams, Mendocino Co., California.

Salmo gairdnerii beardslei Jordan and Seale, Proc. Calif. Acad. Sci., Ser. 2, 6; 1896:209. Crescent L., Washington

Salmo nelsoni Evermann, Proc. Biol. Soc. Wash., 21; 1908:26.

San Pedro Martir Mountains, Baja California

Salmo irideus morpha argentatus Baijkov, Contr. Canad. Biol. and Fish., 3(16); 1927: 387.

Salmo regalis Snyder, Bull. U.S. Bur. Fish., 32; 1912: 26.

Lake Tahoe, Nevada.

Salmo smaragdus Snyder, Bull. U.S. Bur. Fish., 35; 1917: 80.

Pyramid Lake, Nevada.

THE RAINBOW TROUT SERIES

Salmo gairdnerii Richardson

The following discussion includes consideration of both anadromous and resident coastal rainbows, proceeding from ~~south~~ north to ~~north~~ south. ~~in western North America.~~

correct heading

(Alaska)

In the rainbow series only Salmo gairdnerii has been described from Alaskan waters. The northernmost record of S. gairdnerii is from the Kuskokwim drainage. There are no records of native rainbow trout from the Yukon River system. We have seen no specimens from the Kuskokwim but Alaskan fish and game workers have told us that rainbows are rare there. Our Alaskan material is based on 166 specimens representing collections from 10 localities. These samples probably represent mostly resident fish, although most of these areas have access to the sea (~~Fig.~~). The size range of the specimens does not suggest that these trout were either pre-seaward migrants or returning steelhead. ~~Many~~ Some specimens ~~have spotting on the first pectoral ray~~ and some of the larger from Whiskey Lake. ~~specimens have~~ A ~~a~~ weak cutthroat mark was noted on some specimens. ~~but no other character suggests a cutthroat influence.~~

Table ____ compares the numbers of gill rakers, vertebrae and scales in the lateral series of ten groups of Alaskan rainbows.

Insert Table ____.

~~Gill rakers:~~ The mean gill raker number of 20.6 for seven Brooks River specimens is the highest of any sample of coastal rainbow. But

Table . -- Numbers of Gillrakers, Vertebrae and Scales in Lateral Series of Ten Groups of Alaskan Rainbow Trout

Area	No.	Gillrakers		Vertebrae		Scales Lateral Series	
		Range	Mean	Range	Mean	Range	Mean
Alagnak River	29	18-21	19.5	61-64	63.3	125-145	133.4
Bedlam Lake	20	18-20	19.4	60-63	61.7	111-135	121.6
Big Kitoi Creek	5	17-19	18.3	63-64	63.2	-=-	--
Big Kitoi Lake	5	18-20	18.6	63-64	63.8	121-135	128.6
Brooks Lake	16	18-24	20.2	62-64	63.3	120-146	136.9
Brooks River	7	19-22	20.6	63-64	63.1	120-141	130.1
Tebay Lake	22	18-22	20.3	62-65	63.2	123-142	130.9
Tikchik River	11	19-21	19.7	62-64	62.8	119-134	125.5
Whiskey Lake	21	18-21	19.5	62-65	63.0	120-141	128.9
Wood River	30	18-22	19.5	61-64	62.7	116-144	126.8

the variation in this character is not as great among rainbows as it is ~~in~~ the various forms of cutthroat ~~species~~ trout. The sample with the lowest gill raker count (16-20 (17.5)) came from Clairborne Creek, California, ~~and has~~ 16-20 (17.5).

The distinctive characters of specimens from Bedlam Lake and Tebay Lake suggest a longer period of isolation and perhaps stronger selective pressures. Bedlam Lake is a shallow body of water on the Kenai Peninsula. It is open to the sea by a small outlet stream and young silver salmon, Oncorhynchus kisutch (Walbaum), were found in the lake. The vertebra~~e~~l count of 60-63 ~~with a mean of~~ (61.7) and ~~is one of~~ among the lowest among coastal rainbows. The lateral series scale count are ~~is also low, but they resemble typical rainbows in all other respects~~. they?

Tebay Lake is in the Copper River drainage in southern Alaska, about ~~100~~ 60 miles north east of Cordova. These rainbows are isolated by falls which prevent anadromous fish from reaching the lake. The Dolly Varden char, Salvelinus malma (Walbaum), is also found in the lake. Considering the whole rainbow series, the Tebay Lake trout have the shortest distance between the snout tip and the origin of the dorsal fin, .457-.495 (.479) ~~in thousandths~~ of the standard length; the shortest head length, .206-.236 (.225); the shortest upper jaw length, .101-.129 (.110); the shortest adipose fin, .049-.070 (.061); and the least body depth, .199-.242 (.225). These trout were heavily parasitized by ~~a~~ nematode (Philonema sp.) and cestode (Diphyllobothrium sp.) (NOB) in the body cavity which causes heavy sheaths of tissue to completely encase the internal organs. It is not known to what extent the effects of the parasites influence the ~~many distinctions~~ may be attributed to the direct effect of the environment and ~~perhaps the heavy infestation of nematodes~~, but the trout of Tebay ~~Lake stand out in many morphological characters.~~

Canada

In Canada, the rainbow was indigenous to all suitable Pacific Coast drainages and in the Mackenzie River system ~~they~~ it occurred in the Athabasca and probably the Peace River drainages. It was not found originally in the Saskatchewan system of the Hudson Bay drainage in Alberta, where only cutthroats were native. The large, resident rainbow of the lakes in the upper Fraser and Columbia River systems of British Columbia is commonly referred to as the Kamloops trout and often given the specific or sub-specific name kamloops.

Our Canadian coastal rainbow material ~~is represented by~~ consists of 198 specimens. This includes 30 specimens of anadromous steelhead from the Coquihalla River, B.C.; a sample of 32 trout from Moberly Creek, Alberta, in the Athabasca system of the Mackenzie drainage; and 17 specimens also from Lower Kathleen Lake in the Alsek drainage in the Yukon Territory; and 119 specimens from six localities in the upper Fraser and Columbia systems, ~~all~~ representing the "Kamloops" rainbow trout.

- discussed w/ Kamloops -

~~Kamloops Trout~~

Kamloops Trouts: Jordan (1892a) described Oncorhynchus kamloops from Kamloops Lake, B.C. He stated it was a landlocked salmon with its closest affinities to the king salmon O. tshawytscha. Almost immediately, Jordan, (1892b) described Salmo kamloops. This time the relationship was stated to be with Salmo gairdnerii, but he believed the Kamloops trout was intermediate between Salmo and Oncorhynchus. Bean (1892), reviewing the California report in which S. kamloops was described, said:

"One of the types upon which the description is based was deposited in the National Museum at Washington, and we have examined this specimen. After having studied the fish, we find it difficult to understand why the describer of the species failed to recognize in it the Gairdner's trout of Richardson".

Jordan and Evermann (1896; 499) relegated kamloops to subspecific status under gairdnerii and wrote:

"Somewhat different in appearance from the ordinary 'Steelhead', but not distinguished by any technical character of any importance, and doubtless intergrading fully with the latter".

Jordan, Evermann, and Clark (1930) considered kamloops as a synonym of gairdnerii. Dymond (1928, 1932, 1947) recognized kamloops as a full species, admitting the variability between populations and environmental influences on certain characters but stated that kamloops was a purely freshwater form with many structural differences.

Dymond (1931) described the rainbow of the high mountain lakes of British Columbia as a new subspecies, Salmo kamloops whitehousei. Dymond (1932: 26) discussed his views on taxonomic recognition of British Columbia trout and stated:

"The question as to whether some of the striking variations exhibited are in the nature of specific differences has been discussed and the conclusion reached that they are not. Every gradation of difference between the most extreme forms is found. It has seemed advisable, however, to designate the extremes by subspecific names and therefore, the small, heavily-spotted, bright coloured Kamloops trout characteristic of small lakes at high altitudes, has been designated as the Mountain Kamloops trout (<u>Salmo</u> <u>kamloops</u> <u>whitehousei</u>), the typical form of large lakes at lower altitudes become then recognized as (<u>Salmo</u> <u>kamloops</u> <u>kamloops</u>)".

Mottley (1934b, 1936a, 1937) demonstrated that the characters used by Dymond to distinguish Kamloops trout from other rainbows ~~were~~ are considerably influenced by environmental conditions. In one experiment, Mottley (1934b) ~~took eggs and sperm from~~ progeny derived ~~the~~ parent trout ~~with~~ had lateral series scale counts of 148 and 149. ~~Their progeny~~ were raised under relatively high water temperatures. The scale counts of 100 of the progeny were compared; they ranged from 120-135 (127.5) ~~with a mean of 127.46~~, ~~more than 20 fewer scales than either of the parents~~. As a result of his experiments, Mottley (1936b) concluded that all the British Columbia rainbows were of a single species. He recognized S. <u>kamloops</u> and S. <u>whitehousei</u> as varieties of S. <u>gairdnerii</u> but did not ~~suggest~~ indicate if that these "varieties" should be considered ~~as~~ subspecies.

Neave (1943) raised Kamloops trout and Cowichan River steelhead in the Cowichan hatchery under similar conditions. The Kamloops retained a mean value of eleven more scales than the steelhead, demonstrating a genetic basis for this character (142.6 scales in the Kamloops, 131.5 in the steelhead).

The following table presents some meristic counts of our specimens of "Kamloops" trout.

Insert Table _____ here.

Table . -- Meristic Variation in Kamloops Trout of British Columbia

Area	Gillrakers			Vertebrae			Pelvic Rays			Scales Lateral Series		
	No.	Range	Mean	No.	Range	Mean	8	9	10	No.	Range	Mean
Bear Lake ("whitehousei")	7	18-21	19.3	7	63-65	64.0	--	7	--	7	approx.	160*
Fish Lake	32	17-20	18.4	32	62-64	63.0	1	13	18	32	123-148	136.8
Loon Lake	25	17-20	18.7	25	60-64	62.9	--	20	5	25	121-159	136.9
Peachland Res.	5	17-20	18.4	5	62-64	63.2	--	2	3	5	136-160	147.4
Riske Creek	24	18-22	19.6	24	61-65	62.9	--	5	19	24	122-140	132.8
Trout Lake	26	18-22	20.3	26	62-65	63.0	--	3	23	26	133-151	140.5

*Dymond (1932)

It can be observed that Kamloops trout tend to have more scales than coastal rainbows but the differences are not large and there is much overlap. Many Kamloops have 9 pelvic rays instead of the 10 typical of rainbows. The Peachland Reservoir specimens have a distinctive appearance with fine spotting mostly above the lateral line. The Loon Lake specimens also have a spotting somewhat similar to this type while the Fish Lake trout have more typical coastal rainbow spotting. The Peachland Reservoir trout are also distinctive in that four of the five specimens have only 12 pectoral rays as contrasted with the usual 14 or 15 typical for both rainbows and cutthroats.

The lateral series scale count reported by Lindsey, et.al. (1959), for Loon Lake rainbows in central British Columbia is ~~much~~ considerably higher than our counts made on specimens from the same lake. The mean value obtained by Lindsey for trout spawning in the outlet stream was 155.5 and those from the inlet, 150.9. Dr. Lindsey has written that the counts were made ~~four to~~ six rows above the lateral line and continued to the scale in contact with the caudal rays, while our count ~~we~~ terminates ~~the count~~ at the end ~~base~~ of the vertebral column.

Northcote ~~(1960)~~ graphically ~~depicted the number of~~ pyloric caeca ~~in~~ Loon Lake Kamloops trout, ~~His figure reveals~~ typically have ~~that for trout over 30 mm.,~~ most specimens have from 40 to 60 caeca.

Mottley (1937) reported vertebra~~e~~l counts on hundreds of Kamloops trout. He demonstrated the effects of water temperature by comparing Paul Lake trout raised at Lloyds Creek hatchery in 1931 and 1932. In 1931 the water temperature at the hatchery was 3 to 4°C colder than normal and the vertebra~~e~~l number of the trout raised that year ranged from

Mr. Cronemiller phoned - 6/1/1959

In the book Wilderness Men by O'Hagan , p. 187

speaks of Athabasca Pass

The river at one time flowed into the Fraser -

now into the Athabasca and eventually to the

Arctic via the McKenzie

Denver

LA 6-8649

-Mir ~~6~~15

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1644

lunch (2): sand. soup, bev

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TG-35163

2423 1/2 Locust

24

62-65 (63.9). In 1932 with warmer water, the vertebrae number increased to 63-67 (64.5). This is the highest mean value yet reported in the literature for any Salmo. Mottley (op.cit.) listed a count of 63-66 (64.4) for 25 Kamloops from Cottonwood Lake. This is the identical range and mean reported by Needham and Gard (1959) for rainbows from the Rio Tabacatiado in Mexico and the highest reported for any Salmo from a natural environment.

Taxonomic Status: ~~Based on our data, we would hesitate to recognize the landlocked rainbows of the Frazer River system as specifically or even subspecifically distinct.~~ The wide distribution, ~~however~~, of a more fine scaled rainbow with some cutthroat-like characters in the Frazer and in the upper and middle Columbia river systems indicate that probably during the late Pleistocene a landlocked rainbow was differentiating in these areas, isolated from the anadromous coastal rainbow. Although intergradation appears to be complete between the Kamloops rainbow and the coastal rainbow, there are many distinctive populations of fine-scaled rainbows in the Columbia and Frazer river systems. It is a matter of personal judgment if one should stress the extreme types and recognize Salmo gairdnerii kamloops or emphasize the intergradation and relegate kamloops to synonymy. Our material is not comprehensive enough to make a firm decision on the matter. ~~We can only point out that~~ by most criteria, kamloops is not a "good" taxonomic entity. but

The "Kamloops" rainbow in Kootenay Lake, B.C., may consist of two or more races differing in their growth rate, age of spawning and spawning areas (Cartwright,(1961). Cartwright (letter, Jan 1964) has written that offspring of the two "races" are being reared under identical conditions and that real genetic differences are apparant. The kokanee salmon, Oncorhynchus nerka, of Kootenay Lake consists of three races according to Vernon (1957).

Mackenzie River System: Rainbows were known to be native to the Athabasca river system of the Mackenzie drainage in Alberta. The only taxonomic work to appear on these trout to date seems to be misleading. Bajkov (1927) reported two types of rainbows from the Athabasca system in Jasper National

Park. He recognized one as Salmo irideus with 120-140 scales and a long head. The other he called Salmo irideus morpha argentatus. This type was characterized by a shorter head, a more silvery appearance, 75-100 scales (not stated how counted) and a different shape to the scales. Bajkov claimed that these two forms of rainbow lived together in Buffalo Prairie Lake, Caledonia Lake and the Athabasca River.

Bajkov said the term "morpha" meant mutation. He used "morpha" to designate mutant types such as albinos and the silver pike, Esox luscius, described by Lawler (1960), ~~and~~ albinos. This is not the "morpha" as defined by ~~of~~ Berg (1935).

It is doubtful if there were two distinct types of ~~such~~ rainbows trout in the Athabasca system as Bajkov described. Our sample from Moberly Creek ~~is certainly~~ represents a homogeneous group. Bajkov stated the trout of Minaga Creek were like argentatus but with red spots. Because no rainbow has red spots it seems probable that he may have based argentatus, in part, upon silvery-appearing, introduced brown trout, Salmo trutta. Mr. J. S. Nelson of the Zoology Department of Alberta University ~~has written~~ wrote that hatchery rainbows ~~had~~ ~~had~~ already ~~were~~ been ~~been previously~~ introduced into the waters of Jasper Park ~~sampled by Bajkov~~ prior at the time of Bajkov's study. ~~prior to his study~~ ~~This suggests another explanation for morpha argentatus.~~ Bajkov's counts of gill rakers and vertebrae in the trout and char of Jasper National Park are much lower than any hitherto reported. Evidently, he counted only fully developed gill rakers and omitted the last 5 or 6 vertebrae which support the caudal rays. ~~hypural plates~~. He listed pyloric caecal counts of 31-41 for the rainbows of Jasper National Park.

Our sample of Athabascan rainbow was collected from Moberly Creek, a tributary of the Wild Hay River near Entrance, Alberta. The 32 specimens have ~~had~~ 17-21 gill rakers (19.4); vertebrae, 63-66 (64.0); scales in the lateral series, 119-149 (133.2). The scale count above the lateral line of 29-36 (32.6) is the highest count for any group of coastal or Kamloops rainbows used in this study~~, exclusive of the fine-scaled Kern River and upper Sacramento River forms~~. The Moberly Creek rainbows were small fish from 104 to 172 mm. in standard length. They were typically rainbow in their spotting and coloration. Faint parr marks were observed on all specimens. ~~Although~~ The ~~native~~ ~~endemic~~ rainbows in the Athabasca system ~~may~~ have been derived ~~come up the Mackenzie River system when conditions were more favorable for the occurrence of rainbows in the Arctic waters of North America, it is more plausible to assume~~ they were derived by were prob. derived stream transfers from the Fraser River system, ~~because~~ The lack of differentiation in our sample indicates a relatively recent invasion and does not suggest a relict stock. Lindsey (1956) collected rainbows from Summit Lake, the headwaters of the Parsnip River (Mackenzie system). He mentioned that these trout had a definite reddish-orange cutthroat mark, but resembled rainbows in all other characteristics. Lindsey collected rainbows from three other Parsnip River tributaries and stated that rainbows were known to occur in the Peace River drainage at least as far downstream as Dawson Creek, B.C. He wrote that this distribution may be partially attributed to fish cultural activities. The ~~endemic~~ indigenous occurrence of rainbows in the Parsnip River seems logical on geographical grounds because the headwaters of the Parsnip River are contiguous with ~~the~~ headwaters of the Fraser drainage ~~and headwater stream transfers probably took place~~. ~~Also, the Peace River connects to the Athabasca drainage below Athabasca Lake, although no rainbows are known to occur in this area today.~~

Yukon Territory Rainbows: In the Yukon Territory non-anadromous rainbows are present in the Alsek River system (Edwards-Wynne, 1952). Our ~~collection~~ materiel ~~was made in~~ came from Lower Kathleen Lake near Haines Junction. They are typically rainbow in every character and do not seem differentiated in any way from other coastal rainbows. The 17 specimens in our collection have 63-66 (63.9) vertebrae; the number of gill rakers range from 15-20 (18.1); all have 10 pelvic rays; the scales in the lateral series for 10 specimens counted are 126-138 (131.4). The Kathleen Lake trout are heavily spotted with rather large, irregularly shaped spots extending about half way below the lateral line. Landlocked sockeye salmon, Oncorhynchus nerka (Walbaum), lake trout, Salvelinus namaycush (Walbaum), and grayling, Thymallus arcticus (Pallas), occur with the rainbows in Kathleen Lake. No ~~endemic~~ cutthroat~~s~~ trout are known from the Alsek drainage in the Yukon Territory.

Canadian Steelhead: Anadromous Canadian rainbows are represented ~~in our collection~~ by 30 pre-seaward migrant specimens from the Coquihalla River, a tributary of the Fraser, near Hope, B.C. These are a typical coarse-scaled, coastal type with from 111-138 (124.5) scales in the lateral series; the vertebral number is 62-65 (63.5); gill rakers, 18-22 (19.2); and pelvic rays, 9-11 (10.2). These specimens ranged from 100-172 mm. in standard length. Neave (1949) described both anadromous steelhead and resident rainbow from the Cowichan River, B.C. The steelhead, in turn, had both summer and winter races. Neave (1944) collected samples of steelhead and resident rainbow from the Cowichan and found there was a mean difference of ten scales in the lateral series between the two populations (steelhead 132, resident rainbow 122). When raised in a hatchery under similar conditions the steelhead still ~~had~~ averaged five more scales, demonstrating a genetic difference. There appeared to be an overlap in both the time and place of spawning in the Cowichan River ~~between~~ of the anadromous and non-anadromous trout, but Neave did not discuss how the two populations maintained genetic isolation. In some river systems the resident trout may be more coarsely scaled ~~that~~ than the anadromous trout, but the situation is reversed in the Fraser, Columbia and Sacramento systems. Actually, a whole mosaic of populations may exist in a large river system ~~and this~~ which demonstrates the futility of attempting to force all non-anadromous rainbows into a unit which can be given subspecific status. As Neave (1949) pointed out, many British Columbian rivers have both summer and winter races of steelhead. Smith (1960) described work in progress to affirm the genetic distinction between distinct steelhead runs in the same river. Although we do not recognize anadromous from non-anadromous populations nor the various races of anadromous trout, with formal taxonomic nomenclature, these differences are very real for the management of the species and this type of "micro-incipient" speciation deserves ~~research~~ study by systematists.

enlarge

moved up

to p. 2

~~Taxonomic Status of Kamloops Rainbow: Based on our data, we would hesitate to recognize the landlocked rainbows of the Frazer River system as specifically or even subspecifically distinct. The wide distribution, however, of a more fine scaled rainbow with some cutthroat-like characters in the Frazer and in the upper and middle Columbia River systems indicate that probably during the late Pleistocene a landlocked rainbow was differentiating in these areas, isolated from the anadromous coastal rainbow. Although intergradation appears to be complete between the Kamloops rainbow and the coastal rainbow, there are many distinctive populations of fine scaled rainbows in the Columbia and Frazer River systems. It is a matter of personal judgement if one should stress the extreme types and recognize Salmo gairdnerii kamloops or emphasize the intergradation and relegate kamloops to synonymy. Our material is not comprehensive enough to make a firm decision on the matter. We can only point out that by most criteria, kamloops is not a "good" taxonomic entity.~~

INDIGENOUS AMERICAN RAINBOWS

The Columbia River System: ~~We can add little to what has been previously written on the occurrence of both fine and coarse scaled rainbow~~ Trout ~~in the Columbia River.~~ Jordan and Evermann (1896:498) claimed a sample of Salmo gairdnerii from Astoria, Oregon, had from 137-177 scales. It is not known ~~certain~~ if these were ~~actually~~ steelhead, however, because no other information was given concerning this collection. Jordan and Evermann (op.cit.: 489) wrote:

start of comments

> "Dr. Gilbert has verified the fact discovered by him in 1880, that in the streams around Astoria, near the mouth of the Columbia, Salmo mykiss /=S. clarkii/ and Salmo gairdnerii occur together and are perfectly distinct and both easily and unquestionably distinguishable from a third form, here called masoni, found in the brooks of the same region and not descending to the sea".

Apr. 75 these are redband trout

Three specimens of S. gairdnerii rainbows in the Stanford collection (S.U.2028), collected by Gilbert and Rutter, probably in the late 19th century, from the Umatilla River, Pendleton, Oregon, have 142, 153 and 154 scales in the lateral series. Another Stanford specimen (S.U.2025) from the Natches River, North Yakima, Washington, collected by Gilbert and Jenkins has 146 scales. There is little information concerning the degree of intergradation between these fine scaled rainbows of the middle Columbia drainage and the typical coarse scaled coastal rainbow. Gilbert and Evermann (1894) told of their confusion in trying to distinguish cutthroats from rainbows in the middle Columbia system. Evidently, they considered what we call here the fine scaled rainbow or Kamloops trout, to be intermediates or hybrids between the rainbow and cutthroat. Jordan and Evermann (1903:175) claimed that gairdnerii-clarkii intermediates occurred in the Columbia basin, represented by a medly of forms in the lower Snake River. Schultz (1935) wrote of both fine and coarse scaled steelhead at the mouth of the Columbia and speculated that the fine scaled trout may have been anadromous ~~"~~Kamloops~~"~~ trout.

The fine scaled rainbow of the Columbia River basin shares close affinities and, probably, a common origin to the Kamloops trout of the Fra~~z~~ser drainage discussed above. The native rainbows of the upper Columbia River drainage are often classified as S. g. kamloops. The type locality of the finest scaled Kamloops form named S. kamloops whitehousei by Dymond (1931) is in the Columbia River drainage of British Columbia.

It should be noted that Suckley (1858) described Salmo gibbsii from the Columbia River at Fort Dalles, Oregon. He said it occurred also in the larger tributaries of the Columbia, specifically in the Yakima and John Day River. It is not known if Suckley's specimen was a fine scaled rainbow for he gave no scale counts. It was claimed that this fish had a red band on its side and resembled S. gairdnerii but did not go to sea.

no ¶ Jordan and Evermann (1903:179) considered S. gibbsii with the cutthroat series and said it occurred in tributaries of the Columbia system between Shoshone Falls and the Cascades in lakes and large streams. Their description of what they considered gibbsii was of a fish with small spots mostly above the lateral line, a rosy wash on the side, scarcely any red on throat and with scales 140-145. Jordan, Evermann and Clark (1930) ~~maintained~~ retained gibbsii as a distinct species.

Because of the stocking of hatchery trout and the changes in the environment wrought by an encroaching civilization, a detailed taxonomic study of the ~~endemic~~ indigenous trout in the Columbia River system would be extremely difficult.

A few ~~rainbow~~ specimens of S. gairdneri were collected from Snake River tributaries in Elko County, Nevada. A single specimen from Deep Creek, tributary to the East Fork Owyhee River above Wildhorse Reservoir, had typical rainbow spotting and coloration; scale counts of 141 in the lateral series and 31 above the lateral line; 21 gillrakers and 36 pyloric caeca. Four specimens from the North Fork Sweet Creek, also a tributary to Wildhorse Reservoir were typical of hatchery rainbows. The scale counts on these trout were 121-133 in the lateral series and 26-28 above the lateral line. They had 19-20 gill rakers. Wildhorse Reservoir is heavily stocked with hatchery rainbows and we hesitate to use these fish as representative of endemic Snake River rainbow.

- These are redband trout - again collected in 1972 (in 83°F. Temp.) - Apr. 75

Four specimens from Chino Creek, tributary to the South Fork Owyhee near Tuscarora, Nevada, are enigmatic in appearance and characters. Two specimens have the spotting, general morphology and scale counts of typical interior cutthroat trout. These trout have large, roundish spots, a long head and jaw, 151 and 158 scales in the lateral series and 32 and 34 scales above the lateral line. One specimen has 9 pelvic rays and the other 10. Both lack basibranchial teeth. A third specimen resembles a cutthroat-rainbow hybrid in its appearance and spotting, with ~~has~~ 149 scales in the lateral series and 32 above the lateral line. The fourth specimen is typically rainbow in all respects. It has 126 scales in the lateral series and 27 above the lateral line. All specimens lack posterior gill rakers on the first gill arch and in this character, they are typical of rainbow trout. ~~Unfortunately, specimens were poorly preserved and no color notes were made by the collector. These specimens indicate that there has been a definite cutthroat influence on a rainbow population in Chino Creek.~~ Mr. William Nisbet, Nevada Fish and Game Department Biologist in Elko, could find no record that Chino Creek was ever stocked. ~~On such a small sample from a single locality, it is~~

difficult to speculate on the significance of the cutthroat-like rainbows in Chino Creek in regards to the taxonomy of the endemic trout of the Snake and Columbia drainages.

The taxonomy of the trouts in the Columbia River system remains one of the most unsatisfactory segments in the classification of rainbow and cutthroat trout.

The Blueback Trout of Crescent Lake: Jordan (1897) described two new subspecies from Crescent Lake on the Olympic Peninsula, Washington. These trout were brought to Jordan's attention by Admiral Beardslee for whom one of the species was named. Jordan stated:

> "I find myself forced to agree with Admiral Beardslee in the opinion that each of these forms is distinct from any previously named or recorded. The two are allied to each other, rather than to any other form and the nearest affinity of both seem to be with the steelhead trout *S. gairdnerii*".

Actually, the trouts of Crescent Lake represented a coastal rainbow and a coastal cutthroat. The blue-back trout described as *Salmo beardslei* is a rainbow and considred inseparable from *S. gairdnerii*.

The speckled trout of Crescent Lake, ~~named~~ described as *S. gairdnerii crescentis*, is considered ~~with~~ as *S. clarkii clarkii*. The type specimen of *crescentis* lacked basibranchial teeth and this probably caused Jordan to consider it with the rainbow series. Meek (1899) gave further descriptions of the Crescent Lake trouts and contributed to the indiscriminate naming of species by describing another ~~cutthroat~~ species from Crescent Lake and two ~~cutthroat~~ species of S. clarkii from Lake Sutherland which lies just to the south of Crescent Lake. sob

Three specimens of S. beardslei from the U.S. National Museum were examined. These fish range were from 170-179 mm. standard length. A silvery sheen and dark colored back, described as characteristic of these trout was apparent. This smolt-like appearance coloration is common in rainbow trout, especially those from lakes. The Crescent Lake rainbow, although landlocked, may retain the stage in its ontogeny ~~may have~~ undergone smoltification, a characteristic held over from its steelhead progenitors. Lateral series scale counts of these specimens were 124, 125 and 130. Three specimens in the Stanford collection from a fish hatchery at Quilicene, Washington are listed as Salmo gairdnerii beardslei. The date of preservation was January, 1952. These trout appeared to be quite typical of coastal rainbow. Their scale counts were 122-124.

Robert C. Meigs, Chief of the Fish and Game Management Division of the Washington Game Department has kindly supplied the stocking records for Crescent Lake from 1933 to 1941. Hatchery rainbows, steelhead and interior cutthroats (S. c. lewisi) have been introduced into Crescent Lake. The present population probably represents a mixture of many strains. Because there is no evidence that the original beardslei had any real distinction worthy of taxonomic recognition, we consider it proper to relegate beardslei to synonymy under Salmo gairdnerii gairdnerii.

Other Coastal Rainbows: A collection of 30 resident rainbows was made from the headwaters of the North Fork of the Salmonberry River, a tributary of the Nehalem River, just south of the Columbia drainage in Tillamook County, Oregon. ~~This stream courses through a fire ravaged watershed.~~ The specimens ranged from 88-150 mm. standard length. Barrier falls isolate this part of the river against invasion ~~from~~ of anadromous steelhead. These trout ~~were~~ are all coarse scaled with from 117-to 143 (126.6) scales in vertebrae the lateral series for eleven specimens counted. The vertebrae counts were 62 to 64 (63.2). Twelve of the 30 specimens had 9 pelvic rays instead ? of the typical rainbow number, 10.

KLAMATH RIVER ~~RAINBOWS~~ TROUT

~~The Klamath River and its tributaries are noted for the large winter and summer runs of steelhead.~~ ? offer The upper Klamath River and Lake, above Klamath Falls, has a fauna distinct from that of the lower river. The evidence suggests that the upper Klamath system was once connected to the interior basins from which it derived many of its fishes and only in recent geological times became part of the Klamath River (Gilbert, 1898; Hubbs and Miller, 1948). ~~It is not known if both rainbow and cutthroat trout were endemic to Klamath Lake~~. The early literature is confusing as to the species of trout in Klamath Lake. Cope (1878) wrote that Salmo iridea was abundant in Klamath Lake and tributary streams, but made no mention of cutthroats. Cope (1884, 1889) mentioned only the cutthroat, then called Salmo purpuratus, from ~~this region~~ Klamath Lake. Evermann and Meek (1898) said trout were very common in Upper Klamath Lake but from their remark that only two specimens of S. gairdnerii were collected, they implied that the cutthroat was the more abundant species. Gilbert (1898) said rainbows were very abundant in Upper Klamath Lake and River, but made no mention of cutthroat. No specimens ~~of~~ from the upper Klamath ~~rainbows or cutthroats~~ drainage have been located in any collection, and intensive stocking of hatchery trout in this area makes discovery of a pure strain of native trout doubtful.

Girard (1858) named a ~~rainbow~~ trout from the upper Klamath River, Salmo newberrii. Jordan and Evermann (1896:499) claimed the type of S. newberrii had 146 scales. Gilbert (1898) gave scale counts of five rainbows from upper Klamath Lake. His counts ranged from 134 to 146 (138.8). Gilbert said he could not distinguish the rainbows of upper Klamath Lake from typical S. gairdnerii.

Because we have no data of our own, we can not authoritatively designate newberrii as a synonym of S. gairdnerii.

The upper Klamath watershed is contiguous with the Chewaucan and Goose Lake desiccating basins and may have had previous connections with these drainages. The native trout of the Chewaucan and Goose Lake drainages, to be discussed later, have been considered as S. clarkii by Snyder (1908a) and Hubbs and Miller (1948). Examination of collections from these basins, however, revealed a distinctive trout which cannot definitely be placed with either the rainbow or the cutthroat species (Table .). The native trout of the upper Klamath drainage may have been derived from this intermediate type. Below Klamath Falls, the typical coastal rainbow is found. Three specimens of steelhead from Spencer Creek, a Klamath tributary, were examined. These trout had 133, 134 and 137 scales in the lateral series. Spencer Creek has been an important source of many hatchery stocks of rainbow trout. Snyder (1940) presented vertebrae counts from 175 Klamath River steelhead. His counts ranged from 60-65 (62.2).

vertebrae ?

SACRAMENTO RIVER SYSTEM

cyprinids ?

The Sacramento River System is noted for its endemic cyprinids. It also has had more species and subspecies of trout named from its waters than any other drainage basin. Besides shasta and stonei named from the McCloud River, five species were named from the Kern drainage in the San Joaquin system. Also, Salmo rivularis Ayres (1855) was described from a tributary in the lower Sacramento and Salmo irideus Gibbons (1855) from San Leandro Creek, a small tributary of San Francisco Bay. The Eagle Lake trout named Salmo aquilarum by Snyder (1917) has its affinities with the trout of the upper Sacramento.

Cutthroat trout were probably not native to the Sacramento system in recent times. Some of the upper Sacramento trout populations resemble cutthroats in their coloration, spotting, scale counts and morphology. This may be due to an early invasion of interior cutthroats, probably from Goose Lake and perhaps the Lahontan basin, and subsequent hybridization with the native rainbows. It was probably on such intermediate specimens that Snyder (1908) based his records of cutthroat from the Pit River and from Burney Creek, a tributary of the Pit. Miller (1950:31) believed that the cutthroat occurred in the Sacramento during historic times. He based his belief on Snyder's record and on Jordan and Henshaw (1878), who described a trout from the McCloud River with 184 scales and identified it with the Lahontan cutthroat (S. henshawi). Dr. Ralph Taylor of the U.S. National Museum examined this specimen and revealed that it is actually the type specimen of henshawi from Lake Tahoe. The mix-up in the data on the McCloud River and Lake Tahoe specimens was probably due to a typesetter's error which reversed the headings in the report of Jordan and Henshaw.

Rutter (1908) presented lateral series scale counts on a number of rainbows from various localities in the upper Sacramento system. His counts on McCloud River specimens ranged from 146-165. Specimens from the South Fork of Battle Creek had 151-176 (163.), which is typically cutthroat. Upper Sacramento and Pit River trout averaged 147 scales and those from tributaries of the Feather River averaged 143, according to Rutter.

Six specimens collected in 1898 from the North Fork of the Pit River at the mouth of Joseph Creek, Modoc County, California, revealed definite indications of cutthroat influence. The specimens had scale counts which ranged from 138 to 155 (148). Five of the six had 9 pelvic rays, a cutthroat character. The gillraker count ranged from 19-23 (21.3), indicating Lahontan cutthroat influence. The long head and jaw and spotting pattern was also indicative of cutthroat or rainbow-cutthroat hybrids. None had basibranchial teeth. This collection may represent the result of an early hybridization between interior cutthroats and the native rainbow. ~~It must also be kept in mind that~~ Lahontan cutthroats were widely introduced into California waters in the late nineteenth century, and could have influenced some local populations.

Such fine-scaled intermediate populations still exist in a few isolated tributaries of the upper Sacramento system. Wales (1939) ~~described~~ mentioned a "golden" trout from small tributaries of the McCloud in Siskiyou County, California. At that time, he thought they might be introduced aguabonita. Examination of five "golden" trout specimens collected by Wales in 1956 from Edson Creek, a tributary of the McCloud, revealed that these are not aguabonita but represent a population of the ~~intermediate~~ native upper Sacramento trout. Scale counts ranged from 140 to 156 (148). One specimen has 61 vertebrae, four have 62. Three specimens have 10 pelvic rays, two have 9. The spotting pattern ~~was~~ is erratic, resembling cutthroat-rainbow hybrids. Another "golden" trout collection was made by Wales in 1956 from Moosehead Creek, a tributary ~~of~~ in the Pit, River system ~~via Clark Creek~~ in Shasta County, California. These trout have scale counts of 149, 157 and 174. The vertebrae counts ~~were~~ are 61 (1) and 62 (2); all have 10 pelvic rays. Mr. Wales kindly supplied a copy of his color notes made from a living fish; it reads as follows:

> "Back and upper sides light olive, immaculate except for jet black spots. Lateral band rose red, about 1 to 1½ width of eye, starting just behind opercle and ending in a point under adipose. Lower sides very pale golden fading to milk white on belly. Large irregular saffron patch on belly, starting at posterior point of pectorals and extending to vent. This patch is not solid but somewhat broken with white showing through. Opercle iridescent rose red. Pectorals solid

ranged

vertebral

olive gold. Ventrals immaculate olive gold except for interior border of white not sharply differentiated from the golden. Anal immaculate olive gold with white anterior border, but not sharply differentiated from remainder. Caudal olive and spotted. Some marks of gold on mandible and a definite small red streak on left side of isthmus".

Another characteristic noted on the fine-scaled trout of the upper Sacramento is that an opercular or cheek blotch is faint to well developed. This blotch is generally well developed on cutthroats, especially interior cutthroats but is weak or absent on rainbows.

It is well established that non-anadromous fine-scaled trout with intermediate cutthroat-rainbow characters were native to the upper Sacramento River system. Before the construction of Shasta Dam, steelhead ran into the upper Sacramento, McCloud and Pit rivers and their tributaries, but there has never been a report of fine-scaled steelhead from the Sacramento system. Twenty-one specimens of pre-seaward migrant steelhead were examined from the San Lorenzo River, Waddell Creek and the Russian River. These are all within 75 miles of the mouth of the Sacramento River. The following table shows eome of their meristic characters.

Insert Table Here

It may be noted that these steelhead near the southern limit of anadromous North American Salmo are among the coarsest scaled of all rainbows. It is unlikely that such consistent differences in scale counts between the coastal rainbows and the resident trout of the tributaries of the upper

31

Table . -- Meristic Characters of Pre-Seward Migrant Steelhead

Area	No.	Gillrakers		Vertebrae		Scales Lateral Series	
		Range	Mean	Range	Mean	Range	Mean
Russian River	7	18-20	18.6	61-63	62.0	118-132	123.6
San Lorenzo River	9	18-21	19.1	61-63	62.1	117-127	120.6
Waddell Creek	5	19-21	20.2	60-62	61.0	118-132	123.4

Sacramento is merely the by-product of environmental differences. ~~The number of vertebrae is also among the lowest of the rainbow samples used in this study.~~

When Livingston Stone began taking rainbow trout spawn for fish culture operations on the McCloud River in 1879, he was puzzled by the trout and speculated on the possibility that he was dealing with more than one form. Stone (1884) observed that the large trout of the main stream were coarse scaled and those of the tributary streams were fine scaled. Wales (1939) ~~indicated~~ said that steelhead were known to frequent the McCloud before the construction of Shasta Dam. Because the stocks used in the early fish cultural work were taken from both the main river and from the tributaries and indiscriminantly mixed, the original hatchery rainbow was probably an amalgamation of the fine-scaled resident trout and the anadromous steelhead. This matter is discussed more fully by Needham and Behnke (1962). Jordan (1883) believed that the finescaled rainbow of the upper Sacramento was an environmental phenomenon and that there was but one species of trout in the Sacramento and that it was "*Salmo irideus*".

? on Jordan (1894) changed his mind, and on specimens sent to him by Stone from the McCloud, he named the no-shee trout, *Salmo irideus stonei* and the Shasta trout, *Salmo gairdnerii shasta*. Except for the statement that *shasta* had some red under the lower jaw which was lacking in *stonei*, there is nothing in the original descriptions which suggests that *shasta* and *stonei* were not taken from a single population. Wales (1939) believed that *stonei* may have represented a steelhead. ~~The conclusions of~~ Hubbs and ~~Follett, discussed in~~ Hubbs and Wallis (1948), considered *shasta* identical with the steelhead, which they mistakenly assumed to be fine scaled.

Although both steelhead and resident trout inhabited the McCloud River at the time of the original description of *shasta* and *stonei*, the type material at Stanford University on which shasta and stonei were described, represents the fine-scaled resident trout. Twelve type specimens were examined. Scales from three trout of 315 to 402 mm. standard length were analyzed by projection in a scale-reading machine. These trout were in their fourth or fifth year and there was no evidence of ocean growth. Lateral series scale counts of seven of the types ranged from 139 to 160. The spotting ~~was~~ is ~~extremely~~ variable, suggesting that shasta and stonei were based on extremes of a single population. The name

?, page priority

stonei has page priority over shasta, thus, if the fine-scaled upper Sacramento trout is recognized, the name should be Salmo gairdnerii stonei. Although the degree of intergradation between the coarse-scaled and the fine-scaled rainbows in the Sacramento is not known, the available material and literature indicate~~s~~ that before the influence of the white man, a fine-scaled resident trout displaying some cutthroat-like characters in varying degrees was sufficiently differentiated from the coarse-scaled anadromous steelhead to warrant subspecific recognition. In some waters, such as the McCloud and Pit rivers, the steelhead and resident trout may have occurred

earlier? above?

sympatrically, behaving as two distinct species. As noted earlier, ~~here;~~ Neave (1944, 1949) found anadromous and resident rainbows occurring sympatrically in the Cowichan River, British Columbia, with no evidence of hybridization.

The type locality of shasta and stonei is now beneath the waters of Shasta Lake. Intensive stocking with hatchery rainbows has changed the original genotype of the resident McCloud River trout. Nine specimens were collected from the McCloud River in 1953. The scale counts ranged from 119 to 154 with a mean of 134.4, somewhat intermediate between typical hatchery rainbows and the fine-scaled McCloud resident rainbow.

A collection of 23 specimens from Clairborne Creek, a tributary of
the McCloud, forms an interesting sample. These trout are isolated above
an impassable falls. They are not representative of the fine-scaled
rainbow of surrounding regions but are a coarse-scaled trout. Twenty
specimens counted had from 115-134 (124.6) scales in the lateral series.
They sharply differ from other trout in their low number of branchiostegal
had rays. Twenty-two of 23 specimens had only 9 branchiostegal rays on the
had right side and 17 had 9 rays on the left side. The typical branchiostegal
ray count for rainbows and cutthroats is 10-12. Only the Mexican golden
trout have fewer branchiostegal rays. Six specimens taken from below the
had falls on Clairborne Creek at the same time had 11 and 12 branchiostegal
had rays. Eight of the specimens from above the falls had 9 pelvic rays.
Perhaps the Clairborne Creek trout had their origin from coarse-scaled
anadromous rainbows that were isolated before the cutthroat influence spread
through the upper Sacramento rainbow populations. On the other hand, they
may ~~have been~~ be derived from fine-scaled ancestors, typical of other upper
Sacramento tributaries, and independently evolved a lower scale number.
The gillraker count of the Clairborne trout ranges from 16 to 20. The
mean of 17.5 is the lowest of any rainbow sample used in this study. The
is vertebral counts range from 63-65 (63.5) and is slightly higher than other
Sacramento trout.

EAGLE LAKE TROUT

Eagle Lake, Lassen County, California, is a disrupted part of the Lahontan basin. Except for the trout, which belong to the rainbow series, the fish fauna of Eagle Lake is made up of typical Lahontan minnows and suckers. From this evidence it would be expected that the native trout of Eagle Lake would be the Lahontan cutthroat. The Eagle Lake trout, however, appears to be quite typical of the rainbows of the upper Sacramento system. Snyder (1917) described the Eagle Lake trout as _Salmo aquilarum_. Except for the fact that Eagle Lake is an isolated basin and that the other fishes are of Lahontan origin, there is nothing in Snyder's description which ~~really~~ distinguishes this trout from the upper Sacramento rainbow. ~~From the faunal and geographical evidence, one would suspect that the Eagle Lake trout may have resulted from hybridization, between the Lahontan cutthroat and a rainbow either introduced by man or entering by natural headwater transfer from the Pit or Feather River systems.~~ Hubbs and Miller (1948:38) said:

> "The trout, _Salmo aquilarum_, which Snyder described from Eagle Lake as an endemic representative of the Pacific drainage rainbow series, appears from a re-examination of the types to have been based on hybrids between the native cutthroat and an introduced rainbow trout".

Miller (1950:6) remarked that a hybrid origin theory may be erroneous. He stated that if _aquilarum_ was a valid entity it should be considered as a subspecies of _gairdnerii_. Needham and Gard (1959) based their discussion of the Eagle Lake rainbow on eight large specimens collected in 1951. These eight specimens had the highest mean number of gillrakers (20.1) of any of the 17 samples used in that study. But they believed that the Eagle Lake trout was not recognizable even as a subspecies. The present opinions on the Eagle Lake trout are based on the four specimens described by Snyder (1917), the eight specimens used in the study of Needham and Gard, 20 specimens from the Crystal Lake hatchery, kindly donated by Mr. Harry A. Hanson, ~~formerly~~ retired, of the California Department of Fish and Game, and four specimens collected in 1939 and 1940 from Pine Creek, the only tributary of Eagle Lake.

Table . -- Meristic Characters of the Eagle Lake Rainbow

Sample	Gillrakers									Vertebrae							Scales, Lateral Series		
	N	16	17	18	19	20	21	22	Mean	N	61	62	63	64	65	Mean	N	Range	Mean
(from Snyder-1917)	4	1		2	1				17.8								4	136-140	138.0
Crystal Lake Hatchery (1957)	20	1	6	8	4		1		18.0	19	3	10	4	2		62.3	10	122-142	130.5
Eagle Lake (1951)	8				1	5	2		20.1	8	3	1	1	4	2	63.9	8	135-155	143.4
Pine Creek (1939-40)	4			1	1		1	1	20.0	2		1		1		63.0	4	129-137	133.0

The following tables indicate some of the meristic characters of the Eagle Lake rainbow:

Insert tables ___, ___, ___ here.

There were many introductions of hatchery trout into Eagle Lake; however, the personnel of the California Fish and Game Department who worked with the Eagle Lake trout claim that no other trout but the native can survive the alkaline conditions in the lake. It is difficult to believe that the original genotype has not been influenced by hatchery introductions. The population residing in the headwaters of Pine Creek ~~may now be~~ is probably predominantly of hatchery rainbow stock. The scale counts reported by Snyder and those of the 1951 specimens, indicate affinities with the upper Sacramento rainbows. The pelvic fin ray count also tends to confirm such relationships. Grouping all of the specimens, one has 8 pelvic rays, twenty-one have 9 pelvic rays and eleven have 10 such rays. The spotting pattern is variable, ~~and~~ with large, irregularly shaped spots ~~are~~ concentrated above the lateral line, ~~It is much~~ and more typically ~~of~~ rainbow than cutthroat. Except for slightly fewer scales and more typical rainbow-like spotting and coloration ~~(Snyder, 1917)~~ and probably physiological adaptation to the alkaline conditions of Eagle Lake, this trout appears quite identical to the rainbow once native to the northern division of the Sacramento system. Because of the lack of clear-cut differentiating characters, the Eagle Lake trout does not represent a valid subspecies itself. ~~If the subspecies stonei is recognized, then~~ The Eagle Lake trout may be considered ~~with this group~~ as a slightly differentiated pop. as S. g. stonei.

only spawn + rt.

At the present time the California Fish and Game Department has undertaken intensive hatchery production of Eagle Lake rainbows in an effort to maintain ~~and have established~~ ~~a popular~~ the fishery for this large rainbow.

THE TROUTS OF THE KERN RIVER DRAINAGE

Five species and subspecies of trouts were described from the Kern River and its tributaries. These descriptions were based on variations in the California golden trout, *S. aguabonita*, the Kern River rainbow, *S. g. gilberti*, and intergrades between these two forms.

Jordan and Henshaw (1878) discussed the trout of the Kern River area under the names, *Salmo tsuppitch* (a name also used by Jordan at that time for Lahontan cutthroat trout), *S. irideus* and *S. pleuriticus* (Colorado River cutthroat). Jordan (1892) described the golden trout as *Salmo mykiss aguabonita.* Jordan (1894a) named the Kern River rainbow, *S. gairdnerii gilberti*, from specimens taken in the Kern River at Soda Springs. Evermann (1906) described two species, *Salmo roosevelti*, ~~named~~ for the golden trout of Volcano Creek (now Golden Trout Creek) and *Salmo whitei* for a more heavily spotted golden-like trout collected from certain Kern River tributaries. *Salmo rosei* was described by Jordan and McGregor (1924) from Culver Lake, Tulare County. Dill and Shapovalov (1954) presented evidence that Culver Lake was originally barren and was stocked with trout about 1916 from the Big Arroyo which is tributary to the Kern. On these facts, they considered *rosei* as a synonym of *S. g. gilberti*. Evermann (1906), however, listed stocking records which showed that the Big Arroyo had been stocked with trout from the Little Kern where *whitei* was native. The three type specimens of *rosei* at Stanford have higher scale counts and gillraker counts than the typical *gilberti* and, in this they agree with the trout of the Little Kern. If *whitei* is recognized as a subspecies, then *rosei* should be considered a synonym of *whitei* and not of *gilberti*. But, because we consider *whitei* as a synonym of *gilberti* or as a *gilberti-aguabonita* intergrade, the decision of Dill and Shapovalov may stand.

