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A New Fish of the Genus *Xiphophorus* from Guatemala, with Remarks on the Taxonomy of Endemic Forms

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Of all the species of the poeciliid genus *Xiphophorus,* the green swordtail, *X. helleri* Heckel, has the largest range, occupies the greatest number of distinct habitats, and shows the most marked local and subspecific differentiation. Its known range extends from the Río Nautla, Veracruz, southward to the independent Atlantic coastal tributaries of northwestern Honduras. Within this 800-mile expanse of the Atlantic slope of Middle America the green swordtail inhabits more than 20 principal and subsidiary drainage systems. Although much of its north-south variation is distinctly clinal, the species may be divided into four subspecies of unequal but always recognizable distinctiveness. The three principal subspecies from north to south are: *Xiphophorus helleri helleri* (Mexico: Río Nautla, Río Antigua, Río Chachalacas, Río Jamapa), *X. h. strigatus* Regan (Mexico: Río Papaloapan, Río Coatzacoalcos), and *X. h. guentheri,* Jordan and Evermann (Mexico: Laguna Sontecomapan, Río Grijalva; the basin of the Río Usumacinta of southern Mexico and northern Guatemala; and the Atlantic rivers and streams of British Honduras, Guatemala, and northwestern Honduras). Of the three forms, the southernmost, *X. h. guentheri,* has the greatest range and also the greatest

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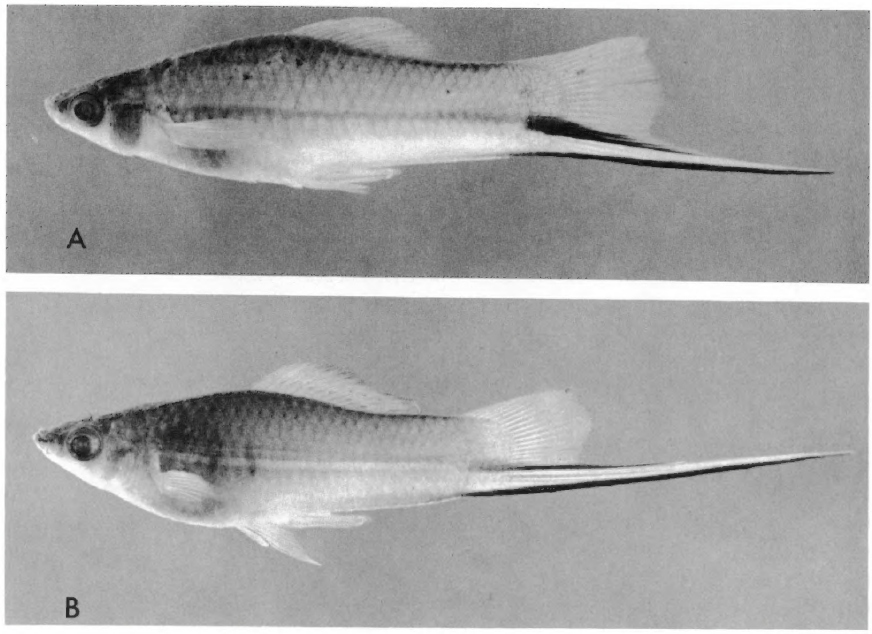

FIG. 1. A. *Xiphophorus helleri signum,* holotype, A.M.N.H. No. 27675. B. Male from the geographically closest population of *X. h. guentheri,* upper Río Sebol, A.M.N.H. No. 27676. In *signum,* note more angulate dorsal and caudal fins and denser proximal pigment along dorsal margin of base of caudal appendage.

amount of morphological variation. The tendency of populations of *guentheri* to differentiate locally is most manifest in the upland tributaries of the Río Usumacinta Basin where in one major branch, the Río Lacantún, another distinct form has arisen, *X. h. alvarezi* Rosen, which in a sense mimics the northern swordtail *X. h. helleri.* The present paper describes a second, and even more dramatic case of the effects of headwater isolation and subsequent differentiation of a population of *guentheri* into an extremely well-marked and, in pigmentation, unique subspecies. The interest in this particular instance of subspecific differentiation is heightened by the occurrence of perfectly typical *guentheri* only 8 kilometers downstream from the collection site of the newly discovered population. The new form apparently is confined to the Río Chajmaic, an intermontane basin that is one of the headwater sources of the Río de la Pasión. The Río Chajmaic flows eastward in an isolated valley for more than 40 kilometers before turning abruptly north and then passing under a low east-west-oriented ridge of 300 to 400 meters in elevation at the point of entry of the river. That low ridge is one of

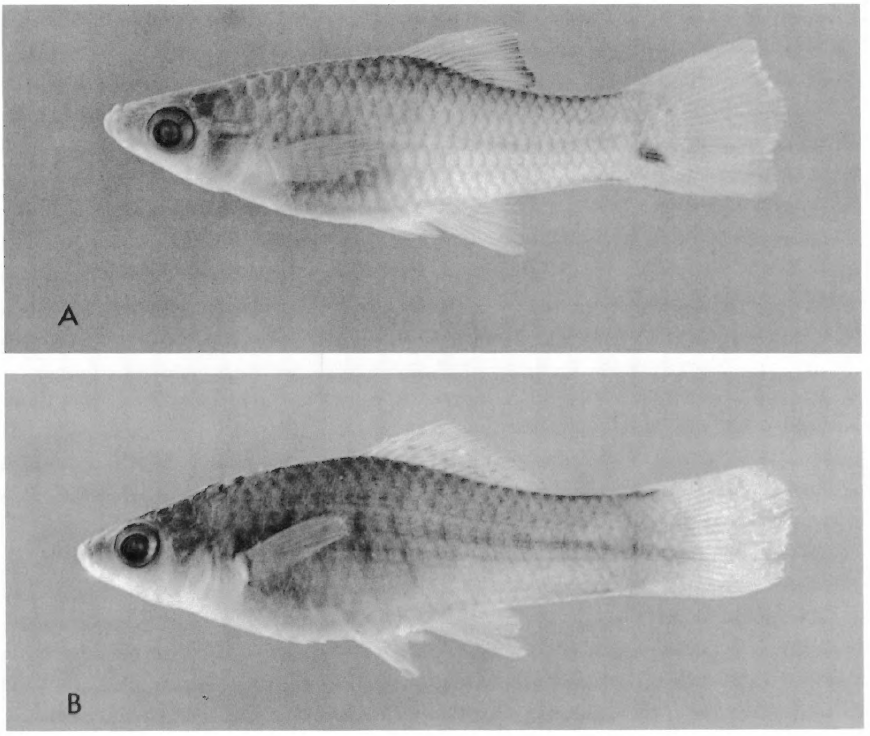

FIG. 2. A. *Xiphophorus helleri signum,* paratype, adult female, A.M.N.H. No. 27671. B. Female from the geographically closest population of *X. h. guentheri,* upper Río Sebol, A.M.N.H. No. 27676. In *signum,* note more angulate dorsal and caudal fins and elongate black spot on the bases of lower caudal rays.

the northernmost foothills of the Sierra de Chamá in Alta Verapaz, Guatemala, and the Río Chajmaic emerges due north of its point of entry from the Chajmaic Valley. North of the ridge it becomes the Río Sebol which, farther north, flows into the Río de la Pasión. The straight-line distance between the points of entry and emergence is about 4 kilometers. The new swordtail was first collected in 1963 in a southeasterly tributary of the Río Chajmaic, the Río Semococh, and again in 1968 in other tributaries farther west and in ponds and backwaters north in the Chajmaic Valley.

