A SYSTEMATIC STUDY OF THE FAMILY SALMONIDAE WITH SPECIAL REFERENCE TO THE GENUS *SALMO*

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Abstract

The salmonoid phyletic line is of great antiquity, perhaps, of Cretac~~i~~eous origin. Basic characters indicate affinities to other primitive teleost groups; however, an assemblage of characters such as the adipose fin, true abdominal pores, two "post terminal" vertebrae (upturned caudal skeleton) spiral valve-like intestine and dentition shows that the suborder Salmonoidei could not have its origin from any present group of Clupeoid fishes as commonly believed.

The family Salmonidae retains most of the primitive characters of the suborder. Most of the present genera and species in Salmonidae appear to be of relatively recent origin, probably Pliocene or Pleistocene. A detailed fossil record is lacking for Salmonoidei. Recent discoveries of Pliocene and perhaps Miocene salmonids (*Salmo*?) were made in western North America.

The Salmonidae are distinguished from other salmonoid families by the presence of two "post terminal" vertebrae, a pelvic appendage, a mesocoracoid, and the absence of mesopterygoid teeth. The Salmonidae is considered to consist of three subfamilies, Salmoninae, Coregoninae, and Thymallinae. The Salmoninae are distinct from the Coregoninae and Thymallinae by the separated parietal bones and a supra preopercle. The Coregoninae have an edentulous maxillary bone. The Thymallinae lack an orbitosphenoid bone, possess an extremely large dorsal fin, and distinctively fluted scales. The subfamilies are well separated. The genus *Prosopium*

of Coregoninae shares some basic features with the Salmoninae and Thymallinae such as a single nasal flap and parr marks. *Prosopium*, however, is well diverged in the coregonine direction from the stem form which gave rise to Coregoninae and Thymallinae.

Salmoninae is the most primitive subfamily. Primitive and advanced characters and phylogenies are based on Dollo's "Principle" i.e., once a character is lost it will not be regained. A group like Coregoninae without teeth on the jaws, could not give rise to Salmoninae with toothed jaws. Likewise, the absence of the orbitosphenoid in Thymalline is judged as an advanced character. It is not known when the subfamilies diverged but it is estimated the separation took place in the Miocene or earlier.

Six genera of Salmoninae are recognized: *Salmo*, *Salmothymus*, *Oncorhynchus*, *Salvelinus*, *Hucho*, *Brachymystax*; but evidence indicates a more natural arrangement would place *Brachymystax* as a subgenus of *Hucho*. *Oncorhynchus* was derived from *Salmo* and is the most recent and specialized genus.

Salmo is arranged as two subgenera: (*Salmo*) for Atlantic species and *Parasalmo* for Pacific species. *Salmothymus* is considered as the most primitive genus because of its dentition, low vertebral number and general morphology. An ancestral species with characters similar to *Salmothymus ohridanus*, but with joined parietals, might be envisioned as the progenitor of the family.

Salvelinus is subdivided into three subgenera, and five species. The *Salvelinus alpinus* group, however, may prove to consist of several additional species.

Hucho and *Brachymystax* are of common ancestry. *Hucho perryi* retains the characters of this hypothetical ancestor, suggesting *Brachymystax* diverged off of the *Hucho* line. *Hucho bleekeri* of central China occurs far outside the range of other salmonids.

Coregoninae has three well-defined genera: *Prosopium* with six valid species; *Stenodus* with a single species; and *Coregonus* which is divided into two subgenera. Convergence has obscured the true phylogenies in some species. There is such taxonomic confusion in *Coregonus* that the number of valid species can only be estimated. Perhaps 25-35 species belong to this genus.

Thymallinae has only four generally recognized species, all in the genus *Thymallus*. It is suggested that the genus *Phylogephyra* be retained until more is known of the thymallines of the Altai Mountain region.

The ancestral salmonid probably had a high number of chromosomes. The evolutionary trend has been for fusion of chromosomes and reduction in number.

Intralacustrine speciation and "micro" divergence allowing closely related populations to occur sympatrically, has caused much confusion in salmonid systematics, but has not played an important role in the evolution of the family.

INTRODUCTION

The goal of this study is to create a systematic arrangement of the family Salmonidae reflecting phylogenetic relationships as accurately and confidently as the available information permits. Many outstanding ichthyologists such as Gunther, Regan, Jordan and Berg have attempted systematic arrangements of the Salmonidae and an enormous amount of literature on the subject has been produced. The systematics of this group is notable for the diversity of opinion concerning the number and relationships of the subfamilies, genera and species. Heretofore, no comprehensive comparative study of the Salmonidae of the world has been attempted. I consider the Salmonidae to represent three subfamilies, the trouts, Salmoninae; the whitefishes, Coregoninae; and the graylings, Thymallinae. The major emphasis of this study is on the Salmoninae.

Besides the standard taxonomic procedures of comparative anatomy and morphology I have utilized evidence from the fields of ecology, zoogeography and cytogenetics in forming my opinions. Except in a few notable instances, where it appears impractical, I apply the biological species concept as a basis for my systematic arrangement.

I object to the opinions of Sokal and Sneath (1963) that real knowledge of phylogenies cannot be had from a comparative study of extant forms. I believe that to a perceptive and judicious student, a thorough comparative study of a group of fishes reveals that characters such as dentition, jaw structure, scales, fins, and body form are more than mere items to be counted and measured for a quantitative statement on degree of differences. Accurate interpretation will yield real information on evolutionary histories and relationships. Granted, many conclusions will be tentative and open to question; but the very nature of such a study inculcates insight and understanding of evolutionary theory obtainable in no other way.

Certain gaps necessary for a thoroughly confident arrangement have not been adequately closed. I have attempted to sharpen the focus on the problems of these obscure areas and suggest an outline for possible solutions. I consider this thesis more as a beginning, rather than a culmination of my work on salmonid systematics.

MATERIALS AND METHODS

The specimens used in this study came from many sources. I utilized museum material both in the United States and in Europe. Personal collections were made of North American trouts from 1957 through 1964 and of European salmonids in 1960. Specimens from Formosa and Japan were shipped damp packed in formalin, sealed in plastic bags. Personal collections were preserved in the field in 10 percent formalin and later transferred to 40 percent isopropyl alcohol. A summary of my European collecting trip was published in Copeia (1961,(3):365-68). Collections were obtained by angling, with nets and electric shocking and by purchase from commercial fishermen.

Linear and Meristic Characters

Counts and measurements were made on the left side of the fish and, unless otherwise noted, were made according to Hubbs and Lagler (1949). Linear measurements were converted to thousandths of the standard length.

Scale Counts

The lateral series and lateral line scale counts have the same demarcation points. They begin with the first scale in contact with the pectoral girdle and terminate at the structural base of the caudal, found by flexing the tail and noting the crease formed. This crease is the posterior limit of the standard length measurement. Lateral series scale counts were made at a level of two rows above the lateral line. Much confusion exists in the literature about this character. It is difficult to make with accuracy and most authors do not state precisely how their counts were performed. European workers, typically, count to the last scale on the body, in contact with the caudal rays. This adds approximately five scales to the lateral series count. Scale counts were made after the epidermis was scraped off with a scalpel. Often a malachite green stain was applied over the region to facilitate accurate counts. A three-power binocular microscope was used for magnification.

The scale count above the lateral line is made from the first scale in front of the origin of the dorsal fin, down and back following an oblique row to the lateral line, but not including the lateral line scale.

Fin Ray Counts

Pectoral and pelvic fin rays are all fully developed and an accurate count is relatively simple. The anal ray count, useful in separating *Oncorhynchus* from *Salmo*, is more complex. The typical salmonid anal fin begins with two small splinter-like elements followed by a full length unbranched ray, then a series of branched rays. I use what is called the principal ray count, i.e. all the branched rays plus the full length unbranched ray.

Vertebrae

Vertebrae counts were made by x-raying the specimen and examining the negative. Every ossified centrum in the vertebrae column, including the last three upturned centra, supporting the hypural plates, were counted.

Basibranchial teeth

This count was made according to Miller (1950:23).

Most authors incorrectly call basibranchial teeth hyoid teeth. These teeth are borne on a thin, flattened bony plate applied over the basibranchial bones and cartilage which lie in a median series forming the floor of the pharynx.

Pyloric Caeca

Each caecal element, no matter how small, was counted. Counts were made under a binocular microscope by removing each caecum with a forceps.

Gillrakers

Gillraker counts were made on the first left arch. Each raker, including rudiments, were counted. The number of gillrakers increase with the size and age of the individual. Only specimens of 100 mm. or more were used for this character.

Osteology

Cleared and stained specimens, skulls, chondrocrania and other skeletal material were prepared. Specimens, preserved in formalin, may be cleared and stained by placing them in 4% KOH solution and adding a few drops of alizarin red stain. If more brightly stained specimens are desired, a few more drops of alizarin may be added the following day. After two to six days depending on the size of the specimen and the intensity of staining, the specimen is removed and washed. It may be stored in alcohol, glycerin or a mixture of the two. Glycerin maintains the cleared and stained specimen in better condition, but is objectionable to work with. Vladykov (1962) presented details on staining bones.

In analyzing osteological characters I follow "Dollo's Principle," that once a character is lost, it will not be regained. For example, if it is established that the presence of an orbitosphenoid bone in the skull is a primitive character, then a group lacking this bone could not be considered ancestral to a group retaining it.

Deposition of Material

The specimens collected for this study and the comparative osteological material will be deposited in the ichthyology collection of the California Academy of Sciences and readily available for use by future investigators.

Terminology and Nomenclature

Race

I frequently use the word race to describe a population or subpopulation. I follow the current ichthyological use of the term which denotes a genetic difference and at least semi-isolation of the gene pool. Contrary to ornithological literature, however, race is not equivalent to subspecies.

Intralacustrine speciation

To obviate the stigma attached to the term sympatric speciation, I use Brooks (1950) phrase intralacustrine speciation. This merely denotes that two or more species (or races) have diverged from a single population in a lake. The lake may have undergone great changes in levels through geological time periods, affording opportunities for separation of the original population and the initiation of speciation. The emphasis is on the fact that the separation and differentiation is endemic to the lake basin where the species are now living.

THE SUBORDER SALMONOIDEI

The suborder Salmonoidei represents a group which probably had its origin from the earliest teleost or "proteleost" fishes perhaps, in the late Mesozoic. I believe their origin is much more ancient than commonly believed. The suborder Salmonoidei is considered in the order Isospondyli or Clupeiformes of Berg (1940). Opinions have varied on the number of Salmonoid families and their relationships. Much of the difficulties involved in a systematic arrangement of the suborder is due to an array of bizarre, highly specialized, deep-sea species for which many families have been created.

Regan (1913, 1929) recognized the suborder Salmonoidei as fishes usually with an adipose fin, parietals well developed, oviducts absent or incomplete, abdominal pelvic fins, a pneumatic duct to the air bladder and ribs not ossified to the vertebral centra. In his 1913 paper, Regan recognized the following families: Salmonidae, Argentinidae, Microstomidae, Osmeridae, Retropinnidae, Salangidae, Galaxudae and Aplochitonidae. In 1929, he recognized one more family, Ophisthoproctidae. Most subsequent authors have accepted the family Plecoglossidae which Regan had considered with the Osmeridae. Regan's Salmonidae has been variously considered as two or three families, Salmonidae for the trouts, Coregonidae for whitefishes and Thymallidae for graylings.

Berg (1940) had the following families in the suborder Salmonoidei: Salmonidae, Thymallidae, Plecoglossidae, Osmeridae, Salangidae, Retropinnidae, Aplochitonidae, Argentinidae, Bathylagidae, Microstomidae, Xenopthalmichthyidae and a fossil family, the Thaumaturidae. Berg placed the Opisthoproctidae in a separate suborder and created a new order, Galaxiiformes for the Galaxiidae, evidently because the olfactory lobes of the brain in galaxids are close to the nasal capsules.

Chapman (1941a, 1941b, 1942a, 1942b, 1948b) published his osteological investigations on many salmonoid species. Much of what is known on the systematic characters of many of the families is based on Chapman's work, which is detailed and comprehensive. His conclusions, however, on relationships and classification are open to question. Chapman (1942b) expanded Berg's suborder Opisthoproctoidei to include the deep sea salmonoid families, Macropinnidae, Xenopthalmichthyidae, Bathylagidae, Microstomidae, Argentinidae and a new family

Winteriidae. Chapman (1944) considered the Aplochitonidae to belong to the haplomous or pike group of fishes (Regan's order Haplomi, Berg's suborder Esocoidei). He stated that probably the Galaxiidae and Retropinnidae should also be removed from Salmonoidei and placed in the Esocoidei.

Hubbs (1953) concluded that the distinguishing features of the Salmonoid-like deep sea fishes were the result of extreme specialization and degeneration and that they had radiated from an argentenid ancestor. Hubbs expanded the salmonoid family Argentinidae to include Berg's suborder Opisthoproctoidei as revised by Chapman. Hubbs also included the Dolichopterygidae which Berg had placed in the suborder Clupeiodei.

