MASS HYBRIDIZATION BETWEEN TWO GENERA OF CYPRINID FISHES IN THE MOHAVE DESERT, CALIFORNIA

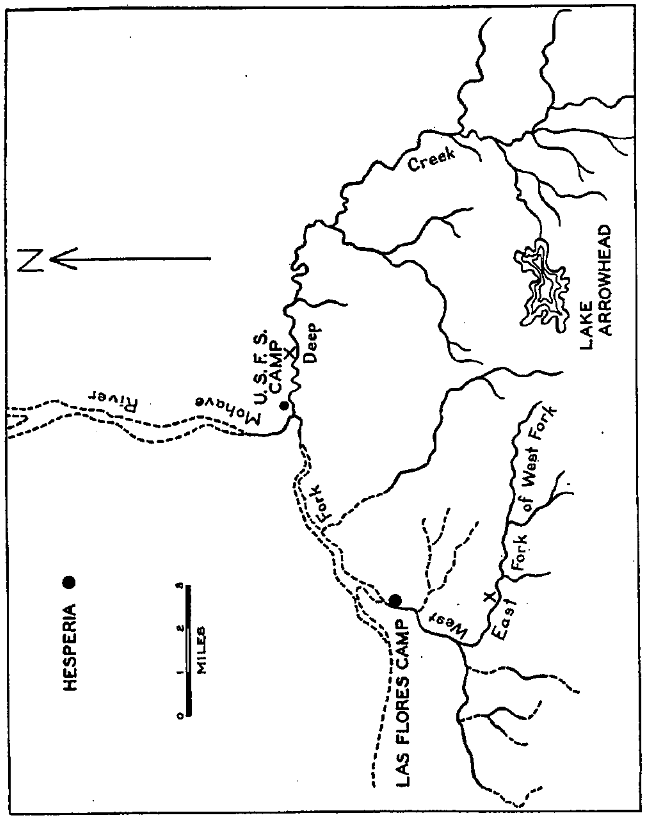
CARL L. HUBBS AND ROBERT R. MILLER

HYBRIDIZATION in nature between fish species is being analyzed by the senior author and his associates in a series of papers of which this is one. Each of these publications emphasizes a distinct point in the biological significance of natural hybridization. The present contribution [1] stresses the high frequency of interspecific hybridization that may result when a changed environment sets the stage for extensive miscegenation. To appreciate this relation between ecology and hybridization it is necessary to picture briefly the present and past hydrography of the Mohave River Basin.

HYDROGRAPHY OF THE MOHAVE DESERT

The Mohave Desert is properly included within the Great Basin, since all its permanent waters are characterized by interior drainage. The principal stream crossing this arid waste is the Mohave River (Fig. 1). Its headwaters (Fig. 2) rise high on the northern slopes of the San Bernardino Mountains of southern California, and it follows a generally northeasterly course for more than one hundred miles across the desert to "The Sink of the Mohave" (Soda Lake, a large discharging playa just south of the town of Baker). Within the river basin there are five major regions of perennial flow, where fishes may be found: (1) the headwater region, comprising fully 90 per cent of the total water supply and lying above the point where Deep Creek (the east fork) and West Fork unite (in high water) to

[1] In this study we have been materially aided by a research grant from the Horace H. Rackham School of Graduate Studies, of the University of Michigan. Sidney Shapiro, who served well as research assistant, made a considerable proportion of the counts and measurements. As usual, Laura C. Hubbs has borne the brunt of the statistical calculations. Professor Elliot Blackwelder, of Stanford University, kindly reviewed the geological discussion.



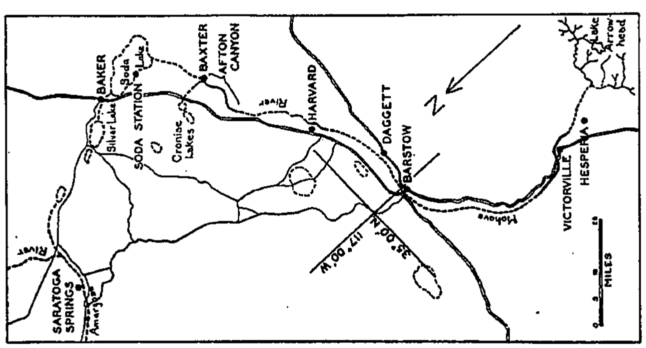


FIG. 1 (left). The present drainage features of the Mohave River system and vicinity. Perennial flows are indicated by solid lines; intermittent flows and the border of playas by dashed lines. Highways and dirt roads are also shown

FIG. 2. Detail of the headwater portion of the Mohave River system. X marks the uppermost points from which minnows have been obtained (Thomas Rodgers assisted in the drafting of both maps)

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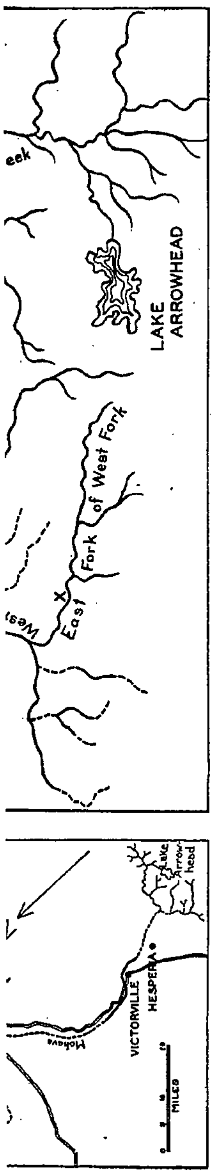

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form the river proper; (2) the vicinity of Victorville, where there is a flow about seven miles in length; (3) a point south of Harvard (a railroad station about twenty miles east of Barstow), where there is a short flow; (4) Afton Canyon (about forty miles east of Barstow), where the river again flows six or seven miles; and (5) the west side of Soda Lake, at the railroad station of Soda, where a spring pool retains permanent water. Since this pond is higher than the adjacent playa bed, it is not subject to the effects of floodwaters, but all the other regions experience severe washouts from time to time.

Precipitation in the headwater region is relatively great, ranging from about 13 to 35 inches (Thompson, 1929 : 94). As a result, particularly in the Deep Creek basin, there are a considerable number of permanent and cool mountain creeks, but the stream mileage available to the native minnows is greatly restricted (Fig. 2). It is not certain to what extent the introduced trout rather than physical conditions limit the waters inhabited by minnows. As the river channel debouches from the base of the mountains onto the desert, a very rapid drop in rainfall occurs. Thus at Victorville, less than fifteen miles distant, the yearly fall is about five inches, and near Afton Canyon the precipitation is less than two inches (Thompson, 1929 : 80, 94). Consequently the occasional severe downpours in the mountainous region literally flush out the entire river (more particularly the lower portions), causing widespread change in the stream conditions and in the populations of aquatic organisms. Such a disastrous flood occurred in March, 1938, at which time the discharge not only filled Soda Lake but also overflowed into the playa of Silver Lake (the extreme flood terminus of Mohave River) just to the north. The effect of this washout on the native fishes is detailed in Table I.

The geological record clearly indicates that at some time during the Pleistocene, probably contemporaneously with lakes Lahontan and Bonneville, the waters of the Quaternary Mohave River formed a large body of water over the present playas of Silver and Soda lakes. This lake, the maximum area of which was about one hundred square miles, was named Lake Mohave by Thompson (1921 : 424). The level of its impounded waters eventually rose high enough to cut at the northern end a small outlet channel that served, for a time at least, to connect the Mohave River with the southeastern arm of Death Valley (Thompson, 1929 : 563–568). Here the stream joined the

Amargosa River, which flowed down from the north (Fig. 1). The conjoined waters contributed to the great lake (Lake Manly) which then existed in Death Valley.

Another body of water, considerably larger than Lake Mohave, is known to have covered the northeastern part of the flat valley east of Daggett. It has been called Manix Lake by Buwalda (1914 : 444). Recent studies of its deposits by Blackwelder and Ellsworth (1936) show that this lake had three stages, the first two correlated with two moist epochs during late Pleistocene time and the third possibly coincident with the close of the last ice advance. Whether it was strictly contemporaneous with Lake Mohave is not certain, but is highly probable, in the opinion of Blackwelder (personal communication).

A third Pleistocene lake, covering the present playas of East and West Cronise lakes, was formed by the Mohave River in Cronise Valley, about seventeen miles southwest of Baker (Fig. 1). Little Mohave Lake, as this body of water was named by Thompson (1921 : 424), was very much smaller than either Lake Mohave or Manix Lake, and appears to have had a very intermittent existence. Its eastern portion (East Cronise Lake) is still occasionally filled by distributary floodwaters from the Mohave River. The junior author saw minnows in that basin in 1937. According to local testimony the lake contained water from 1941 to the summer of 1942, when many fish perished as the lake dried up.

All these ancient lakes probably supported a dense population of the Mohave lake chub, *Siphateles mohavensis*, for, as is later pointed out, this species is particularly fitted for lacustrine conditions. Moreover, the record of fragmentary fish bones, identified as those of *Siphateles mohavensis*, from the first lake stage of Manix Lake (Blackwelder and Ellsworth, 1936 : 459), and another record by Buwalda (1914 : 449) of fish vertebrae (unidentified) from the same basin substantiate the presumed presence of *Siphateles* in such environments. With the disappearance of these bodies of water *Siphateles mohavensis* was largely forced to disperse into the headwater habitat of *Gila orcuttii*.

This study is one of several by which we are attempting to determine how the distribution and speciation of the fishes of the American desert have been affected by the profound hydrographic changes that occurred during and after Quaternary times (Hubbs, 1940b).

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FISH FAUNA OF THE MOHAVE BASIN

With the exception of the disconnected springs and creeks of the Death Valley region, which harbor a limited fish fauna unrelated to that under consideration, as well as a few springs and short creeks that seem devoid of native fishes, all permanent waters of the Mohave Desert that have persisted into the present dry epoch are portions of the Mohave River system. These waters, now connected only in flood periods and at present probably never united into a single connected pattern, contain only two species of native fish (Pl. II). Both are members of the Cyprinidae and represent two genera that are widespread through the West. Except for brief indications by Miller (1938) and by Hubbs (1940b : 62), only one of the species, *Siphateles mohavensis* Snyder (1918), has been recorded from the basin. The second minnow seems to be inseparable specifically from *Gila* [2] *orcuttii* (Eigenmann and Eigenmann), which has hitherto been regarded as confined to the coastal streams of southern California. There are several hints that some catostomid fish occurred in the Mohave system until recently, but if it did, our extensive collecting from 1934 to 1940 indicates that it has been extirpated there.

Trout (*Salmo gairdnerii irideus*), introduced into the mountain headwaters, have probably restricted the numbers and range of the minnows. The several other exotic fishes recently added to the Mohave fauna have probably had as yet little effect on the native fish life.

Gila orcuttii and *Siphateles mohavensis* occur together, with hybrids, in nearly all parts of the generally disrupted Mohave River system (Fig. 1). The only place where the *Siphateles* appears to occur alone is in the spring pool on the ancient shore line of Quaternary Lake Mohave, of which the present southern remnant (Soda Lake) is the sump of the Mohave River. Regularly the *Gila* appears to ascend the streams farther than the *Siphateles* commonly goes, and shows more preference for the current. In the flowing streams the *Siphateles* tends to select the quieter pools.

That the *Gila* is better adapted than the *Siphateles* to stream life was dramatically proved in March, 1938, when a great flood raged

[2] The reference of this species to the genus *Gila* follows from the discovery that representatives of the nominal genera *Tigoma* and *Gila* merely represent ecological subspecies (Hubbs, 1940a : 200; 1941b : 186–187).

down the mountain sides and transformed the dry sands of the Mohave River bed into a torrent that filled the normal sump basin of Soda Lake and overflowed into the usually dry playa known as Silver Lake (Fig. 1). The force of the flood was so great that the stream beds were profoundly altered; for example, the lower end of the normal flow of Deep Creek was transformed from a large and beautiful pool (Pl. I, Fig. 4), five feet deep, into a sand-choked channel. The *Siphateles* population was swept out upon the desert in far greater proportion than was the stock of *Gila orcuttii*. As a result, the relative numbers of the two species were greatly altered. Comparing the samples of 1934 and 1937 with those taken in 1939 and 1940, we have estimated that the *Gila* population showed a relative increase of 66, 365, and 1,437 per cent in three portions of the stream system where the *Siphateles* stock decreased 89 to 93 per cent (Table I). *Siphateles* is estimated (p. 353) to have constituted 35 per cent of the Mohave minnow population in 1934 and 1937, but only 14 per cent of the total after the flood (from May, 1938, to August, 1940). That *Siphateles* was carried farther than *Gila* by the flood is indicated later (p. 355).

