BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 5 Number 4

MIDDLE-AMERICAN POECILIID FISHES OF THE GENUS XIPHOPHORUS

Donn Eric Rosen

1853

UNIVERSITY OF FLORIDA
Gainesville
1960

The numbers of THE BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

All communications concerning purchase or exchange of the publication should be addressed to the Curator of Biological Sciences, Florida State Museum, Seagle Building, Gainesville, Florida. Manuscripts should be sent to the Editor of the BULLETIN, Flint Hall, University of Florida, Gainesville, Florida.

Published 14 June 1960 Price for this issue $2.80

MIDDLE-AMERICAN POECILIID FISHES OF THE GENUS *XIPHOPHORUS*

DONN ERIC ROSEN[1]

SYNOPSIS. Drawing upon information from the present studies of the comparative and functional morphology, distribution, and ecology of the forms of *Xiphophorus* (Cyprinodontiformes: Poeciliidae) and those made during the last quarter of a century on their genetics, cytology, embryology, endocrinology, and ethology, the species are classified and arranged to indicate their probable phylogenetic relationships. Their evolution and zoogeography are considered in relation to a proposed center of adaptive radiation on Mexico's Atlantic coastal plain. Five new forms are described: *X. variatus evelynae*, new subspecies; *X. milleri*, new species; *X. montezumae cortezi*, new subspecies; *X. pygmaeus nigrensis*, new subspecies; *X. helleri alvarezi*, new subspecies.

To the memory of

MYRON GORDON, 1899-1959

for his quarter century of contributions to
the biology of this and other groups of fishes.

---

[1] This paper is a revision of a thesis presented to the Biology Department of the Graduate School of Arts and Sciences of New York University in partial fulfillment of the Ph.D. degree. The work was carried out while the author was associated with New York University and the Genetics Laboratory of the New York Aquarium. It was supported by a National Science Foundation grant to the New York Zoological Society for Dr. Myron Gordon (project: A Biological Synthesis of the Poeciliid Fishes). Now at the University of Florida, the author serves the Department of Biology as Assistant Professor and the Florida State Museum as Assistant Curator of Natural Sciences. Manuscript submitted 24 July 1959.

TABLE OF CONTENTS

PAGE
Introduction 59
Acknowledgments 61
Materials and methods 62
The genus *Xiphophorus* 64
Accounts of the species and subspecies 66
  Xiphophorus couchianus (Girard) 66
  Xiphophorus maculatus (Guenther) 69
  Xiphophorus variatus (Meek) 78
    Xiphophorus variatus xiphidium (Gordon) 81
    Xiphophorus variatus variatus (Meek) 84
    Xiphophorus variatus evelynae, new subspecies 87
  Xiphophorus milleri, new species 89
  Xiphophorus montezumae Jordan and Snyder 92
    Xiphophorus montezumae montezumae Jordan and Snyder 93
    Xiphophorus montezumae cortezi, new subspecies 96
  Xiphophorus pygmaeus Hubbs and Gordon 98
    Xiphophorus pygmaeus nigrensis, new subspecies 100
    Xiphophorus pygmaeus pygmaeus Hubbs and Gordon 102
  Xiphophorus clemenciae Alvarez 104
  Xiphophorus helleri Heckel 106
    Xiphophorus helleri helleri Heckel 116
    Xiphophorus helleri strigatus Regan 118
    Xiphophorus helleri guentheri Jordan and Evermann 122
    Xiphophorus helleri alvarezi, new subspecies 126
Distribution and ecology of *Xiphophorus* 156
  Distribution patterns of *Xiphophorus* in relation to habitat preferences 156
    Ecological restrictions 156
    Types of topographical and ecological isolation 162
    Adaptive modifications to the environment and patterns of distribution 169
  Routes of dispersal 172
Relationships within *Xiphophorus* 175
  Assessment of characters 175
    Gonopodium 175
    Pigmentation 180
    Metamerism and body form in relation to habitat 182
    Comparative behavior 188
    Skeletal elements 189
  Viability, development, and morphology of interspecific hybrids as systematic criteria in *Xiphophorus* 201
    Embryonic development, fertility, and sexuality of interspecific hybrids in relation to their genetic background 201
    Pigment cell abnormalities in hybrids 205
    Abnormalities of the external genitalia of hybrids 208
  Species groups in *Xiphophorus* 212
    The *maculatus* species group (*couchianus, maculatus, variatus*) 214
    The *montezumae* species groups (*milleri, montezumae, pygmaeus*) 216
    The *helleri* species group (*clemenciae, helleri*) 218
Summary and conclusions 219
Appendix 1: Notes on meristic characters 223
Appendix 2: Key to the species *Xiphophorus* 226
Literature cited 229

INTRODUCTION

The genus *Xiphophorus* (Cyprinodontiformes: Poeciliidae), which includes the platyfishes and swordtails, presents an exceptional opportunity for taxonomic research. It is outstanding among fish groups in that its natural range is comparatively well known and its members adapt readily to laboratory conditions. During the last quarter century it has been the subject of an unusual number of diverse experimental and descriptive studies. Investigations of its genetics, cytology, embryology, endocrinology, and ethology have produced a background of general biological information that gives an added perspective to the basic morphologic and zoogeographic criteria of the taxonomist. The objective of this revision is a systematic reappraisal of *Xiphophorus* that combines data from all these diverse yet complementary fields. The following species and subspecies are recognized:

- *Xiphophorus couchianus* (Girard) (Northern platyfish)
- *Xiphophorus maculatus* (Guenther) (Southern platyfish)
- *Xiphophorus variatus* (Meek) (Variable platyfish)
    - *Xiphophorus variatus variatus* (Meek)
    - *Xiphophorus variatus evelynae*, new subspecies
    - *Xiphophorus variatus xiphidium* (Gordon)
- *Xiphophorus milleri*, new species (Catemaco livebearer)
- *Xiphophorus montezumae* Jordan and Snyder (Montezuma swordtail)
    - *Xiphophorus montezumae montezumae* Jordon and Snyder
    - *Xiphophorus montezumae cortezi*, new subspecies
- *Xiphophorus pygmaeus* Hubbs and Gordon (Pygmy swordtail)
    - *Xiphophorus pygmaeus pygmaeus* Hubbs and Gordon
    - *Xiphophorus pygmaeus nigrensis*, new subspecies
- *Xiphophorus clemenciae* Alvarez (Yellow swordtail)
- *Xiphophorus helleri* Heckel (Green swordtail)
    - *Xiphophorus helleri helleri* Heckel
    - *Xiphophorus helleri strigatus* Regan
    - *Xiphophorus helleri guentheri* Jordan and Evermann
    - *Xiphophorus helleri alvarezi*, new subspecies

The formal generic separation of the swordtails (*Xiphophorus* Heckel, 1848) and the platyfishes (*Platypoecilus* Guenther, 1866) grew unchallenged out of early imperfect diagnoses of the species for which the two genera were first erected . *Xiphophorus* was applied by Heckel to three quite unrelated forms, *X. helleri, Pseudoxiphophorus bimaculatus,* and *Gambusia gracilis*, a species of uncertain status. Weyenburgh (1874) described three new forms as *Xiphophorus Heckelii*, *X. obscurus* and *X. minor*, species since assigned to the Jenynsiidae. For many years, *Platypoecilus* was misapplied to various cyprinodontiforms, as follows:

Platypoecilus mentalis Gill (1876: 335) = *Mollienesia sphenops* Cuvier and Valenciennes, a poeciliid.

Platypoecilus quitzeoensis Bean (1898: 540, 1 fig.) = *Zoogoneticus quitzeoensis* (Bean), a goodeid.

Platypoecilus nelsoni Meek (1904: 147, Fig. 46) = *Mollienesia sphenops* Cuvier and Valenciennes, a poeciliid.

Platypoecilus perugiae Evermann and Clark (1906: 851-52, Fig. 1) = *Limia perugiae* (Evermann and Clark), a poeciliid.

Platypoecilus dominicensis Evermann and Clark (1906: 852-53, Fig. 2) = *Mollienesia (Psychropoecilia) dominicensis* (Evermann and Clark), a poeciliid.

Platypoecilus tropicus Meek (1907: 146-47) = *Mollienesia sphenops* Cuvier and Valenciennes, a poeciliid.

The above corrections in identification were indicated by Meek (1902, 1904), Regan (1907, 1913), and Myers (1935). Not until the gonopodial characters of the Poeciliidae were thoroughly studied (Regan, 1913) were the relationships of *Platypoecilus* demonstrated.

Early knowledge of *Xiphophorus* came largely from its comparison with *Poecilia* and *Mollienesia* to which some thought it bore a close relationship. The delimiting criteria for *Poecilia* eventually served also, in part, for *Xiphophorus*. When *Platypoecilus* was named during this early period and separated nomenclaturally from *Poecilia* and its allies, it was natural to regard *Platypoecilus* and *Xiphophorus* as distinct.

Summarizing the historical events up to 1911, three distinct groups of *Xiphophorus* (as presently constituted) were formally recognized, largely on the basis of their fin structure and dentition. 1) Both *helleri* and *montezumae* possess the caudal appendage or sword and biserial dentition (*Xiphophorus*); 2) *maculatus* and *variatus* lack a sword and have but a single series of small teeth (*Platypoecilus*); 3) *couchianus* also lacks the sword but possesses biserial dentition (*Poecilia*).

Regan (1913) decided that the species of *Platypoecilus* and *Xiphophorus*, which previously had been widely separated, were in reality closely related. He also showed that the alleged dentitional differences in the two genera are not real, and that all the members of both genera do, in fact, have biserial dentition, a fact which was presaged when he (1907) distinguished between an outer row and inner band of teeth in *P. maculatus*. He showed that *Xiphophorus helleri* Heckel (1848) and *Xiphophorus montezumae* Jordan and Snyder (1899) were correctly associated as were *Platypoecilus maculatus* Guenther (1866) and *Platypoecilus couchianus* (Girard, 1859).

Langer (1913), after analyzing the anatomy of the gonopodia and their suspensoria in *Xiphophorus helleri* and *Platypoecilus maculatus*, suggested joining the genera, but did not do so. The similarity of these genera was appreciated also by Hubbs (1924) who erected the tribe Xiphophorini to contain them.

When Hubbs and Gordon (1943) described *Xiphophorus pygmaeus,* they pointed out that the distinctions between *Platypoecilus* and *Xiphophorus* are uncertain, and assigned *pygmaeus* to the older genus, *Xiphophorus,* in anticipation of possible taxonomic joining of the platyfishes and swordtails.

Gordon and Rosen (1951) studied the genetics of species differences in the morphology of the gonopodia of two "structurally divergent" species, *X. helleri* and *P. maculatus.* They pointed out that even the measurable differences in genital structure between these two species were not sufficient to prevent hybridization under laboratory conditions. They recommended that, in view of the genetic continuity within the xiphophorin species, a single generic term, *Xiphophorus,* be applied to them all. They suggested, however, that the name *Platypoecilus* be retained as a subgeneric grouping to reflect what they believed to be a real but subtle difference between the platyfishes and swordtails, though statistical and taxonomic evaluations showed no line of demarcation between them.

It is now believed that even subgeneric separation is unwarranted.

ACKNOWLEDGMENTS

It is with great pleasure that I extend my warmest thanks to many persons whose generosity and interest facilitated this work. I am particularly indebted to the late Myron Gordon under whose guidance this work was begun. In addition to making available an unusual variety of equipment and technical facilities, and an always congenial and stimulating atmosphere in which to work, Dr. Gordon provided for my use much unpublished information on the biology of this group of fishes. Among other things, this included a folder of typewritten material relating to the ecology, distribution, and polymorphism of six of the eight recognized species of *Xiphophorus.* These notes have been incorporated wherever possible.

To Reeve M. Bailey I offer special thanks for numerous stimulating discussions of the present study and for reviewing in detail the manuscript as a whole during the final stages of the work. For reading and criticizing various parts of the manuscript I thank James W. Atz, H. Clark Dalton, Hugh M. Gordon, Robert R. Miller, Bobb Schaeffer, and Pamela Alexander.

Robert R. Miller brought to my attention material from two of his recent expeditions to Middle America that included a new species of *Xiphophorus*. I also thank Carl L. Hubbs for making available detailed locality maps of his and Myron Gordon's early collections of *Xiphophorus* in Mexico.

For the loans or gifts of specimens used in this study, I thank Jose Alvarez del Villar, Reeve M. Bailey, James Boehlke, Richard T. Gregg, Ernest A. Lachner, Robert R. Miller, George S. Myers, Leonard P. Schultz, William I. Follett, Loren P. Woods, Myvanwy Dick, and Margaret Story, and the institutions that they represent: The Academy of Natural Sciences of Philadelphia, California Academy of Sciences, Chicago Natural History Museum, Louisiana State University Museum of Zoology, Museum of Comparative Zoology, Stanford University Natural History Museum, United States National Museum, and the University of Michigan Museum of Zoology.

To my wife, Mel, I extend deepest thanks for her editorial aid. Elwood Logan supplied numerous and excellent photographic services.

MATERIALS AND METHODS

MATERIAL. Preserved material of *Xiphophorus* used in this study is from the University of Michigan Museum of Zoology (UMMZ), Louisiana State University Museum of Zoology (LSU), United States National Museum (USNM), Stanford University of Natural History Museum (SU), Chicago Natural History Museum (CNHM), and the Academy of Natural Sciences of Philadelphia (ANSP). Many specimens formerly maintained in the collection of the Genetics Laboratory of the New York Zoological Society have been deposited in the University of Michigan Museum of Zoology; these are herein designated by the symbol UMMZ-NYZS-GL.

Laboratory born and reared inter- and intra-specific hybrids of *Xiphophorus* also were studied (table 34); this is the same material examined in greater detail by Atz (Ms.) in his analyses of the effects of hybridization in this genus.

Laboratory reared descendants of wild caught fish also were analyzed. Living *Xiphophorus* maintained in the Genetics Laboratory of the New York Aquarium were derived from nine expeditions to Mexico and northern Central America, as follows:

Clarence L. Turner and party, 1932; Mexico.
Myron Gordon, John Ross, and Joseph Whetzel, 1932; Mexico.
Myron and Evelyn Gordon, and James W. Atz, 1939; Mexico.
Myron Gordon, James W. Atz, and Forest G. Wood, 1948; Mexico.

Myron Gordon and Gerald Fairweather, 1949; British Honduras.
Myron Gordon and Alphonse Chable, 1951; Honduras.
Myron Gordon and Jesus Garcia, 1952; Mexico.
Myron Gordon and party, 1954; British Honduras and Guatemala.
Myron Gordon, Malcolm Gordon, and Donn E. Rosen, 1957; Mexico.

COUNTS AND MEASUREMENTS. The methods of counting and measuring are those described by Miller (1948: 8-14). Dorsal fin ray counts include small anterior rays; the last ray as counted actually consists of two lepidotrichia that are separate to their bases. Scales in a lateral series are counted from the upper angle of the gill aperture to the caudal base at midside; each scale in this row almost invariably contains a central pit. The vertebral count includes all cervical elements as well as the urostylar vertebra. Standard length is measured from snout tip to caudal base. Head length is taken to the opercular margin. Length of caudal peduncle is measured from the anal origin to the caudal base at midside. Greatest depth is taken from the origin of the dorsal to the origin of the anal fin. Least depth is taken across the caudal peduncle just forward of the caudal base. Caudal fin length is measured from the caudal base to the distal tip of the longest bifurcate ray at midfin. Length of caudal appendage of adult males is taken from the ventral edge of the caudal base to the tip of the longest modified fin ray. All measurements are recorded to tenths of millimeters. Indices of body proportion are obtained by arithmetically dividing each measurement into standard length.

SKELETAL MATERIAL. Preparation of skeletal material follows the method outlined by Rosen and Bailey (1959). Terminology of elements in the gonopodial suspensorium is that employed by Gordon and Benzer (1945) as modified by Rosen and Gordon (1953). Terminology of cranial elements is that used by Ramaswami (1946).

PREPARATION AND STUDY OF GONOPODIA OF ADULT MALES. Gonopodia to be used in statistical comparisons of species or populations were always removed from the fish and mounted on standard microscope slides in the following manner:

1. The fin was excised as close as possible to the body without damaging scales or adjoining bones of the gonopodial suspensorium.

2. Each fin was immersed successively for 15 minutes in each of a graded series of alcohols (70%, 95%, 100%, 100%) and then transferred for 20 to 30 minutes to xylol.

3. When completely cleared in xylol, the fin was transferred to a drop of Canada balsam on a microscope slide and then covered with a number 2 cover slip.

4. The cover slip was pressed down with the blunt end of a pencil, or other wooden rod, to flatten the gonopodium and spread the balsam.

5. Slides prepared in this way were transferred quickly to the warming table where the mounting medium hardened in about 2 days.

The terminology used for the bony elements at the distal tip of the gonopodium of *Xiphophorus* is that given by Rosen and Gordon (1953: 8, text-figure 12A).

THE GENUS *XIPHOPHORUS*

Xiphophorus Heckel, 1848: 291 (original description of *X. helleri*, designated type species).

Platypoecilus Guenther, 1866: 350-351 (original description of *P. maculatus*.)

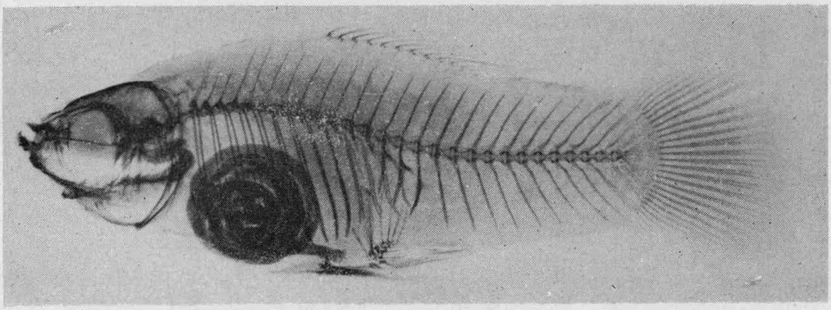


Figure 1. Radiograph of an adult male *Xiphophorus variatus evelynae*, n. ssp. (UMMZ: 124317), 36.2 mm. in standard length, illustrating skeletal plan in *Xiphophorus*.

Body moderately deep and compressed, without severely angulated dorsal and ventral margins, covered with large cycloid scales. Caudal fin usually with variously developed extensions of the lower rays as a "sword." Dorsal fin usually rounded, the first two rays simple, other rays bifurcate one or more times (in adults). In adult males pelvic fin with fleshy appendage developed along distal third of first short unbranched ray, the second and third rays somewhat prolonged. Anal rays 9 or 10, rarely 11. Gonopodium bilaterally symmetrical, I-beam-like in cross section; ray 5a forming a broad lanceolate platform that is flanked by erect, ridgelike elements of 5p, the whole framework forming a long, shallow, trough-like area; ultimate segment of 5a usually modified as claw or hook; ray 4p terminated by erect distal and retrorse subdistal serrae, the two series being separated by several simple oblong or cuboidal segments; proximal portion of 4p developed as a compressed ridge of raised, slender segments directly beneath the lanceolate platform of ray 5a; ray 4a simple, except distally where it is modified as a ramus that arches or hooks ventrally (anteriorly); well-developed hook at terminus of ray 3, followed by several irregularly oval or cuboidal subterminal segments, and a series of large more or less erect spines with angulated shafts; a dense blade of tough membranous tissue separating tips of rays 3 and 4a, its anterior edge merging with hook (ray 3), its posterior edge following contour of terminal ramus (ray 4a); posterior margin of ray 3 proximal to spines raised to meet anterior margin of ray 4a, the two rays together forming a ball and socket joint in cross section; tips of rays 6 and 7 swollen and club-shaped. Gonopodial suspensorium (fig. 1) with three erect, more or less linear gonapophyses; parapophyses present and well-developed on first and second gonapophyses, variously developed or absent on third; uncini usually absent, minute and irregular when present; ligastyle long and rodlike, almost as long as first gonapophysis; primary gonactinostal complex moderately dilated anteroposteriorly, inclined slightly forward, its upper edge deeply notched. Vertebrae 26 to 31. Pleural ribs approximately 12 to 14 in number; distal tips of ribs 7 to 10, counting anteroposteriorly, arched slightly downward and forward just above or posterior to pelvic girdle (fig. 1). Pectoral girdle somewhat triangular in outline, its longest dimension vertical; four actinosts recessed within posterior margins of scapula and coracoid, usually discrete but occasionally showing varying degrees of consolidation; upper part of cleithrum produced backward above scapula as large spatulate process; posterior edge of coracoid usually produced backward as flat process similar in outline to cleithral process but smaller. Skull deep and wedge-shaped (fig. 1), with well-developed supraoccipital processes and variously developed epiotic processes; jaws weak, consisting of slender elements with delicate articulations; premaxillae and dentaries flattened in front, the paired elements not joined at midline and separated by a distinct tissue space, each with an outer series of movable, compressed or narrow incisorlike teeth in a single, largely transverse row that is weakly indented near midline, and an inner series of minute pointed teeth in a band that is broad laterally, becoming narrow medially.

ACCOUNTS OF THE SPECIES AND SUBSPECIES

Xiphophorus couchianus (Girard)

Northern Platyfish, figures 2-4, tables 1-6

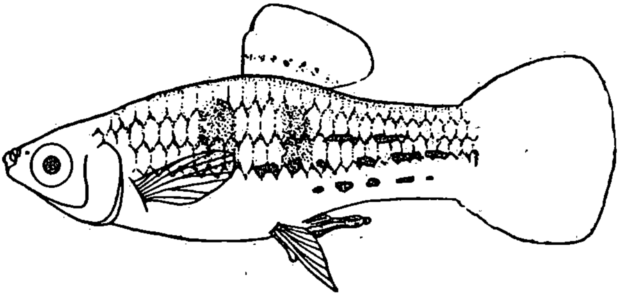


Figure 2. Diagram of the pigment patterns in a male *Xiphophorus couchianus* (Girard). Note three broken rows of black dashes posteriorly. These markings are deep-lying (dermal and subdermal) and are composed entirely of micromelanophores.

Limia couchiana Girard, 1859: 116 (original description; Monterrey).

Gambusia couchiana, Bleeker, 1860: 485 (characters).

Mollienesia couchiana, Jordan and Copeland, 1876: 143 (Nuevo Leon); Jordan, 1878: 434 (Nuevo Leon).

Poecilia couchiana, Jordan and Gilbert, 1883: 348 (description; Nuevo Leon); Jordan, 1885: 838 (name only); Evermann and Kendall, 1894: 76, 84, 87, 89, 92, 108 (Rio San Juan at Cadareita and Monterrey); Jordan and Evermann, 1896: 695 (description; Cadareita, Monterrey); Meek, 1904: 152 (description; Monterrey); Regan, 1906-1908: 104-105 (description).

Platypoecilus couchianus, Regan, 1913: 1003-1004 (description; gonopodium; close relative of *P. maculatus*); Gordon, 1932a: 287 (characters; distribution); 1932c: 89 (distribution); 1932b: 5 (ecology; hybrids); Breder, 1932: 7-9 (figure); Ralston, 1933: 124-125 (misspelled *couchiana;* chromosomes); Stoye, 1933: 307 (aquarium introduction); 1934: 86 (characters); Friedman and Gordon, 1934: 446-455 (chromosomes; distribution); Gordon, 1935a: 8-9 (characters; distribution); 1935b: 186 (ecology); Stoye, 1935: 53 (description); "Anonymous," 1937: 46 (figure; record mapped); Gordon and Smith, 1938a: 543-565 (distribution; hybridization; melanosarcoma); De Buen, 1940: 43 (name only); Dobzhansky, 1941: 280 (genetics; species or race); Gordon, 1941a: 39 (color factor E); 1941b: 112-113 (Rio Grande; hybridization with *Platypoecilus maculatus*); Mayr, 1942: 171 (member of superspecies or subspecies); Gordon, 1943c: 65, 68 (ecology, variation); Gordon, Cohen and Nigrelli, 1943: 569 (caudal fin; Rio San Juan system); Gordon and Lansing, 1943: 231-235 (tumors in hybrids with *Platypoecilus maculatus*); Gordon and Benzer, 1945: 57-70 (vertebrae; ribs; gonopodial suspensoria); Gordon, 1946d: 81, 83 (wagtail pattern in hybrids; introgressive hybridization); 1946b: 317-320 (sex-determining mechanism); 1947a: 117, 129 (ecological communities); 1950b: 19 (hybridization with *Platypoecilus maculatus*; melanomas); Gordon and Rosen, 1951: 417, 423-424, 427-429, 431-433, 457-458 (genetics and morphology of gonopodia; *Platypoecilus* as a subgenus of *Xiphophorus*); Gordon, 1951c: 194-197, 216 (genetics of atypical pigment cell growth); 1953c: 789-790 (distribution; taxonomic history).

Xiphophorus couchianus, Rosen and Gordon, 1953: 23 (gonopodial specializations).

Poecilia couchii, Guenther, 1866: 347 (emendation of *couchiana*).

Platypoecilus variatus, Rachow, 1936: sheets 145-146 (in part; erroneous synonymic reference).

MATERIAL EXAMINED

Mexico, Nuevo Leon

Rio Grande system

1. Springs of Huasteca Canyon, 2 mi. W Santa Catarina, Rio San Juan. UMMZ 124163. 8 half-grown to subadult males; these constitute basis of laboratory stock.
2. Rio Santa Catarina, 1½ mi. S Santa Catarina, Rio San Juan. UMMZ 97572. 25 half-grown to adults.
3. Branch of Rio San Juan in Huasteca Canyon, 4 mi. W Monterrey. UMMZ 108609. 20 half-grown to adults.
4. Headwaters of Rio Santa Catarina, mouth of Santa Catarina, Rio San Juan. UMMZ 97571. 432 half-grown to adults.
5. Rio Santa Catarina in Huasteca Canyon. UMMZ NYZS-GL. 30 young to adults, 15 taken alive.

DIAGNOSIS. A small, moderately deep-bodied species of *Xiphophorus* (tables 4 and 5). Lower caudal rays not developed as a "sword" in adult males. With a weakly developed zigzag midlateral stripe separating the darker heavily reticulated dorsum from the paler ventral surface; usually with a variable number of deep-lying black spots in one to three rows on the caudal peduncle along the line where the myomeres are abruptly angulated. Without a deep-lying ridge of black pigment midventrally on caudal peduncle. Dorsal fin distinctly rounded, occasionally with a weakly developed row of spots or more often a diffuse band of dusky pigment near base. Claw wanting at tip of ray 5a of gonopodium; distal serrae of ray 4p well developed, 4 to 6 in number, their tips converging, the spread of the two outermost ones from base to base four times the distance from tip to tip; ramus of ray 4a curved downward over blade, not hooked; hook of ray 3 long and slender. Vertebrae 28, rarely 27. Scales in a lateral series 26 or 27, usually 26. Dorsal fin rays 8 to 11, usually 9 or 10.

