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Systemic Studies of the Genus Gila (Cyprinidae) of the Colorado River Basin

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SYSTEMATIC STUDIES OF THE GENUS *GILA* (CYPRINIDAE) OF THE COLORADO RIVER BASIN

by

Paul Bernard Holden

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Paul B. Holden

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

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of the Colorado River Basin

by

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Utah State University, 1968

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Three hundred and nine specimens of Gila from the Colorado River basin were studied. A form of numerical taxonomy, taximetrics, was used to help classify the specimens. The data from these fish indicate that many of the present hypotheses concerning their taxonomy are not valid. The concept of ecosubspecies or ecological subspecies does not fit the Colorado basin Gila. The roundtail and bonytail chubs, G. robusta Baird and Girard and G. elegans Baird and Girard respectively, currently treated as subspecies, are well separated morphologically, ecologically and reproductively and therefore are better considered two valid species. The relationship between G. cypha Miller and G. elegans is clouded by the presence of what appear to be intergrade forms. Future investigations are needed to piece together the puzzle surrounding these two fish. The subspecies name seminuda (Cope and Yarrow), presently attributed to fish from throughout the Colorado basin, more correctly is allied to the robusta of the Virgin River. Preliminary study indicates this population may be sufficiently different to warrent subspecies recognition. No specimens of G. robusta intermedia (Girard) were examined but the literature suggests this form may also be a valid species.

(74 pages)

INTRODUCTION

The cyprinid genus *Gila* is presently divided into three subgenera; *Gila*, *Siphateles* and *Snyderichthyes* (Uyeno, 1960). *Richardsonius* is included as another subgenus by some authors (Eddy, 1957). This study is concerned with the systematics of the subgenus *Gila* of the Colorado River basin with emphasis on the upper basin forms presently recognized as *G. r. robusta* (Baird and Girard), *G. robusta elegans* (Baird and Girard) and *G. cypha* Miller.

Baird and Girard (1853), working on fish collected in the Zuni River, New Mexico, described the genus *Gila* and three species, *G. robusta*, *G. elegans* and *G. gracilis* (Baird and Girard also published the descriptions in the 1853 Proceedings of the Academy of Natural Sciences of Philadelphia, published in 1854). Cope and Yarrow (1875) named several *Gila* from collections of the Wheeler Survey in southwestern United States; included was *G. seminuda* from the Virgin River, Utah. By 1896, 13 species and five genera had been used for the Colorado River basin *Gila*. The revision by Jordan and Evermann (1896) reduced these to two genera (*Gila* and *Leuciscus*) and five species. Listed in *Gila* were three species, *robusta*, *elegans* and *seminuda*, with six synonyms. *Leuciscus* contained two species, *intermedius* (Girard) and *niger* (Cope) with two synonyms.

Ellis (1914), with little critical examination, suggested that *robusta* and *elegans* might be considered one polymorphic species with a subspecies *seminuda*. Also, he listed *G. pandora* (Cope) and *G. egregia* (Girard) as synonyms of *robusta* in error. *G. pandora* refers to the *Gila* of the upper Rio Grande basin, *G. egregia* refers to the genus *Richardsonius*.

Jordan, Evermann and Clark (1930) retained robusta, elegans and seminuda as full species, and the two species of Leuciscus listed by Jordan and Evermann (1896) were both included under Tigoma gibbosa Girard. Miller (1946) described a new species, G. cypha, from the Grand Canyon of Arizona and suggested that robusta, elegans, seminuda and intermedia (Tigoma gibbosa) were only subspecies of a single species, robusta. Tanner (1950) named a new species, G. jordani, from the White River of Nevada. La Rivers (1962) considers this form a subspecies of G. robusta. The American Fisheries Society (1960) mentioned only G. robusta and G. cypha as full species. Uyeno (1960) established some of the relationships between fishes allied to the genus Gila in an osteological study. His work primarily considered the taxonomy of this group above the species level. Appendix A is an annotated synonymy of the subgenus Gila of the Colorado basin.

The present classification of robusta and elegans as subspecies does not fit the idea of subspecies being geographical units of species, for these forms are sympatric. It suggests rather that these forms are ecosubspecies or ecological subspecies (Hubbs, 1943) which show rapid parallel evolution in disjunct yet similar habitats, and therefore precludes the idea of a single evolutionary line for each form. Although these fish have been named several times by different authors, no thorough taxonomic study has been undertaken. Many of the hypotheses concerning the taxonomic status of these forms have never been tested. The intent of this study was to contribute towards a better understanding of the populations referred to as the Gila complex. The objectives of the study were:

1. To determine the systematic relationships between the members of the *Gila* complex in the upper Colorado River basin.

2. To determine the amount of intraspecific variation exhibited by the several members of this complex.

DESCRIPTION AND DISTRIBUTION OF THE FORMS

The large amount of taxonomic confusion in these forms can be attributed to: instability of a few morphologic characters, notably squamation; and an apparent cline in morphology believed to be adapted for varying current conditions which is the basis for the present ecosubspecies concept. At one end of the apparent cline is the small, chubby, generalized intermedia of the Gila River basin (Arizona), thought of as a small stream form; robusta is hypothesized to be a slow to moderately swift current form of medium sized rivers; elegans is the intermediate form with characters adapted for life in large swift rivers; the morphology of cypha is hypothesized to be highly adapted for life at or near the bottom of torrential, turbid channels (Miller, 1946).

As the most generalized of the three forms considered in detail here, robusta is usually fully scaled, more robust than the other two, and a nuchal hump is absent or greatly reduced. The very streamlined elegans has a pencil-like caudal peduncle, reduced squamation on dorsal, ventral and peduncle regions and a well developed nuchal hump. The extreme form, cypha, is characterized by a long, fleshy snout, a very abrupt nuchal hump, thin caudal peduncle and reduced squamation (refer to Figure 1). All three are endemic to the Colorado River basin; robusta and elegans were once common throughout the basin, but now are scarce in the Gila River division and most of the lower Colorado River (Miller, 1961). Little is known of the distribution and abundance of cypha. The type speciman of cypha was collected in the Grand Canyon of Arizona.

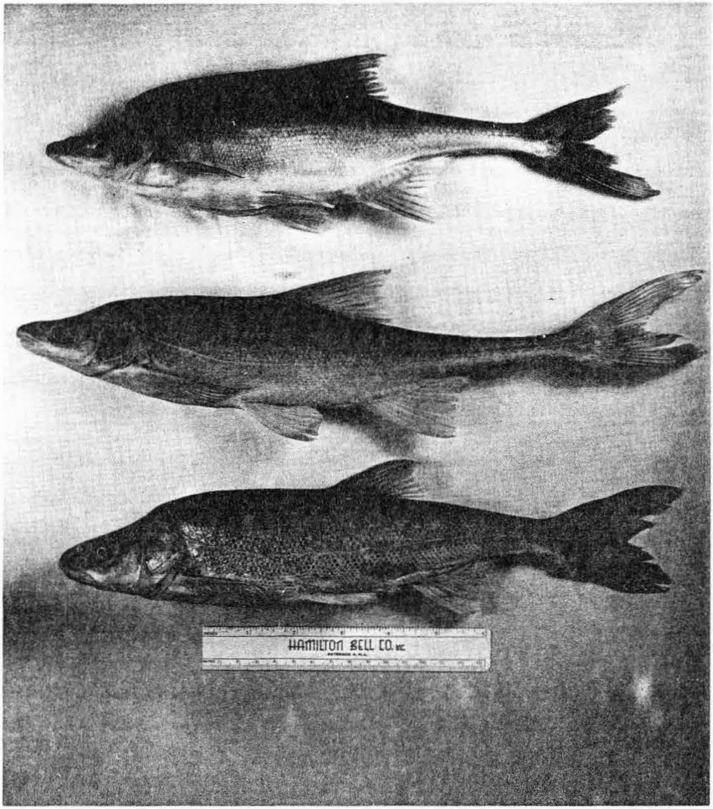

Figure 1. G. cypha, G. elegans and G. robusta from top to bottom.

It has been reported from the Dinosaur National Monument area of the Green River in eastern Utah, and several specimens from the Lake Powell area of northern Arizona and southern Utah which morphologically fit the description of cypha were used in this study.

The small stream form, intermedia, appears much like robusta but is more robust or chubby and has fewer lateral line scales and dorsal fin rays. It is restricted to the Gila River division of the Colorado basin and has been steadily declining in numbers the last few years because of a reduction in suitable habitat (Miller, 1961). The subspecies seminuda supposedly has characters that are intermediate between robusta and elegans. The type material came from the Virgin River, Utah, and the Gila of that river are reportedly distinct (personal communication between James Deacon and Robert Behnke), therefore the author is retaining the name seminuda for fish of the Virgin River. Miller (1946) considers this form to be an intermediate subspecies between robusta and elegans found throughout the Colorado basin.

PROCEDURES

Several hundred Gila specimens were examined; of these, 309 specimens ranging in standard length from 159 to 439 mm were intensively studied. A minimum size of 210 mm standard length was enforced for the fish studied except in the Virgin River collection where all were less than 200 mm. This limitation ensured that all fish examined were mature since some morphologic characteristics (nuchal hump, squamation) are not fully developed in immature fish. The specimens represent collections from (refer to Figure 2): the Green River from its confluence with the White River, upstream to Names Hill, Wyoming (162);[1] Desolation Canyon of the middle Green River (6); the White River in Colorado (19); the San Juan River in New Mexico (24); the Colorado River in Colorado including its tributary the Gunnison (16); Lake Powell (45); Lee's Ferry to Glen Canyon Dam (15); the Virgin River Utah (6); Lake Mohave of the lower Colorado River (6) and the Black River of the Gila River division in Arizona (10).

A total of 35 morphometric characters were recorded for each fish at the beginning of the study. Most of these characters were measured according to Hubbs and Lagler (1958). This number has subsequently been reduced, after several characters were found to be of little value as taxonomic criteria at the species level. Pelvic, pectoral and caudal fin ray counts, lateral line scale count, pharyngeal teeth formulae and

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[1] Refers to number of specimens from that general area used in the study.

