

AN ABSTRACT OF THE THESIS OF

FREDERICK TAYLOR BILLS for the degree of MASTER OF SCIENCE

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Title: TAXONOMIC STATUS OF THE ISOLATED POPULATIONS OF TUI
CHUB REFERRED TO GILA BICOLOR OREGONENSIS (SNYDER)

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The Oregon tui chub, Gila bicolor oregonensis (Snyder), is composed of six allopatric populations that inhabit five endorheic basins of south-central Oregon. Paleohydrographic evidence indicates that these populations have been isolated from one another for 4,000 to 50,000 years. Because tui chub populations elsewhere in the Great Basin have shown remarkable morphological divergence after isolation of a few thousand years, there was reason to believe that G. b. oregonensis might contain more than one subspecies.

To investigate this possibility, I examined 21 morphometric and 12 meristic characters in samples from the six populations. Most of the differences found among populations reflect trophic adaptations and are correlated with habitat. The lacustrine population of the Warner Basin exhibits many features peculiar to lake dwelling fishes. The Hutton Spring population typifies, in most respects, the form of tui chubs inhabiting extremely small bodies of

water. The river populations of the Silver Basin and Chewaucan River are generally intermediate in form between the lake and spring types. The XL Spring tui chub does not exhibit many of the characters associated with spring dwelling fishes. The tui chub of the Summer Basin was excluded from consideration because of recent fish control operations and the introduction of tui chubs from other basins.

On the basis of 15 of the 33 characters examined, I conclude that the six populations referred to G. b. oregonensis constitute four discrete subspecies. Only the tui chub populations of XL Spring and the Chewaucan River are retained in Snyder's oregonensis. Tui chub populations of Hutton Spring, Silver Basin, and Warner Basin represent three additional subspecies.

Except for the populations of XL Spring and the Chewaucan River, morphological affinities among populations do not clearly reflect past hydrographic connections or length of isolation. Similarities and differences among populations appear better correlated with similarities and differences of the respective habitats.

Taxonomic Status of the Isolated Populations
of Tui Chub referred to Gila bicolor
oregonensis (Snyder)

by

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TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
SYNONYMY	5
LITERATURE REVIEW.	8
TOPOGRAPHY AND HABITAT DESCRIPTION OF STUDY AREA . . .	10
HYDROGRAPHIC HISTORY	16
MATERIALS AND METHODS.	22
RESULTS AND INTERPRETATION	26
Introduction.	26
Vertical and Paired Fin Rays.	29
Scale Rows.	35
Vertebrae	41
Gill Rakers	42
Pharyngeal Arch and Teeth	46
Interosseus Space	52
Morphometrics	52
Intestinal Tract.	92
CONCLUSION	114
LITERATURE CITED	117

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Drainage basins of south-central Oregon . . .	2
2	Maximum extent of the Pleistocene lakes of south-central Oregon.	17
3	Variation in the number of scales around caudal peduncle and in the number of pre-dorsal scales in <u>Gila bicolor</u> from Summer Basin, Oregon	27
4	Variation in the number of dorsal fin rays in populations of <u>Gila bicolor</u> from south-central Oregon.	31
5	Variation in the number of scales from lateral line to pelvic fin insertion in populations of <u>Gila bicolor</u> from south-central Oregon.	36
6	Variation in the number of scales around caudal peduncle in populations of <u>Gila bicolor</u> from south-central Oregon	38
7	Variation in the number of gill rakers in populations of <u>Gila bicolor</u> from south-central Oregon.	44
8	Dorsal, lateral, and mesial aspects of the left pharyngeal arches of two populations of <u>Gila bicolor</u> from south-central Oregon . .	49
9	Relationship between dentigerous length/ anterior edentulous length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon	53
10	Representative specimens of five populations of <u>Gila bicolor</u> from south-central Oregon . .	55
11	Variation in the length of head in populations of <u>Gila bicolor</u> from south-central Oregon.	57
12	Variation in the depth of head in populations of <u>Gila bicolor</u> from south-central Oregon.	60

List of Figures -- continued

<u>Figure</u>		<u>Page</u>
13	Relationship between standardized orbit width and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	62
14	Relationship between standardized orbit width and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	64
15	Relationship between standardized orbit width and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	66
16	Variation in the length of mandible in populations of <u>Gila bicolor</u> from south-central Oregon.	69
17	Variation in the width of head in populations of <u>Gila bicolor</u> from south-central Oregon . .	71
18	Variation in predorsal length in populations of <u>Gila bicolor</u> from south-central Oregon . .	73
19	Variation in pelvic-anal length in populations of <u>Gila bicolor</u> from south-central Oregon.	75
20	Relationship between standardized pectoral fin length and standard length for females of two populations of <u>Gila bicolor</u> from south-central Oregon.	79
21	Relationship between standardized pectoral fin length and standard length for females of two populations of <u>Gila bicolor</u> from south-central Oregon.	81
22	Variation in dorsal fin height in populations of <u>Gila bicolor</u> from south-central Oregon.	84
23	Variation in dorsal fin base length in populations of <u>Gila bicolor</u> from south-central Oregon.	86
24	Relationship between mean standardized dorsal fin base length and mean number of dorsal fin rays in populations of <u>Gila bicolor</u> from south-central Oregon	88

List of Figures -- continued

<u>Figure</u>		<u>Page</u>
25	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	93
26	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	95
27	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	97
28	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	99
29	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	101
30	Relationship between standardized gut length and standard length for two populations of <u>Gila bicolor</u> from south-central Oregon. . . .	103
31	Intestinal configurations found in populations of <u>Gila bicolor</u> from south-central Oregon.	107

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Morphometric and meristic characters examined in populations of <u>Gila bicolor</u> from south-Oregon	23
2	Frequency and mean of anal fin ray counts in populations of <u>Gila bicolor</u> from south-central Oregon	30
3	Frequency and mean of pectoral fin ray counts in populations of <u>Gila bicolor</u> from south-central Oregon	33
4	Frequency and mean of pelvic fin ray counts in populations of <u>Gila bicolor</u> from south-central Oregon	34
5	Total mean number of fin rays in populations of <u>Gila bicolor</u> from south-central Oregon. . .	35
6	Total mean number of scales in populations of <u>Gila bicolor</u> from south-central Oregon. . .	40
7	Frequency and mean of vertebral counts in populations of <u>Gila bicolor</u> from south-central Oregon	41
8	Frequency of pharyngeal tooth formulae in populations of <u>Gila bicolor</u> from south-central Oregon	46
9	Number of males and females in different size ranges in <u>Gila bicolor</u> from XL Spring, Oregon	77
10	Mean pectoral fin length, pelvic fin length, and height of dorsal fin for males and females in populations of <u>Gila bicolor</u> from south-central Oregon	78
11	Summary of significant differences among populations of <u>Gila bicolor</u> from south-central Oregon	90

TAXONOMIC STATUS OF THE ISOLATED POPULATIONS
OF TUI CHUB REFERRED TO GILA BICOLOR
OREGONENSIS (SNYDER)

INTRODUCTION

The Oregon tui chub, referred to Gila bicolor oregonensis (Snyder) by recent authors, is composed of six allopatric populations that inhabit five endorheic basins of south-central Oregon: Silver, Summer, Abert, Alkali, and Warner (Fig. 1). Paleohydrographic evidence indicates that these six populations, presently occupying diverse environments, have been isolated for varying periods of time, ranging from 4,000 to 50,000 years or more. The extended isolation under disparate ecological conditions raises the question of differentiation in these allopatric populations now considered to represent a single subspecies. This question is of particular consequence in light of the fact that tui chub populations elsewhere in the Great Basin have shown remarkable morphological divergence after a maximum isolation of a few thousand years (Hubbs et al., 1974). Ichthyologists have long suspected that two or more of the populations referred to G. b. oregonensis are sufficiently distinct to warrant subspecific recognition, but the problem has not been resolved (Hubbs and Miller, 1948a; C. E. Bond, pers. comm.).

G. b. oregonensis is one of eleven presently recognized subspecies of the tui chub, Gila bicolor (Girard),

Figure 1. Drainage basins of south-central Oregon.
Circles and arrows indicate sites of fish
collections.

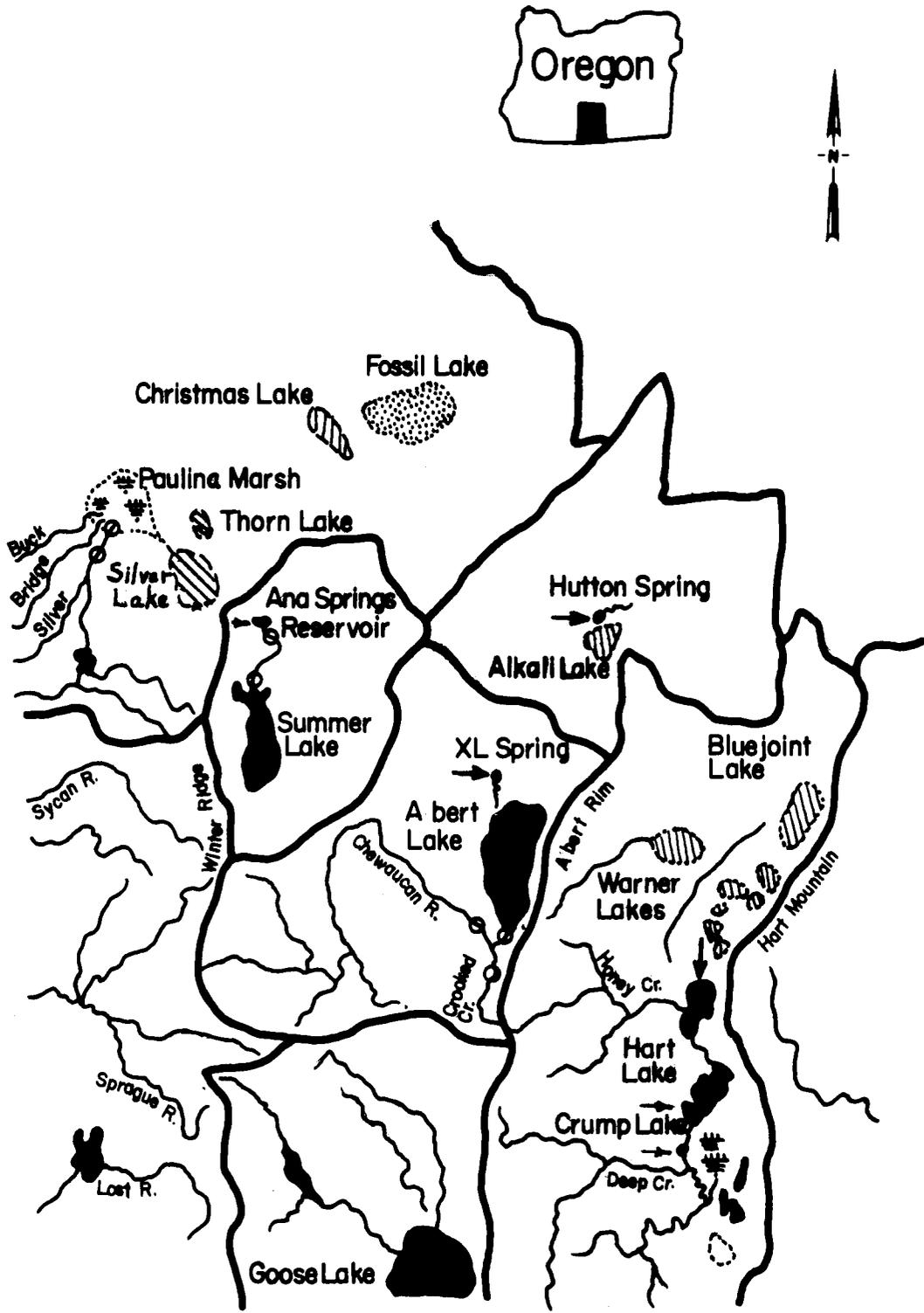


Figure 1

which is a ubiquitous fish species in the western Great Basin and the adjacent Pacific drainage systems. The polytypic and polytopic nature of Gila bicolor is the result of a complex hydrographic history combined with the remarkable ability of the tui chub to adapt to a wide range of ecological conditions (Hubbs and Miller, 1948a; Miller, 1965; Moyle, 1976). Populations occupy nearly the entire range of available aquatic habitats: springs, lakes, and rivers. In most instances, the tui chubs in each of these different environments possess a distinct complex of morphological characters peculiar to their respective habitats (Hubbs et al., 1974).

The objectives of this thesis are to (1) define the meristic and morphometric variation in the geographically isolated populations of G. b. oregonensis, (2) to determine the relationships of such variation to the hydrographic history and ecological characteristics of the habitats, and (3) to reassess the taxonomic status of the populations referred to this subspecies.

SYNONYMY

Gila bicolor, viewed in its entirety, presents an extensive array of morphological variation. Incomplete understanding of the nature and range of this variation has produced an abundance of synonyms with the concomitant problems of a complex and chaotic nomenclature (Uyeno, 1960; Hubbs et al., 1974).

Gila bicolor oregonensis (Snyder) - Oregon Tui Chub

Leucos bicolor, Jordan and Henshaw, 1878:1615, (in part).

Specimens collected from Warner Lake.

Leucos bicolor, Jordan and Gilbert, 1882:143, (in part).

"Streams of Oregon, Nevada, etc."

Myloleucus formosus, Cope, 1883:143, 1889, (in part).

Chewaucan River and Abert, Silver, and Warner Lakes.

Rutilus bicolor, Jordan and Evermann, 1896:244, (in part).

"Lakes of southeastern Oregon..."

Rutilus oregonensis, Snyder, 1908:87, original description.

XL Spring (type locality), Chewaucan River, Ana River, Bridge Creek, Warner Creek, spring at Alkali Lake (= Hutton Spring?).

Rutilus formosus, Fowler, 1913:70, (in part ?). "Also 38

other examples from: Chewaucan (Cope), Warner's Third Lake (Cope), Silver Lake (Cope), Oregon; Mohave River (Hammond), Pose Creek (Heerman), California."

Siphateles oregonensis, Snyder, 1917:60.

Siphateles bicolor oregonensis, Schultz and DeLacy, 1935:
380.

Siphateles obesus oregonensis, Hubbs and Miller, 1942:152.

"Subspecies of S. obesus occur in ... the Warner Lakes and the other Oregon lake basins ..."

Gila bicolor oregonensis, Bailey and Uyeno, 1964: 239.

Since the last half of the nineteenth century, the six populations of G. b. oregonensis have been referred to, in whole or in part, to five genera and four species. The major nomenclatural changes resulted from shifts in prevailing opinion as to whether or not American and European cyprinids were separable at the generic level. At the specific level, I can provide no unequivocal explanations for all the taxonomic decisions.

Jordan and Henshaw (1878) were the first authorities to assign any of the six Oregon tui chub populations to a species. Jordan and Evermann (1896) synonymized Myloleucus and Leucos with Rutilus. Leucos, not Leucus, is the proper spelling of Heckel's genus of cyprinids; the latter name is preoccupied in Aves by Leucus Kaup. Jordan and Evermann (1896) did not include Myloleucus formosus as a specific synonym of Rutilus bicolor. Snyder (1908) described Rutilus oregonensis (= G. b. oregonensis), but he presented no synonymy. The subsequent use of R. formosus by Fowler is enigmatic. Snyder (1917) removed the American species

that had been referred to the European genus Rutilus and assigned them to Siphateles Cope. Schultz and DeLacy (1935) considered the five nominal species of Siphateles as conspecific and relegated the five forms to subspecies of Siphateles bicolor. Bailey and Uyeno (1964), who resolved the nomenclatural confusion surrounding Siphateles and Gila, credit Schultz (1936) with combining the five nominal forms of Siphateles into the single species Siphateles bicolor, but Schultz and DeLacy (1935) predates Schultz (1936). In fact, Schultz (1936:110) cites Schultz and DeLacy (1935). There was disagreement or confusion concerning the actions of Schultz and DeLacy (1935), for in 1942 and 1948 Hubbs and Miller referred subspecies of the tui chub to Siphateles obesus.

The chaos was finally resolved by Bailey and Uyeno (1964). To summarize their decisions pertinent to oregonensis, they placed Siphateles in the synonymy of Gila, and retained bicolor as the specific name for the tui chub.

LITERATURE REVIEW

In the original description of G. b. oregonensis, Snyder (1908) included meristic and morphometric data for all populations, but the sample sizes were not adequate by present statistical standards, and Snyder did not consider many of the morphological characters that have since proven useful for discriminating among tui chub populations. In a subsequent paper, Snyder (1917) briefly discussed the meristic differences between Siphateles oregonensis and the other nominal forms of Siphateles. Because of the great similarities between S. oregonensis and S. obesus, he doubted whether the former should be recognized at all. On the basis of gill raker counts, Snyder (1917) stated that well defined races of S. oregonensis might be identified, but he did not consider them of any distributional significance.

Hubbs and Miller (1948a) stated that differentiation at the subspecific level had definitely occurred in at least the Warner population, and they recognized the need for further examination of the populations referred to S. obesus oregonensis. Drs. Hubbs and Miller were at one time in the process of revising Siphateles, = Gila (Siphateles), (R. R. Miller, pers. comm.). Dr. Miller very kindly provided me with data they had collected on five populations of the Oregon tui chub. Manuscript names were assigned to two of the populations, indicating their belief

that subspecifically distinct populations exist within the oregonensis complex.

Variation and its relationships to habitat have long been of primary concern in the systematics of Gila. Hubbs (1940; 1941a; 1941b), Hubbs and Miller (1948a; 1948b), and Hopkirk (1973) have observed and documented the morphological trends exhibited by fluviatile, lacustrine, and spring populations. Spring dwelling chubs tend to be dwarfed; head, body, and fin contours are generally much rounded; anterior body parts are enlarged, whereas posterior portions are diminished in size; and meristic features such as fin rays, gill rakers, and scales are reduced in number. At the other extreme, lacustrine populations are characterized by a more terete body; the head is straight or concave along its dorsal contour; gill rakers are more numerous and are of greater length; pharyngeal teeth tend to be greater in number and less robust; and the reductions noted for spring chubs are not present. Chubs of the subgenus Gila possess remarkable modifications for fluviatile life. The body is streamlined with a conspicuous nuchal hump; the scales are small and deeply imbricated; and the fins are falcate with more numerous rays. The stability of these characters, on which the validity of the taxa are predicated, through time and under differing conditions has been attested to by Hubbs (1941b), Hubbs et al. (1974), and Rinne (1976).

TOPOGRAPHY AND HABITAT DESCRIPTION OF STUDY AREA

The five basins inhabited by G. b. oregonensis lie within the northern extension of the Great Basin and are collectively known as the Oregon Lakes System. In this semi-arid region of southern Oregon, the most prominent topographical features are the north-south, parallel series of uplifted fault blocks and the intervening grabens (Russell, 1884; Fuller and Waters, 1929). Four of the five basins occupy an expansive 60 km wide tectonic depression bounded on the west and east by the precipitous Winter and Abert fault scarps, respectively (Fuller and Waters, 1929; Newton and Baggs, 1971). Silver and Summer basins are found along the western margin, whereas Alkali and Abert basins border the eastern side of the depression. Smaller fault blocks and other geographical features separate these basins from one another (Donath, 1962). The long narrow Warner Basin is the result of compound faulting (Russell, 1884). Uplifted and/or down-dropped portions of fault blocks form the basin's boundaries.

Silver Basin is the lowest depression of the more encompassing Fort Rock Basin. Buck, Bridge, and Silver creeks drain the mountains to the west and flow through Paulina Marsh before reaching the Silver Lake sump. The lower courses of the creeks are much modified for irrigation, and the lake, when present, is very shallow. Salmo

gairdneri, Ictalurus nebulosus, Rhinichthys osculus, and Gila bicolor inhabit the three creeks. The chubs show a definite preference for the slower waters of the irrigation ditches and canals.

South of Silver Lake, over a divide 150 m above the valley floor, is the Summer Basin. Ana Springs, dammed in the 1920's to form a reservoir, is the major source of water. Ana River flows south from the reservoir to the broad Summer Lake playa. As the river approaches the playa, its waters become progressively more mineral-laden, as evidenced by the white alkaline salts encrusting the banks at the water's edge. The ephemeral Summer Lake is extremely alkaline and devoid of fish life (Cope, 1883; Snyder, 1908).

Both the introduced rainbow trout and the tui chub inhabit the reservoir and upper portions of Ana River. In the lower courses of the river, I observed and collected chubs but not trout. A third species, the California roach, Hesperoleucus symmetricus, was found with the tui chub. Presence of the roach most likely represents a recent introduction by live-bait fishermen, for Cope (1883), Snyder (1908), and Hubbs and Miller (1948a) made no mention of the occurrence of Hesperoleucus in the Summer Basin.

Abert Basin lies to the south of the Summer Lake playa, separated by a relatively low divide of 73 m

(Allison, 1945). The Chewaucan River, Crooked Creek, and a number of small seeps and springs drain into Abert Lake, the largest permanent body of water in the five basins.

The Chewaucan River arises in the high mountains bordering the Klamath drainage. Use for irrigation is extensive, and the river is markedly more turbid in its lower sections. Crooked Creek joins the Chewaucan a short distance before the latter spills over a small falls and enters the south end of Abert Lake. Tui chub, speckled dace, and a single largemouth bass were collected from the lower courses of the Chewaucan River, but only trout and speckled dace were found in upper Crooked Creek. The absence of chubs from the colder headwaters is not unexpected. Snyder (1917) observed that members of this species prefer the quieter portions of rivers to the swifter tributaries.

Another population of tui chubs occupies XL Spring, located 6 km north of Abert Lake. The main pool is approximately 30 m in diameter and 2 m deep, not 5 m as Snyder (1908) reported. I found on three occasions a water temperature of 18 C at one of the spring orifices. The periphery of the spring is soft mud supporting tules and rushes. Matted filamentous algae covers most of the hard rock bottom. Although bass and trout were at one time planted in XL Spring, I observed and collected only

tui chub. The number of mature chubs in the spring and marshy outflow is probably less than 500.

No fish are known to inhabit Abert Lake. Its waters are the most intensely alkaline of any lake in the five basins (Phillips and Van Denburgh, 1971). Total dissolved solids range from 20,000 to 100,000 ppm; major constituents are sodium, chloride, and carbonate ions. The lake effectively isolates the tui chub populations of XL Spring and Chewaucan River.

Twenty-five km north of Abert Lake is the Alkali Basin. In this arid region, evaporation averages five times precipitation, so that the only permanent waters containing fish are two small springs bordering the northwest edge of the playa: Hutton Spring and an unnamed spring.

