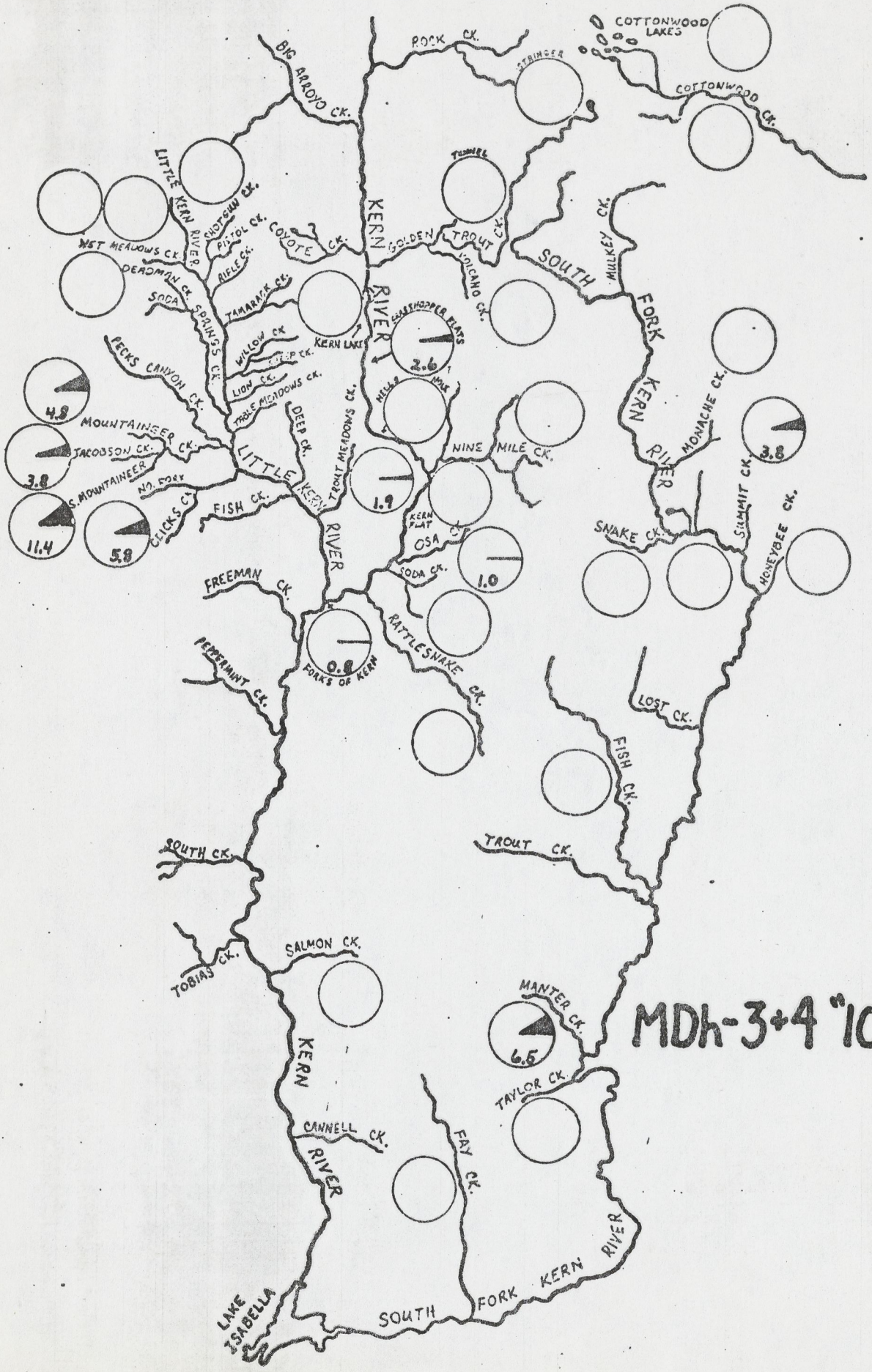
DIAGRAM 12



MDh-3+4 "107" ALLELE

Table II Means for 10 meristic characters of the three proposed subspecific groups of Kern River basin trout. Character means not significantly different at P =.05 are denoted by identical superscripts. Abbreviations are: Dorsal Proximal Pterygiophores (D.P.), Anal Proximal Pterygiophores (A.P.) and Branchiostegals (B.O.).

Subspecies group	Pyloric caeca	D.P.	A.P.	Pectoral fin rays	Pelvic fin rays	B.O.	Vertebrae	Gill rakers	Lateral scales	Scales above lateral line
									155–160	
S. a. whitei	34.3[a]	14.6	12.5[a]	15.4	9.8[a]	22.7[a]	60.4	20.2	168.9	33.7
S. a. aguabonita	27.9	13.6	12.5[a]	14.3	9.1	20.4	59.4	19.4[a]	173.8	34.7
S. a. gilberti	35.3[a]	14.4	12.4[a]	15.0	9.8[a]	22.8[a]	62.2	19.2[a]	148.7	30.5
							60–62(61)		145	36

N = 10
1893, 1904

PROGRESS REPORT

TROUT OF THE KERN RIVER BASIN

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Presented to:

California Department of Fish and Game
Threatened Trout Committee
Fresno, California

July 8-9, 1981

TABLE 1. KERN RIVER TROUT POPULATIONS SAMPLED 1978-1980

Location and Designation	Sample Size
Little Kern River	
River near Broder's Cabin (ULKR)	16
Trout Meadows Cr. (TRMCB)	13
Deadman Cr. Lowest Sect. (DMCC)	14
Wet Meadows Cr., Mid-Sect. (MWM)	21
Wet Meadows Cr., Lowest (LWMD)	24
Jacobsen Cr. (JCB)	20
North Mountaineer Cr.(NMCB)	22
South Mountaineer Cr. (SMCB)	11
North Clicks Cr. (NCCB)	13
Main Kern River	
Hell Hole (HH)	25
Nine Mile Cr., Upper (UNMC)	20
Osa Cr., Lower Sect. (LOC)	27
Rattlesnake Cr. Upper (URC)	24
Salmon Cr., Above Falls (SAC)	24
Forks of the Kern (FORK)	34
Soda Cr. (SODA)	24
Kern Flats (KFL)	18
Kern Lake (KLK)	18
Grasshopper Flats (GRF)	29
Golden Trout Cr.	
Golden Trout Cr. at Tunnel Meadow (GTC)	20
Golden Trout Cr. at Stringer (GTCS)	16
Volcano Cr. (VOL)	19
Cottonwood Cr.	
Cottonwood Cr. (CWC)	27
Cottonwood Lake, 3 (CWLC)	21
South Fork Kern River	
Fish Cr. (SFFC)	17
Fay Cr. (FAY)	20
Monache Cr. (MOC)	19
Honeybee Cr. (HON)	20
Summit Cr. (SUM)	20
Snake Cr. (SNK)	32
Taylor Cr. (TC)	36
Manter Cr. (MAN)	35
South Fork Kern at Monache Meadow (SFKM)	30
Hatchery Rainbow	
Pit River Rainbow (RTP)	45
Shasta (RTS)	28

INTRODUCTION

The taxonomic status of the Kern River trouts has been in dispute since they were first described in the late 1800s and early 1900s. There have been many conflicting theories and taxonomies proposed to organize and clarify the confusing situation that exists in the Kern River basin. This confusion has been compounded by the introduction of domestic rainbow trout stocks into various parts of the basin. These introductions have led to introgression with the native stocks.

Electrophoretic and meristic techniques have been employed to successfully identify and characterize populations of Salmo aguabonita whitei in the Little Kern basin. Populations throughout the Kern River basin have been sampled to elucidate the relationships among the various trouts.

RESULTS

Using Nei's method of estimating genetic similarity for electrophoretic data, several distinct groups of trout are present in the Kern River basin. The results of an analysis of twenty diagnostic electrophoretic loci are presented in dendogramic form in Figure 1.

The thirty-five populations sampled in 1979 and 1980 cluster into four groups (Fig. 1). The first group (Soda Creek through Hell Hole) were collected from the historic range of S. gairdneri gilberti (Kern River Rainbow) and may be considered to be representative of the Kern River Rainbow. They can be characterized by an intermediate frequency of the fast PA 1, 2 (105) allele (Dia. 1), high frequencies of the IDH-3,4 (100) allele (Dia. 2), the slow SOD (60) allele (Dia. 4), the fast LGG (150) allele (Dia. 6), and the presence of the fast AGPD (140) allele (Dia. 9).

The next clearly defined cluster is S. a. whitei (Little Kern Golden Trout), (Lower Wet Meadows Creek through Deadman Creek). This group can be characterized

by low frequency of the fast PA-1,2 (105) allele (Dia. 1), high frequencies of the IDH-3,4 (100) allele (Dia. 2), the fast 6PGD (120) allele (Dia. 3), the slow SOD (60) allele (Dia. 4) and the fast GL-2 (120) allele (Dia. 5).

The next cluster represents populations from the South Fork Kern River (Monache Meadows through Honeybee Creek) and the Mountaineer group (Jacobsen Creek through North Mountaineer Creek). The South Fork subgroup can be characterized by the presence of MDH-3,4 (95) allele (Dia. 7) and the slow PHAP 90 allele (Dia.10) while the Mountaineer subgroup can be characterized by low frequencies of the IDH-3,4 (100) allele (Dia. 2), the presence of the MDH-3,4 (107) allele (Dia. 12). and intermediate frequency of the SOD (140) allele (Dia. 11).

The last cluster represents S. a. aguabonita (Cottonwood Lake 3 through Fish Creek, SFK). It is characterized by low frequency of the IDH-3,4 (100) allele (Dia. 2), absence of the SOD (60) allele (Dia. 4) and high frequency of the PHAP (90) allele (Dia. 10).

The subgroup closely allied to the Kern River rainbow group (Salmon Creek) through Trout Meadows Creek) and the Subgroup closely allied to the South Fork Kern group (Manter Creek through RT Shasta) will be considered in the discussion.

Meristics were done for 10 characters on all populations and are summarized in the appendix. A dendrogram generated from the data is presented in Fig. 2. The clusters in the dendrogram follow the general trend of the electrophoretic dendrogram and they are not as clearly defined geographically. Meristic characterizations of S. a. gilberti, S. a. whitei and S. a. aguabonita are presented in Table II.

DISCUSSION

The evolutionary relationships of the groups represented in the dendrograms should not be inferred on the basis of dendrogram morphology. Rather, the relationships among the trout of the Kern River basin must be considered from

a historical and geographical perspective to fully appreciate the complex changes that have taken place including interactions of the trouts with each other.

The Little Kern goldens and the S. a. aguabonita group appear to represent the remnants of the earliest invasion of trout into Central Valley streams. The Kern River basin served as a glacial refugium, similar to the upper McCloud River, that isolated these forms and allowed them to differentiate. The Kern River rainbow, S. a. gilberti, probably represents the second invasion of trout into the Kern River basin. The South Fork fish are closely allied to rainbows (Fig. 3) and appear to be influenced by the S. a. aguabonita populations upstream from them. This influence is clearly evidenced by the electrophoretic intermediacy of the South Fork group. The frequencies of most of the alleles of the South Fork group fall midway between the values of the Kern River rainbow and S. a. aguabonita. The Mountaineer group represents S. gairdneri (Fig. 3), their origin is rather puzzling, and suggests that the Mountaineer-Clicks Creek systems did not contain a native trout and these fish represent the planted stock.

The two subgroups (Salmon Creek through Trout Meadows Creek) and (Manter Creek through RT Shasta) donot have a geographical communality and appear to represent very recently introgressed populations. This is further supported by planting records and their groupng with other suspect populations in Fig. 3.

The three proposed subspecific forms are distinct taxonomically and should be managed accordingly.

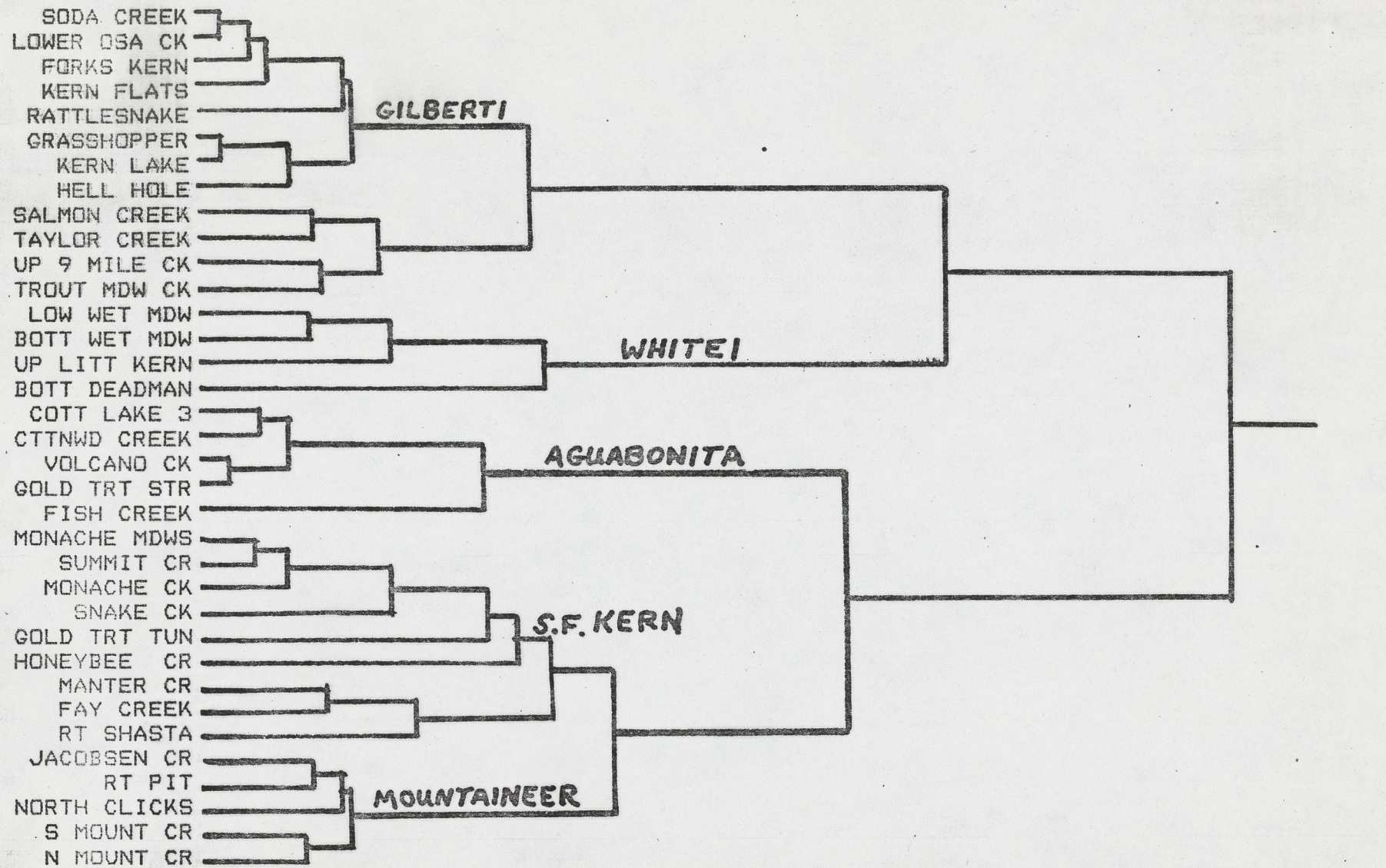

SODA CREEK
LOWER OSA CK
FORKS KERN
KERN FLATS
RATTLESNAKE
GRASSHOPPER
KERN LAKE
HELL HOLE
SALMON CREEK
TAYLOR CREEK
UP 9 MILE CK
TROUT MDW CK
LOW WET MDW
BOTT WET MDW
UP LITT KERN
BOTT DEADMAN
COTT LAKE 3
CTTNWD CREEK
VOLCANO CK
GOLD TRT STR
FISH CREEK
MONACHE MDWS
SUMMIT CR
MONACHE CK
SNAKE CK
GOLD TRT TUN
HONEYBEE CR
MANTER CR
FAY CREEK
RT SHASTA
JACOBSEN CR
RT PIT
NORTH CLICKS
S MOUNT CR
N MOUNT CR
GILBERTI
WHITEI
AGUABONITA
S.F. KERN
MOUNTAINEER
1.00
.99
.98
.97
.96
.95
.94
.93
.92
.91
.90
Genetic Similarity (UPGMA)

FIGURE 1

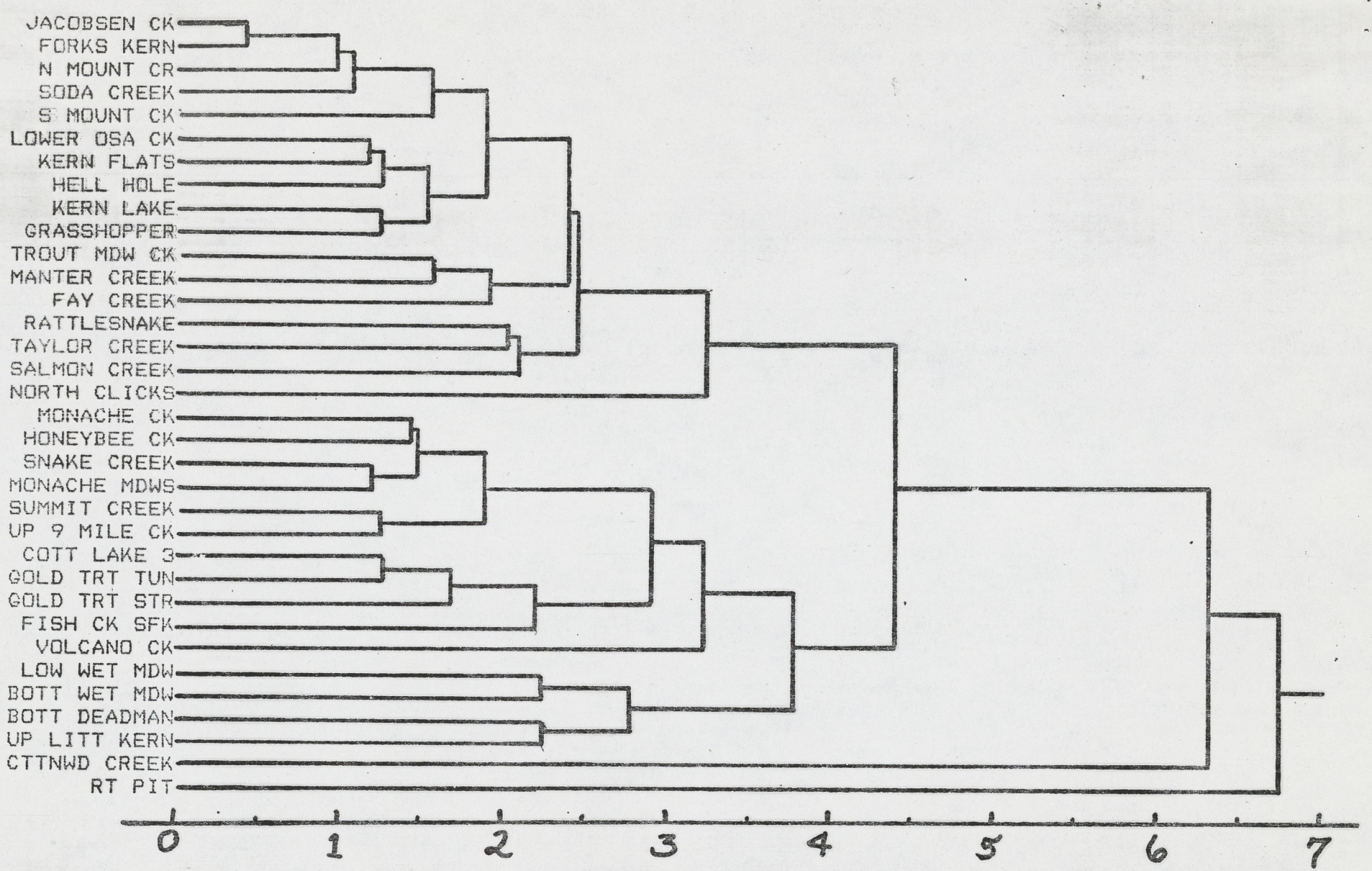
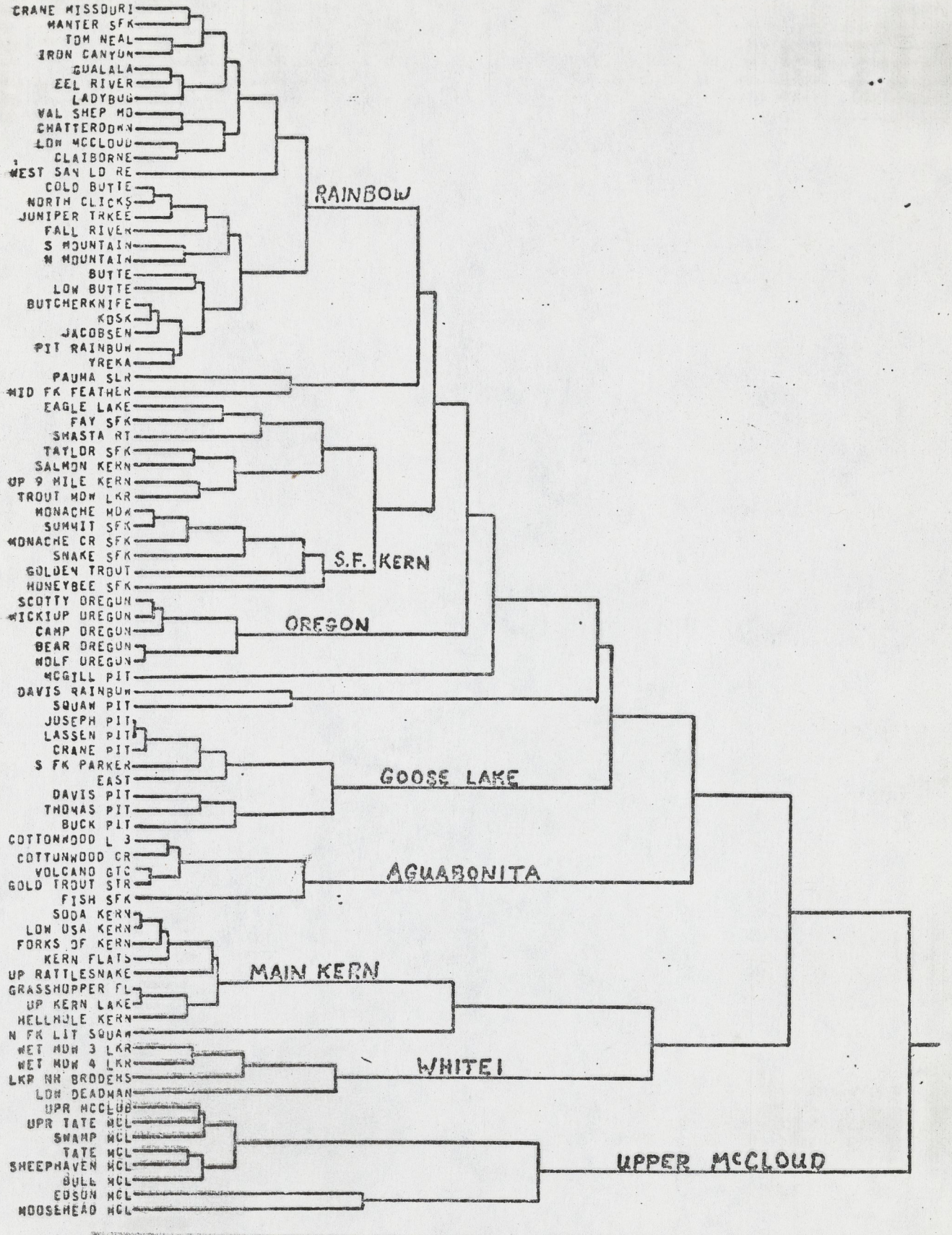
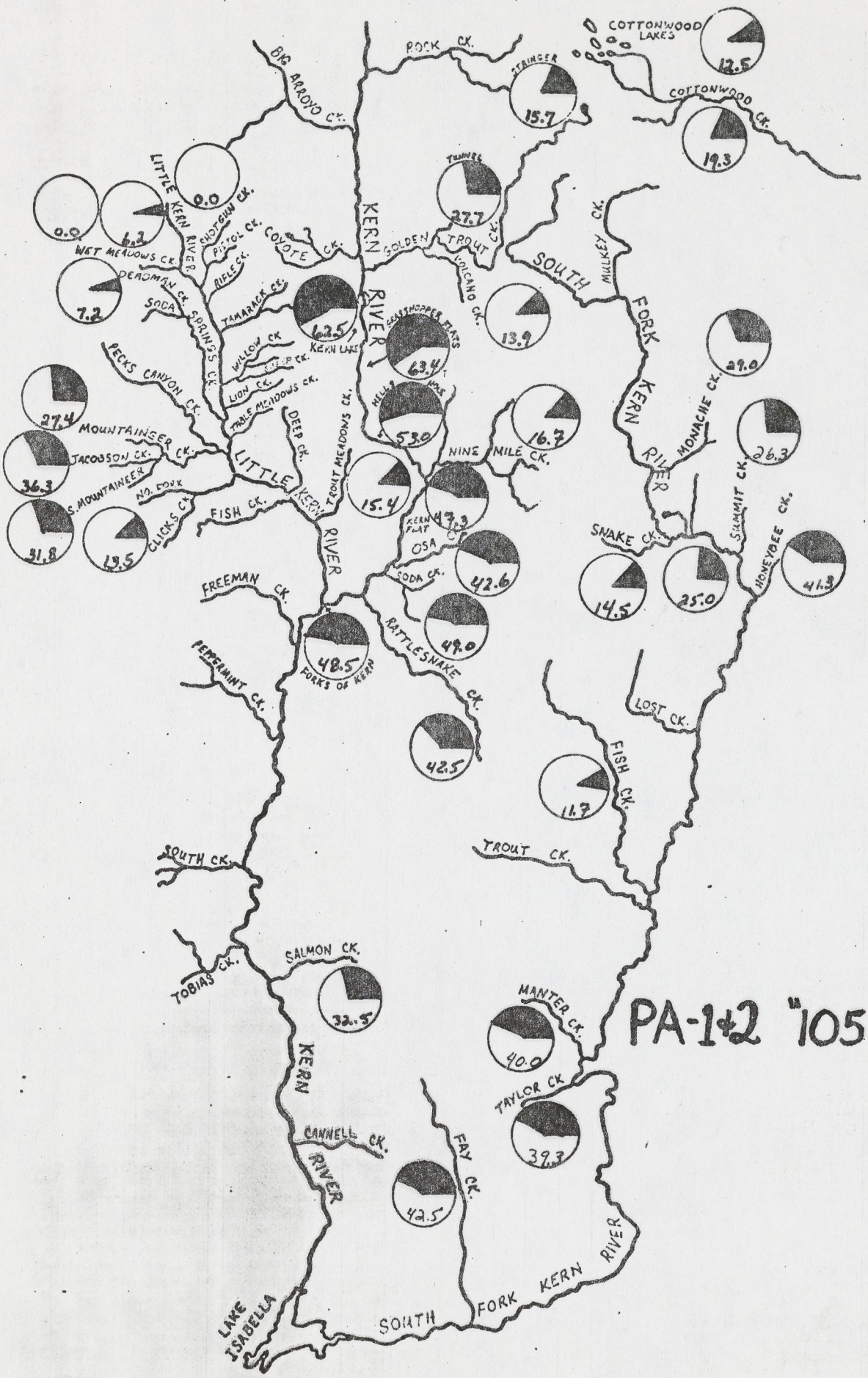