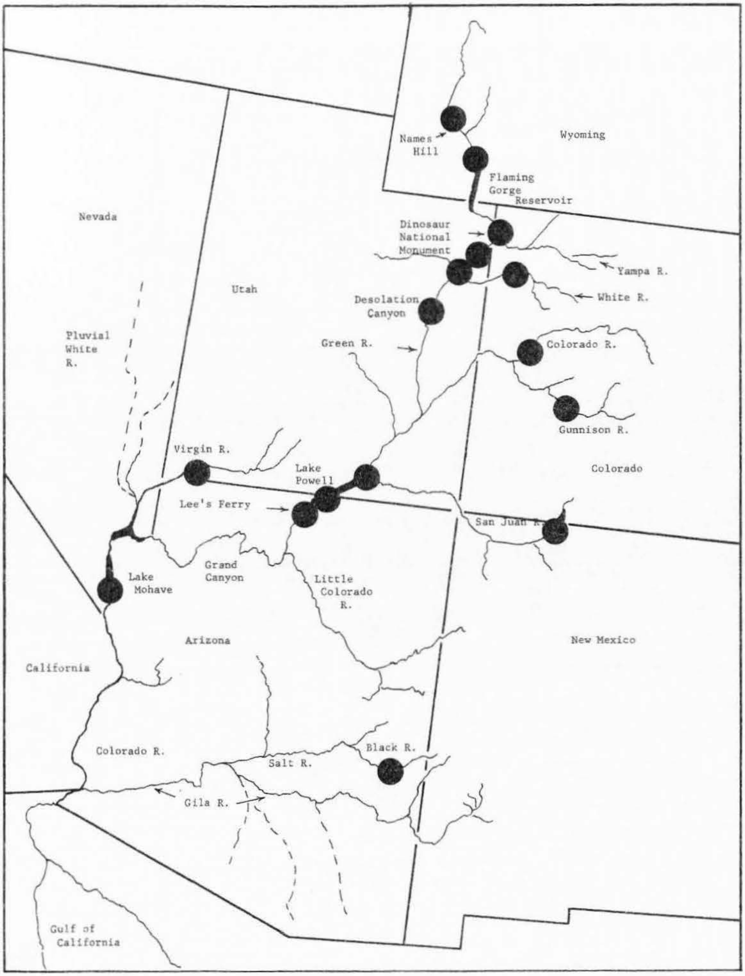

Figure 2. Map of the Colorado River basin showing rivers and localities mentioned in the text. (Dots (●) represent areas of collections.)

several body measurements were deleted because of almost total overlap in ranges and nearness of means between the forms. These characters in the upper Colorado basin Gila are more useful as generic and subgeneric characters than species or subspecies criteria. X-rays were taken for vertebral and fin ray counts. The vertebral count includes the urostyle but not the four Weberian ossicles. The gill raker count as used here represents the summation of the anterior and posterior rows of the first, left gill arch. Appendix B lists the 19 characters most useful in separating the Colorado basin Gila.

The taximetrics program for computers outlined by Estabrook and Rogers (1966) was used to help classify the fish. This program has demonstrated efficacy in problems such as this and proved quite useful in this study. The author will not attempt to outline the mathematical model underlying this program. Estabrook and Rogers (1966) and Wirth, Estabrook and Rogers (1966) may be consulted for a more detailed understanding of the theory behind this method. The 19 characters of Appendix B were used in the program.

The taximetrics program was developed as a tool the biologist may use in analyzing large amounts of taxonomic data. It is a reflection of the biologists' methods and ideas expressed in mathematical terms. It has been most useful for this study in showing where questionable specimens are most closely aligned and in showing the intraspecific variation exhibited by the specimens. A general abstract of the program follows.

A study is composed of objects (specimens) which are described by characters (number of dorsal fin rays) which are dividable into character states (8, 9, 10). For each possible pair of objects in the study, a similarity value (C) is calculated based on the similarity of the character states. A value of 1.0000 connates total similarity (the same as), a value of 0.0000 connates total dissimilarity. Values between one and zero reflect some degree of similarity. A value is found for each pair of objects in the study for each character. A final C value for each pair is then calculated by averaging the values for all the characters.

Once the similarity values have been calculated, the clustering of the objects begins. A cluster may be defined as a group of objects which are more similar to at least one other member (object) of the group than to any object not in the group. The program starts by selecting the pairs with the highest similarity value, that is closest to 1.0000, and clusters them. It then drops to the next highest C value found in the study and brings all pairs that similar into the clustering. These pairs may consist of a member of a previous cluster and a new member, two new objects which will result in the formation of a new cluster, or objects in two previous clusters which results in making one cluster from two. The program continues dropping the similarity value until all objects in the study are clustered together. The stages or C values at which new members are added to the clustering are termed levels (L). The numerical difference in similarity values between levels varies with the study and the number of characters. Many characters will usually create short distances between levels. The clusters are arranged in an hierarchical pattern in that later levels include all the clustering that took place in previous levels.

An example may help explain the clustering better. Let us assume the highest similarity value is .9500, and that three pairs of objects are this similar, (4,6), (6,8) and (7,5). There will be two clusters at Level 1, one consisting of objects 4, 6 and 8; the other of 5 and 7. At Level 2, C = .9000, three pairs are this similar, (1,5), (2,4) and (4,8). The clusters of Level 1 remain but object 1 is added to the 5 and 7 cluster, and 2 is added to 4, 6 and 8. Also 4 and 8, although already in the same cluster have a C value of .9000 and are now also connected. These "internal connections" by members already in the cluster are very important for they indicate the relative strength or homogeniety found within the cluster, and they point out subclusters that may form within the main cluster. Adjectives such as strong and tight indicate very similar clusters internally.

RESULTS

Table 1 summarizes the inter- and intraspecific relationships of robusta, elegans and cypha. The first 19 of the characters listed were used in the taximetrics program. Several characters that typified robusta were: no nuchal humping or very slight humping in larger specimens; dorsal fin rays usually 9; head length[1] range 244-305, mean of 268.9; head depth range 86-123, mean of 101.8; and upper jaw length range 83-117, mean of 96.4. Several characters that typified elegans were: a uniform nuchal hump; dorsal fin rays usually 10; head length range 194-246, mean of 222.7; head depth range 59-88, mean of 74.1; and upper jaw length range 56-84, mean of 68.4. G. cypha was typified by an abrupt nuchal hump, fleshy snout that overhangs the lower lip, and head length range 234-260, mean of 244.1. Peduncle depth showed extremely little overlap between these three forms: robusta ranged from 51-81, mean of 64.1; elegans ranged from 35-49, mean of 41.2; and cypha ranged from 49-57, mean of 52.8.

Tables 2, 3 and 4 indicate the variation expressed in each form from various parts of their ranges for four meristic characters, vertegrae number, dorsal and anal fin rays and gill raker number. G. robusta was collected from the upper Green River, White River, upper Colorado River, San Juan River and the Black River. G. robusta showed little variation in the mean number of vertebrae (42.0-42.3), dorsal fin rays (8.9-9.0), anal fin rays (8.9-9.2) and gill raker number (23.1-24.6) among the five areas collected. G. elegans was collected in the upper

[1]All body measurements are expressed in thousandths of standard length.

Table 1. Summary of the intra- and interspecific morphologic relationships of robusta, elegans and cypha as determined in this study

Character	Robusta		Elegans		Cypha	
	Range	Mean	Range	Mean	Range	Mean
Dorsal fin rays	8-9	9.0	9-11	10.1	9-10	9.5
Anal fin rays	7-10	9.1	9-12	10.1	10-11	10.1
Gill rakers	20-28	23.8	23-36	29.8	22-28	25.6
Vertebrae	41-44	42.2	42-47	44.8	42-45	43.3
Predorsal length[a]	491-569	523.6	451-498	477.1	464-508	487.6
Anal origin to caudal base	317-398	352.1	371-443	409.5	398-468	417.4
Head length	244-305	268.9	194-246	222.7	234-260	244.1
Head depth	86-123	101.8	59-88	74.1	68-92	79.9
Snout length	76-102	88.6	59-85	69.3	77-100	88.8
Interorbital length	74-114	86.7	67-90	76.6	81-94	88.5
Pelvic insertion to pectoral insertion	200-296	239.2	175-247	201.2	186-218	202.8
Snout to occiput length	175-217	196.0	143-179	158.8	148-177	160.7
Upper jaw length	83-117	96.4	56-84	68.4	74-89	82.6
Dorsal fin base length	111-145	125.6	126-168	139.0	132-162	147.1
Least depth of peduncle	51-81	64.1	35-49	41.2	49-57	52.8
Squamation	fully scaled		scaled except for dorsal, ventral and peduncle areas		Same pattern as in elegans only with fewer scales	

[a] All body measurements expressed as thousandths of the standard length.

Table 1. Continued

Character	Robusta		Elegans		Cypha	
	Range	Mean	Range	Mean	Range	Mean
Nuchal hump	none		uniform from head to back		abrupt in occiput region	
Fleshy snout	none		none		present	
Eye diameter	9.0-12.0 mm		8.5-10.0 mm		6.0-7.5 mm	
Pelvic fin rays	9-9 (8-8)		9-9 (8-8)		9-9	
Caudal fin rays	19		19		19	
Lateral line scales	75-96		75-99		72-87	
Pharyngeal teeth	extremely variable in all forms, usually 2,4-5,2 but possible (1,2,3),(4,5)-(4,5),(1,2,3)					

Table 2. Comparison of vertebrae numbers between members of the *Gila* complex

Species and location	Number	40	41	42	43	44	45	46	47	Ave.
robusta										
Upper Green River	60		4	38	16	2				42.3
White River	17		2	13	1	1				42.1
Colorado River	16		1	10	5					42.3
San Juan River	24		7	11	6					42.0
Black River	10		8	2						42.2
seminuda										
Virgin River	6	3	2	1						40.7
elegans										
Upper Green River	91			1	1	28	41	19	1	44.7
Lake Powell	1					1				44.0
Lake Mohave	6					1	4	1		45.0
cypha										
Upper Green River	1					1				44.0
Lake Powell	5			1	2	1	1			43.4
Lee's Ferry[a]	10			1	6	3				43.2
elegans x *cypha*[b]										
Upper Green River	6		1	2	3					42.5
Desolation Canyon	6		1	2	2	1				42.5
Lake Powell	38	1	2	5	12	14	3	1		43.5
Lee's Ferry	5			1	3	1				43.0
robusta x *elegans*[c]										
Upper Green River	2				2					43.0
White River	1			1						42.0

[a]Refers to the area from Lee's Ferry, Arizona upstream to Glen Canyon Dam.

[b]Refers to specimens that appear between *cypha* and *elegans* morphologically.

[c]Refers to specimens that appear between *robusta* and *elegans* morphologically.

