Proceedings of the Iowa Academy of Science

Volume 69 | Annual Issue   Article 87

1962

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Recommended Citation

Schiller, E. L. 1959c. Experimental studies on morphological variation in the cestode genus *Hymenolepis*. III. X-irradiation as a mechanism for facilitating analyses in *H. nana*. Exp. Par. 8-427-470.

Voge, M., and Heyneman, D. 1957. Development of *Hymenolepis nana* and *Hymenolepis diminuta* (Cestoda: Hymenolepididae) in the intermediate host *Tribolium confusum*. University of California Publications in Zoology 59:549-579.

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Development and Comparative Morphology of the Gonopodium of Goodeid Fishes[1]

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Abstract. The Goodeidae, one of four families of the cyprinodont fishes and all of whose species are viviparous, have a modified anal fin in males for intromission of sperm. This gonopodium, with structures specific for each species, develop under the dual controls of genetically determined patterns and endogenous androgenic hormones. In males of all species of the family, rays 2 to 7 of the anal fin are shorter than the other rays and in some species they are single instead of bifurcated. The rays of this complex are strongly recurved and slender in some species. A comparative study of rays 2 to 7 in adult males of different species reveals that the primitive unspecialized structure of the juvenile fin is basic and that, in the modifications in the male fin, evolution has proceeded independently and in varying degrees in the several subfamilies.

INTRODUCTION

Four of the families of the cyprinodont fishes have developed independently ovoviviparity or viviparity. Internal fertilization, essential to these types of reproduction, occurs in each family and in each, parts of the anal fin of the male have become modified for the purpose of intromission of sperm. These specialized structures, known as gonopodia, are radically different in structure and in use in the four families. In the family Poeciliidae rays 3, 4, and 5 of the anal fin are elongated and in addition there are ray enlargements, fusions of rays and additions in specific positions of hooks, spines, serrations and other structures which are species specific. Taxonomists have taken advantage of this specificity to use the characters for the separation of genera and

species. Numerous studies have been made on the endocrine control of the development of the gonopodial features by the senior author. A study of the development of the gonopodium and the adult morphology has now been completed by the senior author and will be published soon. Induction of male characters in the anal fins of females of this species by steroid hormones has been carried out successfully.

Attention has been given to the peculiarities of the male anal fin of the Goodeidae since the taxonomic importance of the specialized anal fin of the male has been recognized. Recent studies (Hubbs and Turner, 1939), (de Buen, 1942), (Alvarez, 1949), have used male anal fin features for taxonomic purposes but no studies have been made to date comparable to those on the Poeciliidae on the development and comparative morphology of the gonopodium in the various species of the Goodeidae. The present study has been made to: 1) compare the skeletal structure of the gonopodium in the various species of the Goodeidae, 2) study the morphogenesis of the gonopodium in a single species, and 3) lay a ground work for endocrinological studies on the control of morphogenesis by androgenic hormones.

MATERIALS AND METHODS

Most of the specimens used in this work were collected in the field in Mexico and fixed in formalin. Some of the species were donated by the Museum of Zoology, University of Michigan. A breeding stock of *Characodon eisen*[5], collected in Mexico by Dr. Robert Miller of the Museum of Zoology, University of Michigan, and maintained at Grinnell College by Dr. Mendoza, has furnished the material for the developmental study. Anal fins were dissected out, the rays stained with alizarin and then cleared for study in glycerine. The drawings are camera lucida tracings of the fin rays.

MORPHOGENESIS OF THE ANAL FIN

This description of the development of the anal fin is confined to changes in the rays of the fins of males and females of *Characodon eiseni* from the time of birth until the specimens have become sexually mature.

At birth the fin contains fifteen rays and rarely an additional ray at the posterior end of the fin. The first and the last rays are much shorter than the others. There is no appreciable difference between male and female fins at this stage.

Sixty days after birth there are still no marked differences be-

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[5] The classification of this species is uncertain and its taxonomic position is being studied by Miller and Mendoza. It probably belongs to the genus *Xenotoca* instead of *Characodon* but the name *Characodon eiseni* will be used for this species in this paper.

