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An Intricate Genetic System that Controls Nine Pigment Cell Patterns in the Platyfish

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(Plate I; Text-figure 1)

THE genetic theory to account for the initiation and development of melanomas in platyfish-swordtail hybrids states that one principal gene, which controls the normal growth of large black pigment cells in the platyfish, interacts with a number of growth-modifying genes of the swordtail; as a consequence, the melanocytes, which normally would develop into macromelanophores, do not mature but retain their generalized juvenile characteristics and, as neotenous cells, the melanocytes accumulate, proliferate and eventually produce the melanoma in the hybrid organism (Gordon, in press).

One of the practical consequences of this theory is that it explains how it is possible for two normal parents (each representing a stock in which cancer has never been known) to have offspring in which cancer will develop in response to purely hereditary factors. The fortuitous combination of some primary gene for a specific cell and its growth-modifying genes may account for some puzzling manifestations of normal as well as atypical cell growth.

In view of the important role of gene modifiers (genes which have no apparent visible effect when present alone but which may have a profound effect when they are associated with an appropriate primary gene), it is valuable to have additional evidence of their specific genetic activities. The genetic reaction which will be described produces no atypical growth, but it establishes more firmly than before that some genes are capable of modifying the usual pattern of pigment cell growth. This paper is concerned with the transformation, through gene action, of one pigmentary pattern known as the *twin-spot* into another called the *Guatemala-crescent.*

In an examination of 5,019 sexually mature platyfish, *Xiphophorus maculatus,* that represented four natural populations from Mexico and Guatemala, Gordon (1947) detected only two specimens, both collected in 1931 from Lago de Petén, Guatemala, that had a unique color pattern which he called the *Guatemala-crescent.* He gave the rare pattern the genetic symbol of *Cg* to distinguish it from each of seven other common, hereditary patterns which some platyfish have at, or near, the caudal fin. He pointed out that the *Guatemala-crescent* closely resembled the *single crescent, C,* pattern but that *Cg* was "broader overall and particularly so at the ends of the crescent."

Additional collections of the platyfish from four other rivers in southern Mexico and British Honduras have now swelled the total number of adult platyfish examined to more than 9,000, and yet no other fish with the *Guatemala-crescent* pattern was found under natural conditions (Gordon & Gordon, in press). Several years ago, however, the author did find some live platyfish with the *Cg* pattern that were being maintained by a New York aquarist.

It is most unlikely that the aquarium-bred platyfish with the *Guatemala-crescent* pattern are traceable to the natural population of platyfish from the Lago de Petén, a location which is, and has been, inaccessible to the commercial aquarium fish collector. Gordon (1954) suggested that the earliest shipment of platyfish from "Central America" to Europe, in 1907, consisted of a few specimens that were most

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probably collected in the vicinity of Belize in British Honduras.

In a preliminary statement on the problem, Gordon (1951) had suggested that the *Guatemala-crescent* pattern may be referred to the complementary action of two dominant genes, one a primary allele, *T*, for *twin-spot*, which produces two discrete groups of small pigment cells near the tail fin, and a complementary gene, *Cg; Cg* produces no visible expression by itself, but in combination with *T* it acts to bring an additional number of small pigment cells to the area between the two discrete groups of micromelanophores. The result is that a crescent-like bridge of pigment cells is formed that unites the two outer dark clusters; the whole effect is then categorized as the *Guatemala-crescent*, Plate I, Fig. 1.

The Genetic Results

The general method of inheritance of the *Guatemala-crescent* pattern was demonstrated in the offspring of the mating of a purchased female platyfish having a *Guatemala-crescent* to a double recessive. From the results in the F_1, the P_1 were of the genetic constitution set forth in Table 1.

In another and apparently similar mating, slightly different results were obtained which indicated that the parents in the second mating were of the following genetic constitution:

Female		Male
T Cg/+ +	×	+ +/+ +

Phenotypes in F_1	Observed	Expected
1. *Guatemala-crescent, T Cg*	6	5.5
2. *Twin-spot, T*	6	5.5
3. No tail patterns, +	10	11.0

Autosomal or Sex-linked

The determination of whether the modifier *Cg* is sex-linked or autosomal was accomplished, in part, from a mating involving the dominant, sex-linked gene, *Sp*, for generalized black (macromelanophore) spotting on the body. A black-spotted female, (W) + (Y) *Sp*, was mated with a male that was recessive for the sex-linked gene, (Y) + (Y) +, but dominant for the *twin-spot* gene, *T*. The results in the F_1 were as shown in Table 2.