Siphateles mohavensis is obviously maladjusted to its present environment. Its survival may be accredited to lack of competition. There are only the two native fishes, and they are presumably complementary to a large degree in their food habits and other ecological relations.

These data on population ecology confirm the morphological evidence that had led us to regard *Gila orcuttii* as a fluviatile fish and *Siphateles mohavensis* as a lacustrine type. The *Gila* is the more streamlined: it has more turgid contours, is more terete (less slab-sided), and has a slenderer caudal peduncle (Pl. II). The *Gila* is darker and more mottled, like bottom-dwelling fishes in general; the *Siphateles* has a more uniform and more metallic color, approaching the appearance of pelagic fishes (see color descriptions, p. 372). The *Gila* has a more leathery integument and less fragile fin rays. The strong pharyngeal teeth of *Gila orcuttii* are adapted by their strong hooks and narrow grinding surfaces to a rapacious diet, presumably of stream insects; the weaker teeth of *Siphateles mohavensis*, with slight hooks and broad grinding surfaces (Pl. III), are fitted for the grinding of plankton, which is essentially a lake rather than a creek product. Correspondingly, the pharyngeal

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RELATIVE NUMBERS OF *GILA*
MOHAVENSIS BEFORE AND

General locality and years	Nu	
	Gila	HYB
West Fork, Mohave River		
1934, 1937 (A) ...	22	1
1939, 1940 (B) ...	1,401	8
Change in percentage (B—A) ...	...	..
Hybrid index	...	..
Deep Creek		
1934, 1937 (A) ...	862	13
1939, 1940 (B) ...	317	1
Change in percentage (B—A) ...	...	..
Hybrid index	...	..
Mohave River near Victorville		
(1915)	...	..
1934, 1937 (A) ...	2	..
1939, 1940 (B) ...	332	2
Change in percentage (B—A) ...	...	..
Hybrid index	...	..

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TABLE I

RELATIVE NUMBERS OF *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS* BEFORE AND AFTER THE GREAT FLOOD OF 1938

General locality and years	Numbers			Percentages		
	Gila	HYBRIDS	*Siphateles*	*Gila*	HYBRIDS	*Siphateles*
West Fork, Mohave River						
1934, 1937 (A) ...	22	16	78	19.0	13.8	67.2
1939, 1940 (B) ...	1,401	82	102	88.4	5.2	6.4
Change in percentage (B—A) ...	...	...	...	69.4	− 8.6	− 60.8
Hybrid index	...	...	...	...	60	...
Deep Creek						
1934, 1937 (A) ...	862	135	518	56.9	8.9	34.2
1939, 1940 (B) ...	317	10	8	94.6	3.0	2.4
Change in percentage (B—A) ...	...	...	...	37.7	− 5.9	− 31.8
Hybrid index	...	...	...	...	63	...
Mohave River near Victorville						
(1915)	...	...	(121)	...	...	(100.0)
1934, 1937 (A) ...	2	...	35	5.4	...	94.6
1939, 1940 (B) ...	332	28	40	83.0	7.0	10.0
Change in percentage (B—A) ...	...	...	...	77.6	?	− 84.6
Hybrid index	...	...	...	...	?	...

arches are stronger in *Gila* than in *Siphateles.* The long gill slits (Table XI) and numerous gillrakers (Table V) of the *Siphateles,* contrasting strongly with the similar characters of the *Gila,* are still more obvious adaptations to a plankton diet (Pl. IV). The characters of *Gila orcuttii* fit it for stream life; those of *Siphateles mohavensis* are adaptations to a lacustrine existence.

FREQUENCY OF HYBRIDIZATION

The interspecific hybridization discussed in this paper[3] was one of the two main cases that resulted in the following generalization (Hubbs, 1940b : 67): "Desiccation of waters has led to fusion as well as differentiation. Species which by their habits and by their feeding

[3] The hybridization between *Gila* and *Siphateles* was first mentioned by Miller (1938) and by Hubbs (1940b : 62).

TABLE II

RELATIVE NUMBERS OF *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS* IN ALL AVAILABLE COLLECTIONS FROM THE MOHAVE RIVER BASIN

Locality (from headwaters to sump of Mohave River)	Numbers			Percentages		
	Gila	HYBRIDS	*Siphateles*	*Gila*	HYBRID	*Siphateles*
East Fork of West Fork of Mohave River, April 5, 1939	30	1	...	96.8	3.4	...
Same locality, Aug. 13, 1940	210	12	17	87.9	5.0	7.1
West Fork of Mohave River, Las Flores, June 29, 1937	5	4	20	17.2	13.8	69.0
Same locality, April 5, 1939	89	43	69	44.3	21.4	34.3
Same locality, July 11, 1940	176	19	12	85.0	9.2	5.8
Tributary to West Fork, Elliot Ranch, June 28, 1937	3	...	1	75(?)	...	25(?)
West Fork, Summit Valley, Aug. 31, 1934	7	4	45	12.5	7.1	80.4
Same locality, June 29, 1937	7	8	12	25.9	29.6	44.4
Same locality, July 12, 1940	518	2	3	99.0	0.4	0.6
West Fork just above Deep Creek, July 11, 1940	378	5	1	98.4	1.3	0.3
Deep Creek, about 1 mile above U. S. F. S. Camp, Sept. 27, 1931 *	...	1	2	...	33(?)	67(?)
Deep Creek at U. S. F. S. Camp, Sept. 1, 1934 (Pl. I, Fig. 4)	839	121	511	57.0	8.2	34.7
Same locality, June 30, 1937 *	23	14	7	52.3	31.8	15.9
Same locality, July 12, 1940	317	10	8	94.6	3.0	2.4
Mohave River about one fourth mile below Deep Creek, July 2, 1937	137	6	14	87.3	3.8	8.9
Mohave River about 5 miles below Deep Creek, April 5, 1939	17	...	...	100	...	...

* Sample taken with hook and line.

TABLE

(Locality from headwaters to sump of Mohave River)	
	Gila	H
Floodwater pond, Mohave River, near Thorn, July 11, 1940	6
Spring tributary of Mohave River, near Victorville, Aug. 5, 1940	129
Mohave River, Victorville, Aug. 14, 1915	...
Same locality, Sept. 1, 1934	2
Same locality, April 8, 1939	91
Same locality, July 11, 1940	112
Mohave River, Daggett, March, April, May, 1903	...
Mohave River (stream), Afton Canyon, April 6, 1939	7
Same locality, July 26, 1940	212
Ponds in river, Afton Canyon, May 22, 1938	2
Same locality, April 7, 1939	6
Same locality, July 26, 1940	11
Isolated pond, Afton Canyon, April 6, 1939	16
Soda Lake spring, 1937–1940	...
Where species occur together (Soda Lake spring excepted)	3,350
1934 and 1937 (before 1938 flood)	1,023
1938 (after flood) – 1940	2,327
Grand total	3,350

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had a complementary distribut

TABLE II (*Concluded*)

(Locality from headwaters to sump of Mohave River)	Numbers			Percentages		
	Gila	Hybrids	*Siphateles*	*Gila*	Hybrids	*Siphateles*
Floodwater pond, Mohave River, near Thorn, July 11, 1940	6	...	...	100	...	...
Spring tributary of Mohave River, near Victorville, Aug. 5, 1940	129	10	17	82.7	6.4	10.9
Mohave River, Victorville, Aug. 14, 1915 ...	...	...	121	...	...	100
Same locality, Sept. 1, 1934	2	...	35	5.4	...	94.6
Same locality, April 8, 1939	91	18	22	69.5	13.7	16.8
Same locality, July 11, 1940	112	...	1	99.1	...	0.9
Mohave River, Daggett, March, April, May, 1903	...	...	9	...	...	100
Mohave River (stream), Afton Canyon, April 6, 1939	7	12	67	8.1	14.0	77.9
Same locality, July 26, 1940	212	63	65	62.4	18.5	19.1
Ponds in river, Afton Canyon, May 22, 1938	2	9	...	18.2	81.8	...
Same locality, April 7, 1939	6	37	122	3.6	22.4	74.0
Same locality, July 26, 1940	11	33	10	20.4	61.1	18.5
Isolated pond, Afton Canyon, April 6, 1939	16	10	13	41.0	25.6	33.3
Soda Lake spring, 1937–1940	...	...	608	...	...	100
Where species occur together (Soda Lake spring excepted)	3,350	442	1,204	67.2	8.9	24.0
1934 and 1937 (before 1938 flood)	1,023	157	645	56.1	8.6	35.3
1938 (after flood) – 1940	2,327	284	427	76.6	9.3	14.1
Grand total	3,350	442	1,812	59.9	7.9	32.2

apparatus and other structures are adapted respectively to lake life and to stream life, and which in periods of ample water no doubt had a complementary distribution, have hybridized *very extensively* now that the two types have been forced into intimate contact in the isolated trickles and springs which represent the remnants of once expansive water systems."

The other case, that of the fluviatile *Siphateles obesus obesus* and the lacustrine *Siphateles obesus pectinifer*, of the Lahontan system, is almost exactly parallel in genetic as well as in historical and ecological respects. Almost the same difference in number of gillrakers is involved. It is somewhat arbitrary that we regard the second case as one of subspecific intergradation rather than one of interspecific hybridization. Failing to recognize the numerous intermediates that occur where the two kinds meet, Snyder (1917: 60–67, figs. 4–6) treated *Siphateles obesus* and *Leucidius pectinifer* as even generically distinct. Furthermore, he described (pp. 58–59), on the basis of only four specimens from Lake Tahoe, a new species, *Richardsonius microdon*, which is obviously a hybrid between *Richardsonius egregius* and *Siphateles obesus*. This hybrid has many features in common with the one we are describing — particularly the intermediate character of dentition, gillrakers, and scales.

An abundance of material, taken in 1934 and 1937 (before the deluge of March, 1938), as well as after the flood, in 1938, 1939, and 1940, makes it possible for us to estimate the relative numbers of the parent species and the hybrids (Table II) in the Mohave basin. From the entire stream system we have random samples totaling 5,604 cyprinids,[4] of which the percentage composition is approximately:

Gila, 60; hybrids, 8; *Siphateles*, 32.

Exclusive of the *Siphateles* samples (608 specimens) from the Soda Lake spring, where this genus alone occurs, the percentages are about:

Gila, 67; hybrids, 9; *Siphateles*, 24.

The most significant single collection was that made in the lowest pool on Deep Creek (p. 348; Pl. I, Fig. 4), where the entire popula-

[4] Most of the material studied is in the fish collection of the University of Michigan Museum of Zoology. One collection in the Natural History Museum of Stanford University and one at Field Museum have also been studied, with the kind permission of the authorities of these institutions. The available collections, taken over several years, we judge to constitute between 1 and 10 per cent of the total standing population in the entire river system, at times when the surface waters are at a very low stage.

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[5] This canyon contained fish in
fish in 1937 (Miller, 1938). The i
Canyon in 1936 is uncertain, thoug
some hybrids as well as *Siphateles* w

n forced into intimate contact in
which represent the remnants of

luviatile *Siphateles obesus obesus*
s *pectinifer*, of the Lahontan sys-
enetic as well as in historical and
ame difference in number of gill-
at arbitrary that we regard the
ntergradation rather than one of
ng to recognize the numerous
e two kinds meet, Snyder (1917:
s *obesus* and *Leucidius pectinifer*
ermore, he described (pp. 58–59),
from Lake Tahoe, a new species,
bviously a hybrid between *Rich-*
obesus. This hybrid has many
we are describing — particularly
tion, gillrakers, and scales.
n in 1934 and 1937 (before the
fter the flood, in 1938, 1939, and
stimate the relative numbers of
(Table II) in the Mohave basin.
have random samples totaling
centage composition is approx-

3; *Siphateles*, 32.

