# PHENETICS AND GENETICS OF HIGH SIERRAN GOLDEN TROUT

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Abstract. Seven populations of golden trout (Salmo aguabonita Jordan) from the Sierra Nevada, California, and four populations of rainbow trout (Salmo gairdneri Richardson) from California and Mexico, were compared for differences in ten meristic characters. Six of the golden trout populations were also examined for differences in chromosome karyotype. The results indicate that at least three, possibly four, phenetically distinct forms of golden-like trout now inhabit the region of the southern Sierra Nevada thought to circumscribe the endemic range of S. aguabonita. Based on phenetic distance estimates between pairs of the eleven populations of trout, and the karyotypes of the six golden trout populations examined, two of the golden trout populations sampled from the Little Kern River basin were suspected of having a recent hybrid origin resultant from crossing of introduced rainbow trout and native Little Kern golden trout, S. a. whitei Evermann. Two other golden trout populations sampled from the Little Kern River basin were tentatively identified as "pure" S. a. whitei.

## INTRODUCTION

During the past year, my colleague, Dr. G. A. E. Gall, and I have undertaken a series of investigations designed to examine the current status of the High Sierran golden trout, Salmo aguabonita. Our attention has been focused primarily on the genetic and taxonomic characterization of golden trout in the Little Kern River and its tributary streams. We also have examined numerous golden trout specimens from tributary streams of the upper Kern and South Fork of the Kern Rivers.

The impetus for these studies stemmed from the concern of California Department of Fish and Game biologists who feared the extinction of Little Kern River basin golden trout because of introgressive hybridization between endemic goldens and introduced rainbow trout, S. gairdneri. Actually, the alarm had been sounded earlier by William A. Dill (1945 & 1950), a district

