REPRINT FROM
*Calif. Fish and Game*, 67(4) : 204–230. 1981

# SYSTEMATICS OF GOLDEN TROUT, *SALMO AGUABONITA,* FROM THE SIERRA NEVADA [1]

J. R. GOLD
Genetics Section
Texas A & M University
College Station, TX 77843
and
G. A. E. GALL
Department of Animal Science
University of California
Davis, CA 95616

**We examined the meristics, morphology, and dentition of 504 specimens from 14 trout populations in the Little Kern River basin area of the Sierra Nevada, California. This region is thought to circumscribe the range of the golden trout subspecies *Salmo aguabonita whitei.* On the basis of mean similarities, Euclidian distances, and projections from canonical analysis, the 14 populations were separated into two distinct phenetic groups: one represented by a sample from the headwaters of Deadman Creek (DMC), and the other by the remaining samples. Little Kern River samples were compared with those from the upper Kern River and upper South Fork Kern River (SFKR) known to represent the golden trout subspecies *Salmo aguabonita aguabonita,* and with two samples of domesticated strains of rainbow trout, *Salmo gairdneri.* The number of trout populations surveyed from the Little Kern basin through 1974 totals 15 and includes samples from headwaters and other portions of most of the permanently flowing streams north of Soda Spring Creek. Data reported in different studies are in agreement and may be summarized as follows: (i) two isolated headwater trout populations, one from DMC and the other from upper Soda Spring Creek (USSC), are virtually the same, but differ markedly from other upper Little Kern trout; (ii) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (iii) phenetically, DMC-USSC trout are nearly identical to *S. a. aguabonita;* and (iv) in multivariate orientation, most upper Little Kern trout occupy positions between DMC-USSC trout and *S. gairdneri.* These patterns of geographic variation among Little Kern trouts are not easily explained by models based on chance, adaptive, or non-genetic effects. We suggest that the DMC-USSC trout are most closely related evolutionarily or phyletically to *S. a. aguabonita* and are descended from among the first trouts to enter Kern basin waters either before or during the last glacial retreat. Other present-day upper Little Kern trout populations, and several named forms from the Little Kern and elsewhere in the upper Kern basin, may reflect varying degrees of introgression from past hybridizations of native goldens with introduced non-native trout such as *S. gairdneri.* They may also be derivatives of a redband-like trout which later entered the upper Kern basin, or, alternatively, they may be natural derivatives of the original endemic golden trout. The DMC-USSC trout are best referred to *S. aguabonita,* a species which at present includes trout from DMC, USSC, SFKR, GTC (Golden Trout Creek), and perhaps a few other streams in the upper Kern River basin.**

## INTRODUCTION

The systematics and taxonomy of the trouts native to the Kern River basin in the Sierra Nevada, California, are not well understood. At least four golden trout-like forms, initially recognized as full species, and one subspecies of rainbow trout have been described from the region, although the taxonomic validity

[1] Accepted for publication November 1980.

of some of these forms has been the subject of considerable debate. At present, the general consensus is that only one golden trout species, *Salmo aguabonita* Jordan, and possibly one subspecies of rainbow trout, *Salmo gairdneri gilberti* Jordan, are endemic to Kern basin waters. An excellent historical critique of the early literature on Kern basin trouts may be found in Schreck and Behnke (1971).

For primarily historic and distributional reasons, *S. aguabonita* is considered to comprise two subspecies. One of these, *S. a. aguabonita,* is restricted to the northeastern part of the upper Kern River basin, and includes populations [2] from Golden Trout Creek and the South Fork Kern River (Gold and Gall 1975*a*). The other subspecies, referred to as either *S. a. whitei* or *S. a. gilberti,* includes trouts from the upper Little Kern River basin (Shapovalov, Dill, and Cordone 1959, Schreck 1969, Schreck and Behnke 1971, Legendre, Schreck, and Behnke 1972, Gold and Gall 1975*a, b*). Recognizable morphological differences between these two geographically disjunct subspecies are few. Populations of *S. a. aguabonita* usually are distinguished from those of *S. a. whitei* by less intense spotting and greater brilliance in colors (Evermann 1906).

The status of the Kern River rainbow, *S. g. gilberti,* is questionable. Schreck (1969) and Schreck and Behnke (1971) synonomized *S. g. gilberti* with *S. aguabonita* from the Little Kern basin (formerly *S.* (*a.*) *whitei* Evermann) on the basis of similarities in the ranges and means of a few meristic characters (principally lateral series scale rows) between trout collected from the Kern and Little Kern Rivers in 1893 and 1904 and limited samples collected in 1967–1968. Since *gilberti* had priority over *whitei* in the literature, they suggested that the Little Kern golden trout be referred to as *S. a. gilberti.* They further noted that there was no geologic evidence that trout from the Kern River and the Little Kern River were ever physically isolated from each other. However, a thorough survey by Evans, Smith, and Bell (1973) revealed the existence of several natural barriers both near the confluence of the Little Kern and Kern rivers and throughout the Little Kern River basin.

The central problem confounding evolutionary relationships among upper Kern basin trout is that many present-day stream populations are of mixed or unknown ancestry. During the late 1800's and early 1900's biologists and the first Kern plateau settlers indiscriminately introduced several non-native trouts throughout the basin and transplanted many native stocks from their streams of origin to other nearby waters. Although many introductions and transplants were recorded (Evermann 1906, Ellis and Bryant 1920, Meyer 1965, Schreck 1969), it is certain that many were not. Further, several recorded 'stockings' involved trout of unknown provenance. It is important to note that a few introductions and transplants occurred before and during the time of the original descriptions of Kern basin trout.

A second source of confoundment, primarily involving Little Kern trout, is the hybridization which may have occurred between endemic goldens and rainbows introduced for recreational purposes. Between 1930–1941, almost 100,000 rainbow fingerlings were planted annually in waters throughout the Little Kern basin (Dill 1941, 1945, 1950), and stocking records list a few earlier rainbow

[2] The term population is used throughout to represent a localized random mating population. Fish taken from a restricted sampling area are assumed to represent such a population (McGlade and MacCrimmon 1979).

introductions. The degree of golden x rainbow hybridization in the Little Kern basin has not been critically assessed, but the considerable phenotypic heterogeneity observed among Little Kern trouts generally has been taken as evidence that both hybridization and backcrossing were extensive (Dill 1945, 1950, Needham and Gard 1959, Schreck 1969, Schreck and Behnke 1971, Gold and Gall 1975*a*, Christenson 1978). Certainly, the laboratory successes of hybridization among these and other western trouts (Hartman 1956, Gould 1966, Dangel 1973, Gold, Pipkin, and Gall 1976, 1979) suggest that reproductive isolating mechanisms are far from complete.

A final problem is the lability in external meristic morphology which characterizes most salmonid fishes. Much of this variation is presumably a response to differing environmental conditions during early stages of development. Several examples among salmonids in nature are cited in Mayr (1973:p. 145), and examples from laboratory experiments are abundant (Tåning 1952, Garside 1966, Kwain 1975). Salmonids, particularly western trouts, also are noted for numerous instances of convergent or parallel evolution (Behnke 1970, 1972), which further tends to obscure actual evolutionary relationships.

Previously (Gold and Gall 1975*a, b, c,* Gold 1975, Gall *et al.* 1976), we reported the occurrence of at least two significantly distinct phenetic groups of golden-like trout in Little Kern waters. One group, represented by samples from upper Soda Spring Creek (USSC) and Deadman Creek (DMC), had close phenetic and genetic affinities to geographically disjunct *S. a. aguabonita.* A second group, represented by samples from lower Soda Spring Creek (LSSC) and the Little Kern River (LKR) near Peck's Canyon Creek, was roughly intermediate in morphology, karyology, and biochemical-genetic profile between *S. a. aguabonita* and *S. gairdneri.* We suggested that the DMC-USSC trout were pure populations of an endemic Little Kern golden trout; whereas the LSSC-LKR trout probably represented remnants of golden x rainbow hybridization. In this paper, we continue our survey of geographic variation among present-day Little Kern trouts. Included are morphological analyses of samples from 14 populations (504 individuals), an assessment of the variation among present-day trout from the upper portion of the Little Kern basin, and a consideration of this variation in regard to systematics and classification of Kern basin trout.

## MATERIALS AND METHODS

Thirteen samples of trout from the Little Kern River and one sample from the headwaters of the South Fork of the Kaweah River were collected between 19 August and 23 September 1974. Approximate collection localities and positions of barriers to upstream migration are provided (Figure 1), as well as geographic information and keys to sample sites (Appendix Table 1). Two Little Kern localities (DMC and LSSC) previously sampled (Gold and Gall 1975*a, b*) were included to allow comparisons between years as well as among all populations examined through 1974. The South Fork Kaweah sample was included since Evermann (1906) described *Salmo whitei* from there, where it had been introduced from Soda Spring Creek. Other trout populations examined for comparative purposes included one sample of *S. a. aguabonita* from the South Fork Kern River (provided by E. P. Pister, Fishery Biologist, Calif. Dept. Fish and Game), and two samples of domesticated rainbow trout (provided by Mt. Shasta State Hatchery personnel). Specimens were returned to the laboratory, sacrificed,

tagged for identification, preserved in ethanol, and deposited in reference collections at the Department of Wildlife and Fisheries Science, Texas A&M University.

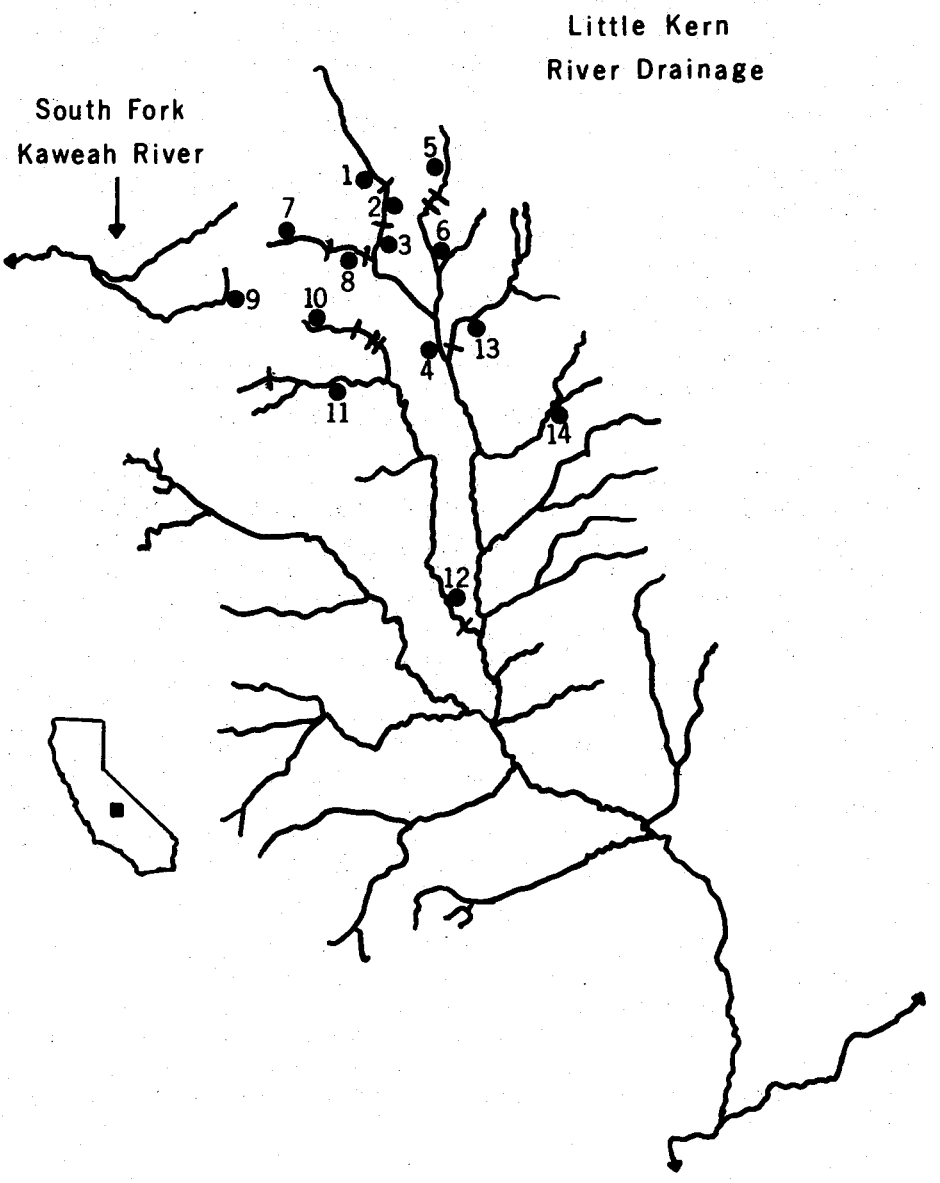


FIGURE 1. A map of the Little Kern River drainage showing the locations of fourteen 1974 collection sites, and the locations of natural barriers to upstream migration. Collection sites are as follows: 1-LKR-1; 2-LKR-2; 3-LKR-3; 4-LKR-4; 5-USGC; 6-LSGC; 7-UWMC; 8-LWMC; 9-GM; 10-DMC; 11-MSSC; 12-LSSC; 13-RC; and 14-TMC (cf. text for further details).

