GENETICS OF PLATYPOECILUS MACULATUS. IV. THE SEX DETERMINING MECHANISM IN TWO WILD POPULATIONS OF THE MEXICAN PLATYFISH[1]

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THE genetic mechanism for sex determination in *Platypoecilus maculatus* where ZZ = male and WZ = female was established by BELLAMY in 1922 and confirmed independently by GORDON in 1927. This was more firmly established in 1929 when FRASER and GORDON indicated that crossing over between W and Z occurred. One result of such crossing over was the development of a genetic strain which was characterized by "mother-to-daughter" inheritance; this was effected by W-borne dominant genes *R* and *Sp*, expressed in red body coloring and black spotting. This type of sex determination for the platyfish was confirmed repeatedly by the above workers (BELLAMY 1928; GORDON 1937) and by others, notably KOSSWIG (1938) and BREIDER (1937, 1942).

Recently GORDON (1944) announced that "wild" stocks of *Platypoecilus maculatus* from the Rio Jamapa, Veracruz, Mexico had a type of genetic mechanism for sex determination in which XY = male and XX = female—just opposite to the established type for the species. He also pointed out that the "domesticated" types of the platyfish retained their special type of sex determination in which ZZ = male and WZ = female. When a "wild" female (XX) was crossed with a "domesticated" male (ZZ) all the offspring were males (ZX).

In view of these unusual results a revaluation is necessary of sex determining mechanisms suggested for fishes of the group, the Xiphophorini. In line with the need of clarifying the situation, and substantiating the fact of dual genetic systems in the same species, data will be presented on sex linkage in two "wild" populations, one from the Rio Jamapa and the other from the Rio Papaloapan, Mexico.

MATERIAL

In 1932 one hundred and one *P. maculatus* (platyfish) were caught in a pool of an arroyo leading to the Rio Tonto, a tributary of the Rio Papaloapan in Oaxaca (GORDON, 1940). Within the same pool a smaller number of *Xiphophorus hellerii* (swordtails) were taken. No hybrids between the swordtail and the platyfish have yet been discovered in nature. The fishes were shipped to the genetical laboratory then at CORNELL UNIVERSITY in Ithaca, New York. The following types of platyfish were represented: the spotted-belly (or black-

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bottom) controlled by the sex-linked gene *Sb*, the spot-sided, controlled by the sex-linked gene *Sp*, the spotted-dorsal (or black-topper) controlled by another sex-linked gene *Sd*, and the unmarked recessive +. The genetic analysis of these color varieties is given in Table 1.

