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with Respect to Phylogenetic Divergences**



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TAXIMETRIC ANALYSIS OF SELECTED GROUPS OF WESTERN NORTH AMERICAN SALMO WITH RESPECT TO PHYLOGENETIC DIVERGENCES^{1,2}

PIERRE LEGENDRE, CARL B. SCHRECK, AND ROBERT J. BEHNKE

Abstract

Legendre, Pierre (Dept. of Biology, Univ. of Colorado, Boulder, Colorado 80302, present address: Genetiska Institutionen, Lunds Universitet, Sölvegatan 29, S-223 62 Lund, Sweden) Carl B. Schreck and Robert J. Behnke (Colorado Cooperative Fishery Unit, Colorado State University, Fort Collins, Colorado, 80521) 1972. Taximetric analysis of selected groups of Western North American *Salmo* with respect to phylogenetic divergences. Syst. Zool. 21:292-307.—Two computer-aided techniques, the clustering analysis of the Graph Theory Model and the CHARANAL program which finds a succession of characters best classifying the objects under study, were used to indicate phenotypic similarities existing within certain members of the genus *Salmo*. Eight characters from 104 objects consisting of 849 specimens from 44 collections representing 5 described species and unnamed forms of western North American trouts were analyzed. Results of the Graph Theory Model and CHARANAL program were almost identical, and the former clustered the same form of trout at high similarity levels.

Considering only the computer-aided analyses, the Apache (unnamed), red-banded (unnamed) and Kern River (*S. aguabonita gilberti*) trouts seem to be a closely-linked group slightly distinct from the Gila trout (*S. gilae*). The California golden trout (*S. a. aguabonita*) joins the cutthroat trout (*S. clarki*) before any other group; the trouts of the "golden trout complex" are phenotypically more similar to cutthroat trout than to rainbow trout. The rainbow trout (*S. gairdneri*) is connected only to trout from the Rio Truchas, also a rainbow-like trout, before the lowest level of similarity. The Mexican golden trout (*S. chrysogaster*) is unique in that it joins the above trouts at the lowest level of similarity. Other taxonomic informations support these contentions.

The taximetric analysis shows that the trout from the upper Little Kern River basin, named *S. whitei*, correctly should be considered a synonym of *S. a. gilberti*.

This paper demonstrates the efficiency of the two computer programs as a method to facilitate data analysis for systematic investigation. It is, however, also an attempt to consider all the known divergent forms of endemic western trouts in a comparative study and is a step toward a sounder understanding of the phylogenies involved.

Résumé

Un modèle de groupement en théorie des graphes, ainsi que le programme CHARANAL (analyse de caractères) qui permet de découvrir les caractères permettant de mieux classifier les objets sous étude, sont les deux méthodes d'analyse par ordinateur qui furent utilisées pour l'étude des relations phénotypiques existant entre certains groupes de poissons du genre *Salmo*. L'analyse, basée sur 8 caractères, a porté plus précisément sur 104 objets qui représentent 849 spécimens provenant de 44 collections de 5 espèces reconnues, ainsi que d'autres truites sans statut en nomenclature, de l'ouest de l'Amérique du Nord. Les résultats obtenus à l'aide des deux méthodes d'analyse sont très fortement comparables; le modèle en théorie des graphes groupait dès les premiers niveaux de similarité les objets appartenant à la même forme, comme on pouvait s'y attendre.

Ces analyses indiquent que les truites désignées ici sous les noms de Apache et "red-banded", ainsi que *Salmo aguabonita gilberti*, forment un seul groupe, légèrement distinct de *S. gilae*. *S. a. aguabonita* rejoint *S. clarki* avant toute autre forme. Les truites du groupe *S. aguabonita*, ainsi que *S. gilae*, sont phénotypiquement plus similaires à *S. clarki* qu'à *S. gairdneri*. *S. gairdneri* n'est relié, avant le niveau de similarité le plus bas, qu'à une autre truite, aussi de type arc-en-ciel, provenant du Rio Truchas. *S. chrysogaster*, pour sa

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part, n'établit des connections de similarité avec les truites sus-mentionnées qu'au plus bas niveau de similarité de cette étude. Des indications taxonomiques d'autres types sont présentées à l'appui de ces relations.

L'analyse montre aussi que le nom *S. whitei*, donné à la truite provenant de la partie supérieure du bassin de la rivière Little Kern, devrait être considéré comme un synonyme de *S. a. gilberti*.

Cette étude démontre l'efficacité des deux programmes d'ordinateurs utilisés, en tant que méthodes de traitement des données pour des fins taxonomiques. Et en tant que tentative de considération comparative simultanée de toutes les formes divergentes connues de truites endémiques de l'ouest, elle représente un pas en avant dans la compréhension de leur phylogénèse.

INTRODUCTION

The teleost family Salmonidae is noted for abundant examples of convergence, phenotypic plasticity and sympatric sibling species and, consequently, frustrating taxonomic problems (Behnke, 1970). In this paper we treat a particular group of salmonid fishes, the indigenous trouts of the genus *Salmo* of western North America with two techniques of similarity clustering.

A major systematic problem with western North American *Salmo* concerns the detection of major and minor evolutionary divergences and the phylogenetic affinities of the diverse forms comprising this group of trouts.

The taxonomic history of western North American *Salmo* has followed contemporary trends of splitting into more than 40 species and lumping all the diverse populations into a single, polytypic species. Vladykov (1963) proposed recognition of the western North American trouts as a subgenus or genus, *Parasalmo*, to emphasize the distinctions separating them from the other members of the genus *Salmo*. In recent years, the trend has been to recognize two basic evolutionary groups or complexes, the rainbow trout series, *Salmo gairdneri* Richardson, and the cutthroat trout series, *S. clarki* Richardson, and to assign other recognized species as derivatives of one or the other series (Miller, 1950; Needham and Gard, 1959). However, as pointed out by Behnke (1970), such a scheme lacks evolutionary reality because some forms such as the California and Mexican golden trouts, Gila trout, Apache trout and a diverse group we call

the red-banded trout do not appear to be recently derived from the rainbow trout or the cutthroat trout but represent an independent phylogenetic divergence (or divergences) from a more distant common ancestor.