Measurements and meristic data were taken from the left side following methods described in Gold and Gall (1975*a*). Branchiostegal rays were counted on both left and right sides. Interneurals (dorsal fin pterygiophores), interhaemals (anal fin pterygiophores), and epurals were enumerated from radiographs. Basibranchial and other dentition were examined using a technique suggested by R. J. Behnke (outlined in Gold 1977:p. 1860). All specimens were examined in a random sequence and identified only by tag number. Observed means, standard deviations, and ranges for 13 meristic characters and fork length for each of the 14 samples are provided (Appendix Tables 2*a–b*). Values for males and females are combined since tests of sex and sex x location interaction effects for each character were non-significant.

All data were initially subjected to univariate statistical analyses using the mean, variance, and Fisher's third and fourth moment statistics. Of 14 characters, only distributions for parr marks and epural number appeared non-normal. Homogeneity of means for all characters was tested using two-way (sex by locality) analysis of variance. Sex and sex x locality interaction effects were non-significant ($P > 0.05$); however, significant heterogeneity ($P < 0.01$) among means due to locality was detected for all characters except epural number. Mean separation tests involving only the 12 normally distributed characters were accomplished using Duncan's multiple range analysis weighing the least significant ranges for unequal sample sizes (Sokal and Rohlf 1969).

Multivariate statistical analyses using only the 11 normally distributed meristic characters were employed to project phenetic affinities and relationships among samples. Specific procedures included UPGMA cluster analysis of a Euclidian distance matrix, multivariate analysis of variance (MANOVA), and canonical analysis. Each multivariate procedure was carried out using computer programs in SAS, the Statistical Analysis Series designed and implemented by Barr *et al.* (1976). Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilks's Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect in the MANOVA. All four tests produced significant F values ($P < 0.01$), indicating significant morphological heterogeneity among samples due to locality.

Canonical analysis of the data provided weighted combinations of characters which maximized the distinction among samples. Characteristic roots and orthogonal vectors were extracted from the variance-covariance matrix, and means for each sample or locality were computed along each vector. Each successive orthogonal axis, termed a canonical variate, extracted the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate (characteristic root) represented an identifiable fraction of the total variation. The relative importance of each original character to a particular canonical variate was computed by multiplying the vector variable coefficient by the grand mean of the dependent variable (individual character), summing all variable values for a particular vector, and then computing the percent of relative importance of each character per vector.

## RESULTS

Results of mean separation tests involving the 11 normally distributed meristic characters and fork length are shown in Tables 1*a* and *b*, in addition to estimates of grand means and error mean squares from analysis of variance. Since age data

were not recorded, the observed differences in mean fork length could stem from several factors, including heterogeneous age distributions within and among populations. Comparisons among samples with significantly different means generally revealed no consistent associations between mean value of any single meristic character and geographic location. No clinal trends with latitude or with altitude were apparent, and geographically contiguous samples (e.g., UWMC-LWMC, USGC-LSGC, etc.) were not necessarily more similar than geographically discontinuous ones. Exceptions to the latter were the LKR-2, 3, and 4 samples which were very similar if not identical for means of all characters.

**TABLE 1a. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance *) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.**

| *Sample* | *Fork length* | *Pyloric caecae* | *Dorsal rays* | *Anal rays* | *Pectoral rays* | *Pelvic rays* |
|---|---|---|---|---|---|---|
| LKR-1 | 15.0$^{a}$ | 35.86$^{b}$ | 12.57$^{cde}$ | 11.14$^{cd}$ | 14.76$^{a}$ | 9.78$^{de}$ |
| LKR-2 | 14.1$^{bcde}$ | 36.78$^{bc}$ | 12.78$^{a}$ | 11.08$^{bc}$ | 15.30$^{cd}$ | 9.78$^{de}$ |
| LKR-3 | 13.6$^{ebcd}$ | 37.39$^{bcde}$ | 12.58$^{cde}$ | 10.94$^{abc}$ | 15.61$^{def}$ | 9.79$^{e}$ |
| LKR-4 | 13.3$^{abc}$ | 39.32$^{de}$ | 12.29$^{abc}$ | 11.10$^{bcd}$ | 15.59$^{def}$ | 9.63$^{bcde}$ |
| USGC | 14.6$^{de}$ | 36.79$^{bcd}$ | 12.32$^{abcd}$ | 11.00$^{bc}$ | 15.41$^{cde}$ | 9.47$^{bc}$ |
| LSGC | 14.0$^{bcd}$ | 38.55$^{bcde}$ | 12.35$^{abcd}$ | 11.06$^{bc}$ | 15.61$^{def}$ | 9.71$^{cde}$ |
| RC | 14.7$^{de}$ | 37.29$^{bcde}$ | 12.69$^{de}$ | 11.37$^{d}$ | 15.09$^{abc}$ | 9.77$^{de}$ |
| UWMC | 14.6$^{de}$ | 36.16$^{b}$ | 12.29$^{abc}$ | 10.97$^{bc}$ | 14.79$^{a}$ | 9.39$^{b}$ |
| LWMC | 13.3$^{abc}$ | 38.83$^{cde}$ | 12.46$^{bcde}$ | 11.34$^{d}$ | 15.69$^{ef}$ | 9.54$^{bcde}$ |
| DMC | 12.5$^{a}$ | 33.24$^{a}$ | 12.15$^{ab}$ | 10.68$^{a}$ | 15.68$^{ef}$ | 9.00$^{a}$ |
| MSSC | 13.0$^{ab}$ | 35.97$^{b}$ | 12.05$^{a}$ | 10.90$^{abc}$ | 15.33$^{cd}$ | 9.51$^{bcd}$ |
| LSSC | 14.5$^{cde}$ | 37.52$^{bcde}$ | 12.06$^{a}$ | 11.10$^{bcd}$ | 15.16$^{bc}$ | 9.71$^{cde}$ |
| TMC | 14.1$^{bcde}$ | 39.68$^{e}$ | 12.15$^{ab}$ | 11.03$^{bc}$ | 15.80$^{f}$ | 9.60$^{bcde}$ |
| GM | 14.8$^{de}$ | 43.67$^{f}$ | 12.11$^{ab}$ | 10.83$^{ab}$ | 14.97$^{ab}$ | 9.67$^{cde}$ |
| $\bar{X}$ | 14.0 | 37.66 | 12.35 | 11.04 | 15.34 | 9.60 |
| EMS | ... | 23.48 | 0.46 | 0.26 | 0.43 | 0.25 |

* Means with identical superscripts are not different at $P \leq 0.05$.

The striking feature revealed by the mean separation tests was the marked distinctness of the DMC sample. For 7 of the 11 meristic characters, DMC fish possessed either the lowest or highest observed mean value; for the remaining 4, DMC means were not significantly different from the observed low (or high) sample mean. This distinctness was especially apparent in number of pyloric caecae, pelvic fin rays, vertebrae, and lateral series scale rows, where DMC fish were essentially unique among the 14 samples.

Comparisons of the number of shared means (Table 2) provided a qualitative measure of morphological similarities among samples. DMC was easily the most dissimilar, sharing an average of only 3.0 means in common with all other samples. LWMC and GM were the next most dissimilar, sharing an average of 5.85 means with other samples. The remaining 11 samples from the Little Kern River appeared to form a relatively close, cohesive grouping, having among them over 8 of 11 means in common. Three sets of pairwise comparisons (LKR-2 and LKR-3; LKR-3 and LKR-4; and TMC and LSGC) were statistically identical for means of all 11 characters.

**TABLE 1*b*. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance *) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.**

| *Sample* | *Branchiostegal rays (total)* | *Vertebrae* | *Gill rakers (I)* | *Scales in lateral series* | *Interneurals* | *Interhaemals* |
|---|---|---|---|---|---|---|
| LKR-1 | $23.22^{bcd}$ | $61.62^{g}$ | $20.49^{cdef}$ | $155.5^{a}$ | $14.51^{bcd}$ | $12.30^{bcde}$ |
| LKR-2 | $23.18^{bc}$ | $61.50^{efg}$ | $20.53^{def}$ | $162.4^{bcd}$ | $14.78^{de}$ | $12.15^{bcd}$ |
| LKR-3 | $22.79^{b}$ | $61.55^{fg}$ | $20.58^{def}$ | $164.5^{bcde}$ | $14.73^{cde}$ | $12.24^{bcde}$ |
| LKR-4 | $23.32^{bcde}$ | $61.10^{cdef}$ | $20.27^{bcde}$ | $161.4^{bc}$ | $14.49^{bcd}$ | $12.12^{bcd}$ |
| USGC | $23.29^{bcde}$ | $60.41^{ab}$ | $20.71^{ef}$ | $160.5^{b}$ | $14.32^{bc}$ | $12.00^{abc}$ |
| LSGC | $23.00^{bc}$ | $61.03^{cde}$ | $20.97^{f}$ | $165.2^{cde}$ | $14.81^{de}$ | $12.32^{cde}$ |
| RC | $22.86^{b}$ | $60.80^{bc}$ | $19.86^{ab}$ | $165.4^{cde}$ | $15.06^{e}$ | $12.54^{ef}$ |
| UWMC | $22.97^{bc}$ | $60.97^{cd}$ | $19.50^{a}$ | $166.3^{de}$ | $14.29^{bc}$ | $12.16^{bcd}$ |
| LWMC | $23.83^{de}$ | $61.31^{defg}$ | $19.91^{abc}$ | $174.1^{f}$ | $14.63^{cd}$ | $12.83^{f}$ |
| DMC | $23.91^{e}$ | $60.06^{a}$ | $19.97^{abcd}$ | $183.5^{g}$ | $13.82^{a}$ | $11.71^{a}$ |
| MSSC | $22.97^{bc}$ | $61.05^{cde}$ | $20.31^{bcde}$ | $175.8^{f}$ | $14.33^{bc}$ | $11.95^{ab}$ |
| LSSC | $22.13^{a}$ | $61.26^{cdefg}$ | $20.13^{bcde}$ | $161.2^{bc}$ | $14.13^{ab}$ | $12.45^{de}$ |
| TMC | $23.08^{bc}$ | $61.18^{cdefg}$ | $20.38^{bcdef}$ | $166.7^{e}$ | $14.45^{bcd}$ | $12.15^{bcd}$ |
| GM | $23.56^{cde}$ | $61.42^{defg}$ | $19.94^{abcd}$ | $166.2^{de}$ | $13.81^{a}$ | $11.75^{a}$ |
| $\bar{\bar{X}}$ | 23.16 | 61.10 | 20.25 | 166.3 | 14.44 | 12.18 |
| EMS | 1.43 | 0.82 | 1.29 | 69.9 | 0.63 | 0.44 |

* Means with identical superscripts are not different at $P \leq 0.05$.