Gosline (1960) studying the caudal skeletons of various isospondylous groups made some significant contributions to the classification of these fishes. One of the main criteria distinguishing teleostean from holostean fishes is the caudal skeleton and the mechanism of caudal fin attachment to the skeleton. The heterocercal or upturned tail of pre-teleost fishes has a number of vertebrae, the last few upturned, associated with a number of other bony elements functioning in support of the caudal fin. The typical teleost caudal region is characterized by much reduction and fusion of elements with only a single terminal vertebrae, often called the urostyle, supporting the caudal fin. Many isospondylous fishes, the Salmonidae among them, retain a primitive intermediate stage with the last three vertebrae upturned, all functioning in fin ray support. Gosline calls the vertebral centra which becomes the last vertebrae or urostyle in advanced teleosts, the terminal vertebrae. There has been a trend in many phyletic lines of isospondylous fishes towards elimination of "post terminal" vertebrae. The retention of "post terminal" vertebrae must be considered as a primitive character. In the Salmonoidei only the Salmonidae have two "post terminal" vertebrae. The Argentinidae have a single "post terminal" vertebrae and the other families have none. Undoubtedly, evolution has proceeded in the direction of fusion and reduction of caudal elements, thus, the Salmonidae could not be derived from any of the present families in the suborder and may be considered as the family retaining the most primitive features. A finding of Gosline pertinent to salmonoid classification is that the Salmonidae, Osmeridae, Plecoglossidae, Retropinnidae, Aplochitonidae, Galaxidae and Argentinidae all have the neural and haemal spines associated with the caudal region, expanded laterally, distinguishing them from all other groups. These expanded spines are absent in the neotenic family, Salangidae and <u>Lovettia seali</u>, a neotenic species in the family Aplochitonidae. Gosline arranged the suborder Salmonoidei to include three superfamilies: the Salmonoidae with the single family Salmonidae, the Argentinoidae, with the family Argentinidae as expanded by Hubbs (1953), and the Osmeroidae with six families. The Osmeroidae were considered to consist of a northern group of three families; Osmeridae, Plecoglossidae and Salangidae, and a southern group; the Galaxiidae, Aplochitonidae, and Retropinnidae. Figure 1 diagrams my hypothetical relationships of Salmonoidei. Table 1 summarizes the characters and pertinent data on the families. As can be noted the Salmonoidei are an extremely diverse group and, at present, systematic arrangements of most of the families are not based on sound evidence. The deep sea forms referred to the Argentinoidae, the Galaxiidae, Aplochitonidae and Retropinnidae are in acute need of further systematic study.

Fossil Evidence

The fossil record for salmonoid fishes is almost nonexistent and adds little to our knowledge. The earliest fossil reputed to be of salmonoid relationship is the Eocene-Miocene genus Thaumaturus Ruess. Jordan (1923) included this fossil genus under Salmonidae. Voight (1934) defined and described the family Thaumaturidae. He believed they were salmonoid fishes. Berg (1940) considered Thaumaturidae with the Salmonoidei. Weitzman (1960), however, surveyed the osteological evidence and suggested Thaumaturus has its relationships with the haplomous group (Esocoidei). Gosline (1960) stated that Thaumaturus lacks the expanded neural and haemal spines in the caudal region, characteristic of Salmonoidei. Gosline also believed Thaumaturus is more indicative of haplomous than of salmonoid fishes.

Origin of Salmonoidei

Because of the absence of a detailed fossil record, one may only indulge in speculation, based on a study of comparative characters, for an estimation of antiquity of the origin of the salmonoid line. Opinions vary greatly on the relative time of origin of Salmonoidei. Berg (1940) places their origin in the Lower Eocene. Gunther (1866) and Jordan and Evermann (1896:460) believed the family Salmonidae was of recent origin because the instability of the species suggested they were still in the early stages of their evolutionary process. Gregory (1933:155) also concluded that: ". . . the Salmonidae are a modern offshoot of the old clupeid-elopid stock, which runs back through the leptolepids into early Mesozoic times." On the other hand, Garstang (1931) believed the salmonoid group to be the most primitive teleosts. He based this assumption mainly on his belief that the salmonoid adipose fin is homologous to the second dorsal fin of crossopterygian and elasmobranch fishes of the Devonian. Besides the adipose fin, salmonoid fishes share other traits found in pre teleostean fishes. As discussed previously, the Salmonidae retain a primitive caudal skeleton. The intestine, especially of Salmonidae, has a spiral valve-like arrangement. The spiral valve in salmonoids, however, may not be truly homologous to the spiral valve of pre teleosts. (Cohen, 1958, presented a brief review of the salmonoid spiral valve). Also, true abdominal pores are present in salmonoids as they are in pre teleost fishes and elasmobranchs. Weber (1886) cleared up many errors in the literature and gave an excellent review of abdominal pores. Little attention has been given to this character since then. The absence of oviducts in salmonoid fishes is probably a primitive feature but it may be specialized. There is still much confusion in the literature on salmonoid oviducts. Kendall (1921, 1922) described functional oviducts, formed from the ventral mesentary in salmonids. Many authors such as Berg (1940) still quote Kendall's work. Percival (1937) studying spawning in Salmo trutta wrote: "The question arises as to the meaning of the membranes which form the alleged oviducal groove. They may be simply regarded as extensions of the mesovarium which have established a connexion with the posterior mesentery. When the posterior mesentery has separated from the mid-dorsal line it has carried downwards the associated mesovaria, and the groove so formed is clearly the mechanical result of a growth process and has nothing immediately to do with oviposition. . . On the so-called oviducts of Kendall--whatever may be their function in other species of Salmonidae, they clearly play no significant part as oviducts in Salmo trutta." Vladykov (1956) stated there were no oviducts in Salvelinus and Yamamoto (1955) found a similar lack of oviducts in Oncorhynchus. I have personally observed ripe ova in the coelom of Salmo; no membrane surrounds it.

Although the lack of oviducts and the presence of a spiral valve-like intestine are suggestive of primitive ancestors these characters may be specialized. The adipose fin, abdominal pores and the caudal skeleton, however, make a strong case for the great antiquity of salmonoids and negate the view that salmonids or salmonoids could have been relatively recently derived from the clupeid phyletic line. Freihofer (1963) compared the patterns of facial nerve innervation and attributed the most primitive type to salmonids.

The earliest known teleost fossils, abundant in Cretaceous deposits, is the extinct genus, Leptolepis. Leptolepis has affinities to the present Elops-Albula group (Gregory, 1933), and sometimes is considered in the suborder Albuloidei of the order Clupeiformes. There is no trace of an adipose fin in leptolepid fossils. If the adipose fin is considered a primitive character--a relict from a pre-teleostean ancestor--then a salmonoid ancestral type was already separated from the leptolepid stock in the Cretaceous.

Elops is often considered the most primitive of living teleosts. They retain a gular plate and parasphenoid teeth, similar to their pre-teleostean ancestors. No known salmonoids have a gular plate or parasphenoid teeth.

Probably, the ancestral salmonoid had both of these characters but they were lost prior to the radiation of the group. In the Salmonoidei teeth may be found on all other primitive tooth bearing bones except the parasphenoid.

FAMILY SALMONIDAE

Linnaeus (1758:308-312), following the classification of Peter Artedi, described the present species of Salmonidae either as *Coregonus* or *Salmo*. Included under the *Salmo* of Linnaeus, however, were also species now placed in different families and orders. The first use of the name Salmonidae, according to Gill (1894) was by Bonaparte in 1832. Since then there has been considerable diversity of opinions on the number of subfamilies, genera and species included in Salmonidae. Gunther's (1866) interpretation of Salmonidae is similar to the present suborder Salmonoidei. Cope (1871) separated Coregonidae, the whitefishes, as a distinct family based on the fact that the parietal bones meet on the surface of the skull. Gill (1894) erroneously stated that the coregonids were like *Salmo* in the position of the parietal bones and that only *Thymallus* have the parietals joined. Gill declared that *Thymallus* was distinct from other salmonids in the possession of epipleural ribs. He created the family Thymallidae for the graylings and considered the whitefishes a subfamily, Coreginae, of Salmonidae. Gill also made a subfamily, Stenodontinae, for the Arctic whitefish genus *Stenodus*.

Boulenger (1895) corrected Gill's error on the condition of the parietals in coregonine fishes and claimed that coregonine and salmonine species do have epipleural ribs like *Thymallus*. He concluded there was no valid reason for separating *Coregonus* or *Thymallus* from Salmonidae. Actually, *Thymallus* is distinct in having well developed epipleural ribs. Norden (1959) found no epipleural ribs in any of the species of coregonines he examined and five of fourteen *Salvelinus fontinalis* (Mitchill) had some epipleural ribs among the salmonines. I have not observed epipleural ribs in *Salmo*. Jordan and Evermann (1896) followed Gill and recognized Thymallidae. Regan (1914), however, agreed with Boulenger and arranged the Salmonidae to include two subfamilies; Salmoninae for the trouts and Coregoninae for the whitefishes and graylings. Jordan (1923) recognized Salmonidae, Coregonidae and Thymallidae but added that it might be more correct to consider them as a single family. Berg (1940, 1948a) distinguished the family Thymallidae mainly on the basis of the absence of the orbitosphenoid bone in the skull. He treated the Salmonidae as two subfamilies, Salmonini for the trouts and Coregonini for whitefishes. The ending ini for subfamilies was defended by Berg (1932) on the basis of grammatical rectitude. Gosline (1949) cited the reasons why the traditional inae subfamiliar endings should stand.

Norden (1959) presented the most detailed and comprehensive comparative osteological study of the trouts, whitefishes and graylings and arranged the Salmonidae in three subfamilies, Salmoninae, Coregoninae and Thymallinae, a decision with which I concur.

In considering the suborder Salmonoidei as summarized in table 1, some fundamental characters link the trouts, whitefishes and graylings together as a natural group and set them apart from the other salmonoid families. The Salmonidae is the only family with the complete primitive caudal skeleton, i.e. two post terminal centra and the associated elements. No salmonid species has teeth on the mesopterygoid bone. Dentition on this bone is found among the other families. Salmonidae have a well developed pelvic appendage, a fleshy lobe from the body adjoining the first pelvic fin ray. This character has not been mentioned from other salmonoid families. I found a tiny scale-like pelvic appendage in Plecoglossus but no other representative salmonoid which I examined have a trace of a pelvic appendage. A critical analysis of salmonoid systematics convinces me that the most natural phyletic arrangement is attained by considering the Salmonidae to consist of three subfamilies.

Distinctions of the Subfamilies

Table 2 summarizes the differentiating characters of the subfamilies. Norden (1959, table 5) lists more characters, some of which I consider unimportant or in error. A distinctive character of Thymallinae which immediately separates them from other salmonids is that the scales on the body continue onto the caudal rays. These caudal or alar scales are important characters for certain clupeid species (Svetovidov, 1964). Norden (1959) and other authors failed to mention this character.

Berg (1940) and Norden (1959) both state that Salmoninae lack a dermosphenotic bone which is present in the whitefishes and graylings. Norden illustrates skulls of Coregonus artedi, Thymallus arcticus and Salvelinus fontinalis, showing what Norden terms three postorbital bones plus a dermosphenotic in ~~the~~ Coregonus and Thymallus while Salvelinus as representative of Salmoninae has only three post orbitals. The problem is: what constitutes a dermosphenotic? Harrington (1955:285) presented a review of the synonymy of the dermosphenotic and mentioned the apparent contradiction in Berg's (1940) statement that Salmonines lack a dermosphenotic while Gregory (1933, fig. 45) illustrates a Salmo with a dermosphenotic. Norden (1959:688) defines the dermosphenotic as: "the pair of small dermal postorbital bones which bear triradiate sensory canals. They are absent in the Salmoninae." There has been considerable variation in the terms used to describe the orbital series of bones in fishes. Weitzman (1962:28) reviews the nomenclature of the orbital series. The dermosphenotic designates the last bone in the orbital series, dorsally and posteriorly. On this bone the infraorbital sensory canal communicates anteriorly with the supraorbital canal and posteriorly with the lateral canal from the pterotic bone.

The confusion on the presence or absence of a dermosphenotic in Salmoninae is due to the fact that individual variation occurs in the number of infraorbital bones and the structure of the infraorbital canal and its branches. Examination of a series of stained heads of representative salmonids revealed a tendency for coregonines and thymallinines to have one more infraorbital bone than the salmonines. Often in the uppermost posterior infraorbital in salmonines the infraorbital canal does not branch on the bone but above it. When comparing such material, the impression is conveyed that the last infraorbital bone with the typically branched sensory canals (dermosphenotic) is absent in Salmoninae. This is not true. In a series of cleared and stained heads of Lahontan cutthroat trout, *Salmo clarkii henshawi* Gill and Jordan, I found the following variations. Four had 4 postorbital bones (as defined by Norden, 1959:690) and three had 3. Six had the sensory canal on the last postorbital ("dermosphenotic") branched (triradiate) and one was unbranched. Surveying other *Salmo* skulls (*clarkii*, *gairdnerii*, *trutta*, *aguab~~m~~onita*), the ratio of four versus three postorbitals and branched versus unbranched sensory canals was noted to display variation. One specimen of cutthroat trout has three postorbitals with the canal branched on the right side while the left side has four postorbitals with an unbranched canal on the "dermosphenotic." It was probably on salmonine specimens with three postorbital and an unbranched canal that led Berg (1940) and Norden (1959) to state Salmonines lack a dermosphenotic. My sample of *S. c. henshawi* from a single population has both the "Coregoninae" and "Salmoninae" condition as depicted by Norden not only among individuals but also in a single specimen. Ridewood (1904) described the individual variations found in the orbital bones and cautioned on the dangers inherent for their use in taxonomy.