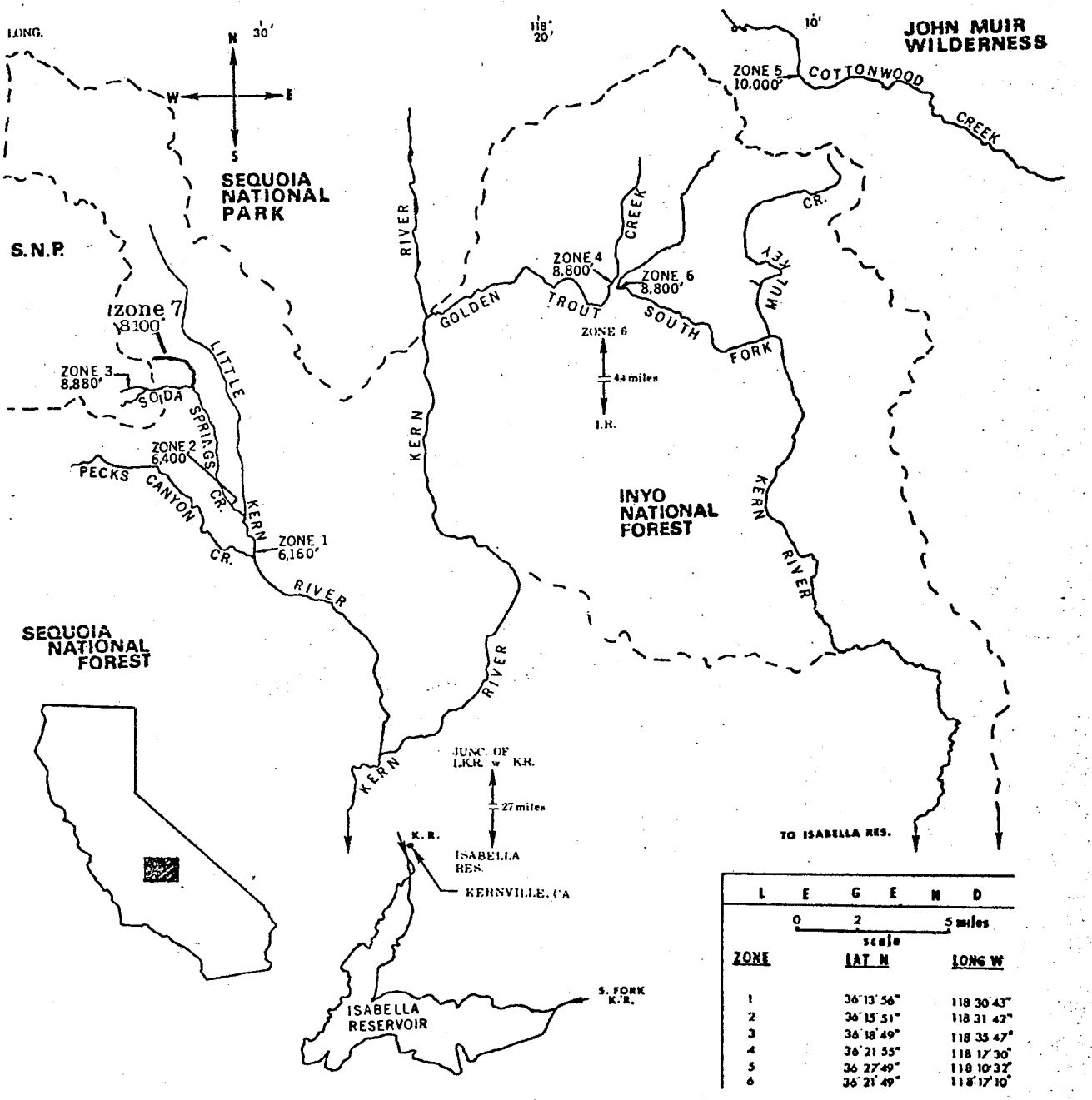



Fig. 1. A map showing the relative locations of seven samples of golden trout. The collection sites are identified as Zones 1-7, where LKR = 1; LSSC = 2; USSC = 3; GTC = 4; CWC = 5; SFK = 6; and DMC = 7.

fisheries biologist during the late 1940's with the then California Division of Fish and Game. Dill made two important observations. First, he observed that individual specimens collected throughout the Little Kern River drainage demonstrated a wide variety of coloration and spotting patterns, ranging from lightly to moderately spotted and brilliantly colored forms (characteristic of golden trout) to heavily spotted and pale colored forms (characteristic of rainbow trout). Secondly, he noted that ca. 100,000 rainbow trout fingerlings had been planted yearly from 1931-1941 in various streams of the Little Kern River basin. These two observations led Dill to the dual conclusions that the endemic Little Kern golden trout were in danger of "hybrid" swamping, and that future biologists would be faced with the problem of distinguishing "pure" stocks from those of hybrid origin.

At present, golden trout of the Little Kern are recognized by the California Department of Fish and Game as a subspecies, S. a. whitei Evermann (Shapovalov, et al. 1959; Fisk 1972). Others, including Dr. Robert Behnke and the U. S. Department of the Interior (1973), recognize the Little Kern golden trout as the subspecies, S. a. gilberti. The latter was based on a study by Schreck and Behnke (1971), who examined various museum specimens collected at the turn of the century from the Little Kern and main Kern Rivers, and concluded that the Little Kern golden trout and the Gilbert rainbow trout, S. g. gilberti Jordan, were synonymous. In accord with taxonomic protocol, they changed "whitei" to "gilberti".

In the present report, two aspects of our studies are presented. The results appear to confirm Dill's (1945 & 1950) conclusion that introgressive hybridization between endemic goldens and planted rainbows has occurred. However, our evidence also suggests that "pure" populations of golden trout still remain in a few isolated headwater streams of the Little Kern drainage. Further, these isolated "pure" populations of Little Kern goldens are not taxonomically synonymous with S. g. gilberti, as suggested by Schreck and Behnke (1971), but are closer to the geographically distant golden trout subspecies, S. a. aguabonita Jordan.

## MATERIALS AND METHODS

Meristic and chromosomal analyses were carried out on seven samples of golden trout, collected by angling and electroshock during the summers of 1973 and 1974. The location of each collection is shown in Figure 1. Four of the samples were from the Little Kern basin: Little Kern River (LKR); lower Soda Springs Creek (LSSC); upper Soda Springs Creek (USSC); and Deadman Creek (DMC). Two samples were from the upper Kern River basin; Golden Trout Creek (GTC); and South Fork of the Kern River (SFK). The remaining sample was from Cottonwood Creek (CWC), a tributary of the Owens River drainage. For comparative purposes, one sample of 19 rainbow trout (RTH) was obtained from the California state fish hatchery at Hot Creek, California. With the exception of the DMC sample, all specimens were brought live to Davis and held until sacrifice.

### Phenetic analysis:

Counts of 10 meristic characters were taken from the left side of each specimen as described in Gold and Gall (1975a). The following characters were examined: pyloric caeca; branchiostegal rays; vertebra; the principle rays of the ventral, dorsal, anal, and pectoral fins; gill rakers; scales in the lateral series (2-4 rows above the lateral line); and scales above the lateral line. All data were subjected initially to frequency distribution analysis using the mean, variance, and Fisher's third and fourth moment statistics (Sokal and Rohlf 1969). Within each sample the distributions of all 10 characters were approximately normal.