GENERAL ACCOUNT. *Xiphophorus couchianus* agrees with *X. variatus* in having a slender caudal peduncle. From *variatus* it may usually be told by the lack of distinctive horizontal zigzag dark stripes, and in being browner in life and more sharply bicolored—

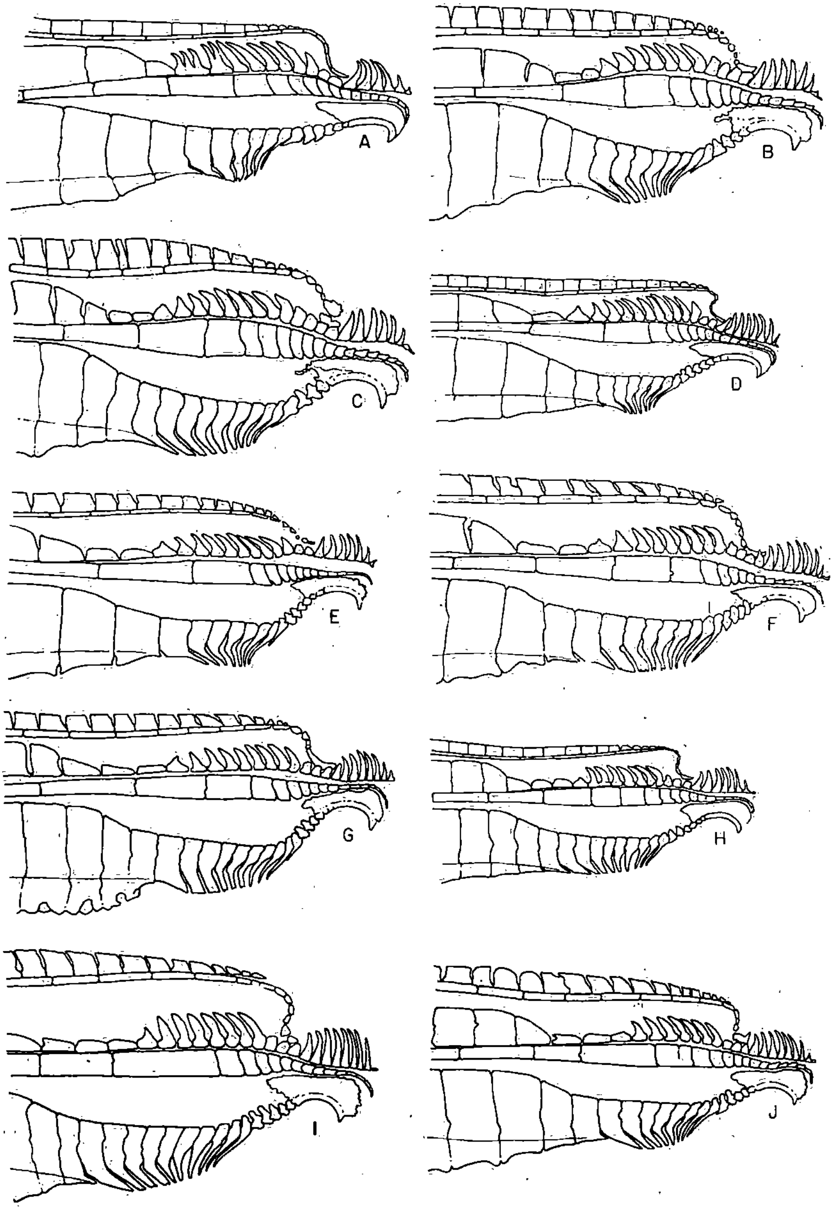


Figure 3. Distal tips of the gonopodia of males of the species and subspecies of platyfishes. A. *X. couchianus* (Girard) (UMMZ: 97571). B-C. *X. maculatus* (Gunther) (UMMZ: 124255). D-E. *X. variatus xiphidium* (Gordon) (UMMZ: 124416). F-H. *X. variatus variatus* (Meek) (UMMZ:NYZS-GL, Rio Nautla). I-J. *X. variatus evelynae*, n. ssp. (UMMZ: 124318).

darker above and paler below. Rarely, individuals of *variatus* may be as dark and bicolored as *couchianus*. This northern species differs from the allied southern species *variatus* and *maculatus* in lacking the variable black markings, other than vertical bars, that appear in varying frequency in those species. *X. couchianus* usually shows a variable number of deep-lying black spots on the caudal peduncle, in one to three rows along the line where the myomeres are abruptly angulated. Specimens collected at Monterrey by Cope show in addition a similar but more conspicuous row of spots or streaks along the line where the superior muscles are sharply bent. All three rows of spots are present in some live specimens of the stock from Huasteca Canyon. These markings, lying deep in the muscles, probably have a histological and a genetic basis different from that of the more superficial black spotting (Sp) of the other species.

This species is confined to the Rio Grande basin in Nuevo Leon, Mexico.

Xiphophorus maculatus (Guenther)

Southern Platyfish, figures 3-5, tables 1-5, 7-8

Platypoecilus maculatus Guenther, 1866: 350-351 (original description; Mexico); Eigenmann, 1893: 57 (Mexico); Garman, 1895: 48-49 (after Guenther; except reference to *P. mentalis* in synonymy); Jordan and Evermann, 1896: 686 (after Guenther); Meek, 1904: 145-146 (records; description; variation); Gerlach, 1909: 25-27 (aquarium introduction); Regan, 1913: 1004 (gonopodium; synonymy; description; range in part); Brind, 1914: 22 (as aquarium fish); Gerschler, 1914: 73-96 (hybridization); Bellamy, 1922: 419-420 (genetics); 1924: 513-529 (biometry); Gordon, 1927: 253-283 (history; taxonomy; genetics); Bellamy, 1928: 226-232 (genetics); Goodrich, 1929: 83-99 (review of genetics); Gordon, 1931a: 732-787 (morphology of color patterns); 1931b: 1495-1523 (history of intergeneric hybrids); Gordon and Fraser, 1931: 169-185 (genetic analysis of natural color variations); Myers, 1932: 403 (reference to *P. nigra* Brind); Shaw, 1932: 263-278 (conditioned water and growth rate); Gordon, 1934b: 79-92 (history of introduction of color varieties; habitat); Stoye, 1934: 84-86; 1935: 50-52 (color varieties); Kosswig, 1935: 40-48 (genetics); Hubbs, 1935: 10 (characters; aguada at Uaxactun, Guatemala); "Anonymous," 1937: 46 (figure; records mapped); Goldschmidt, 1937: 429-39 (sex determination); Gordon, 1937: 376-392 (genetics; references); Breider, 1938: 784-828 (genetic and cytological basis of tumors); Brind, 1938: 40 (color variation); Gordon and Smith, 1938b: 255-272 (interspecific hybridization and tumors); 1938a: 543-565 (hybridization and tumors); Crozier and Wolf, 1939a: 463-485; 1939c: 143-163; 1939d: 176-179 (flicker response); Goodrich, 1939: 198-207 (chromatophores); Grobstein and Bellamy, 1939: 363-365 (thyroid feeding); De Buen, 1940: 43 (literature records, in part); Gordon, 1940b: 3-5; 1940c: 22-24; 1940d: 63-64 (genetics of pigment cells; habitats); 1940e: 171-172 (ecological isolation; no hybrids in nature; Rios Papaloapan, Coatzacoalcos, Usumacinta); Grobstein, 1940a: 1-22 (structure and development of gonopodium); 1940b: 484-486 (testosterone, effects on gonopodium development); Turner, 1940: 64-67 (fetal membrane); Dobzhansky, 1941: 279-280 (genetics; hybridization); Baker and Furgeson, 1942: 116-119 (growth in bacteria-free cultures); Goodrich, Hill and Arrick, 1941: 573-586 (chemistry of pigments); Gordon, 1941a: 38-39 (abstract, hybridization); 1942c: 76 (gene frequencies; genetics; Rios Jamapa, Papaloapan, Coatzacoalcos, Usumacinta); Grobstein, 1942a: 477-478; 1942b: 305-328 (effect, steroids; gonopodia in females); Needham, 1942: 387, 442 (tumors; regeneration of gonopodium); Mayr, 1942: 75-76, 79, 171 (genetic phases; member of subspecies or superspecies); Gordon, 1943a: 71-72 (mutant strain); 1943b: 28 (genetics in relation to melanomas); 1943c: 64-71 (variation; dorsal rays; hybridization; origin of races; genetics; Rios Jamapa, Papaloapan, Coatzacoalcos, Grijalva, Usumacinta); Gordon and Flathman, 1943: 9-12 (genetics of melanomas in hybrids); Goldsmith, Nigrelli, Gordon, Charipper and Gordon, 1944: 132 (effects, thiourea); Nigrelli and Gordon, 1944: 45 (tumors); Gordon and Benzer, 1945: 57-61, 63-70 (vertebrae; ribs; gonopodial suspensoria); Levine and Gordon, 1946: 197-198, 200-204 (ocular tumors); Gordon, 1946c: 87, 92 (ocular tumors); 1946d: 77-78, 81, 83-86 (introgressive hybridization); 1946b: 307-313, 315-320 (sex determination); 1947a: 95-101, 103, 105-112, 114-131 (speciation); 1947b: 8-9, 12, 14-17 (sex determination); 1948a: 216, 219-221, 223, 225, 227, 245 (color genes and melanomas); 1948b: 254, 256, 258 (genetics of tumor development); 1950a: 405, 410-413 (genetics, in part); 1950b: 19 (pigment cell growth); 1950c: 26-34 (heredity of tumors); Gordon and Gordon, 1950: 61, 64, 71-72 (gene frequencies); Gordon and Rosen, 1951: 414-417, 423, 427-430, 432-436, 438-451, 454, 456-459 (genetics of gonopodia; *Platypoecilus* as subgenus of *Xiphophorus*); Nigrelli and Gordon, 1951: 122 (tumors); Gordon, 1951a: 127, 129-130, 133 (sex determination); 1951b: 155, 157-158, 160, 163, 194-197, 199-206, 211, 216 (pigment cell growth; geographical distribution; hybridization); 1951b: 676-677, 679 (genetic expressivity); Chavin and Gordon, 1951: 135-145 (genetics; sex determination); Nigrelli, Jakowska and Gordon, 1951: 54 (peoplastic growths); Gordon, 1953c: 787-792 (pigment cell growth).

Platypoecilia maculata, Taubles, 1916: 16 (aquarium notes).

Poecilia maculata, Regan, 1906-1908: 105 (synonymy; description; records, in part; El Hule, Obispo, Perez).

Xiphophorus (Platypoecilus) maculatus, Gordon, 1952b: 988 (melanomas); 1952a: 91, 94-98 (sex determination); Berg and Gordon, 1953: 44, 46, 58 (gonads).

Xiphophorus maculatus, Gordon, 1953a: 192 (pigment cell growth); Rosen and Gordon, 1953: 20, 22-23, 38-40, 42 (morphology and mechanics of gonopodia); Rubin and Gordon, 1953: 646-647 (gonopodial suspensorium); Gordon and Gordon, 1954: 37-58 (biometry).

Platypoecilia var. *maculatus*, Beldt, 1917: 17 (red spotted form).

Platypoecilus maculata nigra, Brind, 1919: 167 (lapsus for gender of specific name; black banded form).

Platypoecilus maculatus var. *aurata* Stoye, 1935: 51 (aquarium variety).

Platypoecilus maculatus var. *cyanellus* Meinken, 1934: 261-263 (description; aquarium introduction).

Platypoecilus maculatus immaculatus Myers, 1922a: 1-22 (aquarium fish) 1922b: 89 (aquarium fish); Bayliss, 1929: 76-78 (characters); 1943: 74 (description).

Platypoecilus maculatus niger, Myers, 1922a: 1-22 (characters).

Platypoecilus maculatus nigra, Stoye, 1935: 51 (characters).

Platypoecilus maculatus pulcher, Myers, 1922a: 1-22 (characters).

Platypoecilus maculatus pulchre, Troemner, 1943: 1-3 (aquarium notes).

Platypoecilus maculatus ruber, Myers, 1922a: 1-22 (characters).

Platypoecilus maculatus var. *sanguinea,* Stoye, 1935: 51 (description).

Platypoecilus nigra Brind, 1914: 22 (original description; southern Mexico).

Platypoecilus pulchra Brind, 1914: 22 (as aquarium fish).

Platypoecilus rubra Brind, 1914: 22 (as aquarium fish).

Platypoecilus sp., Schreitmuller, 1910a: 177-178; 1910b: 573-576 (spotted variety later called *pulchra*).

MATERIAL EXAMINED

Mexico, Veracruz

Rio Jamapa system

1. Plaza de Agua near El Tejar, 8 mi. S Veracruz. UMMZ 124296. 828 half-grown to adults; others kept alive.

Rio Papaloapan system

2. Southern tributary of Rio Tonto, 10 km. upstream from Papaloapan. UMMZ 108583. 10 half-grown to adults preserved; 91 taken alive.
3. Same locality. UMMZ 124178. 1 mature male.
4. Rio Papaloapan at San Bartolo. UMMZ 124473. 1 transforming male.
5. Lagoon beside Rio Papaloapan, 3 km. N San Bartolo. UMMZ 124255. 567 young and adults.
6. Pool, 5 km. S Papaloapan at 148½ km. mark on railroad. UMMZ 124284. 5,148 young and adults preserved; others taken alive.
7. Lagoon and pool, 4 km. S Papaloapan at 149 km. mark on railroad. UMMZ 124227. 1,473 young and adults preserved; others taken alive.
8. Arroyo Zacatispan and lagoon, 4.5 km. S Papaloapan. UMMZ 124220. 48 young to adults.
9. Pool, part of lagoon, 4.5 km. S Papaloapan. UMMZ 124261. 413 young to adults.
10. Arroyo Zacatispan 6 km. E Papaloapan. UMMZ 124195. 5 half-grown to sub-adults.

Rio Coatzacoalcos system

11. Laguna del Aserradero near pool 200 m. from Rio de Jaltepec in vicinity Santa Lucrecia (Jesus Carranza). UMMZ 157657. 1 subadult male.
12. Lagunitas near Jesus Carranza. UMMZ 124452. 5 half-grown to adults.
13. Arroyo de "La Llorona" about 350 m. from Estacion de Juile. UMMZ 157661. 1 subadult male.
14. Laguna de "El Tule" about 3 to 4 km. from El Juile. UMMZ 157663. 18 young to adults.

15a. Small unnamed arroyo emptying into Arroyo Aguazate near Estacion de Almagres. UMMZ 157662. 90 young to adults.

Mexico, Tabasco

Rio Tonala system

15b. Arroyo de La Venta at La Venta. 30 adults taken alive.

Rio Grijalva system

16. Rio Muerto tributary to Rio Teapa on Finca de Pablo Pratts 4 km. N Teapa. UMMZ NYZS-GL. 38 young to adult males and females.
17. Tierra Colorado pond 5 km. N of Villahermosa. UMMZ NYZS-GL. 203 young to adult males and females.
18. Same locality UMMZ NYZS-GL. 478 young to adult males and females.

Guatemala

Rio Usumacinta system

19. Upper Rio de la Pasion (Rio Chajmayic) at La Ceiba. UMMZ 143788. 1 young.
20. Near mouth of Rio Chajmayic, Cahabon, an upper tributary of Rio de la Pasion. UMMZ 143787. 16 subadults and adults.
21. Mouth of arroyo tributary to the upper Rio de la Pasion between La Ceiba and Arroyo San Simon. UMMZ 143789. 109 young to adults.
22. In and just above mouth of first arroyo tributary to upper Rio de la Pasion from east below Arroyo San Simon. UMMZ 143790. 14 young to adults.
23. Arroyo Subin at Santa Teresa 13 mi. S of La Libertad. UMMZ 143786. 3 subadults and adult.
24. Arroyo Subin at second rapids above mouth in Rio de la Pasion. UMMZ 143791. 3 subadults.
25. Laguna de Yalac, in course of Rio San Pedro de Martir above El Paso de los Caballos. UMMZ 143782, 143783. 2 adults taken by seine and by poison.
26. Rio San Pedro de Martir about ¼ mi. below Laguna de Yalac. UMMZ 143784. 3 half-grown to adult.
27. Rio San Pedro at Desempeno just below El Paso de los Caballos. UMMZ 143781. 17 young to adults.

Interior lakes

28. Laguna de Zotz W Laguna de Peten. UMMZ 143780. 558 young to adults.
29. Laguna de Eckixil E southern arm of Laguna de Peten. UMMZ 143778. 1 adult.
30. Outlet of Laguna de Petenxil, tributary of Laguna de Peten. UMMZ 143779. 20 subadults and adults.
31. Tributary creek to short stream which forms outlet of Laguna de Petenxil. UMMZ 143785. 31 young to adults.
32. Flooded "rio" at E end southern arm Laguna de Peten. UMMZ 143777. 2 young.
33. Arroyo de Ponteil at head of standing water about 1 mi. from mouth. UMMZ 143774. 1 adult.
34. Arroyo de Ponteil at forks about ¾ mi. from mouth, a southern tributary of southern arm Laguna de Peten. UMMZ 143775. 6 young to adults.
35. Laguna de Peten along airfield near middle southern shore of southern arm of lake. UMMZ 143771, 143776. 22 young to adults, 1 adult.
36. Arroyo de Puebla Nueva near head of standing water (flood waters of Laguna de Peten). UMMZ 143773. 9 young to adults.
37. Flores, Lake Peten, Arroyo San Helena, opposite Flores. UMMZ NYZS-GL. 1 male and 2 females.
38. Flores, Lake Peten, Arroyo Ponteil, Peten. UMMZ NYZS-GL. 1 male and 1 female.

Guatemala, British Honduras

Rio Hondo system

39. Aguada at Uaxactun, Guat. UMMZ 97873. 3 adults.
40. Cenote Creek, 8 mi. SE Gallon Jug, Orange Walk, B. Hond. UMMZ NYZS-GL. 2 adult females.

41. Lagoon and creek on E bank of E branch of Rio Hondo opposite San Antonio, B. Hond. UMMZ NYZS-GL. 9 males, 17 females and 16 half-grown.
42. Lagoon opposite San Antonio, connected with creek to east branch of Rio Hondo, Orange Walk, B. Hond. UMMZ NYZS-GL. 144 males, 98 females, 150 young to half-grown.
43. Chorro 4 mi. N Corozal on highway to Santa Helena (Chetumal), Northern District, B. Hond. UMMZ NYZS-GL. 1 adult male.
44. Corozal, Back Street (extreme north B. Hond.) UMMZ 158391. 191 young to adult.

British Honduras

Independent Tributaries to Baluo de Chetumal

45. Chorro at Back and Queen Streets, Corozal, Northern District. UMMZ NYZS-GL. 40 young to adult males and females.
46. Chorro, Northern District. UMMZ NYZS-GL. 9 young to adult males and females.
47. Hill Bank opposite campsite, inlet to lagoon of New River. UMMZ NYZS-GL. 1 male, 1 female and 1 half-grown.
48. San Estevan 1 mile on road to Progreso, Orange Walk. UMMZ NYZS-GL. 8 males, 2 females and 4 half-grown.

Belize River system

49. Lower extension of Gabourel Creek ½ mi. E Belize airport, Belize. UMMZ NYZS-GL. 1 half-grown.
50. Gabourel Creek near Belize Airport, Belize. UMMZ NYZS-GL. 500 young to adult males and females.
51. Johnny Pond Creek 1 mi. from Boom, Belize. UMMZ NYZS-GL. 8 young to adult males and females.
52. Arroyo W of western branch Belize River, near Benque Viejo, Cayo. UMMZ NYZS-GL. 26 young to adult males and females.

DIAGNOSIS. A small, deep-bodied species of *Xiphophorus* (tables 4 and 5). Lower caudal rays not developed as a "sword" in adult males. Midlateral stripe wanting. Without a deep-lying ridge of black pigment midventrally on caudal peduncle. Dorsal and anal fins distinctly rounded. Dorsal fin not usually dimorphic, rounded, usually with a faint or moderate diffuse dusky band near base. Gonopodium with claw usually wanting at tip of ray 5a, rarely with a minute scythe-shaped or crescentic element; distal serrae on ray 4p well developed and erect, seldom retrorse, 4 to 7 in number; ramus of ray 4a curved downward over blade, not hooked, and extending to tip of ray 4p; hook of ray 3 long and slender. Vertebrae usually 27, rarely 26. Scales in a lateral series 22 to 25, usually 23 or 24. Dorsal fin rays 7 to 11, usually 9 or 10.

GENERAL ACCOUNT. The two females on which Guenther based his description of this species were examined in the British Museum by Myron Gordon, who supplied the following information: One, 32 mm in standard length, has a spotted dorsal fin pattern (Sd), and a one spot (O) on the tail base. The other, 30 mm in standard length, has two tail patterns, a comet (Co) and one spot (O), but no macromelano-

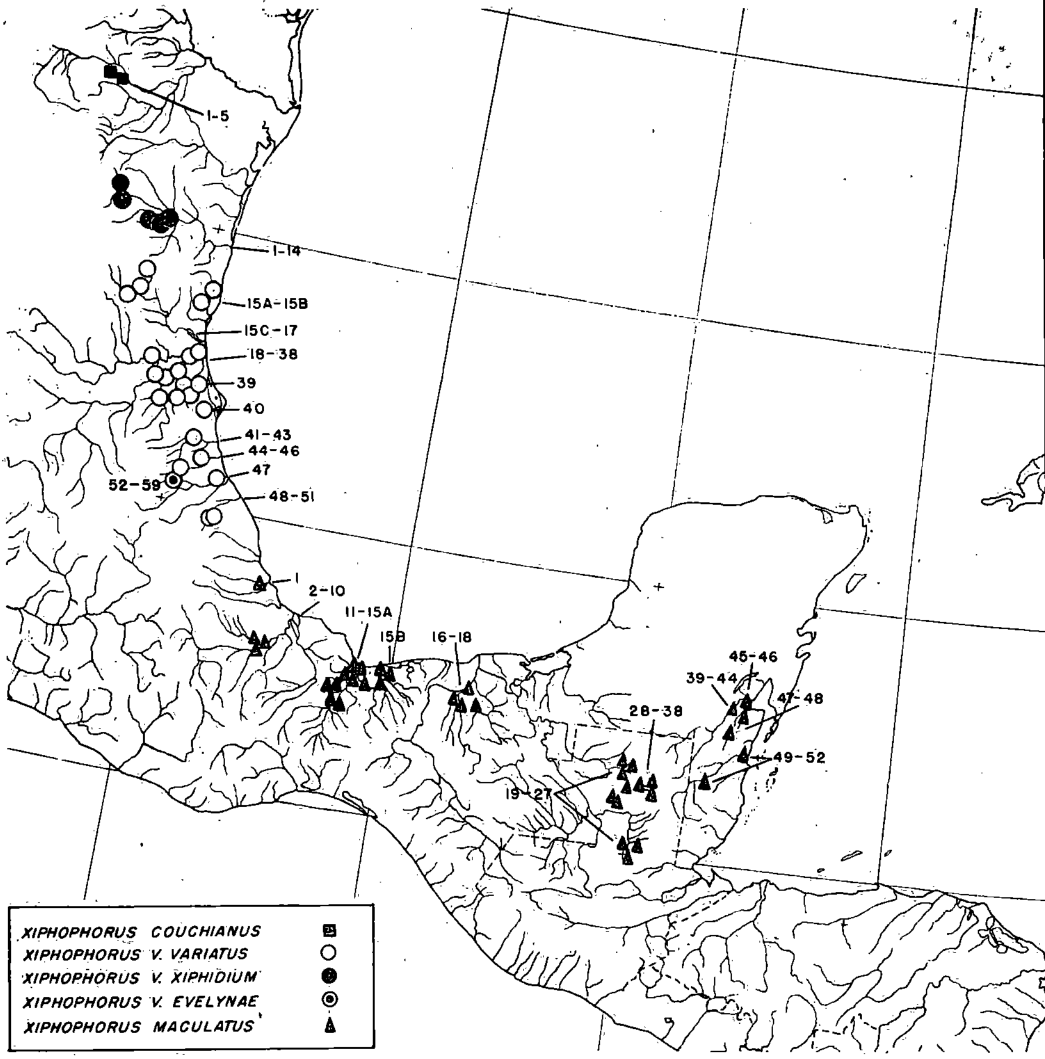


Figure 4. Distribution by record stations for the species and subspecies of platyfishes. Additional records in the Rio Tonala and Rio Grijalva from Gordon and Gordon (1954) are included.

phore patterns (see below and fig. 5). Both have a dorsal ray count of 9, treating the last two rays as one.

Also seen was a small series of specimens in rather poor condition collected at Orizaba in 1867 by Professor Sumichrast (ANSP 14684-85, 14686, 14671-83, 15927-28, 15929, 39893), as well as Meek's specimens from Obispo (SU 21462).

The color phases (fig. 5) which make this species one of the most variable of all wild vertebrates occur together in nature, and these polymorphs differ in no other respects. Some of these polymorphs have been given scientific names (see synonymy) which have no proper place in systematic nomenclature. These color phases, however, are significant in the study of the comparative genetics of species and the composition of natural populations (Gordon and Gordon, 1950, 1954).

In *X. maculatus* seven basic tail patterns are known. The morphological and histological features of four of these patterns were first described by Gordon (1931a). When, later, he described the remaining three patterns, Gordon (1947a) showed that all the tail patterns in this species are controlled by autosomal genes that constitute a single series of dominant epistatic multiple alleles. All seven patterns are formed by characteristic groupings of many small melanophores.

A rare and exceptional tail pattern called the Guatemala crescent pattern was first discovered by Gordon (1947a) in a population of platyfish from the Laguna Petenxil and Arroyo Ponteil in Guatemala. This pattern resembles the simple crescent pattern but is broader throughout and particularly where the ends of the crescent bulge cephalad to form two distinct nodes. Its presence in *X. maculatus* is always associated with two small black dots in the integument at the tip of the lower jaw known as lip markings. This is the only known example of a micromelanophore tail pattern in *Xiphophorus* associated with a far-removed accessory pattern.

Other seldom encountered tail patterns are: The anterior or trapezoidal element of the complete crescent occurring alone; the upper and lower elements of the cut crescent pattern occurring alone; and the upper and lower elements of the comet pattern occurring alone. Possibly the occurrence of only one element of either the cut crescent or comet patterns may be due to localized interference with the expression of the complete pattern during ontogeny. As yet no evidence suggests that these patterns reflect distinct genotypes.

Genetic analyses reveal that all the fundamental tail patterns of *X. maculatus* are controlled entirely by the action of autosomal genes (Gordon, 1947a), and that none so far as known is sex limited.

Gordon (1947a) indicated that in *X. maculatus* any two of the seven basic tail patterns theoretically may occur together to produce a net phenotypical effect of both patterns combined. Such a dual pattern often is difficult to recognize because most of the seven basic patterns occupy similar areas at the base of the caudal peduncle and a certain amount of superimposition is inevitable. This point is well illustrated by a dual pattern consisting of the complete crescent and the simple moon patterns in which the single element of the simple moon pattern occupies approximately the same position on the caudal peduncle as the anterior or trapezoidal element of the complete crescent. As the moon pattern is somewhat larger and more rounded than the crescent pattern, careful observation reveals its presence with the single complete crescent. But the moon pattern is also known to occur with the simple crescent in which the anterior trapezoidal element is lacking. In such cases only careful analysis of the intensity and limits of the pigmented mass will show whether or not a superimposed pattern is present. Many dual patterns probably are overlooked or misinterpreted (Gordon, 1931a; Gordon and Gordon, 1950).

In addition to the seven basic tail patterns in *X. maculatus,* 17 double, but no triple or more complex combinations have been recorded. The presence of double, but no more complex patterns, suggests the operation of seven dominant multiple alleles, as indicated earlier. Evidence from genetic experiments supports this suggestion. The following tabulation, from Gordon (1947a), lists all the types possible in *X. maculatus* (fig. 5).

	O	M	Mc	C	Cc	Co	T
O	O						
M	OM	M					
Mc	OMc	(MMc)	Mc				
C	OC	MC	(McC)	C			
Cc	OCc	MCc	McCc	(CCc)	Cc		
Co	OCo	MCo	McCo	CCo	CcCo	Co	
T	OT	MT	(McT)	CT	CcT	CoT	T

O = one spot; M = simple moon; Mc = complete moon; C = simple crescent; Cc = complete crescent; Co = comet; T = twin spot. Dual patterns shown in parentheses are theoretically possible but have never been detected.

The macromelanophore patterns are composed of cells that are both morphologically and genetically distinct from those responsible for the tail patterns. The macromelanophore patterns (fig. 5) are sex linked, or, at least, incompletely sex linked, and they are not all members of a single allelic series. Two or more patterns may occur together in a single individual.

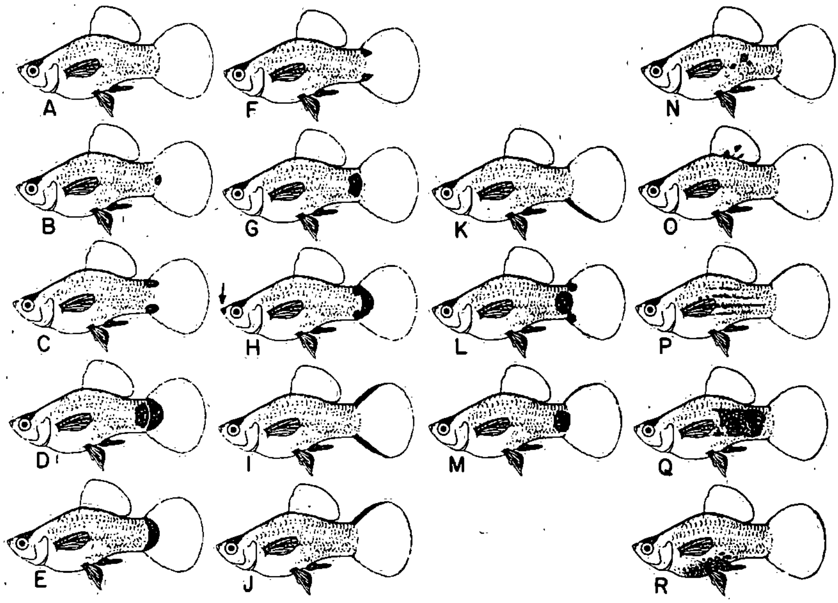


Figure 5. Diagrams of the pigment patterns in *Xiphophorus maculatus* (Guenther).

A. Unmarked except for basic reticular patterns.

B-M. Micromelanophore tail patterns. B. One spot. C. Twin spot. D. Complete crescent. E. Simple crescent. F. Cut crescent. G. Ax-head. H. Guatemala crescent (note lip markings). I. Comet. J. Upper comet. K. Lower comet. L. Complete moon. M. Simple moon. Only patterns B-F, and L are common in natural populations and have been studied genetically. The other tail patterns, except for the Guatemala crescent, are rare and may be only partial expressions of other more common patterns.

N-R. Macromelanophore patterns. N. Spotted. O. Spotted dorsal. P. Striped. Q. Black banded. R. Black belly.

The macromelanophores are chiefly in the dermis, both above and below the scales. Macromelanophores are sometimes seen in the epidermis, and occasionally, when the scales are removed from their dermal pockets, they may be seen adhering to the scale substance. In such cases the pigment granules within the scale macromelanophores are more diffuse and the cell's dendritic processes are less delicate than those within the dermal melanophores.