The evolution of endemic forms of *Xiphophorus* is at present known also to have occurred in Mexico in the drainage of Lago de Catemaco, Veracruz (*X. milleri* Rosen), and in Cuatro Cíenegas, Coahuila (*X. gordoni* Miller and Minckley). The question of the taxonomic status of these endemics, as well as of a number of other representatives of the genus,

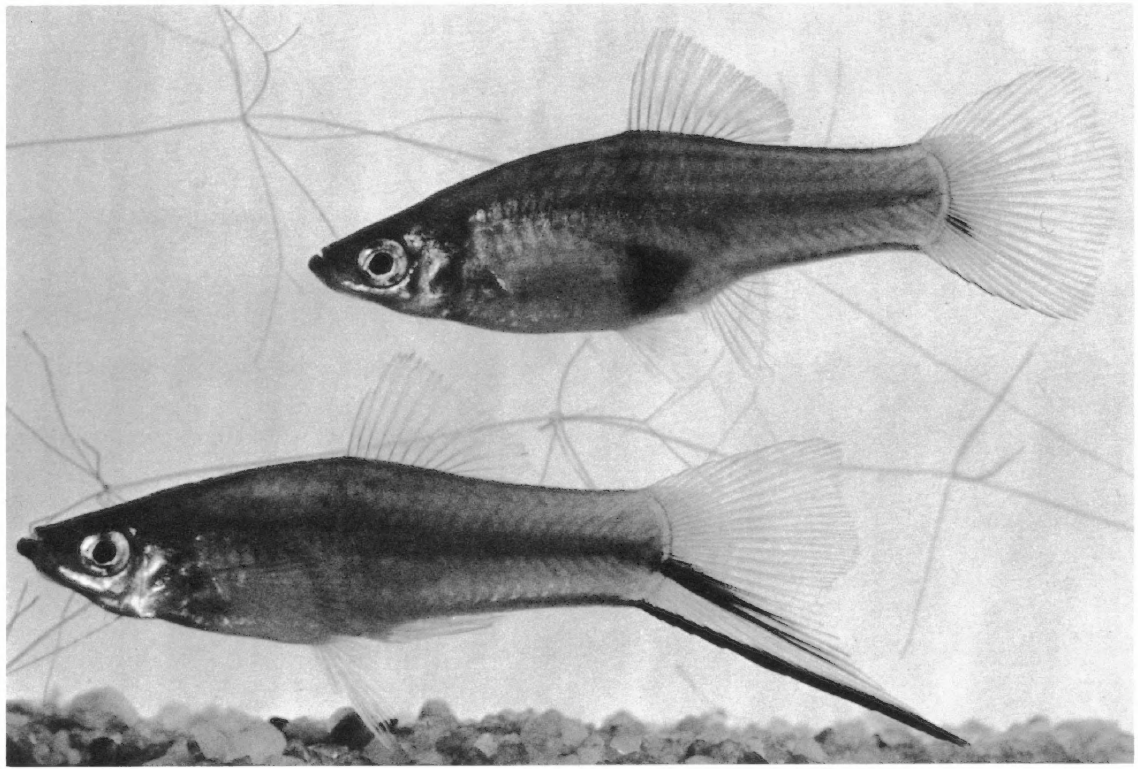

FIG. 3. Laboratory-reared individuals of *Xiphophorus helleri signum. Above:* Adult female. *Below:* Adult male.

has continued to be contentious, mostly, it seems to us, because of the often marked phenotypic differences that have developed even in neighboring populations of swordtails and platyfishes. The issue of what rank to assign *gordoni,* as well as the new form of the green swordtail, is made difficult by the allopatry of the most nearly related populations; and it is clear that the issue cannot be resolved by fiat. It is therefore a secondary aim of the present paper to comment on the evidence for subspecific differentiation within *Xiphophorus.*

Xiphophorus helleri signum, new subspecies

Figures 1A, 2A, 3, 4A, 5–7; tables 1–5

Xiphophorus helleri KALLMAN AND ATZ, 1967, p. 123 (Ch strain; Río Chajmaic; pl. 5, fig. 11, adult male and female).

MATERIAL: The holotype (A.M.N.H. No. 27675) is an adult male, 63.2 mm. in standard length, obtained with rotenone in the Río Semococh, tributary to the Río Chajmaic, a headwater source of the Río de la Pasión (Río Usumacinta Basin) 15 kilometers by road south of Sebol, Alta Verapaz, Guatemala, on March 14, 1963, by the writers. Taken with the holotype were 413 juveniles and adult males and females (A.M.N.H. No. 27671), 10 mm. to 70 mm. in standard length. Additional live material was secured at the same locality on March 16, 1963 by the present writers, which became the basis for the present stock of this swordtail being maintained by the Genetics Laboratory of the New York Zoological Society. Later collections of this form, made during the winter of 1968 by R. M. Bailey, R. C. Dorion, R. Anzueto, and D. E. Rosen, yielded the following specimens: 18 juveniles and subadults (A.M.N.H. No. 27677), 19 mm. to 37 mm. in standard length, from the second arroyo above the mouth of the Arroyo Semococh into the Río Chajmaic; 205 juveniles, adult males, and females (U.M.M.Z. No. 187935), 13 mm. to 74 mm. in standard length, from the lower 200 meters above the mouth of the Arroyo Salaguna into the Río Chajmaic; 441 juveniles to subadults (U.M.M.Z. No. 187941), 24 mm. to 33 mm. in standard length, from a small, drying pool in the bed of an intermittent arroyo 12.3 kilometers southwest of Sebol in the Chajmaic Valley; 551 juveniles to subadults (A.M.N.H. No. 27678), 5 mm. to 35 mm. in standard length, from a woodland pool 13 kilometers southwest of Sebol in the Chajmaic Valley; 305 juveniles to subadults (U.M.M.Z. No. 187951), 15 mm. to 42 mm. in standard length, from the original site of the 1963 collections.

DIAGNOSIS: A deep-bodied form of green swordtail, *Xiphophorus helleri,*

TABLE 1

DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN THE LATERAL LINE OF THE SOUTHERN FORMS OF *Xiphophorus helleri*

	Lateral Line Scales						Mean and Standard Error
	25	26	27	28	29	*N*	
X. h. signum							
Río Chajmaic	—	—	—	20	—	20	28.00—
X. h. guentheri							
Río Sebol (upper Río de la Pasión)	—	4	10	1	—	15	26.80±0.14
X. h. guentheri [a]							
Río Tonala	2	2	4	—	—	8	26.25±0.32
Río Grijalva	4	21	7	—	—	32	26.09±0.10
Río Usumacinta (1 locality)	—	2	—	—	—	2	26.00 —
Río Hondo, Uaxactun	6	7	4	—	—	17	25.88±0.19
Belize River (2 localities)	1	17	8	—	—	26	26.27±0.10
Río Grande (British Honduras)	1	5	1	—	—	7	26.00±0.22
Río Motagua	—	3	3	—	—	6	26.50±0.24
Honduras (5 localities)	7	34	37	6	—	84	26.50±0.08
X. h. alvarezi [a]							
Upper Río Lacantún	—	5	15	—	1	21	26.86±0.14

[a] Data from Rosen (1960).

similar in proportions to *X. h. guentheri,* but differing from that form and from all other subspecies of *X. helleri* in that the half-grown fish of both sexes and adult females have an elongate black spot on the lower half of the caudal fin near the fin base, and have the anterior dorsal rays notably longer than the posterior ones, which gives the elevated fin a subtriangular rather than a parallelogram-like outline. From *X. h. guentheri* (figs. 1B, 2B, 4B) it differs also in having a somewhat broader and more angular caudal fin margin, a constant 28 scales along the midlateral scale row (instead of modally 26 or 27), and, on the average, fewer dorsal fin rays and more numerous distal serrae on ray 4p of the gonopodium than most populations of *X. h. guentheri* (tables 1–3). From *X. h. guentheri* it differs also in life colors: the body is predominantly greenish (instead of bluish green) and has a dusky or brown stripe at midside (instead of a dusky stripe and two or more brick-red stripes along the side); the dorsal and caudal fins are clear or they have an orange-yellow wash in subadult males and in adults of both sexes; the dorsal fin has a faint dusky proximal bar and a broader, darker marginal bar (instead of rows of discrete red and black spots proximally and subdistally on the interradial membrane).

DESCRIPTION: Dorsal fin rays, 12(11), 13(9); distal serrae on gonopodial

TABLE 2

DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS OF THE SOUTHERN FORMS OF *Xiphophorus helleri*

	Dorsal Fin Rays								Mean and Standard Error
	11	12	13	14	15	16	17	*N*	
X. h. signum									
Río Chajmaic	—	11	9	—	—	—	—	20	12.45±0.11
X. h. guentheri									
Río Sebol (upper Río de la Pasión)	—	—	3	9	3	—	—	15	14.00±0.17
X. h. guentheri [a]									
Río Tonala	—	—	4	6	2	1	—	12	13.83±0.21
Río Grijalva	—	—	14	20	2	—	—	37	13.72±0.11
Río Usumacinta (4 localities)	—	5	63	142	17	1	—	228	13.51±0.04
Río Hondo, Uaxactun	—	—	61	92	14	—	—	167	13.72±0.05
Belize River (3 localities)	1	20	146	57	1	—	—	225	13.16±0.04
Río Grande (British Honduras	—	—	1	7	2	—	—	10	14.10±0.10
Río Motagua	1	3	2	—	—	—	—	6	12.17±0.34
Honduras (5 localities)	—	5	36	30	16	3	1	91	13.77±0.10
X. h. alvarezi [a]									
Upper Río Lacantún	16	5	—	—	—	—	—	21	11.23±0.10

[a] Data from Rosen (1960).

ray 4p, 4(8), 5(14), 6(6); scales in midlateral series, 28(20); vertebrae, 30(20). Proportional measurements that distinguish *signum* from the two southern subspecies of green swordtail are given in figures 5–7. For comparisons with the northern forms of *X. helleri,* i.e., *helleri* and *strigatus,* see comparative tables in Rosen (1960).