Snyder (1908) supposedly collected tui chubs, which he referred to Rutilus oregonensis, from a spring in the southwest corner of Alkali Lake. However, Hubbs (1941a), Hubbs and Miller (1948a), and Waring (1908) stated that the only spring of any size containing chubs is Hutton. During a recent geological investigation of the basin, no spring (inhabited by fish) was found in the area indicated by Snyder's map (R. E. Goulding, Oregon State University, pers. comm.). Examination of N.A.S.A. high altitude infrared photographs also failed to reveal any spring in the southwest playa. I therefore conclude that Snyder's specimens were collected from Hutton Spring and that his map is in error.

Hutton Spring has recently been widened and diked to increase its water storage capacity. The present diameter is approximately 12 m; Waring (1908) recorded a maximum depth of 4.5 m. Dredging has removed all except a dense patch of rushes in the center of the pool. Only tui chubs inhabit the spring, and their numbers certainly do not exceed 300.

One half km southeast of Hutton is another spring of much smaller dimensions. Water upwells from a small orifice and is contained in a saucer shaped pool about 3.3 m across and 0.74 m deep. Water drains out onto the playa in an ill-defined channel choked with water parsley, Oenanthe. About 150 small tui chubs occupy the spring and a few deep pot-holes in the outflow channel.

Directly east of the Abert and Alkali basins, and physically separated by the 800 m high Abert fault scarp, is the Warner Basin. The valley floor contains a 60 km north-south chain of lakes. Twentymile, Deep, and Honey creeks feed the southern lakes of the series, and water then flows or seeps to the north, filling the lakes in succession. Only Crump and Hart Lakes are perennial, and because they are the first to receive stream runoff, their waters are also the lowest in mineral content (Phillips and Van Denburgh, 1971).

Of the five basins considered, the Warner Basin possess the greatest number of indigenous, endemic, and introduced

fishes. Hubbs and Miller (1948a) recognized endemic forms of Catostomus, Hesperoleucus, Rhinichthys osculus, and Siphateles obesus (= Gila bicolor). The history of trout (Salmo sp.) in the basin is not well known. Possibly only introduced rainbow trout (S. gairdneri) are now present. Four warm-water species have been introduced: Ictalurus nebulosus, Pomoxis nigromaculatus, P. annularis, and Micropterus salmoides. The tui chub abounds in the shallow turbid waters of Hart and Crump lakes.

In summary, the six populations referred to G. b. oregonensis have a wide ecological as well as geographical distribution. Chubs from the Alkali and Abert basins inhabit a small and large spring respectively. The Warner chub is lacustrine. The Silver Basin, Summer Basin, and Chewaucan River populations can be characterized as fluviatile.

HYDROGRAPHIC HISTORY

Presence of the tui chub in the Oregon Lakes System obviously requires former hydrologic connections among the five basins, but these connections were not necessarily contemporaneous nor direct. Gila bicolor inhabits all the adjoining drainage systems, and dispersal was probably circuitous, involving several intermediate basins. Cope (1883) considered the possibility of one large "Oregon Lake," which would have encompassed the Warner, Abert, Summer, and Silver basins, but current physiographic and paleo-hydrographic data do not support the existence of a pluvial lake of such magnitude.

During the last two pluvial periods of the late Pleistocene, all five basins contained lakes considerably larger than any they now possess (Russell, 1884; Waring, 1908). The first pluvial, synchronous with the Tahoe glaciation, was well advanced 46,000 years B.P. and lasted until 32,000 years B.P. (Flint and Gale, 1958; Hansen, 1961). Within this time range, the lakes of south-central Oregon attained their greatest known depths. Present evidence supports only two definite inter-basin connections: Summer-Abert and Alkali-Fort Rock (Fig. 2).

The Summer and Abert basins were united by a single body of water, Pluvial Lake Chewaucan (Russell, 1884). At its maximum depth of 113 m, the lake surface was 40 m above

Figure 2. Maximum extent of the Pleistocene lakes of south-central Oregon. Modified after Snyder et al. (1964). Heavy lines represent basin boundaries.

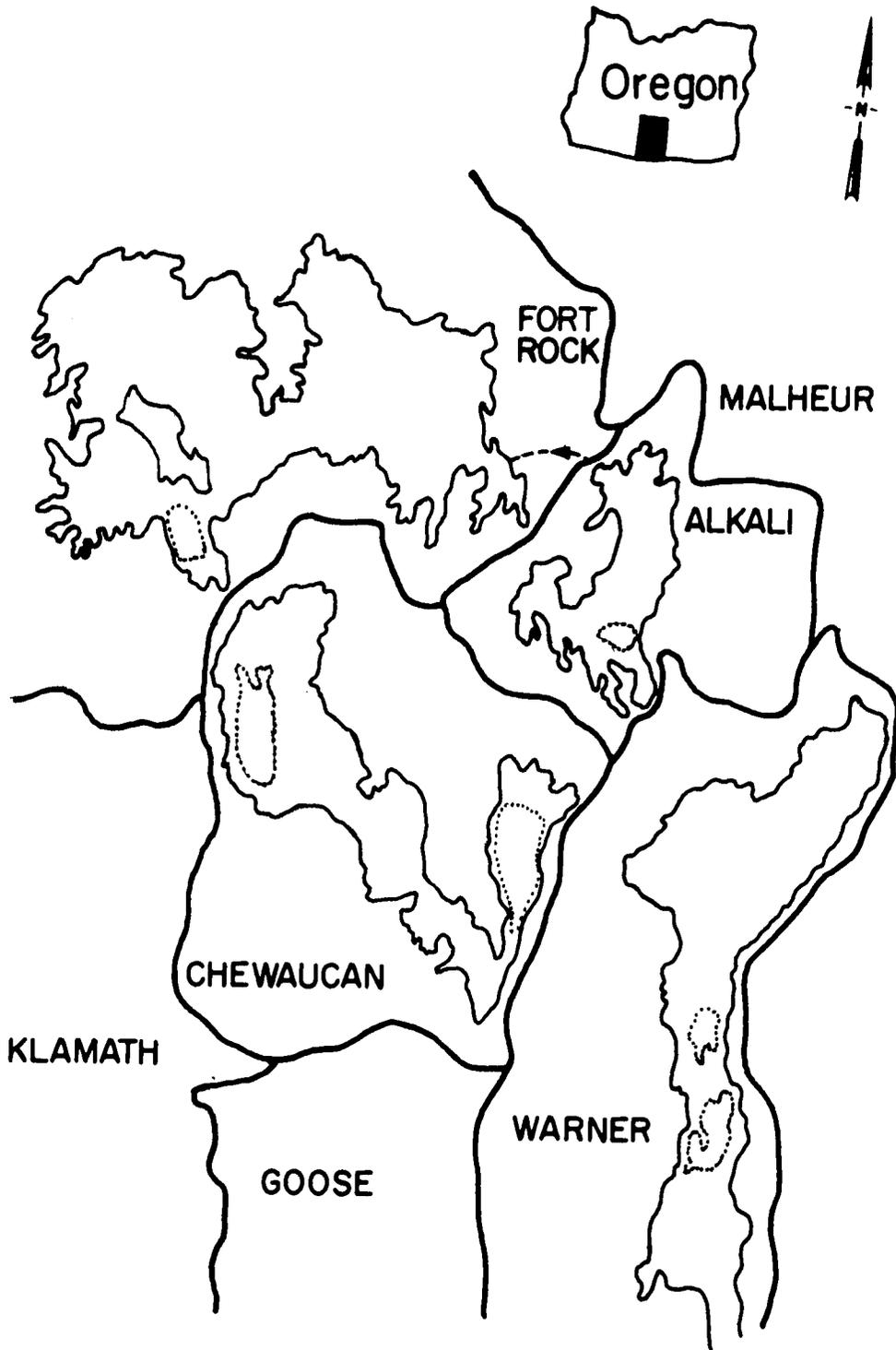


Figure 2

the divide presently separating the two drainages (Allison, 1945; 1954). This lake did not overflow into the adjoining Fort Rock Basin, although Van Winkle (1914), without providing any supporting evidence, thought the lake may have spilled into the Alkali Basin. On the basis of fish distribution and faunal affinities, Hubbs and Miller (1948a) proposed that, during a much earlier pluvial period the Chewaucan Basin had connections with one of the surrounding basins, probably Alkali.

Waring (1908) reported that the pluvial lake that occupied the Alkali Basin, reached a depth of 84 m, but he did not propose an outlet. However, I. S. Allison (pers. comm.) stated that the lake did overflow into the Fort Rock Basin.

Pluvial Lake Fort Rock inundated Silver, Thorn, Christmas, and Fort Rock valleys to a depth of 98 m (Phillips and Van Denburgh, 1971). Other than the overflow received from Pluvial Lake Alkali, the basin had no substantiated connections with the other three interior drainages. According to Hubbs and Miller (1948a), the Silver Basin tui chub most closely resembles Siphateles obesus bicolor (= Gila bicolor bicolor) of the Klamath drainage. Therefore, these authors believe that the Klamath chub may have entered Silver Basin via stream capture.

At its maximum extent, Pluvial Lake Warner reached an elevation of about 1,448 m, whereas the lowest point in

the basin boundary is 1,463+ m, located in Mule Springs Valley (Phillips and Van Denburgh, 1971). If this pluvial lake ever did overflow, the water would have drained north through the Mule Springs Valley and eventually into the Malheur Basin (Van Winkle, 1914). The lowest divides leading to the adjoining Abert and Alkali basins are at least 60 to 90 m higher than the pass to Malheur Basin.

From 32,000 to 25,000 years B.P., the climatic conditions reversed and the lakes either dried completely or were at very low levels. A second pluvial period, contemporaneous with the Tioga glaciation, commenced about 24,000 years B.P. and ended 10,000 or 12,000 years B.P. (Flint and Gale, 1958; Hansen, 1947). Lakes again filled the basins of south-central Oregon but not to the depths attained during the first pluvial. No interbasin connections are recorded. Allison (1945, 1954) stated that Pluvial Lake Winter of the Summer Basin was approximately 9 m lower than the Summer-Abert divide.

Following the end of the last glaciation, the climate became progressively more arid. The warming increased to a maximum 4,000 to 8,000 years B.P. (Hansen, 1947). Dessication was widespread and the lakes of south-central Oregon dried completely (Russell, 1884; Van Winkle, 1914). Cooler, moister conditions have prevailed for the last 4,000 years (Hansen, 1947; Heusser, 1966), although large fluctuations in lake levels have occurred (Phillips and Van Denburgh, 1971).

On the basis of the known hydrographic history, the approximate length of isolation of the six tui chub populations can be inferred. The Warner Basin chub has been isolated from the other five populations for at least 46,000 years and probably much longer. Abert and Summer populations were separated 25,000 to 32,000 years ago, as were the Alkali and Silver basin tui chubs. Chewaucan River and XL Spring populations have been isolated since the thermal maximum, 4,000 to 8,000 years B.P.

MATERIALS AND METHODS

Tui chub specimens examined in this study are retained in the fish collections of Oregon State University Department of Fisheries and Wildlife and California Academy of Sciences.

Field investigations were conducted during 1975 and 1976 to secure adequate numbers of specimens and to obtain descriptions of the habitats. A variety of collecting techniques was employed at each locality in an attempt to avoid non-random sampling of the populations: electroshocker, seine, hook and line, gill net, and minnow traps.

I examined 40 fish from each of the six populations for 21 morphometric and 12 meristic characters (Table 1). The methods of Hubbs and Lagler (1958) were used to determine counts and measurements. The technique for enumerating gill rakers was especially critical. Detection of rudiments near the ends of the upper and lower limbs necessitated complete removal of the arch for examination under 30X magnification. Often, these rudiments were embedded in surrounding tissue, and dissection was required to expose them.

Radiographs were used to determine numbers of vertebrae and vertical fin rays. In accordance with current practice, the Weberian apparatus was counted as four vertebrae and the hypural plate as one.

Table 1. Morphometric and meristic characters examined in populations of Gila bicolor from south central Oregon.

Total length
Standard length
Predorsal length
Anal-caudal length
Head length
Body depth
Pelvic-anal length
Head depth
Dorsal height
Head width
Pectoral fin length
Pelvic fin length
Caudal peduncle depth
Mandible length
Orbit width
Upper jaw length
Snout length
Dorsal fin base length
Gut length
Anterior edentulous length
Dentigerous length
Number of dorsal fin rays
Number of anal fin rays
Number of pectoral fin rays
Number of pelvic fin rays
Number of lateral line scales
Number of scales above lateral line
Number of scales from lateral line to pelvic insertion
Number of scales around caudal peduncle
Number of predorsal scales
Number of vertebrae
Number of pharyngeal teeth
Number of gill rakers

The gut was straightened and measured from its juncture with the transverse septum to the anus. Because of the coiling and elasticity of the intestine, the length was determined only to the nearest 5 mm. All other morphometric characters were measured with dial calipers to 0.1 mm.

The terminology of Uyeno (1961) is used in discussion of pharyngeal arch and tooth morphology.

In order to standardize expression of morphometric characters, I divided measurements by the standard length (SL) of their respective specimen. Each morphometric character in each of the six samples was then examined for allometric growth by plotting the standardized values against standard length. If the line deviated from the horizontal, I concluded that allometry was present. The graphed data points were also identified as to sex so as to check for sexual dimorphism.

Meristic characters and those morphometric characters that exhibited no allometry or sexual dimorphism were analyzed by the graphical methods of Hubbs and Hubbs (1953). The basal line indicates the sample range and the hatched bar outlines plus and minus two standard errors of the mean (vertical line). The graphs have been modified so that the white bar represents 0.675 standard deviations on either side of the mean. If the white bars of two samples do not overlap, the populations are considered significantly

different for that character at the 75% level, the minimum accepted value for subspecific separation of two populations (Hubbs and Hubbs, 1953).

RESULTS AND INTERPRETATION

Introduction

Prior to comparing meristic characters among populations, meristic characters within populations were examined for temporal stability. Data obtained from R. R. Miller, dated 1943, and from Snyder (1908) were compared with present meristic findings, 1975-1976. Counts I recorded from paratypes of Rutilus oregonensis were included.

Large discrepancies were found among the three different collections of Summer Basin chubs, especially in predorsal scale rows and scales around caudal peduncle (Fig. 3). In each instance, the counts of Snyder and Miller are very similar, whereas my counts are considerably lower; the magnitude of the differences are greater than required for subspecific separation. The disparity cannot be entirely attributed to differences in methods, because data from all three sources for the other populations are in close agreement.

The shift in meristic characters since 1943 is undoubtedly related to fish control operations and introductions of chubs from other basins. In 1957, 1961, and 1970, the Summer Basin tui chub was the object of a "rough fish" eradication program, however the three rotenone treatments were not completely successful. Scuba divers reported that

Figure 3. Variation in (a.) the number of scales around caudal peduncle and (b.) in the number of pre-dorsal scales in Gila bicolor from Summer Basin, Oregon. Dates indicate year of collection. See page 24 for explanation of figure.

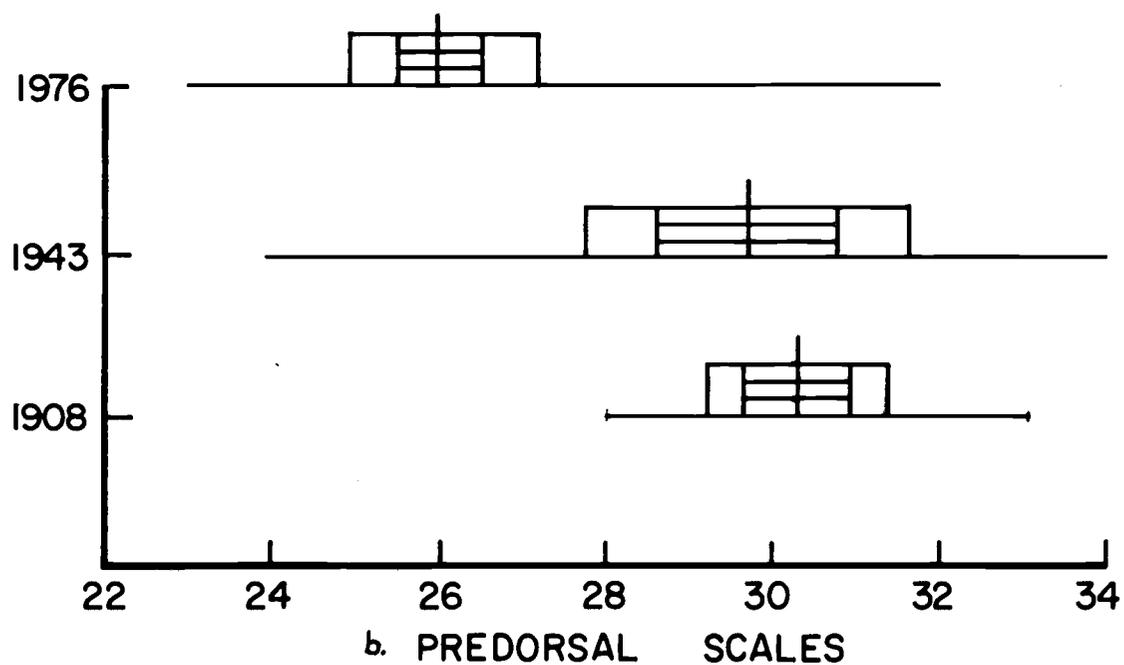
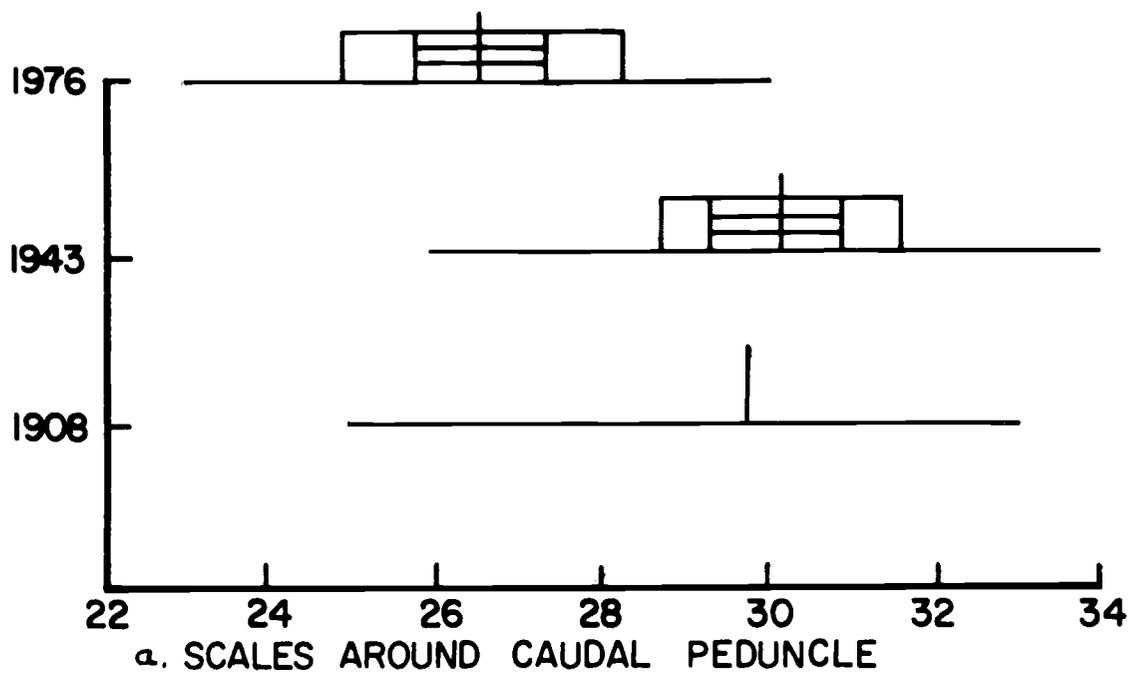


Figure 3

a small number of chubs retreated deep into the springs of Ana Reservoir and therefore avoided poisoning (R. Swan, Oregon Department of Fish and Wildlife, pers. comm.). The variation in these few surviving chubs was possibly not representative of the original population. The second probable cause is that fishermen, using live minnows for bait, introduced chubs from one of the surrounding basins. The recent appearance of the roach, Hesperoleucus symmetricus, strongly suggests this possibility. Subsequent intergradation between the resident and introduced tui chubs could have contributed to the significant shift in meristic characters.

The tui chub and roach were collected together in late June in the lower section of Ana River. The water temperature was 17 C, and males and females of both species were in breeding condition. I suspect but did not observe spawning between these two cyprinids, nor did I find any specimens intermediate in character, which would intimate past hybridization.

The uncertain nature of the Summer Basin "chub" precludes interpretation and comparison of the data from that population.

Vertical and Paired Fin Rays

The narrowest range of any meristic character is in the number of dorsal fin rays, there being eight or nine.

The XL Spring, Hutton Spring, Chewaucan River, and Silver Basin populations are modal at eight, which is typical of the species. In contrast, the Warner chub is modal at nine. When presented in the graphical form of Hubbs and Hubbs (1953), the data reveal significant separation of the Warner populations from all except the Silver Basin collection (Fig. 4). The trend toward nine dorsal fin rays is exhibited by only two other populations of Gila bicolor: G. b. columbiana and G. b. formosa, also a lacustrine chub.

Anal fin ray counts range from seven to nine. All populations are modal at eight. Only three of the 200 chubs examined had nine. No significant difference among the populations was found for this character. Nor do the means reflect a consistent trend toward a reduction of anal fin ray number in spring populations; the Hutton Spring and XL Spring samples have the highest and lowest means respectively (Table 2). These results contrast with the

Table 2. Frequency and mean of anal fin ray counts in populations of Gila bicolor from south-central Oregon.