tween the fins of males and females in regard to length of rays (Diagrams I and II). There is a difference, however, that involves bifurcation of rays. In the male of this age all of the rays of the fin are single and unbranched. In the female, rays 3 to 14 are bifurcated, the branches carrying from one to three segments.
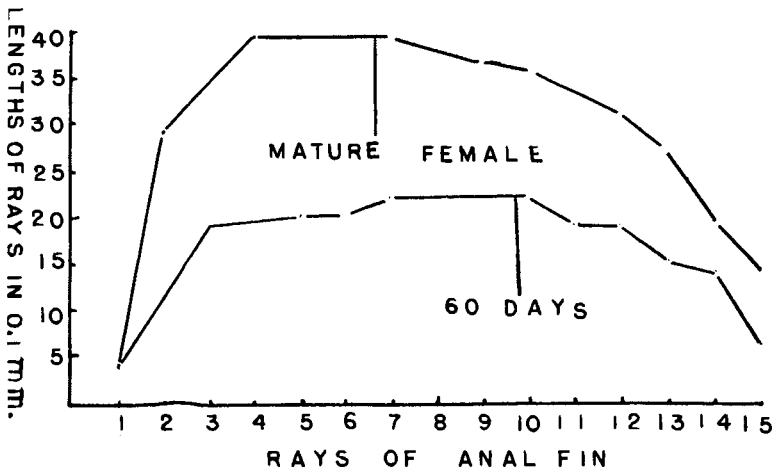
DIAGRAM I

Diagram I
Diagram illustrating length of the rays in anal fins of a female of *Characodon eiseni* in a specimen 60 days after birth and a mature female 42 mm in standard length.

There is a steady growth of the fin in the female (Diagram I) characterized by elongation of rays and terminal addition of segments, particularly in rays 3 to 12, and secondary and even tertiary branching of rays in older specimens. In the adult female the fin is rounded at the margins with the region containing rays 2 to 12 somewhat longer. Rays 4, 5, 6, and 7 are longest in a mature female. There is also a progressive anchylosis of basal segments in all rays, the fusion reaching the point of the primary bifurcation in old specimens.

The first indication of sexual dimorphism in the anal fin appears in the developing young at about 60 days after birth. Between birth and the 60-day stage there is some increase in the length of all rays in both males and females but there is no significant difference between the sexes (Diagrams I and II). At this stage all of the rays of the anal fins of males are single linear units, but in females of a comparable age rays 3 to 14 are branched, each branch containing one to three segments. It appears, particularly in the light of this sexual difference in later stages, that at this stage some agent is effective in preventing

bifurcation of rays in the male fin and that the effect extends to all rays except the extreme anterior and posterior ones.

Seventy-eight days after birth the effect of the retarding agent upon bifurcation of rays in male fins is localized in the area containing rays 2 to 7 (Diagram II). Rays 8 to 13 have become bifurcated and from this stage on to maturity they follow the same course of development as rays in a female fin.

Another sexual difference appears at this stage in the area containing rays 2 to 7. Rays 2, 3, and 4 have become barely elongated during the interval between 60 and 78 days after birth (Diagram II). Rays 5, 6, and 7 have elongated somewhat more than rays 2, 3, and 4 but not as much as the comparable rays in a female fin of the same age (Diagrams I and II). It is apparent that a retarding influence is being exerted upon the rays in the 2- to 7-ray complex and that at this stage the retardation is greater upon rays 2, 3, and 4.

DIAGRAM II

Diagram II
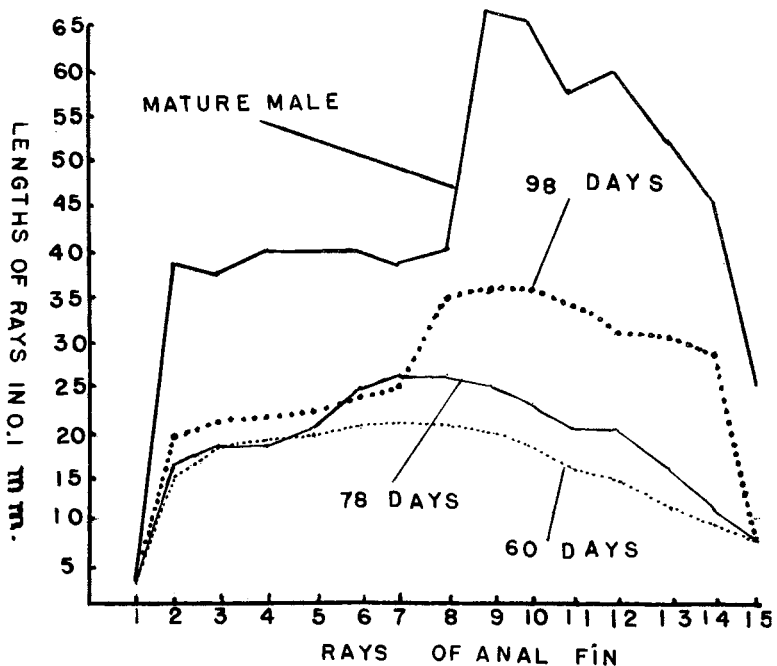Diagram illustrating the lengths of the rays in the anal fin of a male *Characodon eiseni*. Attention is directed particularly to rays 2 to 7 in the specimens 60, 78, and 98 days after birth and to rays 2 to 8 in mature specimens. Comparisons with other rays of the male fin and with comparable rays in the female fins shown in Diagram I will demonstrate the degree of abbreviation of rays in the 2 to 7 complex.