Observations on males reared in the laboratory show that the elongate black spot on the base of the lower caudal rays becomes incorporated into the upper black border of the caudal extension or "sword," so is more or less masked. The presence of the spot in males is nevertheless evident from the fact that the dorsal pigment of the sword in *signum* is denser and more extensive than is the comparable area of the caudal fin in *guentheri* (see fig. 1B). The caudal spot is not evident in newborn fish, appearing clearly only after it attains a size greater than 10 mm.

ETYMOLOGY: The substantive *signum* (Latin, a mark, token, or sign) is employed in reference to the black mark near the bases of the lower caudal fin rays in all half-grown and adult members of this subspecies of the green swordtail.

RELATIONSHIPS: *Xiphophorus helleri signum* is the most distinctive of the

TABLE 3

DISTRIBUTION AND VARIATION IN THE NUMBER OF DISTAL SERRAE IN THE FOURTH POSTERIOR RAY (4p) OF THE GONOPODIUM OF THE SOUTHERN FORMS OF *Xiphophorus helleri*

	Distal Serrae				*N*	Mean and Standard Error
	3	4	5	6		
X. h. signum						
Río Chajmaic	—	8	14	6	28	4.93±0.13
X. h. guentheri						
Río Sebol (upper Río de la Pasión)	3	1	1	—	5	3.60±0.40
X. h. guentheri[a]						
Río Grijalva	6	10	2	1	19	3.89±0.18
Río Hondo	—	11	8	—	19	4.42±0.12
Río Frío	4	5	1	1	11	3.91±0.28
La Lima, Honduras	—	—	1	—	1	5.0—
X. h. alvarezi[a]						
Upper Río Lacantún	1	—	—	—	1	3.0—

[a] Data from Rosen (1960).

forms of the green swordtail. It is the only population thus far known in which all the individuals differ in color pattern from all other populations of the species. Apart from the caudal fin blotch and the barred, rather than spotted, dorsal fin, patterns that are not found in previously known *helleri, signum* differs from all other subspecies in having the anterior dorsal rays notably longer than the posterior ones. As a consequence, the fin appears to be shorter-based than that of other green swordtails, and has a distinctive subtriangular outline when partly elevated. The caudal fin is somewhat more fan-shaped and has a distinctly more angulate appearance posteriorly than that in other forms. In females of *signum* the head, the snout in particular, appears to taper more acutely.

This subspecies resembles the northern swordtail, *Xiphophorus helleri helleri,* in its largely greenish, rather than bluish, hue and in the presence of a single dusky or brownish midlateral stripe, rather than one or more brick-red stripes. It further resembles the northern-latitude *helleri* and the high-altitude *alvarezi* in being slightly more slender-bodied, in having more scales in the midlateral series, and in having fewer dorsal fin rays than the widespread southern subspecies *guentheri.* It differs from both *h. helleri* and *alvarezi* in having a relatively large number of distal serrae in gonopodial ray 4p, the average number of serrae approximating the highest average number for *guentheri.* The vertebral count of *signum,* 30, is equal to the modal count for *helleri helleri,* and is one higher than the

TABLE 4

DISTRIBUTION OF THE NUMBER OF VERTEBRAE IN TWO POPULATIONS OF *Xiphophorus helleri* FROM ALTA VERAPAZ, GUATEMALA

	Males										Females									
	Precaudal					Caudal					Precaudal					Caudal				
	12	13	14	15	16	13	14	15	16	17	12	13	14	15	16	13	14	15	16	17
X. h. signum																				
Río Chajmaic	—	10	—	—	—	—	—	—	—	10	—	—	—	—	10	—	10	—	—	—
X. h. guentheri																				
Upper Río Sebol	1	8	—	—	—	—	—	—	7	2	—	—	—	7	5	4	7	1	—	—

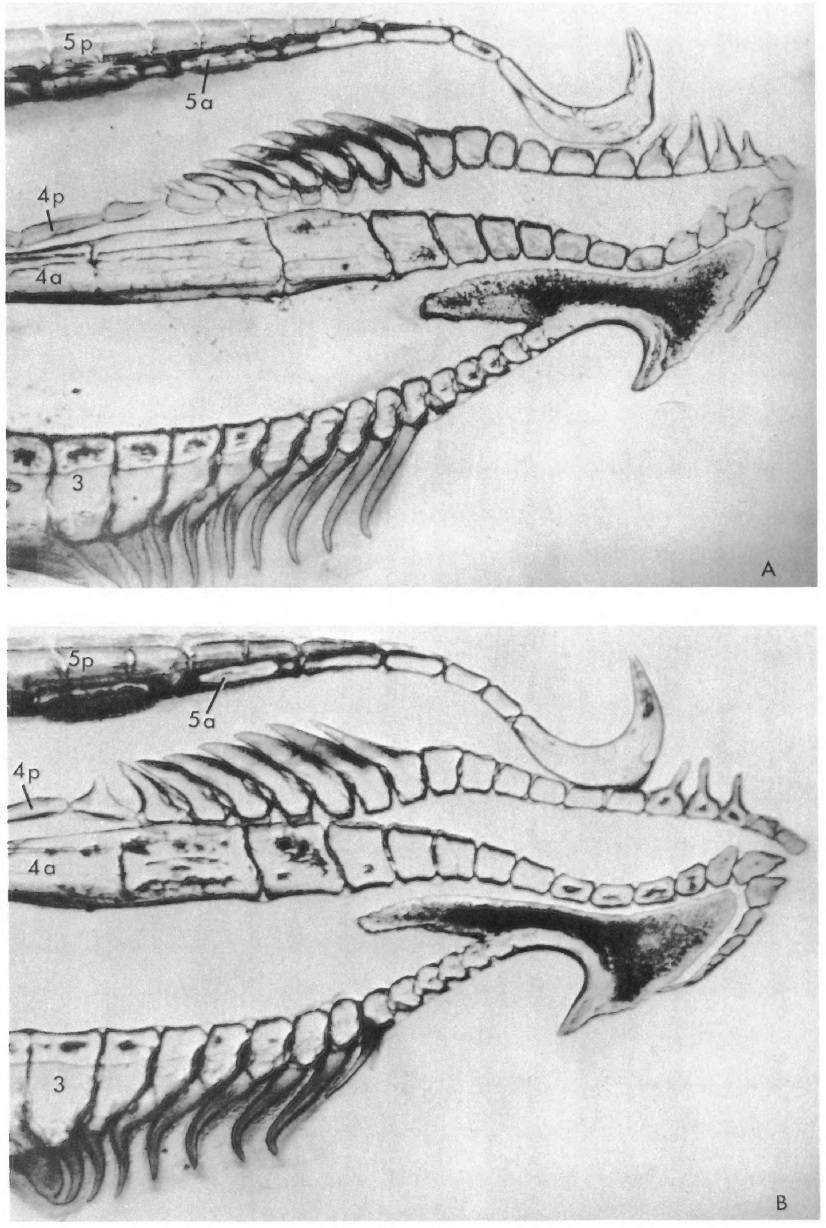

FIG. 4. Tip of gonopodia of adult males. A. *Xiphophorus helleri signum* from the Río Chajmaic. B. *X. h. guentheri* from 8 kilometers downstream from the Río Sebol (upper Río de la Pasión). Anterior to the left. See text for explanation. Ray numbers shown at left.

modal count for neighboring *guentheri* (table 4). It has, however, the relatively long caudal fin of *strigatus, guentheri,* and *alvarezi.*

From the above comparisons, and the geographical position of *signum* between the northern and southern range limits of *guentheri,* it may be surmised that *signum* was derived from the ancestor of *guentheri* and that during the period of its headwater isolation it had developed some of the meristic and pigmentary characteristics of the northern *helleri helleri,* along with its own pigmentation and shape of the dorsal and caudal fins.

The matter is, however, not so simply settled. *Xiphophorus helleri signum* coexists in the Río Chajmaic with two other fish species that are confined to this short stretch of river, the minute poeciliid *Scolichthys iota* Rosen, and a form of *Bramocharax* soon to be described. The genus *Bramocharax* was previously known only from the region between the great lakes of Nicaragua and the Costa Rican lowlands (Bussing, 1967), and the genus *Scolichthys* is represented by one other species besides *iota, S. greenwayi* Rosen, which is confined to western upland regions of the Río Usumacinta Basin. Rosen (1967) speculated that these fishes may be remnants of an older Usumacinta fauna which has been partly eliminated by competitor species that had gradually penetrated upriver from the Grijalva-Usumacinta delta region of Tabasco and Campeche, Mexico. If that hypothesis is correct, then *signum* may already have been in the river, together with *Scolichthys iota* and *Bramocharax,* before the invasion by *guentheri.* Faunal replacement of that kind obviously involves sympatry, but if sympatry existed it would appear not to have been accompanied by hybridization. None of the distinctive features of *signum* has ever been seen by us in Usumacinta *guentheri,* which in all respects are comparable with *guentheri* elsewhere in its extensive range. *Xiphophorus helleri guentheri* and *signum* would have been behaving, *ex hypothesis,* as non-interbreeding sympatric populations, hence as distinct and closely related species.

