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THE ROLE OF THE PELVIC FINS IN THE COPULATORY ACT OF CERTAIN POECILIID FISHES[1]

By Eugenie Clark[2] and Robert P. Kamrin

INTRODUCTION

In adult poeciliid fishes there is a marked sexual dimorphism particularly in reference to body size, coloration, and fin structure. While considerable effort has been expended over the years in studying the structure and function of the gonopodium (modified anal fin of the mature male), relatively little attention has been directed to an understanding of the pelvic fins which also become modified as the males mature. In the latter, particularly the first and second rays of the pelvic fins show considerable specialization. It has been reasoned from the fin anatomy in such cyprinodont genera as *Poecilia*, *Molliensia*, *Limia*, *Xiphophorus* (Henn, 1916), and *Lebistes* (Purser, 1941; Fraser-Brunner, 1947) that the elongated pelvic fins of the males, acting in conjunction with the modified anal fin, help to form a tube through which spermatozoa pass during copulation. Observations on the sexual behavior of *Lebistes reticulatus*, *Platypoecilus maculatus*,

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[2] Post-doctoral fellow of the Atomic Energy Commission in the Biological and Agricultural Sciences of the National Research Council at the American Museum of Natural History.

and *Xiphophorus hellerii* (Christman, MS; Clark and Aronson, in press; Clark, Aronson, and Gordon, MS) show that during sex-

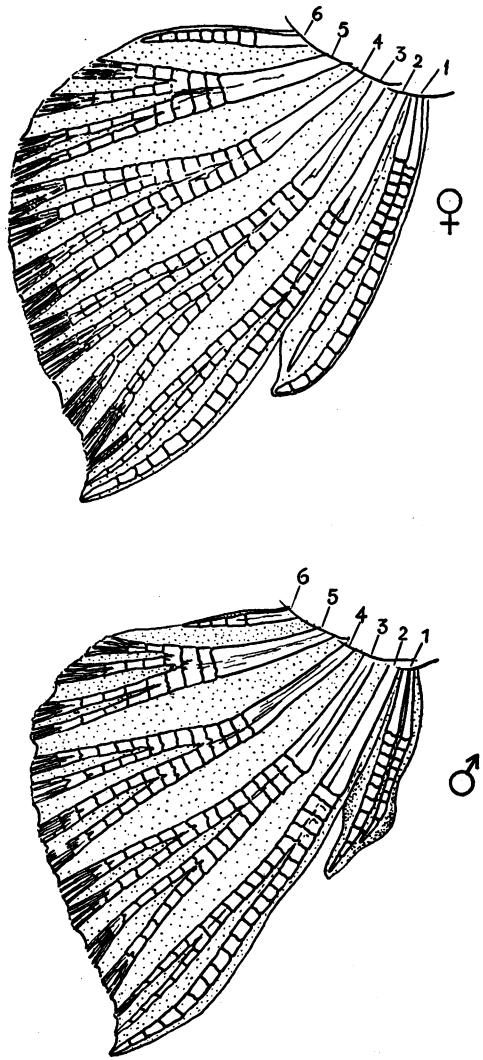

FIG. 1. Pelvic fins of a male and female *Platypoecilus maculatus*. *Ca.* × 15.

ual activity, when the anal fin or gonopodium of the male is moved forward and to one side towards the female, the pelvic fin on that side is also coordinated with a forward motion

