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Genetics of plate morphology in an unusual population of threespine sticklebacks (*Gasterosteus aculeatus*)

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SUMMARY

A collection of *Gasterosteus aculeatus* from a single locality (Friant) in Madera County, California, contains individuals with low and high lateral plate morphology, and very few intermediates. Electrophoretic evidence on protein similarities at 15 genetic loci is compatible with the thesis that members of these two morphs belong to a single interbreeding population. This thesis is also supported by broods from laboratory crosses between morphs, which segregate for low and high plate counts. Laboratory crosses between Friant fish and those from geographically isolated populations often yield some progeny with intermediate plate counts. The demonstration of significantly different patterns of plate development in intralocality versus interlocality crosses evidences a contrasting genetic basis for plate determination in different populations of sticklebacks.

1. INTRODUCTION

The three-spined stickleback, *Gasterosteus aculeatus*, is found in northern coastal regions worldwide (Hagen & Gilbertson, 1972; Munzing, 1963; Muramoto *et al.* 1969). An anadramous form, '*trachurus*' (recognized by some authors as a distinct species from freshwater forms), typically exhibits a complete series of bony plates along the sides of the body. Permanent freshwater residents, '*leiurus*', exhibit a more complex pattern of lateral plate development. Individuals may be assigned to one of three morphs (Fig. 1). A low plate morph has anterior plates only, a partially plated morph has anterior plates plus a caudal keel of plates, and a high plate morph has a continuous series of lateral plates. Plate morph development in a population of *G. aculeatus* ('*leiurus*' form) from Washington State is controlled by at least two genes, each with two alleles (Hagen & Gilbertson, 1973). Variation in plate counts within each morph is polygenically controlled, with heritabilities as high as 0·84 (Hagen, 1973).

An examination of more than 50 populations of *leiurus* in North America indicates that populations may be monomorphic for any morph, polymorphic with all three morphs, or polymorphic with only lows and partials present (Hagen & Gilbertson, 1972, 1973). Polymorphism in freshwater populations has been attributed to hybridization with *trachurus* (Miller & Hubbs, 1969) or to effects of natural selection independent of hybridization with the marine form (Hagen & McPhail, 1970; Hagen, 1967).

In this study, a freshwater population of *Gasterosteus aculeatus* is described

which exhibits an unusual pattern of lateral plate development. Most individuals collected from a single locality in Madera County, California, are either high plated or low plated. Very few partials are present. If this collection represents a single panmictic population, the genetic basis of morph development has apparently been modified relative to that of typical populations of *Gasterosteus aculeatus*.

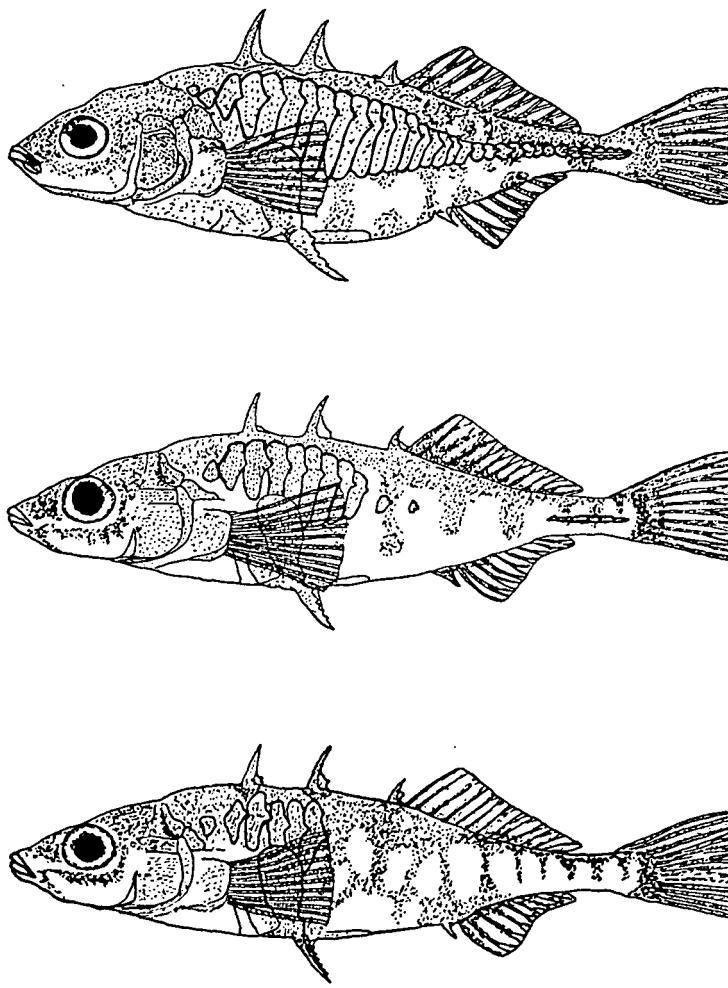

Fig. 1. The three plate morphs typically found in freshwater populations of *Gasterosteus aculeatus*. From top to bottom: high, partial, and low plate morphs.