The criss-cross inheritance of the sex-linked *Sp* gene from the mother to her sons is characteristic of the domesticated strain of the platyfish in which the female is WY, the male YY, (Gordon, 1931); the *Sp* gene was presumably carried on the Y chromosome of the P_1 female. The *Cg* gene must have been carried by the *Sp* female parent because the male parent had the *twin-spot, T*, pattern only. The *Cg* gene, since it appeared in both sexes among the F_1, could not have been sex-linked. These results in addition to those obtained from the first mating, in which the female parent carried *Cg*, indicate that *Cg* is autosomal in its inheritance.

Test for Linkage to the Autosomal Gene *St* (+)

The inheritance of *Cg* was studied in association with a previously determined dominant, autosomal gene for *stippling, St* (Gordon, 1937). The gray color that the *St* gene produces, by a show of many micromelanophores, contrasts sharply with *golden*, which is its recessive effect. The P_1 were as shown in Table 3.

The results favor the conclusion that *Cg* is inherited independently of the *stipple* gene (*St*, +). Although the data are few, indeed, they indicate that if *Cg* were linked completely to *St* in the *Stippled* parent (*Cg St*) no *Stippled, Twin-spot* (*T* + *St*) F_1 should have appeared, yet nine did. If *Cg* were completely linked to the recessive + of the *Stippled* gene in the *Stippled* parent, *Cg* +, then no *Golden, Twin-spots* (*T* + +) F_1 should have appeared, yet four did.

While *Cg* and *T* appear in the expected ratios, the stippled fish outnumber the golden disproportionately. This has been observed and discussed by the author in previous papers but it is not pertinent to the study of the *T Cg* reaction.

Tests with Alleles, *Cc, C* and *O*

In the next series of experiments, the possible effects of *Cg* were tested on some of the other alleles of *T*, such as *Cc* for *complete-crescent, C* for *single crescent, O* for *one-spot* and *Co* for *comet* (Gordon, 1947).

1. Test with *Cc*, Complete-crescent

In order to determine whether *Cg* had any visible effect on the *complete-crescent* pattern, the genes *Cc* and *Cg* were combined in the following manner:

Guatemala-crescent		*Complete-crescent*
T Cg/+ +	×	*Cc* +/+ +

F_1 Phenotypes	Observed	Expected
1. *Complete-crescent, Guatemala-crescent, TCc Cg*	14	14.5
2. *Complete-crescent, Twin-spot, TCc*	7	14.5
3. *Complete-crescent, Cc*	35	29.0
4. *Guatemala-crescent, T Cg*	11	14.5
5. *Twin-spot, T*	16	14.5
6. No tail patterns, +	35	29.0
Totals	118	116.0

In counting the various F_1 phenotypes, the *complete-crescent, Cc,* pattern was identifiable in combination with the overlapping *T* and *T Cg* patterns, owing to the unobscured wedge-shaped mark of *Cc,* which is outside the range of *T* and *T Cg.*

In a follow-up experiment, the complete segregation of *T* from *Cc,* in the presence of *Cg,* was demonstrated by mating a platyfish with both a *complete-crescent* and a *Guatemala-crescent* back to one without a tail pattern as follows:

Complete-crescent, Guatemala-crescent *T Cg/Cc +* × No Pattern *+ Cg/+ Cg*

F_1 Phenotypes	Observed	Expected
Guatemala-crescent, T Cg	12	11
Complete-crescent, Cc	10	11

2. Test with Single Crescent

In order to determine whether *Cg* has any effect on the *single-crescent* gene, *C,* a platyfish with a *Guatemala-crescent* was mated to one with the *C* pattern. Results are seen in Table 4.

The expected frequencies given above are based upon two assumptions. First, that the genotypes of the parents were one or the other of the following:

Guatemala-crescent	×	*Single-crescent*
1. *T Cg/+ Cg*		*C +/+ +*
2. *T Cg/+ +*		*C Cg/+ Cg*

The second assumption is that when *C* is present in combination with *T Cg* the *single-crescent* pattern is completely obscured; *C* is not changed, and, certainly, *C* is not extended.

3. Test with One-spot

The ineffectiveness of the modifier *Cg* in changing the phenotypic expression of the *O*

Table 1.

Female *T Cg/T +* × Male *+ +/+ +*

Phenotypes in F_1	Female	Male	Observed	Expected
1. *Guatemala-crescent, T Cg*	11	7	18	21.5
2. *Twin-spot, T*	16	9	25	21.5

Table 2.

	Females		Males	
Phenotypes in F_1	Observed	Expected	Observed	Expected
1. *Spotted, Guatemala-crescent, Sp T Cg*	0	0	7	7
2. *Spotted, Twin-spot, Sp T*	0	0	7	7
3. *Guatemala-crescent, T Cg*	6	7	0	0
4. *Twin-spot, T*	8	7	0	0

Table 3.