Table 1

Observed means for seven populations of golden trout and four populations of rainbow* trout. Numbers in parentheses refer to sample sizes.

| Character | Pylor. caec. | BO rays | #Vert-ebra | Vent. | Dors. | Anal | Pect. | Gill rakers | Scales in lat. ser. | Scales above L.L. |
|---|---|---|---|---|---|---|---|---|---|---|
| Population: | | | | | | | | | | |
| LKR (56) | 36.0 | 11.1 | 61.4 | 9.8 | 12.3 | 11.4 | 15.0 | 17.7 | 156.8 | 30.2 |
| LSSC (36) | 34.6 | 11.1 | 61.3 | 9.4 | 12.2 | 11.6 | 14.9 | 17.5 | 157.7 | 31.1 |
| USSC (93) | 32.2 | 11.3 | 60.8 | 9.5 | 11.9 | 11.5 | 15.5 | 18.2 | 181.8 | 36.6 |
| DMC (20) | 30.6 | 11.1 | 59.9 | 9.6 | 12.2 | 11.5 | 15.4 | 17.8 | 181.0 | 35.2 |
| GTC (38) | 30.7 | 10.5 | 59.7 | 9.2 | 11.6 | 11.1 | 14.7 | 17.7 | 181.9 | 37.7 |
| CWC (25) | 29.0 | 10.7 | 59.6 | 9.1 | 11.1 | 11.2 | 14.6 | 17.9 | 198.5 | 42.4 |
| SFK (40) | 31.1 | 10.3 | 60.0 | 9.2 | 11.5 | 11.2 | 14.7 | 17.7 | 180.2 | 35.0 |
| SPC (30) | NC† | 10.9 | 63.2 | 9.8 | 10.7 | 10.6 | 14.5 | 18.1 | 133.0 | 25.6 |
| RSD (25) | NC† | 11.2 | 61.9 | 10.1 | 10.9 | 10.3 | 14.7 | 18.3 | 132.0 | 25.7 |
| RH (30) | NC† | 10.9 | 64.3 | 10.0 | 11.5 | 10.6 | 14.0 | 18.4 | 137.0 | 25.9 |
| RTH (19) | 55.1 | 11.7 | 63.7 | 10.5 | 11.0 | 11.1 | 15.4 | 18.6 | 140.8 | 25.8 |

*Means for three rainbow trout populations (SPC, RSD, & RH) were taken from NEEDHAM and GARD (1959).

†NC - No comparison.

The sample means for each character were then transformed into standard deviation units to remove scaling effects (Gold and Gall 1975a). Euclidian, or phenetic, distances between pairs of populations were computed from the transformed data matrix. Distance (D) was estimated from the general formula

$$D_{ij} = [\Sigma_{k=1}^{k=10} (z_{ik} - z_{jk})^2]^{1/2}$$

where

$D_{ij}$ = the distance between the $i^{th}$ and $j^{th}$ sample

$z_{ik}$ = the transformed value of the $k^{th}$ character mean in the $i^{th}$ sample

$z_{jk}$ = the transformed value of the $k^{th}$ character mean in the $j^{th}$ sample

The value D represents the phenetic distance between two samples in standard deviation units in a 10 dimensional hyperspace (Sokal 1961; Goodman 1972). From the phenetic distance matrix, a non-overlapping, hierarchial phenogram was generated using the average linkage UPGMA algorithm outlined by Sokal and Michener (1958) and Sneath and Sokal (1973).

Chromosome analysis:

Chromosome karyotype analyses were carried out on the six golden trout samples which were transferred live to Davis. The method of chromosome preparation is outlined in Gold (1974).

Counts of mitotic chromosome numbers were scored from 1,318 cells prepared from anterior kidney tissue of 92 specimens. Details can be found in Gold and Gall (1975b).

## RESULTS

Phenetic analysis:

The observed means for the 10 characters in each of the seven golden trout and one rainbow trout samples are shown in Table 1. Included in the table are means for 9 of the 10 characters (pyloric caeca excluded) from three rainbow trout populations studied by Needham and Gard (1959); San Pablo Creek (SPC) near Berkeley, California; Rio Santo Domingo (RSD) in Baja California; and Rio Hondo (RH) from central Mexico.