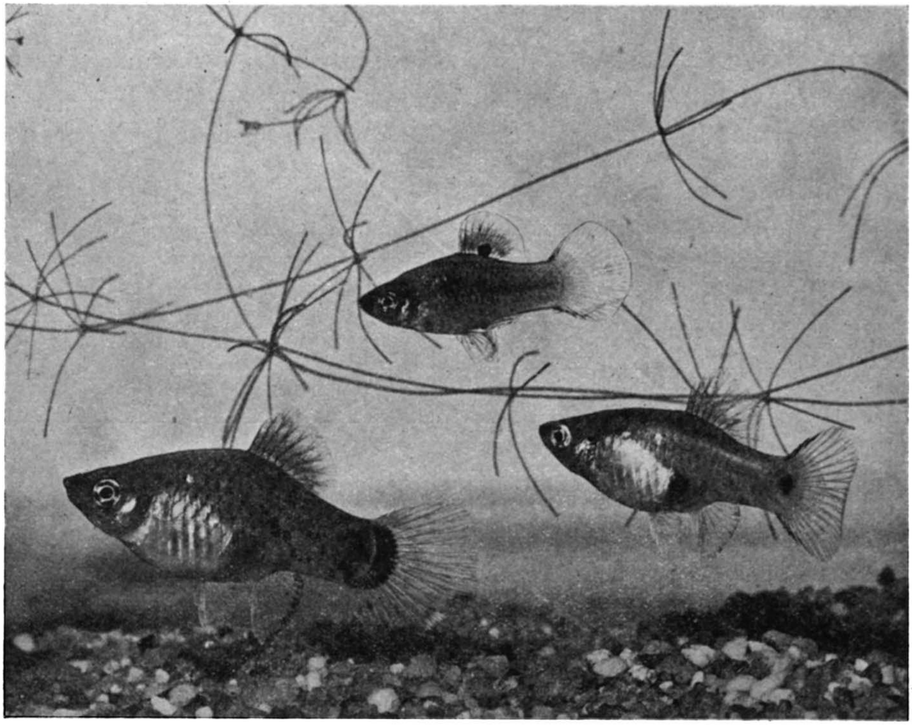

FIGURE 1.—Wild *Platypoecilus maculatus*, the Mexican Platyfish, from the Rio Jamapa, Veracruz, Mexico. This composite photograph shows, on the upper center, a male platyfish having the following sex-linked characters: dorsal-spotted (*Sd*) and stripe-sided (*Sr*); the latter is distinguished by a faint row of macromelanophores along the sides. In the lower left, a female platyfish shows the character spot-sided (*Sp*) prominently and the character stripe-sided (*Sr*) faintly. The female on the lower right is the multiple recessive (+). The other patterns they show, all on, or just in front of, the tail fin are autosomal. The male has the comet (P^{Co}); the left female has the completed crescent (P^{Cc}) and the right female has the comet (P^{Co}) and the one-spot (P^{O}). The sex-linked characters are discussed in this paper; the autosomal, multiple allelic series are discussed in another paper, GORDON (1947). The fish are life size. Photographs by S. C. DUNTON, Staff Photographer, NEW YORK ZOOLOGICAL SOCIETY.

In 1939 on another expedition to Mexico, several thousand platyfish and swordtails were found living side by side in branches of the Rio Papaloapan; no hybrids were found among them (GORDON 1940). At Plaza de Agua, El Tejar, a few miles from Veracruz, a large colony of *P. maculatus* (but no swordtails) was caught and shipped to our laboratory at the New York Aquarium. These represented the platyfish population of the Rio Jamapa system and contained the following sex-linked genes: *Sp*, *Sd*, and *Sr* (striped-sided). All the sex-linked genes mentioned produce their pattern effects by differential distribution of *macromelanophores*. An analysis of the patterns representative of the Rio Jamapa population is given in Table 2. In addition to the color types mentioned, the platyfish of the two river system have a series of patterns controlled by autosomal genes; an analysis of their genetic behavior is soon to be published (GORDON 1947).

GENETIC ANALYSIS OF THE RIO PAPALOAPAN POPULATION

Only a limited number of tests were made of the Rio Papaloapan population of the platyfish. It was for this reason that results from these tests were not

TABLE 1

Platypoecilus maculatus population from the Rio Papaloapan system.

EXP. NO.	PARENTS: CULTURE ♀	CULTURE ♂	TYPE ♀	TYPE ♂	FIRST GENERATION: + ♀	+ ♂	*Sb* ♀	*Sb* ♂	*Sp* ♀	*Sp* ♂	*Sd* ♀	*Sd* ♂	TOTAL	χ^2
1	12	21	+/+	+/*Sb*	20	0	0	15					35	0.706
2	17	21	+/+	+/*Sb*	19	0	0	17					36	0.111
3	2	?	+/*Sp*	(+/*Sb*)	6	0	0	13*	10	0			29	2.310
4	9	?	+/*Sp*	(+/+)	5	4			9	5			23	2.565
5	18	?	+/*Sd*	(+/+)	9	7					5	3	24	3.332

* The 13 fish listed as *Sb* consisted of *Sb* and *Sb*/*Sp* but at the time they were not distinguishable.

given the consideration they deserved at the time they were obtained. In the light of the data obtained later with wild fish from the Rio Jamapa, listed in Table 2, the genetic behavior demonstrated may be explained on the basis of the sex determining mechanism where XX = female, XY = male, and where the Y may carry dominant genes.

In experiment number 1 where the female parent was normally colored, (X)+/(X)+, and the male had the black-bottom pattern, the male presumably carried the gene on its Y chromosome: (X)+/(Y)*Sb* because the dominant *Sb* was transmitted from father to son. This patroclinus mode of inheritance was repeated in the second experiment.