Golden, Guatemala-crescent T Cg +/+ + + × *Stippled + Cg St/+ + +*

			Expected if linked	
F_1 Phenotypes	Observed	No linkage	*Cg St*	*Cg +*
1. *Stippled, Guatemala-crescent, T Cg St*	23	18	24	12
2. *Stippled, Twin-spot, T + St*	9	6	0	12
3. *Stippled, + St*	29	24	24	24
4. *Golden, Guatemala-crescent, T Cg +*	14	18	12	24
5. *Golden, Twin-spot, T + +*	4	6	12	0
6. *Golden, + +*	16	24	12	24
	95	96	96	96

Table 4.

Phenotypes in F_1	Presumed Genotypes	Observed	Expected
1. *Guatemala-crescent*	*T Cg/C +* or *T Cg/+ +*	10	12.5
2. *Single-crescent*	*+ Cg/C +*	7	6.25
3. No tail pattern	*+ Cg/+ +*	8	6.25

allele for *one-spot* was clearly demonstrated in three matings.

1. *O +/Cc +* × *T Cg/+ +*

F_1 Phenotypes	Observed	Expected
1. *One-spot, Guatemala-crescent, OT Cg*	6	7.5
2. *One-spot, twin-spot, OT*	9	7.5
3. *One-spot only, O*	19	15.0
4. *Crescent-complete, Guatemala-crescent, CcT Cg*	6	7.5
5. *Crescent-complete, twin-spot, CcT*	5	7.5
6. *Crescent-complete, Cc*	15	15.0

The 19 *one-spots* were not modified in appearance.

2. *O +/T +* × *Cc +/T Cg*

F_1 Phenotypes	Observed	Expected
1. *OT Cg*	7	6
2. *OT*	2	6
3. *OCc*	10	12
4. *CcT Cg*	8	6
5. *CcT*	8	6
6. *TT Cg*	6	6
7. *TT*	7	6

The *one-spot, O,* pattern was not modified in any of the three phenotypes in which it appeared.

3. The third mating involves, in addition to *O, T* and *Cg,* the independent autosomal gene *St* for the stippling effect of many micromelanophores which cover the entire body; the recessive (*stst*) effect is *golden* since most micromelanophores are lacking. One parent had *stipple, St, one-spot, O,* and *twin-spot, T;* the other was *golden* without tail markings, + + +. From the results of the mating it was demonstrated that the *golden* parent had been homozygous dominant for the *Cg* modifier.

O + St/T + + × *+ Cg +/+ Cg +*

F_1 Phenotypes	Observed	Expected
1. *Stippled, One-spot, O Cg St*	21	17.5
2. *Golden, One-spot, O Cg*	16	17.5
3. *Stippled, Guatemala-crescent, T Cg St*	16	17.5
4. *Golden, Guatemala-crescent, T Cg*	17	17.5

Separation of *Cg* from the Modifier *E*

The testing of the effect of *Cg* on the *comet, Co,* allele was complicated because the expression of *Co* is radically extended and changed by its own specific modifier *E.* Gordon (1946) showed that the combination *Co E* produces the *wagtail* pattern, in which all the fins and extremities are blackened by small black pigment cells. The question that needed clarification was whether the modifier *E* was synonymous with *Cg,* or whether there were, as originally suspected, two independent genetic modifiers, *E* that acts on *Co* and *Cg* that acts on *T.*

In two matings, a platyfish with *Co* and *T* was mated to a melanin-free, albino swordtail, *X. helleri,* because it was previously established by Gordon (1946) that many swordtails carry the modifier *E.* The following results were obtained in the F_1:

Phenotypes F_1	
1. *Wagtails, Co E*	26
2. *Guatemala-crescents, T Cg*	18

From the above results it was not clear whether there were one or two gene modifiers.

In some measure the distinctness of *Cg* was demonstrated by the results of mating a *comet* platyfish with one having a *twin-spot* pattern. The presumed genotypes of the P_1 were:

Comet *Co +/+ +* × *Twin-spot* *T E/+ +*

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Wagtail*	*Co E/T +*	3	3.50
Wagtail	*Co E/+ +*		
2. *Comet, twin*	*Co +/T +*	2	1.75
3. *Comet*	*Co +/+ +*	2	1.75
4. *Twin-spot*	*T E/+ +*	3	3.50
Twin-spot	*T +/+ +*		
5. No pattern	*+ E/+ +*	4	3.50
No pattern	*+ +/+ +*		
		14	14.0

The significant fact is that 3 of the 14 offspring had the *wagtail* pattern. This meant that the *E* modifier was carried by the *T* parent but that it had had no effect on the expression of *T.* Phenotypically, *Co E T* and *Co E* look alike and must be classified as *wagtails.*

In another mating a reverse effect was obtained, namely, the *comet* parent was harboring the *Cg* modifier. This was revealed when a *comet* was mated with a *twin-spot* platy as is indicated in Table 5.