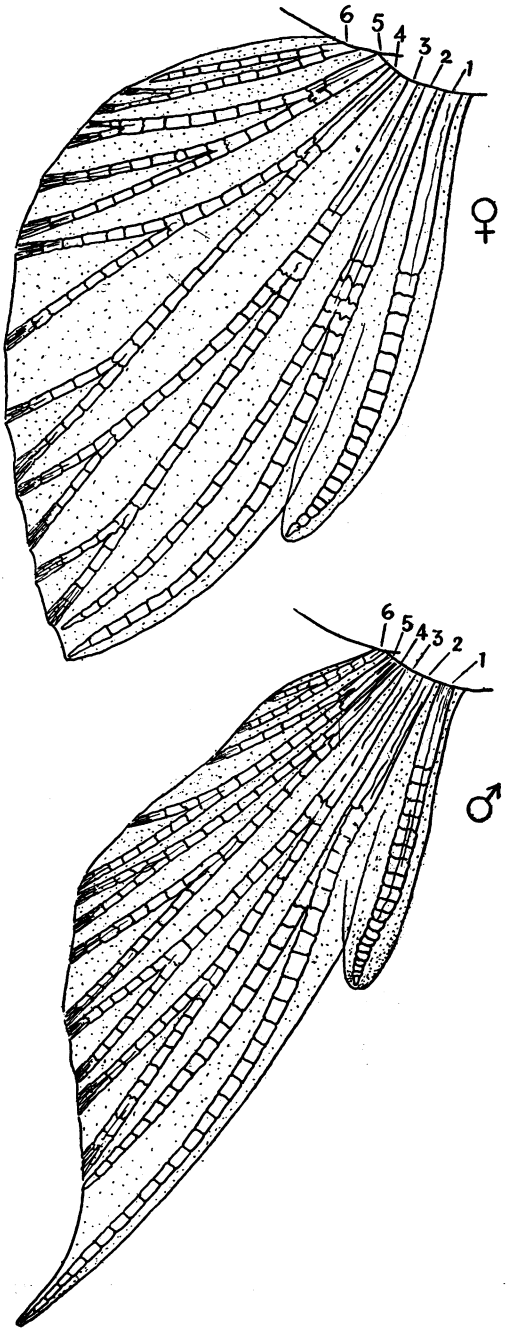

FIG. 2. Pelvic fins of a male and female *Xiphophorus hellerii*. *Ca.* × 15.

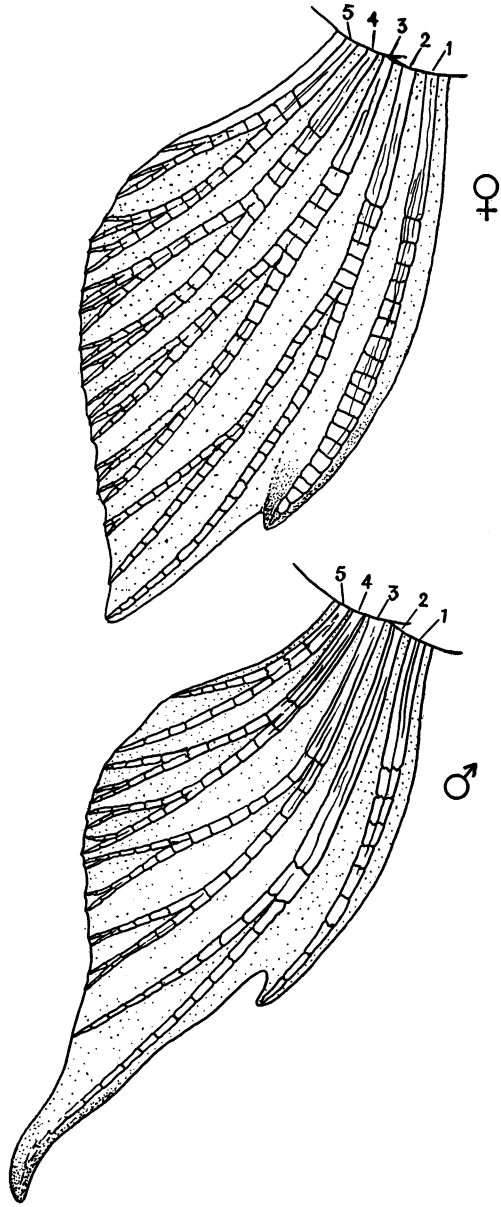

FIG. 3. Pelvic fins of a male and female *Lebistes reticulatus*. *Ca.* × 15.