Table 3. Comparison of principal dorsal and anal fin ray counts between members of the *Gila* complex

Species and location	Number	Dorsal rays 8	9	10	11	Ave.	Anal rays 7	8	9	10	11	12	Ave.
robusta													
Upper Green River	61	1	60			9.0			50	11			9.2
White River	18		18			9.0			16	2			9.1
Colorado River	17		17			9.0		1	14	2			9.1
San Juan River	24	2	22			8.9			22	2			9.1
Black River	10		10			9.0	1		8	1			8.9
seminuda													
Virgin River	6		4	2		9.3			4	2			9.3
elegans													
Upper Green River	92		2	84	6	10.0			1	70	20	1	10.1
Lake Powell	1			1		10.0				1			10.0
Lake Mohave	6		1	5		9.8				2	4		10.7
cypha													
Upper Green River	1		1			9.0				1			10.0
Lake Powell	5		2	3		9.6				3	2		10.4
Lee's Ferry	10		6	4		9.4				10			10.0
elegans x *cypha*													
Upper Green River	6		6			9.0			2	4			9.7
Desoltation Canyon	6		6			9.0			2	4			9.7
Lake Powell	38	2	18	18		9.4				36	2		10.1
Lee's Ferry	5		5			9.0				5			10.0
robusta x *elegans*													
Upper Green River	2		1	1		9.5			1	1			9.5
White River	1			1		10.0				1			10.0

Table 4. Comparison of gill raker number between members of the *Gila* complex

Species and location	Number	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Ave.
robusta																			
Upper Green River	60	2	2	6	20	17	6	3	2	2									23.8
White River	18			1	4	4	3	5	1										24.6
Colorado River	17		1		3	5	4	2	1	1									24.6
San Juan River	23		3	3	7	8	2												23.1
Black River	10			1	6		1	2											23.7
seminuda																			
Virgin River	6					1	1	1	2				1						27.7
elegans																			
Upper Green River	92				1	1	1	5	7	12	16	13	23	10	3				29.4
Lake Powell	1													1					32.0
Lake Mohave	6										1	1		1		1	1	1	32.7
cypha																			
Upper Green River	1						1												25.0
Lake Powell	5				1		2		1	1									25.6
Lee's Ferry	10			1		2	1	2	3	1									25.6
elegans x *cypha*																			
Upper Green River	6			1		2	1	1	1										24.7
Desolation Canyon	6								3	2		1							27.8
Lake Powell	38					1	1	3	6	5	12	4	3	1	1	1			28.6
Lee's Ferry	5							1	1	2		1							28.0
robusta x *elegans*																			
Upper Green River	2						1	1											25.5
White River	1									1									28.0

Green River, Lake Powell and Lake Mohave. This form showed little variation in the means of vertebrae number (44.0-45.0), dorsal fin rays (9.8-10.0) and anal fin rays (10.0-10.7) among the three areas collected. A somewhat larger variation in gill raker number (29.4 for Green River fish and 32.7 for Lake Mohave specimens) was attributed to the larger size of the six Lake Mohave fish (335-439mm standard length). G. cypha was collected in the upper Green River, Lake Powell and Lee's Ferry. This form varied from 43.2-44.0 for mean vertebrae number, 9.0-9.6 for dorsal fin rays, 10.0-10.4 for anal fin rays and 25.0-25.6 for gill rakers for the three areas collected. Collections in the upper Green River, Desolation Canyon, Lake Powell and Lee's Ferry produced specimens referred to as elegans x cypha intergrades. Mean vertebrae numbers in these intergrades were 42.5 from the upper Green River and Desolation Canyon, 43.5 from Lake Powell and 43.0 from Lee's Ferry. Mean dorsal fin ray numbers were 9.0 for all collections except those of Lake Powell which averaged 9.4. Mean anal fin rays were 9.7 for the upper Green River and Desolation Canyon fish, 10.1 from Lake Powell and 10.0 from Lee's Ferry. Mean gill raker number was lowest in the upper Green River fish (24.7), highest in Lake Powell fish (28.6) and quite similar in the Desolation Canyon (27.8) and Lee's Ferry (28.0) specimens. Two fish from the upper Green River and one from the White River had meristic characters between the means of robusta and elegans, and therefore were referred to as robusta x elegans intergrades. The mean values for the characters were: vertebrae number, robusta 42.2, elegans 44.8, intergrades 42.7; dorsal fin rays, robusta 9.0, elegans 10.1, intergrades 9.7; anal fin rays, robusta 9.1, elegans 10.1, intergrades 9.7; and gill rakers, robusta 23.8, elegans 29.8, intergrades 26.3. G. robusta seminuda differed from robusta in mean values of vertebrae number (40.7 and 43.3 respectively) and gill raker number (27.7 and 23.8 respectively).

Figure 3 is a diagram of the results of the taximetrics program comparing 309 Gila on the basis of 19 characters.

Results of the taximetric program by level

Level 1. The clustering started with two clusters being formed at a similarity value of 1.00000. One cluster of 15 fish all from the upper Green River included all typical elegans. The other cluster included four fish from the upper Green River, four from the upper Colorado River, three from the White River and eight from the San Juan River. All 19 of these fish were typical robusta. Therefore these clusters are referred to as the elegans and robusta clusters in this and the remaining levels of the presentation of results. It should be noted here that not all the fish included in these clusters in later levels are typical elegans or robusta, but the majority are and therefore these names will still apply.

Level 2. The similarity value lowered to .94373 and the two previous clusters increased in number of members. Also a third cluster formed. The elegans cluster was joined by 74 new members; 68 were from the upper Green River, four from Lake Mohave and two from Lake Powell. This cluster contained 89 members. Additional members to the robusta cluster included 45 fish from the upper Green River, 12 from the Colorado River, 11 from the San Juan River, nine from the Black River, 13 from the White River and one from the Virgin River. The robusta cluster at Level 2 contained 110 members. A third cluster was also formed; it was composed

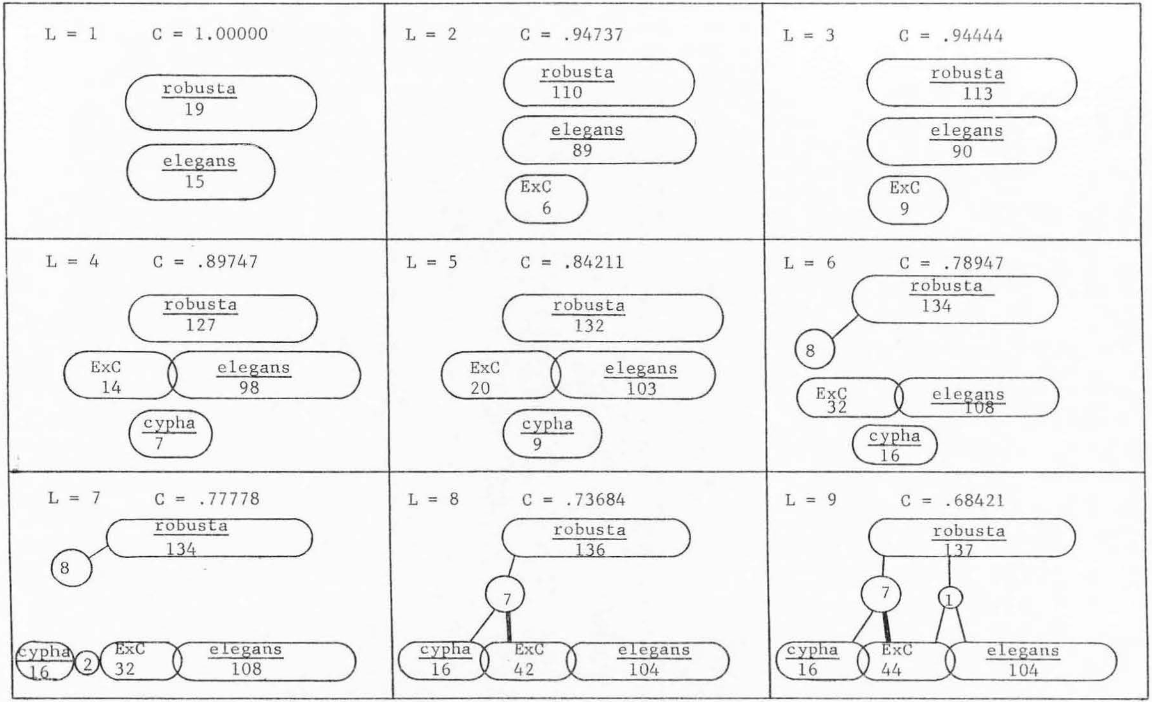

Figure 3. Results of the taximetrics program for 309 Gila specimens. (Number of specimens indicated within each cluster; ExC = intergrades between elegans and cypha; L = Level; C = similarity value.)

of six fish from Lake Powell all of which were considered to be elegans x cypha intergrades due to intermediate morphology.

Level 3. The similarity value lowered only a short amount to .94444, therefore few new members were added. One fish from the upper Green River joined the elegans cluster but otherwise this cluster remained as in Level 2. Three new members joined the robusta cluster; two of these were from the upper Green River, and the other was from the White River. The elegans x cypha cluster did not change from Level 2.

Level 4. The similarity value lowered to .89747 and several important changes occurred. A group of 14 fish from Lake Powell centered around the six member elegans x cypha intergrade cluster of Level 3 and connected to the elegans cluster by only 8 connections. Ten of the 14 had three or more connections to other members of this small group. Therefore this group was defined as the elegans x cypha subcluster since it appeared as a segregated entity and its members fit this intergrade category. Eight new members were added to the elegans cluster; five were from the upper Green River, two from Lake Mohave and one fish from Lake Powell (which in later levels aligned itself with the elegans x cypha subcluster). The robusta cluster was joined by 14 new members; six were from the upper Green River, five from the San Juan River, one from the White River, one from the Virgin River and one from the Black River. A new cluster of seven members was formed; four were from the Lee's Ferry collections, the other three from Lake Powell. This cluster was considered to be the cypha cluster for it behaved somewhat independently in future levels and the specimens had an abrupt nuchal hump and a well developed snout, both characteristic of cypha.