As against the above highly speculative argument in favor of treating *signum* as a full species, we may examine the evidence of comparative morphology and meristics within the species *helleri* and between *helleri* and related swordtail species as a means of estimating the phylogenetic significance of the size of the gap that separates *signum* from *guentheri.* When intraspecific variation within *helleri* is considered, it is clear that *signum* is more different from *guentheri* than the latter is from either *strigatus* or *alvarezi.* The comparison with *alvarezi* cannot be well documented, mainly because that form is known only from relatively few individuals. The numerous similarities between *guentheri* and *strigatus* are based on

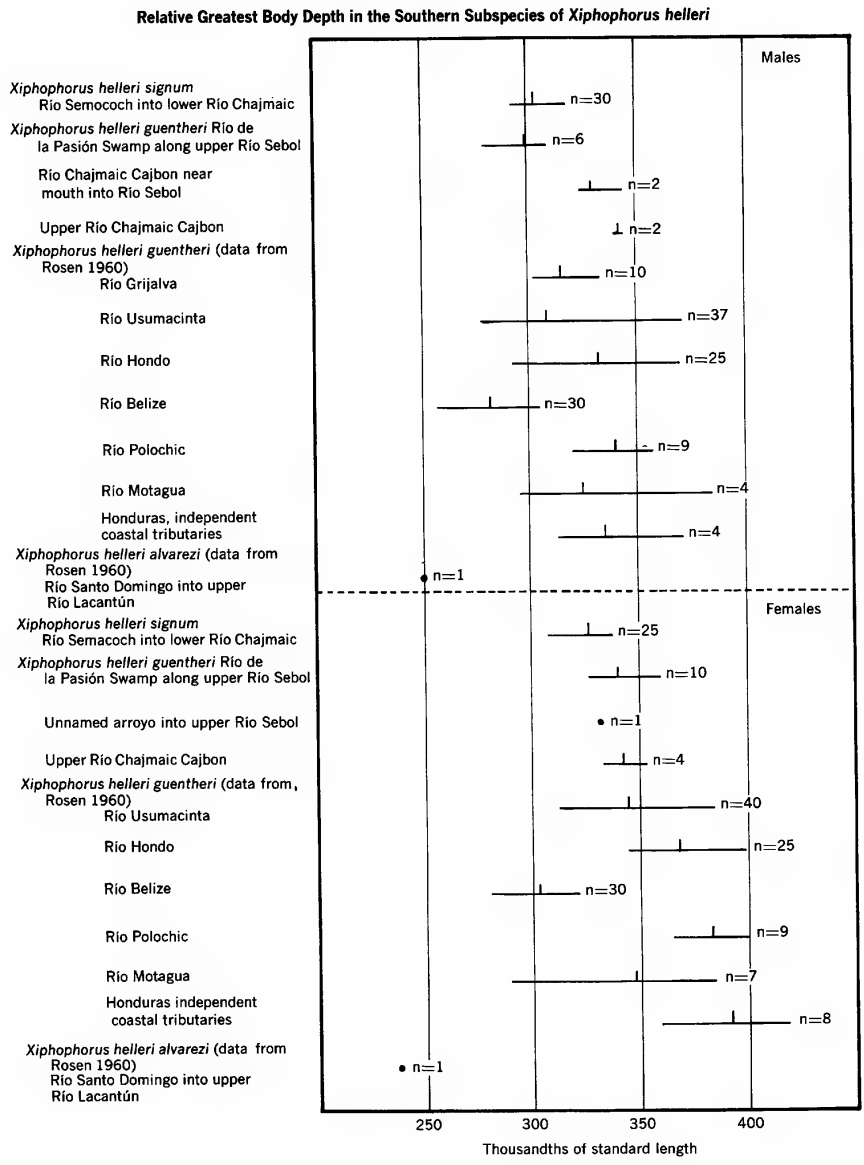

FIG. 5. Relative greatest body depth in the southern subspecies of *Xiphophorus helleri,* showing the range of values (horizontal line) and the arithmetic mean (vertical line).

comparison of hundreds of specimens from throughout the range of both (see Rosen, 1960). The differences between *signum* and *guentheri* are more

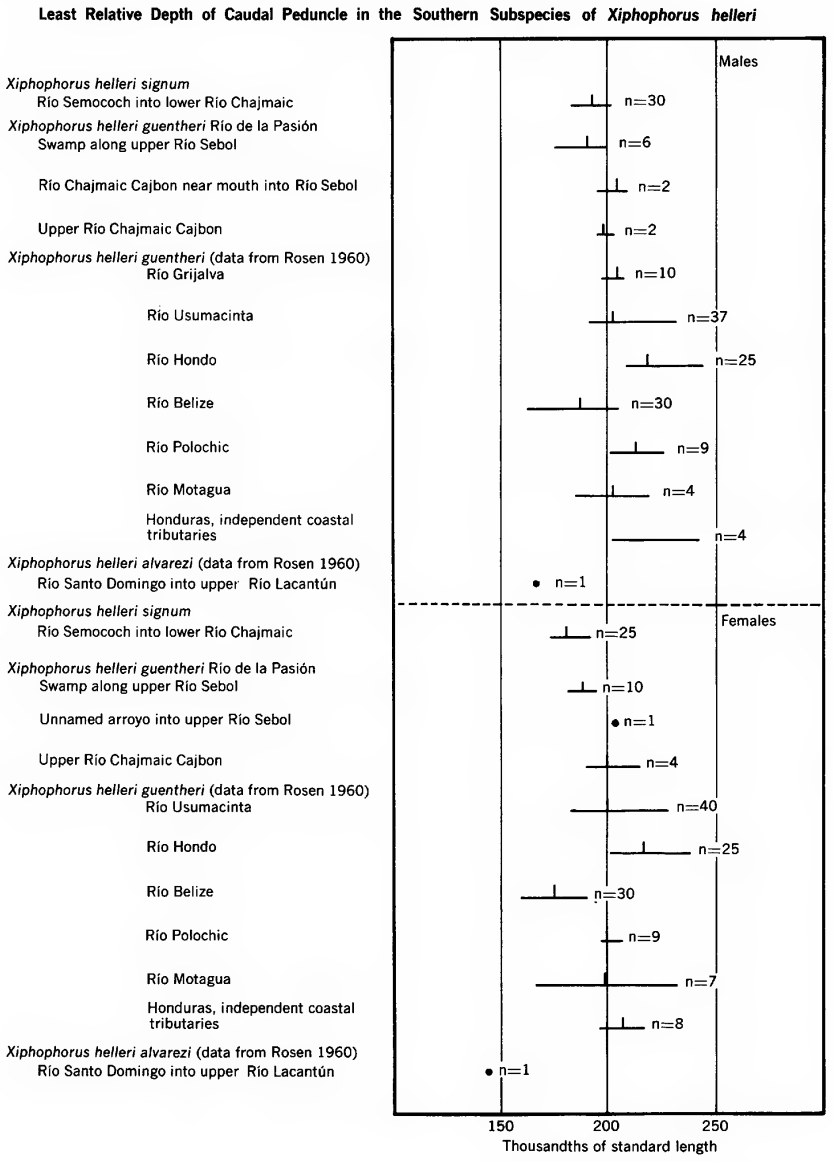

FIG. 6. Least relative depth of caudal peduncle in the southern subspecies of *Xiphophorus helleri,* showing the range of values (horizontal line) and the arithmetic mean (vertical line).

nearly comparable with the differences between the most extreme representatives of *helleri helleri* and *guentheri,* although each of these subspecies