Taxonomic Characters of Kern Trout: No one has attempted an evaluation of the Kern River trout complex since the early writings of Jordan and Evermann. Besides _S. aguabonita_ of the South Fork of the Kern and Golden Trout Creek, we recognize only S. g. gilberti as a valid form. Our interpretation of _gilberti_ includes all the various intergrades between it and _S. aguabonita_ which have been called _whitei_. Besides ~~Other than~~ spotting and coloration, _gilberti_ is distinguished from _aguabonita_ by having ~~a larger number~~ more ~~of~~ pyloric caeca, vertebrae, and ~~and~~ pelvic fin rays and fewer scales.

Because of the intergradation with _gilberti_ and ready hybridization with introduced rainbows, it would seem logical to consider _aguabonita_ as a subspecies of _gairdnerii_. We believe, however, that this would obscure the true origin and relationship of _aguabonita_ which appears to have closer affinities to the interior cutthroat than to the coastal rainbow. The golden trout will be discussed in a separate section.

Our data on the Kern River trout are based on early museum specimens and a comprehensive collection made by Dr. Richard Gard in 1956. The most distinguishing feature separating _gilberti_ from the typical coastal rainbow is the fine scalation of _gilberti_.

Insert Table here.

Table . -- Some Meristic Characters of Kern River Trout Populations (exclusive of aguabonita)

Sample and Collection Date	Gillrakers			Vertebrae			Pyloric Caeca			Scales-Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
gilberti												
Kern River (1876-1912)	17	18-23	19.9	17	60-63	61.5	--	--	--	13	137-172	153.4
Kern River (1956)	3	18-20	19.0	3	59-63	61.3	3	35-52	43.7	3	139-148	143.3
Coyote Creek (1956) (below falls)	12	18-22	19.8	12	61-63	62.2	1	40	--	12	138-154	144.8
"whitei"												
Little Kern River and Coyote Creek (1904)	7	20-21	20.6	8	60-63	61.5	--	--	--	8	148-167	159.0
Coyote Creek (1956)	33	19-23	21.0	33	59-63	61.2	15	29-46	39.8	20	135-182	150.5
Rifle Creek (1956)	22	18-22	20.0	22	60-62	61.2	15	29-48	37.1	15	139-172	154.7
Little Kern River (1956)	5	20-22	21.2	5	60-63	61.4	5	36-43	39.2	5	151-164	155.4
Salmon Creek (1961)	10	18-21	19.2	10	59-61	60.1	10	24-35	28.8	10	128-154	141.0
"rosei"												
Culver Lake (1923)	3	21-23	22.0	3	60-62	61.0	--	--	--	3	155-170	162.1

It may be seen that the Kern River trout are fine scaled rainbows. The form called _whitei_ from the Little Kern and its tributaries and from Coyote Creek, a tributary of the main Kern, is a golden-colored trout but its meristic characters are closer to _gilberti_ than to _aguabonita_. The official view of the California Fish and Game Department, as stated by Dill (1950) is to regard _whitei_ as a golden trout and a subspecies of _aguabonita_. The _whitei_ of Coyote Creek is often marked by a well developed cutthroat mark. This was described by Evermann (1906) and in the field notes of Dr. Richard Gard. Both Evermann and Gard commented on the great variation in coloration and spotting in the Coyote Creek trout. Other isolated streams in the Kern drainage such as Salmon Creek, contain golden-like trout. The trout of Salmon Creek, tributary to the Kern was mentioned by Dill (1950:5), who claimed that they may be, "some type of golden". Mr. Eric Gerstung of the California Department of Fish and Game collected 10 specimens from Salmon Creek in 1961 and donated them for this study. Even after preservation in Formalin, the golden and red colors on these specimens were apparent. The spotting is profuse and in this character they resemble _gilberti_. In the low number of pyloric caeca and vertebrae they resemble _aguabonita_. The scale counts were the lowest of any sample from the Kern drainage. How many other distinct populations exist in isolated waters of the Kern system is not known. These waters of the upper Kern drainage, especially those isolated by falls, should be protected against introduction of hatchery rainbows and other species of trout. The trout of the main Kern River has been influenced by heavy stocking of hatchery trout. Three rainbows collected by Gard in 1956 from the main Kern are intermediate in their scale counts between typical _gilberti_ and typical hatchery rainbows. Also, the fifteen specimens from below the falls of Coyote Creek collected in 1956 have lower scale counts and higher vertebral counts than the type material of _gilberti_.

The spotting pattern pictured in Evermann (1906) for the Kern River rainbow is not typical. The trout pictured is spotted profusely and has spots on the ventral and anal fins. Of the 18 specimens at Stanford University, only three have such spots on these fins. One specimen of gilberti (S.U. 4747) has two basibranchial teeth. Evermann's (1906) ~~stocking list~~ list of introductions shows that cutthroat~~s~~ trout were widely distributed throughout the Kern River area in the late nineteenth century. ~~This may be the explanation for the basibranchial teeth in this specimen.~~

Before the introduction of hatchery rainbows, the endemic Kern River rainbow probably represented a distinctive subspecies. Hubbs and Miller (1948:71) discussed how the Kern, Kings, K~~e~~aweah and Tule rivers ~~have been~~ are semi-isolated from the San Joaquin River by alluvial fans ~~for a long time~~. The Kern River is semi-isolated also from the Kings, K~~e~~aweah and Tule rivers by an alluvial fan. Thus, the endemic trout of the Kern River could only intergrade with the golden trout and not with the coarse scaled anadromous steelhead. ~~All specimens of gilberti and "whitei" indicate that this was the case.~~

Our treatment of S. g. gilberti ~~is to~~ considers it as a group of populations with various degrees of intergradation between the coastal rainbow and the golden trout S. aguabonita.

THE ROYAL SILVER TROUT OF LAKE TAHOE ~~AND THE EMERALD TROUT OF PYRAMID LAKE~~

Snyder (191~~9~~7) in describing Salmo regalis from Lake Tahoe stated:

> "Salmo regalis is distinguished above all else by its unusual color. A fresh specimen (the writer has not seen a living example) is of deep steel blue on the dorsal surface which in some lights seems to be tinted with olive, the blue extending downward on the sides to about the sixth row of scales above the lateral line, where it gives place

to the most brillian and highly burnish silver.

Structurally the species differs from the other native trout, S. henshawi, in having a shorter head, a shorter and more rounded snout, a much smaller maxillary, larger scales, narrower and more pointed fins, perfectly smooth basibranchials without teeth, and fewer gill rakers".

Snyder based his description on four specimens. Two of these are in the Stanford collection and two are in the U.S. National Museum. Since Snyder's description, two specimens, tentatively identified as S. regalis, have been added to collections. One collected in 1949 is at Stanford (S.U. 17136) and the other, caught in 1960, was donated to the University of California. Miller (1950) believed regalis was extinct. The 1949 and 1960 specimens are typical of the original description in their coloration and almost complete lack of spots. Experienced fishermen claim that the royal silver trout is still caught in Tahoe and it is very distinct from the introduced rainbow. The fact that S. regalis was not described until many years after rainbow and rainbow-cutthroat hybrids were stocked in the lake (Miller and Alcorn, 1945) casts doubt on the validity of S. regalis. Although Snyder claimed that regalis had smooth basibranchials, examination under a binocular microscope revealed that the type and two of the three paratypes have evidence of basibranchial teeth. This was manifested either as tooth-like projections on the basibranchial plate or pits in the plate which indicated teeth were once present; they numbered from 1 to 8 in the three specimens. These basibranchial teeth are not typical of the fang-like teeth on the basibranchial plate of cutthroats but are blunt and minute. The scale counts on the type specimens are suggestive of a hybrid origin.

Can hatchery rainbows be introduced into Lake Tahoe and assume the distinctive appearance of the royal silver trout? Concerning this, Mr. Almo Cordone, biologist with the California Department of Fish and Game, who has worked at Tahoe, wrote:

> "We are continually amazed at the beauty and variety of spotting and coloration on Tahoe rainbows. Many of them have the characters, at least superficially, of <u>regalis</u> and the anglers call them "silvers"....a small group of large rainbows (average size 14 inches) planted at Zephyr Cove by a South Tahoe sportsmens' group on May 30, 1961, are now being taken as typical Tahoe "silvers". Aside from coloration, however, other observations have not been made". (letter dated August 15, 1961).

The striking coloration of the royal silver trout is very similar to that described for the rainbow of Crescent Lake, Washington (<u>beardslei</u>). It is the typical transformation or smoltification which prepare anadromous salmonids ~~undergo before~~ for their sojourn in the sea. Many steelheads were stocked into Tahoe, but the basibranchial teeth and the high scale counts of the types cannot be explained from steelhead introduction.

Insert Table ____ Here

The four type specimens are fine scaled for rainbows, but these counts would be expected from <u>S</u>. <u>gairdnerii</u>-<u>S</u>. <u>c</u>. clarkii <u>henshawi</u> hybrids. The 1949 and 1960 specimens have the more typical coarse scalation of hatchery or coastal rainbows. The most obvious distinction of <u>S</u>. <u>regalis</u> is an almost complete lack of spots. Rainbows are typically heavily spotted on the dorsal, adipose and caudal fins; generally there is also an abundance of small to medium sized, Table . -- Some Meristic Characters of <u>Salmo regalis</u>

Collection Date	Gillrakers			Vertebrae			Scales Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
1912	4	19-22	20.5	2	64	--	4	144-153	149.8
1949	1	21	--	1	63	--	1	136	--
1960	1	19	--	1	62	--	1	127	--

irregularly shaped spots on the side of the body and on~~to~~ the head. Three of the six regalis specimens have no spots on the dorsal and adipose fins and two have no spots on the tail. The other specimens have only a few faint spots on these fins. Under close examination, a few faint, large spots can be made out on the body above the lateral line on most specimens. The 1960 specimen has 55 pyloric caeca, a typical rainbow number. All of the six specimens have 10 pelvic rays.

The basibranchial teeth and the scale counts of the type material indicates a hybrid origin. The ~~activities~~ crossing of rainbow and cutthroat by fish culturists at Lake Tahoe also support such an assumption. The two recent specimens have smooth basibranchials and coarse scalation and may be introduced rainbows.

Kinsey (1950) explained how transfers between the Lahontan basin and the Sacramento system was feasible. Miller Lake, Placer County, California, in the Sacramento drainage, once was probably a tributary of Tahoe. The separation between Miller Creek and McKinney Creek, a Tahoe tributary, is slight. By this route, Sacramento rainbows may have made their way into Lake Tahoe. If this transfer occurred in ancient times when Pluvial Lake Lahontan was extant, and if the rainbows were not completely hybridized into the abundant cutthroat populations, ~~we~~ would be expected ~~endemic~~ native rainbows from the other remnant waters in the Lahontan basin, especially in the many mountain streams.

Shapovalov, Dill and Cordone (1959) considered _S. regalis_ as a subspecies of _S. gairdnerii_. If _regalis_ is still maintaining itself as a distinct entity in Tahoe despite massive introductions of rainbows, then it should be regarded as a distinct species. However, on the little material and factual evidence available, we believe _S. regalis_ was based on rainbow-cutthroat hybrids and is not a valid species. ~~A thorough investigation of the present "royal silver" trout in Lake Tahoe might be enlightening.~~

THE EMERALD TROUT OF PYRAMID LAKE

Snyder (1917:80) described another silvery trout as _Salmo smaragdus_. He stated:

> "The trout here described for the first time is a native of Pyramid and Winnemucca Lakes and does not seem to occur elsewhere. It is apparently a representative of _S. regalis_ of Lake Tahoe, and in common with that form it is characterized by its peculiar color, remarkably different from that of other species of the region. The upper parts of the head and body are deep emerald green, with a few small evanescent, dark spots scattered here and there, the sides of polished silver, and the ventral surface, dead white. The body is long and slender, the head rather short and rounded, eyes large, maxillary weak, basibranchials without teeth, gillrakers few, slender and sharp, the scales large and very loosely attached, and the fins thin and pointed. The entire appearance of the fish suggesting the depths of th e lake as its habitat rather than the river or the mountain torrent. From _S. regalis_ this species differs in being green above instead of blue, in having larger scales (there being 124 lateral series -- 144 to 153 in S. regalis) a more slender body, longer and more pointed snout, and a gill cover distinctly different in shape, the upper or opercular part presenting a rounded, broad shoulder, while the posterior margin is relatively truncate.
>
> "The species is recognized by the older Piute Indians. To them it is the trout, "A-gaih", in contradistinction to

'Tomoo-agaih', or the winter trout, the larger migrants of S. henshawi which appear in the lower Truckee River early in winter, and the 'Tama-agaih' or spring trout ('Tommy' of anglers), a smaller fish, also of S. henshawi, though of a later run".

The type specimen at the U.S. National Museum (75596) is the only specimen of smaragdus known to exist. This specimen has retained the striking appearance mentioned by Snyder. In all of its meristic characters it is typical of an introduced rainbow. In contrast with "regalis", there are spots on the dorsal, adipose and caudal fins ~~of "smaragdus"~~. The basibranchials are smooth. Snyder gave a gillraker count of 20 and a lateral series scale counts of 124. Counts made at the U.S. National Museum were gillrakers 18 and scales 131. If regalis was endemic to Tahoe, then it would be expected that it would have established a population in Pyramid Lake because these two lakes are connected by the Truckee River. Nothing more was known about smaragdus besides what Snyder wrote in his original description. If it was an endemic form it was probably exterminated along with the native cutthroats of Pyramid Lake when the Truckee River was completely diverted for irrigation in the 1930's ~~and all spawning grounds were lost~~. It seems more likely, however, that smaragdus was based on a silvery specimen of introduced rainbow.

MEXICAN TROUT

The Mexican trout were fully discussed by Needham and Gard (1959) and will be mentioned only briefly here. No new collections have been made. When comparing the Mexican trout with other western North American Salmo it is evident that they fall into two groups. A typical rainbow is found in

Rio Santo Domingo ~~River~~ in Baja California and in the San Lorenzo and Rio del Presidio ~~river~~ systems in the province of Durango ~~Province~~. The Mexican golden trout of the Verde, Sinaloa and Culiacan drainages ~~in Durango~~ forms a very distinct group which will be discussed under the golden trout section. These were named as S. chrysogaster by Needham and Gard, (1964).

Evermann (1908) described the Santo Domingo rainbow as Salmo nelsoni. The high scale counts reported by Evermann for this trout ~~was~~ were found to be erroneous by Miller (1950) who recounted the type~~s~~ material. Snyder (1926) and Needham and Gard (1959) found the scale counts to range from 120 to about 140 in the Baja rainbow. Hubbs (1946) wrote that S. nelsoni did not seem distinguishable, even as a subspecies. Needham and Gard (op.cit.) agreed with this conclusion. The vertebral counts on Santo Domingo trout range from 61 to 63. Three specimens ~~had~~ have pyloric caeca counts of 46, 47 and 53.

The specimens collected from headwater ~~streams~~ tributaries of the Rio San Lorenzo and Rio del Presidio ~~rivers~~ represent the southernmost ~~endemic~~ indigenous populations of Salmo in North America. We can not state with certainty however, that these trout are truly ~~endemic~~ native. The sample from the Rio Truchas, a headwater tributary of the San Lorenzo may represent a population of McCloud River rainbows. Wales (1939:279) lists the shipment of 33,000 McCloud River rainbow eggs to Senor Chazari of the Mexican Fish Commission in 1888. About that time, trout cultural operations were undertaken at Lerma, Mexico (Meek, 1904). Needham and Gard (1959:58) mention that the Truchas is beautiful trout water, thus, if it did not have a ~~n endemic population~~ native trout it would be a likely candidate for introduction. The scale counts on the Truchas sample ~~is~~ are almost identical with three of the fine scaled rainbow formerly resident in the McCloud River. Sixteen specimens had from 133-161 (149) scales in the lateral series. ~~xxxhxaxxx~~ The mean number of vertebrae in the Truchas sample is ~~more than~~ three less than the value found for two samples taken from tributaries of the Rio del Presidio ~~River~~, just to the south of the Rio Truchas. The scale counts on the trout samples in these two streams south of the Rio Truchas, ranged from 123-150 with means of 137 and 138. The caecal counts of these Mexican trout are low for rainbows. Five specimens from the Rio Truchas ha~~d~~ve from 31 to 39 ~~caeca~~ (33.4). Ten specimens from the Rio Tabactiado ha~~d~~ve 33 to 43 (37.4) and two from the Rio Hondo ha~~d~~ve 34 and 37. These latter two streams are tributary to the Rio del Presidio. Invasions during the Pleistocene may have established coastal rainbows in the San Lorenzo and del Presidio and probably man has made introductions of hatchery rainbows into these streams. The Mexican golden trout ~~described as S. chrysogaster by Needham and Gard (1964)~~ from the Rio Verde, Rio Sinaloa and Rio Culiacan drainages just to the north of the Rio Truchas are quite distinct and are probably of a different origin. ~~This distribution of two types of trout in Mexican waters is not easily explained.~~

The mean vertebral counts of 64.3 and 64.4 for the Rio Hondo and Rio Tabacatiado samples are higher than ~~that of~~ any sample used in ~~our~~ this study, although these trout represent the most southerly North American collection. One of ~~our~~ the most northerly collections, from Bedlam Lake, Alaska, ~~had~~ have a mean vertebral count of 61.7, one of the lowest of the coastal rainbow samples. This seems to be a reversal of "Jordan's Law" (1894c). Actually, there is no discernable ____ cline in vertebral numbers among the coastal rainbows,

THE CUTTHROAT SERIES

Because of their widespread distribution in interior waters accompanied by much isolation and local variation, the systematic problems presented by the cutthroat series are complex. The coastal cutthroat trout have more variation in spotting pattern and number of scales than is found in the coastal rainbows. The coastal cutthroat, like the rainbow, has both resident and sea-run populations, and similar to the conclusions reached on the rainbow, we find no basis for the recognition of more than a single species and subspecies for all coastal cutthroats. The interior cutthroats consist of a montage of forms. ~~We must admit that despite the large series of cutthroats examined in this study, it remains a cursory, and for some areas an inadequate, study.~~

The Coastal Cutthroat

The following is a synonymy of species recognized by Jordan, Evermann and Clark (1930) which we consider as Salmo clarkii clarkii.

Salmo clarkii clarkii

The coast cutthroat, both anadromous and resident forms.

Salmo clarkii Richardson, Fauna Bor. - Amer., 3; 1836:221. Cathlapootl R. stat

Salmo gairdneri crescentis Jordan and Beardslee, Proc. Calif. Acad. Sci., 2nd ser., 6; 1896:207. Crescent Lake, Washington.

Salmo bathoecetor Meek, Field Col. Mus., Zool., 1(12); 1899:227. Crescent Lake, Washington.

Salmo clarki jordani Meek, ibid. 229. Lake Sutherland, Washington.

Salmo clarki declivifrons Meek, ibid; 230. Lake Sutherland, Washington.

The coastal cutthroat occurs from the Eel River, California, to Prince William Sound, Alaska. Throughout its range it has both resident and anadromous populations. Rounsefell (1958:180) claimed that only anadromous populations occurred in Alaska. This is not true, for some of our Alaskan samples were taken from lakes isolated from the sea by barrier falls. From our ~~limited~~ observations it appears that the coastal cutthroat does not occur far from the sea. It frequents the smaller streams or is associated with the mouths and estuaries of the larger rivers. ~~Much is yet to be known on their distribution and the factors which determine it.~~ Anadromy is not as strongly developed in the sea-run cutthroat~~s~~ as in the sea-run ~~steelhead~~ rainbow. Evidently the anadromous cutthroat does not migrate much beyond the bays and estuaries. There are no records of cutthroat from the open ocean.

Comparatively little recent work has appeared on the systematics and ecology of coastal cutthroats. Cope (1950) published a useful, annotated bibliography on cutthroat trout; Sumner (1962) described the life history of cutthroat from a small Oregon stream and DeWitt (1954) presented much information on the coastal cutthroat of California.

The coastal form is typically profusely spotted with irregularly shaped spots, evenly distributed over the sides of the body and on the head (figs. ____and____). The dorsal, adipose and caudal fins are always spotted, as in the rainbow. In some populations the spots occur on the pectoral, pelvic and anal fins and on the abdomen. This type of spotting appears to be more common among the Canadian and Alaskan populations. The lower fins are usually red, orange or yellow ~~in color~~ and the pelvics and anal fins are often tipped with white. The gillrakers of the coastal cutthroat are typically shorter, more stubby and fewer ~~in number~~ than are the gillrakers of rainbows or interior cutthroats. Generally there are no posterior gillrakers on the first gill arch in coastal cutthroats, whereas interior cutthroat almost invariably possess posterior gillrakers on the first arch. Rainbow trout, like the coastal cutthroat, typically ~~generally~~ lack posterior gillrakers on the first gill arch except in the larger specimens where one or two may be seen. In general, over-all comparison between coastal and interior

Table . -- Meristic Data on Cutthroat Trout From Alaska and British Columbia

Sample	Gillrakers			Vertebrae			Basibranchial Teeth			Pelvic Rays			Scales--Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	8	9	10	No.	Range	Mean
ALASKA															
Lake Baranof and Parlof Creek	6	18-20	19.2	6	61-62	61.8	6	6-28	17.5	--	6	--	--	---	--
Makaka Pt. Stream, Hawkins Is.	30	16-21	18.0	30	60-63	62.0	30	2-46	11.0	--	22	8	16	136-178	155.4
Lake No. 1, Hawkins Island	19	16-20	17.7	19	62-64	63.1	19	5-44	17.1	--	17	2	10	144-168	155.8
Hasselberg Lake	25	15-21	18.2	25	61-64	62.0	25	3-35	13.9	--	24	1	10	137-160	147.8
Long Lake	8	17-18	17.5	8	61-62	61.4	8	4-40	19.2	--	3	5	8	148-186	167.4
Luck Lake -- Cutthroats	16	16-19	17.8	16	60-63	61.9	16	1-20	12.0	--	16	--	10	142-171	158.7
Luck Lake --Rainbows or Hybrids	4	18-21	19.3	4	63-64	63.8	4	0	--	--	--	4	4	126-132	129.3
Herman Creek, Behm Canal	11	17-20	18.1	11	60-63	61.2	11	7-14	10.7	--	11	--	11	152-168	156.9
BRITISH COLUMBIA															
Flannigan Slough, Taku River	3	17-20	19.0	3	61	--	3	6-12	9.7	--	3	--	--	---	--
Lake near Stukine River mouth	5	17-21	18.6	5	60-61	60.8	5	12-18	15.7	--	5	--	--	---	--
Quinsam Lake -- Cutthroats	26	16-23	17.9	26	61-63	61.7	26	1-27	12.8	--	26	--	--	---	--
Quinsam L.--Rainbows or Hybrids	8	19-20	19.6	8	62-65	63.5	1 7	11 0	-- --	--	1	7	--	---	--
Middle Quinsam Lake	30	14-20	17.4	30	60-64	62.0	29 1	1-25 0	13.3 --	--	30	--	--	---	--

cutthroats, there is a trend for the coastal cutthroat to have fewer scales and vertebrae, a more narrow caudal peduncle and more basibranchial teeth. Also, the presence of basibranchial teeth is, ~~generally~~, more consistent in the coastal cutthroats.

Alaska and British Columbia: -- Eleven samples were examined from Alaskan and British Columbian waters. The following table indicates some of the meristic variation found in these samples.

Insert Table ___ here.

It can be seen that except for some local exceptions, the cutthroats have predominantly 9 pelvic rays. In the lateral series scale count there is a very slight overlap between northern coastal rainbows and cutthroats, but no overlap in the mean values between the two species. Neave (1943) reported that the lateral series scale count for coastal cutthroats raised at the Veitch Creek hatchery, British Columbia, ranged from 122 to 154 (137.4). ~~Also, the coastal cutthroats used by Hartman (1956) from Chilliwack Lake, B.C., were relatively coarse scaled~~. A sample of Cowichan River, B.C., cutthroats had a mean value of 160.4 scales in the lateral series, according to Neave (1943). Although certain resident populations of coastal cutthroats may tend to have low scale counts, there is a good separation in the number of scales between cutthroats and coastal rainbows in the waters of British Columbia and Alaska, according to our data.

In specimens of 100 mm. or more in standard length, 178 of 179 specimens possess~~ed~~ basibranchial teeth. The sole specimen~~s~~ which lacked these teeth came from Middle Quinsam Lake where rainbows also occur. This specimen had 64 vertebrae and may ~~have~~ represent~~ed~~ a hybrid. The vertebral counts of ~~our~~ the northern cutthroat samples are consistently lower than that of rainbow samples from the same general area. In Alaskan and British Columbian waters the coastal cutthroat typically has one or two less vertebrae than the rainbow.

Samples from Luck Lake, Alaska and Quinsam and Middle Quinsam lakes, B.C., contained some rainbows and some cutthroat-rainbow hybrids. The following criteria were used to distinguish between rainbows and cutthroats: spotting pattern, scale counts, vertebral number, number of pelvic rays, presence or absence of basibranchial teeth and length and thickness of gillrakers. Some specimens appeared to be hybrids and could not definitely be placed with either species. The Luck Lake cutthroat exhibited erratic spotting and patches of gaudy, golden colors typical of hybrids. It is noted, however, that the cutthroats from areas of suspected hybridization are quite distinct from rainbows in all meristic characters and although hybridization probably occurs, it must be limited. This is in contrast to most situations where interior cutthroats have hybridized with rainbows and produced hybrid swarms.

~~American~~ Coastal Cutthroats of the United States: -- Of the material examined from Washington, Oregon and California, only one group represents the sea-run form. The other samples are all resident trout. The sea-run group was collected from four small streams near Tillamook, Oregon. These Oregon, sea-run cutthroats are quite similar in all respects to the more northern samples, except that none have any spots on the pectoral, pelvic or anal fins nor on the abdomen. They appear to be identical to the California cutthroats described by De Witt (1954). The anadromous coastal cutthroat probably represents a rather homogeneous group from California to Alaska. This would be expected from a species where a slight degree of wandering from stream to stream prevents complete isolation of gene pools. Our data show no evident clines in the number of scales, vertebrae or gillrakers. Throughout the range of sea-run cutthroats, the lateral series scale count typically ranges from 135 to 180 and the mean value of a sample may be expected to fall between 145 and 160.

Two samples of resident cutthroat, isolated above barrier falls, have lateral series scale counts which are lower than any cutthroat heretofore mentioned in the literature. Thirty specimens from Grassy Lake Stream, a tributary of the Nehalem River, Clatsop County, Oregon, have 117 to 138 (126.3) scales in the lateral series. Thirteen of the thirty have 10 pelvic rays and two lack basibranchial teeth. This could suggest rainbow influence, but the vertebral count ranges from 59 to 62 (60.4) the lowest mean value of any coastal cutthroat sample used in this study. Penn Creek, a small stream emptying into the ocean at Patrick's Point State Park, Humboldt County, California, yielded a sample of twelve specimens. The lateral series scale counts of these specimens ranged from 118 to 135 (126.1). There was no evidence of rainbow influence on these trout. Two have only 8 pelvic rays and the pectoral ray count of 12 to 14 is lower than the typical cutthroat or rainbow. The Penn Creek cutthroats have from 15 to 18 (16.5) gillrakers and the mean value of 16.5 is the lowest of any cutthroat or rainbow sample known from North America except a sample of cutthroat from Gorge Creek, Alberta, Canada, which has an identical mean value.

Schultz (1934, 1936) reported coarse scaled cutthroats from streams in the Puget Sound drainage. He claimed these cutthroats typically have from 125 to 130 scales. Shultz (1934) believed the coarse scaled type evidently represented a new subspecies, but stated that much work had to be done before such a decision was justified. Suckley (1862) named <u>Salmo</u> <u>brevicauda</u> for a Puget Sound trout which appeared to be a cutthroat from his description. Suckley claimed that <u>brevicauda</u> was coarse scaled but presented no counts. Shultz (1936:136) suggested that ~~such~~ differences in the number of scales may be due to temperature differences in the stream during the development of the eggs.

Bible Creek, a tributary of the Nestucca River, Tillamook County, Oregon, appears to have almost identical physical characteristics as Grassy

Lake Stream. A sample of 15 cutthroat taken from above a barrier falls on Bible Creek have scale counts ranging from 148 to 184 (166.5); forty scales more than the mean value of the Grassy Lake Stream sample. We believe that the bulk of this difference in number of scales between the samples from these two streams which are so similar as to geographic location and physical characteristics, can be attributed to genetic differences.

Do the coarse scaled cutthroats mentioned by Schultz from the Puget Sound area in Washington, and our samples from Grassy Lake Stream, Oregon, and Penn Creek, California represent a monophyletic group which was once widespread along the Pacific Coast, then subsequently replaced by a finer scaled race of cutthroats, and now persist only in isolated localities? We believe that they do not. The interior cutthroat are fine scaled, thus it appears the primitive cutthroat which gave rise to them was also a fine scaled form. If the coarse scaled populations represent a relict form, consistent differentiation in other characters would be expected. Although the Penn Creek trout have a mean of only 16.5 gillrakers, the Grassy Lake Stream sample have a mean gillraker number of 18.7 which is relatively high for coastal cutthroats. It appears that small, isolated populations may independently evolve a coarse scaled type from a fine scaled progenitor. The samples from Gate Creek, Oregon, and Clearwater Creek, Washington, suggests that there are all degrees of intermdiacy between coarse and fine scaled non-anadromous coastal cutthroats.

The Cutthroats Trout _of Crescent Lake and Lake Sutherland_ Washington: -- Four species of cutthroat trout were named from Crescent Lake and Lake Sutherland on the Olympic Peninsula, ~~of~~ Washington. We consider all of these four species to be synonymous with _Salmo clarkii clarkii_. Jordan and Beardslee named

Salmo gairdneri crescentis (Jordan, 1896). The type specimen (S.U.11863) lacks basibranchial teeth and although the lateral series scale count ~~was~~ is 151, Jordan considered it with the rainbow series. Thirteen specimens of crescentis were examined. One other specimen besides the holotype lacks basibranchial teeth. Seven specimens have 10 pelvic rays and the vertebral count is relatively high for a cutthroat. It was claimed that crescentis lacked a cutthroat mark. This indicates that there may have been some rainbow introgression into this cutthroat population. As previously mentioned, a rainbow named S. g. beardslei was also ~~endemic~~ indigenous to Crescent Lake and introductions of hatchery trout may have occurred prior to 1896. Our crescentis material was collected in 1896, 1898 and 1909. The gillrakers number 18 to 21 (19.0). The rakers are short, typical of coastal cutthroat. Meek (1899) named Salmo bathoeceter from Crescent Lake, based on a specimen caught in deep water. No specimen of S. bathoeceter was examined, but from Meek's original description there is no evidence to support the assumption that two distinct forms of cutthroat occurred in Crescent Lake. All the counts and measurements of S. bathoeceter listed by Meek fall within the range of S. g. crescentis. The local fishermen at Crescent Lake believed that the trout caught at depths of more than 100 feet represented a distinct species. Evidently it was on this basis that bathoeceter was named. It is a most logical assumption that bathoeceter and crescentis were from a single cutthroat population. Although this population exhibited a slight degree of differentiation from typical coastal cutthroats, there is little valid argument for taxonomic recognition, and S. g. crescentis and S. bathoeceter are considered synonyms of S. c. clarkii. Heavy stocking of various strains of rainbow and especially the interior cutthroat, S. c. lewisi make it doubtful that the original cutthroat of Crescent Lake persists as a pure strain.

Meek (1899) named two cutthroat species from Lake Sutherland (spelled Southerland by Meek). LakeSutherland, tributary to the Elwah River, lies just to the south of Crescent Lake. Salmo clarki jordani and Salmo clarki declivifrons probably were based on individuals from the same population. Meek described these as subspecies but Jordan, Evermann and Clark (1931) considered them ~~S. c. jordani and S. c. declivifrons~~ as distinct species. Nine paratypes of S. c. jordani collected in 1898, and one specimen collected in 1930 were examined. The most distinctive character of S. c. jordani is the high number of basibranchial teeth. These teeth occur in one or two dense patches and number from 15 to 52. The mean value of 29.2 is higher than any other sample except the Lahontan cutthroat from Independence Lake, California. Some of the specimens have spots on the anal fin and the abdomen. According to Meek, S. c. jordani had a conspicuous cutthroat mark. The scale counts ranged from 131 to 158 (145.5). This is similar to the range and mean given by Meek (1899) for S. c. jordani. His scale counts ranged from 135 to 154 (146.1).

The species named S. c. declivifrons by Meek (1899) was based on a single specimen from Lake Sutherland. Meek claimed that this trout had a wide gape of the mouth, hence its name. It was also stated that this trout was distinguished from S. c. jordani by the color of its fins, which were yellowish instead of orange and that S. c. declivifrons had spots only on the tail. No specimens of S. c. declivifrons were examined. The possibility that two distinct populations of cutthroat existed in Lake Sutherland is remote. When one is aware of the great variation in color, spotting and general morphology which may be evident within a single population, the evidence for the recognition of S. c. declivifrons is not convincing.

Mr. Robert Meigs of the W shington Game Department has supplied a copy of the stocking record for Lake Sutherland. Steelhead rainbow, hatchery rainbow, interior cutthroat (S. c. lewisi) and the rainbow and cutthroat

Table . -- Meristic Data on American Coastal Cutthroat Trout

Sample	Gillrakers			Vertebrae			Basibranchial Teeth			Pelvic Rays			Scales--Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	8	9	10	No.	Range	Mean
CALIFORNIA															
Penn Creek	11	15-18	16.5	12	59-63	60.9	11	1-15	6.6	2	10	--	12	118-135	126.1
OREGON															
Bible Creek	15	17-19	17.9	15	59-63	61.1	15	4-33	15.2	--	15	1	15	148-184	166.5
Gate Creek	17	16-20	18.1	23	60-65	61.8	13 4	2-17 0	5.8 --	--	17	--	12	129-158	142.6
Grassy Lake Stream	30	17-20	18.7	30	59-62	60.4	28 2	2-18 0	8.4 --	--	17	13	30	117-138	126.3
Tillamook Area	13	17-22	18.4	19	61-63	61.6	13	8-22	14.9	--	13	--	13	139-180	154.5
WASHINGTON															
Clearwater Creek	4	18-19	18.3	4	60-63	61.8	3 1	4-25 0	11.8 --	--	4	--	4	139-144	141.8
Lake Crescent--"crescentis"	12	18-21	19.0	10	62-65	63.1	11 2	3-12 0	7.6	--	6	7	6	150-162	155.2
Lake Sutherland--"jordani"	10	17-19	17.7	9	60-63	61.7	9	15-52	29.2	--	8	2	8	131-158	145.5

from Crescent Lake have been introduced. Because Lake Sutherland is a popular resort area on a main highway, the stocking has been intense. Thus, as with the trout of Crescent Lake, the ~~present~~ genotype has most likely been modified by introductions. ~~Perhaps an estimation of the degree of influence that introductions have made can be obtained by counting the basibranchial teeth on a present day sample of Lake Sutherland cutthroats.~~

<u>Salmo</u> <u>clarki</u> <u>jordani</u> is considered synonymous with <u>Salmo</u> <u>clarkii</u> <u>clarkii</u>. <u>Salmo</u> <u>clarki</u> <u>declivifrons</u> was most likely based on a variant of "<u>jordani</u>" and is also considered a synonym of <u>S</u>. <u>c</u>. <u>clarkii</u>.

Table ___ indicates some meristic characters of American coastal cutthroats.

Insert Table ____ here.

DeWitt (1954) presented scale counts of 78 ~~California~~ coastal cutthroats from various California streams; they ranged from 122 to 188 (151.7). His pyloric caeca counts were from 23 to 60 (40.3) for 71 specimens. Of 79 specimens, 73 had from one to 34 basibranchial teeth (8.8). The size of the specimens lacking basibranchial teeth was not mentioned.

Interior Cutthroat Trout

– Heading similar to Coastal Cut.

Typically, the cutthroat found in the interior waters of North America are more highly colored and more sparsely spotted than the coastal cutthroats. The interior waters considered here include the upper Missouri, Colorado, and Rio Grande river systems; the South Sasketchewan drainage; the Great Basin, as defined by Hubbs and Miller (1948) and the middle and upper Columbia River basin. The changing climate and geological history of these areas alternately formed and desiccated large lakes, coalesced and isolated various drainage basins and formed barrier falls on many rivers. The consequences of such a history provided many opportunities for fish speciation.

The endemic minnows and suckers of the interior waters, however, have attained a much higher degree of differentiation than the trout. To explain this, it may be assumed that the trout invaded the interior waters at a much later date than the minnows and suckers. The trout's proclivity for the colder headwaters where stream transfer between drainage basins is more probable, has hindered the formation of discrete species and subspecies. The morphology and physiology of trout may also play an important role in their lack of pronounced speciation in interior waters. The fact that they are able to inhabit a wide range of waters, such as small mountain brooks, large streams and lakes, and utilize a broad spectrum of foods, allows adaptations to new environments without major genetic changes.

The interior cutthroat exhibits much local variation in size, coloration, spotting pattern and habitat which has led to the description of many species and subspecies.

Jordan, Evermann and Clark (1930) recognized eleven species of interior cutthroat. Miller (1950), following other authors, provisionally considered the interior cutthroats to contain ten subspecies. It is our opinion that all the ~~endemic~~ native, interior trout north of the Little Colorado River belong to a single species, Salmo clarkii. The recognition of subspecies presents many problems. Not only is there great variation, but this variation may be as great within a drainage basin as it is between two separate basins. We may roughly group the interior cutthroats into three general types. These are the Lahontan, S. c. henshawi; the Yellowstone or black-spotted trout, S. c. lewisi, and the greenback, S. c. stomias. The Lahontan cutthroat is native to the Lahontan basin of Nevada and California. It is recognized by its more numerous gillrakers and the large spots, more or less evenly distributed ~~spots~~ on the side of the body. The Humboldt River system in the Lahontan basin and the

Alvord

desiccating ~~basins~~ basin in southeast Oregon have some interesting populations which are somewhat intermediate between S. c. henshawi and S. c. lewisi. The Humboldt group is named as a new subspecies. The Piute trout, S. c. seleniris is a Lahontan trout isolated above a falls. The Piute trout differs from other Lahontan cutthroats only by its lack of spots on the body. The greenback trout, S. c. stomias, of the Arkansas and Platte rivers in the state of Colorado, is distinguished by its large spots and fine scalation. The Yellowstone trout, S. c. lewisi, is considered a polytypic subspecies. We extend the traditional range of S. c. lewisi to include the cutthroat of the Colorado, Rio Grande and Bonneville basins. The variation in color, spotting and number of scales is great but intergradations between extremes appear to be complete.

Salmo clarkii lewisi

~~The following synonymy is composed of species listed by Jordan, Evermann and Clark (1930) which we treat as S. c. lewisi.~~

Salar lewisi Girard, Proc. Acad. Nat. Sci., Phila., 8, 1857: 219. Falls of Missouri River.

Salar virginalis Girard, ibid.: 220. Utah Crk., Colo. (Rio Grande system).

Salmo carinatus Cope, Hayden's Geol. Surv. Mont., 1872:469. Missouri R.

Salmo pleuriticus Cope, ~~Hayden's Geol. Surv. Mont.,~~ ibid. 1872:471. Green R., Wyo.

Salmo spilurus Cope, ibid, 1872:470. Rio Grande.

Salmo utah Suckley, Rept. U.S. Fish Comm. 1872-73; 1874:136. Utah Lake.

Salmo purpuratus bouvieri Bendire, Proc. U.S. Nat. Mus., 4; 1882:86. Waha Lake, Idaho.

Salmo mykiss macdonaldi Jordan and Evermann, Proc. U.S. Nat. Mus., 12; 1890:453. Twin Lakes, Colo.

Salmo eremogenes Evermann and Nichols, Proc. Biol. Soc. Wash., 22; 1909:93. Crab Creek, Ritzville, Wash.

The precise range of S. c. lewisi has never been defined. Generally, the upper Missouri system in Montana and Wyoming, the South Saskatchewan drainage in Alberta, Canada, and the middle and upper Columbia basin, Table . -- Meristic variation in "typical" *Salmo clarkii lewisi*.

Sample	Gillrakers			Vertebrae			Basibranchial Teeth			Scales Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
ALBERTA, CANADA,												
S. Sasketchewan System												
Pickle Jar Lake	36	17-21	18.9	35	59-61	60.2	32 4	2-26 0	9.6	15	162-182	172.1
Gorge Creek	27	14-19	16.5	28	60-62	61.0	21 5	1-16 0	6.6	10	153-188	170.4
Ware Creek	34	16-22	18.7	35	60-64	61.8	28 4	1-16 0	7.2	15	131-172	153.8
U.S.A.												
Yellowstone Lake	30	19-23	20.6	30	60-63	61.5	29	1-27	13.7	30	149-202	170.3
Snake River Drainage												
Fish Creek, Wyoming	4	19-22	19.8	4	61-63	62.5	4	12-26	19.2	4	169-196	182.5
Game Creek, Wyoming	26	17-21	19.0	25	61-64	62.1	26	4-38	12.5	14	146-166	157.5
Goose Creek, Nevada	39	18-21	19.6	21	60-63	61.7	26 2	1-17 0	5.3	28	143-177	158.7
Irving Creek, Idaho (now isolated drainage)	5	20-22	20.4	10	62-64	63.0	5	6-14	9.4	5	175-189	179.4

including the Snake River have been accepted as the range of S. c. lewisi. There is great variation in spotting, coloration and number of scales in the native trout of these areas. Because this range of variation encompasses the endemic cutthroat of the Colorado and Rio Grande systems and most of the Bonneville basin, we consider the native cutthroat trout of these areas as S. c. lewisi.

The typical lewisi spotting pattern has a concentration of spots on the caudal peduncle. The spots anteriorly are mainly above the lateral line. The spots may be large and roundish or small and irregularly shaped. The size, shape and distribution of spots may vary from population to population and between individuals in a single population. The lower fins are generally rose, orange or yellow, typically, without a prominant white edge as is found in rainbows and many coastal cutthroats. The following table indicates some meristic variations in cutthroat from the South Sasketchewan and Snake river drainages, and from Yellowstone Lake.

Insert Table ___ here.

Only samples from Pickle Jar Lakes, Alberta, and Yellowstone Lake are known to be uncontaminated by rainbow and other cutthroat introductions. The Gorge Creek and Ware Creek populations are known to have rainbow influence. Introductions in the South Sasketchewan ~~system~~ has resulted in the introgression of rainbow genes throughout the native cutthroat population, except where isolation occurs, such as in Pickle Jar Lake. R. B. Miller (1957) discussed the rainbow introgression in the South Sasketchewan drainage. Although 5 of 26 Gorge Creek specimens lack basibranchial teeth, there is little evidence from the meristic data that hybridization has occurred. The erratic spotting pattern and gaudy coloration observed in the living specimens, however, immediately suggested hybridization with rainbows. The

Ware Creek trout are more obvious hybrids. They also exhibited gaudy coloration, some quite golden, typical of rainbow-cutthroat hybrids. The Pickle Jar Lake specimens were uniform as to color and spotting. The spotting pattern of the Pickle Jar Lake fish is typical of the fine spotted type of interior cutthroat (fig.__). The vertebral count of 59 to 61 (60.2) is the lowest of any cutthroat sample used in this study except S. c. stomias.

Yellowstone Lake, Wyoming, has no other trout except the native cutthroat and there has been no introduction of non-native trout (Cope, 1957). The Yellowstone Lake specimens have a variety of spotting patterns. Most have large, round spots concentrated posteriorly, but some are more evenly spotted on the sides of the body; a few have spots on the abdomen, and appear identical to the Lahontan cutthroat, S. c. henshawi. A more quantitative description of the variation in spotting and coloration in Yellowstone Lake trout and closely related populations is given by Bulkley (1963). The more numerous gillrakers in the Yellowstone Lake sample suggests an incipient specialization for the lacustrine environment.

The specimens from Game Creek and Fish Creek are intensely spotted with tiny irregularly shaped spots (fig.___). These samples are similar except for the divergence in scale counts. Goose Creek, Nevada, is a Snake River tributary which enters the main stream above Shoshone Falls. The spotting in the Goose Creek trout is quite distinct from the Game Creek and Fish Creek specimens. The Goose Creek cutthroats have large, round spots, sparsely distributed (fig.___). They appear much like the trout of Yellowstone Lake. It is interesting that, in contrast to most other interior waters, the Goose Creek cutthroats appear to be a pure stock despite introductions of rainbow trout into Goose Creek by both the Idaho and Nevada Fish and Game Departments. Thirty-nine specimens were collected from a two-mile stretch of Goose Creek, just south of the Idaho border. They all appeared to be of pure and uniform cutthroat stock. These trout apparently are well adapted to the conditions of Goose Creek. There is an abundance of minnows in Goose Creek. *Rhinichthys osculus*, *R. cataractae* and *Gila* (*Snyderichthys*) *copei* were collected with the trout, the latter two species were new records for the fauna of Nevada.

The stomach contents of trout, 12 inches or more, were almost exclusively composed of smaller fish. Being an effective predator may favor the native cutthroat over the introduced rainbow. Hybrids produced are probably at a competitive disadvantage and removed from the population by natural selection.

Irving Creek, Clark County, Idaho, belongs to a disrupted segment of Snake River system. This area, in southeastern Idaho, was called the Snake River Lava Plateau by Hubbs and Miller (1948). The cutthroat trout of this area was considered to represent an endemic subspecies by Hubbs and Miller, although they did not name it. ~~It is interesting to note that~~ Relict populations of Dolly Varden char, *Salvelinus malma*, were also collected from isolated streams in this area. The specimens from Irving Creek are fine scaled and have a high vertebral count for cutthroats, but they are quite typical of *S. c. lewisi* in most meristic characters. The trout of Irving Creek may have been isolated for a long period, but they have not differentiated enough from other Snake River trout to be subspecifically recognized.

Salmo bouvieri: -- Bendire (1882) described a trout from Waha Lake in western Idaho as *Salmo purpuratus* var. *Bouvieri*. This trout had large, round spots sparsely scattered, mainly on the caudal peduncle (fig.___). Garman (1883) considered *bouvieri* as a synonym of *S. c. lewisi*. Jordan (1885) disagreed with Garman but stated: "*bouvieri* is only a color variety and its color not that of a typical *lewisi*". Considering the variation of the interior cutthroat throughout the range of S. c. lewisi, the selection of a "typical" color or spotting pattern is an impossible task. Jordan and Evermann (1903:187) published a confusing statement concerning the spotting of bouvieri. They said:

> "Spots only on the dorsal, caudal and adipose fins, and on the caudal peduncle behind front of anal where the spots are very profuse smaller than the pupil".

This was printed beneath an illustration of bouvieri which depicts a specimen with only about 15 large, round spots on the caudal peduncle. Evidently, they meant to say that profuse, smaller spots occurred on the tail. The spots on the body behind the front of the anal fins are large, round and sparsely distributed, much like Salmo clarkii stomias.

A single ancient specimen of bouvieri was examined. The scale count was 157 in the lateral series and 34 above the lateral line. There were 61 vertebrae and 17 gillrakers; basibranchial teeth were present. Jordan and Evermann (1896:496) gave a scale count of 175 and the same authors (1903:187) said bouvieri had 173 scales. The cutthroat ~~trout~~ that was ~~once found in~~ native to Waha Lake may be considered as a sparsely spotted S. c. lewisi and bouvieri as a synonym of S. c. lewisi.