Although rainbow trout and cutthroat trout occur in natural sympatry in coastal drainages from northern California to southern Alaska, providing the basis for the recognition of two valid species, isolating mechanisms break down when rainbow trout are introduced into waters outside their native range. In such cases where the cutthroat trout populations have probably never been exposed to the natural presence of rainbow trout in their evolutionary history, hybrid swarms are the typical result. Isolating mechanisms allowing sympatric occurrence evidently are lacking in all the diverse populations of western North American *Salmo*, except for the rainbow trout and coastal subspecies of cutthroat trout. Massive hatchery propagation and stocking of rainbow trout, and to a lesser extent, transplants of cutthroat trout, have produced large scale hybridization causing the virtual disappearance of indigenous genotypes of several subspecies of cutthroat trout and of the Gila and Apache trouts.

In addition to the rainbow and cutthroat trouts, the western North American *Salmo* includes relict populations of trout of limited distribution which cannot be readily assigned to either *S. gairdneri* or *S. clarki*. For practical purposes, these forms are accorded full species status, although admittedly they can not pass the test of sym-

patry and meet the criterion of a biological species. These include: (1) the California golden trout, *S. aguabonita* Jordan, native only to the headwaters of the South Fork of the Kern River and Golden Trout Creek, tributary to the Main Kern River, California; (2) the Gila trout, *S. gilae* Miller, found in historical times in the headwaters of the Gila River, New Mexico (now restricted to three, tiny isolated streams); (3) the Mexican golden trout, *S. chrysogaster* Needham and Gard, indigenous to three Pacific Coast river systems in Durango and Sinaloa, Mexico; (4) the Apache trout, yet unnamed, known from headwater tributaries of the White and Black rivers of the Salt River drainage, Arizona—now very rare in its pure form due to hybridization with introduced rainbow trout; and (5) the Kern River trout, *S. aguabonita gilberti*, originally found only in the main Kern River and lower Little Kern River, southern California, but now found only in some upper tributaries; and (6) another unnamed group of diverse populations persisting as disjunct isolated relicts in the upper Sacramento River system in northern California and several desiccating basins in southern Oregon for which we apply the name “red-banded” trout.

It is likely that even after more definitive information is accumulated and evaluated on the systematics of the western trouts, allowing a more reasonable estimation of the phylogenetic affinities of all the groups and sub groups involved, it will prove to be impossible to produce a taxonomic arrangement with binomial (or trinomial) nomenclature accurately reflecting evolutionary reality. Before any nomenclatural revision can be attempted in a meaningful manner, however, it will first be necessary to detect the major and minor evolutionary divergences responsible for the present diversity of distinct forms and to assess phylogenetic affinities between them. Schreck and Behnke (1971) discussed the red-banded trout complex and its possible position in *Salmo* phylogeny. The present paper is the first effort to

bring together information on all of the major divergent groups of western North American *Salmo* specimens by techniques revealing phenotypic similarities. Two computer-aided methods were used and compared: the clustering analysis of the Graph Theory Model and the CHARANAL program.

The clustering analysis used in this paper has been designed in such a way that it reproduces as closely as possible the process of thought that the “classical” taxonomists have been using for decades. Its advantage is that one can obtain in seconds an appreciation of the overall phenotypic similarity existing between many objects, for several characters.

The method derived from CHARANAL, on the other hand, is even more closely related to classical taxonomy, because it consists of finding a succession of characters that best classify the objects under study. The strong concordance of the results obtained with the CHARANAL method with those obtained with the clustering technique is due only to the fact that the characters used were well selected to partition the objects.

However, as pointed out by Rogers and Appan (1969), when one tries to apply the biological species concept to a group of organisms and not a typological or nominalistic concept, one has to consider phenotypic relationships simply as indications of the biological relationships, and other biosystematic evidence must be used to confront and supplement them.

METHODS

Specimens

Choice of specimens best representing the forms under study was based on evidence presented by Needham and Gard (1959, 1964), Miller (1950), Schreck (MS., 1969), Behnke (1970) and Schreck and Behnke (1971). Table 1 lists the specimens used in the analysis, collection sites and dates, number of specimens or populations included in the sample and the

TABLE 1. COLLECTION SITE AND DATE AND IDENTIFYING OBJECT NUMBERS OF THE TROUTS EXAMINED.

Species or form	Source	Date collected	Sample size	Object number
Rainbow	Whiskey L. Outlet, Alaska	1957	21	101
Rainbow	Wood R., Alaska	1957	30	102
Rainbow	Brooks L., Alaska	1957	16	103
Rainbow	Tebay L., Alaska	1957	22	104
Rainbow	Tikchik R., Alaska	1957	11	105
Rainbow	Alagnak R. (or Branch R.), Alaska	1957	29	106
Rainbow	Coquihaila R., Alaska	1957	30	107
Rainbow	N. Fork Salmonberry R., Alaska	1957	28	108
Rainbow	Lwr. Kathleen L., Yukon	1957	17	109
Rainbow	Mulberly C., Alberta, Canada	1957	32	110
Rainbow	Ruby Valley Fish Hatchery, Nevada	1957	30	111
Rainbow	San Pablo C., W. fork, California	1953	30	112
Gila	Diamond C., New Mexico	1939	14	201-214
Mexican golden	Rio Verde (Fuerte), Mexico	1952	5	301-305
Mexican golden	Rio Sinaloa, Mexico	1954	5	311-315
Mexican golden	Rio Culiacan, Mexico	1954	5	321-325
Rio Truchas	Rio Truchas, Mexico	1951	16	401-416
Apache	Ord C., Arizona	1966	9	501-509
Cutthroat	Yellowstone L., Wyoming	1967	30	601
Cutthroat	Reservoir Canyon near Pine Valley, Utah	1958	13	602
Cutthroat	Indian C. and Rio Seco, Colorado	1958	33	603
Cutthroat	Headwaters Big Thompson R., Colorado	1968	20	604
Cutthroat	L. Victor, N. Fk. Boulder C., Wyoming	1969	15	605
Cutthroat	R. Arriba, Canones C., Trib. R. Chama, New Mexico	1969	6	606
Cutthroat	Pacific C., Wyoming	1967	8	607
Cutthroat	Cottonwood C., Wyoming	1969	21	608
Cutthroat	Home C., Wyoming	1969	8	609
Cutthroat	Big Sandstone C., Douglas C., Wyoming	1969	41	610
Red-banded	Sheephaven C., California	1968	13	701-713
Calif. golden	Alpine L., Wyoming	1969	10	801
Calif. golden	Cottonwood L. & C., California	1912	9	802
Calif. golden	Golden Trout C., California—types	1904	24	803
Calif. golden	Golden Trout C., California	1967-1968	13	804
Calif. golden	Whitney C., California	1967	10	805
Calif. golden	Golden Trout C., California	1956	31	806
Calif. golden	Cottonwood C., California	1956	39	807
Calif. golden	S. Fk. Kern R., California	1956	34	808
Calif. golden	Salley Keyes L., California	1959	22	809
Kern River	Kern R., California—types	1893	7	901
Kern River	Soda Spg., S. Fk. Kaweah, Little Kern, Coyote C., California	1904	8	902
Kern River	Rifle C., Calif.	1956	22	903
Kern River	Coyote C., Calif.	1956	33	904
Kern River	Soda Springs C., California	1968	12	905
Kern River	Wet Meadows C., California	1968	17	906