Level 5. The similarity value lowered to .84211. The robusta cluster was joined by five new members, two from the upper Green River, two from the Virgin River and one from Lake Powell, making a total of 132 members. This cluster was quite homogeneous with only 20 members having less than 15 connections to other members and only 7 members with less than 10 connections. These twenty included, ten from the upper Green River, one from the Black River, three from the Virgin River, five from the San Juan River and one from Lake Powell. Six new members to the elegans x cypha subcluster included four fish from Lake Powell connected only to the subcluster. Two others from Lake Powell had connections to both the elegans cluster and the elegans x cypha subcluster. One had one connection to each of the two groups; the other had one connection to the elegans cluster and two to the intergrade group. This intergrade subcluster contained 20 members at Level 5. The elegans cluster was joined by five new members, two from the upper Green River, one from Desolation Canyon, one from Lake Powell and one from Lee's Ferry, making a total of 103 fish. The cypha cluster increased by two, one from Lake Powell and one from Lee's Ferry. Six of the nine members had at least three connections to other members.

Level 6. The similarity value lowered to .78947. A group of eight fish attached to the robusta cluster, but by only one connection from one of the eight. This subcluster included three fish from the upper Green River, three from Desolation Canyon, one from Lake Powell and one from the White River. New members to the robusta cluster made a total of 134; the two new members were one from the Virgin River and one from the upper Green River. New members to the elegans x cypha subcluster were four fish from Lake Powell, four from Lee's Ferry and two from

Desolation Canyon. Two fish from Lake Powell had connections to both the _elegans_ cluster and the _elegans_ x _cypha_ subcluster; one had two and three connections respectively; the other had two to both. Connections in later levels indicated these two fish were most similar to the _elegans_ x _cypha_ group, making a total of 32 members at Level 6. One fish from the upper Green River and three from Lake Powell joined the _elegans_ cluster. Another fish from Lake Powell had one connection to both the _elegans_ cluster and the _elegans_ x _cypha_ subcluster, but later connections associated it with the _elegans_ cluster. The _elegans_ cluster became very tight in Level 6 with only nine members having less than 15 connections to other members. The nine included five fish from the upper Green River, three from Lake Powell and one from Desolation Canyon. The _cypha_ cluster was increased to 16 members by the addition of one fish from the upper Green River, two from Lake Powell and four from Lee's Ferry. Twelve of the 16 members had connections to at least three other members, indicating a fairly tight cluster.

Level 7. The similarity value dropped very little to .77778. The most important change here was a connection between the _cypha_ cluster and the _elegans_ x _cypha_ intergrade subcluster. This was facilitated through a new member to the clustering that had two connections to the _cypha_ cluster and one to the intergrade subcluster. Another new member was connected to the above "linking" fish. No other clustering occurred at Level 7 and the only notable change was that the _robusta_ cluster included only five members with less than 15 connections to other members at this level. This cluster still remained attached to the eight member subcluster mentioned in Level 6 by only one connection.

Level 8. The similarity value dropped to .73686. The *robusta* cluster and its attached subcluster connected to the *elegans*-*cypha* complex by six connections. Five of these connections were from the small attached subcluster to the *elegans* x *cypha* subcluster; the other was from the small attached subcluster to the *cypha* subcluster. This small subcluster of eight members became a bridge between the two large complexes, yet it was connected to the *robusta* cluster by only two connections. One of the fish from the upper Green River included in this bridging subcluster became more similar to the *robusta* cluster and was included there; thus only seven members appeared in the bridging subcluster (Figure 3). The two linking specimens of Level 7 between the *cypha* and *elegans* x *cypha* subclusters were included in the latter group in Level 8, for they were similar to this group. Also two fish from Lake Powell that had entered the *elegans* cluster at Level 6 and one fish from Lee's Ferry and one from Lake Powell that entered the *elegans* cluster at Level 5 now became more similar to the *elegans* x *cypha* subcluster and these four were included there. New members to the clustering included: one fish from the upper Green River connected to the *robusta* cluster; one fish from the upper Green River with one connection to both the *elegans* x *cypha* group and the seven member bridging subcluster; one fish from the upper Green River and one from Lake Powell each with a connection to both the *cypha* cluster and the *elegans* x *cypha* group; one fish from Lake Powell with two connections to the *elegans* cluster, two connections to the *elegans* x *cypha* subcluster, one connection to the *cypha* subcluster and one connection to the bridging subcluster. These last four fish were included in the *elegans* x *cypha* subcluster at this level.

Level 9. The similarity value declined to .68421. This was the last level of the program and therefore all specimens were included. There were only 22 connections between the robusta complex and the elegans-cypha complex at this level. Twenty of these were between the cypha and elegans x cypha subclusters and the bridging subcluster. The other two connections were through a new member to the clustering that had five connections to the elegans cluster, two connections to the robusta cluster and one connection to the elegans x cypha subcluster. The bridging subcluster had only four connections to the robusta cluster at this level. New members to the clustering in addition to the one above included: one fish from the upper Green River that connected to the elegans x cypha subcluster and the elegans cluster by one connection to each, one fish from the upper Green River that connected only to the above new member, one fish from the Virgin River that connected to the robusta cluster. The first two fish mentioned above were included in the elegans x cypha subcluster; the last specimen mentioned was included in the robusta cluster.

Several things happened during the program that weren't indicated in Figure 3 or in the above results. In Level 4 several specimens of robusta from the San Juan River formed a noticeable extension of the robusta cluster. These fish stayed as such until Level 6 when they connected strongly with the other robusta. Also three fish were considered robusta x elegans intergrades for they were quite dissimilar to anything else in the program, and they appeared between robusta and elegans for the meristic characters (Tables 2, 3 and 4).

It was noticeable in the program that by Level 4 most of the robusta from the upper Green River, White River, Colorado River, San Juan River and Black River were clustered. Similarly most of the _elegans_ from the upper Green River and Lake Mohave had been clustered by Level 4. These areas contained what could be considered the "typical" _robusta_ and _elegans._ Later levels clustered primarily fish from Lake Powell, Lee's Ferry, Desolation Canyon and a few from the upper Green River. These were primarily grouped as intergrades and it was through these fish that the several clusters were brought together.

DISCUSSION

G. robusta and G. elegans

The data collected in this study indicate that robusta and elegans are well separated morphologically. The taximetrics program showed no similarity between the clusters representing these two forms, indicating a large morphologic separation. By level 2 of the program, 89 per cent of the elegans and 81 per cent of the robusta had been clustered. This and the high similarity value of .94737 at this level indicates a high degree of homogeneity in each form. Both clusters contain members from all of the general geographical areas in which robusta or elegans were collected. For elegans these areas were: the upper Green River, Lake Powell and Lake Mohave. For robusta these areas were: the upper Green River, White River, upper Colorado River, San Juan River and the Black River of Arizona. These data show that each form is the same throughout the Colorado basin and indicates two distinct evolutionary lines rather than parallel evolution. The last few levels of the program primarily included objects to these main clusters that were not typical robusta or elegans.

The robusta of the San Juan River and the Virgin River appear to be diverging more from the typical than are those from other areas collected. Some of the fish from these two areas were not clustered tightly to the main robusta cluster until later levels or not at all. The Virgin River collection is discussed later as G. robusta seminuda. Most of the San Juan collection were typical robusta, but a few retained their individuality until later levels. This does not suggest that the San Juan population should be regarded as a subspecies but indicates a greater degree of divergence than is found in the other areas collected.

Table 1 indicates, as did the taximetrics program, the distinctiveness of robusta and elegans. Thirteen of the 23 characters show a distinct separation between these two forms with four other characters indicating a lesser degree of difference. The four meristic characters of Tables 2, 3 and 4 support the relationships between robusta and elegans suggested by the taximetrics program. In each of these characters there is a small area of overlap, yet two distinct populations are evident. These meristic characters show the uniformity of each type among the several areas collected, this is especially noticeable in the fin ray counts (Table 3).

Vanicek (1967) found several life history differences which support the morphometric separation. His study revealed the following from specimens collected in the Green River in Dinosaur National Monument, Utah and Colorado.

1. Food habits: robusta appears rather opportunistic eating fish, and terrestial and aquatic insects; elegans is more selective, feeding primarily on terrestial insects with plant debris and algae also taken. This may be correlated with elegans' often seen practice of feeding on the surface.

2. Growth rate: robusta grows fastest its first year of life with growth rate decreasing afterward; elegans grows slowly its first few years, with the fastest growth rate around the fourth year.

3. Length-weight: robusta becomes relatively heavier than elegans as length increases.

4. Spawning area preference: both forms were caught in spawning condition at the same time but never in the same net. This may indicate a spatial difference in spawning. Both were caught in the same net other times of the year.

Another bit of life history information that suggests two quite different populations is general habitat preference. Collection data indicates that robusta is found in smaller rivers than elegans. Tributary rivers (White, San Juan) harbored robusta, whereas elegans was collected only in the main rivers (Green, Colorado). There is an area of overlap in ranges yet this difference appears valid.

Three fish were collected that appear between robusta and elegans morphologically. The taximetrics program indicated that these fish were quite distinct. One of the three was clustered at Level 7, one at Level 8 and one at Level 9. One was most similar to robusta, the other two were closer to elegans. None of them show high similarity to any other specimens in the study, indicating that they are very different. Tables 2 and 3 show that for fin ray counts and gill raker number these three fish appear between the means of robusta and elegans. Therefore they may possibly be hybrids, or they may just be extreme morphologic variants of one or the other of the forms.

Nevertheless, based on the specimens examined, no mass hybridization between the two forms is evident, and reproductive isolation between the two sympatric populations appears well established. This, along with the strong morphologic and life history separation, strongly suggests that robusta and elegans should be treated as full species.

G. elegans and G. cypha

Whereas robusta and elegans are well separated, the relationships between elegans and cypha are not so clear. A large number of specimens that morphologically appear to bridge the gap between these two have been collected. Figure 4 shows the intergradation between these two forms.

Both elegans and cypha have previously been described in general morphology. The name elegans is used here as is commonly accepted in recent literature (La Rivers, 1962; Sigler and Miller, 1963), which is in agreement with the type description and picture (Baird and Girard, 1853). Only two specimens of cypha have been characterized in the literature (Miller, 1946); thus the intraspecific variation of this form is unclear. Several criteria outlined by Miller for distinguishing cypha are: (1) An abrupt nuchal hump (compare cypha and elegans in Figure 1). (2) A prominent fleshy snout and subterminal mouth. (3) A small eye in comparison to either robusta or elegans. (4) A peduncle depth intermediate between those of robusta and elegans.