(608 specimens) from the Soda
ccurs, the percentages are about:

; *Siphateles*, 24.

n was that made in the lowest
Fig. 4), where the entire popula-

he fish collection of the University of
tion in the Natural History Museum
Museum have also been studied, with
hese institutions. The available col-
e to constitute between 1 and 10 per
entire river system, at times when the

tion of 1,471 minnows was preserved on September 1, 1934. Here the percentages are as follows:

Gila, 57; hybrids, 8; *Siphateles*, 35.

The hybrid ratio for the whole basin was scarcely affected by the great flood of March, 1938:

Data for 1934 and 1937: *Gila*, 56.1 %; hybrids, 8.6 %; *Siphateles*, 35.3 %.
Data for 1938 (May) to 1940: *Gila*, 76.6 %; hybrids, 9.3 %; *Siphateles*, 14.1 %.

The flood of March, 1938, did cause some local changes in the hybrid ratio. The percentage of the hybrids in the population decreased in the headwater streams after 1938 (Table I). This loss was compensated for by the extremely high percentage of hybrids in the river and ponds in Afton Canyon from May, 1938, to August, 1940:[5]

Gila, 254 (37 per cent)
HYBRIDS, 164 (24 per cent)
Siphateles, 277 (40 per cent)

An average hybrid ratio of 8 or 9 per cent of the total population, increasing locally to at least 24 per cent, is indeed very exceptional, even in the Cyprinidae. Such a transgression of specific (and generic) lines involves a severe breakdown in the isolating mechanism. It would be expected, from observations as well as from theoretical considerations, that because of its biotic inefficiency such extensive hybridization between species would ordinarily be selected against. Interspecific hybrids are ordinarily infertile, in at least one sex, yet they compete for food and often for spawning sites. Some crosses endowed with hybrid vigor more than hold their own in such competition (as do the sunfishes — Hubbs and Hubbs, 1931–33).

Such a frequency of interspecific hybridization is rarely encountered, except where certain species, as *Salmo clarkii* and *Salmo gairdnerii*, are mixed by introductions. There is a possibility that the present case of hybridization is due to the introduction of *Gila orcuttii* from southern California, as a bait minnow, into the realm of *Siphateles mohavensis*. Only *Siphateles* is represented in the Mo-

[5] This canyon contained fish in 1936 (Miller, 1936), but neither pools nor fish in 1937 (Miller, 1938). The identification of the fish occurring in Afton Canyon in 1936 is uncertain, though the published tooth counts suggest that some hybrids as well as *Siphateles* were present.

have River collections of 1903 and 1915 — the only available series that were taken prior to 1931 (Table II). Slight differences between the specimens from the desert and those from the coastal streams, however, suggest that *Gila* is native to the Mohave River system.

We interpret the mass hybridization between *Gila orcuttii* and *Siphateles mohavensis* as having been made possible by reason of the very limited competition that exists between these species. They appear to be the only native fishes of the Mohave basin, and they are to a large degree complementary in their ecology (p. 347). In these desert waters the physical rather than the biotic environment seems to be the dominant factor in the struggle for existence.

EVIDENCE FOR HYBRID INTERPRETATION

The evidence that *Gila orcuttii* and *Siphateles mohavensis* hybridize in the Mohave River system is circumstantial rather than experimental, but nevertheless trustworthy, in our opinion. This type of evidence for natural hybridization has been discussed and, we think, validated in recent papers (Hubbs and Kuronuma, 1942; Hubbs, Hubbs, and Johnson, *in press*; Hubbs, Walker, and Johnson, *in press*). In these publications there is a detailed consideration of the character index, the hybrid index, and other analytical methods now being used in the interpretation of natural hybrids. In the present study the percentage *hybrid index* is computed on the basis of fixing the average values of the characters of the more primitive parental form, *Gila orcuttii*, as 0, and the values for *Siphateles mohavensis* as 100.

The theory that *Gila orcuttii* and *Siphateles mohavensis* hybridize extensively throughout most of the Mohave River system is thoroughly in line with the ecological picture. As noted on page 351, these species were probably complementary in habitat during the Pluvial period, but are now forced into cohabitation. The spring at Soda Lake is the only place in the whole system where the two species have not been taken together (Table II). They probably segregate to some degree ecologically, but they very commonly swim together.

The main reason for considering certain of the Mohave minnows hybrids is the intermediacy that they display in many respects. The *Gila* × *Siphateles* show an intermediate physiological characteristic, namely, the ability to withstand great floods. We have already pointed out that the populations of the stream type *Gila orcuttii* were proportionately much less decimated by the great flood of March,

1938, than were the headwat
mohavensis. The changes i
species and the hybrids in th
River, namely, West Fork a
intermediate capacity of th
(Table I). The hybrid ind
numbers of hybrids in the tw
are respectively 60 and 63
semblance to the *Siphateles* t

The extent to which the
washed out on the desert by
mediacy of the hybrids. Tl
creased in the upper portion
of West Fork and Deep Cree
to the region of Victorville (F
brids were washed farther, fo
of the total population in
Siphateles was presumably l
playa lakes (Soda and Silver)
doubtless perished in large nu
of 1916, when they formed
1929 : 566).

In the generic characters
hybrids display not only interr
that would not be expected i
characteristics do not reasonal
is rather consistently displaye

The pharyngeal-tooth for
sistently 2, 5—4, 2; that of *S*
0, and commonly 0, 5—4, 0; t
5—4, 1 (Table III; Pl. III).
two rare variant formulae app
ation in the *Siphateles*, wherea
by 62.5 per cent of the hybrid
veloped by the hybrids on the s
This is particularly true of the
almost always has 2 strong teet
has none; the hybrids have 0 t
This is contrary to the expecte

915 — the only available series
II). Slight differences between
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tion between *Gila orcuttii* and
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between these species. They
the Mohave basin, and they are
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INTERPRETATION

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ite physiological characteristic,
eat floods. We have already
e stream type *Gila orcuttii* were
by the great flood of March,

1938, than were the headwater stocks of the lacustrine type *Siphateles mohavensis*. The changes in the relative numbers of the parental species and the hybrids in the two headwater branches of the Mohave River, namely, West Fork and Deep Creek, demonstrate clearly the intermediate capacity of the hybrids to resist the scouring wash (Table I). The hybrid indexes for the difference in the relative numbers of hybrids in the two headwaters before and after the flood are respectively 60 and 63 (an indication of a slightly greater resemblance to the *Siphateles* than to the *Gila*).

The extent to which the parental species and the hybrids were washed out on the desert by the 1938 flood also indicates the intermediacy of the hybrids. The *Gila* population was enormously increased in the upper portion of the Mohave River, from the junction of West Fork and Deep Creek, near the base of the mountains, out to the region of Victorville (Fig. 1; Tables I–II). As a rule, the hybrids were washed farther, for the hybrid ratio rose to 24 per cent of the total population in Afton Canyon (p. 353 and Table II). *Siphateles* was presumably largely carried still farther, out to the playa lakes (Soda and Silver). When these lakes dried up the fish doubtless perished in large numbers, as they did after the major flood of 1916, when they formed windrows of mummies (Thompson, 1929: 566).

In the generic characters of pharyngeal teeth and gillrakers the hybrids display not only intermediacy, but also a degree of variability that would not be expected in a fixed species. Furthermore, their characteristics do not reasonably fit into the systematic pattern that is rather consistently displayed by Western fishes.

The pharyngeal-tooth formula of *Gila orcuttii* is almost consistently 2, 5—4, 2; that of *Siphateles mohavensis*, typically 0, 5—5, 0, and commonly 0, 5—4, 0; that of the hybrids, most commonly 1, 5—4, 1 (Table III; Pl. III). In forty counts of each unit only two rare variant formulae appear in the *Gila*, and only the one variation in the *Siphateles*, whereas eight variant formulae are displayed by 62.5 per cent of the hybrids counted. The number of teeth developed by the hybrids on the several rows is intermediate (Table IV). This is particularly true of the teeth in the outer (lesser) row: *Gila* almost always has 2 strong teeth in this row, on each arch: *Siphateles* has none; the hybrids have 0 to 2 (typically 1), usually weak teeth. This is contrary to the expected pattern, for the Western species of

TABLE III

FREQUENCIES OF PHARYNGEAL-TOOTH FORMULAE IN *GILA*, HYBRIDS, AND *SIPHATELES*

The frequencies of teeth in each series are given in Table IV; forty specimens of each kind were counted.

Kind	Formula*	Frequency
Gila orcuttii	2, 5—4, 2	36
	2, 5—4, 1	2
	2, 5—5, 2	2
HYBRIDS	1, 5—4, 1	15
	0, 5—4, 0	6
	1, 5—5, 1	5
	1, 5—4, 0	5
	1, 5—4, 2	3
	0, 5—4, 1	2
	0, 5—5, 0	2
	1, 5—5, 0	1
	2, 4—5, 2	1
Siphateles mohavensis	0, 5—5, 0	30
	0, 5—4, 0	10

* Frequently individual teeth are lost, and in the older fish often are not replaced. Almost always the loss can be accounted for by the presence of alveoli and by the spacing. Missing teeth were counted, of course. In a few hybrids and in one or two of the *Gila* specimens one tooth of the outer row may have been falsely enumerated, on the basis of what appeared to be a nearly filled-in alveolus.

Cyprinidae normally have either 0 or 2 teeth in this row. The presence of a single weak tooth in the outer row may be taken as a sign of hybridization — as it is for "*Richardsonius microdon*" (p. 352).

Hybridity is also indicated by other characters of the pharyngeal teeth and by the form of the arch (Pl. III). In *Gila orcuttii* the teeth, notably the lowermost one of the main row, are wider toward the base than those of *Siphateles mohavensis;* they are strongly instead of slightly hooked; they have narrow and weak, rather than broad and conspicuous, grinding surfaces. In the *Gila* the two limbs of the arch (as measured above the uppermost tooth and below the lowermost one) are subequal; in *Siphateles* the lower limb is definitely the longer. The lower limb near the teeth is narrow and rounded in the *Gila* (particularly in the adults), but is broad and flat in the Mohave *Siphateles*. The outer face of the arch bears a shelf for the insertion

FREQUENCIES OF PHARYNG
AN

The formula

	0	
INNER (MAIN) ROW		
Left side		
Gila orcuttii	..	.
HYBRIDS	..	.
Siphateles mohavensis	..	.
Right side		
Gila orcuttii	..	.
HYBRIDS	..	.
Siphateles mohavensis	..	.
Both sides (sum)		
Gila orcuttii	..	.
HYBRIDS	..	.
Siphateles mohavensis	..	.
OUTER (LESSER) ROW		
Left side		
Gila orcuttii	..	.
HYBRIDS	10	2
Siphateles mohavensis	40	.
Right side		
Gila orcuttii	..	.
HYBRIDS	14	2
Siphateles mohavensis	40	.
Both sides (sum)		
Gila orcuttii	..	.
HYBRIDS	8	.
Siphateles mohavensis	40	.

of the two outer teeth in *Gila*,
slope, so that teeth could harc
In all these features of teeth
or, commonly, they show a r
types. It seems that dental
as well as in heterogeneous cr
Johnson, 1941 : 367–383).

Similarly impressive varia
characters of the gill arches (

III

ı FORMULAE IN *GILA*, HYBRIDS,
ʳELES

are given in Table IV; forty speci-

mula*	Frequency
;—4, 2	36
;—4, 1	2
;—5, 2	2
;—4, 1	15
;—4, 0	6
;—5, 1	5
;—4, 0	5
;—4, 2	3
—4, 1	2
—5, 0	2
—5, 0	1
—5, 2	1
—5, 0	30
—4, 0	10

and in the older fish often are not
ounted for by the presence of alveoli
unted, of course. In a few hybrids
e tooth of the outer row may have
ıat appeared to be a nearly filled-in

ɔr 2 teeth in this row. The
: outer row may be taken as a
:hardsonius microdon" (p. 352).
:r characters of the pharyngeal
II). In *Gila orcuttii* the teeth,
in row, are wider toward the
sis; they are strongly instead
and weak, rather than broad
ı the *Gila* the two limbs of the
st tooth and below the lower-
:he lower limb is definitely the
is narrow and rounded in the
broad and flat in the Mohave
bears a shelf for the insertion

TABLE IV

FREQUENCIES OF PHARYNGEAL-TOOTH COUNTS IN *GILA*, HYBRIDS, AND *SIPHATELES*

The formulae are given in Table III.