While the matings involving *Co* and *T* yielded relatively few individuals, the very existence and recognition of some of the combinations support the conclusion that there are two specific modifiers, *E* and *Cg,* each of which reacts with its own specific primary gene, *Co* and *T,* respectively. For example, the combination of *Co Cg/T +* appeared four times in the last mating. If *Cg* modified *Co* as well as *T,* these four would have appeared as *wagtails,* but actually the patterns in the four were clearly recognized as being *comet* and *Guatemala-crescent;* there were no *wagtails* at all, Plate I, Fig. 2.

In order to get more evidence of this sort, another experiment was performed with similar phenotypes, that is, a *comet* platyfish was mated with a *twin-spot* as shown in Table 6.

In the F_1, 18 *comet, Guatemala-crescent* platyfish were observed, showing that the *Co* is not modified by the *Cg* gene. When one of the *Co Cg/T +* (*Comet, Guatemala-crescent*) F_1 platyfish was backcrossed to a platyfish that lacked a tail pattern, the results indicated that the parents must have had the genotypes set forth in Table 7.

No *twin-spot* patterns appeared among the F_1. From these results, it is clear that *Cg* has no visible effect on *Co* but rather that its action is restricted to the modification of *T*.

Presence of *Cg* in a Related Species

In a previous study of the modifier *E*, Gordon (1946) showed that this gene is found frequently in the swordtail, a close relative of the platyfish. In order to determine whether the swordtail, *Xiphophorus helleri*, carries the *Cg* gene, a *twin-spot* platyfish from a commercial stock was mated to a swordtail that belonged to a stock originally obtained from the Río Papaloapan in Mexico.

Twin-spot Platyfish		Plain Swordtail
T+/+ +	×	*+ Cg/+ Cg*

F_1 Phenotypes	
1. *Guatemala-crescent, T Cg*	35
2. No tail patterns, *Cg*	32

Since about 50% of the platyfish-swordtail hybrids showed the *Guatemala-crescent* and half showed no peduncular marking, the swordtail must have been homozygous for the modifier *Cg*. This indicates that some swordtails taken from natural habitats harbor a gene which apparently has no visible effect upon the members of its own species but which is capable of interacting with a specific gene of a different species, Plate I, Figs. 3 & 4.

Discussion

The data presented in this paper support the

Table 5.

Comet Co Cg/+ + × *Twin-spot T +/+ +*

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Comet, Guatemala-crescent*	*Co Cg/T +*	4	1.5
2. *Comet, twin-spot*	*Co +/T +*	0	1.5
3. *Comet*	*Co Cg/+ +*	3	3.0
Comet	*Co +/+ +*		
4. *Guatemala-crescent*	*T Cg/+ +*	1	1.5
5. *Twin-spot*	*T +/+ +*	1	1.5
6. No pattern	*+ Cg/+ +*	3	3.0
No pattern	*+ +/+ +*		
		12	12.0

Table 6.

Comet *Co Cg/+ +* × *Twin-spot* *T +/T +*

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Comet, Guatemala-crescent*	*Co Cg/T +*	18	23
2. *Comet, twin-spot*	*Co +/T +*	23	23
3. *Guatemala-crescent*	*+ Cg/T +*	32	23
4. *Twin-spot*	*+ +/T +*	19	23
		92	92

Table 7.

Comet, Guatemala-crescent *Co Cg/T +* × No Pattern *+ Cg/+ Cg*

Phenotypes in F_1	Genotypes	Observed	Expected
1. *Comet* only	*Co Cg/+ Cg; Co Cg/+ +*	14	15
2. *Guatemala-crescent*	*T Cg/+ Cg; T Cg/+ +*	16	15
		30	30

conclusion that in platyfish the *Cg* gene is a specific autosomal modifier of the *twin-spot* gene, *T; Cg* is not linked to *E*, which is a specific modifier of *comet, Co*. Nevertheless *T* and *Co* are alleles; both belong to a common series of seven dominant multiple alleles (Gordon, 1947). These facts reveal the existence of an intricate and interlocking genetic system for the production of nine distinctive patterns, all of which may appear only at the posterior region of the platyfish, and all of which are composed of a specific type of pigment cell, the micromelanophore. This interlocking and precise genetic system depends not only upon seven multiple alleles (plus one universal recessive), but also upon two independently inherited specific gene modifiers. In graphic form, the genetic system is represented by Text-fig. 1.