The ~~endemic~~ native cutthroat of Waha Lake is now certainly extinct. Mr. James Simpson, Chief of Fisheries, Idaho Fish and Game Department, has informed us that Waha Lake was twice poisoned to remove carp and other undesirable fish. The second poisoning resulted in a complete fish kill. The importance of the Waha Lake trout is the fact that these trout had large and sparse spots although Waha Lake is in the Snake River drainage, about 350 miles downstream below Shoshone Falls. Snake River specimens show a reverse in an expected trend that the cutthroats of the upper river would be more typical of interior trout, i.e., larger and fewer spots while the downstream trout may be expected to intergrade with the finer and more heavily spotted coastal cutthroat. The trout most resembling coastal cutthroats in their spotting are the samples from the headwater areas -- Game and Fish creeks, Wyoming. On the basis of our meager material, it is difficult to speculate on the phylogenetic significanc e of the diverse spotting pattern found in Snake River cutthroats. It may be merely local responses, independently evolved in each area or it may represent diverse origins. The lack of any other character differentiating the fine spotted and large spotted trout suggests the former opinion is more correct.

these fine-spotted trout are indeed distinct - subject of Trojnar & Behnke paper in 1974 Trans. Am. Fish. Soc. - Apr. 75

The range of variation and the distribution of cutthroat trout in the Snake River system below the Falls and in the middle Columbia drainage in general is not known. Shultz (1935) stated:

> "The range of the fine scaled form or Montana black-spotted trout overlaps that of the coastal form in the region east of the Cascade Mountains of eastern Washington. In the latter area we have seen certain specimens which we identify as intergrades between the coastal cutthroat and the fine scaled form".

Gilbert and Evermann (1894) seemed to have cutthroats and the fine-scaled "Kamloops" rainbow confused in their Columbia River investigations, claiming the cutthroat and rainbow intergraded so thoroughly that they might be considered as a single species.

Salmo eremogenes: -- Evermann and Nichols (1909) described Salmo eremogenes from Crab Creek in eastern Washington. Crab Creek flows into Moses Lake, a disrupted part of the Columbia River system. Hubbs and Miller (1948) considered eremogenes as a subspecies of Salmo clarkii and believed it to be extinct.

There is nothing in the original description to suggest that eremogenes is distinct from S. c. lewisi. Shultz (1935) has stated that the cutthroat trout of the upper Columbia drainage in eastern Washington are S. c. lewisi. Thus, it would be expected that an isolated, former tributary of the Columbia would contain S. c. lewisi. If isolation ~~were~~ was of long duration and selection rigorous in a new environment, we should expect some apparent changes in the isolated fauna. However, from the illustration of S. eremogenes and the description, there is nothing that tends to validate the claim for specific or even subspecific recognition. Scale counts for three specimens of S. eremogenes are given as 165, 174 and 175. Evermann and Nichols (1909) stated:

> "In the number, size and arrangement of spots, this species most resembles Salmo stomias, the trout of the headwaters of the Platte and Arkansas. It differs from that species, however, in the shorter snout, large eye and the somewhat larger scales. The Waha Lake trout (S. bouvieri) differs from the Crab Creek species in the entire absence of black spots anteriorly".

Although there is no reason to believe that trout were not native to Crab Creek, it must be noted that S. eremogenes was collected in 1908 and may have been the result of an introduction. Whether S. eremogenes was ~~endemic~~ native or introduced into Crab Creek, we consider it as a synonym of S. c. lewisi.

Salmo clarkii alpestris: ~~--~~ Dymond (1931) named ~~the mountain cutthroat trout, Salmo clarkii alpestris~~. This trout was from specimens collected from Isaac, Frog, and Canyon creeks, in the Columbia River drainage near Revelstoke, British Columbia, and from other Columbia tributaries. In the Frazer River system, this trout was listed from Crazy, Yard and Frog creeks. In this area ~~in~~ of British Columbia, the Kamloops rainbow is the dominant trout and the sporadically occurring cutthroat populations were grouped as a new subspecies. The type came from Canyon Creek and five paratypes were preserved from Isaac Creek. Dymond believed the most diagnostic character of *S. c. alpestris* was its extremely numerous scales. According to Dymond's counts, there were 200 to 230 diagonal rows and the mean value for five specimens was 214. Four paratypes from Isaac Creek were examined; our scale counts, made two rows above the lateral line on three specimens were 195, 207 and 210. This is somewhat lower than Dymond's counts but the Isaac Creek specimens do represent a fine scaled trout. Qadri (1959) admitted that *S. c. alpestris* had slightly more scales than other interior cutthroat of British Columbia, but synonymized *S. c. alpestris* with *S. c. lewisi*. Qadri used the scale counting method of Neave (1943) and did not make full lateral series counts. We would agree with Qadri that the fine scalation in the Isaac Creek specimens is not enough distinction to give subspecific recognition to *S. c. alpestris*. There is another character, however, which makes the Isaac Creek trout unique. This is the number of scales (pores) in the lateral line. As mentioned by Neave (1943) it is typical for trout to have approximately two pores in the lateral line for every vertebra. This has essentially held true for all the rainbow and cutthroat specimens used in our study. Most trout have from 110 to 130 pores in the lateral line, counting to the end of the vertebral column (standard length). Because lateral line scale counts are so closely correlated with vertebral counts we have not stressed it as a taxonomic character. It is rare to find a trout with more than 130 scales in the lateral line. The four specimens examined from Isaac Creek have 145, 146, 149 and 150 scales in the lateral line, yet they have only 61 or 62 vertebrae. Two specimens of cutthroat trout collected from Hill Creek, Rio Blanco County, Colorado, in the Colorado River system, have 138 and 148 scales in the lateral line and 61 and 62 vertebrae. The Hill Creek trout are the only specimens used in this study which are comparable to the Isaac Creek S. c. alpestris in the number of scales in the lateral line. The pink salmon, Oncorhynchus gorbuscha, also has about 2.5 times as many lateral line scales as it does vertebrae. Neave (1943) believed this may be due to the large size attained before scale formation begins. It is not known if the other trout considered by Dymond as S. c. alpestris from the other isolated localities all possess this distinctive character or if only ? the Isaac Creek trout should be considered S. c. alpestris.

The Isaac Creek specimens have an abundance of basibranchial teeth, numbering from 15 to 40 in the four specimens.

In all other respects, the Isaac Creek specimens appear to be typical of S. c. lewisi. The presence of interior cutthroat trout in a few headwater tributaries in the Fra~~z~~ser River system can most logically be explained by stream capture from the Columbia River area. Dr. C. C. Lindsey has written that such a stream transfer could have taken place easily in the area from which alpestris was described.

It remains to be seen if the number of scales in the lateral line in alpestris is a local phenomenon restricted to Isaac Creek or is representative of a relict form of cutthroat which inhabited this general area before being replaced by the Kamloops rainbow.

Dr. Lindsey has written that he plans to have a student carry out a comprehensive study of S. c. alpestris. Until more data is available, we withhold our judgment on the validity of the subspecies, S. c. alpestris.

Colorado River Cutthroat

Cope (1872a) described Salmo pleuriticus based on specimens from the Green, Platte and Yellowstone rivers and other streams in Idaho and Montana.

Although Cope did not designate a type, the name *S. pleuriticus* has been associated with Colorado River cutthroat because the Green River is in the Colorado system. Cope distinguished his species *pleuriticus* by the presence of a cranial keel and the possession of 40 to 45 scales above the lateral line. No one since Cope has used cranial keels in trout taxonomy. The scattered geographical areas from which the specimens were taken for the description of *S. pleuriticus* suggests that the cranial keel was an artifact of the method of preservation in the specimens selected by Cope.

Variation in the color and spotting of Colorado drainage cutthroats was recognized by Cope (1872) and Jordan (1891). Jordan listed scale counts and spotting patterns of a few specimens and claimed that *S. pleuriticus* always had a red lateral band and the lower fins were more or less red. In Trapper's Lake, Colorado, Snyder and Tanner (1960) separated what they considered *S. pleuriticus* from introduced *S. c. lewisi* from Yellowstone Lake. They recognized the specimens with red on their sides and bellies as *S. pleuriticus*. When the stocking records and hatchery operations at Trapper's Lake are examined, it seems improbable that the native and introduced forms have not completely merged. The red on the side and belly is probably an expression of polymorphism within a single population. The occurrence of red on the sides and lower fins of interior cutthroat is a common feature and does not allow separation of the Colorado drainage trout from other interior cutthroat.

Colorado River cutthroat are typically fine scaled. But this character, as with spotting and coloration, is variable among various populations.

Distribution: -- The southern limit of the range of Colorado River cutthroat has not been satisfactorily settled. The specimens of trout listed as *S. pleuriticus* from the White River, Arizona, described by Cope and Yarrow (1875) were examined and were found to be a distinct group which we call the Arizona golden trout in this paper. Jordan and Evermann (1896:496) and subsequent authors give the range of S. pleuriticus as "throughout Arizona". Miller (1961:389) examined the specimens of "pleuriticus" mentioned by Jordan and Evermann (1896:496) from the Little Colorado and found them to be the native Arizona golden trout. The records of S. pleuriticus from the Salton Sea, California, were summarized by Dill (1944) and found to be doubtful. Miller (1950) stated that the "pleuriticus" records for the Salton Sea and the lower Colorado River drainages were actually based on introduced rainbow trout. Miller (1961) claimed that cutthroat trout were not native to Arizona, the only endemic trout being the native "golden". The southernmost population of an ~~ou~~undoubted cutthroat trout from the Colorado River system is a collection made near Pine Valley, Washington County, Utah, from an intermittent stream of the Virgin River drainage. Besides the Pine Valley, Utah, collection, our Colorado River cutthroat material consists of 40 specimens borrowed from the University of Michigan. These specimens represent 12 samples from Wyoming, Colorado and Utah. Most were collected in the 1930's and 40's. Although most of the localities are remote, the influence of introductions cannot be ignored.

- These are Bonneville cutts - Apr. 75

The following generalizations can be made on our Colorado River material: The cutthroat from the northern headwaters of the Colorado, such as the Green River, were characterized by small irregularly shaped spots, scattered on the caudal peduncle and above the lateral line anteriorly. These finely spotted trout are typically fine scaled, generally with from 180 to 200 scales in the lateral series. This type of trout seems identical to the yellowfin trout ~~of~~ once native to Twin Lakes, Colorado, ~~named Salmo macdonaldi~~.

In September, 1962, a single specimen of cutthroat trout was collected from the Green River, Sweetwater County, Wyoming, when that river was ~~poisoned~~ chemically treated to remove rough fish. This trout had large, round spots and ~~had~~ 173 scales in the lateral series. Perhaps, it represents an introduction of Yellowstone Lake stock.

Bonneville cutts

Our southernmost sample from Pine Valley, Utah, are quite distinct from Green River specimens. The Pine Valley trout have larger, more round spots, more or less evenly distributed on the sides of the body (fig.___), resembling the Lahontan cutthroat, S. c. henshawi. They have about 30 less scales in the lateral series than the fine scaled Colorado trout from more northern tributaries. ~~As might be anticipated, the~~ Trout from intermediate areas exhibit intermediate spotting patterns and scale counts. Generally, Colorado River drainage cutthroats have more scales than most other populations of S. c. lewisi, but the distinction is not sharp.

The Pine Valley Cutthroat Trout: -- A few miles north of the small community of Pine Valley, Washington County, Utah, a stream which drains Reservoir Canyon, contains a pure stock of cutthroat trout. These trout are isolated above barrier falls; below, in Main Canyon, the stream has a population of rainbow-cutthroat hybrids. This stream and its trout were discussed by Miller (1961:391). The Reservoir Canyon stream is tributary to the Santa Clara River, in the Virgin River drainage. The Virgin River enters the Colorado in what is now the Overton Arm of Lake Mead, about 150 miles downstream from the confluence of the Little Colorado River. The question arises: If cutthroats were native to the Pine Valley, Utah, area in the Virgin River drainage, why were they not found throughout the Little Colorado system and other Colorado River tributaries in Arizona, at least as far downstream as the Virgin River? The Virgin River drains a relatively large area in southwestern Utah and southeastern Nevada but, except for the Pine Valley area, no other populations of native trout have been reported from this drainage. Only a few headwater streams in the Virgin system provide suitable environmental requirements for trout today and these may have been inaccessible to invasion in previous times or more drastic conditions in the past may have eliminated all other established populations.

Table . -- Comparison of cutthroat and rainbow-cutthroat hybrids, Reservoir Canyon, Pine Valley, Utah.

Sample	Pelvic Rays				Vertebrae			Basibranchial Teeth			Scales Lateral Series			Scales Above Lateral Line		
	8	9	10	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
Headwater (cutthroat)	1	14	3	9.1	18	61-64	62.2	16 2	1-9 0	4.9	18	139-167	157.3	18	39-44	41.5
Mid-Section (cutthroat)	--	13	--	9.0	13	61-64	62.0	12 1	1-7 0	2.5	12	145-182	159.2	13	38-46	42.1
Lower Section (hybrids)	--	23	16	9.4	39	59-65	62.5	13 26	1-11 0	5.3	15	126-163	146.4	34	29-48	38.5

The upper Santa Clara drainage, around Pine Valley, borders on the southwestern segment of the Bonneville b ~~B~~asin. It is more plausible that the cutthroat trout ~~endemic to~~ of the Pine Valley area were derived from the Bonneville basin via stream transfer or introductions by early settlers and did not originate from the Colorado River. The spotting pattern and scale counts of the Pine Valley trout suggests affinities with the trout of the Southwestern Bonneville basin.

According to Mr. Jack Rencher of Pine Valley, the headwaters of Reservoir Canyon were originally barren of fish. ~~An introduction of~~ Cutthroats ~~was made~~ were introduced about the turn of the century from fish taken in the lower section of the stream.

Our collection is divided into three samples. The lower stream contains only rainbow-cutthroat hybrids. A sample of 39 specimens shows all degrees of spotting and morphological variation. Some appear to be typically rainbow and others resemble pure cutthroats, but most exhibit great variation in spotting and gaudy coloration (fig.___). Only 13 of 39 hybrids ~~had~~ have basibranchial teeth; 16 ~~had~~ have 10 pelvic rays. Table ___ indicates the meristic variations found. The fact that the morphological features and meristic characters formed a continuous variation, which when plotted form a unimodal curve of distribution suggests that the hybrids are not selected against either by the environment or differential fertility. Gonads were removed from these trout and a ratio of gonad weight to body weight was compared between the hybrids and the pure cutthroats from above the barriers. There was no difference in the relative size of the gonads. Histological sections were made on ovaries and testes. Deterioration between time of capture and preservation prevented a clear picture of the fine details. Close examination of the preparations, however, show the gross development of sperm and eggs in the hybrids to be identical with the pure cutthroats. The middle and upper stream samples represent a pure strain of cutthroat and are identical. ~~to each other~~.

In summary, the Colorado River cutthroat populations have ~~both~~ fine scaled and medium scaled types and ~~also~~ large spotted and fine spotted forms. This parallels the variation in other interior drainages. Because no single character allows separation of Colorado River cutthroat from other S. c. lewisi, we consider S. pleuriticus as a synonym of S. c. lewisi.

The Yellowfin Cutthroat

One of the most interesting situations ~~from the standpoint of the~~ concerning the speciation of cutthroat trout occurred in Twin Lakes near Leadville, Colorado. Twin Lakes lies just to the east of the Continental Divide. It drains into the Arkansas River but may have had previous connections, perhaps from stream capture, with the Colorado River. Representative trout from these two river systems once lived in Twin Lakes, evidently behaving as two distinct species. Salmo clarkii stomias was once abundant in Twin Lakes. It was identical to the stomias of the Arkansas and Platte rivers. A larger trout, more finely spotted, probably identical with the cutthroat of the upper Colorado system, also inhabited Twin Lakes. This latter form was named Salmo mykiss macdonaldi by Jordan and Evermann (1890). Concerning macdonaldi, Jordan and Evermann stated:

> "This form of trout occurs in company with subspecies stomias, but in Twin Lakes, the two are entirely distinct, the habits, size, and coloration being notably different. If we were to consider the Arkansas Basin, alone, the two must be ranked as distinct species, but these and all other American trout seem to be connected by intergradations. Apparently macdonaldi is derived from the Colorado River pleuriticus".

Jordan (1922, vol. 1:334-35) related the details of the discovery of macdonaldi:

> "Visiting Twin Lakes, a glacial excavation in the midst of Saguache range and separated into two parts by an old

moraine, we found the common greenback to be very abundant there. As we were preparing to leave, an enthusiastic young angler, George R. Fisher, then of Leadville, told us that another trout we had not seen, a great big fellow with yellow fins, lived in the depths of the lower lake.

"Though decidedly skeptical, I was nevertheless induced to go out before sunrise in search of a new species. To my delight we caught some half-dozen fine large specimens weighing from eight to ten pounds. At a hint from Marshall Macdonald, then the excellent United States Commissioner of Fisheries, we named the new form for him, though the appellation I had originally in mind would have forever associated it with the high cliffs and eternal snow of the Saguache range, several peaks of which exceed 14,000 feet. It was years before macdonaldi was again brought in by a naturalist. Recently, however, it has been successfully introduced into France from eggs sent out from the Mount Massive hatchery near Leadville".

omit

It appears that ~~S. m.~~ macdonaldi became extinct soon after its discovery. Juday (1907) found no specimens during his work on the lake in 1902 and 1903 although S. c. stomias was still present. At that time, Salvelinus fontinalis, Salvelinus namaycush, Salmo salar and Salmo gairdnerii had been introduced and established in Twin Lakes. Ellis (1914) claimed that no specimens of macdonaldi had been taken in several years and presumed it extinct. Jordan and Evermann (1890) and Jordan (1891) claimed the ecologies of ~~S. c.~~ stomias and ~~S. m.~~ macdonaldi were distinct in Twin Lakes. There was supposedly a great difference in size; ~~S. c.~~ stomias rarely exceeded one pound while

S. m. macdonaldi attained a much greater weight. The feeding habits were were reputed to be distinct; The smaller S. c. stomias was a crustacean feeder and had red flesh while S. m. macdonaldi was piscivorous with white flesh. These premises, however, were actually based on scant detailed observations. Jordan believed that S. c. stomias spawned only in the streams and S. m. macdonaldi spawned mainly in the lake, but no [redacted] evidence was presented to support this supposition. Juday (1907) studied the food utilized by the Twin Lakes trouts and found that S. c. stomias did eat more crustaceans and less fish than did the introduced rainbow trout but S. gairdnerii utilized a greater variety of food than the native S. c. stomias. Jordan (1891) said the length of the types were from 6 to 10 inches, that S. m. macdonaldi had 184 scales in the lateral series and 40 above the lateral line. Although the two specimens of S. m. macdonaldi examined have more gillrakers than would be expected from Colorado River drainage trout, they appear to be identical in all other respects (table _). It is possible that the early settlers in the Twin Lakes area were not content with the small size of S. c. stomias in Twin Lakes and introduced larger trout from tributaries of the Colorado, only a short distance away. The evidence is convincing, however, that whether S. m. macdonaldi was endemic or introduced into Twin Lakes, it occurred sympatrically and with a reproductively isolated from S. c. stomias. -omit Because S. m. macdonaldi evidently had such close affinities with the upper Colorado River cutthroat, and because we consider pleuriticus as a synonym of S. c. lewisi, we also submerge S. m. macdonaldi under S. c. lewisi. The subtle ecological factors which allowed two subspecies of the cutthroat trout to occur sympatrically in Twin Lakes can only be theorized on. It would be enlightening and interesting if pure populations of S. c. stomias and the fine spotted Colorado cutthroat were introduced into various waters to observe if the original Twin Lakes situation could be duplicated.

Table . -- Comparison of Salmo clarkii macdonaldi and Salmo clarkii stomias collected from Twin Lakes, Colorado, 1889.

	Gillrakers			Basibranchial Teeth			Scales Lateral Series			Scales Above Lateral Line		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
S. c. macdonaldi	2	21-22		2	15-16		1	182		2	38-46	
S. c. stomias	8	18-20	19.5	8	6-14	10.6	7	170-202	186.9	7	46-53	49.0

Recognizing the great amount of inherent variability in trout and the dearth of material on ~~S. m.~~ macdonaldi, it might be assumed that Twin Lakes had a single Salmo population and ~~S. m.~~ macdonaldi was based on some large specimens of ~~S. c.~~ stomias. Examination of museum material collected in 1899, however, strongly supports the view that two distinct types of cutthroat trout existed in Twin Lakes. Two specimens in the Stanford collection (SU 512) are listed as types of macdonaldi. These trout are 164 and 223 mm. in standard length. They are silvery specimens with fine spotting, appearing quite identical to the cutthroats once native to the upper Colorado River system and entirely distinct from the dark, large spotted S. c. stomias taken at the same time from Twin Lakes. Table ___ compares the specimens of ~~S. m.~~ macdonaldi and ~~S. c.~~ stomias collected from Twin Lakes in 1889. The ~~S. c.~~ stomias specimens ranged from 176 to 217 mm. standard length. Both the ~~S. m.~~ macdonaldi and the ~~S. c.~~ stomias specimens have 61 or 62 vertebrae.

Rio Grande ~~System~~ cutthroat

Girard (185~~4~~6) named Salar virginalis for specimens from Utah Creek, Colorado, a headwater tributary of the Rio Grande. Cope (1872b) named Salmo spilurus for trout he examined from Sangre de Christo Pass, Colorado, another headwater tributary of the Rio Grande. Cope recognized that S. spilurus and S. virginalis were similar but said S. spilurus was a distinct species because it was "not so slender". Later authors used S. spilurus as the name for the Rio Grande cutthroat under the mistaken assumption that Girard's type locality was actually Utah Lake of the Bonneville basin. Snyder (1919) and Jordan (1920) corrected this mistake and restored the name S. virginalis to the Rio Grande trout.

The original distribution of Rio Grande cutthroats and their distinguishing characters are nebulous. Concerning the Rio Grande cutthroats, Jordan (1891:14) said:

"...abounding in all its tributaries and extending southward in the mountains of Chihuahua. This form is apparently wholly identical with var. pleuriticus except that in the specimens examined the scales are less crowded forward, so that the number in a lengthwise series is less. I count 155 to 160 in Rio Grande specimens; 185 to 190 in those from the Colorado. From the trout of the Great Basin (virginalis) spilurus differs chiefly in the arrangement of its spots".

Figures 7 and 8 in Jordan (1891) portray a fine spotted Rio Grande trout which is listed as an adult and a large spotted specimen noted as young. Cope (1872) described his type specimens of S. spilurus from Sangre de Christo Pass as: "thickly spotted with large irregular black spots". Cope (1875) observed "spilurus" in the Brazos River, New Mexico, as having small spots concentrated posteriorly. In this same work he described large and small spotted trout from the Rio Grande in Colorado which he considered as separate varieties or subspecies of pleuriticus. Ellis (1914:82) wrote:

"Specimens taken in the Rio Grande at Creede in 1912 were quite silvery and had very small black spots; the lateral band was pale rose red color".

The reference to the Rio Grande cutthroat in Chihuahua, Mexico, is from Cope's (1884) note on Mexican trout in ~~which he~~ referred to as S. purpuratus ~~the cutthroat species~~ but did not give the precise locality of the collection. It is entirely credible that cutthroat were native to, and may still persist in the Rio Grande drainage of Chihuahua, but there are no authentic records of such trout. Needham and Gard (1959) described trout collected in the Rio Casas Grande in Chihuahua. The Casas Grande is a disrupted tributary of the

Rio Grande, but the trout of this stream are quite identical to the trout of the Rio Yaqui and resemble the Gila trout, S. gilae. These trout form a most interesting complex, showing characters in many ways intermediate between cutthroats and rainbows but are quite distinct from the cutthroats of the upper Rio Grande. ~~Perhaps the Casas Grande was without trout and the present population the result of introductions from the headwater tributaries of the Yaqui, only a short distance away.~~ ¶ Rostlund (1952:25) records that the first mention of western trout by Europeans was a statement of the Coronado expedition finding "very good trout in the upper Pecos River". The Pecos is tributary to the Rio Grande joining it on the Texas-Mexican border, far downstream from known trout populations today. This indicates that formerly trout were more widespread in the Rio Grande system.

From the available evidence, the Rio Grande had populations of both fine spotted and large spotted cutthroats, paralleling the condition found in the Colorado drainage. Specimens in the Stanford University and California Academy of Sciences collections, collected by Jordan from the Rio Grande at del Norte, Colorado, in 1889, are finely spotted. In August, 1958, ~~collections of~~ cutthroat trout were ~~made~~ collected in the Rio Seco and Indian Creek, Costillo County, Colorado, and sent to the University of Michigan. These localities are in the Rio Grande system and the trout probably represent the native stock. The samples from the two localities are similar and will be considered together. They are large spotted trout, the spots are concentrated on the caudal peduncle and occur only sparsely anterior ~~of~~ to the dorsal fin (fig.___). The adipose fin is distinctively edged with a pronounced black border. There cheek and opercle blotches are distinct. A few specimens have spots on the sides of the head, but there are no spots on the top of the head. In the preserved specimens, the anterior tip of the dorsal fin is marked by a light area. The specimens have a robust appearance. ~~The following~~ Table (?) ~~gives~~ presents some meristic data on these trout.

Table . -- Meristic Data on Rio Grande Cutthroats from Indian Creek and Rio Seco

Gillrakers			Vertebrae			Basibranchial Teeth			Scales Lateral Series			Pelvic Rays	
No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	8	9
34	18-21	19.5	30	61-63	61.8	28 5	1-6 0	3.2	26	146-186	164.3	4	29

Insert table ____ here.

Except for this 1958 collection, good material of Rio Grande cutthroats is lacking and probably the original situation will never be known. The early literature and the sparse museum material available all indicate that the Rió Grande, like most other interior drainages contained a mosaic of forms intergrading in all respects. We find no reason to maintain virginalis as a subspecies and consider it a synonym of S. c. lewisi.

The Bonneville Basin Cutthroat

The Bonneville basin is the largest single unit of the Great Basin. Pluvial Lake Bonneville attained a maximum size of 346 by 145 miles with a surface area of 19,750 acres. ~~almost the size of present-day Lake Michigan~~. The geological history of Lake Bonneville was described by Gilbert (1890). At its peak, Lake Bonneville's outlet was north into the Snake River. Like other Great Basin waters, Lake Bonneville fluctuated with changing climatic conditions during the late Pleistocene. ~~A time of decreased aridity which brings about the formation of large lakes is known as a Pluvial period.~~ It is believed that Lake Bonneville rose to high levels three times during ~~such~~ Pluvial periods. Broecker and Watson (1959) claim that the present remnant of Lake Bonneville, Great Salt Lake, has been a constant lacustrine environment since the last interglacial period, at least 73,000 years. The Bonneville "cisco" Prosopium gemmiferum (Snyder), endemic to Bear Lake, Utah and Idaho, in the Bonneville basin, is a highly specialized lacustrine species of a primitive whitefish genus. A constant lacustrine environment for a very long period was probably necessary for the evolution of such a species. Broecker and Orr (1958) believe the connection with the Snake River occurred more recently than 16,000 years ago. The similarity of Bonneville and upper Snake River fishes also argues for a connection during a relatively recent period.

The Bonneville basin and Pluvial Lake Bonneville probably played an important role in the speciation of cutthroat trout. The native Bonneville cutthroat is quite typical of the large-spotted *S. c. lewisi*. This lack of differentiation in Bonneville trout indicates that isolation was not of long duration nor was it very complete.

Some material from the western part of the Bonneville basin indicates a trout differentiated from the trout native to the eastern section. These western Bonneville specimens appear to be closely related to the Humboldt River subspecies of the Lahontan basin.

Taxonomy of the Native Trout

Yarrow (1874) called the trout of Utah Lake *Salmo virginalis*. Cope and Yarrow (1875) reported both *S. virginalis* and *S. pleuriticus* in the Bonneville basin. Jordan and Gilbert (1881) commented on the trout of Utah Lake as follows:

> "Specimens obtained do not differ in any visible respect from others taken in salt water in Puget Sound. This is apparently the parent stock from which *S. spilurus*, *S. irideus*, and *S. gairdnerii*, have scarcely yet become completely differentiated".

The name *Salmo utah* was applied by Suckley (1874) as a provisional name only for the trout of Utah Lake, which he distinguished by its silvery color, larger size and smaller spots. Suckley referred to the other Bonneville trout as *S. virginalis*. Most authors used the name *S. virginalis* for Bonneville trout until Snyder (1919) and Jordan (1920) pointed out that the name *S. virginalis* belonged to Rio Grande trout and *S. utah* should be the specific name for Bonneville trout.

The sparse data in the literature on the systematics of Bonneville trout has been largely based on a few Utah Lake specimens. Jordan (1891) was very likely correct when he said that the distinctive appearance of Utah Lake specimens was due to the alkaline conditions in that body of water. The fact that specimens from the Provo River, the main tributary of Utah Lake, are typical of large-spotted interior cutthroat, indistinguishable from any other large-spotted *lewisi*, supports the idea that the distinctive appearance of the Utah Lake trout was a phenotypic response to the alkaline environment of the lake.

Jordan and Evermann (1896:495) distinguished the Bonneville trout by its coarser scales; 140 to 150 in the lateral series. Tanner and Mayes (1933) presented scale counts of five Provo River and Utah Lake specimens;

their counts ranged from 177 to 205 but it was not stated precisely how the counts were made. Tanner and Hayes (op.cit.) said the identity of the original trout of Utah was a puzzle and that the mixing of various stocks and hybridization with rainbows had confused the situation. These authors claimed they had never taken any trout in the Bonneville basin with scale counts as low as the counts listed by Jordan and Evermann for Salmo utah (140-150). Our lateral series scale counts of 23 Bonneville trout collected from 1872 to 1939 ranged from 146 to 193. These trout were collected from the Salt Lake-Utah Lake-Bear Lake drainage and from the Sevier River. Specimens collected from Pine Creek, Nevada, where they had been introduced from the western Bonneville basin have fewer scales and more gillrakers. The Pine Creek specimens have their affinities with the cutthroat native to the Humboldt system of the Lahontan basin and will be discussed more fully under the Lahontan section.

Meristic Variation

Of the various Bonneville samples examined, none were of the fine-spotted type. When compared with upper Snake River cutthroats, the Bonneville trout are more similar to those of Goose Creek, Nevada (fig.___) and do not resemble the fine-spotted specimens of Game Creek, Wyoming (fig.___). No distinguishing characters were found which allow separation of Bonneville cutthroat trout from S. c. lewisi. Variation within the basin, however, suggests an increase in the number of gillrakers and a decrease in the number of scales in the trout indigenous ~~endemic~~ to the western part of the basin, perhaps indicating a stronger lacustrine influence in their past history.

Scales: -- Counts on specimens from the Salt Lake-Utah Lake-Bear Lake drainages typically range from 150 to 180 scales in the lateral series. Two USNM specimens collected by Jordan from Utah Lake in 1889 have 148 and 157 scales. These specimens may have been the basis for the claim by Jordan and Evermann (1896) that Bonneville trout have 140 to 150 scales. Three Utah Lake specimens, also collected by Jordan in 1889, in the collection of the California Academy of Sciences, have lateral series scale counts of 167, 176 and 186. A count of 193 was obtained from a specimen collected from Utah Lake in 1939. A Provo River trout, collected by H. C. Yarrow in 1872, has 164 scales. One collected from the same river in 1889 has a count of 152 and a 1934 specimen has 173 scales. Seven specimens collected from Bear Lake, Idaho and Utah in 1915 have from 157 to 178 scales with a mean value of 168.4. Five specimens collected in 1915 from Mammoth Creek in the Sevier River drainage have 146 to 162 (153.6) scales. ~~The Bonneville trout introduced into~~ The Pine Creek, Nevada, samples have from 133 to 156 (143.0) scales in 28 specimens counted.

Gillrakers: -- Nineteen trout from the Salt Lake-Utah Lake drainage have 17 to 22 (19.7) gillrakers, quite typical of interior cutthroat trout. The seven Bear Lake specimens have 18 or 19 (18.6) rakers. The five specimens from the Sevier River drainage have 19-23 (20.8). H.C. Yarrow collected eight specimens from the Beaver River, probably in southern Utah; four have 20 gillrakers and four have 21. ~~The Bonneville trout introduced into~~ The Pine Creek, Nevada, sample have the highest number of gillrakers found in Bonneville trout. Thirty-one specimens have from 19 to 23 (21.5) gillrakers.

Vertebrae: -- Vertebral counts on 19 specimens from the Salt-Lake-Utah Lake drainage ranged from 61 to 65 (63.0); the highest mean number of vertebrae of any sample of interior cutthroat used in this study. There is not much variation in the number of vertebrae in interior cutthroat trout. The maximum difference between the mean values of any two samples of what we consider as _S_. _c_. _lewisi_ is 2.8 vertebrae. The collection from Pickle Jar Lake, Alberta, has the lowest mean, 60.2.

Basibranchial teeth: -- In 22 specimens of Bonneville cutthroat more than 100 mm. standard length, 20 possessed from 3 to 13 basibranchial teeth (7.1). Two specimens had smooth basibranchials.

~~S. c. utah, A Synonym of S. c. lewisi~~

The native cutthroat trout of the Salt Lake-Utah Lake area were typical, large-spotted, interior cutthroat with no characters differentiating them from other S. c. lewisi. The name, Salmo utah, therefore is considered a synonym of Salmo clarkii lewisi. ~~The Bonneville trout introduced into Pine Creek, Nevada, is most similar to the Humboldt drainage subspecies of the Lahontan basin.~~ ~~The degree of intergradation between the trout native to the northeastern part of the basin and those endemic to the western section is not known.~~

Present Status of the native Bonneville Trout — Actually 2 distinct forms (subsp.) of Bonneville trout. Apr. 75

Miller (1950) believed the native Bonneville trout to be extinct in its pure form. Cope (1955) described how the native trout in Utah had been replaced by rainbows and Yellowstone cutthroats. Perhaps most Bonneville waters where cutthroat trout still persist are similar to Bear Lake where, although the native type cutthroat dominates the introduced rainbow, hybridization has occurred and repeated introductions have influenced the original genotype (M'Connell, Clark and Sigler, 1957). We have made no collection of trout from the Bonneville basin and cannot state if any pure strains of native cutthroat yet remain. From our experience in other areas in the West, however, it is likely that uncontaminated populations still exist in a few, remote, isolated streams. ~~Material from such populations, especially from the southern and western parts of the Bonneville basin, would make valuable contributions to the systematic study of cutthroat trout.~~

Cope

Salmo clarkii stomias

The endemic cutthroat trout of the upper Arkansas and Platte drainages in the Missouri River system form a distinctive group worthy of taxonomic recognition at the subspecific level. These trout are fine scaled, typically with 175-210 scales in the lateral series and 40 to 52 scales above the lateral line. They have large, roundish spots, sparsely distributed and concentrated on the caudal peduncle (fig.___).

Historical Notes

A confusing situation exists concerning the original distribution and type locality of S. c. stomias. Cope (1872a) described Salmo (Salar) stomias, based on two specimens collected by Dr. William A. Hammond, M.D. from; "The Platte River, from near Fort Riley, Kansas". Cope distinguished stomias by its large head and mouth and 42 scales above the lateral line. The Platte River does not flow through Kansas. Fort Riley is at the junction of the Republican and Kansas rivers. Later, Cope (1872b) stated that; "Its habitat, so far as is known, is the Kansas River, far to the eastward of the Rocky Mountains". He claimed that his earlier reference to the Platte River was erroneous. Cope and Yarrow (1875) maintained that the type locality of stomias was the Kansas River and not the Platte. Jordan (1891) said there were no trout in the Kansas River and that there was no suitable habitat for trout within 500 miles of Fort Riley. Jordan considered the type locality to be the Platte River and the name, stomias, was applied to the cutthroat trout of the Arkansas and Platte rivers. Cope (1872b) considered the trout of the Platte River to be Salmo pleuriticus.

Dr. R. R. Miller of the University of Michigan, examined the two type specimens of stomias at the National Museum. The specimens are in poor condition and an accurate scale count was difficult but his counts of 150

Phila. Acad. Sci. #7825-7826

original Rept.
cool water
and
Fowler's

GEORGE R. CLARK, CHAIRMAN OF THE BOARD

THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA

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NINETEENTH AND THE PARKWAY, PHILADELPHIA, PENNA. 19103 LOCUST 4-3921

JOHN W. BODINE
PRESIDENT

H. RADCLYFFE ROBERTS
DIRECTOR

27 February 1967

Dr. Robert Behnke
Colorado Cooperative Fishery Unit
Colorado State University
Fort Collins, Colorado

Dear Dr. Behnke:

I fear I can do no more on the trout question than give you all the data from our catalogs and labels and hope you can make something of them.

7825-7826: An ancient red-lined 'type' label has written on it "Trutta lewisi Gir.", with "lewisi" crossed out and "stomias Cope" written above it. This label further gives "Ft. Riley, Kansas," "Dr. Hammond", and the word "Types". Fowler later labels and the catalog (also written by Fowler) give Types (or Cotypes) of Salmo stomias Cope, and no new information.

14869: The oldest label in the bottle reads simply "Hammond". The catalog (in Fowler's writing) gives "Salmo" and "Dr. Hammond" only. Later bottle labels by H.W.F. read "Salmo clarkii stomias (Cope) Kansas? Dr. W.A. Hammond."

18985-87: The oldest label in the bottle is a printed "field label" of the "U.S. Engineer Department", "Explorations west of the 100th Meridian", "Locality, etc. Ute Creek, Camp Garlan" [unfortunately I cannot determine if there was or was not a -d on the end], July 30, 1872, Collector Cope and Shedd, and "No. 81." Later, in the catalog, Fowler wrote "Ute Creek, Camp Garland" with no further locality. On the bottle labels, Fowler has the additional locality, "Ute Creek, Canadian River, Arkansas River, New Mexico" and "Hayden Survey" [On one of these labels someone has recently added "= Wheeler Survey"].

20453: The oldest bottle label reads "Trout", "N. Fork St. Vrain R.," "Sept. 10", and has at the bottom what appear to be the initials W. L. Ç. The catalog says simply "Salmo", "North Fork of St. Vrain R.," "Donated by Cope." On the more recent bottle label by Fowler is the further locality information "North Fork Saint Vrain River, South Platte River, Colorado".

I hope the above will mean something to you, for I know nothing further about these collections or their history.

Sincerely,

James E. Böhlke

James E. Böhlke
Department of Ichthyology
and Herpetology

JEB: lw

— *stomias*

Fowler, H.W. 1912. Notes on salmonoid and related fishes. Proc. Phila. Acad. Sci., 63:551-571.

#7825; 7826. - cotypes *stomias*. One probably from Kansas? one from N. Fk. St. Vrain Crk. S. Platte R. basin, Boulder Co. Colo. + 3 small ones from Ute Crk. at Camp Garlan in Canadian R. basin - Union? Co., N. Mex..

syn. of *lewisi*

Salmo carinatus Cope, Rep. Geol. Surv. Hayden 1871:471 - unknown locality - probably Yellowstone.

Insert Page 93

Salmo Texas - New Mex

Canadian R.

Forest & Stream - Daniel

Salmonidae in Texas (cont.)

- a distinct recollection of having taken the speckled trout from this stream. At Fort Davis I remained several months during which time I caught many trout from the Limpia. This was in Texas, (all above mentions)

- In New Mexico I saw many fine specimens of speckled trout from the Rio Benito at Ft. Stanton.

- [Ed. note The ~~origin~~ of the question whether speckled trout of the family Salmonidae existed in Texas, arose from a disputed statement made in "Hallock's Gazetteer" - Ample testimony has been printed in Forest and Stream, from Army officers and others, supporting the assertions of the Gazetteer. - drawing Picture of Salmo spilurus portrayed

- ibid - May 2, 1878, 10(13): 236

letter from N.A.T. (Taylor) - In answer to an (inquiry by editor of Forest & Stream prob. Hallock's Gazetteer) Salmo fontinalis in Texas

- Looked into the matter - met Dr. H.I. Hunter - confederate surgeon during war at Ft. Davis. He said he found a fish he took to be fontinalis abundant in the Limpia and in streams to the north. - Limpia flows thru region 5000 ft. - cool - sparkling clear - Buffalo hunter told me he can catch wagon loads of of speckled trout in Pan Handle region of Texas - headwaters of Canadian and Red R. "Maj. D.W. Hinkle who was with Emory's Boundary Comm., and whose acquaintance I formed ~~there~~, says the Buffalo hunter is about right. He has been all over the Pan Handle. I am convinced you are right in your Gazetteer".

- mentions First Biennial Rept. 'Comm. Fisheries St. Kansas 1877-8 ..

★ Salmo — Texas
Forest & Stream . Trout - Rocky Mtns.

Jan. 24 1878 vol. 9 no. 25 : "Trout in the Rocky Mts." : 468-69.

Trout decimated now around centers of pop. - favorite spot.

15 18 years ago - Bear Crk. 16 mi. west of Denver - at mouth of canyon -

delightful camp spot, - - largest trout caught by author 18 1/2 in.

- But now R. R. station - hotel & noisy village there.

★ 16 mi. north of the Thompson is Cache-a-la-Poudre River -

the trout stream par excellence east of the snowy range in

northern Colo. It has nearly 100 mi. of fishing water, with

much open valley easy of access, and many of our best

sportsmen still go there summer after summer for a camping tour.

trout are still very abundant, and many are large. - Also great

variety game -

- ibid 1878 10(19): 357 Trout in the Rocky Mts. -

In 1863 - crossed over the snowy range to Middle Park - center

of Colo. trout abundant easily caught by bag fulls - up to

6-7 lb. - mentions Williams R. - smallest days catch weighed 72 lbs.

near Grand L. -

---

ibid p. 339 ~~S~~ W. C. June 6, 1878 vol. 10 no. 18

★ The Salmonidae of Texas. - letter by J. W. Daniel, M.D.

- Saw letter from Mr. N. A. Taylor said *Salmo fontinalis*

in Texas - I am familiar w/ *fontinalis* - formerly in New Haven -

- Served as asst. surgeon 2nd Texas Rifles - accompanied expedition

thru northwest Texas & New Mex. - "If my recollection

serves me at this distance of time, that being 1861, I think

I have taken *Salmo fontinalis* from the San Felipe Springs,

25 mi. above Ft. Clark. "Of this however, I will not be positive.

- I was stationed at Ft. Hudson, on the Devil's R. and have

J. F. R. B. C.

Bull. 1939 no. 56 : 39-50

QH1
C22

Jour. 1953 10(2) : 51-60

QH1
C245

Univ. Toronto Ser. QH1
T57

Dymond 1928 : 31 1-6
Pritchard 7-25
Pritchard 1931 : 35

(Pac. herring: Crawford 1922 append. VII)

Bull. U.S. Bur. Fish. Kendall 1920 Atlantic smelts : Append. II . Rept. U.S. Fish c. for 1920 : 5-6.

1902 22 : 353-68

Sci. E. 1911 29(8-34)

Occ. Pap. Mus. Zool. U. Mich.

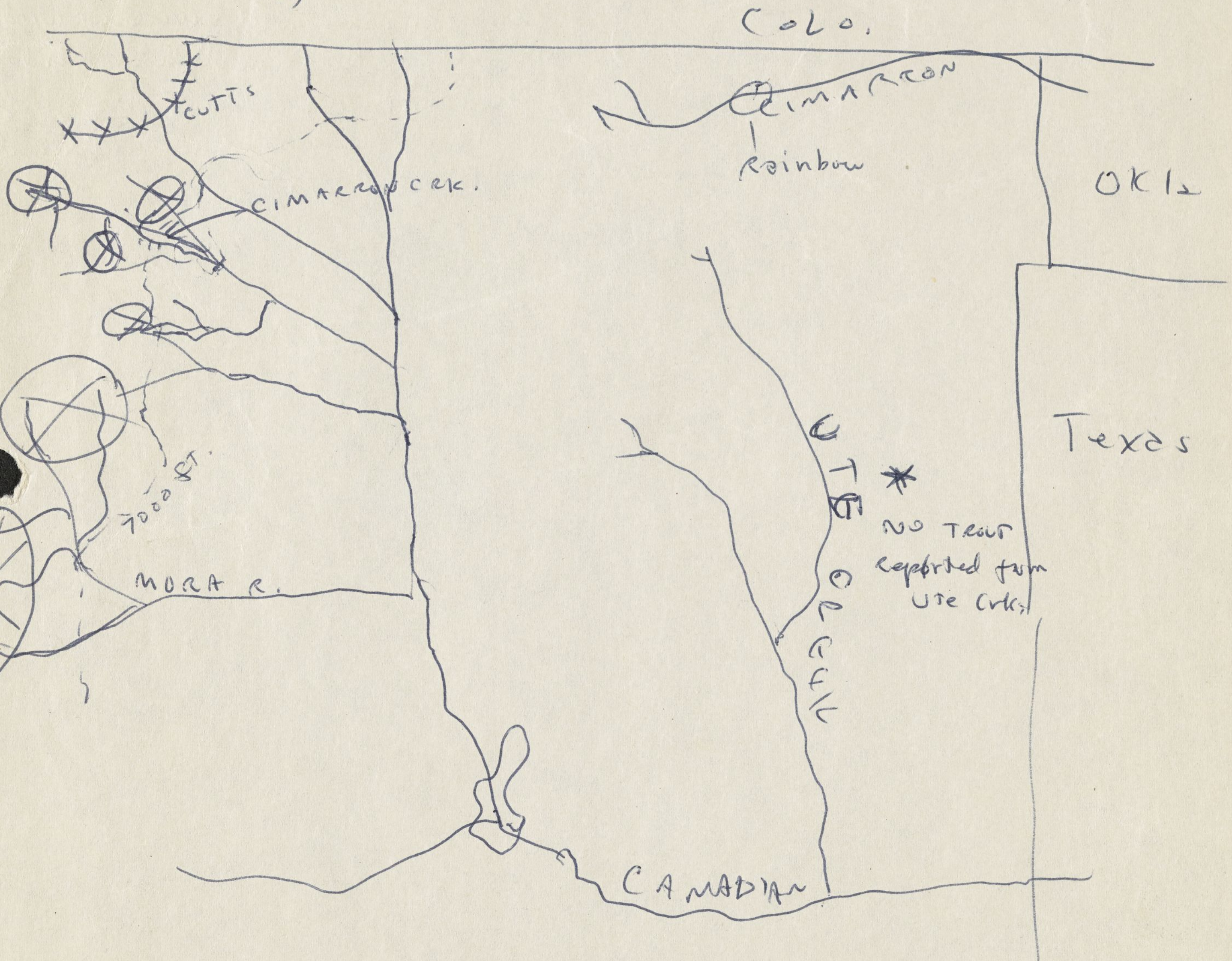
no. 204

QL1
M5

+ no. 158
1925

Rep. Brit. Ass. Adv. Sci. for 1925 : 75-87.

New Mex. Dept. F. & G.
Job Completion Rept.
Fish. Surv. Canadian & Cimarron river drainages in N.M. 1953-56.
William H. Wolfrum project leader
(Mar. 1956)



Western headwaters - Eastern Sangre de Cristo Mtns. - to 13,100 ft., "
"only native salmonid in area is cutthroat
"no differentiation attempted between Yellowstone cutt. & Rio Grande cutt. both of which widely planted - and possible other subsp. that have been introduced

(ibid) - N. Mex. Dept.
Mar. 1959 - Completion Rept.
D. Jester - Proj. Leader
- includes surveys of Rio Grande trib.

"natives" appear to dominate most headwater streams. - no attempt to distinguish virginalis

- ~~wa~~

high P.H. assoc. with excessive weed growth - high mortality & blindness of trout - in weed beds - O.K. in open water - alkalinities to 1000 and 152 scales in the lateral series are much lower than any known specimens of stomias from the Arkansas and Platte river systems. Information provided to Dr. Miller by James Cole, biologist with the National Park Service, indicates that the Republican River as far south as Fort Riley, Kansas, may original have provided trout habitat as recently as 1870. The topography of the area between the South Platte and the Arkansas rivers suggests the probability that trout occurred in Kansas when environmental conditions were favorable. There are, however, no authentic records of native trout from any rivers between the South Platte and Arkansas drainages and the origin of the type specimens of stomias remains a mystery.

Some of the locality records of ~~the~~ specimens described by ~~of~~ Cope and Yarrow are known to be in error. The exactness of the data of the early western explorers who gathered the specimens was probably not of the highest order. The type specimens of stomias may actually represent Rio Grande trout.

¶ Taxonomy:

Museum material on stomias is not abundant. Until recently, it was feared that stomias was extinct, but in the past few years, some collections of stomias were made in isolated tributaries of the Platte River. All the specimens of stomias examined are fine scaled and large spotted trout. Their characters show less variability between samples than the cutthroat trout from other interior drainage basins. Besides this relatively high degree of homogeneity, the fact that stomias once occurred sympatrically in Twin Lakes with a cutthroat of Colorado River origin, indicates that stomias has been isolated more completely and for a longer duration than any other group of cutthroat trout except, perhaps, the Lahontan cutthroat S. c. henshawi.