JACOBSEN CK
FORKS KERN
N MOUNT CR
SODA CREEK
S MOUNT CK
LOWER OSA CK
KERN FLATS
HELL HOLE
KERN LAKE
GRASSHOPPER
TROUT MDW CK
MANTER CREEK
FAY CREEK
RATTLESNAKE
TAYLOR CREEK
SALMON CREEK
NORTH CLICKS
MONACHE CK
HONEYBEE CK
SNAKE CREEK
MONACHE MDWS
SUMMIT CREEK
UP 9 MILE CK
COTT LAKE 3
GOLD TRT TUN
GOLD TRT STR
FISH CK SFK
VOLCANO CK
LOW WET MDW
BOTT WET MDW
BOTT DEADMAN
UP LITT KERN
CTTNWD CREEK
RT PIT
0
1
2
3
4
5
6
7
EUCLIDEAN DISTANCE (UPGMA)

FIGURE 2

FIGURE 3

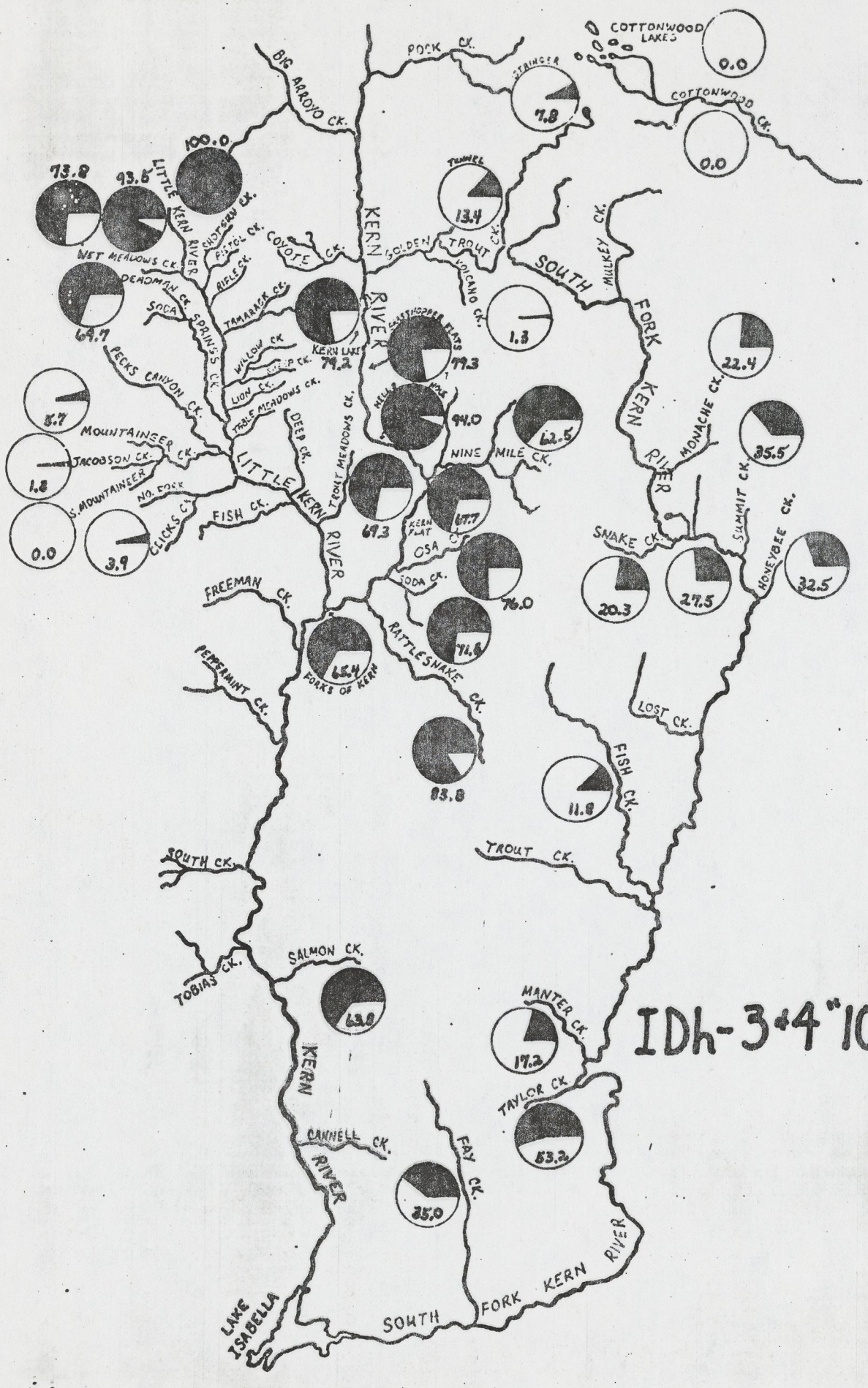


GENETIC SIMILARITY (UPGMA)