Though micro- and macromelanophores are morphologically and genetically distinct, the two types of patterns interact when they occur together in the same individual according to observations by Gordon (1928). He found that the occurrence of a macromelanophore spot on the side in *X. maculatus* is correlated with the loss of micromelanophore reticulation in the same region. Conversely, he found that the micromelanophore pattern enhances the expression of the macromelanophore spotting in this species. Gordon's experiments show that these reciprocal relations are referable to the interaction of an autosomal gene, St, for reticulations with a sex linked gene, Sp, for spotting.

The southward dispersal of *X. maculatus* is limited by the swift waters that arise in the Maya mountains and intervene between British Honduras and the Honduras lowlands. Recent collections in British Honduras suggest that the species of *Phallichthys* compete with *maculatus* and entirely replace it ecologically to the south, thereby reinforcing the topographical barriers that block further extension of its range.

Where this species occurs together with *Phallichthys* in the New River and Rio Hondo systems (see Rosen and Bailey, 1959, for distribution of *Phallichthys*), the two species become stratified and occupy alternative microhabitats. The platyfish are caught deep in the cooler mud, and the *Phallichthys* on top. When separated in different drainages or in different sections of the same drainage, they appear to occupy almost identical ecological niches.

This species ranges from Veracruz, Mexico to northern British Honduras, usually at lower elevations.

Xiphophorus variatus (Meek)

Variable Platyfish, figures 1, 3-4, 6-7, tables 1-5, 9-13

Platypoecilus variatus Meek, 1904: 146-147 (original description; records, including those of the Rio Soto la Marina system).

DIAGNOSIS. A small to moderate, deep-bodied species of *Xiphophorus* (tables 4 and 5), rarely with a minute unpigmented caudal appendage in adult males (Rio Soto la Marina system only); usually with two or more variably complete zigzag black midlateral stripes running from base of caudal peduncle to opercular membrane; with two or more oblique black lines extending downward from the midlateral stripes just behind pectoral base. Without a deep-lying ridge of black pigment midventrally on caudal peduncle. Dorsal fin usually rounded, higher and more smoothly rounded in adult males than females. Claw wanting at tip of ray 5a of gonopodium; distal serrae on ray 4p well developed and retrorse, 5 to 8 in number; ramus of ray

4a curved downward over blade, not hooked, and extending to tip of ray 4p; hook of ray 3 long and slender. Vertebrae 28 or 29, rarely 27 or 30. Scales in a lateral series 24 to 28, usually 26. Dorsal fin rays 9 to 14, rarely 14.

GENERAL ACCOUNT. Most of the present material corresponds well with Meek's (1904) account of *Platypoecilus variatus.* Three distinct subspecies may be separated however, *X. v. xiphidium,* long regarded by authors as a full species, *X. v. evelynae* from the headwaters of the Rio Tecolutla, and the nominate form. Even after excluding *xiphidium* and *evelynae, variatus* remains far from a simple unit. It shows marked geographical variation, as well as the spectacular individual variation in micromelanophore tail patterns and macromelanophore spotting exhibited by *maculatus* (see fig. 5). Aquarists have tended to select the brightest of the distinctive color phases of *variatus.* Frequently, large males have lemon yellow or orange caudal and dorsal fins, and a coppery red spot on the base of the caudal peduncle never seen in *maculatus.*

The position of *variatus* in the genus *Xiphophorus* is perhaps unique, for it combines the pigmentary polymorphism of *maculatus* with the structural and metameric variability of *helleri.* Unlike members of the *helleri* complex, however, the morphometric differences distinguishing the subspecies of *variatus* show no evidence of any common trends or uniting features. Only within *X. v. variatus* does there appear a marked north-south trend in values of least relative depth of caudal peduncle (table 5) and in the frequencies of the micromelanophore tail patterns. The geographical distribution of other traits is distinctively mosaic (see tables).

Gordon and others early appreciated the special features of the numerous forms of *X. v. variatus.* These were found to differ chiefly in average numbers of dorsal fin rays and certain pigmentary traits, but a number of other features have nevertheless been examined. This information may be summarized as follows:

1. Greatest depth of body. *X. v. variatus* in the Rio Axtla (Rio Panuco system), Estero Tancochin system, Rio Cazones system, and Rio Nautla system are most slender bodied.

2. Least depth of caudal peduncle. In *X. v. variatus* the least depth of the caudal peduncle shows a gradual increase from north (Rio Tamesi) to south (Rio Nautla).

3. Length of head. Members of the Estero Tancochin and Rio Cazones populations have relatively long heads.

4. Length of caudal peduncle. Platyfish in the Arroyo Sin Nombre (lower reaches of the Rio Tecolutla system) have the shortest average length of caudal peduncle.

5. Length of caudal fin. Platyfish in the Rio Cazones system possess the longest caudal fins.

6. Dorsal fin ray counts. *X. v. variatus* in the Rio Cazones system average one more fin ray than the other nine populations (table 9).

7. Scales in a lateral series. Scale counts in all populations are relatively uniform (table 10).

Of the three subspecies, only *variatus* and *xiphidium* possess micromelanophore tail patterns. Four have been identified so far, all evidently members of a single allelic series. A tabulation of their tail pattern combinations follows:

	O	Cu	Ct	C
O	O			
Cu	CuO	Cu		
Ct	CtO	CtCu	Ct	
C	CO	(CCu)	CCt	C

O = one spot; Cu = upper portion only of cut-crescent; Ct = cut crescent; C = simple crescent. Dual patterns shown in parentheses are theoretically possible but have never been detected.

In *variatus* from the Rio Nautla, a pattern occurs that strongly resembles the complete crescent of *maculatus*, having a peduncular segment and crescentlike extension on the base of the caudal fin. The crescentic portion is believed to result from a "spilling over" of pigment from an unusually well developed one spot onto the fin base. In addition, some one-spot patterns of *variatus* may become sufficiently large and well defined that they resemble the simple moon pattern of *maculatus*, or by conforming to the limits of the sharply bent posterior myomeres they resemble the axlike portion of the complete crescent of *maculatus*.

As indicated, only *X. v. evelynae* lacks tail patterns. *X. v. variatus* from the Rio Moctezuma and Rio Calaboza (Rio Panuco system) have but a single pattern, though a different one in each case. Three populations, those of the Rio Tuxpam, the lower reaches of the Rio Tecolutla, and the headwaters of the Rio Nautla, have only two patterns, and the remaining populations of *X. v. variatus* have three, four, and five in various combinations.

Four macromelanophore patterns occur in *variatus*, a caudal spot, a black banded pattern, and two types of spotting (blotches and speckles) along the sides. The banded and speckled patterns and caudal spot are found only in the Rio Cazones population, and in less than 10 percent of the adult individuals. The blotched pattern occurs throughout all populations of *variatus* in numbers ranging from 15 to 96 percent of each adult sample.

Atz (Ms.) has found genetic evidence that some of the tail patterns, as well as certain macromelanophore markings, are controlled by homologous genes in *variatus variatus, v., xiphidium,* and *maculatus*. He also provides evidence that the genetic sex-determining mechanisms (female homogametic, male heterogametic) in *variatus* and in *maculatus* north of the Rio Usumacinta system are similar, while *maculatus* from the rivers of British Honduras are female heterogametic, and those from the Peten district of Guatemala do not behave consistently according to either system. This genetic information, considered in the light of the morphological and ecological similarities between *maculatus* and *variatus*, is taken as direct evidence of their close relationship. Nevertheless it will be shown below that, despite their many similarities and their allopatric distributions, good evidence favors recognizing *maculatus* and *variatus* as distinct species.

Xiphophorus variatus ranges throughout most of the Atlantic coastal rivers and streams of southern Tamaulipas, eastern San Luis Potosi, and northern Veracruz over a straight line distance of approximately 350 miles. Within this range it occurs at altitudes ranging from 100 to 4000 feet (table 33).

Xiphophorus variatus xiphidium (Gordon)

Figures 3-4, 6, tables 3-5, 9-11

Platypoecilus xiphidium Gordon, 1932a: 287 (original description; small sword mentioned); 1932c: 89 (Rio Soto la Marina); 1933a: 143-146 (habitat; characters; not mentioned by name); 1933c: 77-78 (polymorphism); Stoye, 1934: 86 (characters); Friedman and Gordon, 1934: 446-455 (chromosomes and distribution); Stoye, 1935: 53 (description); Kosswig, 1935: 46-48; 1937: 491-528 (hybrids); Gordon, 1935a: 8-9; 1937: 388-389 (characters and sex determination); Anonymous, 1937: 46 (figure; records mapped); Hubbs, 1937: 296 (tributary of Arroyo San Carlos); Gordon, 1938: 21 (coloration); Gordon and Smith, 1938a: 543-565 (hybridization); Gordon, 1940a: 96-106 (habitat); De Buen, 1940: 44 (cuenca del Rio Soto la Marina); Dobzhansky, 1941: 280 (genetics; species or race); Gordon, 1941b: 112-113 (Rio Soto la Marina; hybridization); 1943c: 65-66 (Rio Soto la Marina system; patterns; variation;

dorsal fin rays); Gordon, Cohen and Nigrelli, 1943: 569-572 (*xiphidium*-like sword in *maculatus*); Hubbs and Gordon, 1943: 31 (caudal appendage); Gordon and Benzer, 1945: 58-70 (vertebrae; gonopodial suspensorium); Gordon, 1946b: 316-317, 320 (sex determination); 1947a: 117, 129 (speciation); Gordon and Rosen, 1951: 417, 423-433, 456-458 (genetics of gonopodia); Nigrelli and Gordon, 1951: 121-125 (spontaneous neoplasms; hybrids with *variatus*); Gordon and Aronowitz, 1951: 151 (sex determination); Gordon, 1951c: 194-197 (species hybridization; distribution).

Xiphophorus xiphidium, Rosen and Gordon, 1953: 23, 47 (evolution of genitalia); Gordon, 1953c: 789 (mating systems; distribution).

Platypoecilus variatus (in part), Meek, 1904: 146 (records for Garza Valdez, Santa Engracia, Victoria).

Poecilia maculata (misidentification; not *Platypoecilus maculatus* Guenther), Regan, 1906-1908: 105 (in part; records for Garza Valdez, Santa Engracia, and Victoria).

Platypoecilus maculatus, Regan, 1913: 1004 (in part); De Buen, 1940: 44 (literature records; in part).

Platypoecilus xiphodium (misspelling), Needham, 1942: 387 (tumors).

Platypoecilus xiphidinus (lapsus for *xiphidium*), Mayr, 1942: 171 (subspecies or member of superspecies).

Platypoecilus n. sp. Stoye, 1933: 307 (discovery; coloration).

MATERIAL EXAMINED

Mexico, Tamaulipas

Rio Soto la Marina system

1. Arroyo Marmolejo, tributary of Arroyo San Carlos. UMMZ 92310. 4 half-grown to adult females.
2. Rio Santa Lucia at Villagran. UMMZ 108664. 8 half-grown to adult males and females.
3. Rio Purificacion above Cruz. UMMZ 108662. 121 half-grown to adult males and females.
4. Spring tributary of Rio Purificacion 2 mi. W Cruz. UMMZ 124168. 2 half-grown.
5. Rio Purificacion, above Cruz. UMMZ 108661. 12 half-grown to adult males and females.
6. Chorro, ½ mi. above junction Rios Pilon and Purificacion, Rancho Santana, 8 mi. SE Padillo. UMMZ 169671. 17 half-grown.
7. Manantial de Rio Santa Engracia near Hacienda Santa Engracia. UMMZ 124416. 282 young to adult males and females.
8. Rio Corona (Rio Santa Engracia) at La Corona. UMMZ 108663, 97573. 164 half-grown to adult males and females plus the lectotype.
9. Arroyo de la Presa 16 km. N Ciudad Victoria. UMMZ 124404. 54 large young to adult males and females.
10. Rio Corona 3 mi. NE Guemes. UMMZ 124398. 36 large young to adult males and females.
11. Rio San Marcos S Ciudad Victoria. UMMZ 124389. 17 half-grown to adult males and females.
12. Rio Santa Engracia, 17 mi. N Victoria at bridge, highway 1 to Monterrey. UMMZ 169600. 13 half-grown to adults.
13. Rio Corona where road from Guemes to Padilla crosses Rio Corona. UMMZ 169610. 8 adults.

14. Rio Caballero, 729 km. N Mexico City. UMMZ 162151. 234 half-grown to adult males and females.

DIAGNOSIS. A consistently deep-bodied, robust subspecies of *variatus*; with a single weak zigzag dark mid-lateral stripe, two or more stripes, or with a diffuse, dusky midlateral black band; frequently with irregular black speckling along middle sides and on caudal peduncle. Adult males with a short, broad, pointed appendage developed from the lower angle of the caudal fin as a sword. Vertebrae 27 or 28, usually 28. Dorsal fin rays 9 to 11, usually 10.

REMARKS. Though in all sections of the *variatus* complex the adult male shows distinctive "parr" markings along the sides and flanks, these are intensified and very broad in *xiphidium*. They vary with age and in very old males the vertical bars become broad bands of deep purple or black. This subspecies differs from *variatus* proper in the above mentioned color character, in averaging one less dorsal fin ray and one less vertebra, in the invariable presence of the minute caudal sword in adult males, and in proportional measurements (see table 29).

Though this well known form has been described many times (see synonymy above), no holotype was ever designated and the name *xiphidium* thus rests upon a syntypic series from the Rio Corona at La Corona, Tamaulipas, Mexico. From this syntypic material a lectotype is herewith designated:

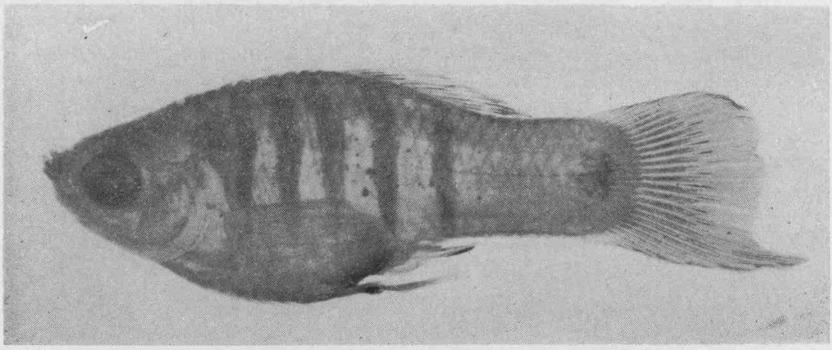


Figure 6. Lectotype of *Xiphophorus variatus xiphidium* (Gordon), (UMMZ: 97573), adult male 29.0 mm in standard length.

Lectotype, an adult male (UMMZ 97573) 29.0 mm in standard length, collected at Rio Corona (Rio Santa Engracia) at La Corona, 15 miles north of Ciudad, Victoria, Rio Soto la Marina system, Tamualipas, Mexico, by Gordon, Creaser, and Ostos on 25 April 1930, together with 164 half-grown to adult males and females (UMMZ 108663).

Reasons for regrouping *xiphidium* and *variatus* as a single species are discussed below. The specimens reported by Meek as *Platypoecilus variatus* from Garza Valdez, Santa Engracia, and Victoria, represent this subspecies.

Xiphophorus variatus variatus (Meek)

Figures 3-4, tables 3-5, 9-13

Platypoecilus variatus Meek, 1904: 146-147 (in part; original description; Valles; records, excluding those of Rio Soto la Marina system); Gordon, 1932a: 287 (Valles); 1932c: 89 (distribution); 1933b: 518-522 (habitat; colorvariations); Meinken, 1933: 89-92 (nomenclature; as aquarium fish; Tampico); Peters, 1933: 9-10 (variations [lowermost figure *X. montezumae*]); Friedman and Gordon, 1934: 446-455 (chromosomes; distribution; hybrids); Kosswig, 1935: 43-46 (distribution; synonymy in part; characters); Gordon, 1935a: 7-10 (distribution; synonymy in part; characters); Bellamy, 1936: 531-535 (hybrids); Anonymous, 1937: 46 (figure; records mapped); Goldschmidt, 1937: 429-439 (sex determination); Gordon, 1937: 388-389 (sex); 1938: 21 (coloration); Breider, 1938: 784-828 (in part; genetic and cytological basis of tumors); Grobstein and Bellamy, 1939: 363-365 (effect of thyroid feeding); Rust, 1939: 172-176 (heterogamety); Gordon and Smith, 1938a: 543-565 (hybridization); Grobstein, 1940a: 1-22 (structure and development of gonopodium); 1940b: 484-486 (hormones; gonopodium; gonopodium in females); Turner, 1940: 64-67 (fetal membranes); Dobzhansky, 1941: 280 (genetics; species or race); Gordon, 1941a: 38-39 (sex); 1941b: 112-113 (Rio Panuco, Rio Cazones; hybridization); Mayr, 1942: 171 (as subspecies or member of superspecies); Potts, 1942: 85-88, 90-93, 95 (hypophysis); Needham, 1942: 387 (tumors); Hubbs and Gordon, 1943: 31 (comparisons); Gordon, Cohen and Nigrelli, 1943: 569 (hormones; caudal fin appendage); Gordon and Benzer, 1945: 58-70 (gonopodial suspensorium; vertebrae); Gordon 1946b: 316-318, 320 (sex determination); 1947a: 117, 129 (speciation; three subspecies); 1950a: 408 (25 pairs of chromosomes); 1950b: 19 (hybrids; Rio Panuco); Gordon and Rosen, 1951: 415, 417, 424-425, 427-433, 454, 457 (genetics of gonopodia); Nigrelli and Gordon, 1951: 121-124 (spontaneous neoplasm in *xiphidium-variatus* hybrid); Gordon and Aronowitz, 1951: 151 (sex determination); Gordon, 1951c: 194-197 (hybridization; distribution; spotting); 1953c: 789-790 (spotting; distribution; hybrids).

Platypoecilus variatus variatus Gordon, 1940e: 172 (habitat; ecological segregation; Rio Axtla); 1943c: 65-67 (dorsal rays; habitat; Guayalejo, Panuco, Valles, Axtla, Cucharas, Tancochin, Tuxpam).

Platypoecilus variatus dorsalis Stoye, 1933: 306-307 (misuse of name in 1932 for *P. v. variatus*); Gordon, 1933b: 6 (explanation of name).

Platypoecilus variatus ssp. Gordon, 1943c: 65-67 (Rio Cazones).

Xiphophorus (Platypoecilus) variatus, Aronowitz, Nigrelli and Gordon, 1951: 239-240 (spontaeous epithelioma); Gordon, 1953b: 148-150 (habitat; association with *X. montezumae*, *X. pygmaeus*).

Platypoecilus maculatus, Regan, 1913: 1004 (in part; diagnosis, Meek's specimens only).

Poecilia maculata (not of Guenther) Regan, 1906-1908: 105 (description; records).

Mollienisia formosa (misidentification, not *Limia formosa* Girard), Rachow, 1932: 705; Roth, 1932: 249 (as aquarium fish).

Mollienesia formosa, Wheeler and Ingle, 1953: 266 (misidentification).

MATERIAL EXAMINED

Mexico, Tamaulipas

Independent Atlantic tributaries

15a. Tributary of Rio San Rafael, 3 mi. S San Rafael. UMMZ M59 195 young to adult.

15b. Rio Tigre at road crossing just north Aldama. UMMZ 59 22 young to adult.

Rio Tamesi system

15c. Rio Guayalejo near Llara, 45 mi. SE Ciudad Victoria. UMMZ 108669. 19 half-grown to adults.

16. Tributary of Rio Guayalejo 16 mi. N Xicotencatl. UMMZ 108668. 75 half-grown to adults.

17. Canal 5 mi. S Limon. UMMZ 97574. 1 young.

Mexico, San Luis Potosi and Veracruz

Rio Panuco system

18. Rio Valles at Valles. UMMZ 108667. 115 half-grown to adults.

19. Same locality. UMMZ 108616. 2 adult females.

20. De los Puercos, Valles. UMMZ NYZS-GL. 21 young to adults.

21. Arroyo near Valles. UMMZ 124437. 3 subadult to adult.

22. El Nilo, Pujal. UMMZ NYZS-GL. 25 half-grown to adult.

23. Pool reputed to have connection with Cueva Chica, Pujal. UMMZ NYZS-GL. ? half-grown to adults.

24. Open pond at Pujal near Cueva Chica. UMMZ NYZS-GL. 2 half-grown.

25. Arroyo Santa Isabel, tributary of Rio del Coy. UMMZ 124383. 10 half-grown to adults.

26. Small arroyo between Rio Axtla and Rio Moctezuma. UMMZ NYZS-GL. 31 half-grown to adults.

27. Rio Matlapa at Matlapa, 8 mi. N Tamazunchale. UMMZ 124338. 11 half-grown to adults.

28. Rio Matlapa. UMMZ NYZS-GL. 9 half-grown to adults.

29. Arroyo Plan de Jalpilla, 18 mi. N Tamazunchale. UMMZ 124351. 18 half-grown to adults.

30. Danubio, Rio Axtla 4 mi. upstream from Axtla. UMMZ NYZS-GL. 22 young to adult males and females.

31. Rio Axtla 2 mi. W Axtla. UMMZ 108604. 123 half-grown to adults.

32. Arroyo Matlapa at Comeca 2 mi. NW Axtla. UMMZ 124375. 3 adults.

33. Rio Axtla at Axtla. UMMZ 124363. 1 mature male.

34. Rio Calaboza 9 mi. SW Tantoyuca. UMMZ 108666. 32 half-grown to adults.

35. Rio de los Hules 11 mi. SW Tantoyuca. UMMZ 108670. 3 adults.

36. Junction of Rio de los Hules and Rio Calaboza. UMMZ 108665. 7 half-grown to adults.

37. Tributary of Rio Tempoal 2.5 mi. N Tempoal. UMMZ 108672. 184 half-grown to adults.

38. Tributary of Rio Panuco 3 mi. N El Higo. UMMZ 108671. 5 half-grown to adults.

Mexico, Veracruz
Estero Cucharas system

39. Estero Cucharas near Cucharas. UMMZ 97575. 203 half-grown to adults.

Estero Tancochin system.

40. Tributary of Estero Tancochin E. Naranjos. UMMZ 108675. 92 half-grown to adults.

Rio Tuxpan system

41. Tributary of Rio Tuxpan 14 mi. S Alamo. UMMZ 108676. 27 half-grown to small adults.
42. Rio Frio, 10 mi. N Juarez (or Mante). UMMZ 162105. 5 specimens not seen but probably subadult since their stand. lengths are given as 24.0-25.0 mm.
43. Drainage canal, 1 mi. N Juarez (or Mante). UMMZ 162119. 4 adults.

Rio Cazones system

44. Tributary of Rio Cazones 12 mi. S Miahuapam. UMMZ 108673. 28 half-grown to adults.
45. Tributary of Rio Cazones near Tihuatlan. UMMZ 108674. 47 half-grown to adults.
46. Arroyo Mariandrea on road to Apapantilla from Papantla at Mariandrea about 10 mi. W Poza Rica (Puebla, Mexico). UMMZ NYZS-GL. 63 half-grown to adult males and females.

Rio Tecolutla system

47. Arroyo Sin Nombre between Guitierrez Zamora and Papantla. UMMZ NYZS-GL. 87 half-grown to adult males and females.

Rio Nautla system

48. Rio Nautla 6 mi. from Tlapacoyan on road to Nautla. UMMZ NYZS-GL. 146 adult males and females.
49. Rio Nautla 4 mi. from Martinez de la Torre on road to Nautla. UMMZ NYZS-GL. 235 young to adult males and females.
50. Stream 2.3 mi. W Ixtacocoa, 3.9 mi. W Martinez de la Torre, on Teziutlan-Casita Highway. UMMZ 167485. 11 half-grown to adult.
51. Ditch 1.8 mi. SW Nautla turnoff towards Martinez de la Torre. UMMZ 167496. 4 adults.

DIAGNOSIS. A variably deep-bodied, moderately robust subspecies of *variatus*; with two or more variably developed zigzag black midlateral stripes; without black speckling along middle sides or on caudal peduncle. Adult males lacking short, broad, pointed caudal appendage or sword. Vertebrae 28 or 29, rarely 30. Dorsal fin rays 9 to 14, usually 11.

REMARKS. Also examined were some of Meek's original collections of this form from Tamaulipas and San Luis Potosi (CNHM 4449, 4461, 4471, 4486, 4502, 14360, 14361, 14435, 14436). An adult specimen from "30 kilometers back of Tampico" (Stoye, 1935: 52) was from the German aquarium stock introduced first as *Mollienisia formosa*, according to an identification by Rachow (1932). The first specimens introduced into German aquaria in 1931 were all young. They were collected by Conrad from a cattle hole near Tampico (Rachow, 1936: 145-146).

Wheeler and Ingle (1953) misidentified *variatus* as *Mollienesia formosa* in a published photograph, showing a female (above) and a male (below), that bears the caption "Male and female *M. formosa.*"

The name "*dorsalis*" is an erroneous application of a manuscript name, but apparently sufficient to fix the name on *X. v. variatus,* which was the only other form mentioned in connection with this first use of the name "*dorsalis*". The originally intended (manuscript) use of the name "*dorsalis*" was later explained by Gordon (1933b: 6). The fish to which this name refers are confined entirely to the Rio Cazones basin and are not at present regarded as being subspecifically separable from other geographical populations of *X. v. variatus.*

Xiphophorus variatus evelynae, new subspecies

Figures 1, 4, 7, tables 3-5, 9-13

Platypoecilus variatus, Gordon, 1941b: 112-113 (Rio Tecolutla record only).
Platypoecilus variatus ssp., Gordon, 1943c: 65-67 (Rio Necaxa).

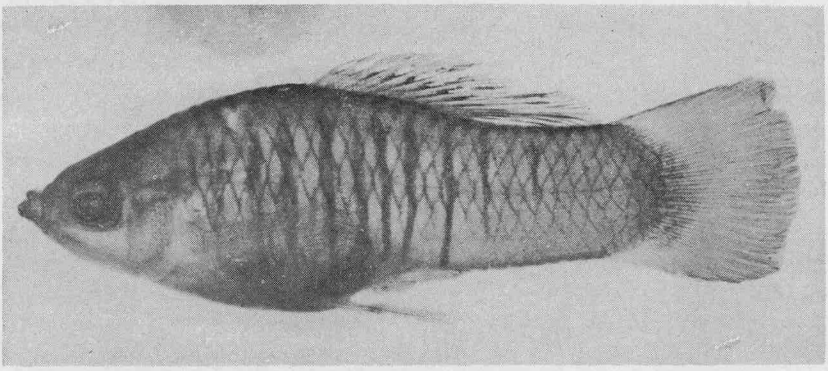


Figure 7. Holotype of *Xiphophorus variatus evelynae,* n. ssp. (UMMZ: 177306), adult male 33.0 mm in standard length.

TYPES. Holotype, an adult male 33.0 mm. in standard length (UMMZ 177306) from station number 58 below. Allotype, an adult female 36.3 mm. in standard length (UMMZ 177307) from same locality.

MATERIAL EXAMINED

Mexico, Puebla

Rio Tecolutla system

52. Rio Tezcapa (= Rio Necaxa) and mouths of two small tributaries 4 mi. W La Mesa (= Necaxa). UMMZ 124313. 20 half-grown to adults.
53. Rio Acatlan entering Vaso de Tenango near La Mesa. UMMZ 124312. 25 subadults to adults.

54. Vaso de Necaxa at La Mesa. UMMZ 124309. 1 mature male.
55. Old Rio Necaxa at foot of dam of Vaso de Necaxa at La Mesa. UMMZ 124303. 12 adults.
56. Tributary of Rio Necaxa draining Vaso de Tenango, ca. 2 km. E Necaxa. 18 adult males and females shipped alive to Genetics Laboratory, New York Zoological Society; this is the basis for present living stock.
57. Rio Necaxa at Tepexic 2 mi. downstream from La Mesa. UMMZ 124317. 40 half-grown to adult.
58. Side branch of the Rio Xaltepuztla where it meets the Rio Necaxa at Tepexic. M. and E. Gordon. 6 April 1939. UMMZ 124318. 9 subadults to adults; excluding holotype and allotype.
59. Manantial de Tepexic entering Rio Necaxa below mouth of Rio Xaltepuztla. UMMZ 124321. 17 half-grown to adults.

DIAGNOSIS. A moderately deep bodied and long headed subspecies of *variatus*, with a relatively short caudal peduncle and long caudal fin (tables 12 and 13). Adult males consistently with 8 to 12 slender, close-set dusky to black vertical bars along midsides that are best developed anteriorly. Vertebrae 28, rarely 27. Dorsal fin rays 12 or 13, rarely 11 or 14.

REMARKS. In addition to the distinguishing criteria listed in the diagnosis, this subspecies is exceptional in lacking micromelanophore tail patterns. Some specimens of each sex show along the sides a speckling of small spots composed of macromelanophores. In adult males, orange-yellow coloring is confined to the proximal half of the caudal fin as a diffuse band whereas in *X. v. variatus* the entire fin becomes pigmented.