In order to quantitatively assess phenetic similarities among the 14 samples, Euclidian distances between sample pairs were computed from a standardized data matrix, basically following the methodology of Gold and Gall (1975*a*:p. 256). The resulting distance matrix (Table 2) was then clustered using UPGMA average linkage analysis to produce a non-overlapping, hierarchical phenogram (Figure 2). The cophenetic correlation coefficient (matrix with phenogram) was 0.911.

The phenetic affinities among samples depicted in the phenogram essentially paralleled similarities revealed by the comparisons of the number of shared means. DMC was the last group to cluster, being well separated in average distance (21.79 units) from the rest. The fact that DMC has closest affinity to MSSC (13.55 units, Table 2) was not reflected in the phenogram, and may be attributed in part to the distortion at lower clustering levels which usually accompanies cluster analyses (Sneath and Sokal 1973). The similarity between DMC and MSSC stemmed primarily from the high number of lateral series scale rows in these two samples as compared to considerably lower numbers in other samples (Table 1*b*). However, MSSC was closer in average distance (11.65 units) to all other samples than to DMC.

The other 13 samples were closer to one another in average Euclidian distance than any was to DMC. GM, LWMC, MSSC, and LKR-1 were the most divergent, joining the group individually at successively higher clustering levels (14.19, 13.39, 12.51, and 11.37 units, respectively). Individual characters affecting the distinctness of these four samples were high number of pyloric caecae (GM), high number of vertebrae and low number of lateral series scale rows (LKR-1), and high number of lateral series scale rows (MSSC and LWMC). The remaining

nine samples divided into two groups, one containing UWMC and LSSC (9.43 units), and the other LKR-2, 3, 4, TMC, LSGC, USGC, and RC (10.46 units). Separation between these two groups could not be attributed to any single character or suite of characters and appeared to result from small differences in several characters. No further inferences regarding phenetic affinities were made since higher level clusters were apparently affected by sampling variation. This was indicated by the fact that LKR-3 and LKR-4 did not join until 7.08 units, yet the two samples were statistically identical for means of all 11 characters (Table 2).

Canonical analysis of the 11 character data set yielded 11 characteristic roots (canonical variates) which accounted for all of the phenetic variation. Of these, only the first explained an appreciable proportion (48.3%) of the variation and had an eigenvalue greater than 1.0. Characteristic root II accounted for 14.1% of the variation, but its eigenvalue of 0.327 was not significantly different from zero (Wilks's lambda test). Uni-dimensional Hubbs-o-grams displaying univariate statistics of each sample along canonical variate I are provided (Figure 3). Characters contributing heavily to separation along this vector included number of vertebrae, lateral series scale rows, pelvic fin rays, and pectoral fin rays (Table 3).

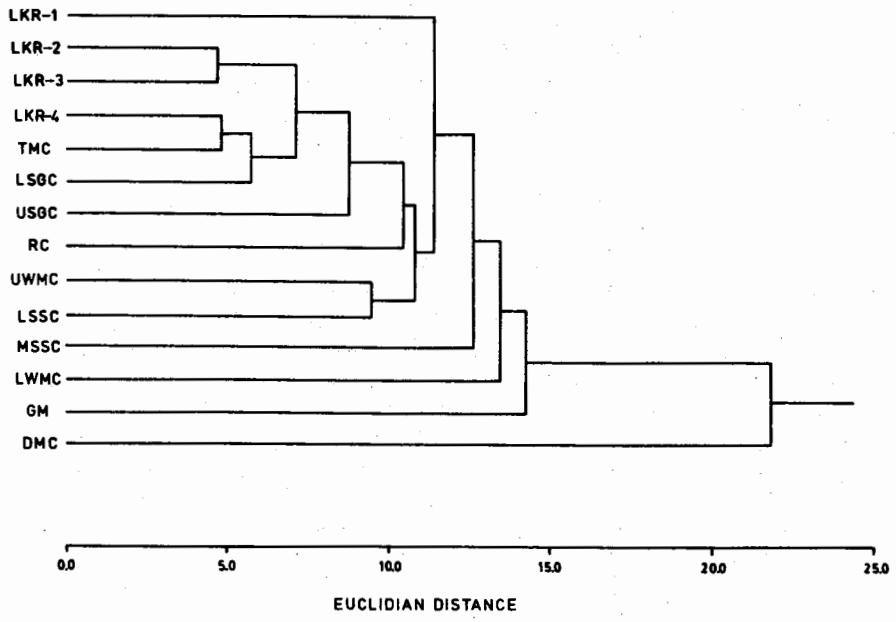


FIGURE 2. Phenogram from UPGMA cluster analysis of the Euclidian distance matrix. The cophenetic correlation $r_{cs}$ was 0.911.

**TABLE 2. Matrices of Mean Similarity * (lower left) and Euclidian Distances (upper right) Between Pairs of Fourteen Samples of Trout from the Little Kern River Basin Area.**

| *Sample* | *LKR-1* | *LKR-2* | *LKR-3* | *LKR-4* | *USGC* | *LSGC* | *RC* | *UWMC* | *LWMC* | *DMC* | *MSSC* | *LSSC* | *TMC* | *GM* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LKR-1 | — | 7.77 | 10.88 | 10.61 | 12.48 | 12.33 | 11.67 | 11.96 | 17.96 | 28.13 | 17.48 | 10.21 | 14.39 | 15.87 |
| LKR-2 | 9 | — | 4.63 | 7.02 | 10.31 | 7.08 | 8.61 | 11.33 | 13.27 | 24.06 | 13.24 | 10.50 | 9.51 | 14.62 |
| LKR-3 | 9 | 11 | — | 6.66 | 10.58 | 5.23 | 10.10 | 12.17 | 12.40 | 23.06 | 11.74 | 9.59 | 6.96 | 14.51 |
| LKR-4 | 7 | 9 | 11 | — | 6.10 | 5.85 | 10.19 | 10.40 | 12.19 | 21.80 | 11.92 | 8.70 | 4.90 | 11.84 |
| USGC | 7 | 7 | 9 | 10 | — | 8.13 | 12.32 | 10.88 | 15.53 | 20.48 | 12.78 | 10.74 | 8.46 | 12.92 |
| LSGC | 8 | 10 | 10 | 10 | 8 | — | 9.59 | 12.58 | 11.48 | 22.00 | 11.25 | 10.08 | 5.61 | 14.60 |
| RC | 7 | 7 | 7 | 7 | 5 | 8 | — | 10.74 | 11.66 | 24.26 | 14.21 | 11.20 | 11.94 | 17.31 |
| UWMC | 7 | 5 | 7 | 7 | 7 | 7 | 6 | — | 14.30 | 18.91 | 9.98 | 9.43 | 11.69 | 12.43 |
| LWMC | 7 | 5 | 6 | 9 | 6 | 6 | 6 | 5 | — | 20.24 | 12.59 | 15.33 | 10.57 | 17.13 |
| DMC | 1 | 1 | 3 | 4 | 5 | 2 | 1 | 2 | 4 | — | 13.55 | 24.36 | 19.78 | 22.61 |
| MSSC | 7 | 8 | 7 | 9 | 9 | 7 | 6 | 8 | 5 | 4 | — | 13.01 | 9.54 | 13.77 |
| LSSC | 7 | 8 | 7 | 9 | 8 | 7 | 8 | 6 | 5 | 3 | 8 | — | 9.85 | 13.51 |
| TMC | 7 | 7 | 10 | 10 | 7 | 11 | 6 | 8 | 7 | 3 | 8 | 8 | — | 11.72 |
| GM | 5 | 6 | 5 | 6 | 5 | 6 | 4 | 7 | 5 | 6 | 7 | 7 | 7 | — |

* Values in each pairwise comparison refer to the number of characters with similar means.

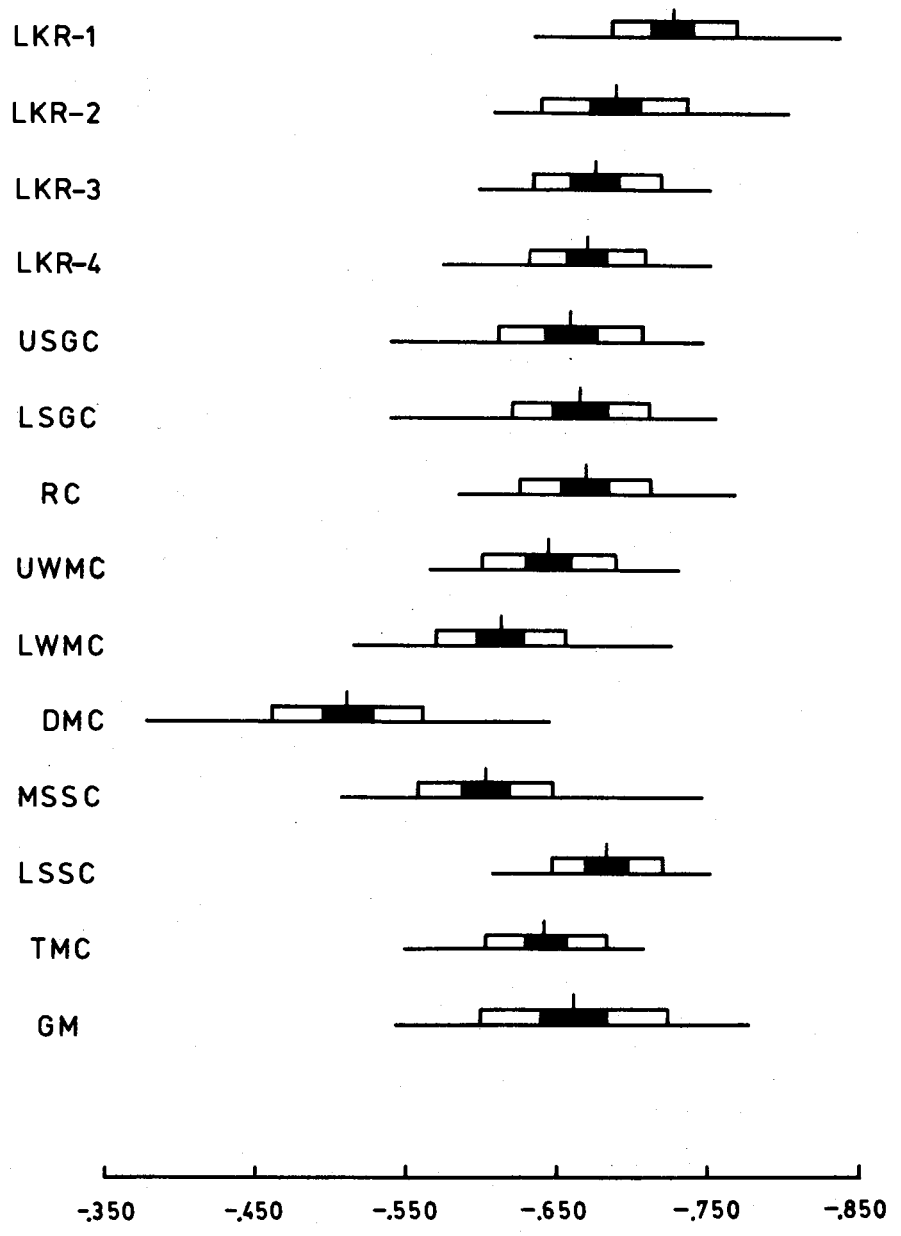


FIGURE 3. Hubbs-o-grams illustrating the phenetic positions of fourteen trout samples along canonical vector I. For each sample, the mean is indicated by the short black vertical line. Two standard errors on either side of the mean are shown by the solid black bar, and one standard deviation on either side of the mean by the white bar plus the black bar. The range is indicated by the solid black horizontal line.