(figs. 4 and 5). These studies support the hypothesis that the pelvic fins function in some manner during copulation.

A preliminary experiment on the function of the pelvic fin during copulation in *Platypoecilus maculatus* (Clark, Aronson, and Gordon, MS) indicates that insemination of the female is not possible by a male without pelvic fins. The present study represents an expansion of this approach, using the swordtail, *Xiphophorus hellerii* Heckel, and the guppy, *Lebistes reticulatus* (Peters), as well as the platyfish, *Platypoecilus maculatus* Günther. The extended pelvic fins of these species are shown in figures 1, 2, and 3. In the platyfish (fig. 1) and the swordtail (fig. 2), the first ray of the male is considerably shorter and the epidermal covering thicker than in the female. In the guppy (fig. 3), the second ray shows the most noticeable dimorphism and in the male is longer, less branched, and has a thicker covering than in the female.

MATERIAL AND METHODS

For each of the three species, 14 mature males were used. Of the 14, four were kept as controls, the right pelvic fin was cut off three males, the left pelvic fin was cut off three other males, and the four remaining males had both pelvic fins cut off. Each male was then paired with a female for a test period of approximately four weeks, or until she had been inseminated by the test male.

When noticeable regeneration of an amputated pelvic fin took place, the fin was immediately trimmed (after a week some males showed some regeneration). During the time of pairing, the females were checked for sperm periodically (table 1) by a smear technique developed previously in these fishes (Clark and Aronson, in press; Clark, Aronson, and Gordon, 1948, 1949, MS). Prior to testing, the swordtail and platyfish females were virgins, and the guppy females had been isolated for several weeks until sperm could no longer be recovered from their genital tracts by the smear technique.

RESULTS

In the four control pairings for these species and in the six experimental pairings for each species where males had only one pelvic fin removed, the females were all inseminated by the twenty-first day in the platyfish, the twentieth day in the sword-

TABLE 1

INSEMINATION OF FEMALES PAIRED WITH MALES HAVING ONE OR BOTH PELVIC FINS REMOVED

Species	Smears on Various Days of Test Period 4	6	11	14	18	21	28	Total	Pelvic Fin Amputated
Platypoecilus maculatus									
1	—[a]	+						+	Neither (controls)
2	—	—	×	—	+			+	
3	+							+	
4	—	—	+					+	
5	—	+						+	Right fin only
6	—	—	×	+				+	
7	+							+	
8	—	—	—	+				+	Left fin only
9	—	×	—	—	×	+		+	
10	—	—	—	—	+			+	
11	—	×	—	—	—	—	—	—	Both
12	—	—	—	×	—	—	—	—	
13	—	—	—	—	—	+×	—	+	
14	—	—	—	—	—	—	—	—	
Xiphophorus hellerii	4	7	14	17	20	26	29		
1	—	—	—	+				+	Neither (controls)
2	—	—	+					+	
3	+							+	
4	+							+	
5	—	—	+					+	Right fin only
6	+							+	
7	+							+	
8	—	—	—	—	+			+	Left fin only
9	+							+	
10	—	—	—	—	—	—	—	—	
11	—	—	—	—	—	—	—	—	Both
12	—	—	—	—	—	—	—	—	
13	—	—	—	×	—	+×	—	+	
14	—	—	—	—	—	—	—	—	
Lebistes reticulatus	3	7	11	16	22	26			
1	—	—	—	+				+	Neither (controls)
2	—	+						+	
3	—	—	—	—	+			+	
4	+							+	
5	—	+						+	Right fin only
6	—	—	×	+				+	
7	—	+						+	
8	—	—	—	—	×	+		+	Left fin only
9	—	—	—	—	—	—		—	
10	—	+						+	
11	—	—	—	—	+×	—		+	Both
12	—	—	—	—	—	—		—	
13	—	—	—	—	—	—		—	
14	—	—	×	—	—	—		—	

[a] Symbols: —, smear contained no sperm; +, smear contained sperm; ×, female replaced.

tail, and the twenty-sixth day in the guppy (table 1). Two exceptions were noted, as follows:

Lebistes reticulatus male No. 9 and *X. hellerii* male No. 10 did not inseminate the females with which they were paired by the end of the test period. At this time these two males were examined. The sperm of the guppy male was found to be abnormally low in motility and loose rather than in spermatophores. Examination of the swordtail male yielded no plausible explanation for its failure to inseminate the female paired with it.