The purposes of this study are: (1) to determine whether the two morphs in this unique collection of sticklebacks belong to a single interbreeding population and (2) if so, to determine the nature of the genetic basis of this pattern of plate development. Data from two major sources are described: (1) electrophoretic mobilities of proteins encoded by 15–19 genetic loci and (2) progenies reared in laboratory crosses among morphs in the Madera County population, and between these fish and others from geographically isolated populations.

2. THE *GASTEROSTEUS* POPULATIONS

G. aculeatus were collected from a ¼ mile section of the San Joaquin River, in the Lost Lake County Park, about 1 mile below the Friant Dam, Madera County, California. This will be referred to as the 'Friant' population. Several collections were made in the spring and summer of 1973 and 1974. The Friant population is at least 200 miles upstream from the river's outlet to the Pacific Ocean in the Sacramento–San Joaquin Delta, and is undoubtedly permanently restricted to fresh water, and probably to this locality. Very few sticklebacks have been found immediately above or below this site.

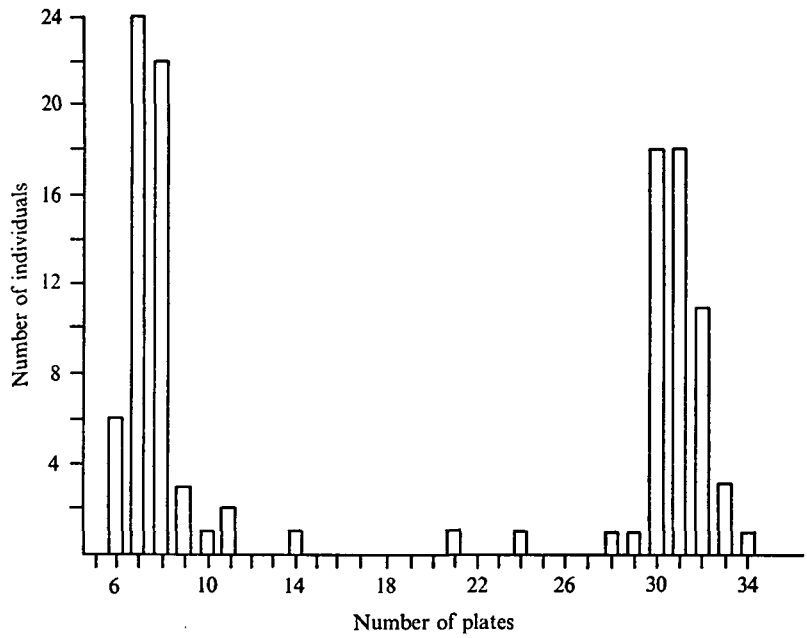

Fig. 2. Frequency distribution of plate numbers in a typical collection of *Gasterosteus aculeatus* from the Friant population. Fish with 6-11 plates belonged to the low plate morph. Those with 28–34 plates belonged to the high plate morph. A total of 49 individuals in this collection showed 7 plates (only 24 are graphed).

The distribution of plate counts for a typical collection of 139 fish from Friant is given in Fig. 2. Most fish belong to either the high morph (about 28–34 plates) or to the low morph (about 6–11 plates), although a few fish exhibiting intermediate plate conditions have been observed (see Results and Analysis). Both morphs are abundant in short seine hauls, and appear to be distributed throughout this section of stream. The unusual nature of plate morph development in the Friant population was first noticed in 1934 (Miller & Hubbs, 1969), and hence appears to be a stable condition (see Table 4).

Friant fish exhibiting high and low plate counts are remarkably similar in other morphological features. Spines are uniform in length and sharpness, anal and cauda fins are uniformly falcate, and body shape and size are similar (Miller &

Hubbs, 1969). In addition, both forms are parasitized by procercoids of intestinal cestodes. Proportions of infected individuals in the present collection were 0·43 and 0·41 for the high and low morph samples, respectively.

Two other populations were used in breeding and electrophoretic studies. A population of '*leiurus*' (*G. a. microcephalus*, Miller & Hubbs, 1969) monomorphic for the low plate morph, was sampled from Conn Creek near Rutherford, Napa County, California, and will be referred to as the 'Napa' population. A sample of '*trachurus*' (*G. a. aculeatus*, Miller & Hubbs, 1969) was collected about 1 mile upstream from the mouth of the Navarro River, near Albion, Mendocino County, California. This population was monomorphic for the high plate morph and will be referred to as the 'Navarro' population. These fish were large, and exhibited much wider plates than those in high plate individuals from Friant.