The hump and snout characteristics are the key characters here. However, the specimens vary from a typical elegans (smooth hump and no snout) to a "typical" cypha (abrupt hump and long snout). The transition from elegans to these intergrades is more abrupt and noticeable than that between the intergrades and cypha. At Level 6 a group of 16 fish is clustered as a separate unit by the taximetrics program. At Level 7 this group joins the elegans cluster, but by only one connection and this to the intergrade subcluster. In Levels 8 and 9 this group of 16 fish and the elegans cluster remain separate but each becomes more similar to the intergrades. The major characters separating

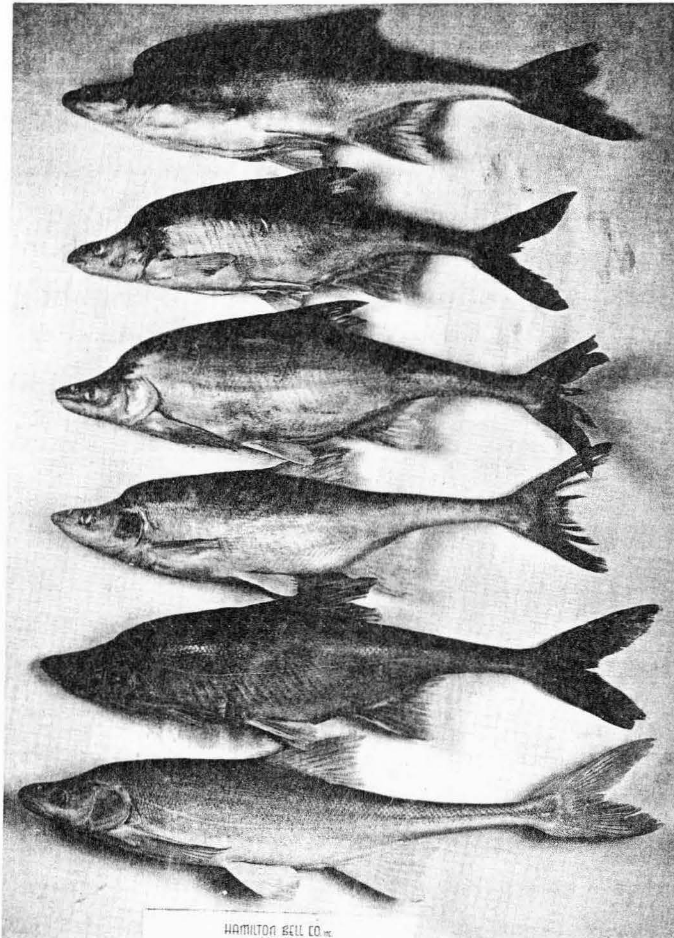

Figure 4. Intergradation in morphology between G. cypha (top) and G. elegans (bottom).

this group of 16 fish from the intergrades are; a more abrupt nuchal hump, eye less than 7.5mm in diameter and head more elongate (including snout), yet these distinctions are not very sharp. Therefore the author has considered these 16 fish to be cypha based on the taximetrics program clustering. Present knowledge is not sufficient to unravel the mystery that surrounds this fish, but the cypha morphology is a reality and therefore it seems most logical to recognize it until future investigations prove otherwise. The last three levels of the program indicate rather strongly that cypha and elegans are two separate entities, but they are completely bridged by a third group of specimens. This intergrade cluster does not show the internal homogeneity of the other two. Some of its members are very similar to elegans, while others are most similar to cypha. Tables 2, 3 and 4 illustrate the somewhat cloudy distinction between elegans and cypha and the position of the intergrades. The knowledge that cypha is not easily defined and that there are intergrade forms is the basic idea extended here.

The fact that cypha is a very elusive and arbitrary entity does not seem apparent in the literature. The reason for this is that few collections have been made in areas cypha may inhabit, therefore few cypha or extreme types have been collected. Gaufin, Smith and Dotson (1960) reported collecting 15 cypha from the Hideout Flat area of the Green River (river mile 306), now under Flaming Gorge Reservoir. These fish were unavailable for examination by the author. A picture that undoubtedly represents one of these fish appeared in an article in National Parks Magazine (Miller, 1963). Although it is somewhat difficult to judge from a picture, the fish appeared more like an integrade than a cypha as used here. Also, two specimens used in this study (tag numbers

2790, 2791) and collected at Little Hole (river mile 282) of the Green River in 1963, were intergrades, not cypha. The problem seems to be that collectors can distinguish quite easily between elegans and fish with a more extreme morphology, but that collections up to this time have not been sufficiently large to illustrate the total bridging of the morphologic difference between elegans and cypha. Therefore many of the specimens presently referred to cypha probably represent intergrades as defined here.

Miller (1963) indicated that the Green River in the area of the Flaming Gorge basin and Dinosaur National Monument probably represented the only area where cypha was common. This statement probably was based on Gaufin, Smith and Dotson's (1960) collection which represented the largest group of fish with the extreme morphology taken to that date. These fish were taken 61 miles upstream from Dinosaur National Monument. Hagen and Banks (1963) reported collecting two fish with the extreme morphology, one in 1961 and one in 1962, in the Monument. The Monument was intensively collected during 1964-1966 by Vanicek (1967), his collections were used in this study. They contained no cypha and only two intergrades, but one cypha and one intergrade were taken in the Monument in 1963 (collected by the late Donald R. Franklin, Leader, Utah Cooperative Fishery Unit). Vanicek indicated the reason he collected no cypha was its extreme rarity, rather than its supposed eradication by the 1962 poisoning of the Flaming Gorge basin. This is supported by the fact that the other native fishes were not severely diminished in the Monument by the eradication program. The site from which Gaufin, Smith and Dotson (1960) collected cypha in the upper Green River has been obliterated by Flaming Gorge Reservoir. Of the 16 fish defined as cypha in the present study, only one was from the Green River, all others being from the northern Arizona canyons. This suggests that _cypha_, or fish with the extreme morphology, are most abundant in the middle Colorado River canyons with smaller numbers at least at one time inhabiting the upper Green River.

Lake Powell was represented in this study by 45 specimens; of which one was a typical _robusta_, one a typical _elegans_, five were _cypha_ and 38 were intergrades between _elegans_ and _cypha_. The upper Green River was represented by 92 _elegans_, 61 _robusta_, one _cypha_ and six intergrades. Desolation Canyon of the middle Green River, only collected once, produced six specimens all of which were most similar to the intergrades, yet were distinct in themselves. Of 15 fish collected just below Glen Canyon Dam (Lake Powell) to Lee's Ferry, ten were _cypha_ and the remaining five intergrades. All six specimens from Lake Mohave were _elegans_. These data indicate that the most extreme form, _cypha_, is found most abundantly in the northern Arizona canyons of the middle Colorado basin, whereas the less extreme form, _elegans_, is most abundant in the upper basin. Minckley and Deacon (1968) report that _elegans_ has become depleted in the lower basin. The intergrades from Lake Powell are not very similar to the intergrades from the upper Green River or Desolation Canyon. Nor are the intergrades from the upper Green very similar to those from Desolation Canyon. Therefore there are three groups of fish which are not very similar to each other but are provisionally assigned as intergrades between _elegans_ and _cypha_.

This large number of intermediate forms presents a problem. The most probable explanation appears to be introgressive hybridization. Two parent or end forms bridged by an assortment of intergrades seems apparent. Yet the data also suggest a general cline in morphology, from an extreme form in northern Arizona to a less extreme form in northern Utah, associated with differences at least historically in river volume and velocity. The proponents of the ecosubspecies concept for the Colorado basin Gila have used as the basis of their hypothesis this idea of different morphologies being related to their adaptive value for varying current conditions. The author feels the idea of ecosubspecies does not apply and these fish represent distinct evolutionary lines throughout the basin and are not the result of parallel evolution. Yet the immediate environment may have a role in shaping the phenotype of these fish.

From the data collected to date, elegans and cypha appear very closely related. Intergrades between the two suggest either introgressive hybridization or phenotypic variability associated with environmental conditions. Either of these situations suggest one polytypic species with two or possibly more subspecies. If future investigations find these two forms living sympatrically without hybridization, and/or find the present hybrids were a result of some disturbing force such as man's activity, the two species concept would be correct. But present information suggests these two forms are only subspecifically separated.

G. robusta seminuda

As mentioned earlier, this form is tentatively being retained here as a distinct form from the Virgin River. The small number of specimens (6) used in this study and their small size (159.0 mm - 199.5 mm) limits what can be said about this population. Slight differences in the averages of the characters in Tables 2, 3 and 4 indicate that seminuda may be a distinct entity at the subspecies level. The vertebrae and gill raker counts seem to set it off from either robusta or elegans. The taximetrics program shows the Virgin River specimens to be very close to robusta, yet somewhat distinct. None of the six fish became strongly attached to the main robusta cluster until they had been in the group for several levels. The six fish did not act as a population, e.g., they were not very homogenious, for one entered at Level 2, one at Level 4, two at Level 5, one at Level 6 and one at Level 9. Also there were few connections between these six fish. Therefore some evidence for recognizing seminuda as a distinct subspecies exists, but it is not conclusive.

Miller (1946) considers seminuda an intermediate subspecies between robusta and elegans. He examined the five type specimens collected by Cope and Yarrow (1875), which range from 90 mm to 128 mm standard length. He suggests, as does Ellis (1914), that this form is found throughout the Colorado basin, but the type material came from the Virgin River, Utah. Ellis considered this form to be a typical robusta except for reduced squamation on ventral and dorsal areas. The author found several specimens matching this description and since they agree in all other characters with the typical robusta, has considered them only as phenotypic variants for this one character. Miller (1946) probably classified seminuda on the basis of the ecosubspecies concept. Since it appears between robusta and elegans for a few morphologic characters, it fit into this concept quite well and therefore would be expected to be found throughout the basin in suitable ecological situations. The ecosubspecies concept does not appear valid for the Colorado basin Gila, and the Virgin River population of robusta appears as a distinct entity. Therefore seminuda most correctly refers to the Virgin River population only. Miller's (1946) data on the type material shows seminuda to be distinct from either robusta or elegans, supporting the hypothesis presented here for a geographic subspecies in the Virgin River.

The fish from the Virgin River used in the present study were quite fully scaled. Lack of scales on dorsal and ventral areas was the key character used by Cope and Yarrow (1875) for distinguishing seminuda and was used by subsequent workers. Squamation has been found by the author to be somewhat variable and may not be as genetically fixed as some of the other characters of these fish.