As females become mature a differential growth rate develops in the rays of the anal fin with rays 3 to 10 becoming somewhat longer than the others (Diagram I).

The anal fin of the male offers a sharp contrast in development (Diagram II). The retardation of growth in the 2- to 7-ray complex becomes quite pronounced in a male 98 days old. The rays of the remainder of the fin continue to elongate and to bifurcate as they do in female fins. The effect of retardation upon the rays in the 2- to 7-ray complex is continuous throughout gonopodial development but it is not total, the rays continuing to grow at a rate which is slow compared to that of rays 8 to 15. The rays of the 2 to 7 complex in a mature male of 55 mm in standard length are more than twice as long as they were at 60 days of age, and they contrast sharply in length with the longer rays of the male fin and with comparable rays in the female fin. An interesting feature of the area in which retardation of growth occurs is the extension of the area posteriorly as development of the fin progresses so that ray 8 becomes included in the area.

Some minor sexual differences developing in the morphogenesis of the anal fin are: crowding of rays in the anterior portion, thickness of rays, anchylosis of basal segments, and recurvature of rays. Anchylosis of basal segments begins at an early stage and is apparent in both males and females at the age of 60 days. From this stage to maturity there is a progressive anchylosis in the rays of females. The progress of basal segment fusion in rays 2 to 5 is slow but it is relatively rapid in rays 6 and 7, producing in mature females a marked difference in the lengths of the fused bases of rays 5 and 6 (Fig. 13). This feature, present in males also (Fig. 6) but not so prominent, is a unique character by which goodeid fishes may be recognized. Rays of the 2 to 7 complex in males remain thin with segments little fused so that this portion of the fin is flexible and movable in contrast to the more rigid condition in the comparable part of the fin of the female. Crowding of rays in the area persists to some extent in both males and females but it is more conspicuous in males. Recurvature likewise is better developed in male fins. It is developed only slightly in mature males of some species (Fig. 5) but it is exaggerated in others (Fig. 8).

COMPARATIVE STRUCTURE OF MALE ANAL FINS

No males of the Goodeidae now possess what was probably the most primitive condition of the anal fin. Presumably the condition would be one in which the structures would resemble closely those of the female. Specializations in the male fin have involved: 1) Prevention of bifurcation in rays 2 to 7, 2) Retardation of growth in the same rays, 3) Recurvature of all or a part

of the rays of the 2 to 7 complex. To a lesser extent three other specializations are involved: 1) Increase or decrease of the diameter of some or all of the rays of the complex, 2) Crowding of the rays so that they occupy less space on the fin and, 3) More or less anchylosis of the basal segments of some of the rays in the anal fin.

Prevention of bifurcation. In the account of the development of the anal fin in males and females of *Characodon eiseni* it was demonstrated that bifurcation of all rays except 1, 2, and 15 undergo bifurcation in the female at about 60 days after birth but that rays 2 to 7 undergo bifurcation in the male. It was assumed that an area of susceptible tissue involving the terminal parts of these rays existed in all males, and possibly in females as well, and that some effective agent acted upon this target area preventing bifurcation of the rays. The effective agent is probably an endogenous androgenic hormone secreted by the testis as it is in two other families (Poeciliidae and Jenynsiidae) in this order of fishes. In other species, if the agent were weak or the area was weakly susceptible to the agent, the effect would be less pronounced. Those species might be considered primitive in which the male fin most closely resembled that of the female.

Table I. Distribution in subfamilies and in some species of bifurcation in rays 1 to 7 in the anal fins of adult males. B indicates a bifurcated ray. Several species described in the text are not included in the table.

Species	Rays 1 to 7 of the anal fin							Sub family
	1	2	3	4	5	6	7	
Ataeniobius toweri			B	B	B	B	B	Ataeniobiinae
Characodon lateralis								Characodontinae
Allotoca dugesii								
Neoophorus diazi			B	B	B	B	B	Goodeinae I
Goodea luitpoldii			B	B	B	B	B	
Alloophorus robustus			B	B	B	B	B	
Chapalichthys encaustus				B	B	B		
Xenotoca variata								Goodeinae II
Zoogoneticus cuitzeoensis								
Characodon eiseni								
Balsadichthys whitei						B	B	
Skiffia lermae								
Neotoca bilineata								Girardinichthyinae
Girardinichthys inn.								
Lermichthys mult.								