1. Frequency of the *Cg* Gene in Natural Populations

The frequency of the *Cg* gene modifier in the upper Río Usumacinta and the Lago de Petén area may be estimated on the basis of the frequency of the *T* allele; because only when the *T* allele is present can the presence of the *Cg* gene be detected. Gordon (1947) found that of 552 adult platyfish, which represented the entire Guatemala collection made in 1935, 31 specimens had the *T* allele either alone (13) or in combination with other members of its allelic series (18). In 2 of the 31, the *T* allele was modified by the *Cg* gene to produce the *Guatemala-crescent* pattern. The presence of the *Cg* gene on the basis of the 31 *twin-spot* platyfish is therefore 6.4%. In contrast, the presence of the *T* allele on the basis of 31 platyfish out of 552 is 5.6%. Thus, it would appear that the frequency of the *Cg* gene in the Río Usumacinta population as a whole is slightly greater than the frequency of the *T* allele it modifies. Actually, however, the frequency of the *Cg* gene might better be calculated from the limited number of platyfish from the Lago de Petén basin because the modifier *Cg* has been detected only in this area. In the Lago de Petén, which includes Petenxil and Ponteil but excludes Laguna de Zotz (Stations 12 to 20, Gordon, 1947), 79 platyfish were collected of which 14 had the *T* allele, the gene frequency of *T* in the platyfish from the Lago de Petén basin is 0.093, and of *Cg* 0.074; both calculated by the usual formula $f = 1 - \sqrt{1-p}$.

The distribution of the *Cg* gene is restricted not only in the platyfish of Guatemala, but it is probably non-existent among all the other known natural populations of the platyfish. For example, Gordon & Gordon (in press) evaluated the frequencies of the *twin-spot* and six other tail patterns among the platyfish of eight large river populations. To attain maximum accuracy, they based their evaluation on the frequencies of *single* tail patterns only; double patterns were deliberately excluded because many of them were difficult to identify with complete assurance. The frequencies of the single *twin-spot* patterns in each of eight natural populations of the platyfish were as follows:

	Number of Platyfish	Single *Twin-spots*	%
1. Jamapa	860	54	6.3
2. Papaloapan	3,492	138	4.0
3. Coatzacoalcos	1,334	252	18.9
4. Tonala	178	5	2.3
5. Grijalva	651	50	7.7
6. Usumacinta	552	13	2.4
7. Hondo	327	10	3.1
8. Belize	1,526	78	5.1

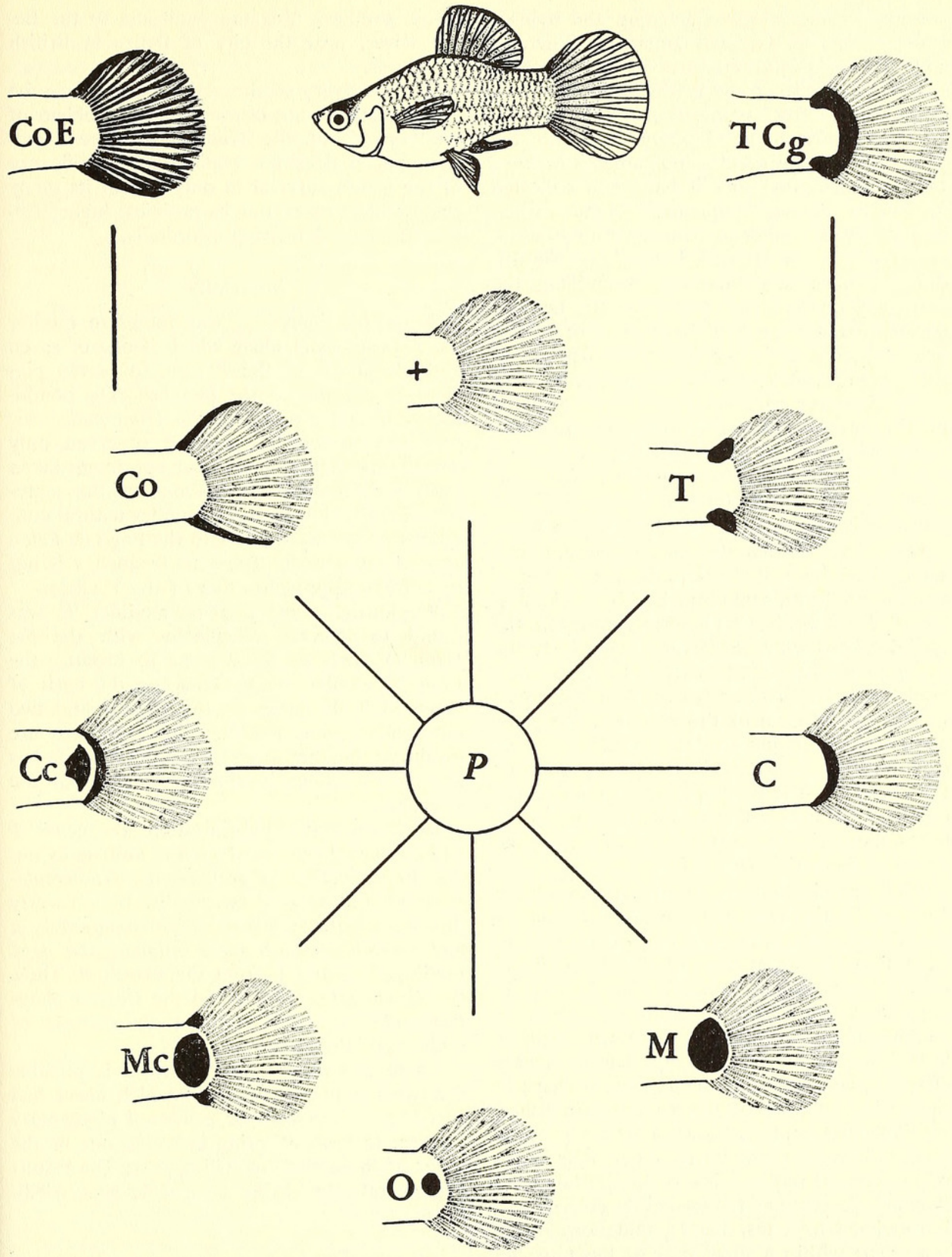
On the basis of this sample of Gordon & Gordon's (in press) data, it is evident that the *Cg* gene is either lacking in the eight river populations (except in Lago de Petén) or it is extremely rare. While the platyfish of the Lago de Petén have been assigned to the Río Usumacinta population, this analysis points up the fact that a local population within an assigned river system may differ genetically from its other local populations.