In experiment number 3, a male of the constitution (X)+/(Y)*Sb* must have mated with the spotted female, presumably heterozygous (X)+/(X)*Sp*, to account for the results obtained. Some of the daughters were normally colored (+) while others were spotted (*Sp*). The sons were black-bottomed and presumably about half carried the *Sp* gene in addition to the *Sb*, but at the time the record was made they were all listed as only black-bottomed.

Additional evidence that the *Sp* in females is carried by the X chromosome is given in mating number 4. Here the spotted female presumably was heterozygous (X)+/(X)*Sp*, the male was normally colored (X)+/(Y)+ and the offspring were spotted and non-spotted; in this brood the sexes were equally distributed among the two phenotypes. Essentially similar results were obtained in the next mating, 5, with the use of the spotted dorsal female (X)+/(X)*Sd*.

Summing up, the Rio Papaloapan fish populations showed that one gene, *Sb*, was transmitted through the Y chromosome and the genes *Sp* and *Sd* were transmitted through the X chromosome. This conclusion, apparently so obvious now, was not appreciated because the bulk of the published data available at the time clearly indicated that WZ = female, ZZ = male.

GENETIC ANALYSIS OF THE RIO JAMAPA POPULATION

A number of young female platyfish were isolated for two or more months. Those which did not produce any offspring within that time were paired with males as indicated in Table 2. In Exp. 1, the spot-sided female transmitted its *Sp* gene (when mated to a recessive male) to half of its daughters and sons; the other half of the offspring, both female and male, were normally colored. These results may be explained on this basis: (X)*Sp*/(X)+ × (X)+(Y)+ = (X)+/(X)+, (X)*Sp*/(X)+, (X)*Sp*/(Y)+, (X)+/(Y)+. These results cannot be explained on the basis of WZ = female, ZZ = male, worked out for this species (*P. maculatus*) from domesticated stocks. If the *Sp* had been borne on the *Z* chromosome, criss-cross inheritance would have been expected; if the *Sp* has been borne on the W chromosome then matroclinus inheritance would have been expected.

The results of Exp. 2 are noteworthy in light of later work, in that they show that a wild platyfish female may carry the *Sd* gene on its X chromosome. One or the other or both of the parents must have been homozygous for the *Sd* gene since all of the offspring showed up with a spotted dorsal fin. At a later point an instance of crossing over of the sex chromosomes (experiment 7) was found in which the *Sd* gene was transferred from the Y to the X.

A first case of a Y borne gene involving *Sd* was detected in mating number 3. Here the male carried *Sr* and *Sd* in this manner: (X)*Sr*/(Y)*Sd*, while the female was homozygous recessive (X)+/(X)+. The female offspring were (X)*Sr*/(X)+ while the males were all (X)+/(Y)*Sd*.

In the 4th and 5th experiments, the male used was homozygous for *Sr*. When mated with an (X)*Sr*/(X)*Sd* female, half of its young were *Sr*, the others were *Sr*/*Sd*; when it was mated with a homozygous recessive female, all its offspring were *Sr*.

The spotted female in mating 6 (1–18) was first mated to an *Sr* male and several broods were produced; then after a two month period of unproductiveness, the same spotted female (X)*Sp*/(X)+ was mated (number 7) to an (X)*Sr*/(Y)*Sd* male. From the second mating (7) its male offspring were (X)+/(Y)*Sd* and (X)*Sr*/(Y)*Sd*; the females were (X)*Sr*/(X)+, (X)*Sr*/(X)*Sp* and an exceptional marked individual, presumably (X)*Sd*/(X)+. This exceptional female (28 *Sd* 1) was tested at a later date (see mating number 14) with a homozygous *Sr* male (30^3–11). Since mating number 14 produced sons and daughters in the *Sr*/+ group and in the *Sr*/*Sd* group, the presumed constitution of the exceptional (28 *Sd* 1) female was (X)*Sd*/(X)+; and apparently it was traceable to a crossover in its male parent (16–12 in mating number 7) in which one (X)*Sr*/(Y)*Sd* germ cell produced an (X)*Sd* gamete, see figure 2.