Fossil Salmonidae

Until recently, fossils reliably referable to Salmonidae have been known only from Pleistocene and Upper Pliocene deposits. *Rhabdifaris lacustris* was described by Cope (1870) from Idaho. Uyeno and Miller (1963) examined the type and other material and synonymized *Rhabdifario* with *Salmo*. Because *Salmo lacustris* Linn. has priority, Uyeno and Miller renamed *Rhabdifario lacustris* as *Salmo copei*. They date this fossil in the Upper Pliocene or Lower Pleistocene. They also mention mid Pliocene salmonid fossils from Jefferson County, Oregon. Uyeno elaborated further on salmonid fossils in an unpublished paper he presented at the 1963 annual meeting of the American Society of Ichthyologists and Herpetologists. In an abstract, Uyeno made the following statement on salmonid fossils: "The earliest known materials are of early

Pliocene age from Gateway and Juntura, Oregon, and west central Nevada. The specimen from Gateway is of enormous size and probably represents a distinct genus, being remarkable in the possession of a strong keel of the parasphenoid, large teeth, and a broad jaw. The fossils from Juntura and west central Nevada consist of pieces of tooth-bearing bones and are too fragmentary to support any speculations on their systematic status. Specimens of Rhabdofario lacustris Cope from Late Pliocene to Early Pleistocene beds of Idaho and Oregon were discovered in considerable number and the genus is indistinguishable from the genus Salmo."

Mr. Camm Swift, a graduate student in ichthyology at the University of Michigan examined the fossil dentaries of the Gateway, Oregon material and wrote me that they dwarf those taken from a 40 pound king salmon, Oncorhynchus tshawytscha (Walbaum).

Vladimirov (1946) named Salmo derzhavini from reputed Pliocene deposits in Armenia. Berg (1948b) stated that this fossil cannot be positively placed with Salmo.

La Rivers (1964) described Salmo cyniclope based on fossil fragments from Pershing County, Nevada. He dates his find as Middle or Upper Miocene. If this dating is correct, La River's fossils are the oldest known salmonid material. La Rivers has fragments of several specimens representing a wide size range. His type specimen material is from a fish of about 20 inches. He states that the jaw is more massive in Salmo cyniclope than in present Salmo, but believed there are no generic differences.

I have examined vertebrae centra and a fragment of a toothed dentary bone, given to me by Dave Webb, a graduate student in Paleontology on the Berkeley campus. This material was collected south of Walker Lake, Nevada and Webb felt confident it was from an Upper Miocene deposit. Besides myself, I had the material examined by Mr. W. I. Follett, curator of fishes at the California Academy of Sciences, and Dr. Stanley Weitzman, now at the U.S. National Museum. We all agreed that the material was from a salmonid. The dentary fragment is larger than any comparative material I have seen from Salmo or Oncorhynchus. If the rest of the specimen possessing this dentary was comparable to present day Salmo or Oncorhynchus, I would estimate it would have been 40 to 50 pounds or more in size.

If the upsurge in interest in salmonid fossils continues and more material is uncovered we may soon have some data on the ancestral forms in the ~~sub~~family and an estimate of when the subfamilies diverged.

Marine or Freshwater Origin

Concerning the question of a marine or freshwater origin of Salmonidae, plausible arguments can be advanced for both sides. Tchernavin (1939) reviewed the positions of various authors and presented his own case, concluding that the salmonids are of freshwater origin, mainly on the basis that all species must reproduce in freshwater.

The argument will never be firmly decided because, when considering hypothetical ancestral forms and arbitrary limits of the family an obscure area is reached for which we lack factual evidence. On the basis of the eggs and larval stages and considering the ecologies and distribution of the present Salmonidae it is reasonable to assume that the immediate ancestors of the present groups were primarily freshwater species. The large egg size and advanced larval stage at hatching, characteristic of the subfamily Salmoninae, is an adaptation for the harsh environment typical of cold, running waters (Svardson, 1949). Orton (1955) stated that the salmonid larval form is a secondary adaptation from the primitive isospondylous marine larval type. When considering the suborder Salmonoidei, the complete spectrum of ichthyological life cycles is encountered; marine, freshwater, anadromous and catadromous. The Argentinidae is the only completely marine salmonoid family. Certainly there must have been a marine or at least a euryhaline influence in the phyletic line leading to Salmonidae. Evidently, in salmonoid species, adaptation of eggs and larvae to environments of varying salinity may come about relatively rapidly without major genetic changes producing radical divergence in the adult form. For example, in the smelts, Osmeridae, a single genus, Hypomesus has a completely marine species, H. pretiosus (Girard); a completely freshwater species, H. olidus (Pallas); and freshwater or euryhaline species, H. transpacificus McAllister (M'Allister, 1963). The pink salmon Oncorhynchus gorbuscha (Walbaum) is known to successfully reproduce in intertidal zones in waters of intermittent high salinity (Hanavan and Skud, 1954). Berg (1948b) cited reports that some races of a typical freshwater whitefish, Coregonus autumnalis (Pallas), probably spawns in brackish water in certain areas.

SUBFAMILY SALMONINAE

My arrangement of this subfamily consists of six genera; Salmo, Salvelinus, Oncorhynchus, Hucho, Brachymystax, and Salmothymus.

GENUS SALMO LINNAEUS

Salmo Linnaeus, Syst. Nat., ed. 10, 1758:308 (type: S. salar).

Fario Valenciennes in Cuvier and Valenciennes, Hist, Nat. des Poissons; 21, 1848:277.

Salar Valenciennes, loc. cit., 314.

Trutta Siebold, Susswasserfische von Mitteleuropa, 1863:292.

The genus Salmo consists of species which are often referred to as the "true" trouts. They are characterized by black spots on the body, a completely toothed vomer, relatively long head and jaws and moderately small scales.

The sporting qualities and beauty of the trouts has stimulated the imagination and pens of man since earliest times. Probably no other fish genus has had so much literature devoted to it. The species of *Salmo* exhibit the most diverse habitats of any salmonid genera. Within a single species (and subspecies, in my arrangement) anadromous, fluvialite, and lacustrine populations may be encountered.

As I interpret it, *Salmo* is not a sharply defined genus. There are many similarities with *Oncorhynchus* and *Salmothymus*. The limits of the genus and the number of species contained is still open to question and individual interpretation. The *Salmo* of Linnaeus included not only all the family Salmonidae, except the whitefishes, but also the smelts, Osmeridae; and the characins of the present suborder Characinoidei of the order Cypriniformes. Gunther (1866) treated Salmo to include two subgenera *Salmones* (= *Salmo*) and *Salvelini* (= *Salvelinus*). Gunther recognized 32 species of *Salmo* for Europe, almost all of these are now considered synonyms of *S. salar* or *S. trutta*. Siebold (1863) had *Salvelinus* and *Hucho* in the genus *Salmo*. His genus *Trutta* represented the genus *Salmo* as presently interpreted. Regan (1914, 1920) regarded *Salmothymus obtusirostris* as a subspecies of *Salmo salar*. Regan also stated his belief that all species of *Oncorhynchus* and the North American rainbow and cutthroat trouts represented but a single variable species. Despite Regan's inordinate lumping of *Salmo*, he recognized each local variation in British Char (*Salvelinus* *alpinus*) as a distinct species. In fairness, it should be noted that Gunther and Regan were deservedly recognized as outstanding ichthylogists. Their trouble with salmonid systematics was due to their belief in the stability of a species with limited variation from the type and an ignorance of a biological species concept. Most Scandanavian workers persist in regarding *Salvelinus* as a subgenus of *Salmo*. Norden (1959) thought *Salmothymus* should be considered a synonym of *Salmo*. It was common practice among former workers to divide *Salmo* into subgenera such as *Salmo*, *Salar*, *Trutta*, and *Fario*, based on the arrangement of vomerine teeth and anadromy. These divisions have proved to be useless and erroneous. Dr. V. D. Vladykov, of the University of Ottawa informed me that he plans to distinguish the North American rainbow and cutthroat trouts as a separate genus called *Parasalmo*. I disagree with his opinion because it promotes a degree of splitting misleading for a natural arrangement of the family.

My taxonomic arrangement of *Salmo* emphasizes four main phyletic lines, or species groups. These are the Atlantic salmon, *S. salar*; the European brown trout and its allies, *S. trutta*; and the less sharply differentiated North American rainbow and cutthroat trout series, *S. gairdnerii* and *S. clarkii*.

Distribution of the Genus

In the Eastern Hemisphere the genus is widespread throughout Europe with representatives of S. salar and S. trutta and allied species. The southern limit is the Atlas Mountains in Algeria and Morocco. Northward, they reach the Kara River, but not the Ob, in northern Russia. Various subspecies of trutta extend eastward to the Aral Sea and its tributaries. In the Western Hemisphere, S. salar occurs from northern New England to James Bay. The distribution in western North America extends from the Kuskokwim River, just south of the Yukon River in Alaska, to northern Mexico and eastward through the Rocky Mountains. Salmo is very sparsely represented in the Pacific drainages of the Far East. S. mykiss occurs sporadically from Kamchatka, south to the mouth of the Amur River.

The native range has been greatly extended. S. trutta and S. gairdnerii have been successfully introduced throughout the world and are now common in South America, Africa, Australia and New Zealand.

THE RAINBOW TROUT, SALMO GAIRDNERII RICHARDSON

Complete coverage of our present knowledge on the systematics of the rainbow, cutthroat and golden trouts can be found in Needham and Behnke's monograph on western North American Salmo, which is planned as a Publication in Zoology, University of California Press. The voluminous material will not be entirely duplicated here, but I shall present a summary of our findings and conclusions.

Despite the fact that I found the rainbow trout, at least when compared with the cutthroat species, to be relatively stable with limited variability, numerous species and subspecies were named. Jordan Evermann and Clark (1930) recognized 16 species and Miller (1950) listed 12 species and subspecies referable to the rainbow series. At the other extreme, Needham and Gard (1959) recognized only Salmo gairdnerii with no subspecies, for all of the rainbow trout and golden trout. Needham and Gard (1964), however, changed their opinion on the Mexican golden trout and named it as a new species, Salmo chrysogaster.

My own arrangement considers Salmo gairdnerii to consist of four subspecies. These subspecies, however, have much intergradation and overlap in their characters and do not form neat discrete units. There are (or were) some populations in desiccating basins of northern California and southern Oregon which are intermediate between the cutthroat and rainbow species. The golden trout, Salmo aquabonita Jordan, undoubtedly is closely related to the rainbow, but for reasons explained later, is considered a separate species.

Distribution

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

The original distribution of S. garidnerii, characterized by a lack of isolated, rel~~e~~ict interior populations, suggests the species as we know it, probably is of relatively recent origin and arrived on the scene in North America after the cutthroat species was established in the interior waters. Based on chromosome numbers and morphology, Simon and Dollar (1963) believed the rainbow was derived from the cutthroat.

Salmo mykiss of Kamchatka is closely related to S. gairdnerii. Table 3 lists the taxonomic characters of gairdnerii.

Salmo gairdnerii Richardson, The Coast Rainbow

Salmo gairdnerii Richardson, Fauna Bor. -Amer., 3:1836:221. Columbia River at Ft. Vancouver.

Salmo ~~I~~iridea Gibbons, Proc. Calif. Acad. Nat. Sc., 1; 1855:35. San Leandro Creek, Alameda Co., Calif.

Salmo rivularis Ayres, Proc. Calif. Acad. Nat. Sci., 1; 1855:42. Martinez, California

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

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

Salmo masoni Suckley, Pac.R.R. Surv., 12, pt. 2; 1860:345. Small tributaries of Columbia River.

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

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

Salmo nelsoni Evermann, Proc. Biol. Soc. Wash., 21; 1908:26. San Pedro Martir Mountains, Baja California.

Salmo irideus morpha *argentatus* Baijkov, Contr. Canad. Biol. and Fish., 3(16): 1927:387. Jasper Park, Canada.