Locality or basin	Frequency			Mean
	7	8	9	
Warner Basin	2	38		7.950
Hutton Spring	1	37	2	8.025
Silver Basin	1	39		7.975
XL Spring	10	30		7.750
Chewaucan River	5	34	1	7.900

Figure 4. Variation in the number of dorsal fin rays in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

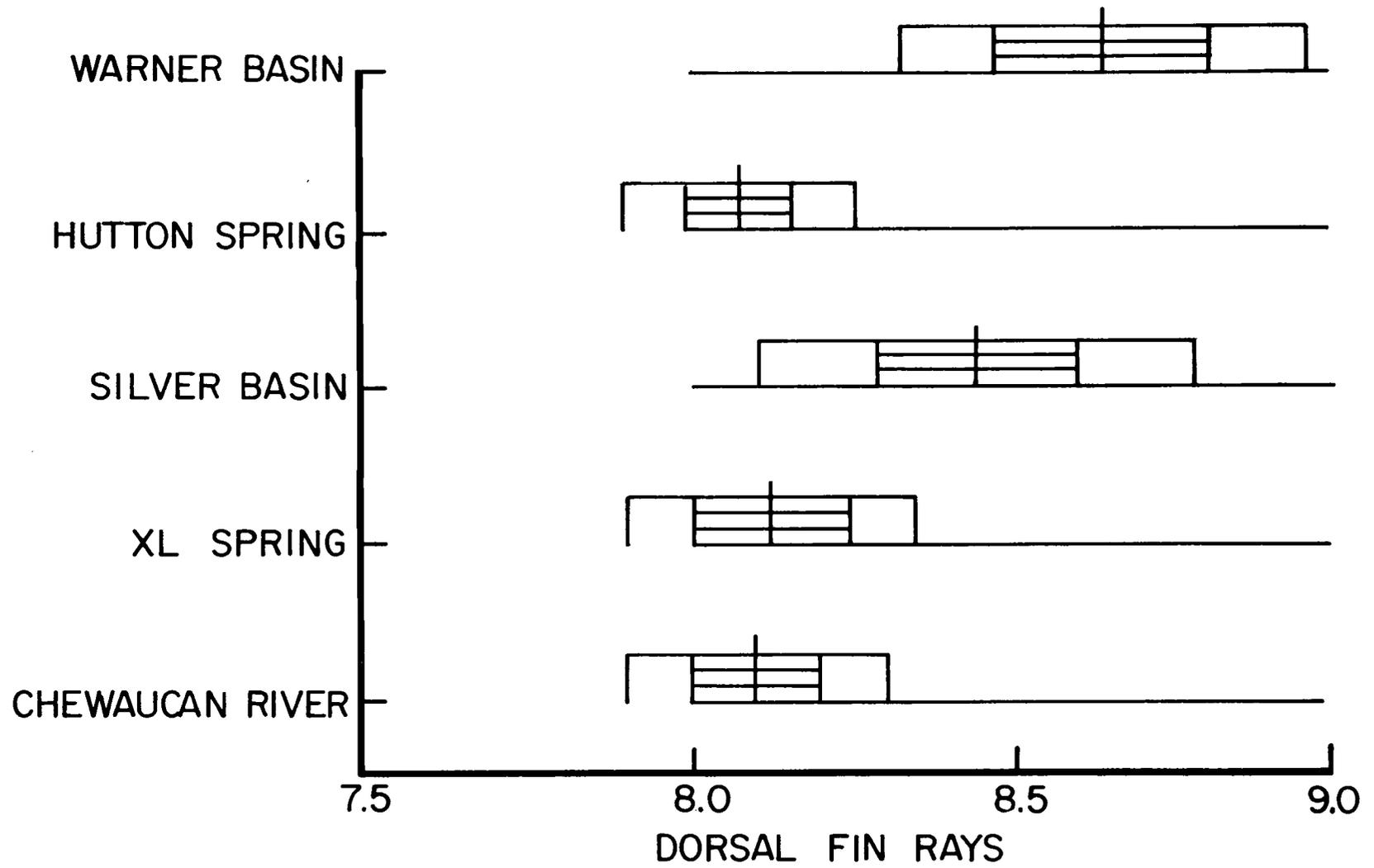


Figure 4

findings of Hubbs et al. (1974) for three spring tui chubs of north-central Nevada: G. b. euchila, G. b. isolata, and G. b. newarkensis. The anal fin ray counts of these three subspecies are modal at seven with occasional counts of six, whereas their fluviatile and lacustrine conspecifics are modal at eight.

Examination of paired fin ray data disclosed no significant differences, and the trends within the two characters are contradictory. Pectoral fin ray counts of 16 occur in highest frequency in all samples except Hutton Spring, which is modal at 15; the lowest count recorded for any tui chub population (Table 3). An expected concomitant reduction of pelvic fin rays for either spring population is not

Table 3. Frequency and mean of pectoral fin ray counts in populations of Gila bicolor from south-central Oregon.

Locality or basin	Frequency				Mean
	15	16	17	18	
Warner Basin	2	22	13	3	16.425
Hutton Spring	21	14	3	2	15.650
Silver Basin	4	24	10	2	16.250
XL Spring	4	22	12	2	16.300
Chewaucan River	7	25	7	1	16.050

observed. Approximately 60% of the XL Spring specimens have counts of 10, whereas the remaining populations are modal at nine (Table 4). Within this latter group, the Hutton Spring population has the highest mean. The data

Table 4. Frequency and mean of pelvic fin ray counts in populations of Gila bicolor from south-central Oregon.

Locality or basin	Frequency			Mean
	8	9	10	
Warner Basin	2	30	8	9.150
Hutton Spring		26	14	9.350
Silver Basin	3	34	3	9.000
XL Spring		17	23	9.575
Chewaucan River	1	29	10	9.225

appear to indicate a tendency for an increase of pelvic fin rays and a decrease of pectoral fin rays in spring dwelling chubs. Hubbs et al. (1974) presented evidence supporting the opposite trend.

In summary, fin ray characters are of relatively low value for discriminating among the five populations. Counts from all samples overlap considerably, and the maximum separation of means for any of these four characters does not exceed one fin ray. The anticipated reduction of fin ray numbers in spring populations is not realized for every character. Within a given population, the number of dorsal, anal, pectoral, and pelvic fin rays appears to vary independently, and there is no consistency in the pattern of variation from one sample to the next. The discrepancies for individual characters noted above between my findings and those of Hubbs et al. (1974) are exemplary. However, when the means of all four counts are totaled for each population, the predicted trends emerge (Table 5). In

Table 5. Total mean number of fin rays in populations of Gila bicolor from south-central Oregon.

Locality or basin	Total mean number of fin rays
Warner Basin	42.200
Hutton Spring	41.100
Silver Basin	41.675
XL Spring	41.750
Chewaucan River	41.275

spite of the inconsistency among individual characters, the Hutton Spring sample, as expected, possess the lowest overall fin ray number, whereas the Warner population has the highest total average. The divergence of these two populations is commensurate with the disparity of their respective habitats. The greater total fin ray number of XL Spring chubs over their Chewaucan River congeners appears contrary to the above mentioned trends, but the difference between the two means is very small, less than 0.5 fin rays.

Scale Rows

Only two of the five scale counts are of discriminating value (Figs. 5, 6). Chubs from the Warner and Silver basins have significantly fewer scale rows around the caudal peduncle than do specimens collected from the Chewaucan River. The Warner Basin population also differs significantly in this character from the XL Spring chub. The differences among samples in the number of scales from

Figure 5. Variation in the number of scales from lateral line to pelvic fin insertion in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

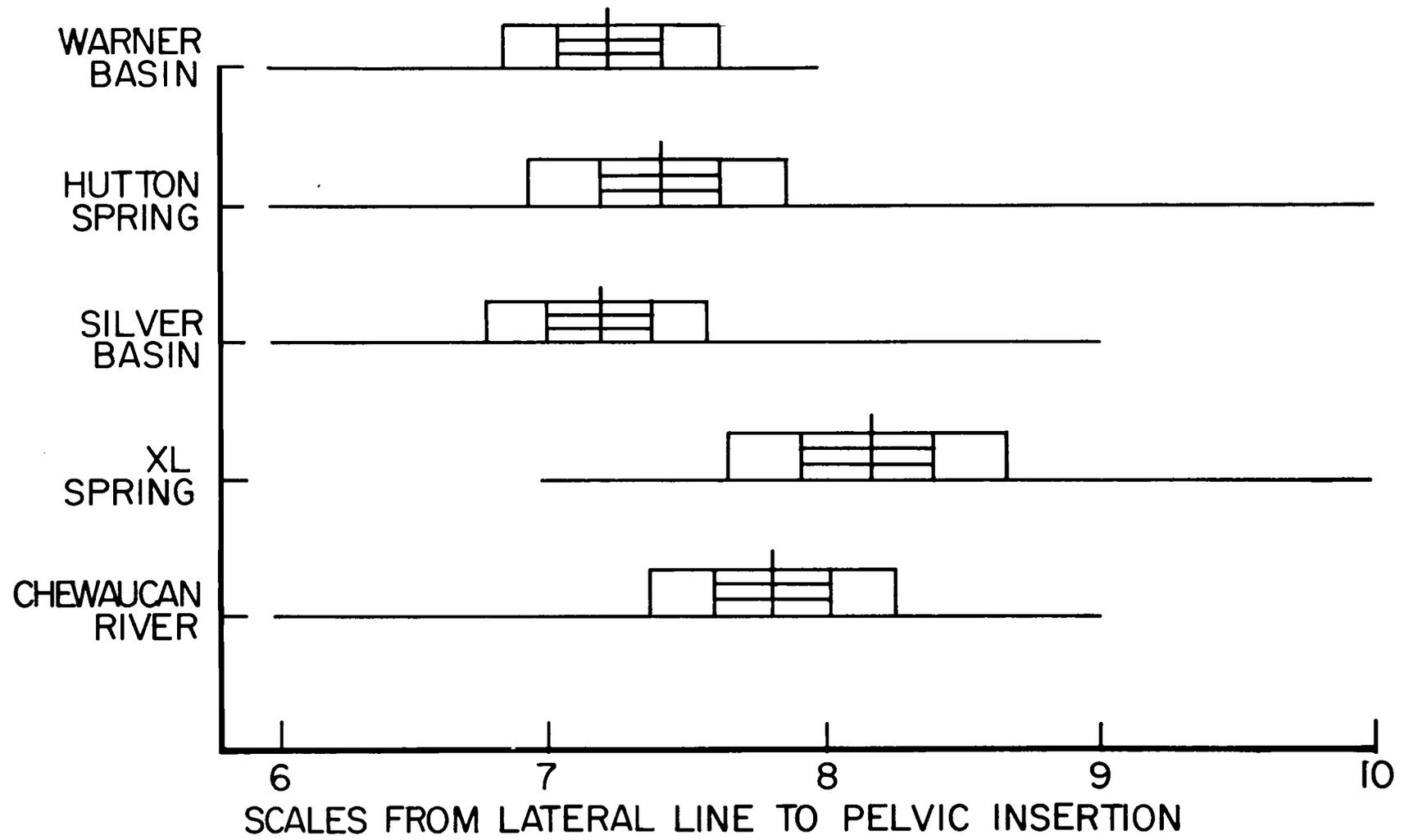


Figure 5

Figure 6. Variation in the number of scales around caudal peduncle in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

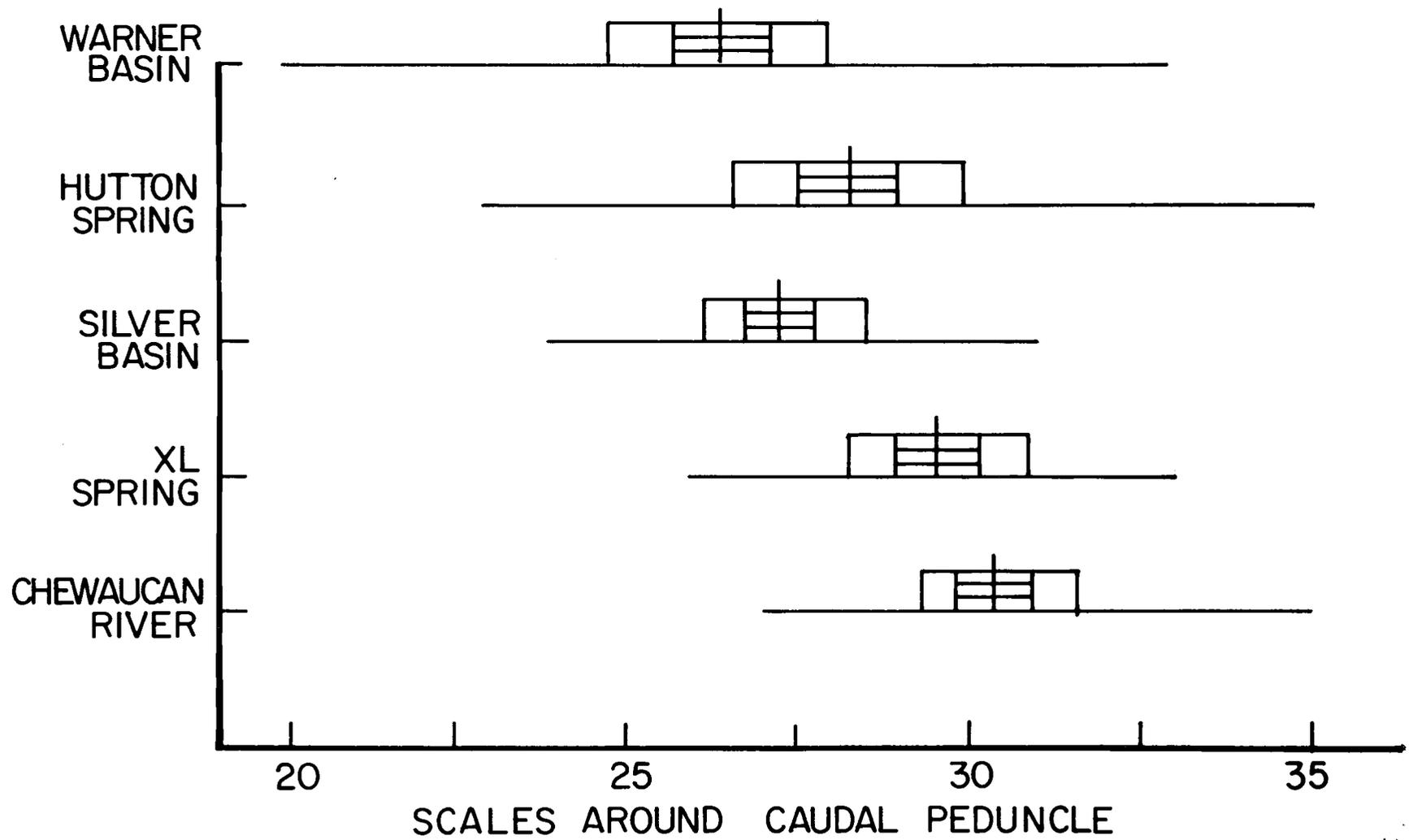


Figure 6

lateral line to pelvic fin insertion are less distinct. Separation of the XL Spring chubs from the Warner and Silver basin chubs is barely significant. There is wide overlap among the five populations in the remaining scale counts.

As opposed to fin ray characters, the pattern of variation of scale counts is more consistent. The relative position of the means of each of the five populations is fairly constant for every scale character. The Chewaucan River sample has the highest mean number of scales in four of the five scale counts. The two spring samples are consistently intermediate in scale numbers, and without exception, the Silver or Warner basin chubs possess the lowest mean scale counts. When the means of all five counts are totaled for each population, this same pattern is evident (Table 6). With respect to all five populations, these results do not exhibit the expected trend for lower meristic counts in spring chubs. However,

Table 6. Total mean number of scales in populations of Gila bicolor from south-central Oregon.

Locality or basin	Total mean number of scales
Warner Basin	125.250
Hutton Spring	130.025
Silver Basin	125.200
XL Spring	130.875
Chewaucan River	133.950

the XL Spring population does show a small reduction in total scale number relative to its presumed ancestor of the Chewaucan River.

Examination of scale structure revealed no consistent differences in scale shape or in the number and distribution of radii. The typical scale is well imbricated and characterized by a strong basal shield, well defined shoulders, and radii in the apical field only.

Vertebrae

Vertebral number does not vary significantly among the five populations. The majority of counts (94%) range from 39 to 41. The Silver Basin, Chewaucan River, and XL Spring populations have modes of 40, whereas the Hutton Spring population is modal at 41, the highest reported for Gila bicolor (Table 7).

Table 7. Frequency and mean of vertebral counts in populations of Gila bicolor from south-central Oregon.

Locality or basin	Frequency						Mean
	37	38	39	40	41	42	
Warner Basin	1		10	21	7	1	39.90
Hutton Spring	1	1		10	21	7	40.75
Silver Basin			12	25	3		39.77
XL Spring			4	19	17		40.32
Chewaucan River			11	22	6	1	39.92

Gill Rakers

The value of gill rakers for discriminating among the numerous populations of Gila bicolor is well documented (Hubbs et al., 1974). The disparity in both gill raker number and form among the populations reflects the wide trophic divergence of this polytypic species. Lacustrine forms, subsisting mainly on zooplankton, possess up to 40, long closely spaced gill rakers. Omnivorous tui chubs, especially spring dwellers, bear as few as eight gill rakers, and many of these tend to be stubby or reduced to rudiments.

Gill raker number is of greater importance than gill raker form for distinguishing the populations under present study. Counts range from nine to 23. In consonance with the above mentioned trends, the XL Spring and Hutton Spring populations possess the lowest mean gill raker number. Both populations are modal at 12 and approximately 12% of their specimens have 11 or fewer rakers. These results are comparable to the findings of Hubbs et al. (1974) for G. b. euchila, G. b. isolata, and G. b. newarkensis.

Chewaucan River and Silver Basin populations average about one gill raker higher than the spring populations. The difference between the spring and river chubs is mainly the result of a shift in the modes from 12 to 14 rather than an upward extension of the range in the latter group.

Gill raker counts of the Warner Basin chub are the most distinctive for any character examined. This lacustrine population possesses significantly greater number of gill rakers than the other four populations (Fig. 7). Maximum overlap of ranges of gill raker number with the spring or river chubs is two rakers. There is no overlap with the topotype population of G. b. oregonensis, XL Spring. Of the currently recognized subspecies, only G. b. mohavensis and G. b. pectinifer exceed the Warner chub in mean gill raker number.

Separation of adjoining gill rakers is least at the juncture of the upper and lower gill arch limbs, the space being equal to or slightly greater than the width of a gill raker base. The inter-gill raker distance increases to a maximum about halfway down the lower limb. In this region, the separation is 1.5 times the width of a gill raker base in Warner chubs, 2.0 to 2.5 in Chewaucan River and Silver Basin chubs, and 3.0 to 4.0 in XL Spring and Hutton Spring chubs.

Warner Basin and Silver Basin chubs have relatively longer gill rakers than the Chewaucan River population, but not consistently longer than the XL Spring or Hutton Spring populations. Gill raker length is extremely variable among individuals from these two springs. The length of gill rakers ranges from less than half to slightly greater than those found in chubs from Warner Basin. Regardless of

Figure 7. Variation in the number of gill rakers in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

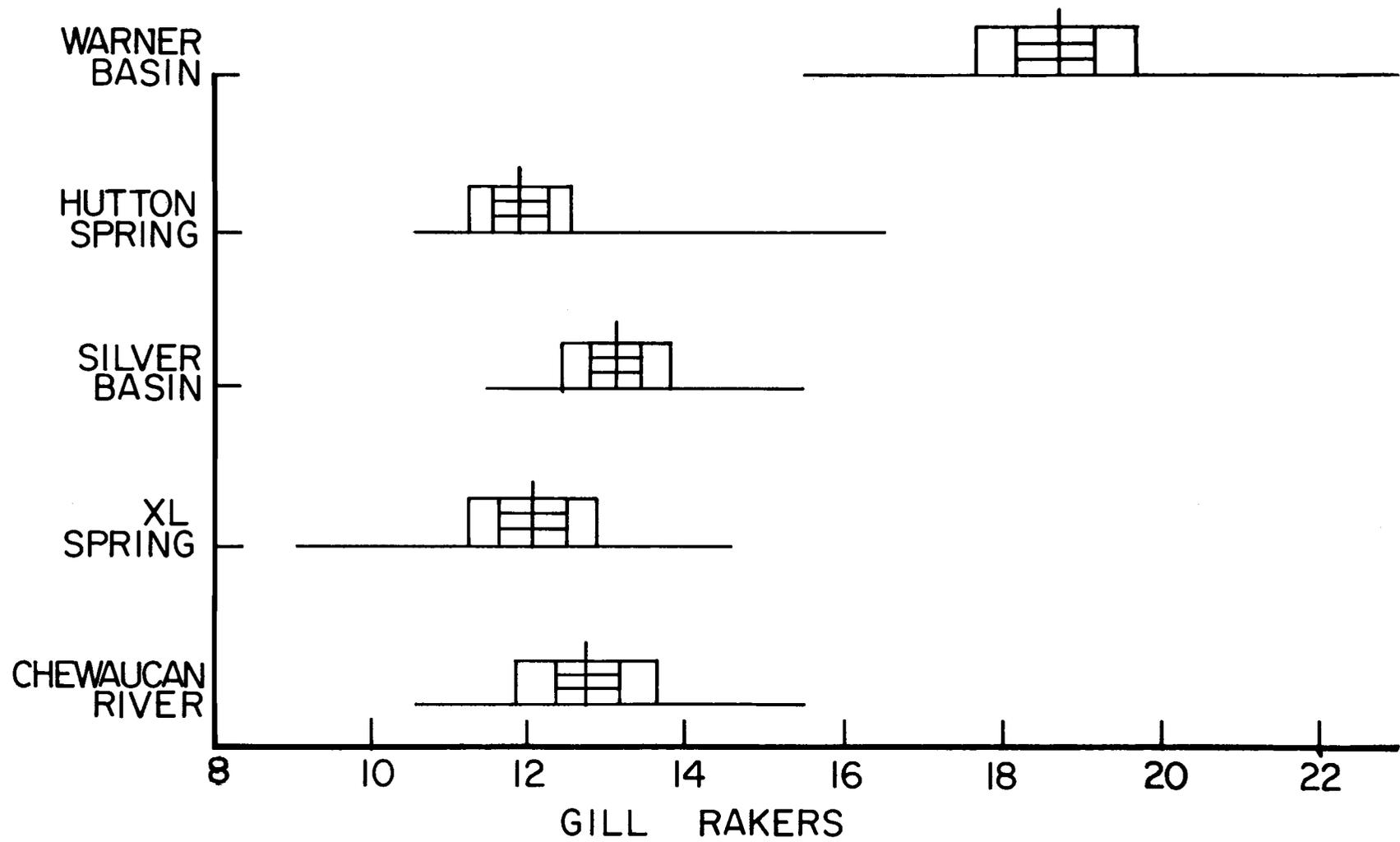


Figure 7

length, the gill rakers of the XL Spring and Hutton Spring chubs appear unsuited for any straining function. Instead of being directed cephalad and therefore extending beyond the anterior edge of the arch, the rakers, especially the longer ones on the lower limb, project sharply downward and then curve medially.

The tissue between the inner and outer gill raker rows is greatly thickened in specimens from the two springs. In freshly caught specimens, this tissue appears white, puffy, and somewhat papillose. No chubs collected from the other basins exhibited this degree of thickening of gill arch tissue.

Pharyngeal Arch and Teeth

There is little variation in either pharyngeal tooth number or formula (Table 8). Approximately 92% of all

Table 8. Frequency of pharyngeal tooth formulae in populations of Gila bicolor from south-central Oregon.