Insert Table Here

Table ____ displays some of the meristic variation in our samples of stomias. In 60 specimens from 8 localities, the scale counts range from

Table . -- <u>Salmo</u> <u>clarkii</u> <u>stomias</u>

Sample and Date of Collection	Gillrakers			Vertebrae			Basibranchial Teeth			Scales Lateral Series			Scales Above Lateral Line		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
SOUTH PLATTE SYSTEM															
Moraine Park Colorado - 1889	1	19	--	1	59	--	1	0	--	1	195	--	1	44	--
Bear Creek, Morrison, Colorado - 1889	4	16-20	18.3	4	62-63	62.5	1 3	1 0	-- --	--	--	--	4	41-44	42.7
Pingaree Park Colorado - 1932	2	18-20	--	--	--	--	2	1-6	--	2	196-213	--	2	47-48	--
Albion Creek, Boulder Co. Colorado - 1955	9	18-22	19.4	9	59-61	60.1	7	1-23	6.9	9	178-205	191.2	9	44-51	47.2
Big Thompson River Rocky Mtn. Nat. Park Colorado - 1959	20	18-21	19.1	20	59-62	60.8	19 1	1-10 0	7.1 --	19	177-215	199.8	11	43-51	47.5
NORTH PLATTE SYSTEM															
Red Canyon, Jackson Co., Colorado - 1950	20	18-22	19.6	20	59-61	59.9	15 5	1-13 0	4.2 --	20	172-194	184.5	20	40-49	44.0
ARKANSAS SYSTEM															
Arkansas R., Leadville Colorado - 1889	2	21-22	--	4	60-62	61.0	2	2-12	--	2	198-213	--	2	46-49	--
Twin Lakes, Leadville Colorado - 1889	8	18-20	19.5	7	61-62	61.7	8	6-14	10.6	7	170-202	186.9	7	46-53	49.0

170 to 215, the highest scale counts in the cutthroat species. Some populations have low vertebral counts. The mean value of 59.95 for the Red Canyon sample is the lowest of any cutthroat sample used in this study. Some populations have a tendency for the loss of basibranchial teeth which is a common occurrence among small, isolated populations of interior cutthroat. The arrangement of the basibranchial teeth is, typically, in a single row in stomias although exceptions to this were noted, particularly in the Twin Lakes specimens.

Twenty specimens from the Big Thompson River have from 22 to 40 (31.4) pyloric caeca.

¶ General Comments

~~We do not know to what extend stomias will hybridize with introduced cutthroat and rainbow trout or how significant a role hybridization has played in the drastic reduction in the range of stomias.~~ The area where the 1959 collection of stomias was made, in the Big Thompson River, was stocked with 160,000 Yellowstone cutthroats in 1922 and with 130,000 in 1923. This fact was disclosed in a letter from O. L. Wallis to Dr. R. R. Miller. The effect that these introductions had on the native stomias appears to be nil. Based on spotting, scale, vertebral and caecal counts, the 1959 collection seems to represent essentially a pure strain. ~~Every effort should be made to certify the purity of present populations and protect them from introductions.~~

The sample from Red Canyon, Jackson County, Colorado, is the only known trout collection from the North Platte drainage. These were collected by Dr. John Greenbank and his field notes indicate that the area is extremely remote and not likely to have introduced trout. Jordan (1920a) recounted the notes of Mr. Ralph Montega, who said there were no trout in the tributaries of the North Platte in 1887. Land (1913) also stated that the North Platte had no indigenous trout but "native trout" were stocked in the headwaters of the North Platte at North Park, Colorado, in 1891 and 1892, as well as in the headwaters of the Big Laramie River in Laramie County, Colorado. The characteristics of the Red Canyon trout are somewhat distinct from the typical South Platte and Arkansas River stomias. They have fewer scales and vertebrae, 12 of the 20 have 10 pelvic rays and the spots are smaller and more numerous than in the other stomias examined.

Although our material on stomias is not comprehensive, the data indicate that the endemic trout of the Arkansas and Platte drainages should be retained as a valid subspecies. Unless it can be demonstrated conclusively that the type specimens of stomias did not come from the Platte or Arkansas drainages, the name stomias may continue to be applied in its present interpretation.

Lahontan Cutthroat Trout

Salmo henshawi Gill and Jordan, in Jordan, Man. Vert. ed. 2, 1878:258. Lake Tahoe.

Salmo tsuppitch Richardon, Jordan and Henshaw, Rept. Chief Engineers, Part 3, 1878: 196 App. NN. Lake Tahoe.

Salmo purpuratus henshawi Jordan and Jouy, Proc. U.S. Nat. Mus. (4): 14, 1882. Lahontan basin.

Salmo mykiss henshawi Jordan and Evermann, Bull. 47, U.S. Nat. Mus.: 493, 1896. Lahontan basin.

Salmo clarkii henshawi Jordan and Evermann, ibid.: 2819, 1898. Lahontan basin.

Salmo clarkii tahoensis Jordan and Evermann, ibid.: 2870, 1898. Lake Tahoe.

Salmo evermanni Jordan and Grinnell, Proc.Biol.Soc.Wash.21:31, 1908. Santa Ana River, California.

The cutthroat trout, endemic to the Lahontan basin, forms the most distinctive group in the cutthroat series. The Lahontan cutthroat may be distinguished from other cutthroat by its more numerous gillrakers. ~~The spotting pattern is also distinctive with large or medium-large, roundish spots, evenly distributed on the sides of the body, both above and below the lateral line, often onto the abdomen (fig. ___).~~ ~~Actually,~~ We recognize two other subspecies of Lahontan cutthroat trout, besides S. c. henshawi. The Piute trout, ~~Salmo clarkii~~ S. c. seleniris, is a typical Lahontan cutthroat in every respect except for the absence of spotting on the body. The endemic trout of the Humboldt River drainage of the Lahontan basin is intermediate in its gillraker number between lewisi and henshawi but has fewer scales than either. The Humboldt cutthroat trout is described as a new subspecies here, ~~in this paper~~.

Hydrographic History

Most of the present Lahontan fish species and their distribution can probably be attributed to events of the Pleistocene. ~~The Pluvial periods provided opportunities for faunal connections and lacustrine adaptations.~~ Pluvial Lake Lahontan may have reached its maximum level about 11,700 years ago and had its final recession about 9,000 years ago (Broecker and Orr, 1958). Broecker and Watson (1959) believed that Pyramid Lake, Nevada, has been a continual lacustrine environment for at least 73,000 years. No outlet for Lake Lahontan has been found. The high degree of endemism in the Lahontan fishes suggests that no broad connections with other drainages have existed, perhaps, since the Pliocene. The closest affinities of Lahontan fishes are with Klamath Lake and Bonneville species. A more comprehensive coverage of Lahontan history and fishes is found in Hubbs and Miller (1948) and La Rivers (1962).

The Native Trout

The Lahontan cutthroat trout appears to be the most lacustrine adapted of North American trouts. Its degree of differentiation from other cutthroats suggests a long period of isolation. The cutthroat probably entered the Lahontan basin via headwater stream transfers from the Bonneville and, perhaps, the Snake River systems. It probably arrived much later than the minnows and suckers. This is indicated by many independent basins, contiguous with the Lahontan drainage, containing differentiated Lahontan fauna but no ~~endemic~~ native trout (Hubbs and Miller, 1948).

Today, the Lahontan basin consists of four main river systems: the Truckee, Carson, Walker and Humboldt. Examination of specimens indicate that the trout from the Truckee, Carson and Walker drainages comprise a uniform group which may be called the Lahontan cutthroat trout, S. c. henshawi. The trout endemic to the Humboldt system may represent intergrades with S. c. lewisi or a more fluviatile adapted ancestor of S. c. henshawi.

Taxonomy of S. c. henshawi

From the earliest mention of Lahontan trout in the Biennial Reports of the California Fish Commission, there was constant reference to two types of trout, especially in Lake Tahoe. These trout were distinguished because the larger type was more silvery. Jordan and Henshaw (1878) called the silver trout, Salmo henshawi Gill and Jordan and the black trout, Salmo tsuppitch Richardson. Jordan and Evermann (1896:494) made the following statement concerning the trout in Lake Tahoe:

> "In Lake Tahoe there are two forms of this type, (1) the ordinary Tahoe trout (locally known to fishermen as "Pogy", the young as "Snipe") weighing from 3 to 6 pounds, dark in color, with coppery sides, ascending the streams to spawn,

> and (2) the "Silver Trout", a large robust trout profusely spotted, the spots often oblong, the coloration more silvery. These trout live in deep water and spawn in the lake itself. A careful comparison of specimens convinces us that there is no specific nor varietal difference between the one and the other".

But on page 2,870 in volume 3 of this same work they describe the silver trout as _Salmo_ _clarkii_ _tahoensis_, using the same criteria published on page 494. A gillraker count of 18 is given for the type specimen of _S_. _c_. _tahoensis_. This is outside the range of _S_. _henshawi_. The holotype of _S_. _c_. _tahoensis_ (Stanford University 4370) was examined and the first left gill arch was found to have 9 rakers on the upper limb and 16 on the lower, for a total of 25. These could be counted without magnification. It is difficult to understand how an error of this magnitude was made in describing _tahoensis_. We have observed large specimens of _henshawi_ which assumed a silvery appearance with concomitant alteration of the spotting pattern, as was described in the discussion on the trout of Utah Lake. Snyder (1917) recognized _tahoensis_ but later (1940) found no justification for it and considered it synonymous with _henshawi_. The type specimen of _tahoensis_ appears to be identical to _henshawi_. The name, _tahoensis_, is considered a synonym of _S_. _c_. _henshawi_. Although the history of the Lahontan basin with its Pluvial and Interpluvial periods provided opportunities for speciation, there is no valid evidence to support the assumption that two distinct forms of cutthroat trout occurred sympatrically in Lake Tahoe.

The nomenclature is further confused by the fact that Jordan and Henshaw (1878) called the silver trout _henshawi_, while Jordan and Evermann (1898) called the black trout _henshawi_ and the silver trout _tahoensis_.

Table . -- Salmo clarkii henshawi

Sample and Date of Collection	Gillrakers			Vertebrae			Scales Lateral Series		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
CARSON RIVER DRAINAGE E.Carson R., Alpine Co., California, 1959	4	22-25	23.3	4	61-62	61.8	4	156-173	167.5
Murray Canyon Creek, Alpine Co., Calif, 1959	6	22-25	23.3	6	60-62	61.1	6	152-176	166.7
Summit Lake, Humboldt Co., Nevada (independent basin), 1939 and 1942	38	23-28	25.2	28	59-63	61.5	13	139-165	154.1
TRUCKEE RIVER DRAINAGE Independence Lake, Sierra-Nevada Co., Calif., 1952-1959	19	21-28	24.0	10	61-63	62.2	9	146-172	160.5
Lake Tahoe, Calif.-Nevada, 1872-1915	19	21-26	22.8	8	61-64	62.5	10*	156-170*	163.1*
Pole Creek., Placer Co., California, 1962	28	23-28	25.1	12	61-63	61.7	12	142-171	159.8
Pyramid Lake & Truckee R. Nevada, 1913	7	21-26	23.6	6	62-64	62.8	--	---	--
Truckee River, Nevada.*	45	22-27	23.6	--	--	--	20	149-169	158.7
WALKER RIVER DRAINAGE Dog Creek, Mono Co., California, 1959	2	24	--	2	62-63	--	2	162-168	--

*From Snyder, 1917

Meristic variation.

~~Table ___ lists the number of gillrakers, scales and vertebrae in various samples of *S. c. henshawi*~~. (Table ___) The range in gillraker number, 21 to 28, has only a slight overlap with the subspecies *S. c. clarkii*, *S. c. lewisi* and *S. c. stomias*. The Lahontan trout has a moderate number of scales, typically from 145 to 170. The number of vertebrae is quite typical of cutthroat trout in general.

Snyder (1917:73) claimed than *S. c. henshawi* had 70 to 85 pyloric caeca. This is much higher than counts reported in the literature for cutthroat and rainbow trout. We have relatively few caecal counts, but among those counted, the following figures were obtained: Independence Lake, 46 and 54; nine from Pole Creek ha~~d~~ve 49 to 64 (59.2) and four from the hatchery stock of *S. c. henshawi* at Heenan Lake, California, ha~~d~~ve from 47 to 64 (54.3). Although Snyder's caecal number was too high, *S. c. henshawi* does tend to have more pyloric caeca than reported for other cutthroat populations.

Most samples of *henshawi* are similar to other cutthroats in basibranchial teeth. Generally 5 to 10 percent of a population may be expected to lack these teeth, while the remainder will have one to 15 teeth. However, the cutthroat of Independence Lake, Sierra-Nevada County, California, is entirely distinct in the number and arrangement of the basibranchial teeth. Figures ___ and ___ compare the typical arrangement of basibranchial teeth of cutthroat trout with the condition found in Independence Lake specimens. Whereas most cutthroat have only a few teeth, seldom more than 20, arranged in one or two rows, the arrangement of basibranchial teeth in the Independence Lake specimens is unique. The teeth proliferate in two masses on the basibranchial plate. In most specimens a few clumps of teeth will be visible on the hypobranchial segments of the gill arches also. A precise count is virtually impossible, but there are approximately 100 basibranchial teeth in Independence Lake cutthroats. All of the 19 specimens collected from Independence Lake exhibit this distinctive character. Records of the California Fish & Game Department show that Independence Lake was formerly stocked with Tahoe cutthroats and in recent years more than one million fingerling rainbows and Heenan Lake cutthroats have been planted. It is difficult to understand how the ~~endemic~~ native cutthroat have been able to maintain their identity. It is assumed that the native cutthroat is highly adapted to conditions in Independence Lake. The spawning run in the single tributary stream has been observed every year since 1950 and no rainbow trout has been observed with the cutthroats during the spring spawning periods.

Independence Lake is at an elevation of ~~approximately 7,000~~ 6950 feet, or about 2,~~600~~ 550 feet above the maximum level attained by Pluvial Lake Lahontan. The outlet stream, Independence Creek, ~~forms~~ one of the headwaters of the Little Truckee River has barrier falls that prevents migration, into the lake. The other fishes of Independence Lake appear to be undifferentiated Lahontan fauna, but detailed comparisons have not been made.

Ecological Notes:

Due to the activities of man, pure populations of Lahontan cutthroat trout are extremely rare. What we consider uncontaminated S. c. henshawi, are known only from the collections made from 1939 to 1962 from the localities listed in Table ___. Only in Pole Creek and Independence Lake does the native cutthroat occur with other species. This suggests that the Lahontan cutthroat is not successful when in competition with introduced trouts, but this, ~~however~~, may not be true.

When the progenitor of S. c. henshawi entered the Lahontan basin, it probably encountered an environment rich with cyprinid forage. It should be expected that natural selection would favor the development of a large, predatory type. ~~Although growth rates and maximum size of trout is a most variable character~~, The size ~~records~~ attained by Lahontan cutthroats far exceeds that ~~those of~~ other cutthroat subspecies of ~~trout~~. A specimen on display at the Nevada State Museum in Carson City weighed 41 pounds when taken from Pyramid Lake in 1921. Specimens of 60 pounds have been reported but not authenticated

Before obstruction of tributary spawning streams ~~from~~ of Lake Tahoe and diversion of Truckee River water from Pyramid Lake, the native cutthroat completely dominated the fisheries of these lakes despite intensive introduction of brown, rainbow, eastern brook and other subspecies of cutthroat trout. Rainbow-cutthroat hybrids were produced at the hatchery on Lake Tahoe from 1905 to 1910 and stocked in the lake (Miller and Alcorn, 1945). Examination of specimens and a review of the literature indicates that hybridization, either natural or artificial, with rainbows had little effect on the purity of the native ~~endemic~~ cutthroat. In the many streams of the Lahontan basin, S. c. henshawi readily hybridized with introduced rainbows and soon lost their identity. The three areas where S. c. henshawi were collected from the Carson and Walker River systems are all isolated above barrier falls and only the cutthroat trout was found there. In Pole Creek, tributary to the Truckee River, however, the cutthroat occurs with eastern brook and brown trout and the cutthroat dominates the introduced species in the headwater section of this tiny stream. We have found similar situations in the Humboldt drainage of Nevada. ~~Perhaps the Lahontan cutthroat, and other subspecies of cutthroat, are more adaptable in the colder headwater areas. Further investigation of such an assumption may prove useful in fish management work, besides promoting the perpetuation and appreciation of native types.~~

Present Status:

The unfortunate effects of civilization on the fate of native Lahontan trout is typified by the extermination of the trout in Pyramid Lake, ~~the~~

~~to diversion of the water from the Truckee River.~~ Sumner (1939) reported on the last spawning run from Pyramid Lake. From February to May in 1938 he recorded 1069 large trout taken from the Truckee River above the lake. He weighed a sample of 195 specimens. The average weight of these trout was 20 pounds. Evidently, successful spawning had not occurred for ~~a few~~ some years prior to 1938 and the population was made up almost exclusively of older individuals. Today, Pyramid Lake is stocked with both cutthroats and rainbows ~~from Heenan Lake and Summit Lake stocks~~, but ~~they do~~ they have yet not attained the sizes reported for the original population; ~~it must be pointed out that the lake level has dropped more than 50 feet in the past 30 years~~.

~~As mentioned previously, the only known pure populations of S. c. henshawi are from the six localities collected from 1939 to 1962, listed in Table ___. Undoubtedly, more populations exist in isolated streams in the Truckee, Carson and Walker river systems and, as these areas are more thoroughly explored and more people become aware of the Lahontan cutthroat, our known stocks of native S. c. henshawi should increase.~~

Unfortunately, the Heenan Lake stock of cutthroat which is most extensively used by California and Nevada in the propagation of henshawi, probably does not represent a pure strain of Lahontan cutthroat. Heenan Lake, Alpine County, California, is an artificial lake, first stocked with cutthroats from Blue Lake in 1935 (Anon.1956). Blue Lake in the Sacramento River drainage is near Heenan Lake but at a higher elevation. It was originally barren of trout but was stocked with cutthroats from the Carson River in 1864 and with rainbows from the Mokelumne River in 1873 (Evermann, 1906:35). Another ~~stocking with~~ plant of 5,000 rainbows was made in 1924 (Calhoun, 1944). Mr. Gus Giebel, director of the Elk Grove Hatchery of the California Department of Fish and Game, told us of the egg collecting operations at Blue Lake during the 1930's. He said that rainbows and hybrids were destroyed and eggs were taken only from what they considered to be cutthroats. The present Heenan Lake cutthroat is a beautiful trout; its spotting and morphology appears to be typical of Lahontan cutthroats. However, examination of 146 specimens of Heenan Lake stock, raised at four hatcheries, indicates introgression of rainbow genes. Gillraker counts ranged from 20 to 26, instead of 21 to 28 expected in pure henshawi. The mean values varied from 22.1 to 22.8 for the four samples, or about one or two fewer than expected for henshawi. Lateral series scale counts on fifteen Heenan Lake trout raised at Hot Creek, California, ranged from 128 to 147 (136.7), about 20 fewer than is typical of S. c. henshawi.

Summit Lake

Summit Lake occupies a small, independent basin in northwestern Nevada between the Lahontan basin to the south and the Alvord basin to the north. Hubbs and Miller (1948:61) mention that the cutthroat trout is the only fish present. LaRivers (1962:172-74) discussed Summit Lake and the possible origins of the trout. If the lake was originally without trout, it seems probable that men from an Army camp on the lake, which was in operation prior to 1890, would have introduced trout from neighboring Lahontan streams. Whatever their origin, Summit Lake sustains a pure type of henshawi. In the number of gillrakers, the mean value of 25.2 is the highest of any sample used in this study and higher than any heretofore reported for the genus Salmo. The Summit Lake specimens have slightly fewer scales than other henshawi and about 50 percent of the specimens have only eight pelvic rays. LaRivers (op.cit.) said the Summit Lake population represented the last remnant of pure henshawi of which he was aware.

Salmo evermanni, A Synonym of Salmo clarkii henshawi

Jordan and Grinnell (1908) described a new species, Salmo evermanni from the upper Santa Ana River, San Bernardino County, California. Most subsequent authors placed S. evermanni with the rainbow series until Miller (1950:9) recognized that the type specimens represented a cutthroat trout. Miller (1950:31) considered S. evermanni as a relict cutthroat trout which occurred in coastal waters as far south as the Santa Ana River in Pleistocene times.

Hybridization with introduced rainbows soon eliminated the Santa Ana River cutthroat population. Only the five type specimens are known to exist, three at Stanford University and two at the U.S. National Museum. Examination of the type material at Stanford revealed that in their spottern pattern, scale counts and gillraker counts, S. evermanni was identical to S. c. henshawi. The most logical answer to the question of how Lahontan cutthroat trout became established in the Santa Ana River was found in the stocking records published in the Biennial Report of the California Fish Commission for 1895 and 1896. In these years cutthroat trout derived from spawn taken at Lake Tahoe were stocked in the Santa Ana River "above the falls". Benson and Behnke (1961) presented more complete details on the history of S. evermanni and placed evermanni in synonymy.

The Piute Trout

J. O. Snyder (1933) described the Piute trout, Salmo seleniris, based on a sample from a population isolated above Llewellyn Falls on Silver King Creek, a tributary of the East Carson River, Alpine County, California. The name, seleniris, was suggested by "a fancied resemblance of its evanescent tints to the lunar rainbow" (Snyder, 1934). Silver King Creek is in the Lahontan drainage and Snyder recognized the affinities of S. seleniris to S. c. henshawi. The only character which differentiates S. seleniris from S. c. henshawi is that S. seleniris has no spots on its body, although there are a few spots on the dorsal, adipose and caudal fins (fig. ___). Sixty-two specimens of S. seleniris were examined. The number of gillrakers ranged from 21 to 27 with a mode of 24 and a mean value of 24.2. Other meristic characters are typical of S. henshawi. Snyder mentioned that S. seleniris possessed a slim, terete body form. When 14 specimens, collected in 1956, were compared with 26 specimens, collected in 1933, it could be observed that the average size and body depth was greater in the more recent specimens. The figures are as follows:

		Standard length (mm)		Body depth (1000ths of the standard length)	
Year	No.	Range	Mean	Range	Mean
1933	26	112-169	133.1	200-221	207.3
1956	14	113-200	160.1	201-253	236.4

A slim, terete body form does not distinguish S. seleniris from S. henshawi or any other cutthroat trout. The opening of Silver King Creek to public fishing and the lure of a rare, newly described trout probably increased the fishing pressure on the small stream, which resulted in a reduction of the population and better growth, as reflected in the recent collection.

There is probably only a relatively slight genetic difference between S. henshawi and S. seleniris but because this difference results in a most easily recognized character, i.e., spots versus no spots on the body, we retain the Piute trout as a subspecies in the cutthroat series.

Miller (1950:8,9) said:

> "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 two forms (henshawi and seleniris) thus intergrade in one of the most striking features thought to characterize seleniris".

Twenty specimens in the collection of the California Academy of Sciences, collected from below Llewellyn Falls in 1933, represented hybrids between introduced rainbows and native S. henshawi and perhaps some S. seleniris which could have migrated over the falls. This was evident from counts of scales, vertebrae, gillrakers, pelvic rays and basibranchial teeth and from the erratic spotting patterns. Most likely, the specimens examined by Miller from below Llewellyn Falls were also hybrids between the rainbow and Lahontan cutthroat and not intergrades between S. henshawi and S. seleniris.

In 1949, the California Department of Fish and Game inadvertently stocked Silver King Creek above the falls with fingerling rainbows. Although the 14 specimens collected in 1956 were uniform in their characters and lack of spots, recent reports claim the effects of hybridization are rapidly spreading and the Piute trout of Silver King Creek will soon be eliminated in its pure form. The Piute trout has been introduced into a few other waters and it is hoped that representative populations of the original race will continue to maintain this beautiful and interesting fish.

The Humboldt Cutthroat Trout, Salmo clarki humboldtensis, new subspecies

In his study of Lahontan fishes, Snyder (1917), collected trout from many areas including the Humboldt River and its tributaries, but his systematic data were limited to cutthroats collected from the Truckee River system. Our examination of Humboldt River specimens collected by Snyder from 1911 to 1915, demonstrated that the Humboldt cutthroat is distinct from S. henshawi of other Lahontan waters. The Humboldt cutthroat typically has 2 to 4 fewer gillrakers than henshawi. Some samples from isolated headwater tributaries have fewer scales in the lateral series than any other interior cutthroat yet examined. Our humboldtensis material has been separated into a coarse scaled group and a moderate scaled group (Tables__and__). The type specimen is from a coarse scaled sample.

The endemic cutthroat has been exterminated from the main stream of the Humboldt and its immediate tributaries. In almost all of the easily accessible waters in the Humboldt drainage, only introduced eastern brook, (*Salvelinus fontinalis*), brown and rainbow trouts are found.

The field activities of William Nisbet and Donald King, Fisheries Biologists for the Nevada Fish and Game Commission in Elko County, uncovered many populations of the native trout in remote headwater tributaries. Collections were made in Elko County in 1961, 1962 and 1963, resulting in ~~More~~ more than 130 specimens from many localities ~~were collected~~.

Description

Holotype. An adult female 189 mm standard length, 220 mm total length; California Academy of Sciences no. 22561. Collected from the very headwaters of the South Fork Little Humboldt, about 5 miles west of Midas, Elko County, Nevada, on July 16, 1961; elevation 6,400 ft. The collection was made by William Nisbet, John Schlechteweg and Robert Behnke, using an electric shocker. Specimens were preserved in the field in ten percent formalin and later transferred to 40 percent isopropyl alcohol. Cutthroat trout were the only fish found in this section of the stream. A series of falls in a canyon about one half mile downstream from the collecting site isolates this population from upstream invasion.

Scale counts: Lateral series (2 rows above the lateral line), 128; above the lateral line, 35; in the lateral line, 116; origin of adipose to the lateral line, 24. Gillrakers on first left arch, 8 + 14. Posterior rakers on first left arch 4 + 7; well developed. Branchiostegal rays, 10, both left and right sides. Fin rays; pectoral, 14; pelvic, 9; dorsal, 2, 10; anal, 3, 9 (10 principal rays). Vertebrae, 61. Pyloric caeca, 45. Basibranchial teeth, 11.

Parr marks~~:--~~ These are ill defined, consisting of narrow vertical bands along the lateral line with smaller markings above and below the lateral line. Smaller specimens have more pronounced parr marks. Typically, the parr marks are narrow and not uniform in S[redacted]. humboldtensis.

Spotting pattern~~:--~~ This resembles S[redacted] henshawi, but anterior spots are smaller and more irregularly shaped than in typical S[redacted]. henshawi. The spots are larger and more distinctly round on the caudal peduncle. No spots appear on the abdomen or lower fins. Dorsal, adipose and caudal fins are spotted. A few, tiny spots appear on the head, dorsal and posterior to the eye. Two cheek blotches are distinct, the larger approximates the diameter of the pupil.

The life colors are burnished silvery background with golden-olive hues and tints of rose along sides of body and on the opercle; cutthroat mark distinct, bright red; fins drab olive-brown; lower fins slightly tinged with pink; lighter colored trim completely absent on all fins.

Meristic Variation of Paratypes

Tables ___ and ___ list scale counts and gillraker counts. The samples have been separated into a coarse scaled group with mean values of less than 140 scales in the lateral series and less than 35 above the lateral line, and a moderate scaled group with mean values of more than 145 in the lateral series and more than 35 above the lateral line. There is much overlap in the ranges of the two groups and most samples contain only one to five specimens, thus, they may not be truly representative of their populations.

The coarse scaled group ~~apparently~~ generally consists of populations from isolated headwater localities. Specimens more typical of S[redacted]. henshawi in scale number tend to be associated with waters which have a more direct connection to the main Humboldt River.

Table . -- Comparative scale and gillraker counts in S. c. humboldtensis.

Sample	Gillrakers									Scales Lateral Scales			Scales Above Lateral Line		
	No.	18	19	20	21	22	23	24	Mean	No.	Range	Mean	No.	Range	Mean
Moderate scaled sample (mean value over 140)															
Humboldt R & Marys R.*	21			5	5	11		**	21.3	6	145-164	154.4	22	31-39	35.4
N.Fork, Humboldt R.	6			1	3	2			21.2	5	139-154	147.0	4	34-38	36.3
Foreman Creek	2				1	1			--	2	144-146	--	2	38-39	--
Kleckner Creek	3		1	1	1				--	3	145-156	152.0	3	37-38	37.3
Green Mtn. Creek	2				1	1			--	2	136-156	--	2	35-37	--
Cold Creek	2					1	1		--	2	146-153	--	2	37-39	--
Talbot Creek	1				1				--	1	165	--	1	35	--
Coyote Creek	2		1		1				--	2	137-149	--	2	33-37	--
Genette Creek	1				1				--	1	156	--	1	36	--
Carville Creek	5					3	1	1	22.6	2	144-146	--	2	33-35	--
Big Creek	2					2			--	2	160-163	--	2	36-38	--
Frazier Creek	3		1	1		1			--	2	148-157	--	1	36	--
Sub-total	50	--	3	8	14	22	2	1	21.3						
Coarse scaled sample (mean value under 140)															
Ganz Creek	17	1	3	7	2	3	1		20.4	17	117-140	126.0	16	28-36	31.2
S.Fork,Little Humboldt	13			2	3	7		1	21.7	13	121-148	130.3	13	30-39	32.6
S.Fork, Rock Creek	17		3	5	4	5			20.6	17	120-156	138.9	17	31-36	32.8
Beaver Creek	23		4	4	6	6	3		21.0	15	125-146	138.4	23	32-38	34.9
Nelson Creek	5			3		2			21.3	5	131-146	138.4	5	30-33	31.6
Lewis Creek	2				1	1			--	2	130-132	--	2	31-32	--
Rock Creek	3	1			1			1	--	3	113-133	121.7	3	26-32	29.7
Tea Creek	2		1				1		--	4	120-128	124.3	3	30-31	30.7
Mahala Creek	2		1	1					--	2	118-122	--	2	29-31	--
Conrad Creek	3		1	1	1				--	3	133-142	138.0	3	32-36	34.0
Sub-total	87	2	12	23	18	25	5	2	20.9						
Total	137	2	15	31	32	47	7	3							

*Collected from 1911-1915 except 3 specimens from upper Marys R. collected in 1962.

**A specimen collected at Carlin, Nev. in 1911 has 26 gillrakers. This may have been an introduced henshawi and is omitted.

Table . -- Number of Gillrakers in S. c. henshawi and S. c. humboldtensis

	N	18	19	20	21	22	23	24	25	26	27	28	Mean
Combined henshawi data from Table .	161				3	18	32	47	32	14	11	4	24.2
Combined humboldtensis data from Tables and	137	2	15	31	32	47	7	3					21.0

A somewhat distinct sub-group of coarse-scaled trout is probably a reality and not an artifact of inadequate sampling. There is no overlap between 11 coarse-scaled specimens from Lewis, Rock, Tea and Mahala creeks when compared with 28 moderate-scaled specimens from 11 localities. The Ganz Creek specimens show almost no overlap with the moderate-scaled samples. The mean value of 126.0 for 17 Ganz Creek trout is the lowest of any sample of more than 10 specimens from any cutthroat population investigated during this study. Only two coastal cutthroat samples are comparable; Penn Creek, California (126.1) and Grassy Lake Stream, Oregon (126.3). No other interior cutthroat approaches the low scale counts found in certain populations of ~~S. c~~. *humboldtensis*.

Scale counts above the lateral line and from the origin of the adipose fin to the lateral line are related to the lateral series count. Most moderate-scaled specimens have from 24 to 29 scales from the adipose to the lateral line, whereas coarse-scaled specimens typically have 20 to 25 such scales. In all other characters no differences have been noted between the coarse-scaled and moderate-scaled groups. The implications of the coarse-scaled group in relation to the origin and affinities of *humboldtensis* will be discussed later. We believe that the amount of intergradation is sufficient to prohibit the separation of the Humboldt system cutthroat into more than a single subspecies. ~~Russian ichthyologists often use a category called "natio" (sub-subspecies) for such situations~~.

Gillrakers, ~~--~~ the modal values are typically 22. The distribution is skewed to the right. Table ___ compares the gillraker distribution between ~~S. c~~. *henshawi* and ~~S. c~~. *humboldtensis*.

Insert Table Here

Posterior gillrakers are well developed on the first gill arch in both ~~S. c~~. *henshawi* and ~~S. c~~. *humboldtensis*.

Vertebrae. Counts of 79 specimens from 10 localities revealed that two specimens have 60, ~~30~~ thirty - 61, ~~42~~ forty two - 62 and ~~5~~ five - 63, with a mean of 61.6.

Basibranchial teeth. Humboldt cutthroat trout generally have slightly fewer basibranchial teeth than most samples of other subspecies. In specimens more than 100 mm. in standard length, 115 of 121 have from one to 13 teeth; six have smooth basibranchials. These figures do not include specimens from the type locality, the South Fork Little Humboldt. The South Fork sample indicates that most individuals in this population may not develop basibranchial teeth until they are well over 100 mm.; three specimens from 93 to 98 mm. all lack basibranchial teeth and in seven specimens from 100 to 119 mm., four have no teeth and three have 2 or 3 teeth. The largest specimens of 150, 165 and 189 mm. have 6, 7 and 11 teeth, respectively.

In samples of five or more specimens, the mean values vary from 2.9 to 6.5. This low number of basibranchial teeth follows a common trend that small isolated populations tend to have a reduced number of basibranchial teeth.

Pelvic rays. Typical of the cutthroat species, the predominant number is 9. Only 7 of 137 specimens have 10 pelvic rays.

Pectoral rays. The range is from 13 to 15. Most specimens have 14.

Branchiostegal rays. The range is from 9 to 12 on both sides. Most specimens have 10 or 11.

Pyloric caeca. Relatively few caecal counts were made because it did not appear to be a differentiating character from ~~S. c.~~ henshawi. Eleven specimens from Mahala, Tea, Forman and Ganz Creeks and from the North Fork of the Humboldt and Marys Rivers have from 40 to 56 caeca with a mean of 49.9. This is slightly lower than ~~our~~ the counts for ~~S. c.~~ henshawi.

Spotting and Coloration

The spotting pattern is somewhat similar to ~~S. c.~~ henshawi. There is, however, typically a concentration of the larger spots on the caudal peduncle area, with the spots on the anterior part of the body more sparse and reduced in size. In ~~S. c.~~ henshawi, large spots are evenly distributed on the body and often onto the ventral surface.

The parr marks are narrower and more irregular in their shape and distribution than is typical for other cutthroat trout.

In coloration, ~~S. c.~~ humboldtensis resembles interior cutthroat trout in general but the golden and red hues are more subdued. The lower fins have a drab, pinkish tint and are never brightly colored.

Speculation on Speciation

The most probable routes of entry of cutthroat trout into the Lahontan basin would have been either from the Snake River or Bonneville drainages. The first area of colonization by the new invaders then would have been in the Humboldt River system. Most of the present Humboldt drainage was never submerged by Pluvial Lake Lahontan. Thus, a continuous and extensive fluvatile environment was maintained during the Pluvial and Interpluvial periods of the Pleistocene. During these periods, the headwater streams in the Humboldt drainage, probably had resident populations of cutthroat, essentially isolated from the lacustrine adapted form (henshawi) evolving in the great lake. The Humboldt River was the largest tributary of Pluvial Lake Lahontan and must have been an important spawning area for the lacustrine trout. Some introgression between the fluvial and adfluvial forms undoubtedly occurred. The amount of genetic interchange, however, was not enough to break down the incipient divergence. The final recession of Lake Lahontan, about 9,000 years ago, completely isolated ~~S. c.~~ henshawi and ~~S. c.~~ humboldtensis.

It would be expected that the ~~S. c.~~ *humboldtensis* associated with the main stream and its immediate tributaries would be more influenced by ~~S. c.~~ *henshawi* introgression than remote headwater populations. This may explain the difference in scale counts among ~~S. c.~~ *humboldtensis*. It is likely that the coarse-scaled character was evolved in the Humboldt system, because no other group of interior cutthroat has such few scales.

Other interior cutthroat (*lewisi*) typically have 18 to 21 gillrakers. On this evidence we would expect that the first invader of the Lahontan basin had a lower gillraker number than ~~S. c.~~ *humboldtensis*. If this is true, it is logical to assume that the intermediate number of gillrakers in ~~S. c.~~ *humboldtensis* was due to ~~S. c.~~ *henshawi* introgression. We should then expect that the coarse-scaled populations, if they have less ~~S. c.~~ *henshawi* influence, should also have fewer gillrakers than the moderate-scaled group but there is no such correlation. It is possible that the progenitor of the Lahontan cutthroat entered from the Bonneville basin and already had 20 to 23 gillrakers. Some interesting questions are raised by a collection of reputed Bonneville cutthroat from a stream on Mt. Wheeler, White Pine County, Nevada, which are apparently closely related to ~~S. c.~~ *humboldtensis* and quite distinct from the eastern Bonneville trout.

The Collection From Mount Wheeler

Pine Creek, a small stream tumbling down the western slope of Mt. Wheeler, the highest peak in Nevada, was believed to contain a pure strain of Bonneville cutthroats. Pine Creek is a tributary to Spring Valley, White Pine County, Nevada, an independent, desiccating basin between the Lahontan and Bonneville drainages. Pine Creek was originally barren of fish but was among those streams in this area planted by early settlers with trout from the Bonneville basin. The streams draining the eastern slope of Mt. Wheeler are part of the

Table . -- Characters of Pine Creek and Lehman Creek Specimens

Character	Pine Creek, Nevada			Lehman Creek
	N	Range	Mean	(N=2) Mean
Scales, lateral series	28	133-156	143.8	148.0
Scales above lateral line	21	37-44	40.1	42.0
Vertebrae	28	60-63	62.3	62.0
Gillrakers	31	19-23	21.5	20.5
Basibranchial teeth	31	6-46	22.5	18.5
Caudal peduncle, depth	31	98-120	112.9*	120.5*
Dorsal fin length	31	203-248	223.5*	219.5*
Head length	31	266-321	294.9*	283.0*
Upper jaw length	31	153-197	172.6*	165.5*

*In thousandths of the standard length

Bonneville basin. Miller and Alcorn (1945:177-78) said that the source of the Bonneville trout in this area was Trout Creek, Utah; but some streams may have received trout from other sources such as the South Fork of the Humboldt.

In September, 1958, a sample of 31 specimens was collected from Pine Creek, between the elevations of 8,000 and 8,500 feet. The Pine Creek trout appears to be closely related to *S. c. humboldtensis*. The spotting pattern (fig.___), coloration, and especially the gillraker number indicates such affinities.

The Pine Creek trout is distinctive in some characters. It has a chunky body with a long head and jaw, a long dorsal fin and a deep caudal peduncle. In these characters it is not only differentiated from *S. c. humboldtensis* but from other interior cutthroats. Such morphological characters may be easily influenced by the environment and perhaps too much importance should not be placed on them, but the number of basibranchial teeth is higher than in any other interior cutthroat except the Independence Lake, California, population. Table ___ lists some characters of the Pine Creek sample and the mean values of two specimens from Lehman Creek on the Bonneville side of Mt. Wheeler.

Insert Table Here.

Graphically plotting the range and mean of the measurements of body proportions in our material demonstrates that the Pine Creek sample markedly stands out in the above listed morphometric characters. This trout is quite distinct from the cutthroat trout of the eastern part of the Bonneville basin which was discussed previously.

On this evidence, it would seem logical that the Pine Creek trout were actually derived from some slightly differentiated population of *S. c. humboldtensis* from the Humboldt system. Two specimens (UMMZ 141701) collected from Lehman Creek on the Bonneville side of Mt. Wheeler, however, indicate that the Pine Creek population did come from a Bonneville stream.

The spotting pattern, the morphometric measurements, and especially the number of basibranchial teeth demonstrate that the trout of Pine Creek and Lehman Creek may be considered identical and of common origin. It seems unlikely that Lehman Creek on the Bonneville side would have been stocked with trout from the Humboldt River system. It is also unlikely that this distinctive trout was originally restricted to Lehman Creek alone. Unfortunately, we may never know if the "humboldtensis" type of cutthroat was truly native ~~endemic~~ to western Bonneville waters or how widely it was distributed. Biologists of the Nevada Fish and Game Department know of no indigenous ~~endemic~~ cutthroat population~~s~~ still persisting in western Bonneville waters. ~~It is hoped that some may soon be discovered and compared with humboldtensis.~~

The Pine and Lehman creeks material indicate~~s~~ that the western Bonneville trout and the Humboldt drainage trout share common affinities, much more so than they do with the cutthroat native ~~endemic~~ to their own basins (henshawi and lewisi). This could have resulted from headwater stream transfer between the two areas after the recession of the Pluvial lakes. Certainly, there has been no large connection between the two basins since perhaps Pliocene times, because the other fish species, except for Rhinichthys osculus, are quite distinct and show a high degree of endemism.

We may also speculate that humboldtensis and the western Bonneville trout represents a more primitive Bonneville trout, much like the form which first invaded the Lahontan basin.

Ecological Notes

The waters where S. humboldtensis lives are mainly headwater tributaries which are subjected to periods of flood and drought. During late summer, the total suitable trout environment in some of these streams may be restricted to a few pools fed by spring seepage. Flood drift lines visible on stream-bank vegetation depict the violent fluctuations that occur. The native cutthroat seems well adapted to these conditions. Records of introductions and observations on the trout in the North Fork of the Humboldt indicate that in headwater areas the endemic cutthroat resists hybridization with rainbows and other introduced cutthroats and is the most successful trout.

According to the records at the Elko Office of the Nevada Fish and Game Department, many of the waters which sustain what we consider as pure strains of ~~S. c.~~ humboldtensis had been stocked previously with eastern brook, brown, rainbow and Yellowstone cutthroat trout. On July 5, 1962, a collection was made from the headwaters of the North Fork of the Humboldt above the U.S. Forest Service campground at an elevation of about 7,000 feet. Snowbanks were still on the hillsides and the stream temperature was 50°F at noon. Approximately 700 pounds of catchable size eastern brook trout are stocked in this area each year. There is a series of beaver dams and the stream appears to be typical of good eastern brook trout water. When trout were collected by the electric shocking method, the ~~endemic~~ cutthroat outnumbered the brook trout by about five to one. We found no evidence of natural reproduction by brook trout. ~~It is probably only because of the yearly stocking with adult fish that the brook trout can maintain a population in competition with the native cutthroat.~~

21	22	23	24	25	26	27	28
	1	3	2	1			
			2	1			
1			1	1			
		1	1	2			
			1				1
1	1	4	7	5			1

Independence Lake

Creel census sample July 1963 - Richard Beland C.F.G. Biologist in charge

Cutthroat trout heads.

- cleared and stained in KOH + alizarin red

gillrakers N = 32

N	21	22	23	24	25	26	27	28	mean
32	1	3	13	4	5	2	3	1	24.0
1949-1959 19	1	1	4	7	5			1	24.0
51	2	4	17	11	10	2	3	2	24.0

All have the proliferation of basibranchial and hypobranchial teeth - tiny, bony plates occur on floor of mouth & on arches * - Pharyngobranchial teeth also present - some specimens have pharyngobranchial tufts of teeth on every arch - giving each arch "pharyngeal teeth" - like ling cod.

Posterior gillrakers well developed on first arch as many as 6+11 counted.

Osmeridae - dental cement bone

page 96 (Chapman's paper Dusmerissidae)

Taylor, D. W., 1960 (cont.)

Klamath
Pit
Snake R
+
Bonneville

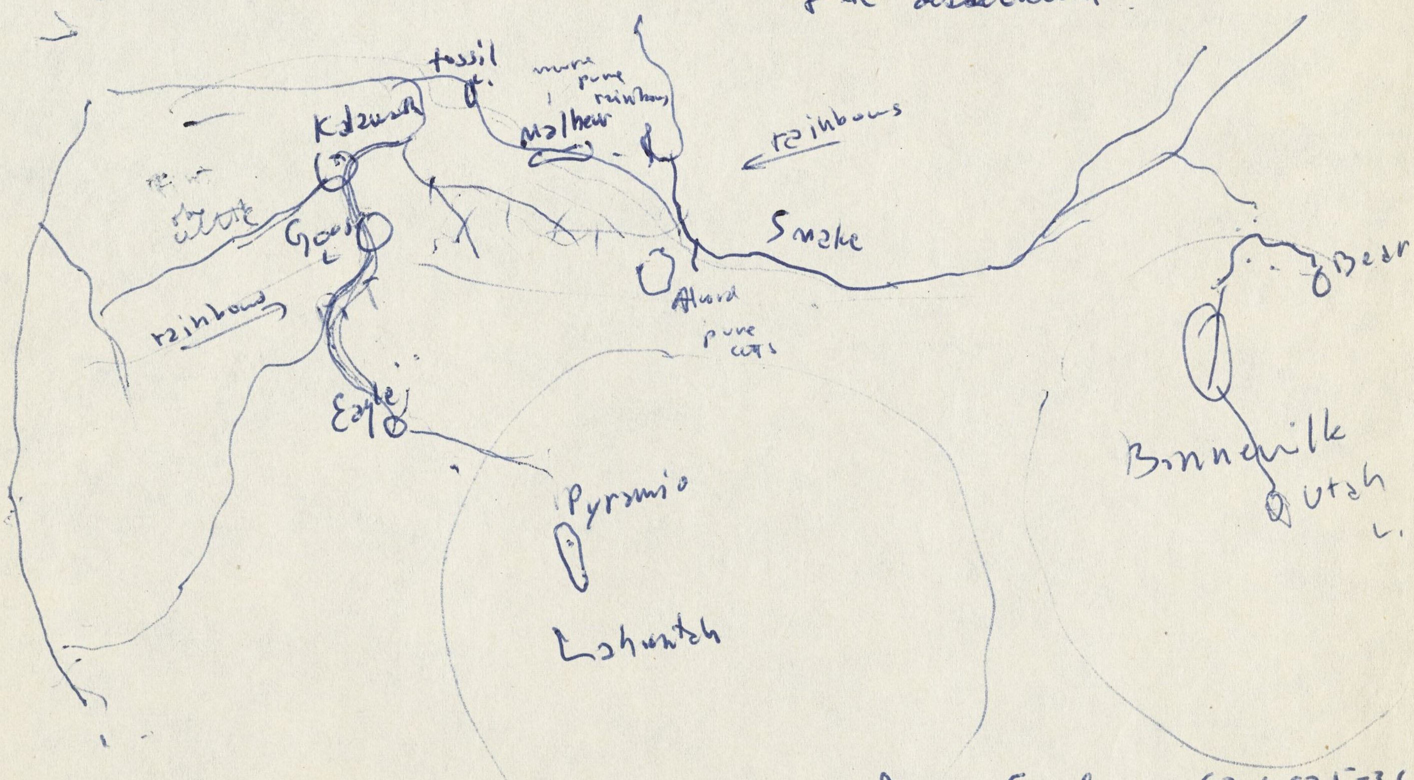
Age of this distribution (linking Lahontan cannot be precisely determined - probably as old as Pliocene - and at least as early Pleistocene. - Estimated on degree of differentiation and estimated age of mid Pleistocene Snake R. capture. - + Restricted distribution & lack of fossils for Carinifex and Pyrgulopsis.

now in Utah L.
& no fossils in Bonneville.

now Pyramid L.
& sulphsail Walker
not other Lahontan
fossils.

2 other snail species in Utah L. w/ no Bonneville fossils.

- Why not spread through Bonneville & Lahontan lakes?? & introduced after desiccation?



- Wheeler & Cook 1954. Snake R. capture. Jour. Geology 62: 525-36.
, also Cook & Larrison - 54. Late Pleistocene age of Snake R. diversion - abst. - Bull. Geol. Soc. Am. 65: 1241.

Robins & Miller - Cottus - 1957. Calif. Fish & Game 43: 213-33.

See - Prosopium fossils in Bonneville deposits - (Proc. Utah Acad.) - 64 -

western Lahontan - Pit. - Klamath connections

Klamath L. 3 sp. Chasmistes all 3 lacustrine relicts
w/ P. u. snail Carinifex

only other Chasmistes - C. liorus Utah L.
& C. cujus Pyramid L.

fossil Chasmistes from Fossil L. ~~Idaho~~ Ore.

Carinifex only 2 sp. living one - only in Clear L. Calif.
other - C. newberryi - over much of western U.S.
- striking correlation of distribution w/ Chasmistes, Pyrgulopsis & P. u. - again shows Klamath - Lahontan connection via upper Pit & Eagle L.
- Fossil L, Ore. - fossil Chasmistes & Carinifex (Christmas L.) suggest w/ Klamath - presently only a chub living ~~...~~ which seem similar to Klamath chub.
- Fm. Ore. → Wyo. & Utah ' Malheur - fossil Carinifex link between Fossil L. & Snake R. - modern Malheur fishes close to Snake - probably best connection relatively recently.
- Utah L. Chasmistes & Carinifex but not P. u. - links to Klamath L. - Pyramid L.
- Bear L. - 3 endemic whitefishes - but no molluscs.
- Gentile Valley Idaho - Once Bear R. flowed here - lava flow created lake - flowed over into Bonneville basin & present course of Bear R. - fossil molluscs fm. lacustrine deposits in Gentile Valley incl. P. u.; Valvata utahensis (also Utah L.) - Stagnicola utahensis & Carinifex -
- faunal links - Chain fm. - Walker L. Nev. - Eagle L. - Pit R. - Klamath L. - Fossil L. - Malheur Basin & Snake R. - Gentile Valley - Bear L - Utah L. - all thought to be coversal & connected by series of rivers and lakes - but not all at once.