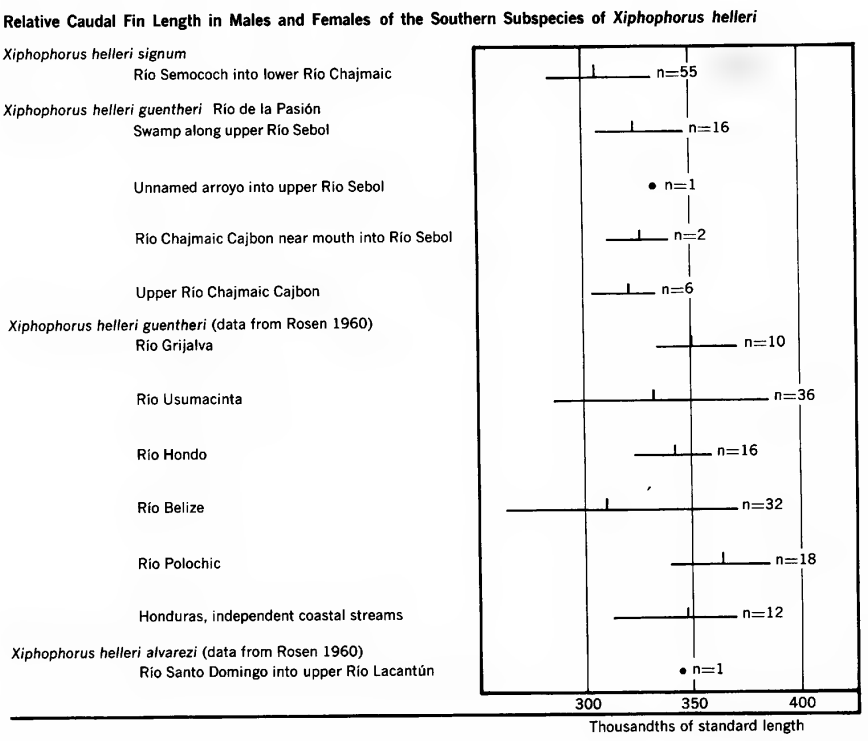

FIG. 7. Relative caudal-fin length in males and females of the southern subspecies of *Xiphophorus helleri,* showing the range of values (horizontal line) and the arithmetic mean (vertical line).

shows evidences of intergradation with the morphologically and geographically intermediate *strigatus* (Rosen, 1960, pp. 106–116). Nevertheless, it is impossible to make an objective judgment as to whether the pigmentary and morphological features of the caudal and dorsal fins of *signum* are of lesser, equal, or greater value evolutionarily than the extremely high or low meristics and exceptionally short caudal fin of *helleri helleri.*

If one compares, however, the previously described forms of *helleri* with the closely related and sympatric yellow swordtail, *Xiphophorus clemenciae* Alvarez, another insight into the status of *signum* may be gained. If the sympatry of *helleri* (fig. 8) and *clemenciae* (fig. 9) in the Río Sarábia in southern Mexico be disregarded for the moment, the yellow swordtail in over-all pigmentation, body shape, and meristic characters might be interpreted simply as one more distinct subspecies of

helleri. One important feature of its anatomy, however, is at variance with that interpretation, and that is the relationship of the size and shape of the bony elements in the external male genitalium, or gonopodium. In the gonopodium of *helleri* (fig. 10A) the terminal portion of ray 4a is unusually heavy, the component irregular bony segments being as high or higher than long and the terminal members turning back sharply away from the tip of the fin; at the tip of ray 5a the large, upturned, bony, clawlike segment is constantly higher than the nearby distal serrae of ray 4p. Adult males from all populations of *helleri* exhibit these gonopodial modifications, as do males of *signum.* In the gonopodium of *clemenciae* (fig. 10B), by contrast, the terminal portion of ray 4a is composed of slender bony segments of regular outline that are invariably longer than high, the terminal members curving gently down around the gonopodial tip and not turning back; the claw at the tip of ray 5a is variably developed, but it is not higher than the serrae of ray 4p. *Xiphophorus clemenciae,* by virtue of its sympatry and the invariably recognizable distinctive combination of features, must certainly be regarded as specifically distinct from *helleri,* whereas *signum* bears the unmistakable imprint of *helleri* in genitalic characters, body form, at least some aspects of pigmentation, and in showing pigmentary and meristic differences from *guentheri* that, within the range of the species, are associated with headwater isolation or northern latitude. Needless to say, the evidence for or against subspecific status for *signum* is entirely circumstantial and the matter cannot be considered closed, but we are at least in a position to state unequivocally that no information about *signum* gathered to date is inconsistent with its status as a very distinct subspecies of *helleri.*[1]

THE CUATRO CIÉNEGAS PROBLEM

There is, among the various species of *Xiphophorus,* one other known instance of involvement in a topographic isolation of a population be-

[1] It may be noted, however, that this argument would be quite irrelevant if, as Zander (1967) claimed, no such animal as *clemenciae* exists. Zander figured the gonopodium of the same specimens of *clemenciae* illustrated by Rosen (1960) and, concerning these, commented rather mysteriously that he was at a loss to explain the "anomalous" appearance of the gonopodia. His comments include an analysis of the clawlike element of gonopodial ray 5a but do not touch on the more significant, and more obvious, details of the tip of ray 4a. We are at present maintaining both *helleri* and *clemenciae* from the Río Sarábia alive in laboratory aquaria (figs. 8, 9), and there is no question of their morphological distinctiveness. A further comparison of these two species will be presented in a forthcoming paper by the present authors.

FIG. 8. *Xiphophorus helleri strigatus.* Fish taken together with *X. clemenciae,* photographed seven months after capture. Both sexes possess a single red lateral stripe and a median and subdistal row of red spots in dorsal fin, absent from *X. clemenciae.* See figure 9.

FIG. 9. *Xiphophorus clemenciae.* Fish collected February 8, 1968, by R. R. Miller, University of Michigan, in a tributary of Río Sarábia, Oaxaca, Mexico, photographed seven months later. Males and females exhibit two salmon-colored lateral stripes and red or orange spots on proximal portion of caudal fin and caudal peduncle.

cause of basic changes in drainage pattern, and the subsequent evolution of a distinct endemic fauna in the now-isolated region. The region is the Cuatro Ciénegas Basin of the Río Grande drainage area in northern Coahuila, Mexico. The fish is *Xiphophorus gordoni* Miller and Minckley. The problem of its specific distinctness or of its specific identity with the northern platyfish, *Xiphophorus couchianus* (Girard), also from Río Grande drainage mirrors all of the difficulties we face in dealing with the taxonomic status of *Xiphophorus helleri signum.*

The two forms, *gordoni* and *couchianus,* have in common certain pigmentary features that are unique in *Xiphophorus* (figs. 11, 12). The most striking of these are the two or three rows of widely spaced, rather oblong groups of deep-lying dermal melanophores on the upper, middle, and lower parts of the caudal peduncle. Miller and Minckley (1963) commented on other aspects of their resemblances in color pattern, as follows: "The corresponding color patterns of *Xiphophorus gordoni* and *X. couchianus,* and their geographic proximity, suggest that these two species are more closely related than is either to the southern species of platyfishes. Both lack macromelanophore markings and tail patterns,

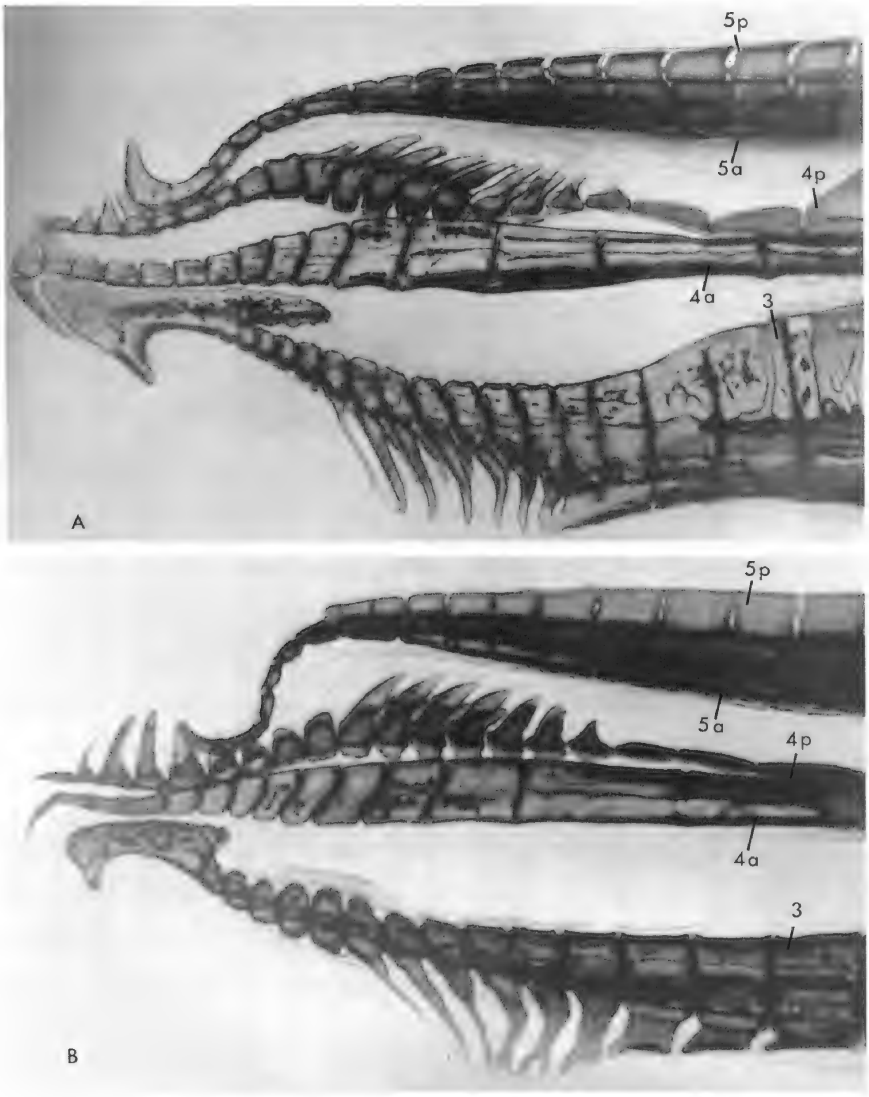

FIG. 10. Tip of gonopodia of adult males of two sympatric species of swordtails from the Río Sarábia, Río Coatzacoalcos drainage, Oaxaca, Mexico. A. *Xiphophorus helleri strigatus.* B. *Xiphophorus clemenciae.* Anterior to the right. Ray numbers shown at the right.