**TABLE 3. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of each Variable on the Vector for Fourteen Samples of Trout from the Little Kern River Basin Area.**

| *Character* | *Variable coefficient* | *Percent influence* |
|---|---|---|
| Pyloric caecae | −0.00154 | 1.97 |
| Dorsal rays | −0.00161 | 0.68 |
| Anal rays | −0.00573 | 2.15 |
| Pectoral rays | 0.02236 | 11.63 |
| Pelvic rays | −0.03645 | 11.86 |
| Branchiostegal rays | 0.00557 | 4.38 |
| Vertebrae | −0.01600 | 33.16 |
| Gill rakers (I) | −0.00884 | 6.07 |
| Scales, lateral series | 0.00407 | 22.99 |
| Interneurals | −0.00842 | 4.13 |
| Interhaemals | −0.00239 | 0.99 |

The relative positions of each sample along vector I closely agree with affinities indicated by the mean similarity and Euclidian distance comparisons. DMC was well separated in 11 character space, and appeared to comprise a single, distinct phenetic group. MSSC and LWMC occupied positions somewhat less than halfway between DMC and a broad group containing the remaining 11 samples. Within the latter, most samples were phenetically similar except for LKR-1 and LSSC, which were displaced slightly to the right of the main group, and UWMC which was displaced slightly to the left (towards DMC). The affinity between UWMC and LSSC, and the distinctness of GM, suggested by the distance phenogram, were not corroborated by canonical analysis. The sample means for these groupings of the two characters (vertebrae and lateral series scale rows) which most heavily influenced vector I were: DMC (60.06, 183.5); LWMC plus MSSC (61.17, 175.0); GM (61.42, 166.2); LKR-1 plus LSSC (61.46, 158.1); and the rest (61.08, 164.0). Separation from left to right along vector I followed a trend of increasing vertebrae number and decreasing lateral series scale row number.

The foregoing indicates the presence of at least two phenetically distinct forms of trout among the 14 samples. One distinct type, represented by DMC fish, is characterized principally by low number of vertebrae and high number of lateral series scale rows. The other 13 samples form a generally homogeneous grouping, although small differences in several characters are often evident. "Marginal" samples (e.g., LKR-1, MSSC, LWMC) show divergences in apparently key characters such as lateral series scale rows, but are more similar to the main group than to DMC.

To examine these differences in relation to other trout forms, MANOVA and canonical analysis were carried out on a new data set which included samples from two populations of domesticated rainbow trout and two populations of *S. a. aguabonita* from the northeastern part of the upper Kern basin. The two rainbow trout samples were designated RTS (Shasta strain) and RTV (Virginia strain), and the two *S. a. aguabonita* samples as SFKR (South Fork Kern River) and GTC (Golden Trout Creek). Observed means, standard deviations, and ranges for several meristic characters in RTS, RTV, and SFKR are shown in Appendix Table 3. Meristic data for GTC may be found in Gold and Gall (1975*a*: p. 253). The meristic data set included only 7 of the 11 characters used earlier

since counts of interneurals, interhaemals, branchiostegal rays, and gill rakers were not available for all samples. The loss of information, however, should be minimal as these four characters usually are not discriminating among these trout (Table 3, Schreck and Behnke 1971, Gold and Gall 1975*a*).

The hypothesis of no overall locality effect in the MANOVA among the 18 samples was rejected ($P < 0.01$) by four different criteria (cf. METHODS). Canonical analysis yielded seven characteristic roots, the first of which explained 78.8% of the variation and had an eigenvalue of 4.725. Characteristic root II accounted for only 7.9% of the variation, and its eigenvalue of 0.476 was not significantly different from zero (Wilks's lambda test). Hubbs-o-grams displaying the positions of each sample along canonical variate I are shown in Figure 4, and character contributions to the vector appear in Table 4. Again, vertebrae and lateral series scale rows most heavily influenced separation, but in this analysis vertebrae number appeared to exert a relatively greater effect.

**TABLE 4. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of Each Variable on the Vector for Eighteen Samples of Trout.**

| *Character* | *Variable coefficient* | *Percent influence* |
|---|---|---|
| Pyloric caecae | 0.00519 | 8.78 |
| Dorsal rays | 0.00832 | 4.45 |
| Anal rays | −0.00392 | 1.88 |
| Pectoral rays | −0.01599 | 10.57 |
| Pelvic rays | 0.01641 | 6.84 |
| Vertebrae | 0.01679 | 44.64 |
| Scales, lateral series | −0.00318 | 22.84 |

The relative positions of the Little Kern samples and GM were only slightly changed in this analysis. DMC remained clearly distinct from the others, and the latter were more or less phenetically the same. MSSC was still positioned approximately halfway between DMC and the main group, but LWMC appeared to be slightly displaced to the right (away from DMC). GM was definitely displaced to the right. These differences are attributable to the greater effect in this analysis of vertebrae number on separation along vector I.

Of the four comparison populations, the two rainbow samples (RTS and RTV) were well displaced to the right and markedly distinct from all other samples. The short distance between RTS and RTV is explained by the increased number of lateral series scale rows in RTS (cf. Appendix Table 3). The two *S. a. aguabonita* samples also differed slightly from one another. GTC was virtually identical to DMC in both multivariate mean (0.552 *vs.* 0.553) and variance (0.0015 *vs* 0.0017); whereas SFKR occupied a position roughly halfway between MSSC and DMC-GTC. Again, the gradient (left to right) along the vector appeared to reflect increasing vertebral number and decreasing lateral series scale row number. Considered together, all samples of Little Kern trout, GM, and the two representatives of *S. a. aguabonita* were more similar to one another than any were to the rainbow trout. A few samples (e.g., LKR-1 and GM) which were displaced to the right appeared more "rainbow-like", but the clearly distinct samples (DMC, GTC, SFKR, and perhaps MSSC) were divergent in a direction

away from rainbow trout. The similarity between DMC and GTC substantiates our earlier findings (Gold and Gall 1975*a, b*) that DMC trout are much more closely related phenetically to *S. a. aguabonita* than to trout from nearby locations in the Little Kern basin.

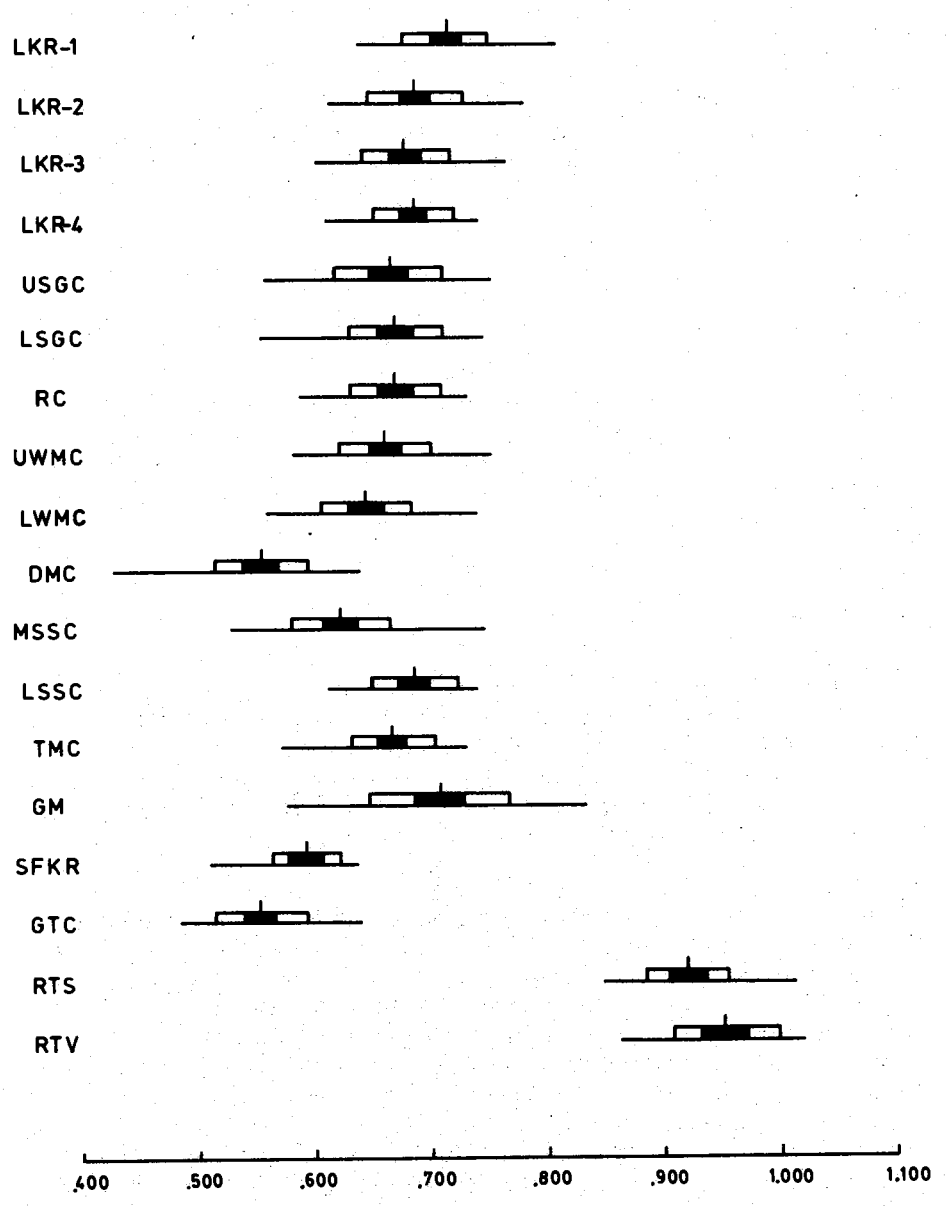


FIGURE 4. Hubbs-o-grams illustrating the phenetic positions of eighteen trout samples along canonical vector I. For further details, see Figure 3.

The last morphological examination performed on the 14 samples was a careful search for the presence of basibranchial or other unusual dentition. Of the 504 specimens examined, 88 (17.5%) possessed at least one basibranchial tooth, and a few specimens had as many as five (Table 5). In only a few instances were these teeth prominent and well developed. All samples except DMC contained individuals with basibranchial dentition, the numbers per sample ranging from 2 of 36 (5.5%) in GM to 12 of 34 (35.3%) in USGC (Table 5). The SFKR fish also were examined for dentition, but only one individual with one poorly developed basibranchial tooth was found.

**TABLE 5. Distribution of Basibranchial Teeth Among Individuals in Fourteen Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Refer to Sample Sizes.**

| *Sample* | *Number of individuals w/basibranchial dentition* | *Number of basibranchial teeth* | | | | |
|---|---|---|---|---|---|---|
| | | *1* | *2* | *3* | *4* | *5* |
| LKR-1 (37) | 7 | 6 | 1 | — | — | — |
| LKR-2 (40) | 4 | 2 | — | 2 | — | — |
| LKR-3 (33) | 7 | 6 | 1 | — | — | — |
| LKR-4 (41) | 6 | 5 | — | 1 | — | — |
| USGC (34) | 12 | 7 | 2 | 2 | 1 | — |
| LSGC (31) | 4 | 2 | — | — | 1 | 1 |
| RC (35) | 10 | 7 | 2 | — | — | 1 |
| UWMC (38) | 9 | 4 | 2 | 2 | — | 1 |
| LWMC (35) | 9 | 8 | 1 | — | — | — |
| DMC (34) | 0 | — | — | — | — | — |
| MSSC (39) | 4 | 4 | — | — | — | — |
| LSSC (31) | 5 | 3 | 1 | — | 1 | — |
| TMC (40) | 9 | 7 | 1 | 1 | — | — |
| GM (36) | 2 | 2 | — | — | — | — |

The unusual "glossohyal" dentition described previously from a few specimens of *S. a. gilberti* (Schreck and Behnke 1971) and the unnamed redband trout (Schreck and Behnke 1971, Gold 1977) were found on only 13 of the 504 specimens examined. Twelve individuals possessed only one of these teeth, and one (from LWMC) had two. Samples with this type of dentition included: LSGC (4), RC (4), LKR-4 (3), LWMC (1), and LKR-1 (1).