In the subfamily Ataeniobiinae there is a single species, *Ataeniobius toweri*. The species may be considered primitive in respect to bifurcation of the critical rays of the 2 to 7 complex, for all of the rays except 2 are bifurcated in the adult male (Fig. I).

The subfamily Characodontinae also is represented by a single species, *Characodon lateralis*. None of the rays of the 2 to 7 complex in the anal fin of adult males (Fig. 11) is bifurcated

and the species is considered highly specialized, since all of these rays except 2, 3, and 4 are divided in the female (Fig. 15).

The species in the subfamily Goodeinae may be divided roughly into two groups on the basis of the type of trophotaeniae which each possesses (Table I). One group, represented in this study by *Neoophorus diazi, Goodea luitpoldii, Goodea atripinnis, Goodea gracilis,* and *Allotoca dugesii* have the rosette type of trophotaeinae while the other group, represented by *Xenoophorus exsul, Alloophorus robustus, Chapalichthys encaustus, Xenotoca variata, Zoogoneticus cuitzeoensis,* and *Characodon eiseni* have the ribbon type of trophotaeniae. In the first group (Table I) all species except *Allotoca dugesii* have rays 3 to 7 bifurcated in adult males (Figs. 9 and 10) while none of the these rays is branched in males of *Allotoca dugesii.* The latter is assumed to be highly specialized since it has departed most from the basic fin pattern exhibited in the females of the group (Fig. 12). In the second group (Table I) rays 3 to 7 are all branched in two species, *Xenoophorus exsul* and *Alloophorus robustus.* Rays 4, 5, and 6 of the fin in males of *Chapalichthys encaustus* are branched (Fig. 5) but in the other three species, *Xenotoca variata* (Fig. 3), *Zoogoneticus cuitzeoensis* (Fig. 4), and *Characodon eiseni* none of the first seven rays of the male fin is divided. Presumably in this group evolution has proceeded from the primitive type represented by *Xenoophorus, Allophorus,* and *Chapalichthys* in which all or most of the rays of the 2 to 7 complex are divided to a type represented by *Xenotoca, Zoogoneticus* and *Characodon eiseni* in which branching of these rays has been partially or completely supressed.

The members of the subfamily *Girardinichthyinae* (Table I) represented in this study fall into two distinct groups. In one group, composed of the genera *Allodontichthys, Skiffia, Neotoca, Girardinichthys,* and *Lermichthys* (Figs. 2, 6, 8), the 2- to 7-ray complex in adult males has only single, unbranched rays. In the other group, including *Balsadichthys xantusi* and *Xenotaenia resolanae,* all the members of the 2- to 7-ray complex are divided. *Balsadichthys whitei* is intermediate with bifurcations only in rays 6 and 7 (Fig. 7). *Xenotaenia resolanae* and *Balsadichthys xantusi* represent the more primitive condition found in the fins of females of the group (Fig. 13) with *Balsadichthys whitei* representing a stage of transition toward the specialized condition occurring in the other five species.

The mechanism of change from primitive to specialized structure in each of the groups described above appears to lie in the "bifurcation field." In the most specialized cases the target organ, the field, has developed a greater sensitivity to the retarding

influence of the androgenic hormone or the hormone has been increased in its potency.

Differential growth of the 2- to 7-ray complex. Ray 1 might be included in this complex as it is always shorter in adult males than in adult females. Ray 2 is properly included because it is segmented and is much shorter in males than it is in females, although it is not bifurcated in males of any species and in females only rarely.

It has been demonstrated in *Characodon eiseni* that males and females are practically identical in anal fin structure up to the age of 60 days (Diagrams I and II), At 78 days after birth there is a marked retardation in the males in rays 2, 3, and 4, some retardation in ray 5, but none in rays 6, 7, or 8. At 98 days after birth all of the rays of the 2 to 7 complex have elongated somewhat but all are retarded as compared to rays 8 to 14. In a fully matured male, 55 mm in standard length, the rays of the entire 2 to 8 complex are now roughly equal in length but much shorter than rays 9 to 14. However, they are longer than at any previous stage. The interpretation is offered that as the testis develops and the output of androgen increases, the field represented by the 2- to 8-ray complex is affected differentially while the remainder of the fin is not. It is assumed that there is a differential susceptibility in the 2- to 8-ray complex with rays 2, 3, and 4 being most susceptible to the retarding effect of the androgen and with rays 5 to 8 becoming progressively retarded as the concentration of androgen is increased in the developing testis.