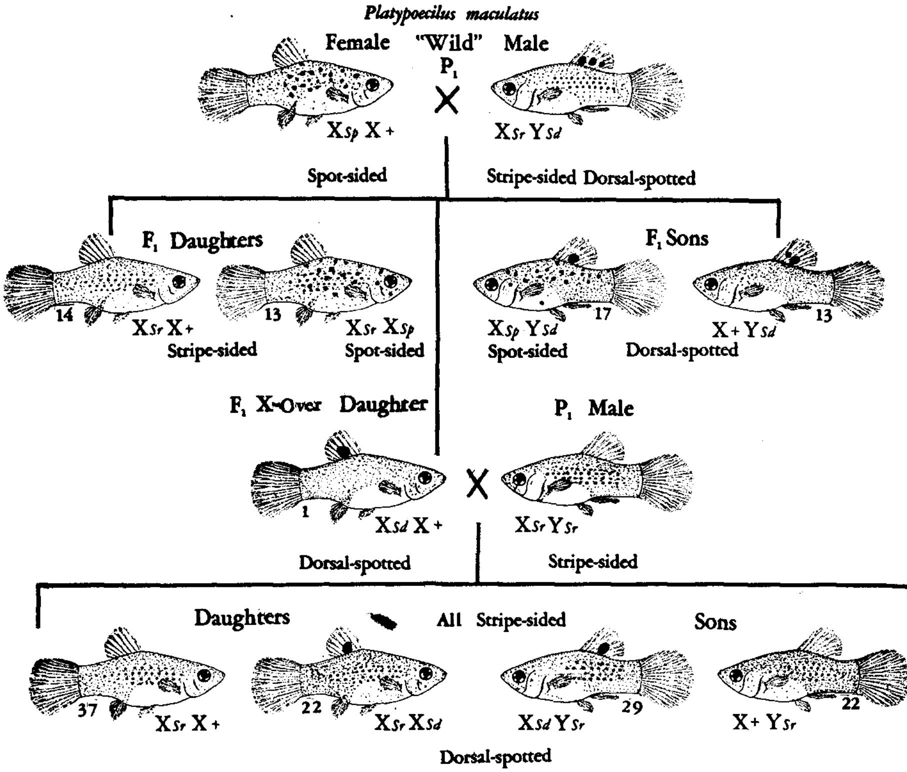

FIGURE 2.—Crossing Over of the X and Y Chromosomes in Mating Number 7. The diagram shows the P_1 male carrying the *Sd* gene on the Y chromosome mated to a *Sp* female. They produced 30 *Sd* sons, 1 *Sd* daughter and 27 non-spotted dorsal daughters. When the exceptional *Sd* daughter was mated to a *Sr* male (Mating Number 14) it produced *Sd* sons and daughters in equal proportions. This supports the supposition that *Sd*, originally on the Y chromosome, was transferred to the X.

The results obtained from matings number 8, 9, 10 and 11 were in accordance with the general results obtained previously where XX = female and XY = male. In these matings no exceptions were detected.

An exceptional individual appeared from mating number 12. Here a female (X)*Sr*/(X)*Sp* was mated to an (X)+/(Y)*Sd* male. Their young were as follows: females = (X)*Sp*/(X)+, (X)*Sr*/(X)+; males = (X)*Sp*/(Y)*Sd*, (X)*Sr*/(Y)*Sd*, and a single exceptional male which was presumably (X)*Sp*/(Y)+. Two explanations may be suggested for its appearance: (1) it may have been the product of crossing over of the sex chromosomes in its male parent (60a14) in which an (X)+/(Y)*Sd* germ cell produced an (Y)+ sperm; (2) it may have represented an incomplete case of sex reversal in which the exceptional male may not have been of the constitution (X)*Sp*/(Y)+ but (X)*Sp*/(X)+. Since it was sterile, it was not possible to decide just what occurred.