2. Introgression of the *Cg* Gene from One Species to Another

With regard to the mechanism of inheritance of the *Cg* gene in the platyfish, it is exactly similar to that of an equivalent color pattern of the domesticated swordtail which was previously analyzed by Kerrigan (1934) and confirmed by Gordon (1937). The genetic symbols these authors used varied, however:

	Xiphophorus maculatus	*Xiphophorus helleri*	
Phenotype	Gordon (in press)	Kerrigan (1934)	Gordon (1937)
Guatemala-crescent	*T Cg*	*C P*	*C P*
Twin-spot	*T* +	*C p*	*T P*
No pattern	+ *Cg*	*c P*	*C p*
No pattern	+ +	*c p*	*T p*

It seems strange that the inheritance of the *twin-spot* and *Guatemala-crescent* patterns should have been worked out first in the swordtail, because *X. helleri* in its many native habitats does not have any of these patterns. Aquarium-reared swordtails, however, obtained the *T* gene from the platyfish about 1911 by experimental introgressive hybridization made



TEXT-FIG. 1. Nine Pigment Cell Patterns. The intricate genetic system that controls nine specific pigment cell patterns in the platyfish, *Xiphophorus maculatus*, is built around the central gene *P* for seven melanic patterns located in the anterior part of the caudal fin and the posterior part of the caudal peduncle. The gene *P* has a series of seven dominant, autosomal, multiple alleles: *PT*, *PC*, *PM*, *PO*, *PMc*, *PCc*, *PCo* plus the multiple recessive *P+*. For convenience the symbol *P* is deleted from the formulae for the patterns which are written *T* for *PT*, etc.

Superimposed upon the *P* series of alleles are two independent, autosomal gene modifiers: *Cg* that interacts specifically with *T*, and *E* that interacts exclusively with *Co*. Neither *Cg* nor *E* have any visible expression by themselves, nor any visible effect upon the *P* multiple alleles other than *T* and *Co*.

T = *Twin-spot* *C* = *Crescent* *O* = *One-spot* *Co E* = *Wagtail complex* *Mc* = *Moon-complete*
Co = *Comet* *M* = *Moon* *T Cg* = *Guatemala-crescent* *Cc* = *Complete-crescent* + = No tail pattern

possible by the selective breeding and hybridization trials of German aquarists. When in 1911 the *twin-spotted* swordtails were sent by German aquarists to the British Museum (Natural History) for identification, Regan (1911) at first regarded the *Xiphophorus* with the *twin-spot* as a new species and named it *rachovii* on the assumption that it had been collected at Puerto Barrios, Guatemala. Later, when Regan (1913) obtained swordtails unquestionably from Puerto Barrios, he saw that the fish did not have any markings resembling the *twin-spot* or *crescent*. Consequently he suspected that the *"rachovii"* type was of hybrid origin, produced in the aquarium. He therefore recommended that the name *Xiphophorus rachovii* be regarded as invalid. As indicated in the present paper, a *twin-spot* platyfish mated with a swordtail produced a hybrid that had the *Guatemala-crescent* pattern. This confirms Regan's suggestion that *X. rachovii* was a fish of hybrid origin, Plate I, Figs. 5 & 6.