	Tooth counts								No.	Av.	Hybrid index
	0	1	2	3	4	5	9	10			
INNER (MAIN) ROW											
Left side											
Gila orcuttii	..	..	..	..	..	40	..	..	40	5.00	..
HYBRIDS	..	..	..	..	1	39	..	..	40	4.98	..
Siphateles mohavensis	..	..	..	..	..	40	..	..	40	5.00	..
Right side											
Gila orcuttii	..	..	..	..	38	2	..	..	40	4.05	..
HYBRIDS	..	..	..	..	31	9	..	..	40	4.23	33
Siphateles mohavensis	..	..	..	..	10	30	..	..	40	4.75	..
Both sides (sum)											
Gila orcuttii	..	..	..	..	..	..	38	2	40	9.05	..
HYBRIDS	..	..	..	..	..	..	32	8	40	9.20	21
Siphateles mohavensis	..	..	..	..	..	..	10	30	40	9.75	..
OUTER (LESSER) ROW											
Left side											
Gila orcuttii	..	..	40	..	..	..	..	..	40	2.00	..
HYBRIDS	10	29	1	..	..	..	..	..	40	0.77	61
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..
Right side											
Gila orcuttii	..	2	38	..	..	..	..	..	40	1.95	..
HYBRIDS	14	22	4	..	..	..	..	..	40	0.75	62
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..
Both sides (sum)											
Gila orcuttii	..	..	..	2	38	..	..	..	40	3.95	..
HYBRIDS	8	8	20	3	1	..	..	..	40	1.53	61
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..

of the two outer teeth in *Gila*, but in *Siphateles* has an even and steep slope, so that teeth could hardly find a base if they ever were present. In all these features of teeth and arch the hybrids are intermediate; or, commonly, they show a mixture of the features of the parental types. It seems that dental maladjustments occur in fish hybrids as well as in heterogeneous crosses in man and in dogs (Stockard and Johnson, 1941 : 367–383).

Similarly impressive variable intermediacy is exhibited by the characters of the gill arches (Pl. IV). In harmony with its presum-

TABLE V

FREQUENCIES OF GILLRAKER COUNTS IN *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS*

Locality (see next page)	Kind	Number of gillrakers 6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
A	*Gila*	..	9	22	10	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A	HYBRIDS	..	..	...	...	2	3	10	13	5	1	2	2	..	..	..	..	..	..	..	..	..	..	..	..
A	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	3	3	6	7	11	10	9	3	3	2	..
B	*Gila*	5	16	63	27	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
B	HYBRIDS	..	..	...	...	2	3	16	32	41	16	2	2	..	..	..	..	..	..	..	..	..	..	..	..
B	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	2	2	2	1	5	20	21	25	20	8	4	..
C	*Gila*	5	28	77	39	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
C	HYBRIDS	..	..	...	...	..	1	3	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
C	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	2	..	..	..	3	3	2	2	1	1	..
D	*Gila*	1	15	19	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
D	HYBRIDS	..	..	...	...	..	..	3	11	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
D	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	..	..	2	2	3	7	4	2	1	..	1
E	*Gila*	2	9	38	21	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
E	HYBRIDS	..	..	2*	1*	11	11	7	15	7	2	4	5	1	..	..	..	..	..	..	..	..	..	..	..
E	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	3	8	10	21	13	7	3	..	..
F	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	4	6	17	19	20	9	2	2	..
A–F	*Gila*	13	77	219	102	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A–F	HYBRIDS	..	..	2*	1*	15	18	39	71	56	22	8	9	1	..	..	..	..	..	..	..	..	..	..	..
A–F	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	2	7	7	16	28	64	81	73	43	18	9	1

* Each count of 8 or 9 on one side of a hybrid is matched by a count of 11 on the other side; only a few specimens were counted on both sides.

TABLE V (*Concluded*)

STATISTICAL COMPUTATIONS

Locality	Kind	Range	No.	$M \pm \sigma_M$	Coefficient of variability (%)	Hybrid index
(A) West Fork of Mohave River	*Gila*	7–10	43	8.12 ± 0.15	9.65	..
	HYBRIDS	10–17	38	12.97 ± 0.26	12.44	32
	Siphateles	19–28	57	23.33 ± 0.28	9.13	..
(B) Deep Creek	*Gila*	6–10	123	8.20 ± 0.08	10.20	..
	HYBRIDS	10–17	114	13.52 ± 0.11	9.04	22

D	*Gila*	1	15	19	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Hybrids ...	..	..	...	...	..	..	3	11	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Siphateles ...	..	..	...	...	..	..	..	..	..	..	..	..	..	..	..	2	2	3	7	4	2	1	..	1
E	*Gila*	2	9	38	21	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Hybrids ...	..	..	2*	1*	11	11	7	15	7	2	4	5	1	..	..	..	..	..	..	..	..	..	..	..
	Siphateles ...	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	3	8	10	21	13	7	3	..	..
F	*Siphateles* ...	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	4	6	17	19	20	9	2	2	..
A–F	*Gila*	13	77	219	102	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Hybrids ...	..	..	2*	1*	15	18	39	71	56	22	8	9	1	..	..	..	..	..	..	..	..	..	..	..
	Siphateles ...	..	..	...	...	..	..	..	..	..	..	..	..	2	7	7	16	28	64	81	73	43	18	9	1

* Each count of 8 or 9 on one side of a hybrid is matched by a count of 11 on the other side; only a few specimens were counted on both sides.

TABLE V (*Concluded*)

Statistical Computations

Locality	Kind	Range	No.	$M \pm \sigma_M$	Coefficient of variability (%)	Hybrid index
(A) West Fork of Mohave River ...	*Gila*	7–10	43	8.12 ± 0.15	9.65	..
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(B) Deep Creek	*Gila*	6–10	123	8.20 ± 0.08	10.20	..
	Hybrids	10–17	114	13.52 ± 0.11	9.04	33
	Siphateles	18–28	110	24.38 ± 0.18	7.90	..
(C) Mohave River, ¼ to 5 miles below Deep Creek	*Gila*	6–10	154	8.07 ± 0.07	10.29	..
	Hybrids	11–15	6	12.67 ± 0.61	10.85	29
	Siphateles	19–28	14	24.00 ± 0.67	10.45	..
(D) Mohave River, Victorville	*Gila*	6–9	40	7.70 ± 0.11	9.28	..
	Hybrids	12–15	18	13.17 ± 0.20	6.33	33
	Siphateles	21–29	22	24.14 ± 0.39	7.63	..
(E) Mohave River, Afton Canyon ..	*Gila*	6–10	71	8.14 ± 0.09	9.29	..
	Hybrids	8–18	66	12.58 ± 0.29	18.57	28
	Siphateles	20–27	66	23.95 ± 0.19	6.35	..
(F) Soda Lake spring	*Siphateles*	20–28	80	24.09 ± 0.18	6.54	..
(A–F) All localities	*Gila*	6–10	431	8.09 ± 0.04	10.44	..
	Hybrids	8–18	242	13.13 ± 0.11	12.87	32
	Siphateles	18–29	349	24.03 ± 0.10	7.89	..

ably entomophagous habits, *Gila orcuttii* has the short gill slit and the few almost rudimentary gillrakers that are typical of the genus. In correlation with a probable plankton diet *Siphateles mohavensis* has deeply cleft gill slits and numerous slender functional gillrakers. In the hybrids the first gill slit is of almost exactly intermediate length (Table XI, second item); the values for the hybrid fill the gap between those for the parental species. The gillrakers number 6 to 10 in the *Gila*, 18 to 29 in the *Siphateles* (Table V). The values for the hybrids again fill the gap. Consistently through the river system the gillrakers average about 8 in the *Gila*, 13 in the hybrids, and 24 in the *Siphateles*. Only 19 of the 242 counts for the hybrids overlap the range of counts for both parental types. The coefficient of variability is about 10 per cent for the *Gila* and 8 per cent for the *Siphateles*, but definitely higher, 13 per cent, for the hybrids. A variation of 11 in the gillraker counts that average only 13 would be quite unexpected in any single form of fish that does not vary geographically in this respect. No explanation other than hybridization would be plausible.

Similar intermediacy is displayed by the scale structure (Pl. I, Figs. 1–3), which is strikingly different in *Gila orcuttii* and *Siphateles mohavensis*. The lateral scales of the *Gila* are typically much longer than high, have straightish upper and lower edges, and do not appear shield-shaped. Those of the *Siphateles* have more nearly equal axes and are strongly shield-shaped. The *Gila* scales have more radii, which extend onto the lateral (dorsal and ventral) fields and often occur on the basal field. The radii of the *Siphateles* are fewer, generally stronger, and more regular, and do not extend onto the lateral fields. In all these respects the hybrids cry out their intermediacy. Counts of radii for twenty adults of each form are given in Table VI.

The difference in the number of scales is not great, but the averages for all twelve enumerations (Table VII) are higher in the *Gila* than in the *Siphateles*. The averages for the hybrids are in general nicely intermediate, but with notable exceptions. The transverse counts tend to be high, and that from the origin of the dorsal fin to the lateral line is even higher than that in the *Gila*, giving a strange hybrid index of − 24. This aberrancy in the scale count is quite in agreement, however, with the fact that the measurement of the line along which this count was made, from the origin of the dorsal fin to the lateral line, averages definitely higher in the

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Frequencies of Counts
ANI

Based on adults used in Tabl
margin were counted. The scale se
lateral line, directly over the insert

Kind	Number of				
	6–8	9–11	12–14	15–17	18 2
Gila orcuttii	..	..	4	3	.
Hybrids	..	10	5	2	:
Siphateles mohavensis	14	5	1	..	.

hybrids than in either paren
portionately greater depth of
well become established at t
there. It is a principle of le
down where there is greater sp

The hybrids are interjacen
one significant exception. Th
of pelvic rays, which typically
and 10 in the *Siphateles* (Tal
series counted the hybrid ind
somewhat greater similarity t

Intermediacy, again with
the *Siphateles* parent, is shown
rays (Table IX). The *Gila* t
The hybrids usually have 8 ray
quently than in the *Siphateles*
averaging 78. Correspondin
anal base is about as great in t
XIII).

The dorsal rays show a sli
in average number in the pa
23 (Table X). The difference
and those for the *Siphateles* is
for the hybrids and the *Gila* a

TABLE VI

FREQUENCIES OF COUNTS OF SCALE RADII IN *GILA*, HYBRIDS, AND *SIPHATELES*

Based on adults used in Table XIII. Only those radii reaching the scale margin were counted. The scale selected was the one in the row next above the lateral line, directly over the insertion of the pelvic fin.

Kind	Number of scale radii									No.	Range	Av.	Hybrid index
	6–8	9–11	12–14	15–17	18–20	21–23	24–26	27–29	30–32				
Gila orcuttii	..	..	4	3	4	5	..	2	2	20	12–32	20.30	..
HYBRIDS	..	10	5	2	3	..	..	..	..	20	10–19	12.60	61
Siphateles mohavensis	14	5	1	..	..	..	..	..	..	20	6–12	7.75	..

hybrids than in either parental species (Table XIII). This proportionately greater depth of the hybrids above the lateral line may well become established at the stage when the scales are formed there. It is a principle of lepidogenesis that more scales are laid down where there is greater space (Hubbs, 1941a).

The hybrids are interjacent in the number of fin rays, again with one significant exception. The sharpest differences lie in the number of pelvic rays, which typically number 8 in the *Gila*, 9 in the hybrids, and 10 in the *Siphateles* (Table VIII, first item). In the two large series counted the hybrid indices are 63 and 73, which indicates a somewhat greater similarity to the *Siphateles* than to the *Gila*.