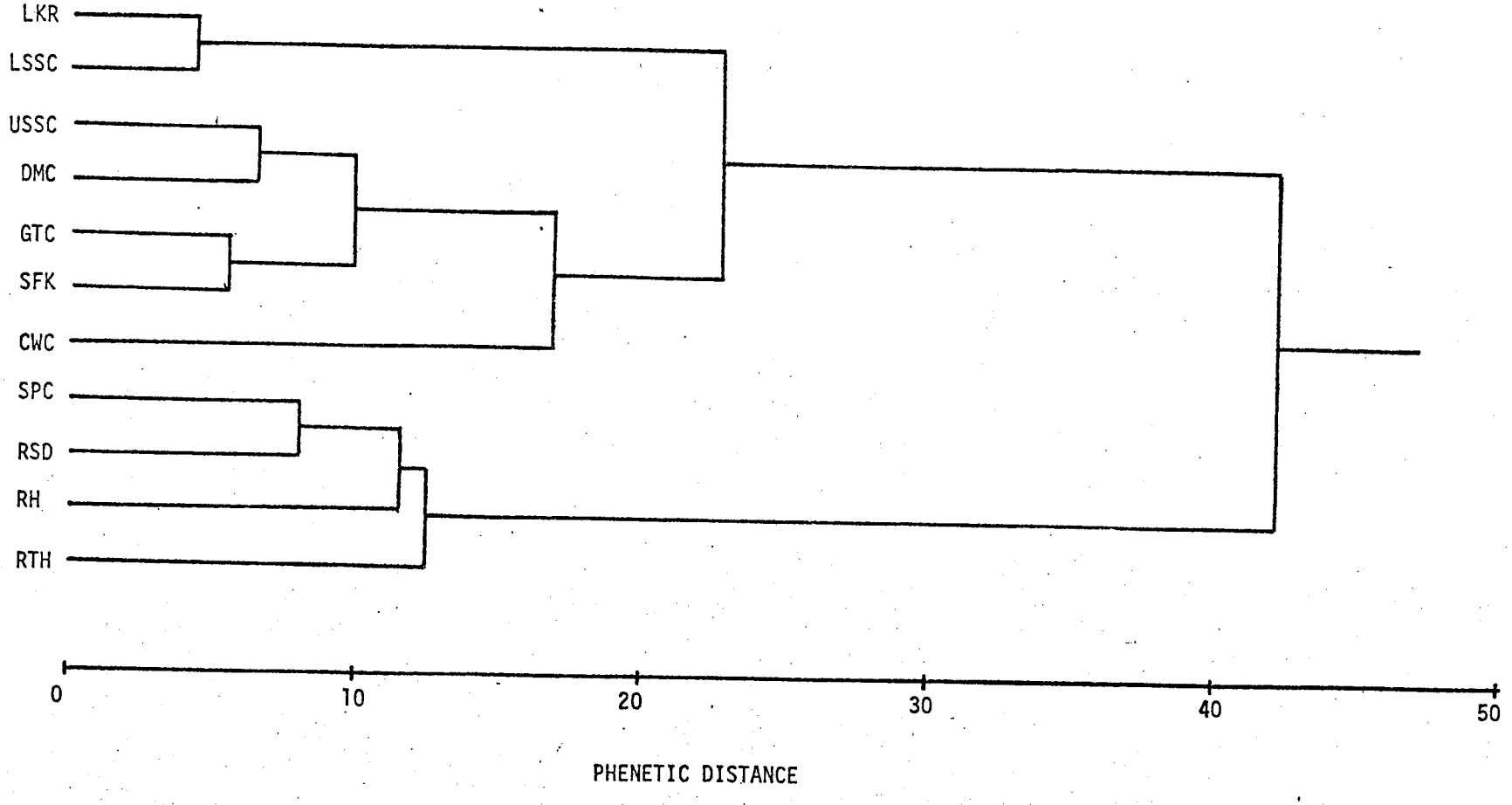
A number of marked differences in mean values are evident among the 11 samples of trout. The four rainbow samples tended to have fewer scales both in the lateral series and above the lateral line, but more vertebra and ventral fin rays than did the seven golden trout samples. Further, in the one rainbow sample (RTH) where counts of pyloric caeca were made, a much higher mean (55.1) was found than in any golden trout sample.

Similar, but less marked distinctions were found among the seven golden trout samples. LKR and LSSC trout tended to have higher numbers of vertebra and pyloric caeca, but fewer scales in the lateral series and above the lateral line. CWC trout had the highest number of scales in the lateral series and above the lateral line, and the lowest number of vertebra, pyloric caeca, and ventral fin rays. The differences among samples for the remaining characters, did not appear to follow consistent patterns.

The distance phenogram (Figure 2) derived from the above data shows two major groupings: (1) the rainbow trout group consisting of RTH, RH, SPC, and RSD; and (2) the golden trout group consisting of LKR, LSSC, USSC, DMC, GTC, CWC, and SFK. The major divergences between the two groups are in

Figure 2

The phenogram of UPGMA clustering of the data in the matrix of euclidian distances. The cophenetic correlation coefficient, $r_{CS}$, was 0.883.



scale number (both in the lateral series and above the lateral line), pyloric caeca number, and vertebrae number (Table 1). The separation by these characters is in accord with other published descriptions of rainbow trout (Miller 1950; Needham and Gard 1959) and Kern River golden trout (Schreck 1969; Schreck and Behnke 1971). Within the rainbow trout cluster, the differences among the four samples were minor. Slight differences in all character means were found (Table 1), but they were small and precluded major separation. The SPC and RSD rainbows were the most closely related, followed by the inclusion of the RH and RTH samples, respectively, into the cluster.