Two more exceptions were found in mating number 13 when an (X)*Sp*/(X)+ female (17–1) was crossed with an (X)*Sr*/(Y)*Sd* male (24–11); they produced two unexpected male offspring presumably having the following constitution: (X)+/(Y)*Sr* which was fertile and (X)*Sp*/(Y)*Sr* which was sterile. The fertile male exception (number 62–12) was mated to a spotted female (159–1) which had the following genetic constitution: (X)*Sp*/(X)+. The results listed in mating number 21 indicate that the *Sr* gene had crossed over from the X to the Y chromosome in male number 24–11 of mating number 13. The results indicate the probable sequence of events as follows:

No. 17-1 P_1 No. 24-11
(X)*Sp*/(X)+ × (X)*Sr*/(Y)*Sd*
F_1
19 (X)+/(X)*Sr*, 24 (X)*Sp*/(X)*Sr*, 20 (X)*Sp*/(Y)*Sd*, 18 (X)+/(Y)*Sd*
1 (X)+/(Y)*Sr**, 1 (X)*Sp*/(Y)*Sr*
Fertile* Sterile

No. 159-1 = (X)*Sp*/(X)+ × (X)+/(Y)*Sr** = No. 62-12

12 (X)+/(X)+, 12 (X)*Sp*/(X)+, 13 (X)+/(Y)*Sr*, 13 (X)*Sp*/(Y)*Sr*

Conclusion: *Sr* crossed over from X to Y in the germ cells of the P_1 male no. 24–11. The exceptional offspring (X)+/(Y)*Sr* (No. 62–12) subsequently transmitted its *Sr* gene to its sons only through the Y chromosome.

Mating number 14 has previously been discussed and numbers 15 and 16 did not produce any unusual results: criss-cross inheritance was observed for *Sp* and *Sr* and patroclinus inheritance for *Sd*. From mating number 17 a remarkable example of sex reversal was found in an exceptional male offspring (GORDON 1946c).

SEXUAL TRANSFORMATION OF A GENETICALLY CONSTITUTED FEMALE INTO A FUNCTIONAL MALE

The events leading to the discovery of a functional male with a genetic constitution of a female are as follows. A stripe-sided female (63–1) was mated to a spot-sided and spotted dorsal male (62–11). This mating and their offspring may be expressed as follows:

(X)*Sr*/(X)+ × (X)*Sp*/(Y)*Sd*
♀♀ F_1 ♂♂
32 (X)*Sr*/(X)*Sp*, 34 (X)*Sp*/(X)+ 29 (X)*Sr*/(Y)*Sd*, 27 (X)+/(Y)*Sd*
1 (X)*Sp*/(X)+* = exceptional ♂

(X)*Sr*/(X)*Sr* × (X)*Sp*/(X)+* = exceptional ♂
F_2
79 ♀♀ (X)*Sr*/(X)*Sp* No males
74 ♀♀ (X)*Sr*/(X)+

TABLE 2

Platypoecilus maculatus population from the Rio Jamapa at El Tejar, Veracruz.

PARENTS						FIRST GENERATION															
EXP. NO.	♀	♂	X/X	X/Y	PED. NO.	+/+ ♀	+/+ ♂	Sd/+ ♀	Sd/+ ♂	Sp/+ ♀	Sp/+ ♂	Sr/+ ♀	Sr/+ ♂	Sd/Sp ♀	Sd/Sp ♂	Sd/Sr ♀	Sd/Sr ♂	Sp/Sr ♀	Sp/Sr ♂	TOTAL	x^2
1	1-7	1-17	*Sp/+*	*+/+*	17	16	13			12	10									51	1.961
2	1-10	1-20	*Sd/+*	*Sd/Sd*	20			23	15											38	1.684
3	1-12	1-22	*+/+*	*Sr/Sd*	22			0	14			18	0							32	0.500
4	1-16	1-34	*Sr/Sd*	*Sr/Sr*	26							13	14			13	8			48	1.833
5	1-17	1-34	*+/+*	*Sr/Sr*	27							25	25							50	0.000
6	1-18	16-11	*Sp/+*	*Sr/+*	28a	0	7			0	5	6	0					8	0	26	0.746
7	1-18	16-12	*Sp/+*	*Sr/Sd*	28b			1	13			14	0	0	17			13	0	58	0.719*
8	1-19	1-36	*Sr/+*	*+/Sr*	29	12	0					11	17							40	0.950
9	27-1	27-11	*Sr/+*	*+/Sr*	30	7	0					14	22							43	2.872
10	27-2	12-11	*Sr/+*	*+/Sd*	60a	16	0	0	16			12	0			0	14			58	0.759
11	27-3	21-11	*Sr/+*	*+/+*	60b	9	9					6	5							29	1.513
12	28a3	60a14	*Sr/Sp*	*+/Sd*	61					12	1	16	0	0	11	0	16			56	1.473*
13	17-1	24-11	*Sp/+*	*Sr/Sd*	62			0	18			19	1	0	20			24	1	83	1.047*
14	28Sd1	30^{3}-11	*Sd/+*	*Sr/Sr*	63							37	22			29	22			110	4.654
15	60a3	28b11	*+/+*	*Sp/Sd*	64			0	9	8	0									17	0.059
16	60a5	60a11	*+/+*	*Sr/Sd*	65			0	16			18	0							34	0.118
17	63-1	62-11	*Sr/+*	*Sp/Sd*	159			0	27	34	1					0	29	32	0	123	0.950*
18	63-2	63-12	*Sd/Sr*	*Sd/Sr*	160			18	0			1	12			12	17			70	3.337*
19	61-1	28b17	*Sp/+*	*+/Sd*	161	15	0	0	12	12	0			0	13					52	0.461
20	64-1	63-11	*Sp/+*	*Sd/Sr*	163			5	0			0	6	6	0			0	6	23	0.130
21	159-1	62-12	*Sp/+*	*+/Sr*	178	12	0			12	0	0	13					0	13	50	0.082
22	30^{4}-1	159-21	*Sr/Sr*	*Sp*	167							79	0					74	0	153	0.163