3. MATERIALS AMD METHODS

Electrophoresis

Fish were scored for plate morph and number of lateral plates, and then individually ground in a glass tissue homogenizer with an equivalent volume of deionized water. The homogenate was centrifuged at 49000 ***g*** for 20 min at 4 °C, and the supernantant stored at − 60 °C until electrophoresis could be carried out. Adults from the Navarro and Napa populations were usually longer than 55 mm total length and individual tissues (muscle and liver) were electrophoresed separately. Mature adults in the Friant population were considerably smaller (about 45 mm) and the whole animal was homogenized for electrophoresis.

Electrophoretic techniques and buffer stains and recipes are fully described by Ayala *et al.* (1972), as modified for fish by Avise *et al.* (1975) and Avise & Ayala (1975). The following buffer systems and tissues provided the best resolution for various proteins in this study: muscle tissue, C buffer for 6-phosphogluconate dehydrogenases (loci *Pgd-1*, *Pgd-2*), malate dehydrogenases (*Mdh-1*, *Mdh-2*), isocitrate dehydrogenase (*Idh-1*) and α-glycerophosphate dehydrogenase (*Gpd-1*); muscle tissue, A buffer for esterase (*Est-1*), general proteins (*Pt-1*, *Pt-2*, *Pt-3*), lactate dehydrogenase (*Ldh-1*), phosphoglucose isomerases (*Pgi-1*, *Pgi-2*), phosphoglucomutase (*Pgm-1*), tetrazolium oxidase (*To-1*, appearing on gels stained for alcohol dehydrogenase) and glutamate oxalate transaminase (*Got-2*); liver tissue, A buffer for glutamate oxalate transaminase (*Got-1*), general protein (*Pt-0*), and triosephosphate isomerase (*Tpi-1*).

Laboratory crosses

Fish were collected by seine and transferred to the laboratory in aerated styrofoam coolers. Eggs from ripe females were artificially stripped into a moist petri dish. Testes were dissected from males and placed in a watch glass with a few drops of water, where they were chopped into fine shreds with a probe and forceps. The testes homogenate was poured onto the eggs and allowed to remain for 5 min. Mucous and sperm residue around the eggs were removed with a dropper (in order

to retard fungus development), and the egg masses were placed in a plastic-screen-bottomed container with plexiglass divider walls. This container was placed in a trough with gently flowing well water (20 °C) until the eggs hatched in about 7–8 days.

Samples of fry from each cross were placed in 16 l plastic dishpans fitted into troughs with slowly moving water. Small holes were punched in the dishpans to allow some water exchange. Fry were fed infusoria for several days and then transferred to nauplii of brine shrimp. At about 15 mm. total length, they were fed tubifex worms and frozen brine shrimp until they reached a length of about 28–45 mm, when they were preserved in formaldehyde for analysis of morph development. Time to development of this length was about 7 months. Studies by Hagen (1973) indicate that plate development in sticklebacks is essentially complete at a length of 28 mm, and I had no difficulty scoring fish greater than 30 mm. Mean size of fish scored is $33{\cdot}29 \pm 0{\cdot}31$ mm.

With limited laboratory space and facilities, a decision had to be made whether to raise a few large families, or a large number of smaller families. For purposes of this study, the latter option is preferable. In addition, mortality was higher than anticipated, and hence family sizes are small.

4. RESULTS AND ANALYSIS

Protein similarities

A total of 15 genetic loci encoding nine enzymes and four general proteins was assayed in samples of *Gasterosteus* from the Friant locality. Initially, data were treated separately for fish exhibiting high and low plate morphology. For most systems, 84 low plate and 55 high plate individuals were scored (some proteins which appeared monomorphic in the first 40 animals were not examined further). Of the 15 loci, 4 or 27% were polymorphic (frequency of common allele $< 0{\cdot}99$) in both the high and low plate sticklebacks. The other 11 loci were monomorphic, and the same allele was shared by all fish. Mean percentages of individuals heterozygous per locus were $9{\cdot}0 \pm 4{\cdot}4$ and $7{\cdot}5 \pm 3{\cdot}7$% for low and high plate fish, respectively. These heterozygosity estimates are close to the mean heterozygosity value of 5·8% calculated by Selander & Kaufman for all vertebrates previously studied. They are well within the range of values reported in fishes (Avise & Selander, 1972; Avise & Smith, 1974).