In order to compare the degree of retardation of the 2 to 7 complex in males of different species it is necessary to compare the length of the rays in the complex with some unaffected fixed point in the remainder of the fin, representing the same point of departure in all species. The point selected is the level of the bifurcation point of ray 8 (Figs. 1 to 11). At the level of development in which the bifurcation occurred there was no retardation in the rays of the 2 to 7 complex and once the bifurcation had occurred the location was fixed and recognizable at any later stage of development. The ray of the 2 to 7 complex selected for comparison is either 5 or 6, whichever is the longer. Ray 7 is not selected because it is more variable than 5 and 6, being slightly shorter than 4, 5, or 6 in some species and forming the basis for a notch in the peripheral margin of the fin.

If a line is drawn through the bases of the rays 2 to 7 and another line parallel to it is drawn through the point of the bifurcation of ray 8, the projection of rays 2 to 7 distal to this second line will indicate approximately the elongations of the rays of

the 2 to 7 complex after that stage in development in which ray 8 became branched. The lengths of the rays within the complex may then be compared to each other or to the lengths of the rays in the unspecialized part of the fin.

The species in which the lengths of the rays of the 2- to 7-ray complex are least retarded possess the least sexual dimorphism in this respect. The least specialized are *Ataeniobius toweri* (Fig. 1), *Neophorus diazi* (Fig. 9), and *Alloophorus robustus*. These three species, in three separate groups, are also the least specialized in regard to the bifurcation of the rays of the 2 to 7 complex. The species showing the greatest degree of retardation of the complex in male fins are *Characodon lateralis* (Fig. 11), *Neotoca bilineata* (Fig. 6), and *Lermichthys multiradiatus*. *Goodea luitpoldii* (Fig. 10) shows a considerable degree of retardation and all of the others are intermediate.

There are two separate fields in which the rays of the 2 to 7 complex are involved. Each field, susceptible to the appropriate concentration of androgen, responds differentially. The "prevention of bifurcation" field originates first in development and, in *Charcodon eiseni*, involves rays 3 to 7 at the same time. There is no axis of differential susceptibility. The "retardation of growth" field in *Characodon eiseni* (Diagram II) is affected first at the 78-day stage with rays 2, 3, and 4 affected. When the male of this species is fully mature at 55 mm in standard length, rays 2 to 7, although retarded as compared to other rays of the fin, are double the length represented in the 98-day stage. It must be concluded that the retarding effect upon these rays is partial instead of total. Also in older males the retardation field will have extended to include ray 8.

A comparison of the anal fins of adult males of different species reveals that some species are relatively unspecialized in both features described above, some are specialized in both and in still other species one feature represents a high degree of specialization while the other does not. The genera having little specialization of either feature are *Ataeniobius* (Fig. 1), *Neoophorus* (Fig. 9), and *Allophorus*. Within the group of species studied, the species showing the highest degree of specialization in both characters are *Characodon lateralis* (Fig. 11), *Neotoca bilineata* (Fig. 6), and *Lermichthys multiradiatus*. *Goodea luitpoldii* illustrates a case in which inhibition of growth has occurred but bifurcation has not been prevented (Fig. 10). Increase in length of rays without bifurcation occurs in the rays of the 2 to 7 complex in several species, *Girardinichthys innominatus* (Fig. 2), *Zoogonelicus* (Fig. 4), and others; but the most extreme cases occur in *Skiffia lermae* (Fig. 8), *Xenotoca variata* (Fig. 3), and *Characodon eiseni* in which the critical rays con-

tinue to elongate and segment with bifurcation, doubling their length and adding as many as 7 new segments in stages later than the one in which the ray 8 became bifurcated.

Curvature and crowding of rays.

There is little difference among the females of the various species of the goodeid fishes in regard to curvature of the rays of the anal fin. There is a tendency for the rays to be parallel and straight (Fig. 14) or to curve slightly backward (Fig. 15).

In the anal fin of mature males of all species studied, the backward curvature of rays of the 2 to 7 complex is more noticeable than in females of the same species. Recurvature anteriorly of the distal half of the rays of the complex is present but slight in most species but it is exaggerated in *Skiffia lermae* (Fig. 8). Strong backward curvature, accompanied by recurvature anteriorly of the distal parts of the rays, is best developed in the members of the subfamilies *Girardinichthyinae* and *Characodontinae* and is most completely developed in *Neotoca* (Fig. 6), *Characodon lateralis* (Fig. 11), and *Skiffia lermae* (Fig. 8). Specialization in regard to recurvature and crowding of the recurved rays appears to accompany specialization in abbreviation and bifurcation of rays. In practically every case in which crowding has occurred, there has been a decrease in the diameter of the crowded rays (Figs. 6, 8, and 11); but single rays (ray 2 in Fig. 8) may sometimes become enlarged to serve for the attachment of large muscles.