G. robusta intermedia

The author is familiar with this form only through the literature; therefore any remarks made here are merely speculation at this time. G. r. intermedia as characterized by Miller (1946) and Barber and Minckley (1966) seems to be a distinct form. It differs from robusta in dorsal and anal fin ray counts (8-8 as opposed to 9-9 for robusta) and general body morphology, especially the peduncle depth (deeper in intermedia). This form has been reported to live sympatrically with robusta and elegans, but no reports of hybridization between intermedia and either of the other two have appeared in the literature. Specimens of the three forms collected together from the Salt River of Arizona by Gilbert and Scolfield (1898) were examined by Dr. Minckley (Arizona State University), and he reported them as being distinct from each other (personal communication to Dr, Robert Behnke, Colorado State University). This suggests that intermedia may be a distinct and valid species as well as robusta and elegans.

G. robusta jordani

This Pluvial White River form is definitely referable to the species *robusta*. The author examined the type specimens (BYU 9958, 9959) and found them to be the same as *robusta* except they were somewhat shorter and chunkier on the average and had dark mottling on their bodies. The Virgin River and Pluvial White River are faunistically and geographically close. Several fish species are common to both, yet each has its endemics. It is possible that the White River *Gila* are closely allied to the Virgin River *Gila*. If so the name *seminuda* may apply to both. However, current knowledge suggests the subspecies taxon, e.g., *G. robusta jordani*, for the Pluvial White River population (La Rivers, 1962).

EVOLUTION AND PHYLOGENY

Members of the genus Gila are found in all major U. S. basins, and in several small, isolated basins, west of the Continental Divide. They are also found in several drainages in Mexico and in one U. S. basin east of the Divide, the Rio Grande. There appears to be two major phylogenetic lines within the subgenus Gila. The larger of the two centers around G. robusta and G. robusta intermedia of the Colorado basin, the other around G. atraria (Girard) and the Bonneville and more westerly basins. Uyeno (1960) considers atraria of the Bonneville basin to be the most primitive North American cyprinid. An ataria-like form probably gave rise to G. caerulea (Girard) of the Klamath River basin of Oregon and California and G. crassacauda (Baird and Girard) of the Sacramento-San Juaquin system of California. G. crassacauda has not been collected since about 1950 and is feared extinct.

The evolution of the Colorado basin Gila is undoubtedly integrally tied with the geological history of that basin. Unfortunately this history is somewhat obscure at the present time. Several general trends seem to be indicated, most of the following are from McKee, et. al. (1967).

1. The Colorado River did not become the through flowing river of today until the mid-late Pliocene.

2. Before the mid-Pliocene the upper Colorado basin drained southeastward from the Kaibab Upwarp, following closely what is presently the Little Colorado River but in an opposite direction. It may have drained into the Rio Grande basin. West of the Kaibab Upwarp the Hualapai Drainage System was well established and probably drained southwestward.

Smith (1966) suggests that these two basins were connected in the Miocene but became separated by the Kaibab Upwarp.

3. The Hualapai Drainage System cut through the Kaibab Upwarp from west to east in mid-late Pliocene thus creating a channel for the Colorado River to follow. This was the beginning of the Grand Canyon and the Colorado River as we know them today.

4. The increased waters of the early Pleistocene produced connections between the Colorado basin and outlying areas. Central and southern Nevada were connected to the Colorado River primarily through the Pluvial White River system. The Gila River of Arizona probably was connected to basins in northern Mexico, principally the Yaqui River basin. These connections became severed in the late Pleistocene as the northern glaciers receded.

The fish fauna of the present Colorado basin reflects an origin from an upper and lower part, the Grand Canyon area being the separating point. This concurs with the geologic evidence. The lower basin (Hualapai Drainage System) was characterized by relatively short drainage patterns indicating small rivers and streams (McKee, et al., 1967). The endemic fish of this area are typically small river and stream forms, as is seen in the five species of the tribe Plagopterini that inhabit this area. The upper basin is geologically older than the lower basin and during the Pliocene the Ancestral Colorado River was well established. This may have provided an environment that selected towards large river fish such as Ptychocheilus lucius Girard, Catostomus latipinnis Baird and Girard and Catostomus (Pantosteus) discobolus Cope. A mid-Pliocene fossil of Ptychocheilus has been found in the Bidahochi Formation of northeastern Arizona (Uyeno and Miller, 1965). McKee, et al. (1967)

indicate that this formation was deposited before the Colorado River started flowing through the Kaibab Upwarp; this suggests that Ptychocheilus may have evolved in the upper basin. When the two sections of the river were joined, the large river forms of the upper basin could have easily moved into the lower basin; but the large river environment would have acted as a barrior to the small river and stream forms. This would explain the limited range of the Plagopterini and other forms that evolved in the lower basin, and the presence of the large river forms throughout the basin.

This hypothesis is supported by the fish fauna of the widely separated Gila River and White-Virgin River basins. The fish of these basins appear closely related and a few species are or were found in both (Plagopterus argentissimus Cope, Catostomus (Pantosteus) clarki Baird and Girard), yet each has several endemics. This indicates a period of general connectedness and a period of isolation as suggested above. The time element also seems fairly well correlated. Many of the Colorado basin endemic fish species evolved in the Pliocene; this is indicated for the genus Catostomus (Smith, 1966), the Plagopterini (Miller and Hubbs, 1965), the genus Gila (Miller, 1958; Uyeno, 1966) and the genus Ptychocheilus (Miller, 1965). Therefore these fish had probably evolved to about their present forms by the time the Colorado River became the through flowing river we know today.

There is also some support for the theory that the Colorado River once flowed from Arizona across southern California to the Pacific Ocean (Smith, 1966). Smith suggests this diversion of the Colorado River occurred in the premiddle Pliocene, before the Kaibab Upwarp appeared. Faunistic evidence for this is shown by one species of Gila and one of

Pantosteus found presently in the Los Angeles Plain area. These fish were derived from the Colorado River basin. Also the golden trouts of California appear very closely related to the endemic trouts (Gila and Apache) of the lower Colorado basin (personal communication with Dr. Robert Behnke). There is little present geologic data to support this theory one way or the other, but a connection at some earlier time does seem very probable.

Where do the Gila fit into this picture? Gila is considered the most primitive American cyprinid genus (Miller, 1958). Ptychocheilus and Richardsonius were probably derived from a Gila-like ancestor (Uyeno, 1960), as was the tribe Plagopterini (Miller and Hubbs, 1960). Therefore Gila was probably represented in both the upper and lower basins before they became separated by the Kaibab Upwarp. This also was before Gila became differentiated which suggests a late Miocene or early Pliocene time period which is the approximate time of the Kaibab Upwarp.

If the above hypothesis should prove to be true, then robusta and possibly elegans could have evolved in the upper basin. Both are fairly large river fish, elegans more so than robusta. This idea of upper basin speciation for robusta is supported by a Pliocene fossil Gila from the Bidahochi Formation reported by Uyeno and Miller (1965) which appears to be robusta or at least very closely related. The similarities between robusta and the elegans suggest that an early robusta probably gave rise to the more specialized elegans. No present information suggests a relative time or place for elegans speciation. The many endemic species of fish in the Colorado basin speaks for the geographical isolation that must have occurred at various times. It is possible that some of the isolation in the basin was more ecological in nature than strictly geologic. Therefore it is possible that elegans speciated in the upper basin also.

The extreme morphology of cypha suggests a more recent speciation. Its close affinity to elegans and the apparent gradation in a few morphologic characters between the two, suggest that it evolved from an elegans-like form. The present distribution of cypha, though based on very meager collections, suggests that it evolved in the northern Arizona canyons. It also suggests that this form is best adapted to swift, canyon areas, as has been hypothesized based on its extreme morphology. Cutting of the Grand Canyon by a continuous Colorado River began in the mid-Pliocene, and the Canyon was cut to within 50 feet of its present depth by the early Pleistocene (McKee, et. al., 1967).

This would indicate a very torrential environment for several million years and a relatively quiet area for the last million. If cypha's morphology was indeed selected for in a torrential environment as Miller (1946) suggested, the early Grand Canyon certainly provided a place that could have guided this speciation.

As mentioned earlier, the many intergrades between elegans and cypha most likely are hybrids. If this is so, the following hypothesized sequence of events may explain the situation as we find it today. The evolution of the extreme cypha morphology took place during the time of rapid cutting in the Grand Canyon area. This area was effectively isolated from the rest of the river by some mechanism, possibly the violent conditions. More recently as the area became less torrential, cypha began moving into other parts of the river and came into contact with elegans. Although morphologically diverse, no reproductive barriers existed between these forms and hybridization occurred. In the area where the ranges of the parent forms met, a zone of intergradation was established. Subsequent introgression produced a population almost entirely of intergrades in this zone. Lake Powell fits this zone both geographically and faunistically. Movements of some of these hybrids into the Green River explain the presence of this morphology in this area and the few extreme cypha types. Evidence that cypha inhabited parts of the lower Colorado basin in recent times has been found (Dr. W. Minckley, personal communication). Data at hand suggest the extreme morphology was more successful in the upper basin for no cypha have been reported in the lower basin. This hypothesis is based on very circumstantial evidence. It would be supported if Grand Canyon collections contain primarily cypha and collections from the lower Green River produce primarily elegans and intergrades.

The Virgin River population, if it is distinct, probably differentiated in the Pleistocene, or possibly since the Pleistocene.

The White River form, jordani, undoubtedly represents a population of robusta that has been isolated since the Pleistocene in a restricted type of habitat. The aridity of the late Pleistocene changed the large, through flowing White River to a series of isolated springs and short streams, thus also isolating the fish fauna.

The Gila River form, intermedia, undoubtedly evolved in the lower basin. Uyeno (1960) says this form is the closest of the Colorado basin forms to atraria. This would indicate that intermedia branched off fairly early from the parent stock. G. orcutti (Eigenmann and Eigenmann) of the Los Angeles Plain of southern California appears to have evolved from *intermedia*. This also suggests an early evolution for *intermedia*, probably before the upper and lower basins became joined. Uyeno (1960) indicates that *intermedia* probably gave rise to several species of *Gila* in Mexico and the Rio Grande basin. The Pleistocene is the hypothesized time of this speciation. Studies of several of these Mexican forms and *intermedia* are presently being conducted at Arizona State University. The several species possibly evolving from *intermedia* stock, and the apparent early evolution of this form certainly do not support the subspecies standing for this fish.

SUMMARY AND CONCLUSIONS

A study was made of the morphologic relationships among and within the several members of the *Gila* complex. A form of numerical taxonomy, taximetrics, was used to help analyze the data. Additional morphologic and life history data from the literature were used to formulate as complete a picture of the relationships as possible. The tables of Appendix C show the relationships among the various forms for the 11 body measurements used in the taximetrics program.