The second main cluster, the golden trout group, can be divided into three successively smaller clusters. The first division was the splitting of the LKR and LSSC trout from the main cluster, and appeared to stem primarily from the large differences in scale number between the two groups; although less pronounced differences also were apparent in the numbers of pyloric caeca, vertebra, and ventral fin rays (Table 1).

The next division was the splitting of the CWC trout from the USSC-DMC-GTC-SFK cluster, and appeared to reflect the greater number of scales found in the CWC trout. Differences in other characters were minor, with scale number having the greatest effect.

The final division was between the USSC-DMC and GTC-SFK clusters. In this case, separation did not appear to be the result of differences in scale number, but rather the result of small differences in all characters.

At the lowest level, the LSSC and LKR, GTC and SFK, and USSC and DMC samples were clustered very early, and indicated close taxonomic affinity. Differences between individual samples in each cluster were attributed to slight variations in a few characters.

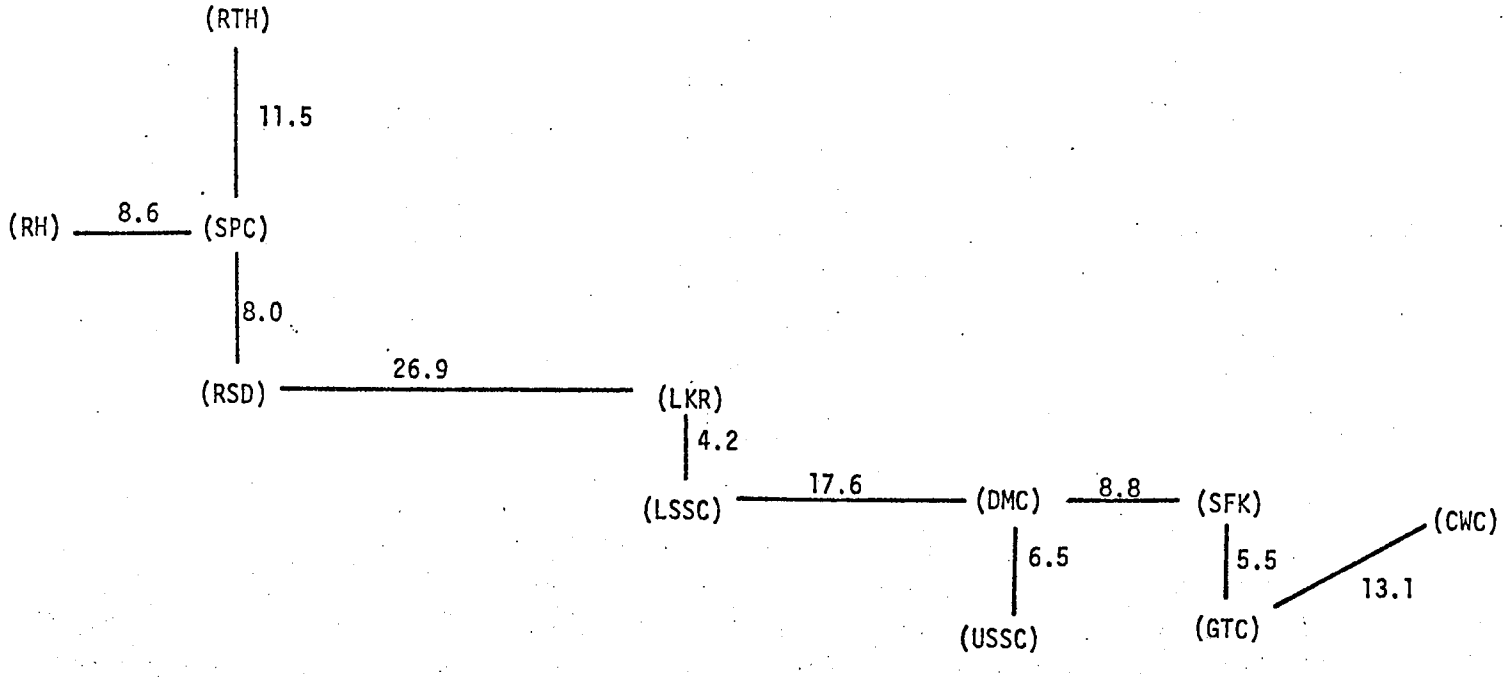
When these data were summarized into a two dimensional model by single-linkage clustering of the original Euclidian distance data matrix, a spatial arrangement shown as a shortest spanning tree was produced (Figure 3). The phenetic relationships among the 11 samples projected by the model do not differ from those revealed by the phenogram of UPGMA clustering. The model does, however, more accurately reflect the two dimensional phenetic position of each cluster relative to other clusters. It should be noted that the model does not necessarily depict phylogenetic divergences per se, but rather differences only in phenetic distances between all samples.