## DISCUSSION

The number of trout populations surveyed from the Little Kern basin through 1974 totals 15, and includes samples from headwaters and other portions of most of the permanently flowing streams north of the mouth of Soda Spring Creek. Morphological data reported in different studies (Gold and Gall 1975*a, b,* Gold 1975, this paper) are essentially in agreement and may be summarized as follows: (i) two isolated headwater populations, one from DMC and the other from USSC, are virtually the same in meristic morphology, but differ markedly from trout in all other upper Little Kern streams sampled; (ii) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (iii) phenetically, DMC-USSC trout are nearly identical to *S. a. aguabonita,* as represented by samples from GTC and SFKR; (iv) most other upper Little Kern trout are morphologically similar, but a few (e.g., MSSC, LWMC) are generally intermediate between

DMC-USSC and the rest; (v) all upper Little Kern trouts, upper South Fork Kaweah trout (GM), and *S. a. aguabonita* are more similar to one another than any are to rainbow trout (as represented by RTS and RTV in this study, and four other rainbow samples in Gold 1975); and (vi) in multivariate orientation, most upper Little Kern trout occupy positions between DMC-USSC and rainbow trout. Repeat samples from 1973–1975 (Table 6) suggest these differences are relatively stable and do not stem from sampling error. Patterns of karyotypic and biochemical-genetic variation also have been studied in a few of these populations (Gold and Gall 1975*c*, Gall *et al.* 1976), and are congruent with the morphological data.

**TABLE 6. Selected Meristic Data (mean ± one standard error) from Repeat Samplings of Kern Basin Trout. Numbers in Parentheses Refer to Year Collected.**

| *Sample* | *N* | *Pyloric caecae* | *Pectoral fin rays* | *Pelvic fin rays* | *Vertebrae* | *Scales, lateral series* |
|---|---|---|---|---|---|---|
| DMC (73) [1] | 20 | 30.6±0.4 | 15.4±0.1 | 9.6±0.1 | 59.9±0.1 | 181.0±1.2 |
| DMC (74) [4] | 34 | 33.2±0.6 | 15.7±0.1 | 9.0±0.1 | 60.1±0.1 | 183.5±1.2 |
| DMC (75) [3] | 26 | 35.0±0.7 | 15.5±0.1 | 10.0±0.1 | 60.4±0.1 | 178.9±1.8 |
| USSC (73) [2] | 93 | 32.2±0.4 | 15.5±0.1 | 9.5±0.1 | 60.8±0.1 | 181.8±0.9 |
| USSC-1 (75) [3] | 25 | 34.3±0.7 | 15.8±0.1 | 9.9±0.1 | 60.7±0.2 | 173.0±2.0 |
| USSC-2 (75) [3] | 24 | 39.8±0.9 | 15.2±0.1 | 9.6±0.1 | 60.6±0.2 | 176.4±2.0 |
| SFKR (73) [2] | 40 | 31.1±0.7 | 14.7±0.1 | 9.2±0.1 | 60.0±0.2 | 180.2±2.0 |
| SFKR (74) [4] | 19 | 31.5±0.8 | 14.5±0.1 | 9.0±0.0 | 59.8±0.2 | 172.7±1.8 |
| LSSC (73) [2] | 36 | 34.6±0.7 | 14.9±0.1 | 9.4±0.1 | 61.3±0.2 | 157.7±1.9 |
| LSSC (74) [4] | 31 | 37.5±0.8 | 15.2±0.1 | 9.7±0.1 | 61.3±0.2 | 161.2±1.4 |
| LKR (73) [2] | 56 | 36.0±0.7 | 15.0±0.1 | 9.8±0.1 | 61.4±0.2 | 156.8±1.5 |
| LKR-3 (74) [4] | 33 | 37.4±1.0 | 15.6±0.1 | 9.8±0.1 | 61.5±0.2 | 164.5±1.5 |
| LKR-4 (74) [4] | 41 | 39.3±0.8 | 15.6±0.1 | 9.6±0.1 | 61.1±0.1 | 161.4±1.3 |

Data are from [1]Gold and Gall (1975*b*); [2]Gold and Gall (1975*a*); [3]Smith (1980); and [4]this paper. LKR samples represent different localities not separated by physical barriers.

The observed patterns of geographic variation among Little Kern trouts are not easily explained by models based only on chance or adaptive effects. Under a chance model, divergence should be random in direction and inversely proportional to effective population size in magnitude. Both DMC and USSC are isolated headwater populations, and both apparently have limited population levels and low fecundity (Smith 1977). However, similar conditions prevail in many upper Little Kern streams, and thus far none of the other isolated headwater populations (LKR-1, USGC, UWMC, and TMC) have been anywhere near as divergent as DMC-USSC. It also would be difficult under a chance model to explain why the overall change in direction and magnitude in the geographically separate DMC and USSC populations is nearly the same, and why these differences appear stable from year to year. If both populations are or have been subjected to unusually severe stochastic effects, then at least some degree of divergence between the two might be expected.

Under an adaptive model, the observed patterns of variation would best be explained by assuming past or present directional selective pressures which affected only trout in DMC and USSC. However, there are no obvious ecological or habitat differences which distinguish DMC and USSC from other upper Little Kern streams (Evans, Smith, and Bell 1973; Smith 1977), and we have found no evidence of clinal variation in any meristic character. Further, if selection alone

has produced the constellation of characteristics which typify DMC-USSC trout, then similar selective pressures also must exist in GTC and SFKR. Certainly, it would be difficult to argue that habitat conditions and selective pressures in DMC and USSC are more similar to those in the distant drainages of Golden Trout Creek and the South Fork Kern River than to those in the same basin.

A third possibility is that the variation stems from differential "non-genetic" or environmental effects that radically alter embryonic developmental rate and duration (Hubbs 1922, 1926; Hamor and Garside 1976). Laboratory experiments on several fishes, including salmonids, have shown that segment numbers for most meristic characters generally increase under growth retarding conditions, and decrease under accelerating conditions (Gabriel 1944, Tåning 1952, Garside 1966, Kwain 1975). The extent of these effects in natural trout populations, however, is apparently fairly small (Behnke 1979). Schreck and Behnke (unpub. data, see 1971: p. 990) compared morphologies of introduced populations with their parental stocks in four different trout taxa (including *S. aguabonita*) and found that no more than 2% of the differences in mean values for most meristic characters (up to 5% in scale rows) could be attributed to nongenetic effects. Since the percent differences among upper Little Kern trout meristic means are considerably greater than 2% (15% in scale rows), the observed variation would appear to be the result of true genetic differentiation. There also was no indication of a parallel response in the direction of character divergence (e.g., the gradient along vector I in canonical analysis), which further argues against an environmental effects model.

The foregoing considerations suggest that the patterns of morphological and genetic variation among present-day Little Kern trouts cannot logically be accounted for by those evolutionary forces which normally promote differentiation among natural populations. The DMC and USSC trout apparently represent a unique form in the upper Little Kern basin; but given the geographic separation and absence of gene flow between the two populations, it is difficult to explain how trout in both have diverged in the same direction and to nearly the same extent. The key to the problem, however, may not lie in the dissimilarities among Little Kern trouts, but rather in the similarities between DMC-USSC trout and *S. a. aguabonita*. In almost every criterion thus far examined, including meristic morphology, karyotype, and biochemical-genetic profile, DMC-USSC trout have been more similar to *S. a. aguabonita* than to trout only a few miles distant in the same basin (Gold and Gall 1975*a, b, c,* unpubl. data, Gall *et al.* 1976). The only noticeable differences we have found, aside from geographic separation, are slight variations in number and location of body spots. DMC-USSC trout are similar, on the average, to the color plate of *S. whitei* shown in Evermann (1906), and tend to have more body spots, particularly below the lateral line. However, there is considerable variation in spotting among DMC-USSC trout, and individuals with patterns typical of present-day *S. a. aguabonita* are not infrequent (Gold and Gall unpubl. data, Smith 1977: Figures 1–3). Further, DMC-USSC trout are actually more similar in spotting to *S. a. aguabonita* than to certain Little Kern populations (e.g., LSSC) where individuals often display the profuse spotting typical of *S. gairdneri*. In short, the present evidence strongly suggests that DMC-USSC trout are little more than isolated populations of a form now considered to represent *S. a. aguabonita*.

If our interpretations are correct, and DMC-USSC trout are the same as *S. a.*

*aguabonita*, then their presence in the Little Kern basin may be explained under one of two hypotheses: either (i) DMC-USSC trout are relicts of a trout form which once occupied much of the upper Kern basin, and is now represented only by stocks in DMC, USSC, GTC, SFKR, and perhaps a few other streams; or (ii) they are vestiges of earlier transplants of *S. a. aguabonita* into the Little Kern basin. Unfortunately, the present data cannot distinguish between these two alternatives since both predict morphological and genetic similarity between DMC-USSC trout and *S. a. aguabonita*. However, stocking records compiled by Schreck (1969) do not list any official introductions of *S. a. aguabonita* into the Little Kern basin, and given the remoteness and terrain surrounding the DMC and USSC headwater sites it is unlikely that any introductions ever were made. On this basis we favor the first hypothesis, but note that the second cannot presently (if ever) be falsified.

What about the trout elsewhere in the upper Little Kern basin? The morphological and genetic intermediateness of most of these populations between *S. a. aguabonita* (including DMC and USSC trout) and *S. gairdneri* suggests a hybrid origin, or at least introgression (Anderson 1949) of rainbow genes into native golden populations. Stocking records (Schreck 1969) show that almost every Little Kern site thus far examined, excepting DMC, USSC, and UWMC, either received or was accessible to hatchery or other rainbow trout planted in the basin. The UWMC site, however, received a transplant of trout in 1892 from somewhere in the Little Kern River (Ellis and Bryant 1920), and also happens to be located in a small meadow adjacent to a major trail, an ideal spot for packers to have planted non-native trout.

Several aspects of the data support an introgression hypothesis. First, most upper Little Kern populations are not strictly intermediate in morphology between the two presumed parental types, but are more similar to DMC-USSC trout. This would be expected if not all planted fish crossed with natives, or if backcrossing to golden trout took place in the 30 years since the last official rainbow introductions. Secondly, trout from tributaries entering the Little Kern River below Soda Spring Creek (e.g., Alpine Creek or Mountaineer Creek), where extremely heavy rainbow introductions are known to have occurred, are morphologically more similar to *S. gairdneri* than to *S. aguabonita* (Smith 1981). Finally, the karyotypic and biochemical-genetic data suggest a small, but detectable rainbow influence (Gold and Gall 1975*c*, Gall *et al.* 1976).

As pointed out by Miller (1972) 'critical' evidence of hybrid fertility often is lacking in western *Salmo*, and it is important to note that much of the evidence for introgression in the Little Kern basin is circumstantial. Schreck (1969) and Schreck and Behnke (1971) faced the same problem in their studies of Little Kern trouts, and could only tentatively identify hybrid populations by greater meristic variability and heavier spotting patterns. In a few populations we have examined (e.g., LSSC and LKR from Gold and Gall 1975*a*) there are fish with the profuse spotting typical of *S. gairdneri*. But in others (e.g., RC) most individuals resemble Evermann's *S. whitei*. Since the genetic basis of spotting in western *Salmo* is virtually unknown, identification of 'purity' based solely on this characteristic seems a dubious prospect. There also were no apparent differences in meristic variability (Table 7) among the 14 populations (including DMC) examined in the present study. This does not falsify an introgression hypothesis, but rather demonstrates the difficulty of the problem. One might expect, for exam-

ple, that after 30 years populations would have achieved morphological stability, particularly if the amount of introgression were small.