Confidence in the allelic basis of the polymorphisms scored on the gels stems from two considerations: (1) the banding patterns are typical of those observed in a wide variety of vertebrates and invertebrates (e.g. three bands for individuals presumed to be heterozygous at loci encoding dimeric enzymes) and (2) in most cases the genotypic proportions agree well with those predicted from observed gene frequencies assuming the populations are in random-mating equilibrium. However, at a single locus, *Idh*-1, there was a significant ($P < 0{\cdot}05$) deficit of individuals homozygous for the 'slow' allele among fish exhibiting the low plate morph. This presumed deficit of 'slow' homozygotes appears common among

populations of sticklebacks in northern California (unpublished data) and requires further study.

The electrophoretic data are fully compatible with the thesis that the high and low morph samples were taken from a single interbreeding population. Alleles are shared at the monomorphic loci. At polymorphic loci, allele frequencies are nearly identical (Table 1). Furthermore, when data for the two morphs are pooled, there are no significant departures of genotypic proportions from Hardy–Weinberg expectations (Table 2). The observed F values give no strong indication of 'Wahlund effect' (a phenomenon of apparent deficits of heterozygotes due to the artifact of pooling samples from genetically distinct populations).

Table 1. *Allele frequencies at four polymorphic loci in low and high plate morph sticklebacks from the Friant collection*

(Significant allele frequency differences between the morphs were not observed. Enzyme abbreviations are given in the text).

			Allele frequency	
Locus	Sample size	Morph	F	S
Mdh-2	84	Low	0·411	0·589
	55	High	0·409	0·591
Pgi-2	84	Low	0·185	0·815
	55	High	0·200	0·800
Idh-1	84	Low	0·816	0·184
	55	High	0·836	0·164
Pgi-1	84	Low	0·059	0·941
	55	High	0·028	0·972

Table 2. *Correspondence of observed genotypes to those expected on the basis of Hardy–Weinberg equilibrium for pooled samples of high and low plate fish from the Friant collection*

(Enzyme abbreviations are given in the text).

	Genotype (observed (expected*))				
Locus	FF	FS	SS	χ^2	Fixation index F†
Mdh-2	22 (23·25)	70 (67·49)	47 (48·25)	0·19, N.S.	−0·039
Pgi-2	3 (4·97)	47 (43·05)	89 (90·97)	1·18, N.S.	−0·090
Idh-1	91 (94·25)	47 (40·51)	1 (4·25)	3·63, N.S.	−0·162
Pgi-1	1 (0·28)	11 (12·44)	127 (126·28)	2·00, N.S.	0·122

* Calculated according to Levene's (1949) formula for small samples, assuming random mating equilibrium.

† Calculated as $(H_{exp}-H_{obs})/H_{exp}$, where H_{exp} and H_{obs} refer to the expected and observed frequencies of heterozygotes, respectively.

Nei (1972) has developed an expression which estimates the normalized identity of genes (I, or genetic similarity) between two populations at the j locus. The formula is $I_j = (\Sigma x_i y_i)/(\Sigma x_i^2 \Sigma y_i^2)^{\frac{1}{2}}$ where x_i and y_i are the frequencies of the i allele in populations X and Y, respectively. When all loci are considered, $I = J_{xy}/$

$(J_x J_y)^{\frac{1}{2}}$, where J_x, J_y, and J_{xy} are the arithmetic means over all loci of Σx_i^2, Σy_i^2 and $\Sigma x_i \Sigma y_i$, respectively. I values may range from 0 to 1, with 1 indicating genetic identity. Between the high and low morph samples of the Friant collection, I is greater than 0·999 over the 15 assayed loci.

Small samples (10 individuals each) from the Napa and Navarro populations were assayed electrophoretically at 19 genetic loci (*Pgd*-1, *Pgd*-2, *Est*-1, and *Got*-1 were scored in addition to those loci examined in the Friant fish). Proportions of polymorphic loci (frequency of common allele < 0·99) were 0·21 and 0·42 for Napa and Navarro fish, respectively, and the mean proportions of individuals heterozygous per locus ($\overline{H}$) were $0{\cdot}10 \pm 0{\cdot}05$ and $0{\cdot}13 \pm 0{\cdot}04$. Polymorphisms involving the same alleles were observed at three loci (*Est-1*, *Pt-1*, and *Pgi-2*). At a single locus, *Pt-3*, the Napa population was highly polymorphic ($H = 0{\cdot}40$) but the Navarro population appeared monomorphic. At five additional loci (*Mdh-1*, *Mdh-2*, *Idh-1*, *Pgm-1*, and *Tpi-1*) heterozygotes were observed in the Navarro sample and not in the Napa sample.