both are sharply bicolored, and both have rows of spots on the caudal peduncle, although these are very weak in *gordoni* which also lacks the 2 to 5 prominent dark, oval to quadrate spots on the mid-sides of

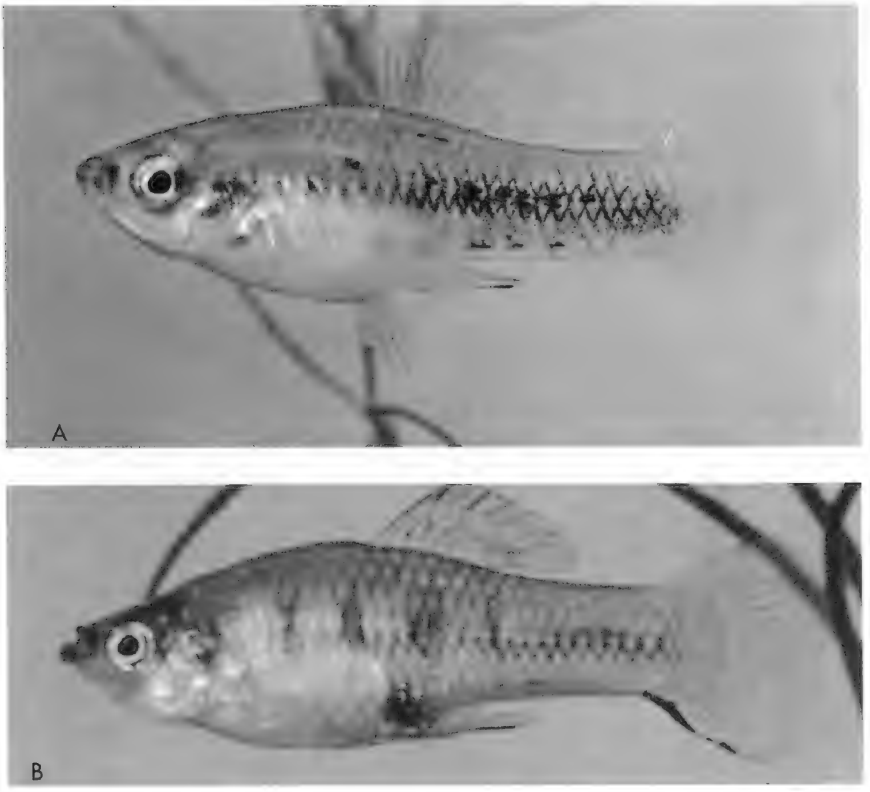

FIG. 11. Living, laboratory-reared adult males of the subspecies of *Xiphophorus couchianus*. A. *X. c. couchianus*. B. *X. c. gordoni*. In both note black-edged gonopodium. The rows of subdermal, flecklike melanophores in A are only faintly indicated in B. See also figure 12.

couchianus (best developed in mature males)." On the basis of observations of living individuals of *gordoni*, which have been maintained for several years in the laboratory, we find that the peculiar spots on the caudal peduncle are equally well developed in both forms and that the older adults of *gordoni* develop the oval to quadrate bars at midside on the trunk (fig. 12B, C). The two forms differ somewhat in the intensity of the dorsal reticular markings, *gordoni* being the more sharply bicolored. Miller and Minckley also pointed out that in *gordoni* and in *variatus xiphidium* (Gordon) there is a conspicuous accumulation of melanophores in the distal part of the third ray of the gonopodium, a pattern they had not seen in *X. couchianus*. The pattern is known to occur, however, in some individuals of our laboratory populations of *couchianus* (fig.

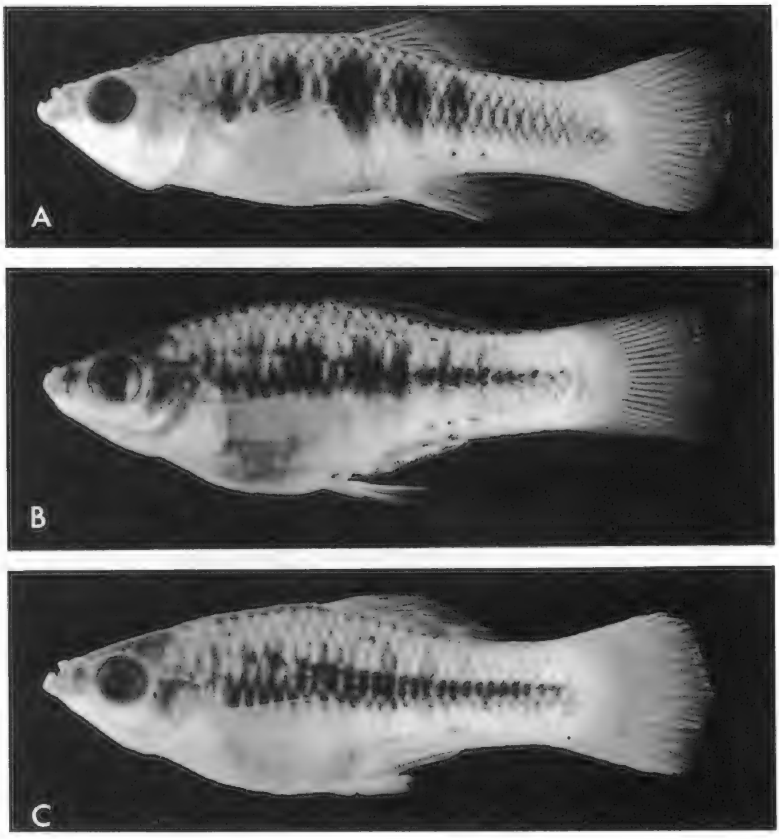

FIG. 12. Preserved, laboratory-reared examples of the subspecies of *Xiphophorus couchianus.* A. *X. c. couchianus,* adult female. B, C. *X. c. gordoni,* adult males. In both forms, note sharply bicolored appearance, broad bars best developed anteriorly, and the rows of deep-lying (subdermal), flecklike, black markings on the caudal peduncle. The last-named pattern does not occur in any other species of *Xiphophorus.*

11A). Moreover, *Xiphophorus variatus* (Meek), *X. milleri* Rosen, and *X. maculatus* (Günther) are polymorphic for this pattern. In those species the entire gonopodium may turn jet black. The black gonopodium of *milleri* was illustrated by Kallman and Atz (1967, pl. 2, fig. 5); and that of *maculatus,* by Gordon (1931, pl. 3, fig. 23).

From our observations of laboratory-reared specimens, males of *gordoni,* if they are maintained long enough, may also develop a black ventral emargination on the caudal fin (fig. 11B), a pattern not seen in *couchianus,* but one for which *maculatus* and *helleri* are polymorphic.

TABLE 5

DISTRIBUTION OF SIX PIGMENTARY SYSTEMS IN THE SPECIES AND SUBSPECIES OF *Xiphophorus*

	1 Vertical Barring	2 Deep-Lying Spots	3 Tail-Spot Pattern	4 Macromelanophore Pattern	5 Black Gonopodium	6 Black Ventral Margin of Caudal Fin
X. couchianus gordoni	+[a]	+	−	−	+	+
X. couchianus couchianus	+	+	−	−	±	−
X. variatus xiphidium	+	−	P+	P+	P+	−
X. variatus variatus	+	−	P+	P+	P+	−
X. variatus evelynae	+	−	−	P+	−	−
X. maculatus	+	−	P+	P+	P+	P+
X. milleri	+	−	+	P+	±	−
X. pygmaeus nigrensis	−	−	+	−	−	+
X. pygmaeus pygmaeus	−	−	−	−	−	−
X. montezumae cortezi	+	−	P+	P+	−	−
X. montezumae montezumae	+	−	P+	P+	−	−
X. helleri signum	−	−	+	−	−	+
X. helleri guentheri	+	−	−	P+	−	+
X. helleri strigatus	+	−	−	P+	−	+
X. helleri helleri	−	−	−	−	−	+
X. helleri alvarezi	−	−	−	−	−	+
X. clemenciae	−	−	−	−	−	+

[a] *Symbols:* +, present; −, absent; ±, rarely present; P+, polymorphic.