Taylor, D.W. 1960. Distribution of the freshwater clam *Pisidium ultramontanum*; a zoogeographic inquiry. Am. Jour. Sci., Bradley Vol., 258-A: 325-334.

P. u. lives now only in N.E. California & s. central Ore. but in Pleistocene and Pliocene - eastward, at least to s.e. Idaho. - Some early Pliocene deposits.

There are faunal ties between Pliocene & Pleistocene Snake R. of southern Idaho & recent fauna of Northeast Calif. & S. Ore. - evident among snails also.

- Present course of Snake R. relatively young - once flowed to Pacific independent of Columbia & Sacramento.

2 fossil snails assc. w/ *P. u.* in southern Idaho - share similar affinities - one now lives in upper Pit R. & Honey L. basin. the other lives in Sacramento R. drainage.

3 species of Prosobranch genus *Pyrgulopsis* are closely related. *P. archimedis* Klamath L. Ore. - *P. nevadensis* - Pyramid L. Nev. subfossil in Walker L. - and a Pliocene fossil form from southern Idaho. - comparing Late Pliocene molluscs from S.W. Idaho w/ Central Valley Calif. - so distinct that believes Snake didn't flow down Sacramento - living molluscs & fish suggests closer relations w/ Klamath.

faunal ties (1). Klamath - upper Pit. (2) upper Pit - Lahontan by other animals besides molluscs.

(1). *Entosphenus* known only from here, *Siphateles bicolor* & *Cottus klamathensis*, *C. tenuis* of Klamath L. close to *C. asperimus* of Pit. (Robins & Miller 57)

~~taxa~~ none of endemic Sacramento - *Hesperoleucas*, *Mylopharodon*, *Ptychocheilus*, *Hysterocarpus* in Klamath - connection to Klamath lost before these gained entrance to Pit.

Carinifex acutifilosa: Pit R. - Lahontan (Honey L.),

P. ultra. - Pit. - Klamath - Eagle L.

—These are the redband trout (exept. Alvord basin)

Independent Basins North of the Lahontan System

Snyder (1908a) and Hubbs and Miller (1948) collected trout from the following independent basins: Goose, Fort Rock (including Silver Lake), Chewaucan (including Summer and Abert lakes), Warner, Malheur and Alvord. All of these basins contained large lakes during Pluvial periods of the Pleistocene, but today the trout habitat in this arid region is restricted to headwater streams. The names of the basins used hereare those used by Hubbs and Miller (1948).

From the standpoint of cutthroat and rainbow systematics, these desiccating basins in southeastern Oregon are an important region. Almost nothing is known of the native trout of these basins. The non-trout fishes have affinities to species found in the Sacramento and Columbia river systems, the Lahontan basin and Klamath Lake.

Although the material examined is very incomplete, it indicates that cutthroat trout from the Columbia River system and, perhaps, the Lahontan basin and rainbow trout from the Columbia and possibly the Sacramento river systems invaded these basins during Pluvial periods. In some areas, hybridization probably occurred and a series of local forms were produced whose affinities are difficult to ascertain.

Snyder (1908a) considered all the trout he collected from these basins as Salmo clarkii. He mentioned great variation in spotting, coloration and presence of the cutthroat mark. Snyder gave lateral series scale counts on 50 specimens from five localities, ranging from 146 to 174. Bond (1961) said that isolated basins in eastern Oregon contain rainbow trout which are fine scaled and superficially resemble cutthroats.

Discussion of Basins and their Trout

Goose Lake: -- This basin lies partly in California and partly in Oregon. It had a relatively recent overflow into the Pit River of the

Sacramento system and the native fishes of the Goose Lake basin have close affinities to Sacramento species. Snyder (1908a) collected trout which he described as Salmo clarkii from three Goose Lake tributaries. He also mentioned S. clarkii from two localities in the Pit River system. As discussed previously, we believe the "S. clarkii" from the Pit River were actually based on S. gairdnerii stonei specimens which oftem have pronounced cutthroat-like characters. Six specimens collected by Snyder in 1904 from Cottonwood Creek, tributary to Goose Lake were examined. Although labeled as Salmo clarkii by Snyder, these specimens have a morphology and spotting pattern suggestive of rainbow and all of the specimens have smooth basibranchials. Our scale counts on these specimens (Table) are much lower than the counts of 153-168 reported by Snyder (1908a) for ten Cottonwood Creek specimens. The gillraker counts of 21 to 24 indicate a lacustrine influence during their evolution. Two specimens have a single posterior gillraker on the first arch, suggesting interior cutthroat influence. If more material becomes available, the native Goose Lake trout may be considered as a subspecies, but it can not be confidently allied to either the cutthroat or rainbow species. If all Goose Lake basin trout lack basibranchial teeth, it would seem practical to assign them to the rainbow series, although they appear to have their closest affinities with the Chewaucan and Fort Rock basin trout, which have more cutthroat-like characters.

Fort Rock Basin, Lake County, Oregon: -- This basin is considered a disrupted part of the Columbia River system by Hubbs and Miller (1948:73). Silver Lake is the only permanent body of water. Cope (1889) said Silver Lake was too alkaline to support fish life, but its tributary, Silver Creek, abounded with "Salmo purpuratus" [=S. clarkii]. Snyder (1908a) collected trout from Silver, Buck and Bridge creeks, all tributaries of Silver Lake.

Willow Creek, Oregon
Undescribed subsp. S. clarki

Locality	Vertebrae 59	60	61	62	63	64	65	66	Vertebrae $\bar{X}$	Gillrakers 15	16	17	18	19	20	21	22	23	24	Gillrakers $\bar{X}$
Willow Crk. 1934		1	1	5	2				61.9				1	2	2	4	4	1		20.8
1946	1	1	0	1	2	1			61.8					3	1	1	2			20.3
1952			1	4	2				62.1						2	2	3	1		21.4
1972		3	6	10	5				61.7					4	6	3	10	5		21.2
Sum of 4	1	5	8	20	11	1			N: 46 59-64 61.8				1	9	11	10	19	7		N: 57 18-23 21.0

Locality	Pyloric caeca (N, range, $\bar{X}$)	Scales, lat. ser. and above lat. line (N, range, $\bar{X}$)	Branchiostegal rays (N, range, $\bar{X}$)	Pelvic fin rays (N, range, $\bar{X}$)	Basibranchial teeth (N)
Willow Crk. 1934	—	14 36-45 40.5 —	9-11	9	1 no teeth 13: 2-13 (6)
1946	6 41-49 45.7	6 40-42 40.7 143-163 (152)	..	..	7 2-7 (4)
1952	—	8 — 149-162 (154)	"	..	2: no teeth 6: 5-12 (8)
1972	28 39-59 (48)	28 36-44 (41) 141-163 (151)	..	..	28 1-10 (6)
Sum of 4	34 39-59 (47-48)	56 36-45 (41) 141-163 (151-152)	..	..	3 of 57 w/o teeth 1-13 (6)

Whitehorse & Little Whitehorse Crks. Oregon

undescribed subsp. Salmo clarki

Locality	Vertebrae 60	61	62	63	64	65	66	Gillrakers 15	16	17	18	19	20	21	22	23	24	Pyloric caeca (N, range, $\overline{X}$)	Scales, lat. ser. and above lat. line (N, range, $\overline{X}$)	Branchiostegal rays (N, range, $\overline{X}$)	Pelvic fin rays (N, range, $\overline{X}$)	Basibranchial teeth (N)
Whitehorse Crk. 1969		2	5	1										3	1	2	2	1 41	8 35-40 36.9; 131-164 142.	9-11	9	1: no teeth; 7: 2-8 (5)
						61.8									22.4							
1971	1	2	10	4								1	2	11	4	1	1	10 40-49 44.7	10 35-42 37.9; 127-154 144.	..	..	10 1-8 (5.5)
						62.0									21.25							
1972	3	3	9	5							1	1	2	6	6	6	1	23 37-52 46.3	23 34-43 38.2; 127-148 141.	..	..	23 1-14 (5.2)
						61.8									21.4							
Sum of 3	4	7	24	10							1	2	4	20	11	9	4	N = 34 37-52 (45.46)	N=41 (37-38) 34-43; (142) 127-164	..	..	1 of 41 w/o teeth 1-14 (5)
	N = 45 60-63					61.9		N=51 18-24							21.6							
Little Whitehorse Crk. 1972		4	7										4 (20)	3 (21)	6 (22)	2 (23)		15 37-76 (48.1)	15 34-42 37.5; 126-149 136.3	..	..	2: no teeth; 13: 1-7 (3.7)
		61.6													21.4							

Salmo clarki "alvordensis" ms.   Trout & Virgin Crks

Locality	Vertebrae 60	61	62	63	64	65	66	Gillrakers 15	16	17	18	19	20	21	22	23	24	25	26	Pyloric caeca N range $\bar{X}$	Scales, lat. ser. and above lat. line N range $\bar{X}$	Branchio-stegal rays N range $\bar{X}$	Pelvic fin rays N range $\bar{X}$	Basi-branchial teeth N
Trout Crk. 1934 UMMZ 130493	2	2		1									1		3	1				5 46.4 41-59	5 35.8 33-38 135.6 131-140	10-11	8/1 9/3 10/1	4 w/o teeth 1 w/ 4 teeth
					61.0											21.8								
Trout/Little Trout 1934 UMMZ 130491 N=1	?																1			53	37 120	12-12	9	2 teeth present
	- hybrid ?																							
Trout Crk. below canyon UMMZ 130494 hybrids	3	1	2	1							1	3	6	7	2	1				–	–	–	-	17 w/o teeth 3 w/ one tooth each
	?				60.5											20.45								
Virgin Crk. Nev. UMMZ 130532 1934 T 44N R25E	2	17	8	2									1	1	5	11	8	4	1	20 (42.0) 34-49	20 (35.1) 33-37 (135.0) 122-152	9-10	8/9 9/21	N=19 10 w/o teeth 9 w/ 1-5 mainly 1 or 2
	59-63 61.2				61.3						20-26					23.3 (4)								
Virgin Crk. Nev. 1971 T43N R25E			2	4						1	1	3	1							6 (47.2) 41-54	6 (29) 28-31 (122.8) 116-130	6 10-12	9/3 10/3	6 all w/o teeth
Typical S. gairdneri					62.7											18.7								
Lower Trout Crk. 1972			2	1	1		1	1			1	3	2							7 (52) 45-64	7 (28) 25-30 (132) 120-145	9-12		7 all w/o teeth
typical S. gairdneri					63.4											18.6								
headwaters E. Fk. Trout Crk. 1972		1	4	2	1						3	5								8 (53) 41-66	8 28.1 26-30 127.0 117-131	9-12		8 all w/o teeth
S. gairdneri					62.4											18.6								

INVOICE OF SPECIMENS

THE UNIVERSITY OF MICHIGAN, MUSEUM OF ZOOLOGY

DIVISION OF ~~Fishes~~

ANN ARBOR, MICHIGAN, U. S. A. 48104

To ~~Dr. Robert Behnke~~
Colorado Cooperative Fishery Unit
Colorado State University
~~Fort Collins, Colorado 80521~~

Attention

Loan XX Exchange
Gift Transfer

LOANS ARE ORDINARILY MADE FOR A PERIOD OF SIX MONTHS OR LESS. A REQUEST FOR RENEWAL SHOULD BE MADE IF IT IS NECESSARY TO KEEP SPECIMENS FOR A LONGER PERIOD.

CATALOGUE NO.	NAME		DATA
UMMZ 130493	Salmo clarki	(5)	Oregon: Trout Cr., Harney Co. C. L. Hubbs & family - VII:26:1934.
130532	" "	~~(88)~~ 41	Nevada: Virgin Cr., Humboldt Co. C. L. Hubbs & family - VIII:2:1934.
191644	" "	(2)	Utah: Trout Cr., ~~J~~uab Co. H. B. Stafford - VII:26:1933.
130492	Salmo gairdneri	(27)	Oregon: Trout Cr., Harney Co. C. L. Hubbs & family. - VII:26:1934. and Little Trout Cr.
130491	S. clarki X S. gairdneri (hybrid)	(1)	Oregon: Trout Cr., Harney Co. C. L. Hubbs and family - VII:26:1934.
130494	" "	(49)	Oregon: Trout Cr., Harney Co. C. L. Hubbs and family - VII:26:1934.

spec. #14 tentatively selected as type

PLEASE DATE, SIGN, AND RETURN THIS COPY.

Returned May 29, 74
R. J. B.

Date of shipment April 24, 1973
Method of shipment Library Rate

Sent by Mike L. Smith for R. R. Miller
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Form 5510

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UNITED STATES
DEPARTMENT OF THE INTERIOR
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BUREAU OF SPORT FISHERIES AND WILDLIFE
COLORADO COOPERATIVE FISHERY UNIT
COLORADO STATE UNIVERSITY
FORT COLLINS, COLORADO 80521

June 4, 1974

Dr. R.R. Miller
Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104

Dear Bob:

I had a request for an address from your father-in-law. He wrote that he was leaving for Ann Arbor, via Boulder, Colorado, so I will enclose a letter for you to present to him when he arrives.

Under separate cover the specimens are being returned. The enclosed data sheets summarize the meristic characters of the trout in Willow and Whitehorse creeks on one hand and Trout and Virgin creeks on the other. It includes UMM2 specimens from 1934 and recent collections of my own plus some borrowed from Carl Bond. You will note that the Willow and Whitehorse samples are quite distinct from the Virgin Creek trout, particularly in number of gillrakers, scales and number and presence or absence of basibranchial teeth. If they are of common origin they have been separated for a long time. The populations in Willow and Whitehorse creeks appear to be unchanged (no introductions-except perhaps in Little Whitehorse Creek which has a road crossing it). In contrast, no trace of the original trout is now apparant in the present populations in the Trout Creek and Virgin Creek drainages, sampled in the vicinity of the 1934 collections--I also sampled from the very headwaters of E. Fk. Trout Creek and a tributary to Pueblo Slough--only typical rainbow trout can be found. It looks like "alvordensis" is extinct before it could be named. I have alerted BLM biologists to look for cutthroat populations in the Virgin-Thousand Creek drainage. I covered the Trout Creek watershed in 1972 and I could find no isolated sections where the native trout might persist. The phenomenon of rapid elimination of native cutthroat trout by introduced rainbow trout is particularly evident in those groups with a pluvial lacustrine ancestry. It appears they have never "re-adapted" to stream life and are completely vulnerable to extinction by introduced trout in small stream habitat. In contrast, my recent studies on the native cutthroat trout of the upper Columbia River basin in Idaho and Montana revealed large areas where at least a predominantly cutthroat trout phenotype is the dominant trout, despite continued stocking of massive numbers of rainbow trout.

The pertinent questions now are: What are the origins and affinities of the Willow-Whitehorse Creek trout, the original Trout Creek-Virgin Creek trout and the present Summit Lake stock, in relation to each other and to S. c. henshawi and S. c. "humboldtensis" of the Humboldt drainage of the Lahontan, ~~but~~ I believe this is convergentce rather than direct descendency. The headwater drainage of Willow Creek virtually intertwine with Trout Creek and a headwater transfer may

5

have been the route of entry rather than a pluvial connection from Alvord Lake. There is also only a slight divide from the "Whitehorse" desert to the Owyhee drainage.

From previous communications, I assume that Summit Lake formed from a lava dam across a Lahontan tributary but may have overflowed or at least provided a potential connection to Virgin Creek. This might have isolated a Lahontan cutthroat in Summit Lake and transferred it later to Virgin Creek. But why are no other Lahontan fishes in Summit Lake? On the other hand, the lava flows may have exterminated all fishes prior to the formation of Summit Lake and the trout gained entrance from Virgin Creek. Comparisons of characters don't reveal any obvious answers. The Summit Lake trout have more gillrakers than typical henshawi (25.2 vs. ca. 24). They have an average of about 36 scales above the l.l. and 155 in the lateral series (henshawi is typically about 36-40 and 160-175). The evidence of affinities of Summit Lake trout to Virgin Creek trout is the pelvic rays (many with 8), the common occurrence of fused vertebrae in both stocks and reduced number of basibranchial teeth (3 of 27 small specimens of Summit L. stock lack teeth and average only about 4). In the Virgin Creek trout, 50% or more lack teeth and of those with teeth, most have only one or two. I would suspect that the 1934 sample was already hybridized, except they look like good cutthroat trout in all other respects (except, perhaps, the low scale counts).

I have never seen a large, fresh specimen of Summit Lake trout to critically examine the spots. Virgin Creek trout appear to be typical of the generalized interior cutthroat in their spotting. S. c. henshawi has a distinctive pattern with spots evenly distributed over the body, onto the head and often on the abdomen.

That is where the matter now stands and I would like to hear any opinions you and Dr. Hubbs might have when I see you in Ottawa.

I just received a call from a BLM biologist in Salt Lake City. BLM people have been conducting studies in the Deep Creek Mtns. (Trout Creek and Deep Crk. drainages) of western Utah, and I had urged they be on the lookout for cutthroat trout. The message was that cutthroat trout were found in one of the headwaters forks of Trout Creek, above a barrier. Only rainbows and hybrids were found below the barrier and in other streams sampled. Twelve specimens were preserved and will be sent to me next week. I'll let you know about these trout when I see you, but my hopes are high. I will now try to stimulate more searching for cutthroat in the Virgin Creek drainage of Nevada--perhaps alvordensis can be rediscovered.

I received your letter of May 23, before I had this letter typed so I'll add on some replies. Thanks for bringing me up-to-date on Cyprinodon. There is no problem with types of alvordensis. The specimens have small, numbered tags under the right operculum. When I would select a type, I'll let you know the number of the specimen and it can be assigned a new UMMZ number as the holotype of the subspecies.

I have a student finishing up a thesis on comparison of fine-spotted and large-spotted Snake River cutthroat. We've learned quite a bit but there are still some unknowns. Both fine-spotted and large-spotted cutthroat are in the Gros Vente drainage but don't appear to be truly sympatric. The large-spotted populations are in the smaller tributaries and there are intergrades which suggests hybridization does occur here.

It seems unusual that Jordan, Evermann and Gilbert never mentioned the distinctive fine-spotted form during their investigations on the Snake River. Most likely, they didn't sample where the fine-spotted form occurred. But what were the original limits of their distribution. Today it extends to Palisades Reservoir--all tributaries below here--Henry's Fork, Raft River, Goose Creek have large-spotted cutthroat. Perhaps you can locate some of the collections made in the 1890's at the USNM which might shed light on the form of trout native to the Snake River down to Shoshone Falls. Also we know little about the native trout from Shoshone Falls to the Cascade Range. If you can find any of the specimens collected by Evermann, Gilbert, Thoburn, Rutter and others in the 1890's from this area, they would be valuable. I found a few at the California Academy last summer. A large-spotted cutthroat was native to a stream near Walla Walla, Washington and Wood River, Idaho specimens, labled S. mykiss are red-banded trout (The Wood River trout were called "S. gibbsi" in the Gilbert and Evermann publication). What is the native resident trout of the Payette Owyhee, Grande Ronde, John Day and Deschutes rivers? If you can find any specimens at the USNM from these areas, let me know. Also, Don Seigrist once told me he saw the type of S. gibbsi at the USNM (just a skin or a stuffed specimen, I believe). The name "gibbsi" was used for a trout which I believe to be the red-banded complex--at least in part (Wood R., Payette Lakes), but I suspect the type is S. gairdneri (taken from the Dalles, Oregon). Seegrist said it seemed coarse-scaled like a rainbow.

When at the USNM, you should try to find a steel tank containing W.C. Kendall's personal collections. Harry Everhart told me it was at the University of Maine and he sent it to the USNM several years ago. Of particular interest would be the possibility that Kendall had specimens of "S. agassizi" from Christine Lake, New Hampshire and another lake (which he never named in print) where he claimed it was found. I am curious to find out what is in Kendall's tank. I have heard it is stored in the basement and has not been cataloged. You might want to examine USNM 34710, 35355 and 39327 and convince yourself that agassizi was quite divergent from fontinalis.

Yes, Don Seegrist is correct, I'm terminating my employment with the Fish and Wildlife Service in June. There has been no great disagreement or unpleasant relationships involved, but the Bureau is taking a new course which is centralizing authority and tightening the reins. The existence of a loosely attached and ill-defined position such as I have doesn't fit the new reorganization and they wanted me to move my operations to Buelah, Wyoming. There isn't a worthwhile library within 400 miles of Buelah, among other things.

My long range plans are not definite. I have accepted an offer from Targi Farvar in Iran to go there in July and help set up a fisheries program and start a graduate education project. I would return in December and then see what develops here at C.S.U.

If you hear of opportunities for a "free-lance" ichthyologist for one to six month periods of employment in 1975, let me know.

Sincerely yours,

Robert Behnke

RB:vv

Enclosures

[illegible] Great Basin.
Summit L.: Miller, R. R.
Carl L. Hubbs
NOV 22 1965

MAR 20 1973
Xeroxed for Behnke

November 22, 1965

Dr. Robert Rush Miller
Museum of Zoology
University of Michigan
Ann Arbor, Michigan

Dear Bob:

As a carbon copy of my apologetic letter to Starker Leopold has indicated, I have been up to my neck in the swamp of the Needham-Behnke opus. I am doing a lot of editing but only a minimal amount of comment on substantial points. They obviously did not use Michigan material (or ideas) extensively enough. As I go through the MS word by word evidence keeps accumulating of significant data and interpretations, along with some glaring lacks.

I would like to comment in particular on the treatment of the Summit Lake trout, because we should be looking forward to a discussion of this lake and its fauna. I will start by copying what the MS now says (with a few editorial changes):

Summit Lake

"Summit Lake occupies a small independent basin in northwestern Nevada between the Lahontan basin to the south and Alvord basin to the north. Hubbs and Miller (1948: 61) mention that the cutthroat trout is the only fish present. LaRivers (1962: 172-74) discussed Summit Lake and the possible origins of the trout. If the lake was originally without trout, it seems probable that men in the Army camp on the lake that was in operation prior to 1890 would have introduced trout from neighboring Lahontan streams. Whatever their origin, Summit Lake sustains a pure type of S. c. henshawi. The mean number of gill rakers (25.2) is the highest of any sample used in this study; in fact, higher than any heretofore reported for the genus Salmo. The Summit Lake specimens have slightly fewer scales than in other samples of S. c. henshawi and about 50 percent of the specimens have only 8 pelvic rays. LaRivers (op. cit.) thought that the Summit Lake population represented the last remnant of pure henshawi of which he was aware."

Now let's check a bit. N. & B. placed almost full reliance on their gill-raker counts, which they summarized as follows (from different tables):

		18	19	20	21	22	23	24	25	26	27	28	Range	Mean	No.
Summit Lake		..	..	..	..	—	—	—	—	—	—	—	23-28	25.2	38
Lake Tahoe	1872-1915	..	..	..	—	—	—	—	—	—	..	..	21-26	22.8	19
Independence L.		..	..	..	—	—	—	—	—	—	—	—	21-28	24.0	19
Total, henshawi		..	..	..	3	18	32	47	32	14	11	4	21-28	24.2	161
Total, humbold.		2	15	31	32	47	7	3	..	..	..	..	18-24	21.0	137
Virgin Cr., Nev.		..	..	—	—	—	—	—	—	—	..	..	20-26	23.4	30
Willow Cr., Ore.		—	—	—	—	—	—	..	..	..	..	..	18-23	21.0	22

As presented the percentage identifiable is 87% for henshawi and 93% for humboldtensis---not bad, but the high values for henshawi is heavily sustained by the Summit Lake data and by that for Independence Lake, the population of which, unless N. & B. are cockeyed, has vastly greater right for separation, possibly even as a species, for the basibranchial teeth seem to be quite different. Now if we look at details, we find that N. & B. arbitrarily omitted a count of 26 from humboldtensis (from Carlin), because it may have been an introduced henshawi, and we find under humboldtensis 2 means, of 22.5 and 22.6, not strikingly different than the mean of 22.8 for 19 from Lake Tahoe based on 1872-1915 collections! If we eliminate the Summit Lake and Independence Lake counts as likely to represent other forms, I calculate the mean as 23.8---still near upper limit for humboldtensis. But that is barely above the mean for Virgin Creek (23.4).

The "lateral-series scale count" for Summit Lake is the lowest for any "henshawi." N. & B. do not give this count for the Virgin Creek trout.

A point of possible significance is the pelvic ray count, giving as about 50% 8's for Summit Lake and 12 8's to 18 9's in Virgin Creek. I find no pelvic-ray counts for "henshawi" and for humboldtensis only this text statement: "typical of the cutthroat species, the predominant number is 9. Only 7 of 137 specimens have 10 pelvic rays [none with 8?]." I suppose we may assume they counted 9 usually in "henshawi."

In very briefly and non-committingly discussing the trout of Alvord Basin N. & B. do not refer to Summit Lake.

It does appear probable, in line with N. & B.'s explicit indications, that the Lahontan system in Pluvial times was occupied by a lake-adapted (henshawi) type and a stream adapted one (humboldtensis)---much as for the Gila obesa subspecies. The Lahontan type presumably spawned in streams and probably dominated shorter tributaries, such as Soldier Creek. The lava flow we found presumably cut off a population of the henshawi type, which in the lack of fish prey and probable rich plankton in shallow Summit Lake underwent a little further increase in raker number. If the cutoff was in Pluvial or Little Pluvial time, the lake probably overflowed for a time into Virgin Creek and carried over a similar type---different from the trout of eastern tributaries to Lake Alvord. This may have been before the final further increase in rakers in Summit Lake, or the same stock as now in Summit Lake may have regressed a bit in the creek.

Obviously we need to do some careful comparing or have you done so? Does UMMZ have Virgin Creek cutthroats?

Cordially,

Carl L. Hubbs

Table . -- Meristic Variation is Salmo from Desiccating Basins North of the Lahontan System.

	Gillrakers			Vertebrae			Pelvic Rays			Scales Lateral Series			Scales Above Lateral Line		
	No.	Range	Mean	No.	Range	Mean	8	9	10	No.	Range	Mean	No.	Range	Mean
ALVORD BASIN															
Virgin Crk., Nevada	30	20-26	23.4	29	60-63	61.3	12	18	--	--	--	--	23	33-43	36.3
Willow Crk., Oregon	22	18-23	21.0	16	60-63	62.0	3	18	1	7	154-167	159.9	10	36-45	40.5
CHEWAUCAN BASIN															
Chewaucan R., Ore.	6	20-23	22.3	6	61-64 --	62.8 --		6		6	132-143	138.0	6	27-30	28.3
FORT ROCK BASIN															
Buck Crk., Ore.	6	19-22	20.2	6	63-65	63.7		4	3	6	138-147	141.7	6	28-33	29.8
GOOSE LAKE BASIN															
Cottonwood Crk. Ore.	6	21-24	22.8	6	63-64 --	63.3 --		2	3	6	132-149	139.0	6	29-34	30.2
MALHEUR BASIN															
Silvies R., Oregon	4	20-22	21.0	4	64-66	65.0		2	2	4	146-154	150.8	4	29-32	30.3

Seven specimens from Buck Creek (S.U.37966) collected by Snyder in 1904 form a most interesting group. Some of their meristic characters are listed in Table .

Although the general morphology and spotting pattern is cutthroat-like and four specimens of 126 mm. or more in standard length have basibranchial teeth, thenumber of vertebrae is typical of rainbow trout and the scale counts and pelvic ray number indicate rainbow influence. The Buck Creek specimens appear to represent rainbow introgression in a predominant cutthroat genotype. These specimens have affinities to the Chewaucan and Goose Lake basin trout but have stronger cutthroat characters and fewer gillrakers. It is not known if native trout still persist in the Fort Rock basin.

Warner basin, Lake County, Oregon: -- Snyder (1908a) collected trout from tributaries of Warner Lakes. He mentioned that some of the local people said the trout were introduced, but others claimed they were native. No specimens from Warner Lake basin were examined.

Chewaucan basin, Lake County, Oregon: -- A Pluvial lake once covered the Chewaucan Marsh, Summer Lake and Abert Lake (Hubbs and Miller, 1948:66). Cope (1884) reported trout to be abundant in the Chewaucan River. Six specimens collected by Snyder in 1904 from the Chewaucan River were examined. These trout appear almost identical to the sample from Cottonwood Creek of the Goose Lake basin, except that one specimen has a single basibranchial tooth. The small amount of data available implies that a series of intergrading populations existed in the desiccating basins of Oregon. Considering the specimens examined, including S. g. stonei of the upper Sacramento River system in California and proceeding with the samples from the Goose Lake, Chewaucan and Fort Rock basins, the demarcation between the cutthroat and rainbow species breaks down.

As with the Cottonwood Creek sample from the Goose Lake basin, our scale counts of 132 to 143 for the Chewaucan River sample disagrees with the counts obtained by Snyder(1908a) (147 to 151) for ~~the~~ Chewaucan River specimens. ~~Miller~~ Hubbs and Miller (1948:67) believe the native trout have hybridized with introduced rainbows.

Malheur basin, Harney County, Oregon: -- Snyder (op.cit.) thought the connection of this desiccating basin to the Columbia River system was in recent times. He found the fishes to be typical Columbia River species. Hubbs and Miller (op,cit.:75) recognized four or five endemic subspecies and suggested there may have been "...a somewhat prolonged isolation".

Four specimens (S.U. 28770) collected by Snyder in 1904 from the Silvies River, tributary to Malheur Lake, resemble rainbow trout in their spotting and morphology. All lack basibranchial teeth. The vertebrae number (64-66) is higher than any other rainbow sample, Except for the Alvord basin samples which are unmistakably derived from the cutthroat species, the Silvies River specimens have more scales in the lateral series than the samples with more obvious cutthorat characters from the desiccating basins mentioned above. The native trout of the Malheur basin may represent an endemic subspecies with affinities to the "Kamloops" rainbow of the Columbia River system. The present status of ~~these~~ this Malheur trout is not known.

Alvord basin, Humboldt County, Nevada, Harney and Malheur Counties, Oregon: -- Hubbs and Miller (1948:60) believed the Alvord basin has been isolated since Prepluvial times. Cutthroat trout samples from two localities were examined. Thirty specimens from Virgin Creek, tributary to Thousand Creek, Humboldt County, Nevada, appear to be quite typical of S. c. henshawi. These trout may have entered the Alvord basin from the Lahontan basin by headwater stream transfer or, perhaps, through introductions by man. Bond (1961) lists henshawi from the Alvord basin. Specimens from Willow Creek, tributary to Whitehorse Valley, Harney County, Oregon, are distinct from the Virgin Creek specimens and may represent an endemic subspecies. These trout have medium-large, round spots concentrated on the caudal peduncle and sparsely scattered anteriorly above the lateral line. The number of gillrakers is similar to humboldtensis, but the spotting pattern and scale counts resmeble Columbia River drainage lewisi. Nineteen specimens have from 2 to 13 basibranchial teeth. Three specimens over 100 mm. have smooth basibranchials.

The native trout of the Alvord basin were probably derived, at least in part, from the Snake River drainage. Incipient speciation in the lacustrine environment of Pluvial Lake Alvord may have resulted in an increased number of gillrakers. The Willow Creek specimens probably represent a relict stock of the native Alvord trout. The Trout Creek specimens apparantly are of Lahontan origin and perhaps entered the Alvord basin after the recession of Pluvial Lake Alvord and the subsequent isolation of the various stream systems in the basin.

The Willow Creek cutthroat trout probably should be recognized as a subspecies, but we would prefer to examine more specimens from more localities.

– I now believe these (Virgin Crk – Willow + Whitehorse Crk) – are 2 separate basins w/ 2 endemic subsp.

THE GOLDEN TROUT COMPLEX

Golden colored trout populations native to Kern River tributaries in California, to tributaries of the Salt River and the Little Colorado River, Arizona, to tributaries of the Gila River, New Mexico, and to the Río Verdi, Río Sinaloa and Río Culiacan ~~river~~ systems in [redacted], Mexico, share a number of distinctive traits which suggest a monophyletic origin. ~~It has been assumed that these trouts represent localized offshoots of the rainbow species.~~ ~~We believe, however, that~~ As was stated above The available evidence [redacted] strongly supports the theory that the golden trout have their closest affinities to each other and may represent the result of an ancient hybridization between a primitive rainbow-like trout and a primitive cutthroat-like ancestor.

California Golden Trout

The question concerning the number of forms of California golden trout has never been settled. Despite the great interest aroused by this beautiful trout, no detailed systematic data, or critical comparisons with other forms, have appeared in the literature.

Jordan and Henshaw (1878) first mentioned the golden trout from the South Fork of the Kern. They called it Salmo irideus. In this same paper they also mention the Colorado River cutthroat, Salmo pleuriticus, from the South of the Fork Kern. Jordan (1892) described the California golden trout as a subspecies of the cutthroat, naming it Salmo mykiss aguabonita. Jordan said its closest affinities were to the Colorado River cutthroat and it was "...not in any way related to the Rainbow trout". Jordan (1893) essentially repeated the same description of S. aguabonita in the Proceedings of the U.S. National Museum. Evermann (1906) and Jordan, Evermann and

Clark (1931) erroneously list the 1893 paper as the original description . Jordan (1894d) placed the California golden trout as a subspecies of the rainbow, calling it S. gairdnerii aguabonita, considering it an offshoot of the Kern River rainbow, S. g. gilberti. Jordan and Evermann (1896:504) referred to it as S. irideus aguabonita and wrote:

> "This form is apparantly derived from the Kern river trout, var. gilberti, but is so much modified that unless intermediate specimens now exist, it may be ranked as a distinct species".

Most subsequent authors have accepted the assumption that the California golden trout was derived from the rainbow.

In the original description, Jordan believed the type locality to be Whitney Creek, also called Volcano Creek (now called Golden Trout Creek). Actually, the type material came from Cottonwood Creek where the trout were introduced in 1876 from Mulky Creek, a tributary of the South Fork of the Kern. Evermann (1906) corrected these errors and documented the history of the events leading to the description of aguabonita. Evermann (op.cit.) considered the population in Golden Trout Creek to be specifically distinct and named them Salmo roosevelti. He also named another golden-like trout from various Kern River tributaries as Salmo whitei, in this same work. Jordan and McGregor (1924) described yet another golden-like trout from a lake in the Kern system as Salmo rosei. As discussed under the Kern River ~~rainbow~~ section, we consider Salmo whitei to represent intergrades between S. aguabonita and S. g. gilberti with closer affinities to ~~S. g~~. gilberti. As previously mentioned, S. rosei was based on introductions whose original source was the Little Kern. This leaves only the question of the validity of S. roosevelti to be settled.

X date? Mulky?

Evermann (1906) distinguished roosevelti from aguabonita mainly on the basis of the arrangement of spots on the body. He claimed the population in Golden Trout Creek (*roosevelti*) had spots restricted to the caudal peduncle area with no spots anterior to the dorsal fin, whereas, *aguabonita* from the South Fork Kern typically had spots anterior to the dorsal fin. About the only meristic character mentioned by Evermann which might suggest a difference between *aguabonita* and *roosevelti* was his statement that *aguabonita* was relatively coarse scaled while *roosevelti* had about 50 scales above the lateral line, about 200 in the lateral series and about 140 to 150 scales with pores in the lateral line. Our counts are lower than Evermann's and indicate no real differences between *aguabonita* and *roosevelti* in scale counts or any other character (Table___). The California golden trout typically have only 110 to 115 pores in the lateral line.

Curtis (1934, 1935) claimed the spotting pattern of golden trout was variable and that both the "*roosevelti*" type and the *aguabonita* type were found among all populations, although the "*roosevelti*" type predominated in Golden Trout Creek. He suggested *roosevelti* should be considered a synonym of *aguabonita* and most subsequent authors have accepted this view. ~~Miller (1950:9), however, pointed out that no critical systematic study has been published on *roosevelti* and *aguabonita* and left open the question concerning the validity of *roosevelti*.~~

~~Table ___ indicates no obvious difference between specimens from Golden Trout Creek and other waters.~~

Specimens collected from various localities in 1956 were separated into two groups -- those with spots anterior to the origin of the dorsal fin (*aguabonita*), and those with spots only posterior to the origin of the dorsal fin (*roosevelti*). The following distribution was obtained (Table __).

Table ? Spotting pattern of California golden trout

Locality	roosevelti-type	aguabonita-type
Golden Trout Creek	10	22
South Fork Kern	5	33
Mulky Creek	15	17
Cottonwood Creek	15	9

Curtis (1935) judged 22 of 28 specimens from Golden Trout Creek and 6 of 17 from Mulky Creek to be of the "roosevelti" type.

Evermann (1906) recognized that Golden Trout Creek was once tributary to the South Fork Kern and that its golden trout population was derived from the aguabonita there. He believed, however, that the lava flow which changed the drainage of Golden Trout Creek to make it tributary to the main Kern River, provided isolation of sufficient duration to develop a distinct species. Our data indicate that the population in Golden Trout Creek may be considered identical with the aguabonita of the South Fork Kern. We consider the true, California golden trout a single taxonomic entity, Salmo aguabonita, whose original range was the South Fork Kern and its tributaries and Golden Trout Creek.

Characters andComparisons

The coloration of S. aguabonita is distinct from any rainbow or cutthroat trout (plate 1, Evermann, 1906). The bright red and yellow hues, however, are much more similar to interior cutthroat than to rainbow trout. The spotting pattern is typical of interior cutthroat. In the absence of basibranchial teeth it is rainbow-like. The general morphology, its long head and jaw are more suggestive of cutthroat than rainbow. A bright crimson generally covers the ventral surface and the underside of the lower jaw so that a cutthroat mark is not discernable. The scale counts of *aguabonita* are quite typical~~ly~~ of cutthroat. We have examined no rainbow or cutthroat samples with such low numbers of vertebrae and pyloric caeca as found in *aguabonita*. Except for other golden trouts, some samples of *S. c. stomias* are closest to *S. aguabonita* in vertebra~~e~~l and caecal counts. As mentioned previously, a low vertebral number is considered a primitive character and this is one of the most forceful arguments against the theory that *aguabonita* is a localized offshoot of the rainbow, at least of rainbows stocks existing ~~today~~. Overall, the California golden trout appears to have closer affinities to the interior cutthroat than to the rainbow. The closest affinities, however, apparantly are with the other members of the golden trout complex.

Table ___ discloses that a low number of vertebrae and pyloric caeca are common to all the known populations of the golden trout complex. Besides sharing golden coloration, all of the golden trout group have distinctively colored lower fins, typically shades of red, yellow or orange with the pelvics and anal fins tipped with white. The anterior tip of the dorsal fin is, typically, yellow or orange. Also, all of the golden trouts have a relatively long dorsal fin, typically .225 to .275 of the standard length. In most samples of rainbows and cutthroats, the dorsal fin is .180 to .230 of the standard length. *S. aguabonita*, typically has nine pelvic rays, like a cutthroat. The Mexican golden trout also has predominantly nine pelvic rays, while the Gila trout and the Arizona golden trout mostly have ten pelvic rays.

Arizona Golden Trout

Native trout were known to exist in tributaries of the Colorado River system in Arizona, but until recently these trout were considered as Colorado River cutthroats. Cope and Yarrow (1875) listed three specimens of that a cutthroat mark is not discernable. The scale counts of S. aguabonita are quite typically of cutthroat. We have examined no rainbow or cutthroat samples with such low numbers of vertebrae and pyloric caeca in aguabonita. Except for other golden trouts, some samples of S. c. stomias are closest to S. aguabonita in vertebral and caecal counts. As mentioned previously, a low vertebral number is considered a primitive character and this is one of the most forceful arguments against the theory that aguabonita is a localized offshoot of the rainbow, at least rainbows existing today. Overall, the California golden trout appears to have closer affinities to the interior cutthroat than to the rainbow. The closest affinities, however, apparently are with the other members of the golden trout complex.

Uyeno & Miller 1965
Copeia (1) – Colorado Pliocene cyprinids
– rapid current – early cyprinid

Table ___ discloses that a low number of vertebrae and pyloric caeca are common to all the known populations of the golden trout complex. Besides sharing golden coloration, all of the golden trout group have distinctively colored lower fins, typically shades of red, yellow or orange with the pelvic and anal fins tipped with white. The anterior tip of the dorsal fin is typically yellow or orange. Also, all of the golden trouts have a relatively long dorsal fin, typically .225 to .275 of the standard length. In most samples of rainbows and cutthroats, the dorsal fin is .160 to .180 of the standard length. S. aguabonita, typically has nine pelvic rays, like a cutthroat. The Mexican golden trout also has predominantly nine pelvic rays, while the Gila trout and the Arizona golden trout mostly have ten pelvic rays.

Arizona Golden Trout

Native trout were known to exist in tributaries of the Colorado River system in Arizona, but until recently these trout were considered as Colorado River cutthroats. Cope and Yarrow (1875) listed three specimens of

S. pleuriticus, collected from the White Mountains of Arizona. These specimens were borrowed from the National Museum (USNM 15999) where they are erroneously labeled, Panguitch Lake, Utah. The three specimens range ~~were~~ from 101 to 166 mm. in standard length. They have a striking appearance with an extremely long head, jaw and dorsal fin. Table ___ indicates the meristic characters are similar to other golden trout, especially to a sample collected by Dr. R. R. Miller in 1950 from the East Fork White River, a tributary in the Salt River system, Apache County, Arizona. Although Jordan and Evermann (1896:496) state that the Colorado River cutthroat occurred throughout Arizona, Miller (1961:389) said that the only indigenous Arizona trout ~~to Arizona waters~~ ~~was~~ is what we here call the Arizona golden trout, which Miller (1950:34) tentatively referred to as S. gilae. Mulch and Gamble (1954) considered the Arizona golden trout as S. gilae, although their colored illustration depicts a trout quite differently spotted than S. gilae. The specimens examined from the East Fork of the White River (fig.___) appear to be more similar to S. aguabonita in their spotting than to S. gilae. Table ___ indicates the White River golden trout have more scales than S. gilae from Diamond Creek, New Mexico. The spots are considerably larger and fewer in number on the White River golden trout than in S. gilae. It must be noted that similar ~~such~~ variation in spotting and scale counts are found among S. c. lewisi populations. It is not known if continual intergradation occurs or if the Arizona golden trout of the Salt River tributaries should be recognized as a valid taxonomic entity. So few pure populations remain that the original situation may never be known. The Arizona Game and Fish Department kindly supplied two completion reports on the distribution and abundance of their native golden trout in the tributaries of the White and Black rivers. They found that most native populations had hybridized with introduced rainbow trout.

Table . -- Meristic Variation in the Golden Trout Complex

Sample	Gillrakers			Vertebrae			Pyloric Caeca			Pelvic Rays			Scales Lateral Series			Scales -- above Lateral Line		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	8	9	10	No.	Range	Mean	No.	Range	Mean
<u>Salmo aguabonita</u>																		
Cottonwood Creek and Lakes - 1912	9	18-22	20.2	9	58-61	59.7	--	--	--	--	9	--	8	156-186	175.8	7	35-44	39.4
Cottonwood Creek, 1954	16	19-21	19.8	39	58-61	59.7	16	22-36	28.9	--	16	1	5	176-211	187.4	7	38-43	40.9
South Fork Kern River, 1954	16	17-21	19.2	34	58-62	59.4	10	24-36	29.8	1	14	1	15	151-182	168.0	9	38-43	39.8
Golden Trout Creek, 1891, 1904, 1912	23	18-20	19.0	24	58-61	59.3	--	--	--	1	20	1	22	148-182	164.6	22	35-45	38.8
Golden Trout Creek, 1954	15	17-21	19.4	31	58-61	59.3	15	26-40	31.7		12	3	11	163-212	174.9	13	38-45	40.5
Sally Keyes Lake, Fresno Co., Calif. 1961	32	18-20	18.7	22	58-61	59.4	17	21-33	26.9	1	16	5	18	151-175	164.8	14	34-42	39.1
Arizona "native" trout																		
White Mtns, Ariz. 1872*	3	18-19	18.7	3	58-60	59.0	--	--	--	--	--	3	2	141-158	--	2	37-40	--
E. Fork, White River, Apache Co. Ariz. 1950	20	18-21	19.5	20	58-61	59.5	2	30-31	--	--	7	13	16	144-168	155.4	10	32-36	34.2
<u>Salmo gilae</u>**	25	18-20	19.0	20	59-62	60.2	10	31-42	34.9	--	15	19	25	133-151	141.2	25	24-29	
<u>Salmo gilae</u>***	25	18-21	19.1	25	59-63	60.7	--	--	--	--	--	--	17	138-153	146.0	17	28-35	31.8
<u>Salmo chrysogaster</u>***	82	15-20	17.5	81	55-61	57.5	81	10-30	22.0	10	98	--	typically 120-150 (variable among populations)			typically 18-25		

*Collected by Yarrow
**From Miller (1950)
***From Needham and Gard (1959)

A native golden trout was also present in the Little Colorado and Verdi river systems (Miller, 1961). It is not known if these were identical to the White River trout. Miller (1961:390) doubted ~~that~~ the existence of a pure stock of native trout ~~persisted~~ in the Verdi drainage. (F just received 2 sample of Verdi trout - Apr. 75)

The Gila Trout

Miller (1950) named Salmo gilae from Diamond Creek, New Mexico, tributary to the Gila River. This trout has some characters intermediate between cutthroat and rainbow. It has a weak cutthroat mark and golden hues. It is coarser scaled and finer spotted than the California golden trout or the Arizona golden trout ~~from the East Fork of the White River~~. S. gilae has an extremely long adipose fin, longer than any other sample examined in this study. More complete meristic and morphometric data on the Gila trout is presented by Miller (1950) and Needham and Gard (1959). Today the native trout of the Gila River is found in only a few headwater tributaries in New Mexico (Miller, 1950:17) and perhaps in Greenlee County, Arizona (Mulch and Gamble, 1954). The trout of the Rio Yaqui and Rio Casas Grandes in Mexico, just south of the Gila drainage, described by Needham and Gard (1959), appear somewhat intermediate between S. gilae of Diamond Creek and the Mexican golden trout.

Miller (1950) believed the Gila trout was derived from the rainbow series but regarded it as a full species because of its distinctive coloration and spotting.

Mexican Golden Trout

This trout was fully described by Needham and Gard (1959) and named Salmo chrysogaster by the same authors (1964). Its native range is the Verdi, Sinaloa and Culiacan river systems in ~~Durango~~, Mexico.

In most characters the Mexican golden trout is the most distinctive of the golden trout complex. It has a shorter head and jaw and its spotting pattern is more typical of rainbow trout.(plate 1, Needham and Gard, 1959). The scale counts are variable among the different samples but tend to be the lowest of the golden trout group. The count above the lateral line, 18 to 25, is especially low -- lower than any rainbow sample and only slightly more than one-half as many as is typically found in the California golden trout. The number of vertebrae is the lowest yet reported for any western North American Salmo. The pyloric caeca counts are the lowest known in the genus Salmo. The Mexican golden trout may represent the most primitive of the golden trout complex.

Discussion

If all of the golden trouts mentioned above are of common origin, the waters of the lower Colorado River area ~~was~~ were probably the ~~site~~ center of speciation. The fishes of the lower Colorado system form a distinct group from the northern elements of the Colorado drainage (Miller, 1958). Blackwelder (1936) believed that the Colorado River was not a continuous river system until the Pleistocene. A primitive rainbow-like trout, perhaps somewhat similar to the Mexican golden trout, may have been established in the lower Colorado River area; ~~and~~ when the lower Colorado became connected with the upper basin, a primitive interior cutthroat trout may have invaded the more southern waters, resulting in hybridization. Long isolation from other cutthroats and rainbows and then from each other could have produced the golden trouts as we know them today. The distribution of the Arizona and Mexican golden trout and the Gila trout fit this scheme well. The occurrence of S. aguabonita in the Kern drainage in California is not so easily explained. To cross the Sierras and enter a Pacific slope stream would necessitate gaining entrance into the Pluvial waters of Death Valley and its connectives.