The specific name *gairdnerii* is now generally accepted for the rainbow trout although many foreign authors continue to use *S. irideus* or sometimes *S. shasta*. Gunther (1866:118) thought Richardson's description of *S. gairdnerii* inadequate and stated: "The material on which this species has been founded was quite insufficient for that purpose, and the species for which this name has been intended is not likely ever to be recognized." Jordan changed his opinion many times on the specific name of rainbow trout and on the recognition of anadromous and non-anadromous forms of rainbow. In a statement that is not entirely clear, Jordan (1919) said:

> There has been much discussion as to whether the steelhead is a species really distinct from the rainbow trout, and on this question the writer has at different times held different opinions.
> My final judgment (1919) is this: The coastwise trout of California are the young of the species which in the sea and the large rivers is called the steelhead, *Salmo rivularis*; the original rainbow is therefore the young of *Salmo rivularis* or as we used to call it, wrongly I now believe, *Salmo gairdneri*, as *irideus* (misspelled iridia) is the oldest name it must stand."

I understand this to mean that Jordan recognized the coastal rainbow as a single entity, *Salmo irideus*. His "final judgment" of 1919 was altered when he (Jordan, 1923a) designated the steelhead as *Salmo rivularis* again, because he believed Richardson's description of *S. gairdnerii* was based on *Oncorhynchus nerka*. Jordan, Evermann, and Clark (1930) recognized *S. gairdnerii* and *S. irideus* as considered *S. rivularis* as synonym of *S. irideus*. Actually, Richardson's description of a specimen from the Columbia River with 11-12 branchiostegal rays, 64 vertebrae and 12 anal rays, readily distinguishes it from the species of *Oncorhynchus* and leaves little doubt that the type specimen of *gairdnerii* was indeed a rainbow trout.

The coastal rainbow has both anadromous (steelhead) and non-migratory populations in all major river systems throughout its range. Often the non-migratory populations are recognized as S. irideus or S. g. irideus. This is doubly objectionable. First, the non-migratory populations are not monophyletic, i.e., they have arisen from anadromous rainbows independently many times in many places. Every major river system has both forms, and unless barriers are present on tributary streams, isolation is not complete. Fish culture work has demonstrated that supposed non-migratory rainbows may turn into steelhead and steelhead have been used to establish landlocked populations. Shapovalov and Taft (1954) describe the situation in Waddell Creek, California, a small coastal stream which has a run of steelhead but some individuals complete their life cycle without going to sea. Also Waddell Creek has a section isolated by a barrier falls where a non-migratory population maintained itself. Although the basis for anadromous or non-migratory behavior is mainly genetic, the genetic difference must be slight and easily modified. The result is that no constant character can separate non-migratory from anadromous populations. Thus, whether one endorses a phyletic or purely practical concept of the subspecies, the taxonomic recognition of the two forms is not tenable. The second objection for using the name irideus for the non-migratory form is that Gibbons' description of "S. iridea" from San Leandro Creek, a small tributary of San Francisco Bay, was very probably based on a young, pre-seaward steelhead.

Taxonomic Characters

In discussing taxonomic characters of rainbow trout it is important to clarify the question concerning the typical number of scales found in coastal rainbows. Diagnostic criteria often list 180 scales as the upper limit for *S. g. gairdnerii*. I have never encountered a specimen of coastal rainbow which approaches this figure. My samples, from Baja, California to Alaska, typically have 120-140 scales in the lateral series.

The source of the belief that the coastal rainbow has up to 180 scales can be traced to the statements of Jordan and Evermann (1896:498) who give the variation as from 130 to 180, averaging 155. These counts were based on a sample collected at Astoria, Oregon, from the mouth of the Columbia River. A fine scaled race of anadromous rainbow may be native to the Columbia River as suggested by Schultz (1935). The values obtained by Jordan and Evermann may have been based on such a fine scaled population, or the high counts might be an artifact due to counting techniques. Another possible explanation is that the collection actually consisted of coastal cutthroat, *S. c. clarkii*, which typically average about 155 scales with an upper limit of approximately 180. In any event, I consider lateral series scale counts of more than 140 as unusual for coastal rainbow specimens.

Kendall (1921b) stated that the coastal rainbow and steelhead were coarse scaled trout, averaging about 130 scales in the lateral series. He was in error, however, in his remark that the steelhead have only 60 vertebrae. The vertebrae count of 58 for S. gairdnerii given by Jordan and Evermann (1896:498) should be considered erroneous. Typically, the coastal rainbow has 62-65 vertebrae, counting every ossified centrum. I have never examined a specimen of S. g. gairdnerii with as few as 58 vertebrae. Typically, S. gairdnerii, has more vertebrae than any other species of Salmo, although there is much overlap in vertebrae number with S. clarkii.

As demonstrated in Table 3, scale counts are the only constant characters distinguishing the subspecies of rainbow trout. The other meristic characters are quite similar except for lower vertebrae and caecal counts in the Kern River rainbow S. g. gilberti.

From other species of Salmo, S. gairdnerii may be distinguished from S. trutta and S. salar by gairdnerii's higher vertebrae number; spots on the dorsal, adipose and caudal fins; an absence of well developed posterior gill-rakers on the first arch; no red spots on the body at any stage of life; and a red band on the sides of the body, especially pronounced in mature specimens. From the cut-throat trout, gairdnerii typically has fewer scales and more vertebrae. The most absolute character is the presence of basibranchial teeth in S. clarkii; these are lacking in all other Salmo. I have found no osteological character which absolutely characterizes any species of Salmo. S. gairdnerii does tend to have a somewhat distinct ethmoid bone, more broad in its anterior end and more shallowly forked posteriorly than the ethmoid of other species of Salmo.

Kamloops Trout, Salmo gairdnerii kamloops (Jordan)

Oncorhynchus kamloops Jordan, Forest and Stream, 39(12); 1892:405. Kamloops L., B.C.

Salmo kamloops whitehousei Dymond, Contrb. Canad. Biol. Fish., 6(16):391. Selkirk Mtns., B.C.

Jordan (1892a) described Oncorhynchus kamloops from Kamloops Lake, British Columbia. He thought it was a landlocked salmon with close affinities to the king salmon, O. tshawytscha. He immediately changed his mind and sent off the same description but substituting the word trout for salmon and Salmo for Oncorhynchus (Jordan, 1982b). Jordan and Evermann (1896:499) relegated kamloops to subspecific status under S. gairdnerii. Jordan, Evermann, and Clark (1930) considered kamloops synonymous with gairdnerii.

Dymond (1928, 1932, 1947) gave kamloops full species status and described a subspecies of it, S. kamloops whitehousei (Dymond, 1931). Mottley (1934b, 1936, 1937) demonstrated that the number of scales and vertebrae in trout can be influenced by environmental conditions and concluded that all the rainbow trout of British Columbia were of a single species, S. gairdnerii. Neave (1943) demonstrated a genetic difference in the number of scales of Kamloops trout. He raised Kamloops trout and Cowichan River steelhead under identical conditions and found the Kamloops had a mean value of 142.6 scales in the lateral series and the steelhead 131.5.

Opinions have varied on the taxonomic recognition of the Kamloops rainbow trout. My own work, as discussed in Needham and Behnke's manuscript, revealed that a rainbow trout typically possessing 10 to 20 more scales than the coastal rainbow is (or was) widespread throughout the Fraser and Columbia river systems. Some populations have bright coloration and slight cutthroat marks. There appears to be complete intergradation with the coastal rainbow and the Kamloops do not form a sharply defined group. I believe, however, that recognition should be given to such a widespread group which probably had its origin during the late Pleistocene in large glacial lakes associated with the present Columbia and Fraser river systems. It is possible that the original Kamloops trout was influenced by hybridization with cutthroat trout during isolation from coastal waters in the Pleistocene. After free access to the sea was established, the Kamloops may have thoroughly interbred with invading coastal rainbows, resulting in the intergradation found today.

Kootenay Lake

Examples of incipient intralacustrine speciation of salmonids are found in Kootenay Lake, British Columbia. Kootenay Lake is a narrow body of water about 50 miles in length in the upper Columbia River drainage. Vernon (1957) found the kokanee salmon, *Oncorhynchus nerka*, consisted of three races in Kootenay Lake. These races were separated by spatial isolation during spawning. Cartwright (1961) studied the Kamloops trout in Kootenay Lake, and claimed there were two races, differing in their growth rate, age of spawning and spawning areas. In a letter of January, 1964, Cartwright wrote me that offspring of the two "races" are being reared under identical conditions and real genetic differences are apparent. Intralacustrine speciation is discussed in more detail in a later section.

The Shasta Rainbow, *Salmo gairdnerii stonei* Jordan

Salmo irideus stonei Jordan, Thirteenth Biennial Rept. Calif. Fish. Comm., 1894:142. McCloud River, Calif.

Salmo gairdnerii shasta Jordan, *ibid*:142. McCloud River.

Salmo aquilarum Snyder, Bull. U.S. Bur. Fish. 35; 1917:35. Eagle Lake, Calif.

In the 1880's the Fish Culturist, Livingston Stone, of the U.S. Fish Commission, was active on the McCloud River, California, taking eggs of salmon and trout for artificial propagation. He was confused by two forms of trout, one with fine scales he obtained from small tributary streams, the other, a large fish (5-10 lbs.) he found in the main stream. Undoubtedly, the large trout associated with the main river were steelhead (Needham and Behnke, 1962). Stone observed that the eggs and sperm of both types were indiscriminately mixed; and so the original hatchery rainbow was created born. Stone sent specimens and queries to Jordan about these McCloud River trout. Jordan (1883) said the trout of the upper Sacramento basin were all one species (*Salmo irideus*); the differences noted by Stone attributable to environmental phenomena. Jordan (1894) reversed himself and described two new subspecies based on Stone's specimens from the McCloud River. *Salmo irideus stonei* and *S. gairdnerii shasta* were based on the fine scaled non-migratory rainbow from tributaries of the McCloud. The original description and the type material at Stanford University indicates no valid differences between *stonei* and *shasta* (Needham and Behnke, 1962). The name *stonei* has ~~page~~ priority over *shasta*. Jordan (1905, 1925) said that *shasta* was the McCloud River trout and *stonei* was found in the Klamath River. He did not elaborate on this opinion which ignored the fact that the type locality of *stonei* is the McCloud. Pure populations of the native non-migratory trout of the upper Sacramento River area are now virtually extinct, due to indiscriminate stocking of exotics policies. Examination of museum specimens and two recent

and hatchery rainbows

collections made by Mr. Joe Wales, formerly with the California Fish and Game Department, and analysis of the literature, demonstrates that there was once a widespread occurrence in the Upper Sacramento system of a fine-scaled rainbow trout with some cutthroat-like characters. Variability is great between samples I have examined. Some appear to be typically cutthroat with a long head and jaw, 9 pelvic rays, large, distinct spots, but lacking basibranchial teeth. Often gaudy golden coloration and a well developed cutthroat mark is present. Scale counts typically range from 140-170. The unusual appearance of these trout has confused other investigators besides Livingston Stone. Jordan and Henshaw (1878) identified the trout of the McCloud River with the cutthroat from Lake Tahoe. Snyder (1908) described specimens from the Pit River and Burney Creek as S clarkii cutthroats. Wales (1939) believed a population he found in a small tributary of the McCloud were golden trout, S. aquabonita.

There appears to be a strong cutthroat influence in extreme forms of stonei. I believe that interior cutthroats and coastal rainbows hybridized when the upper Sacramento system tapped the present desiccating Goose Lake basin, to the north. The native trout of Goose Lake basin and Fort Rock basin in southern Oregon were described as cutthroats, S. clarkii, by Snyder (1908), but they are intermediate between gairdnerii and clarkii and cannot be authoratatively placed with either species. The material is limited, but there is a strong indication that a transitional series from rainbow to cutthroat once occurred from the upper Sacramento drainage (stonei) into the Oregon basins. These forms will be discussed further later in this paper.

The Eagle Lake Trout

Eagle Lake, Lassen County, California is a desiccating basin which was once part of the Lahontan system. The minnow and sucker species are typical Lahontan fauna but the native trout is a an emigrant rainbow and not a Lahontan cutthroat. Snyder (1917) named Salmo aquilarum on specimens from Eagle Lake. Hubbs and Miller (1948:38) believed the Eagle Lake trout had its origin from hybridization between Lahontan cutthroat and introduced rainbow. Miller (1950:6) thought this conclusion may be in error and left the status of aquilarum open. Needham and Gard (1959) didn't believe the Eagle Lake trout deserved recognition even as a subspecies.

There is no evidence from the characters of the Eagle Lake trout to indicate a rainbow-cutthroat hybrid origin. My opinion, stated more completely in the Needham and Behnke manuscript, is that the Eagle Lake trout was derived from headwater stream transfer from the Pit River system and could be considered a synonym of stonei. The few authentic specimens available of aquilarum have slightly lower scale counts (135-155) than the typical stonei.

Kern River Rainbow, Salmo gairdnerii gilberti Jordan

Salmo gairdnerii gilberti Jordan, Thirteenth Biennial Rept. Calif. Fish Comm., 1894:143. Kern River, Calif.

Salmo whitei Evermann, Bull. U.S. Bur. Fish., 25; 1906:20. Tributaries of Kern River.

Salmo rosei Jordan and McGregor, Proc. Acad. Nat. Sci. Phila., 76; 1924:19. Lake Culver.