identification or object numbers for each specimen or population.

For representatives of the cutthroat trout species, *S. clarki*, only the large-spotted, interior forms were used. The only consistent difference between the interior

subspecies and the coastal subspecies yet found is the number of chromosomes (Behnke, 1970). The 104 objects consist of a total of 849 specimens representing 44 collections of the 5 described species and the undescribed forms. In cases where the

trout is restricted in distribution to one or only a few waters, the individual fish themselves were treated as objects. In widespread forms occupying diverse habitats the characters from an entire collection sample were averaged, and this mean of the population was treated as a theoretical individual and considered as a single object. For example, 12 samples of populations of rainbow trout consisting of a total of 296 specimens were evaluated, but each individual sample was treated as if it were a single fish, thus giving 12 "rainbow trout" objects. This was done in an effort to be more representative of the group as a whole and to include the spectrum of variability in the species. The need to handle several hundred specimens was thus eliminated. Almost an equal number of objects in each group was obtained, enabling us to use the Graph Theory Model for the analysis. Each object has a three digit identification number. The first digit refers to the main group in which the object is included (Table 1); the second and third digits designate the individual fish or individual population (theoretical individual).

The Graph Theory Model used by us shows the relationship between the individual objects and not directly between the groups of objects as do statistical models. Consequently, the sample used to represent each group of trouts does not have to be statistically representative to indicate true relations between the objects. Similarity indices found between pairs of specimens would be the same even if 500 more specimens were included.

Characters

Taxonomic characters used in our comparison, given in Table 2, were those found to be diagnostic for the fishes under consideration by Schreck and Behnke (1971) and were obtained following their methods. Characters were also selected on the basis of their being available for each object. Morphometric characters were shown by Needham and Gard (1959) to be of lit-

tle discriminatory value in western North American *Salmo* taxonomy. We also found in a preliminary study that these characters are subject to much allometric and/or nongenetic ecological variation. For the taximetric analysis, therefore, we used 5 ordered meristic characters and 3 nonordered characters relating to coloration and markings.

The term "ordered" used above refers to the concept of character states. For example, a nonordered character such as the color of the cutthroat mark consists of "red, yellow, and blank" (no cutthroat marks). States are ordered when variation of the character can be associated with a sequence of real numbers. The Graph Theory Model allowed us to establish a partial relationship between neighboring states of such a character. For a detailed discussion of the concept of character and state see Estabrook and Rogers (1966), Estabrook (1967), Rogers, Fleming and Estabrook (1967), and Legendre and Rogers (1972).

The division of characters into states was made by plotting the frequency distribution of characters and then dividing them where natural breaks occurred. Characters were weighted by use of a property of the Graph Theory Model—when there are fewer states in a character, then this character weighs more than a character with more states. No weighted values were utilized, however. This principle of weighting is discussed more thoroughly by Legendre and Rogers (1972). Table 2 defines the states for characters used in this study, and Table 3 lists the character states for each specimen.

First Method of Determining Similarity—Clustering Analysis

The program for the Graph Theory Model has been described in detail by Wirth et al. (1966) and by Estabrook (1966). It first calculates a similarity value for each pair of objects, which is basically the number of characters with matching states in both individuals of the pair, di-

TABLE 2. DEFINITION OF CHARACTER STATES.

1: <i>Pyloric caeca number</i>		2: <i>Number of vertebrae</i>	
State	Number	State	Number
1	17-26	1	56-60
2	26.1-35.9	2	60.1-62.6
3	36-44	3	62.7-64.0
4	45-60		
3: <i>Number of scales in lateral series</i>		4: <i>Rows of scales above lateral line</i>	
State	Number	State	Number
1	121-137	1	20-24
2	138-148	2	(void state)
3	148.1-159.0	3	25.0-32.9
4	159.1-200.0	4	33.0-37.9
		5	38-48
5: <i>Rays in pelvic fin</i>		6: <i>Color of the top of dorsal fin</i>	
State	Number	State	Color
1	8.0-9.2	1	bright orange or cream
2	9.3-10.2	2	tip not of a bright color
7: <i>Color of the cutthroat marks</i>		8: <i>Size and location of the spotting</i>	
State	Color	State	Description
1	red	1	large, posterior
2	yellow	2	medium, posterior and more anterior
3	blank (no cutthroat marks)	3	fine and profuse, generalized

vided by the total number of characters for which information is available. The various measures of similarity thus obtained are then ranked in order of decreasing similarity; in a final step, and proceeding from high to low similarity, clusters are obtained by establishing connections between pairs of objects between which there exists a calculated similarity at least as high as the value of the similarity level considered. The most dissimilar groups of objects cluster together at the lowest levels.