Of the males that had both pelvic fins removed, only one out of four inseminated a female in each of the species tested. In the case of the guppy, a typical positive smear was obtained, consisting of hundreds of motile sperm. The single platyfish and swordtail positive smears resulting from pairings with males without pelvic fins were, however, definitely abnormal. In the platyfish, only four sperm were recovered in the smears, and in the swordtail, six were recovered. All the positive smears obtained from the control females, as well as those from females paired with males having one pelvic fin, contained hundreds of motile sperm, as would normally be expected.

It was evident from the above results that in males without pelvic fins the ability to inseminate females is considerably lessened. But from these data, conclusions cannot be drawn concerning copulatory behavior, since it has been found frequently that copulations do not always result in insemination (Clark and Aronson, in press; Clark, Aronson, and Gordon, 1948, and MS). Moreover, if the pelvic fin functions as an accessory structure to the gonopodium for the passage of sperm from the male genital opening to the female genital opening, males without pelvic fins may well be copulating but ejaculating into the water. In order to ascertain if the absence of pelvic fins actually hinders copulatory behavior, we conducted observational studies on the sexual behavior of males after pelvic fin amputation.

For these observational studies we used only *P. maculatus*. Six untreated males served as controls, and on a second group of six males, both pelvic fins were removed. Each male was placed in a 2-gallon aquarium and presented with a virgin female for a 10-minute observation period on six different days. The number of times he thrust his gonopodium at the female's genital region and the number of copulations that took place were recorded. This

observational technique is the same as that described by Clark, Aronson, and Gordon (1948, 1949, MS).

The results given in table 2 show that the six control fish made a total of 738 thrusts and copulated 18 times, whereas the fish without pelvic fins made 1058 thrusts without copulating once.

On two occasions an experimental male thrust at the female and for an instant appeared to have gripped her in a manner suggesting the beginning of a copulation. However, the male then seemed to lose his balance, tumbled backward, and the action terminated without insemination.

DISCUSSION

Our results indicate that the pelvic fins of the male platyfish, swordtail, and guppy play a role in copulatory behavior and that they are an important part in the mechanism for internal fertilization.

In all but two cases out of 30, males with one or two pelvic fins were able to inseminate females within a test period of four weeks; half of these males inseminated females within the first week. The males with only one pelvic fin probably inseminated females by copulating with the gonopodium held to the side having the intact pelvic fin. It is shown elsewhere that the males of these species are ambidextrous in their ability to thrust and copulate (Aronson and Clark, MS).

Males lacking both pelvic fins were considerably handicapped in their ability to inseminate females. Only one out of four transferred sperm to females and then only after a period of nearly three weeks in the tank with the female. In the case of the platyfish and swordtail, the smears indicated that the number of sperm transferred was abnormally low. There was no evidence that males without pelvic fins were appreciably handicapped in their general swimming or maneuvering for position prior to thrusting. Nor were males that were rendered asymmetrical by the removal of only one pelvic fin handicapped in this manner. Actually, our experiments show no apparent difference between the times it took the control males and the times it took males minus one pelvic fin to inseminate their females. Thus it appears that males with both pelvic fins removed were prevented from inseminating females because of a specific defect in the total copulatory apparatus.