Locality or basin	Frequency				
	3-4	4-3	4-4	5-4	5-5
Warner Basin			2	37	1
Hutton Spring			2	38	
Silver Basin		1	5	34	
XL Spring			1	37	2
Chewaucan River	1		2	37	

specimens examined bear five teeth on the left arch and four on the right (5-4), which is, with the notable exception of

G. b. pectinifer, a characteristic of the species. Snyder (1908), in the original description of oregonensis, gave the normal pharyngeal tooth formula as 4-5, but his convention for expressing tooth distribution is the reverse of that currently used.

Variants found are 3-4, 4-3, 4-4, and 5-5. Of these, 4-4 is the most numerous. The loss of tooth V on the left arch appears to produce this symmetric condition. Three specimens with the formula 5-5 represent the only observed cases of supernumerary teeth. The reduction of tooth number to three on either arch is very uncommon. Although 4-3 has previously been recorded from populations of Gila bicolor, the reverse condition, 3-4, has not. The presence of only three teeth on the left arch is a rare occurrence among North American cyprinids (Hubbs et al., 1974). The 3-4 formula is also of interest, because it is an exception to the empirical generalization of Hubbs and Hubbs (1945): the sinistrality of bilateral asymmetrical counts.

A few aberrant arches were found in the collections from Silver Lake and Chewaucan River basins. There are as many as eight teeth on a single arch variously arranged in what could erroneously be interpreted as two rows. These anomalous or "additional" teeth are quite unlike those characteristically found in the minor row of chubs of the subgenus Gila. The typical minor row teeth are relatively small, spike-shaped, and lateral to the major row, whereas

the anomalous teeth discovered in the present collections are large, irregularly arranged, and medial to the major row. Additional teeth or tooth rows have been found in other cyprinid species (Evans and Deubler, 1955; Eastman and Underhill, 1973). Evans and Deubler (loc. cit.) attributed the presence of additional teeth to a dysfunction of the natural tooth replacement process. The replacement tooth becomes ankylosed to the arch, but the original tooth fails to detach.

Pharyngeal arch and tooth morphology, generally typical of the subgenus Siphateles as described by Uyeno (1960), differs remarkably among populations referred to this single subspecies. The most divergent and unique arch and teeth are those of the Hutton Spring chub. Of the four populations, that from the Warner Basin contrasts most sharply with the Hutton Spring population (Fig. 8). In every respect, the arch and especially the teeth of the Hutton Spring chub are considerably more robust for a given standard length or arch length. Bases of these teeth, which form the dentigerous area of the arch, are greatly swollen. Only the teeth of a few large specimens, greater than 150 mm SL, from XL Springs approach this degree of development. In marked contrast, the arch of the Warner Basin chub is lighter and more attenuate. The teeth are greatly reduced in size, laterally compressed, and are without the enlarged bases. Hubbs et al. (1974) and Snyder (1918) noted a

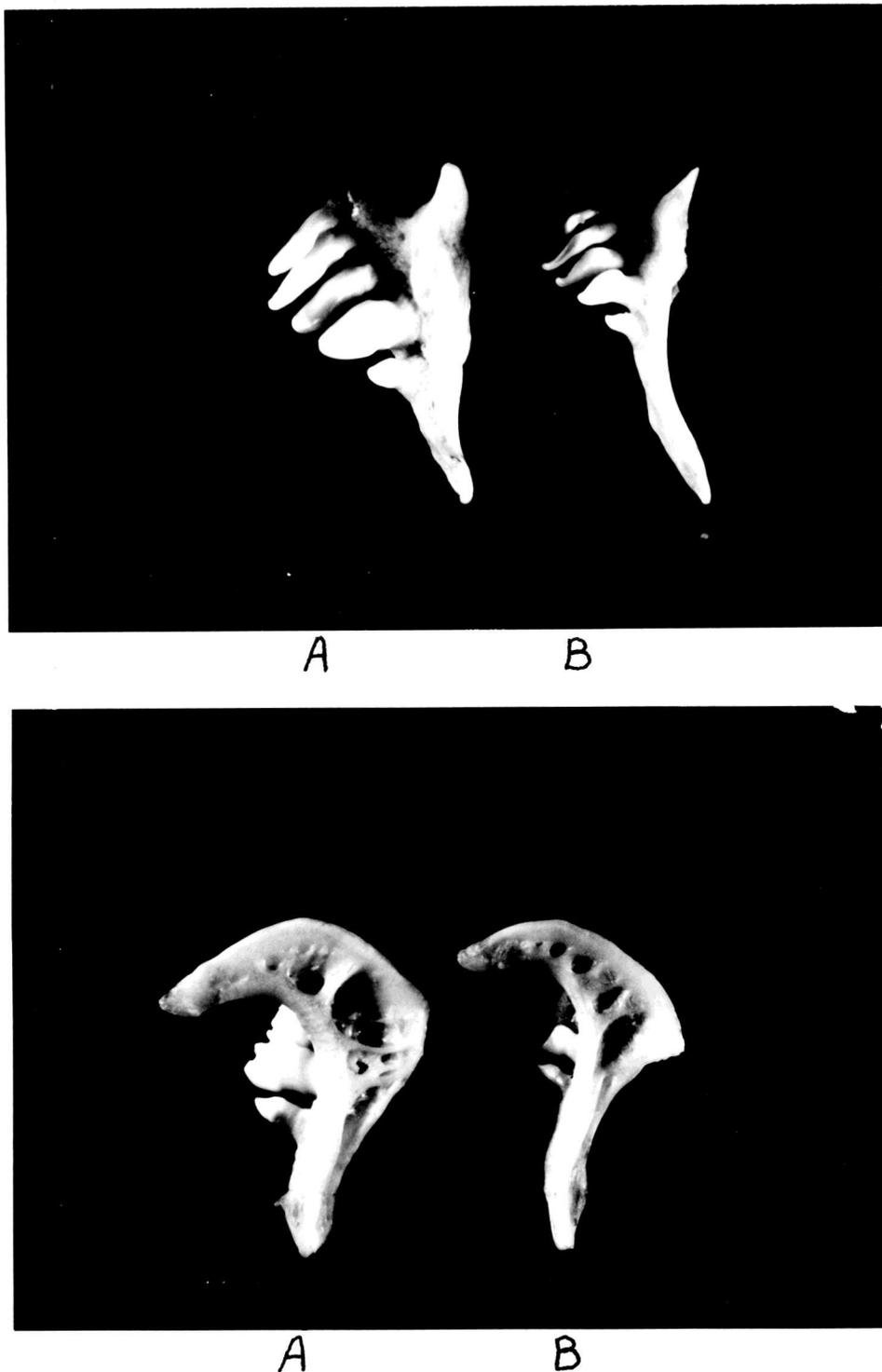


Figure 8. Dorsal, lateral, and mesial aspects of the left pharyngeal arches of two populations of Gila bicolor from south-central Oregon. A, Hutton Spring tui chub; B, Warner Basin tui chub.



A

B

Figure 8. Continued.

relatively less robust arch and teeth in the lacustrine chub G. b. pectinifer than in its congener G. b. obesa. The former authors consider the lighter arch to be an adaptation parallel to numerous gill rakers for a planktivorous diet. Hopkirk (1973) noticed this same trend.

The ventral contour of the arch, from the anterior angle to the tip of the anterior limb, is concave in Warner Basin chubs and straight or slightly concave in Hutton Spring chubs. This difference in arch profiles reflects to some degree the development of a shield at the posterior end of the anterior limb. A shield is most consistently present in specimens from XL Springs and Warner Basin, and poorly developed or absent in the collection from Hutton Spring. Other populations are intermediate in shield development.

Equally as remarkable as the gross disparity in tooth size is the difference between Warner Basin and Hutton Spring chubs in the relative length of the anterior edentulous process. In Warner Basin specimens, this untoothed portion of the anterior limb is elongate, approximately equal in length to the dentigerous surface. The ratio of these two measurements remains fairly constant with growth. The same process in Hutton Spring chubs is greatly abbreviated, however the fundamental difference is that the ratio of the anterior edentulous length and dentigerous length changes drastically with growth in this spring population

(Fig. 9). As the standard length increases, the size of the teeth increases at a faster rate than does the anterior limb.

Interosseus Space

In specimens from XL Spring and Hutton Spring, the interosseus space, an aperture in the pectoral girdle bordered by the coracoid and cleithrum, is often greatly reduced or absent. The other populations show no tendency towards reduction. Starks (1930) stated that the interosseus space is present in the typical teleost pectoral girdle, yet in a single specimen of Cyprinus carpio he found the space present on one side and absent on the other. No functional significance is presently attributed to this structure.

Morphometrics

Morphology of the trunk, fins, and especially the head is of the utmost value for discriminating among the populations. The morphology of certain populations under present study is so distinct that small samples or even individuals can be correctly assigned to their respective localities solely on the basis of external examination. That differences are found in these tui chubs from diverse environments is not unexpected, for the correlation between body form and habitat type is well established for this species.

A number of distinguishing features of the head, which I did not quantify, are discernible in Figure 10. In the

Figure 9. Relationship between dentigerous length/anterior edentulous length and standard length for two populations of Gila bicolor from south-central Oregon. Lines fitted by least-squares method.

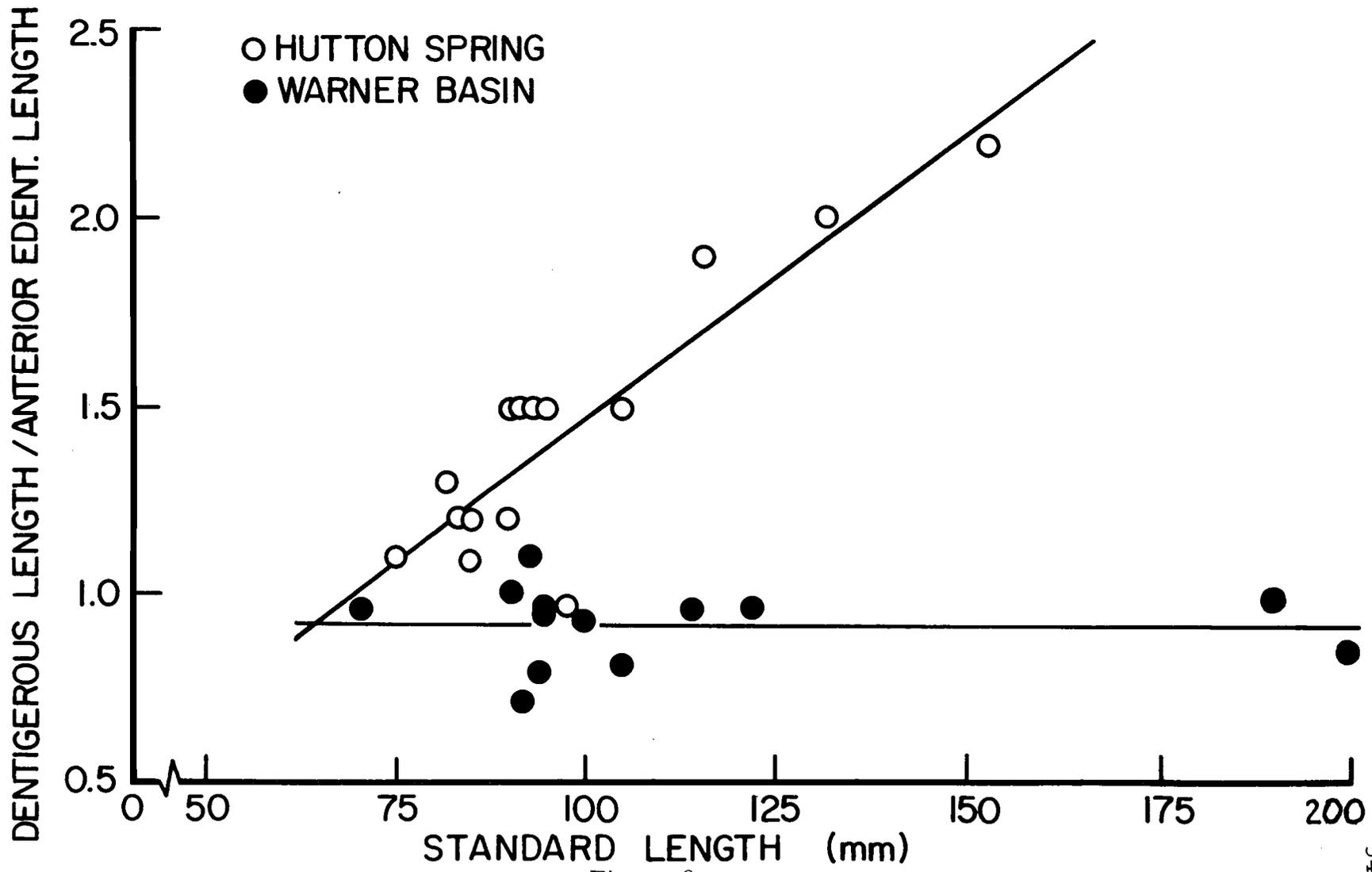


Figure 9



Figure 10. Representative specimens of five populations of Gila bicolor from south-central Oregon. A, XL Spring; B, Chewaucan River; C, Hutton Spring, D, Silver Basin; E, Warner Basin.

typical Hutton Spring chub, the dorsal contour of the head, from snout to occiput is distinctly convex, whereas the ventral outline is broken by the sharply angled oblique mouth. The Chewaucan River and XL Spring chubs are the most similar in general body form than any other two populations. The heads are subconical. Dorsal and ventral contours are symmetric about the longitudinal axis, and the snout is gently rounded. The moderately oblique mouth does not disrupt the conformation. In contrast, the head of the Warner Basin chub is markedly angular. The straight to slightly concave dorsal outline combined with the long oblique mouth produces the distinct profile. These last remarks apply to a lesser degree to the Silver Basin chub, which the Warner Basin chub most closely resembles.

The Hutton Spring chub has a significantly longer head than either the Chewaucan River or Silver Basin chubs (Fig. 11). Although Figure 11 indicates significant separation of the Hutton Spring and XL Spring populations, the difference is not conclusive. The problem with the comparison stems from the limited size range overlap between the two samples. The collection from XL Spring contains predominantly large chubs, greater than 140 mm SL, whereas Hutton Spring chubs rarely exceed 120 mm SL. The lack of Hutton Spring specimens greater than 120 mm SL precludes direct comparison with the majority of the XL Spring collection. Within the common size range of 50 mm to 120 mm

Figure 11. Variation in the length of head in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

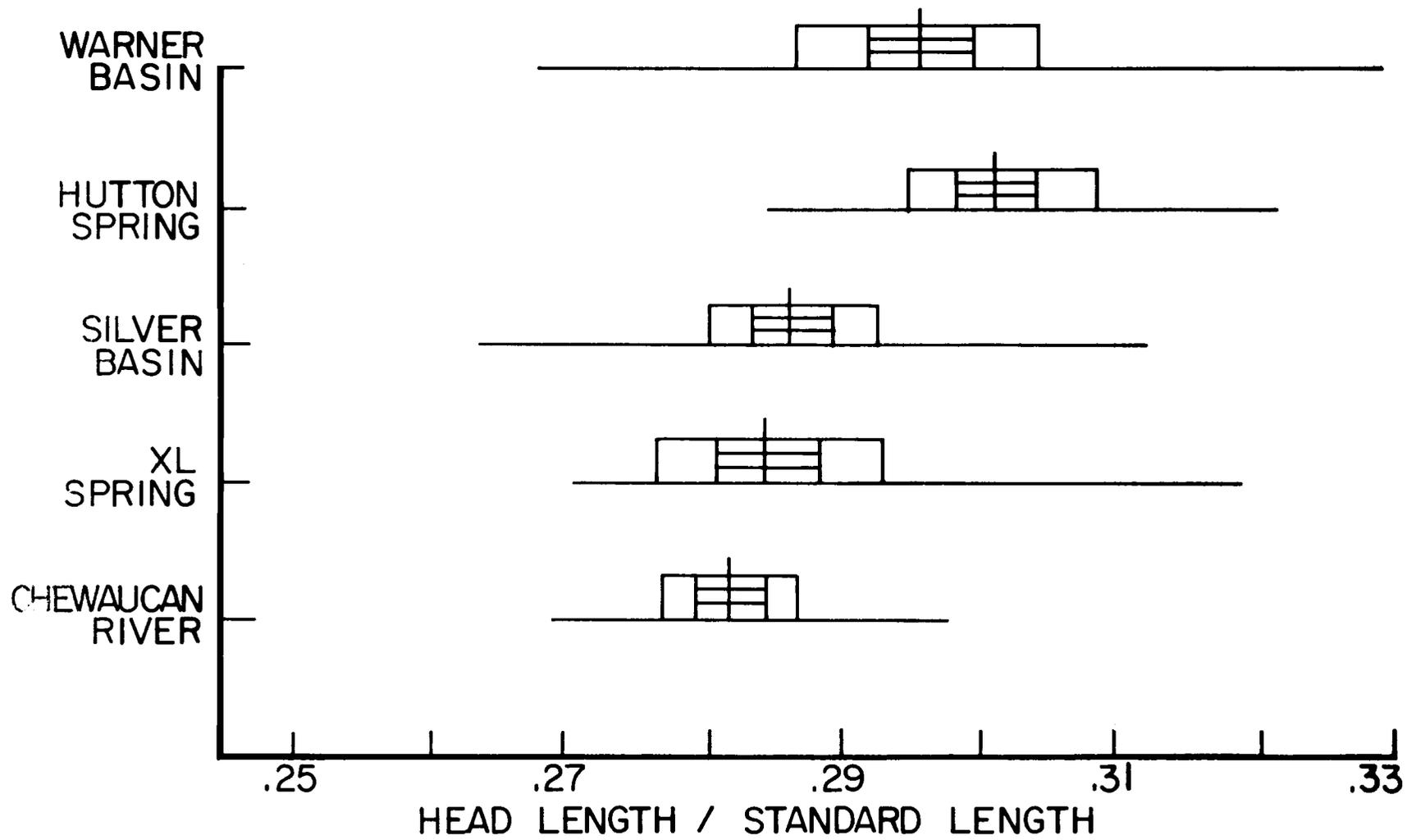


Figure 11

SL, the populations appear separable. The situation is further complicated by the apparent increased variability of head length-standard length ratio, HL/SL, in larger XL Spring chubs. The greater HL/SL of these larger fish is unlikely due to allometry. Plots of head measurements of chubs from other basins exhibit no allometry or a slight negative relationship between HL/SL and SL, not positive as suggested by the XL Spring data. HL/SL data presented by Hubbs et al. (1974) showed a slight inverse relationship with standard length.

The separation of Warner Basin and Chewaucan River populations on the basis of head length is not definite. The difference can be negated by a single datum point.

Hutton Spring chubs are also distinct with respect to depth of head (Fig. 12). Members of this population have deeper heads than chubs from Warner, Chewaucan, or Silver basins. The difference between Silver Basin and XL Spring populations is borderline and is complicated by the same factors mentioned for head length.

Orbit width is one of the most diagnostic morphometric features. Separation of the Hutton Spring population from the Chewaucan River and Silver Basin populations is greater than 90% (Figs. 13, 14). Hutton Spring chubs also have a greater orbit width than XL Spring chubs of the same standard length, but the disparity in size ranges of the two collections again precludes definite separation (Fig. 15).

Figure 12. Variation in the depth of head in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

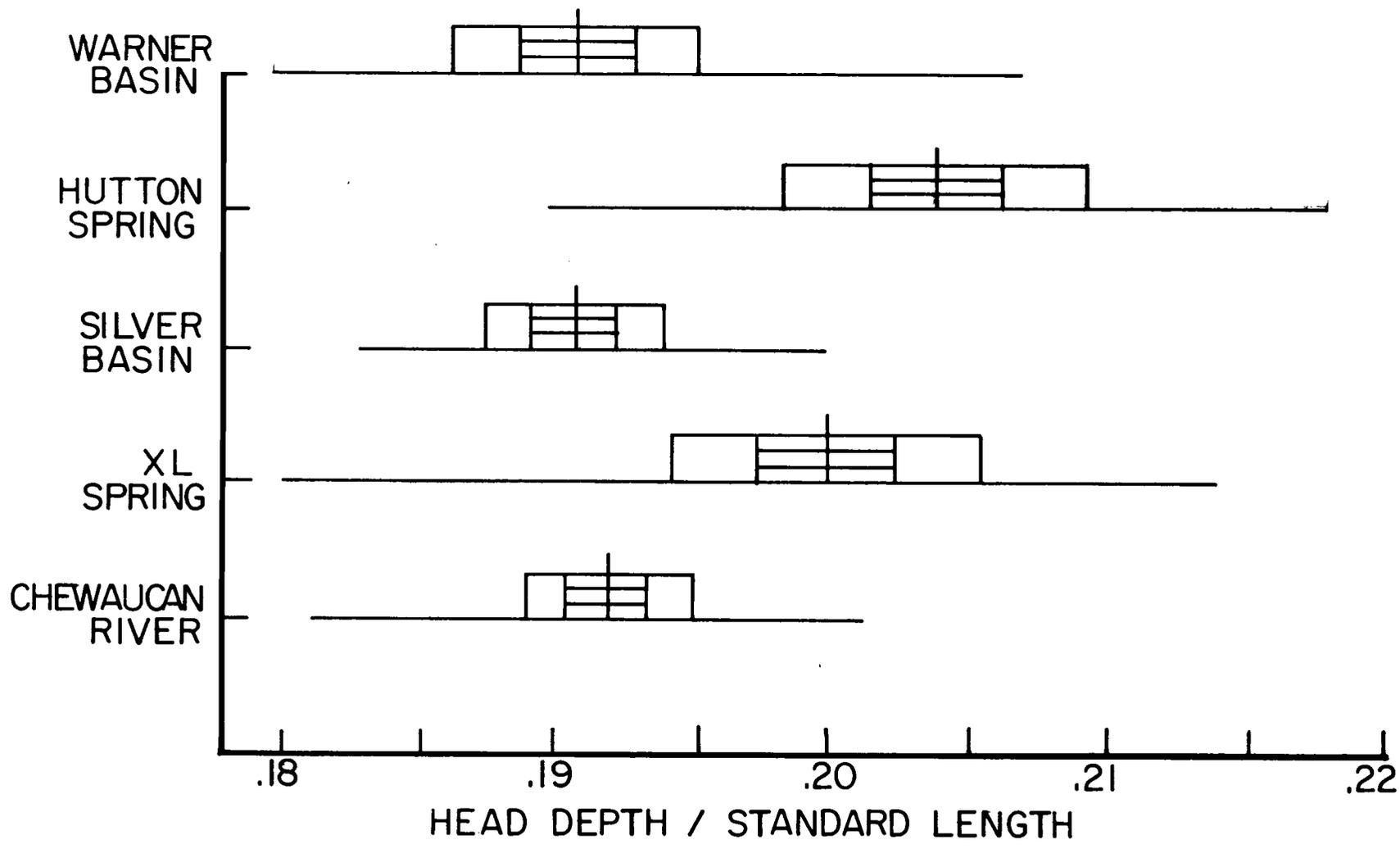


Figure 12

Figure 13. Relationship between standardized orbit width and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