Five species and subspecies of trout were named from the Kern River drainage. These were based on the Kern River rainbow, the golden trout, S. aquabonita, and intergrades between these two forms. My contention is that the distinctive characters, such as bright coloration, low vertebrae and caecal counts and high scale counts found in gilberti are due to hybridization of a coastal rainbow form with the California golden trout and subsequent isolation of the Kern River from the San Joaquin system.

In 116 specimens of Kern River rainbows representing 9 samples, I found considerable variation in spotting pattern and scale counts. Vertebrae numbers are the lowest of the rainbow series, 59-63 with mean values of 60.1 to 61.5. Pyloric caeca numbers are also the lowest reported for rainbow trout, mean values ranged from 28.8 to 39.8. The lateral series scale counts ranged from 128 to 182 with means of 141.0 to 159.0. All of these above mentioned characters are intermediate between S. aquabonita and S. g. gairdnerii. Although the genotype of the trout of the main Kern has been altered by hatchery introductions, S. aquabonita can still enter the population by migration downstream from the South Fork of the Kern and from Golden Trout Creek. "Salmo whitei" which I consider a synonym of gilberti because its meristic characters are similar to gilberti, consists of disjunct populations of golden colored trout. S. whitei is considered by most workers with the golden trout S. aquabonita, but no one heretofore has bothered to undertake critical analysis of their characters. Salmo rosei was named by Jordan and McGregor from Culver Lake. Dill and Shapavalov (1954) made rosei a synonym of gilberti when they discovered the fact that Culver Lake was originally a barren lake and was stocked with trout from the Big Arroyo, tributary to the Kern River. Evermann (1906) listed a stocking record showing the Big Arroyo had been stocked with trout from the Little Kern where "white" is native. Thus, if one recognizes whitei, then rosei should be considered a synonym of it. In Jordan and McGregor's original description of rosei they claim it to be a form of golden trout.

Before introductions by man, the Kern River rainbow probably was the most distinctive group in the rainbow series. Hubbs and Miller (1948:71) discussed how the Kern has been isolated for a long period from the San Joaquin system by an alluvial fan. Thus, gilberti could only intergrade with *aquabonita*. Table 4 lists the meristic characters of *S. g. gilberti*.

Lahontan Basin Rainbows, Salmo regalis Snyder and Salmo smaragdus Snyder

Snyder (1912) described the royal silver trout from Lake Tahoe. He also (1917) named the emerald trout, *Salmo smaragdus*, from Pyramid Lake. Both Lake Tahoe and Pyramid Lake are in the Truckee River drainage of the Lahontan basin where the cutthroat is the native trout. Jordan (1925) was impressed by the apparent distinctness of *regalis* and *smaragdus* and wrote that in North America there are three series of trouts; the rainbows, the cutthroats and the "silvers." Jordan, Evermann, and Clark (1930) separated *regalis*, but not *smaragdus* from all other rainbow and cutthroat trout by placing *regalis* in the subgenus *Salmo* with *S. salar* and *S. mykiss*. The other North American *Salmo* were put in the subgenus *Trutta*.

Hubbs and Miller (1948) cited the occurrence of the "lacustrine adapted *S. regalis*" as evidence for the great age of Lake Tahoe. Hutchinson (1937) in discussing the age of Pyramid Lake cited the occurrence of *smaragdus* as a lacustrine relict. In my Master Degree thesis on Great Basin trout, and in the manuscript of Needham and Behnke, I expressed a strong suspicion that *regalis* and *smaragdus* were not valid species but the result of introductions by man. The reasons for this opinion were based on the fact that these trout were described long after rainbows were stocked in Lake Tahoe and Pyramid Lake and that the distinctive character of the "silver" trout was identical to the transformation or smolt stage that young steelhead and other anadromous salmonids undergo before they migrate to sea (see later section on the physiology of anadromy). I have often noted this silvery smolt-like stage in many populations of landlocked rainbows. Also, if a species derived from the rainbow was native to the Lahontan basin, it would be expected to be found in other waters besides Lake Tahoe and Pyramid Lake.

I examined all of the type material of S. regalis (two at Stanford University, two at the U.S. National Museum). I found these specimens had higher than expected scale counts for rainbows (144-153). I also noted that three of the four type specimens had evidence of basibranchial teeth. These characters suggested that regalis had its origin from the deliberate hybridization of rainbows and cutthroats carried on at the Lake Tahoe hatchery from 1905-1910 (Miller and Alcorn 1945). The type specimen of smaragdus and subsequent specimens of the "silver" trout, have the meristic characters of a typical coastal rainbow. In the original Needham and Behnke manuscript I made the statement that it would be interesting to observe introduced trout of known origin taken from Tahoe. In July, 1964, Mr. Almo Cordone of the California Fish and Game Department, in charge of Lake Tahoe trout investigations, provided such an opportunity. He sent me 34 specimens of Tahoe "silver" trout taken in gillnets from the lake. Most of these trout appeared strikingly identical to the type material of *regalis*, with dark dorsal regions, bright silvery sides, and a lack of distinct spots. Twelve of these specimens had fins clipped and originated from Diamond Lake, Oregon or Williams Lake, Idaho.

It cannot be proved beyond reasonable doubt that *regalis* and *smaragdus* were not true endemics, but the evidence convinces me that these "species" did not occur in Lake Tahoe and Pyramid Lake before the era of fish cultural activities. La Rivers (1962) was similarly inclined on this matter and expressed his belief that *regalis* and *smaragdus* were not "pre-Caucasian" relicts.

THE CUTTHROAT TROUT *SALMO* *CLARKII* RICHARDSON

The cutthroat species is comprised of two well defined groups. The coastal subspecies is relatively homogeneous and uniform in its characters, but the interior cutthroat are made up of an array of forms which almost defy a logical systematic arrangement. Simon (1964, unpub.) found the diploid chromosome number in the coastal cutthroat to be 70 and these chromosomes have a distinctive morphology. He counted 64 chromosomes in samples of the interior cutthroat, *S*. *c*. *lewisi* and *S*. *c*. *henshawi*. On chromosomal evidence alone, it could be argued that the coastal and interior cutthroat should be considered as two separate species. I believe, however, that subspecific ranking is more correct. Schultz (1935) claimed the coastal and interior forms intergraded east of the Cascade Mountains in the Columbia River system.

The interior cutthroat has been virtually exterminated throughout most of its native range by man's use and misuse of water, and by the introductions of other trouts, especially rainbow, which readily hybridize with the native cutthroat.

Jordan, Evermann and Clark (1930) listed 16 species and Miller (1950) had 12 species or subspecies of cutthroat trout. The Needham and Behnke manuscript recognizes a single species with six subspecies and the possibility that more will be recognized in the future.

The Coastal Cutthroat, Salmo clarkii clarkii

Salmo clarkii Richardson, Fauna Bor. - Amer., 3; 1836:221. Katpootl R. (now N. Fork Lewis River, Washington).

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

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

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

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

The coastal cutthroat occurs from the Eel River, California, to Prince William Sound, Alaska. Throughout its range it has both resident and anadromous populations. Anadromy is not as strongly developed in the sea-run cutthroat as in the steelhead rainbow. Evidently the anadromous cutthroat does not migrate much beyond the bays and estuaries. There are no records of cutthroat from the open ocean. The average period spent in salt water by the cutthroat is only a few months, and many individuals in coastal streams complete their life cycle in freshwater (Sumner, 1962). Rounsefell (1958) rated the cutthroat low on his scale of anadromy.

Table 5 compares the meristic characters of the subspecies of cutthroat trout. The coastal cutthroat is the most heavily spotted of all trouts; often spots occur on the lower fins and or the abdomen. The gillrakers of the coastal cutthroat are short and stubby in comparison with the gillrakers of rainbow and interior cutthroat trout. The posterior region of the first gill arch lacks gillrakers and in this character the coastal cutthroat resembles the rainbow. The interior cutthroats have well developed posterior gillrakers.

The most fascinating aspect of the systematics of rainbow and cutthroat trouts is the fact that they occur sympatrically in coastal waters from California to Alaska, but rainbows introduced into interior waters where only the cutthroat is native almost always produce a hybrid swarm. Based on ~~a~~ comparison of characters, the rainbow is more similar to the coastal cutthroat than to the interior forms. Hartman (1958, unpub.) made reciprocal crosses between coastal cutthroats and Kamloops rainbow and found no loss in fertility through two generations. The coastal cutthroat has ten more chromosomes than the rainbow but the genetic material must be similar enough for normal pairing at meiosis. I have examined samples from Luck Lake, Alaska and Quinsam Lake, B.C., which I believe contained rainbow-cutthroat hybrid. It could be noted, however, that only a small proportion of the sample could be regarded as hybrids and both parent species could be readily distinguished. This is in contrast to the hybrid swarms produced in interior waters and indicates the hybrids are selected against. I believe the coastal cutthroat and rainbow are able to maintain their identity due to ecological factors and not genetic incompatibility. The cutthroat seeks the smaller, colder streams than the rainbow, especially for spawning. Idyll (1942) found the cutthroat considerably more piscivorous than the rainbow. The cutthroat and rainbow species utilize the "trout niche" in such a way that hybrids are at a disadvantage. In interior waters, where the cutthroat evolved without competition from other trout or salmon, there was no such selection for ecological specialization allowing coexistance with the rainbow species.

Interior Cutthroat Trout

Typically, the cutthroat found in the interior waters of North America are more highly colored and more sparsely spotted than the coastal cutthroats. The interior waters considered here include the upper Missouri, Colorado, and Rio Grande river systems; the South Sasketchewan drainage; the Great Basin, as defined by Hubbs and Miller (1948), and the middle and upper Columbia River basin. The changing climate and geological history of these areas alternately formed and desiccated large lakes, coalesced and isolated various drainage basins, and formed barrier falls on many rivers. The consequences of such a history provided many opportunities for fish speciation. The endemic minnows and suckers of the interior waters, however, have attained a much higher degree of differentiation than the trout. To explain this, it may be assumed that the trout invaded the interior waters at a much later date than the minnows and suckers. The trout's proclivity for the colder headwaters, where stream transfer between drainage basins is more probable, has hindered the formation of discrete species and subspecies. The morphology and physiology of trout may also play an important role in their lack of pronounced speciation in interior waters. The fact that they are able to inhabit a wide range of waters, such as small mountain brooks, large streams and lakes, and utilize a broad spectrum of foods, allows adaptations to new environments without major genetic changes.

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

Jordan, Evermann, and Clark (1930) recognized eleven species of interior cutthroat. Miller (1950), following other authors, provisionally considered the interior cutthroats to contain ten subspecies. It is my opinion that all the native, interior trout north of the Little Colorado River belong to a single species, <u>Salmo clarkii</u>. The recognition of subspecies presents many problems. Not only is there great variation, but this variation may be as great within a drainage basin as it is between two separate basins. In the Lahontan basin I found the native trout of the Humboldt River system distinct from the other ~~rest of~~ Lahontan trout and ~~Needham and Behnke described~~ the Humboldt trout was described as a new subspecies in the Needham and Behnke ~~our~~ manuscript. Throughout most of the interior waters, however, from the Columbia River to the Colorado and Rio Grande no character was found which could distinguish the various samples and all were included in a single subspecies, S. c. lewisi.

The interior cutthroats may be grouped into three general types. These are the Lahontan, S. c. henshawi; the Yellowstone or black-spotted trout, S. c. lewisi; and the greenback, S. c. stomias. The Lahontan cutthroat is native to the Lahontan basin of Nevada and California. It is recognized by its more numerous gillrakers and the large, evenly distributed spots on the side of the body. The Humboldt River system in the Lahontan basin and the Alvord desiccating basin in southeast Oregon have some interesting populations which are somewhat intermediate between S. c. henshawi and S. c. lewisi. The Piute trout, S. c. seleniris is a Lahontan trout isolated above a falls. The Piute trout differs from other Lahontan cutthroats only by its lack of spots on the body. The greenback trout, S. c. stomias, of the Arkansas and Platte rivers in the state of Colorado, is distinguished by its large spots and fine scalation. The Yellowstone trout, S. c. lewisi, is considered a polytypic subspecies. ~~We~~ I extend the traditional range of S. c. lewisi to include the cutthroat of the Colorado, Rio Grande and Bonneville basins. The variation in color, spotting and number of scales is great but intergradations between extremes appears to be complete.

The Yellowstone or Black-Spotted Trout, Salmo clarkii lewisi

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

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

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

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

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

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

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

The precise range of *S. c. lewisi* has never been defined. Generally, the upper Missouri system in Montana and Wyoming, the South Sasketchewan drainage in Alberta, Canada, and the middle and upper Columbia basin, including the Snake River, have been accepted as the range of *S. c. lewisi*. There is great variation in spotting, coloration and number of scales in the native trout of these areas. Because this range of variation encompasses the endemic cutthroat of the Colorado and Rio Grande systems and most of the Bonneville basin, I consider the native cutthroat trout of these areas as *S. c. lewisi*.