Most of the known specimens were collected above a series of cataracts at or around the village of Necaxa (= La Mesa), principally in the Mexican Light and Power Company's reservoirs (*vasos*) and their tributaries at elevations estimated higher than 4000 feet (Stations 52-56). The waters that at one time cascaded sharply from the plateaulike reservoir area down into the gorge of the Rio Necaxa are now deflected into large conduits that lead to the hydroelectric generators. At a small village, Tepexic, on the banks of the Rio Necaxa, almost at the foot of the precipitous 1900-foot drop below the reservoir area (stations 57-59), approximately 70 fish were collected in 1939, some in manantiales near the base of the mountain, others directly in the torrential boulder-strewn riverbed. The latter specimens are the largest and most strikingly marked *X. v. evelynae* in the total sample; the dorsal fins of adult males are greatly developed, extending posteriorly in two examples almost to the caudal base. In 1957 no platyfish were taken below the falls at Tepexic in 2 days of seining, although *Mollienesia sphenops* and *Pseudoxiphophorus bimaculatus* were abundant in both the river and the manantiales. Many *X. v. evelynae* were seined, however, above the falls in the vicinity of Necaxa; this form is undoubtedly plentiful in the reservoirs. According to the engineers of the Mexican Light and Power Company, the Rio Necaxa valley was scoured out and locally modified by flood waters that followed a severe hurricane during the 1940's.

Apparently *variatus* has not become reestablished in its former habitat at Tepexic, although two other poeciliid species have done so. This raises the question of the source of the original Necaxa (reservoir area) and Tepexic populations. Did *X. v. evelynae* derive from a lowland Rio Tecolutla *variatus* population, or from one in a neighboring drainage by headwater transfer? It is difficult to see how lowland forms reaching Tepexic in the past could possibly have overcome the 1900-foot cataracts to establish a population above the falls at Necaxa; also why some *variatus* have not repenetrated to Tepexic from the lowlands.

On the other hand, derivation of *X. v. evelynae* from the headwaters of an adjacent drainage at some former time could account for the large populations in the reservoir area as well as for smaller numbers at Tepexic that floods may have swept downstream. Though they do not now merge, the headwaters of the Rio Necaxa and Rio Cazones approach one another to the north in a network of small streams and tributaries. The fish in these two systems have high dorsal fin ray counts, low vertebral counts, and rather long caudal fins, but the two populations differ in many relative body measurements and in several micromelanophore tail patterns and macromelanophore spotted patterns. It may also be asked why some of the Necaxa fish have not again been washed downstream into Tepexic since their habitat was disrupted. Perhaps the deflection of the larger streams into the conduits and generators of the hydroelectric plants has effectively reduced or eliminated this possibility. In this regard it would be important to know definitely if the *Mollienesia* and *Pseudoxiphophorus* at present around Tepexic are recent immigrants (within the last 10 years) and, if so, from where they came.

This subspecies is named for Mrs. Evelyn Gordon, who, in 1939, was instrumental in collecting the first known examples.

Xiphophorus milleri, new species

Catemaco Livebearer. Figures 8-10, tables 1-5, 14

TYPES. Holotype, an adult male (UMMZ 177308) 23.2 mm in standard length (station 1 below); allotype (UMMZ 177309), an adult female 28.5 mm in standard length (same data).

MATERIAL EXAMINED

Mexico, Veracruz
Rio Papaloapan system

1. A small tributary of Laguna Catemaco about 2 mi. SE Catemaco. R. R. and M. Miller; 29 March 1957. UMMZ 177310. 241 young to adult males and females, excluding holotype and allotype.
2. Same locality. UMMZ M59-25. 93 young to adult males and females.

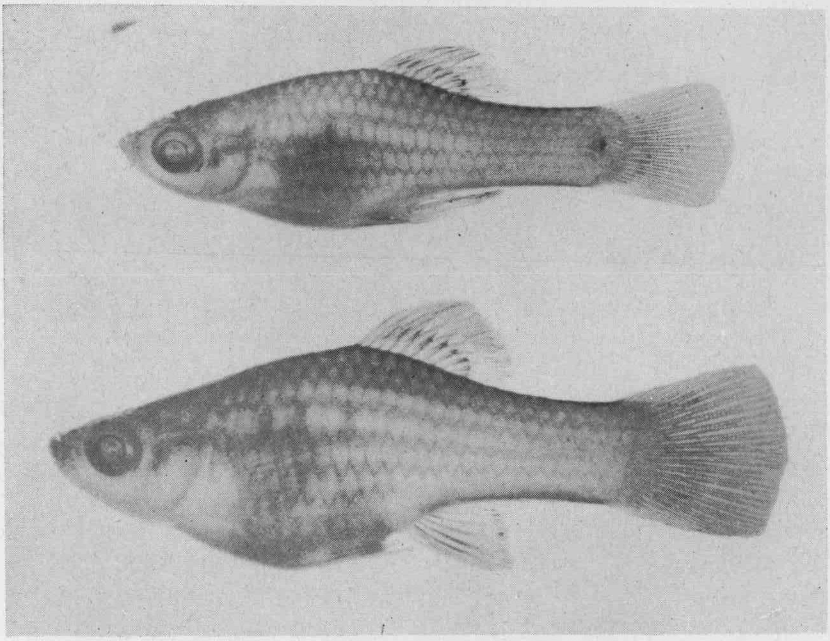


Figure 8. Holotype and allotype of *Xiphophorus milleri*, n. sp. Holotype above, adult male (UMMZ: 177308), 23.2 mm in standard length. Allotype below, adult female (UMMZ: 177309), 28.5 mm in standard length.

DIAGNOSIS. A small to medium, slender-bodied species of *Xiphophorus* (tables 4 and 5), with caudal peduncle extremely slender and much compressed laterally; with 6 to 8 variably developed dusky bands along sides that follow the scale rows and a deep lying ridge of darker black pigment midventrally on caudal peduncle. Adult males without pointed appendage on ventral rays of the caudal fin. Dorsal fin with a broad marginal dusky band and a median row of distinct black dashes that are oriented parallel with the fin rays and lie in the interradial membrane. Claw at tip of ray 5a of gonopodium thin, one half as thick as hook on ray 3, with weakly developed or obsolescent terminal cusp, present only in about half of the specimens; distal serrae on ray 4p well developed, 8 to 11 in number; ramus of ray 4a curved downward over blade, extending to tip of ray 4p; hook on ray 3 long and slender. Vertebrae 28, rarely 29. Scales in a lateral series 25 to 27, usually 26. Dorsal fin rays 9 to 11, usually 10.

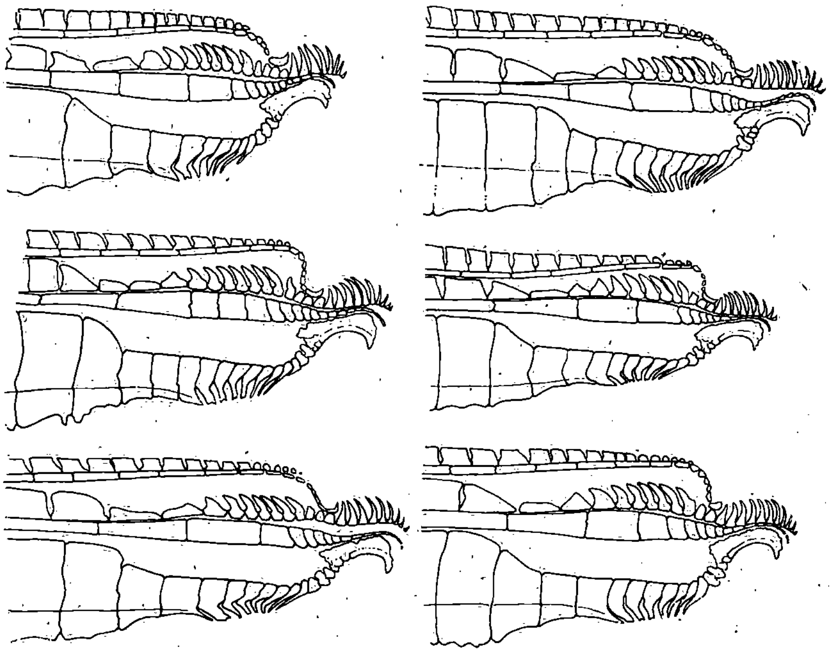


Figure 9. Distal tips of the gonopodia of males of *Xiphophorus milleri*, n. sp. (UMMZ: 177310).

GENERAL ACCOUNT. Among the many distinctive features of this rather small species is the presence in slightly less than half the specimens of both sexes of several different micro- and macromelanophore markings. There are three tail patterns (composed of micromelanophores), a one spot similar to that of *maculatus* and *variatus*, a large one spot similar to that of some *variatus*, and a barlike pattern resembling one found in *montezumae* and *pygmaeus*. Two macromelanophore patterns may be distinguished phenotypically, one of irregular spots on the body, and another of more or less definite rows of spots arranged along the dusky bands on the side. Similar macromelanophore patterns are found in *montezumae*, *maculatus*, and *variatus*. According to the field notes of R. R. Miller, who collected this species, the side and belly of adult males are deep yellow-orange (in late March).

This species is of particular importance for establishing the taxonomic integrity of the platyfishes and swordtails. It combines traits that in each group were hitherto used for generic separation. Body form, pigmentation, and ecology ally it to the swordtails. It resembles the platyfishes in certain secondary sexual characters, in the absence of a well-developed caudal appendage, and in showing pigmentary polymorphism. Its probable relationships are discussed below.

Xiphophorus milleri, known only from the single locality listed, is named for Dr. Robert Rush Miller who collected this and many other forms of *Xiphophorus.*

Xiphophorus montezumae Jordan and Snyder

Montezuma Swordtail, figures 10-13, 30, tables 1-5, 15-19

Xiphophorus montezumae Jordan and Snyder, 1900: 131-133 (original description; color variation; Rio Verde near Rascon, San Luis Potosi).

DIAGNOSIS. A moderate to large, rather deep-bodied species of *Xiphophorus* (tables 4 and 5) with a moderately to well developed caudal appendage that is conspicuously edged with black on its upper and lower margins, and having a continuous solid or zigzag black midlateral stripe running from base of caudal peduncle through eye to lips. With a deep-lying ridge of black pigment midventrally on caudal peduncle. Dorsal fin rounded, with broad marginal dusky band. Caudal fin above swordlike appendage without marginal pigment. Claw at tip of ray 5a of gonopodium thin, one half as thick as hook on ray 3, with weakly developed terminal cusp; distal serrae on ray 4p well developed, 5 to 12 in number; ramus of ray 4a curved downward over blade, extending to tip of ray 4p; hook on ray 3 long and slender. Vertebrae 28 to 30, usually 29. Scales in a lateral series 25 to 28, usually 27 or 28. Dorsal fin rays 10 to 14, usually 11 or 12.

GENERAL ACCOUNT. This species apparently is confined to the Rio Panuco drainage system. The typical form occurs in the headwaters of the Rio Tamesi, and in the Panuco proper, in the headwaters of a tributary to the Rio Tampaon, the type locality. A second form of *montezumae* occurs to the south in the Rio Moctezuma. Each of these populations is distinct in pigmentation, in shape and relative size of the caudal appendage, and to a lesser extent in morphometric traits (see tables 15-19 and discussion above). The form from the Rio Moctezuma is treated here as a distinct subspecies.

This species has become well known from genetic and correlated studies by Gordon and others on *m. cortezi.* This is the most southern representative (Rio Moctezuma) and until recently the only subspecies maintained alive for laboratory study. Living examples of *m. montezumae* recently secured in Mexico have been successfully crossed with *m. cortezi.* So far 200 fertile hybrids have been obtained.

Four macromelanophore patterns occur in this species, a striped pattern, two kinds of spotting on the side, and a caudal marking. Morphologically the cells composing these patterns resemble those of the platyfish (see above). At least one of the *montezumae* patterns, spotted caudal (Sc), produces melanotic and melanomatous growth in *montezumae* x *helleri* hybrids.

A single micromelanophore tail pattern occurs in this species, exclusive of pigmentation associated with the "sword." This pattern is indistinguishable from one occurring in *pygmaeus nigrensis.* It is similar to the moon pattern of *maculatus,* though larger and more diffuse, and usually dusky rather than black.

Xiphophorus montezumae montezumae Jordan and Snyder

Figures 11-12, 30, tables 3-5, 15-19

Xiphophorus montezumae Jordan and Snyder, 1900: 131-133 (original description; Rio Verde near Rascon); Jordan and Evermann, 1900: 3154-3156 (after Jordan and Snyder); Meek, 1904: 158-159 (description; Rascon); Regan, 1906-1908: 107 (diagnosis; Rascon); 1913: 1004 (diagnosis; relationships; Rio Panuco).

MATERIAL EXAMINED

Mexico, Tamaulipas

Rio Panuco system
Rio Tamesi

1. Nacimiento of Rio Sabinas, about 5 mi. W NW of El Porvenir (near km. mark 613 on Pan American Highway). 30 young to adult males and females taken alive.
2. Nacimiento of Rio Sabinas, tributary to Rio Guayalejo, 11 mi. N Gomez Farias. UMMZ NYZS-GL. 45 half-grown to adult males and females.
3. Pano Ayuctle, Rio Sabinas about 2 mi. W of km. mark 610 on Pan American Highway. 1 adult male taken alive.

Mexico, San Luis Potosi

Rio Panuco system
Rio Salto

4. Pools adjacent to Rio Salto de Agua 12 km. NW of road from Antigua Morelos to San Luis Potosi. 26 young to adult males and females taken alive.
5. Same locality and pools as above. LSU 6262. 55 half-grown to adult males and females.
6. Rio Verde near Rascon. SU 6145, 6146, 6194. 132 half-grown to adult males and females, including holotype and paratypes.
7. Rascon. SU 23876. 13 subadults.

DIAGNOSIS. A short-headed subspecies of *montezumae,* adults ranging from 27 to 54 mm. in standard length. Caudal appendage

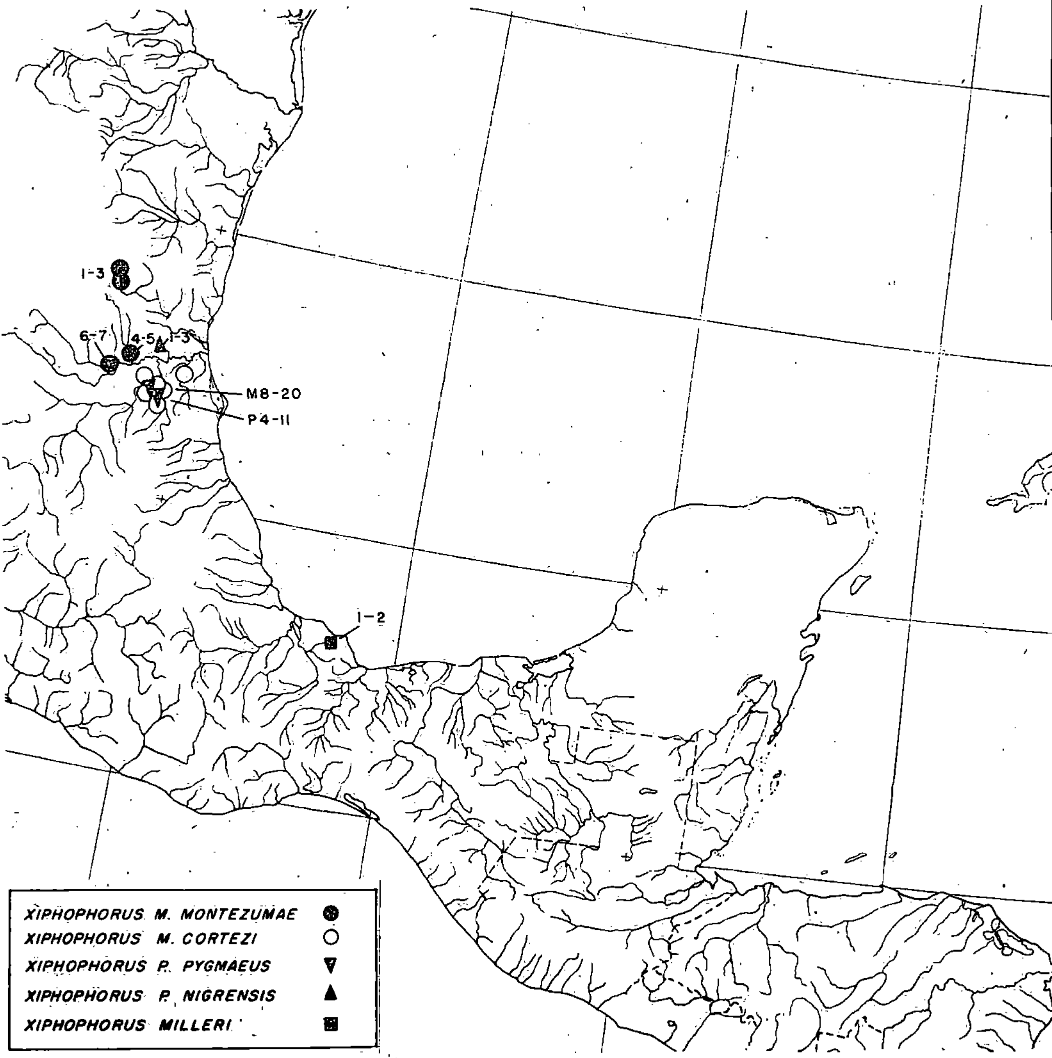


Figure 10. Distribution by record stations for *X. milleri*, and the forms of *X. montezumae* and *X. pygmaeus*.

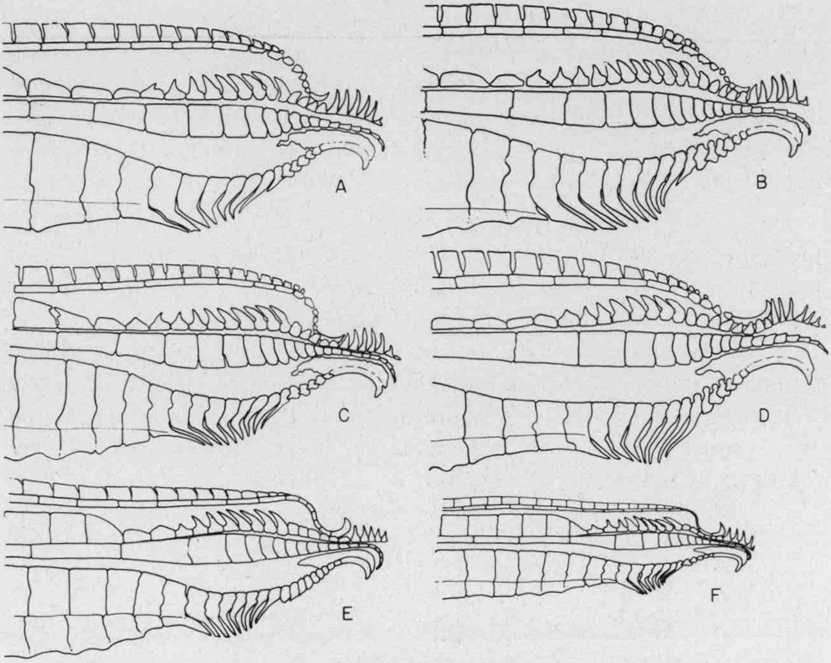


Figure 11. Distal tips of the gonopodia of males of the forms of *X. montezumae* and *X. pygmaeus*. A-C. *X. montezumae cortezi*, n. ssp. (LSU: 6261). D. *X. montezumae montezumae* Jordan and Snyder (SU: 6146). E. *X. pygmaeus nigrensis*, n. ssp. (UMMZ:NYZS-GL, Rio Choy). F. *X. pygmaeus pygmaeus* Hubbs and Gordon (laboratory stock).

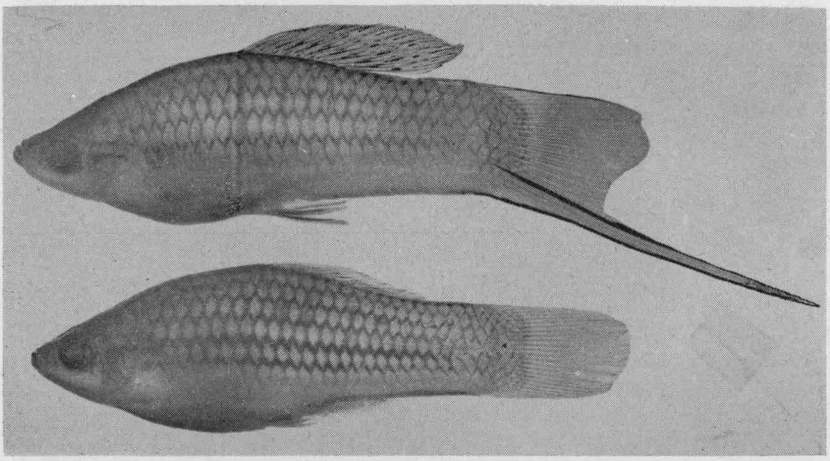


Figure 12. *Xiphophorus montezumae montezumae* Jordan and Snyder (LSU: 6262), from the Rio Salto de Agua. Male above, 55.0 mm, and female below, 54.0 mm in standard length. Retouched photo.

always long, straight, and rather wide, particularly at the base. Black markings along sides and flanks arranged in more or less definable rows that are joined together to form a reticulum, the midlateral row always the most prominent and developed as a zigzag line, never as a solid band. In adult males, dorsal fin with a distinct median row of black spots on interradial membrane. Vertebrae 28 to 30, usually 29.

REMARKS. I found this form to be most common in small spring pools that are periodically connected with the main river at times of high water. They occur in small numbers together with *Astyanax*, *Dionda*, and *Gambusia* in the main channel.

Two macromelanophore patterns have been recorded, a striped pattern in which the spots are confined to regions delimited by the horizontal sections of the reticulum, especially the midlateral stripe, and a spotted pattern in which larger irregular blotches dot the middle side below the dorsal fin.

Xiphophorus montezumae cortezi, new subspecies

Figures 10-11, 13, 30, tables 3-5, 15-19

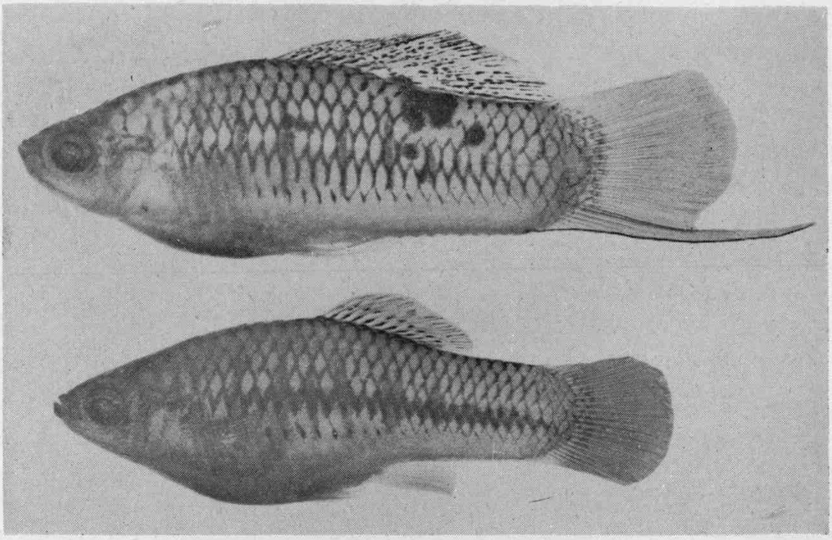


Figure 13. Holotype and allotype of *Xiphophorus montezumae cortezi*, n. ssp. Holotype above, adult male (UMMZ: 177302), 38.5 mm in standard length. Allotype below, adult female (UMMZ: 177303), 34.9 mm in standard length.

Xiphophorus montezumae, Gordon, 1933b: 518-522; 1934a: 107-110 (habitat; coloration; "*X. montezumae*" of aquarists cleared from synonymy); Friedman and Gordon, 1934: 446-455 (chromosomes; distribution); Gordon, 1938: 19-29 (history of name "*montezumae*" as applied to a variety of *X. helleri*); 1940e: 172 (habitat and ecological separation; Rio Axtla); 1941b: 112-113 (northern and upland parts of Rio Panuco system; differential ecology; hybrids with *X. maculatus*); 1942b: 196-197 (as aquarium fish; confusion of name; Rio Axtla); 1943c: 68-69 (habitat; gonopodium; variant patterns; Rio Axtla; no hybrids in nature); Gordon, Cohen and Nigrelli, 1943: 571 (caudal fin appendage in light of hormone experiments); Hubbs and Gordon, 1943: 31-32 (gonopodium; dorsal rays); Gordon and Benzer, 1945; 58, 60-61, 63-67, 69-70 (vertebrae; ribs; suspensorium; comparisons); Gordon, 1946d: 84-85 (introgressive hybridization; color patterns); 1948a: 258 (melanomas and hybrids); 1950a: 406 (spotting in hybrids with *X. helleri*); Gordon and Rosen, 1951: 414, 417, 424-429, 432-433, 454, 456-457 (genetics and morphology of gonopodia); Gordon and Aronowitz, 1951: 151 (sex determination unknown); Aronowitz, Nigrelli and Gordon, 1951: 240 (tumors); Gordon, 1951c: 172, 196-198 (tumors; distribution; hybrids); Rosen and Gordon, 1953: 22-23 (gonopodial adaptations); Gordon, 1953b: 148-150 (habitat); 1953c: 789-790 (distribution; spotting).

Platypoecilus variatus, Peters, 1933b: 9 (in part; misidentification; lowermost figure only).

TYPES. Holotype, an adult male (UMMZ 177302) 38.5 mm. in standard length and allotype, an adult female (UMMZ 177303) 34.9 mm. in standard length, both from station 16.

MATERIAL EXAMINED

Mexico, San Luis Potosi
Rio Panuco system
Rio Moctezuma

8. Arroyo near Valles. UMMZ 124436. 3 subadults.
9. Arroyo Palitla at Palitla, 8 mi. N Tamazunchale. UMMZ 124331. 312 young to adult males and females.
10. Small arroyo between Rio Axtla and Rio Moctezuma. UMMZ NYZS-GL. 67 half-grown to adult males and females.
11. Rio Matlapa at Matlapa, 13 mi. N Tamazunchale. UMMZ 124341. 46 half-grown to adult males and females.
12. Arroyo Matlapa. UMMZ NYZS-GL. 37 half-grown to adult males and females.
13. Arroyo Plan de Jalpilla, 18 mi. N Tamazunchale. UMMZ 124353. 55 large young to subadults.
14. Danubio, Rio Axtla 4 mi. upstream from Axtla. UMMZ NYZS-GL. 53 young to adult males and females.
15. Rio Axtla 2 mi. W Axtla. UMMZ 108602. 21 half-grown to adult males and females.
16. Arroyo Matlapa at Comoca, 2 mi. N of Axtla. M. Gordon, S. Coronad, and H. F. Gandy; 14-15 April 1939. UMMZ 124374. 128 young to adult males and females excluding holotype and allotype.
17. Rio Axtla at Axtla. UMMZ 124364. 9 young to adult males and females.
18. Pool in river bed of Rio Axtla at Axtla. UMMZ 124174. 4 large young to subadults.
19. Tributary of Rio Calaboza 20 mi. S Tantoyuca. UMMZ 108679. 3 half-grown.
20. Rio de los Hules 11 mi. SW Tantoyuca. UMMZ 108678. 1 half-grown.

Diagnosis. A long-headed subspecies of *montezumae*, adults variable in size, averaging about 30 mm. in standard length. Caudal appendage usually short and curved upward at tip; and rather slender. Black pigment along sides and flanks evenly arranged in a uniform reticulum, except along midlateral line where it usually forms a prominent zigzag line or a solid black band. In adult males, dorsal fin lacking a distinct median row of black spots on interradial membrane. Vertebrae 29, rarely 28.

Remarks. Though never before recognized as a distinct subspecies, this form is well known in the literature and has been described many times. The above diagnosis is sufficient to set it off clearly from the lesser known typical form.

The midlateral stripe in adult male *cortezi* may be rather faint, incomplete, or lacking. Its expression is affected by the physiological state of the animal at time of fixation, i.e., excitation versus quiescence, and by the background shade of the environment. Some living specimens maintained in the laboratory for years show heavy deposition of guanine along the side and flank giving the fish a silvery hue. Perhaps guanine competes with the black pigment, for in some instances where the silvery coloring pervades the entire fish even the characteristic reticulum may be absent.

Two macromelanophore patterns and one micromelanophore tail pattern occur in this subspecies. One or more variable black spots may occur on the interradial membrane of the caudal fin. In both size and position on the fin this pattern is inconstant, though it usually follows the fin's long axis. A spotted pattern on the upper side near the dorsal fin may spread to the base of this fin, rarely to its distal margin.

The name *cortezi* is a historical reference to the Spanish conquistador, Hernando Cortez (1485-1547).

Xiphophorus pygmaeus Hubbs and Gordon

Pygmy Swordtail, figures 10-11, 14-16, 31, tables 1-5, 20-23

Xiphophorus pygmaeus Hubbs and Gordon, 1943: 31-33 (Rio Axtla).