Objects in neighboring states of characters 1-5 (Table 2) are not totally independent from each other with respect to the character. Different objects of the same form of trout may be on either side of the somewhat arbitrary boundary between two states. To correct for this an equation described by Estabrook and Rogers (1966: 792) has been incorporated into the program. According to it, the partial similarity between objects placed in different states of a character is, for this character,

$2(k+1-d)/(2k+2+dk)$ whenever $d \leq k$, and 0 when $d > k$, where d is the "distance" between two states of an ordered character, and k is a parameter which indicates the largest "distance" between character states in the sequence, for which the worker wants to get a non-0 assignment of partial similarity. Using the value $k=1$, a degree of similarity of 0.4 was assigned to pairs of objects in neighboring states ($d=1$) of characters 1 to 5. The use of this equation results, in the case of adjacent character states, in a lowering of the intensity of the separation caused by placing objects in different states of a character.

We used the partial similarity value for character 4, but we also desired to express the large gap in its frequency distribution separating the Mexican golden trouts from all other objects except specimen 402 from the Rio Truchas. This explains why object 402 does not cluster with others of its group until level 4. We have created a void state for this character which con-

TABLE 3. THE STATES IN WHICH EACH SPECIMEN FALLS FOR EVERY CHARACTER. EACH COLUMN UNDER "CHARACTER STATES" CORRESPONDS IN ORDER TO ONE OF THE 8 CHARACTERS SHOWN IN TABLE 2.

object number	character states	object number	character states	object number	character states	object number	character states	object number	character states
101	43132233	210	21241123	402	32112233	507	21342122	709	32451122
102	43132233	211	22332123	403	31332233	508	21342122	710	42452122
103	43132233	212	22242123	404	32332233	509	21242122	711	32452122
104	43132233	213	21241123	405	33232233	601	32451211	712	42451122
105	43132233	214	22341123	406	32332233	602	32451211	713	32452122
106	43132233	301	11111112	407	31432233	603	32451211	801	11451111
107	43132233	302	11111112	408	32232233	604	22451211	802	21451111
108	43132233	303	11211112	409	32232233	605	32451211	803	21451111
109	43132233	304	11111112	410	32332233	606	32451211	804	21451111
110	43132233	305	11111112	411	32232233	607	22451211	805	21451111
111	43132233	311	11111112	412	31332233	608	32451211	806	21451111
112	43132233	312	11111112	413	31342233	609	32452211	807	21451111
201	21342123	313	11111112	414	31432233	610	32451211	808	21451111
202	21232123	314	11111112	415	32332233	701	21341122	809	21451111
203	22332123	315	11111112	416	32231233	702	32441122	901	32342122
204	22232123	321	11111112	501	21451122	703	32442122	902	32342122
205	22232123	322	11111112	502	21441122	704	22442122	903	32342122
206	22242123	323	11211112	503	12242122	705	42442122	904	32342122
207	21232123	324	11111112	504	11242122	706	22442122	905	22352122
208	21332123	325	11111112	505	11252122	707	42441122	906	32342122
209	21232123	401	32232233	506	11442122	708	32452122		

tains no object, thus eliminating the possibility of partial similarity between specimens in state 1 and all others.

Second Method of Determining Similarity—CHARANAL Program

The same data used above was processed in a program called CHARANAL. Estabrook (1967) and Legendre and Rogers (1972) discuss this program more fully. The program has been designed to get various information-theoretic measures: the information held by the frequency distribution of objects in the states of a character is calculated following the well-known

measure of entropy $H = -\sum_{i=1}^n p_i \log p_i$ where p_i is the probability of an object to be found in state i of the character; in a similar manner, the information held in common by pairs of characters is calculated from the matrix of combined frequency distribution. This measure can be understood as the correlation between characters, since it shows to what extent pairs of characters carry the same partitioning, or classificatory, power for the set of objects under study.

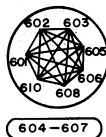
Two equations of this program, SUMRAT and SAMRAT, indicate what charac-

FIG. 1. Results from the clustering analysis. The values of similarity or C-values are represented on the abscissa. The levels of similarity L_i are those at which the clusters are modified by addition of new objects. Inside each circle, only the connections formed at the given level of similarity are shown. —: indicates external connections, connecting the cluster to an object that was not in this cluster at the preceding level. ----: indicates internal connections between two objects that were already members of the cluster. At level 6, only the connections between the presumed taxa are shown, because of the large number of internal connections formed at this level. For more detail, see Table 4. The fraction following each cluster is the ratio of the actual number of connections formed before and at the given level to the total number of possible connections between the objects in the cluster. Circles and oblongs represent the same thing; they are drawn differently for graphical convenience.

LEVELS → L₀
C-VALUES → 1.000

L₁
0.925

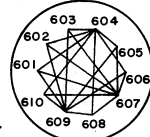
CALIF. GOLDEN CUTHROAT



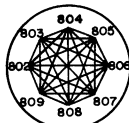
21/21

1/1

604-607



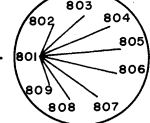
GILA



28/28

1/1

210-213



3/3

1/1

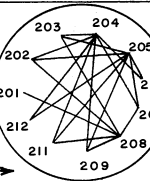
203-211

1/1

204-208

1/1

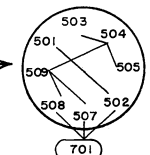
206-212



APACHE

507-508

1/1



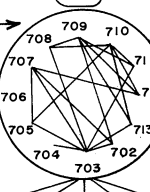
RED-BANDED

704-706

1/1



3/3



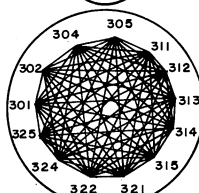
KERN RIV.