Intermediacy, again with a somewhat greater approach toward the *Siphateles* parent, is shown by the hybrids in the number of anal rays (Table IX). The *Gila* typically has 7 anals; the *Siphateles*, 8. The hybrids usually have 8 rays in this fin, but 7 rays occur more frequently than in the *Siphateles*. The hybrid index of course is high, averaging 78. Correspondingly, the proportionate length of the anal base is about as great in the hybrids as in the *Siphateles* (Table XIII).

The dorsal rays show a slight but probably significant difference in average number in the parental species, with a hybrid index of 23 (Table X). The difference between the averages for the hybrids and those for the *Siphateles* is probably significant; but the averages for the hybrids and the *Gila* are not reliably different.

TABLE VII

SCALE COUNTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Based on twenty specimens of each category, all collected in lowest pool of Deep Creek, Mohave Desert, California, September 1, 1934.

Location of count	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*	Hybrid index
Lateral line	52–63 (57.25)	49–58 (53.45)	44–55 (51.10)	62
Dorsal to lateral line	12–14 (13.20)	12–15 (13.55)	11–12 (11.75)	– 24
Anal to lateral line	8–10 (8.85)	8–9 (8.60)	7–9 (7.70)	22
Pelvic to lateral line	7–9 (7.90)	7–8 (7.55)	5–8 (6.90)	35
Predorsal scales	29–38 (34.15)	28–32 (30.20)	25–34 (28.25)	67
Predorsal rows	29–36 (32.75)	26–31 (28.60)	24–28 (26.35)	65
Around body				
above	26–29 (27.85)	25–29 (27.40)	23–27 (24.95)	16
below	23–27 (24.90)	22–27 (23.90)	20–24 (22.70)	45
total	53–58 (54.80)	49–58 (53.30)	45–52 (49.65)	29
Around peduncle				
above	14–16 (14.80)	13–16 (14.55)	12–15 (13.45)	19
below	13–15 (13.65)	12–15 (13.10)	11–14 (12.65)	55
total	29–33 (30.45)	28–32 (29.65)	25–31 (28.10)	34
			Average hybrid index	35

In the average number of pectoral rays (Table VIII) the hybrids exceed either parental species. The differences are small but almost certainly significant. The t values (ratios of the differences between the means to the standard error of the differences) are as follows:

Deep Creek collection:

Difference between hybrids and *Gila*, 1.29; standard error of this difference, 0.06; t value, 21.

I

›s, and *Siphateles*

›ry, all collected in lowest pool of
mber 1, 1934.

Hybrids	*Siphateles mohavensis*	Hybrid index
49–58 (53.45)	44–55 (51.10)	62
12–15 (13.55)	11–12 (11.75)	– 24
8–9 (8.60)	7–9 (7.70)	22
7–8 (7.55)	5–8 (6.90)	35
28–32 (30.20)	25–34 (28.25)	67
26–31 (28.60)	24–28 (26.35)	65
25–29 (27.40)	23–27 (24,95)	16
22–27 (23.90)	20–24 (22.70)	45
49–58 (53.30)	45–52 (49.65)	29
13–16 (14.55)	12–15 (13.45)	19
12–15 (13.10)	11–14 (12.65)	55
28–32 (29.65)	25–31 (28.10)	34
Average hybrid index		35

ys (Table VIII) the hybrids
:rences are small but almost
›s of the differences between
fferences) are as follows:

standard error of this difference,

Difference between hybrids and *Siphateles*, 0.36; standard error of this difference, 0.06; *t* value, 6.

Afton Canyon collection:

Difference between hybrids and *Gila*, 0.90; standard error of this difference, 0.9; *t* value, 10.

Difference between hybrids and *Siphateles*, 0.50; standard error of this difference, 0.8; *t* value, 6.

TABLE VIII

Number of Pelvic and Pectoral Rays in *Gila*, Hybrids, and *Siphateles*

Collection and kind	Number of pelvic rays					No. of counts*	$M \pm \sigma_M$	Hybrid index
	7	8	9	10	11			
Deep Creek collection, September 1, 1934								
Gila orcuttii ...	4	174	22	..	..	200	8.09 ± .02	...
Hybrids	..	5	137	58	..	200	9.27 ± .04	73
Siphateles	..	4	50	146	..	200	9.71 ± .04	...
Afton Canyon collection, July 26, 1940								
Gila orcuttii ...	1	332	68	..	..	406	8.17 ± .02	...
Hybrids	..	9	96	21	..	126	9.10 ± .04	63
Siphateles	..	1	47	80	2	130	9.64 ± .05	...

Collection and kind	Number of pectoral rays							No. of counts*	$M \pm \sigma_M$	Hybrid index
	13	14	15	16	17	18	19			
Deep Creek collection, September, 1, 1934										
Gila orcuttii ...	1	26	113	58	2	..	..	200	15.17 ± .04	...
Hybrids	..	..	16	86	89	8	1	200	16.46 ± .05	139
Siphateles	..	..	33	120	42	5	..	200	16.10 ± .04	...
Afton Canyon collection, July 26, 1940										
Gila orcuttii ...	..	10	61	54	12	3	..	140	15.55 ± .07	...
Hybrids	..	1	9	51	59	4	..	124 †	16.45† ± .06	220
Siphateles	..	..	43	53	31	3	..	130	15.95 ± .06	...

* Both fins were separately enumerated.

† Not including one count of 0 rays (pectoral fin absent on one side of one fish).

TABLE IX

NUMBER OF ANAL RAYS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Collection and kind	Number of anal rays					No. of speci-mens	Av.	Hybrid index
	6	7	8	9	10			
West Fork of Mohave River								
Gila orcuttii	..	124	2	..	..	126	7.02	..
HYBRIDS	..	14	38	..	..	52	7.73	75
Siphateles mohavensis	..	1	80	..	..	81	7.99	..
Deep Creek								
Gila orcuttii	3	115	5	..	..	123	7.02	..
HYBRIDS	..	22	91	1	..	114	7.82	84
Siphateles mohavensis	..	3	101	3	..	107	8.00	..
Mohave River, ½ to 5 miles below Deep Creek								
Gila orcuttii	..	152	2	..	..	154	7.01	..
HYBRIDS	..	3	3	..	..	6	7.50	51
Siphateles mohavensis	..	1	12	1	..	14	8.00	..
Mohave River, Victorville								
Gila orcuttii	1	90	1	..	..	92	7.00	..
HYBRIDS	..	3	15	..	..	18	7.83	86
Siphateles mohavensis	..	2	55	..	..	57	7.96	..
Mohave River, Afton Canyon								
Gila orcuttii	4	87	6	..	..	97	7.02	..
HYBRIDS	1	34	67	4	1	107	7.72	79
Siphateles mohavensis	1	13	176	1	..	191	7.93	..
Soda Lake spring								
Siphateles mohavensis	..	1	75	4	..	80	8.04	..
All localities								
Gila orcuttii	8	568	16	..	..	592	7.01*	..
HYBRIDS	1	76	214	5	1	297	7.76†	78
Siphateles mohavensis	1	21	499	9	..	530	7.97§	..

* Standard error, 0.01.
† Standard error, 0.03.
§ Standard error, 0.01.

This is a most unexpected result, but the increased pectoral-ray count in the hybrid harmonizes with the fact that the pectoral fin in the hybrids is larger than in either parental species, just as the

T

NUMBER OF DORSAL RAYS

Collection and kind
West Fork of Mohave River
Gila orcuttii
HYBRIDS
Siphateles mohavensis
Deep Creek
Gila orcuttii
HYBRIDS
Siphateles mohavensis
Mohave River, ½ to 5 miles below Deep Creek
Gila orcuttii
HYBRIDS
Siphateles mohavensis
Mohave River, Victorville
Gila orcuttii
HYBRIDS
Siphateles mohavensis
Mohave River, Afton Canyon
Gila orcuttii
HYBRIDS
Siphateles mohavensis
Soda Lake spring
Siphateles mohavensis
All localities
Gila orcuttii
HYBRIDS
Siphateles mohavensis

* Standard errc
† Standard errc
§ Standard erro

higher count of scales betweer the hybrids is consistent with same region. Something in th have been responsible for a be

The fins of the hybrids sh structural feature. The apper

TABLE X

NUMBER OF DORSAL RAYS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Collection and kind	Number of dorsal rays				No. of specimens	Av.
	7	8	9	10		
West Fork of Mohave River						
Gila orcuttii	3	122	1	..	126	7.98
HYBRIDS	1	43	8	..	52	8.13
Siphateles mohavensis	..	69	11	1	81	8.16
Deep Creek						
Gila orcuttii	3	119	1	..	123	7.98
HYBRIDS	21	89	4	..	114	7.85
Siphateles mohavensis	1	97	9	..	107	8.07
Mohave River, ½ to 5 miles below Deep Creek						
Gila orcuttii	1	151	2	..	154	8.01
HYBRIDS	..	5	1	..	6	8.17
Siphateles mohavensis	..	11	3	..	14	8.21
Mohave River, Victorville						
Gila orcuttii	4	84	3	..	91	7.99
HYBRIDS	..	18	..	..	18	8.00
Siphateles mohavensis	..	22	..	..	22	8.00
Mohave River, Afton Canyon						
Gila orcuttii	2	65	3	..	70	8.01
HYBRIDS	..	48	15	..	63	8.24
Siphateles mohavensis	..	52	13	..	65	8.20
Soda Lake spring						
Siphateles mohavensis	..	73	7	..	80	8.09
All localities						
Gila orcuttii	13	541	10	..	564	7.99 *
HYBRIDS	22	203	28	..	253	8.02 †
Siphateles mohavensis	1	324	43	1	369	8.12 §

* Standard error, 0.01.
† Standard error, 0.03; hybrid index, 23.
§ Standard error, 0.02.

higher count of scales between the dorsal fin and the lateral line in the hybrids is consistent with the greater depth of the body in the same region. Something in the constitution of the hybrids seems to have been responsible for a better-developed pectoral fin.

The fins of the hybrids show intermediacy in a very interesting structural feature. The appendages of the *Gila* are very tough and

TABLE XI

FREQUENCIES OF BODY-PROPORTION RATIOS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Based on the data used for Table XIII.

100 × standard length / Dorsal to occiput	31	32	33	34	35	36	37	38	39	40	41	No.	Av.	Hybrid index
Males														
Gila orcuttii	..	..	..	1	2	4	1	..	2	..	..	10	36.3	..
HYBRIDS	..	1	1	5	2	1	..	..	..	..	..	10	34.2	62
Siphateles mohavensis	1	2	5	2	..	..	..	..	..	..	..	10	32.9	..
Females														
Gila orcuttii	..	..	..	..	1	..	..	3	5	..	1	10	38.3	..
HYBRIDS	..	..	..	1	1	3	4	..	1	..	..	10	36.3	62.5
Siphateles mohavensis	..	..	..	3	3	4	..	..	..	..	..	10	35.1	..
1000 × standard length / First gill-slit length		**67–70**	**71–74**	**75–78**	**79–82**	**83–86**	**87–90**	**91–94**	**95–98**	**99–102**	**103–106**	**No.**	**Av.**	**Hybrid index**
Gila orcuttii		11	4	5	..	..	..	..	..	..	..	20	72	..
HYBRIDS		..	..	..	4	9	3	3	1	..	..	20	86	58
Siphateles mohavensis		..	..	..	..	..	2	5	3	9	1	20	97	..
Eye to preopercle / Internarial width		**0.75–0.80**	**0.81–0.86**	**0.87–0.92**	**0.93–0.98**	**0.99–1.04**	**1.05–1.10**	**1.11–1.16**	**1.17–1.22**	**1.23–1.28**	**1.29–1.34**	**No.**	**Av.**	**Hybrid index**
Gila orcuttii		2	3	7	4	3	1	..	..	..	..	20	0.915	..
HYBRIDS		..	..	..	2	8	6	1	2	1	..	20	1.06	55
Siphateles mohavensis		..	..	..	..	..	4	3	9	1	3	20	1.18	..
Dorsal height / Anal height	**1.07–1.09**	**1.10–1.12**	**1.13–1.15**	**1.16–1.18**	**1.19–1.21**	**1.22–1.24**	**1.25–1.27**	**1.28–1.30**	**1.31–1.33**	**1.34–1.36**	**1.37–1.39**	**No.**	**Av.**	**Hybrid index**
Gila orcuttii	2	4	7	6	1	..	..	..	..	..	..	20	1.14	..
HYBRIDS	..	..	1	2	5	8	2	2	..	..	..	20	1.22	50
Siphateles mohavensis	..	..	..	1	..	..	3	6	3	3	2	18	1.30	..

leathery, perhaps in correlati
fin rays are very strong. The
rays thinner and more fragil
served and handled together
the *Gila* specimens, but are br
hybrids and in almost all the
difference between the parent
ness of the skin over the bod
are intermediate.