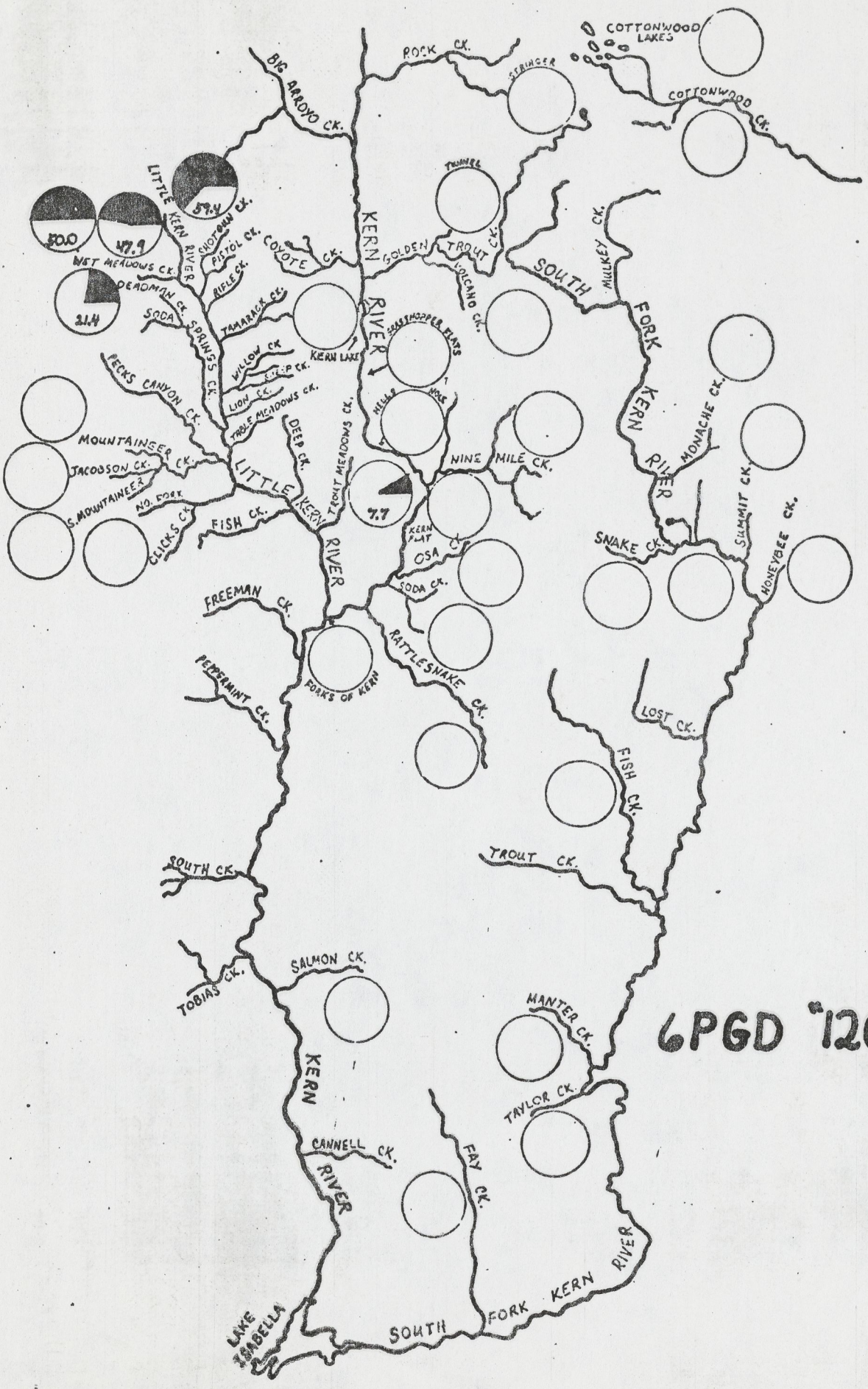


PA-1+2 "105" ALLELE

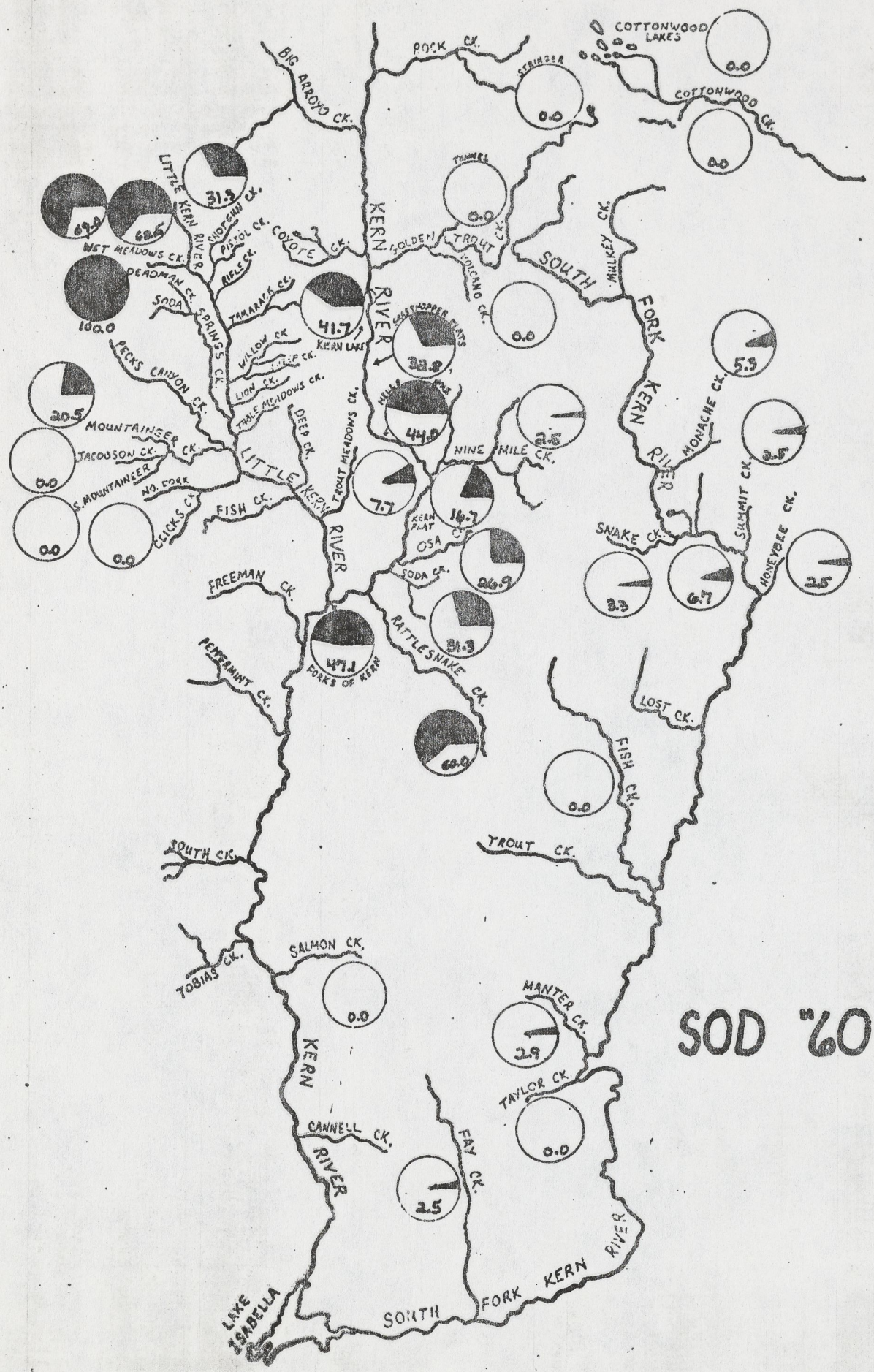
DIAGRAM 2



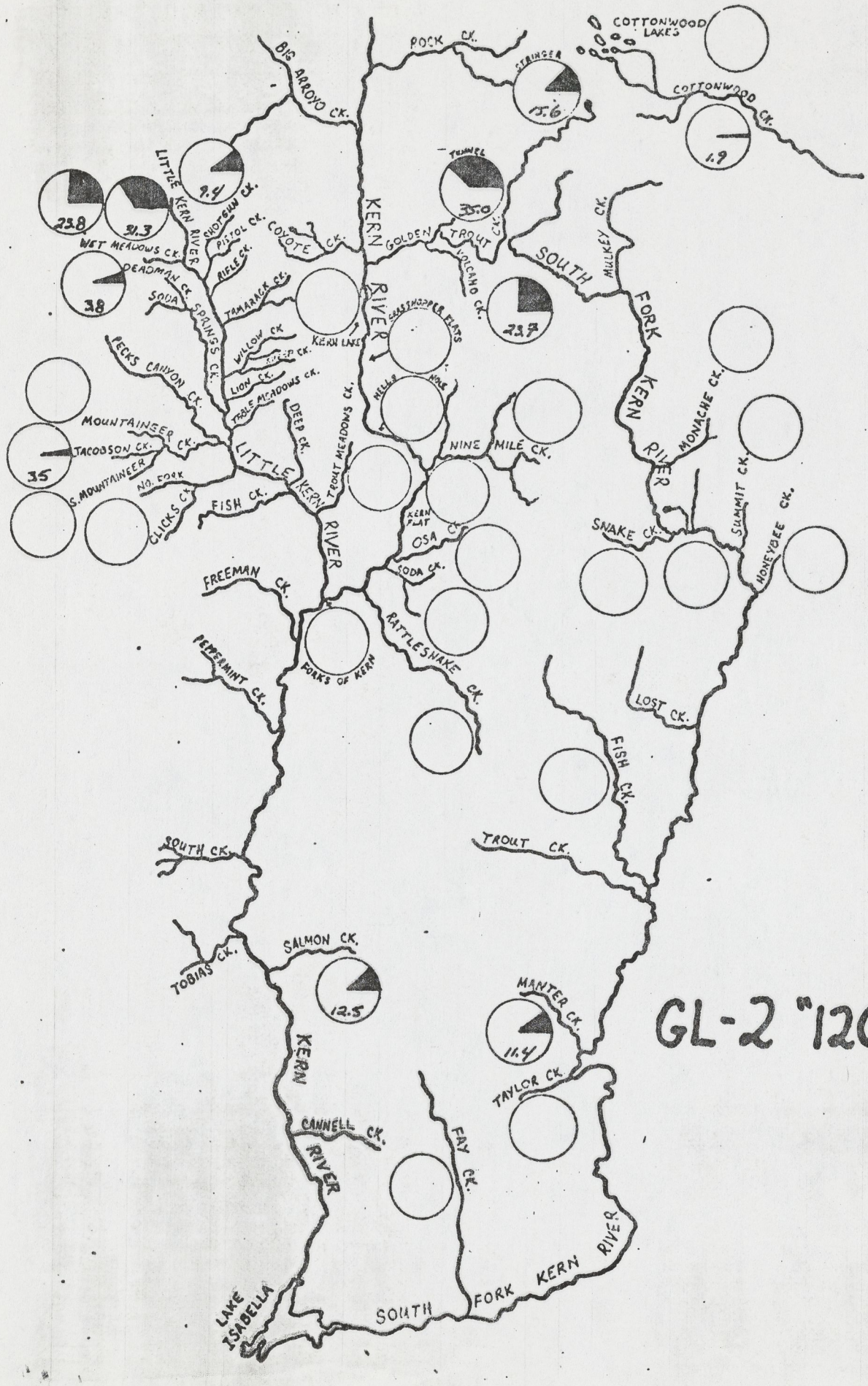
IDh-3•4 "100" ALLELE



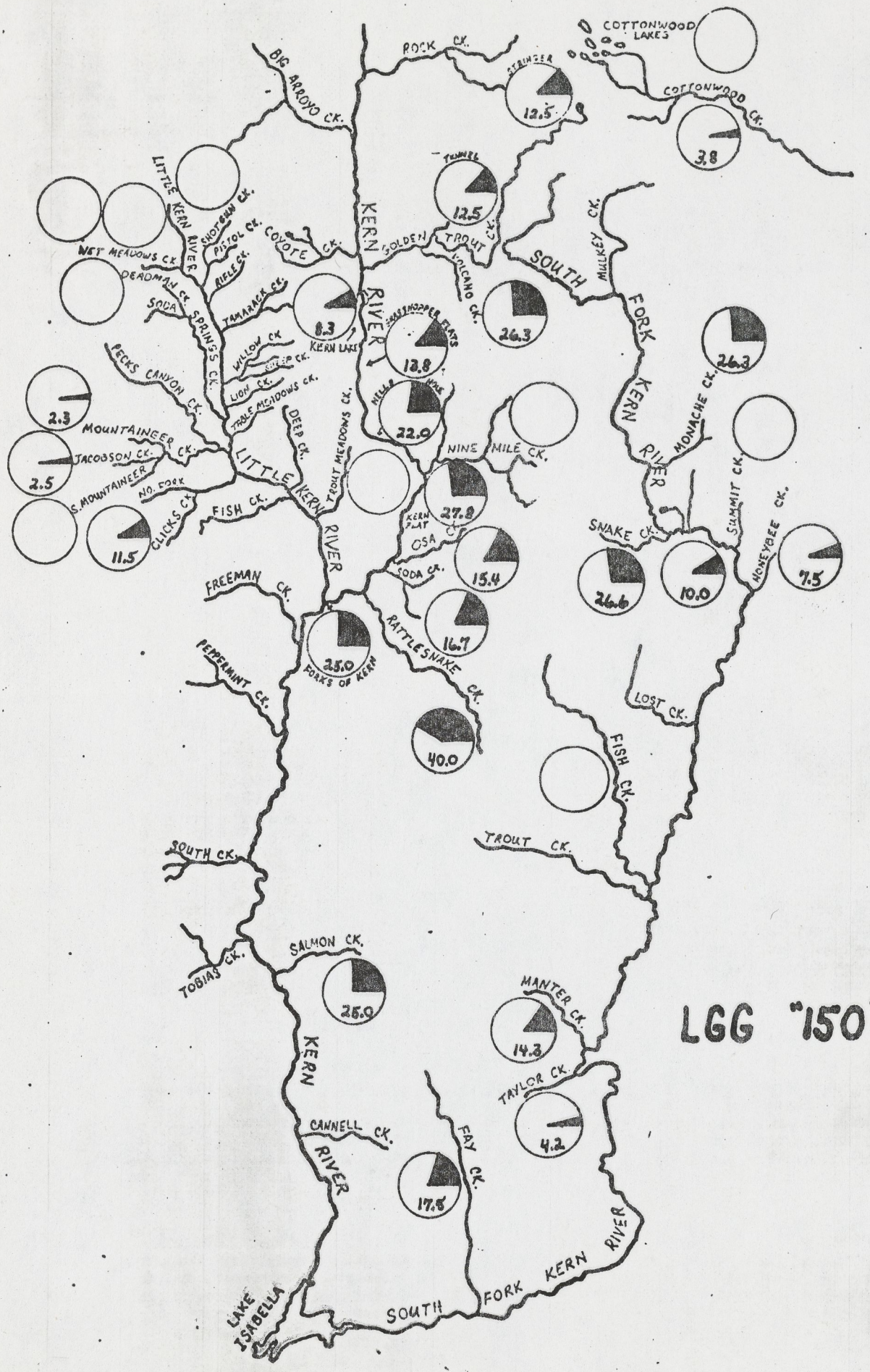
6PGD "120" ALLELE



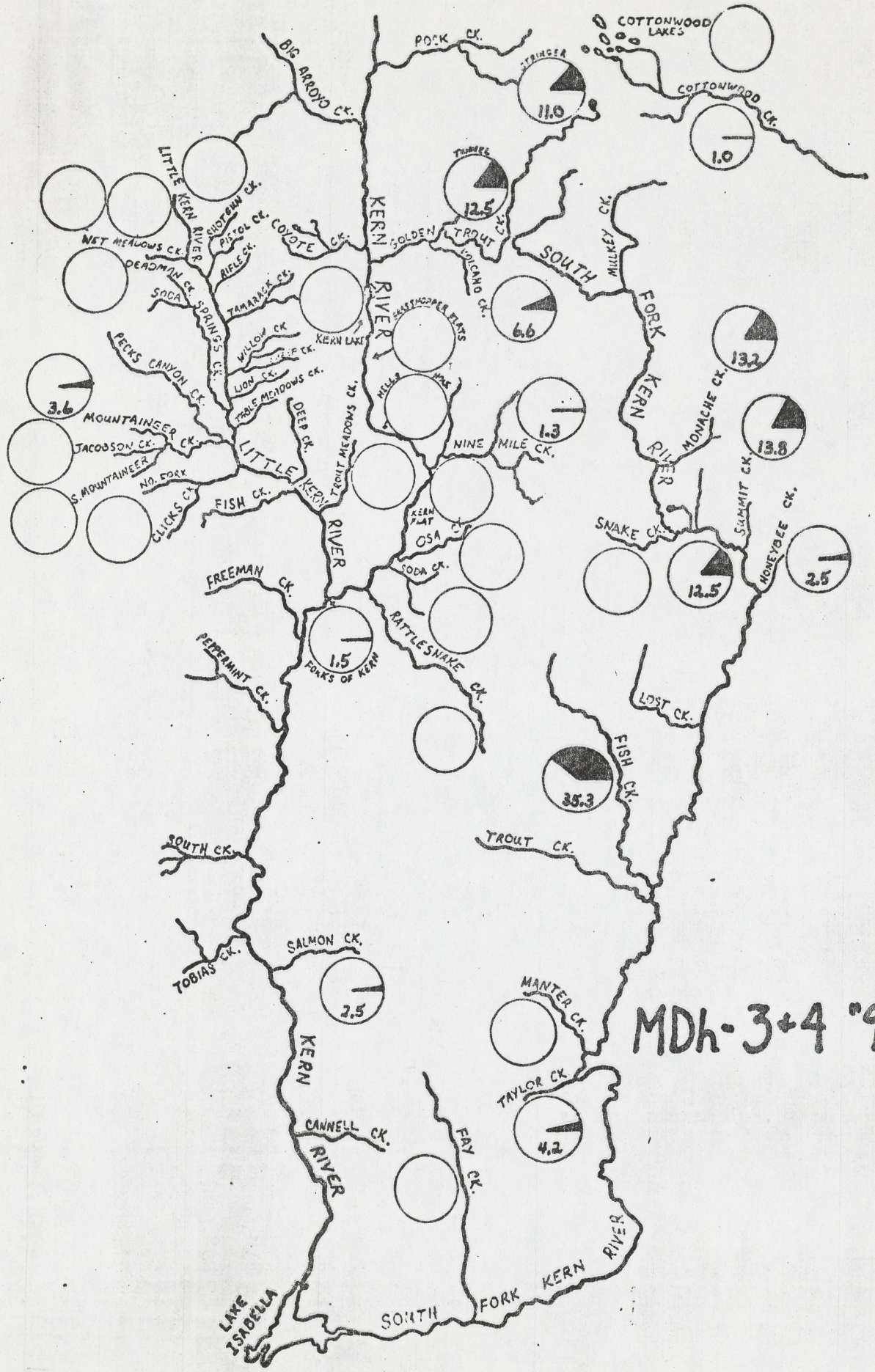
SOD "60" ALLELE



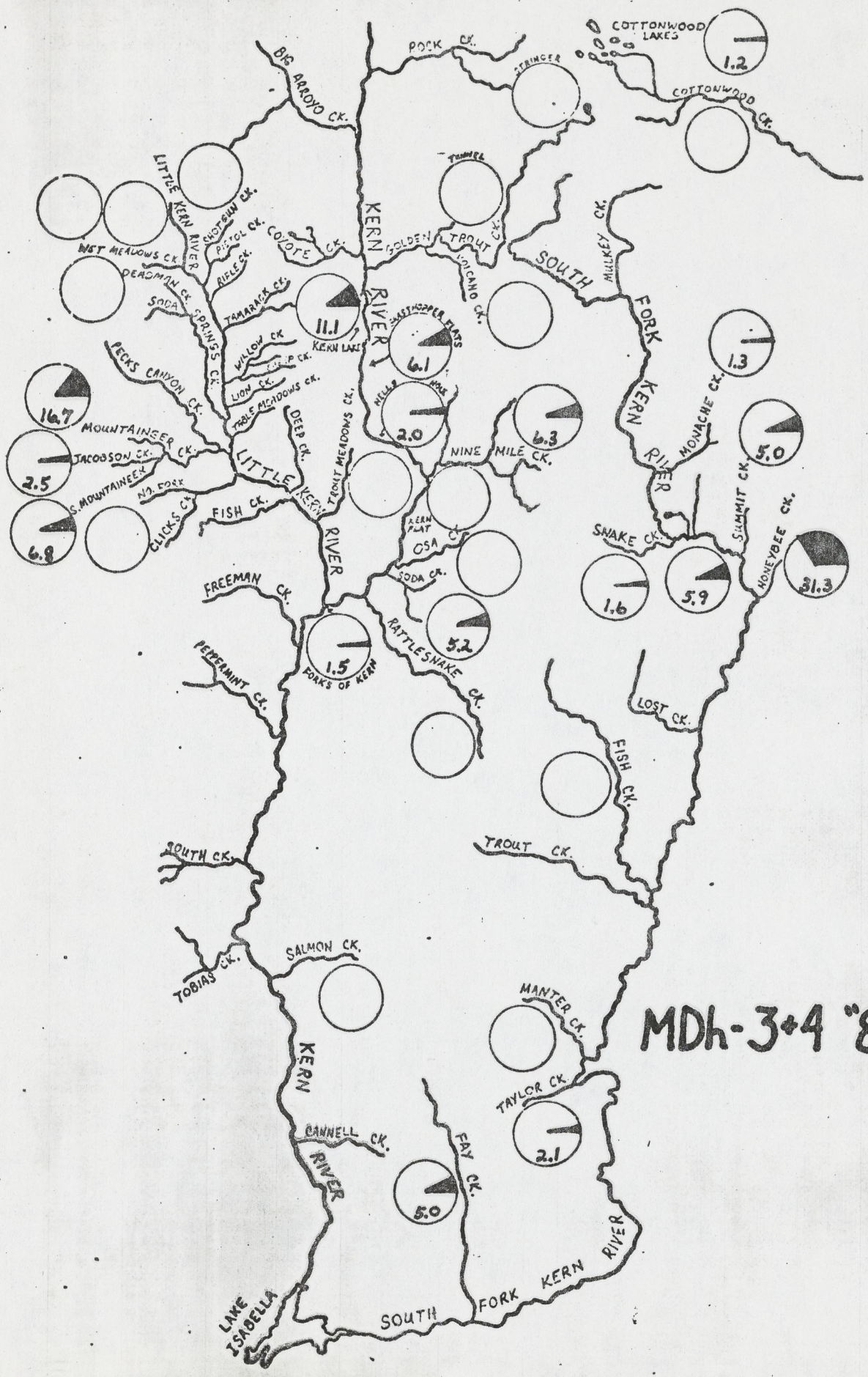
GL-2 "120" ALLELE



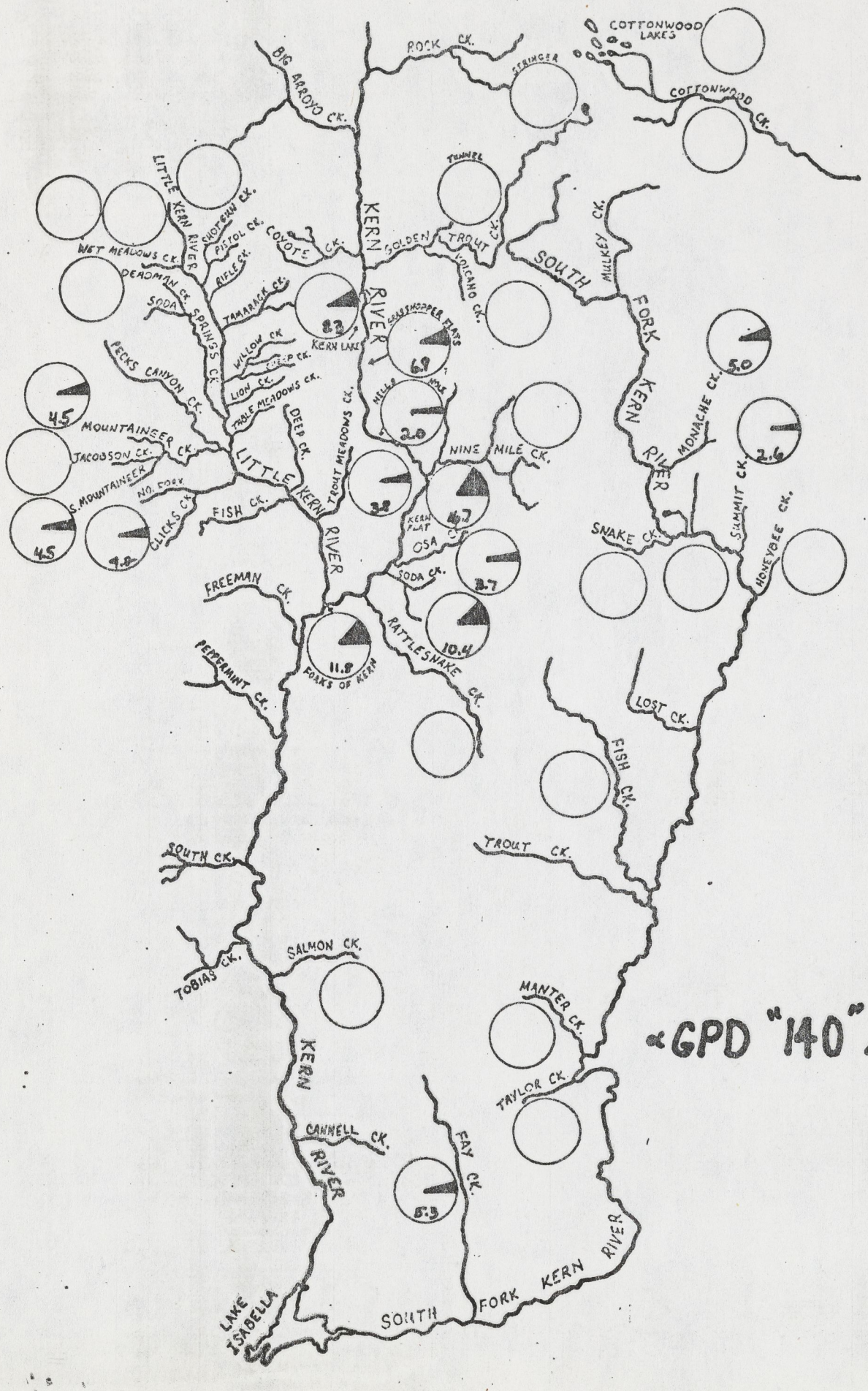
LGG "150" ALLELE



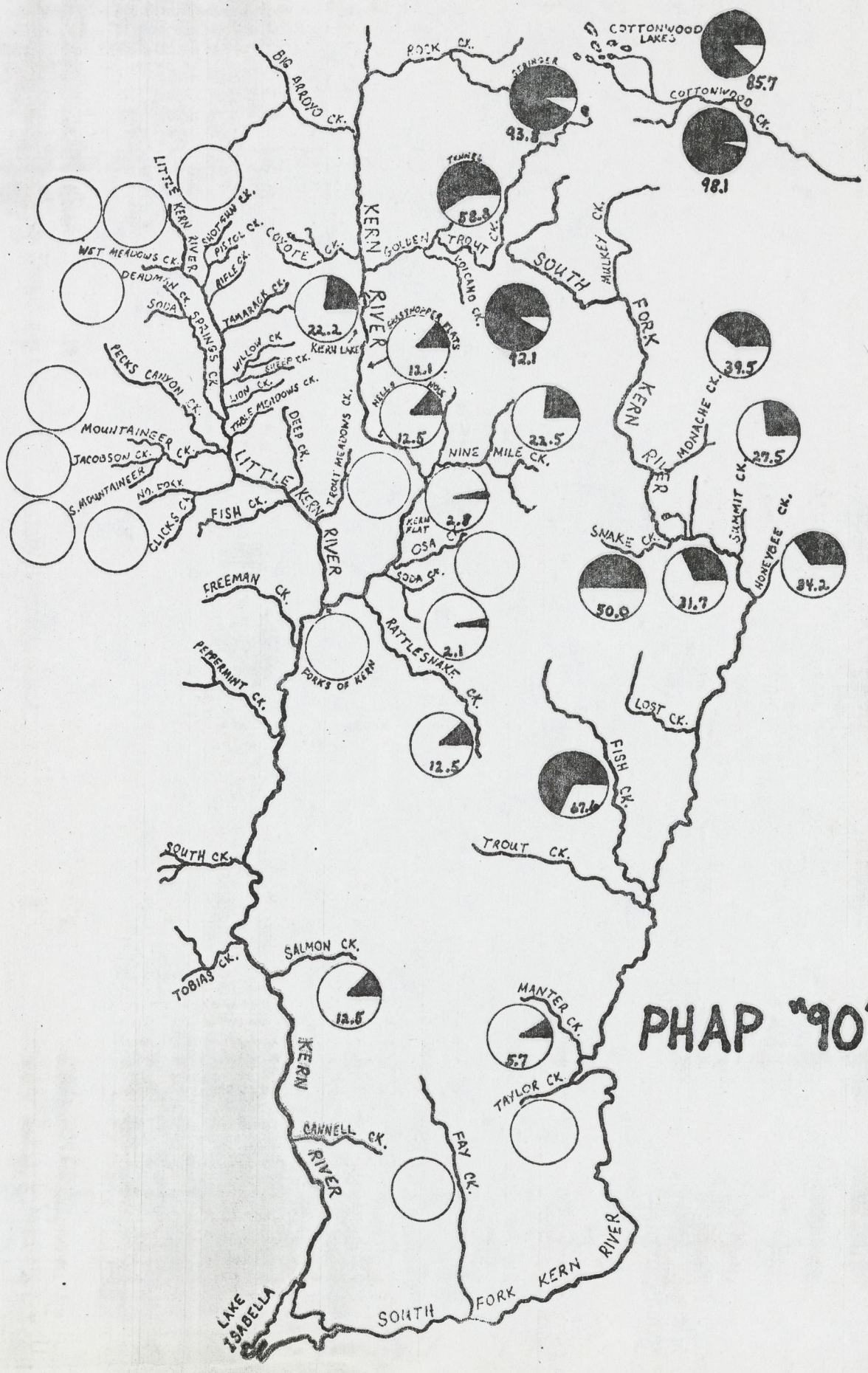
MDh-3+4 "95" ALLELE



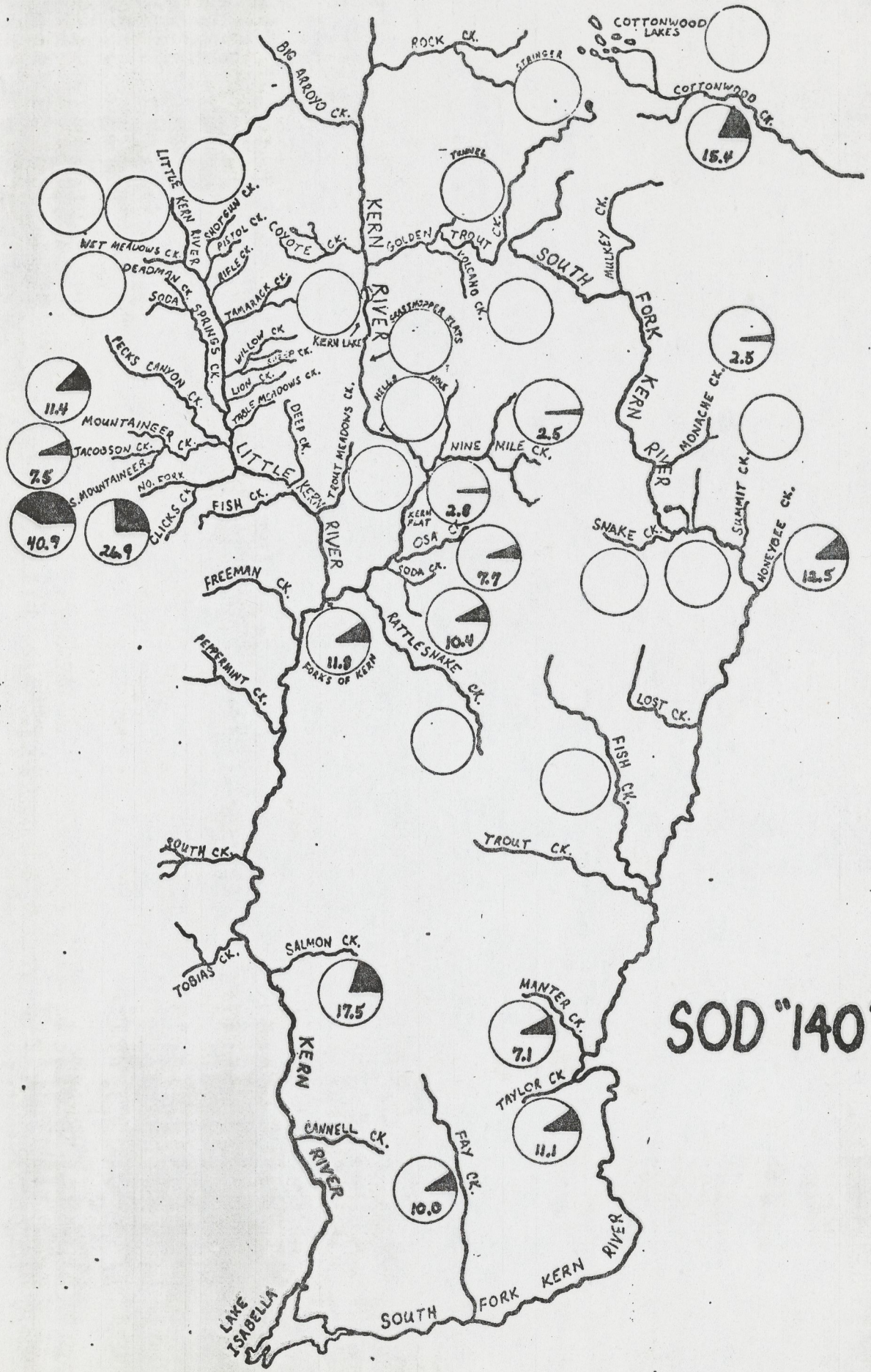
MDh-3•4 "85" ALLELE



«GPD "140" ALLELE



PHAP "90" ALLELE



SOD "140" ALLELE

J6628

A Biochemical-Genetic and Meristic Analysis of the Relationship Between Salmo Aguabonita Whitei Everman and S. A. aguabonita Jordan

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Abstract

The purpose of this study was to analyze and characterize S. a. whitei and S. a. aguabonita. Four hundred and eighty-eight specimens from 14 populations of wild trout in the Kern River basin were analyzed for nine meristic characters and 20 electrophoretic loci. The populations could be classified into two distinct taxonomic groups. Seven populations were identified as S. a. whitei and seven were identified as S. a. aguabonita. The genetic similarity between the two groups was 0.911, a value comparable with other subspecific designations of Salmo. There were significant electrophoretic differences that characterized each subspecies. The meristic data suggested differences between the subspecies but only one character proved to be diagnostic. The high degree of concordance (r = 0.606) between the Euclidean distance and genetic similarity estimates suggests similar trends of biochemical and morphological evolution.