10/10

901 902 903 904 906

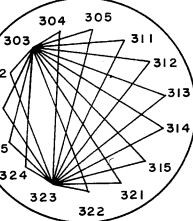
MEXICAN GOLDEN



78/78

1/1

303-323



RIO TRUCHAS



6/6

1/1

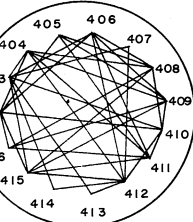
403-412



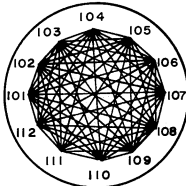
6/6

1/1

407-414



RAINBOW



66/66

L_2
0.875

L_3
0.850

45/45

45/45

36/36

26/55

10/36

39/136

105/105

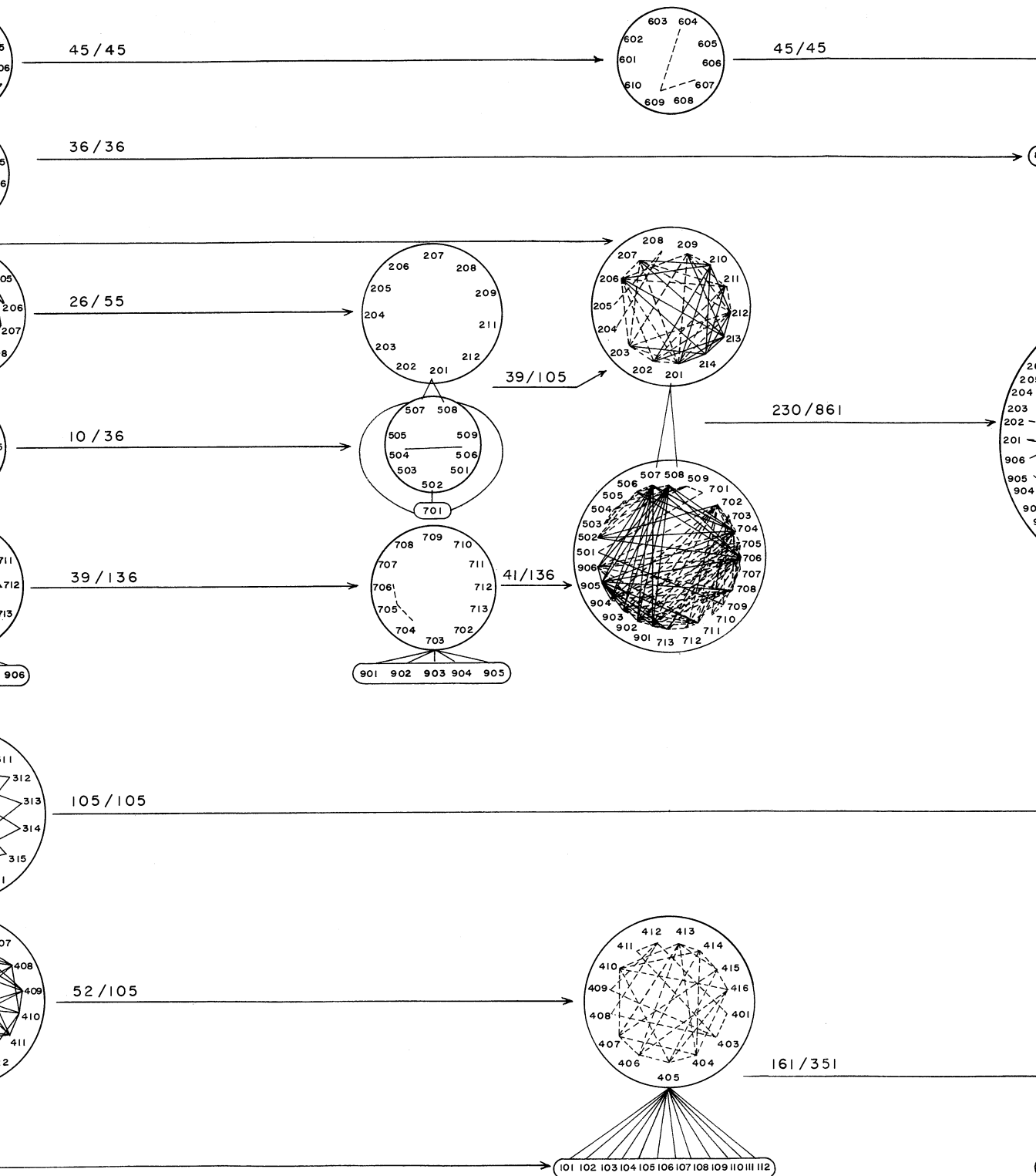
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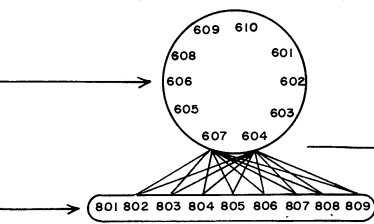
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161/351

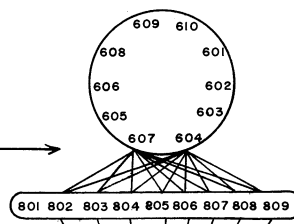


L_4
0.800

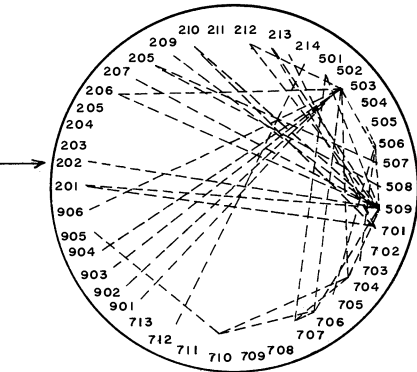
L_5
0.750



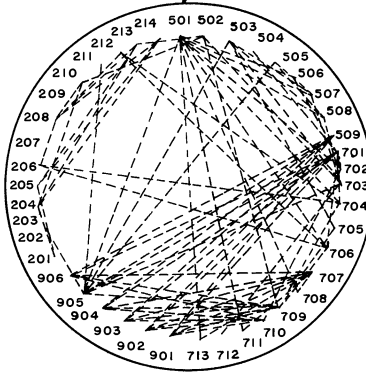
97/171



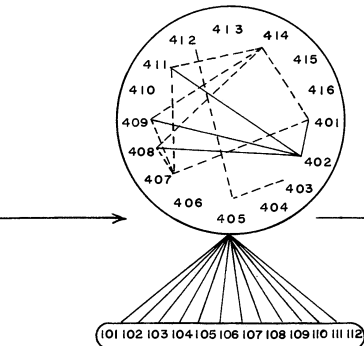
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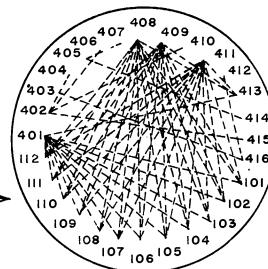
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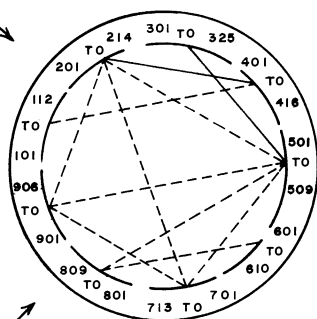
235/378