Observational tests (table 2) on the platyfish indicated that

TABLE 2

THRUSTING AND COPULATORY BEHAVIOR OF MALES WITHOUT PELVIC FINS AS COMPARED TO CONTROL MALES OF *Platypoecilus maculatus*[a]

Dates of Observations	Control Males							Males Without Pelvic Fins						
	1	2	3	4	5	6	Total	1	2	3	4	5	6	Total
10/7/50	0-0	24-2	12-0	0-0	0-0	2-0		0-0	0-0	14-0	7-0	0-0	13-0	
10/10/50	104-1	7-0	64-0	2-0	99-2	8-0		7-0	45-0	9-0	38-0	3-0	0-0	
10/17/50	15-0	9-0	3-0	24-0	14-0	5-0		0-0	69-0[b]	20-0	53-0	18-0	7-0	
10/20/50	5-0	8-1	12-0	98-1	16-0	2-0		1-0	150-0	28-0	134-0	23-0	64-0[b]	
10/22/50	32-3	1-0	0-0	3-0	9-1	0-0		3-0	53-0	0-0	3-0	116-0	0-0	
10/24/50	37-3	18-0	47-2	14-0	39-2	5-0		4-0	26-0	4-0	18-0	127-0	1-0	
Totals	193-7	67-3	138-2	141-1	177-5	22-0	738-18	15-0	343-0	75-0	253-0	287-0	85-0	1058-0
Mean number of thrusts				*123.0*							*176.4*			
Mean difference				*53.4* thrusts; $t = 0.86$; $P = 0.4$										

[a] In this table the first number in each column indicates the number of thrusts, and the second number (after the hyphen) gives the number of copulations.

[b] In these observations the male tumbled backward after a close contact thrust.

males lacking both pelvic fins had considerable mechanical difficulty in effecting the "hold" on the female that is necessary for a copulation. None actually copulated. That their level of sexual responsiveness was up to normal is demonstrated by the amount of thrusting behavior. The number of thrusts appeared appreciably higher in the experimental males compared to the

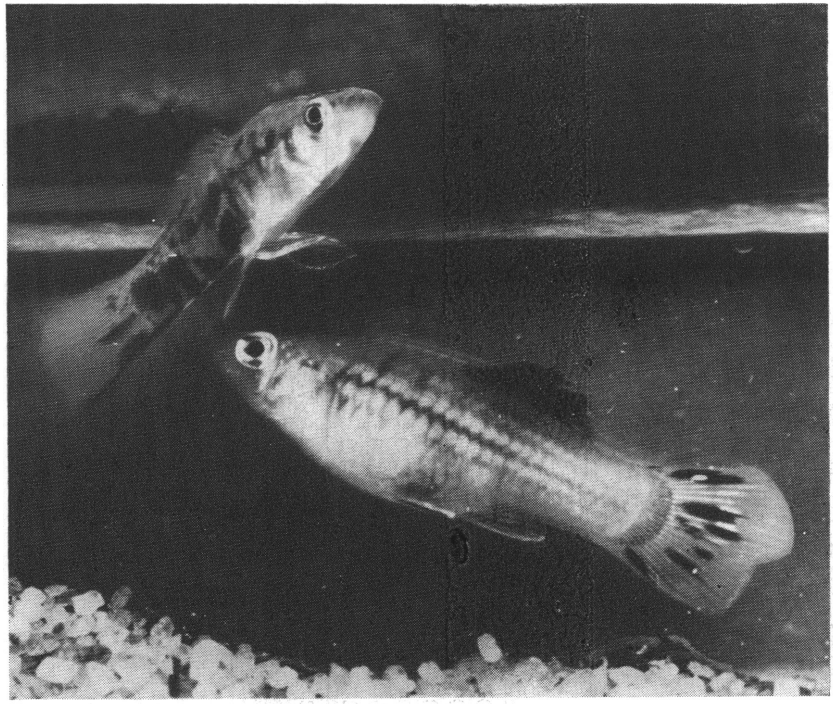

FIG. 4. Photograph of the swinging behavior of a *Platypoecilus maculatus* × *Xiphophorus hellerii* F_1 hybrid male. The left pelvic fin and gonopodium are shown in the forward position. The fish in the lower right is a female resulting from the same cross.

number of thrusts observed in the controls, but because of the small sampling and high variability, no statistically significant difference could be demonstrated. Indication of a higher sexual excitability when copulation is hindered has been noted also when testing platyfish males with amputated gonopodial tips (Clark, Aronson, and Gordon, 1949, MS). Similarly, in certain rodents it has been shown that sympathetic denervation of the genitals

prevents ejaculation, but vigorous mating including persistent copulation continues unabated until the animal is totally exhausted (Beach, 1947, p. 255).