Key words: Salmo aguabonita, subspecies, electrophoresis, meristics, taxonomy, evolution.

Introduction

Since Salmo aguabonita was first described by Jordan in 1892, its taxonomic status and evolutionary history have been greatly disputed. Evermann (1906) described the following species of golden trout: S. aguabonita of the South Fork Kern River and Cottonwood Lakes, S. roosevelti of the Golden Trout Creek drainage, and S. whitei of the Little Kern River drainage. Jordan (1892) originally suggested that S. aguabonita was descended from cutthroat trout, while he later felt it arose from the rainbow trout (Jordan, 1894). Presently, S. aguabonita is considered to be a species with two subspecies: S. a. aguabonita of Golden Trout Creek, Cottonwood Creek, and the South Fork Kern drainages and S. a. whitei of the Little Kern River drainage (Miller, 1950). Recent work of Gold and Gall (1975a,b), Gold (1975), Gall et al. (1976), and Smith (1981) has established the existence of several isolated populations of S. a. whitei in the Little Kern River basin.

The purpose of this study was to determine if S. a. whitei is subspecifically distinct from S. a. aguabonita and if so, what characterizes that distinctness. The samples were analyzed for meristic counts to investigate multigenic traits and starch-gel electrophoresis to investigate single gene differences.

Materials and Methods

Data for 488 fish representing 14 Salmo aguabonita populations was selected from previous studies carried out from 1974 to 1978 (Table I, Fig. 1). The seven populations from the Little Kern River basin are

those reported to be S. a. whitei by Smith (1981), and the other seven were collected from the South Fork Kern and the Cottonwood basin. Identification, transport, and processing of the fish followed the procedures of Gall et al. (1976).

Table I near here

Fig. 1 near here

Electrophoretic Techniques

The tissues were processed according to the methods of Utter et al. (1974), and the horizontal starch-gel electrophoretic and staining techniques of Busack et al. (1979) were the ultimate ones used. Thirteen protein systems encoded by 20 loci were studied and are listed in Table II.

Table II near here

Gels were interpreted according to inheritance models of golden trout and other salmonid species (Utter and Hodgins, 1972; Gall et al., 1976; Busack et al., 1979). The system of nomenclature followed that of Busack et al. (1979), which was originally suggested by Allendorf and Utter (1979). Each locus was given an appropriate acronym. Multiple locus systems were numbered consecutively with increasing migration rate of the protein product. The most common allele at each locus in rainbow trout was designated 100, with the other allelic designations based on relative migration rate to the most common allele.

Coefficients of genetic similarity between operational taxonomic units (OTU) based on the allelic frequencies at the 20 loci were calculated according to Nei (1972). The resulting matrix of genetic similarities was subjected to the unweighted pair-group method using arithmetic averages (UPGMA) method of cluster analysis (Sneath and

Sokal, 1973). Average heterozygosity values were calculated according to Nei and Roychoudhury (1971).

Meristic Techniques

After the fish were sacrificed, identified with numeric tags, and tissues taken for electrophoresis, they were preserved in 10 percent formalin for a week. They were then rinsed for 24 hours in water and stored in 70 percent isopropanol or ethanol according to Minckley (1973).

Fish were checked for basibranchial teeth. Meristic counts were made for nine characters according to procedures of Minckley (1973) and Gold and Gall (1975a). The characters and counting procedures followed Smith (1981).

The data was subjected to descriptive analysis using BMDP program 7 D (Dixon, 1977) to detect obvious departures from normality. This was followed by a least squares analysis of variance using the method of Harvey (1975).

Pairwise, Euclidean distances were calculated using the square root of the Mahalanobis distance after Sneath and Sokal (1973). An Euclidean distance dendrogram was generated using the UPGMA method of Sneath and Sokal (1973).

Results

Electrophoretic analysis. Allele frequencies for the eight polymorphic loci are presented in Table III; the other 12 loci were invariant in all populations.

The invariant loci were PGI 1, 2 and 3, CK-2, DIA, AK, FUM, ADH

and MDH 1, 2, and 3. The banding patterns and genetic interpretations of the polymorphic loci followed those in Busack et al. (1979), except malic enzyme (ME).

Table III near here

Malic enzyme (ME): The variation observed for ME in this study suggested that ME is a tetramer encoded by at least one locus, in agreement with Busack (1977). The one locus model was assumed since no breeding data was available to suggest an alternative model.

Isocitrate dehydrogenase (IDH): Busack et al. (1979) have shown that Isocitrate dehydrogenase is a dimer encoded by two polymorphic loci that have identical alleles. Therefore, the values reported in Table IX are the average of the two loci since calculation of allele frequencies at each locus was impossible. IDH was entered as two identical loci in the calculation of genetic identities.

The principal differences between S. a. whitei and S. a. aguabonita were characterized by significant divergence in two systems, SOD and IDH and limited differentiation for PALB. The average frequency of SOD 60 was high (.87) in S. a. whitei and low in S. a. aguabonita, being present in only MC and SFK. SOD 100 was low in S. a. whitei and high (.91) in S. a. aguabonita. SOD 140 was absent in S. a. whitei and present in four of the seven populations of S. a. aguabonita. Similarly, the average frequency of IDH 100 was high (.79) in S. a. whitei and low (.11) in S. a. aguabonita, while IDH 140 was low (.20) in S. a. whitei and high (.89) in S. a. aguabonita. Two rare alleles, IDH 60 and 170, occurred in one S. a. whitei population and two S. a. aguabonita populations.

The average heterozygosity value for each population is the principle diagonal in the genetic similarity matrix (Table IV). The average heterozygosity of all the fish sampled was 4.9 percent, with the average of the S. a. whitei populations being 5.2 compared to 4.8 for S. a. aguabonita. The values ranged from 1.9 (CLC) to 7.3 (LWM) percent.

Table IV near here

The normalized genetic identity (I) of Nei (1972) was used to determine the similarity among all populations based on gene frequencies (Table IV). The range of values was from 0.999 (FC-LWM, DMCA-WC, DMCA-CC, DMCA-DMCB, DMCB-USSCA, CWLB-SFK, TRC-CWLC) to 0.860 (USSCA-CWLA). A genetic similarity dendrogram based on the similarity matrix in Table IV is given in Figure 2. The cophenetic correlation coefficient was 0.973, which indicates little distortion due to clustering (Sneath and Sokal, 1973).

Fig. 2 near here

There were two distinct clusters of populations based on a variance calculated from all pairwise comparisons of the similarity matrix (Sneath and Sokal, 1973). The average similarity among the S. a. whitei group is 0.998 while the average among the S. a. aguabonita is 0.996. The S. a. whitei group and the S. a. aguabonita group joined into a single cluster at an average identity of 0.911. The average similarity between the two clusters is within the range of 0.937 to 0.754 reported by Loudenslager and Gall (1980) for S. clarki subspecies, which had an average similarity of .852.

Meristic analysis. Table V presents the observed means and error mean square (EMS) for all characters in all samples. No true basibranchial

teeth were observed in any population. All characters appeared to be distributed normally, based on Fischers third and fourth moments, which follows the results of Gold and Gall (1975).

Table V near here

Although analysis of variance revealed that there were significant differences between the subspecies for five characters, the populations within the subspecies were significantly heterogeneous for all characters (Table VI). This suggested that while there were characteristic average differences between the subspecies, the overlap among populations was great enough to prevent the differences from being diagnostic for all populations of a subspecies (Table V). The one exception was pyloric caeca, where S. a. whitei populations had a larger number of pyloric caecas than any of the S. a. aguabonita populations.

Table VI near here

Euclidean distance estimates based on all meristic characters are presented in Table VII. Distances ranged from .76 (CLWA-CLWB) to 6.97 (MC-WC). A dendrogram (Fig. 3) was generated from the Euclidean distance matrix. The cophenetic correlation coefficient of 0.834 indicated little distortion due to clustering (Sneath and Sokal, 1973).

Table VII near here

Fig. 3 near here

The FC sample is geographically and electrophoretically an S. a. whitei population; however, meristically it falls in with the S. a. aguabonita group. This apparent discrepancy will be discussed later.

While the two subgroups cluster separately, with the S. a. whitei group (DMCA, USSCA, LWM, DMCB, WC, and CC) joining the S. a. aguabonita group (SFK, SFFIS, MC, TRC, CWLA, CWLB, and CWLC) group at 4.31 (Fig. 3), there were eight clusters of populations that were distinct, based on a variance calculated from the Euclidean distance

matrix (Sneath and Sokal, 1973). There was, however, a high degree ($r = .606$) of concordance between the Euclidean distance and biochemical similarity matrices. This suggested that even though the meristic data was not as conclusive as the biochemical, the meristic data tended to suggest a similar pattern of relationships existing among the population and subgroups as was demonstrated by the biochemical data.

Discussion

The systematics of western North American Salmo has been based on morphological differences and geographical isolation (Miller, 1972) or "degree of difference," as Hubbs (1943) expressed it. This was because of the apparent lack of genetic isolating mechanisms (Gould, 1966; Gold and Gall, 1975a; and Gold et al., 1977). Consequently, the Salmo species do not fit the biological species criteria of Mayr (1973). Subspecific differences, therefore, are even less clear cut and more arbitrary.

There were significant electrophoretic differences between the two subspecies for the populations sampled in this study. The meristic differences were not as clearcut, however, the high concordance between the meristic, genetic, and geographical data support the separation of S. a. whitei and S. a. aguabonita as at least subspecific entities.

The only population that clustered in one group electrophoretically (S. a. whitei) and the other group meristically (S. a. aguabonita) was FC. Smith (1981) and Evans et al. (1973) have

noted that it was the only sample site in the Little Kern River basin which has been subjected to tremendous erosion and destruction of suitable habitat.

The habitat on Fish Creek (FC) is very similar to TRC, MC, SFFIS, and SFK, having little stream cover and high water temperatures (Dill, 1945; Smith, unpublished data). Garside (1966) and Kwain (1975) have demonstrated that higher than normal water temperatures causes significant changes in meristic counts in embryonic S. gairdneri. So it is not suprising that FC would cluster with TRC, MC, SFFIS, and SFK. Electrophoretic characters are less subject to environment effects than meristic ones (Avise and Ayala, 1975). Therefore, based on electrophoretic and geographical evidence, FC is considered a S. a. whitei population rather than a S. a. aguabonita population.

Although much has been written about the phylogenetic relationships of S. a. whitei and S. a. aguabonita, little has been done to define the two forms systematically. It is critical to clearly define the forms before beginning to suggest possible phylogenies and evolutionary histories. It was, then, the purpose of this study to clearly define S. a. whitei and S. a. aguabonita.

Evermann's (1906) description of S. a. whitei and Jordan's (1892) description of S. a. aguabonita contain little information beyond a general observation about coloration, spotting patterns, and scale size. Their type collections have been examined by Schreck and Behnke (1971) and Legendre, Schreck, and Behnke (1972) and compared with collections made in the Little Kern River basin during 1967 to 1969. Their conclusion was that S. a. whitei was synonymous with S. a.

gilberti (Kern River Rainbow); however, this conclusion was based primarily on lateral series scale counts. All of the populations listed by Schreck and Behnke (1971) as being S. a. whitei have been shown to be introgressed with S. gairdneri (Smith, 1981). It is not surprising that Schreck and Behnke (1971) felt that the fish they examined were closely related to S. gairdneri.

Gold and Gall (1975a) critically examined several isolated populations of fish in the Little Kern River basin, Cottonwood Creek, South Fork Kern, and Golden Trout Creek. On the basis of 11 meristic characters, they divided the populations into three distinct taxonomic groups. Cottonwood Creek, South Fork Kern, and Golden Trout Creek were identified as S. a. aguabonita. An isolated population in Soda Springs Creek, a tributary of the Little Kern, was identified as a S. a. whitei based on its greater similarity to the S. a. aguabonita populations than the populations down stream from it. The remaining two populations, located just down stream from the S. a. whitei population, demonstrated characteristics suggestive of a recent hybrid origin with S. gairdneri (Gold, 1975). Gold and Gall (1975b) meristically identified another isolated population in Deadman Creek of S. a. whitei in the Little Kern basin. Gall et al. (1976) have corroborated electrophoretically the work of Gold and Gall (1975a,b).

Smith (this paper) has examined, electrophoretically and meristically, 31 populations of fish from the Little Kern basin and has found a close correlation between electrophoretic and meristic evidence that suggested the existence of three distinct taxonomic groups in the Little Kern basin. Seven isolated populations scattered

throughout the Little Kern basin represented S. a. whitei. Nineteen populations show evidence of introgression and have a history of being planted with S. gairdneri (Dill, 1940,1945). Five isolated populations, geographically adjunct, have been tentatively identified as S. a. gilberti (pending further ongoing investigation).

It is interesting that all investigators examining a similar locality get very similar results. However, the conclusions arrived at by each investigator seemed to be completely contrary until Smith (this paper) demonstrated the complex relationships that existed among populations in the Little Kern basin. The findings of Gold and Gall (1975a,b), Gall et al. (1976), Schreck (1969), and Schreck and Behnke (1971) are comparable with the much broader overview presented by Smith (1981).

The biochemical similarity or "degree of difference" between S. a. whitei and S. a. aguabonita of 0.911 is comparable to that reported for S. clarki subspecies (0.937 to 0.754) (Loudenslager and Gall, 1980). Smith (1981) found similarity between S. gairdneri and S. a. whitei of 0.894, while Utter et al. (1973) report a value of .90 between S. gairdneri and S. clarki. Turner (1974) reported values of .969 to .834 for species of Cyprinodon. Therefore, the level of similarity observed between S. a. whitei and S. a. aguabonita is not unexpected for fish.

There appeared to be greater differences biochemically than meristically between S. a. whitei and S. a. aguabonita suggesting that both levels of genetic organization are undergoing different rates of evolution. This is the reverse of the results of Busack (1977) where

there are no biochemical differences between S. clarki henshawi and S. c. seleniris, yet meristically the two subspecies have characteristic differences. The lack of a clear cut trend between biochemical and meristic evolution in western Salmo is reason for a more cautious and thorough meristic and biochemical approach to questions of phylogeny and evolution in western Salmo.

The resolution of the phylogeny and evolution of S. a. whitei and S. a. aguabonita must, then, wait until the status of S. a. gilberti is more clearly defined since it may represent the link between S. a. whitei and S. a. aguabonita or S. aguabonita spp. and S. gairdneri.

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Table I. Locations and designations of Trout collected from 1974 to 1978. The site number refers to figure 1.

Population	Site Number	Acronym	Sub-Species	N
Cottonwood Lakes 1-3	1	CWLA	aguabonita	40
Cottonwood Lakes 4-5	2	CWLB	aguabonita	40
Cottonwood Lake 3	3	CWLC	aguabonita	21
Coyote Creek	4	CC	whitei	40
[1]Deadman Creek, Lower	5	DMCB	whitei	34
Deadman Creek, Upper	6	DMCA	whitei	26
Fish Creek, Little Kern	7	FC	whitei	40
Fish Creek, South Fork Kern	8	SFFIS	aguabonita	21
Mulkey Creek	9	MC	aguabonita	40
Soda Springs Creek, Upper	10	USSCA	whitei	25
South Fork Kern River	11	SFK	aguabonita	41
Trout Creek	12	TRC	aguabonita	47
[1]Wet Meadows Creek, Lower	13	LWM	whitei	35
Willow Creek	14	WC	whitei	38

[1] Meristic data collected by J. R. Gold (1981).

Table II. Protein systems studied, with number of loci, tissue examined and quarternary structure.

Protein	Acronym	Loci	Tissue	Quarternary Structure	
Alcohol dehydrogenase	ADH	1	Liver	Dimer	(3)
Alpha-glycerophosphate dehydrogenase	AGPDH	1	Muscle	Dimer	(1)
Adenylate Kinase	AK	1	Muscle	———	
Creatine Kinase	CK	2	Muscle	Monomer	(3)
Diaphorase	DIA	1	Liver	———	
Fumarase	FUM	1	Muscle	Monomer	(5)
Isocitrate dehydrogenase	IDH	2	Liver	Dimer	(2)
Malate dehydrogenase	MDH	4	Heart	Dimer	(1)
Para-albumin	PALB	1	Blood	Monomer	(2)
Phosphoglucoisomerase	PGI	3	Muscle	Dimer	(3)
Phosphoglucomutase	PGM	1	Muscle	Monomer	(1)
Superoxide dismutase	SOD	1	Liver	Dimer	(1)
Malic enzyme	ME	1	Liver	Tetramer	(4)

(1) Utter and Hodgins, 1972; (2) Busack et al., 1979; (3) Allendorf, 1975;

(4) Busack, 1977; (5) Unpublished data.

Table ~~IX.~~ III. Gene frequencies for 8 variable protein systems for 14 trout populations. IDH is composed of 2 loci with identical alleles, so is reported as one system.

	PALB		SOD			IDH				ME		PGM		CK-1		MDH-4			AGPD	
	100	105	60	100	140	60	100	140	170	70	100	85	100	70	100	85	100	125	100	140
FC	1.00	0	.70	.30	0	.05	.75	.19	.01	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
WC	.90	.10	.99	.01	0	0	.73	.27	0	.03	.97	0	1.00	0	1.00	0	1.00	0	1.00	0
CC	.78	.22	.87	.13	0	0	.68	.32	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
DMCA	.91	.09	.86	.14	0	0	.78	.22	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
DMCB	.99	.01	.96	.04	0	0	.88	.12	0	0	1.00	01	.99	.01	.99	0	1.00	0	1.00	0
USSCA	.88	.12	1.00	0	0	0	.97	.03	0	0	1.00	0	1.00	.02	.98	0	1.00	0	.98	.02
LWM	.93	.07	.71	.29	0	0	.77	.23	0	.11	.89	0	1.00	0	1.00	0	1.00	0	1.00	0
SFK	.68	.32	.05	.91	.04	.01	.17	.78	.04	.03	.97	0	1.00	0	1.00	0	1.00	0	1.00	0
WL	.68	.32	0	.94	.06	.01	.05	.94	0	.05	.95	0	1.00	0.	1.00	.06	.94	0	.86	.14
WL	.75	.25	0	.99	.01	0	.12	.88	0	0	1.00	0	1.00	0	1.00	.06	.94	0	.99	.01
CWLC	.94	.06	0	1.00	0	0	.07	.93	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
SFFIS	.86	.14	0	1.00	0	0	.11	.89	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
MC	.73	.27	.33	.55	.12	0	0	1.00	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0
TRC	.96	.04	0	1.00	0	0	.22	.78	0	0	1.00	0	1.00	0	1.00	0	1.00	0	1.00	0

Table IV. Biochemical similarity coefficients (I) among 14 populations of trout calculated according to Nei (1972). Average heterozygosity in principle diagonal.

	FC	WC	CC	DMCA	DMCB	USSCA	LWM	SKF	CLWA	CLWB	CLC	SFFIS	MC	TRC
FC	.061	.995	.995	.998	.996	.992	.999	.936	.913	.925	.921	.919	.926	.943
WC		.052	.998	.999	.998	.997	.995	.922	.899	.908	.904	.902	.922	.923
CC			.072	.999	.995	.994	.996	.940	.918	.927	.920	.919	.938	.938
DMCA				.055	.999	.997	.998	.927	.903	.914	.909	.908	.922	.930
DMCB					.029	.999	.995	.904	.877	.889	.886	.884	.898	.909
USSCA						.019	.993	.891	.860	.873	.867	.866	.882	.893
LWM							.073	.938	.915	.926	.922	.919	.928	.942
SFK								.068	.997	.999	.994	.991	.992	.995
CLWA									.061	.998	.994	.993	.991	.992
CLWB										.048	.997	.995	.990	.997
CWLC											.019	.993	.988	.999
SFFIS												.054	.983	.993
MC													.049	.985
TRC														.040

Table ~~XI~~ V. Means for 10 meristic characters in 14 trout populations. The error mean square (EMS) and sample sizes are provided for calculation of significant differences among means. Fork length is in millimeters. DP = Dorsal Proximal Pterygiophores; AP = Anal Proximal Pterygiophores; BO = Branchiostegals. Means with identical superscripts are not significantly different at P = .05.