The data indicate that the present concepts concerning the taxonomy of these fish do not fit what is actually present. The idea of ecosubspecies for the several subspecies of *G. robusta* does not appear valid. *G. r. robusta* and *G. robusta elegans* appear as two distinct evolutionary lines throughout the basin, not as products of parallel evolution in various parts of the basin. The distinction between *robusta* and *elegans* is well founded morphologically, ecologically and apparently reproductively. Therefore these forms are better considered full species, e.g. *G. robusta* and *G. elegans*.

The relationship between *cypha* and *elegans* is not as simple as previously thought. A large number of intergrades morphologically bridge the gap between these two forms. This makes it extremely hard to delineate *cypha* and raises the question of validity in the use of the species taxon. It also questions the distinctiveness of *elegans*. Just what kind of biological process is operating on these fish is not known. Specimens from the lower Green River and the Grand Canyon area may help explain this problem.

The Virgin River population of G. robusta may be distinct enough to be a subspecies, seminuda. Only six specimens were available for use in the study, and no conclusive statement can be made at this time. A more intensive study of the Virgin River must be made before this problem can be resolved.

An isolated form of robusta from the Pluvial White River of Nevada is considered as the subspecies G. robusta jordani.

No specimens of G. robusta intermedia of the Gila River division were examined although the literature of this form was studied. It appears that intermedia may also be a valid species for it seems to be morphologically distinct and reproductively isolated from G. robusta robusta.

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APPENDIXES

Appendix A

Annotated synonymy of the subgenus Gila[1] of the Colorado River basin

Gila elegans--Widely distributed in the Colorado River basin.

Gila elegans Baird and Girard, *In* Cap. L. Sitgreaves. Report of an expedition down the Zuni and Colorado Rivers, 1853, 150, Zuni River, New Mexico. Listed as synonymous with *G. robusta* by Ellis (1914). Placed as a subspecies of *G. robusta* by Miller (1946).

Gila emoryi Baird and Girard, Proc. Acad. Nat. Sci. Phil., VI, 1854 (1853),[2] 388, Gila River, Arizona. Listed as *G. emorii* by Jordan and Gilbert (1882). Synonymized by Jordan and Evermann (1896).

Gila robusta--Widely distributed in the Colorado River basin.

Gila robusta robusta

Gila robusta Baird and Girard, *In* Cap. L. Sitgreaves. Report of an expedition down the Zuni and Colorado Rivers, 1853, 148, Zuni River, New Mexico.

Gila gracilis Baird and Girard, *In* Cap. L. Sitgreaves. Report of an expedition down the Zuni and Colorado Rivers, 1853, 148, Zuni River, New Mexico. Syn. Jor. and Ever. (1896). Gunther, Catalog Fishes, VII, 1868, 241: placed *Gila* in the genus *Leuciscus* and substituted *L. zunnensis* for *G. gracilis* because *gracilis* was occupied in *Leuciscus*.

Gila grahami Baird and Girard, Proc. Acad. Nat. Sci. Phil., VI, 1854 (1853), 389, Rio San Pedro, tributary to Rio Gila, Arizona. Syn. by Jor. and Ever. (1896).

Ptychocheilus vorax Girard, Proc. Acad. Nat. Sci. Phil., VIII, 1857 (1856), 209, Locality unknown. Syn. by Jor. and Gil. (1882).

Gila affinis Abbot, Proc. Acad. Nat. Sci. Phil., X, 1861 (1860), 474, type erroneously ascribed to Kansas River. Syn. by Jor. and Ever. (1896).

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[1] As recognized by Uyeno (1960).

[2] Refers to the Proceeding of 1853 published in 1854.

Gila nacrea Cope, Hayden's Geol. Surv., Wyoming, for 1870. 1872, 441, tributary of Green River, Fort Bridger, Wyoming. Syn. by Jor. and Ever. (1896).

Gila robusta seminuda--Virgin River of Utah, Nevada and Arizona.

Gila seminuda Cope and Yarrow, Zool., Wheeler's Expl. W. 100th Mer., V, 1875, 666, Rio Virgin, Utah. Tentatively retained here as a distinct subspecies pending further study.

Gila robusta jordani--Remnant White River of Nevada.

Gila jordani Tanner, Great Basin Nat., X, 1950, 31-36, White River, Lincoln Co., Nevada. Reduced to a subspecies by La Rivers (1962).

Gila robusta intermedia--Restricted to the Gila River division of the Colorado basin in Arizona and New Mexico. (See below.)

Gila gibbosa Baird and Girard, Proc. Acad. Nat. Sci. Phil., VII, 1856 (1854), 28, Rio Santa Cruz, Arizona. Placed in genus *Tigoma* by Girard (1856). Syn. in *Squalius niger* by Jor. and Gil. (1882). Placed in *Leuciscus niger* by Jor. and Ever. (1896). Put in *Tigoma gibbosa* by Jor., Ever. and Clark, (1930).

Tigoma intermedia Girard, Proc. Acad. Nat. Sci. Phil., VIII, 1857 (1856), 206, Rio San Pedro, Arizona. Listed as *Squalius intermedius* by Jor. and Gil. (1882). Listed as *Leuciscus intermedius* by Jor. and Ever. (1896). Syn. under *Tigoma gibbosa* by Jor. Ever. and Clark (1930).

Gila nigra Cope, Zool. Wheeler's Expl. W. 100th Mer., V, 1875, 663, Ash and San Carlos Creeks, Arizona. Listed as *Squalius niger* by Jor. and Gil. (1882). Listed as *Leuciscus niger* by Jor. and Ever. (1896). Syn. under *Tigoma gibbosa* by Jor., Ever. and Clark (1930).

Squalius lemmoni Rosa Smith, Proc. Calif. Acad. Sci., 1884, 3, Rillito Creek, Arizona. Syn under *Leuciscus intermedius* by Jor. and Ever. (1896).

Gila cypha Miller, Jour. Wash. Acad. Sci., 36, 1946, 409-415, Colorado River in Grand Canyon, Arizona.

An explanation of the synonymy of *intermedia* is appropriate. This form was described three times, twice in *Gila* and once in *Tigoma*, before 1880. Jordan and Gilbert (1882) placed them in the genus *Squalius* and synonymized G. gibbosa and G. nigra to S. niger for gibbosa was preoccupied in Squalius. Tigoma intermedia became S. intermedius. Jordan and Evermann (1896) kept the two species recognized by Jordan and Gilbert (1882) but changed the genus from Squalius to Leuciscus, and synonymized under intermedius, S. lemmoni. Jordan, Evermann and Clark (1930) combined the two Leuciscus species of Jordan and Evermann (1896) to Tigoma gibbosa. Since this time the form has been placed as a subspecies of Gila robusta under the name intermedia. Although the species name gibbosa is the oldest and appears to have priority, Art. 59 of the International Code of Zoological Nomenclature (1961) states the rule that once a name is made a homonyn, even if incorrectly, it must always be considered a homonym.

Appendix B

Characters and States as Used in the Taximetrics Program

Characters	States
1. Dorsal fin rays	A. 7 B. 8 C. 9 D. 10-11
2. Anal fin rays	A. 7-8 B. 9 C. 10-11
3. Squamation	A. naked except for lateral line B. sides partially scaled C. Scaled except for dorsal, ventral and peduncle regions D. Fully scaled
4. Gill rakers	A. 23 and below B. 24-26 C. 27 and above
5. Body humping	A. no hump B. slight hump C. well humped D. abrupt hump
6. Vertebrae count	A. 42 and below B. 43 C. 44 D. 45 and above
7. Eye diameter	A. 7.5mm and below B. 8.0-9.5mm C. 10.0mm and above
8. Fleshy snout	A. large B. small C. none
9. Predorsal length[a]	A. above 512 B. 512-476 C. below 476
10. Anal origin to caudal base	A. above 400 B. 400 and below
11. Head length	A. above 250 B. 250-233 C. below 233
12. Head depth	A. above 91 B. 91-83 C. below 83
13. Snout length	A. above 77 B. 77 and below
14. Interorbital length	A. above 83 B. 83 and below
15. Insertion of pelvic fin to insertion of pectoral fin	A. 220 and above B. below 220

[a]All body measurements expressed in thousandths of standard length.

16.	Snout to occiput	A. 174 and above B. below 174
17.	Upper jaw length	A. above 87 B. 87-77 C. below 77
18.	Dorsal fine base length	A. 132 and above B. below 132
19.	Least depth of caudal peduncle	A. above 57 B. 57-50 C. below 50

Appendix C

Tables[a]

Table 5. Comparison of predorsal lengths between members of the *Gila* complex

Form and location	No.	441-460	461-480	481-500	501-520	521-540	541-560	561-580	Mean
robusta									
Upper Green River	61			2	27	27	5		523.0
White River	18				6	11	1		524.8
Colorado River	17			1	4	7	5		530.3
San Juan River	24			3	16	5			513.75
Black River	10					7	2	1	536.7
seminuda									
Virgin River	6			3	3				500.3
elegans									
Upper Green River	92	10	65	17					478.1
Lake Powell	1		1						472.0
Lake Mohave	6	3	3						462.0
cypha									
Upper Green River	1		1						476.0
Lake Powell	5		1	3	1				488.0
Lee's Ferry	10		2	7	1				488.6
elegans x *cypha*									
Upper Green River	6		1	4	1				493.0
Desolation Canyon	6		2	3	1				488.9
Lake Powell	38	1	10	20	5	2			487.6
Lee's Ferry	5		4	1					474.2
robusta x *elegans*									
Upper Green River	2			2					489.0
White River	1				1				511.0

[a]All the measurements are expressed in thousandths of the standard length.