It can be seen in figures 4 and 5 that when the gonopodium is brought forward and to the side, the pelvic fin is moved forward with it somewhat under or alongside the gonopodium in the position of a buttress. The photographs were taken during the "swinging" behavior (Clark, Aronson, and Gordon, 1948, and MS), when the gonopodium and pelvic fin are in the same relative positions as in thrusting and copulation. From our evidence it appears that the modified pelvic fin of the male platyfish, swordtail, and guppy act at least in part as a supporting organ for the gonopodium during copulation. The three cases of males without pelvic fins that eventually inseminated females can be explained by compensatory adjustment.

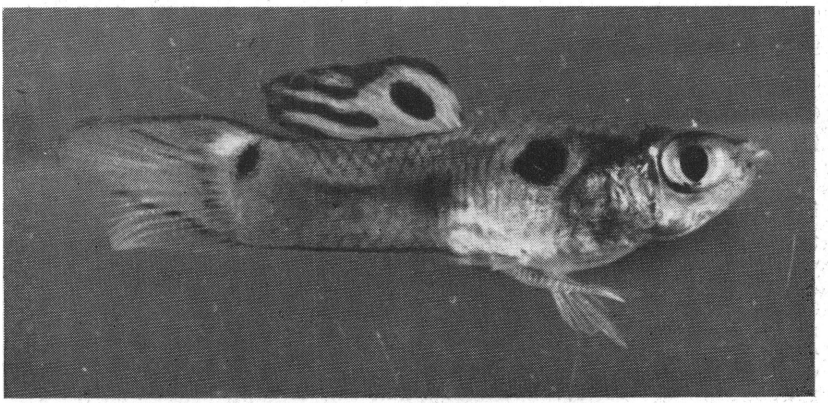

FIG. 5. Photograph of the swinging behavior of a male *Lebistes reticulatus*. The left pelvic fin and gonopodium are shown in the forward position.

That the male pelvic fin may also act to help form an enclosure for the passage of sperm is still a possibility. It can be easily demonstrated on living specimens, and Rosen and Gordon (MS) show by a mechanical model that when the gonopodium of the platyfish or swordtail is brought forward into the position attained in copulation, certain mechanical adjustments occur in rays 3, 4, and 5 which lead to the formation of a groove along one side of the gonopodium. What appears to be the more obvious function of the gonopodial groove is that of a passageway for the

sperm which is released in bundles or "spermatophores." The diameter of the individual spermatophores, however, is considerably less than the open side of the gonopodial groove. It seems logical to assume that when the pelvic fin moves forward and alongside of the gonopodium it completes the enclosure and thus forms a broad passageway along the gonopodium which directs the sperm towards the female. If this is true, it might account for the abnormally low numbers of sperm obtained in the smears in the two cases of insemination by a male platyfish and male swordtail lacking both pelvic fins. These males succeeded in holding a female *in copula* without the aid of a pelvic fin (possibly through a process of learning), but during ejaculation, without the proper enclosure of the gonopodial groove, most of the spermatophores may have been lost into the water.

However, the heavy sperm smear obtained from the female guppy paired with a male lacking both pelvic fins does not support the hypothesis that the pelvic fin is part of an enclosure for the passage of sperm. It should be noted, however, that some aspects of gonopodial morphology and copulatory behavior of the guppy (Clark and Aronson, in press) are considerably different from those of the closely related platyfish and swordtail (Clark, Aronson, and Gordon, 1948, MS). It may well be that the pelvic fins of the guppy function in a slightly different manner than those of the platyfish and swordtail.