The typical *lewisi* spotting pattern has a concentration of spots on the caudal peduncle. The spots anteriorly are mainly above the lateral line. The spots may be large and roundish or small and irregularly shaped. The size, shape and distribution of spots may vary from population to population and between individuals in a single population. The lower fins are generally rose, orange or yellow, typically, without a prominant white edge as is found in rainbows and many coastal cutthroats. In all of the major river systems containing lewisi, both small spotted and large spotted populations are found. Figures 4, 5, and 6 in Needham and Behnke's monograph depict three distinctively different patterns of spotting; yet, the three populations exhibiting such divergence in the size and arrangement of spots all were native to the Snake River drainage. It is understandable how one not familiar with the range of variation and the intergradation of characters in the black-spotted trout, might recognize many invalid species or subspecies.

I have lumped the native cutthroat from most of the interior waters into a single subspecies. It is possible, however, that some local populations within the range of lewisi may be analogous to the Piute trout, S. c. seleniris, of the Lahontan basin, by possessing some unique character worthy of subspecific recognition. Possibly, such an example is the mountain cutthroat of British Columbia, named Salmo clarkii alpestris by Dymond (1931). Until more data are available I have not committed myself on the status of alpestris. The mountain cutthroat was named for a few disjunct populations in the upper Columbia and Fraser river systems. The dominant trout of this area is the Kamloops rainbow. Dymond believed the sparsely distributed cutthroat populations, restricted to a few headwater streams, were a relict worthy of taxonomic recognition. Qadri (1959) found no difference between alpestris and the typical lewisi from other areas and considered alpestris a synonym of lewisi. I examined four type specimens of alpestris from Isaac Creek, B.C. and noted that although they appear to be typical of lewisi in most characters, they have from 145 to 150 scales in the lateral line, or about 25 more scales than the average cutthroat (or rainbow) trout. I have never examined a specimen of Salmo with so many scales in the lateral line. In most species of salmonids, the number of scales in the lateral line is approximately twice the number of vertebrae. Oncorhynchus gorbuscha is the only species which constantly has more than a 2 to 1 ratio of lateral line scales to vertebrae; they have approximately 2.5 scales per vertebrae. The Isaac Creek specimens have 60 or 61 vertebrae so their ratio is also about 2.5 scales per vertebrae. Neave (1943) believed that O. gorbuscha had a high number of lateral line scales because the scales were not laid down until the young gorbuscha had reached a comparatively large size.

If all of the trout of Isaac Creek have such a high number of lateral line scales they could be readily separated from any other group of trout. The question is: should they be taxonomically recognized? My opinion in this case is based on the belief that for subspecies to have meaning they must be designated with forbearance and not wantonly proliferated. If all of the disjunct cutthroat populations in the Kamloops area of British Columbia possess the genetic combination resulting in a high lateral line scale count, distinguishing them from the typical lewisi, then I would recognize alpestris as a subspecies because these trout would represent a relict, differentiated group. If, however, only the Isaac Creek population is distinct in this character, I would not recognize them with subspecific designation. To do so would promote the naming of every small population which has incorporated some mutation into their genotype resulting in an abberant form, and thus lessen the value and meaning of my systematic arrangement.

Another situation leading to nomenclatorial problems and of real significance from the standpoint of speciation studies, was found in Twin Lakes, Colorado. The facts are obscure and only a few specimens exist, but it appears that two populations of cutthroat trout lived in Twin Lakes, behaving as two distinct species before introductions of exotic species exterminated both of the native forms.

Twin Lakes is at the headwaters of the Arkansas River, just east of the Continental Divide. The common trout of Twin Lakes was S. c. stomias, native to the Arkansas River drainage. Another trout, called the yellowfin trout and given the scientific name of Salmo mykiss macdonaldi by Jordan and Evermann (1890), was described from Twin Lakes. In the description of macdonaldi the authors stated:

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

On the statements of Jordan and Evermann alone, I would not accept as fact, the sympatric occurrence of two cutthroat trout populations in Twin Lakes. These same authors (1898) described Salmo clarkii tahoensis from Lake Tahoe. As discussed later, there is no valid evidence indicating that more than a single population of trout was native to Tahoe. Jordan also believed subspecies of rainbow trout occurred sympatrically in the McCloud River, California, and Crescent Lake, Washington. These are now considered synonyms as mentioned previously. Examination of two specimens of macdonaldi from the Stanford University collection and eight specimens of stomias from the California Academy of Sciences, all collected by Jordan from Twin Lakes in 1889, convinced me that "macdonaldi" and stomias were of different genotypes and the differences observed were not due to any environmental phenomena or to age, sex or growth rate. All the specimens were of comparable size, 164 and 223 mm. for "macdonaldi" and 176 to 217 mm. for stomias. Even after 75 years preservation a sharp difference could be noted in the spotting and basic coloration of the two forms. The two samples could also be distinguished on meristic characters. The two "macdonaldi" have 21 and 22 gillrakers versus 18-20 for the eight stomias specimens. In the number of basibranchial teeth, I counted 15 and 16 in "macdonaldi" and 6 to 14 in stomias. There are 38 and 46 scales above the lateral line in the "macdonaldi" specimens; the stomias have from 46 to 53 such scales.

The geography of the Twin Lakes basin and the characters of the specimens leaves little doubt that the populations were derived, from each side of the Continental Divide. The stomias appear to be undifferentiated from other Arkansas drainage stomias. I cannot make a firm decision based on only two specimens of "macdonaldi," but I consider them typical of Colorado River cutthroat and treat them as a synonym of lewisi.

Nothing more is known about macdonaldi; no more specimens were collected and any subsequent mention in the literature referred to it as extinct. S. c. stomias persisted in Twin Lakes until after the turn of the century. There is the possibility that "macdonaldi" was introduced into Twin Lakes by man. Perhaps this was not a case of long co-existence by two closely related populations. In any event, this was not a case of intralacustrine speciation, but is an indication that two slightly differentiated trout populations might occur sympatrically if the environment provides the niches for their ecological separation.

The Greenback Trout Salmo clarkii stomias

Salmo stomias Cope, Hayden's Geol. Surv. Wyo., 1871:433. South Platte River?

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

Historical Notes

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

Dr. R. R. Miller of the University of Michigan, examined the two type specimens of *stomias* at the National Museum. The specimens are in poor condition and an accurate scale count was difficult but his counts of 150 and 152 scales in the lateral series are much lower than any known specimens of *stomias* from the Arkansas and Platte river systems. Information provided to Dr. Miller by James Cole, biologist with the National Park Service, indicates that the Republican River as far south as Fort Riley, Kansas, may have provided trout habitat as recently as 1870. The topography of the area between the South Platte and the Arkansas rivers suggests the probability that trout occurred in Kansas when environmental conditions were favorable. There are, however, no authentic records of native trout from any rivers between the South Platte and Arkansas drainages and the origin of the type specimens of _stomias_ remains a mystery.

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

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

Table 6 displays some of the meristic variation in samples of *stomias*. In 60 specimens from 8 localities, the scale counts range from 170 to 215, the highest scale counts in the cutthroat species. Some populations have low vertebral counts. The mean value of 59.95 for the Red Canyon sample is the lowest of any cutthroat sample used in this study. Some populations have a tendency for the loss of basibranchial teeth which is a common occurrence among small, isolated populations of interior cutthroat. The arrangement of the basibranchial teeth is, typically, in a single row in *stomias* although exceptions to this were noted, particularly in the Twin Lakes specimens.

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

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

Lahontan Cutthroat Trout, *Salmo clarkii henshawi*

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

Salmo clarkii taheensis Jordan and Evermann, Bull. 47, U.S. Nat. Mus., 1898:2812. Lake Tahoe.

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

The cutthroat trout, endemic to the Lahontan basin, is the most distinctive group of interior cutthroat trout. The Lahontan cutthroat may be distinguished from other cutthroat by its more numerous gillrakers. Actually, I recognize two other subspecies of Lahontan cutthroat trout, besides S. c. henshawi. The Piute trout, S. c. seleniris, is a typical Lahontan cutthroat in every respect except for the absence of spots on the body. The endemic trout of the Humboldt River drainage of the Lahontan basin is intermediate in its gillraker number between lewisi and henshawi but has fewer scales than either. The Humboldt cutthroat trout is described as a new subspecies in the Needham and Behnke manuscript.

Hydrographic History

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

The Native Trout

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

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

Taxonomy of S. c. henshawi

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

> In Lake Tahoe there are two forms of this type, (1) the ordinary Tahoe trout (locally known to fishermen as "Pogy," the young as "Snipe") weighing from 3 to 6 pounds, dark in color, with coppery sides, ascending the streams to spawn, and (2) the "Silver Trout," a large robust trout profusely spotted, the spots often oblong, the coloration more silvery. These trout live in deep water and spawn in the lake itself. A careful comparison of specimens convinces us that there is no specific nor varietal difference between the one and the other.

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

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

Meristic variation. The range in gillraker number, 21 to 28, has only a slight overlap with the subspecies S. c. clarkii, S. c. lewisi and S. c. stomias. The Lahontan trout has a moderate number of scales, typically from 145 to 170. The number of vertebrae is quite typical of cutthroat trout in general.

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

Most samples of _henshawi_ are similar to other cutthroats in basibranchial teeth. Generally 5 to 10 percent of a population may be expected to lack these teeth, while the remainder will have one to 15 teeth. However, the cutthroat of Independence Lake, Sierra-Nevada County, California, is entirely distinct in the number and arrangement of the basibranchial teeth.

Most cutthroat have only a few teeth, seldom more than 20, arranged in one or two rows on the basibranchial plate. The arrangement of basibranchial teeth in the Independence Lake specimens is unique. The teeth proliferate in two masses on the basibranchial plate. In most specimens a few clumps of teeth are visible on the hypobranchial segments of the gillarch and on the pharyngobranchials on the roof of the mouth. This type of dentition, ~~typical~~ found ~~of~~ in this small population of Lahontan cutthroats, is ~~found~~ known in no other species of Salmonidae. It was mainly on this type of teeth arrangement that Chapman (1948a) distinguished the round herring family, Dussumierudae, separating them from Clupeidae. The Independence Lake cutthroat trout are typical of Lahontan cutthreats, *S. c. henshawi*, in all other characters. The other fishes in Independence Lake appear to be undifferentiated Lahontan fauna. Evidently certain mutations have been incorporated into the Independence Lake cutthroat genotype which result in a strikingly distinct teeth pattern in the pharyngeal region, but are not reflected in other characters. This example stresses the caution one must use in the emphasis placed on certain characters which we may believe to be basic in a taxonomic arrangement. A character associated with categories above the species level, may originally come about from a relatively slight genetic change. Long isolation under diverse environmental conditions could lead to a new phyletic line which may greatly accentuate this character and irreversably incorporate it into the genotype.

Provisionally I am treating the Independence Lake cutthroat as *S. c. henshawi*, for the same reasons I would not taxonomically recognize a single population in Isaacs Creek, B.C., with a high lateral line scale count.

Salmo evermanni, A Synonym of Salmo clarkii henshawi

Jordan and Grinnell (1908) described a new species, *Salmo evermanni* from the upper Santa Ana River, San Bernardino County, California. Most subsequent authors placed

S. evermanni with the rainbow series until Miller (1950:9) recognized that the type specimens represented a cutthroat trout. Miller (1950:31) considered *S. evermanni* as a relict cutthroat trout which occurred in coastal waters as far south as the Santa Ana River in Pleistocene times.

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

Piute Trout, Salmo clarkii seleniris

Salmo seleniris Snyder, Proc. Calif. Acad. Sci., 20 (11), 1933:471, Silver King Creek, Alpine Co., Calif.

J. O. Snyder (1933) described the Piute trout, *Salmo seleniris*, based on a sample from a population isolated above Llewellyn Falls on Silver King Creek, a tributary of the East Carson River, Alpine County, California. The name, seleniris, was suggested by "a fancied resemblance of its evanescent tints to the lunar rainbow" (Snyder, 1934). Silver King Creek is in the Lahontan drainage and Snyder recognized the affinities of seleniris to henshawi. The only character which differentiates seleniris from henshawi is that seleniris has no spots on its body, although there are a few spots on the dorsal, adipose and caudal fins.

Snyder published a brief article in the magazine, Pacific Sportsman, recounting the discovery of the Piute trout. A drawing accompanied the article and the scientific name Salmo seleniris accompanied it, but not a taxonomic description. This issue of the magazine, November, 1933, bears the University of California date of November 10, 1933. The official type description in the Proceedings of the California Academy of Sciences has the date of November 16, 1933. Thus, the name seleniris appeared first as a nomen nudem.

There is probably no greater genetic differentiation producing the spot free body in the Piute trout than there is resulting in the dentition pattern of the Independence Lake population or the high number of lateral line scales in the Isaac Creek population, however, the Piute's character is obvious and readily apparent to the naked eye. The Piute Trout is the only ~~group of~~ Salmo which completely lack spots on the body.