Diagnosis. A small, slender species of *Xiphophorus* (tables 4 and 5) with a slightly to well-developed caudal appendage, having a continuous solid black midlateral stripe running from base of caudal peduncle through eye to lips that is separated from a series of black to dusky blotches on the dorsum by a light, almost unpigmented area. Without a deep-lying ridge of black pigment midventrally on caudal

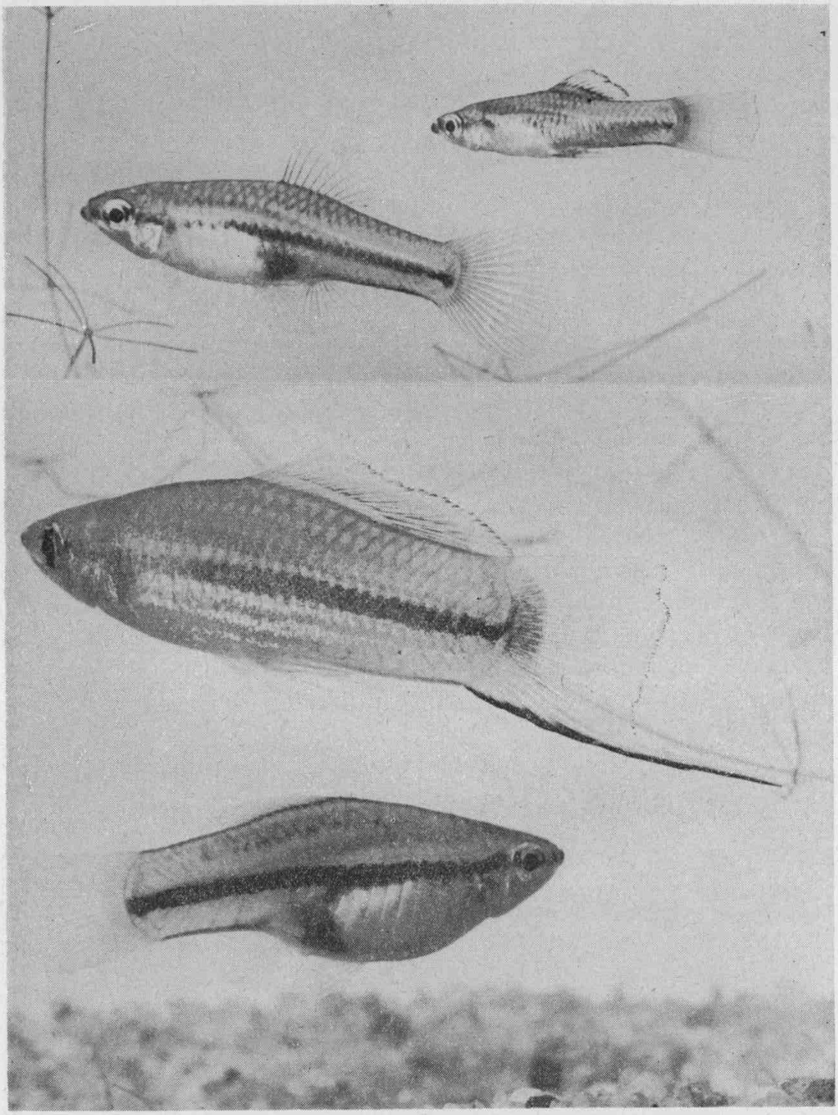


Figure 14. Living laboratory born and reared breeding pairs of *Xiphophorus pygmaeus pygmaeus* Hubbs and Gordon (above) and *Xiphophorus pygmaeus nigrensis*, n. ssp. (below). Males are on top; note thin line of dark pigment along the edges of their dorsal and caudal fins and their partly faded midlateral black stripes.

peduncle. Dorsal fin rounded, with fine dusky margin and basal or median row of black or dusky spots on interradial membrane in adult males. Caudal fin above "sword" truncate, usually with a fine dusky margin on posterior edge in adult males. Claw at tip of ray 5a of gonopodium thick, two times as thick as hook on ray 3, with moderately developed terminal cusp; distal serrae on ray 4p only moderately developed, approximately 4 in number; ramus of ray 4a slightly curved downward over blade, extending to tip of 4p but sometimes falling slightly short; hook on ray 3 long and slender. Vertebrae 28 or 29. Scales in a lateral series 25 to 28. Dorsal fin rays 9 to 14.

General Account. Until recently this species was thought to be confined to the Rio Axtla (Rio Panuco system) above the town of Axtla, the type locality of this small swordtail (Hubbs and Gordon, 1943). In 1952 R. T. Gregg collected another distinctive form of the pygmy swordtail in the north arm of the Rio Panuco below Valles, a little over 100 miles by water from Axtla.

Both forms of the pygmy swordtail are restricted, for the most part, to deep pools and the waters along undercut slopes of river and stream beds. *X. p. pygmaeus* is infrequently encountered in dense stands of submerged aquatics and along exposed shoreline in shallow water on the slip-off slope of the Rio Axtla at Axtla. *X. p. nigrensis* is known only from deep, swiftly flowing water at depths as great as 10 feet.

Xiphophorus pygmaeus nigrensis, new subspecies

Figures 10-11, 14-15, 31, tables 3-5, 20-23

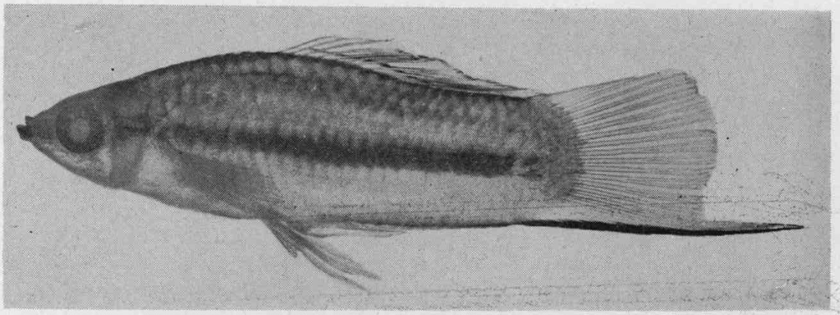


Figure 15. Holotype of *Xiphophorus pygmaeus nigrensis*, n. ssp. (UMMZ: 177301), adult male 29.0 mm in standard length. Retouched photo.

Holotype. An adult male (UMMZ 177301) 29.0 mm standard length from Station 1.

MATERIAL EXAMINED

Mexico, San Luis Potosi
Rio Panuco system
Rio Choy

1. Nacimiento del Rio Choy, 4 km. N Hotel Taninul, 3 km. N of road from Route 110 (Valles-Tampico Highway). D. E. Rosen, M. S. Gordon, and M. Gordon; 19 January 1957. UMMZ NYZS-GL. 30 adults to half-grown including holotype; 8 adult males and 12 adult females and young taken alive.
2. Nacimiento del Rio Choy. LSU 6265, 6388. 6 adults to half-grown.
3. Rio Choy at Rancho Colandria 2 mi. W Tamuin. LSU 6264. 1 adult male.

DIAGNOSIS. A large, deep-bodied subspecies of *pygmaeus*, with a moderately to well-developed caudal appendage that is set off by a distinct black line on its ventral margin. In pregnant adult female, a small indistinct dusky patch or weakly developed triangular black mark on side directly above vent. Vertebrae 29. Scales in a lateral series 25 to 28, usually 27. Dorsal fin rays 11 to 14, usually 12.

REMARKS. A large oval or rectangular black spot may occur at the base of the caudal peduncle. In the two available samples it appears to be normal for a single population of *nigrensis* to contain adult males of quite diverse sizes (fig. 28). The smallest ones (about 20 mm) are slender, have short swords and an intensely black lateral stripe. With increase in size (standard length) the body becomes proportionally deeper, the sword longer, and a brilliant iridescent blue develops along the side and flank, partly obscuring the midlateral black stripe. In the largest males (30 mm plus) the lateral stripe may not be in evidence during times of inactivity, but during courtship or feeding it may be pronounced. The polymorphism exhibited by adult males of *p. nigrensis* appears to be most closely related to factors affecting absolute size, e.g. body growth in the vertical dimension and sword growth are positively allometric with axial lengthening. (See values of maximum and minimum relative depths, tables 4 and 5, and discussion below).

This distinctive form is closely allied to the pygmy swordtail on the basis of overall pigmentation, the structure of the gonopodium of the adult male, and ecology. In coloration it differs primarily in having a pigmented caudal appendage and in the character of the anal blotch in adult females, as noted in the diagnoses. Its gonopodium cannot be clearly distinguished from that of the nominate form. Like *p. pygmaeus*, it prefers deep and clear fast waters along undercut slopes. Other characters are listed in the diagnosis and in tables 7, 8, 21, 22, 23, and 24.

The young of *p. nigrensis* apparently are born larger than those of the nominate form, and they may be slower growing. Precise data on these two points are not yet available. Despite these and other differences, the two pygmy swordtails form such a manifestly compact group that they are treated as conspecific. On the one hand, their differences are not greater than those that separate the subspecies of *helleri, montezumae* or *variatus,* whereas on the other, heterotypic matings are as readily effected as homotypic matings of *p. nigrensis,* and the comparatively large numbers of young so produced (about 14 per brood as compared with 11, 9, 7, and 4) develop into vigorous and healthy adults. The two forms are allopatric.

As discussed below, large adult males of *p. nigrensis* are strikingly similar to the smaller, silvery males of *m. cortezi,* and in this way aid in defining the relationships of these two swordtail species.

The name *nigrensis,* compounded from the Latin, *niger* = black, and *ensis* = sword, refers to the diagnostic ventral margin of black pigment on the caudal appendage of adult males.

Xiphophorus pygmaeus pygmaeus Hubbs and Gordon

Figures 10-11, 14, 16, 31, tables 3-5, 20-23

Xiphophorus pygmaeus Hubbs and Gordon, 1943: 31-33 (original description; comparisons; variation; Rio Axtla at Axtla; between Rio Axtla and Rio Moctezuma); Gordon, Cohen and Nigrelli, 1943: 571 (caudal fin character in light of hormone experiments with *Platypoecilus* [=*Xiphophorus*] *maculatus;* Gordon and Rosen, 1951: 424-433 (gonopodium); Gordon, 1953: 148-150 (ecology); Rosen and Gordon, 1953: 21-23 (mechanics of gonopodium).

Xiphophorus sp., Gordon, 1940e: 172; 1943c: 68 (ecological isolation; habitat).

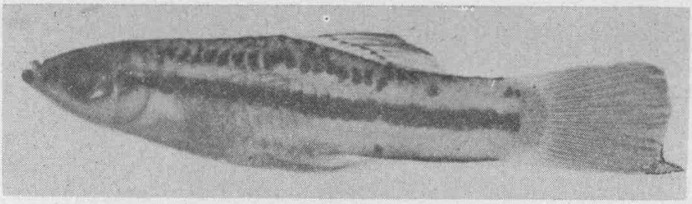


Figure 16. Adult male of *Xiphophorus pygmaeus pygmaeus* Hubbs and Gordon, 22.0 mm in standard length. Wild caught specimen from the Rio Axtla (NYZS-GL).

MATERIAL EXAMINED

Mexico, San Luis Potosi

Rio Panuco system

Rio Axtla

4. Small arroyo between Rio Axtla and Rio Moctezuma. UMMZ NYZS-GL. 1 adult female.
5. Rio Matlapa at Matlapa 8 mi. N Tamazunchale. UMMZ 124340. 1 adult female.

6. Danubio, Rio Axtla, 4 mi. upstream from Axtla. UMMZ NYZS-GL. 29 young to adult males and females.
7. Rio Axtla, 2 mi. W Axtla. UMMZ 108601. 1 subadult male.
8. Rio Axtla at Axtla. UMMZ 124366, 124365. 174 young to adult males and females, one of which, a male, is holotype.
9. Rio Axtla at Axtla. UMMZ NYZS-GL. 28 young to adult males and females.
10. Rio Axtla at ferry to Xilitla. LSU 6311. 23 half-grown to adult males and females.
11. Rio Axtla at ferry to Xilitla. UMMZ NYZS-GL. 50 adult males and females, some taken alive.

DIAGNOSIS. A small, slender form of *pygmaeus*, with a weakly developed caudal appendage that lacks black ventral emargination. In pregnant adult female, a well-developed subtriangular black patch on side directly above vent. Vertebrae 28, rarely 29. Scales in a lateral series 25 or 26, usually 26. Dorsal fin rays 9 to 12, usually 10 or 11.

REMARKS. The nominate form of the pygmy swordtail appears to have a restricted distribution in the upper part of the Rio Panuco system of northeastern Mexico. Most of the known specimens have come from the Rio Axtla, tributary of the Rio Moctezuma, San Luis Potosi. Here it was found in the same cross section of the stream with *Xiphophorus v. variatus* and *Xiphophorus montezumae cortezi*, but almost always in a different ecological niche.

Since, with one exception, all of the known specimens came from the Rio Axtla at Axtla, and from an "arroyo between Rio Axtla and Rio Moctezuma," or have been bred from stock obtained at Axtla, little can be said regarding geographical variation. The one fish, an adult female 40 mm. in standard length, that was taken in the Rio Matlapa at Matlapa (misspelled Matalpa in Hubbs and Gordon, 1943), is 8 mm. longer than any of the large series from Axtla and is not fully typical in appearance. The black band is not set off as strongly as in most of the specimens, though it can be matched by some of the Axtla fish. Its low dorsal fin ray count of 10 suggests that it is correctly assigned to this subspecies.

Like other *Xiphophorus*, with the probable exception of *couchianus*, the stock of *Xiphophorus pygmaeus* from Axtla is polymorphic. Golden or slaty-blue variants appear and lines of each color have been established by breeding. The usually broad, black, rather even-edged lateral band may be narrow and zigzag, much as in *X. montezumae*. The dark blotches on the upper parts may be absent, or may connect with the lateral band. A ventrolateral band of dusky blotches develops in some fish.

Xiphophorus clemenciae Alvarez

Yellow Swordtail. Figures 17-19, tables 1-5, 24

Xiphophorus clemenciae Alvarez, 1959: 69-71 (original description; Rio Sarabia, Oaxaca).

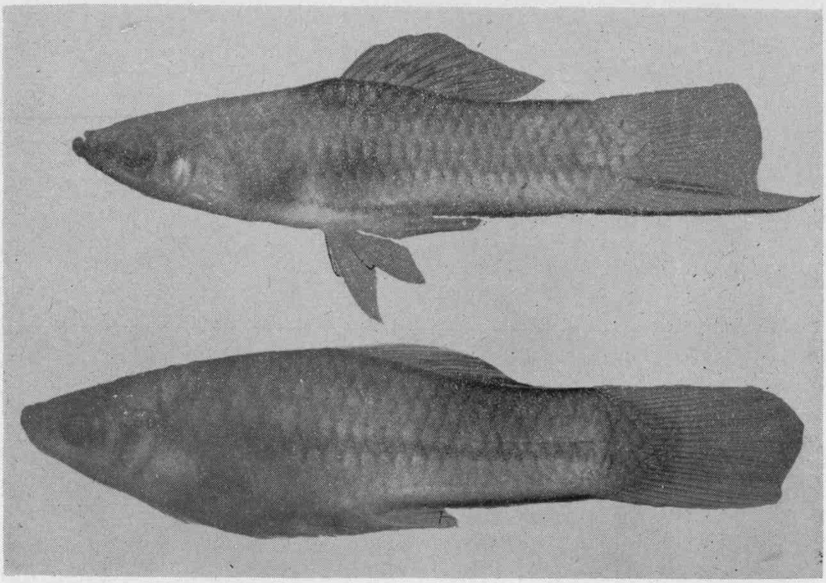


Figure 17. Topotypes of *Xiphophorus clemenciae* Alvarez. Above, adult male (UMMZ: 177311), 30.0 mm in standard length, and below, an adult male (UMMZ: M57-55) 33.9 mm. in standard length.

Material Examined

Mexico, Oaxaca
Rio Coatzacoalcos system

1. Small tributary of Rio Sarabia, about 75 mi. S Acayucan (Veracruz). UMMZ M57-55. 33 young to subadult.
2. Same locality. UMMZ 177311, 177312. 15 young to adult.
3. Stream running east-west crossed by Trans-Isthmian Highway, 5 mi. N Donaji. UMMZ M57-56. 13 young to subadults.

Diagnosis. A small to moderate, slender bodied species of *Xiphophorus* (tables 4 and 5), with a well-developed caudal appendage that is conspicuously edged with black on its upper and lower margins; two continuous solid red lateral stripes extending from caudal base to opercle; a small black band passing from in front of eye forward to lips; a well-developed dusky axillary stripe extending from ventral margin of pectoral base posteriorly along belly to base of gonopodium or beyond; a deep-lying ridge of black pigment midventrally on caudal peduncle; and a group of from 3 to 6 small red or orange spots proximally on base of caudal fin. Dorsal fin with last few rays elongate in adult male and rounded in female and young, with a row of triangular black or dusky markings along its proximal third and a diffuse band of dusky pigment along its distal third. Caudal fin above "sword" distinctly convex without definite marginal pigment. Claw at tip of ray 5a of gonopodium variable, but occasionally moderately developed and formed as in *helleri;* distal serrae on ray 4p moderately developed, 5 or 6 in number; ramus of ray 4a slender, but definitely hooked backward over bluntly pointed blade, extending slightly beyond tip of ray 4p; hook on ray 3 rather short and broad, sickle-shaped.

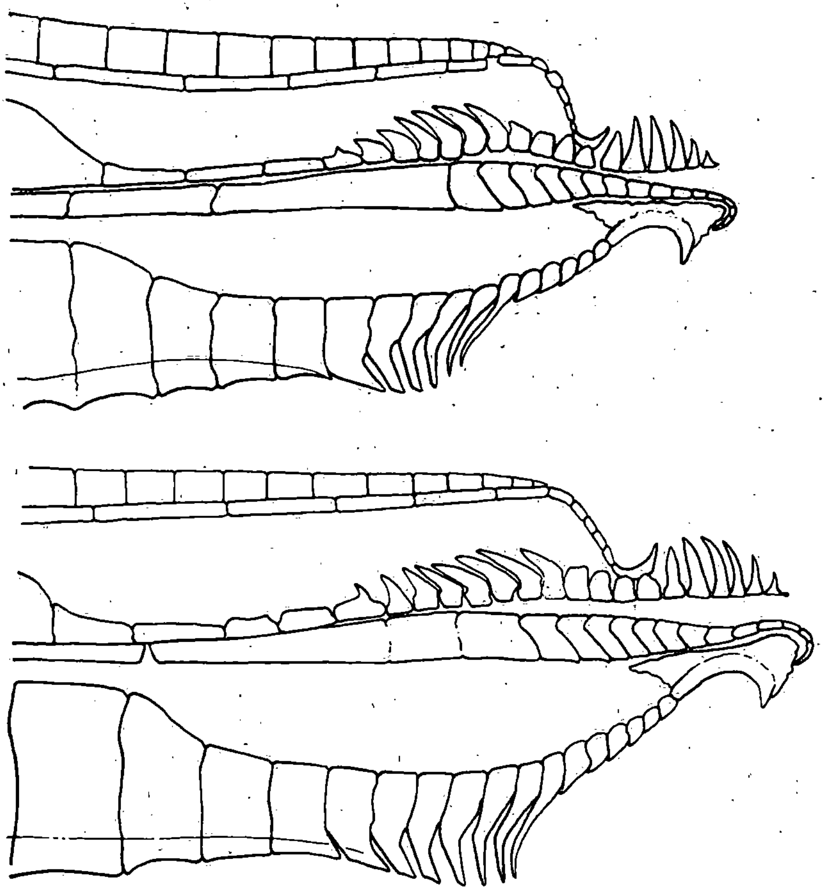


Figure 18. Distal tips of the gonopodia of males of *Xiphophorus clemenciae* Alvarez (UMMZ: 177312).

Vertebrae 29, rarely 28. Scales in a lateral series 26 or 27, usually 27. Dorsal fin rays 11 or 12, rarely 10 or 13.

General Account. When first encountered in 1957 in collections of swordtails from the Rio Coatzacoalcos system, this species was overlooked, primarily because of its strong superficial resemblance in size, coloration, and proportion to *X. helleri strigatus*. It is known only from three collections in Oaxaca and was taken together with the green swordtail each time. It lives sympatrically with *helleri* and is certainly that species' closest relative. The two are readily separated by gonopodial characters and dorsal fin markings.

According to field observation of Robert R. Miller, who first collected this new species, its habitat appears to be typical of *helleri* and other swordtail species. His records for March 1957 state the water was clear, vegetation none, the bottom consisted of mud, silt and brush, and the current was moderate to almost none. The stream averaged about 4 feet wide and was bordered by a steep bank of dense, tropical vegetation (rain forest). In February 1959 he obtained many living specimens in the same stream, which was then a torrent of significant proportions.

Alvarez (1959) reported that some of the males were bright yellow, a color not noted in my specimens. A male and female paratype of *clemenciae* are identical to my material in all other respects.

Xiphophorus helleri Heckel

Green Swordtail, figures 19-23, 32, tables 1-5, 25-31

Xiphophorus hellerii Heckel, 1848: 291, pl. 8.

Diagnosis. A large, slender bodied species of *Xiphophorus* (tables 4 and 5), with a well-developed caudal appendage that is conspicuously edged with black on its upper and lower margins, and having one or more continuous solid or zigzag black or red lateral stripes, the midlateral stripe only running from base of caudal peduncle, where it may be continuous with pigment of caudal appendage, forward through eye to lips. With a deep-lying ridge of black pigment midventrally on caudal peduncle. Dorsal fin usually rounded, rarely with the last few rays produced; dorsal fin in adult males only, usually with a median and a subdistal row of subspherical black or red spots. Caudal fin above "sword" without distinct marginal pigment. Claw at tip of ray 5a of gonopodium large, as large as hook on ray 3, distinctly scythe-shaped, the terminal cusp being as large as or larger than proximal section; distal serrae on ray 4p variably developed, usually small and blunt, rarely obsolescent, 2 to 7 in number when typically formed;

ramus of ray 4a heavy, hooked sharply downward over distinctly or bluntly pointed blade, extending to tip of ray 4a; hook on ray 3 short and broad. Vertebrae usually 28 to 30, rarely 31. Scales in a lateral series 25 to 29, usually 26 or 27. Dorsal fin rays 11 to 17, usually 12 to 14.

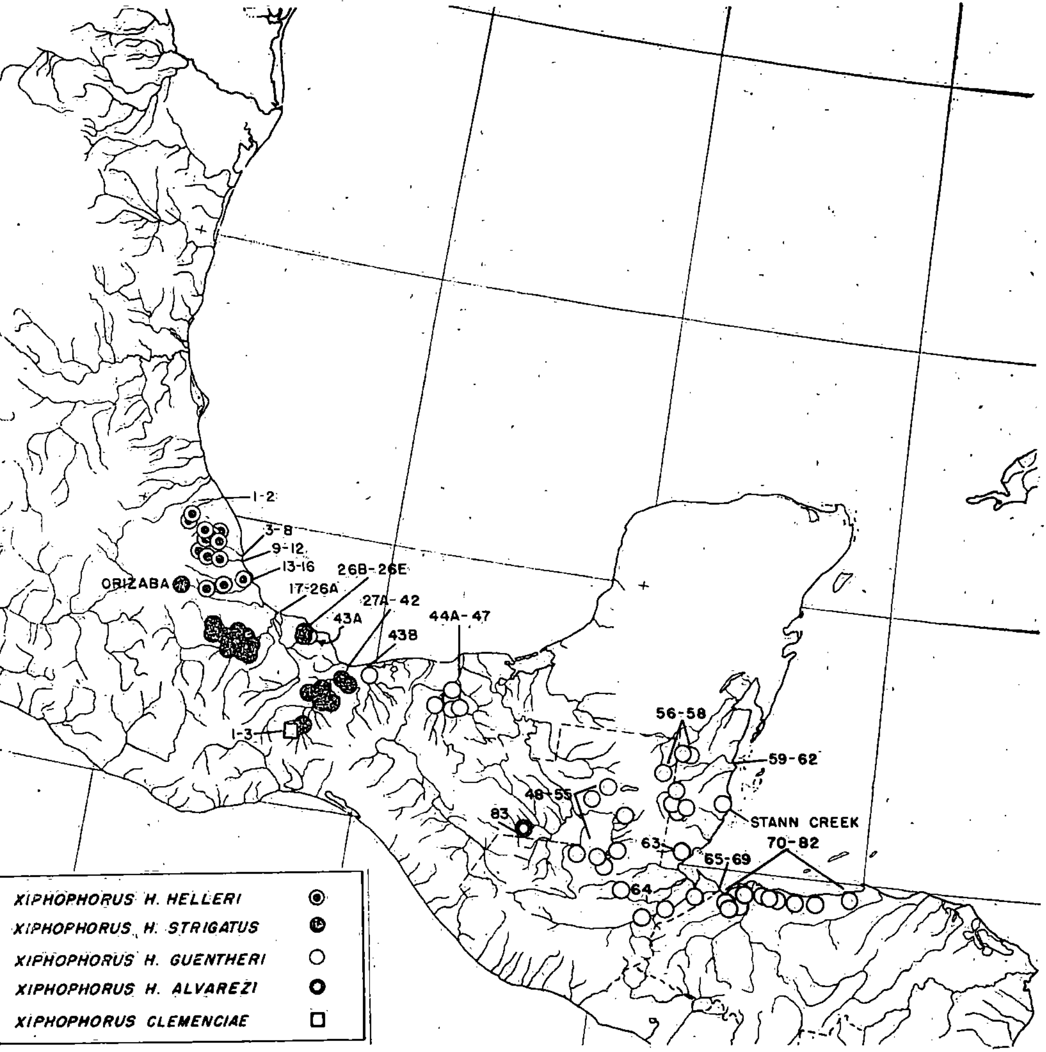


Figure 19. Distribution by record stations for *X. clemenciae* and the forms of *X. helleri*. See text for a discussion of the Orizaba swordtail. The Stann Creek record is from Regan (1907).

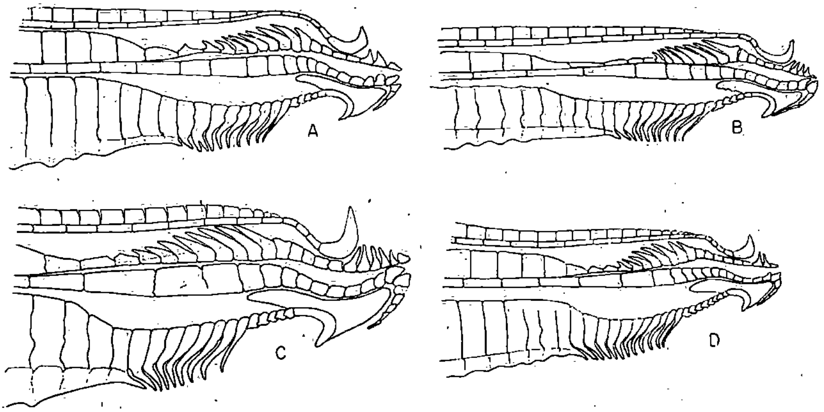


Figure 20. Distal tips of the gonopodia of males of the subspecies of *X. helleri*. A. *X. helleri helleri* Heckel (UMMZ: 97579). B. *X. helleri strigatus* Regan (laboratory stock, Rio Papaloapan). C. *X. helleri guentheri* Jordan and Evermann (UMMZ: 97871). D. *X. helleri alvarezi*, n. ssp. (UMMZ: 177304).

General Account. The green swordtail has the most extensive natural range of any species of *Xiphophorus*, from the Rio Nautla, Veracruz southward to the independent Atlantic coastal tributaries of northwestern Honduras, a straight line distance of almost 800 miles. Within the separate drainage areas of this extensive natural range, the species breaks up into a great number of morphologically distinct geographic and microgeographic races. Early recognition of the green swordtail's great geographic variation led some workers to describe many of the river populations as distinct species (see synonymy). Hubbs (1935), Martin del Campo (1938) and Hubbs and Gordon (1943) are chiefly responsible for indicating the conspecificity of all these forms. These authors recognized four subspecies: *X. helleri helleri, X. h. strigatus, X. h. guentheri* and *X. h. brevis*.

A collective view of all the geographic races of *X. helleri* clearly shows a north-south oriented morphocline involving a constellation of traits. In the north, for example, the swordtails are slender with short heads, intensely black lateral striping and a preponderance of black in the dorsal fin, relatively short caudal fins (excluding the appendage or "sword"), few distal serrae on ray 4p of their gonopodia (the distal serrae may even be obsolescent), relatively high scale count, and relatively low dorsal fin ray count. In the intermediate populations the fish are somewhat chunkier with longer heads, have less black and more red in their dorsal fins and in the striping along the sides, their caudal fins (excluding "sword") are relatively longer, the distal serrae in the gonopodium are larger and more numerous (they are never degenerate), the scale counts are slightly lower and dorsal fin ray counts higher. The southernmost populations are generally quite robust with a long head, intense red but little black pigment on the side and dorsal fin, long caudal fin (excluding "sword"), distal serrae at the tip of the gonopodium still further exaggerated and more numerous, the scale count lowest and dorsal fin ray count highest of any of the green swordtail populations.