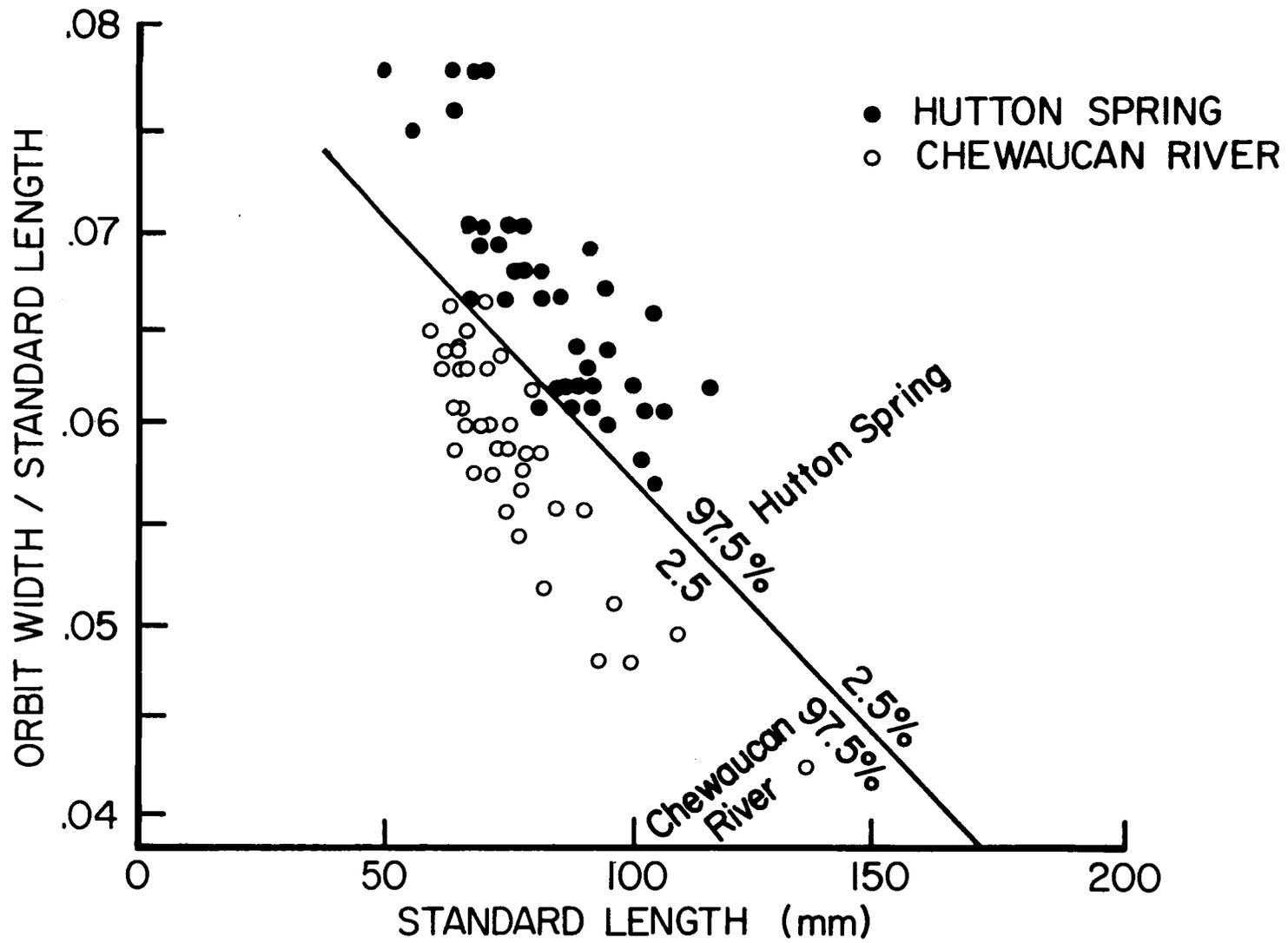


Figure 13

Figure 14. Relationship between standardized orbit width and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

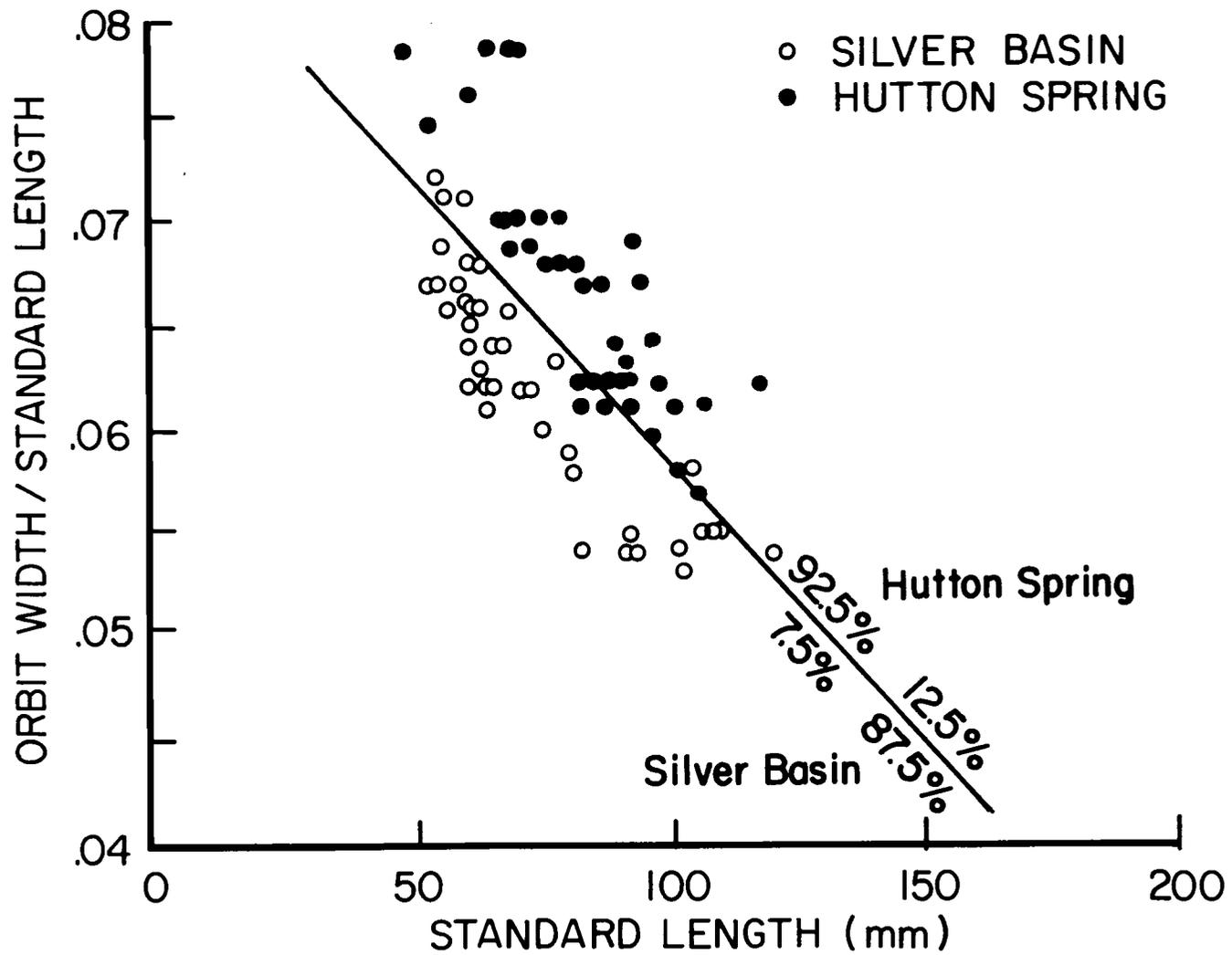


Figure 14

Figure 15. Relationship between standardized orbit width and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

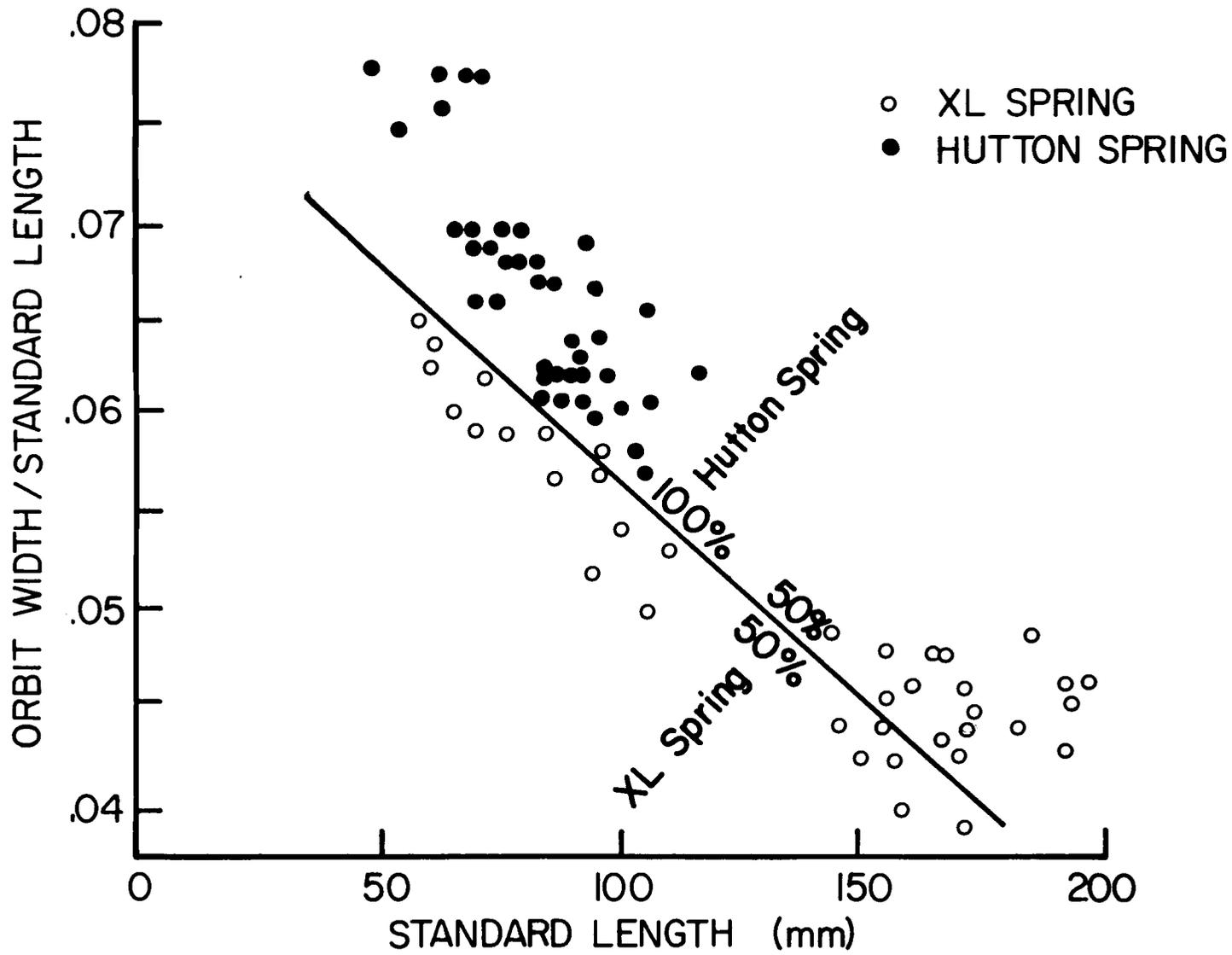


Figure 15

Mandible length is significantly greater in chubs from the Warner Basin than in those from the Chewaucan River and XL Spring (Fig. 16).

There is wide overlap among populations for most of the remaining head measurements. The only character in which populations show definite divergence is that of head width (Fig. 17). Chubs from the two springs and the Chewaucan River exhibit a trend toward wider heads than the other populations.

Only two measurements of the trunk are of discriminating value. Warner Basin chubs differ significantly from the XL Spring chubs in having a greater predorsal length (Fig. 18). Pelvic-anal length is of somewhat greater importance; the XL Spring population exceeds the Warner Basin, Hutton Spring, and Silver Basin populations in this measurement (Fig. 19). Anal-caudal length, body depth, and caudal peduncle depth do not differ significantly among samples.

Comparison among populations of pectoral, pelvic, and dorsal fin measurements is complicated by sexual dimorphism and to a lesser extent by allometry. For those characters in which sexual dimorphism is present, comparison between some populations is not possible because of widely disparate sex ratios. Composition of the XL and Hutton spring samples are noteworthy in this respect; both contain a great majority of females.

Figure 16. Variation in the length of mandible in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

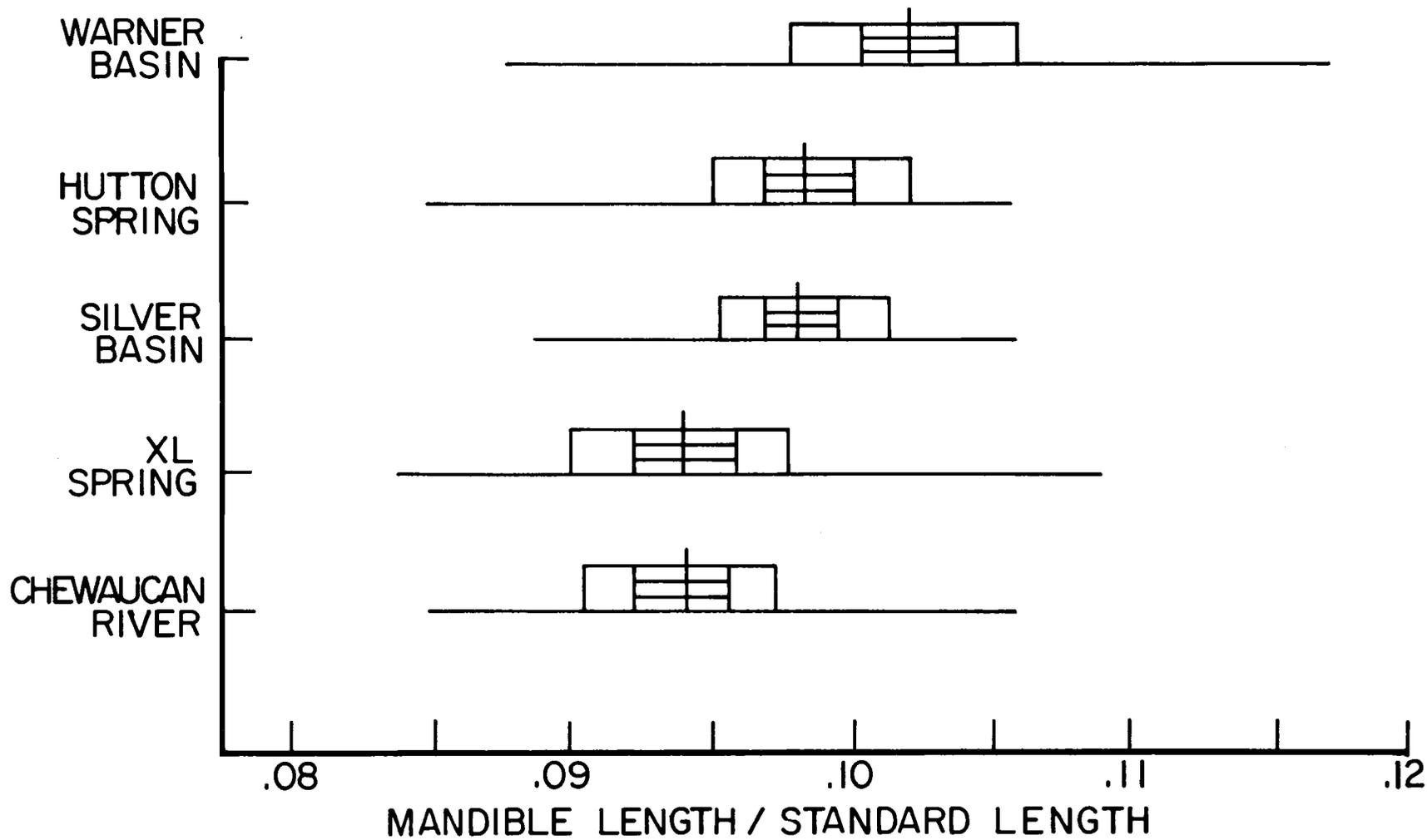


Figure 16

Figure 17. Variation in the width of head in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

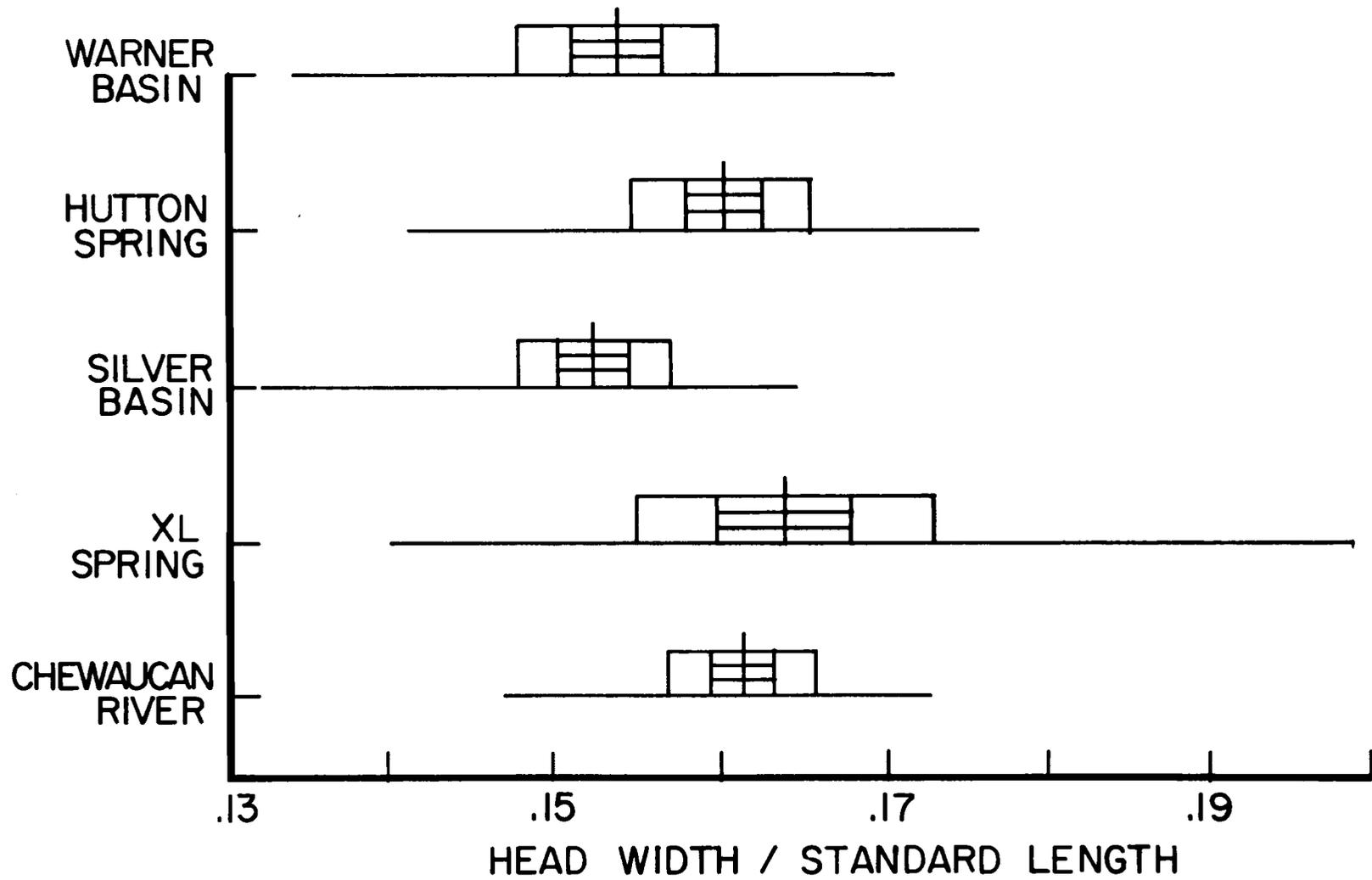


Figure 17

Figure 18. Variation in predorsal length in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

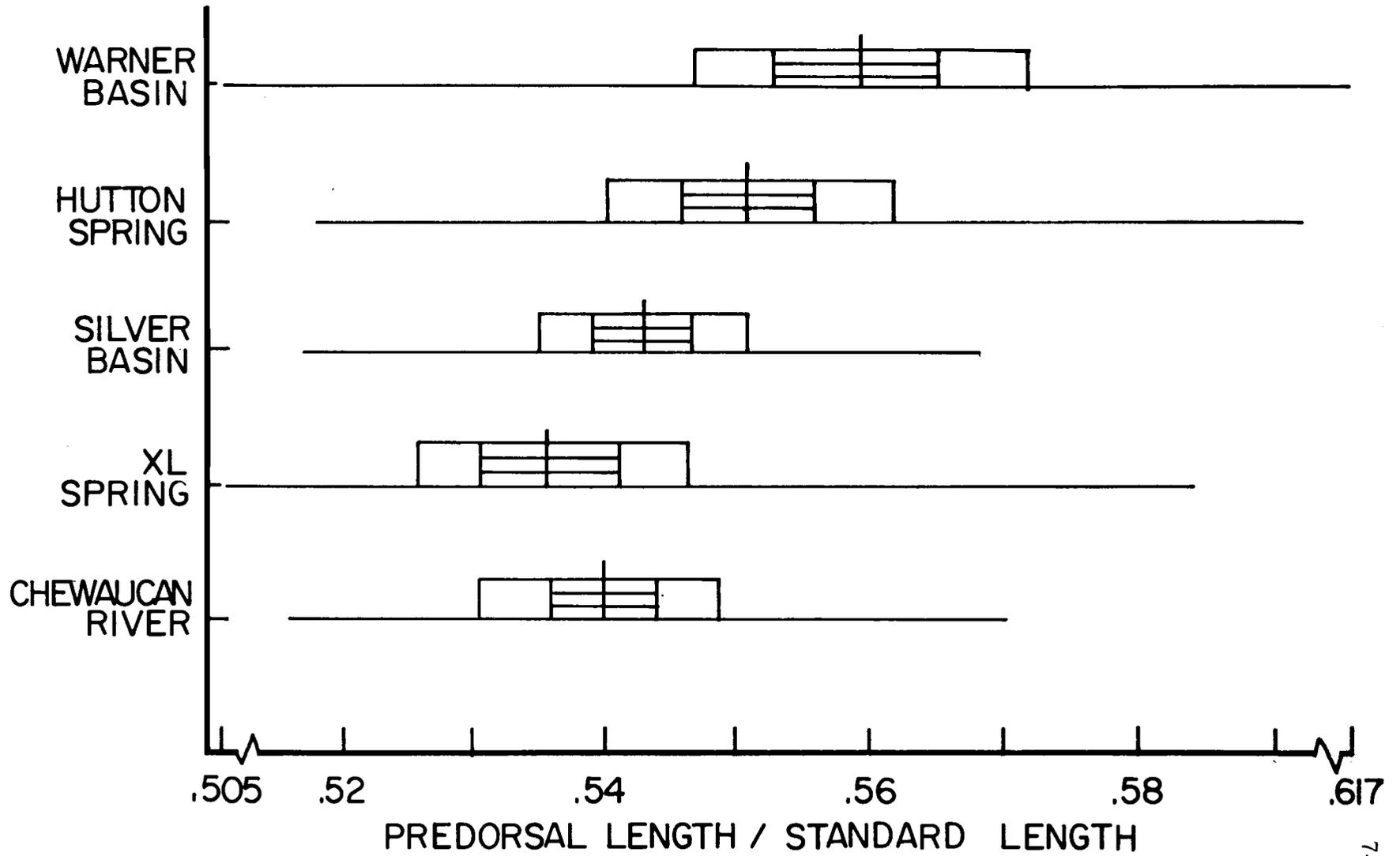


Figure 18

Figure 19. Variation in pelvic-anal length in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