Once the *Guatemala-crescent* pattern was synthesized by fish fanciers in the platyfish-swordtail hybrids, some breeders, by backcrossing *T Cg* hybrids to platyfish, recreated the platyfish body type and distinguished it by the *T Cg* color pattern. Thus, while the aquarium-bred *"rachovii"* swordtails owe their color pattern to the *T* gene of the platyfish, the color pattern in the aquarium-bred *Guatemala-crescent* platyfish is traceable to the *Cg* gene of the swordtail. The development of *Guatemala-crescent* patterns in two related species of fishes illustrates an example of what may be called *reciprocal introgression.*

While precise data on the frequency of the *Cg* gene in the swordtail are not available, it would appear from the experiences of fish fanciers that the frequency of *Cg* is probably much higher in wild *X. helleri* than in wild *X. maculatus*. Just what function *Cg* serves in contemporary swordtails is unknown since, as is the case in the platyfish, *Cg* has no visible effect in the absence of the *T* gene. Perhaps in the early evolution of the xiphophorin fishes, *Cg* imparted some advantage to their members and was by this virtue retained in some of the present day species. It is odd, however, that the *Cg* gene, as far as can be determined, is restricted to a few local populations of *X. maculatus* within a small part of the Lago de Petén basin of Guatemala. This represents a tiny area considering the wide range of *X. maculatus,* which extends southeast from the Río Jamapa, near the city of Veracruz, Mexico, across southern Yucatan peninsula to the Belize River, near the city of Belize in British Honduras.

The discovery of the action of the *Cg* gene in the platyfish has cleared up the problem of the "rarity" of the *Guatemala-crescent* pattern, but it does not explain the significance of the gene's survival in only one of its many geographical races, nor its probable higher frequencies among races of swordtails.

Summary

A specific gene, *Cg,* was found to modify the *T* (*twin-spot*) allele which is one of seven multiple alleles of the *P* gene for seven pigmentary patterns in the platyfish. The combination of *T Cg* produces the *Guatemala-crescent* pattern which has been observed only twice in more than 9,000 adult specimens taken from eight natural populations of the platyfish. The distribution of *Cg,* under natural conditions, is restricted solely to the Lago de Petén area of Guatemala. There its frequency is not rare, for it approaches that of the *T* allele.

Previously, another gene modifier *E* was found to interact specifically with the *Co* (*comet*) allele of the *P* gene to produce the *wagtail* complex, *Co E*. Thus, on the basis of seven multiple alleles of the *P* gene and two independent gene modifiers, nine patterns are produced. Neither modifier *Cg* nor *E* alone has any visible effect in the platyfish or in the swordtail.

By introgressive hybridization, the genes *T* and *Co* have been transferred to swordtails under domestication to produce the *Guatemala-crescent* and *wagtail* swordtails. In a reverse direction aquarium-bred *Guatemala-crescent* and *wagtail* platyfish have obtained the gene modifiers *Cg* and *E* from the swordtail. Thus, the *Guatemala-crescent* and the *wagtail* platyfish and swordtails represent an example of reciprocal introgression.

These experiments show how it is possible for two parents, from stocks which never had a *Guatemala-crescent* or a *wagtail* pigmentary pattern, to have offspring in which one or the other of these patterns will appear. The results demonstrate the reality of specific gene modifiers.

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. A platyfish, *Xiphophorus maculatus*, with a *twin-spot* (*T*) pattern is at the left. The one to the right has a *Guatemala-crescent* (*T Cg*) pattern; note that the *T Cg* complex also involves dot-like markings at the mandibular junction.

FIG. 2. The male platyfish, *Xiphophorus maculatus*, (to the left) has no tail pattern. The female (to the right) has *comet* (*Co*) and *Guatemala-crescent* (*T Cg*) patterns; note the small black dot at the mandibular junction in the female.

FIG. 3. The male platyfish, *Xiphophorus maculatus*, shown in the upper left, having a *comet*, *Co*, and *twin-spot*, *T*, pattern, was mated to a female albino swordtail, *X. helleri*, shown in the lower right. Their F_1 hybrids are shown in Fig. 4.