	Fork Length	Pyloric Caecae	DP	AP	Pectoral Fin Rays	Pelvic Fin Rays	BO	Vertebra	Gill Rakers	Lateral Series	Sample Size
FC	138.9	34.3^{c}	13.7^{abc}	11.9^{de}	14.6^{b}	9.2^{a}	21.3^{ad}	59.8^{abd}	19.0^{cd}	156.3^{a}	40
WC	129.3	42.3^{g}	14.5^{df}	12.8^{bc}	16.0^{d}	9.8^{bc}	23.3^{bc}	60.9^{fh}	20.3^{ab}	152.3^{a}	38
CC	149.6	37.8^{f}	14.1^{bcd}	12.6^{abc}	15.3^{f}	9.8^{bc}	23.3^{bc}	60.1^{abc}	20.6^{b}	153.0^{a}	40
DMCA	128.9	35.0^{c}	14.1^{bcd}	12.0^{de}	15.5^{cf}	10.0^{bc}	23.5^{bc}	60.4^{bcf}	20.4^{ab}	178.9^{bc}	26
DMCB	123.3	33.3^{ce}	13.8^{abc}	11.7^{d}	15.7^{cd}	9.0^{a}	23.9^{b}	60.0^{abc}	19.9^{ab}	183.0^{c}	34
USSCA	127.6	34.3^{c}	14.8^{f}	12.2^{ae}	15.8^{cd}	9.9^{bc}	22.7^{c}	60.7^{cf}	19.6^{ac}	173.0^{b}	25
LWM	133.0	38.8^{f}	14.6^{f}	12.8^{bc}	15.7^{cd}	9.5^{d}	23.8^{b}	61.3^{h}	19.9^{ab}	174.1^{b}	35
SFK	106.7	31.1^{de}	13.6^{ab}	12.3^{a}	14.2^{e}	9.1^{a}	20.1^{ef}	59.5^{ad}	19.0^{cd}	150.7^{a}	41
CWLA	180.4	28.3^{ab}	13.8^{abc}	12.5^{abc}	14.5^{b}	9.2^{a}	21.7^{a}	59.3^{ade}	20.3^{ab}	182.6^{c}	40
CWLB	218.0	27.6^{ab}	14.1^{cd}	12.6^{abc}	14.7^{b}	9.2^{a}	22.0^{a}	59.3^{de}	20.0^{ab}	183.8^{c}	40
CWLC	207.3	29.8^{bd}	13.5^{ae}	12.6^{abc}	14.8^{b}	9.2^{a}	21.5^{ad}	59.3^{ade}	19.7^{ac}	179.8^{bc}	21
SFFIS	194.6	28.1^{ab}	13.4^{ae}	12.5^{abc}	14.0^{ae}	9.0^{a}	20.3^{fg}	59.0^{eg}	19.5^{ac}	161.4^{d}	21
MC	140.4	26.3^{a}	13.6^{a}	12.4^{ab}	13.5^{a}	9.0^{a}	19.6^{e}	58.5^{g}	18.8^{d}	175.4^{b}	40
TRC	118.2	31.2^{de}	13.9^{abc}	12.9^{c}	14.0^{ae}	9.8^{b}	20.8^{dg}	59.9^{bc}	18.5^{d}	154.1^{a}	47
EMS	--	15.8	.49	.34	.34	.17	1.37	.99	1.06	115.07	--

Table VI. An analysis of variance of 9 meristic characters for all 14 populations. The populations are nested within the subspecies.

Means Squares for Each Character

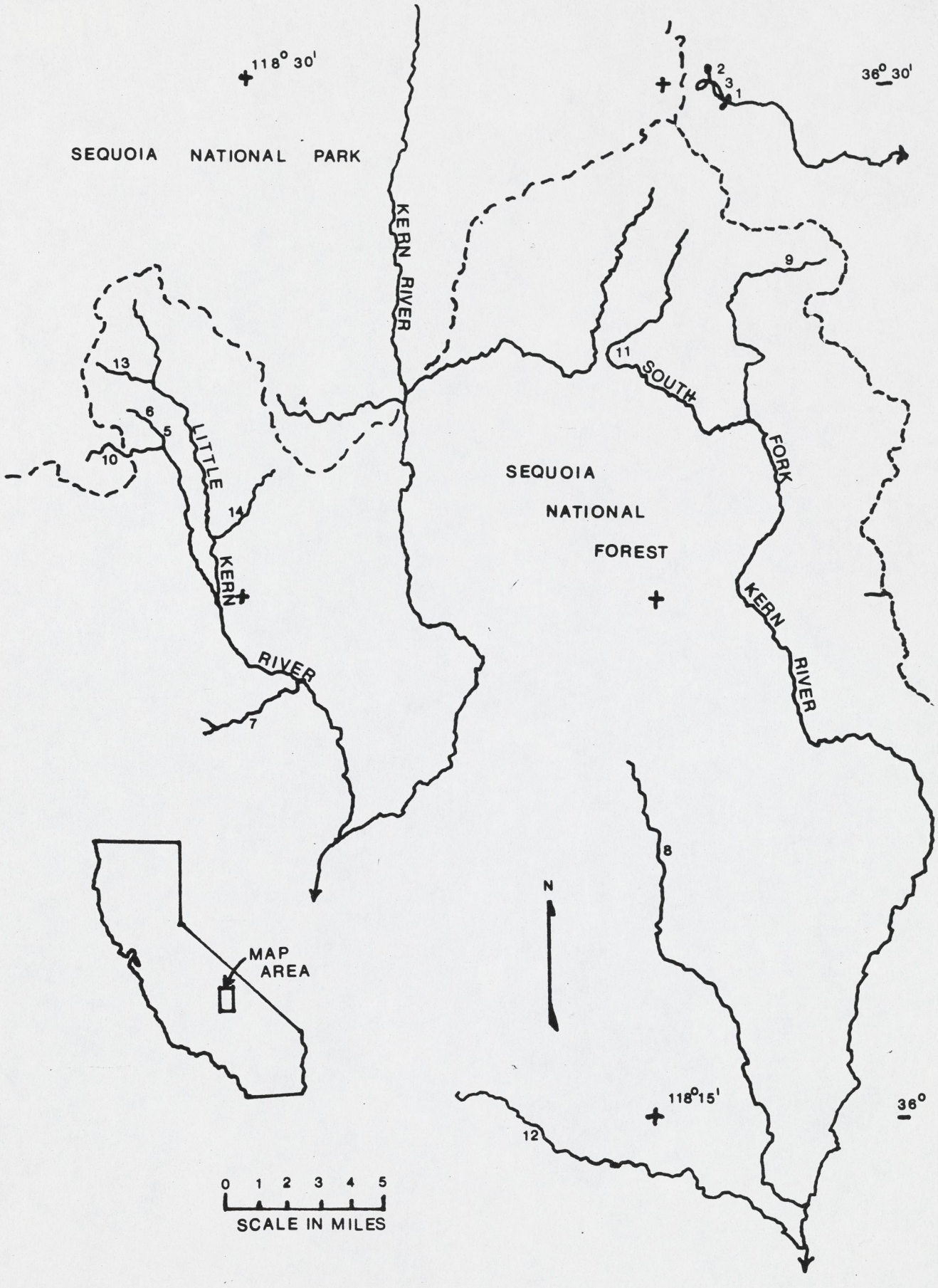
Source	d.f.	Pyloric Caeca	D.P.	A.P.	Pectoral Fin Rays	Pelvic Fin Rays	B.O. Rays	Vertebra	Gill Rakers	Lateral Series
Between subspecies	1	6629.9^{**}	34.1^{*}	9.3^{ns}	173.6^{**}	16.9^{ns}	590.5^{**}	160.2^{**}	38.0^{ns}	699.1^{ns}
Popul. within subspecies	12	260.5^{**}	3.9^{**}	4.3^{*}	6.2^{**}	3.9^{**}	28.6^{**}	10.9^{**}	14.1^{**}	6768.4^{**}
Within Popul.	474	15.9	.5	.3	.3	.2	1.4	1.0	1.1	114.8

Level of significance: * = $P \leq .05$, ** = $P \leq .01$, ns = not significantly different.

Table VII. Euclidean distance matrix of 14 trout populations based on 9 meristic characters.

	WC	CC	DMCA	DMCB	USSCA	LWM	SFK	CWLA	CWLB	CWLC	SFFIS	MC	TRC
FC	3.95	2.93	3.60	3.67	3.38	3.73	1.75	3.54	3.71	3.01	2.87	3.78	2.80
WC		2.02	3.74	4.84	3.17	2.65	4.91	5.82	5.82	5.26	5.93	6.97	4.75
CC			2.84	4.17	2.81	2.76	3.73	4.38	4.49	4.00	4.44	5.61	3.53
DMCA				2.58	1.71	2.43	4.75	3.47	3.51	3.29	4.87	5.33	4.41
DMCB					3.15	3.17	4.99	3.48	3.37	3.26	4.87	5.22	5.43
USSCA						2.13	4.41	3.91	3.75	3.55	4.90	5.32	4.08
LWM							4.86	4.37	4.22	3.98	5.33	5.95	4.44
SFK								3.61	3.84	3.18	1.90	3.03	2.19
CWLA									.76	1.15	2.43	2.46	3.76
CWLB										1.35	2.75	2.66	3.91
CWLC											2.27	2.47	3.41
SFFIS												1.70	2.88
MC													3.59

FIGURES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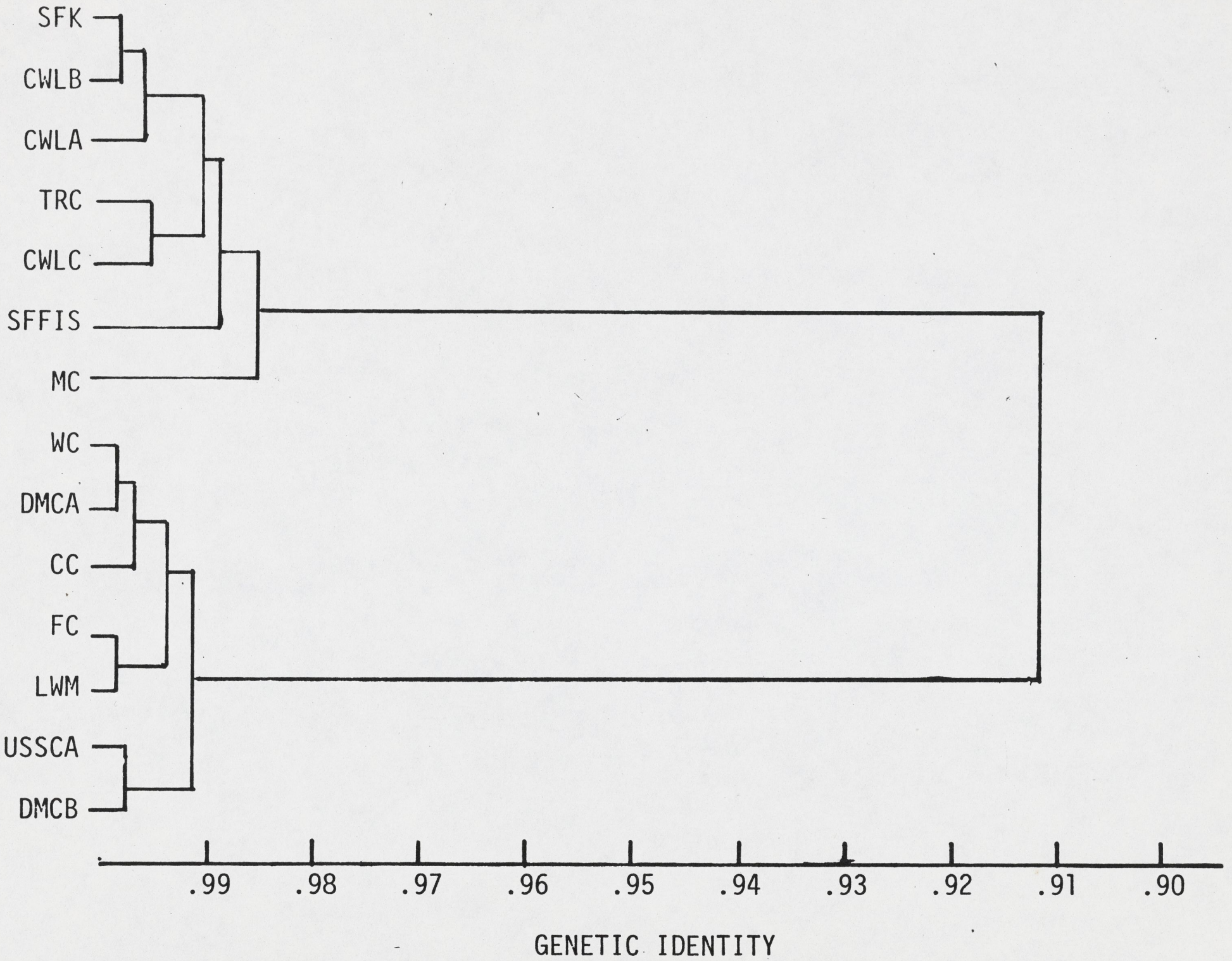
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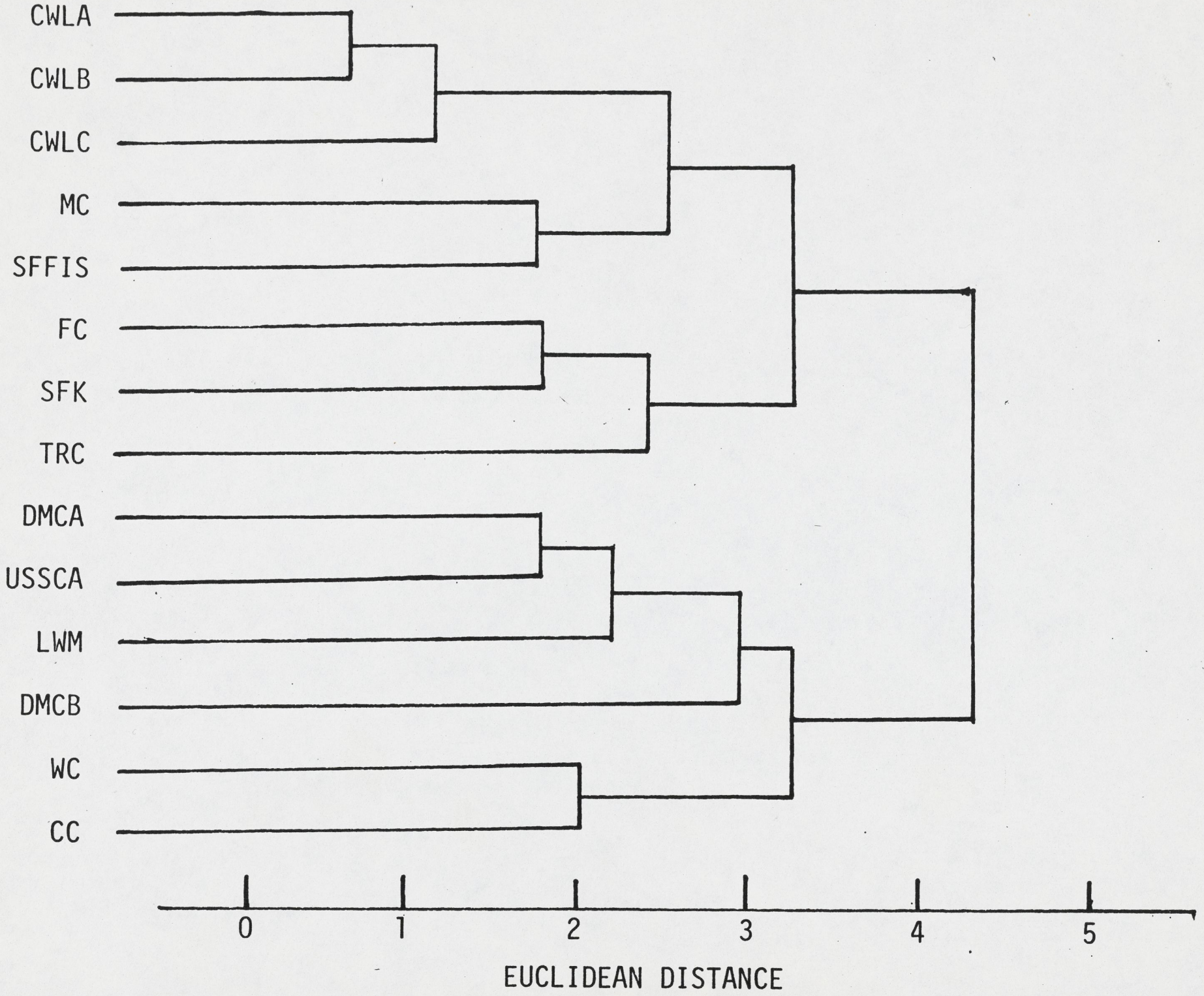
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AUTHOR(S)/AUTEUR(S): R.C. Smith and G.A.E. Gall

TITLE/TITRE: Biochemical-Genetic and Meristic Analyses of Populations Of Little Kern River Basin Golden Trout

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BIOCHEMICAL-GENETIC AND MERISTIC ANALYSES OF POPULATIONS OF LITTLE KERN RIVER BASIN GOLDEN TROUT

R. C. Smith and G. A. E. Gall

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Abstract

A total of 1088 specimens from 31 populations of Little Kern Golden Trout were analyzed for 9 meristic characters and 20 electrophoretic loci. The populations were divided into three distinct taxonomic groups, based on Euclidian distance and genetic similarity estimates. Seven populations were identified as *Salmo aguabonita whitei* Everman; nineteen populations evidenced recent introgression with Rainbow trout, *S. gairdneri* Richardson. The remaining five populations in the southern part of the Little Kern River Basin are difficult to classify but may represent the Kern River Rainbow *S. gairdneri gilberti*. The conclusive definition of this last group would clear up contradictory hypotheses concerning the taxonomic synonomy of *S. a. whitei*.

Genetic identities observed were .894 between *S. a. whitei* and *S. g. gairdneri*; .921 between *S. a. whitei* and *S. g. gilberti*; and .957 between *S. g. gilberti* and *S. gairdneri*. Genetic identity among populations of the *S. a. whitei* group was .996 and among populations of the *S. g. gilberti* group was .994 indicating a high degree of within group similarity.

Key words: *Salmo aguabonita* and *gairdneri*, subspecies, hybridization, electrophoresis, merisrics, taxonomy, evolution.

Introduction

The taxonomic status and distinctiveness of the Little Kern River golden trout, Salmo aguabonita whitei (Evermann) has been disputed since it was first described as one of three species by Evermann 1906. Ellis and Bryant (1920) felt that it descended from the Kern River rainbow S. gairdneri gilberti Jordan. Schreck (1969), Schreck and Behnke (1971), and Legendre, Schreck, and Behnke (1972) proposed that S. a. whitei was synonomous with S. gairdneri gilberti (Jordan), which they called S. a. gilberti. Presently, S. a. whitei is considered to be subspecific to S. a. aguabonita, found in Golden Trout Creek, the south fork of the Kern River and Cottonwood Creek (Miller, 1950; Gold and Gall, 1975). The populations of S. a. whitei are differentiated from S. a. aguabonita by having spots over the entire body, fewer lateral scales than S. a. aguabonita, being duller in coloration and geographically isolated (Evermann, 1906). The problem has become confounded by the planting of rainbow trout in streams of the Little Kern River basin from 1932-1941 (Dill, 1941, 1945 & 1950). Dill (1945 & 1950) has suggested that these plantings have led to extensive hybridization occurring throughout the Little Kern River basin.

Apparently incomplete genetic isolating mechanisms have allowed the golden and rainbow trout to hybridize (Gold and Gall, 1975a; Gold et al., 1977; Pipkin, unpublished data).

The species classification of Western North America Salmo sp. has been based on morphological differences and geographical isolation (Miller, 1972) so these species may not fit the biological species criteria of Mayr (1973). Geological barriers have isolated many discrete populations in the Little Kern River Basin (Evans et al.,

1973). A careful meristic analysis of several discrete populations of fish from Soda Spring Creek and the Little Kern River and their subsequent comparison with S. a. aguabonita populations from Golden Trout Creek, South Fork Kern River and Cottonwood Creek by Gold and Gall (1975a,b) have confirmed the existence of isolated Golden trout populations present in the upper Soda Springs Creek drainage. Gold and Gall (1975a) tentatively classified these populations as S. a. whitei, while the downstream populations exhibited characteristics tending toward those of S. gairdneri and were suspected of having a relatively recent hybrid origin.

Gall et al. (1976) using electrophoretic evidence from the same fish used in the meristic study of Gold and Gall (1975a) have reached a parallel conclusion. This corroboration between meristic and biochemical-genetic evidence strongly suggested that S. a. whitei exists and is a form of S. aguabonita.

The purpose of this study was to assess the status of additional populations in the Little Kern River Basin and to determine whether other populations may have introgressed with S. gairdneri. This was done by comparing Little Kern River populations to S. a. whitei from Upper Soda Spring Creek and the Whitney strain of S. gairdneri as representative of rainbow planted in the drainage. The samples were analyzed on two levels of genetic organization similar to that of Gold and Gall (1975a) and Gall et al. (1976): meristic counts to investigate multiple gene traits and starch-gel electrophoresis to investigate single gene differences.

Materials and Methods

Collection of 1088 fish representing 31 possible S. a. whitei

populations was undertaken from 1974 to 1976 (Table I, Fig. 1). For comparison, 245 S. gairdneri, from the Mt. Whitney Hatchery, were used for electrophoretic analysis and 24 of these were used in the meristic analysis. The Whitney strain (RTW) was chosen because it is the only extant broodstock that predates the planting program in the Little Kern Basin of the 1930's and 1940's (Busack et al., 1979) and it was one of the stocks planted in the Little Kern Basin from 1932 to 1941 (Dill, 1945).

Table I near here
Fig. 1 near here

Electrophoretic Techniques. The fish were fin clipped for population identification and transported live to the Fisheries Biology Research Facility. Each fish was permanently jaw tagged upon sacrifice and all tissue samples were labelled accordingly. The tissues were processed following the methods of Gall et al. (1976). The horizontal starch-gel electrophoresis technique used was modified during the study. This improved resolution and increased efficiency, but did not effect phenotypic interpretation of the protein systems. The horizontal starch-gel electrophoretic and staining techniques of Busack et al. (1979) were the ultimate ones used. The twenty loci for thirteen protein systems studied are listed in Table II.