175/378



L_6
0.675



ter(s) best represent the systematizing power of all other characters:

$$\text{SUMRAT (I)} = \sum_{j=1}^n \frac{(\text{information shared by character I and each character } J_j)}{(\text{information in } J_j)}$$

$$\text{SAMRAT (I)} = \sum_{j=1}^n \frac{(\text{information shared by character I and each character } J_j)}{(\text{information in I})}$$

where n is the number of characters other than I in the study.

Calculations with these equations showed that character 7 had the most information in common with all the other characters. Since it represented best the classificatory power of all the other characters, the objects were then divided according to their particular state within character 7. Another CHARANAL was run for each of the three groups obtained from the split of character 7, and the characters best representing all others were chosen to partition each group into subgroups, just as it had been done with character 7. This process was continued (Figure 4). Sometimes, several characters were partitioning the objects in exactly the same way: for instance, one of the groups obtained after the first partition was split in the same way by characters 1, 3, 4 and 8 (Figure 4).

RESULTS

Analysis of the clusters (Figure 1) obtained from the Graph Theory Model reveals the expected result that, in general, objects of the same group of trout cluster together very early. Many cluster at 1.000 similarity value, denoting complete identity for every character state.

The terms degree of similarity, clustering level and level of similarity will all refer to a point on the axis of decreasing similarity. A C-value is defined as a value of similarity where at least one of the clusters gets modified by addition of at least one new object. Cluster has been

operationally defined in the method section on clustering analysis.

The C-value of 0.675 (level 6) corresponds probably, in this case, to the subgeneric level (Figure 1) because this is the level where *S. clarki* and *S. gairdneri*, considered two valid species, cluster together. There are 5 different units at level 5. Cutthroat and California golden trouts form 16 connections at level 4 ($C = 0.800$); no more connections are added at level 5. These two groups were not included in the same cluster at these levels for two reasons. First, these 16 connections represent a single indication of similarity because specimens 802 to 809 are identical, clustering at the 1.000 level. Specimens 604 and 607 are identical for the same reason. Therefore, 16 connections are the minimum number that can be formed between the objects. This applies to object 501 which forms one connection with each identical object of the 802 to 809 series. Secondly, even if these 16 connections represent 0.178 of all the connections possibly formed between these groups (Table 4), cutthroat and California golden trouts are represented as theoretical individuals based on mean values of samples and thus generally more variable. Such objects are consequently more likely to form similarity connections with populations of related species than would individuals of a single population.

It is justifiable to cluster cutthroat and California golden trouts only at level 6 (compare levels 5 and 6, for these two trouts, in Table 4), indicating that they are two separate species. This is also the case with the Mexican golden trout. They cluster very tightly at levels 0 and 1 (at level 1 on Table 4 all internal connections of series 3 are formed) and stay independent of all other groups until level 6.

After clustering tightly at levels 0 and 1, theoretical individuals of rainbow trout form 12 connections at level 3 with real fish from the Rio Truchas and 48 additional connections at level 5. Because these 12 connections represent only 0.063

TABLE 4. THE RATIO OF CONNECTIONS THAT OCCUR BEFORE AND AT A GIVEN LEVEL TO THE NUMBER OF POSSIBLE CONNECTIONS BETWEEN GROUPS (OR IN A GROUP).

1: rainbow trout; 2: Gila trout; 3: Mexican golden trout; 4: Rio Truchas trout; 5: Apache trout; 6: cutthroat trout; 7: red-banded trout; 8: California golden trout; 9: Kern River trout.

L ₀ : C = 1.000									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	—	1.000
4	—	—	—	—	—	—	—	.117	
3	—	—	—	—	—	—	.752		
9	—	—	—	—	—	.667			
7	—	—	—	—	.051				
5	—	—	—	.028					
2	—	—	.077						
8	—	.778							
6	.489								
L ₁ : C = 0.925									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	—	1.000
4	—	—	—	—	—	—	—	.434	
3	—	—	—	—	—	—	1.000		
9	—	—	—	—	.064	.667			
7	—	—	—	.026	.308				
5	—	—	—	.194					
2	—	—	.297						
8	—	1.000							
6	.956								
L ₂ : C = 0.875									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	—	1.000
4	—	—	—	—	—	—	—	.434	
3	—	—	—	—	—	—	1.000		
9	—	—	—	—	.064	.667			
7	—	—	—	.026	.333				
5	—	—	.016	.222					
2	—	—	.297						
8	—	1.000							
6	.956								
L ₃ : C = 0.850									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	.063	1.000
4	—	—	—	—	—	—	—	.692	
3	—	—	—	—	—	—	1.000		
9	—	—	—	.222	.577	1.000			
7	—	—	—	.128	.667				
5	—	—	.016	.500					
2	—	—	.780						
8	—	1.000							
6	1.000								

TABLE 4. (Continued)

L ₄ : C = 0.800									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	.063	1.000
4	—	—	—	—	—	—	—	.809	
3	—	—	—	—	—	—	1.000		
9	—	—	—	.315	.590	1.000			
7	—	—	.022	.197	.718				
5	—	—	.111	.611					
2	—	—	.780						
8	.178	1.000							
6	1.000								
L ₅ : C = 0.750									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	.313	1.000
4	—	—	—	—	—	—	—	.909	
3	—	—	—	—	—	—	1.000		
9	—	—	.024	.481	.885	1.000			
7	—	—	.044	.299	.859				
5	—	.099	.127	.806					
2	—	—	.923						
8	.178	1.000							
6	1.000								
L ₆ : C = 0.675									
	6	8	2	5	7	9	3	4	1
1	—	—	—	—	—	—	—	.938	1.000
4	—	—	.085	—	—	—	—	1.000	
3	—	—	—	.030	—	—	1.000		
9	—	—	.464	.815	.987	1.000			
7	—	—	.137	.658	.923				
5	—	.210	.460	.889					
2	—	—	1.000						
8	.900	1.000							
6	1.000								

of the possible connections (Table 4) but 60 (= 48 + 12) represent 0.313 of possible connections, we believe it is legitimate to cluster these groups at level 5. This implies the two groups are probably related below the species level, forming a specific cluster at level 0.750.