One other possible function of the male pelvic fin during copulation should be considered here, that of a pressure appliance for the ejaculation of spermatophores. If a fish is held on its back with wet cotton, while the observer works with a dissecting-scope, spermatophores can be released artificially from living male platyfish, swordtails, or guppies by pressure on the abdomen. Quite frequently this can be done by merely rotating the gonopodium forward and to one side of the fish, the spermatophores filling the groove in the gonopodium and spilling around its base. When this method does not work the additional pressure caused by a forward pull of the pelvic fin on the side to which the gonopodium is pointed will often release the spermatophores. However, it must be noted that spermatophores are not ejaculated every time the male swings his gonopodium and pelvic fin forward, but this probably occurs only during copulation, for at this time, along with other mechanisms, movement of the pelvic fin to a forward position may be of material aid.

SUMMARY

The role of the male pelvic fins in the copulatory act of *Lebistes reticulatus*, *Platypoecilus maculatus*, and *Xiphophorus hellerii* has been studied experimentally. Males with one pelvic fin removed appear to be able to transfer sperm to a female as readily as intact control fish. Males with both fins removed are strongly handicapped in this respect, although they may eventually adjust themselves to this condition and transfer sperm without the aid of pelvic fins. The pelvic fins of mature males appear to have three possible functions during copulation: (1) as a supporting mechanism for the gonopodium when the latter is brought forward and to the side during the swinging, thrusting, and copulatory behaviors in courtship, (2) as a mechanism to aid the gonopodium in forming an enclosure for the passage of spermatophores, and (3) as a supplementary part of the ejaculatory mechanism for the release of spermatophores during copulation.

BIBLIOGRAPHY

ARONSON, LESTER R., AND EUGENIE CLARK

[MS.] Evidences of ambidexterity in the sexual behavior of certain poeciliid fishes.

BEACH, FRANK A.

1947. A review of physiological and psychological studies of sexual behavior in mammals. Physiol. Rev., vol. 27, no. 2, pp. 240–307.

CHRISTMAN, GUINEVERE C.

[MS.] The morphology of the primary and accessory genital organs of certain Poeciliidae. (Unpublished Master's thesis, dated 1928, in Cornell University Library, Ithaca, New York.)

CLARK, EUGENIE, AND LESTER R. ARONSON

[In press.] Sexual behavior of the guppy *Lebistes reticulatus* (Peters). Zoologica, New York.

CLARK, EUGENIE, LESTER R. ARONSON, AND MYRON GORDON

1948. An analysis of the sexual behavior of two sympatric species of poeciliid fishes and their laboratory induced hybrids. Anat. Rec., vol. 101, no. 4, p. 42. (Abstract.)

1949. The role of the distal tip of the gonopodium during the copulatory act of the viviparous teleost *Platypoecilus maculatus*. Anat. Rec., vol. 105, no. 3, pp. 26–27. (Abstract.)

[MS.] The sexual behavior of two sympatric species of xiphophorin fishes and their laboratory induced hybrids, with an analysis of the isolating mechanism.

FRASER-BRUNNER, A.

[1947.] The guppy. An "Aquarist" Booklet, Buckley Press, Ltd., Middlesex, England.

GORDON, MYRON, AND DONN ERIC ROSEN
1951. Genetics of species differences in the morphology of the male genitalia of xiphophorin fishes. Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 409–464.
HENN, A. W.
1916. On various South American poeciliid fishes. Ann. Carnegie Mus., vol. 10, pp. 93–142.
PURSER, G. L.
1941. Sex-dimorphism in the fins of *Lebistes reticulatus*. Jour. Quekett Micro. Club, ser. 4, vol. 1, pp. 172-178.
ROSEN, DONN E., AND MYRON GORDON
[MS.] Gonopodial adaptations and speciation in the xiphophorin fishes.