Despite the differences in allele frequencies at polymorphic loci, the samples of *trachurus* (Navarro population) and *leiurus* (Napa population) exhibit high overall biochemical similarity, $I = 0{\cdot}97$. At no loci were these populations monomorphic for different alleles. Hagen (1967) has previously reported a diagnostic protein locus between samples of *leiurus* and *trachurus* in British Columbia, but this is the first reported estimate of overall genic similarity based on a large number of loci. Analyses of geographic variation in allele frequencies at many loci for both *leiurus* and *trachurus* are needed for a fuller understanding of evolutionary relationships among these forms.

Plate morphology

Crosses were made within and between the two morphs from the Friant population (Table 3). A total of 32 of 55 attempted crosses eventually produced mature progeny. There are no apparent postzygotic crossability barriers between high (H) and low (L) morph fish under laboratory conditions. About 62% of H × L crosses produced mature offspring, compared to 66 and 38% success for L × L and H × H crosses, respectively. Most mortality in the unsuccessful crosses occurred when the fertilized eggs were attacked by fungus. Many progeny, and some entire families, also died after hatching, presumably due to effects of crowding or disease.

The genetic data are also compatible with the thesis that the two morphs in the Friant locality belong to a single population. Almost without exception, progeny exhibited high or low plate morphology (Table 3). Only L offspring were observed from crosses of L × L parents. Most H × L crosses produced both H and L offspring, but some small broods were comprised of all H, or all L progeny. Families of H × H crosses contained either all H progeny, or H and L progeny. Thus the Friant population appears to have evolved a genetic system coding for high and low plate morphs, largely without the partial morphs typifying other *leiurus* populations.

The data are generally compatible with a single locus, two allele model, the allele for H dominant to that for L. Under this model, broods from an H × L cross should contain all H individuals, or else H's and L's in equal proportions. Among families segregating for H and L morphs, a total of 26 H and 26 L progeny

Table 3. *Plate morphologies in 148 F_1 progeny from 32 crosses of parents from the Friant population*

(H, L, and P refer to high, low, and partial plate morphs, respectively.)

F_1 brood number	Parents		Progeny		F_1 brood number	Parents		Progeny	
	♂	♀	Number	Morph		♂	♀	Number	Morph
1	L	L	8	L	18	H	L	1	H
								1	L
2	L	L	2	L					
					19	H	L	4	H
3	L	L	4	L					
					20	H	L	2	H
4	L	L	6	L					
					21	H	L	1	H
5	L	L	5	L				3	L
6	L	L	5	L	22	H	L	1	H
								1	P
7	L	L	3	L				1	L
8	L	L	5	L	23	H	L	2	H
								4	L
9	L	L	4	L					
					24	L	H	3	H
10	L	L	10	L				1	L
11	L	L	5	L	25	L	H	4	H
12	L	L	6	L	26	L	H	4	H
								1	L
13	H	L	3	H					
			6	L	27	L	H	2	H
								2	L
14	H	L	2	H					
					28	H	H	7	H
15	H	L	1	L					
					29	H	H	2	H
16	H	L	2	H					
			3	L	30	H	H	1	H
17	H	L	6	H	31	H	H	2	H
			4	L					
					32	H	H	7	H
								1	L

were observed. Progeny in single broods from H × H crosses should be either all H, or H and L in 3:1 ratio, and all progeny from L × L crosses should be L, as observed. Nonetheless, the family sizes do not allow unambiguous determination of the number of genes involved in plate formation in the Friant population. Sampling errors are a serious problem in these small families. For example, one

H × L cross yielded a single offspring, L. If all offspring from such a cross were L, clearly a single locus model with two alleles would be incorrect.

Additional complications arise with the occasional appearance of partially plated fish. In the collections from the Friant locality (Table 4), and among progeny from laboratory crosses (Table 3), fish with various intermediate plate conditions were observed in about 2–6% frequency. For example, two adult females (exhibiting 21 and 24 lateral plates, Fig. 2) showed a gap of several missing plates before the caudal, and another female (14 plates, Fig. 2) showed lateral plates extending further down the side than usual. A single progeny reared from a cross of H × L parents (Table 3) also showed a gap of several missing plates before the caudal. These atypical plate morphologies may suggest interactions of alleles at different loci. Basic patterns of morph development may be altered by particular recombinant genotypes at one or more 'modifier' loci. Alternatively, more than two alleles exhibiting different dominance relationships could be present at the 'major gene'.

Table 4. *Percentages of progeny exhibiting intermediate plate morphologies in laboratory crosses between high plate (H) × low plate (L) parents from various localities*

(P* morphs (Tables 4 and 5) are counted here as high plate fish. Percentages of intermediate plate fish from various Friant collections are also given.)