Miller (1958) believed the connection between Death Valley and the Colorado was probably in the Pliocene. Trout, however, may have made headwater transfers at a later date, after direct connection was lost. If the golden trout did enter the Kern basin from the east slope, some drastic changes must have occurred which wiped out all trace of trout from the Sierran east slope streams, south of the Lahontan basin. Although many east slope waters, such as Cottonwood Creek, the type locality of aguabonita, provide excellent trout habitat today, these waters were barren of ~~fish~~ trout before the activities of man. A sucker, probably of Colorado River origin, Pantosteus santanae Snyder (1928), made it across the divide, perhaps in Pliocene times (Miller, 1958), to establish itself in a Pacific Coast stream.

Systematic Arrangement of Golden Trouts

It will take much more work with much more material, perhaps with the help of serological and chromosomal studies, before the true relationships of the golden trouts are established with confidence. The available evidence indicates that four groups, apparently, are worthy of taxonomic recognition: the California golden trout, Salmo aguabonita, the Gila trout, S. gilae, the Mexican golden trout, S. chrysogaster, and the Arizona golden trout, as yet unnamed. Further collections and study may demonstrate the Arizona golden trout and the Gila trout to form an intergrading series like S. c. lewisi. None of the golden trout make "good" biological species, i.e., they will hybridize with rainbow and probably with cutthroat trout when occurring sympatrically. They may be considered as subspecies of the rainbow or cutthroat species but this would disguise their true affinities, if they do, ~~indeed,~~ actually represent a monophyletic group. The most proper and practical solution seems to be to consider the golden trout complex as a third species of western North American Salmo. Salmo aguabonita has priority. The distinct forms then ~~can~~ could be considered as subspecies of S. aguabonita.

GENERAL DISCUSSION

Assessment of the foregoing material requires further comment on the emphasis placed on certain taxonomic characters, on inter- and intra-specific relationships and on the origin and affinities of western North American fishes in the genus Salmo.

Scale counts: - It is difficult to assess the importance of scale counts and to evaluate the amount of emphasis placed on this character for taxanomic purposes. Formerly, slight differences in scale counts were thought to be an important diagnostic criterion of trout taxonomy. Kendall (1921) believed a higher number of scales indicative of a northern origin. He, and most of his contemporaries, placed great emphasis on scale counts. During the past 30 years, experimental methods have demonstrated the phenotypic plasticity in number of scales, fin rays and vertebrae in a single genotype raised under different environmental conditions. Because of the results of such experiments, many recent authors have minimized differences in scale number. There is no doubt that environmental conditions may influence the number of scales. However, within a subspecies such as S. c. stomias or in a group of populations such as the cutthroats found in the Humboldt drainage in Elko County, Nevada, comparable ranges and means are found between many samples from many localities, and these ranges and means are markedly different from the trout of contiguous areas. It may be assumed that such differences have a genetic basis.

Generally, there is good separation between rainbow and cutthroats in the lateral series count but there are some notable exceptions, especially among small, isolated populations.

Scale counts above the lateral line and from the origin of the adipose fin to the lateral line are generally proportional to the lateral series count.

– Meek 04

Hatchery. at Rio Lerma

Semin Chazarri. 33,000 McCloud R.
1883

Vladykov (1963) – new genus Parasalmo

Page 135

These latter two counts yield about the same degree of separation between cutthroats and rainbows as does the lateral series count. Generally, cutthroats have more than 32 scales above the lateral line, with as many as 50 or more in S. c. stomias, while rainbows usually have less than 32 scales above the lateral line. Mexican golden trout, S. chrysogaster, may have as few as 18 such scales.

The lateral line count, i.e., number of pores, is closely correlated with the number of vertebrae. There is almost no separation between cutthroats and rainbows in this character; but forms with a low number of vertebrae, such as the California golden and Mexican golden trouts, have significantly fewer scales in the lateral line than either the cutthroat or the rainbow trout. The typical count for most cutthroat and rainbow range between 115-125 while the California and Mexican golden trout typically have from 105-118. Four specimens of S. c. alpestris from Isaac Creek, British Columbia, have 145 to 150 scales in the lateral line and, in this character, are distinct from all other trout examined during this study.

According to our material all anadromous rainbows may be considered coarse scaled, usually having from 120 to 140 in the lateral series. What we consider as fine-scaled rainbows occur only in parts of the upper Fraser and Columbia river systems (Kamloops type) and in the Kern and upper Sacramento river systems in California (S. g. gilberti and S. g. stonei). In the cutthroat series, S. c. stomias often have over 200 scales in the lateral series which makes it the finest scaled group in the genus Salmo. In contrast, other cutthroats display extreme variability in this character. The typical cutthroat trout has 140 to 180 scales, but some populations possess fewer scales than the coastal rainbow.

Pelvic Fin Rays: -- The number of pelvic fin rays proved to be a useful character in separating rainbow from cutthroat trout. With some local exceptions, rainbows typically have 10 pelvic rays and the cutthroats have nine. Examination of other salmonids suggests that nine is the primitive Salmo number.

Vertebrae: Cutthroats typically have 60-63 vertebrae and rainbows generally have 62-64. The California, Arizona and Mexican golden trout samples all have mean values of less than 60. An interesting finding (Needham and Gard, 1959) is that the two most southerly samples of rainbows from the Rio del Presidio drainage in Mexico, have the highest mean vertebrae number, 64.3 and 64.4 for 30 and 23 specimens, respectively. Just to the north, samples of the Mexican golden trout from the Rio Sinaloa, Rio Culiacan and Rio Verde systems, comprising 91 specimens have mean counts ranging from 56.9 to 58.4, the lowest vertebrae counts observed in ~~the~~ western North American Salmo. A low vertebrae number is considered a primitive character among Salmonidae. There has been a constant trend in the phylogeny of Salmonidae for a progressive increase in vertebral number. The relict Salmothymus ohridanus (Steindachner) of Lake Ohrid, Yugoslavia, appears to be the most primitive species of the subfamily Salmoninae as delineated by Norden (1961). This belief is based on the presence of basibranchial teeth, a median series of teeth on the tongue, teeth on the shaft of the vomer, and no gap between the vomerine and palatine teeth. This species typically has 54 or 55 vertebrae (Hadzisce, 1961). The progenitor of Salmo may have been a species much like Salmothymus ohridanus. Salmo trutta and S. salar both retain a low number of vertebrae, typically 55 to 61 with S. salar generally slightly higher than S. trutta. If the separation of the primitive Salmo, which gave rise to S. trutta, S. gairdnerii and S. salar, from the basibranchial toothed progenitor of the cutthroat, was monophyletic, then the number of vertebrae in the primitive S. gairdnerii ancestor would be expected to be in the mid-50's. Salmo mykiss of Kamchetka, to be discussed below, may represent a relict rainbow stock. S. mykiss has 57-59 vertebrae.

Many laboratory experiments have demonstrated that the number of vertebrae may be influenced by environmental factors, notably, water temperature during embryonic development. These experiments were reviewed by Needham and Gard (1959:21) and Lindsey (1961). Examination of our data indicate that the number of vertebrae is a relatively stable character among populations from natural environments. Samples of California golden trout transplanted in waters with altitudinal differences of thousands of feet, retain a remarkably constant range and mean vertebral number. In the whole rainbow series, the greatest difference between mean values exhibited by any two samples is less than three. Among cutthroats, both coastal and interior, the maximum difference is slightly more than three.

Basibranchial Teeth: Needham and Gard (1959) noted a single specimen of rainbow trout from the Santo Domingo River, Baja, California, which had three basibranchial teeth. In the present study, no specimen of undoubted pure strain rainbow had basibranchial teeth, but one specimen of S. g. gilberti and three of the four type specimens of S. regalis of Lake Tahoe possess basibranchial teeth. The occurrence of basibranchial teeth in these specimens may have been the result of hybridization with cutthroat. Cutthroats generally have from 1 to 40 basibranchial teeth. These teeth typically appear during the growth stage of between 30 and 100 mm. Some populations are marked by trends for reduction or loss of these teeth. The native cutthroat of Independence Lake, California, S. c. henshawi, have a striking proliferation of basibranchial teeth. Not only is the basibranchial region covered with 50-100 teeth but small tufts of teeth may appear on the hypobranchial elements of the first or second gill arches.

The variability found within a single population and between closely related populations suggests that a slight genetic difference can greatly one tooth in apache

influence the number of basibranchial teeth. Bulkley (1963) reported that in four generations in a hatchery, S. c. lewisi from Yellowstone Lake greatly increased the average number of basibranchial teeth. Rainbow-cutthroat hybrids may or may not have basibranchial teeth. Hartman (1956, unpublished) found 15 out of 23 two-year-old, first generation hybrids to lack these teeth.

The dentigerous condition of the basibranchial plate goes far back in phylogeny, appearing in most of the families of the suborder Salmonoidea and in the primitive isospondylous genera Elops and Albula. S. gairdnerii, S. salar, S. trutta and its derivitives S. ischchan, S. letnica and S. carpio all lack basibranchial teeth. Among other salmonid genera the same situation occurs, with the more advanced species lacking basibranchial teeth. All Salvelinus except S. fontinalis have basibranchial teeth. Hucho perryi of Hokkaido and Sakhalin have these teeth while they are absent in Hucho hucho and H. taimen. Salmothymus ohridanus possesses the dentigerous basibranchial plate while in Salmothymus obtusirostris it is smooth.

Pyloric Caeca: Closely related species, subspecies, and even populations of the same subspecies may have large differences in caecal number, indicating that a slight genetic change can influence caecal development. Miller (1950) grouped data from previous authors and gave a range of 39-80 caeca for rainbows and 27-45 for cutthroats. DeWitt (1954) counted 71 specimens of California coastal cutthroats and found a range of 23 to 60 with a mean of 40.3. Snyder (19~~k8~~ 17) claimed a caecal count of 70-85 for S. c. henshawi, however, our counts for this subspecies ranged from 40-64. Goode (1888) listed 20 caeca~~e~~ as characteristic of "S. purpuratus" which as he delimited it, would at present, include S. c. clarkii and S. c. lewisi in part. We have not encountered such a low count in any cutthroat examined to date.

- no evidence altered by environment.
Nikolsky (63) - neg. correlation of rakers + caeca - more predacious more caeca.

Averette (1962) listed mean values of from 28.1 to 32.3 for five samples of S. c. lewisi from tributaries of the St. Joe River of the Columbia River drainage of Idaho. Our counts and those of other workers suggest that cutthroats generally may be expected to have slightly fewer caeca than rainbows, but the great variability limits the efficacy of caecal counts as a distinguishing criteria between cutthroats and rainbows or between subspecies. It appears, however, that the Gila trout, the Arizona golden trout, the California golden trout and the Mexican golden trout typically have fewer caeca than most cutthroats or rainbows. The Mexican golden trout have the lowest caecal counts of any Salmo yet reported in the literature.

Osteology: A comparison of osteological material indicates no clear-cut distinctions between cutthroat and rainbow trout. Cutthroats tend to have a more deeply notched ethmoid, which typically is broader in its anterior part than the posterior. Rainbows generally have a shallow notch in the ethmoid and the broadest area is the posterior section. The caudal skeleton, believed to be diagnostic in Salvelinus taxonomy by Vladykov (1954), was found to have great individual variation. A more thorough and detailed study, using more specimens may turn up some valid distinctions in the osteology of rainbow and cutthroats. The outcome of the present comparisons only emphasizes again the close relationship of the two species. Norden (1961) included some material of S. gairdnerii in his comparative study of salmonid fishes.

Chromosome Counts: Simon and Dollar (19~~5~~63) reported on chromosome numbers in rainbow and cutthroat trout. 64, 104 S. g. gairdneri S. c. lewisi from the U.S. National Hatchery at Winthrop, Washington, has a diploid number of 60 and an arm number of 104. They concluded that the cutthroat chromosome complement was more primitive. Centric fusion in two pairs of chromosomes could derive the rainbow genotype from a cutthroat ancestor. This work greatly weakens *-

UNIVERSITY OF WASHINGTON
COLLEGE OF FISHERIES
SEATTLE 5, WASHINGTON

March 9, 1964

Mr. Robert Behnke
Department of Zoology
University of California
Berkeley 4, California

Dear Bob;

As I hope you suspected, my delay in answering your last letter has been due to the demands of finishing my thesis. The whole thing is now in final typing stage and I can catch up with my badly-neglected correspondence.

Your manuscript on rainbow and cutthroat trouts sounds very interesting indeed. My procrastination in reply should not be misunderstood to be an indication of waning interest in salmonids, or in your work with them.

All things considered, I don't presently see any major difference between chromosomes of Lahontan and Yellowstone cutthroats. It should be understood that my samples are miserably small and possibly not representative of either group. The golden on the other hand appears to be chromosomally distinct from either the rainbow or cutthroat and thus far has the lowest of <u>Salmo</u> diploid numbers (2n = 58).

The embryonic material of O. mason was preserved too late for good chromosome observation. I was unable to obtain further samples. About 14 counts were made on this material, but chromosomes were very poorly spread. These estimations ranged from 63–70 and were considered to be only scantly reliable. Better confidence was felt in approximation of the arm number as 104, since the decision is not necessary as to whether 4 elements (for example) are 4 acrocentrics, 2 metacentrics, or one metacentric and two acrocentrics. I will try to obtain more material next fall which will hopefully be better.

The reason I expected differences between 2n in S. gairdneri, and O. mason was simply based on the overall implication that centric fusions (or decrease due to hybridization) seem to occur pretty much at random in highly-anadromous species. An additional occurrence of 60 as a diploid number was thus speculated to be unlikely for the simple reason that it already has occurred in a good percentage of the species studied to date. I don't think the absolute diploid number really means a great deal considered by itself. For example, the pink and chum salmon appear to be closely related in a host of morphologic and ecologic attributes, yet their diploid numbers represent the extremes in <u>Oncorhynchus</u>.

My current thinking on species differences is something like this:

(a) an ancestral number included many acrocentrics

(b) development of anadromous habit occurred in response to altered environmental conditions, probably in the form of glacial-pluvial changes

(c) anadromy constituted an escape from rigors of the freshwater habitat which enabled these species to discard some of their freedom of chromosome assortment (i.e. reduction in diploid number, without change in arm number) as a means of producing a new adaptive complex which was specialized to suit new environmental conditions

(d) species which did not develop anadromous habit (chars) could not afford the luxury of the specializing nature of centric fusions (specializing in the sense that centric fusions limit the freedom of random arm assortment to gametes) with the result that those species which are least anadromous (face the most severe environmental conditions) have not diverged very far from the original high number of the primitive condition.

(e) species differences could be postulated to be the consequence of shuffling of very similar genetic information (supported by equivalence in arm number) with each new combination providing a unique linkage grouping offering possible selective value in a new environment.

(f) species similarities might be due in large part to the selective pressures of similar environments.

I realize that this is somewhat vague and confusing and that several points of objection may arise. I believe I have arguments to meet the objections; some of necessity are hypothetical entirely while others are based on experiment.

I think your concept of the duplication of four acrocentrics in the S. alpinus-sort of complex is reasonable. I just wish we knew more of the variability in arm number, or diploid number, in much larger samples of these populations. If this increase has taken place it should be detectible in meiotic chromosome pairing. The usual behavior of these polysomics is a random distribution at diakinesis — thus the interest in variability of diploid numbers. Your proposition is certainly justified, and one which can be tested experimentally. If current reports on the stability of diploid numbers are correct, this would appear to provide a basis for objecting to possible increase in numbers. I am not so sure of the great stability in numbers implied by most authors (myself included).

I tried the leukocyte culture technique ~~of~~ on F_1 hybrids of chum and pink without success. I will try again very shortly now that I've begun to emerge from the thesis. Some excellent, but limited, results have been obtained with the cornea technique.

Could you please pass on any new information that comes your way on the progress of Dr. Svetovidov?

Have you heard any news on your application for the exchange program with the Soviet Union?

Sincerely,

Ray Simon

Bungenberg de Jong, C. M. 1955. QH 301 G4

Cytological Studies on *Salmo irideus*. Genetica, 27: 472-483.

- 2n = 60 - at least 40 metacentrics

- Kupka 1948 - Rev. Suisse Zool. 55: 285-93 - Swiss cutthroat fish

Makino S. 1951 - atlas of Chromosomes

1937 - Chromosomes in Teleosts - Zool. Mag. Tokyo. 49: 75-8

* Pomini - 1939. - Scientia Genetica I: 206-08

Prokofieva - 1934 - Cytologia 5: 498-506.

* White - 46 - Am. Nat. 80. 610-618

C. lavaretus & C. albula - same chromos. as *S. alpinus*

2n = 80 16 meta. 64 acro. = 96 arms.

Thymallus thy. 102 2n. 28? meta. = 130? arms.

- Can't accept polyploidy theory on basis of metacentrics in rainbows - .

- Prakken et al - right after de Jong's art.
- Chromosomes. *Esox lucius* -

over.

* Matthey, R. 1951 - Chromosomes of Vert. - Advances in Genetics 4: 159-80.

Svardson & Wickbom 39. Hereditas 25: 472-7.

Pike - Esox

Prakken, R., J. Bekendam and G. A. Pieters 1955

The Chromosomes of *Esox lucius* L., Genetica, 27: 484-88.

2N = 48 all rod shaped.

- miscounts from orientation ex. / ʃ - 2 acrocentric close together could be considered 1 metacent.

Svardson & Wicklom mentioned *E. l.* had 2N = 18

6 pr. meta - 12

3 pr. acro - 6

use of right embryo stage + preparation & stain.

* J. Fish. res. Bd. Can. 8: 469-52

L. Winnipeg whitefish

Table . -- Chromosome numbers reported in Salmo, Oncorhynchus and Salvelinus

lewisi
aguabonita
letnica ?. Lebow
finland

	Diploid No.	Metacentric	Acrocentric	Total No. of Arms
Salmo				
gairdnerii[1,5]	60	44	16	104
clarkii[1]	64	42	22	106
trutta[2,5]	80	16	64	96
salar[2] (Europe)	60	12	48	72
salar[3] (N.Am.)	56	16	40	72
Oncorhynchus[4]				
keta	74	28	46	102
tschwy~~t~~acha t-cha	68	36	32	104
kisutch	60	52	8	112
nerka	56	46	10	102
gorbuscha	52	52	0	104
Salvelinus				
fontinalis[2,5]	84	16	68	100
namaycush[6]	84	16	68	100
alpinus[2]	80	16	64	96

[1] Simon and Dollar (1963)
[2] Svardson (1945)
[3] Boothroyd (1959)
[4] Simon (1963)
[5] Wright (1955)
[6] Wahl (1960)

Svardson's (1945) argument of polyploid speciation in salmonid fishes. For speciation by polyploidy or from duplication of a group of chromosomes, the arm number would be expected to increase proportionately to the increase in the chromosome number. *S. trutta* has more chromosomes (80) than the cutthroat or rainbow but fewer arms (96). This means that *S. trutta* has more rod-like chromosomes (one arm) and fewer V-shaped or J-shaped chromosomes (two arms) than *S. gairdnerii* or *S. clarkii*. The European *S. salar* has 60 chromosomes, like the rainbow, but only 72 arms, making their chromosomal morphology quite distinct from *S. gairdnerii* (Table). Future chromosome work on other subspecies of cutthroat trout and comparisons with *S. c. lewisi* should yield valuable insight into questions of speciation.

Chromosomal research may be the most fruitful approach to establish the true affinities of the golden trouts.

Hybridization

It would appear obvious from the prevalence of rainbow-cutthroat hybrid populations in interior waters that the rainbow and cutthroat species are fully capable of hybridization with no loss of viability in the offspring. Little detailed work, however, has been performed concerning hybrid fertility between these species. Needham and Gard (1959:71) cite two hatchery experiments producing viable rainbow-cutthroat hybrids. In British Columbia, Hartman (1959, unpublished) made reciprocal crosses between Kamloops rainbow stock from the Cultus Lake hatchery and a coastal cutthroat from Chilliwack Lake. In both instances the eggs from the hybrid parents produced a slightly higher percentage of fry than did the pure matings. The hybrids had a normal sex ratio. Hartman has informed us that the hybrid females were lost in a mishap at the hatchery but the males were backcrossed to both rainbow and cutthroat females and proved to be fully fertile.

It is reasonable to assume that during the evolution of rainbow and cutthroat trouts in coastal waters, there has been a trend of specialization acting to divide the "trout niche" between the two species for the most efficient utilization of environmental resources. Hybrids between rainbows and coastal cutthroat probably are at a competitive disadvantage and selectively removed; thus, the effects of hybridization are kept in check in coastal waters where the two species occur sympatrically.

The typical interior cutthroat, however, evolving as the only trout species in its waters, perhaps, developed to utilize a more generalized niche than the coastal cutthroat. When rainbows are introduced into an interior cutthroat population, rapid and complete hybridization is the rule. Some notable exceptions have been discussed, such as the lacustrine specialized S. c. henshawi in Independence Lake, California, and formerly in Lake Tahoe and Pyramid Lake, Nevada, where, despite massive introductions of rainbows, hybridization had little or no effect on the native populations. Similar examples were also noted in populations of S. c. humboldtensis in many headwater tributaries in the Humboldt drainage, Nevada. We may assume that for certain environments, the native cutthroat is more perfectly adapted than the rainbow or hybrids. In such situations, the effects of hybridizations will be minimal.

Origin and Affinities of Western North American Salmo

Jordan (1894b) envisioned the progenitor of the rainbow and cutthroat trout coming from Asia, moving down the North American Pacific coast, invading the Columbia and Snake Rivers, crossing Two Ocean Pass and entering the Missouri, Arkansas, Platte, Colorado, Rio Grande and the waters of the Great Basin. From the Colorado, he believed the trout made it across the Sierra Nevada Mountains into the Kern River system. This, according to Jordan, initiated the separation of cutthroat and rainbows. The trout which crossed the Sierra lost their basibranchial teeth and, as they populated the Pacific drainages, they speciated into present day rainbows.

The separation and speciation of rainbows and cutthroats may have occurred during an interglacial period when the cutthroat progenitor was isolated in Pacific waters from other *Salmo* by a land bridge across the Bering Straits. The *Salmo* which invaded Asia and Europe gave rise to the Atlantic salmon, *Salmo salar*, and, perhaps the brown trout, *Salmo trutta*. The form which re-entered the Pacific during a subsequent flooding of the Bering Straits became the primitive rainbow. By this time, the cutthroat was established in the interior drainages of the United States and the interior populations, except perhaps in the lower Colorado River, never came in contact with other *Salmo* until the recent activities of man. In the interior drainages of western America, geological and climatic changes, and the proclivity of trout for inhabiting the uppermost headwaters, have undoubtedly caused many interchanges of allopatric, diverging populations. The result is the scrambled mosaic of cutthroat trout populations found today in these waters.

In coastal waters it would be expected that hybridization could occur and this eventually may have influenced the present genotypes of coastal rainbows and cutthroats. Neave (1958) suggested that the primitive *S. gairdnerii* gave rise to the genus *Oncorhynchus* in the region of the Japanese Sea in the early Pleistocene.

Due to greater anadromy and perhaps greater tolerance of warmer waters, the primitive rainbow pushed further south than the cutthroat. This early rainbow made it across or around the Baja California peninsula, as discussed by Miller (1950) and into the waters of the lower Colorado River system. Here, a primitive cutthroat was probably native and hybridization may have occurred. Later, isolation allowed various populations to evolve their own peculiarities. Changing climatic conditions essentially isolated the lower Colorado trout from the more advanced cutthroats and rainbows north and west of this area. This early hybridization may explain the origin of what we call the golden trout complex. By a qualitative treatment of the data gathered from the literature, Rounsefell (1962) has made the most recent attempt to establish relationships among North American Salmonidae. Besides meristic characters, various traits of the species life history and ecology were assessed. Although the work involved is impressive, the results appear to be an incongruous mixture of the phyletic and phenetic schools of classification. In commenting on relationships in the genus *Salmo*, Rounsefell (op.cit.:261) states:

> "Of the three species, *salar*, *trutta* and *gairdnerii*, *S. trutta* shows connections with *Salvelinus marstoni*, only a remote affinity with *Salmo salar*, and none with *Salmo gairdnerii*. *Salmo salar* shows equally remote associations with *Salmo trutta*, *Salvelinus aureolus*, and *Salmo gairdneri*. *Salmo gairdneri* is closely linked with *Oncorhynchus* (*kisutch*) on one hand and with *Salvelinus* (*marstoni*) on the other, and shows only a remote affinity with *Salmo salar* and none with *Salmo trutta*".

Consideration of more basic characters such as dentition and osteology makes it difficult to accept the idea that all species of *Salmo* do not have closer affinities to each other than to a subspecies of Arctic char (*marstoni*). A quantitative study based on limited data or small samples which may not be representative of the species, is likely to produce erroneous conclusions regarding affinities. This is especially true when dealing with variable and polytypic species such as salmonids.

Asiatic *Salmo*

Berg (1948) and other authros considered two species of *Salmo* from Kamchatka, *Salmo mykiss* Walbaum and *Salmo penshinensis* Pallas. Through the kind cooperation of Dr. A. N. Svetovidov and his staff at the Zoological Institute of the Academy of Sciences of the USSR at Leningrad, seven specimens of Kamchatkan *Salmo* were examined by the junior author during a visit there in 1960. Two of the specimens were listed as *S. penshinensis* and five as *S. mykiss*. No differences were found to separate them. The specimens of Kamchatkan *Salmo* at Leningrad may represent but a single species and *Salmo mykiss* is the older name. Based on very limited material, Berg (1948) distinguished *S. mykiss* from *S. penshinensis* by morphometric measurements which are known to be notoriously variable in *Salmo*, and by the number of scales from the insertion of the adipose fin to the lateral line. No such differences were apparent in the specimens examined in Leningrad. It appears that *S. mykiss* represents the resident form and *S. penshinensis* the anadromous form of a single species. Nikolsky (1956) reported *S. penshinensis* from the Amur River. This extends the range of *Salmo* on the Asiatic side of the Pacific. A pyloric caeca count of 53 was reported for the Amur specimen.

Jordan and Evermann (1898:2819) believed that *S. mykiss* of Kamchatka was most closely related to the Atlantic salmon, *S. salar*. Actually, *S. mykiss* is probably closer to *S. gairdnerii*. The Kamchatkan *Salmo* is heavily spotted on its sides, head and on its dorsal, adipose and caudal fins, typical of contemporary North American rainbow trout. In *S. salar*, the spotting on the fins is generally absent or much reduced. A red lateral band, similar to the rainbow, is reported for *S mykiss*. A low number of vertebrae in *S. mykiss* (57-59) and the absence of basibranchial teeth suggests it is close to the ancestral type of *S. gairdnerii*.

Behnke (1959) found basibranchial teeth, as in S. clarkii, in a reputed paratype of Salmo formosanus from Formosa. Behnke, Koh and Needham (1962) discussed the possibility of an endemic Formosan Salmo. The number of species of Far Eastern Salmo is unknown, but the only known species, S. mykiss is close to S. gairdnerii. When more is known concerning the Asiatic Salmo, S. mykiss may be considered eventually as a subspecies of the rainbow trout. This would introduce complications in the nomenclature because S. mykiss has priority over S. gairdnerii and S. mykiss was used for many years as the specific name of the cutthroat trout under the mistaken assumption that the cutthroat had a continuous distribution to Kamchatka.

General Comments on Species and Subspecies

There are similarities between the systematics of rainbow and cutthroats and the complexities of the taxonomy of Notropis cornutus and N. chrysocephalus described by Gilbert (1961). These two minnows behave as ~~a~~ good species in some areas, i.e., they occur sympatrically and maintain reproductive isolation, but in other areas they hyridize. Gilbert (op.cit.) cites other examples and criticizes the definition of a species and subspecies given by Mayr, Linsley and Usinger (1953) that "...Species are groups of actually (or potentially) interbreeding populations which are reproductively isolated from other such groups" and subspecies are "...Geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species". Actually, Mayr, Linsley and Usinger were quite aware of exceptions to the above definitions and they would agree that, primarily, the investigator for each particular group should understand the complete situation and then fit the taxonomy to best describe the ~~true~~ facts.

Essentially, we follow the biological species concept stressing reproductive isolation of sympatric forms. Because the cutthroat and rainbow trout under natural conditions maintain reproductive isolation in coastal waters from California to Alaska, we regard them as two valid species. The California golden trout freely hybridize with the rainbow when given the opportunity. Because of this, the golden trout is commonly considered as a subspecies of S. g. aguabonita. Our data indicate that S. g. aguabonita may have closer affinities to interior cutthroat than to coastal rainbows. Thus, placing it as a subspecies of rainbow may obscure its true relationship. We consider it most proper to maintain ~~S. g~~. aguabonita as a full species although recognizing the fact that it is not a "good" biological species.

For subspecies, easily recognized characters resulting from geographic isolation are stressed. The degree of divergence reflected in one or more characters allows a small sample (3-5 specimens) to be recognized from any other subspecies of the species. The characters used, we believe, generally indicate real genetic divergence; however, a subspecies such as S. c. seleniris, the Piute trout, has an obviously distinctive character (no spots on the body) but the genetic change causing its distinction from S. c. henshawi is probably very small. We do not give separate subspecific recognition to anadromous and resident forms of the coastal rainbow and cutthroat. All anadromous and all non-anadromous populations are certainly not monophyletic, but have risen independently many times within the species. No character can consistently separate resident and sea-run populations.

SUMMARY

To clarify systematic problems, evaluate taxonomic characters and to provide a basis for determining the origin and affinities in native, western, North American Salmo, more than 2,000 specimens from 140 samples taken in representative areas from Mexico into Alaska were examined.

Both anadromous and non-anadromous populations of the coastal rainbow are considered as a single taxonomic unit. All coastal rainbow samples considered in this study were coarse scaled, with 120 to 140 scales in the lateral series.

Fine scaled, non-anadromous rainbow trout populations that are native to the upper Frazer, Columbia, Sacramento and Kern river systems, possess some cutthroat-like characters to varying degrees, suggesting hybridization may have played a role in their speciation.

The recognition of subspecies in the rainbow series is a matter of individual interpretation. The Kern River rainbow, S. g. gilberti, perhaps, best fits most accepted concepts of a subspecies. This trout has more scales and fewer vertebrae than the coastal rainbow and before introductions of hatchery rainbows, apparantly did not intergrade with the coarse scaled coastal form due to isolation of the Kern River. The Kern River rainbows distinctive characters are probably due to influence from the California golden trout, S. aguabonita. Some populations, representing intergrades with aguabonita were named Salmo whitei. S. whitei is considered a synonym of S. g. gilberti.

The fine scaled rainbow native to the upper Sacramento River system, S. g. stonei, exhibits great variation in coloration, spotting and other characters. Some populations are distinctly cutthroat-like. This trout is virtually extinct and the degree of intergradation with the coarse scaled coastal rainbow is not known.

The Kamloops rainbow of the upper Frazer and Columbia river systems, apparantly, fully intergrades with the coastal rainbow and does not make a "good" subspecies. Individual preference, however, may wish to place greater emphasis on the extreme types rather than on the intergrades.

The royal silver trout of Lake Tahoe is probably based, at least in part, on hybrids between the hatchery rainbow and the native cutthroat in Lake Tahoe, *S. clarkii henshawi*.

The cutthroat series consists of a coastal form, considered as a single taxonomic unit, *Salmo clarkii clarkii*, and the interior cutthroat made up of a number of subspecies.

The black-spotted or Yellowstone cutthroat trout, *S. c. lewisi*, may be considered as the typical interior cutthroat. The great variability of *S. c. lewisi* fully covers the cutthroat of the Colorado and Rio Grande river systems and most of the Bonneville basin. Therefore, *S. c. pleuriticus*, *S. c. virginalis* and *S. c. utah* are considered synonyms of *S. c. lewisi*.

The greenback trout, *S. c. stomias* of the Arkansas and Platte river systems in Colorado is regarded as a valid subspecies. They form the finest scaled group in the genus *Salmo*.

The Lahontan cutthroat trout, *S. c. henshawi*, endemic to the Lahontan basin of California and Nevada, has more gillrakers than any other group of cutthroat or rainbow trout.

The cutthroat native to the Humboldt River drainage in the Lahontan Basin, differs from *S. c. henshawi* by having fewer gillrakers and scales. This trout is named as a new subspecies, *S. c. humboldtensis*.

Evidence is presented that the cutthroat, native to the western Bonneville basin, may have closer affinities to *S. c. humboldtensis* than to the *S. c. lewisi* native to the rest of the Bonneville basin.

The Piute trout, S. c. seleniris, is identical to S. c. henshawi except for a complete absence of spots on the body.

Collections from desiccating basins north of the Lahontan drainage may represent undescribed subspecies. Some of these samples cannot yet definitely be assigned to either the cutthroat or rainbow series. They may have had their origin in Pluvial or Postpluvial times from hybridization between the two species.

Distinctive populations sharing a number of characters are native to certain waters of the lower Colorado River drainage in Arizona and New Mexico, tributaries of the Kern River, California and the Rio Verde, Rio Sinaloa and Rio Culiacan river systems in Mexico. These trout are grouped as the golden trout complex. A common origin is hypothesized and a tentative scheme of classification is presented.

Salmo mykiss, the only known Salmo native to the Asiatic side of the Pacific Ocean is close to S. gairdnerii.

Table summarizes our views on the systematic arrangement of western North American Salmo.

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Table . Summary of the Systematic Status of Western North American Salmo Forms Recognized by Jordan, Evermann and Clark (1930), Miller (1950) and Distinctive Groups Reported in This Paper.

Names, Author and Range	Proposed Status	Comments
RAINBOW SERIES		
Salmo gairdnerii Richardson Coastal rainbow or steelhead. Rio del Presidio, Mexico to Kuskokwim R., Alaska.		All coastal rainbows, both anadromous and non-anadromous populations are considered a single taxonomic unit. All samples examined may be considered as coarse scaled rainbows, typically having 120 to 140 scales in the lateral series.
S. irideus Gibbons. Rainbow trout, coast rainbow. Range as above.	Snyonym of S. gairdnerii	Commonly used as designation for non-anadromous coastal rainbow. Actually, irideus was probably based on a young steelhead from San Leandro Creek, tributary to San Francisco Bay, California
S. g. stonei Jordan. No-shee trout or Shasta rainbow Upper Sacramento R., Calif.	Provisionally retained as subspecies	A distinctive rainbow trout with some cutthroat-like characters; was once widespread in the upper Sacramento River system; variability among populations is great and the amount of intergradation with the coarse scaled coastal rainbow is not known.
S. g. shasta Jordan Shasta rainbow, McCloud River rainbow McCloud River, Calif.	Synonym of S. g. stonei	The fine scaled non-anadromous rainbow in the McCloud River provided the type material from which both stonei and shasta were named. S. g. stonei has page priority. The original hatchery rainbow from the McCloud River was probably taken mostly from steelhead stock and not the resident trout as commonly believed.
S. aquilarum Snyder Eagle Lake rainbow Eagle Lake, Calif.	Not a valid subspecies	No real distinguishing characters; probably derived from upper Sacramento River rainbow and could be considered synonym of stonei. Introductions have probably altered original genotype

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Names, Author and Range	Proposed Status	Comments
RAINBOW SERIES--Continued		
S. g. gilberti Jordan Kern River rainbow Kern River, Calif.	A valid subspecies	A distinctive fine scaled rainbow with some golden trout (S. aguabonita) influence. Before introductions of hatchery rainbows, this form was isolated in Kern drainage. Now pure populations are almost extinct.
S. whitei Evermann Kern R. tributaries	Synonym of gilberti	In some Kern R. tributaries, populations of golden colored trout occur. These represent varying degrees of intergradation between S. g. gilberti and S. aguabonita but the meristic characters are closer to gilberti.
S. rosei Jordan and McGregor Rose trout Kern River system	Synonym of gilberti	This trout had its origin from an introduction whose ultimate source was the Little Kern River where "S. whitei" occurred. If whitei is recognized, then rosei would be a synonym of it.
S. newberrii Girard Upper Klamath rainbow Upper Klamath R. drainage, Oregon	Open	The systematics of the native trout of the upper Klamath basin is not known. The other fish species have Great Basin origins and the original trout may have its affinities to the intermediate cutthroat-rainbow populations once native to contiguous desiccating basins.
S. regalis Snyder Royal silver trout of Lake Tahoe, Calif-Nev.	Probably based on rainbow-cutthroat hybrids	Finding basibranchial teeth in three of the four type specimens of this predominantly rainbow-like trout and the fact that hybrids were introduced into Lake Tahoe for a number of years prior to the description of regalis, makes it a highly doubtful form.
S. smaragdus Snyder Emerald Trout Pyramid Lake, Nevada	Synonym of S. g. gairdnerii	No characters suggest distinction from typical coarse scaled rainbow. Probably based on an introduced gairdnerii. If rainbows were native to Lahontan basin, they would not be expected to be restricted to Lake Tahoe and Pyramid Lake.

Names, Author and Range	Proposed Status	Comments
Rainbow Series--Continued		
S. nelsoni Evermann Lower California trout Santo Domingo R.,Baja Calif.	Synonym of S. g. gairdnerii	No differentiating characters from typical coastal rainbow
S. g. beardslei Jordan and Seale Blueback trout Crescent Lake, Washington	Synonym of S. g. gairdnerii	No evidence of distinction from S. g. gairdnerii.
Oncorhynchus kamloops Jordan Kamloops trout Frazer and Columbia river systems	Not a "good" subspecies and may be considered a synonym of S. g. gairdnerii, but this depends on individual point of view, whether to stress the broad intergration or emphasize the extreme types.	In upper Frazer and Columbia river systems a fine scaled non-anadromous rainbow is widely distributed. Intergradation, however, with the coarse-scaled, coastal rainbow is complete.
S. kamloops whitehousei Dymond Mountain Kamloops trout Lakes in Selkirk Mtns., Columbia R. system, B.C.	Synonym of S. gairdnerii	This would represent a good subspecies if intergradation is not complete.
S. gibbsii Suckley Middle Columbia R. system	Synonym of S. gairdnerii	Based on non-anadromous rainbows of uncertain affinities

Table -- Summary of the Systematic Status...--Continued

Names, Author and Range	Proposed Status	Comments
DISTINCTIVE, UNNAMED FORMS		
Malheur desiccating basin Malheur County, Oregon	Probable endemic subspecies of S. gairdnerii.	Four specimens collected from Silvies River, tributary to Malheur Lake in 1904, have 146 to 154 scales in the lateral series and more vertebrae (64-66) than any other rainbow sample examined. It is not known if this trout still exists.
// CUTTHROAT SERIES		
S. clarkii Richardson. Coastal cutthroat Eel R., Calif. to Prince William Sound, Alaska	A valid species and subspecies	As with the coastal rainbow, we consider the coastal cutthroat to represent a single taxonomic unit.
S. c. jordani Meek Spotted trout L. Sutherland, Washington	Synonym of S. c. clarkii.	Typical coastal cutthroat.
S. c. declivifrons Meek Salmon trout Lake Sutherland, Washington	Synonym of S. c. clarkii	Apparently from same population from which jordani was named. No valid distinctions from S. c. clarkii.
S. gairdnerii crescentis Jordan and Beardslee Speckled trout Crescent Lake, Washington	Synonym of S. c. clarkii.	No real distinction from S. c. clarkii.
S. bathoeceter Meek Longheaded trout Crescent Lake, Washington	Synonym of S. c. clarkii	Evidently based on specimens of "crescentis" caught in deeper waters of Crescent Lake.

Names, Author and Range	Proposed Status	Comments
CUTTHROAT SERIES--Continued		
S. c. lewisi Girard Black-spotted or Yellowstone cutthroat Widely distributed in interior waters.	A valid subspecies	Variable, polytypic subspecies. The range of variation includes most of the interior cutthroat trout.
S. pleuriticus Cope Colorado R. cutthroat	Synonym of S c. lewisi	The variability found in lewisi from the Missouri and Columbia river systems fully covers the native cutthroat described from the Colorado, Rio Grande and most of the Bonneville basins.
Salar virginalis Girard Rio Grande cutthroat	Synonym of S. c. lewisi.	
S. utah Suckley Bonneville cutthroat	Synonym of S. c. lewisi	
S. purpuratus var. bouvieri Bendire. Waha L., Idaho, Snake R. drainage.	Synonym of S. c. lewisi.	Represented a population of large-spotted lewisi. Now extinct in Waha L.
S. eremogenes Evermann and Nichols. Crab Creek, Washington	Synonym of S. c. lewisi	Collected from a disrupted part of Columbia R. basin. No evidence for distinction from lewisi in surrounding areas.
S. mykiss macdonaldi Jordan and Evermann. Yellowfin trout Twin Lakes, Colorado	Probable synonym of S. c. lewisi.	Apparently identical to cutthroat of upper Colorado river system. Once occurred sympatrically in Twin Lakes with S. c. stomias. Now both are extinct in Twin Lakes.

Table -- Summary of the Systematic Status...--Continue

Names, Author and Range	Proposed Status	Comments
CUTTHROAT SERIES--Continued		
S. c. alpestris Dymond Mountain cutthroat Certain streams in Frazer and Columbia river systems in British Columbia	Open	Only four specimens examined. Typical of S. c. lewisi except the paratypes from Isaacs Creek have 145 to 150 pores in the lateral line. This is more than any other specimen examined during this study. It is not known if the Isaacs Creek sample is representative of all alpestris.
S. stomias Cope Greenback trout Arkansas and Platte rivers, Colorado	Valid subspecies of S. c. stomias	Typically with more scales (180-210) and larger spots than any other group of Salmo. Once occurred sympatrically with cutthroat of Colorado River origin in Twin Lakes, Colorado.
S. henshawi Gill and Jordan Lahontan cutthroat Lahontan Basin, Nev.& Calif.	Valid subspecies of S. c. henshawi	More gillrakers than any other group of Salmo (typically 22 to 27). Perhaps the most lacustrine adapted cutthroat.
S. tahoensis Jordan and Evermann. The silver trout of Lake Tahoe	Synonym of S. c. henshawi	Probably based on a large, silvery specimen of henshawi.
S. evermanni Jordan and Grinnell. San Gorgonio trout Santa Ana River, Calif.	Synonym of S. c. henshawi	Derived from intorductions of henshawi from L. Tahoe into the Santa Ana River

Table . Summary of the Systematic Status...--continued

Names, Author and Range	Proposed Status	Comments
CUTTHROAT SERIES--Continued		
S. seleniris Snyder Piute trout Silver King Creek, above Llewellyn Falls, Lahontan basin, California	Valid subspecies of S. c. seleniris.	Distinguished by a complete absence of spots on the body, otherwise identical to S. c. henshawi.
S. c. humboldtensis Humboldt R. system, Lahontan basin, Nevada	New subspecies	Resembles henshawi but typically with three fewer gillrakers and fewer scales. Some populations are as coarse scaled as the typical coastal rainbow.
DISTINCTIVE UNNAMED FORMS		
Alvord basin, Nev.,Oregon	Probably Willow Creek population represents a new subspecies of cutthroat.	Two collections examined from this desiccating basin revealed one sample similar to S. c. henshawi; the other from Willow Creek, Harney Co., Ore., appears intermediate between lewisi and henshawi and probably represents an endemic subspecies.
Chewaucan desiccating basin, Lake Co., Oregon	Probably represents an endemic subspecies, but cannot be definitely assigned to cutthroat series.	A small sample from the Chewaucan R., collected in 1904, chave characters intermediate between cutthroat and rainbows. One of 6 specimens has a single basibranchial tooth. High gillraker number (20-23) suggests lacustrine influence in their evolution.
Goose Lake basin, desiccating basin, Oregon, California	As above	Similar to Chewaucan sample but none of six specimens have basibranchial teeth. Gillrakers 21-24.
Fort Rock Basin, Lake Co. Oregon	Probable endemic subspecies of cutthroat	A sample from Buck Creek, trib. to Silver L., has affinities to above two samples but four of six specimens have basibranchial teeth and gillrakers number 19-22. This form and the two above may now be extinct.

Table --- Summary of the Systematic Status...--continued

Names, Author and Range	Proposed Status	Comments
GOLDEN TROUT SERIES		
S. mykiss aguabonita Jordon California golden trout S.Fork Kern R. and Golden Trout Creek	Provisionally retained as a full species, S. aguabonita	Although it freely hybridizes with the rainbow trout, aguabonita's distinctive characters indicate close affinities to the forms mentioned below and suggests a third, intermediate line of western North American Salmo evolution, distinct from the cutthroat and rainbow series.
S. gilae Miller The Gila trout Diamond Creek, N. Mexico	Provisionally retained	Probably once widespread in the Gila river system, this golden-like trout is now almost extinct. The Rio Yaqui, Mexico, has trout somewhat intermediate between gilae and chrysogaster.
S. chrysogaster Needham and Gard Mexican golden trout Rio Verde, Rio Sinaloa and Rio Culiacan systems, Mex.	Provisionally retained	This trout has a number of distinctive characters such as the lowest vertebral and pyloric caecal numbers found in any Salmo.
Arizona golden trout unnamed White R., Apache Co., Arizona	Undetermined status	This trout, also in the Gila river system, is quite distinct from S. gilae in its spotting pattern. It possesses an extremely long dorsal fin and appears close to aguabonita in most characters.