Table II near here

Gels were interpreted according to inheritance models of Golden trout (Gall et al., 1976) and other salmonid species (Busack et al., 1979; Allendorf, 1975; Utter and Hodgins, 1972). The system of nomenclature followed that of Busack et al. (1979), which was originally suggested by Allendorf and Utter (1979). Each locus was given an appropriate acronym. Multiple locus systems were numbered consecutively with increasing migration rate of the protein product. Usually the most common allele at each locus was designated 100 with

the other allelic designations based on migration rate relative to the most common allele.

Coefficient of genetic similarity between operational taxonomic units (OTU) based on the allelic frequencies at the 20 loci were calculated according to Nei (1972). The resulting matrix of genetic similarities was subjected to the unweighted pair-group arithmetic averages (UPGMA) method of cluster analysis (Sneath and Sokal, 1973). Average heterozygosity values were calculated according to Nei and Roychoudbury (1974). An unrooted Wagner network was constructed after Farris (1970) and Sneath and Sokal (1973), using allele frequency data. Allele frequencies were calculated for each electrophoretic group and coded as present if the frequency was greater than .05.

Meristic Techniques

After the fish were sacrificed, labeled and tissues taken for electrophoresis, they were preserved in 10% formalin for a week. They were then rinsed for 24 hours in water and stored in 70% isopropanol or ethanol according to Minckley (1973).

Fish were checked for basibranchial teeth. Meristic counts were made for 9 characters according to procedures of Minckley (1973) and Gold and Gall (1975a). The characters and counting procedures were: pyloric caeca, all tips counted; vertebrae, and dorsal and anal proximal pterygiophores were counted from radiographs; the pectoral and pelvic principle fin rays were counted under a dissecting scope; branchiostegal rays on both left and right sides were counted and sum recorded; all gill rakers on first gill arch including rudiments; lateral scales, counted from the cleithrum to the end of the hypural plate, two scale rows above the lateral line - the end of the hypural

plate was determined by flexure of the caudal peduncle and noting the resulting fold and a scale lying on the fold with more than half its length anterior to the fold was counted; fork length measured to the nearest millimeter was the only measurement made.

The data were subjected to descriptive analysis using BMDP program 7D (Dixon, 1977) to detect obvious departures from normality. Gold and Gall (1975) had also demonstrated by Fisher's third (skewness) and fourth moment (kurtosis) statistics that the meristic characters studied are normally distributed in golden trout. The data were analyzed by least squares analysis of variance using the method of Harvey (1975). A posteriori mean separation was done using Student-Newman-Keuls (SNK) multiple range test (Sokal and Rohlf, 1969).

Pair-wise Euclidean distances were calculated using the square root of the Mahalanobis of Sneath and Sokal (1973). An Euclidean distance dendrogram was generated using the UPGMA method of Sneath and Sokal (1973).

Results

Electrophoretic Analysis. Allele frequencies for the ten polymorphic protein systems representing 11 loci are presented in Table III. Nine loci, invariant in all populations were PGI-1, 2, and 3, CK-2, DIA, AK, and MDH 1-2. The banding patterns and the genetic interpretations followed those in Busack et al. (1979), except as outlined below.

Table III near here

Isocitrate dehydrogenase (IDH); Busack et al. (1979) have shown that IDH was a dimer encoded by two polymorphic loci which have identical alleles. Therefore, the values reported in Table III are the average of the two loci, since calculation of allele frequencies

at each locus was impossible. IDH was entered as two identical loci for calculation of genetic identities.

Fumarase (FUM): The variation observed suggested that FUM is a monomer encoded by a single locus. This is the first report of variability in FUM in salmonids (Allendorf, 1975; Busack et al., 1979).

Alcohol dehydrogenase (ADH): Gall et al. (1976) and Busack et al. (1979) reported that this system was invariant in Rainbow and Golden trout. In the present study, variability was observed to support Allendorf (1975) that ADH is a dimer encoded by a single locus.

Malic enzyme (ME): The variation observed suggests that ME is a tetramer encoded by at least one locus. This is in agreement with Busack (1977). The one locus model was assumed since no breeding data were available to suggest an alternative model.

Four alleles found in the wild populations were not found in the RTW sample: SOD 60, ADH 50, PGM 85 and FUM 105 whereas RTW did not exhibit alleles not found in the wild populations.

Average heterozygosity and the genetic similarity index (I) for all pair-wise comparisons are given in Table IV. The mean heterozygosity for all the wild populations was 7.2 percent, comparable to values found by Gall et al. (1976) and Allendorf and Utter (1978) for other salmonids. The wild population values ranged from 1.9% for USSCA to 10.3% for GM, while RTW had a value of 13.8 percent. The range of values of (I) was from .999 (TRMC-LSGC, LSSC-LKRD) to .893 (RTW-USSCA). The RTW sample had an average identity of .950 with all other populations.

Table IV near here

A genetic similarity dendrogram based on allele frequencies for

the twenty systems is presented in Figure 2. The cophenetic correlation coefficient of .921 indicated little distortion due to clustering (Sneath and Sokal, 1973). There were four distinct clusters of populations based on a variance calculated from all pairwise comparisons of the similarity matrix (Sneath and Sokal, 1973): 1) an apparent "S. a. whitei" group, WC, DMCA, CC, FC, LWM, USSCA, and DMCB, with an average identity of .996; 2) a geographic cluster which we will refer to as the "Mountaineer group", SMC, NCC, JC, MMC and NMC, whose average identity was .994; 3) the RTW population; and 4) an apparent introgressed group, MSSC, UWM, QMC, TRMC, LSGC, USSCB, RC, LSSC, LKRD, GM, TMC, USGC, LKRC, LKRB, LPC, UPC, LKRH, AC, and LKRA, with an average identity of .993. The Mountaineer group joined the introgressed group at an average identity of .974. The S. a. whitei joined the Mountaineer - introgressed group at .963 while these groups then joined the RTW population at .938.

Fig. 2 near here

The average similarity between the whitei group and RTW was .912. This value is comparable to that of .89 reported by Turner (1974) for 5 species of cyprinodon, 0.90 by Utter et al. (1973) for S. gairdneri vs. S. clarki, .85 by Busack (1978) for S. gairdneri vs. S. clarki and .937 to .754 reported for S. clarki subspecies by Loudenslager and Gall (1980). The "degree of difference" between whitei and RTW can be characterized by differences in six systems, PALB, SOD, IDH, ME, CK-1 and MDH-4. The frequency of PALB 100 was high (.91) in whitei and moderate (.45) in RTW. SOD 60 was high (.87) in whitei and absent in RTW, while SOD 140 was present (.12) in RTW and absent in whitei. The IDH 60 allele was rare (.01) in whitei but had a frequency .20 in RTW, while IDH 100 was high (.79) in whitei and low (.08) in RTW. The IDH

170 allele was observed in one heterozygous whitei fish and at a frequency of .38 in RTW. ME 100 was high (.98) in whitei and moderate (.64) in RTW. The MDH-3,4 85 allele was absent in whitei and at .37 in RTW, while MDH-4 100 was fixed in whitei and at a frequency of .62 in RTW. CK-1 70 was at a frequency of .16 in RTW and absent in whitei.

The "Mountaineer" electrophoretic group, JC, NMC, MMC, and SMC had an average similarity of .994. The average similarity to whitei was .921. The degree of divergence between whitei and the Mountaineer group (MG) can be characterized by differences in six systems PALB, SOD, IDH, MDH4, ADH, and FUM. The frequency of PALB 100 was .73 in MG and .91 in whitei. SOD 60 was the dominant SOD allele in whitei (.87), while SOD 100 occurred at .75 in MG. The frequency of SOD 140 was .18 in MG and absent in whitei. The most common IDH allele in whitei was IDH 100 (.79) whereas IDH 140 occurred at a frequency of .81 in MG populations. MG had four rare alleles, ADH 50, FUM 105, MDH 85 and 125, that were absent in whitei.

The "Mountaineer" electrophoretic group had an average similarity to RTW of .957, which is closer to RTW than is whitei (.894). The electrophoretic differences can be characterized by eight systems; PALB, SOD, IDH, ME, MDH-4, ADH, CK-1 and FUM. The frequency of PALB 100 was dominant (.73) in MG and common (.45) in RTW. IDH 140 was the dominant allele (.81) in MG while being only common (.34) in RTW. IDH 60 and 170 were common alleles in RTW and rare in MG. ME 70 was common (.36) in RTW and present in one heterozygote in MG. No fish in MG carried the CK-1 70 allele, however, it was common (.16) in RTW. The MDH-4 85 allele was rare in MG and common (.37) in RTW. MG had

three rare alleles, SOD 60, ADH 50, and FUM 105, not found in RTW.

The Wagner network (Fig. 3) showed that the whitei and "Introgressed" electrophoretic groups have identical allelic configurations, suggesting that their phenetic differentiation is of a very recent origin. The whitei and "Mountaineer" groups are more closely related to each other than either is to S. gairdneri, suggesting they evolved from a common ancestor in the Kern River Basin rather than evolving from S. gairdneri.

Fig. 3 near here

Meristic Analysis. Table V presents the observed means and error mean squares for all characters in all samples. No true basibranchial teeth were observed in any population. All characters appeared to be distributed normally supporting the results of Gold and Gall (1975). An analysis of variance revealed that there were significant differences among populations for all 9 characters. Therefore, all were used in the Student-Newman-Keuls mean separation analysis and in the Euclidean distance calculations. High pyloric caeca and low counts for pectoral fin rays, dorsal proximal pterygiophores, and lateral scales consistently discriminated between RTW and the wild poplations.

Table V near here

Euclidean distance estimates based on Mahalanobis distances are presented in Table VI. Distances ranged from .75 (LKRC-LSGC) to 8.83 (RTW-DMCB). As with the electrophoretic data, RTW is the most distant population with an average value of 6.11.

Table VI near here

A dendrogram (Fig. 4) was generated from the Euclidean distance matrix. The cophenetic correlation coefficient of .834 indicated little distortion due to clustering (Sneath and Sokal, 1973). There were three clusters of populations that were distinct, based on a

variance calculated from all pair-wise comparisons (Sneath and Sokal, 1973) which agree closely with the groupings defined from electrophoretic evidence. The groups are: a group containing whitei populations USSCA, LWM, and DMCA, in addition to, USSCB and MSSC, with an average within group distance of 1.82. The "Mountaineer" group, UPC, LKRA, AC, JC, NMC, LKRH, MMC, and SMC with an average within group distance of 1.82 and the apparent "introgressed" group comprised the third group, with an average distance among populations of 1.73. The "introgressed" group joins the whitei group at 2.21. Then an outlier (GM) joins this group at 2.40. This cluster then joins the "Mountaineer" group at 2.91. FC and DMCB are outliers joining at 3.14 and 3.96 respectively, while NCC and RTW cluster together at 4.18 and complete the dendrogram at 5.31.

Fig. 4 near here

While there is a significant correlation (r = .463) between the genetic similarity matrix (Table IV) and the Euclidean distance matrix (Table VI), there were numerous discrepancies in the population makeup of the three major groups. The whitei electrophoretic and meristic groups have three out of nine populations in common, USSCA, LWM, and DMCA. The "Mountaineer" groups have four common members out of ten possible, JC, NMC MMC, and SMC. The "introgressed" groups have 11 common members out of a total of twenty one.

Means of meristic characters for RTW and the populations which were common to the three groupings based on both meristic and electrophoretic evidence are presented in Table VII. RTW and whitei differed in all but two characters, number of vertebrae and gill rakers. Also, whitei have a brilliant coloration and sparse spotting that readily distinguish them from RTW.

Table VII near here

The "degree of difference" between the whitei and Mountaineer groups can be characterized by differences in all but one meristic character (Table VII), Dorsal proximal pterygiophores. Morphologically, Mountaineer group fish were not as brightly colored and were more densely spotted than whitei group.

The significant meristic differences occurred between the Mountaineer group and RTW at all but one of the nine meristic characters, branchiostegal rays.

Discussion

The classification of western North American Salmo has been based on morphological differences and geographical isolation (Miller, 1972) or "degree of difference," as Hubbs (1943) expressed it. This was necessitated by the apparent lack of genetic isolating mechanisms (Gould, 1966; Gold and Gall, 1975 and Gold et al., 1977). Consequently, the Salmo species don't fit the biological species criteria of Mayr (1973).

The whitei meristic group has three members in common with the whitei electrophoretic group, LWM, USSCA, and DMCA. FC is an outlier which clusters with the whitei and the "introgressed" group. The deviation of FC is probably due to environmental factors effecting all the meristic characters. Fish Creek (FC) is the only sample site which has undergone tremendous erosion and destruction of suitable habitat. The erosion has destroyed the stream cover which invariably causes higher than normal water temperatures (Evans et al., 1973). Garside (1966) and Kwain (1975) have demonstrated that higher than normal temperatures cause rapid embryonic development in Salmo gairdneri, which is inversely related to a decrease number of

vertebrae, gill rakers and fin rays. The means for every character, except lateral scales, in the FC sample were the lowest or nearly so of all the populations sampled. Therefore, it is highly likely that this accounts for the discrepency between the electrophoretic and meristic position of FC.

The environmental correlations demonstrated by Garside (1966) and Kwain (1975) probably account for the presence of MSSC and USSCB in the meristic whitei group, while being absent from the whitei electrophoretic group. MSSC and USSCB are in close proximity to USSCA and DMCA so have a similar environment resulting in similar meristic development in these populations. Electrophoretic characters are monogenic, while most meristic characters are polygenic. Monogenic characters do not exhibit the effects of the complex interactions of genes in a polygenic character. Therefore, the monogenic phenotype is a less ambiguous representation of the genotype than is the multigenic phenotype. So electrophoretic data are much more likely to show the effects of long term hybridization than meristic data.

WC and CC are members of the whitei electrophoretic group, but members of the "Introgressed" group, meristically. CC was planted with fish from the Little Kern River in 1882 (Ellis, 1915) and with fish from Rifle Creek (RC) in 1887 (Ellis and Bryant, 1920). Rifle Creek in this study is a member of the "introgressed" electrophoretic and meristic group and has been planted with S. gairdneri (Dill, 1945). WC has no record of being planted with S. gairdneri (Ellis, 1915; Dill, 1945) so can be presumed to be a native population. WC and CC are very similar meristically as are CC and RC (Fig. 4, Table VI). Therefore, it can be assumed that CC is representative of RC

before the S. gairdneri introduction and its close meristic affinities with WC and RC suggest that the environment has modified the meristics of the fish populations of the eastern streams of the Little Kern Basin in a manner similar to Fish Creek. Past history, as well as the electrophoretic and meristic evidence, suggest that WC and CC are representative of the whitei group and provide further evidence of the phenotypic plastiscity of Salmo (Gold, 1977).

The concurence of the history of the populations, the electrophoretic analysis, and the meristic evidence suggests that the "introgressed" group is the product of hybridization among any and all combinations of endemic and introduced Salmo (Dill, 1945; Schreck and Behnke, 1971) and is consistent with the interpretations of Gold and Gall (1975a,b) and Gall et al. (1976). The high degree of concordance between the meristic and electrophoretic analyses in the present study further substantiates that S. a. whitei does exist in isolated areas of the Little Kern River Basin. Populations of S. a whitei have been identified in CC, DMCA, DMCB, FC, LWM, USSCA, and WC. The extensive number of barriers to upstream migration throughout the Little Kern River drainage has prevented the loss of S. a. whitei through introgression and has allowed the documentation of substantial introgression with introduced salmonids.

A purpose of the present study was to clear up the somewhat confused synonomy of S. a. whitei. Schreck (1969); Schreck and Behnke (1971) and Legendre, Schreck and Behnke (1972) have proposed that S. a. whitei Evermann is synonomous with S. a. gilberti Jordan. Their conclusions were based on samples from the Little Kern some of which are now known to be of mixed origin. Their samples from Soda Springs

Creek, Coyote Creek and Wet Meadows were taken from populations we have shown to be of the whitei group. Their samples from Green Meadows, the Little Kern River and Rifle Creek were from populations we have shown to be introgressed and their sample from Mountaineer Creek was from a population of the Mountaineer group. Therefore, considering the mixed origin of the populations on which they based their conclusions, it is little wonder they proposed that S. a. whitei and S. gairdneri gilberti were synonomous and proposed the classification S. a. gilberti (Schreck and Behnke, 1971). They in fact were looking at populations that were from both forms as well as introgressants between S. a. whitei and S. gairdneri.

The populations in the Mountaineer group occur together geographically in the southwestern part of the Little Kern Basin (Fig. 1). They occur in tributaries to Mountaineer Creek and Clicks Creek. A total of eight populations were sampled from the southwestern area. Three of these (AC, LPC, UPC) were sampled at or below sites of S. gairdneri introductions (Ellis, 1915; Dill, 1945 and 1950). These three samples occur electrophoretically in the introgressed clusters.

The Mountaineer meristic group has 4 members in common with the Mountaineer electrophoretic group, JC, MMC, SMC, and NMC. LKRH is a member of the Mountaineer meristic group, yet a member of the "introgressed" electrophoretic group. It appears that common environmental effects have modified meristic characters to mask an introgressed population (Kwain, 1975). The concurrence of the Mountaineer group populations as electrophoretic, meristic and geographic units suggested that they were remnants of fish inhabiting the lower basin before introductions of exotic salmonids occurred.

Manter Creek, a sourthern tributary to the South Fork Kern sampled in 1978, was found to be nearly identical meristically (1.60) and electrophoretically (I = .994) to the Mountaineer group (Smith, unpublished). Ellis (1915) reported Kern River trout, S. a. gilberti in Manter Creek. There are no confirmed populations of S. aguabonita that are geographically situated between Manter Creek and MG, however, S. a. gilberti has been reported in several streams situated geographically between Manter Creek and the Mountaineer group (Ellis, 1915; Ellis and Bryant, 1920).

The unique geographical distribution of the three genetically distinct groups of fish present in the Little Kern River basin may suggest multiple invasions of ancestral fish. The Mountaineer group was only found in the southwestern part of the basin, the whitei group was only found in isolated headwaters of streams scattered about the basin. The introgressed group was always found in or downstream from areas with a history of S. gairdneri introductions. Whitei and MG populations were never found downstream from each other. The geographic distribution combined with the electrophoretic and meristic analyses suggested an interesting invasionary history of the Little Kern River basin by Salmo sp.

The whitei group appears to have invaded the basin first, probably before the last glacial periods, twenty to fifty thousand years ago, since it was the most genetically distinct from the present day S. gairdneri and was found only in populations geographically isolated from S. gairdneri introductions. Whitei appeared to have historically occupied most of the basin, except in areas of recent glacial activity. The occurrence of whitei at the lower edges of the glacial

advance suggests that it occupied the glaciated areas before they were glaciated and was forced to retreat with the advance of the ice. The mountaineer group was more closely related to the present day S. gairdneri than is whitei. The genetic relationships of the mountaineer group combined with the geographic distribution suggests that the mountaineer group invaded the basin later than whitei and had access to much less of the basin than did whitei. Since no whitei populations exist upstream from MG populations, it is not likely the MG group represented an hybridization event between early S. gairdneri and whitei fish. The MG group probably represented a population of S. gairdneri isolated in the lower Kern River within the last ten thousand years. The recent introductions of S. gairdneri into the Little Kern basin have made it impossible to determine the historical range of the MG group, since introgressants between the whitei and MG groups or whitei and S. gairdneri groups are indistinguishable due to the close genetic relationships of the ancestral stocks.

This study has presented genetic, historic, and geographic evidence confirming the existence and range of S. a. whitei. S. a. whitei has been characterized both meristically and electrophoretically so that further investigations and comparisons can be made to determine the taxonomic status and evolutionary history of S. a. whitei. Therefore, it is tentatively proposed that the Mountaineer group which appears to be distributed throughout the lower reaches of the Kern system represents S. a. gilberti. However, further sampling of the Kern River basin and South Fork basin is necessary to assess this hypothesis. Furthermore, the demonstrated presence and uniqueness of the Mountaineer group may shed some light on the

evolutionary history of the Salmo of the Kern River basin.

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Table I

Alphabetic Listing of Trout Samples Collected From 1974 to 1976.

The acronyms are used in the text and N is the sample size.

The site number refers to Fig. 1.

Population	Acronym	N	Site Number
Alpine Creek	AC	39	21
Clicks Creek, North Fork	NCC	40	26
[1]Coyote Creek	CC	40	30
[1]Deadman Creek, Lower Section	DMCB	34	11
Deadman Creek, Upper Section	DMCA	26	10
[1]Fish Creek	FC	40	27
[1]Green Meadows, South Fork Kaweah River	GM	36	31
[1]Jacobsen Creek	JC	33	23
[1]Little Kern River Above Broder Cabin	LKRA	37	1
[1]Little Kern River Below Broder Cabin	LKRB	39	2
[1]Little Kern River At Wet Meadows Creek	LKRC	33	3
[1]Little Kern River At Rifle Creek	LKRD	41	8
Little Kern River At Horse Bridge	LKRH	34	28
Mountaineer Creek, Middle Section	MMC	44	25
Mountaineer Creek, North Fork	NMC	38	22
Mountaineer Creek, South Fork	SMC	40	24
Pecks Canyon Creek, Lower Section	LPC	32	20
Pecks Canyon Creek, Upper Section	UPC	31	19
[1]Quinn Meadow Creek	QMC	25	12
[1]Rifle Creek	RL	35	9
[1]Shotgun Creek, Lower Section	LSGC	31	7
[1]Shotgun Creek, Upper Section	USGC	34	6
[1]Soda Springs Creek, Lower Section	LSSC	31	16
Soda Springs Creek, Above Barrier	USSCA	25	13
[1]Soda Springs Creek, Below Barrier	USSCB	24	14
[1]Soda Springs Creek, Middle Section	MSSC	39	15
[1]Tamarack Creek	TMC	40	17
[1]Trout Meadows Creek	TRMC	36	29
[1]Wet Meadows Creek, Lower Section	LWM	35	5
[1]Wet Meadows Creek, Upper Section	UWM	38	4
Willow Creek	WC	38*	18
Mt. Whitney Strain Rainbow Trout	RTW	24*	-

*For meristic analysis, 245 were used for electrophoretic analysis.