Laboratory cross	Number of high plus low plate progeny	Number of intermediate plate progeny	Percent intermediate plate progeny
Friant (H) × Friant (L)	64	1	1·5
Friant (H) × Napa (L)	29	4	12·1
Friant (L) × Navarro (H)	39	13	25·0

Collection (year)	Number of high plus low plate fish	Number of intermediate plate fish	Percent intermediate plate fish	Source
Friant (1934)	119	5	4·0	Miller & Hubbs (1969)
Friant (1969–70)	316	20	6·0	Peter Moyle (pers. comm).
Friant (1974)	136	3	2·2	Present study

On the basis of much more extensive breeding data, Hagen & Gilbertson (1973) proposed a dilocus model with dosage effects for morph development in sticklebacks from Washington State. At each locus, one allele is assumed to be dominant to a single alternate. Fish with three or more dominant alleles at these two loci exhibit high morph, those with two dominant alleles show partial morph, and those with zero or one dominant allele develop low plate morphology. Various two-locus models determining H and L morphs are certainly not excluded by the genetic data for the Friant population, although differences in dominance relationships are required to explain the near absence of partially plated fish in H × L crosses.

Interpopulation crosses of Friant × Napa fish gave somewhat different results. As before, all L × L crosses yield only L progeny, but a higher percentage of offspring of H × L crosses are intermediate for plate count (Tables 4 and 5). Two of the three progeny labelled P in brood number 46 showed 14–15 plates extending down the anterior half of the body, but no caudal keel of plates. Other fish labelled P (Table 5) exhibit conspicuous gaps the width of two or more plates before the caudal. In addition, fish labelled P* (Tables 5 and 6) showed smaller gaps, the width of one or perhaps two plates before the caudal. Hagan (1973) noted that fish with these small gaps (P*) typically behave as fully plated fish in laboratory crosses.

Table 5. *Plate morphologies in 60 F_1 progeny from 17 crosses between a parent from the Friant population and a parent from the Napa population*

(H, L, and P refer to high, low, and partial plate morphs, respectively. P* indicates unusual morph, missing one or two plates before the caudal peduncle.)

F_1 brood number	Parents ♂ Friant	Parents ♀ Napa	Progeny Number	Progeny Morph
33	L	L	6	L
34	L	L	2	L
35	L	L	3	L
36	L	L	1	L
37	L	L	5	L
38	L	L	1	L
39	L	L	3	L
40	L	L	6	L
41	H	L	1	L
42	H	L	3	H
			1	L
43	H	L	1	H
			2	L
44	L	H	4	H
45	L	H	2	H
			3	L
46	L	H	3	L
			3	P
47	L	H	3	L
48	L	H	2	H
			1	P
49	L	H	2	H
			1	P*
			1	L

A number of genetic models could be advanced to explain the pattern of morph inheritance in these crosses. As an example, assume a two-locus model, each locus with two alleles (A, a and B, b). In both the F_1 hybrids (Friant × Napa) and in the Napa population, the A_B_ genotype is required for full plate development, A_bb codes for partial plates, and aa_ codes for low plates. The evolution of the pattern of morph development within the Friant population then requires the acquisition of full dominance by the A allele such that, within the genetic backgrounds of the Friant population, A_ genotypes result in high plate development. The expression of the dominant alleles in the Friant population could have evolved through changes in the genetic background, through changes in alleles at the major genes, or both. This particular model can account for the various segregations in Tables 3 and 5, although a number of other models may be equally plausible.

Further evidence for contrasting genetic bases of morph development in different populations is provided by crosses of low plate Friant fish with high plate Navarro fish. Typical broods contain both high and partially plated fish (Table 6) and about a quarter of F_1 hybrids have intermediate plate morphology (Table 4). The normal development of high and low plate morphologies in the Friant population is altered in interlocality F_1 hybrids containing genetic material from the Navarro gene pool.

Table 6. *Plate morphologies in 61 F_1 progeny from 11 crosses between a parent from the Friant population and a parent from the Navarro population*

(H, L, and P refer to high, low, and partial plate morphs, respectively. P* indicates unusual morph, missing one or two plates before the caudal peduncle.)