**TABLE 7. Mean Coefficients of Variance (after Soulé 1972) for Eleven Normally Distributed Meristic Characters of Fourteen Samples of Trout from the Little Kern Basin Area.**

| *Sample* | *Mean C.V. ± S.E.* |
|---|---|
| LKR-1 | 5.25 ± 0.80 |
| LKR-2 | 5.83 ± 0.78 |
| LKR-3 | 5.85 ± 0.96 |
| LKR-4 | 5.65 ± 0.82 |
| USGC | 6.11 ± 0.98 |
| LSGC | 5.28 ± 0.77 |
| RC | 5.48 ± 0.88 |
| UWMC | 5.27 ± 0.62 |
| LWMC | 4.93 ± 0.71 |
| DMC | 4.79 ± 0.71 |
| MSSC | 5.06 ± 0.96 |
| LSSC | 5.36 ± 0.77 |
| TMC | 5.27 ± 0.73 |
| GM | 6.07 ± 1.02 |

Regardless, what is important is that the DMC-USSC trout are different from most other upper Little Kern basin trout. For key meristic characters such as vertebrae, lateral series scale rows, and pyloric caecae, the magnitude of difference invariably exceeds three standard errors of a mean, well beyond the usual limits of statistical confidence. The lone exception are MSSC trout which are divergent from the main group and toward DMC-USSC. This can easily be explained since the MSSC site is directly below both DMC and USSC and must receive occasional migrants of DMC-USSC genotype.

The above discussions have bearing on the systematics and present classifications of Kern basin trout. Briefly, five forms of trout, including four golden species and one rainbow subspecies, have been described from the Kern River drainage. The golden trouts include *S. aguabonita* Jordan (Jordan and Henshaw 1878: listed as *S. pleuriticus* Cope, Jordan 1892, 1893) from the South Fork Kern River; *S. roosevelti* Evermann (1906) from Golden Trout Creek (formerly Volcano Creek); *S. rosei* Jordan and McGregor (1924) from Culver Lake; and *S. whitei* Evermann (1906) from the Little Kern basin. Ironically, Evermann's description of *S. whitei* was based on specimens from the headwaters of the South Fork Kaweah River (Green Meadows site, this paper) where trout had been transplanted from Soda Spring Creek. The rainbow subspecies, *S. gairdneri gilberti* Jordan (Jordan and Henshaw 1878: listed as *S. irideus* and *S. tsuppitch,* Jordan 1894), was described from specimens taken in the Kern River.

Based on studies by Curtis (1934, 1935), *S. aguabonita* and *S. roosevelti* were eventually synonomized, and have gradually become classified as *S. aguabonita aguabonita* (Shapovalov, Dill, and Cordone 1959). Dill and Shapovalov (1954) synonomized *S. rosei* with *S. g. gilberti* because of earlier transplants from Big Arroyo (Creek) to Culver Lake; but Schreck and Behnke (1971) felt that *rosei* might have been a hybrid between *gilberti* and *S. a. aguabonita.* In either case, *S. rosei* is no longer considered a valid taxon. Dill (1945) was the first to refer to *S. whitei* as *S. a. whitei,* a suggestion which later became generally accepted (Shapovalov, Dill, and Cordone 1959). Schreck and Behnke (1971) synonomized *S. a. whitei* and *S. g. gilberti,* and based on karyotypic and meristic

similarities to *S. a. aguabonita* and the priority of *gilberti* over *whitei* in the literature reclassified Little Kern trout as *S. a. gilberti.* They also concurred with the synonomy of *S. aguabonita* and *S. roosevelti,* and the invalidity of *S. rosei.*

Taxonomic data for key meristic characters of pertinent upper Kern trouts and other western *Salmo* are shown in Table 8. Other comparative data for these trouts include dentary characteristics, karyotypes, and spotting patterns. The type specimens of *S. "rosei"* and *S. "whitei",* and present-day specimens of *S. a. aguabonita,* DMC-USSC trout, and *S. gairdneri* apparently do not possess basibranchial dentition; whereas individuals from the remaining groups often have one or a few of these teeth (Schreck and Behnke 1971, Schreck pers. commun., Gold and Gall 1975*a,* Gold 1977, this paper). Diploid karyotypes of *S. a. aguabonita,* DMC-USSC trout, samples from LSSC and LKR, and the redband trout contain 58 chromosomes and 104 chromosome arms (Miller 1972, Wilmot 1974, Gold and Gall 1975*c,* Gold 1977, unpubl. data). North American *S. gairdneri* also possess 104 (diploid) chromosome arms, but chromosome numbers range at least from 58–60 (Thorgaard 1976, 1977, unpubl. data). Spotting patterns on DMC-USSC trout are similar to Evermann's *"whitei"* (see also Smith 1977: Figures 1–3), but the variation in this character render it a poor taxonomic criterion. Most other trout listed in Table 8 (except *S. a. aguabonita* and *S. gairdneri*) have been described as similar in spotting to Evermann's *"whitei"* (Schreck 1969, Schreck and Behnke 1971, Gold and Gall 1975*a,* Gold 1977).

Consideration of these data lead to the following general conclusions. First, the use of *S. a. whitei* for the DMC-USSC trout (e.g., Gold and Gall 1975*a*) may no longer be appropriate. These fish are nearly the same as *S. a. aguabonita,* and may be distinguished from other upper Kern basin trout, including *S. "whitei"* or *S. a. gilberti,* by fewer pyloric caecae and vertebrae, and greater number of lateral series scale rows. On the basis of morphological and meristic criteria, the DMC-USSC trout and *S. a. aguabonita* in our opinion do not warrant formal taxonomic separation.

Secondly, most upper Little Kern trout (including GM) and the types of *S. "rosei", S. "whitei",* and *S. g. gilberti* are not separable from one another. All are more or less intermediate in morphology between *S. a. aguabonita* and *S. gairdneri,* and the few observable differences (Table 8) can easily be attributed to sampling errors because of the small sizes of some samples. Schreck and Behnke (1971) considered a similar data set (minus samples from DMC and USSC) and proposed synonomy of *S. "whitei"* and *S. g. gilberti.* They referred both to *S. aguabonita* because of similarities in karyotype and morphology, and retained the subspecific designation *S. a. gilberti* for Little Kern trout.

Finally, most upper Kern basin trout, including all named forms except *S. (a.) aguabonita,* cannot be distinguished from the redband trout. Although only limited taxonomic data on redband trout are published (Hoopaugh 1974, Gold 1977), the similarities with most Little Kern trout are obvious, and it has been suggested that all Kern basin golden trouts are actually derivatives of an older, more primitive redband phyletic line (Miller 1972, Gold 1977). Schreck and Behnke (1971) cited the similarities between redband trout and their *S. a. gilberti* as evidence that the latter was not of hybrid origin.

**TABLE 8. Meristic Comparisons Among Upper Kern and Other Western *Salmo*.**

| *Character* Group | *Pyloric caecae* | *Vertebrae* | *Scales, lateral series* |
|---|---|---|---|
| *S. a. aguabonita* | 21–41 (31.1)* n=141 | 57–62 (59.6) n=267 | 150–212 (178.5) n=166 |
| DMC-USSC | 24–45 (33.6) n=222 | 57–63 (60.5) n=222 | 155–204 (180.1) n=222 |
| Other upper Little Kern trout | 23–52 (37.1) n=526 | 58–65 (61.2) n=526 | 133–202 (163.6)† n=526 |
| Green Meadows | 33–59 (43.7) n=36 | 59–63 (61.4) n=36 | 150–191 (162.2) n=36 |
| *S. "rosei"* | ... | 60–62 (61.0) n=3 | 155–170 (162.3) n=3 |
| *S. "whitei"* | ... | 60–63 (61.5) n=8 | 148–167 (159.0) n=8 |
| *S. g. gilberti* | 37–43 (40.0) n=2 | 60–64 (61.2) n=16 | 137–160 (152.7) n=10 |
| Redband trout | 29–42 (36.0) n=25 | 60–63 (61.4) n=25 | 153–174 (162.1) n=25 |
| *S. gairdneri* | 31–79 (50.3) n=246 | 58–67 (63.0)‡ n=331 | 115–154 (133.3) n=331 |

* Data are shown as ranges, means (in parentheses), and sample sizes. Sources of the data were as follows: *S. a. aguabonita* (*S. "rooseveltí"* and *S. a. aguabonita* in Table 2 of Schreck and Behnke (1971), and GTC and SFKR in Gold and Gall (1975*a*) and this paper); DMC-USSC trout (Table 6, this paper); other upper Little Kern and Green Meadows trout (Gold and Gall 1975*a*, this paper); *S. "rosei"*, *S. "whitei"*, and *S. g. gilberti* (types and other specimens from collections in 1893, 1904, and 1923, in Table 2 of Schreck and Behnke (1971)); redband trout (Gold 1977); and *S. gairdneri* (RTS and RTV from this paper, four samples in Gold (1975), samples from the Mt. Whitney and Hot Creek hatcheries in California, and samples from two wild steelhead populations along the northern California coast).

† Includes fine-scaled trout from MSSC.

‡ Includes sample with low vertebral number from Mt. Whitney State Hatchery in California.

The picture which emerges is that at least two forms may be identified among past and present upper Kern basin trout: a fine-scaled, low to intermediately spotted, brilliantly colored form represented by Jordan's *S. (a.) aguabonita;* and a second type, which is essentially identical to present-day redband trout, represented by Jordan's *S. g. gilberti,* Evermann's *S. whitei,* and Jordan and McGregor's *S. rosei.* The presence of the first type in both upper Kern and Little Kern waters and at sites located on the southern-most edge of the last glacial advance (Matthes 1965, Schreck 1969: map 4), suggests it is the ancestral form and is descended from among the first trouts to enter the Kern basin either before or during the last glacial retreat. The intermediateness of the second type between *S. a. aguabonita* and *S. gairdneri* suggests a hybrid origin. Stocking records compiled by Schreck (1969) indicate that several introductions and transplants in the upper Kern basin occurred well before Evermann's Little Kern and Kern River collections in 1904, and probably before the 1893 Kern River collections of *S. g. gilberti.* Many of the introductions involved non-natives such as *S. gairdneri* and *S. clarki* (cutthroat trout), and it may be assumed that subsequent transplants often included hybrids between non-natives and endemics.

An alternative view (Schreck and Behnke 1971) is that the *gilberti*-like trout represent a distinct evolutionary lineage which arose either directly from *S. (a.) aguabonita* in the Kern basin, or from a redband-like trout that entered the Kern

at a later time. Geographic considerations do not rule out either possibility since several natural barriers which could engender isolation exist throughout the Kern basin, and infiltration into the Kern by derivatives of the redband trout apparently did occur through adjacent connections in the Sacramento and San Joaquin Valleys.

Our evidence to date suggests that DMC-USSC trout are best referred to *S. (a.) aguabonita,* and that they represent relics of (one of) the earliest trout forms to enter present-day Kern basin waters. Our data unfortunately do not resolve the question of whether other Little Kern basin trout and (by inference) the forms described as *S. g. gilberti* and *S. whitei* merit separate taxonomic status, or whether they represent remnants of hybridization between endemic goldens (*S. (a.) aguabonita*) and introduced (or invading) non-natives. We agree with Behnke (pers. commun.) and Schreck and Behnke (1971) that: (i) many present-day Little Kern trout and those described as *gilberti* and *whitei* are morphologically the same, (ii) this form resembles present-day redband trout, and (iii) more than one trout form probably infiltrated post-glacial Kern basin waters. The problem is that we have not as yet found a consistent, objective criterion for delineating hybrid or introgressed Kern basin trout from those which might represent "pure" *gilberti.* This problem is further confounded by the possibility that introduced (or invading) trout were very likely a heterogeneous mixture of several forms. What is needed in the future are comparative studies using higher resolution genetic techniques (e.g., chromosome banding or DNA sequencing) which will permit direct tests of the hypothesis that Little Kern trout other than those in DMC-USSC warrant separate taxonomic status from the trout originally described as *Salmo aguabonita* Jordan. Electrophoretic studies to determine the amount of biochemical-genetic differentiation between DMC-USSC trout and those recognized as *S. a. aguabonita* are currently in progress.