The hybrids are interjace
relative height of the dorsal a
the average the *Gila* has the
than they are in the *Siphatel*
sequently, are emphasized b
dorsal height and the anal h
crosses are exactly intermedi

The hybrids are also inter
dorsal fin. This is indicated
length and of the distance fr
these are expressed in thous
XIII). When the sexes are
length of the head is elimin
overlap but little, and the hyb

The relatively high dorsa
Siphateles calls for a compa
hybrids in the ratio betwee
the smaller fish the hybrids a
(the hybrid index is 62). In
decreases less in relative lengt
As a result, it becomes about
teles (Table XIII). The hy
height to dorsal–occiput inter
XII).

The other proportionate r
last 6 items) almost equal or e
(or, in the anal height only, th
of the hybrids apparently cau

Another ratio emphasizes
rental species and the interm

Gila orcuttii		11	4	5	..	..	..	..	..	..	..	20	72	..
HYBRIDS		..	..	..	4	9	3	3	1	..	..	20	86	58
Siphateles mohavensis		..	..	..	..	..	2	5	3	9	1	20	97	..
Eye to preopercle / Internarial width		0.75–0.80	0.81–0.86	0.87–0.92	0.93–0.98	0.99–1.04	1.05–1.10	1.11–1.16	1.17–1.22	1.23–1.28	1.29–1.34	No.	Av.	Hybrid index
Gila orcuttii		2	3	7	4	3	1	..	..	..	..	20	0.915	..
HYBRIDS		..	..	..	2	8	6	1	2	1	..	20	1.06	55
Siphateles mohavensis		..	..	..	..	..	4	3	9	1	3	20	1.18	..
Dorsal height / Anal height	1.07–1.09	1.10–1.12	1.13–1.15	1.16–1.18	1.19–1.21	1.22–1.24	1.25–1.27	1.28–1.30	1.31–1.33	1.34–1.36	1.37–1.39	No.	Av.	Hybrid index
Gila orcuttii	2	4	7	6	1	..	..	..	..	..	..	20	1.14	..
HYBRIDS	..	..	1	2	5	8	2	2	..	..	..	20	1.22	50
Siphateles mohavensis	..	..	..	1	..	..	3	6	3	3	2	18	1.30	..

leathery, perhaps in correlation with its life in rapid water, and the fin rays are very strong. The fins of the *Siphateles* have the skin and rays thinner and more fragile. In single collections that were preserved and handled together the caudal fins are intact in nearly all the *Gila* specimens, but are broken in a considerable proportion of the hybrids and in almost all the *Siphateles* specimens. There is a similar difference between the parental species in the thickness and leatheriness of the skin over the body, and in this respect, too, the hybrids are intermediate.

The hybrids are interjacent between the parental species in the relative height of the dorsal and anal fins (Table XI, last item). On the average the *Gila* has the dorsal fin lower but the anal fin higher than they are in the *Siphateles* (Table XIII). The differences, consequently, are emphasized by comparing the ratios between the dorsal height and the anal height. In this ratio the interspecific crosses are exactly intermediate, showing a hybrid index of 50.

The hybrids are also intermediate in the average position of the dorsal fin. This is indicated by the measurements of the predorsal length and of the distance from the dorsal fin to the occiput, when these are expressed in thousandths of the standard length (Table XIII). When the sexes are treated separately and the discordant length of the head is eliminated, the parental species are seen to overlap but little, and the hybrid indices are about 62.

The relatively high dorsal fin and short predorsal space in the *Siphateles* calls for a comparison of the parental species and the hybrids in the ratio between these two values (Table XII). In the smaller fish the hybrids are definitely intermediate in this ratio (the hybrid index is 62). In the adults the dorsal fin of the hybrids decreases less in relative length than it does in either parental species. As a result, it becomes about as long proportionately as in the *Siphateles* (Table XIII). The hybrid index for the quotient, dorsal height to dorsal–occiput interspace, is about 85 in the adult (Table XII).

The other proportionate measurements of the fins (Table XIII, last 6 items) almost equal or even exceed the values for the *Siphateles* (or, in the anal height only, the value for the *Gila*). The constitution of the hybrids apparently causes them to have large fins.

Another ratio emphasizes observed differences between the parental species and the intermediate position of the hybrids. In the

TABLE XII

FREQUENCIES OF PROPORTIONS, DISTANCE FROM ORIGIN OF DORSAL FIN TO OCCIPUT DIVIDED BY DORSAL HEIGHT, IN SPECIMENS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Collection, standard length, and kind	Dorsal fin to occiput / Dorsal height												No.	Av.	Hybrid index
	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1			
West Fork of Mohave River, April 5, 1939; 44 to 85 mm.															
Gila orcuttii	..	..	..	..	..	1	5	3	2	3	2	..	16	1.74	..
HYBRIDS	..	..	1	4	2	3	2	1	..	..	..	..	13	1.43	84
Siphateles mohavensis	..	..	3	6	5	2	2	..	..	..	..	..	18	1.37	..
Deep Creek, September 1, 1934; 51 to 92 mm.															
Gila orcuttii	..	..	..	..	..	1	4	2	5	5	2	1	20	1.79	..
HYBRIDS	..	..	..	..	4	7	2	6	1	..	..	..	20	1.56	85
Siphateles mohavensis	..	..	..	..	8	3	5	2	1	..	..	..	19	1.52	..
Deep Creek, September 1, 1934; 23 to 31 mm.															
Gila orcuttii	..	..	1	7	14	7	1	..	..	..	..	..	30	1.40	..
HYBRIDS	..	3	12	13	2	..	..	..	..	..	..	..	30	1.25	62
Siphateles mohavensis	3	10	12	5	..	..	..	..	..	..	..	..	30	1.16	..

TA

PROPORTIONATE MEASUREM AND

Expressed in thousandths of the s in parenthesis) derived from ten me numbers. Based on a single large co California, September 1, 1934.

	Gila orcuttii	HYBRID
Standard length, mm.	51.3–62.1 (57.1)	55.2–72. (63.0)
Predorsal length	555–592 (570)	531–57 (557)
Dorsal to occiput	343–390 (363)	323–35 (342)
Prepelvic length	533–562 (550)	536–57 (558)
Anal origin to caudal base	292–333 (313)	296–31 (307)
Caudal peduncle, length	193–225 (213)	185–22 (200)
Caudal peduncle, depth	121–142 (132)	130–14 (135)
Lateral line to dorsal origin	156–180 (167)	162–18 (175)
Lateral line to pelvic insertion	99–111 (105)	90–11 (101)
Body depth	270–297 (286)	266–31 (288)
Head length	279–302 (288)	293–315 (306)
Head depth	204–221 (210)	196–215 (208)
Head width	155–169 (162)	149–174 (158)
Interorbital width	86–101 (96)	91–100 (96)
Internarial width	49–62 (55)	48–59 (53)
Suborbital width	31–39 (35)	31–42 (35)
Snout length	73–87 (79)	75–90 (82)
Eye length	61–65 (63)	60–72 (67)

TABLE XIII

PROPORTIONATE MEASUREMENTS OF ADULTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Expressed in thousandths of the standard length. Each item (range, with mean in parenthesis) derived from ten measurements, except as indicated by subscript numbers. Based on a single large collection made in Deep Creek, Mohave Desert, California, September 1, 1934.

	Males			Females		
	Gila orcuttii	HYBRIDS	*Siphateles mohavensis*	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*
Standard length, mm.	51.3–62.1 (57.1)	55.2–72.5 (63.0)	52.1–70.3 (61.6)	55.5–80.8 (67.2)	55.2–87.3 (66.9)	56.0–91.6 (72.5)
Predorsal length	555–592 (570)	531–573 (557)	531–556 (545)	551–615 (585)	567–598 (579)	549–582 (565)
Dorsal to occiput	343–390 (363)	323–359 (342)	315–342 (329)	353–408 (383)	343–386 (363)	336–363 (351)
Prepelvic length	533–562 (550)	536–579 (558)	525–568 (549)	537–565 (551)	554–578 (566)	545–563 (552)
Anal origin to caudal base ..	292–333 (313)	296–317 (307)	292–318 (303)	279–303 (291)	275–308 (292)	277–295 (286)
Caudal peduncle, length	193–225 (213)	185–224 (200)	194–223 (200)	191–212 (203)	184–214 (199)	181–200 (191)
Caudal peduncle, depth	121–142 (132)	130–141 (135)	126–138 (132)	119–131 (124)	123–140 (131)	123–138 (131)
Lateral line to dorsal origin .	156–180 (167)	162–182 (175)	156–179 (165)	143–164 (155)	155–181 (167)	147–168 (161)
Lateral line to pelvic insertion	99–111 (105)	90–119 (101)	86–114 (100)	95–117 (105)	98–108 (103)	82–126 (105)
Body depth	270–297 (286)	266–312 (288)	254–298 (277)	259–300 (278)	276–317 (292)	268–306 (281)
Head length ...	279–302 (288)	293–315 (306)	283–310 (301)	276–305 (290)	302–325 (313)	287–318 (307)
Head depth	204–221 (210)	196–215 (208)	193–216 (204)	198–217 (205)	202–224 (211)	198–214 (205)
Head width	155–169 (162)	149–174 (158)	147–168 (155)	149–176 (163)	156–188 (167)	148–170 (159)
Interorbital width	86–101 (96)	91–100 (96)	85–99 (92)	90–101 (96)	98–111 (103)	90–104 (94)
Internarial width	49–62 (55)	48–59 (53)	45–53 (49)	49–61 (53)	52–61 (58)	45–54 (50)
Suborbital width	31–39 (35)	31–42 (35)	34–40 (37)	35–39 (37)	35–46 (38)	32–42 (37)
Snout length ...	73–87 (79)	75–90 (82)	70–82 (74)	78–88 (82)	79–93 (87)	69–91 (78)
Eye length	61–65 (63)	60–72 (67)	64–73 (68)	54–65 (59)	57–69 (65)	58–69 (65)

TABLE XIII (*Concluded*)

	Males			Females		
	Gila orcuttii	HYBRIDS	*Siphateles mohavensis*	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*
Eye to preopercle	43–53 (48)	53–61 (57)	51–62 (57)	47–56 (50)	55–65 (61)	53–66 (60)
Opercle length .	92–113 (101)	99–107 (104)	96–117 (105)	93–109 (100)	94–114 (106)	101–115 (107)
Upper jaw length	76–87 (81)	77–93 (86)	71–80 (77)	76–98 (85)	85–96 (92)	74–87 (80)
Mandible length	101–112 (107)	100–117 (109)	102–109 (106)	102–116 (108)	107–119 (115)	103–115 (108)
First gill-slit length	68–78 (72)	81–93 (86)	88–101 (97)	68–77 (72)	80–96 (87)	89–105 (97)
Dorsal height . .	208–244 (219)	218–244 (233)	227–239 (234)	183–209 (200)	207–236 (221)	201–226 (215)$_{9}$
Dorsal base	106–135 (119)	118–140 (129)	114–128 (122)	105–121 (109)	111–130 (119)	111–127 (121)
Anal height	179–208 (193)	175–201 (191)	167–184 (178)$_{9}$	164–185 (175)	166–202 (181)	156–177 (166)
Anal base	90–104 (96)	97–114 (103)	91–107 (99)	76–89 (84)	79–102 (93)	85–105 (93)
Caudal, longest ray, lower lobe	228–270 (243)$_{9}$	256–289 (272)$_{9}$	257–290 (279)$_{4}$	208–254 (235)$_{9}$	245–291 (270)$_{8}$	....
Pectoral length .	193–225 (210)	214–241 (228)	217–238 (224)	172–189 (182)	195–217 (198)	183–195 (188)
Pelvic length ...	157–188 (167)	169–197 (183)	173–193 (180)	129–153 (144)	157–183 (164)	156–176 (166)

Gila, as compared with the *Siphateles*, the internarial width (the least distance between the anterior nostrils) is relatively large, but the distance from the eye to the preopercle is relatively small (Table XIII). The ratio between the two proportions (Table XI, third item) shows almost no overlap. The values for the hybrids range between the means for the parental species. The hybrid index of 55 is only 10 per cent above one of exact intermediacy.