Objects of Gila, Apache, red-banded, and Kern River trout groups form a closely related complex below the species level and are distinct from other clusters. Within each group clusters include all objects of each group at levels 0 and 1 except for object 905 of the Kern River trout group and objects 210, 213, and 214 of the

Gila trout group. These 4 objects do not join their respective clusters until level 3 because they were in character states neighboring those of the rest of the group. Actual difference in characters 1 and 4 is small for specimen 905 and small in character 5 for the others.

Apache, red-banded and Kern River trouts are interconnected very early. At level 1 object 703 of the red-banded group connects with the five Kern River trouts which are similar (i.e., connected at level 0). Specimen 701 of the red-banded trout clusters at level 1 with three Apache trouts. It is not until level 5 that this object forms

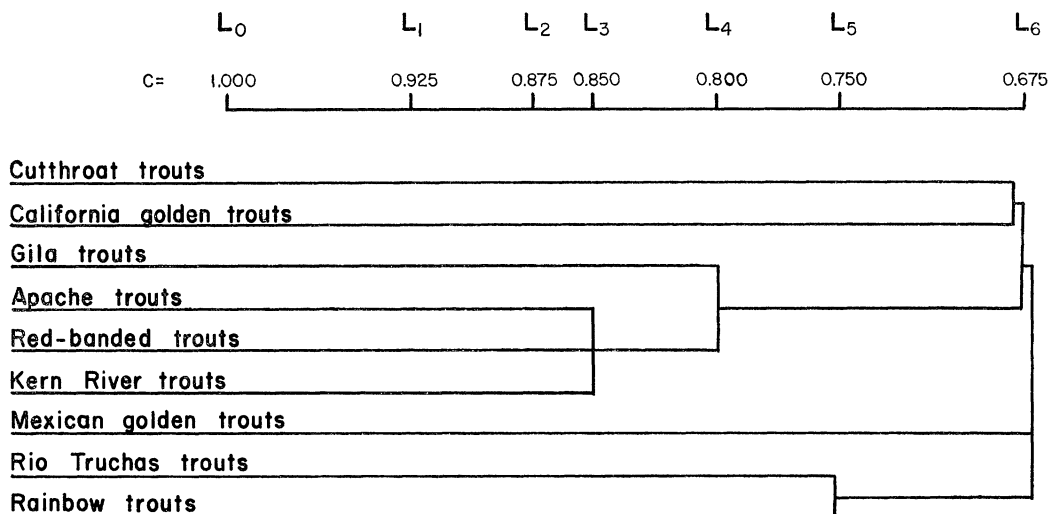


FIG. 2. The relation between groups of salmonid fishes based on data from Figure 1 and Table 4 (see text).

connections with other red-banded trout. This may be attributed to variation in the red-banded trout series together with an effect due to division of character states. At level 3 ($C = 0.850$) Apache, red-banded and Kern River trout groups are interconnected tightly enough to be considered one group.

Object 201 of the Gila trout connects with two specimens of Apache trout, but no more connections form at level 3. At level 4 enough connections are made between Gila and Apache trouts to allow their inclusion in the same cluster with the red-banded, Kern River and Apache trout groups.

Figure 2 shows relation between groups discussed above, and Figure 3, based on data of Table 4, illustrates possible relationships of these forms as determined by the Graph Theory Model.

The resulting grouping from the CHARANAL program is shown in Figure 4, and will be discussed below.

Basibranchial teeth are an important character not included in the programs because of difficulty in treating certain groups in which this character may be present or absent in specimens of the same

population. We found that virtually all cutthroat trouts had these teeth whereas they were always lacking in rainbow, California golden, Mexican golden and Gila trouts. Vestiges of basibranchial teeth were found in some red-banded, Apache, and Kern River trouts.

DISCUSSION

The two classifications obtained from the clustering analysis and the CHARANAL program are almost identical. The only noticeable difference is in the position of the Mexican golden trout. The CHARANAL program shows it joining the cutthroat and California golden trout groups whereas the clustering analysis has it linked to the Apache trout. Taxonomic position of all the kinds of trouts, however, is the same for the two methods; the Mexican golden trout joins the others at the lowest level of similarity.

Considering only the computer-aided analyses, Apache, red-banded and Kern River trouts seem to represent closely-linked groups which are distinct to a certain extent from Gila trout which represents a divergence at level 3. The Mexican

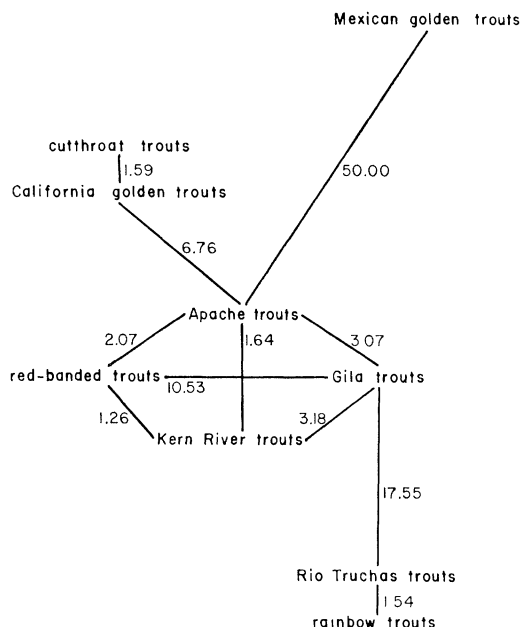


FIG. 3. Phenogram of the probable similarity between the groups of fish studied. The lines are not intended to represent phyletic relationships. The length of the lines between each two taxa has been obtained by the formula

$$1 / \sum_{i=0}^6 C_i N_i \text{ where the } C_i \text{ are the } C\text{-values of the}$$

levels of similarity and the N_i are the number of connections formed between the two presumed taxa at the given levels. The distances between the presumed taxa are approximate because it would have been necessary to use a non-euclidian space to represent them properly. Some very long lines have also been shortened for graphical reasons. The results of the calculations are given on the lines. For more details see Table 4.

golden trout is tied into this group by a very weak link (0.030 of possible connections at level 6) to Apache trout. Contrarily, the California golden trout is joined very strongly to the cutthroat trout group (0.900 of possible connections at level 6) with some connections at level 4. The rainbow trout is connected only to the Rio Truchas trout which is joined very weakly also to Gila trout (0.085 of possible connections at level 6).