	Parents		Progeny			Parents		Progeny	
F_1 brood number	♂ Friant	♀ Navarro	Number	Morph	F_1 brood number	♂ Navarro	♀ Friant	Number	Morph
50	L	H	2	H	58	H	L	3	H
			3	P				2	P*
			1	P*	59	H	H	4	H
51	L	H	4	H	60	H	H	5	H
52	L	H	6	H					
			2	P					
53	L	H	1	H					
			1	P					
			1	P*					
54	L	H	2	H					
			2	P					
55	L	H	6	H					
			1	P					
56	L	H	2	H					
			1	P					
			2	P*					
57	L	H	4	H					
			3	P					
			3	P*					

Hagen (1967) crossed low plate *leiurus* and high plate *trachurus* from Washington State. All offspring were partially plated. In that study, plate counts were $4{\cdot}4 \pm 1{\cdot}0$ and $33{\cdot}1 \pm 1{\cdot}0$ for *leiurus* and *trachurus* parents, respectively, and mean count for 207 F_1 hybrids was $19{\cdot}9 \pm 2{\cdot}7$. In the present study, plate counts for low plate *leiurus* (Friant) and high plate *trachurus* (Navarro) were $7{\cdot}50 \pm 0{\cdot}27$ and $31{\cdot}6 \pm 0{\cdot}22$, respectively, and F_1 hybrids were $28{\cdot}55 \pm 0{\cdot}44$. In Hagen's (1967) study, mean F_1 values were strictly intermediate between the parents, and in the present study they were very strongly skewed toward the *trachurus* phenotype. These data indicate that the nature of plate development in hybrids between *leiurus* and *trachurus* depends upon which particular populations are crossed, and hence upon particular interactions between genes contributed by the parental populations.

5. DISCUSSION

Origin of the Friant population

Miller & Hubbs (1969) argue that Friant fish comprise an introgressed population between *trachurus* and *leiurus*, and they cite three types of supportive evidence: (1) the reduction in plate size in the fully plated fish in comparison to typical *trachurus*, (2) the appearance of some fish with intermediate plate counts and (3) the overall similarity of high and low plate fish in other morphological features. Hagen & Gilbertson's (1972, 1973) demonstration of the genetic basis of morph development and morph distribution in permanent freshwater sticklebacks suggests that fish with intermediate plate counts do not necessarily result from hybridization between *leiurus* and *trachurus*, but may simply arise in *leiurus* populations through recombination of alleles at two genetic loci. However, the possibility that alleles for high plate morphology were originally introduced into *leiurus* through hybridization with *trachurus* is not eliminated.

Similarly, the present data cannot determine the ultimate origin of genes for high plates in the Friant collection. The relatively simple genetic basis of high plate development in Friant sticklebacks could easily have evolved within a *leiurus* population (one model is presented in Results and Analysis) without recourse to hybridization with *trachurus*. Alternatively, the high plate genes in the Friant population may originally have been introduced from *trachurus*.

In British Columbia, *leiurus* and *trachurus* may be distinguished by a number of characters besides plate morphology, including alleles at a general protein locus (Hagen, 1967). Howe (1974) argues that *trachurus* (as described by Hagen) is rare in northern California, and that morphological differences other than plate count cannot readily be used to separate fully plated forms from low plate forms. The *trachurus* (Navarro) and *leiurus* (Napa) populations sampled in the present study show only relatively minor allele frequency differences at a few loci, and high overall biochemical similarity. The discovery of diagnostic alleles for *trachurus* in northern California, and the demonstration that these alleles are present in the Friant gene pool, would strongly argue for hybrid origin of the Friant population. The present biochemical data are compatible with both hybrid and non-hybrid origins for Friant sticklebacks.

Genetics of plate morphology

Crosses between morphs within the Friant population yield high and low plate offspring, usually without intermediates. The Friant population has apparently built up a genetic basis of morph development unusual among known populations of *Gasterosteus aculeatus*. However, crosses between morphs from different drainage basins frequently do produce some partially plated fish (Table 4). Partially plated fish are most abundant in F_1 hybrids between the Friant and Navarro parents. One possible explanation for these results is that genes in the Friant population are 'coadapted' to favour production of the two distinctive morphs. Replacement of

50% of the genome by genetic material from a geographically isolated population (through production of F_1 progeny) frequently results in an alteration of this simple pattern of plate development.

A number of examples of genetic coadaptation revealed by hybridization studies are known among other organisms. For example, the melanic allele in a population of the moth *Biston betularia* from Birmingham, England, requires its normal, mutually evolved genetic background for full dominant expression. When this allele is placed into a hybrid background of a non-melanic population, a greater number of white scales appear on the moth's wings than in the Birmingham heterozygotes (Kettlewell, 1961; Ford, 1964).

A long series of studies by Gordon and associates on the platyfish, *Xiphophorus maculatus* (see Gordon & Gordon, 1957; Gordon & Smith, 1938; Gordon, 1947) provides evidence for genetic coadaptation in fishes. Development of patterns of melanophores within platyfish populations was shown to be controlled by different alleles of a particular genetic locus. Hybrids between members of different populations developed abnormal blotches of melanophores across the sides of the body. Apparently, the normal development of macromelanophores can be disrupted by unfavourable interactions of major genes with the novel genetic background in which they are placed in F_1 hybrids. Background genotypes are different in different river basins, and are coadapted to the major melanophore genes only of that population.