Table 6. Comparison of anal origin to caudal base lengths between members of the *Gila* complex

Form and location	No.	311-330	331-350	351-370	371-390	391-410	411-430	431-450	451-470	Mean
robusta										
Upper Green River	61	1	17	34	8	1				356.8
White River	18	3	1	12	2					355.1
Colorado River	17	1	7	8	1					351.9
San Juan River	24		14	10						349.2
Black River	10	6	4							325.3
seminuda										
Virgin River	6	1	2	2	1					351.3
elegans										
Upper Green River	92				4	43	43	2		409.9
Lake Powell	1					1				400.0
Lake Mohave	6				1	3	1	1		404.7
cypha										
Upper Green River	1					1				410.0
Lake Powell	5					2	2		1	426.8
Lee's Ferry	10					5	4	1		413.5
elegans x *cypha*										
Upper Green River	6				2	3	1			400.5
Desolation Canyon	6				4	2				386.3
Lake Powell	38				5	25	7	1		402.5
Lee's Ferry	5					3	2			407.0
robusta x *elegans*										
Upper Green River	2				2					388.5
White River	1				1					376.0

Table 7. Comparison of head lengths between members of the Gila complex

Form and location	No.	190-205	206-220	221-235	236-250	251-265	266-280	281-295	296-310	Mean
robusta										
Upper Green River	61				3	18	26	13	1	266.0
White River	18					3	11	4		274.0
Colorado River	17					5	8	4		272.9
San Juan River	24				2	11	11			263.0
Black River	10						3	6	1	284.2
seminuda										
Virgin River	6			1	1	4				250.0
elegans										
Upper Green River	92	2	20	66	4					223.9
Lake Powell	1			1						228.0
Lake Mohave	6	3	3							203.5
cypha										
Upper Green River	1				1					238.0
Lake Powell	5			1	2	2				245.8
Lee's Ferry	10			1	7	2				243.8
elegans x cypha										
Upper Green River	6				4	2				248.3
Desolation Canyon	6		1		2	2	1			246.5
Lake Powell	38	1	8	23	5	1				226.6
Lee's Ferry	5		1	3	1					227.8
robusta x elegans										
Upper Green River	2				2					244.0
White River	1						1			268.0

Table 8. Comparison of head depths between members of the *Gila* complex

Form and location	No.	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	Mean
robusta										
Upper Green River	61				3	26	24	8		101.3
White River	18					7	11			102.3
Colorado River	17					3	11	3		104.6
San Juan River	24					20	2	2		97.6
Black River	10						6	3		109.1
seminuda										
Virgin River	6				1	4	1			96.3
elegans										
Upper Green River	92		15	71	6					74.6
Lake Powell	1		1							68.0
Lake Mohave	6	2	2	1	1					67.2
cypha										
Upper Green River	1				1					81
Lake Powell	5		1	2	2					77.6
Lee's Ferry	10			6	3	1				79.4
elegans x *cypha*										
Upper Green River	6			1	5					84.5
Desolation Canyon	6				4	2				86.7
Lake Powell	38		5	27	5	1				75.7
Lee's Ferry	5		1	3	1					75.0
robusta x *elegans*										
Upper Green River	2			1	1					83.0
White River	1				1					81.0

Table 9. Comparison of snout lengths between members of the *Gila* complex

Form and location	No.	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	Mean
robusta												
Upper Green River	61					6	15	17	13	10		88.6
White River	18						3	8	3	4		90.6
Colorado River	17					1	3	5	5	1	2	90.4
San Juan River	24					1	11	8	4			86.1
Black River	10						3	3	4			88.8
seminuda												
Virgin River	6			1	4	1						73.7
elegans												
Upper Green River	92	3	12	37	34	5	1					69.6
Lake Powell	1			1								70.0
Lake Mohave	6	2	2	2								64.0
cypha												
Upper Green River	1					1						77.0
Lake Powell	5						1	2	2			88.6
Lee's Ferry	10						2	4	3	1		90.0
elegans x *cypha*												
Upper Green River	6							5	1			88.2
Desolation Canyon	6				1	1	1	3				86.5
Lake Powell	38	1		6	15	11	3	1	1			74.8
Lee's Ferry	5					2	3					80.6
robusta x *elegans*												
Upper Green River	2					1	1					81.0
White River	1						1					83

Table 10. Comparisons of interorbital lengths between members of the *Gila* complex

Form and location	No.	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-115	Mean
robusta										
Upper Green River	61		1	6	20	28	5		1	85.7
White River	18				2	9	4	3		90.2
Colorado River	17			1	2	8	6			87.2
San Juan River	24				9	12	3			86.6
Black River	10			3	4	2			1	85.5
seminuda										
Virgin River	6			2	2	2				83.5
elegans										
Upper Green River	92	1	31	51	8	1				76.8
Lake Powell	1			1						80.0
Lake Mohave	6	2	1	3						73.7
cypha										
Upper Green River	1				1					83.0
Lake Powell	5				1	2	2			88.6
Lee's Ferry	10				3	3	3	1		89.0
elegans x *cypha*										
Upper Green River	6				2	2	2			87.3
Desolation Canyon	6			1	1	4				85.5
Lake Powell	38		1	5	19	10	3			84.1
Lee's Ferry	5		1	1	2	1				82.4
robusta x *elegans*										
Upper Green River	2			1		1				81.5
White River	1						1			94.0

Table 11. Comparison of pelvic insertion to pectoral insertion lengths between members of the Gila complex

Form and location	No.	171-180	181-190	191-200	201-210	211-220	221-230	231-240	241-250	251-260	261-270	271-280	281-290	291-300	Mean
<u>robusta</u>															
Upper Green River	61			1	2	4	17	15	11	7	2			2	232.6
White River	18					3	2	6	3	2	2				239.4
Colorado River	17				1		2	6	3	3	2				242.8
San Juan River	24					1	3	3	6	8	1	1	1		247.5
Black River	10							3	2	3		1	1		252.9
<u>seminuda</u>															
Virgin River	6						1	3	2						238.0
<u>elegans</u>															
Upper Green River	92	2	11	30	33	12	3	1							201.0
Lake Powell	1				1										210.0
Lake Mohave	6		2	1	2				1						203.0
<u>cypha</u>															
Upper Green River	1			1											194.0
Lake Powell	5		1	2	1	1									199.6
Lee's Ferry	10			3	4	3									205.7
<u>elegans</u> x <u>cypha</u>															
Upper Green River	6		1		4			1							209.2
Desolation Canyon	6			1		4	1								215.8
Lake Powell	38	1	2	5	11	10	5	1	3						212.2
Lee's Ferry	5			1	4										203.6
<u>robusta</u> x <u>elegans</u>															
Upper Green River	2				1	1									210.0
White River	1			1											198.0

Table 12. Comparison of snout to occiput lengths between members of the _Gila_ complex

Form and location	No.	131-140	141-150	151-160	161-170	171-180	181-190	191-200	201-210	211-220	Mean
robusta											
Upper Green River	61					6	13	21	17	4	198.6
White River	18						5	8	5		195.4
Colorado River	17					2	4	5	6		194.8
San Juan River	24					4	13	6	1		186.8
Black River	10							4	3	3	205.1
seminuda											
Virgin River	6			1		3	2				176.7
elegans											
Upper Green River	92		8	45	35	4					159.5
Lake Powell	1			1							150.0
Lake Mohave	6		3	3							149.7
cypha											
Upper Green River	1			1							156.0
Lake Powell	5			4	1						160.6
Lee's Ferry	10		1	4	4	1					161.2
elegans x _cypha_											
Upper Green River	6				2	4					172.0
Desolation Canyon	6			2	1	3					167.5
Lake Powell	38	4	9	20	4	1					153.2
Lee's Ferry	5			4	1						157.4
robusta x _elegans_											
Upper Green River	2					2					174.5
White River	1							1			196.0

Table 13. Comparison of jaw lengths between members of the *Gila* complex

Form and location	No.	51-60	61-70	71-80	81-90	91-100	101-110	111-120	Mean
robusta									
Upper Green River	61				16	29	15	1	95.8
White River	18					10	8		99.9
Colorado River	17				2	7	6	2	100.4
San Juan River	24				9	15			91.0
Black River	10				1	5	4		100.2
seminuda									
Virgin River	6			3	3				80.2
elegans									
Upper Green River	92	2	60	29	1				68.6
Lake Powell	1			1					72.0
Lake Mohave	6	1	5						64.3
cypha									
Upper Green River	1				1				83.0
Lake Powell	5			1	4				80.2
Lee's Ferry	10			3	7				82.7
elegans x *cypha*									
Upper Green River	6				4	2			89.2
Desolation Canyon	6			2	1	3			85.3
Lake Powell	38		11	25	2				72.7
Lee's Ferry	5			5					74.0
robusta x *elegans*									
Upper Green River	2			1	1				83.0
White River	1				1				88.0

Table 14. Comparison of dorsal base lengths between members of the Gila complex

Form and location	No.	101-110	111-120	121-130	131-140	141-150	151-160	161-170	Mean
robusta									
Upper Green River	61		17	30	13	1			125.2
White River	18			14	4				126.4
Colorado River	17		3	11	2	1			125.5
San Juan River	24		1	11	11	1			129.5
Black River	10	1	7	3					117.5
seminuda									
Virgin River	6			2	2	1	1		136.7
elegans									
Upper Green River	92			8	46	32	4	2	139.4
Lake Powell	1				1				140.0
Lake Mohave	6			1	5				133.0
cypha									
Upper Green River	1						1		152.0
Lake Powell	5				3		2		142.8
Lee's Ferry	10				1	6	2	1	148.7
elegans x cypha									
Upper Green River	6				3	1	2		146.0
Desolation Canyon	6			1	3	2			138.2
Lake Powell	38	1		3	16	15	3		139.4
Lee's Ferry	5			1	1	3			137.2
robusta x elegans									
Upper Green River	2			1	1				133.5
White River	1					1			147.0

Table 15. Comparison of peduncle depths between members of the *Gila* complex

Form and location	No.	31-40	41-50	51-60	61-70	71-80	81-90	Mean
robusta								
Upper Green River	61			20	40	1		62.3
White River	18			4	13	1		64.8
Colorado River	17			4	12	1		64.8
San Juan River	24				23	1		65.2
Black River	10				7	2	1	69.9
seminuda								
Virgin River	6			1	5			64.2
elegans								
Upper Green River	92	43	49					41.1
Lake Powell	1		1					46.0
Lake Mohave	6	2	4					41.3
cypha								
Upper Green River	1		1					50.0
Lake Powell	5		1	4				52.4
Lee's Ferry	10		3	7				53.2
elegans x *cypha*								
Upper Green River	6		2	3	1			54.2
Desolation Canyon	6		2	4				51.5
Lake Powell	38		26	12				49.7
Lee's Ferry	5		3	2				49.4
robusta x *elegans*								
Upper Green River	2		2					47.5
White River	1			1				53.0

VITA

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Candidate for the Degree of

Master of Science

Thesis: Systematic Studies of the Genus Gila (Cyprinidae) of the Colorado River Basin

Major Field: Fishery Biology

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