In 1949 the California Department of Fish and Game inadvertently stocked Silver King Creek, above the barrier falls with rainbow trout. Hybridization occurred and the effects spread rapidly through the population. In 1964 I accompanied a Fish and Game Department expedition to Silver King Creek to assess the situation. We found pure Piute populations in headwater areas above barriers to upstream migration. The population in the mainstream was composed mostly of hybrids; these were easily recognized by spots on the body. During August, Silver King Creek was treated with rotenone to remove all fish below the areas ~~where we found the~~ of pure Piute populations.

Humboldt Cutthroat Trout, *Salmo clarkii humboldtensis*

Salmo clarkii humboldtensis Needham and Behnke, The rainbow and cutthroat trouts of North America (unpub.). Humboldt River system, Elko Co., Nevada.

In his study of Lahontan fishes, Snyder (1917), collected trout from many areas including the Humboldt River and its tributaries, but his systemmatic data were limited to cutthroats collected from the Truckee River system. My examination of Humboldt River specimens collected by Snyder from 1911 to 1915, demonstrated that the Humboldt cutthroat is distinct from *henshawi* of other Lahontan waters. The Humboldt cutthroat typically has 2 to 4 fewer gillrakers than *henshawi* (Table 8). Some samples from isolated headwater tributaries have fewer scales in the lateral series than any other interior cutthroat yet examined. A detailed description of humboldtensis and a distribution map is presented in the Needham and Behnke monograph.

It is extremely doubtful that the divergence of the trout of the Humboldt drainage from henshawi of the rest of the Lahontan basin came about during the last period of desiccation within the past 10,000 years. No differentiation was noted among henshawi specimens from the Truckee, Carson and Walker river drainages of the Lahontan basin, which also have been isolated from each other since the final desiccation of Lake Lahontan. Many of the headwater stream sites from which humboldtensis was collected, are intermittant and no longer connected to the main Humboldt River. These populations probably have been essentially isolated for thousands of years, yet they all share the features of lower numbers of gillrakers and scales, distinguishing them from henshawi. I believe humboldtensis represents the more primitive and more fluviatile adapted Lahontan trout which later gave rise to henshawi in Pluvial Lake Lahontan. The significant point is that this divergence probably took place within the Lahontan basin without any physical barriers to insure isolation. This continuous environment, however, may be considered to represent two different ecological spheres; the lacustrine ecosystem of

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

No other group of interior cutthroat trout have maintained themselves as well as the Humboldt cutthroat. Most headwater tributaries in the Humboldt drainage still have the native trout despite repeated introductions of exotic trouts.

Independent Basins North of the Lahontan System

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

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

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

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

Discussion of Basins and their Trout

Goose Lake. This basin lies partly in California and partly in Oregon. It had a relatively recent overflow into the Pit River of the Sacramento system and the native fishes of the Goose Lake basin have close affinities to Sacramento species. Snyder (1908) collected trout which he described as *Salmo clarkii* from three Goose Lake tributaries. He also mentioned *S. clarkii* from two localities in the Pit River system. As discussed previously, I believe the "*S. clarkii*" from the Pit River were actually based on *S. gairdnerii stonei* specimens which often have pronounced cutthroat-like characters. Six specimens collected by Snyder in 1904 from Cottonwood Creek, tributary to Goose Lake were examined. Although labeled as *Salmo clarkii* by Snyder, these specimens have a morphology and spotting pattern suggestive of rainbow and all of the specimens have smooth basibranchials. The scale counts on these specimens (Table 9) are much lower than the counts of 153-168 reported by Snyder (1908a) for ten Cottonwood Creek specimens. The gillraker counts of 21 to 24 indicate a lacustrine influence during their evolution. Two specimens have a single posterior gillraker on the first arch, suggesting interior cutthroat influence. If more material becomes available, the native Goose Lake trout may be considered as a subspecies, but it can not be confidently allied to either the cutthroat or rainbow species. If all

Goose Lake basin trout lack basibranchial teeth, it would seem practical to assign them to the rainbow series, although they appear to have their closest affinities with the Chewaucan and Fort Rock basin trout, which have more cutthroat-like characters.

Fort Rock Basin, Lake County, Oregon: This basin is considered a disrupted part of the Columbia River system by Hubbs and Miller (1948:73). Silver Lake is the only permanent body of water. Cope (1889) said Silver Lake was too alkaline to support fish life, but its tributary, Silver Creek, abounded with "Salmo purpuratus" [= S. clarkii]. Snyder (1908) collected trout from Silver, Buck and Bridge creeks, all tributaries of Silver Lake. Seven specimens from Buck Creek (S.U.37966) collected by Snyder in 1904 form a most interesting group. Some of their meristic characters are listed in Table 9.

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

Rock basin.

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

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

As with the Cottonwood Creek sample from the Goose Lake basin, ~~our~~ my scale counts of 132 to 143 for the Chewaucan River sample disagrees with the counts obtained by Snyder (1908) (147 to 151) for the Chewaucan River specimens.

~~Miller~~ Hubbs and Miller (1948:67) believe the native trout have hybridized with introduced rainbows.

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

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

Alvord basin, Humboldt County, Nevada, Harney and Malheur Counties, Oregon: Hubbs and Miller (1948:60) believed the Alvord basin has been isolated since Prepluvial times.

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

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

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

THE GOLDEN TROUT COMPLEX

Golden colored trout populations native to Kern River tributaries in California, to tributaries of the Salt River and the Little Colorado River, Arizona, to tributaries of the Gila River, New Mexico, and to the Verdi, Sinaloa and Culiacan systems in Mexico, share a number of distinctive traits which suggest a monophyletic origin. The available evidence strongly supports the theory that the golden trout have their closest affinities to each other. In many characters the golden trouts are intermediate between cutthroats and rainbows. They may have had their origin from an ancient hybridization between the cutthroat and rainbow species, or they may represent an early, intermediate stage between the cutthroat and rainbow trouts. They freely hybridize and lose their identity when occurring together with rainbow trout. Because the golden trouts show relationships to both rainbows and cutthroats and because they appear to be a monophyletic group, I give the golden trouts species status and recognize four subspecies.

California Golden Trout
Salmo aquabonita aquabonita Jordan

Salmo mykiss aquabonita Jordan, Bien. Rept. St. Bd.

Fish Comm. Calif.; 1891-92, 1892:62. Cottonwood Lakes (introduced from South Fork Kern River).

Salmo roosevelti Evermann. Bull. U.S. Bur. Fish., 25, 1906:26. Volcano Creek (now Golden Trout Creek).

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

Jordan and Henshaw (1878) first mentioned the golden trout from the South Fork of the Kern. They called it Salmo irideus. In this same paper they also mention the Colorado River cutthroat, Salmo pleuriticus, from the South Fork of the Kern. Jordan (1892c) described the California golden trout as a subspecies of the cutthroat, naming it Salmo mykiss aquabonita. Jordan said its closest affinities were to the Colorado River cutthroat and it was ". . . not in any way related to the Rainbow trout." Jordan (1893) essentially repeated the same description of aquabonita in the Proceedings of the U.S. National Museum. Evermann (1906) and Jordan, Evermann and Clark (1930) erroneously list the 1893 paper as the original description. Jordan (1894b) placed the California golden trout as a subspecies of the rainbow, calling it S. gairdnerii aquabonita, considering it an offshoot of the Kern River rainbow, S. g. gilberti. Jordan and Evermann (1896:504) referred to it as S. irideus aquabonita and wrote:

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

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

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

Evermann (1906) distinguished roosevelti from aguabonita mainly on the basis of the arrangement of spots on the body. He claimed the population in Golden Trout Creek (roosevelti) had spots restricted to the caudal peduncle area with no spots anterior to the dorsal fin, whereas, aguabonita from the South Fork Kern typically had spots anterior to the dorsal fin. About the only meristic character mentioned by Evermann which might suggest a difference between aguabonita and roosevelti was his statement that aguabonita was relatively coarse scaled while roosevelti had about 50 scales above the lateral line, about 200 in the lateral series and about 140 to 150 scales with pores in the lateral line. My counts are lower than Evermann's and indicate no real differences between aguabonita and roosevelti in scale counts or any other character (Table 10). The California golden trout typically have only 110 to 115 pores in the lateral line.

Curtis (1934, 1935) claimed the spotting pattern of golden trout was variable and that both the "roosevelti" type and the aguabonita type were found among all populations, although the "roosevelti" type predominated in Golden Trout Creek. He suggested roosevelti should be considered a synonym of aguabonita and most subsequent authors have accepted this view.

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

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

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

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

Characters and Comparisons

The coloration of aguabonita is distinct from any rainbow or cutthroat trout (plate 1, Evermann, 1906). The bright red and yellow hues, however, are much more similar to interior cutthroat than to rainbow trout. The spotting pattern is typical of interior cutthroat. In the absence of basibranchial teeth it is rainbow-like. The general morphology, its long head and jaw are more suggestive of cutthroat than rainbow. A bright crimson generally covers the ventral surface and the underside of the lower jaw so that a cutthroat mark is not discernable. The scale counts of *aguabonita* are quite typical of cutthroat. I have examined no rainbow or cutthroat samples with such low numbers of vertebrae and pyloric caeca as found in *aguabonita*. Some samples of *S. c. stomias* are close to *S. aguabonita* in vertebral and caecal counts. A low vertebral number is considered a primitive character and this tends to negate the view that *aguabonita* is a local offshoot of the rainbow. Overall, the California golden trout appears to have closer affinities to the interior cutthroat than to the rainbow. The closest affinities, however, apparently are with the other members of the golden trout complex.

Simon (1964, unpub.) found the diploid chromosome number to be 58 in the California golden trout. This is the lowest diploid number reported for any *Salmo*. Although 58 is closer to the rainbow number of 60 than to the interior cutthroat's 64, the cutthroat and the golden both have an arm number of 106 in their diploid compliment; the rainbow has

104 chromosomae arms. In correspondence, Simon wrote me that he detected a golden trout chromosome of distinctive morphology which he had previously observed only in his cutthroat material. Although the chromosome research does not support a hybrid origin theory for golden trout, it does supplement the evidence for considering the golden a distinct phyletic line intermediate between rainbows and cutthroats.

Table 10 discloses that a low number of vertebrae and pyloric caeca are common to all the known populations of the golden trout complex. Besides sharing golden coloration, all of the golden trout group have distinctively colored lower fins, typically shades of red, yellow or orange with the pelvics and anal fins tipped with white. The anterior tip of the dorsal fin is, typically, yellow or orange. Also, all of the golden trouts have a relatively long dorsal fin, typically .225 to .275 of the standard length. In most samples of rainbows and cutthroats, the dorsal fin is .180 to .230 of the standard length. S. aguabonita, typically has nine pelvic rays, like a cutthroat. The Mexican golden trout also has predominantly nine pelvic rays, while the Gila trout and the Arizona golden trout mostly have ten pelvic rays.

Arizona Golden Trout

Salmo aguabonita apache Miller?

Native trout were known to exist in tributaries of the Colorado River system in Arizona, but until recently these trout were considered as Colorado River cutthroats. Cope and Yarrow (1875) listed three specimens of S. pleuriticus, collected from the White Mountains of Arizona. These specimens were borrowed from the National Museum (USNM 15999) where they are erroneously labeled, Paguitch Lake, Utah. The three specimens were from 101 to 166 mm. in standard length. They have a striking appearance with an extremely long head, jaw and dorsal fin. Table 10 indicates the meristic characters are similar to other golden trout, especially to a sample collected by R. R. Miller in 1950 from the East Fork White River, a tributary in the Salt River system, Apache County, Arizona. Although Jordan and Evermann (1896:496) state that the Colorado River cutthroat occurred throughout Arizona, Miller (1961: 389) said that the only indigenous Arizona trout is what I here call the Arizona golden trout, which Miller (1950:34) tentatively referred to as S. gilae. Mulch and Gamble (1954) considered the Arizona golden trout as S. gilae, although their colored illustration depicts a trout quite differently spotted than S. gilae. The specimens examined from the East Fork of the White River appear to be more similar to S. aguabonita in their spotting than to S. gilae. The White River golden trout have more scales than gilae from Diamond Creek, New Mexico. The spots are considerably larger and fewer in number on the White River golden trout than in gilae. It must be noted that similar variation in spotting and scale counts are found among S. c. lewisi populations. It is not known if continual intergradation occurs or if the Arizona golden trout of the Salt River tributaries should be recognized as a valid taxonomic entity. So few pure populations remain that the original situation may never be known. The Arizona Game and Fish Department kindly supplied two completion reports on the distribution and abundance of their native golden trout in the tributaries of the White and Black rivers. They found that most native populations had hybridized with introduced rainbow trout.

A native golden trout was also present in the Little Colorado and Verdi river systems (Miller, 1961). It is not known if these were identical to the White River trout. Miller (1961:390) doubted the present existence of a pure population of native trout in the Verdi drainage.

In correspondence, Dr. Miller disclosed his plans to publish a description of the Arizona golden trout. He had given it a manuscript name of Salmo apache. He found a basibranchial tooth in one speciman of his White River sample. This single tooth definitely indicates cutthroat genes are present in the Arizona golden trout and bolsters my contention of the golden trouts close relationships to the cutthroat line.

The Gila Trout

Salmo aguabonita gilae Miller

Salmo gilae Miller, Occ. Pap. Mus. Zool. Univ.