The projections of the model can be summarized as follows: (1) the two major groups, rainbow trout (RSD, SPC, RH, and RTH) and golden-like trout (LSSC, LKR, USSC, DMC, GTC, SFK, and CWC), are separated linearly by the greatest distance; (2) the divergence of the LKR-LSSC samples from the remainder of the golden trout group (USSC, DMC, GTC, SFK, and CWC) occurs in the direction of the rainbow trout group, and to a position approximately halfway between the rainbow group and the S. a. aguabonita group (GTC, SFK, and CWC); (3) two Little Kern basin samples (DMC, USSC) are more closely related phenetically to the S. a. aguabonita group (represented by the GTC and SFK samples) than to the other two Little Kern basin samples (LKR and LSSC); and (4) the CWC sample is divergent from the GTC and SFK group, but in a direction away from the rainbow trout, i.e., in the golden trout direction.

Chromosome analysis:

Chromosome analyses were made on 92 specimens from six of the samples of trout (LKR, LSSC, USSC, GTC, CWC, and SFK). The results of these investigations have been reported elsewhere (Gold and Gall 1975b), and are only summarized here.

Figure 3
Shortest spanning tree from single linkage clustering of the data in the matrix of euclidian distances.



A clear and consistent mode of 2n = 58 somatic chromosomes was found for all six samples. This is in agreement with previous estimates of diploid chromosome number in S. aguabonita (Simon, R. C. in Schreck and Behnke 1971; Miller 1972), and is distinct from the karyotype of 2n = 60 of the rainbow trout (Ohno, et al. 1965). However, variability of chromosome number within each of the six samples was observed. Cells with chromosome numbers ranging from 2n = 55 to 2n = 60 were found in all six samples, and a few cells were observed with 2n = 61 in three of the six.

Of the modal class of 2n = 58, the most often encountered karyotype (Figure 4) was one containing 44 chromosomes with median centromeres, 2 chromosomes with submedian centromeres, 2 chromosomes with sub-terminal centromeres and 10 chromosomes with terminal centromeres. By scoring chromosomes with median and sub-median centromeres as two armed chromosomes, and chromosomes with sub-terminal and terminal centromeres as one armed chromosomes, the arm number of S. aguabonita was estimated as 104. This estimate is identical to that of S. gairdneri (Ohno, et al. 1965), but not that of S. clarki (106), as previously reported (Schreck and Behnke 1971).

Of the 749 cells on which arm number analyses were made, between 65-85% had 104 chromosome arms despite variability in 2n chromosome number. Moreover, of those cells with other than 104 chromosome arms, between 83-100% were hypodiploid, i.e., had less than 104 chromosome arms. These two observations indicated that variation of chromosome number in S. aguabonita is derived from Robertsonian rearrangements (Robertson 1916), and that the large number of hypodiploid cells stemmed from counting errors and chromosome loss during preparation.

Interpopulation comparisons (Table 2), carried out using data from those cells with 104 chromosome arms, revealed highly significant differences ($P < 0.01$) in chromosome number variability only in the comparison of LKR and LSSC with USSC, GTC, CWC and SFK ($X^2 = 53.4$, 4df). Comparisons of LKR with LSSC ($X^2 = 7.41$, 4df) and among USSC, GTC, CWC, and SFK ($X^2 = 3.07$, 9df) were both non-significant. Considering the proportions of non-modal karyotypes in each sample (Table 2), the difference between the LKR and LSSC group and the USSC, GTC, CWC, and SFK group appears to stem from an increased frequency of hypermodal cells (2n > 58) in the LKR and LSSC samples.

## DISCUSSION

The foregoing data indicate that at least three, and possibly four, phenetically distinct forms of golden-like trout now inhabit the region of the Southern High Sierra thought to circumscribe the endemic range of S. aguabonita (Evermann 1905; Ellis and Bryant 1920; Curtis 1935; Shapovalov, et al. 1959; Schreck 1969).

In the upper Kern River basin the samples from Golden Trout Creek (GTC) and the South Fork of the Kern River (SFK) comprised a single phenetic group which is considered as representative of S. a. aguabonita. Virtually no differences in mean values for the meristic characters examined between the GTC and SFK samples of 1974 and those reported for S. a. aguabonita collected in 1891 and 1968 (Schreck and Behnke 1971) were found. In life, both the GTC and SFK samples of 1974 were as described by Evermann (1905), i.e., brilliantly hued with scarlet abdomen and lateral stripe against an olive background; and very sparsely spotted, particularly below the lateral line.

The sample from Cottonwood Creek (CWC), however, differed from the GTC and SFK samples, and could represent a second phenetic group of upper Kern River golden trout. CWC trout were more finely scaled both in the lateral series and above the lateral line, and had fewer vertebrae and pyloric caeca than did the GTC and SFK trout. However, the CWC trout were almost identical in life colors and spotting to the GTC and SFK trout. Furthermore, they did not differ in karyotype.