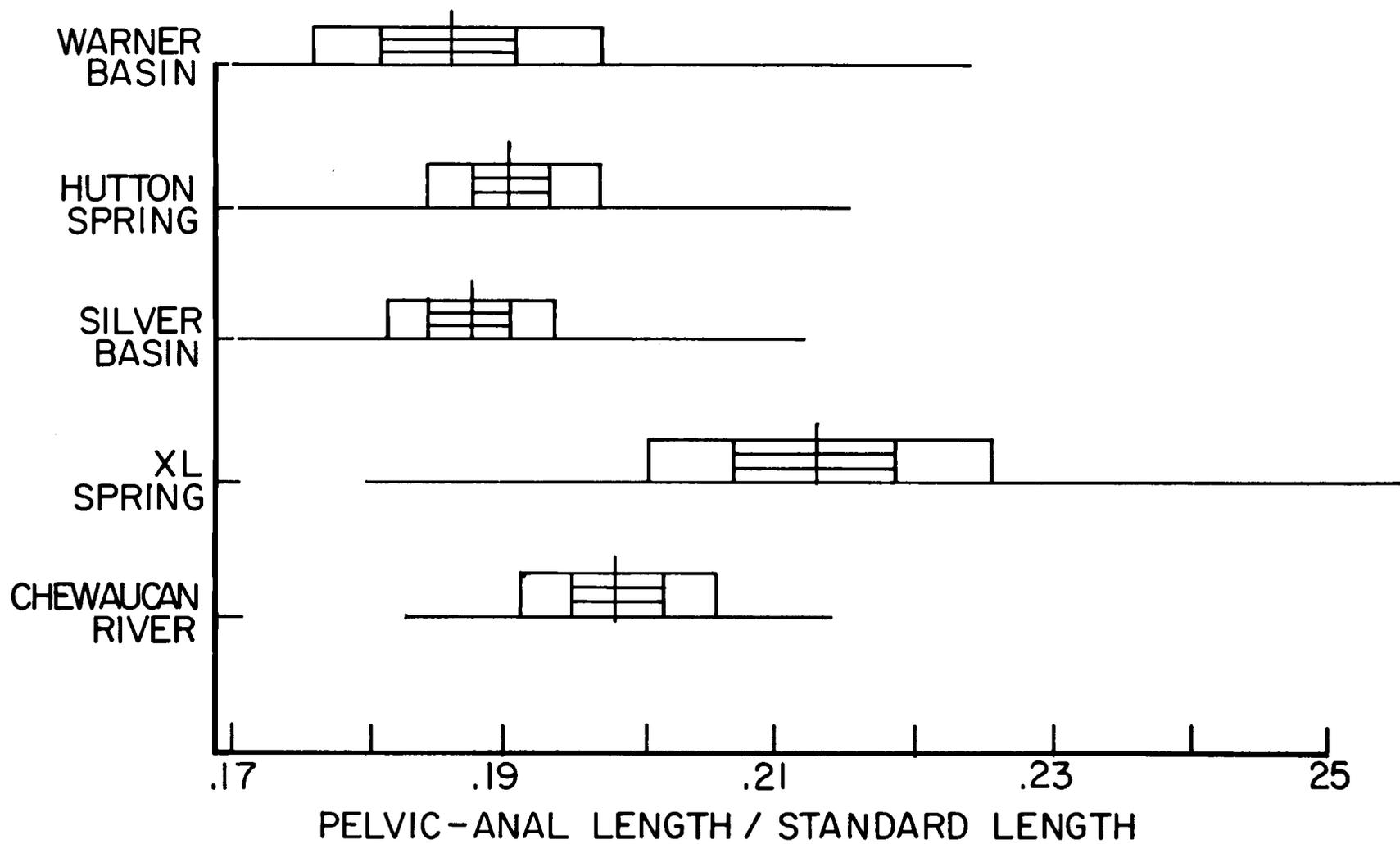


Figure 19

Initial sampling at XL Spring, using a hook and line, produced only large, female chubs. Collections by Snyder (1908) yielded similar results. Minnow traps, small-meshed gill net, and selective shocking were subsequently used to secure smaller specimens. From 40 mm to 50 mm SL, males and females are about equal in numbers, but beyond this size range the proportion of males in the population is very small (Table 9). Hubbs and Miller (1948b) observed

Table 9. Number of males and females in different size ranges in Gila bicolor from XL Spring, Oregon.

Standard length	Number of males	Number of females
45- 59 mm	15	18
60-110 mm	4	10
140-200 mm	1	35
45-200 mm	20	63

approximately three females per male in populations of the desert spring dace Eremichthys arcus. Recently, Hubbs et al. (1974) recorded similar sex ratios in populations of Relictus solitarius. These authors concluded that after sexual maturity, the males either die or stop growing, whereas the females continue to survive and grow. My data tend to support differential mortality as the cause of the highly skewed sex ratios. If the growth of males stopped or slowed markedly after maturity, the proportion of males in a population would be expected to increase sharply in that size range where their growth ceased and then decrease

in the larger size groups. Sex ratios from XL Spring do not reflect this pattern. Furthermore, a check of scales for number of annuli revealed that at 80 mm SL, males and females are of the same age.

The Hutton Spring sample is also predominantly females, but no small chubs were available to determine if and when a change in sex ratio occurs.

Sexual dimorphism is most evident in length of pectoral fin, especially in the Chewaucan River sample (Table 10). The only conclusive differences in pectoral fin

Table 10. Mean pectoral fin length, pelvic fin length, and height of dorsal fin for males and females in populations of Gila bicolor from south-central Oregon. Values expressed as permillage of standard length. Subscripts indicate number of specimens.

Locality or basin	Pectoral fin length		Pelvic fin length		Dorsal fin length	
	♂	♀	♂	♀	♂	♀
Warner Basin	196 ₂₁	170 ₁₉	166	152	212	195
Hutton Spring	192 ₇	174 ₃₃	165	151	189	188
Silver Basin	185 ₁₁	160 ₂₉	162	146	209	205
XL Spring	188 ₃	162 ₃₇	149	147	188	178
Chewaucan River	198 ₂₀	163 ₂₀	162	147	213	201

length are among females. Female chubs from Hutton Spring possess significantly longer pectoral fins than female chubs from XL Spring or Silver Basin (Figs. 20, 21).

Disparity in pelvic fin length between sexes is much less than that encountered in pectoral fin length, and no significant differences were detected.

Figure 20. Relationship between standardized pectoral fin length and standard length for females of two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

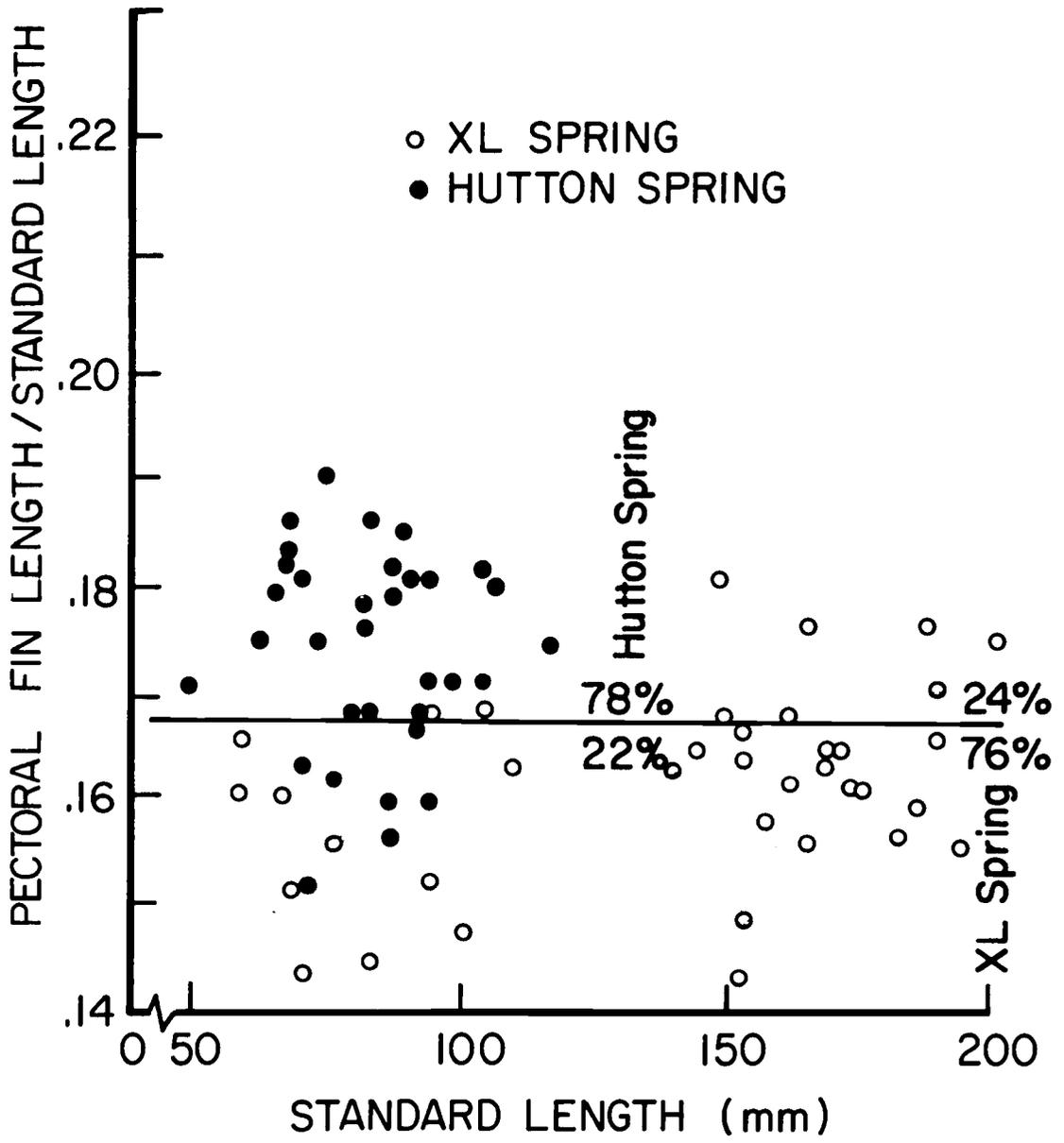


Figure 20

Figure 21. Relationship between standardized pectoral fin length and standard length for females of two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

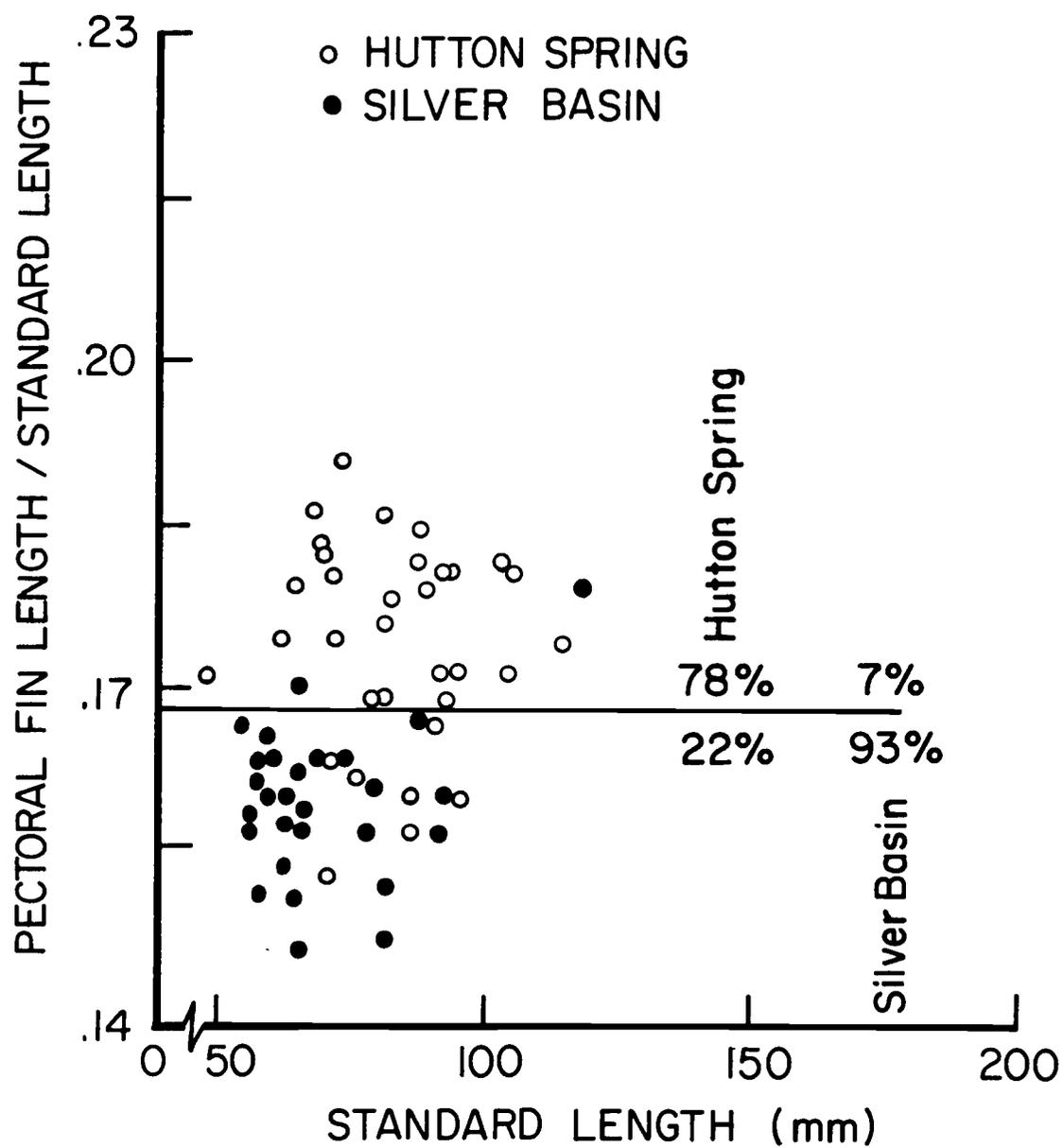


Figure 21

A moderate amount of sexual dimorphism is present in dorsal fin height. However, the differences between sexes is not enough to negate the differences in dorsal fin height among the Hutton Spring, Silver Basin, and Chewaucan River populations (Fig. 22). A plot of only the data of females from these populations produced the same results. The Warner Basin and XL Spring populations are excluded from the figure, because of pronounced allometry. Over the small size ranges of Hutton Spring, Chewaucan River, and Silver Basin samples, allometry is negligible.

Warner Basin population has a significantly longer dorsal fin base than the Hutton Spring population (Fig. 23). The fact that the Warner Basin chubs also possess a greater number of dorsal fin rays, raises the question of character redundancy. To determine the effect of dorsal fin ray number on dorsal fin base length, the mean values of these two characters were plotted for each population (Fig. 24). A regression line was calculated using data from all populations except that of Hutton Spring. The large discrepancy between the actual and predicted length of the Hutton Spring dorsal fin base indicates that the relatively shorter fin base of this population is the result of closer spacing of the fin rays as well as a lower average fin ray number.

A summary of discriminating morphometric characters is included in Table 11. The Hutton Spring chub is

Figure 22. Variation in dorsal fin height in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

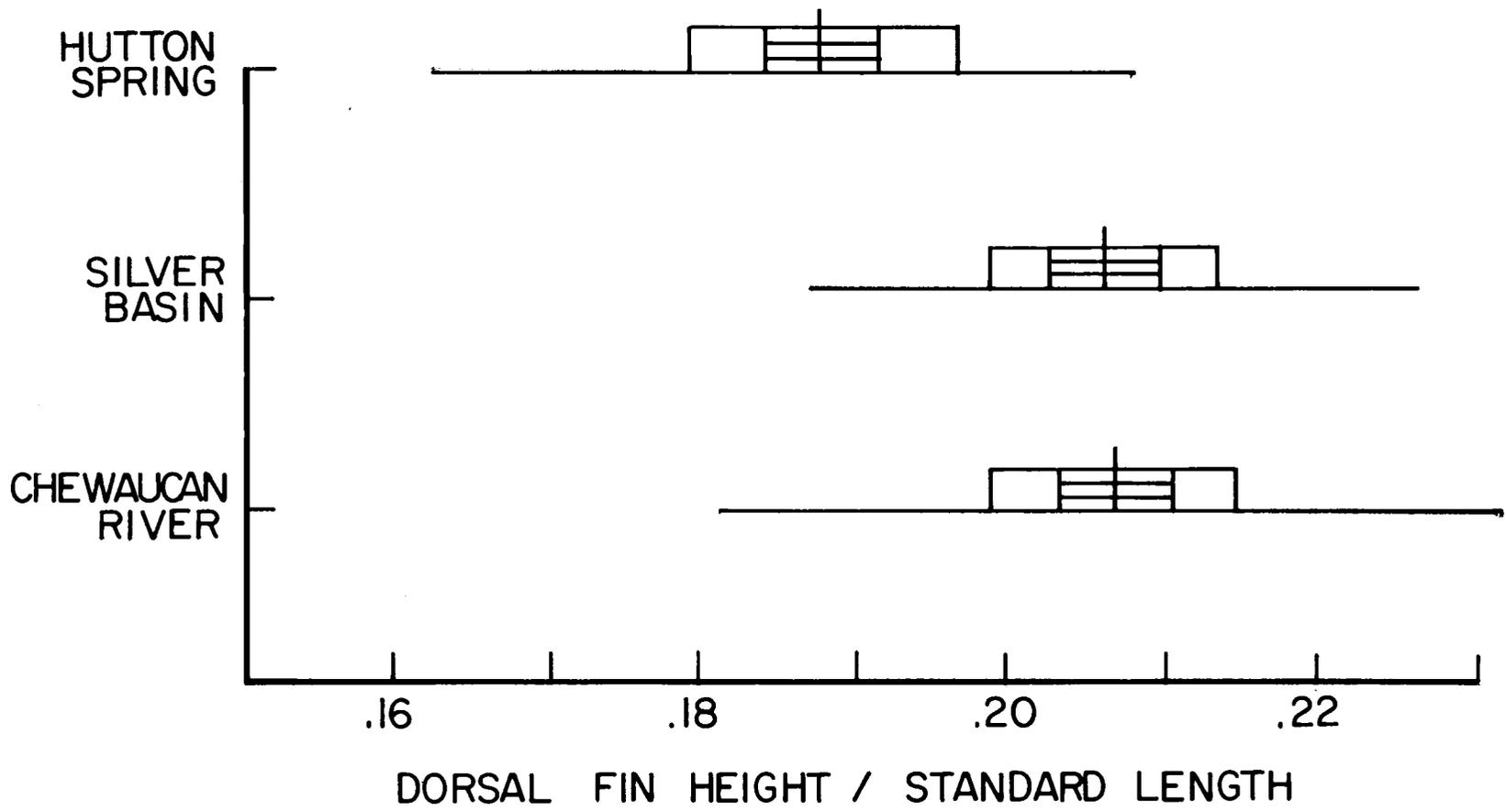


Figure 22

Figure 23. Variation in dorsal fin base length in populations of Gila bicolor from south-central Oregon. See page 24 for explanation of figure.

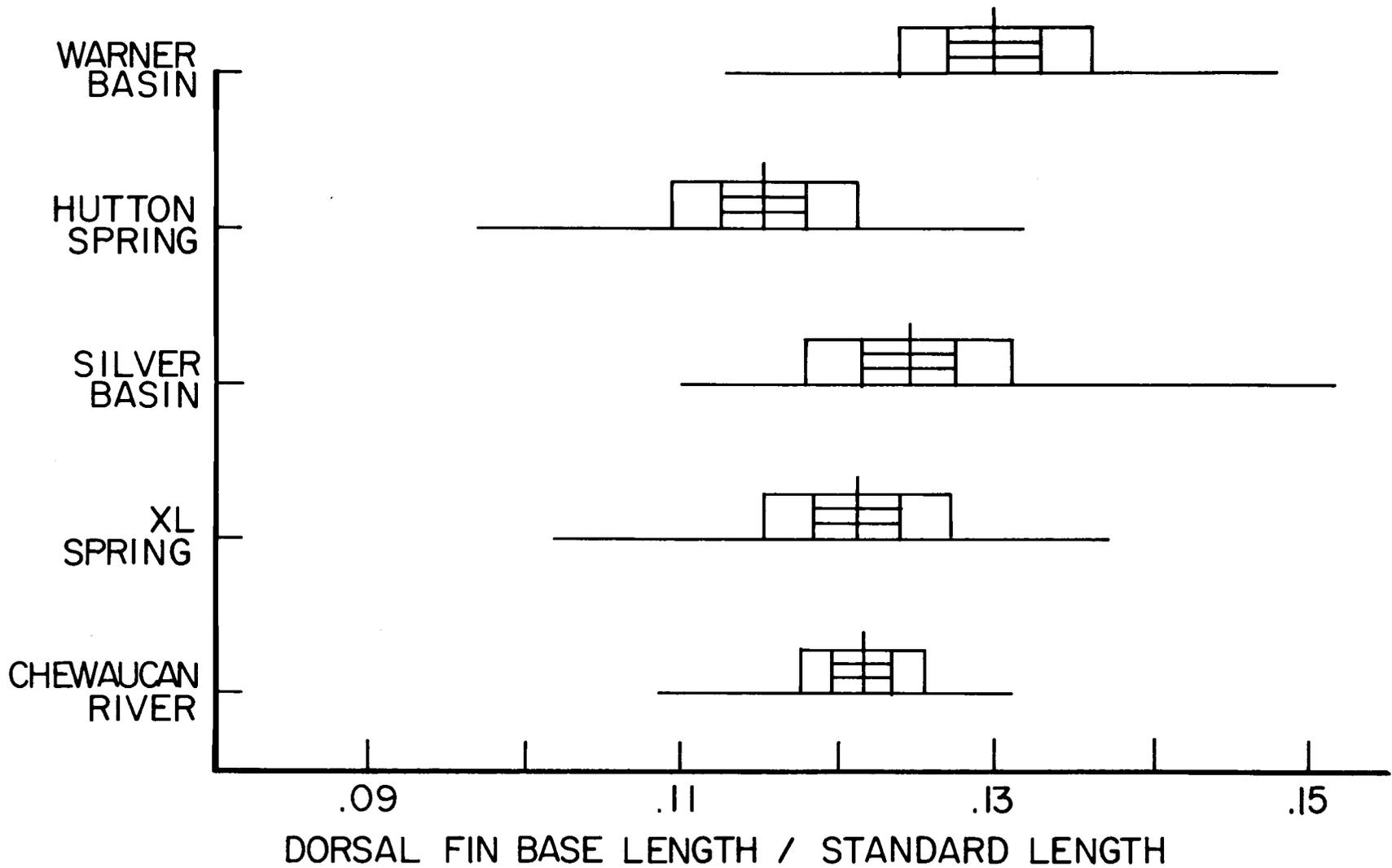


Figure 23

Figure 24. Relationship between mean standardized dorsal fin base length and mean number of dorsal fin rays in populations of Gila bicolor from south-central Oregon. Note: the data from Hutton Spring were not used in calculating the least-squares regression line.