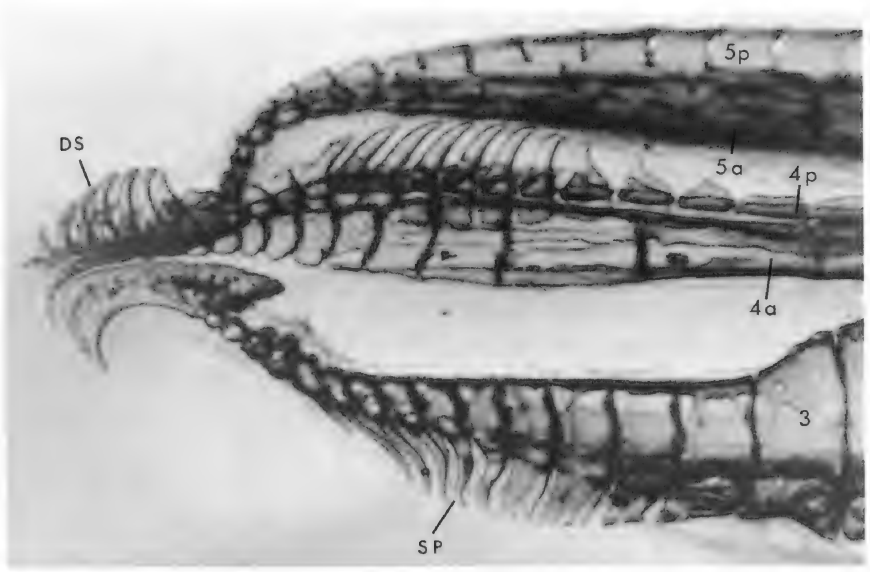

FIG. 13. Tip of gonopodium of adult male of *Xiphophorus couchianus gordoni* from Cuatro Ciénegas, Coahuila, Mexico. Anterior to the right. Note converging distal serrae on ray 4p (DS) and vertical spines with indented tips (SP) on ray 3, both features that characterize the gonopodium of the nominate form, *X. c. couchianus.*

Table 5 shows the manner in which pigment patterns can be used to characterize the known species of *Xiphophorus.* According to this table, pigmentary systems 1 and 5 are of limited use as taxonomic criteria because they are present in most species. The absence of systems 3 and 4 from *couchianus* is interesting only in that the patterns are present in other species belonging to the same species group as *couchianus.* The presence of system 2 in *gordoni* and *couchianus* and its absence from all other *Xiphophorus* may have considerable significance. Pigmentary differences between *gordoni* and *couchianus* are similar to those that separate *variatus evelynae* Rosen from the two other subspecies of *variatus,* and *pygmaeus nigrensis* Rosen from *pygmaeus pygmaeus* Hubbs and Gordon.

The chief structural differences between *gordoni* and *couchianus* concern meristics and a gonopodial trait. The Cuatro Ciénegas form differs from *couchianus* in having, on average, one more vertebra, one or two more dorsal fin rays, and a slightly higher scale and gill-raker count. The gonopodial difference between the two concerns the tendency of the distal serrae on ray 4p to converge at their tips, a feature very marked in *couchianus* and only faintly indicated in about half of our adult male

TABLE 6

DEVELOPMENT OF THE CAUDAL APPENDAGE IN THE SPECIES AND SUBSPECIES OF *Xiphophorus*

Species and Subspecies	Caudal Appendage or "Sword"
X. couchianus couchianus	Absent
X. couchianus gordoni	Absent
X. variatus variatus	Absent
X. variatus xiphidium	Small projection from caudal fin
X. variatus evelynae	Absent
X. maculatus	Usually absent, but arising spontaneously in some fish
X. milleri	Absent
X. pygmaeus pygmaeus	Minute "sword," smaller than that of *variatus xiphidium*
X. pygmaeus nigrensis	Variable from tiny projection to moderately well developed (larger than that in some individuals of *montezumae cortezi*)
X. montezumae montezumae	Small "sword" (Río Tamesí, Río Salto); large "sword" as in *helleri* (Río Verde)
X. montezumae cortezi	Small "sword"
X. helleri (all subspecies)	Large "sword"
X. clemenciae	Large "sword"

specimens (A.M.N.H. Nos. 20448, 20469) of *gordoni* (fig. 13). Although the degree of convergence of the distal serrae may be used to separate the two forms clearly, both *gordoni* and *couchianus* share another gonopodial trait not found in any other species of platyfish, that is, the development of a shallow notch at the tips of the central members of the series of subdistal spines on ray 3 (fig. 13). These central spines in both forms are more or less erect, whereas the comparable spines in the gonopodia of other platyfishes are bent sharply forward.

Miller and Minckley (1963) suggested a possible relationship of *gordoni* with the *variatus* complex rather than with *couchianus* because of the reported occurrence of a small "sword" in *gordoni* resembling that of *variatus xiphidium.* We find no caudal-fin structure in *gordoni* (see figs. 11B, 12B, C) that compares with the "sword" of *variatus xiphidium.* The lower margin of the fin in *gordoni* is more angulate than the same part of the *couchianus* caudal, but we note that a similar difference exists between the caudal fin of adult females of *X. helleri signum* and that of females of *X. helleri guentheri* (fig. 2). Moreover, a small caudal "sword" like that of *variatus xiphidium* has appeared frequently in laboratory stocks of *X. maculatus,* a species of which the sword is not typical. It

would be exceedingly difficult to evaluate the taxonomic meaning of the structure in *gordoni,* even if it occurred in a few individuals. The caudal "sword" appears to be more of a generic than a specific attribute (see table 6).

The sum of the evidence presented above seems clearly to indicate that *gordoni* and *couchianus* are closely related to each other. The question remaining is how one should treat the known order of difference taxonomically.

Geographically, *gordoni* is separated from *couchianus* to the north and to the west by a distance of 100 miles. The factors leading to the isolation of the Cuatro Ciénegas Basin from the tributaries of the Río Grande are unknown, as is also the time of separation. Hubbs and Miller (1965) discussed indirect evidence indicating that the basin has long been isolated and has long contained surface water. They tentatively suggested a Pleistocene age for some of the alluvial deposits of the basin. The Cuatro Ciénegas ichthyofauna is a mixture of a few well-differentiated species, some rather distinct subspecies, and a large number of local variants of widespread forms. Of the fishes there, four of the five cyprinodontoid fishes have been described or indicated as distinct, endemic species. One of these, *Xiphophorus gordoni,* is discussed above as being at least very similar to the northern platyfish, *Xiphophorus couchianus,* of a Río Grande tributary farther southeast. Similarly, the Cuatro Ciénegas forms, *Lucania interioris* Hubbs and Miller and *Gambusia longispinis* Minckley, have their more widespread respective near relatives, *Lucania parva* and *Gambusia nobilis,* in the Río Grande drainage as well as elsewhere. The form of *Cyprinodon* in the basin has not been described but is said by Hubbs and Miller to be a distinct species. Only one other fish is reported to be unique to the Cuatro Ciénegas Basin; it is a subspecies of the minnow *Dionda episcopa.* The remaining fishes, *Gambusia marshi, Astyanax fasciatus, Cichlasoma cyanoguttatum, Ictalurus lupus,* and *Micropterus salmoides,* occur also in North American and Mexican waters, although additional studies of the local cichlids are needed (Miller, personal communication).

Although some quite distinct endemic fishes have evolved in the Cuatro Ciénegas Basin, for any one of these cases it cannot be assumed that a specific level of differentiation has been attained. With regard to *gordoni,* its differences from *couchianus* appear to us to be not greater than the differences separating *Xiphophorus helleri signum* from *X. helleri guentheri,* a conclusion already expressed taxonomically by Rosen and Bailey (1963, p. 63). Our expression of opinion on the level of distinctness of *gordoni* is not intended as criticism of the taxonomic action taken by Miller

FIG. 14. *Xiphophorus pygmaeus nigrensis.* Males, 20 months old, siblings, pedigree 2020. Size disparity between the two siblings is characteristic for the Río Choy population. Both males are fertile and have *Cb* (caudal blot) allele, but pattern is expressed only in large fish. Note that, in small male, elongation of caudal fin rays into a "sword" is barely indicated.