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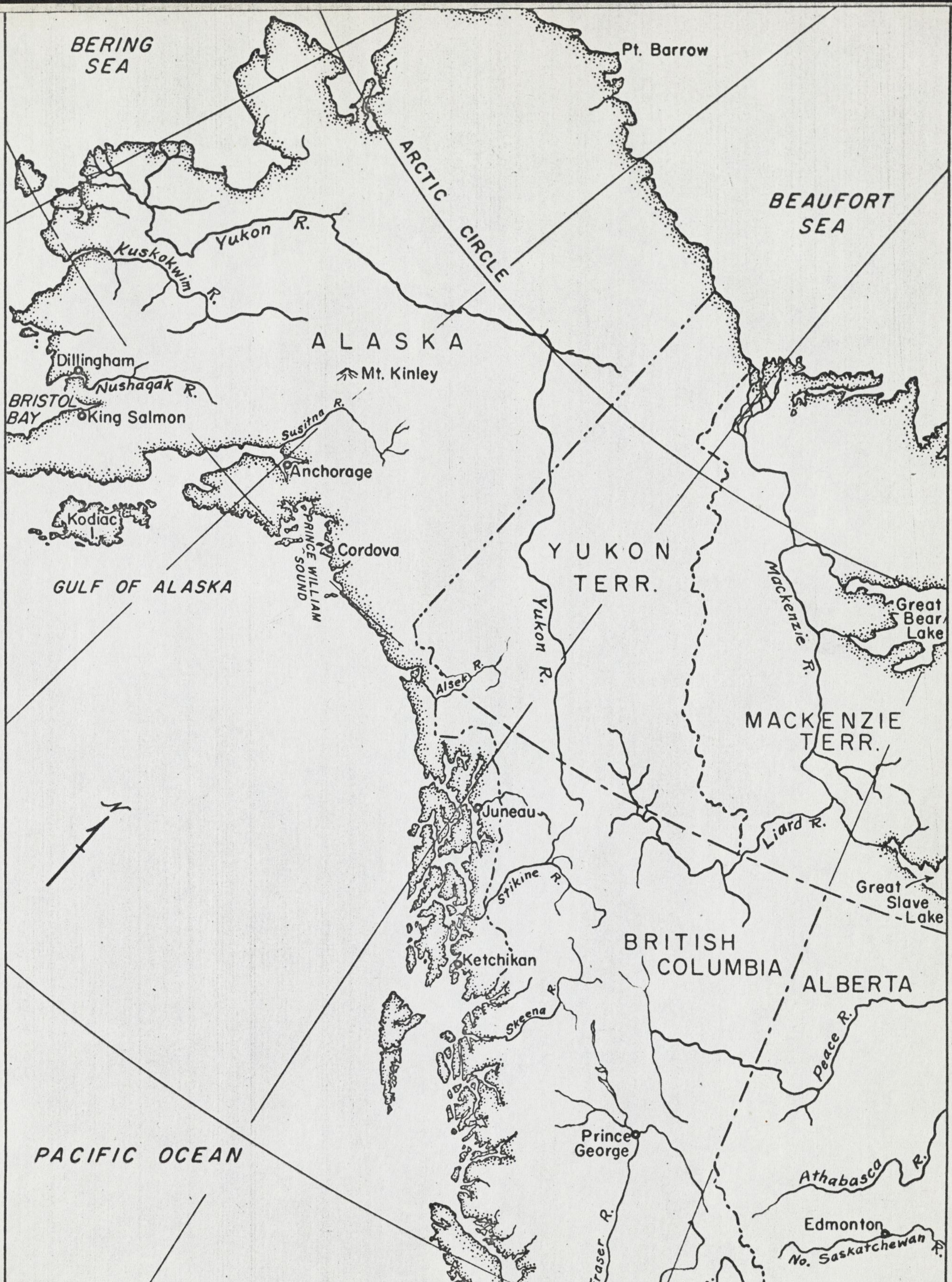
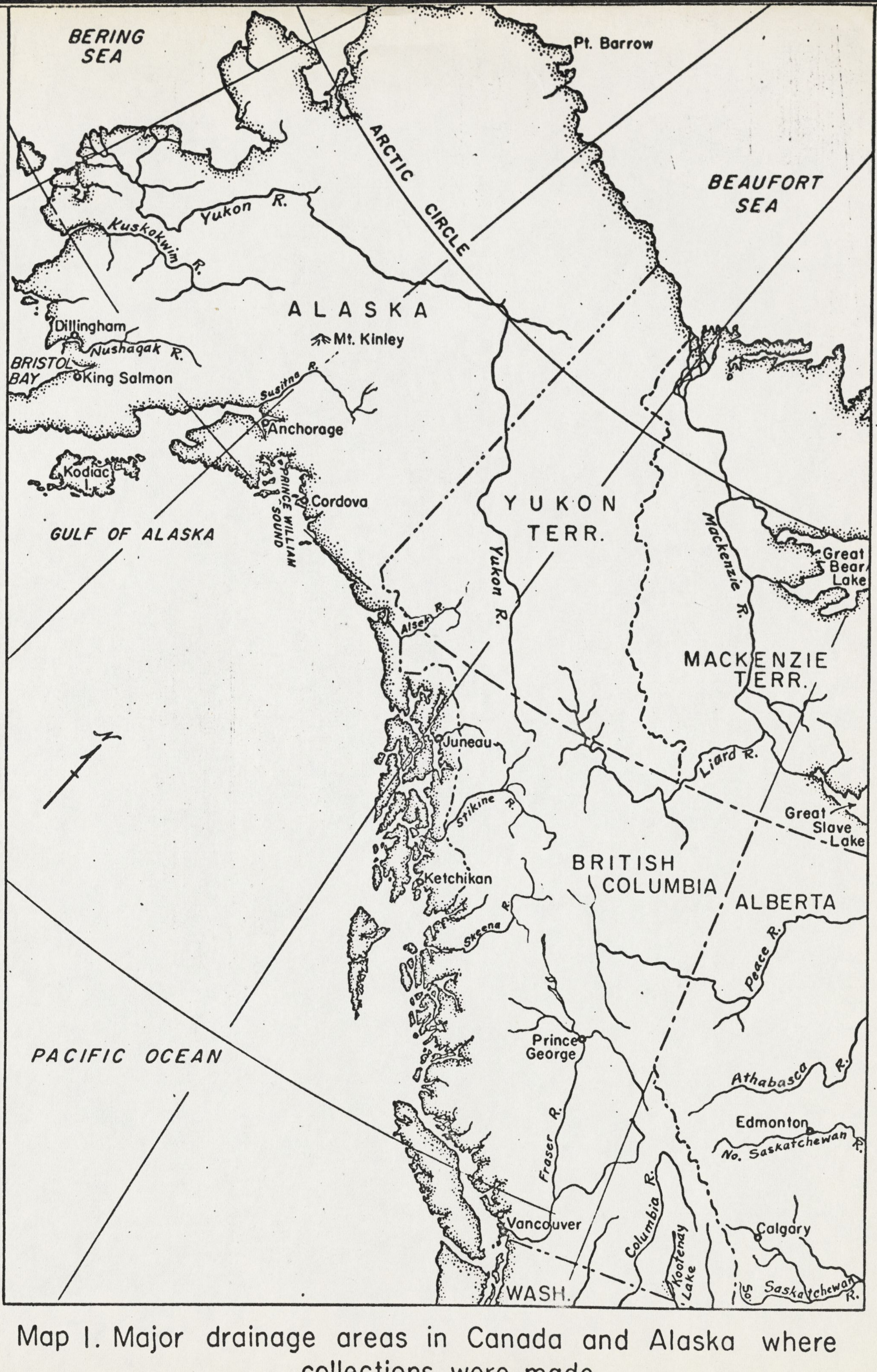


Map I. Major drainage areas in Canada and Alaska where collections were made.



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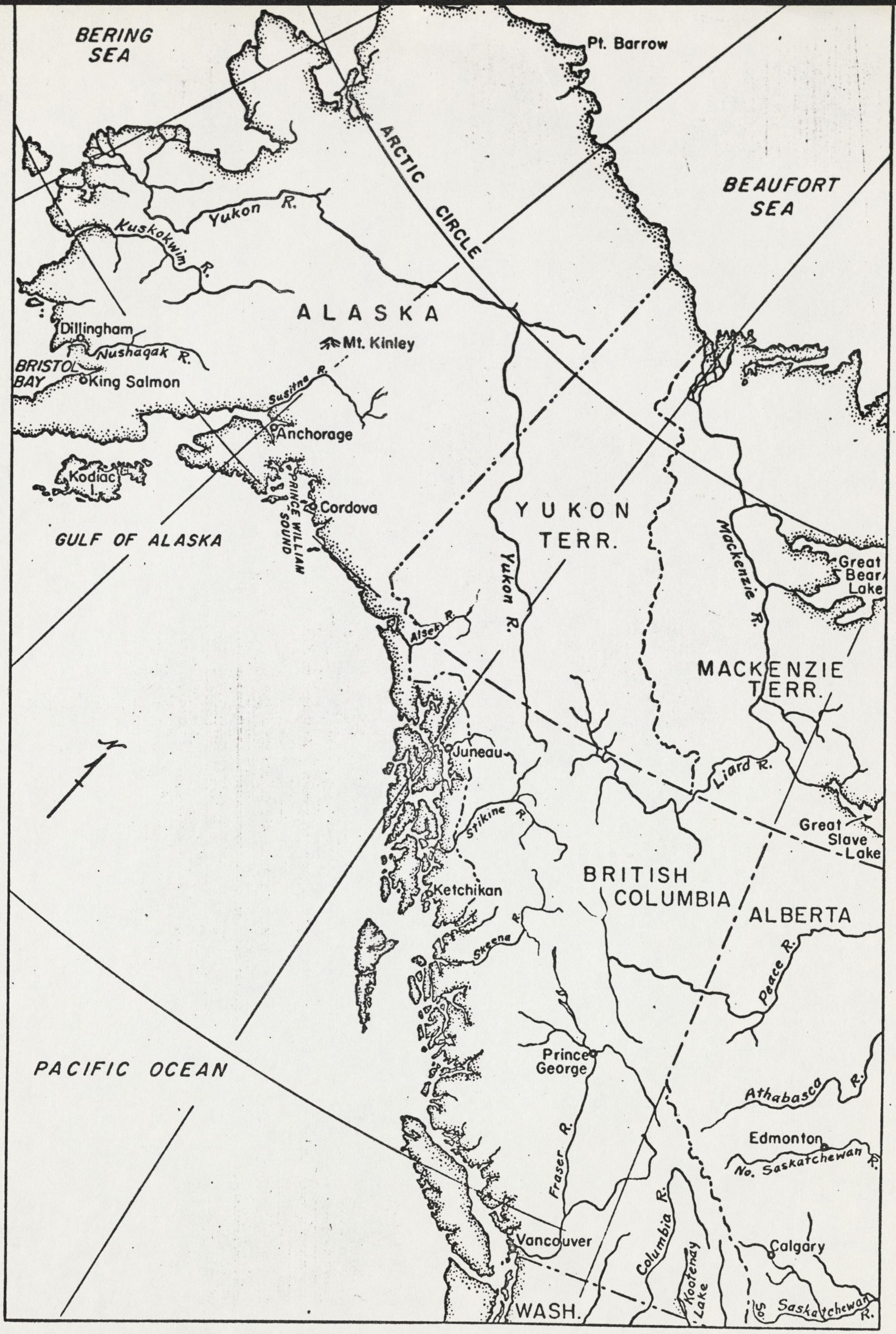

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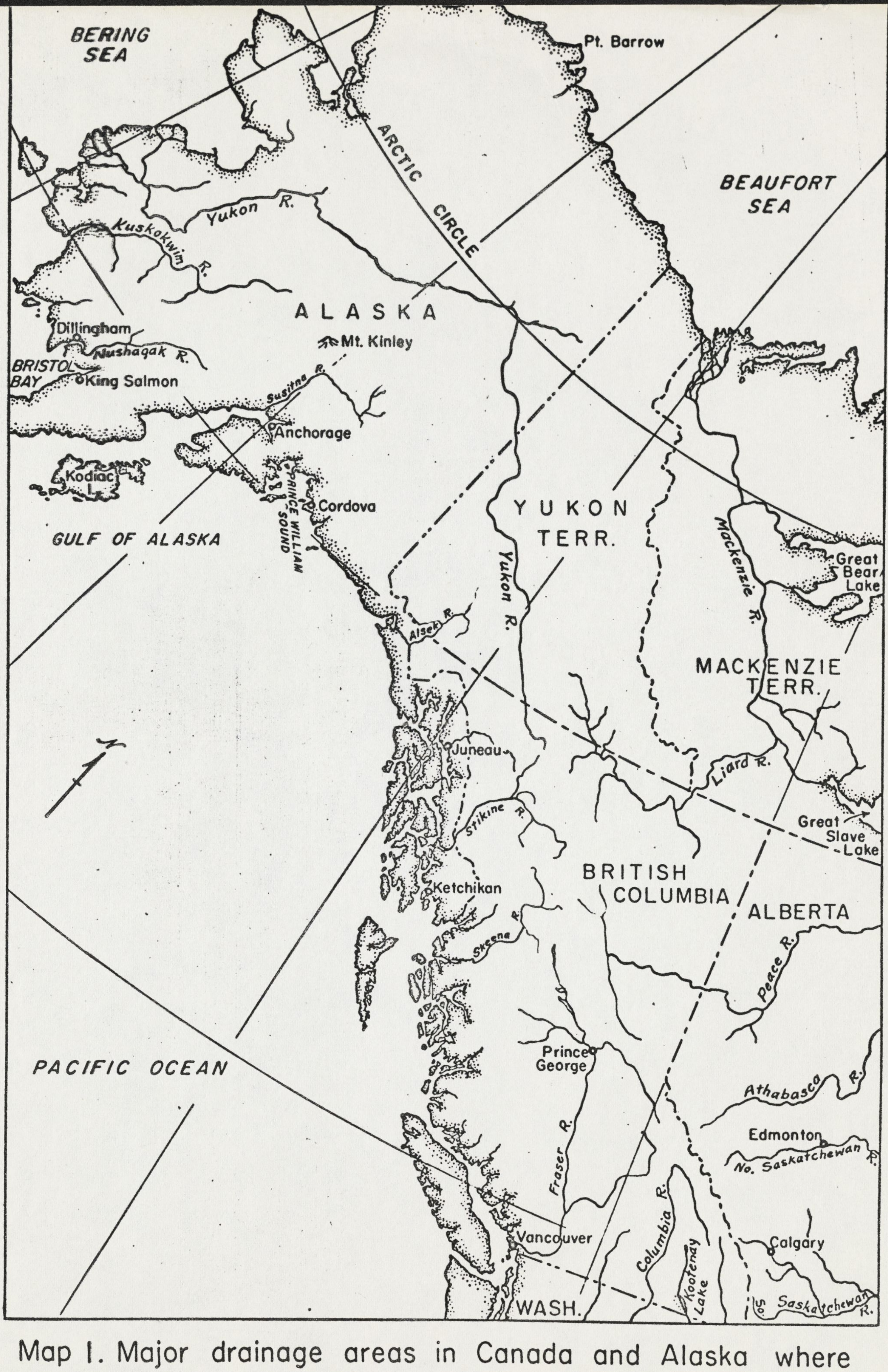

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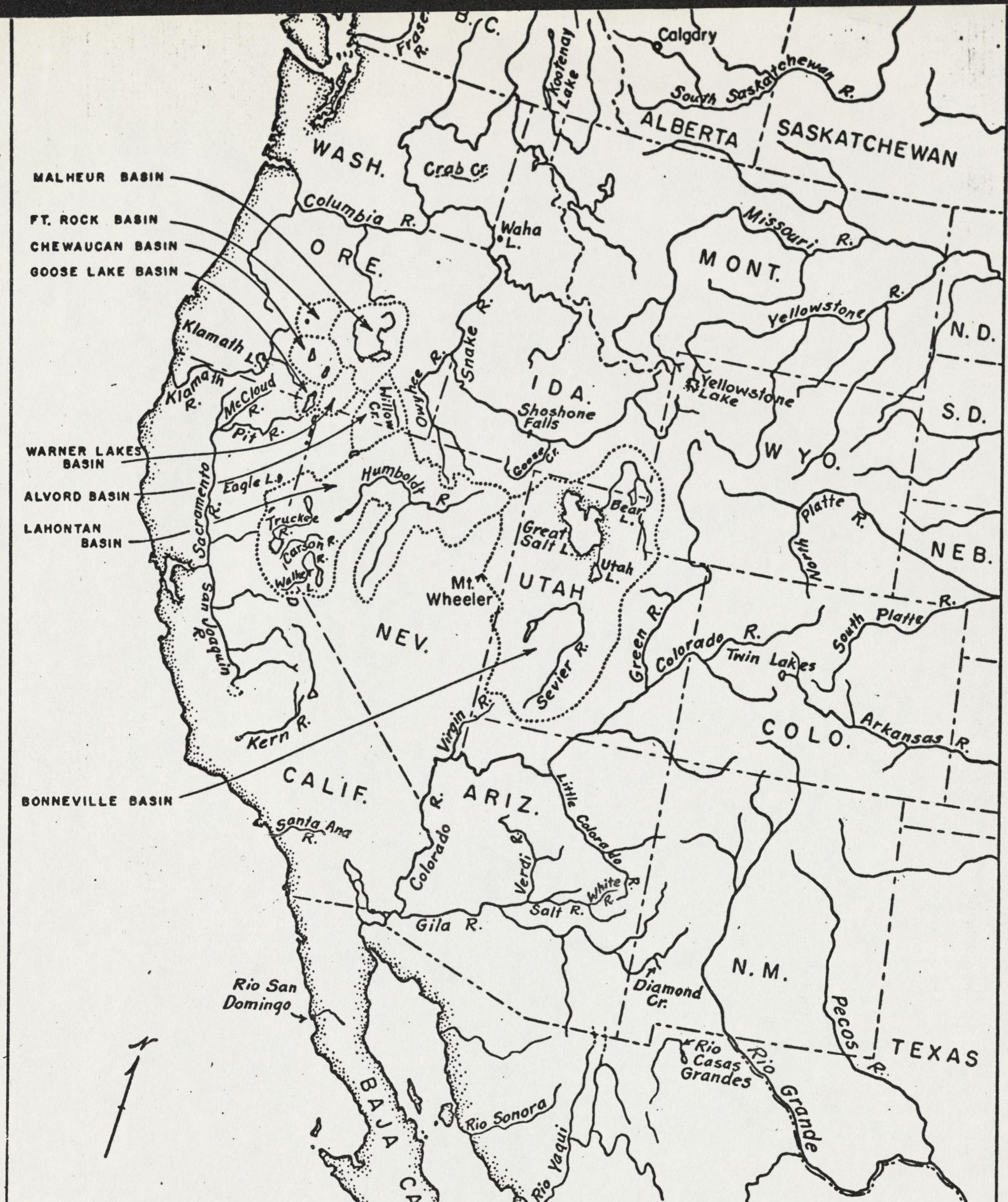

Map 2. Major drainage areas in the United States and Mexico where collections were made.

Some spotting variations in cutthroat trout.

Fig. 1. Coastal cutthroat, Salmo clarkii clarkii, Long Lake, Alaska. Example of extremely profuse spotting; spots extend onto ventral surface.

Fig. 2. Coastal cutthroat, S. c. clarkii, Herman Creek, Alaska. Moderate spotting.

Fig. 3. Greenback trout, S. c. stomias, Twin Lakes, Colorado (coll. 1889). Typically, with large, roundish spots; spots concentrated on caudal peduncle.

Some spotting variations in cutthroat trout.

Fig. 4. Blackspotted or Yellowstone cutthroat trout, S. c. lewisi, Game Creek, Wyoming; Snake River drainage. Example of small, spotted form with spots profusely distributed on sides of body.

Fig. 5. S. c. lewisi, Goose Creek, Nevada; Snake River drainage. This type of spotting is more typical of lewisi throughout most of its range.

Fig. 6. "S. bouvieri" (synonym of S. c. lewisi), Waha Lake, Idaho. Example of an extremely sparsely spotted form.

Some spotting variations in cutthroat trout.

Fig. 7. S. c. lewisi, Pickle Jar Lake, Alberta, Canada; South Sasketchewan drainage. Small spotted form; typical lewisi distribution of spots.

Fig. 8. S. c. lewisi, Indian Creek, Colorado; Rio Grande drainage. Example of the large-spotted type.

Fig. 9. S. c. lewisi, Pine Valley, Utah, Colorado River drainage. The cutthroat population from which this specimen was taken may have been derived from the Bonneville basin. Colorado River drainage cutthroat have both large-spotted and small-spotted populations.

Some spotting variations in cutthroat trout.

Fig. 10. _S_. _c_. _humboldtensis_, type specimen, South Fork Little Humboldt River, Nevada. Spotting pattern similar to _henshawi_. Parr marks typically narrow and irregular.

Fig. 11. Lahontan cutthroat trout, _S_. _c_. _henshawi_, Independence Lake, California. Typically, with an even distribution of spots on the side of body; no concentration of spots on caudal peduncle.

Fig. 12. Piute trout, _S_. _c_. _seleniris_, Silver King Creek, Lahontan basin, California. Complete absence of spots on body.

Basibranchial Teeth

Fig. 13. Typical arrangement in cutthroat trout. S. c. henshawi, Heenan Lake, California.

Fig. 14. Unusual proliferation of teeth found in population of S. c. henshawi in Independence Lake, California. Note clusters of teeth on hypobranchial segments of gill arch.

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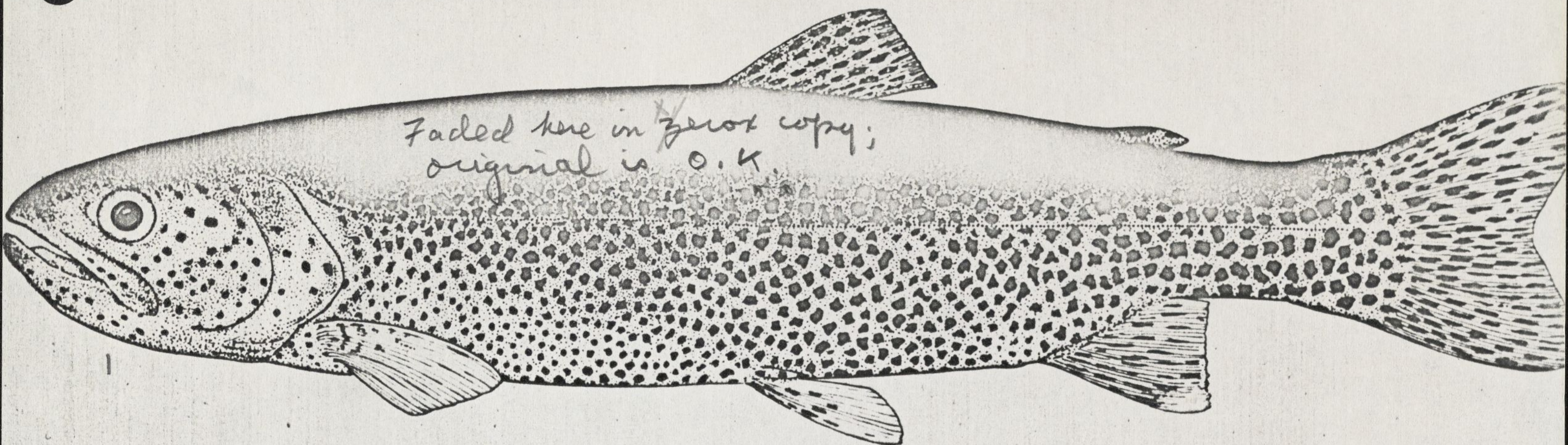

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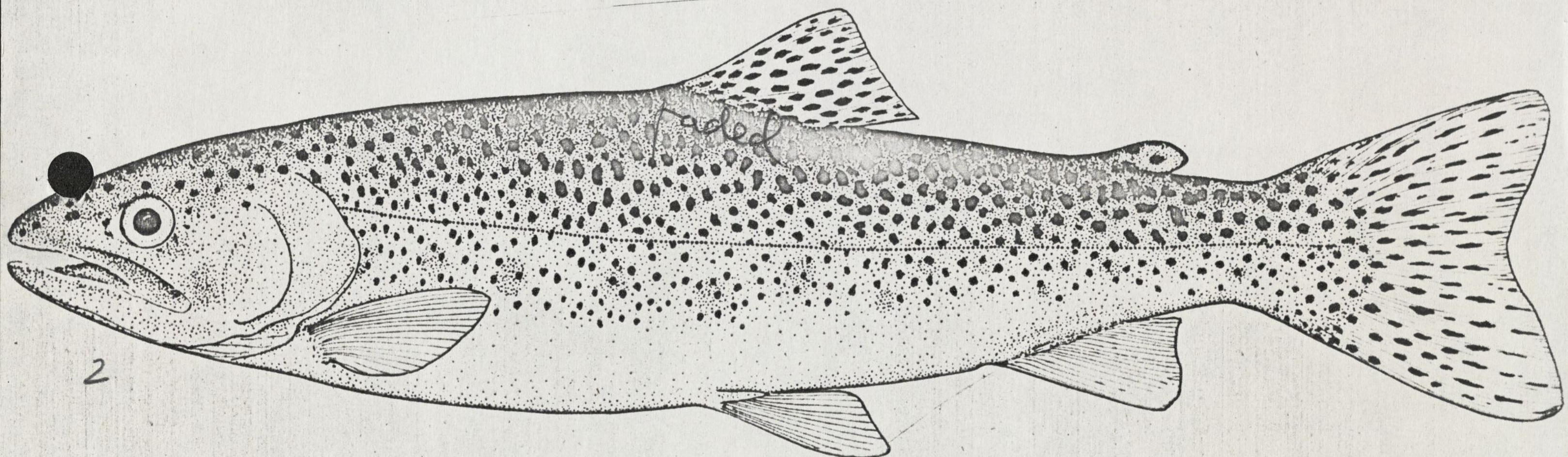

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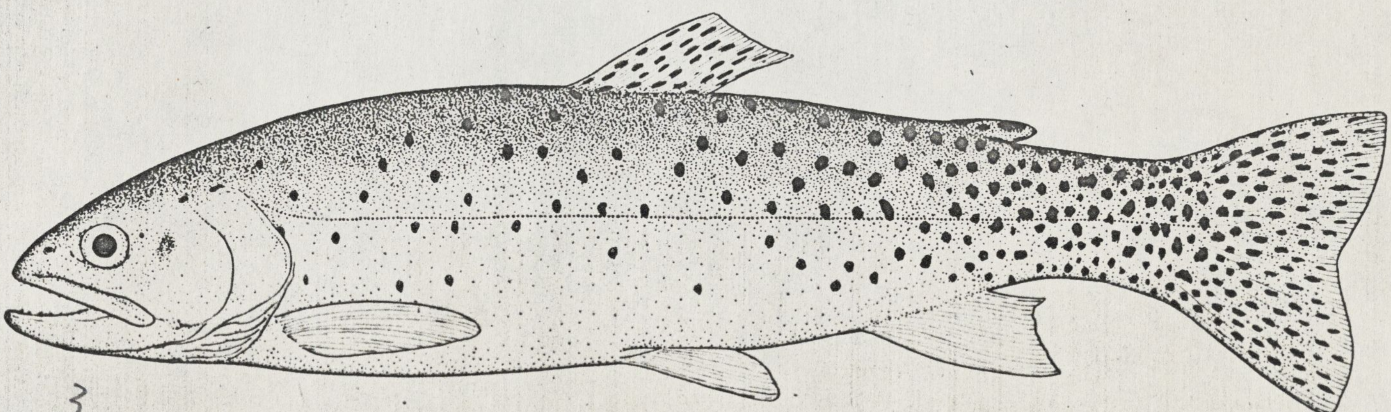

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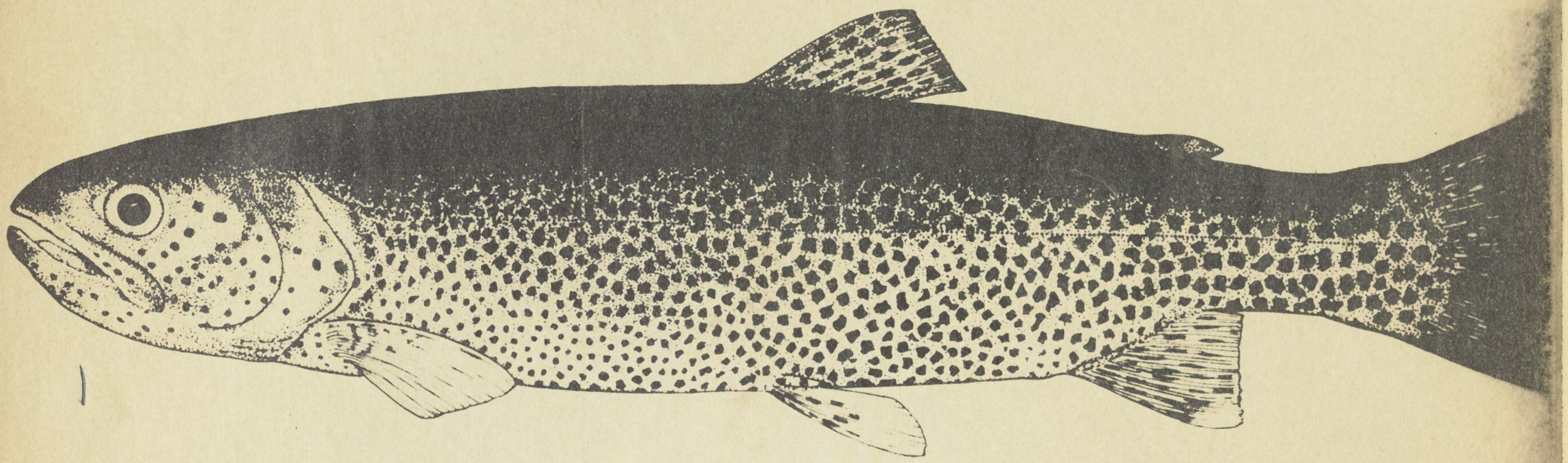

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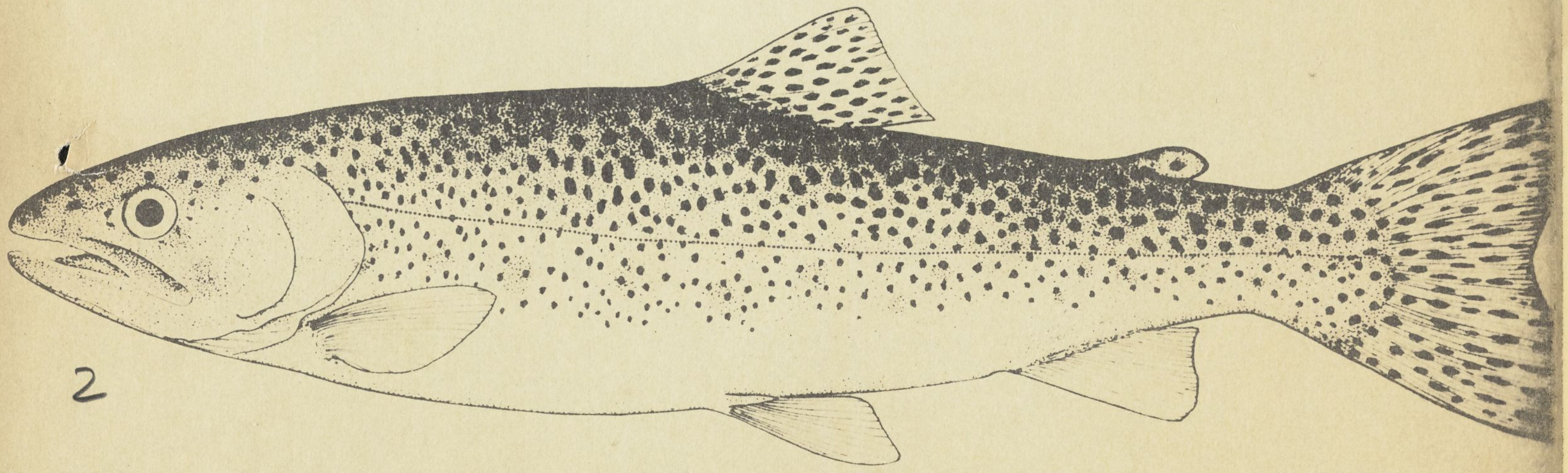

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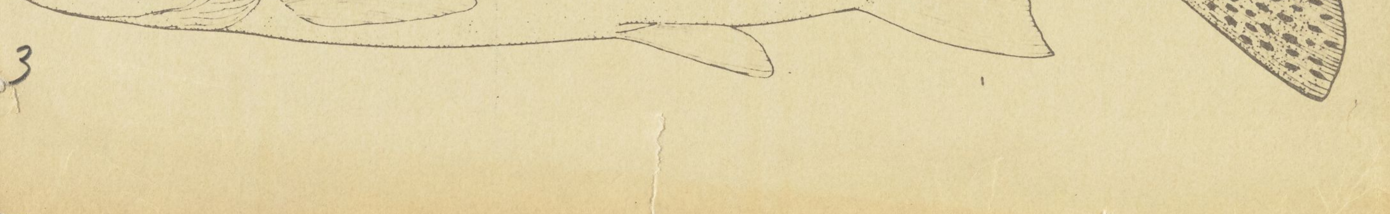

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Some spotting variations in cutthroat trout.

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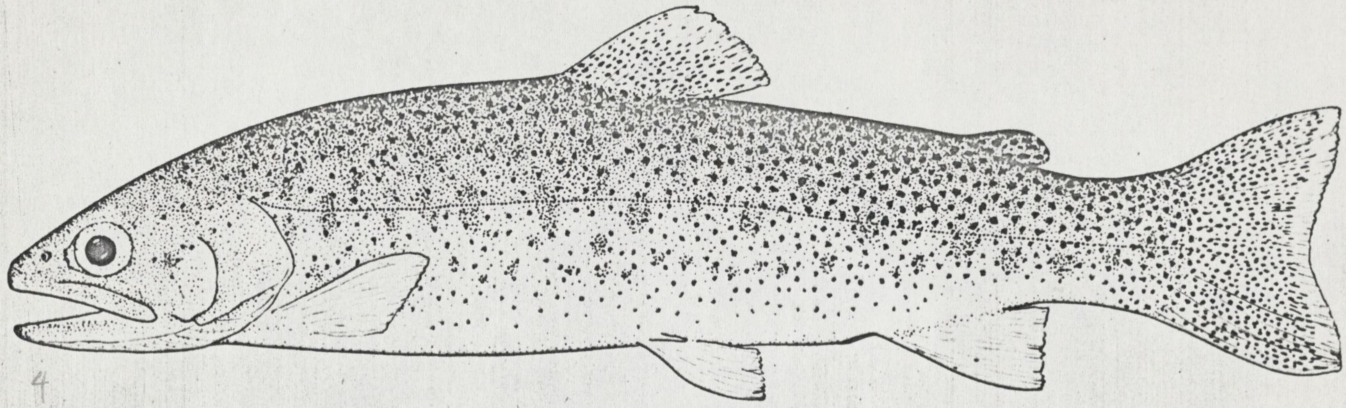

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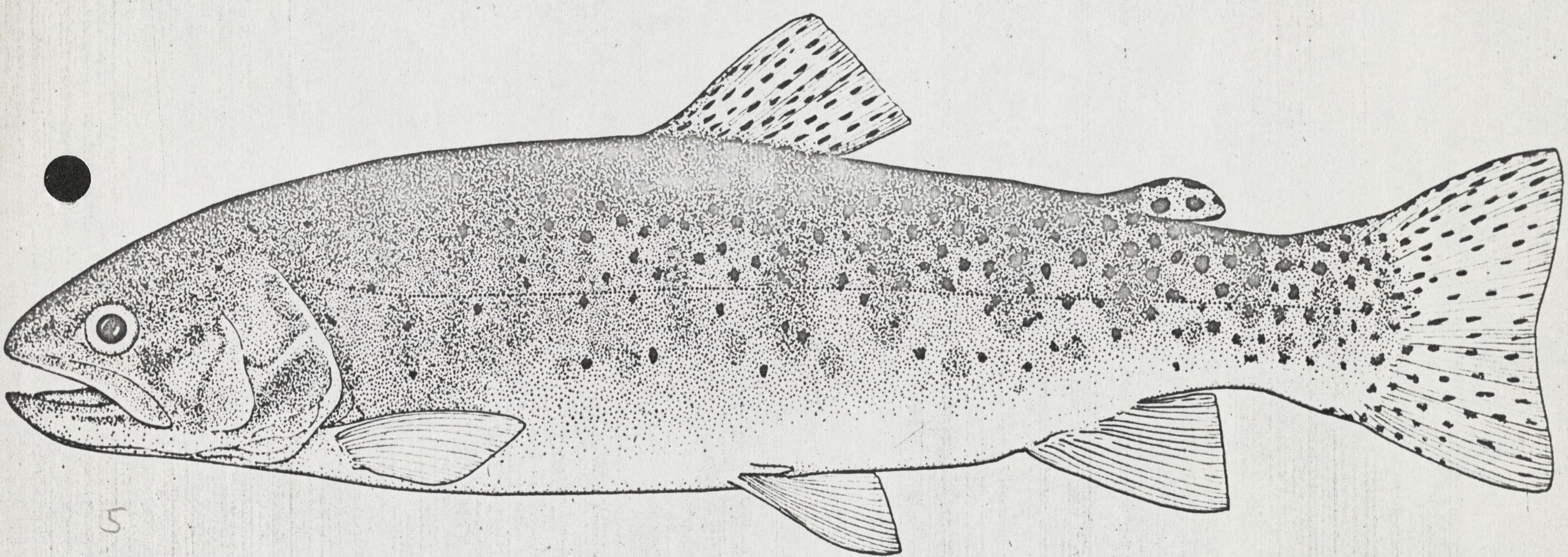

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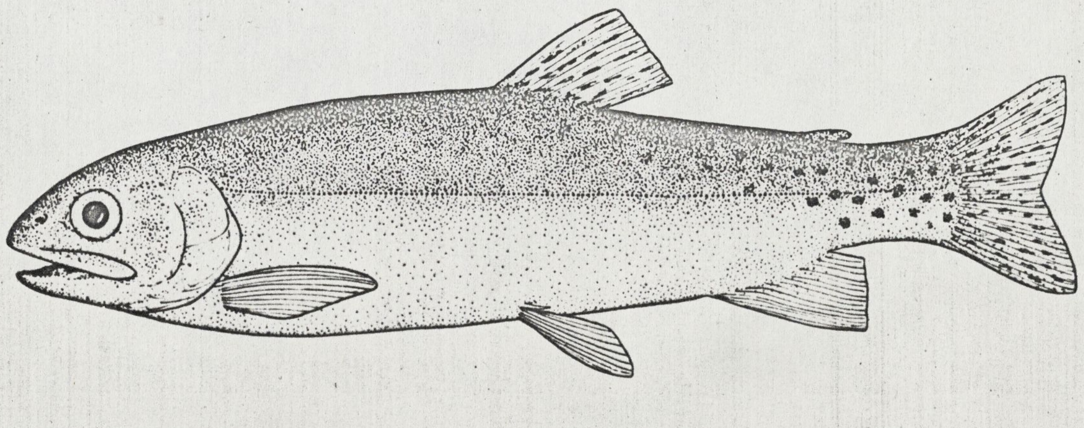

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Basibranchial Teeth

Fig. 13. Typical arrangement in cutthroat trout. _S. c. henshawi_, Heenan Lake, California.

Fig. 14. Unusual proliferation of teeth found in population of _S. c. henshawi_ in Independence Lake, California. Note clusters of teeth on hypobranchial segments of gill arch.

Some spotting variations in cutthroat trout.

Fig. 10. *S*. *c*. *humboldtensis*, type specimen, South Fork Little Humboldt River, Nevada. Spotting pattern similar to *henshawi*. Parr marks typically narrow and irregular.

Fig. 11. Lahontan cutthroat trout, *S*. *c*. *henshawi*, Independence Lake, California. Typically with an even distribution of spots on the side of body; no concentration of spots on caudal peduncle.

Fig. 12. Piute trout, *S*. *c*. *seleniris*, Silver King Creek, Lahontan basin, California. Complete absence of spots on body.

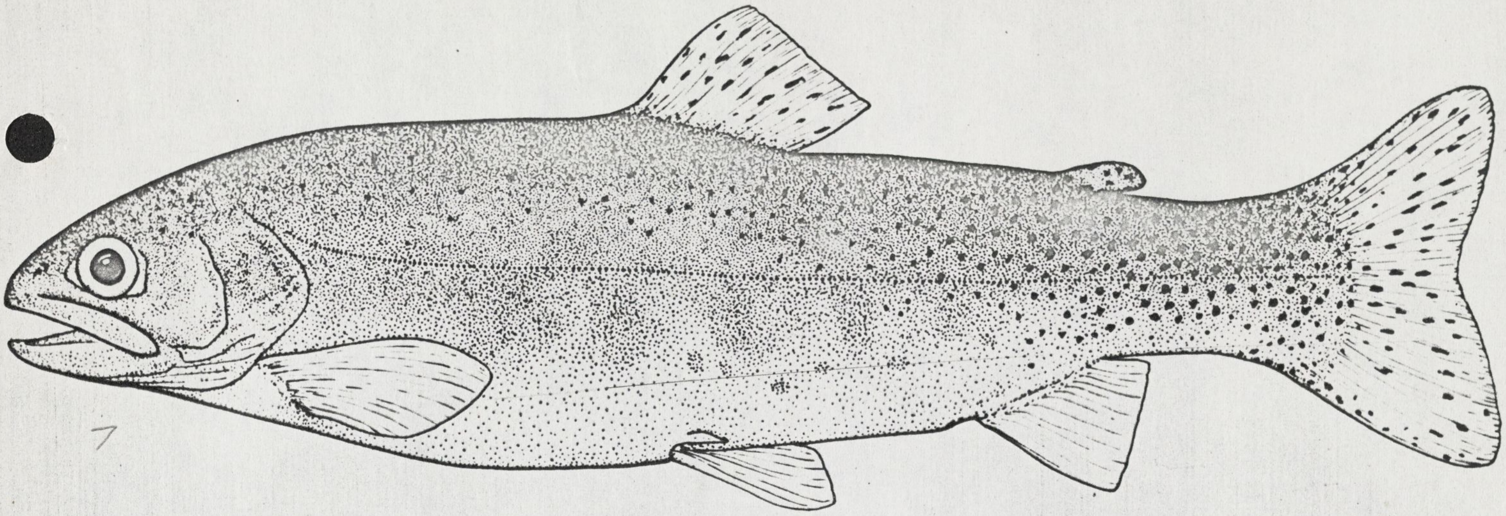
Some spotting variations in cutthroat trout.

Fig. 7. S. c. lewisi, Pickle Jar Lake, Alberta, Canada; South Sasketchewan drainage. Small-spotted form, typical of S. c. lewisi in ~~distribution of spots.~~

Fig. 8. S. c. lewisi, Indian Creek, Colorado; Rio Grande drainage. Example of the large-spotted type.

This is the type I have regarded as a subspecies, S. c. spilurus / or Rio Grande system. R.J.B.

Fig. 9. S. c. lewisi, Pine Valley, Utah, Colorado River drainage. The cutthroat population from which this specimen was taken may have been derived from the Bonneville basin. Colorado River drainage cutthroat have both large-spotted and small-spotted populations.



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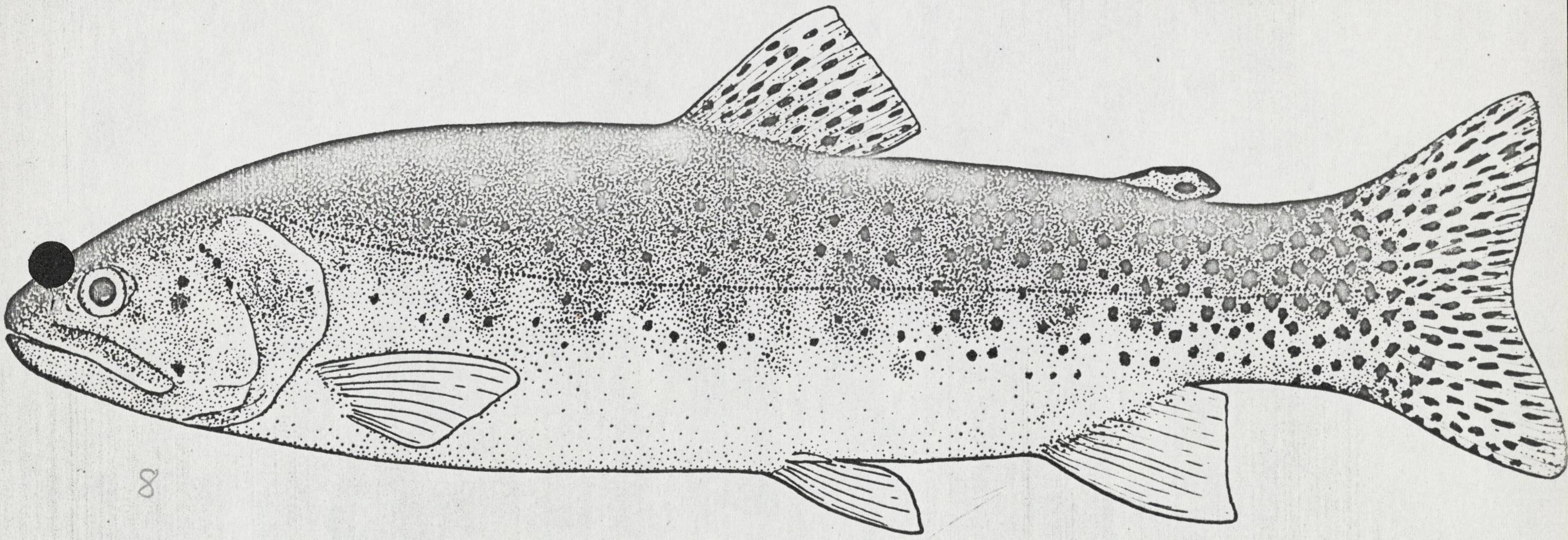

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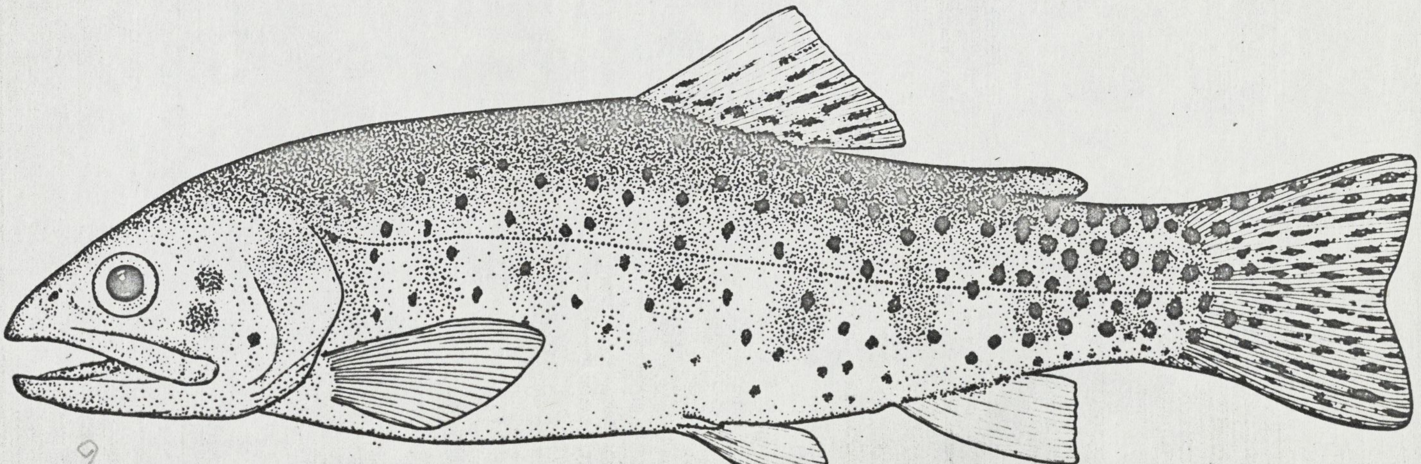

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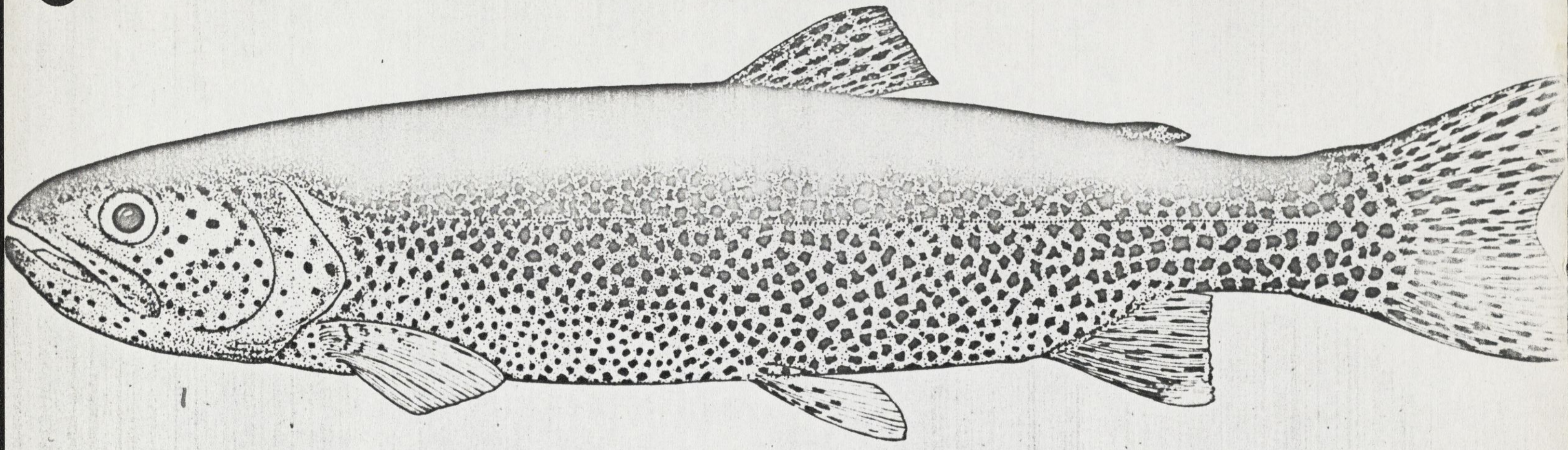

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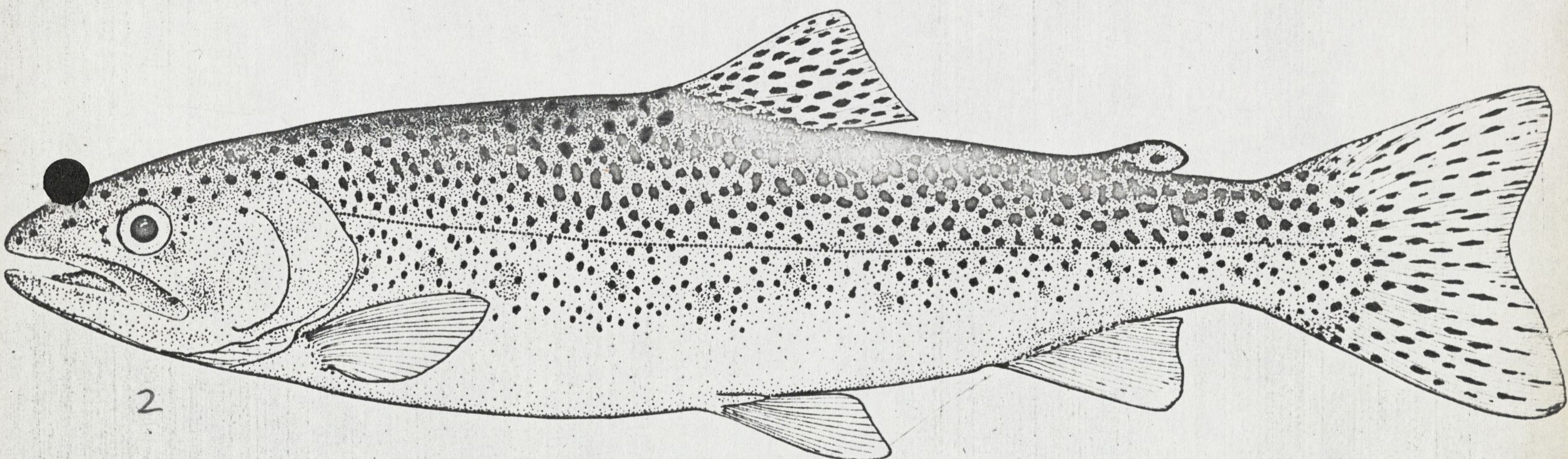