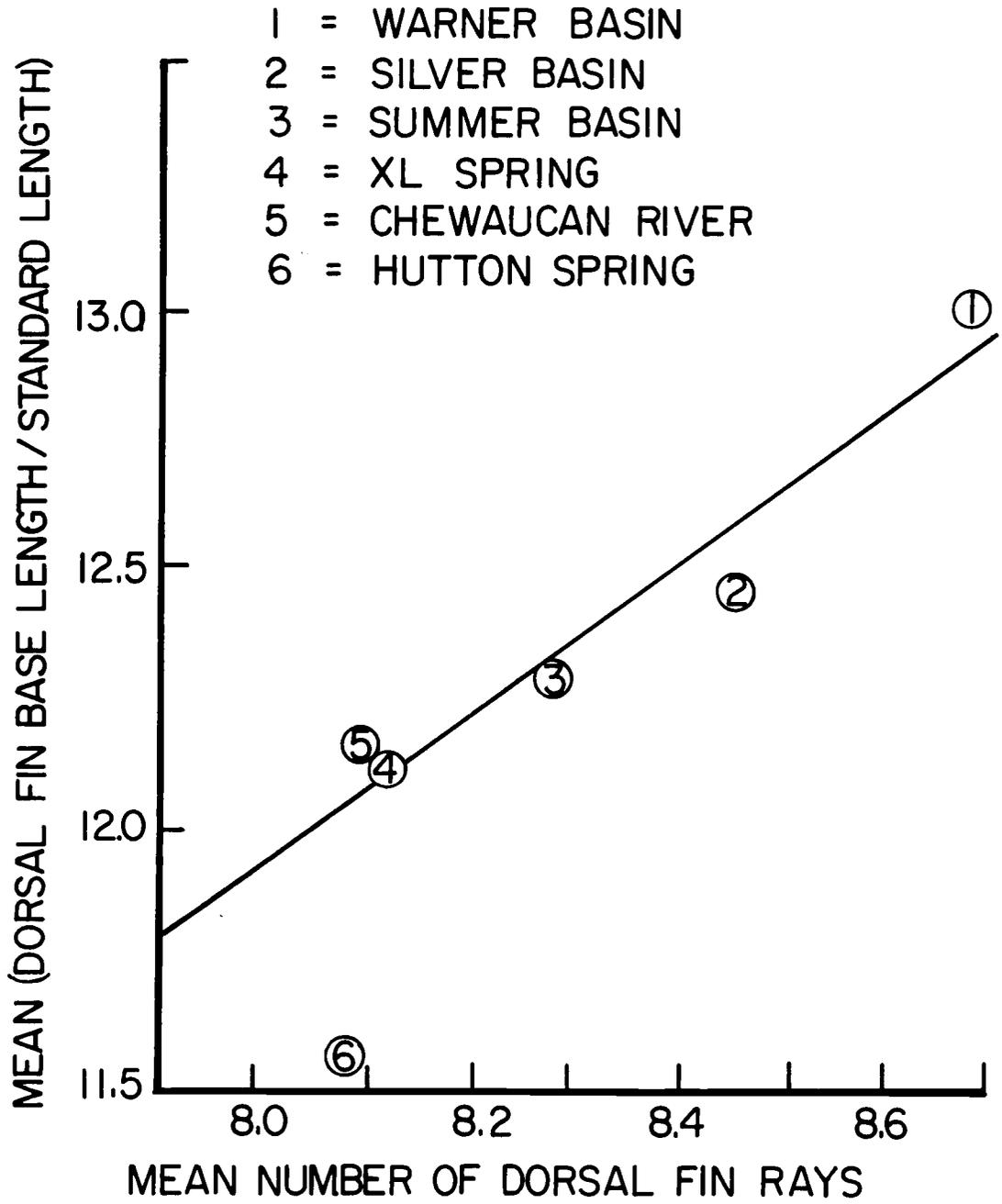


Figure 24

Table 11. Summary of significant differences among populations of Gila bicolor from south-central Oregon. Table to be read across.

	Hutton Spring	Silver Basin	XL Spring	Chewaucan River
Warner Basin	>Number of gill rakers >Number of dorsal fin rays >Dorsal fin base length <Head depth	>Number of gill rakers	>Number of gill rakers >Number of dorsal fin rays <Number of scales around caudal peduncle <Number of scales lateral line to pelvic insertion >Mandible length >Predorsal length <Pelvic-anal length	>Number of gill rakers >Number of dorsal fin rays <Number of scales around caudal peduncle >Mandible length >Head length?
Hutton Spring		>Head length >Head depth <Dorsal height >Orbit width >Pectoral length (♀)	<Pelvic-anal length >Pectoral length (♀) >Head length ? >Orbit width ?	>Head length >Head depth >Orbit width <Dorsal height
Silver Basin			<Number of scales lateral line to pelvic insertion <Pelvic-anal length	<Number of scales around caudal peduncle
XL Spring				No significant differences

distinguished by those features typical of spring dwelling representatives of the species. Most notable among these characteristics is the greater development of the anterior body portions. The head in particular is augmented in almost every dimension: length, depth, and to some degree width. In consonance with this trend, the orbit is of a larger diameter. Reduction of fin size is evident in the smaller height and base of the dorsal fin. The anal fin appears to parallel the dorsal in diminished size. The greater pectoral fin length of females of this population is a noted exception to the general tendency in spring fishes for reduction of vertical and paired fins. Other trends expected but not observed are increases in body and caudal peduncle depth.

The Chewaucan River, Silver Basin and Warner Basin populations are the most divergent from the Hutton Spring chub. The salient morphometric differences are presented above. Of the three former populations, that from the Silver Basin is decidedly intermediate in morphometric character. The Silver Basin chub does not differ significantly in any measured feature from either the Chewaucan River or Warner Basin collections, and is distinct from the XL Spring population only in pelvic-anal length.

With respect to the morphometric characters examined, the XL Spring population differs very little from its presumed closest relative of the Chewaucan River. The XL

Spring chub does not parallel its Hutton Spring congener, but in fact differs from that population in the possession of a shorter head and somewhat smaller orbit. The shorter predorsal distance and the greater pelvic-anal length of the XL Spring chub are also not typical of western cyprinids confined to small bodies of water. Another and most obvious difference is size. Specimens from XL Spring exceed 200 mm SL, whereas Hubbs et al. (1974) recorded a maximum length of 149 mm for G. b. euchila, largest spring tui chub of north-central Nevada.

Intestinal Tract

Gut length and gut configuration vary within and between populations. Length of the gut, but not necessarily its configuration, appears correlated with other structures associated with feeding, and, to the limited extent that could be determined, with feeding habits. The difference observed among populations in these characters indicate trophic divergence within the oregonensis complex.

Relationship of the standardized gut length measurements, GL/SL, to standard length is shown for all collections in Figures 25 through 30. Length of the alimentary tract is definitely greater in chubs from Hutton Spring than in those collected from Silver, Warner, or Chewaucan River basins. The GL/SL ratio increases over the entire size range of the Hutton Spring sample, averaging 1.1 at 60