Table 2

Distribution of metacentric chromosome number in cells with 104 chromosome arms in six populations of golden trout. Numbers in parentheses refer to sample sizes.

| 2n chromosome number / Number of metacentrics | 56 / 48 | 57 / 47 | 58 / 46 | 59 / 45 | 60 / 44 | % of cells 2n<58 | % of cells 2n>58 |
|---|---|---|---|---|---|---|---|
| Population: | | | | | | | |
| LKR (10) | 1 | 3 | 58 | 13 | 15 | 4.4 | 31.1 |
| LSSC (9) | 2 | 2 | 55 | 2 | 14 | 5.3 | 20.1 |
| USSC (12) | .. | 4 | 90 | 8 | 3 | 3.8 | 10.4 |
| GTC (10) | .. | 7 | 87 | 6 | 1 | 6.9 | 6.9 |
| CWC (6) | .. | 6 | 72 | 4 | 2 | 7.1 | 7.1 |
| SFK (9) | .. | 5 | 83 | 6 | 3 | 5.1 | 9.1 |

Tests of significance:

| | | |
|---|---|---|
| LKR + LSSC vs. USSC + GTC + CWC + SFK | $\chi^2$= 53.4, 4 df | P<.005 |
| LKR vs. LSSC | $\chi^2$= 7.41, 4 df | P> .05 |
| USSC vs. GTC vs. CWC vs. SFK | $\chi^2$= 3.07, 9 df | P> .05 |

Since it is known that the barren Cottonwood Creek was initially foundered in 1876 by a plant of 13 trout from Mulkey Creek, a tributary of the South Fork of the Kern River (Evermann 1905), the CWC trout are directly descendant from SFK stock, and hence cannot represent an independent group of different phyletic origin. Possible explanations for the observed differences include: (1) non-random sampling combined with small sample size; (2) environmental modification due to lower ambient temperatures (Taning 1952) since CWC is over 1,000 feet higher in elevation than the GTC and SFK sites; or (3) a "founder effect" since the original introduction into CWC consisted of only 13 trout. Of the three, the latter is the most probable explanation as it has been shown that in some instances "founder effects" can produce quite drastic changes in gene frequency, and hence, in phenotype (Stebbins 1966).

Based on the above, taxonomic splitting of the CWC trout from the GTC and SFK trout does not seem warranted. Therefore, all three should be considered as geographically separate populations of S. a. aguabonita.

In the Little Kern River basin, the taxonomic situation is more difficult to interpret, even though the distinctions between the two major groupings, i.e., the LKR and LSSC samples and the USSC and DMC samples are straightforward. The LKR and LSSC trout were much more coarsely scaled than the USSC and DMC trout, had slightly higher numbers of vertebra and pyloric caeca, and in the case of LKR trout, had more ventral fin rays. All of these meristic character differences between the two groups can be summarized as a significant phenetic shift of the LKR and LSSC trout away from the USSC and DMC trout and in the direction of the rainbow trout. This was illustrated by the two-dimensional, shortest spanning tree model (Figure 3).

The above strongly suggests that the intermediateness of the LKR and LSSC stems from past hybridization between endemic golden trout (now represented by the USSC and DMC trout) and rainbow trout. This is supported by the karyotype evidence. The LKR and LSSC trout differed from the USSC and DMC trout in having a greater proportion of hypermodal ($2n > 58$) cells. This would be the expected result if introgression of rainbow trout chromosomes into the LKR and LSSC, trout had occurred since rainbow trout also have 104 chromosome arms, but $2n = 60$ chromosomes (Ohno, et al. 1965). Moreover, the two groups of Little Kern River basin trout differed markedly in variability of coloration and spotting. In life, the USSC and DMC samples were similar to the descriptions of S. a. whitei by Evermann (1906). The LKR and LSSC samples, on the other hand, exhibited a wide variation of phenotypes, ranging from brightly colored individuals to ones with almost no color at all. Spotting intensity also was variable in the LKR and LSSC samples, ranging from lightly spotted individuals to those which were profusely spotted over the entire body.

The picture which emerges from all the data is that the LKR and LSSC trout are indeed descendant from hybridization between endemic goldens and rainbows, and that the USSC and DMC trout represent vestige populations of the golden trout which first came to Little Kern basin waters. This latter conclusion is supported by the close phenetic relationship and identical karyotype of the USSC and DMC trout to the populations of S. a. aguabonita (GTC and SFK). Furthermore, the close phenetic relationship between the USSC and DMC trout and S. a. aguabonita, strongly indicates that the Little Kern golden trout and S. a. aguabonita do not represent two independent invasions of the Kern River Basin by "already divergent forms of the golden trout complex," as suggested by Schreck and Behnke (1971); but rather that both forms shared the same ancestor. Whether or not this hypothetical ancestor was the Gilbert rainbow trout (Ellis and Bryant 1920), the Shasta rainbow trout (Jordan 1928) or perhaps a form of inland cutthroat trout (Jordan 1894; Schreck 1969) is speculative, and will not be discussed here.