## ACKNOWLEDGMENTS

We wish to thank all the California Department of Fish and Game (CDFG) personnel, especially those in Region 4, who provided or participated in collecting the specimens used in this study. We are particularly indebted to D. Christenson, A. Cordone, S. Nicola, G. Nokes, and P. Pister, and to all members of the CDFG Committee on Threatened Trout for their encouragement and support of the Little Kern project. We also thank B. J. Janak for assistance with the statistical analyses and B. Behnke and S. Nicola for their very valuable comments on the manuscript. The study was supported in part by the Department of Fish and Game, The Resources Agency of California, Contract No. S-813; by Federal Aid to Fish Restoration funds as part of Dingell-Johnson project California F-28-R, 'Trout Genetics'; and by the Texas Agricultural Experiment Station, Texas A&M University.

## REFERENCES

Anderson, E. A. 1949. Introgressive hybridization. John Wiley and Sons, Inc., New York. 109 p.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A user's guide to SAS '76. SAS Inst. Inc., Raleigh, North Carolina, 329 p.

Behnke, R. J. 1970. The application of cytogenetic and biochemical systematics to phylogenetic problems in the family Salmonidae. Amer. Fish. Soc., Trans., 99: 237–248.

_____ 1972. The systematics of salmonid fishes of recently glaciated lakes. Can., Fish. Res. Bd., J., 29: 639–671.

_____ 1979. The native trouts of the genus *Salmo* of western North America. (unpublished monograph).

Christenson, D. P. 1978. A fishery management plan for the Little Kern golden trout. Calif. Fish Game, Inland Fish., Endang. Spec. Progr. Spec. Publ. No. 78-1. 14 p. (mimeo).

Curtis, B. 1934. The golden trout of Cottonwood Lakes (*Salmo agua-bonita* )Jordan. Amer. Fish. Soc., Trans., 64: 259–265.

_____. 193S. The golden trout of Cottonwood Lakes. Calif. Fish Game, 21: 109–121.

Dangel, J. R. 1973. An annotated bibliography of interspecific hybridization of Salmonidae. FAO United Nations Fish. Circ., No. 133. 32 p. (mimeo).

Dill, W. A. 1941. The Little Kern River drainage, Tulare County. Prog. Rep. No. 1, Calif. Fish Game, Inland Fish. Admin. Rep. No. 41-21. 12 p. (mimeo).

_____. 194S. The Little Kern River drainage, Tulare County. Prog. Rep. No. 2, Calif. Fish Game, Inland Fish. Admin. Rep. No. 45-29. 19 p. (mimeo).

_____. 1950. A preliminary report on the status of the golden trout fishery of California. Calif. Fish Game, Inland Fish. Admin. Rep. No. 50-44, 28 p. (mimeo).

Dill, W. A., and L. Shapovalov. 1954. *Salmo rosei,* not a valid species. Calif. Fish Game, 40: 337–338.

Ellis, S. L. N., and H. C. Bryant. 1920. Distribution of the golden trout in California. Calif. Fish Game, 6: 142–152.

Evans, W. A., R. C. Smith, and M. Bell. 1973. A reconnaissance survey of the fish resources of the Little Kern River drainage, California. USDA For. Serv. Region 5, and Calif. Fish Game. 41 p. (mimeo).

Evermann, B. W. 1906. The golden trout of the southern High Sierras. U. S. Bur. Fish., Bull., 2S: 1–51.

Gabriel, M. L. 1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus.* J. Exp. Zool., 95: 105–147.

Gall, G. A. E., C. A. Busack, R. C. Smith, J. R. Gold, and B. J. Kornblatt. 1976. Biochemical genetic variation in populations of golden trout, *Salmo aguabonita:* evidence of the threatened Little Kern River golden trout, *S. a. whitei.* J. Hered., 67: 330–335.

Garside, E. T. 1966. Developmental rate and vertebral number of salmonids. Can., Fish. Res. Bd., J., 23: 1537–1551.

Gold, J. R. 1975. Phenetics and genetics of High Sierran golden trout *(Salmo aguabonita).* Cal-Neva Wildl., Trans., (1975): 13–26.

_____. 1977. Systematics of western North American trout *(Salmo),* with notes on the redband trout of Sheepheaven Creek, California. Can. J. Zool., 55: 1858–1873.

Gold, J. R., and G. A. E. Gall. 1975*a*. The taxonomic structure of six golden trout *(Salmo aguabonita)* populations from the Sierra Nevada, California (Pisces: Salmonidae). Calif. Acad. Sci., Proc., 40(10): 243–263.

_____. 1975*b*. Further record of Little Kern golden trout, *Salmo aguabonita whitei,* in the Little Kern River basin, California. Calif. Fish Game, 61: 248–250.

_____. 1975*c*. Chromosome cytology and polymorphism in the California High Sierra golden trout *(Salmo aguabonita).* Can. J. Genet. Cytol., 17: 41–53.

Gold, J. R., R. E. Pipkin, and G. A. E. Gall. 1976. Artificial hybridization between rainbow *(Salmo gairdneri)* and golden trout *(Salmo aguabonita).* Copeia, 1976(3): 597–598.

_____. 1979. Notes on a hybridization experiment between rainbow and golden trout. Calif. Fish Game, 65: 179–183.

Gould, W. R. 1966. Cutthroat trout (*Salmo clarkii* Richardson) x golden trout (*Salmo aguabonita* Jordan) hybrids. Copeia, 1966(3): 599–600.

Hamor, T., and E. T. Garside. 1976. Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. Can. J. Zool., 54: 1912–1917.

Hartman, G. F. 1956. A taxonomic study of cutthroat trout, *Salmo clarki clarki* Richardson, rainbow trout, *Salmo gairdneri* Richardson, and reciprocal hybrids. Thesis, Univ. British Columbia, Vancouver. 71 p.

Hoopaugh, D. A. 1974. Status of the redband trout (*Salmo* sp.) in California. Calif. Fish Game, Inland Fish. Admin. Rep. No. 74-7. 11 p. (mimeo).

Hubbs, C. L. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of the water during development. Am. Nat., 56: 360–372.

_____. 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. Am. Nat., 60: 57–81.

Jordan, D. S. 1892. Description of the golden trout of Kern River. Calif. St. Bd. Fish Comm., Bienn. Rep., 1891–1892, 12: 62–65.

_____. 1893. A description of the golden trout of Kern River, California, *Salmo mykiss agua-bonita.* U. S. Nat. Mus., Proc., 15: 481–483.

_____. 1894. Descriptions of new varieties of trout. Calif. St. Bd. Fish Comm., Bienn. Rep., 1893–1894, 13: 142–143.

Jordan, D. S., and H. W. Henshaw. 1878. Report upon the fishes collected during the years 1875, 1876, and 1877, in California and Nevada. U. S. Chief Engin., Ann. Rep., part 3: 1609–1622.

Jordan, D. S., and E. A. McGregor. 1924. Description of a new species of trout *(Salmo rosei)* from Lake Culver in the High Sierras of California. Acad. Nat. Sci. Phil., Proc., 76: 19–22.

Kwain, W. 1975. Embryonic development, early growth, and meristic variation in rainbow trout *(Salmo gairdneri)* exposed to combinations of light intensity and temperature. Can., Fish. Res. Bd., J., 32: 397–402.

Legendre, P., C. B. Schreck, and R. J. Behnke. 1972. Taximetric analysis of selected groups of western North American *Salmo* with respect to phylogenetic divergences. Syst. Zool., 21: 292–307.

Matthes, F. E. 1965. Glacial reconnaissance of Sequoia National Park, California. Geol. Surv. Prof. Pap., 504-A: 1–58.

Mayr, E. 1973. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts. 797 p.

McGlade, J., and H. MacCrimmon. 1979. Taxonomic congruence in three populations of Quebec brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool., 57: 1998–2009.

Meyer, F. A. 1965. Golden trout waters of California. Calif. Fish Game, Inland Fish. Admin. Rep. No. 65-1, 24 p. (mimeo).

Miller, R. R. 1972. Classification of the native trouts of Arizona, with the description of a new species, *Salmo apache*. Copeia, 1972(3): 401–422.

Needham, P. R., and R. Gard. 1959. Rainbow trout in Mexico and California: with notes on the cutthroat series. Univ. Calif. Publ. Zool., 67: 1–124.

Schreck, C. B. 1969. Trouts of the upper Kern River basin, California. Thesis, Colo. St. Univ., Ft. Collins, Colo. 120 p.

Schreck, C. B., and R. J. Behnke. 1971. Trouts of the upper Kern River basin, California, with reference to systematics and evolution of western North American *Salmo*. Can., Fish. Res. Bd., J., 28: 987–998.

Shapovalov, L., W. A. Dill, and A. J. Cordone. 1959. A revised checklist of the freshwater and anadromous fishes of California. Calif. Fish Game, 45: 159–180.

Smith, J. R. 1977. Aspects of the reproductive biology and behavior of the Little Kern golden trout. Thesis, Calif. St. Univ., Fresno, Calif. 151 p.

Smith, R. C. 1981. A biochemical-genetic and meristic analysis of populations of Little Kern River golden trout. Dissertation, Univ. Calif., Davis, Calif.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco. 573 p.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco. 776 p.

Soulé, M. 1972. Phenetics of natural populations. III. Variation in insular populations of a lizard. Am. Nat., 106: 429–446.

Tåning, A. V. 1952. Experimental study of meristic characters in fishes. Biol. Rev., 27: 169–193.

Thorgaard, G. H. 1976. Robertsonian polymorphism and constitutive heterochromatin distribution in chromosomes of the rainbow trout *(Salmo gairdneri)*. Cytogenet. Cell Genet., 17: 174–184.

_____. 1977. Heteromorphic sex chromosomes in male rainbow trout. Science, 196: 900–902.

Wilmot, R. L. 1974. A genetic study of the red-band trout. Dissertation, Oregon St. Univ., Corvalis, Oregon. 60 p.

**APPENDIX TABLE 1. Key to Geographic Locations of Collection Sites.**

| *Collection site* | *Longitude W(118°)* | *Latitude N(36°)* | *Altitude (in feet)* |
|---|---|---|---|
| Little Kern River (LKR-1) | 33'8" | 22'12" | 8,800 |
| Little Kern River (LKR-2) | 32'56" | 21'52" | 8,540 |
| Little Kern River (LKR-3) | 33'5" | 21'12" | 8,080 |
| Little Kern River (LKR-4) | 31'48" | 19'24" | 7,200 |
| Upper Shotgun Creek (USGC) | 31'48" | 22'28" | 9,880 |
| Lower Shotgun Creek (LSGC) | 31'55" | 20'48" | 7,720 |
| Rifle Creek (RC) | 31'15" | 20'8" | 7,520 |
| Upper Wet Meadows Creek (UWMC) | 34'42" | 21'14" | 9,200 |
| Lower Wet Meadows Creek (LWMC) | 33'48" | 21'8" | 8,720 |
| Deadman Creek (DMC) | 34'8" | 20'14" | 8,480 |
| Middle Soda Spring Creek (MSSC) | 33'50" | 18'58" | 7,760 |
| Lower Soda Spring Creek (LSSC) | 31'25" | 15'34" | 6,400 |
| Tamarack Creek (TMC) | 29'35" | 18'48" | 7,840 |
| Green Meadows (GM)* | 35'53" | 20'26" | 9,320 |

*Sample from the South Fork Kaweah River (cf. text).