Figure 25. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

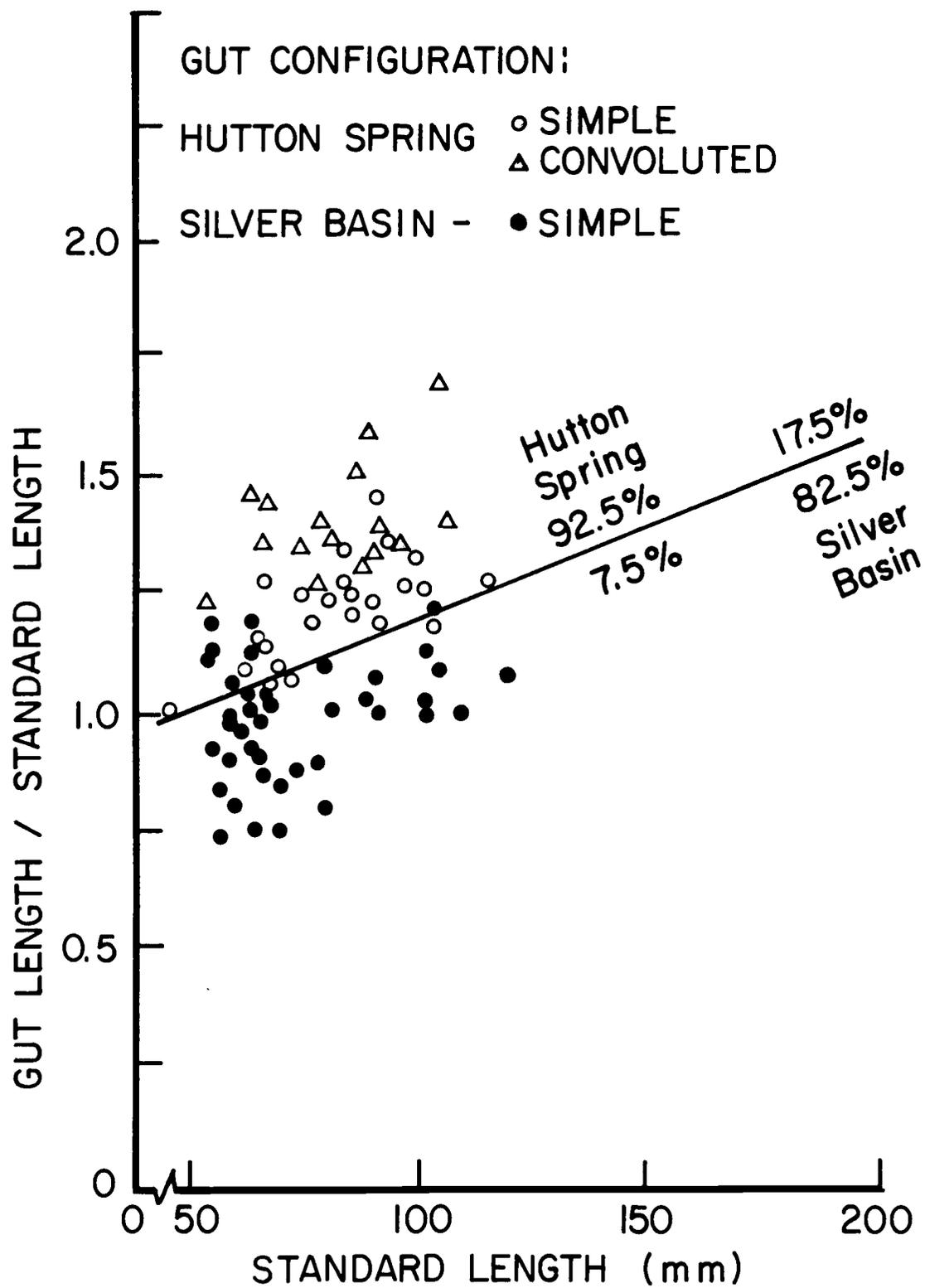


Figure 25

Figure 26. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

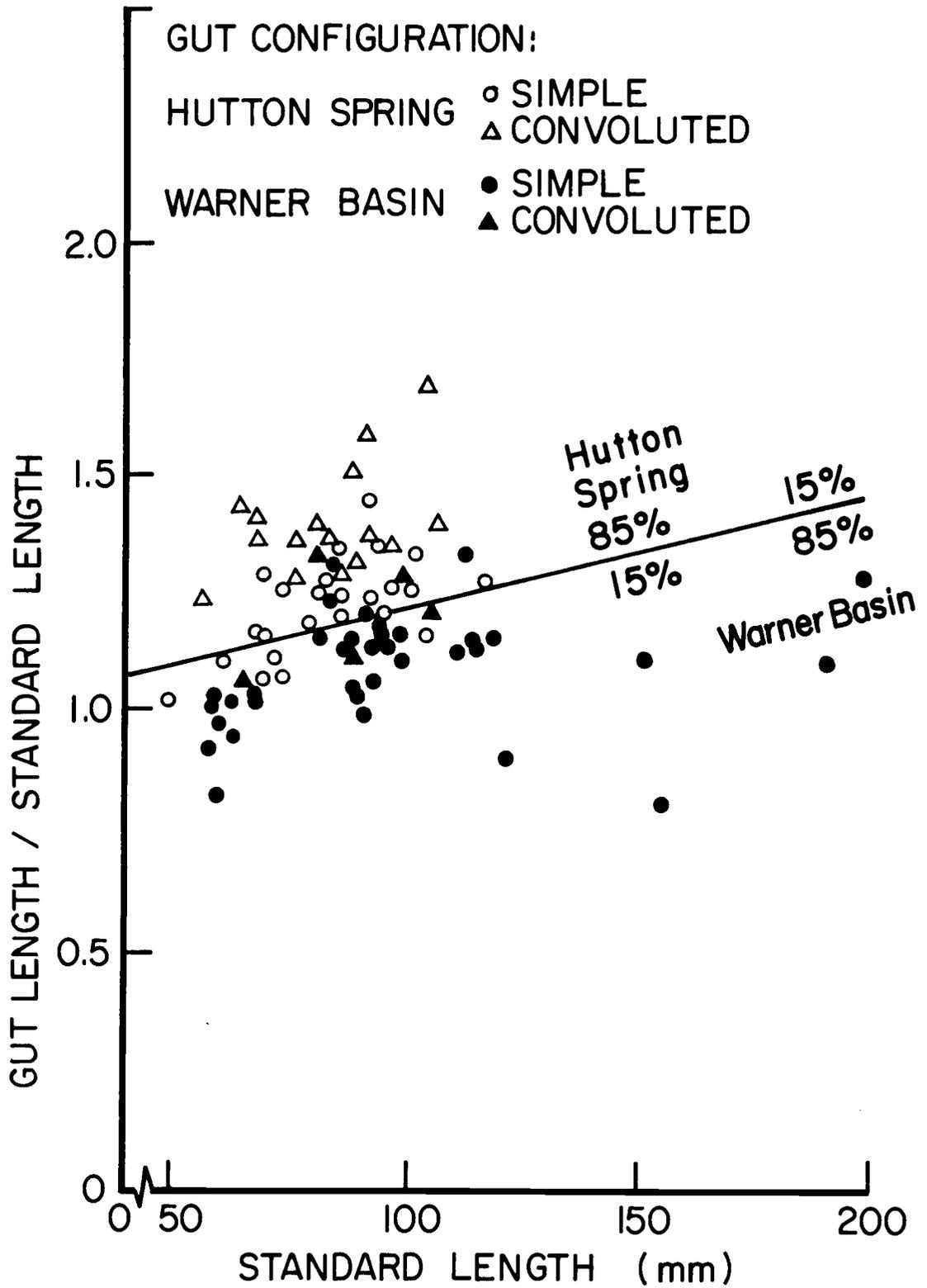


Figure 26

Figure 27. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

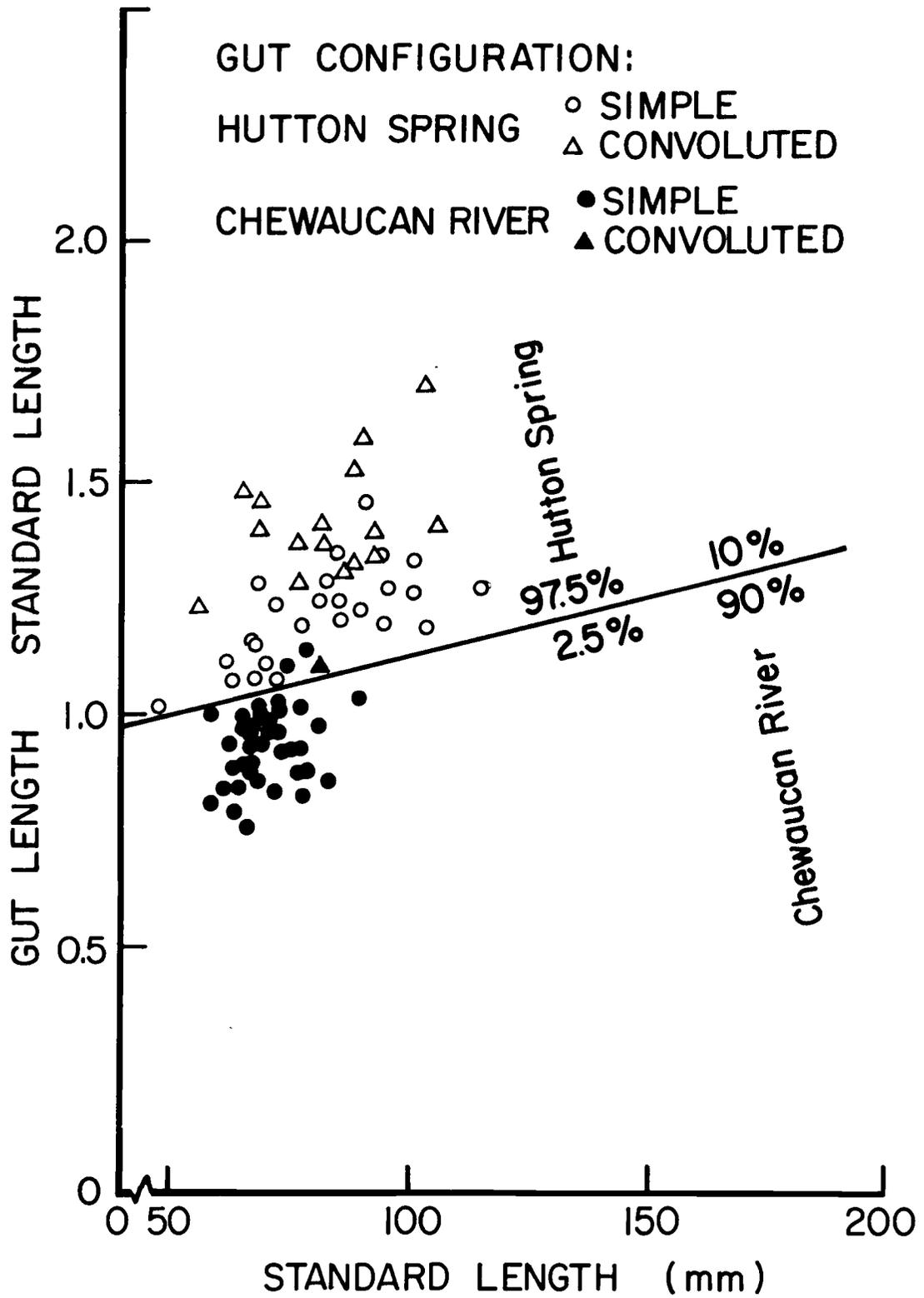


Figure 27

Figure 28. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

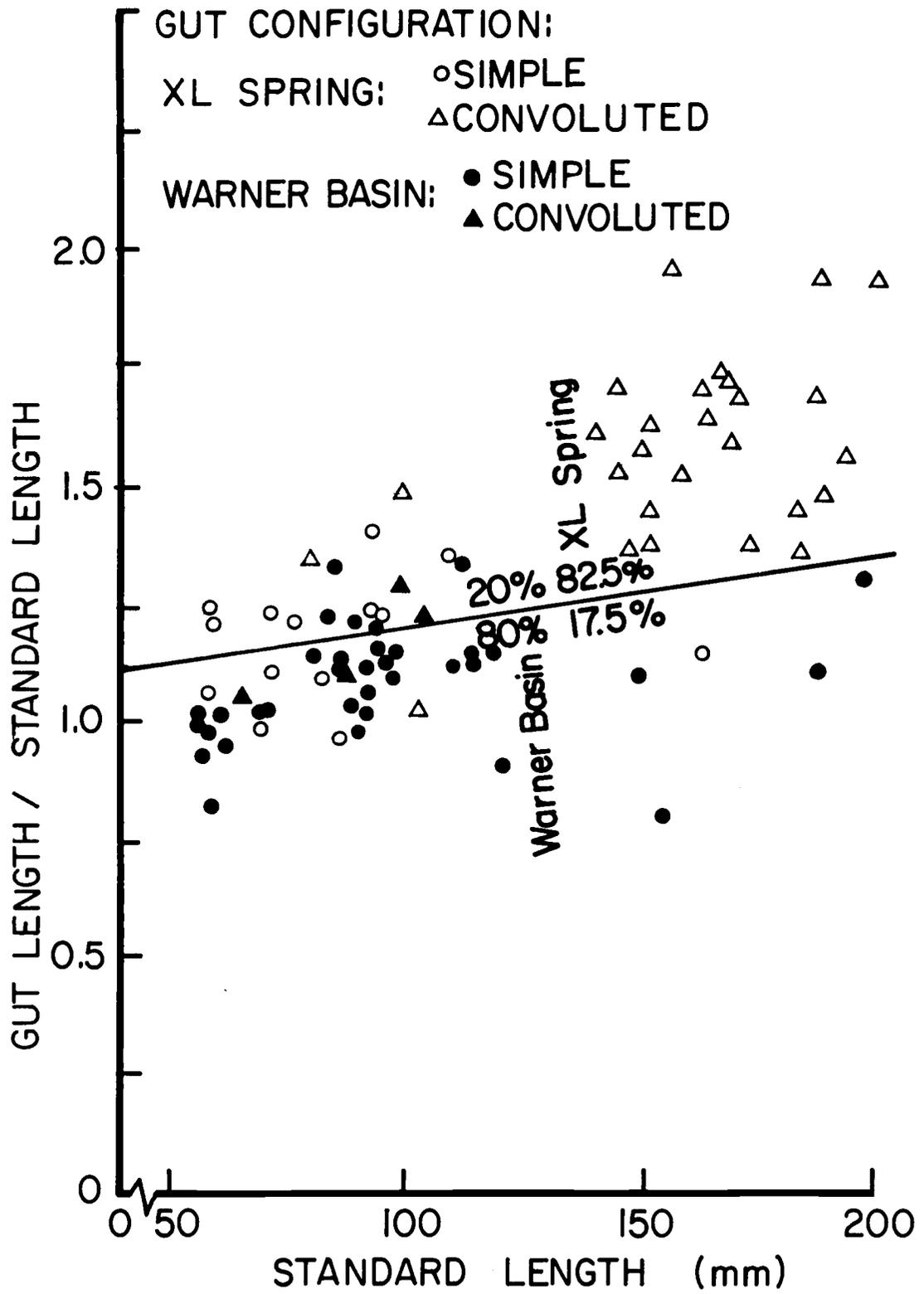


Figure 28

Figure 29. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

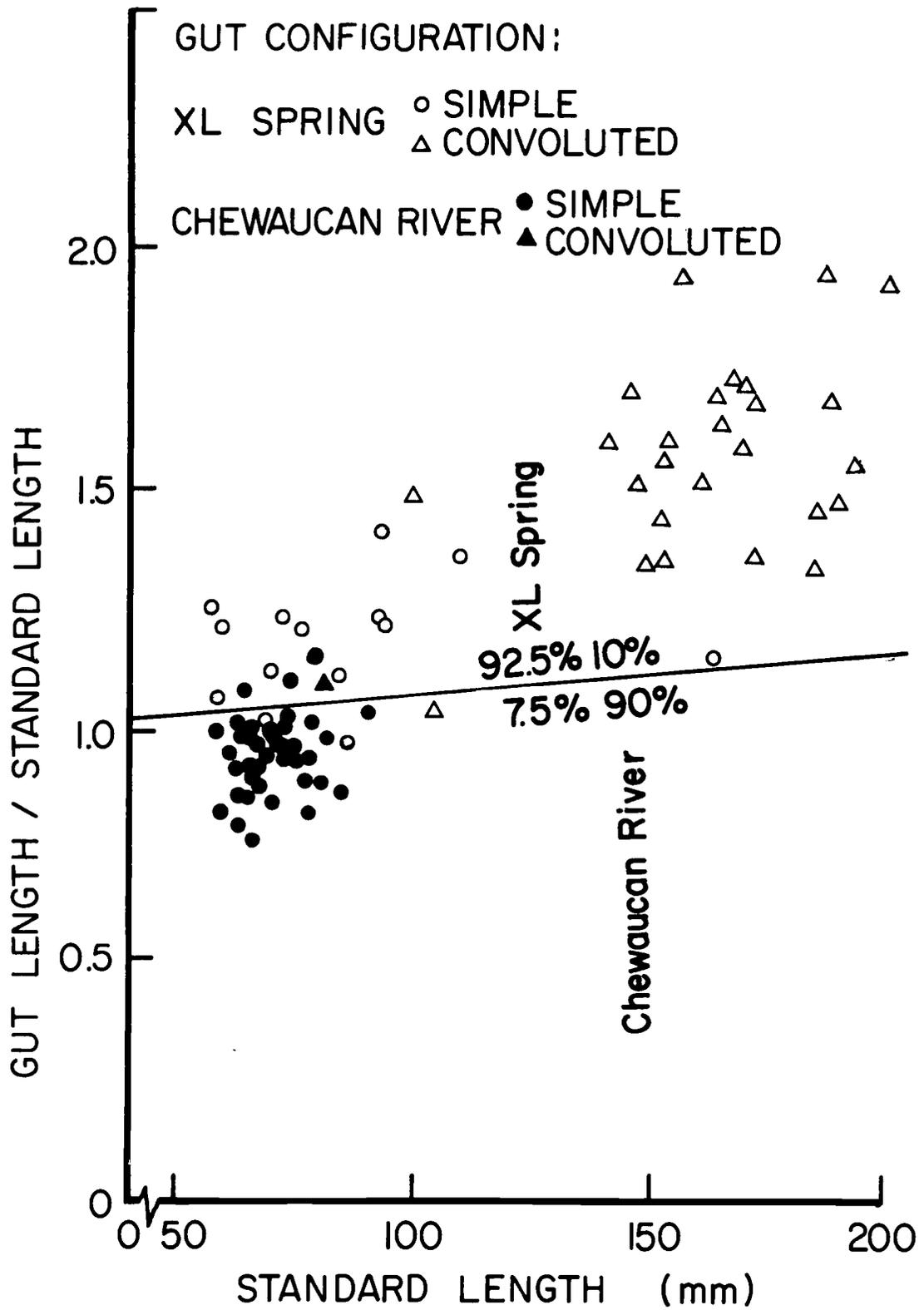


Figure 29

Figure 30. Relationship between standardized gut length and standard length for two populations of Gila bicolor from south-central Oregon. For each population, the number of data points on either side of the line is expressed as a percentage. Line fitted by eye.

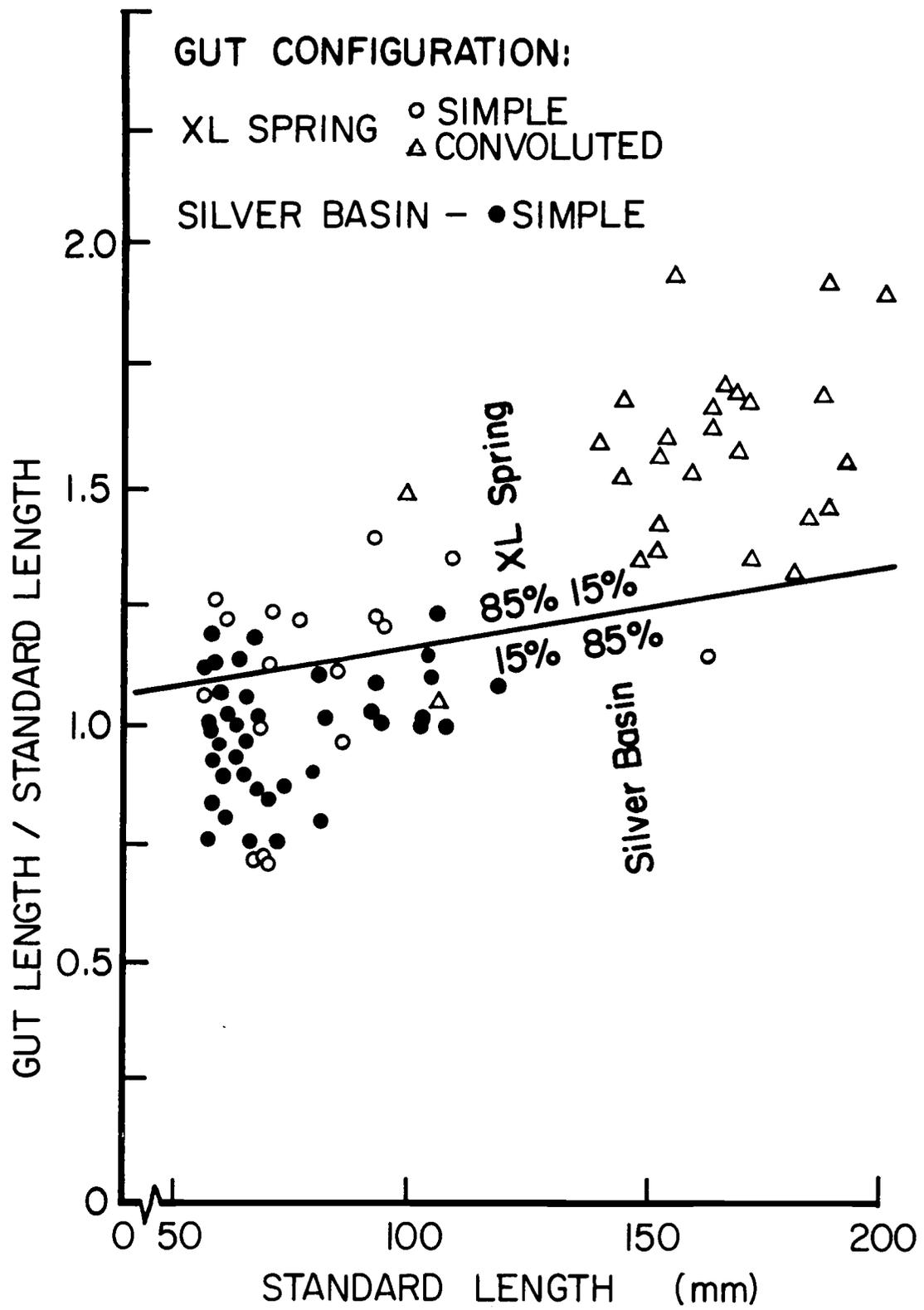


Figure 30

mm SL and 1.4 at 110 mm SL. In the Warner Basin chubs, GL/SL increases from approximately 1.0 at 60 mm SL to 1.1 at 90 mm SL and then evidently remains constant. Data from the Silver Basin collection suggest a similar pattern of intestinal growth, but the lack of larger specimens in this sample and the Chewaucan River sample prevents a complete description of the variation for these two populations.

The GL/SL ratio ranges from 1.0 to almost 2.0 in chubs from XL Spring. Members of this population have longer guts than do those of the Warner Basin population. XL Spring chubs probably also have greater gut length than do chubs from both the Chewaucan River and Silver Basin, but these differences are questionable. As shown for other morphometric characters, especially those exhibiting allometry, comparisons involving the XL Spring collection are difficult to assess.

Results from the two spring populations are comparable to the findings of Snyder (1908). Snyder recorded gut lengths of 1.25 times total length (= 1.6 SL) in chubs from XL Spring, but he did not include for comparison measurements from his Silver Basin, Warner Basin, or Chewaucan River collections. The GL/SL ratios of these latter three populations average between 1.0 and 1.2, which Schultz (1936) reported as typical for the tui chub. Kimsey (1954) and La Rivers (1962) found similar ratios in other populations of Gila bicolor. Snyder (1918) described the gut of

Leucidius pectinifer (= G. b. pectinifer), the planktivorous chub of the Lahonton system, as "short." In the same paper, he reported the alimentary canal of Siphateles obesus (= G. b. obesa) as ". . .about equal in length to the entire length of the specimen." From these statements, I conclude that the GL/TL ratio of G. b. pectinifer to be less than one, or about equal to that found in the Warner Basin chub.

In four of the five collections, two types of intestinal coiling were found (Fig. 31). The simplest form corresponds to the Group 2 of Kafuku (1958); a single loop with a bend. Schultz (1936) and Hubbs et al. (1974) gave similar descriptions. The second, more convoluted, type does not conform exactly to any of Kafuku's Groups, although the coiling does more closely resemble the diagram of Group 4. Hubbs et al. (1974) indicated that variations of Group 2 are found in Gila but did not elaborate.

The simple gut type is present in varying numbers throughout the small size ranges of all samples. In the Silver Basin collection and with one exception the Chewaucan River collection, only the simple form is found. There appears to be no pattern in the distribution of the two gut types in the Warner Basin sample. In chubs from Hutton Spring, gut configuration does not change with standard length; frequency of the two forms is constant over the entire size range. Only in the XL Spring collection is

Figure 31. Intestinal configurations found in populations of Gila bicolor from south-central Oregon. A, Simple gut configuration; B, convoluted gut configuration.

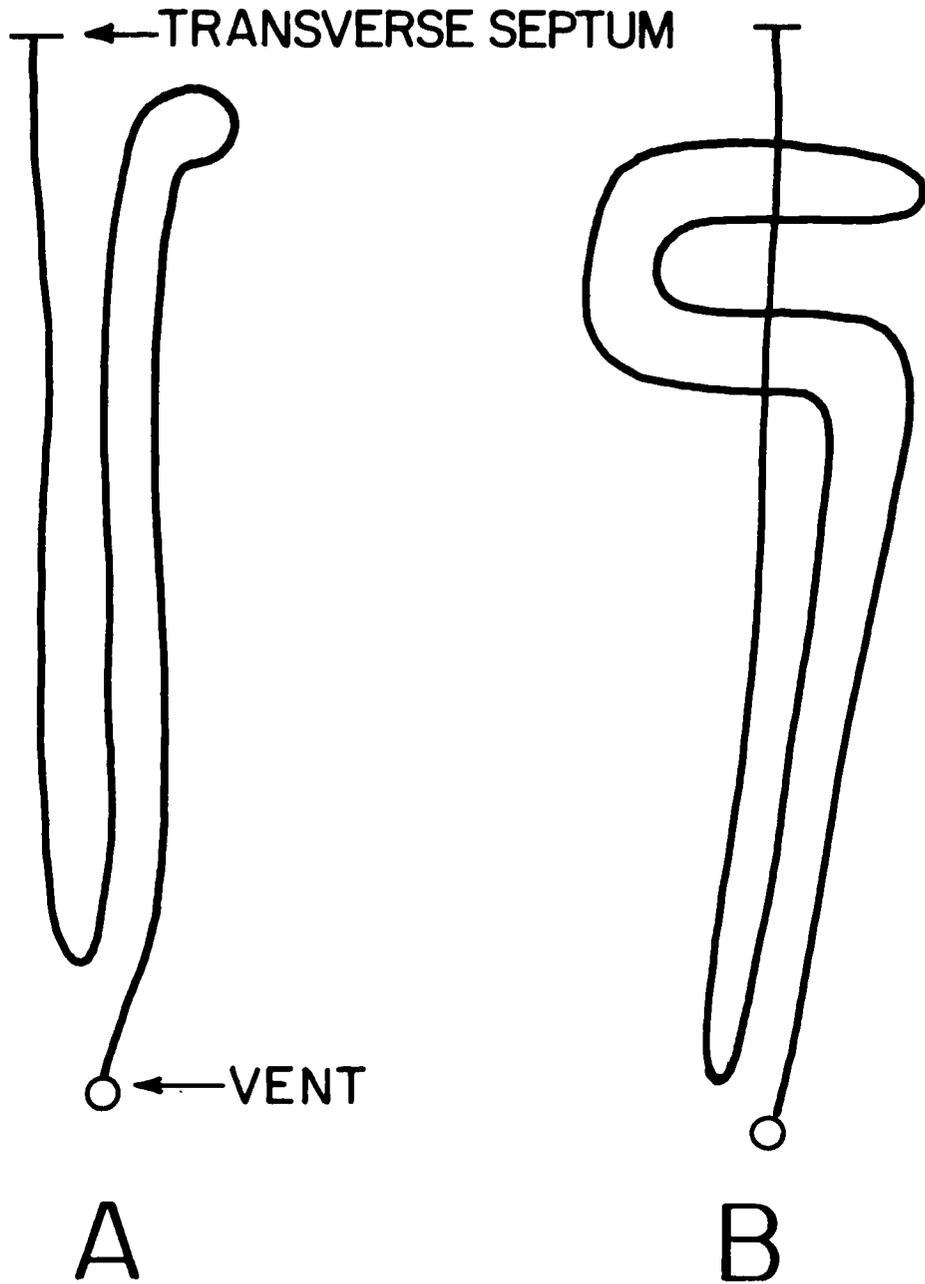


Figure 31

any pattern apparent, which in fact may be due to the greater size range of specimens. Up to 110 mm SL, the simple gut configuration predominates, whereas the convoluted form is found in all except one instance in specimens greater than 140 mm SL. The transition in intestinal coiling from simple to convoluted evidently occurs between 100 mm SL and 140 mm SL.

The only statement applicable to all populations, concerning gut length and configuration is that for a given standard length those fish with the convoluted coiling usually have longer intestines than those with the simple gut configuration. The Hutton Spring data express this relationship most clearly.

In smaller specimens, less than 110 mm SL the convoluted form is apparently not necessary to accommodate a longer gut, but more intensive coiling does seem required for chubs with a GL/SL ration greater than 1.5, such as for the large specimens from XL Spring. No determination was made of the length of the abdominal cavity whose dimensions would probably affect the amount of coiling.

Ontogenetic changes in gut length and form have been reported for variety of fish species. Kafuku (1958) examined populations of Carassius carassius inhabiting diverse environments. He found differences among populations in the adult gut length and gut configuration; differences which he correlated with feeding habits. Within

populations, he also observed changes during growth in gut morphology associated with shifts in diet. Naiman (1975) and Montgomery (1977) found shifts from a carnivorous to herbivorous diet accompanying an increase of the GL/SL ratio in Cyprinodon nevadensis amargosae and Cebidichthys violaceus respectively.

In light of the above mentioned studies, similar relationships would be expected, within and among the present populations, between feeding habits and gut morphology. Only an incomplete survey of feeding habits of the present material was possible. The age, condition, method of capture, and initial preservation rendered many specimens, particularly smaller individuals, unsuitable for study. However, definite statements can be made concerning the diets of the larger specimens from Hutton Spring, XL Spring, and Warner Basin. Both spring populations are omnivorous, with the emphasis on plant material - filamentous algae. Snyder (1908) recorded large amounts of vegetable material and many small gastropods in specimens he collected from XL Spring. In the few chubs I examined from the Warner Basin, no plant material or gastropods were found, but some zooplankton was noted.

Feeding habits of a number of tui chub populations have been examined (Bird, 1975; Kimsey, 1954; Miller, 1951), but none of these investigations correlated gut contents with gut morphology. With regard to shifts in diet

during growth, all studies indicate that, as young, tui chubs subsist predominantly on zooplankton; very little or no plant material is consumed. As adults, there is more diversity among populations in the types of food eaten. Mid-water planktivores, omnivores, and benthic carnivores have been described but there is only one reported case of apparent herbivory. Bond (1948) concluded that the diet of adult tui chubs from Lake of the Woods, Oregon was predominantly plant material.

On the combined basis of these studies, the probable changes in gut morphology and feeding habits can be constructed for populations of the Oregon tui chub. Initially, the young of all five populations have the simple gut form and feed on zooplankton. Then at some size less than 60 mm, the guts of chubs from XL and Hutton springs start to diverge. Their diet shifts from animal to predominantly plant material with a concomitant increase in the GL/SL ratio, and the convoluted gut configuration appears. The GL/SL ratio continues to increase in these omnivorous spring populations, while in the Silver Basin, Chewaucan River, and Warner Basin chubs, the GL/SL ratio levels off at approximately 1.0 or 1.1. In these latter populations, the diet continues to consist of plankton or other animal material.

The observed differences in feeding habits and gut morphology between spring and lacustrine populations are

correlated with other characters of a trophic nature. The Warner Basin chubs are characterized by a long oblique mouth, more numerous gill rakers, and a lighter pharyngeal arch and teeth; these are all typical adaptations of a mid-water planktivore. The Warner Basin chub parallels the noted lacustrine planktivore of the species G. b. pectinifer, in most respects, including length of gut. Differences between these two populations, although significant in many characters, are more a matter of degree than of kind.

Conversely, the reduced gill raker number, more robust arch and teeth, and longer intestinal tract are expected adaptations of spring chubs that consume hard-shelled gastropods and large quantities of filamentous algae. However, the XL Spring and Hutton Spring populations are not typical herbivores. Al-Hussaini (1949) stated that the GL/SL ratio of herbivorous fishes ranges from 3.7 to 6.0. The greatest GL/SL ratio recorded from the XL Spring collection was 1.96.

These conclusions are based largely on circumstantial evidence and extrapolations of other studies. An investigation with sufficient numbers of specimens in all size ranges from all populations will be required to assess the relationships between gut morphology and feeding habits.

There are a number of factors which could lessen or negate some of the differences in gut length found among the present populations. Some samples, e.g. Silver Basin,

contain many specimens collected 10 to 20 years ago. The intestinal tracts of these individuals are very stiff and shrunken. Chubs of relatively recent collections definitely have more elastic intestines. A second and probably more important factor is the degree of gut fullness, which according to Montgomery (1977) greatly affects gut length as well as diameter. The validity of gut length as a taxonomic character is also in serious doubt. Naiman (pers. comm.) found in omnivorous cyprinodonts that the type of food ingested (plant, animal) can affect the length of the alimentary tract and that the length of the gut of individual fish can change during the year depending on the kinds of food available.

CONCLUSION

The six populations referred to Gila bicolor oregonensis do not constitute a single valid subspecies. This taxon, as delimited by Snyder (1908), is a heterogeneous assemblage of populations which differ among themselves as much as they do from other recognized subspecies of Gila bicolor. Only the tui chub populations of XL Spring and the Chewaucan River are here retained in Snyder's oregonensis. The tui chub populations of the Alkali Basin (Hutton Spring, and the small adjacent spring), Silver Basin, and Warner Basin represent three additional subspecies. Because of the drastic morphological changes that have occurred in the Summer Basin chub (resulting from repeated poisonings and introductions), the present population of that basin has no official taxonomic status at the subspecific level.

The degree of morphological divergence among populations does not clearly reflect past hydrographic connections or length of isolation (Table 18). Similarities and differences among populations appear better correlated with habitat. Solely on the basis of hydrographic history, the XL Spring and Hutton Spring chubs would be expected to most closely resemble the Chewaucan River and Silver Basin chubs respectively.

The Chewaucan River and XL Spring populations do most closely resemble one another in body form, counts, and most measurements. Divergence between these two populations is limited primarily to gut length and gut configuration, characters of doubtful taxonomic validity. The XL Spring chub exhibits only small reductions in gill raker and scale counts relative to its fluviatile congener. This lack of trends in meristics and morphometrics associated with the spring habitat may be related to length of isolation or more likely to environment; XL Spring is of such relatively large size that it approaches lacustrine in character.

The Silver Basin and Hutton Spring chubs differ grossly from each other in morphology, especially in the conformation of the head and pharyngeal arch. Some of the divergence may be attributable to the "founder effect" or genetic drift in the small Alkali Basin population, yet the majority of features of the Hutton Spring chub are in accord with the predicted trends for spring populations.

Although the only known hydrographic connection of the late Pleistocene involving the Silver Basin was with the Alkali Basin, the chubs of Silver Basin are more similar to those of the Chewaucan River, XL Spring, and Warner Basin. With the noted exception of gill raker counts, the Silver Basin chub most closely resembles the lacustrine chub of

the Warner Basin. Possibly the Silver Basin chub, presently a stream inhabitant, represents a lacustrine form that subsequently lost its high gill raker number.

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