Other measurements of the hybrids do not conform with the general rule, that the characters of interspecific fish hybrids are intermediate and unlike those of either parental species. Reviewing the figures in Table XIII, we note that the measurements of the hybrids (expressed in thousandths of the standard length) are high and often extreme for the depth of the head, body, and caudal peduncle, for the length of the head and the parts thereof, and, as already noted, II (*Concluded*)

les		Females	
Siphateles mohavensis	*Gila orcuttii*	Hybrids	*Siphateles mohavensis*
51–62 (57)	47–56 (50)	55–65 (61)	53–66 (60)
96–117 (105)	93–109 (100)	94–114 (106)	101–115 (107)
71–80 (77)	76–98 (85)	85–96 (92)	74–87 (80)
102–109 (106)	102–116 (108)	107–119 (115)	103–115 (108)
88–101 (97)	68–77 (72)	80–96 (87)	89–105 (97)
227–239 (234)	183–209 (200)	207–236 (221)	201–226 $(215)_9$
114–128 (122)	105–121 (109)	111–130 (119)	111–127 (121)
167–184 $(178)_9$	164–185 (175)	166–202 (181)	156–177 (166)
91–107 (99)	76–89 (84)	79–102 (93)	85–105 (93)
257–290 $(279)_4$	208–254 $(235)_9$	245–291 $(270)_8$	....
217–238 (224)	172–189 (182)	195–217 (198)	183–195 (188)
173–193 (180)	129–153 (144)	157–183 (164)	156–176 (166)

;iphateles, the internarial width (the
;erior nostrils) is relatively large, but
ıe preopercle is relatively small (Table
ıe two proportions (Table XI, third
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ither parental species. Reviewing the
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he standard length) are high and often
head, body, and caudal peduncle, for
.e parts thereof, and, as already noted,

TABLE XIV

PROPORTIONATE MEASUREMENTS OF HEAD PARTS IN ADULTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Expressed in thousandths of head length. Each item (range, and mean in parenthesis) derived from twenty measurements. Based on data used in Table XIII.

Head part	*Gila orcuttii*	Hybrids	*Siphateles mohavensis*	Hybrid index
Head depth	655–772 (719)	650–715 (675)	626–724 (673)	96
Head width	529–602 (562)	479–602 (525)	484–565 (517)	82
Interorbital width	306–352 (331)	301–353 (321)	282–328 (311)	50
Internarial width	168–213 (187)	156–198 (180)	151–172 (163)	29
Suborbital width	109–136 (124)	100–144 (118)	109–133 (121)	200 ?
Snout length	253–301 (279)	251–298 (272)	232–287 (251)	25
Eye length	187–228 (211)	179–238 (214)	184–241 (219)	37.5
Eye to preopercle	154–186 (171)	173–204 (190)	172–208 (192)	90
Opercle length	318–381 (349)	310–366 (338)	323–380 (349)	...
Upper jaw length	268–299 (284)	247–319 (288)	231–274 (259)	– 16
Mandible length	350–390 (370)	338–390 (363)	338–364 (354)	44
First gill-slit length.	233–271 (249)	245–307 (279)	283–339 (319)	43
Average hybrid index (opercle measurement excluded)				62

for the length of the fins. The high values for the measurements of the head parts, as expressed in relation to the standard length, are due chiefly to the large size of the head, for when the measurements of the head parts are given in thousandths of the head length (Table XIV) intermediacy is generally indicated.

Life colors (noted in the field on September 1, 1934, when the large collection was secured in Deep Creek) give the hybrids an obvious intermediate appearance:

General Tone:
- *Gila:* darker
- Hybrids: variably intermediate
- *Siphateles:* lighter

Upper Parts:
- *Gila:* blotched with olive-blackish and olive-brassy colors
- Hybrids: variably intermediate
- *Siphateles:* relatively uniform, dark olive

Lower Sides:
- *Gila:* silvery, with more gold than in the *Siphateles*, but also with blue reflections; punctulate with olive black
- Hybrids: with a mixture of the gold of the *Gila* and the blue of the *Siphateles*
- *Siphateles:* bluish white, with brilliant blue and gold reflections, the blue predominating

Lower Surface:
- *Gila:* blue white anteriorly; creamy posteriorly
- Hybrids: (not specified)
- *Siphateles:* bluish white; scarcely cream-colored posteriorly

Sides of Head:
- *Gila:* with brilliant gold reflections, brightest in a bar just behind preopercle
- Hybrids: with bright silvery-blue reflections as in the *Siphateles*, and approaching the *Gila* in the amount of gold; a trace of the golden bar behind preopercle in most hybrids (strong in one)
- *Siphateles:* with silvery blue and gold reflections, but with much less gold than in the *Gila;* no golden bar behind preopercle

Region about Base of Paired Fins:
- *Gila:* translucent gold
- Hybrids: with some of this color
- *Siphateles:* (not noted, presumably almost colorless)

Dorsal Fin:
- *Gila:* dusky amber, in some fish with a wash of dull reddish or greenish
- Hybrids: (not recorded)
- *Siphateles:* olive to rich brown

Lower Fins:
- *Gila:* with a wash of translucent gold, especially on the paired fins; yellower than in the *Siphateles*
- Hybrids: varying greatly; in some much as in the *Gila*, in others, about as in *Siphateles;* in still others, rich orange
- *Siphateles:* olive to rich brown basally, paling outward and with a bluish-white border

Preserved specimens (Pl
in coloration, and the hybri
Gila specimens are usually
show a trace of a dark late
variable dusky spots (regen
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Preserved specimens (Pl. II) of *Gila* and *Siphateles* usually differ in coloration, and the hybrids tend to be recognizably intermediate. *Gila* specimens are usually rather dark in general tone, ordinarily show a trace of a dark lateral band, and are typically marked with variable dusky spots (regenerated scales). *Siphateles* specimens are commonly lighter, show little trace of a dusky lateral band, and are not marked with darkened scales; the dark margins of the scale pockets, however, tend to be better defined. The hybrids vary from the one extreme to the other, but commonly exhibit intermediate or mixed characters in their coloration.

EXPLANATION OF EXTREME CHARACTERS OF HYBRIDS

As noted above, the *Gila* × *Siphateles* hybrids are extreme, or tend to be so, in a number of characters. They have a longer and deeper head, bigger fins, and a deeper body (particularly above the axis) than one would expect to find, on the generally well-substantiated theory of hybrid intermediacy. The long distance between the origin of the dorsal fin and the lateral line is correlated with a high scale count along this line. Similarly, on the average the pectoral fin in the hybrid is larger and has more rays than it does in either parental species.

Something in the constitution of these hybrids would seem to grant them an especial development of the head region, of the body depth, and of the fins. We cannot refrain from thinking of this development as due to some factor other than the specific genes. It seems more plausible that a basic feature in the metabolism is responsible; that we are dealing with an expression of hybrid vigor. It will be recalled that the verified hybrids among the sunfishes (Centrarchidae) display what seems to be heterosis in their growth, activity, intensity of color, and heaviness of body (Hubbs and Hubbs, 1931–33). Certain of the *Gila* × *Siphateles* hybrids definitely recall some of the sunfish crosses in having an extreme development of the flesh, which has caused the body to be very robust and the nape region to bulge beyond the occiput. High development of the fins has characterized many of the aquarium-produced hybrids in the Poeciliidae.

The attribution of the large heads, deep body, and high fins of these cyprinid hybrids to heterosis finds support in the similarity of these differences to certain character gradients that are commonly exhibited by fishes. Thus young fish usually differ from old ones in having the head and the fins proportionately larger (but with a slenderer body), and males differ from females in their bigger fins. Southern races typically differ from northern ones, and races living in highly productive waters often contrast with those inhabiting sterile waters by having deeper bodies, larger heads, and bigger fins (Hubbs, 1941b) — in other words, in the same way that the hybrids under treatment differ from the parental species.

EVIDENCE OF BACKCROSSING

There is no indication that the distinctions between *Gila orcuttii* and *Siphateles mohavensis* are being broken down by the mass hybridization between these genera. In a number of characters the hybrids show little overlap with either parental type, and the whole body of evidence on fish hybrids (Hubbs, 1940a: 205–209) leads us to expect that backcrossing, if it occurred, would cause the counts and measurements to overlap. The number of gillrakers is particularly characteristic of the hybrids (p. 360 and Table V), for only 8 per cent of the counts for the hybrids overlap slightly the range of counts for both parental species. The pelvic rays (Table VIII) are typically 8 in *Gila*, 9 in hybrids, and 10 in *Siphateles*. Studies on correlations of counts in species of fish yield no indication that the gillraker and pelvic-ray counts should show any positive correlation within a systematic unit (unless some hybridization is involved). When we examine these counts for the Mohave cyprinids, we find that such a correlation is indicated (Table XV). The Deep Creek specimens of *Gila* with 9 pelvic rays have a higher average number of gillrakers than those with 8 pelvics. The 8 individuals that agree with the hybrids in having 9 pelvic rays and approach them in having 10 gillrakers probably owe this combination of characters to hybridization followed by backcrossing. The hybrids from Afton Canyon show a definitely significant correlation between the number of pelvic rays and gillrakers ($r = 0.34 \pm 0.07$), which indicates that there are included a considerable number of backcrosses with *Gila* and a few with *Siphateles*.

Backcrossing with *Gila orcuttii* is suggested also by the correlation between extremely low (*Gila*-like) counts of gillrakers and a high number (again *Gila*-like) of pharyngeal teeth in the outer row. These again are unrelated characters with no expected correlation. Among

CORRELATION BETWEEN NU
GILLRAKERS IN G

Locality
No. of pelvic rays*
No. of gillrakers*
Gila orcuttii ....
HYBRIDS ....
Siphateles mohavensis ......

* The pelvic rays were counted
were enumerated for the right side
from Deep Creek and for one *Gila*,
Canyon, which were counted on bo
were tallied.

† The hybrid with 8 gillrakers
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TABLE XV

CORRELATION BETWEEN NUMBER OF PELVIC RAYS AND NUMBER OF GILLRAKERS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Locality		Lowest pool of Deep Creek				Mohave River in Afton Canyon			
No. of pelvic rays*		7	8	9	10	8	9	10	11
No. of gillrakers*	6	..	4	..	..	4	..	..	..
	7	2	22	..	..	15	3	..	..
Gila orcuttii	8	2	94	12	..	58	18	..	..
	9	..	42	2	..	29	13	..	..
	10	..	12	8	..	2	..	..	..
	8	..	..	..	..	2 †	2 †	..	..
	9	..	..	..	..	..	2 †	..	..
	10	..	..	4	..	6	18	2	..
	11	..	..	5	1	5	21	2	..
	12	..	2	24	4	..	14	..	..
HYBRIDS	13	..	2	35	17	..	21	9	..
	14	..	..	47	19	..	14	..	..
	15	..	1	20	11	..	2	2	..
	16	..	..	..	4	..	5	3	..
	17	..	..	2	2	..	7	3	..
	18	..	..	..	..	..	4	..	..
	18	..	..	4	..	..	..	..	..
	19	..	..	..	4	..	..	..	..
	20	..	..	1	3	..	..	2	..
	21	..	..	..	2	..	..	6	..
	22	..	..	2	8	..	11	5	..
Siphateles mohavensis	23	..	5	5	26	..	5	15	..
	24	..	..	5	35	..	15	25	2
	25	..	1	15	30	1	10	15	..
	26	..	..	10	28	..	5	9	..
	27	..	..	4	10	..	1	5	..
	28	..	..	6	2	..	..	..	..