[1]Meristic counts from J. R. Gold (1981).

Table II. Protein systems studied, with number of loci, tissue examined and quarternary structure.

Protein	Acronym	Loci	Tissue	Quarternary Structure	
Alcohol dehydrogenase	ADH	1	Liver	Dimer	(3)
Alpha-glycerophosphate dehydrogenase	AGPDH	1	Muscle	Dimer	(1)
Adenylate Kinase	AK	1	Muscle	———	
Creatine Kinase	CK	2	Muscle	Monomer	(3)
Diaphorase	DIA	1	Liver	———	
Fumarase	FUM	1	Muscle	Monomer	(5)
Isocitrate dehydrogenase	IDH	2	Liver	Dimer	(2)
Malate dehydrogenase	MDH	4	Heart	Dimer	(1)
Para-albumin	PALB	1	Blood	Monomer	(2)
Phosphoglucoisomerase	PGI	3	Muscle	Dimer	(3)
Phosphoglucomutase	PGM	1	Muscle	Monomer	(1)
Superoxide dismutase	SOD	1	Liver	Dimer	(1)
Malic enzyme	ME	1	Liver	Tetramer	(4)

(1) Utter and Hodgins, 1972; (2) Busack et al., 1979; (3) Allendorf, 1975;

(4) Busack, 1977; (5) Unpublished data.

Table III. Gene frequencies for 10 variable protein systems for 32 trout populations. IDH is composed of 2 with identical alleles so is reported as one system.

	PALB		SOD			IDH				ME		PGM		CK-1		MDH 3,-4			AGPD		ADH		FUM	
	100	105	60	100	140	60	100	140	170	100	70	85	100	70	100	85	100	125	140	100	50	100	100	105
FC	1.00	0	.70	.30	0	.05	.75	.19	.01	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
SMC	.62	.38	.04	.66	.30	.02	.18	.79	.02	0	1.00	0	1.00	0	1.00	.08	.89	.04	0	1.00	.15	.85	.99	.01
NCC	.73	.27	.02	.64	.34	.08	.10	.81	.01	0	1.00	0	1.00	0	1.00	.09	.83	.09	0	1.00	.02	.98	.94	.06
TRMC	.73	.27	.34	.66	0	.01	.65	.33	0	0	1.00	0	1.00	0	1.00	0	.99	.01	.05	.95	0	1.00	1.00	0
LKRH	.75	.25	.25	.72	.03	0	.42	.58	0	0	1.00	.01	.99	0	1.00	.07	.90	.03	.06	.94	.02	.98	1.00	0
JC	.67	.33	0	.93	.07	0	.11	.89	0	0	1.00	0	1.00	0	1.00	0	1.00	0	.01	.99	.06	.94	1.00	0
NMC	.86	.14	.16	.69	.15	.02	.11	.81	.06	.02	.98	.01	.99	0	1.00	.20	.64	.16	.06	.94	.01	.99	.95	.05
WC	.90	.10	.99	.01	0	0	.73	.27	0	.03	.97	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
AC	.75	.25	.12	.85	.03	.01	.40	.58	.02	.02	.98	.03	.97	0	1.00	.14	.85	.01	0	1.00	0	1.00	1.00	0
MMC	.77	.23	.12	.83	.05	0	.23	.77	0	.03	.97	.15	.85	0	1.00	.06	.88	.06	.06	.94	0	1.00	1.00	0
DMCA	.91	.09	.86	.14	0	0	.78	.22	0	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
QMC	.56	.44	.80	.20	0	0	.44	.56	0	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
USSCB	.76	.24	.34	.66	0	0	.64	.36	0	0	1.00	.07	.93	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
USSCA	.88	.12	1.00	0	0	0	.97	.03	0	0	1.00	0	1.00	.02	.98	0	1.00	0	.02	.98	0	1.00	1.00	0
CC	.78	.22	.87	.13	0	0	.68	.32	0	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LPC	.73	.27	.12	.75	.13	.03	.48	.49	0	0	1.00	0	1.00	0	1.00	.08	.90	.02	.03	.97	0	1.00	1.00	0
UPC	.68	.32	.20	.64	.16	0	.56	.44	0	0	1.00	0	1.00	0	1.00	.10	.90	0	.01	.99	0	1.00	1.00	0
LKRA	.58	.42	.27	.73	0	.01	.41	.56	.02	0	1.00	.03	.97	.03	.97	.15	.85	0	.01	.99	0	1.00	1.00	0
USGC	.74	.26	.35	.65	0	0	.51	.49	0	.06	.94	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LKRB	.64	.36	.42	.57	.01	.03	.46	.51	0	0	1.00	0	1.00	0	1.00	.06	.94	0	0	1.00	0	1.00	1.00	0
DMCB	.99	.01	.96	.04	0	0	.88	.12	0	0	1.00	.01	.99	.01	.99	0	1.00	0	0	1.00	0	1.00	1.00	0
MSSC	.73	.27	.56	.44	0	0	.38	.62	0	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
TMC	.76	.24	.35	.65	0	.01	.60	.40	0	.21	.79	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LSSC	.69	.31	.50	.50	0	0	.60	.40	0	.13	.87	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LWM	.93	.07	.71	.29	0	0	.77	.23	0	.11	.89	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LKRD	.75	.25	.50	.50	0	.01	.63	.37	0	.16	.84	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
GM	.67	.33	.49	.46	.06	.02	.61	.38	0	.10	.90	.03	.97	.02	.98	.04	.96	0	0	1.00	0	1.00	.93	.07
RC	.88	.12	.46	.54	0	.06	.61	.33	0	0	1.00	0	1.00	.01	.99	0	1.00	0	0	1.00	0	1.00	1.00	0
UWM	.83	.17	.65	.35	0	0	.53	.47	0	.11	.89	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LSGC	.75	.25	.38	.62	0	0	.68	.32	0	0	1.00	0	1.00	0	1.00	0	1.00	0	0	1.00	0	1.00	1.00	0
LKRC	.65	.35	.26	.73	.02	.01	.51	.48	0	0	1.00	0	1.00	.03	.97	.03	.97	0	0	1.00	0	1.00	1.00	0
RTW	.45	.55	0	.88	.12	.20	.08	.34	.38	.36	.64	0	1.00	.16	.84	.37	.62	.01	.01	.99	0	1.00	1.00	0

Table IV. Biochemical similarity coefficients among 32 populations of trout calculated by Neis (1972) formula. Average heterozygosity in principle diagonal.

	FC	SMC	NCC	TRMC	LKRH	JC	NMC	WC	AC	MMC	DMCA	QMC	USSCB	USSCA	CC	LPC
FC	.043	.952	.953	.988	.978	.945	.958	.995	.970	.961	.998	.982	.988	.992	.995	.975
SMC		.094	.998	.980	.991	.995	.991	.938	.992	.993	.945	.969	.980	.921	.953	.992
NCC			.087	.977	.990	.994	.995	.938	.991	.994	.945	.966	.978	.919	.952	.991
TRMC				.075	.996	.978	.977	.975	.993	.985	.982	.983	.999	.970	.984	.996
LKRH					.086	.991	.991	.964	.999	.996	.971	.981	.996	.952	.975	.999
JC						.048	.989	.926	.993	.996	.935	.960	.978	.907	.943	.990
NMC							.099	.943	.992	.994	.949	.965	.977	.924	.954	.989
WC								.034	.952	.944	.999	.987	.975	.997	.998	.958
AC									.080	.997	.961	.971	.993	.940	.965	.999
MMC										.087	.952	.968	.987	.927	.957	.994
DMCA											.040	.987	.983	.997	.999	.967
QMC												.068	.983	.977	.994	.975
USSCB													.074	.970	.984	.996
USSCA														.019	.994	.949
CC															.053	.970
LPC																.083
UPC																
LKRA																
USGC																
LKRB																
DMCB																
MSSC																
TMC																
LSSC																
LWM																
LKRD																
GM																
RC																
UWM																
LSGC																
LKRC																
RTW																

Table IV (Cont.)

UPC	LKRA	USGC	LKRB	DMCB	MSSC	TMC	LSSC	LWM	LKRD	GM	RC	UWM	LSGC	LKRC	RTW
.980	.971	.985	.983	.996	.986	.986	.990	.999	.992	.990	.995	.994	.990	.979	.924
.989	.991	.986	.987	.928	.983	.979	.978	.953	.975	.978	.975	.972	.978	.989	.969
.987	.988	.984	.985	.928	.982	.977	.975	.953	.973	.976	.975	.972	.975	.986	.968
.997	.994	.998	.997	.973	.993	.997	.997	.988	.997	.997	.998	.992	.999	.998	.958
.998	.998	.998	.997	.958	.994	.994	.993	.978	.992	.992	.993	.989	.995	.998	.967
.985	.990	.985	.984	.916	.980	.978	.973	.946	.971	.972	.971	.967	.975	.988	.967
.984	.987	.984	.984	.934	.983	.978	.975	.957	.974	.975	.976	.974	.975	.984	.967
.966	.959	.973	.975	.998	.982	.974	.983	.995	.984	.983	.984	.991	.978	.965	.905
.996	.997	.996	.994	.947	.988	.992	.988	.970	.987	.988	.989	.982	.991	.997	.973
.990	.993	.991	.989	.936	.986	.986	.982	.961	.980	.981	.982	.978	.983	.992	.967
.974	.966	.980	.980	.999	.985	.980	.988	.998	.989	.988	.990	.993	.985	.973	.914
.981	.982	.986	.991	.978	.995	.982	.991	.985	.989	.992	.985	.993	.984	.983	.938
.997	.994	.998	.997	.973	.993	.997	.997	.989	.997	.997	.998	.993	.999	.998	.957
.959	.948	.964	.965	.999	.970	.967	.976	.993	.978	.977	.978	.982	.973	.956	.893
.978	.973	.983	.985	.995	.990	.983	.991	.996	.991	.991	.990	.995	.986	.977	.923
.999	.997	.997	.996	.954	.990	.994	.991	.976	.990	.991	.992	.985	.995	.998	.970
.087	.997	.998	.997	.962	.992	.995	.995	.981	.994	.995	.994	.989	.997	.999	.968
	.094	.996	.997	.952	.992	.992	.992	.973	.990	.992	.989	.986	.993	.998	.974
		.076	.999	.969	.996	.998	.998	.987	.997	.997	.997	.994	.998	.999	.963
			.084	.968	.998	.995	.997	.985	.996	.997	.995	.994	.997	.998	.964
				.020	.974	.971	.979	.995	.981	.979	.983	.986	.976	.960	.896
					.071	.992	.996	.987	.995	.995	.994	.997	.993	.994	.952
						.086	.998	.989	.999	.997	.996	.994	.997	.996	.964
							.086	.993	.999	.999	.997	.998	.998	.995	.958
								.058	.994	.992	.994	.996	.991	.980	.929
									.085	.999	.997	.998	.998	.994	.956
										.103	.996	.997	.997	.994	.958
											.066	.996	.998	.994	.949
												.075	.994	.989	.945
													.067	.997	.955
														.078	.968
															.138

Table V. Means for 10 meristic characters in 32 trout populations. The last row is the error mean square for each character. The first column is fork length in millimeters. *Dorsal Proximal Pterygiophores (DP), Anal Proximal Pterygiophores (AP), Branchiostegals (BO). Means with identical superscripts are not significantly different at P = .05.

Population	Fork length	Pyloric caeca	D.P.	A.P.	Pectoral Fin Rays	Pelvic Fin Rays	B.O.	Vertebrae	Gill Rakers	Lateral Scales	Sample Size
FC	138.2	34.3^{bc}	13.7^{g}	11.9^{ghk}	14.6^{fk}	9.2^{f}	21.3^{k}	59.8^{v}	19.0^{hk}	156.3^{dfg}	40
SMC	145.1	35.9^{abc}	14.2^{abcef}	12.7^{abf}	14.2^{ms}	9.8^{abcd}	22.3^{fgh}	62.2^{ptx}	19.0^{hk}	135.6^{h}	40
NCC	137.4	46.0^{f}	13.9^{efg}	12.6^{abcdf}	14.1^{ms}	9.8^{abcd}	21.7^{fk}	63.2	18.5^{k}	132.8^{h}	40
TRMC	130.2	36.0^{abc}	14.4^{abce}	12.7^{abf}	15.4^{abc}	9.8^{abcd}	22.5^{abdfgh}	60.7^{abcds}	20.0^{abcdef}	153.7^{d}	36
LKRH	143.1	35.1^{abc}	14.1^{bcefg}	12.5^{abcdf}	14.8^{efhk}	9.7^{abcde}	21.8^{fgk}	61.7^{eghkmp}	19.3^{fgh}	148.2^{bc}	34
JC	146.5	37.1^{abc}	14.6^{abcd}	12.9^{f}	14.3^{kms}	9.7^{abcde}	22.8^{abdfgh}	62.5^{tx}	19.3^{dfgh}	147.7^{b}	33
NMC	154.7	36.9^{abc}	14.4^{abce}	12.6^{abdf}	14.5^{fks}	9.7^{abcde}	22.6^{abdfgh}	62.0^{kmpt}	20.0^{abcdef}	145.5^{b}	38
WC	129.3	42.3^{de}	14.5^{abcd}	12.8^{bf}	16.0^{g}	9.8^{abcd}	23.3^{abce}	60.9^{abcdf}	20.3^{abcde}	152.3^{cd}	38
AC	144.4	43.8^{ef}	14.7^{abcd}	12.7^{abf}	15.4^{abcd}	10.0^{ac}	22.6^{abdfgh}	61.9^{hkmpt}	20.2^{abcdef}	146.5^{b}	39
MMC	131.2	38.1^{abcd}	14.1^{cefg}	12.4^{abcde}	14.7^{fhk}	9.9^{abc}	22.1^{fghk}	62.1^{mpt}	19.2^{gh}	144.7^{b}	44
DMCA	128.9	35.0^{abc}	14.1^{bcefg}	12.0^{ceghk}	15.5^{abcd}	10.0^{ac}	23.5^{ace}	60.4^{abrs}	20.4^{abce}	178.9^{e}	26
QMC	155.3	38.6^{abcd}	14.8^{abd}	$12.3^{abcdegh}$	14.8^{defh}	9.7^{abcde}	21.6^{fk}	60.5^{abcrs}	20.3^{abcde}	164.2^{a}	25
USSCB	157.0	39.8^{ad}	14.9^{ad}	12.5^{abcdef}	15.2^{abcde}	9.6^{abde}	22.6^{abdfgh}	60.6^{abcdrs}	20.9^{ce}	176.4^{e}	24
USSCA	127.6	34.3^{abc}	14.8^{abd}	$12.2^{abcdegh}$	15.8^{abg}	9.9^{ac}	22.7^{abcdgh}	60.7^{abcdrs}	19.6^{adfgh}	173.0^{e}	25
CC	149.6	37.8^{abc}	14.1^{cefg}	12.6^{abcdf}	15.3^{acde}	9.8^{abcd}	23.3^{abce}	60.1^{rv}	20.6^{bce}	153.0^{cd}	40
LPC	140.1	38.1^{abcd}	14.6^{abcd}	12.5^{abcdf}	15.4^{abcd}	9.9^{abc}	23.4^{ace}	61.9^{ghkmpt}	19.7^{adfgh}	148.5^{bc}	32
UPC	146.0	36.9^{abc}	14.4^{abcef}	12.7^{abdf}	15.4^{abcd}	9.7^{abcde}	23.9^{ce}	61.7^{eghkmp}	19.8^{abdf}	147.7^{bc}	31
LKRA	149.6	35.9^{abc}	14.5^{abcd}	$12.3^{abcdegh}$	14.8^{efhk}	9.8^{abcd}	23.2^{abce}	61.6^{eghkmp}	20.5^{bce}	155.5^{df}	37
USGC	145.5	36.8^{abc}	14.3^{abcef}	12.1^{cegh}	15.4^{abcd}	9.5^{de}	23.3^{abce}	60.4^{abrs}	20.7^{bce}	157.9^{afg}	34
LKRB	141.4	36.8^{abc}	14.8^{ad}	12.2^{acdegh}	15.3^{abcd}	9.8^{abcd}	23.2^{abce}	61.5^{efghkm}	20.5^{abce}	162.5^{a}	39
DMCB	123.3	33.3^{b}	13.8^{efg}	11.7^{gk}	15.7^{abg}	9.0^{f}	23.9^{e}	60.0^{rsv}	19.9^{abcdf}	183.0	34
MSSC	141.4	36.8^{abc}	14.8^{abcef}	12.2^{eghk}	15.3^{abcd}	9.8^{bde}	23.2^{abcd}	61.5^{abcdef}	20.5^{abcde}	162.5^{e}	39
TMC	141.6	39.9^{ad}	14.5^{abcd}	$12.2^{abcdegh}$	15.8^{bg}	9.6^{abde}	23.1^{abcde}	61.2^{acdeg}	20.4^{abce}	166.8^{a}	40
LSSC	140.9	38.4^{abcd}	14.8^{abcefg}	12.3^{abcdf}	15.6^{acde}	9.7^{abcde}	23.0^{bdfgh}	61.1^{acdefh}	20.9^{abcdf}	164.9^{afg}	31
LWM	133.0	38.8^{acd}	14.6^{abcd}	12.8^{bf}	15.7^{abg}	9.5^{abde}	23.8^{ce}	$61.3^{cdefghk}$	19.9^{abcdf}	174.1^{e}	35
LKRD	133.1	39.3^{ad}	14.5^{abcd}	12.1^{cdegh}	15.6^{abcg}	9.6^{abde}	23.3^{abce}	$61.1^{abcdefg}$	20.3^{abcde}	161.4^{ag}	41
GM	147.5	43.7^{ef}	13.8^{fg}	11.8^{gk}	15.0^{defh}	9.7^{abcde}	23.6^{ace}	$61.4^{defghkm}$	19.9^{abcdf}	166.3^{a}	36
RC	146.0	37.6^{abc}	15.1^{d}	12.5^{abcdf}	15.1^{cdeh}	9.8^{abcd}	22.8^{abcdh}	60.8^{abcdf}	19.9^{abcdf}	165.1^{a}	35
UWM	145.1	36.2^{abc}	14.3^{abcef}	12.2^{acdegh}	14.8^{efh}	9.4^{e}	23.0^{abcd}	61.0^{abcdef}	19.5^{adfgh}	165.9^{a}	38
LSGC	140.9	38.4^{abcd}	14.8^{abd}	$12.3^{abcdegh}$	15.6^{abg}	9.7^{abcde}	23.0^{abcde}	61.1^{abcdef}	20.9^{e}	164.9^{a}	31
LKRC	135.8	37.4^{abc}	14.7^{ad}	12.2^{abcdeh}	15.6^{abcg}	9.8^{abcde}	22.8^{abcdh}	$61.6^{efghkmp}$	20.6^{abce}	164.5^{a}	33
RTW	279.7	54.0^{g}	13.0^{h}	11.4^{k}	13.8^{t}	10.1^{c}	21.7^{fgk}	60.3^{brsv}	20.5^{abcdef}	127.0^{j}	24
Error Mean Square	-	25.6	0.5	0.4	0.4	0.2	1.4	0.9	1.2	78.4	-

Table VI. Euclidean distance matrix of 32 trout populations based on 9 meristic characters

	FC	SMC	NCC	TRMC	LKRH	JC	NMC	WC	AC	MMC	DMCA	QMC	USSCB	USSCA	CC	LPC
FC		4.17	5.62	2.61	2.78	3.96	3.50	3.55	4.11	3.41	3.62	2.52	3.52	3.27	2.73	3.67
SMC			2.59	3.28	1.86	1.53	1.53	3.79	2.73	1.41	5.81	4.22	5.45	5.21	3.66	2.47
NCC				4.94	3.61	3.12	3.33	4.83	3.34	2.78	7.21	5.47	6.60	6.65	5.30	3.90
TRMC					1.76	2.76	2.20	1.56	2.28	2.37	3.24	2.00	2.86	2.51	1.28	1.81
LKRH						1.67	1.22	2.67	2.17	.93	4.24	2.71	3.91	3.56	2.49	1.72
JC							1.14	3.28	2.33	1.44	4.91	3.42	4.37	4.35	3.24	2.00
NMC								2.78	1.89	1.10	4.59	2.99	4.09	4.09	2.57	1.59
WC									1.84	2.83	3.79	2.81	3.28	3.14	1.84	1.82
AC										1.82	4.73	3.06	3.96	4.02	2.77	1.53
MMC											4.73	3.18	4.38	4.11	2.91	1.65
DMCA												2.79	2.08	1.64	3.15	4.09
QMC													1.66	2.25	2.33	3.08
USSCB														2.05	2.97	3.87
USSCA															3.00	3.39
CC																2.36
LPC																
UPC																
LKRA																
USGC																
LKRB																
DMCB																
MSSC																
TMC																
LSSC																
LWM																
LKRD																
GM																
RC																
UWM																
LSGC																
LKRC																
RTW																

Table VI (Cont.)