Yet within each of the northern, intermediate, and southern groups, the green swordtails of any particular river basin are usually distinct and characteristic of only that drainage. Descendants of fish from six major drainage areas, Jamapa, Papaloapan, Coatzacoalcos, Grijalva, Belize (British Honduras), and Ulua (Honduras), have been maintained under laboratory conditions for a considerable period (table 25). The members of each river population not only maintain their own morphological characteristics (table 26), but can always be correctly assigned to their appropriate geographical race entirely by their pigment patterns (fig. 21).

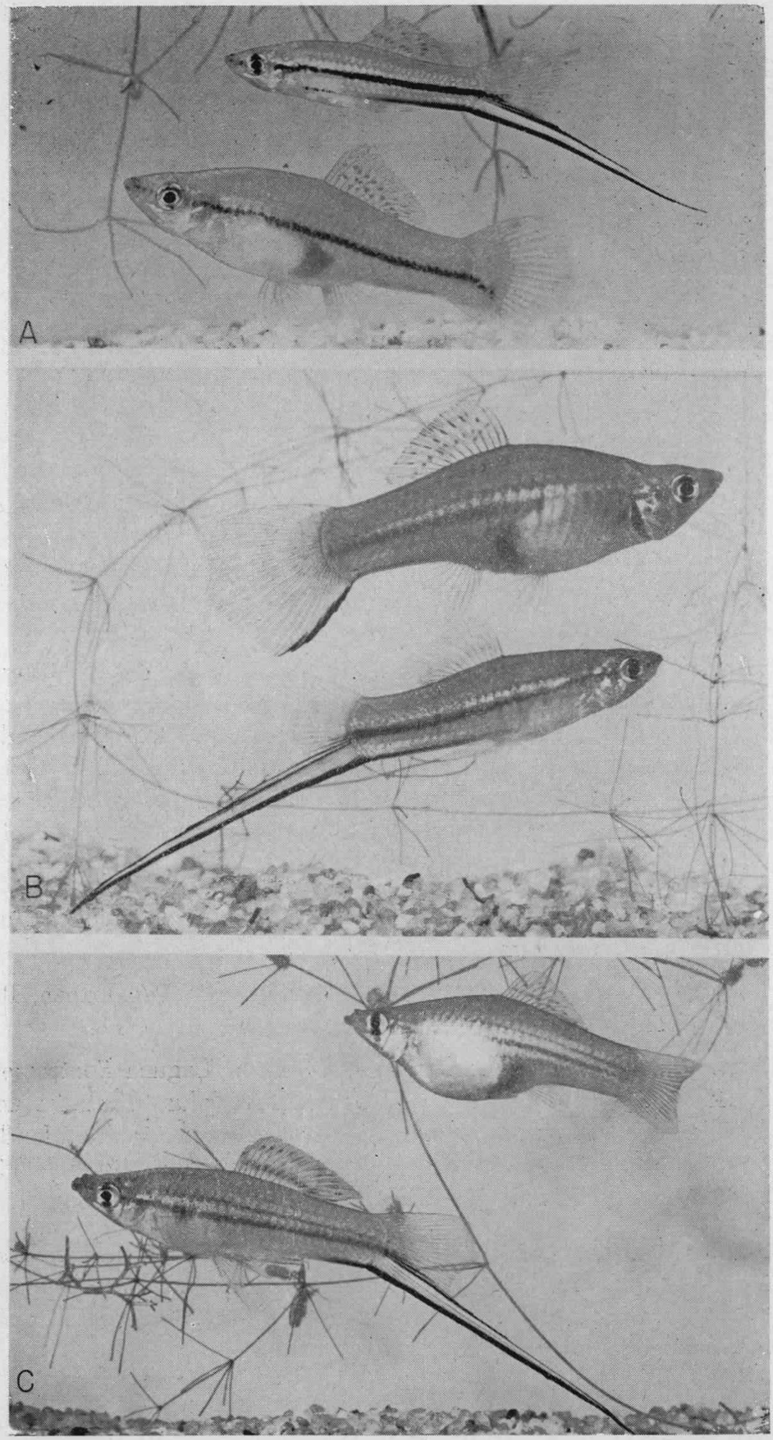
Despite the clinal change from north to south and the great number of distinct geographical populations within this species, three groups with relatively abrupt transitions between them can be defined. These three groups correspond exactly with the northern, intermediate, and southern character complexes indicated above. The members of each of these major allopatric groups may be designated as subspecies, as follows:

Xiphophorus helleri helleri —— Mexico: Rio Nautla, Rio Antigua, Rio Chachalacas, Rio Jamapa.

Xiphophorus helleri strigatus —— Mexico: Rio Papaloapan, Rio Coatzacoalcos.

Xiphophorus helleri guentheri —— Mexico: Laguna Sontecomapan, Rio Tonala, Rio Grijalva, Rio Usumacinta (plus tributaries and interior lakes of Peten, Guatemala). British Honduras: Rio Hondo, Rio Belize, Rio Grande, Stann Creek. Guatemala: Rio Polochic, Rio Motagua. Honduras: Rio Ulua, independent Atlantic tributaries.

A fourth group, from the Rio Santo Domingo in northwestern Chiapas (Usumacinta basin), described below as a new subspecies, *X. helleri alvarezi*, constitutes an important exception to the well-defined step cline already discussed.


A
B
C

MORPHOMETRIC DIFFERENCES

DORSAL FIN RAY COUNTS. Table 27 shows the distribution of counts of numbers of dorsal fin rays in 37 natural populations of *X. helleri.* These data permit separation of the populations into two major groups: 1) those with 11 to 14 dorsal rays (modal number 12), distributed continuously from Nautla southward to Minatitlan, and 2) those with 11 to 17 dorsal fin rays (modal number 14) ranging continuously from Tonala southeastward to Ceiba, Honduras. The relatively sharp transition from low to high fin ray counts occurs in fishes separated geographically at the Isthmus of Tehuantepec by approximately 20 miles of coastline (between the Rio Coatzacoalcos and Rio Tonala). Here two subspecies are separated geographically, *X. helleri strigatus* (Rio Papaloapan and Rio Coatzacoalcos) and *X. helleri guentheri* (Rio Tonala to Ceiba, Honduras). Table 27 reveals no obvious quantitative difference between *X. helleri helleri*, the most northern subspecies, and *X. helleri strigatus*, but it does call attention to the disparate counts of the Rio Santo Domingo (Comitan) swordtails within the southern complex. The Comitan swordtail occurs in the extreme upper reaches of the Rio Usumacinta at an elevation of about 1500 feet, and is thus isolated within the principal geographical limits of the southern form. Its fin ray count is exceptionally low (11 and 12, usually 11) considering its proximity to the southern forms with high modal counts.

To test the significance of the difference in mean dorsal fin ray number in natural populations of this swordtail, an estimate of the standard error of the difference between the means of two samples was obtained.[2] Certain related assumptions were made in setting up the raw data for analysis. It was assumed that 1) with respect to the number of dorsal fin rays swordtail samples from separate collecting

---

[2] The calculation of a value of d/σ_d is designed to test the hypothesis that two samples were drawn from one population or from populations with equal means and variances.

Figure 21. Living laboratory born and reared breeding pairs of three subspecies of *X. helleri.* A. *X. helleri helleri* Heckel from the Rio Jamapa; male above. B. *X. helleri strigatus* Regan from the Rio Papaloapan; male below. C. *X. helleri guentheri* Jordan and Evermann from the Belize River, British Honduras; male below. Note the progressive loss of black pigment along the sides from A to C. The midlateral stripe in the male in B is actually dark red or brown due to the combination of erythrophores and melanophores. In C, the multiple stripes are orange-red. Note vertical barring in the male and the black caudal emargination in the female in B.

stations within a single drainage area are sufficiently alike that they may be treated as microgeographic races of a single, distinct geographic race, and that 2) the collective members of all stations within a single river basin represent distinct biological units that differ genetically from other such units in adjacent river basins. These assumptions were based partly upon observations of the striking similarity of the swordtails from all stations within a single system in overall coloration and body form. All members of local populations of a single drainage area are now or have recently been in close enough contact to inhibit significant local variation.

These assumptions are probably valid for the six drainage areas subsumed by the two northern subspecies, *X. h. helleri* and *X. h. strigatus*. Southward the situation is less clear. Subsamples from the Rio Usumacinta system (excluding the Rio Grijalva) show a gradual increase in mean fin ray number with eastward penetration of headwater areas. From the upper Rio Usumacinta in Chiapas to the streams and lakes of the Peten District of Guatemala, the mean number of dorsal fin rays rises from 12.67 to 14.00, a significant increase of at least one fin ray. Similarly in the swordtails from the Atlantic coastal rivers and streams of Honduras, from the Rio Ulua eastward to Estero Salada, the mean number of dorsal fin rays rises from 13.34 to 15.33, a significant increase of more than one fin ray. If, however, a single mean is obtained for the four subsamples from the Rio Usumacinta system and a single mean is obtained for the five subsamples from Honduras, the overall mean dorsal fin ray counts of the Rio Usumacinta and Honduras swordtails differ by about one one-hundredth, 13.76 and 13.77 respectively. The probability that this small difference between the two mean values represents samples drawn from different populations is inconsiderable, $d/\sigma_d = 0.11$, where the criterion of significance is taken as 3. The statistical trends noted within these two drainage areas may indicate the effects of gradually changing east-west oriented ecogeographical factors. Despite this variability in dorsal fin ray number in the *helleri* populations from the Rio Usumacinta and from Honduras, their mean values are uniformly higher than those of populations north of the Isthmus of Tehuantepec.

Comparisons of the southern members of *X. helleri strigatus* (Rio Coatzacoalcos swordtail) with six of the seven natural populations of *X. helleri guentheri* yield d/σ_d values ranging from 9.12 to 20.24. A comparison of the Rio Grijalva population (*X. h. guentheri,* in part) with the Rio Santo Domingo population (*X. h. alvarezi*) gives the high value of 15.18.

LATERAL SCALE COUNTS. Table 28 shows the distribution of counts of scales in lateral series in 23 natural populations of *X. helleri*. These fall into four groups as follows: 1) fish whose scales range from 26 to 29 (modal number 28), from the Río Nautla, Antigua and Jamapa (*X. h. helleri*); 2) those whose scales range from 26 to 28 (modal number 27), from the Río Papaloapan and Coatzacoalcos (*X. h. strigatus*); 3) those whose scales range from 25 to 28 (modal number 26), from the Rio Tonala to Ceiba, Honduras (*X. h. guentheri*); 4) fish whose scales range from 26 to 29 (modal number 27), from the Rio Santo Domingo (*X. h. alvarezi*). As in the dorsal fin ray counts, the change from a lower to a higher mean value of lateral scales is most abrupt between *X. h. strigatus* and *X. h. guentheri* where they are geographically separated at the Isthmus of Tehuantepec, and between *X. h. guentheri* and *X. h. alvarezi* in the upper reaches of the Rio Usumacinta basin. The separation of *X. h. helleri* from *X. h. strigatus* is poorly defined by both lateral scale and dorsal fin ray counts, particularly as scale counts of fish from Boca del Rio (Rio Jamapa system) appear to be intermediate between the typical mean values for populations north and south of this station.

VERTEBRAL NUMBER. Complementing the dorsal fin ray and scale counts that separate *h. strigatus* from the southern forms, vertebral number and the following study of caudal fin length offer a means of distinguishing between *h. strigatus* and the northern *h. helleri*. The few X-ray data on vertebral number available show that *h. strigatus* from the Rio Coatzacoalcos has one more vertebra than *h. helleri* from the Nautla, Antigua, and Jamapa Rivers (table 3). Between *strigatus, guentheri,* and *alvarezi* no difference in vertebral count is apparent, even in modal number.

RELATIVE LENGTH OF CAUDAL FIN. Relative length of the caudal fin was determined in 31 populations of *X. helleri*. As before, these data are grouped into drainage systems with a single mean for each (table 29). These relative lengths clearly define the separation between the two northern subspecies, *X. h. helleri* and *X. h. strigatus*. Fish from the Rio Nautla, Rio Chachalacas and Rio Jamapa have relatively truncate caudal fins (2.9 to 4.5); those from the Rio Papaloapan and Coatzacoalcos have relatively longer caudal fins in proportion to body length (2.8 to 3.7). On the basis of the combined indices for adult males, females, and subadult fish, no clear separation can be made for the samples of *strigatus, guentheri,* and *alvarezi,* though the increase in low values first appearing in fishes from the Rio Grijalva suggests a possible separation between *strigatus* and *guentheri* at this point.

RELATIVE BODY MEASUREMENTS. Relative body measurements may be used further to define the separation of *X. helleri* into its four component subspecies. Many of the difficulties that beset Gordon and Gordon (1954) in their use of such measurements in their biometric studies of *X. maculatus* are met with here. For reasons discussed below only index values derived from adult males may be safely employed in intraspecific comparisons. In support of arguments based upon more precise data for the formal splitting of *X. helleri* into four subspecies groups, the data summarized, in part, in tables 4 and 5 are generalized as follows:

1) *X. h. helleri* may be separated from both *strigatus* and *guentheri* by relative depth of body; *strigatus* and *guentheri* are indistinguishable on this basis, though the latter is readily separable from *alvarezi*. Both *helleri* and *alvarezi* are slender fish with greatest body depth only 25 percent of standard length. Both *strigatus* and *guentheri* are stouter with the greatest body depth about 30 percent of standard length.

2) *X. h. helleri* may be separated from both *strigatus* and *guentheri* by relative depth of caudal peduncle; *strigatus* and *guentheri* are indistinguishable using these measurements, but *alvarezi* is readily separable from *guentheri*. As in relative body depth, caudal peduncle depth shows both *helleri* and *alvarezi* to be slender forms and *strigatus* and *guentheri* to be considerably heavier bodied.

3) The four subspecies do not differ greatly in their relative head lengths, although the more slender forms, *helleri* and *alvarezi*, appear to have slightly longer heads.

4) An apparent correlation with overall slenderness of form is again suggested by the relatively greater caudal peduncular lengths of *helleri* and *alvarezi*, as compared with those of *strigatus* and *guentheri*.

GENITALIC DIFFERENCES. Differences in the form and frequency of the bony details at the tip of the adult male's gonopodium may be used to separate *X. helleri* into its four component subspecies (table 30). For example, nominate *helleri* has a low distal serrae count (ray 4p) (3.10 and 3.50), *strigatus* a somewhat higher count (3.67), and *guentheri* the highest count (3.89, 3.91, 4.47 and 5). The two adult males of *alvarezi* at hand both show the low distal serrae count of 3. The subterminal segment count (ray 3) of nominate *helleri* is low (5.50 and 5.60), that of *strigatus* intermediate (5.67 and 6.67), and that of *guentheri* high (6.55, 6.60, 8.26 and 10). The two *alvarezi* males show the relatively high count of 8.

A form analysis of the distal serrae on ray 4p of the gonopodium permits a relatively sharp separation of the two northern subspecies. Adult males of nominate *helleri* show small, poorly developed serrae, some of which may be degenerate as in the sample from the Rio Antigua system. Adult males of *strigatus* show taller, more strongly developed serrae that rarely are degenerate or anomalous. In general, the distal serrae seem the most strongly developed in the adult males of *guentheri;* in the two adult males of *alvarezi,* they are rather small, as in the Rio Antigua and Jamapa samples of the nominate form.

ECOGEOGRAPHIC DIFFERENCES. A survey of the characters used to separate the subspecies of *X. helleri* shows that, with the possible exception of *alvarezi,* the subspecies differ from each other in a regular manner when samples are arranged according to north-south geographic position. The absence of any important mosaic distributions of morphological traits within the range of this species and the steady north-south change in the number and/or size or other characters studied suggests that all the geographic and microgeographic races of *X. helleri* are related within a single morphocline. It has been shown that sudden transitions between character complexes, marking morphological stepclines, occur at two geographic points in the species' range. These zones of transition may be taken as geographic limits of definable taxonomic units. It has further been shown that the possibility for gene exchange between members of adjacent drainage areas is remote. Information gained by maintaining stocks of six natural populations of *X. helleri* under uniform laboratory conditions and studying various laboratory produced interriver hybrids (tables 25 and 26) shows conclusively that the members of each population are relatively homogeneous, that the different populations are genetically distinct from one another, and that the differences are therefore not directly induced by the environment.

Table 33, which gives estimated altitudes for all stations where *Xiphophorus* has been collected, reveals that the samples of *helleri* and *alvarezi,* both slender forms, occur almost entirely at higher altitudes (from 1000 to 5000 feet) and samples of more heavy-bodied *strigatus* and *guentheri* at lower altitudes (mostly from 50 to 800 feet). There are exceptions: *strigatus* from Orizaba occurs at 4200 feet; *helleri* from the Rio Jamapa system at Boca del Rio at 50 feet; and some *guentheri* from the Rio Motagua and Rio Belize at about 2000 and 1000 feet elevations respectively. A few of the Motagua and Belize fish are noteworthy for their relatively slender bodies, exceptional pigmentation, and apparently low dorsal ray counts.

Thus the effects of increasing altitude are similar to those of increasing latitude, as shown by the variations in dorsal fin ray and lateral scale counts above. This suggests the possibility that temperature differentials may in part have produced the effects noted (Appendix I). An analysis of the relationships among four relative body dimensions suggests that temperature effects may be quite general in the green swordtail. Not only general body form and metamerism, but probably pigmentation and, to some extent, configurations of gonopodial elements may become involved. It now seems likely that during the swordtail's course of speciation under geographical isolation, many of what may originally have been ecophenotypic variations became incorporated into the genotypes of these animals (see Waddington, 1957: 162-187, and discussion below).

Ecological effects other than climatically induced variations may significantly alter the expressions of certain characters in this species. Green swordtails found in a lily pond at Lancetilla, Honduras, in which competition for food apparently was minimal, grew to an enormous size, were extremely deep bodied, more intensely blue, and had a higher dorsal fin ray count than swordtails taken from adjacent streams (fig. 22). Swordtails taken from the upper Rio Usumacinta system (station 52), on the other hand, were extremely small and slender (28 to 32 mm standard length of adults), darkly pigmented, and had exceptionally short "swords." Although the environmental conditions in which these fish were living are unknown, possibly their comparatively small size resulted from a density factor, either crowding or too keen competition for food. Champy (1924) indicated that similar proportional changes in body form may be produced experimentally in this species by enforced starvation. These changes may be regarded as ontogenetic in contrast to the genetically fixed proportional differences discussed above.

Xiphophorus helleri helleri Heckel

Figures 19-21, 32, tables 3-5, 27-30

Xiphophorus hellerii Heckel, 1848: 291, Pl. 8 (original description); Guenther, 1866: 349-350 (description, in part, var. β only); Jordan and Evermann, 1896: 70 (after Guenther); Gordon, 1935c: 50-51 (habitat; figure of fish inaccurate); 1941b: 112 (Rio Jamapa); 1943c: 64, 68-71 (type species; status of typical subspecies; no hybrids in nature).

Xiphophorus helleri, Meek, 1904: 157 (Cordova record only); Regan, 1907: 109 (synonymy; description; Jalapa, Orizaba); 1913: 1004-1005 (in part; specimens with axillary stripes only); Schauenberg, 1920: 260 (plains near Veracruz and in high mountain streams; identification by locality); De Buen, 1940:

44 (Jalapa record); Turner, 1940: 64-67 (fetal membranes of Cordova specimens).

Xiphophorus hellerii hellerii, Hubbs and Gordon, 1943: 32 (variation, dorsal rays).

Xiphophorus jalapae Meek, 1902: 107 (original description; Jalapa); 1904: 156-157, pl. 9 (description; Jalapa).

Xiphophorus strigatus Regan, 1907: 65 (original diagnosis, in part, not types as hereby restricted to Rio Papaloapan and Rio Coatzacoalcos specimens; Veracruz [Cordova] record only); 1906-1908: 107-108, pl. 14, fig. 7 (diagnosis, in part; Cordova records and references only).

MATERIAL EXAMINED

Mexico, Veracruz

Rio Nautla system

1. Six mi. from Tlapacoyan on road to Nautla. UMMZ NYZS-GL. 15 young to adults.
2. Stream 2.3 mi. W Ixtacocoa, 3.9 mi. W Martinez de la Torre, on Teziutlan-Casita Highway. UMMZ 167487. 18 young to adult.

Rio Chachalacas system

3. L'Encero near Jalapa. UMMZ NYZS-GL. 249 young to adults.
4. Pond at L'Encero 10 mi. SE Jalapa. UMMZ 124288. 93 half-grown to adults; others taken alive.
5. Tributary of Rio Chachalacas at Plan del Rio. UMMZ 108677. 12 half-grown to adults.
6. Pond 12 mi. E Jalapa. UMMZ 157650. 210 half-grown to adults.
7. Pond 14 mi. E Jalapa. UMMZ 157647. 140 half-grown to adults.
8. Tributary of Rio Actopan, Jalapa. UMMZ 162464. 10 adult males and females.

Rio Antigua system

9. Jalapa. UMMZ 66266. 1 adult male.
10. Rio Bejucas 7 mi. S Jalapa. UMMZ 97578. 125 half-grown to adults.
11. Artificial laguna at headwaters of Rio Grande, Jalapa. UMMZ 167701. 131 half-grown to adults.
12. Jalapa. SU 21452, 22338. 18 young and adults. These are topotypes and possibly paratypes of Meek's *X. jalapae.*

Rio Jamapa system

13. Rio Chico, on southern edge of Cordoba. UMMZ 108613. 135 half-grown to adults preserved; others taken alive.
14. Cordoba. USNM 55810. 7 young to adults.
15. Rio Atoyac 4 mi. N Hacienda Portrero Viejo, Paraje Nuevo. UMMZ 162145. 15 young to adults.
16. Rio along highway to Cordoba 7.5 mi. from S shore of Rio Jamapa at Boca del Rio. UMMZ NYZS-GL. 5 adults.

DIAGNOSIS. A long headed, slender bodied subspecies of *helleri.* Midlateral black or dusky stripe strongly developed as a solid band, rarely as a zigzag line; with a variously developed secondary or axillary stripe on the lower side behind and below the pectoral fin base of adult males. Dorsal fin with a median and subdistal row of red or black spots. Caudal fin excluding "sword" truncate; caudal fin of adult females rarely with ventral margin of black pigment. Distal serrae on ray 4a of gonopodium small, blunt, subtriangular in outline, frequently obsolescent, 2 to 4 in number. Vertebrae 30 or 31. Scales in a lateral series 26 to 29, usually 27 or 28. Dorsal fin rays 11 to 14, rarely 14.

REMARKS. Stations 9, 10, and 11 are provisionally assigned to the Rio Antigua system despite poor locality records. The adult male swordtails from these collections show the exaggerated axillary streak that is not found so well developed to the south.

A series of living specimens of Cordoba origin was maintained by C. L. Turner for several years at Northwestern University and subsequently has been continued at the University of Michigan Museum of Zoology and at the Genetics Laboratory of the New York Aquarium.

The Rio Bejucos specimens from Station 8 represent the form called *X. jalapae* by Meek (1902, 1904).

Heckel wrote that his species was taken "in einem klaren Bache des Gebirges Orizaba in Mexico." This northern mountain form of *helleri* with the axillary stripe was taken by Meek and by Myron Gordon only in the Rio Nautla, Rio Antigua, Rio Chachalacas, and Rio Jamapa systems and by Turner at Cordoba. Another subspecies (*strigatus*) is also known from near Cordoba, but to the south near the town of Orizaba, and in waters that drain south into the Rio Papaloapan rather than northward. Specimens in the U. S. National Museum collected long ago by Professor F. Sumichrast in Mexico (USNM 7816) and labelled "Orizaba" appear to represent nominate *helleri*, from the north. Of two developed males, one retains a distinct second or axillary band and the other shows a faint trace of one (an undeveloped male and 12 females show no second band). They are all rather slender.

Xiphophorus helleri strigatus Regan

Figures 19-21, tables 3-5, 27-30

Xiphophorus helleri, Meek, 1904: 157 (record from Sanborn, Rio Coatzacoalcos system); Regan, 1906-1908: 108 (record from Sanborn, Rio Coatzacoalcos system); 1913b: 1004-1005 (material and synonymy, in part); De Buen, 1940: 44 (records, except Jalapa).

Xiphophorus hellerii, Gordon, 1941a: 38-39 (material, in part; genetic color factors); 1941b: 112-113 (Rio Coatzacoalcos record only; abstract on hybridization); 1942a: 73-74, fig. 1 (genetics); 1942b: 197 (in part, confusion with *X. montezumae*); 1942c: 76 (genetics of hybrid mating); 1943b: 28 genetics in relation to melanomas); 1943c: 68-71 (in part; variations; no hybrids in nature; origin of domesticated races); Gordon and Flathman, 1943: 9-12, figs. 1-3 (genetics of melanomas in hybrids); Gordon, Cohen and Nigrelli, 1943: 571 (caudal fin characters in light of hormone experiments with *X. maculatus*).

Xiphophorus helleri helleri, Martin del Campo, 1938: 226 (Laguna Catemaco, Veracruz).

Xiphophorus brevis, Arnold, 1914: 125-126, fig. 3 (identification of figure of type later misidentified as *X. montezumae*, from near Coatzacoalcos).

Xiphophorus hellerii brevis, Hubbs and Gordon, 1943: 32 (material, in part; variation, dorsal fin rays).

Xiphophorus strigatus Regan, 1907: 65 (*helleri* of Meek a synonym; original diagnosis; Veracruz and Oaxaca); 1906-1908: 107 (synonymy, in part; description; Otapa; Motzorongo; Refugio; El Hule [= Papaloapan]; Obispo; Oaxaca).

Xiphophorus helleri strigatus, De Buen, 1940 (after Regan).

Xiphophorus hellerii strigatus Hubbs and Gordon, 1943: 32 (variation, dorsal rays).

MATERIAL EXAMINED

Mexico, Veracruz, Oaxaca

Rio Papaloapan system

17. Southern tributary of Rio Tonto 10 km. upstream from Papaloapan. UMMZ 108585. 59 young to half-grown and one adult female; others taken alive.
18. Same locality. UMMZ 124177. 5 young to adults.
19. Near Arroyo Zacatispan at its headwaters in the hills of San Bartolo. UMMZ 124271. 33 young to subadult specimens preserved; others taken alive.
20. Same locality. UMMZ 124472. 4 adults.
21. Lagoon beside Rio Papaloapan, 3 km. N San Bartolo. UMMZ 124253. 7 adults.
22. Pool 5 km. S Papaloapan, at km. mark 148½ on railroad. UMMZ 124282. 41 half-grown to adults.
23. Lagoon and pool 4 km. S Papaloapan at km. mark 149 on railroad. UMMZ 124236. 60 half-grown to adults.
24. Arroyo Zacatispan and lagoon 4.5 km. S Papaloapan. UMMZ 124217. 19 half-grown to adults.
25. Arroyo Zacatispan 6 km. SE Papaloapan. UMMZ 124194. 4 half-grown to subadults.

26a. Obispo. SU 21463. 23 young to adults.

26b. Laguna Encantada, about 2 mi. by road and trail E SE San Andres Tuxtla. UMMZ M59-23. 155 young to adult.

26c. Tributary of Laguna Catemaco, on W side about 1.5 mi. S Catemaco. UMMZ M57-58. 66 young to adult.

26d. Same locality. UMMZ M59-25. 42 young to adult.

26e. Laguna Catemaco at Playa Azul, about 2 mi. E Catemaco. UMMZ M57-57. 21 young to adult.

Rio Coatzacoalcos system

27a. Small tributary of Rio Sarabia about 7.5 mi. S Acayucan (Veracruz). UMMZ M57-55. 42 young to adult.

27b. Same locality. UMMZ M59-21. 1 adult male.

27c. Stream running east-west, crossed by Trans-Isthmian highway, 5 mi. N Donaji. UMMZ M57-56. 6 young to subadult.

27d. Arroyo de "La Llorona" about 350 m. from Estacion de Juile. UMMZ 157660. 6 subadult to adults.

28. Small unnamed arroyo emptying into Arroyo del Aguagate near Estacion de Almagres. UMMZ 157658. 6 half-grown to adults.
29. Arroyo de Niscalapa, 1 km. S Estacion de Ojapa. UMMZ 157664. 1 half-grown and 1 adult male.
30. Arroyo beneath bridge 30a of same railroad about 400 m. N Estacion Hibueras. UMMZ 157665. 33 half-grown to adults.
31. Acantarilla on railroad 1 km. SW Estacion Hibueras. UMMZ 157659. 8 subadults.
32. Pool along railroad from Jesus Carranza to Veracruz. UMMZ NYZS-GL. 1 subadult male.
33. Arroyo Buena Vista tributary to Rio Uxpanapa 20 km. SE Minatitlan. UMMZ NYZS-GL. 1 adult female.
34. Under and nearby Culvert "G322-57" on railroad from Jesus Carranza to Veracruz. UMMZ NYZS-GL. 4 half-grown to subadults.
35. Pool under Culvert "G3T9-76" on railroad from Jesus Carranza to Veracruz. UMMZ NYZS-GL. 45 young to adults.
36. Arroyo Ojillal tributary to Rio Hondo, Veracruz. UMMZ NYZS-GL. 7 half-grown to adults.
37. Arroyo Chapala 1½ km. W Minatitlan. UMMZ NYZS-GL. 7 half-grown to adults.
38. Rio Viejo about 2 km. E Jesus Carranza, tributary to Rio Jaltepec. UMMZ NYZS-GL. 3 half-grown to adults.
39. Laguna about ½ km. NW of Jesus Carranza. UMMZ NYZS-GL. 6 adults.
40. Arroyo running into Arroyo Santa Lucrecia tributary to Rio Jaltepec about 700 m. from river. UMMZ NYZS-GL. 20 young to adults.
41. Arroyo del Aguagate at village of Almagrez. UMMZ NYZS-GL. 23 young to adults.
42. Arroyo along railorad from Jesus Carranza to Veracruz; tributary to Rio Jaltepec. UMMZ NYZS-GL. 22 young to adults.