* The values starred (*) were obtained by omitting the exceptional cross-overs.

A single spotted-male appeared in the F_1. This phenotype generally characterized the females. When the exceptional spotted male (159–21) was tested by mating it with a homozygous stripe-sided female (30^4–1), the pair produced 153 females and no males (see mating 22). A histological report on the reproductive organs of male number 159–21 is being prepared. The female number 30^4–1 with which 159–21 was mated, after a period of non-productivity, was mated a second time with an (X)+/(Y)+ male. From the latter mating (not indicated in Table 2) it produced approximately as many male as female offspring. This definitely shows that the first male, number 159–21, was responsible for the unusual sex ratio in the first group of young.

In mating number 18 another exceptional individual was discovered; this time it was a female offspring. The simplest explanation for its appearance is that it represented a product of crossing over of the (X)*Sd* and (Y)*Sr* chromosomes of its male parent (63–12): an (X)*Sr* sperm was produced. This suggestion could not be verified owing to the complete sterility of the exceptional female.

Matings number 19 and 20 may be contrasted with regard to the manner in which the gene *Sd* was carried by the male parents. In 19, the male (28b17) *Sd* was carried by the X chromosome whereas in the latter (male, 63–11) *Sd* was carried by the Y. The results are explainable on this basis.

Matings number 21 and 22 were discussed previously in connection with exceptional individuals, 62–12 and 159–21.

DISCUSSION

A general discussion of the genetic sex determining mechanism in "wild" and in "domesticated" stocks of *Platypoecilus maculatus* is presented in another paper by the author (GORDON 1946b). In this paper the consequences of mating a homozygous "domesticated" platyfish male (ZZ) with a homozygous "wild" female (XX) are given: all the offspring are male (ZX). This result and others substantiate the suggestion of CASTLE (1936) that perhaps the usage of ZZ for the "domesticated" male might be discontinued and YY substituted. Apparently Z and Y are homologous. However the W chromosome of the "domesticated" female is not homologous to any X of the platyfish. Indeed, the nature of the W chromosome is not yet clear. GORDON has suggested that perhaps the W chromosome may be traced to a *Xiphophorus hellerii* chromosome which has introgressed through intergeneric hybridization into the genetic structure of the domesticated platyfish. The basis for this suggestion may be found in the results of mating an (X)*Sr*/(Y)*Sd* "wild" male *P. maculatus* with a "wild" female *X. hellerii*. All the *Sr* hybrids are female and fertile; some of the *Sd* hybrids are male, some are female while most of them are sexually indifferent and, of course, sterile. This is as far as the experiment has gone at present. Suppose, however, that the rare fertile male and the rarer fertile female *Sd* platyfish-swordtail hybrids are inbred:

♀♀	F_1	♂♂
(X′)+/(Y)*Sd*	×	(X′)+/(Y)*Sd*

F_2:	1 (X′)+/(X′)+ presumably female,	2 (X′)+/(Y)*Sd* presumably female or male,	1 (Y)*Sd*/(Y)*Sd* presumably male

In the second generation hybrids we would probably find some homozygous females containing two X′ chromosomes from *Xiphophorus hellerii*. And we would probably find some homozygous males carrying two Y chromosomes from *Platypoecilus maculatus*. The others would probably be male or female and most of them might be sterile. If among the latter, an (X′)+/(Y)*Sd* female stock could be stabilized, then the so-called WZ = female and ZZ = male platyfish stock could be reestablished.

Under restricted aquarium conditions *Xiphophorus hellerii* and *Platypoecilus maculatus* hybridized readily and the history of the first reported hybrid between them goes back to 1912. The records show that the first platyfish were imported into Germany in 1907 and the first swordtails in 1909. Under natural conditions, and this phase of research is described by GORDON (1947), the species have never been known to hybridize.

Under commercial tropical fish breeding practices, there are many examples of the transference of platyfish genes into the germ plasm of a swordtail-like hybrid and the subject of introgressive hybridization is discussed by GORDON (1946a).

Both the WZ-ZZ and the XX-XY systems are stable in their respective stocks and are being maintained side by side. According to BREIDER (1942) the stocks maintained by him, at least up to 1942, were still showing the WZ-ZZ mechanism. Indeed, in a remarkable cross he identified an exceptional male platyfish, which by its peculiar phenotype should have been a female. When he tested the unusual male which he suspected had the genetic constitution of (W)*RSp*/(Z)*Dr* with a stock female (W)+/(Z)*R*, he obtained 51 females and 13 males,—that is, 3 females to 1 male. Among the females he claimed to have obtained WW females. This was highly probable but it would have been desirable to have had additional information on the genetical behavior of the WW females. If WW females had been mated with ordinary ZZ males, all of their offspring would have had to be males; this would have verified the genetic constitution of the presumed WW females completely.

The ratio of 3 females to 1 male has been obtained in this laboratory by a method which did not depend upon the sexual transformation of a genetically constituted female into a functional male. A spotted "domesticated" female (W)*Sp*/(Z)+ was mated to a stripe-sided "wild" male, (X)+/(Y)*Sr*. The spotted F_1 hybrids were all females and presumably, (W)*Sp*/(X)+ or (W)*Sp*/(Y)*Sr*; the non-spotted F_1 hybrids were males, half of which were stripe-sided, (Z)+/(Y)*Sr*, and half were normal. (Z)+/(X)+. When some of the spotted F_1 females were tested with "wild" stripe-sided males the following results were obtained:

Mating I		Mating II	
(W)*Sp*/(X)+ ×	(X)+/(Y)*Sr*:	(W)*Sp*/(Y)*Sr* ×	(X)+/(Y)*Sr*:
Daughters:	Sons:	Daughters:	Sons:
(W)*Sp*/(X)+	(X)+/(Y)*Sr*	(W)*Sp*/(X)+	(Y)*Sr*/(Y)*Sr*
(W)*Sp*/(Y)*Sr*		(W)*Sp*/(Y)*Sr*	(Y)*Sr*/(X)+
(X)+/(X)+			

When a WY female was mated with an XY male the sex ratio was 1:1 (mating II). When a WX female was mated with an XY male (mating I) the sex ratio was 3 ♀♀ to 1 ♂♂. A complete report on this mating and other "domesticated-wild" matings will appear in the near future.

SUMMARY

The sex determining mechanism in two wild populations of the Mexican platyfish, *Platypoecilus maculatus*, one from the Rio Papaloapan and the other from the Rio Jamapa may be expressed as follows: XX = female, XY = male.

The domesticated stocks of the same species have a sex determining mechanism which may be expressed as follows: WZ = female, ZZ = male. It is suggested, in view of the probable origin of this mechanism from the wild type that the formula might better be written: WY = female, YY = male.

An instance of sexual transformation of a genetically constituted female of the "wild" stock XX has been reported. When this XX male was mated with a normal "wild" type female, also XX, all the offspring, 153 in all, were females, XX.

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