	UPC	LKRA	USGC	LKRB	DMCB	MSSC	TMC	LSSC	LWM	LKRD	GM	RC	UWM	LSGC	LKRC	RTW
FC	3.53	3.21	2.54	3.22	3.90	3.09	3.10	2.47	3.63	2.91	3.27	2.89	2.16	3.29	3.32	6.02
SMC	2.56	2.91	4.34	3.82	6.93	5.25	4.60	3.56	5.07	4.04	4.32	4.10	4.04	4.49	4.18	4.86
NCC	4.21	4.59	5.84	5.27	8.28	6.52	5.68	4.84	6.21	5.26	4.97	5.55	5.44	5.79	5.45	4.18
TRMC	1.84	1.88	1.82	1.81	4.46	2.83	2.05	1.30	2.63	1.69	2.96	1.76	2.18	1.84	1.81	5.93
LKRH	1.91	1.89	2.92	2.46	5.38	3.62	3.03	1.83	3.61	2.61	3.16	2.69	2.59	3.00	2.6[illegible]	5.34
JC	2.11	2.12	3.71	2.92	6.10	4.28	3.75	2.78	3.93	3.27	3.52	3.09	3.14	3.60	3.29	5.48
NMC	1.72	1.53	3.06	2.46	5.82	3.97	3.32	2.33	3.89	2.77	3.24	2.89	2.94	3.08	2.83	5.00
WC	1.91	2.57	2.23	2.31	4.81	3.35	2.02	2.12	2.71	1.72	2.88	2.48	2.91	2.09	2.18	5.71
AC	2.10	2.41	3.22	2.62	6.05	4.11	2.94	2.46	3.72	2.53	3.14	2.99	3.45	2.83	2.63	4.82
MMC	2.02	2.14	3.40	2.81	5.96	4.13	3.41	2.37	4.03	2.92	3.17	3.14	3.08	3.41	3.03	4.76
DCMA	4.11	3.28	2.45	2.57	2.45	1.39	2.31	2.74	2.23	2.56	2.81	2.42	2.32	2.38	2.51	7.65
QMC	3.30	2.29	2.06	1.89	4.15	2.19	2.05	1.51	2.67	1.99	2.59	1.28	1.86	1.69	1.86	5.96
USSCB	3.97	3.03	2.36	2.28	3.37	1.62	1.96	2.24	1.93	2.29	2.74	1.72	2.21	1.66	2.07	7.12
USSCA	3.58	2.99	2.28	2.04	3.06	1.53	1.80	2.27	1.97	2.06	3.01	1.68	2.10	1.89	1.82	7.57
CC	2.14	2.04	1.64	2.20	4.37	3.03	2.39	1.90	2.91	1.94	2.83	2.16	2.36	2.12	2.39	5.53
LPC	.88	1.67	2.61	1.95	5.27	3.55	2.56	2.21	3.19	1.99	2.88	2.56	2.77	2.54	2.20	5.59
UPC		1.74	2.46	2.17	5.03	3.58	2.70	2.37	3.13	2.10	3.01	2.71	2.68	2.69	2.49	5.79
LKRA			1.97	1.20	4.63	2.73	2.34	1.76	2.94	1.78	2.41	1.94	1.98	1.99	1.78	5.68
USGC				1.48	3.23	1.89	1.42	1.84	2.35	1.08	2.33	1.85	1.69	1.32	1.64	6.26
LKRB					3.93	1.89	1.38	1.54	2.19	1.01	2.19	1.34	1.69	1.03	.75	6.33
DMCB						2.36	3.26	4.03	2.99	3.59	3.84	3.84	3.10	3.67	3.86	8.83
MSSC							1.48	2.08	1.71	1.85	2.25	1.94	1.54	1.72	1.75	7.32
TMC								1.57	1.61	.75	1.96	1.75	1.80	.95	.98	6.57
LSSC									2.22	1.49	2.16	1.62	1.60	1.58	1.39	5.91
LWM										1.92	2.51	1.91	1.93	1.92	2.01	7.46
LKRD											1.82	1.57	1.63	1.00	1.01	6.11
GM												2.48	1.89	2.38	2.31	5.55
RC													1.47	1.42	1.52	6.47
UWM														1.99	1.94	6.42
LSGC															.75	6.53
LKRC																6.55

Table VII. Means for 9 meristic characters of the 4 common member meristic and biochemical clusters of populations, character means not significantly different at P = .01 are denoted by identical superscripts. Only populations that clustered together meristically and electrophoretically in the same group are included.

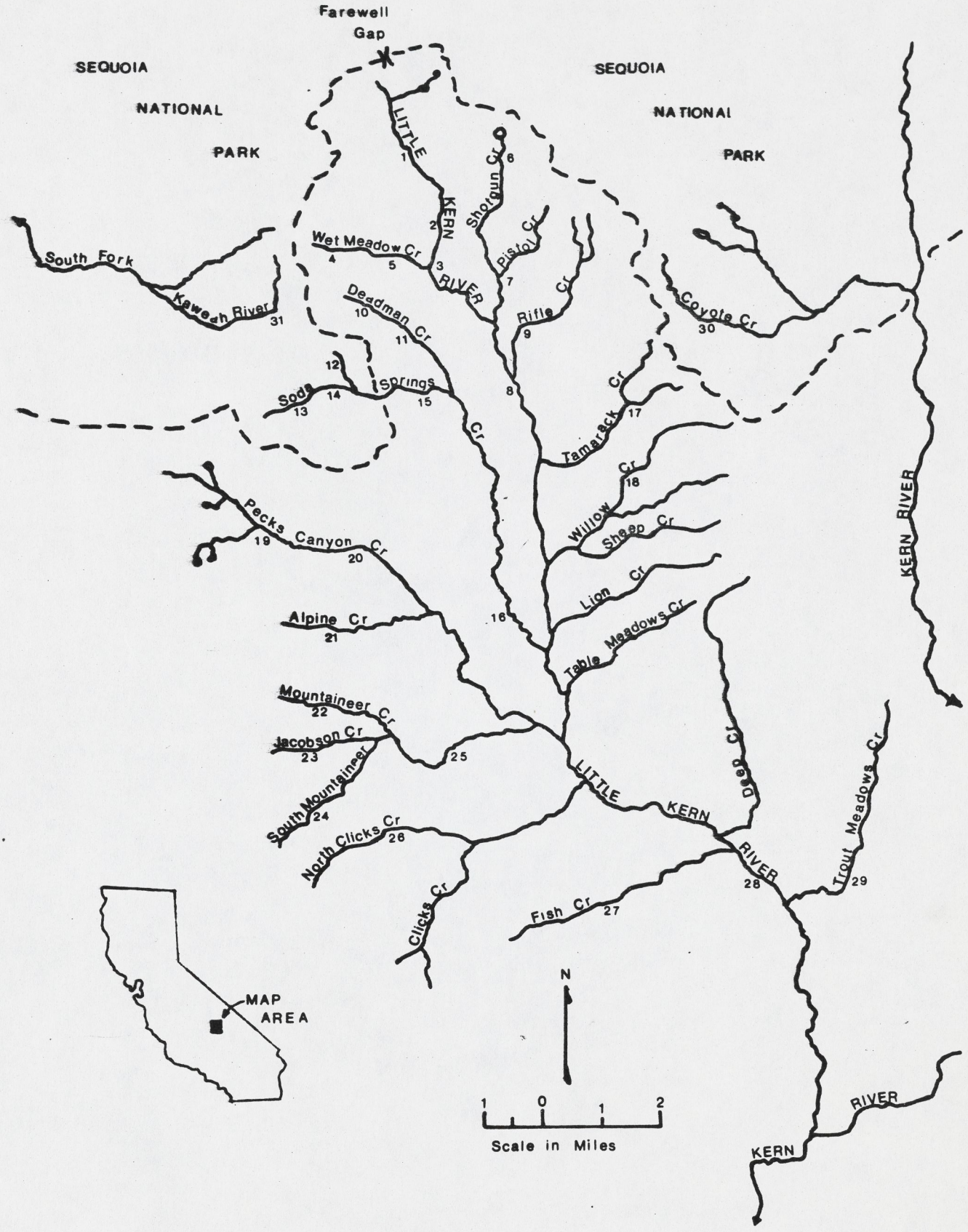
	Pyloric Caeca	D.P.	A.P.	Pectoral Fin Rays	Pelvic Fin Rays	B.O. Rays	Vertebra	Gill Rakers	Lateral Scales
Whitei	36.5	14.2[a]	12.3[a]	15.5	9.8[a]	23.1	60.5[a]	20.0[a]	167.2
Introgressed	38.2[a]	14.6	12.3[a]	15.3	9.7	22.9	61.0[a]	20.3[a]	160.2
Mountaineer	38.8[a]	14.2[a]	12.6	14.4	9.8[a]	22.3	62.4	19.2	141.3
RTW	54.0	13.0	11.4	13.8	10.1	21.7	60.3	20.5[a]	127.0

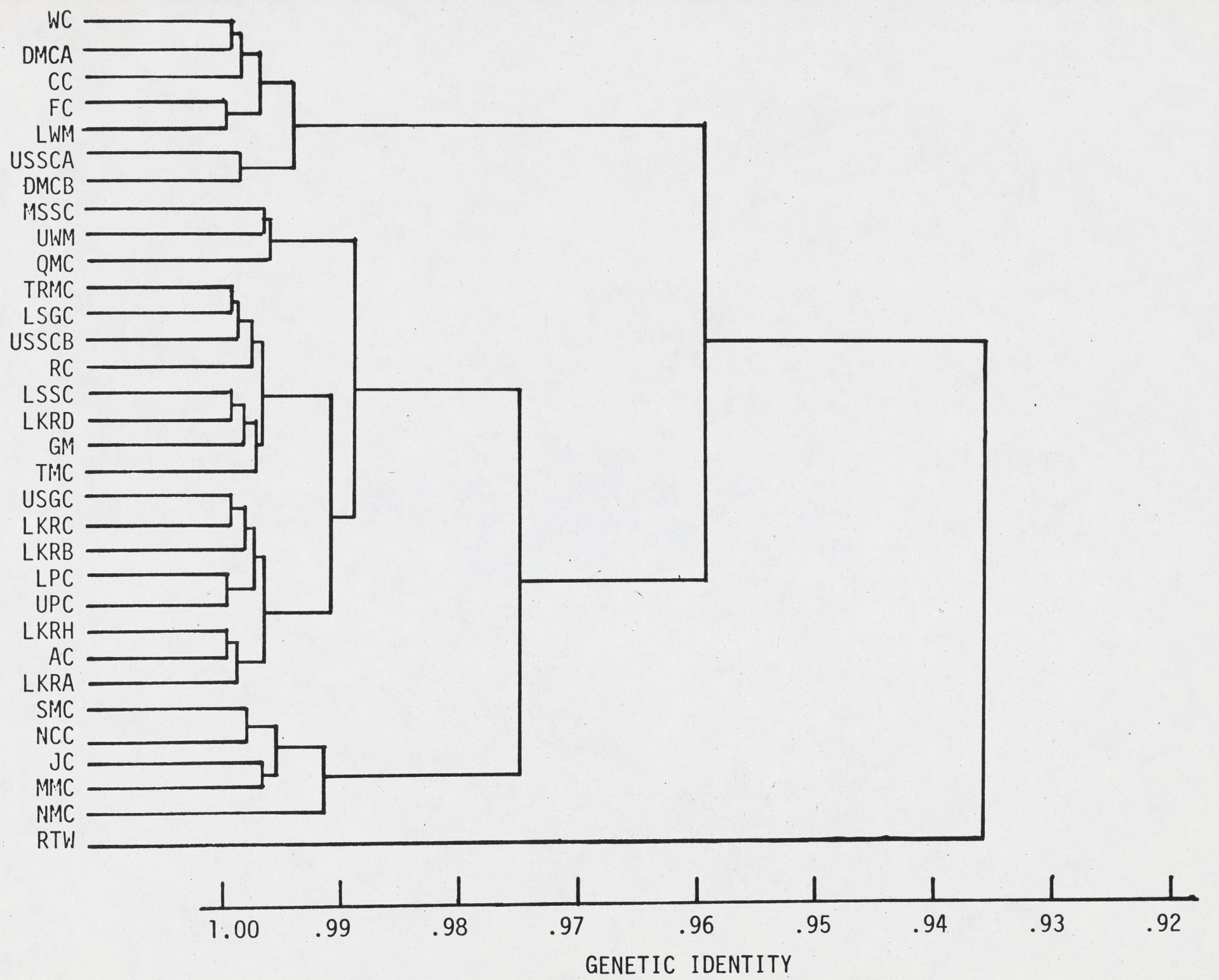
Figure 1. Little Kern River Basin and vicinity with sampling sites.

Figure 2. Biochemical similarity dendrogram of 32 trout populations. The cophenetic correlation coefficient is 0.921.

Figure 3. An unrooted Wagner Network of the proposed evolutionary relationships among the trout of the Little Kern Basin, based on allele frequencies.

Figure 4. Euclidean distance dendrogram based on 9 meristic characters of 32 trout populations. The cophenetic correlation coefficient is 0.834.


Farewell Gap
SEQUOIA NATIONAL PARK
SEQUOIA NATIONAL PARK
LITTLE KERN RIVER
Shotgun Cr
Pistol Cr
Rifle Cr
Wet Meadow Cr
South Fork Kaweah River
Deadman Cr
Soda Springs Cr
Coyote Cr
Tamarack Cr
Willow Cr
Sheep Cr
Lion Cr
Table Meadows Cr
Pecks Canyon Cr
Alpine Cr
Mountaineer Cr
Jacobson Cr
South Mountaineer
North Clicks Cr
Clicks Cr
Fish Cr
Deep Cr
Trout Meadows Cr
KERN RIVER
KERN RIVER
MAP AREA
N
1 0 1 2
Scale in Miles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GM
TMC
USGC
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LPC
UPC
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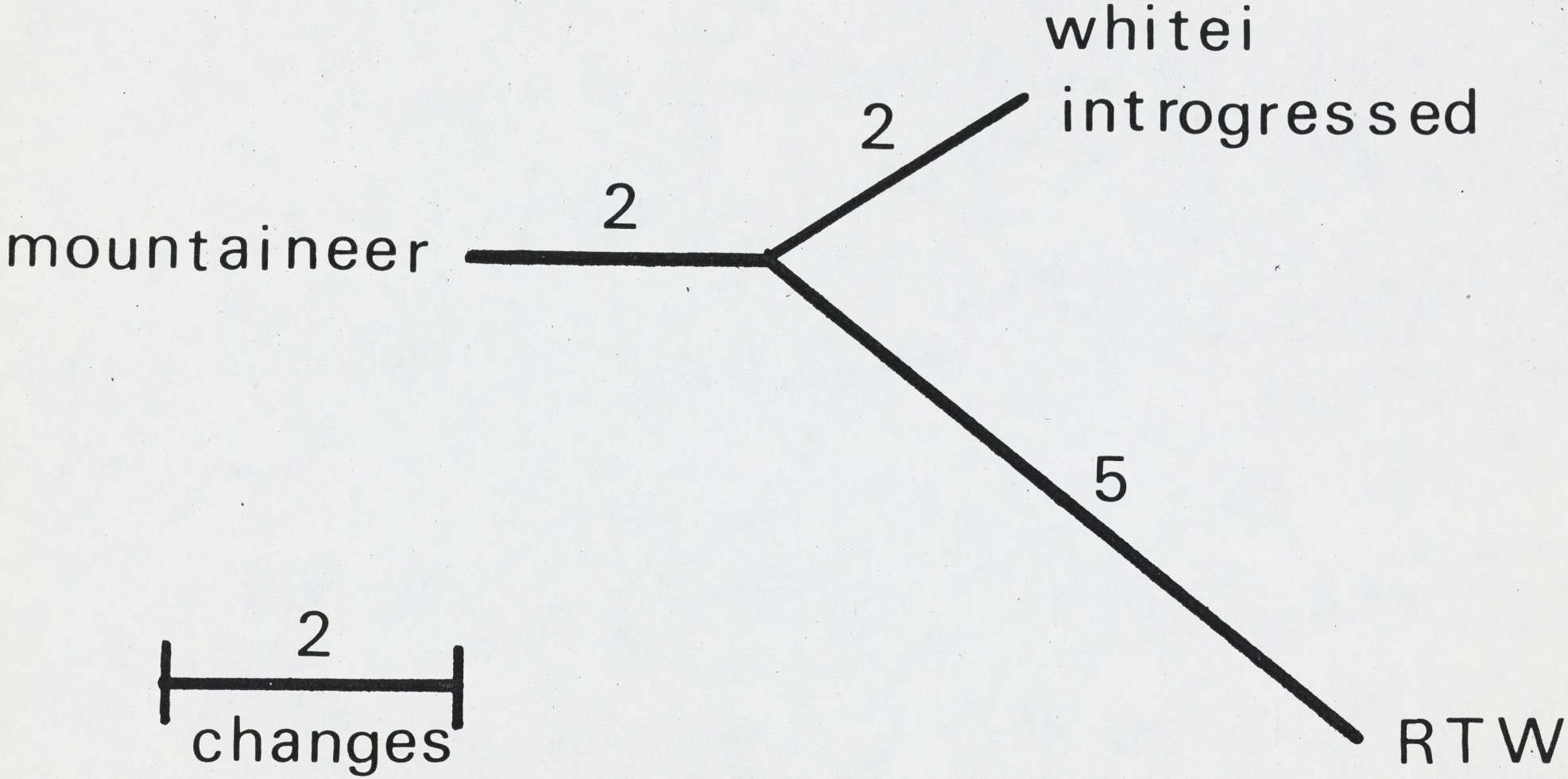
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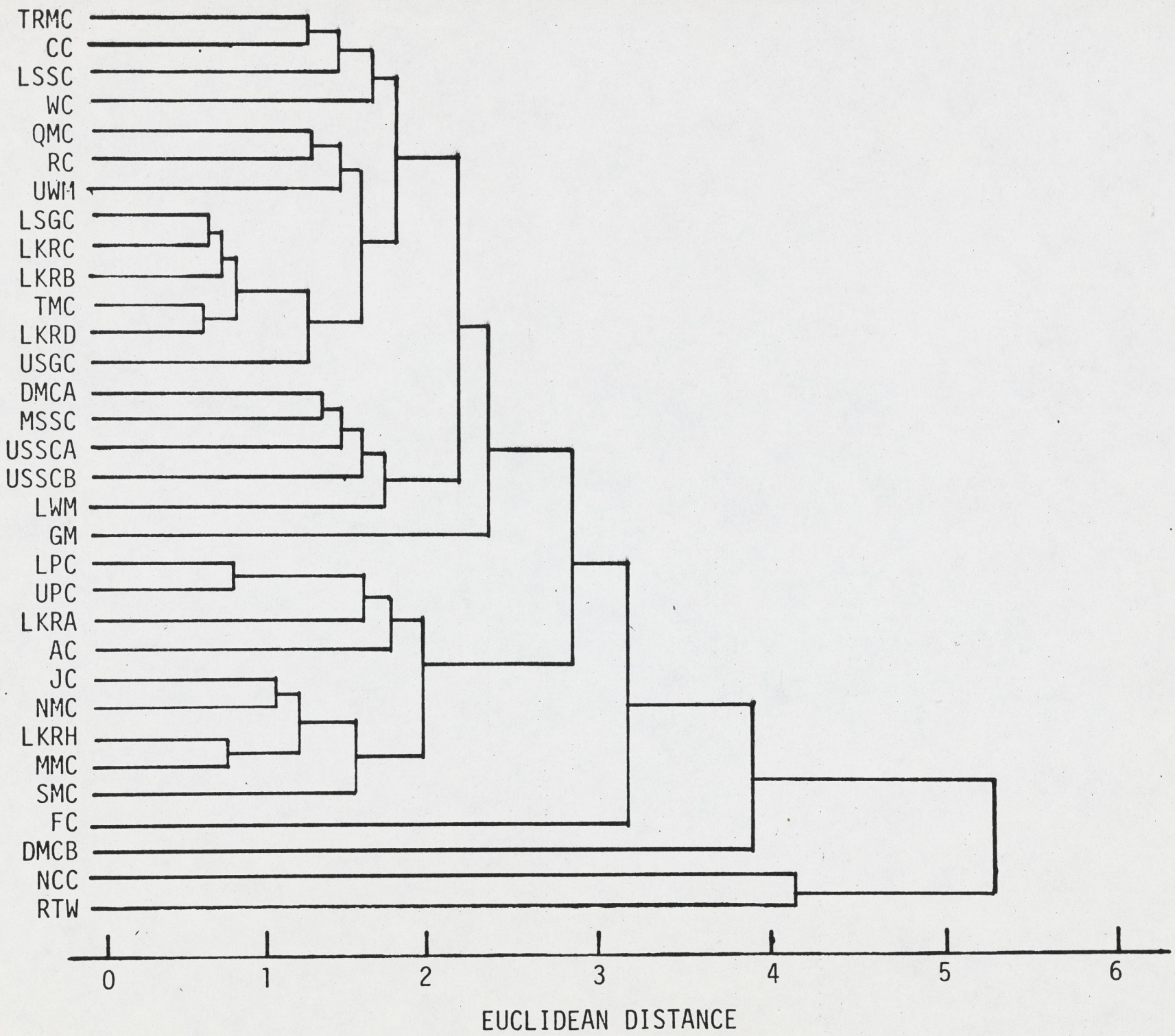
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LSGC
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TMC
LKRD
USGC
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MSSC
USSCA
USSCB
LWM
GM
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Oct. 8-

Dear Bob,

Received your letter re the Smith and Gall manuscript, along w your reviewer's comments. Since I haven't SEEN (or even heard of) the MS, my comments are certainly a bit premature. As far as I know, Smith finished his PhD work a year or so ago, so this must be the fruit of his labor. I recall about two years ago they were convinced the Mountaineer and Clicks Creek trout were S. g. gilberti (whatever that is or was). I mentioned this to you along w my opinion that these were most likely hybrids - in part because they exhibited the profuse spotting typical of S. gairdneri, and in part because of the heavy rainbow introductions there in the 30's. It would appear that they don't believe us, as I infer from your review that the Mountaineer trout, etc., are being referred to as gilberti.

Insofar as the MS by myself and Gall, it's scheduled for publication this fall in the CFG quarterly as "Systematics of Golden Trout, Salmo aguabonita, from the Sierra Nevada". If in fact, the data on basibranchial teeth cited by Smith and Gall include specimens from those I examined, then

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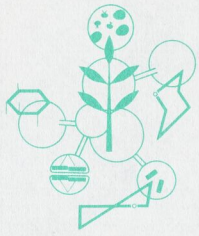

yes 88 of the 504 little Kern fish did have these teeth. I could hazard a guess that the method they used to see if basibranchial teeth were present was to insert a finger into the mouth and feel for the teeth (note: this is a guess!). What I did was the alizarin-soaking business followed by careful observation w/ a good stereo 'scope. What I learned was it's damn hard to see one or a few small teeth - also, the teeth are (as you know) very fragile and tend to break easily. In any event, if they included the specimens I examined, then it would appear that neither read my MS very closely. What can I say?? If the journal does send the MS here, then I guess I'll probably say something similar to what you wrote. Probably, for political, etc. reasons, I won't receive a copy.

Regards,

John

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