DISCUSSION

Endrocrinological Interpretations. It has been shown that gonopodial differences in poeciliid fishes are so constant that they may be used for species separation in taxonomy. It has been demonstrated also that development of specific differential features is mediated through the endogenous androgenic hormones from the developing testis. Conclusive results have been obtained in *Xiphophorus, Platypoecilous, Gambusia, Lebistes* and *Mollienisia* by experiments involving castration and administration of androgenic hormones. It seems likely that the same principle operates in many other species of poeciliid fishes. In these experiments it became apparent that specific concentrations of androgenic hormones were responsible for the development of specific areas in the gonopodium. Unpublished results of similar experiments with another species in another family of viviparous cyprinodont fishes (*Jenynsia lineata,* family Jenynsiidae) indicate that androgenic hormones operate in the same way in the metamorphosis of the anal fin of the male into a gonopodium. Although experimental work on the goodeid fishes has not yet proved that androgenic hormones are concerned in the develop-

ment of the peculiarities of the anal fin in males of different species, there is little doubt that endogenous androgenic hormones from the developing testis act upon target areas of the developing anal fin in members of this family also. Morphological differences in the anal fins of different species would be assignable in part to genetic differences in the target areas themselves, and partly to the reactions of the target areas to appropriate concentrations of endogenous androgenic hormones.

Zoogeographical interpretations. The goodeid fishes are a relatively small family of the Cyprinodontidae and their geographical range is limited. They occur only in the waters of the Mexican plateau and some immediately adjacent lowland streams. Some facts have been deduced concerning migration and isolation of various species but in general the zoogeographical picture is a confusing one. This study supports at least one of the theories concerning distribution but it also raises more questions than it answers.

In a study of the geographical distribution of the members of the subfamily Girardinichthyinae (Turner, 1946) it was postulated that the subfamily originated in the lowland in the area southwest of the plateau near the city of Colima and that new genera arising in this center migrated up and down the coast, up coastal rivers and also into the plateau. The plateau stock then migrated eastward in the plateau with speciation occurring as local barriers produced geographical isolation. The conclusions were based upon a study of ovarian and trophotaenial structures but the present study of gonopodial structure supports these views on the geographical distribution and permits some extension of the details. Presumably the old lowland stock became divided into two groups before migration occurred. *Illyodon furcidens* and *Balsadichthys xantusi* represent the primative condition in the male anal fin with bifurcation in the rays of the 2 to 7 complex and little shortening of these rays. These two species are closely related as hybridization between them occurs freely. This stock did not migrate. *Xenotaenia,* retaining the primitive condition, migrated northward along the coast. Specialization in the direction of shortening the rays of the 2 to 7 complex and prevention of bifurcation in some of these rays began with production of a species (*Balsadichthys whitei,* Fig. 7) which then migrated down the coast to the mouth of the Balsas River and up the Balsas River for several hundred miles to its headwaters in the vicinity of Cuautla. Further specialization in the original lowland center produced a species in which bifurcation of the rays of the 2 to 7 complex in the male was completely suppressed. *Allodontichthys,* remaining in the original site, represents this stock, one strain of which migrated into the plateau.

Ataeniobius toweri possesses the most primitive gonopodial structure in the goodeid family. It was recognized as a primitive group by Hubbs and Turner (1939, p. 39) because of the absence of the trophotaenia and the presence of a well-developed fin fold. It was postulated that this species, occurring only in the Rio Verde, a tributary of the Panuco River, represented an early off-shoot of the stock from which all of the other goodeid arose. The fact that another genus *Xenoophorus* has a primitive gonopodial structure and that it lies partly within the Panuco River system nearby suggests that there may be a close relationship between the two and that this northeastern corner of the plateau may have been another point of entry into the plateau.

Characodon lateralis poses a complete enigma in its location. It is isolated in a restricted area in the northwestern part of the plateau near Durango where it occurs in small lakes and in the headwaters of the Rio Mesquital. It has all of the goodeid characteristics and possesses a highly-specialized gonopod. Presumably the area it occupies was joined at one time to the area to the east and south where the other more generalized goodeids are located. It might be postulated that an an earlier period the intervening plateau was well-watered instead of arid and that the more generalized forms from which *Characodon* arose are now extinct or may still exist in isolated springs or water holes in the region between the range of *Characodon* and the area occupied by the other goodeids.

There appears to be no rational relation between gonopodial types and geography in the body of the plateau itself. Except for the members of the subfamily Giradinichthyinae there appears to be no morphological trend which can be associated with a migrational direction. Some forms with very generalized gonopodia are tightly restricted in range (*Chapalichthys*) while others range widely (*Allophorus*). Some species with very specialized gonopodia have closely restricted ranges (*Skiffia lermae*), but a wide distribution is found in some forms (*Neotoca*) with highly specialized anal structures.