* The pelvic rays were counted on both sides of all specimens. The gillrakers were enumerated for the right side only, except for three specimens of *Siphateles* from Deep Creek and for one *Gila*, twelve hybrids, and one *Siphateles* from Afton Canyon, which were counted on both sides. All possible combinations of counts were tallied.

† The hybrid with 8 gillrakers and the 2 with 9 rakers, on the right side, have 11 rakers on the left side (the entries are doubled because the pelvic rays were counted on both sides).

the hundreds of specimens counted there are only three hybrids with fewer than 10 gillrakers (on one side only), and two of these three are among the four that have two teeth in the outer row on one or both sides. The data for the five specimens involved follow:

Gillrakers, 8–11; pharyngeal teeth, 1, 5—4, 1
Gillrakers, 8–11; pharyngeal teeth, 2, 4—5, 2
Gillrakers, 9–11; pharyngeal teeth, 1, 5—4, 2
Gillrakers, 12–12; pharyngeal teeth, 1, 5—4, 2
Gillrakers, 13–13; pharyngeal teeth, 1, 5—4, 2

No very extensive backcrossing is indicated, however. As a rule, the hybrids are probably first-generation products, with low fertility.

SUMMARY

The two native fishes of the Mohave River system, *Gila orcuttii* and *Siphateles mohavensis*, probably had a complementary distribution during the Pluvial period of the Quaternary, for the *Gila* is adapted for fluviatile life and the *Siphateles* for a lacustrine existence. Despite an obvious maladjustment, the *Siphateles* has been able to survive, with the *Gila*, in isolated creeks that now constitute the only permanent water in this river system. As a result of this cohabitation the two species have engaged in mass hybridization. Hybrids were estimated to constitute 8 per cent of the minnow population in the entire basin; in the area of mutual occurrence the hybrid ratio rose to 9. Interspecific hybridization in fishes is seldom carried to such a degree. Ordinarily it appears to be selected against, because of its biotic inefficiency. The breakdown of the isolating mechanism is apparently due to the circumstance that in these desert waters the physical rather than the biotic environment is dominant in the struggle for existence.

The intergeneric hybrids of the Mohave, like other hybrids between species of Western minnows [6] and of fishes in general, display their mixed origin by a variety of circumstantial evidence. The hybrid interpretation is in complete harmony with the ecological picture. The hybrids were more resistant than the *Siphateles*, but less so than the *Gila*, to the great flood of 1938. They show intermediacy in numerous characters of the pharyngeal arch and dentition, with a variability unexpected in a species. They exhibit similar intermediacy and variability in the length of the gill slit and in the number and form of the gillrakers. The scale structure is also transi-

[6] See papers by Hubbs and Schultz (1931), Schultz and Schaefer (1936), and Calhoun (1940). We have in preparation several additional papers, with conclusions similar to those here proposed.

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several additional papers, with

tional. With a few noteworthy exceptions the scale and fin-ray counts interpose between those for the parental species. The fins and integument are less leathery than those in the *Gila*, but not so fragile as those in the *Siphateles*. Several critical ratios between different measurements provide further evidence of hybridity. The color is likewise intermediate. In general, the proportionate measurements yield averages that are intercalated between those for the parental species.

In certain respects, however, the hybrids are not intermediate. They are large-headed, deep-bodied, and big-finned. In some measurements they are more extreme in these respects than is either parental species. This is true, for example, of the pectoral fin and of the depth of the body above the lateral line, and these aberrant measurements are reflected, respectively, in an increased number of pectoral rays and of scales in the series between the origin of the dorsal fin and the lateral line. The extreme development of certain parts of the body in the hybrids we cannot attribute to the action of specific genes. The similar differences that appear in certain gradients, particularly those between southern races and northern ones, and between races dwelling in highly productive waters and ones existing in sterile habitats, lead us to believe that the aberrant features of the hybrids have some simple physiological basis. We attribute their extremely big heads, robust bodies, and large fins to heterosis.

There is evidence of a small amount of backcrossing between the hybrids and the parental species, particularly with the *Gila*. Certain unrelated counts, which happen to be low in the *Gila* and high in the *Siphateles*, show a positive correlation that would probably not have arisen in any way other than by backcrossing.

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FIG. 1. *Gila orcuttii* FIG.
All

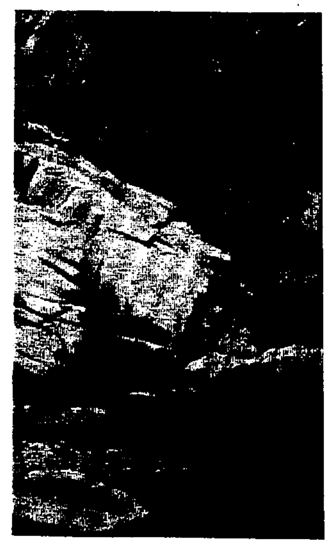

FIG. 4. Lowest pool of Deep Cre
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4, figs. 1–20.

FIG. 1. *Gila orcuttii*

FIG. 2. Hybrid

FIG. 3. *Siphateles mohavensis*

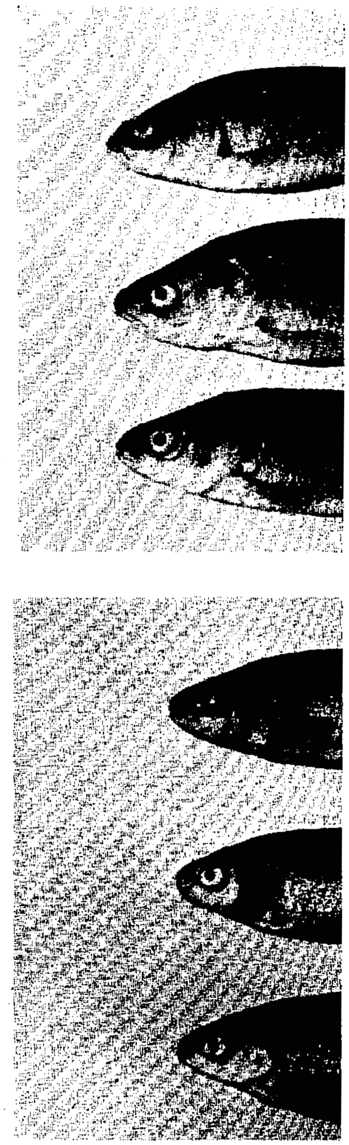
All scales are of adults

FIG. 4. Lowest pool of Deep Creek, photographed by Laura C. Hubbs on September 1, 1934, when the entire fish population was removed and preserved for the analysis of the natural hybrids

EXPLANATION OF PLATE II

FIGS. 1–3. Adult females from Deep Creek, collected September 1, 1934
- FIG. 1. *Gila orcuttii,* 78 mm. in standard length
- FIG. 2. Hybrid, 87 mm. long
- FIG. 3. *Siphateles mohavensis,* 79 mm. long

FIGS. 4–6. Adults from Afton Canyon (main stream), collected April 6, 1939; 57–58 mm. in standard length
- FIG. 4. *Gila orcuttii,* male
- FIG. 5. Hybrid, female
- FIG. 6. *Siphateles mohavensis,* female



Gila orcuttii, hybrids, and *Siphate*

F PLATE II

, collected September 1, 1934
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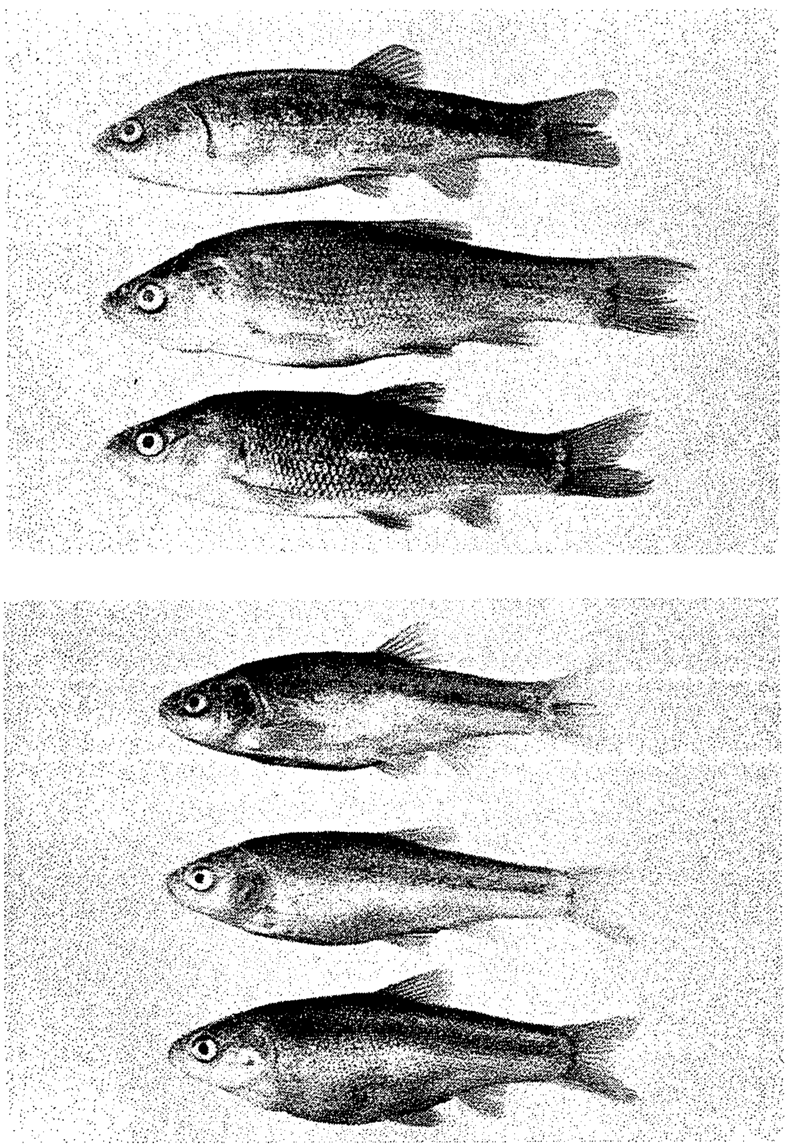
in stream), collected April 6, 1939;



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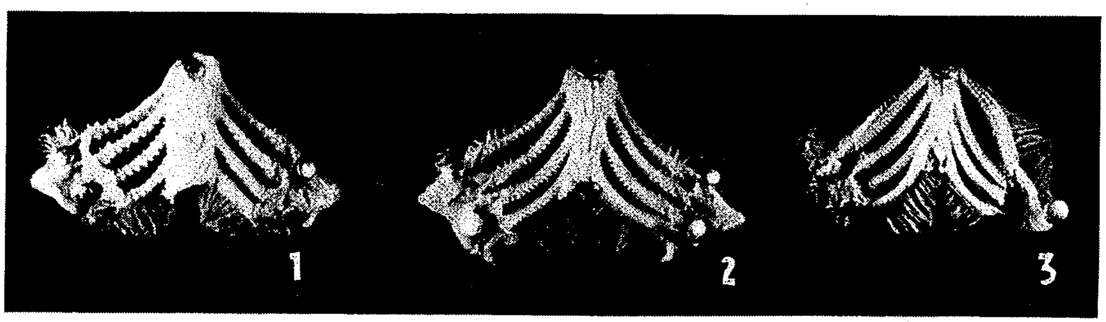
Gila orcuttii, hybrids, and *Siphateles mohavensis* (photographs by Clarence Flaten)

Pharyngeal arches and teeth of *Gila*, hybrids, and *Siphateles* from adults 71–75 mm. long (photographs by Clarence Flaten)

FIGS. 1, 4. *Gila orcuttii*. Teeth, 2, 5 — 4, 2 (one missing on left side represented by alveolus)
FIGS. 2, 5. Hybrid. Teeth, 1, 5 — 5, 1
FIGS. 3, 6. *Siphateles mohavensis*. Teeth, 0, 5 — 5, 0 (one missing on right side represented by alveolus)



Gila orcuttii Hybrid *Siphateles mohavensis*

Gill arches of adult minnows, 91–99 mm. long