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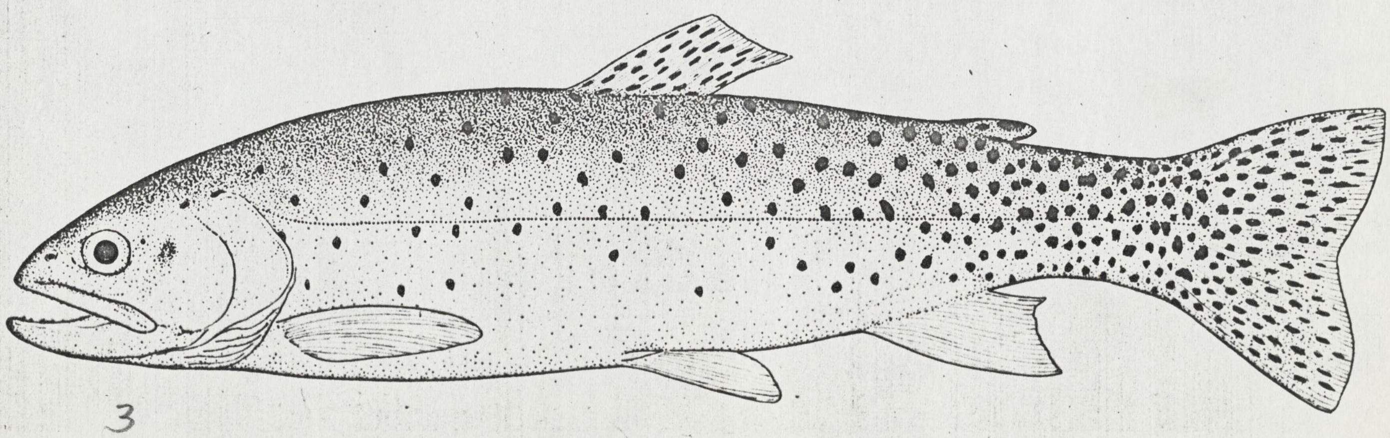

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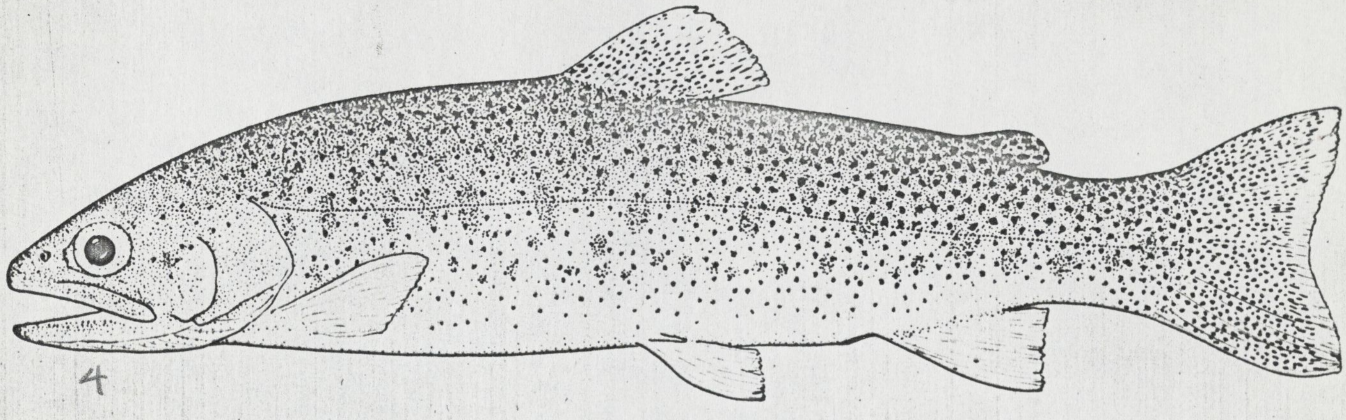

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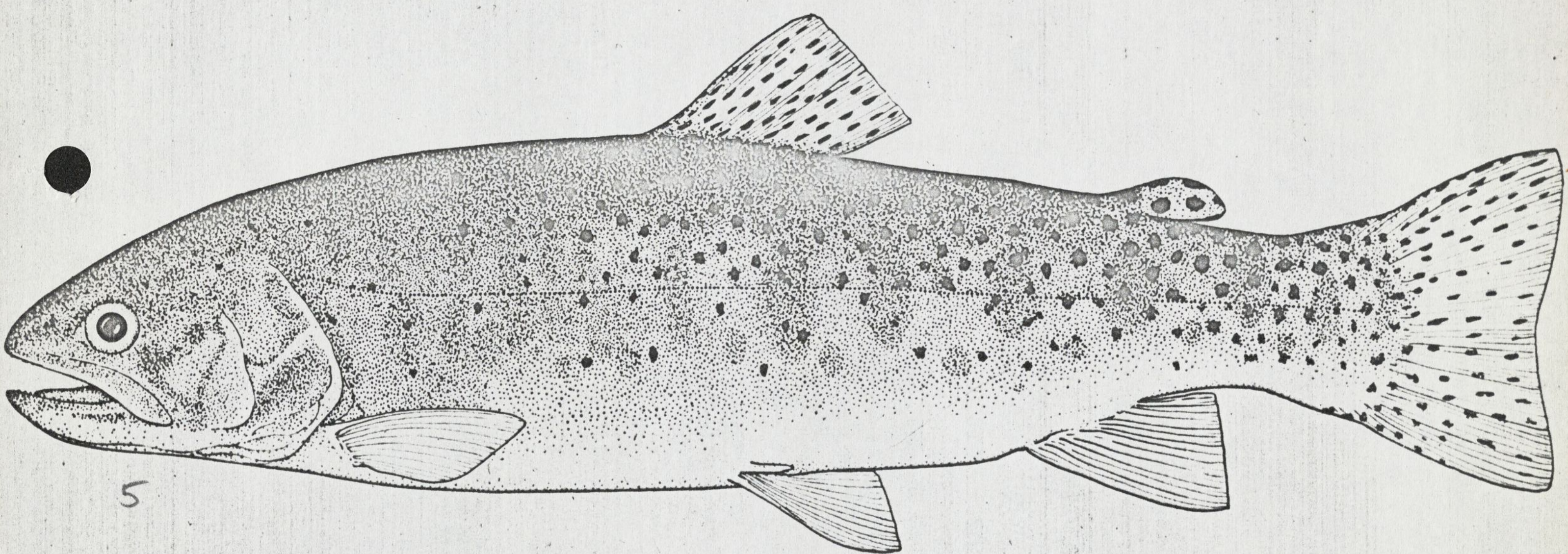

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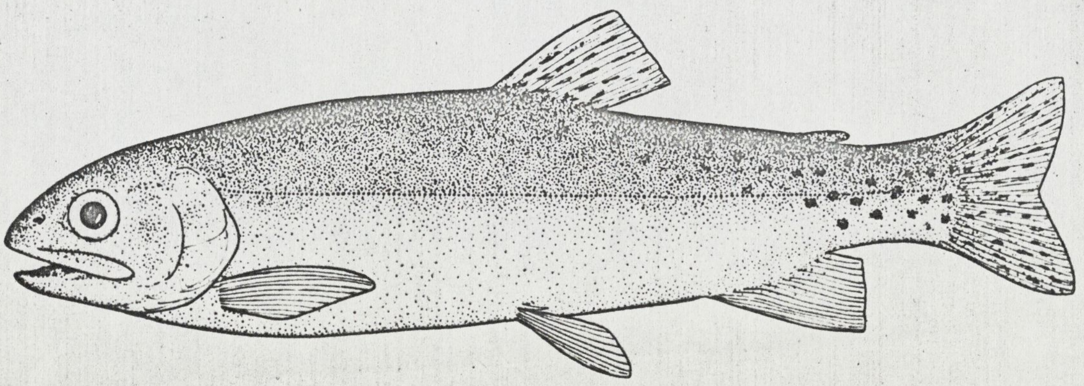

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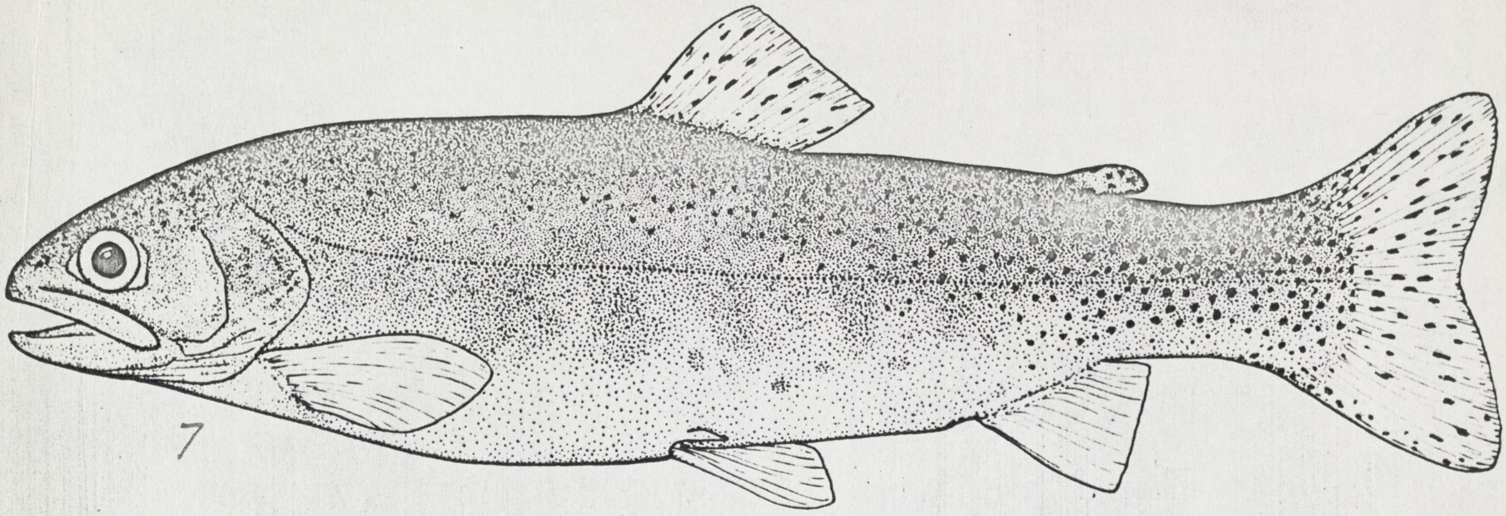

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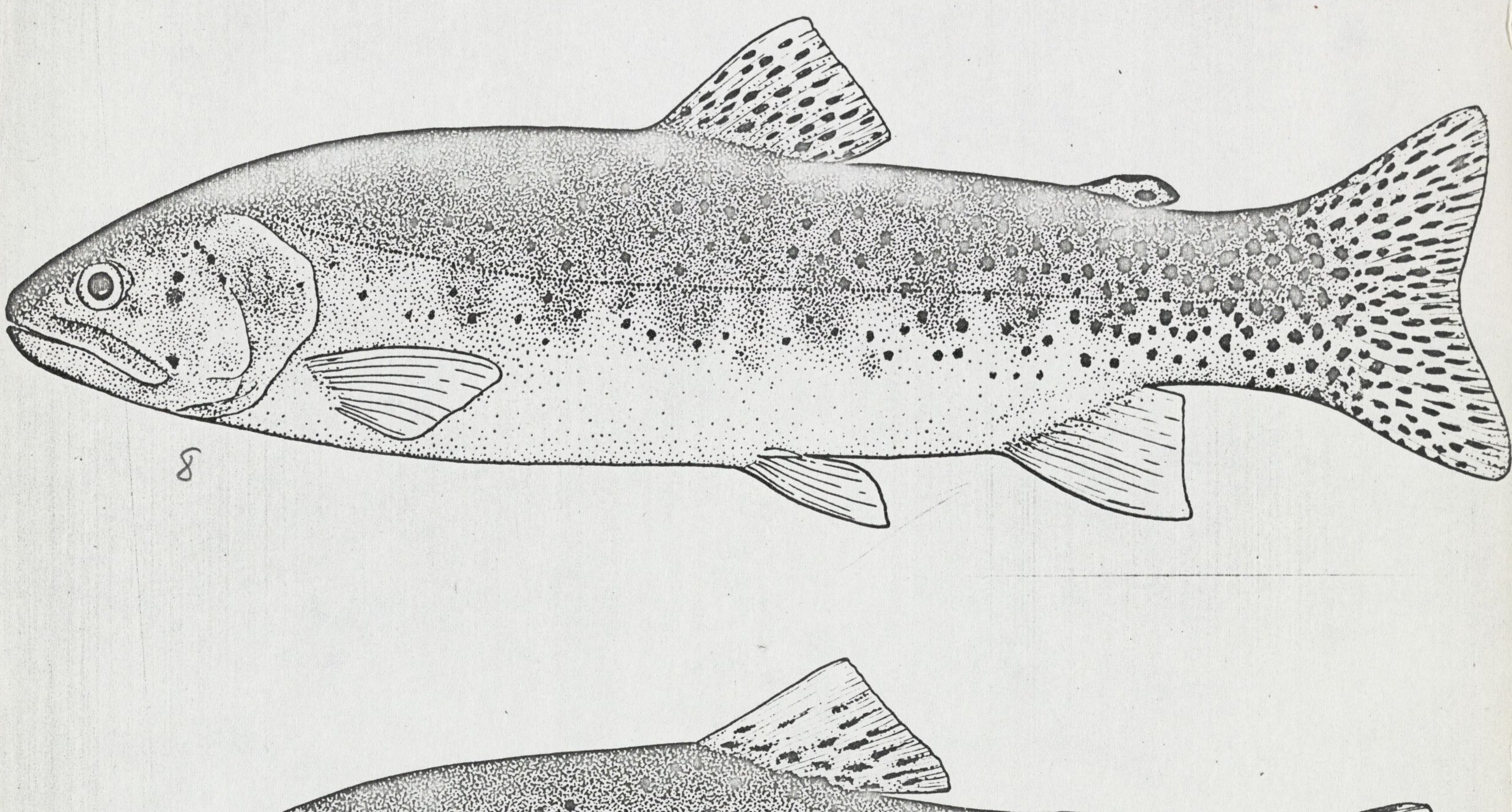

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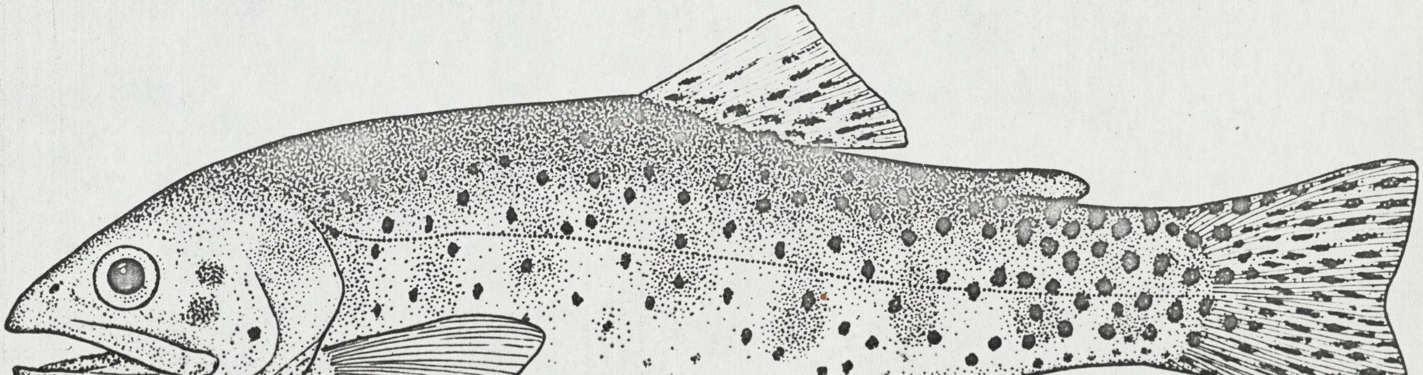

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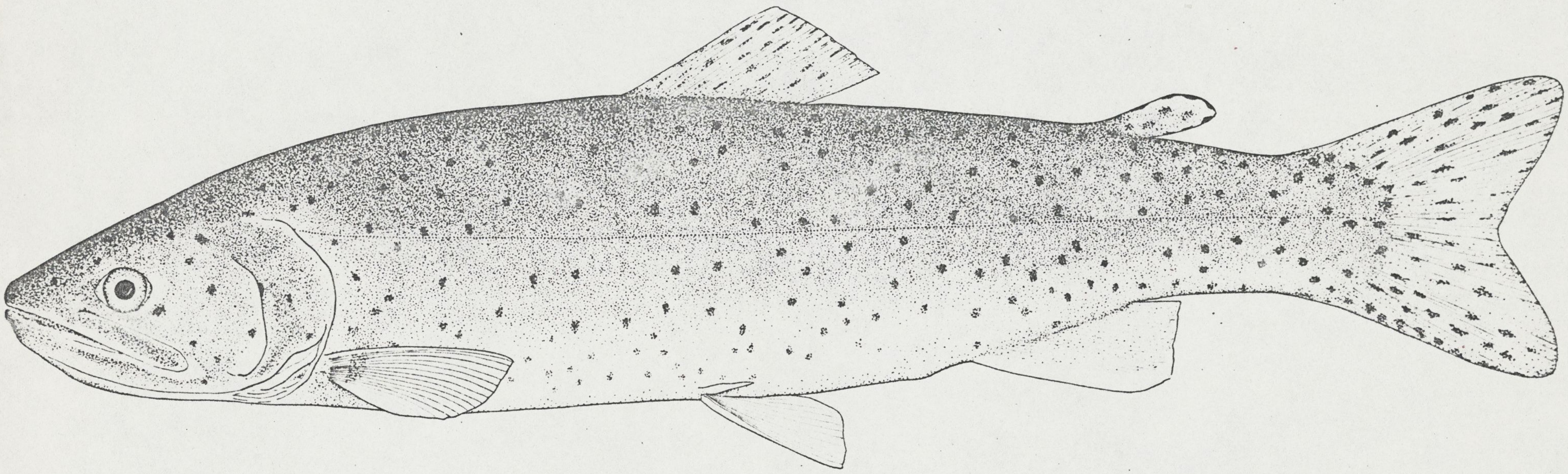
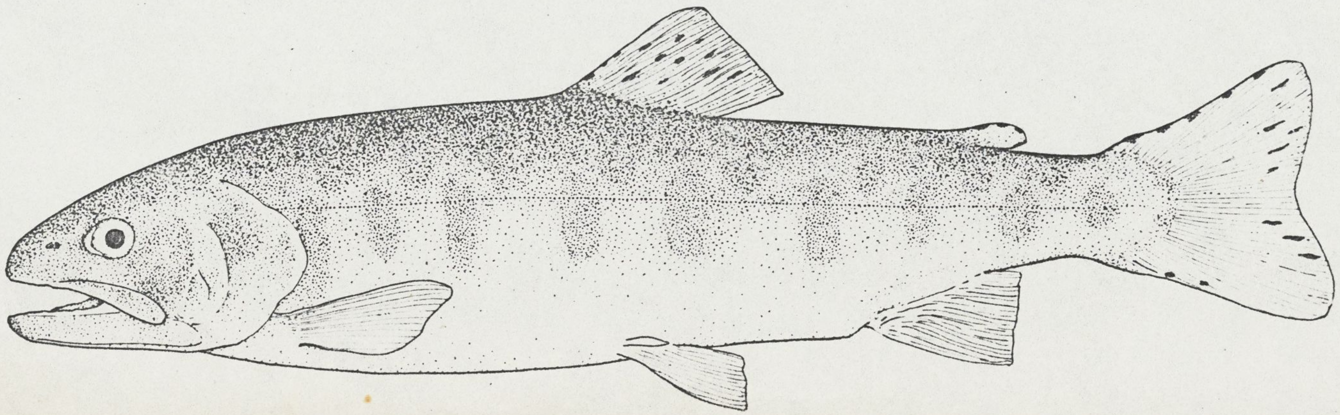
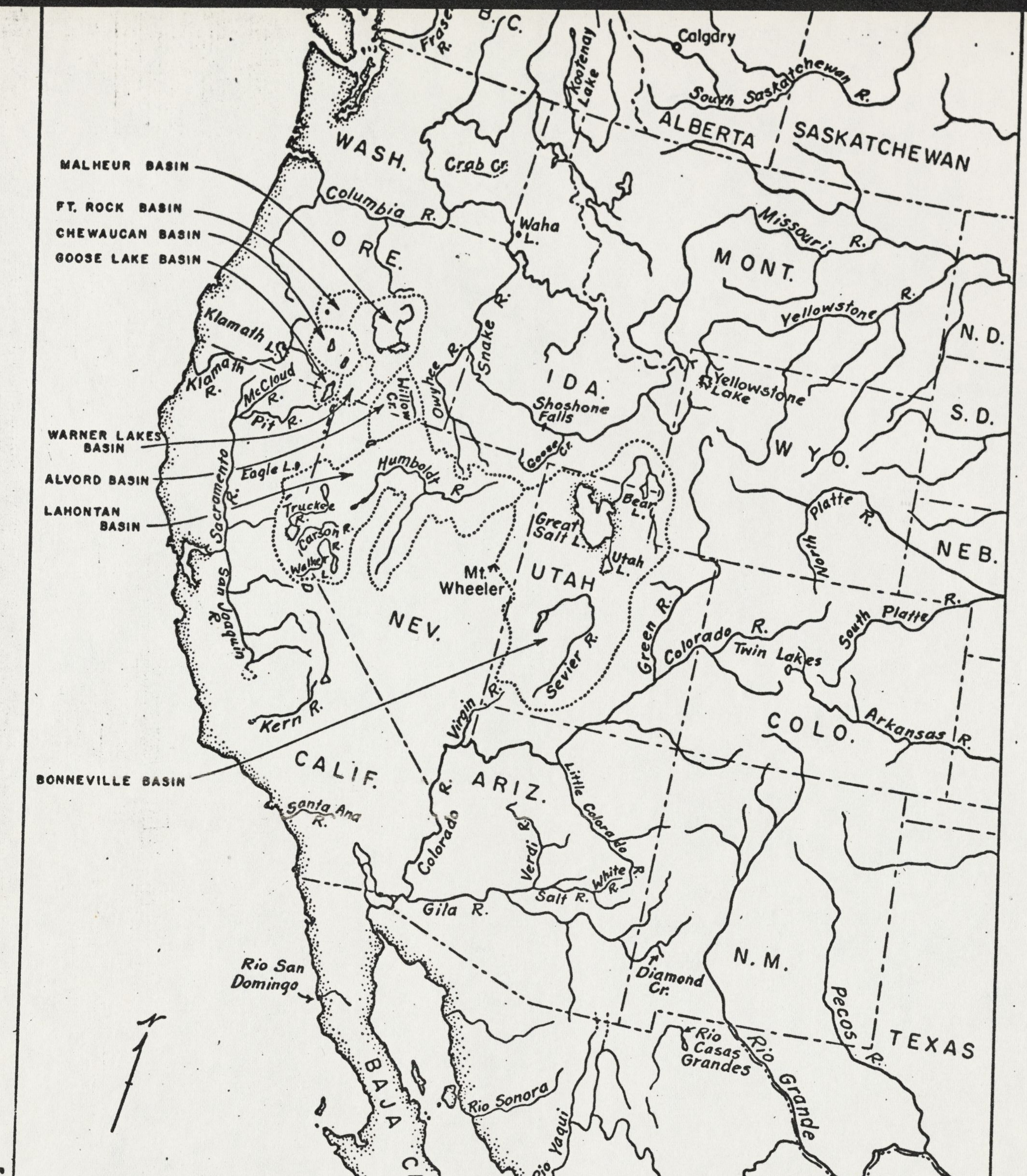
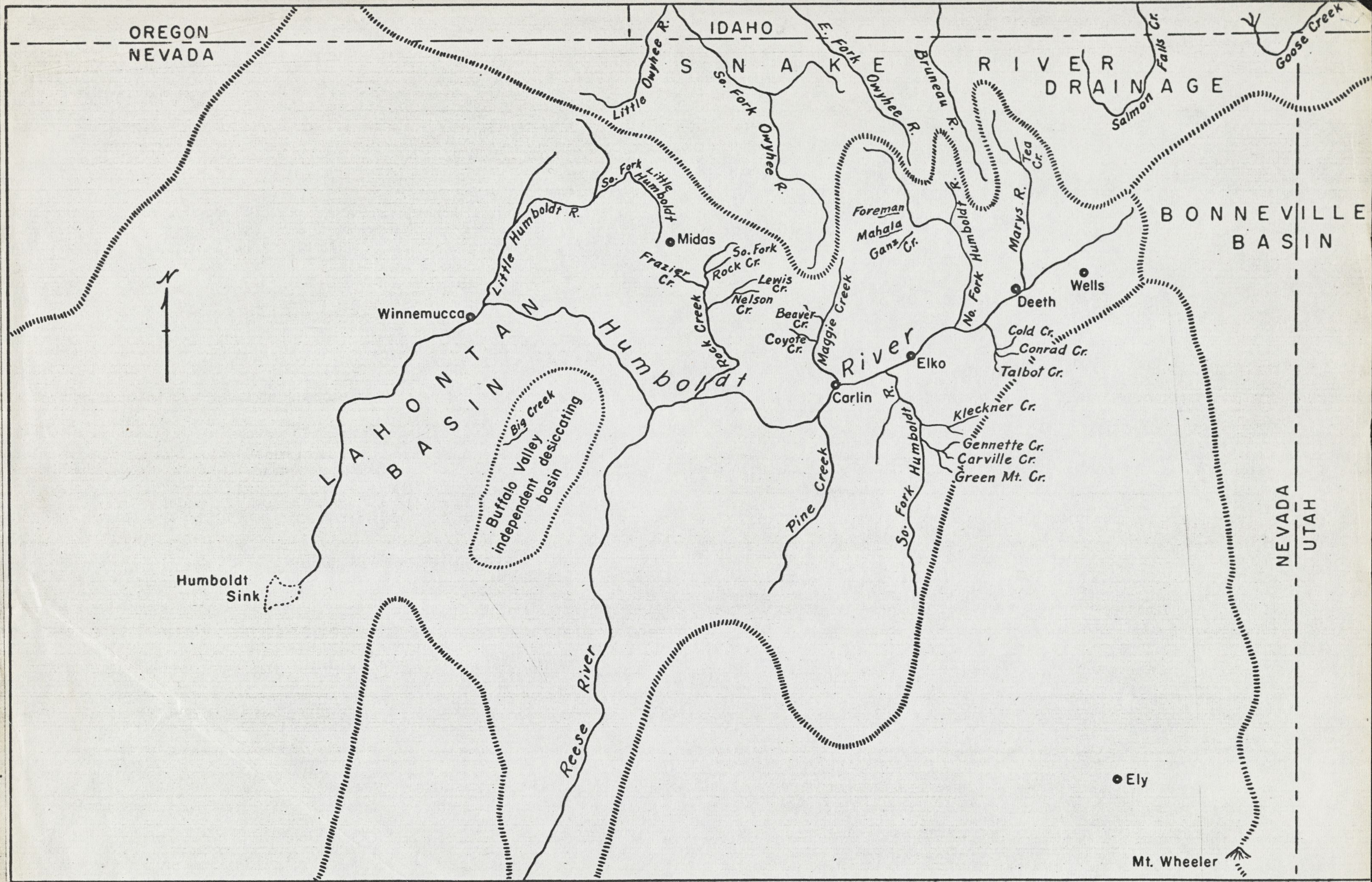


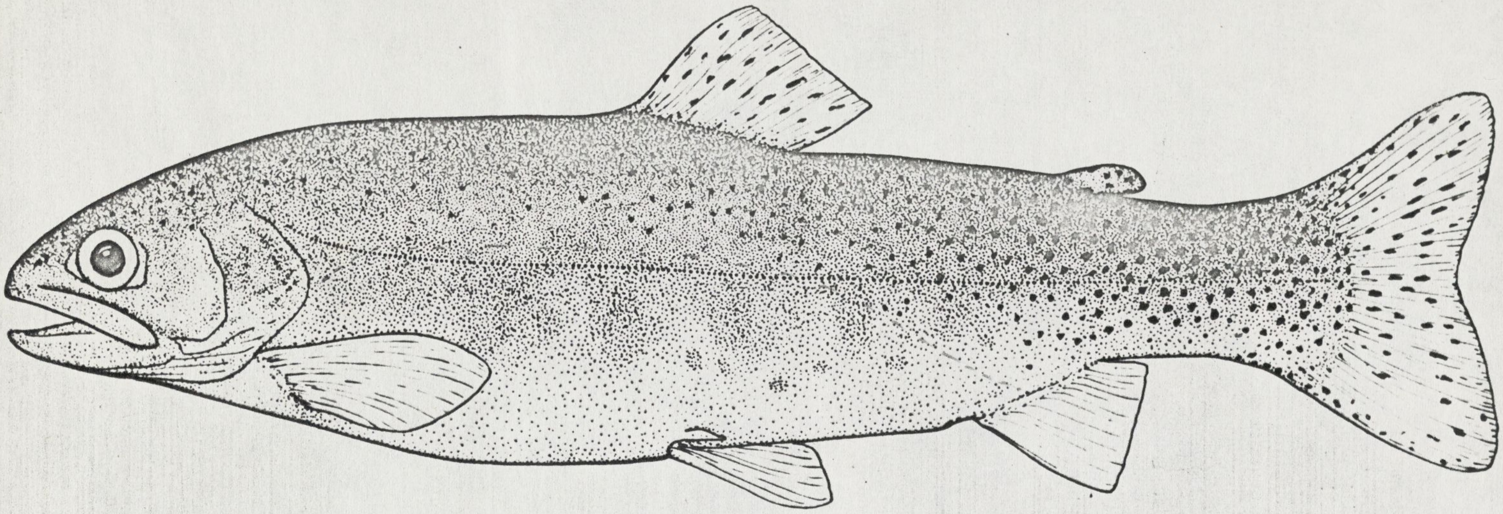


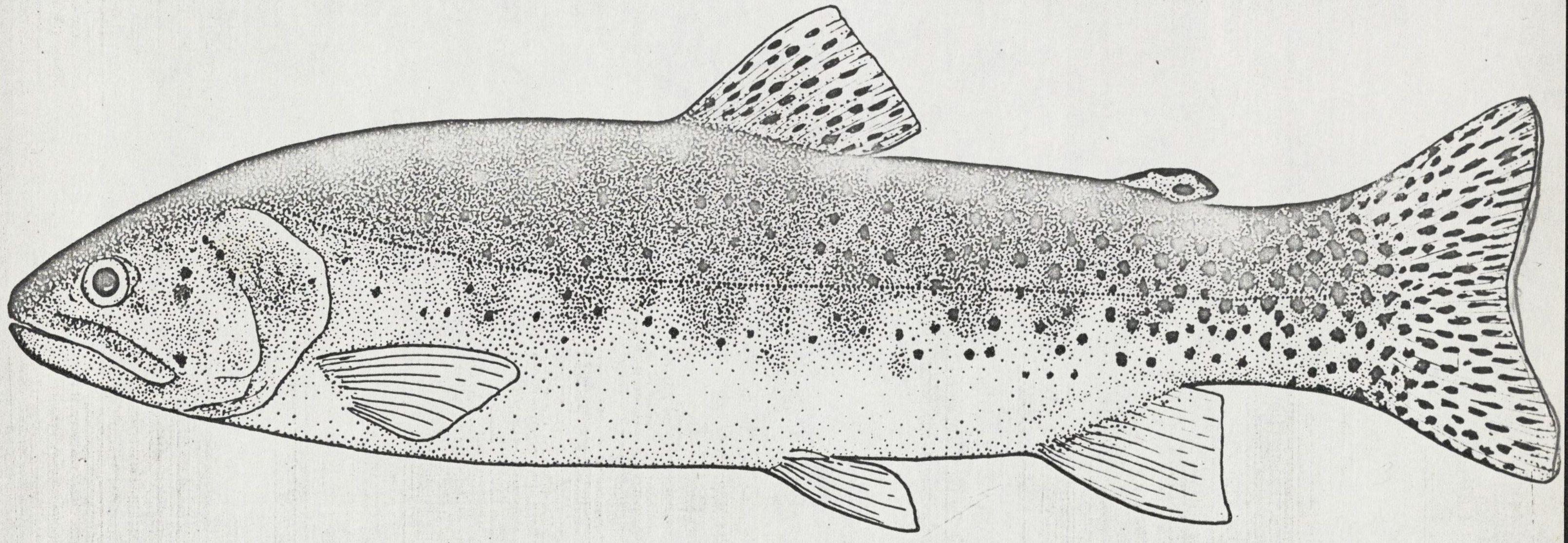


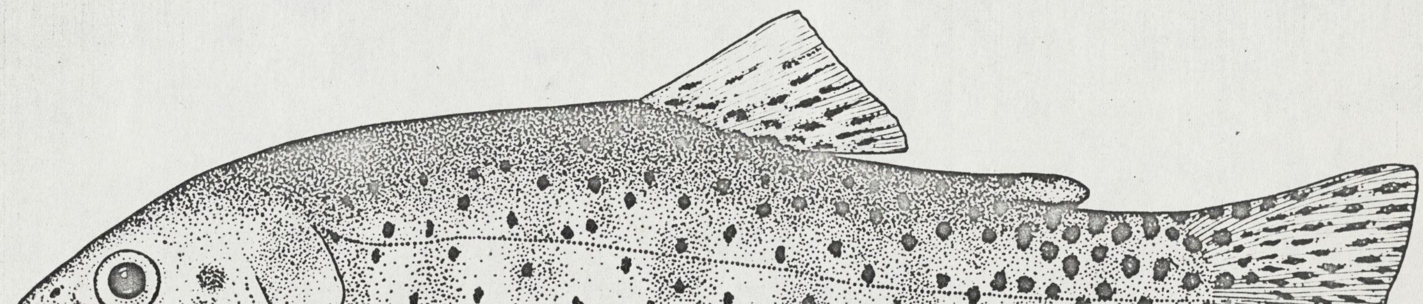
Map 2. Major drainage areas in the United States and Mexico where collections were made.

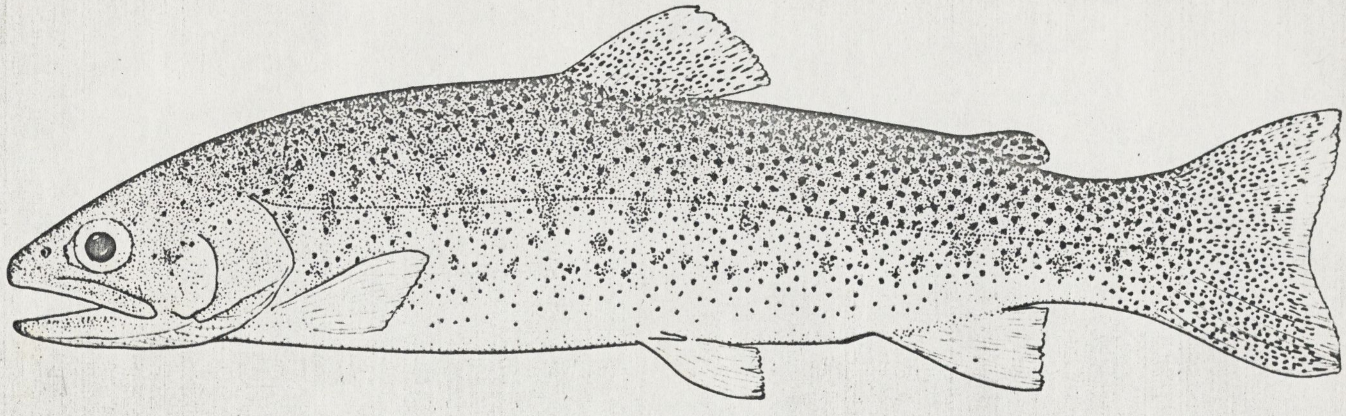


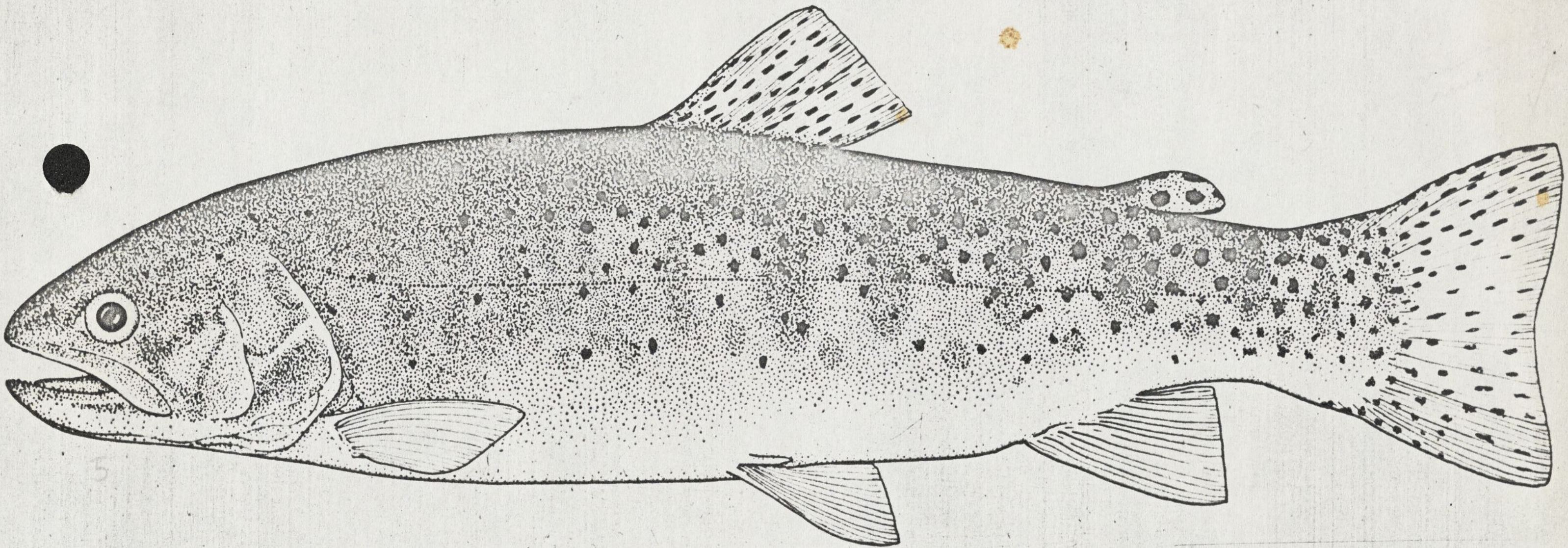
Map 3. Humboldt River system in the Lahontan Basin indicating streams where *S. c. humboldtensis* was collected

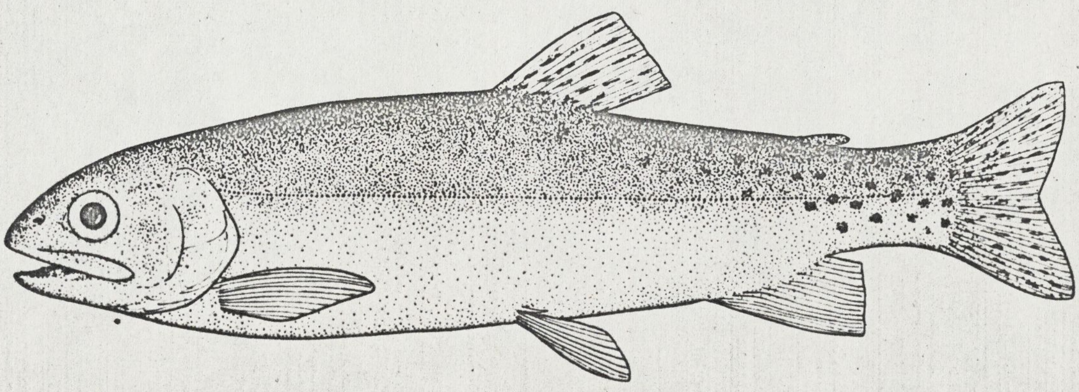


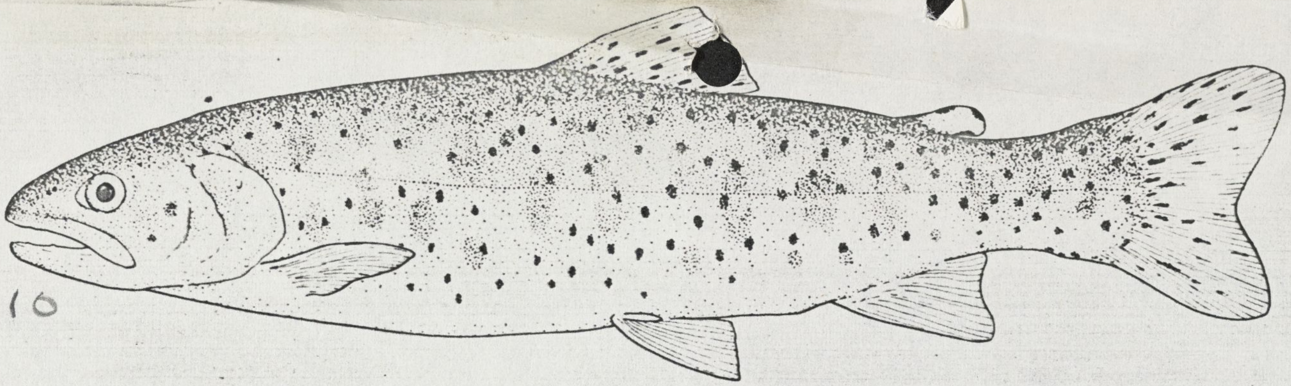












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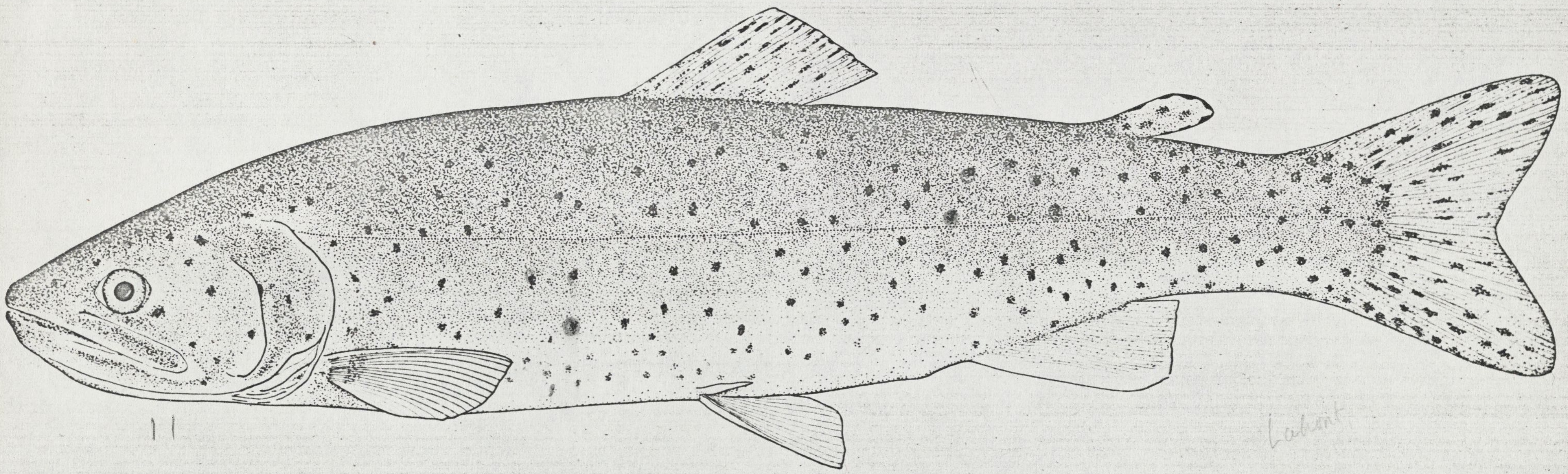

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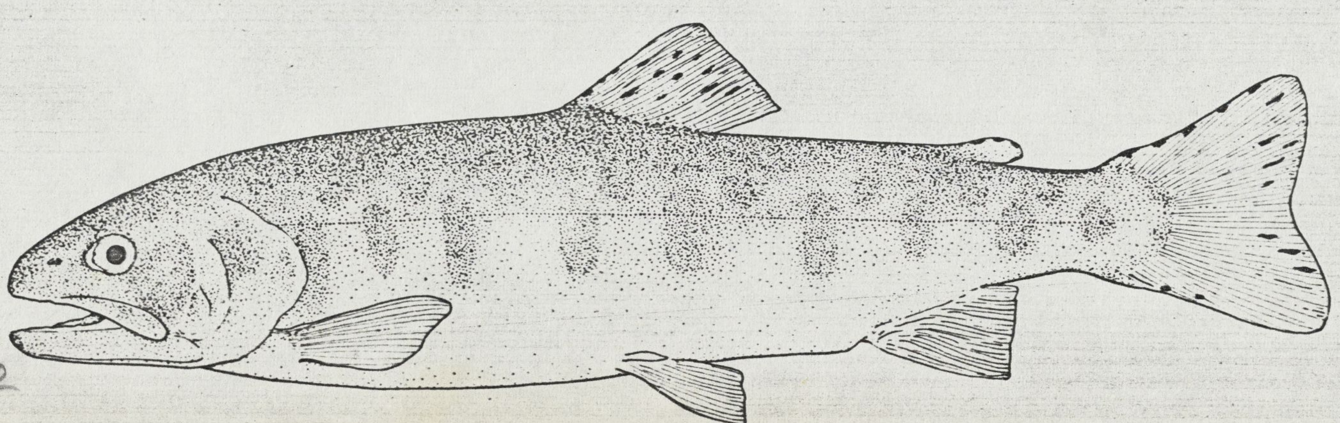
Lahont

Piute



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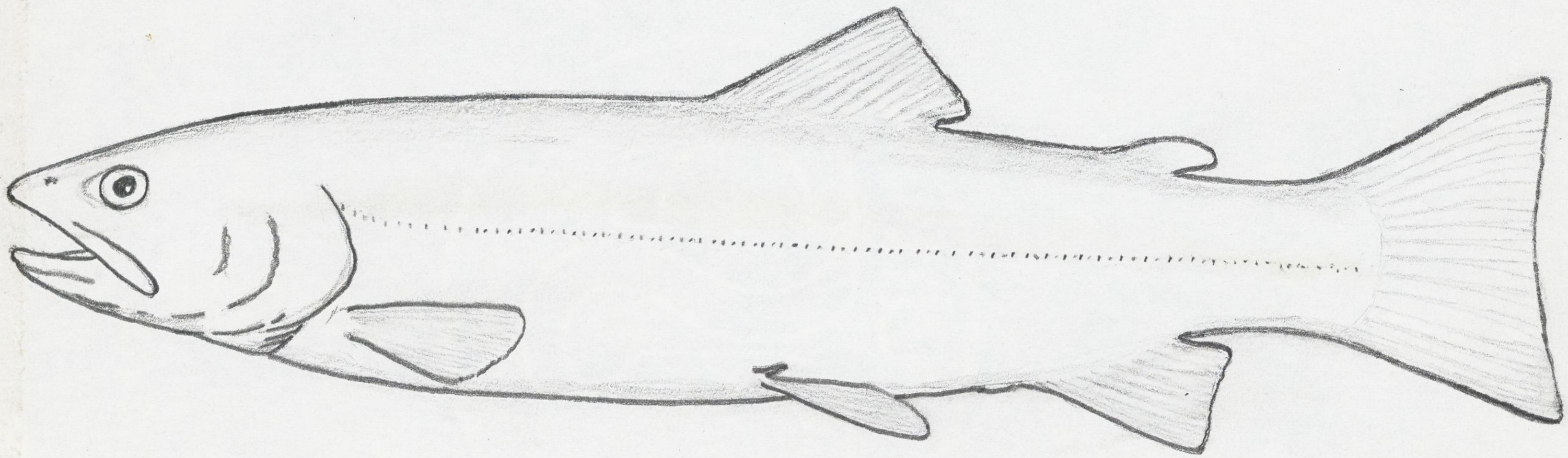

DEPARTMENT OF FISHERY AND WILDLIFE BIOLOGY

MEMORANDUM