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EXPLANATION OF FIGURES

All figures include rays 1 to 8 of the anal fin. The other rays of the fin are omitted. Only rays 1 and 8 are numbered. A 1 mm scale appears with each figure to indicate the scale of magnification.
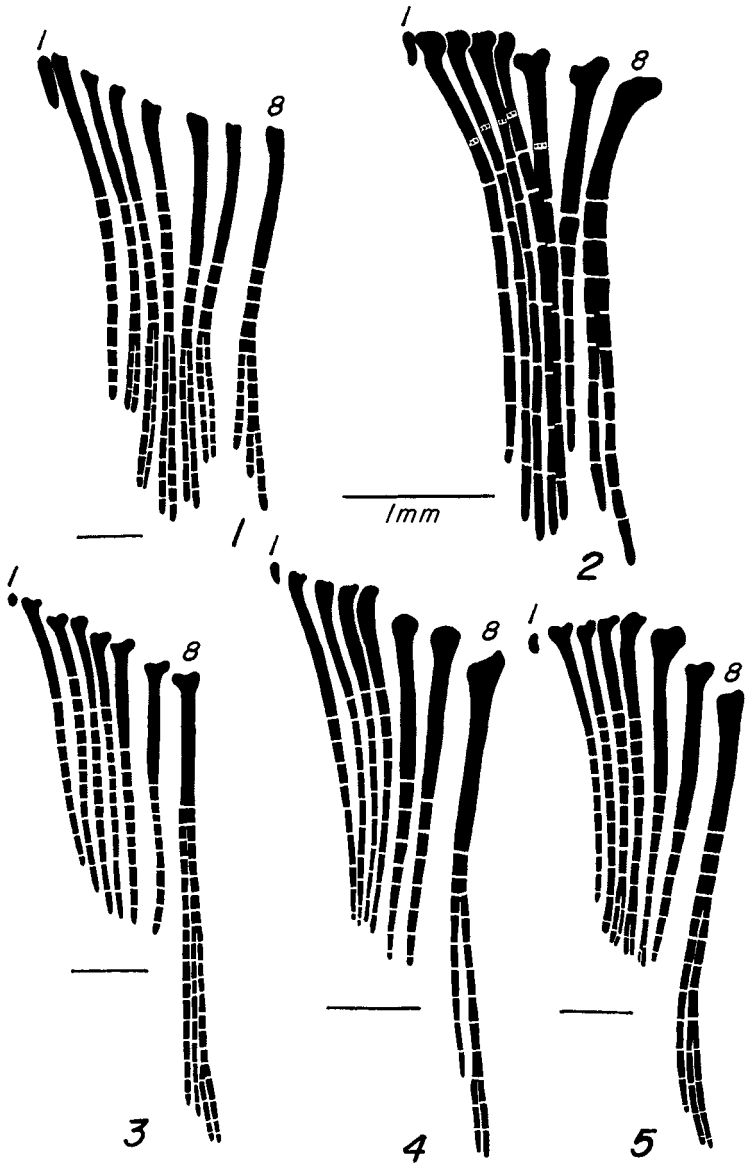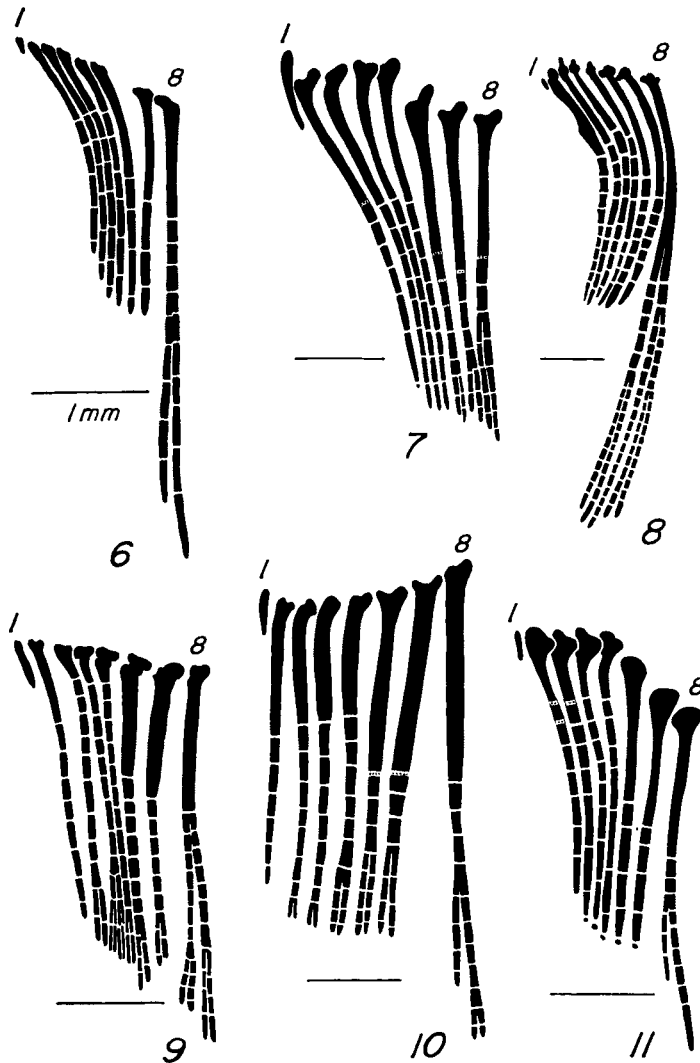
Plate 1