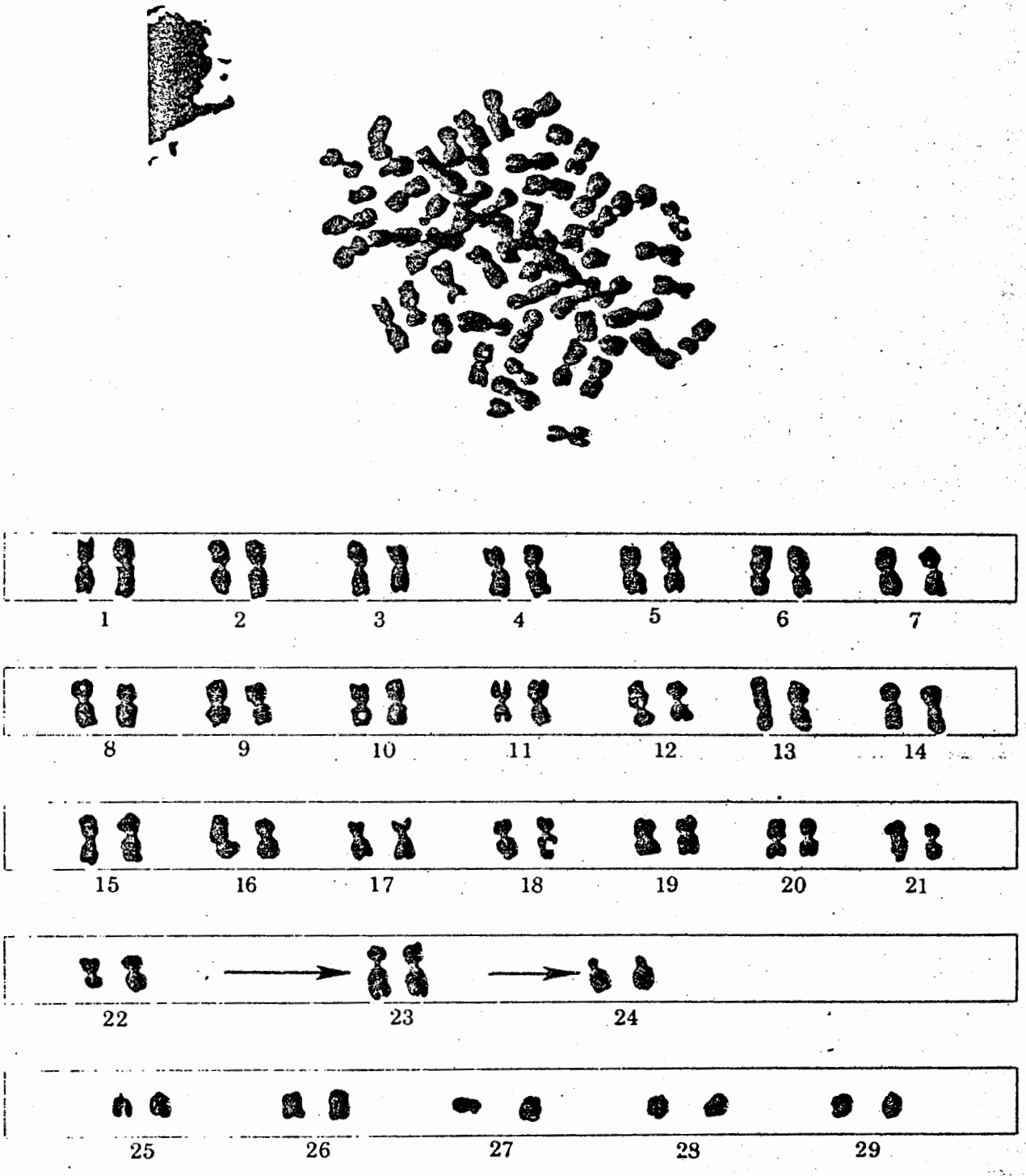



Fig. 4. Metaphase chromosomes from kidney and the karyotype of Salmo aguabonita. The arrows in the karyotype indicate chromosomes with submedian (#23) and subterminal (#24) centromeres.

ACKNOWLEDGEMENTS

The author is grateful to Dr. G. A. E. Gall both for his assistance in analyzing the data and in providing the laboratory space where this work was undertaken. I also wish to thank Mr. Stephen J. Nicola and Mr. Daniel P. Christenson for their help in procuring the specimens. Mr. Stephen J. Nicola and Dr. Charles Taylor have read this manuscript and made several valuable contributions.

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