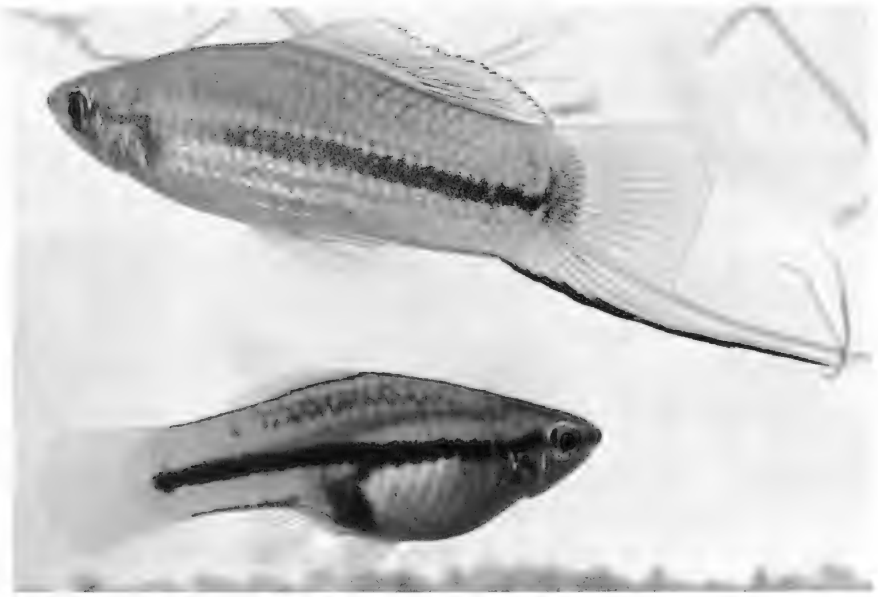

FIG. 15. *Xiphophorus pygmaeus nigrensis.* Male and female. Male is *Cb* (caudal blot), but pattern is poorly expressed; female is +. Prominent midlateral stripe is well developed in females, but only in certain subdominant males. Stripe is similar to one present in *X. montezumae.*

and Minckley, but it emphasizes the difficulty in making objective assignments of the taxonomic level of distinct, wholly allopatric populations. We, in fact, admit to being perhaps over-conservative in our own treatment of *signum* by not giving it full specific status. Our reasoning is that, if *signum* and *gordoni* are given species, rather than subspecies, status, then at least six other distinct subspecies of *Xiphophorus* must be similarly elevated because of the morphological gap that separates them from related, allopatric forms (namely, *variatus xiphidium, variatus evelynae, pygmaeus nigrensis, montezumae cortezi, helleri guentheri,* and *helleri alvarezi*). We oppose such action on the following grounds: it would needlessly multiply the number of working categories (by pushing all categories up one notch); the experimental evidence cited by Rosen (1960), with its limitations, favors a more conservative set of criteria for recognizing species; and there is yet no evidence as might be afforded by local mixing of faunas through stream capture or other natural means in the non-endemic areas that the presently allopatric populations of each of the subspecies pairs involved are potentially reproductively isolated.

However, the most cogent factors, in our opinion, for applying con-

servative criteria in the erection of new species in *Xiphophorus* are that most of the known species are exceptionally polymorphic, and that this polymorphism often is expressed as strongly among siblings or within a single population as it is between allopatric populations. Two distinct kinds of males may occur in a single brood of *pygmaeus nigrensis* (fig. 14), and it is noteworthy that the larger type of *nigrensis* male (see also fig. 15) often is more similar in body proportions and pigmentation to *montezumae cortezi* (fig. 16) than is *cortezi* to *montezumae montezumae* (fig. 17).

With regard to the origin of the most northern subspecies pair, *c. couchianus* and *c. gordoni,* it is suggested that the restriction of the two

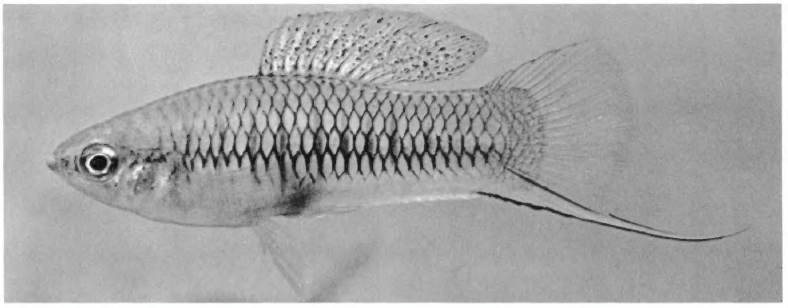

FIG. 16. *Xiphophorus montezumae cortezi.* Adult male from a tributary to the Río Moctezuma, Río Panuco system, San Luis Potosí, Mexico. Note short, slender, caudal appendage, bent upward, characteristic for all individuals of *X. m. cortezi.*

forms to two regions of the Río Grande system more than 100 kilometers apart indicates that the species had a more extensive original distribution, perhaps during more pluvial times. Subsequent environmental changes (primarily increasing aridity and lower temperatures) may have eliminated this platyfish from almost all parts of its former range, for it survives today only in several spring-fed pools, streams, and lagunas near Monterrey (*X. c. couchianus*) and in Cuatro Ciénegas (*X. c. gordoni*). In both areas the fish are found only in dense aquatic vegetation close to the banks. In this respect they occupy typical platyfish habitats and do not differ much from *Xiphophorus variatus xiphidium,* their closest neighbor, which lives in the Río Soto La Marina system to the south. *Xiphophorus v. xiphidium,* however, is not restricted to spring pools, but is also abundant in backwaters and weed-choked ditches which are common just east of the Sierra Madre. North of the Soto

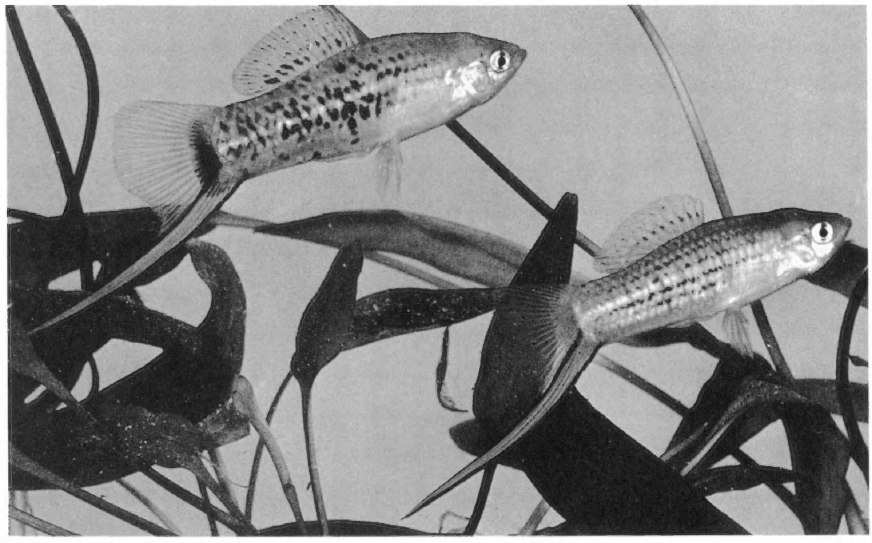

FIG. 17. *Xiphophorus montezumae montezumae.* Males of pedigree 2091, 11 months old, third laboratory generation, descendants from fish collected at Río Salto de Agua, Río Panuco system, San Luis Potosí, Mexico. Upper fish exhibits *Cb* (caudal blot) pattern; lower fish is +. Irregular black markings on flank are caused by macromelanophores. A long, slender, caudal appendage is typical for males of this population.

La Marina system the country becomes increasingly arid, and platyfish habitats are scarce. Such habitats are virtually non-existent in the Río San Fernando, and the few areas that perhaps could support platyfish are characterized by a low volume of water. The absence of platyfish from this river may indicate that the few tributaries of the San Fernando system periodically run dry. The same considerations apply to the Río San Juan and Río Salado of the Río Grande system. In these areas low temperatures during the winter constitute an additional factor that may severely limit the habitats open to species of *Xiphophorus.* Mean January temperatures of 12° C. have been reported for Monterrey (Conover, 1959); presumably temperatures are still lower for the more northern Río Salado area. During cold waves temperatures lower than -5° C. have been recorded for Monterrey (Hann, 1910). Low air temperatures combined with low water conditions lead to rapid cooling of streams and pools. We believe that *X. couchianus* has been able to survive only in regions of spring-fed waters where stable water conditions and sufficiently high temperatures are provided throughout the year.

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