Figure 1. Rays of the anal fin of mature male of *Ataeniobius toweri*.
Figure 2. Rays of the anal fin of adult male of *Girardinichthys innominatus*.
Figure 3. Anal fin rays of mature male of *Xenotoca variata*.
Figure 4. Rays 1 to 8 of the anal fin of a mature *Zoogoneticus cuitzeoensis*.
Figure 5. Anal fin rays 1 to 8 of a mature male of *Chapalichthys encaustus*.

Plate 2

Figure 6. Anal fins of mature male of *Neotoca bilineata.*

Figure 7. First 8 anal fin rays of mature male of *Balsadichthys whitei.*

Figure 8. Rays of the anal fin of *Skiffia lermae* illustrating an extreme case of abbreviated, recurved and crowded single rays of the 2- to 7-ray complex.

Figure 9. Anal fin rays of mature male of *Neophorus diazi.* Rays 3, 4, 5, 6, and 7 resemble those of the female in being relatively long and bifurcated.

Figure 10. Anal fin 1 to 8 in 9 small mature male of *Goodea luitpoldii.*

Figure 11. Rays 1 ot 8 of the highly specialized male anal fin of *Characodon lateralis.*
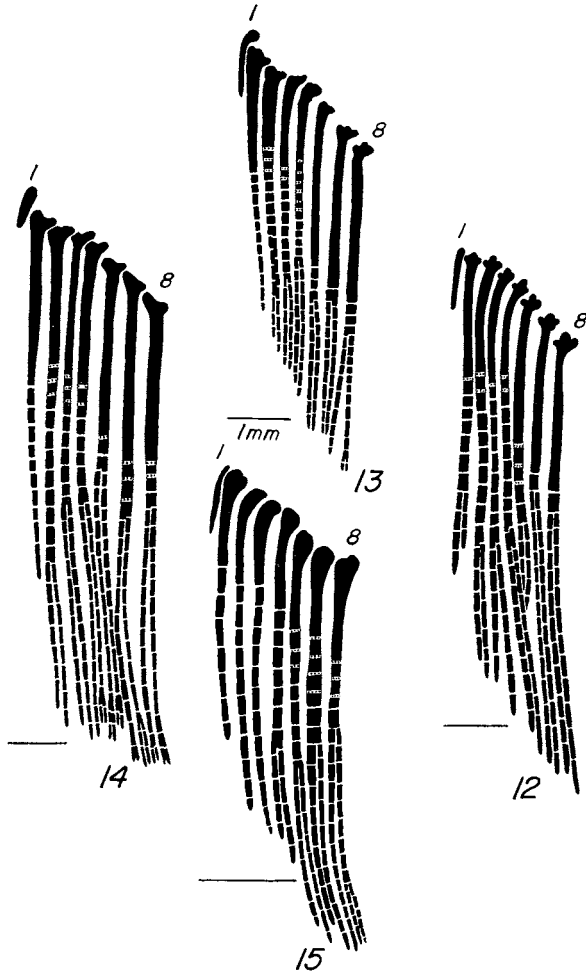
Plate 3

Figure 12. First eight rays of anal fin in mature female of *Goodea luitpoldii*.

Figure 13. Rays 1 to 8 in anal fin of mature female of *Balsadichthys whitei*.

Figure 14. Anterior eight rays of anal fin of adult female of *Chapalichthys encaustus*.

Figure 15. First eight rays of anal fin of mature female of *Characodon lateralis*. Note that rays 2, 3, and 4 are not bifurcated as they are in mature females of other subfamilies.

Female fins shown in plate 3 may be contrasted with male fins shown in other figures as follows:

—Figure 12 with Figure 10
—Figure 13 with Figure 7
—Figure 14 with Figure 5
—Figure 15 with Figure 11