DIAGNOSIS. A short headed, moderately deep bodied subspecies of *helleri*. Midlateral stripe brown or brownish red (dusky in alcohol), usually developed as a zigzag line, rarely as a solid band; rarely an axillary stripe in adult males. Dorsal fin with a median and subdistal row of red or dusky spots, or without definitive spotting. Caudal fin excluding "sword" long and broad; caudal fin of adult females commonly with ventral margin of black pigment. Distal serrae on ray 4a of gonopodium moderately developed, sharply or bluntly pointed, higher than wide with a distinct notch separating base from shaft, never obsolescent, 3 to 5 in number. Vertebrae 28 or 29. Scales in a lateral series 26 to 28, usually 27 or 28. Dorsal fin rays 11 to 14, usually 12 or 13.

REMARKS. A spotted form of this swordtail has been found in the Rio Papaloapan system. Of 14 fish from Motzorongo 4 females are spotted; of 452 specimens collected at Papaloapan and vicinity 2 females and 1 male are spotted; of 27 specimens from Obispo 1 female and 5 males are spotted. This spotting is produced by large black pigment cells or macromelanophores.

In a tributary of the Rio Sarabia (Rio Coatzacoalcos system), Oaxaca, (stations 27, a, b) R. R. and M. Miller collected a small series of *X. helleri* farther upstream than any of the above specimens. In all ways typical of the swordtails from this drainage, they are especially interesting because they occur in true sympatricity with the very similar and closely allied *X. clemenciae.*

Although many of the swordtails from the Papaloapan and Coatzacoalcos rivers show the black or dusky vertical barring that gives them their subspecific name, and other features listed in the diagnosis, the living laboratory populations from each river system have a number of distinctive pigment patterns, many of which, unfortunately, are lost in preservation.

In a laboratory stock of the Rio Papaloapan swordtails the midlateral stripe may be broad posteriorly near the tail base, but it tapers to a very thin line of pigment on the precaudal area. It is never intensely black, usually brownish or reddish. It is composed of both melanophores and erythrophores. Vertical bars, composed of dermal and subdermal concentrations of micromelanophores, are especially numerous and well-developed in males; they may number as many as eight. Dorsal fin spotting consists largely of two or more regular rows of brilliant red dots sometimes surrounded by a few fin melanophores. Adult females show all of these pigmentary characteristics, but to a lesser extent. In addition, adult females from this and the Rio Coatzacoalcos system may show a thin line of black pigment on the lower margin of their caudal fins, a trait found only rarely in the northern and southern green swordtails. The underlying ground coloring of these swordtails is brownish olive with a pale iridescent green on the caudal peduncle. The interradial membrane of the sword of adult males is usually bright yellow.

In general coloration the present laboratory stock of the Rio Coatzacoalcos green swordtails resembles the above. The adult males differ principally in having a golden band directly above the midlateral stripe, fewer vertical bars in some instances, and faint dorsal spotting. The midlateral stripe of the Rio Coatzacoalcos swordtails tends to be redder posteriorly than in the Rio Papaloapan swordtails, and some adult females may show a somewhat less developed black caudal emargination.

The swordtails from a coastal station (43a) between the Papaloapan and Coatzacoalcos rivers are perplexing in that they show definite affinities to the southern *guentheri.* They have, for example, a series of from 3 to 5 distinct red bands that follow the scale rows and they are all rather deep-bodied (table 31). Their dorsal fin ray and lateral scale counts fall within the range of those of *strigatus*. Specimens from farther south in the Rio del Azufre (Rio Grijalva drainage, station 44a) are not separable by measurements from *guentheri* from that general region (table 31), but are noteworthy because each individual possesses both the midlateral black stripe of *strigatus* and the multiple red stripes of *guentheri*. The taxonomic status of these two populations is uncertain. This suggests that *strigatus* and *guentheri* may have come together secondarily following a period of geographical isolation. If so, movement of *guentheri* northward was probably accomplished coastally as indicated by the apparently restricted distribution of the deep-bodied, red-striped form between the Papaloapan and Coatzacoalcos basins in the Laguna de Sontecomapan. These lowland swordtails are strikingly different from those occurring close by at higher elevations in the Laguna Catemaco and Laguna Encantada, particularly from the latter which possess not only a black midlateral stripe but a faint trace of dusky axillary pigment. The swordtails from stations 43a and 44a are tentatively treated as members of the *X. h. guentheri* complex.

Xiphophorus helleri guentheri Jordon and Evermann

Figures 19-22, 32, tables 3-5, 27-31

Xiphophorus helleri, Steindachner, 1863: 184 (coloration; "Gebirgsbachen bei Tepeaca" = "bei Teapa an der Grenze zwischen Chiapas und Tabasco."; Schauenburg, 1920: 261 (Rio Pichucalco on boundary between Tabasco and Chiapas, 3000 feet elevation; natural history).

Xiphophorus hellerii, Guenther, 1866: 349-350 (description in part; var. α and γ, Rio Chisoy, Central America); 1869: 485, pl. 87, Figs. 2-5; Darwin, 1871: 679, Fig. 30 (sexual dimorphism; figure of black spotted form, from Guenther); Gordon, 1941b: 112-113 (Rio Usumacinta material only).

Xiphophorus guentheri Jordan and Evermann, 1896: 702 (original diagnosis, based on Guenther's black spotted variety (γ) from Rio Chisoy, Guatemala); Meek, 1904: 158 (nominal species based upon spotting); Regan, 1906-1908: 108 (synonymy; diagnosis, based on both spotted and unspotted forms from Rio Chisoy).

Xiphophorus hellerii guntheri, Hubbs, 1935: 10-11 (characters; dwarfed and large races; tributary of Belize River, Mountain Pine Ridge, British Honduras; aguada at Uaxactun, Guatemala).

Xiphophorus brevis Regan, 1907: 65 (original diagnosis; Stann Creek, British Honduras); 1906-1908: 108, pl. 14, figs. 8-9 (same material).

Xiphophorus hellerii brevis, Hubbs and Gordon, 1943: 32 (material in part; variation, dorsal rays).

?*Xiphophorus rachovii* Regan, 1913: 1005 (material in part, not of Regan, 1911a: 373; as synonym of *X. helleri*; lacking pair of black spots at caudal base; Puerto Barrios, Guatemala).

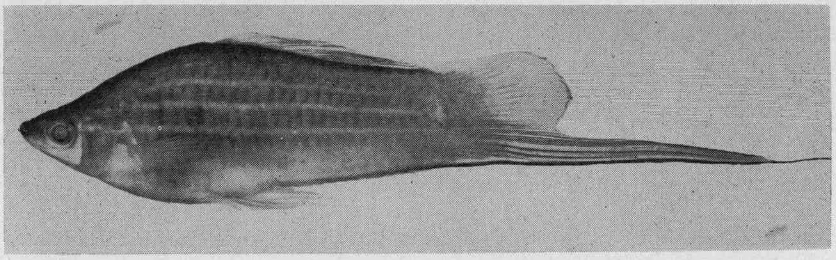


Figure 22. An extremely large and deep-bodied adult male *X. helleri guentheri* Jordan and Evermann (UMMZ:NYZS-GL) approximately 70 mm in standard length, from a lily pond in Lancetilla, Honduras.

MATERIAL EXAMINED

Mexico, Veracruz

Independent Atlantic Tributary

43a. Laguna de Sontecomapan at village of Sontecomapan, 10 mi. by road E Catemaco. UMMZ M59-24. 122 young to adults.

Mexico, Tabasco

Rio Tonala system

43b. Arroyo de La Venta at La Venta. UMMZ NYZS-GL. 12 young to adults.

Rio Grijalva system

44a. Arroyo del Azufre at Banos de Azufre, 4 mi. W Teapa. UMMZ M59-35. 15 half-grown to adult.

44b. Spring washing place at Teapa. UMMZ NYZS-GL. 101 half-grown to adults.

45. Arroyo Cocona tributary to the Rio Puyocatengo 1 mi. N Teapa. UMMZ NYZS-GL. 4 half-grown.

46. Hacienda de Santa Anna in ditch 39 km. from Villahermosa. UMMZ NYZS-GL. 4 young to adults.

47. Arroyo Huasteca 28 km. from Villahermosa to Teapa. UMMZ NYZS-GL. 4 young to adults.

Mexico, Chipas; Guatemala, Peten and Alta Vera Paz.

Rio Usumacinta system

48. Upper Rio de la Pasion (= Rio Chajmayic) at Sebol. UMMZ 143770. 1 half-grown.

49. In and just about mouth of first arroyo tributary to upper Rio de la Pasion from E below Arroyo San Simon. UMMZ 143767. 48 young to adults.

50. Arroyo de Xotal about 7 km. NW of Chicle Station on Laguna Perdida. UMMZ 143769. 151 young to adults.

51. Rio Cenizo tributary to Rio Salinas (= Rio Negro = Rio Chisoy = Rio Chixoy), upper Rio Usumacinta system, 30 mi. NW Coban. UMMZ 105458. 6 subadults.

52. Spring at Santa Toribia, tributary to Rio de la Pasion. UMMZ 158452. 10 half-grown to adults.

53. Upper Rio de la Pasion (= Rio Chajmayic) between Rio San Senora and Rio Ceilia. UMMZ 143776. 21 half-grown to adults.

54. Yaxoquintela, Chiapas (probably Usumacinta drainage). UMMZ 161763. 3 subadults.

55. Laguna de Zotz W Laguna de Peten. UMMZ 143768. 33 young to adults.

Guatemala, British Honduras
Rio Hondo system

56. Aguada at Uxactun, Guat. UMMZ 97871. 172 adults.
57. Broken ridge 4 mi. W Gallon Jug, Rio Chanchic tributary to Rio Hondo, Orange Walk, B. Hond. UMMZ NYZS-GL. 4 half-grown.
58. Cenote Creek 8 mi. SE Gallon Jug, Orange Walk, B. Hond. UMMZ NYZS-GL. 8 half-grown.

British Honduras
Rio Belize system

59. Rio Privacion, an upper tributary to Rio Frio, Mount Pine Ridge 12 mi. S El Cayo, Guatemala border. UMMZ 97884. 84 half-grown to adult.
60. Rio Frio and tributaries in vicinity of San Augustine, Mt. Pine Ridge, El Cayo District. UMMZ 159294. 424 young to adults.
61. Xunantunich Creek, vicinity of Mayan Ruins, Benque Viejo, UMMZ 158408. 50 young to adults.
62. Arroyo Xunantunich W western branch of Rio Belize near Benque Viejo, El Cayo District. UMMZ NYZS-GL. 1 adult male and female.

Rio Grande system

63. Coroso Creek tributary to Jacinto Creek along San Antonio Road, Toledo District. UMMZ NYZS-GL. 10 young to adults.

Guatemala
Rio Polochic system

64. Tributary to Rio Polochic, 14 mi. W Panzos on road to La Tinta. USNM 114256. 51 young to adult males and females.

Rio Motagua system

65. Irrigation ditch W Gualan. USNM 73971. 1 subadult.
66. Brook E of Los Amates. USNM 73932. 10 specimens.
67. Gualan. USNM 73991. 1 specimen.
68. Los Amates. USNM 73931. 2 specimens.
69. Sulphur River, Puerto Barrios. USNM 73930. 1 specimen. This is an independent coastal tributary.

Honduras
Independent Atlantic tributaries

70. Brook at Veracruz emptying into Gulf of Honduras, Cortez. UMMZ NYZS-GL. 70 half-grown to adults.
71. Second Rio Tulian at Tulian, Cortez (the second stream is independent and flows into the Bay of Cortez about ¼ mi. E of large stream, the first Rio Tulian). UMMZ NYZS-GL. 23 half-grown.

Rio Mapache system

72. Rio Mapache at Masca within 40 ft. of ocean, Cortez. UMMZ NYZS-GL. 1 half-grown.

Rio Chamelecon system

73. Rio Benejo, N San Pedro Sula, Cortez. UMMZ NYZS-GL. 64 young to adults.
74. Rio Armenta N San Pedro Sula on Chaloma Road, Cortez. UMMZ NYZS-GL. 3 young to adults.

Rio Lancetilla system

75. Tributary of Rio Lancetilla 1 mi. S Tela, Atlantida. UMMZ NYZS-GL. 1 young.
76. Tributary of Rio Lancetilla at Lancetilla near Royal Palm Avenue, Atlantida. UMMZ NYZS-GL. 4 half-grown.
77. Lily pond fed by creek tributary to Rio Lancetilla, Atlantida. UMMZ NYZS-GL. 4 adults.

Rio Colorado-Rio Lean system

78. Tributary of Santiago branch of Rio San Alejo at San Alejo, Atlantida. Many swordtails seen but not taken.

Rio San Juan system

79. Stream 48.5 km. W Ceiba near San Juan, Atlantida. UMMZ NYZS-GL. 1 half-grown.
80. Stream 47.3 km. W Ceiba along railroad near San Juan, Atlantida. UMMZ NYZS-GL. 11 half-grown.

Rio Bonito system

81. Rio Bonito 10.1 km. W Ceiba, Atlantida. UMMZ NYZS-GL. 7 half-grown to subadults.

Independent Atlantic tributaries

82. Stream 18.3 km. E Ceiba, Atlantida. UMMZ NYZS-GL. 14 half-grown. This station may be in Sambo Creek, a small coastal river between Ceiba and Belfate.

DIAGNOSIS. A short-headed, variably deep-bodied subspecies of *helleri*. Midlateral stripe bright red (paler than the surrounding integument in alcohol), always developed as a solid band, occasionally with dusky or brownish stripe on caudal peduncle; with one to 4 additional solid red bands on sides above, rarely below, midlateral stripe; axillary stripe lacking in adult males. Dorsal fin with a median and subdistal row of red spots, or red spots ringed in black. Caudal fin excluding "sword" long and broad; caudal fin of adult females rarely with ventral margin of black pigment. Distal serrae on ray 4a of gonopodium well developed, sharply or bluntly pointed, higher than wide with a distinct notch separating base from shaft, never obsolescent, 3 to 6 in number. Vertebrae 28 to 30. Scales in a lateral series 25 to 29, usually 26 or 27. Dorsal fin rays 11 to 17, usually 13 to 15.

REMARKS. The types of *X. guentheri* (collected by Godman and Salvin, 26 January 1864) and *X. brevis* (collected by Robertson, 1890), both in the British Museum, were examined by Myron Gordon, who reported that they correspond with the material here referred to *X. helleri guentheri*. Both nominal species are represented by some spotted individuals, although those from the Rio Chisoy (*guentheri*) are more heavily spotted than the ones from British Honduras (*brevis*).

Regan (1907) gave additional records from Stann Creek, British Honduras. This material was the basis for his original description of the nominal species, *X. brevis*. No green swordtails have been taken from the Rio Sibun system, British Honduras. The Sibun descends rather steeply from the northern peaks of the Maya Mountains. Its waters flow rapidly most of the year and during the rains become torrential and flood the banks in the lowland reaches. Possibly green swordtails have not been successfully established here. Similarly, no green swordtails are known from the Rio Sarstun on the southern frontier of British Honduras.

A black-spotted form of this subspecies was taken at stations 62 (Belize system, British Honduras) and 77 (Lancetilla system, Honduras). The number of spotted individuals is probably one percent or less of the total wild populations. The macromelanophore spots in the Belize swordtail are large and irregularly distributed over the side. The spotting in the Lancetilla form is arranged in regular rows, for the most part corresponding to the lateral striping.

Xiphophorus helleri alvarezi, new subspecies

Figures 19-20, 23, 32, tables 3-5, 27-30

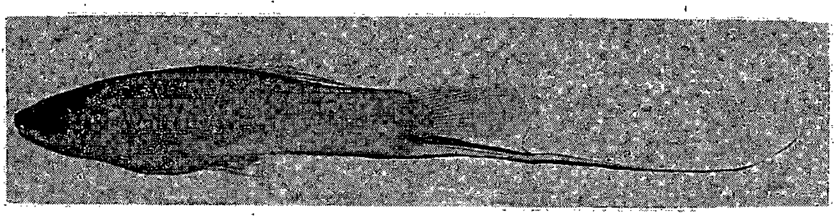


Figure 23. Holotype of *Xiphophorus helleri alvarezi*, n. ssp. (UMMZ: 177304), an adult male 39.0 mm in standard length.

TYPES. Holotype, an adult male (UMMZ 177304) 39.0 mm. in standard length, and allotype, an adult female (UMMZ 177305) 39.4 mm. in standard length, both from a single known locality (station 83) below.

MATERIAL EXAMINED

Mexico, Chiapas

Rio Usumacinta system

83. Rio Santo Domingo, a tributary of the Rio Jatate, upper Rio Usumacinta system, 90 km E Comitan; M. del Toro; August 1948. 19 adults excluding holotype and allotype, only two of which, a male and female (UMMZ 160727) are now available; 16 of the remaining specimens are in the private collection of Sr. Jose Alvarez del Villar, Secretaria de Marina, Mexico, D. F., and one in the British Musuem.

DIAGNOSIS. A long headed, slender bodied subspecies of *helleri*. Midlateral stripe red (paler than the surrounding integument in alcohol), always developed as a solid band, occasionally with an additional red band on sides above midlateral stripe; axillary stripe lacking in adult male. Dorsal fin with a median and subdistal row of red and black spots, or without definitive spotting. Caudal fin excluding "sword" long and broad; caudal fin of adult female without ventral margin of black pigment. Distal serrae on ray 4a of gonopodium small, blunt, subtriangular in outline, never obsolescent, 3 in number. Vertebrae 29. Scales in a lateral series 26 or 27, usually 27. Dorsal fin rays 11 or 12, usually 11.

The striking general features of this swordtail combine a slender body, the absence of the black midlateral stripe and a long, slender, whiplike caudal appendage.

Data available on a specimen sent by Sr. Alvarez to the British Museum (an adult male 43.0 mm. in standard length) correspond well with the present diagnosis: greatest depth of body 10 mm.; least depth of caudal peduncle 8 mm.; length of caudal appendage or "sword" 50 mm.

Remarks. As shown above, this form is readily separable from *X. h. guentheri* from adjacent river basins in southern Mexico and Guatemala by relative body measurements, dorsal fin ray and lateral scale counts, and details at the tip of the gonopodium of adult males. Its red rather than black lateral stripes and its relatively long caudal fin show it to be closely allied to the southern swordtails.

The 21 specimens of this swordtail, collected about 1500 feet above sea level, were given to Jose Alvarez del Villar of the Escuela Nacional de Ciencias Biologicas of Mexico shortly after their capture. Sr. Alvarez had prepared a description of these fish as a new subspecies of *X. helleri,* but its publication was delayed by lack of the comparative material. I gratefully acknowledge that the description given here is based largely upon Sr. Alvarez's original manuscript. Unfortunately the bulk of the material is not presently available to me, but the four adult specimens Sr. Alvarez generously sent to the University of Michigan confirm the new taxonomic status he proposed. The striking differences between *guentheri* and *alvarezi* and the uniformity of the few individuals of *alvarezi* at hand warrant its recognition.

This subspecies is named for Jose Alvarez del Villar who brought the new material to my attention and generously provided many measurements and observations.

TABLE 1

SUMMARY OF THE DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus*

	7	8	9	10	11	12	13	14	15	16	17	(N)	Means	S.E.
X. couchianus		8	134	53	1							(196)	9.24	± 0.04
X. maculatus	2	45	1281	684	11							(2023)	9.32	± 0.01
X. variatus			59	667	1233	386	54	2				(2402)	10.88	± 0.02
X. milleri			3	73	4							(80)	10.01	± 0.01
X. montezumae				3	195	283	26	1				(508)	11.66	± 0.03
X. pygmaeus			1	72	159	20	1	4				(257)	10.84	± 0.03
X. clemenciae				3	11	9	1					(24)	11.33	± 0.02
X. helleri					93	726	555	363	54	5	1	(1797)	12.77	± 0.02

TABLE 2

SUMMARY OF THE DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN A LATERAL SERIES IN *Xiphophorus*

	22	23	24	25	26	27	28	29	(N)	Means	S.E.
*X. couchianus**					36	1			(37)	26.03	± 0.03
X. maculatus	8	396	140	2					(546)	23.25	± 0.02
X. variatus			8	48	135	38	1		(230)	25.90	± 0.05
X. milleri				14	63	2			(79)	25.87	± 0.02
X. montezumae				1	24	42	3		(70)	26.67	± 0.07
X. pygmaeus				6	12	17	3		(38)	26.45	± 0.11
X. clemenciae					6	5			(11)	26.46	± 0.17
X. helleri				21	109	127	83	8	(348)	26.85	± 0.05

* Santa Catarina

TABLE 3

DISTRIBUTION OF NUMBER OF VERTEBRAE IN *Xiphophorus*

	26	27	28	29	30	31
X. couchianus						
Rio Santa Catarina		1	8			
X. maculatus						
Rio Papaloapan		9				
Rio Coatzacoalcos	1	9				
Rio Grijalva			3			
Belize River (B. Hond.)	1	3				
X. variatus						
X. variatus xiphidium						
Rio Corona		2	7			
Rio Caballero			8			
X. variatus variatus						
Rio Moctezuma				8		
Rio Tempoal			2	31	1	
Estero Cucharas			5	27	2	
Rio Cazones			23	3		
X. variatus evelynae						
Rio Necaxa		1	23			
X. milleri						
Laguna Catemaco			20	2		
X. montezumae						
X. montezumae montezumae						
Rio Tamesi			2	15		
Rio Verde				11		
Rio Salto de Agua			3	21	3	
X. montezumae cortezi						
Rio Axtla			1	18		
X. pygmaeus						
X. pygmaeus nigrensis						
Rio Choy				6		
X. pygmaeus pygmaeus						
Rio Axtla			7	1		
X. clemenciae						
Rio Sarabia			1	10		
X. helleri						
X. helleri helleri						
Rio Nautla					7	1
Rio Antigua					42	2
Rio Jamapa					10	1
X. helleri strigatus						
Rio Coatzacoalcos			1	5		
X. helleri guentheri						
Rio de la Pasion (Guat.)				7	6	
Arroyo Xotal (Guat.)			3	13	1	
Laguna de Zotz (Guat.)				6		
Rio Hondo (Guat.)			10	11		
Rio Frio (B. Hond.)			1	8	2	
Belize River (B. Hond.)			3	8		
X. helleri alvarezi						
Rio Santo Domingo				4		

TABLE 4

Variation in greatest relative depth of body in *Xiphophorus*

	Males				Females			
	Min.-Max.	(N)	Mean	S.E.	Min.-Max.	(N)	Mean	S.E.
X. couchianus								
Rio San Juan near Sta. Catarina	2.2-3.8	(66)	3.01	± 0.05	2.3-3.3	(74)	2.66	± 0.02
X. maculatus (Mexico)								
Rio Papaloapan								
Obispo	2.1-2.5	(25)	2.24	± 0.03	2.1-2.6	(41)	2.28	± 0.02
Papaloapan	2.2-2.7	(11)	2.51	± 0.04	2.2-3.0	(17)	2.59	± 0.05
(Guatemala)								
Rio de la Pasion	2.2-2.7	(17)	2.44	± 0.03	2.3-2.6	(31)	2.42	± 0.01
Rio San Pedro de Martir	2.5	(1)	2.5	——	2.4-2.7	(8)	2.54	± 0.04
Laguna de Zotz*	2.7-3.1	(20)	2.89	± 0.02	2.6-3.1	(30)	2.81	± 0.02
Laguna de Peten	2.3-2.7	(8)	2.51	± 0.04	2.3-2.6	(26)	2.48	± 0.01
Uaxactun	2.2-2.4	(2)	2.30	——	2.2	(1)	2.2	——
X. variatus								
X. variatus xiphidium								
Rio Sota la Marina								
Rio Pilon	2.5-3.1	(11)	2.81	± 0.05	2.7-3.9	(27)	3.12	± 0.05
Rio Purificacion and Rio Corona	2.1-2.8	(61)	2.35	± 0.02	2.1-3.0	(62)	2.56	± 0.05
Rio Corona (Meek)	2.5-3.1	(9)	2.70	± 0.07	2.6-3.1	(14)	2.87	± 0.05
X. variatus variatus								
Rio Tamesi								
Rio Guayalejo	2.2-2.8	(10)	2.50	± 0.06	2.4-2.9	(31)	2.59	± 0.02

TABLE 4 (continued)

		Males			Females	
	Min.-Max.	(N)	Mean S.E.	Min.-Max.	(N)	Mean S.E.
Rio Panuco						
Rio Valles	2.1-2.6	(27)	2.32 ± 0.03	2.2-2.7	(35)	2.42 ± 0.02
Rio Axtla	2.7-3.4	(10)	3.05 ± 0.07	3.3-3.8	(9)	3.48 ± 0.07
Rio Calaboza	2.1-3.9	(45)	2.54 ± 0.06	2.3-3.6	(71)	2.61 ± 0.04
Estero Cucharao	2.1-3.5	(50)	2.31 ± 0.02	2.1-2.9	(50)	2.41 ± 0.02
Estero Tancochin	2.4-3.5	(25)	3.05 ± 0.05	2.9-3.7	(31)	3.21 ± 0.04
Rio Tuxpan	2.1-2.3	(5)	2.20 ± 0.04	2.2-2.7	(12)	2.46 ± 0.04
Rio Cazones						
Arroyo Mariandrea	2.9-3.5	(11)	3.14 ± 0.05	2.8-3.6	(16)	3.18 ± 0.06
Rio Tecolutla						
Arroya Sin Nombre	2.4-3.0	(9)	2.45 ± 0.12	2.7-3.0	(10)	2.91 ± 0.04
Rio Nautla						
Tlapacoyan	2.6-3.1	(10)	2.81 ± 0.04	2.7-3.0	(10)	2.94 ± 0.04
Maria de la Torre	2.4-3.1	(10)	2.76 ± 0.08	2.7-3.3	(10)	2.94 ± 0.06
X. *variatus evelynae*						
Rio Tecolutla						
Rio Necaxa	2.9-3.3	(13)	3.12 ± 0.04	3.0-3.7	(14)	3.29 ± 0.05
X. *milleri*						
Rio Papaloapan						
Laguna Catemaco	3.1-3.7	(38)	3.45 ± 0.04	2.9-3.4	(20)	3.19 ± 0.02
X. *montezumae*						
X. *montezumae montezumae*						
Rio Tamesi						
Rio Sabinas	2.9-3.5	(13)	3.16 ± 0.05	3.0-3.4	(15)	3.20 ± 0.03

TABLE 4 (continued)

	Males Min.-Max.	Males (N)	Males Mean	Males S.E.	Females Min.-Max.	Females (N)	Females Mean	Females S.E.
Rio Panuco								
Rio Verde	3.0-3.4	(5)	3.21	± 0.08	2.9-3.4	(16)	3.12	± 0.03
Rio Salto de Agua	2.7-3.1	(15)	2.89	± 0.03	2.8-3.3	(13)	3.07	± 0.04
X. montezumae cortezi								
Rio Panuco								
Rio Moctezuma	3.2-3.4	(5)	3.32	± 0.10	3.2-3.7	(14)	3.53	± 0.04
Rio Axtla	2.7-3.6	(14)	3.15	± 0.07	3.2-3.9	(10)	3.43	± 0.04
Rio Calaboza	——	—	——		3.5	(1)	3.51	——
X. pygmaeus								
X. pygmaeus nigrensis								
Rio Panuco								
Rio Choy	2.7-3.6	(11)	3.08	± 0.10	3.2-3.5	(7)	3.35	± 0.04
X. pygmaeus pygmaeus								
Rio Panuco								
Rio Axtla	3.5-4.5	(17)	4.10	± 0.04	3.7-4.3	(4)	4.01	——
X. clemenciae								
Rio Coatzacoalcos								
Sarabia	2.9-3.7	(6)	3.30	± 0.15	——	—	——	
X. helleri								
X. helleri helleri								
Rio Nautla	3.6-4.0	(3)	3.74	——	3.0-3.2	(6)	3.06	± 0.03
Rio Chacalacas	3.7	(1)	3.7	——	3.0-3.4	(6)	3.27	± 0.06
Rio Antigua								
Pond at Jalapa	4.0-4.4	(23)	4.25	± 0.03	3.6-4.0	(23)	3.77	± 0.02
Rio Bejucos	3.9-4.4	(25)	4.16	± 0.04	3.0-3.7	(23)	3.40	± 0.03

TABLE 4 (continued)