FIG. 4. The first-generation platyfish-swordtail hybrids; the one on the left shows the wagtail complex, *Co E*; the one on the right shows the *Guatemala-crescent* pattern, *T Cg*.

FIGS. 5 & 6. The so-called *"rachovii"* swordtails are actually hybrids reconstructed to look like swordtails. These "swordtails" have been produced by fish culturists by a series of backcrosses of the hybrids to swordtails; that is, by introgressive hybridization. The female swordtail, Fig. 5, shows just the effects of the *T* gene. The *Guatemala-crescent* pattern which characterizes the male, Fig. 6, is traceable to the *T* gene of the platyfish and the *Cg* gene of the swordtail.

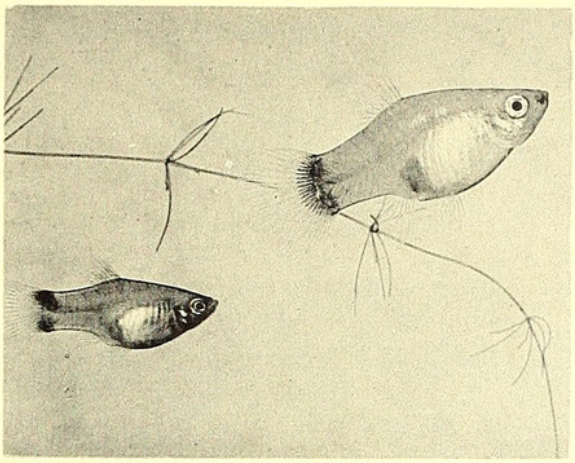

FIG. 1

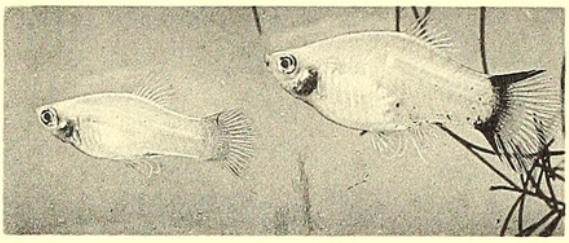

FIG. 2

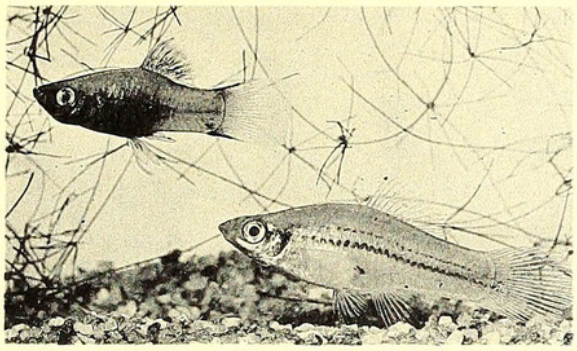

FIG. 3

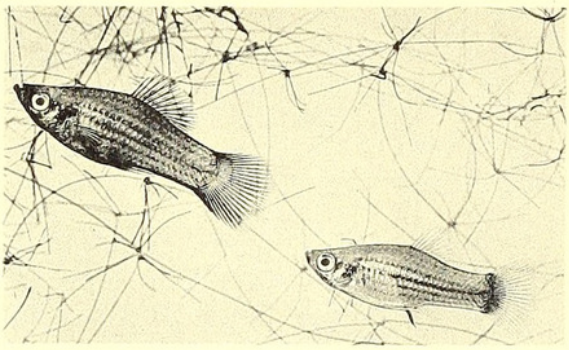

FIG. 4

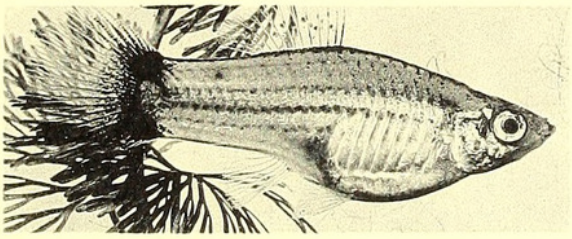

FIG. 5

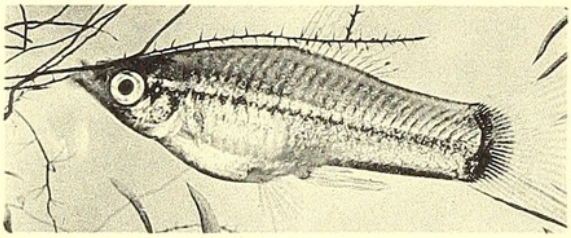

FIG. 6

AN INTRICATE GENETIC SYSTEM THAT CONTROLS NINE PIGMENT CELL PATTERNS IN THE PLATYFISH