Another possible explanation for the results of the present study is that new alleles differing in dominance relationships have evolved within the Friant population, without alterations in background genotype. This hypothesis may be tested. Repeated backcrossing of high plate hybrids between Friant × Napa parents to the Napa population should result in increased proportions of intermediate progeny if the background genotype plays a significant role in morph development. If only major genes are involved, the proportion of intermediate progeny should not increase.

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REFERENCES

Avise, J. C. & Ayala, F. J. (1975). Genetic differentiation in speciose versus depauperate phylads: evidence from the California minnows. *Evolution* (in the Press).

Avise, J. C. & Selander, R. K. (1972). Evolutionary genetics of cave-dwelling fishes of the genus *Astyanax*. *Evolution* **26**, 1–19.

Avise, J. C. & Smith, M. H. (1974). Biochemical genetics of sunfish. II. Genic similarity between hybridizing species. *American Naturalist* **108**, 458–472.

Avise, J. C., Smith, J. J. & Ayala, F. J. (1975). Adaptive differentiation with little genic change between two native California minnows. *Evolution* **29**, 411–426.

AYALA, F. J., POWELL, J. R., TRACEY, M. L., MOURÃO, C. A. & PÉREZ-SALAS, S. (1972). Enzyme variability in the *Drosophila willistoni* group. IV. Genic variation in natural populations of *Drosophila willistoni*. *Genetics* **70**, 113–139.

FORD, E. B. (1964). *Ecological Genetics*. London: Chapman and Hall.

GORDON, H. & GORDON, M. (1957). Maintenance of polymorphism by potentially injurious genes in eight natural populations of the platyfish, *Xiphophorus maculatus*. *Journal of Genetics* **55**, 1–44.

GORDON, M. (1947). Genetics of ocular-tumor development in fishes (preliminary report). *Journal of the National Cancer Institute*, **7**, 87–92.

GORDON, M. & SMITH, G. M. (1938). The production of melanotic neoplastic disease in fishes by selective matings. IV. Genetics of geographical species hybrids. *American Journal of Cancer* **34**, 543–565.

HAGEN, D. W. (1967). Isolating mechanisms in threespine sticklebacks (*Gasterosteus*). *Journal of the Fisheries Research Board of Canada* **24**, 1637–1692.

HAGEN, D. W. (1973). Inheritance of numbers of lateral plates and gill rakers in *Gasterosteus aculeatus*. *Heredity* **30**, 303–312.

HAGEN, D. W. & GILBERTSON, L. G. (1972). Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest, America. *Evolution* **26**, 32–51.

HAGEN, D. W. & GILBERTSON, L. G. (1973). The genetics of plate morphs in freshwater threespine sticklebacks. *Heredity* **31**, 75–84.

HAGEN, D. W. & MCPHAIL, J. D. (1970). The species problem within *Gasterosteus aculeatus* on the Pacific coast of North America. *Journal of the Fisheries Research Board of Canada* **27**, 147–155.

HOWE, K. M. (1974). The systematics of the *Gasterosteus aculeatus* complex in northern California. Unpublished Masters Thesis, California State, Sonoma.

KETTLEWELL, H. B. D. (1961). The phenomenon of industrial melanism in the Lepidoptera. *Annual Review of Entomology* **6**, 245–262.

LEVENE, H. (1949). On a matching problem arising in genetics. *Annals of Mathematical Statistics* **20**, 91–94.

MILLER, R. R. & HUBBS, C. (1969). Systematics of *Gasterosteus aculeatus*, with particular reference to intergradation and introgression along the Pacific coast of North America: a commentary on a recent contribution. *Copeia* **1969**, 52–69.

MUNZING, J. (1963). The evolution of variation and distributional patterns in European populations of the three-spined stickleback, *Gasterosteus aculeatus*. *Evolution* **17**, 320–332.

MURAMOTO, J., IGARASHI, K., ITOH, M. & MAKINO, S. (1969). A study of the chromosomes and enzymatic patterns of sticklebacks of Japan. *Proceedings of the Japan Academy* **45**, 803–807.

NEI, M. (1972). Genetic distance between populations. *American Naturalist* **106**, 283–292.

SELANDER, R. K. & KAUFMAN, D. W. (1973). Genic variability and strategies of adaptation in animals. *Proceedings of the National Academy of Sciences* **70**, 1875–1877.