**APPENDIX TABLE 2*a*. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.**

| *Character* | *LKR-1* (37) | *LKR-2* (40) | *LKR-3* (33) | *LKR-4* (41) | *USGC* (34) | *LSGC* (31) | *RC* (35) |
|---|---|---|---|---|---|---|---|
| Fork length (cm) | 15.0±3.1 (11.0–21.4) | 14.1±1.9 (10.6–16.6) | 13.6±2.4 (10.4–21.3) | 13.3±2.1 (9.1–20.2) | 14.6±1.9 (11.4–18.7) | 14.0±2.3 (10.2–18.3) | 14.7±3.0 (10.6–22.1) |
| Pyloric caecae | 35.86±4.45 (28–45) | 36.78±4.44 (31–47) | 37.39±5.54 (26–48) | 39.32±5.06 (30–50) | 36.79±5.46 (30–52) | 38.55±4.53 (32–51) | 37.29±5.02 (30–52) |
| Dorsal rays | 12.57±0.69 (11–14) | 12.78±0.95 (11–14) | 12.58±0.71 (11–14) | 12.29±0.59 (11–13) | 12.32±0.73 (11–14) | 12.35±0.75 (11–14) | 12.69±0.80 (12–15) |
| Anal rays | 11.14±0.53 (10–12) | 11.08±0.47 (10–12) | 10.94±0.50 (10–12) | 11.10±0.49 (10–12) | 11.00±0.60 (10–12) | 11.06±0.44 (10–12) | 11.37±0.55 (11–13) |
| Pectoral rays | 14.76±0.55 (14–16) | 15.30±0.78 (13–17) | 15.61±0.79 (14–17) | 15.59±0.77 (14–17) | 15.41±0.69 (14–17) | 15.61±0.66 (15–17) | 15.09±0.61 (14–16) |
| Pelvic rays | 9.78±0.48 (9–10) | 9.78±0.42 (9–10) | 9.79±0.48 (9–11) | 9.63±0.49 (9–10) | 9.47±0.51 (9–10) | 9.71±0.53 (9–11) | 9.77±0.41 (9–10) |
| Branchiostegal rays (total) | 23.22±0.95 (21–25) | 23.18±1.09 (21–26) | 22.79±1.22 (20–25) | 23.32±1.31 (21–26) | 23.29±0.98 (22–26) | 23.00±1.38 (18–25) | 22.86±1.18 (20–25) |
| Vertebrae | 61.62±0.92 (60–63) | 61.50±1.23 (59–65) | 61.55±1.03 (60–64) | 61.10±0.94 (59–63) | 60.41±0.90 (59–62) | 61.03±0.76 (59–62) | 60.80±0.83 (59–63) |
| Gill rakers (left) | 20.49±1.12 (18–23) | 20.53±1.34 (17–23) | 20.58±1.30 (18–24) | 20.27±1.02 (19–22) | 20.71±1.33 (18–24) | 20.97±1.19 (18–24) | 19.86±1.09 (17–22) |
| Scales in lateral series | 155.5±8.1 (140–174) | 162.4±7.4 (148–176) | 164.5±8.5 (151–182) | 161.4±8.2 (145–181) | 160.5±10.7 (137–188) | 165.2±6.6 (153–181) | 165.4±8.6 (151–184) |
| Interneurals | 14.51±0.69 (14–16) | 14.78±0.89 (13–16) | 14.73±0.80 (13–16) | 14.49±0.95 (13–16) | 14.32±0.88 (13–16) | 14.81±0.75 (14–17) | 15.06±0.87 (14–17) |
| Interhaemals | 12.30±0.66 (11–13) | 12.15±0.86 (10–16) | 12.24±0.66 (11–14) | 12.12±0.78 (10–14) | 12.00±0.74 (11–14) | 12.32±0.54 (12–14) | 12.54±0.56 (12–13) |
| Epurals | 2.65±0.48 (2–3) | 2.70±0.46 (2–3) | 2.70±0.47 (2–3) | 2.68±0.47 (2–3) | 2.73±0.45 (2–3) | 2.77±0.42 (2–3) | 2.54±0.50 (2–3) |
| Parr marks | 9.66±1.03 (8–12) | 9.58±0.87 (8–12) | 9.67±0.99 (8–12) | 10.00±0.77 (8–11) | 10.35±0.80 (9–12) | 9.69±1.15 (8–12) | 9.87±0.94 (8–12) |

**APPENDIX TABLE 2*b*. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.**

| *Character* | *UWMC (38)* | *LWMC (35)* | *DMC (34)* | *MSSC (39)* | *LSSC (31)* | *TMC (40)* | *GM (36)* |
|---|---|---|---|---|---|---|---|
| Fork length (cm) | 14.6 ± 2.6 (9.2–20.5) | 13.3 ± 2.1 (10.9–19.4) | 12.5 ± 2.5 (8.2–19.7) | 13.0 ± 2.4 (8.8–18.3) | 14.5 ± 2.3 (10.0–20.3) | 14.1 ± 1.9 (10.7–18.1) | 14.8 ± 1.7 (11.0–18.9) |
| Pyloric caecae | 36.16 ± 3.73 (28–44) | 38.83 ± 4.35 (30–48) | 33.24 ± 3.34 (25–43) | 35.97 ± 4.99 (26–47) | 37.52 ± 4.54 (31–46) | 39.68 ± 4.58 (28–48) | 43.67 ± 6.72 (33–59) |
| Dorsal rays | 12.29 ± 0.56 (11–13) | 12.46 ± 0.61 (12–13) | 12.15 ± 0.50 (11–13) | 12.05 ± 0.51 (11–13) | 12.06 ± 0.63 (11–13) | 12.15 ± 0.70 (10–13) | 12.11 ± 0.71 (11–14) |
| Anal rays | 10.97 ± 0.54 (10–12) | 11.34 ± 0.54 (10–12) | 10.68 ± 0.47 (10–11) | 10.90 ± 0.31 (10–11) | 11.10 ± 0.47 (10–12) | 11.03 ± 0.48 (10–12) | 10.83 ± 0.61 (10–12) |
| Pectoral rays | 14.79 ± 0.66 (13–16) | 15.69 ± 0.53 (15–17) | 15.68 ± 0.52 (14–16) | 15.33 ± 0.58 (14–16) | 15.16 ± 0.58 (14–16) | 15.80 ± 0.65 (15–17) | 14.97 ± 0.61 (14–16) |
| Pelvic rays | 9.39 ± 0.50 (9–10) | 9.54 ± 0.50 (9–10) | 9.00 ± 0.70 (8–10) | 9.51 ± 0.51 (9–10) | 9.71 ± 0.46 (9–10) | 9.60 ± 0.49 (9–10) | 9.67 ± 0.48 (9–10) |
| Branchiostegal rays (total) | 22.97 ± 1.39 (21–26) | 23.83 ± 1.04 (21–26) | 23.91 ± 0.91 (21–25) | 22.97 ± 0.84 (21–25) | 22.13 ± 1.38 (19–25) | 23.08 ± 1.37 (21–26) | 23.56 ± 1.40 (22–28) |
| Vertebrae | 60.97 ± 0.86 (60–63) | 61.31 ± 0.87 (59–63) | 60.06 ± 0.61 (59–61) | 61.05 ± 0.86 (60–63) | 61.26 ± 0.89 (59–63) | 61.18 ± 0.87 (59–63) | 61.42 ± 0.87 (59–63) |
| Gill rakers (left) | 19.50 ± 1.12 (18–21) | 19.91 ± 0.95 (18–22) | 19.97 ± 1.07 (18–22) | 20.31 ± 1.15 (18–22) | 20.13 ± 1.06 (18–23) | 20.38 ± 0.89 (19–22) | 19.94 ± 1.12 (18–23) |
| Scales in lateral series | 166.3 ± 8.1 (152–182) | 174.1 ± 7.3 (160–189) | 183.5 ± 6.9 (170–203) | 175.8 ± 9.4 (161–202) | 161.2 ± 7.6 (144–180) | 166.7 ± 7.7 (151–181) | 166.2 ± 10.5 (146–191) |
| Interneurals | 14.29 ± 0.73 (13–15) | 14.63 ± 0.81 (13–16) | 13.82 ± 0.72 (13–15) | 14.33 ± 0.70 (13–15) | 14.13 ± 0.81 (12–15) | 14.45 ± 0.68 (13–16) | 13.81 ± 0.79 (12–15) |
| Interhaemals | 12.16 ± 0.64 (11–14) | 12.83 ± 0.57 (12–14) | 11.71 ± 0.46 (11–12) | 11.95 ± 0.56 (11–13) | 12.45 ± 0.67 (11–14) | 12.15 ± 0.73 (11–14) | 11.75 ± 0.69 (10–13) |
| Epurals | 2.71 ± 0.46 (2–3) | 2.83 ± 0.38 (2–3) | 2.97 ± 0.17 (2–3) | 2.79 ± 0.41 (2–3) | 2.77 ± 0.50 (2–4) | 2.72 ± 0.45 (2–3) | 2.86 ± 0.42 (2–4) |
| Parr marks | 9.97 ± 0.98 (8–12) | 10.03 ± 0.71 (9–12) | 11.25 ± 0.80 (9–13) | 10.53 ± 0.99 (8–12) | 10.18 ± 0.98 (8–12) | 9.86 ± 0.72 (8–11) | 10.40 ± 0.89 (9–12) |

**APPENDIX TABLE 3. Observed Means, Standard Deviations, and Ranges for Three Samples of Trout from California. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.**

| *Character* | *SFKR (19)* | *RTV (24)* | *RTS (24)* |
|---|---|---|---|
| Fork length (cm) | 12.5 ± 1.7 (8.1–14.7) | 23.0 ± 1.0 (20.5–24.5) | 23.2 ± 1.9 (19.0–26.3) |
| Pyloric caecae | 31.53 ± 3.60 (26–37) | 61.50 ± 8.38 (46–75) | 61.36 ± 6.89 (52–79) |
| Dorsal rays | 11.84 ± 0.60 (11–13) | 12.37 ± 0.58 (11–13) | 12.36 ± 0.49 (12–13) |
| Anal rays | 10.84 ± 0.37 (10–11) | 11.08 ± 0.50 (10–13) | 11.20 ± 0.41 (11–12) |
| Pectoral rays | 14.47 ± 0.51 (14–15) | 14.21 ± 0.59 (13–16) | 14.68 ± 0.56 (14–16) |
| Pelvic rays | 9.0 ± 0.0 (9–9) | 10.00 ± 0.0 (10–10) | 9.92 ± 0.28 (9–11) |
| Branchiostegal rays (total) | 21.00 ± 1.00 (20–23) | 21.17 ± 0.76 (20–22) | 21.32 ± 1.25 (19–23) |
| Vertebrae | 59.84 ± 0.96 (58–61) | 62.46 ± 0.78 (61–64) | 63.44 ± 0.65 (62–65) |
| Gill rakers (left) | 19.63 ± 0.76 (18–21) | 18.21 ± 1.10 (16–20) | 18.04 ± 0.93 (16–19) |
| Scales in lateral series | 172.7 ± 7.7 (164–189) | 130.7 ± 5.2 (119–138) | 142.2 ± 4.92 (137–151) |
| Interneurals | 13.10 ± 0.81 (12–14) | 14.67 ± 0.70 (13–16) | 14.68 ± 0.56 (14–16) |
| Interhaemals | 11.95 ± 0.62 (11–13) | 12.71 ± 0.62 (12–14) | 12.68 ± 0.56 (12–14) |
| Epurals | 2.53 ± 0.51 (2–3) | — | — |
| Parr marks | 9.84 ± 1.12 (8–12) | — | — |

75205—800 12-81 175 OSP