This scheme of phenotypic similarity is of interest in the light of discussion and classification proposed by Schreck and Behnke (1971). They considered Apache, Gila, Kern River, California golden and perhaps Mexican golden trouts as being a closely related group sharing a common origin. The red-banded trout may also belong to this complex. All members of this golden trout complex were apparently derived from a cutthroat trout-like progenitor and not from the rainbow trout as previously surmised. The results of this study support such a premise. Some members of the golden trout group form a tightly connected group which are more closely allied with cutthroat trout than with rainbow trout. The Mexican golden trout is unique among the golden trout complex in joining the group at a level similar to rainbow and Rio Truchas trouts and may represent the most divergent group of all of the trouts under consideration.

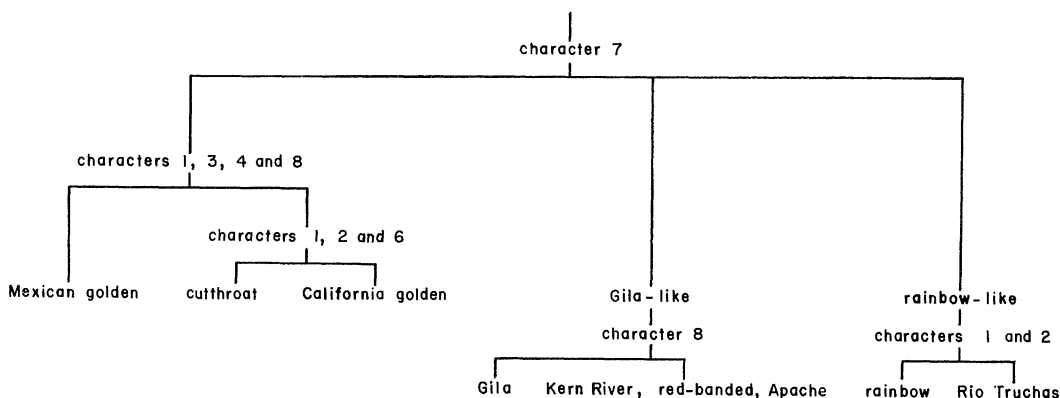


FIG. 4. Classification obtained with CHARANAL.

Relatedness of the golden trout complex to the cutthroat trout series, demonstrated by the computer-aided programs showing phenotypic similarity, is further supported by basibranchial teeth and chromosomal evidence. Cutthroat trout typically have dentition on the basibranchial plate, and it is always lacking in rainbow trout. Because this is a primitive salmonine character, Kern River, red-banded and Apache trouts probably did not independently evolve these teeth from an ancestor lacking this dentition. There is no information on the chromosomes of Gila, Mexican golden, Rio Truchas or red-banded trouts. However, the karyotypes for California golden, cutthroat, rainbow (Simon, MS., 1964) Apache (Behnke, 1970), and Kern River (Schreck and Behnke, 1971) trouts indicate, applying Robertson's rule of centric fusion, that the chromosome counts of Apache, golden, and Kern River trouts, which are identical, can be derived more readily from a *S. clarki* karyotype than from that of *S. gairdneri*.

Evermann (1906) named trout from the upper Little Kern River drainage *S. whitei*. Based on character analyses, stocking records, and original descriptions, Schreck (MS., 1969) and Schreck and Behnke (1971) reported *S. whitei* is actually a synonym for the Kern River trout, *S. aguanbonita gilberti*. Our clustering analysis seems to confirm this classification. The original specimens of *S. a. gilberti* (901) collected in 1893 cluster at level 1 with type specimens of *S. whitei* (902) collected by Evermann in 1904. Existing populations of Kern River trout considered relatively pure by Schreck (MS., 1969) and Schreck and Behnke (1971) also cluster such that they can be included in this group. It is interesting that trout from Coyote Creek (904), a tributary to the upper Kern River, collected in 1956, join with Kern River trouts at level 1 even though they express great internal variation.

Considering the above computer-aided analyses, basibranchial teeth, karyotypes, and zoogeographic evidence, it seems ap-

parent that members of the golden trout complex represent a closely related group, perhaps at the semispecies level in the sense of Mayr (1969:33). Further, it is apparent that this complex shares phenotypic similarity with *S. clarki*-like trouts and with *S. gairdneri*. Rio Truchas trout are definitely rainbow trout-like. This is logical on zoogeographical grounds. The Rio Truchas is tributary to the Rio San Lorenzo, Durango, Mexico. Immediately to the north is the Rio Culiacan, where the Mexican golden trout is found; to the south is the Rio Del Presidio and the southernmost natural distribution of *S. gairdneri*. The Rio Truchas population may be a predominantly rainbow trout genotype introgressed with Mexican golden trout or with another form once having access to the Gulf of Mexico. The position of *S. chrysogaster* in this evolutionary hierarchy is confounded by its independence of the other forms until the lowest level of similarity. The divergent position of the Mexican golden trout is supported by osteological evidence; a supplementary series of orbital bones found in this trout appears to be a character unique among salmonid fishes.

Correlation of evidence presented here with future chromosome preparations and biochemical taxonomy will help in presenting a clearer understanding of phylogenetic patterns. The major goal of this paper is to demonstrate the applicability of a computer-aided taximetric approach to the problem and provide an outline of suggested relationships necessary to base further studies.

ACKNOWLEDGMENT

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