Mich. (529), 1950:11.

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

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

Mexican Golden Trout

Salmo aguabonita chrysogaster Needham and Gard

Salmo chrysogaster Needham and Gard, Copei, (1) 1964:169.

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

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

Discussion

If all of the golden trouts mentioned above are of common origin, the waters of the lower Colorado River area were probably the center of speciation. The fishes of the lower Colorado system form a distinct group from the northern elements of the Colorado drainage (Miller, 1958). Blackwelder (1936) believed that the Colorado River was not a continuous river system until the Pleistocene. A primitive rainbow-like trout, perhaps somewhat similar to the Mexican golden trout may have been established in the lower Colorado River area; when the lower Colorado became connected with the upper basin, a primitive interior cutthroat trout may have invaded the more southern waters, resulting in hybridization. Long isolation from other cutthroats and rainbows and then from each other could have produced the golden trouts as we know them today. The distribution of the Arizona and Mexican golden trout and the Gila trout fit this scheme well. The occurrence of S. aguabonita in the Kern drainage in California is not so easily explained. To cross the Sierras and enter a Pacific slope stream would necessitate gaining entrance into the Pluvial waters of Death Valley and its connectives. Miller (1958) believed the connection between Death Valley and the Colorado was probably in the Pliocene. Trout, however, may have made headwater transfers at a later date, after direct connection was lost. If the golden trout did enter the Kern basin from the east slope, some drastic changes must have occurred which wiped out all trace of trout from the Sierran east slope streams, south of the Lahontan basin. Although many east slope waters, such as Cottonwood Creek, the type locality of aguabonita, provide excellent trout habitat today, these waters were barren of trout before the activities of man. A sucker, probably of Colorado River origin, Pantosteus santanae Snyder, made it across the divide, perhaps in Pliocene times (Miller, 1958), to establish itself in a Pacific Coast stream.

Systematic Arrangement of Golden Trouts

It will take much more work with much more material, perhaps with the help of serological and chromosomal studies, before the true relationships of the golden trouts are established with confidence. The available evidence indicates that four known groups are worthy of taxonomic recognition. None of the golden trout make "good" biological species, i.e., they will hybridize with rainbow and probably with cutthroat trout when occurring sympatrically. They may be considered as subspecies of the rainbow or cutthroat species but this would disguise their true affinities, if they do, actually represent a monophyletic group. The most proper and practical solution is to consider the golden trout complex as a third species of western North American Salmo and recognize four subspecies.

THE KAMCHATKAN TROUT SALMO MYKISS WALBAUM

Salmo mykiss Walbaum, Peter Artedi Sueci Genera Piscium, 1792:59. Kamchatka.

Salmo purpuratus Pallas, Zoographia Rosso-Asiatica, 3; 1814:374. Rivers, west coast of Kamchatka.

Salmo penshinensis Pallas, ibid.:381. Vorovskaya R., Kamchatka.

A trout, typical of the genus Salmo, inhabiting the freshwaters of Kamchatka, has been known to naturalists since the middle of the eighteenth century. Little detailed information or comparative data have appeared on this trout in the past 200 years. Three nominal species, referable to the genus *Salmo* were named from Kamchatka, but the actual number of species and their relationships have not been adequately determined. At various times, Kamchatkan *Salmo* have been considered to be allied to the brown trout, *Salmo trutta* ~~L.~~; the Atlantic salmon, *S. salar* ~~L.~~; the cutthroat trout, *S. clarkii* ~~Richardson~~; and the rainbow trout, *S. gairdnerii* ~~Rich.~~.

Examination of eight specimens of Kamchatkan *Salmo* and analysis of the literature leads to the conclusion that the known endemic *Salmo* fauna of the Far East consists of a single species with both anadromous and non-anadromous populations. It has its closest affinities to the rainbow trout, *S. gairdnerii*.

Historical Review

Salmo mykiss Walbaum 1792 was the first scientific name applied to the Kamchatkan trout. Walbaum took the description from Pennant (1785), who, in turn, got his information from Stellar. Pallas (1814) named *S. purpuratus* and *S. penshinensis* for the anadromous form. The main diagnostic characters distinguishing *purpuratus* from *penshinensis* are slight differences in fin ray numbers. Such differences would be expected in the normal range of variation of a species. If taxonomic recognition is given to the anadromous form, *purpuratus* has page priority over *penshinensis*.

Gunther (1866) considered the American cutthroat trout, *S. clarkii* as a synonym of *S. purpuratus*. Gunther's comparative data for "*purpuratus*" was actually taken from two specimens of *clarkii*; or perhaps *gairdnerii* from British Columbia. Gunther examined a skin of *S. penshinensis* from Kamchatka and claimed it was very close to *S. cambricus* (=*S. trutta*). He mentioned that Valenciennes had identified *S. penshinensis* with *S. rossi* (=*Salvelinus alpinus*).

Jordan and Evermann (1896), following the earlier classifications of Jordan, considered the Kamchatkan *Salmo mykiss* conspecific with the North American cutthroat trout, and ranked the various cutthroat groups as subspecies of *Salmo mykiss*. Jordan and Evermann (1898:2818) noted that the range of the cutthroat trout was not continuous to Kamchatka but extended northward only to southern Alaska. They then considered the Kamchatkan *Salmo mykiss* to be distinct from any North American species. They described a head and skin of a large specimen of Kamchatkan *Salmo* sent by Leonhard Stejneger from the Kalakhtyka River and concluded that *mykiss* was most closely related to the Atlantic salmon, *S. salar*. The Kalakhtyka River specimen mentioned by Jordan and Evermann is in the Stanford University collection (no. 12011) and appears indistinguishable from a steelhead-rainbow trout.

Berg (1916) recognized only *S. mykiss* from Kamchatka mentioning that *mykiss* was close to *gairdnerii*, differing chiefly in the number of scales. Actually, the number of scales in *mykiss* is typical of the coastal rainbow, *S. g. gairdnerii*.

Derzhavin (1930) studied about 50 specimens of the anadromous form of the Kamchatkan *Salmo* and recognized it as a full species, *Salmo penshinensis*. As mentioned earlier, if the anadromous form is taxonomically recognized, the name *purpuratus* has priority. Derzhavin believed, however, that his specimens most closely approximated the description of penshinensis.

Derzhavin claimed that *penshinensis* had more gillrakers (18-21) than *mykiss* (16-17), and fewer scales from the insertion of the adipose fin to the lateral line (11-14 versus 14-15). The comparative data on *mykiss*, however, was taken from Berg (1916) who based his diagnosis of *mykiss* on two specimens collected from the mouth of the Kamchatka River. In 1960, I examined these specimens at the Zoological Institute of the Soviet Academy of Sciences in Leningrad and counted 17 and 19 gillrakers on the first left arch instead of the 16 and 17 reported by Berg. I believe an adequate comparison of anadromous and non-anadromous populations of Kamchatkan Salmo would make it evident that there is the same local variability, typical of *S. g. gairdnerii*, with no constant differences between anadromous and resident populations. It was Derzhavin's (*op. cit.*)

opinion that the relationship of *penshinensis* to *mykiss* was comparable to that of *S. gairdnerii* to *S. irideus* and *S. trutta* to *S. fario*. Most systematists today essentially follow the polytypic and biological species concept and do not give formal taxonomic recognition to such situations as anadromous and non-anadromous populations which undoubtedly have arisen many times independently within a species. Thus, *irideus* is considered a synonym of *gairdnerii* and *fario* a synonym of *trutta*.

After Derzhavin's publication, Berg (1948) and most other Russian authors mentioning Far Eastern *Salmo*, recognized *S. mykiss* and *S. penshinensis* as valid species. Berg (*op. cit.*) stated that *penshinensis* is closely related to *S. gairdnerii* but he thought the relationship of *penshinensis* to *mykiss* analogous to that of *S. salar* to *S. trutta*. He considered *purpuratus* a synonym of *S. mykiss*. Berg (*op. cit.*) cited references extending the known range of the Far Eastern *Salmo*. Besides Kamchatka, it is known from the Commander islands, and on the coast of the mainland bordering the Okhotsk Sea, it has been reported as far south as the mouth of the Amur River.

Meristic Characters of Salmo mykiss

The specimens of Kamchatkan *Salmo* examined cannot be definitely assigned to the anadromous or non-anadromous form. The data are based on the following specimens: Stanford University specimen (S.U. 12011), 853 mm. standard length, from the Kalakhtyrka River. This, apparently, was an anadromous individual. Three specimens listed as *S. mykiss*, at the Zoological institute of the Soviet Academy of Sciences at Leningrad (no. 23596), 367, 414, and 510 mm. standard length are listed as *S. mykiss* from Kamchatka with no other details as to locality. Two specimens (one stuffed) of 664 and 780 mm. standard length in the Leningrad collection are labeled *S. penshinensis* from Kamchatka. Table 11 lists some meristic characters of *S. mykiss*. My limited material does not suggest that more than a single species and subspecies is involved.

Relationships

A red band on the sides of the body, black spots on the body and on the dorsal, adipose and caudal fins, an absence of any red or light colored spots, and a spring spawning habit, all ally *S. mykiss* with western North American *Salmo* and not to *S. salar* or *S. trutta*. Typically, *salar* and *trutta* lack spots on the caudal fin and *salar* generally has no spots on the dorsal fin. I observed no development of gillrakers on the posterior region of the first gill arch in the specimens of *S. mykiss*. Posterior gillrakers on the first arch are always present in *salar* and *trutta* but are absent or only feebly developed in *S. gairdnerii*. Comparison of *mykiss* with *S. gairdnerii* and *S. clarkii* indicates *mykiss* is closest to *gairdnerii*.

The most reliable character distinguishing *gairdnerii* from *clarkii* is the presence of basibranchial teeth in *clarkii*. No other species of *Salmo* retains this primitive character. All the specimens of *mykiss* examined lack basibranchial teeth. The red band, coarse scalation and the predominance of 10 pelvic fin rays are all indicative of *gairdnerii* and not *clarkii*. *S*. *clarkii* and other species of *Salmo* typically have nine pelvic fin rays. If a relict group of trout allied to the cutthroat species occurs in the Far East, they have not yet been discovered and described.

The only apparent distinction between *S*. *mykiss* and *S*. *gairdnerii* is the number of vertebrae. If the specimens of *S*. *mykiss* used in this study are representative of the species throughout its range, then *mykiss*, typically has four or five fewer vertebrae than *gairdnerii*.

I suspect that *mykiss* and *gairdnerii*, if crossed, would prove to be fully fertile and might properly be considered only subspecies. In view of the fact that *mykiss* has priority over the well established name of *gairdnerii* and that *mykiss* was used for many years as the specific name of the cutthroat trout, I believe it prudent not to propose such a solution, at least at this time.

Summary and Review of Pacific Salmo

The *Salmo* endemic to Pacific drainages are a closely related group which could properly be recognized as a subgenus as proposed by Vladykov (1963). I can not agree to Vladykov's further suggestion that his subgenus, *Parasalmo*, really deserves full generic ranking.

I recognize two main phyletic lines, the rainbow series and the cutthroat series. The boundaries of these two species are not definitely established because intermediate types exist. One intermediate group, the golden trouts, I rank as a third North American species. The golden trouts may have resulted from hybridization between the rainbow and cutthroat lines or they may represent an intermediate group on the evolutionary line leading from the cutthroat to the rainbow species.

Although the known variation in chromosome number is from 58 to 70, all the North American Pacific *Salmo* must have quite similar genetic material because the available evidence indicates no genetic incompatibility among hybrids.

The cutthroat species is the only species of *Salmo* which has basibranchial teeth. The present cutthroat genotype has close affinities to the rainbow and golden trouts, but the cutthroat chromosomes ~~number and morphology~~ are ~~is~~ quite distinct from the chromosomes of *Salmo salar* and *S. trutta* and could not be considered ancestral to these ~~latter~~ species. The evidence suggests that there has been rapid evolution at the species level and all of the present species of *Salmo* are of relatively recent origin, probably no earlier than the late Pliocene. No present species can be considered as the progenitor of the genus.

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

In coastal waters it would be expected that hybridization could occur and this eventually may have influenced the present genotypes of coastal rainbows and cutthroats.

Due to greater anadromy and perhaps greater tolerance of warmer waters, the primitive rainbow pushed further south than the cutthroat. This early rainbow made it across or around the Baja California peninsula, as discussed by Miller (1950) and into the waters of the lower Colorado River system. Here, a primitive cutthroat was probably native and hybridization may have occurred. Later, isolation allowed various populations to evolve their own peculiarities. Changing climatic conditions essentially isolated the lower Colorado trout from the more advanced cutthroats and rainbows north and west of this area. This early hybridization may explain the origin of what we call the golden trout complex. The alternative explanation, that the golden trout are an early intermediate group leading to the rainbow species, would indicate that an interior cutthroat, isolated in the lower Colorado River drainage, initiated a new phyletic line, ultimately producing the rainbow species.

Table 12 summarizes my systematic arrangement of western North American Salmo.

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