	Males Min.-Max.	(N)	Mean	S.E.	Females Min.-Max.	(N)	Mean	S.E.
Rio Jamapa								
Rio Chico at Cordoba	3.6-4.4	(15)	3.87	± 0.05	3.1-3.9	(15)	3.41	± 0.05
X. helleri strigatus								
Rio Papaloapan								
Motzorongo	3.0 —	(1)	3.0	——	2.6-3.1	(13)	2.94	± 0.04
El Hule	2.7-3.4	(9)	2.97	± 0.05	2.6-3.1	(11)	2.78	± 0.04
Obispo	2.7-3.4	(21)	3.06	± 0.02	2.6-3.1	(6)	2.80	± 0.06
Achatal	2.9-3.8	(8)	3.38	± 0.05				
Otopa	2.9-4.0	(7)	3.43	± 0.05	3.2-4.0	(4)	3.58	——
Rio Coatzacoalcos	2.9-4.1	(12)	3.25	± 0.04	2.6-3.4	(17)	2.96	± 0.03
X. helleri guentheri								
Rio Grijalva	3.0-3.3	(10)	3.18	± 0.03	——	—	——	
Rio Usumacinta								
Rio de la Pasion	3.0-3.5	(9)	3.24	± 0.05	2.9-3.1	(10)	2.98	± 0.02
Laguna de Zotz	3.2-3.5	(3)	3.37	——	2.9-3.2	(5)	3.00	± 0.06
Rio Xotal	2.7-3.6	(25)	3.17	± 0.04	2.6-2.9	(25)	2.72	± 0.02
Rio Hondo (Uaxactun)	2.7-3.4	(25)	3.00	± 0.04	2.5-2.9	(25)	2.72	± 0.03
Rio Belize								
Rio Privacion	3.3-3.6	(10)	3.46	± 0.03	3.1-3.5	(10)	3.29	± 0.03
Rio Frio	3.4-3.9	(20)	3.63	± 0.03	3.1-3.5	(20)	3.30	± 0.02
Rio Polochic	2.8-3.1	(9)	2.93	± 0.04	2.5-2.7	(9)	2.61	± 0.03
Rio Motagua (Guatemala)	2.6-3.4	(4)	3.08	——	2.6-3.4	(7)	2.87	± 0.04
Independent Atlantic tributaries (Honduras)	2.7-3.2	(4)	2.95	——	2.4-2.8	(8)	2.55	± 0.05
X. helleri alvarezi								
Rio Usumacinta								
Rio Santo Domingo	4.0	(1)	4.0	——	4.2	(1)	4.2	——

---

[*] Mostly small specimens

TABLE 5

VARIATION IN LEAST RELATIVE DEPTH OF CAUDAL PEDUNCLE IN *Xiphophorus*

	Males				Females			
	Min.-Max.	(N)	Mean	S.E.	Min.-Max.	(N)	Mean	S.E.
X. couchianus								
Rio San Juan near Sta. Catarina	4.7-6.7	(66)	5.46 ±	0.12	4.9-6.4	(75)	5.58 ±	0.09
X. maculatus (Mexico)								
Rio Papaloapan								
Obispo	3.1-4.9	(25)	3.74 ±	0.08	3.5-5.5	(41)	4.08 ±	0.05
Cosamaloapan	3.5-3.8	(5)	3.65 ±	0.09	3.8-4.4	(8)	4.10 ±	0.07
Papaloapan	3.9-4.2	(11)	4.03 ±	0.03	3.9-5.0	(17)	4.41 ±	0.07
(Guatemala)								
Rio de la Pasion	3.4-4.6	(17)	3.88 ±	0.07	3.8-4.3	(31)	4.08 ±	0.02
Rio San Pedro de Martir	3.7	(1)	3.7	——	3.8-4.3	(8)	4.04 ±	0.07
Laguna de Zotz*	4.1-4.9	(20)	4.45 ±	0.05	4.3-5.1	(30)	4.61 ±	0.04
Laguna de Peten	3.6-4.4	(8)	3.99 ±	0.08	3.6-4.4	(26)	4.04 ±	0.04
Uaxactun	3.4-3.9	(2)	3.05	——	3.9	(1)	3.9	——
X. variatus								
X. variatus xiphidium								
Rio Sota la Marina								
Rio Pilon	4.5-5.8	(11)	5.23 ±	0.13	5.1-6.4	(27)	5.83 ±	0.06
Rio Purificacion and Rio Corona	4.1-6.1	(61)	5.02 ±	0.03	4.9-6.6	(62)	5.55 ±	0.12
Rio Corona	4.3-5.4	(9)	4.83 ±	0.12	4.7-6.3	(14)	5.10 ±	0.11
X. variatus variatus								
Rio Tamesi								
Rio Guayalejo	5.5-7.0	(10)	5.91 ±	0.15	5.4-7.3	(31)	6.18 ±	0.09

TABLE 5 (continued)

	Males Min.-Max.	Males (N)	Males Mean S.E.	Females Min.-Max.	Females (N)	Females Mean S.E.
Rio Panuco						
Rio Valles	5.0-6.8	(27)	5.79 ± 0.09	5.4-6.8	(35)	6.07 ± 0.06
Rio Axtla	5.0-6.1	(10)	5.51 ± 0.12	4.9-6.9	(9)	6.12 ± 0.25
Rio Calaboza	4.6-6.6	(45)	5.45 ± 0.15	5.2-7.0	(71)	6.04 ± 0.10
Estero Cucharas	4.7-5.8	(50)	5.13 ± 0.04	5.0-6.9	(50)	5.74 ± 0.06
Estero Tancochin*	4.5-6.3	(25)	5.29 ± 0.09	4.8-6.1	(31)	5.53 ± 0.06
Rio Tuxpan	4.8-6.3	(5)	5.52 ± 0.26	5.5-6.7	(12)	5.99 ± 0.09
Rio Cazones						
Arroyo Mariandrea	4.9-5.7	(11)	5.35 ± 0.09	5.4-6.7	(16)	5.92 ± 0.10
Rio Tecolutla						
Arroyo Sin Nombre	4.2-5.3	(9)	4.83 ± 0.13	4.9-5.9	(10)	5.37 ± 0.11
Rio Nautla						
Tlapacoyan	4.6-5.4	(10)	4.84 ± 0.08	5.0-5.5	(10)	5.30 ± 0.05
Maria de la Torre	4.4-5.9	(10)	4.89 ± 0.16	5.2-6.0	(10)	5.50 ± 0.09
X. variatus evelynae						
Rio Tecolutla						
Rio Necaxa	4.7-5.9	(13)	5.19 ± 0.08	4.8-5.9	(14)	5.21 ± 0.07
X. milleri						
Rio Papaloapan						
Laguna Catemaco	5.7-6.7	(38)	6.24 ± 0.05	5.6-6.6	(20)	6.04 ± 0.05
X. montezumae						
X. montezumae montezumae						
Rio Tamesi						
Rio Sabinas	4.3-5.4	(13)	4.71 ± 0.09	5.1-6.1	(15)	5.62 ± 0.07
Rio Panuco						
Rio Verde	4.6-5.0	(5)	4.80 ± 0.08	4.9-6.3	(16)	5.68 ± 0.07
Rio Salto de Agua	3.8-5.0	(15)	4.35 ± 0.07	4.8-5.6	(13)	5.21 ± 0.08

TABLE 5 (continued)

	Males				Females			
	Min.-Max.	(N)	Mean	S.E.	Min.-Max.	(N)	Mean	S.E.
X. Montezumae cortezi								
Rio Panuco								
Rio Moctezuma	4.4-5.0	(5)	4.54	± 0.11	4.8-5.7	(14)	5.37	± 0.05
Rio Axtla	4.1-5.5	(14)	4.74	± 0.10	5.2-6.1	(10)	5.49	± 0.11
Rio Calaboza	——	—	——		5.3	(1)	5.30	——
X. pygmaeus								
X. pygmaeus nigrensis								
Rio Panuco								
Rio Choy	3.7-4.8	(11)	4.28	± 0.12	4.8-5.6	(7)	5.09	± 0.10
X. pygmaeus pygmaeus								
Rio Panuco								
Rio Axtla	5.1-6.5	(17)	5.87	± 0.09	6.7-7.1	(4)	6.99	——
X. clemenciae								
Rio Coatzacoalcos								
Sarabia	4.4-5.0	(6)	4.70	± 0.10	——	—	——	
X. helleri								
X. helleri helleri								
Rio Nautla	4.9-5.2	(3)	5.09	——	5.5-5.8	(6)	5.62	± 0.06
Rio Chachalacas	4.7	(1)	4.7	——	5.0-5.5	(6)	5.33	± 0.09
Rio Antigua								
Pont at Jalapa	5.6-6.5	(23)	5.91	± 0.04	5.8-6.5	(23)	6.23	± 0.04
Rio Bejucos	5.5-6.8	(25)	6.04	± 0.08	5.3-6.0	(25)	5.72	± 0.04
Rio Jamapa								
Rio Chico, Cordoba	5.0-5.8	(15)	5.51	± 0.16	4.9-6.7	(15)	5.71	± 0.11
X. helleri strigatus								

TABLE 5 (continued)

	Males Min.-Max.	(N)	Mean	S.E.	Females Min.-Max.	(N)	Mean	S.E.
Rio Papaloapan								
Motzorongo	4.4	(1)	4.4	——	4.6-5.4	(13)	5.14	± 0.06
El Hule	4.0-4.8	(9)	4.57	± 0.04	4.3-5.4	(11)	4.72	± 0.05
Obispo	4.3-5.0	(21)	4.64	± 0.03	4.3-5.1	(6)	4.75	± 0.07
Achatal	4.3-5.7	(5)	4.85	± 0.09				
Olapa	4.3-6.0	(7)	5.13	± 0.11	5.2-6.0	(4)	5.75	——
Rio Coatzacoalcos	4.3-5.4	(12)	4.80	± 0.07	4.9-6.3	(17)	5.37	± 0.06
X. helleri guentheri								
Rio Grijalva	4.8-5.1	(10)	4.87	± 0.04	——	—	——	
Rio Usumacinta								
Rio de la Pasion	4.9-5.2	(9)	5.06	± 0.03	4.9-5.5	(10)	5.15	± 0.07
Laguna de Zotz	4.8-5.1	(3)	4.97	——	5.0-5.3	(5)	5.10	± 0.06
Rio Xotal	4.3-5.2	(25)	4.69	± 0.05	4.4-5.2	(25)	4.73	± 0.04
Rio Hondo (Uaxactun)	4.1-4.8	(25)	4.46	± 0.04	4.2-5.0	(25)	4.61	± 0.05
Belize River, Brit. Hond.								
Rio Privacion	4.9-5.9	(10)	5.26	± 0.10	5.1-6.3	(10)	5.82	± 0.11
Rio Frio	5.0-6.2	(20)	5.43	± 0.06	5.3-6.1	(20)	5.52	± 0.05
Rio Polochic	4.4-5.0	(9)	4.67	± 0.06	4.8-5.2	(9)	4.99	± 0.06
Rio Motagua (Guatemala)	4.6-5.4	(4)	4.92	——	4.3-6.0	(7)	5.04	± 0.14
Independent Atlantic tributaries (Honduras)	4.1-4.9	(4)	4.49	——	4.6-5.1	(8)	4.82	± 0.07
X. helleri alvarezi								
Rio Usumacinta								
Rio Santo Domingo	6.0	(1)	6.0	——	6.9	(1)	6.9	——

*Mostly small specimens

TABLE 6

DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus couchianus*

	8	9	10	11	(N)	Mean	S.E.
Rio Grande (Mexico)							
Santa Catarina	7	113	20		(140)	9.09	± 0.04
4 mi. west of Monterrey		15	4	1	(20)	9.30	± 0.13
Monterrey	1	6	29		(36)	9.78	± 0.08

TABLE 7

DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus maculatus*

	7	8	9	10	11	(N)	Mean	S.E.
Rio Jamapa		1	27	71	1	(100)	9.72	± 0.05
Rio Papaloapan								
Cosamaloapan 1867			4	7	2	(13)	9.85	± 0.19
Obispo 1902			16	46	1	(63)	9.76	± 0.06
Papaloapan 1932-1939			34	74	4	(112)	9.73	± 0.05
Rio Coatzacoalcos								
Almagrez		2	60	7		(69)	9.07	± 0.03
Jesus Carranza			23	24		(47)	9.51	± 0.07
Minatitlan	1	10	278	21		(310)	9.03	± 0.02
Rio Uxpanapa		2	89	7		(98)	9.05	± 0.03
Coatzacoalcos		2	138	11		(151)	9.06	± 0.02
Rio Tonala								
Huapacal		1	9	1		(11)	9.00	± 0.13
Tres Bocas			8	2		(10)	9.20	± 0.13
La Renal			10	1		(11)	9.09	± 0.09
La Venta		3	124	13		(140)	9.07	± 0.03
Rio Grijalva		5	148	26		(179)	9.12	± 0.02
Rio Usumacinta								
Rio de la Pasion			13	58		(71)	9.82	± 0.05
Rio San Pedro de Martir			17	6		(23)	9.26	± 0.09
Laguna de Zotz			37	160	3	(200)	9.83	± 0.03
Laguna de Eckivil			1			(1)	9	——
Laguna de Peten	1		15	42		(58)	9.69	± 0.07
Rio Hondo, Uaxactun			2	1		(3)	9.33	——
Brook no. 1		2	18	1		(21)	8.96	± 0.08
Brook no. 2		1	5	1		(7)	9.00	± 0.21
Belize River		16	205	104		(325)	9.27	± 0.03

TABLE 8

DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN A LATERAL SERIES IN *Xiphophorus maculatus*

	22	23	24	25	(N)	Mean	S.E.
Rio Jamapa		36	14		(50)	23.28	± 0.06
Rio Papaloapan (Papaloapan)	2	39	9		(50)	23.14	± 0.06
Rio Coatzacoalcos							
Almagrez	1	37	7		(45)	23.13	± 0.06
Jesus Carranza	3	40	11		(54)	23.15	± 0.07
Minatitlan		36	14		(50)	23.28	± 0.06
Rio Uxpanapa		35	15		(50)	23.30	± 0.07
Coatzacoalcos		33	17		(50)	23.34	± 0.07
Rio Tonala (La Venta)		33	17		(50)	23.34	± 0.07
Rio Grijalva	2	40	8		(50)	23.12	± 0.06
Brook no. 1		15	7		(22)	23.32	± 0.10
Belize River	-	52	21	2	(75)	23.33	± 0.06

TABLE 9

DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus variatus*

	9	10	11	12	13	14	(N)	Mean	S.E.
X. variatus xiphidium									
Rio Sota la Marina									
San Carlos		3					(3)	10.0	——
Rio Santa Lucia	2	41	3				(46)	10.02	± 0.05
Rio Purificacion	38	84	2				(124)	9.71	± 0.04
Rio Corona	13	209	13				(235)	10.00	± 0.02
Rio San Marcus	1	29	10				(40)	10.23	± 0.08
X. variatus variatus									
Rio Tamesi		7	65	20	1		(93)	11.16	± 0.06
Rio Panuco									
Inland	2	42	247	28			(319)	10.94	± 0.03
Coastal		59	200	31	2		(292)	10.92	± 0.03
Estero Cucharas		9	163	39	1		(212)	11.15	± 0.03
Estero Tancochin		4	86	7			(97)	11.03	± 0.03
Rio Tuxpan	1	7	38				(46)	10.80	± 0.07
Rio Cazones									
Arroyo Mariandrea			30	91	12	1	(134)	11.88	± 0.05
Tihuatlan		1	33	41			(75)	11.53	± 0.06
Rio Tecolutla									
Arroyo Sin Nombre		1	64	45			(110)	11.40	± 0.05
Rio Nautla									
Tlapacoyan	1	95	61	2			(159)	10.40	± 0.04
Maria de la Torre	1	76	209	3	1		(290)	10.76	± 0.03
X. variatus evelynae									
Rio Tecolutla									
Rio Necaxa			9	80	37	1	(127)	12.24	± 0.05

TABLE 10

DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN A LATERAL SERIES IN *Xiphophorus variatus*

	24	25	26	27	28	(N)	Mean	S.E.
X. variatus xiphidium								
Rio Soto la Marina								
Rio Corona	1	8	25	4		(38)	25.84	± 0.09
X. variatus variatus								
Rio Tamesi			1			(1)	26	——
Rio Panuco (Inland)			24	16	1	(41)	26.44	± 0.09
Estero Cucharas		5	27	11		(43)	26.14	± 0.09
Rio Cazones								
Arroyo Mariandrea	3	11	10	1		(25)	25.36	± 0.16
Tihuatlan	1	1	3			(5)	25.4	——
Rio Tecolutla								
Arroyo Sin Nombre	3	6	11	2		(22)	25.55	± 0.19
Rio Nautla								
Tlapacoyan		9	6			(15)	25.40	± 0.14
Maria de la Torre		8	21	1		(30)	25.77	± 0.09
X. variatus evelynae								
Rio Tecolutla								
Rio Necaxa			7	3		(10)	26.30	± 0.14

TABLE 11

VARIATION IN RELATIVE LENGTH OF HEAD* IN *Xiphophorus variatus*

	Males Min.-Max.	(N)	Mean S.E.	Females Min.-Max.	(N)	Mean S.E.
X. variatus xiphidium						
Rio Sota la Marina						
Rio Pilon (Meek)	3.1-3.7	(11)	3.37 ± 0.05	3.0-3.9	(27)	3.41 ± 0.04
Rio Purificacion and Rio Corona	3.0-3.7	(61)	3.34 ± 0.03	3.2-4.1	(62)	3.56 ± 0.04
Rio Corona (Meek)	2.8-3.7	(9)	3.37 ± 0.09	2.9-3.8	(14)	3.36 ± 0.06
X. variatus variatus						
Rio Tamesi						
Rio Guayalejo	3.4-3.7	(10)	3.51 ± 0.03	3.2-3.9	(31)	3.55 ± 0.03
Rio Panuco						
Rio Valles	3.3-4.1	(27)	3.61 ± 0.04	3.3-3.9	(35)	3.59 ± 0.03
Rio Axtla	3.3-3.6	(10)	3.48 ± 0.03	3.3-3.6	(9)	3.49 ± 0.03
Rio Calaboza	3.2-3.8	(45)	3.46 ± 0.05	3.2-4.1	(71)	3.57 ± 0.05
Estero Cucharas	3.2-3.8	(50)	3.50 ± 0.02	3.3-3.9	(50)	3.53 ± 0.02
Estero Tancochin**	3.1-3.8	(25)	3.34 ± 0.03	3.1-4.0	(31)	3.40 ± 0.04
Rio Tuxpam	3.2-3.7	(5)	3.42 ± 0.10	3.3-3.8	(12)	3.56 ± 0.05
Rio Cazones						
Arroyo Mariandrea	3.3-3.8	(11)	3.57 ± 0.05	3.5-3.7	(16)	3.64 ± 0.02
Rio Tecolutla						
Arroyo Sin Nombre	3.1-3.6	(9)	3.35 ± 0.05	3.4-3.9	(10)	3.57 ± 0.05
Rio Nautla						
Tlapacoyan	3.4-4.0	(10)	3.56 ± 0.05	3.4-3.8	(10)	3.62 ± 0.04
Maria de la Torre	3.4-3.6	(10)	3.54 ± 0.03	3.5-3.9	(10)	3.67 ± 0.04
X. variatus evelynae						
Rio Tecolutla						
Rio Necaxa	3.1-3.5	(13)	3.25 ± 0.03	3.1-3.6	(14)	3.29 ± 0.04

---

* The length of the head from the tip of the lower jaw to the end of the opercular membrane was arithmetically divided into the standard length.

** Mostly small specimens.

TABLE 12

VARIATION IN RELATIVE LENGTH OF CAUDAL PEDUNCLE IN *Xiphophorus variatus variatus* AND *Xiphophorus variatus evelynae*

	Males				Females			
	Min.-Max.	(N)	Mean	S.E.	Min.-Max.	(N)	Mean	S.E.
X. variatus variatus								
Rio Panuco								
Rio Axtla	2.07-2.25	(10)	2.14 ±	0.01	2.24-2.56	(9)	2.43 ±	0.03
Rio Cazones								
Arroyo Mariandrea	2.06-2.24	(11)	2.15 ±	0.01	2.27-2.65	(16)	2.50 ±	0.02
Rio Tecolutla								
Arroyo Sin Nombre	2.09-2.31	(9)	2.20 ±	0.03	2.19-2.60	(10)	2.46 ±	0.04
Rio Nautla								
Tlapacoyan	1.96-2.20	(10)	2.14 ±	0.02	2.30-2.77	(10)	2.48 ±	0.04
Maria de la Torre	2.03-2.22	(10)	2.14 ±	0.06	2.40-2.50	(10)	2.44 ±	0.01
X. variatus evelynae								
Rio Tecolutla								
Rio Necaxa	2.08-2.62	(13)	2.29 ±	0.04	2.54-2.87	(14)	2.69 ±	0.03

TABLE 13

VARIATION IN RELATIVE LENGTH OF CAUDAL FIN IN *Xiphophorus variatus variatus* AND *Xiphophorus variatus evelynae*

	Males Min.-Max.	(N)	Mean S.E.	Females Min.-Max.	(N)	Mean S.E.
X. *variatus variatus*						
Rio Panuco						
Rio Axtla	3.1-3.7	(10)	3.36 ± 0.08	3.6-4.3	(9)	3.79 ± 0.07
Rio Cazones						
Arroyo Mariandrea	2.9-3.5	(9)	3.10 ± 0.07	2.9-3.5	(16)	3.21 ± 0.04
Rio Tecolutla						
Arroyo Sin Nombre	3.1-3.5	(9)	3.29 ± 0.06	3.4-4.0	(10)	3.61 ± 0.07
Rio Nautla						
Tlapacoyan	3.0-3.2	(10)	3.16 ± 0.02	3.1-3.5	(10)	3.34 ± 0.04
Maria de la Torre	3.1-3.5	(10)	3.24 ± 0.04	3.2-3.8	(10)	3.48 ± 0.06
X. *variatus evelynae*						
Rio Tecolutla						
Rio Necaxa	2.7-2.9	(13)	2.84 ± 0.02	2.6-3.0	(12)	2.70 ± 0.03

TABLE 14

VARIATION IN THREE PROPORTIONAL MEASUREMENTS IN *Xiphophorus milleri* FROM LAGUNA CATEMACO (RIO PAPALOAPAN SYSTEM)

	Males Min.-Max.	(N)	Mean S.E.	Females Min.-Max.	(N)	Mean S.E.
Length of Head	3.2-3.6	(38)	3.42 ± 0.02	3.4-3.6	(20)	3.49 ± 0.02
Length of Caudal Peduncle	2.0-2.2	(38)	2.13 ± 0.01	2.3-2.5	(20)	2.38 ± 0.01
Length of Caudal Fin	3.2-4.0	(38)	3.65 ± 0.03	3.5-4.1	(20)	3.85 ± 0.03

TABLE 15

DISTRIBUTION AND VARIATION OF THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus montezumae*

	10	11	12	13	14	(N)	Mean	S.E.
X. *montezumae montezumae*								
Rio Tamesi		20	19	1		(40)	11.53 ±	0.09
Rio Panuco								
Rio Verde at Rascon		13	19	9		(41)	11.90 ±	0.11
Rio Salto de Agua	1	15	12			(28)	11.40 ±	0.10
X. *montezumae cortezi*								
Rio Panuco								
Rio Valles at Valles		1	2			(3)	11.7	
Rio Moctezuma		79	88	1		(169)	11.53 ±	0.04
Rio Axtla	1	82	154	13		(251)	11.71 ±	0.04
Rio Calaboza	2		1	2	1	(4)	13.0	

TABLE 16

DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN A LATERAL SERIES IN *Xiphophorus montezumae*

	25	26	27	28	(N)	Mean	S.E.
X. *montezumae montezumae*							
Rio Tamesi	1	6	25	1	(33)	26.79 ±	0.10
Rio Panuco							
Rio Verde			6	15	(21)	27.70 ±	0.10
Rio Salto de Agua		8	16	4	(28)	26.80 ±	0.10
X. *montezumae cortezi*							
Rio Panuco (Rio Axtla)		18	17	2	(37)	26.57 ±	0.11

TABLE 17

VARIATION IN RELATIVE LENGTH OF HEAD IN *Xiphophorus montezumae*

	Males Min.-Max.	(N)	Mean S.E.	Females Min.-Max.	(N)	Mean S.E.
X. montezumae montezumae						
Rio Tamesi						
Rio Sabinas	3.5-3.9	(13)	3.82 ± 0.03	3.7-3.9	(15)	3.76 ± 0.01
Rio Panuco						
Rio Verde	4.0-4.4	(5)	4.17 ± 0.07	4.2-4.5	(16)	4.30 ± 0.02
Rio Salto de Agua	3.6-4.1	(15)	3.85 ± 0.03	3.6-4.0	(13)	3.82 ± 0.04
X. montezumae cortezi						
Rio Panuco						
Rio Axtla	3.4-4.0	(14)	3.62 ± 0.04	3.4-3.7	(10)	3.53 ± 0.02

TABLE 18

VARIATION IN RELATIVE LENGTH OF CAUDAL PEDUNCLE IN *Xiphophorus montezumae*

	Males Min.-Max.	(N)	Mean S.E.	Females Min.-Max.	(N)	Mean S.E.
X. montezumae montezumae						
Rio Tamesi						
Rio Sabinas	1.9-2.0	(13)	1.99 ± 0.01	2.2-2.6	(15)	2.41 ± 0.02
Rio Panuco						
Rio Verde						
Rio Salto de Agua	2.0-2.5	(15)	2.13 ± 0.03	2.3-2.6	(13)	2.44 ± 0.01
X. montezumae cortezi						
Rio Panuco						
Rio Axtla	1.9-2.2	(14)	2.09 ± 0.02	2.3-2.6	(10)	2.47 ± 0.02

TABLE 19

Variation in relative length of caudal appendage in adult males of *Xiphophorus montezumae*

	Min.-Max.	(N)	Mean	S.E.
X. montezumae montezumae				
Rio Tamesi				
Rio Sabinas	1.5-2.6	(13)	2.02 ±	0.10
Rio Panuco				
Rio Verde	1.0-1.7	(2)	1.37	——
Rio Salto de Agua	1.2-1.9	(6)	1.65 ±	0.12
X. montezumae cortezi				
Rio Panuco				
Rio Axtla	1.6-2.6	(33)	2.01 ±	0.04

TABLE 20

Distribution and variation of the number of dorsal fin rays in *Xiphophorus pygmaeus*

	9	10	11	12	13	14	(N)	Mean	S.E.
X. pygmaeus nigrensis									
Rio Panuco									
Rio Choy			4	15	1	4	(24)	12.21 ±	0.19
X. pygmaeus pygmaeus									
Rio Panuco									
Rio Axtla	1	72	155	5			(233)	10.70 ±	0.03

TABLE 21

Distribution and variation of the number of scales in lateral series in *Xiphophorus pygmaeus*

	25	26	27	28	(N)	Mean	S.E.
X. pygmaeus nigrensis							
Rio Panuco							
Rio Choy	1	1	17	3	(22)	27.00 ±	0.13
X. pygmaeus pygmaeus							
Rio Panuco							
Rio Axtla	5	11			(16)	25.69 ±	0.12

TABLE 22

VARIATION IN RELATIVE LENGTH OF HEAD IN *Xiphophorus pygmaeus*

	Males Min.-Max.	Males (N)	Males Mean S.E.	Females Min.-Max.	Females (N)	Females Mean S.E.
X. pygmaeus nigrensis Rio Panuco Rio Choy	3.6-4.0	(9)	3.81 ± 0.04	3.4-3.7	(7)	3.55 ± 0.03
X. pygmaeus pygmaeus Rio Panuco Rio Axtla	3.4-4.0	(17)	3.77 ± 0.05	3.6-4.2	(4)	3.89 ± 0.12

TABLE 23

VARIATION IN RELATIVE LENGTH OF CAUDAL PEDUNCLE IN *Xiphophorus pygmaeus*

	Males Min.-Max.	Males (N)	Males Mean S.E.	Females Min.-Max.	Females (N)	Females Mean S.E.
X. pygmaeus nigrensis Rio Panuco Rio Choy	2.0-2.3	(11)	2.15 ± 0.03	2.3-2.6	(6)	2.49 ± 0.05
X. pygmaeus pygmaeus Rio Panuco Rio Axtla	2.1-2.3	(16)	2.19 ± 0.02	2.6-2.7	(4)	2.67 —

TABLE 24

VARIATION IN TWO PROPORTIONAL MEASUREMENTS IN MALES OF *Xiphophorus clemenciae* FROM SARABIA (RIO COATZACOALCOS SYSTEM)*

	Min.-Max.	(N)	Mean	S.E.
Length of Head	3.7-4.4	(6)	4.02 ±	0.12
Length of Caudal Peduncle	2.0-2.3	(6)	2.12 ±	0.06

* Only three of the males are adult, ranging in size from 29.0 to 35.5 mm. in standard length. The remaining three are in various stages of development, from very early to late differentiation.

TABLE 25

GEOGRAPHICAL POPULATIONS OF *Xiphophorus helleri* MAINTAINED UNDER LABORATORY CONDITIONS, AND NUMBERS OF INTRASPECIFIC SWORDTAIL HYBRIDS PRODUCED

Subspecies	Period Maintained in Laboratory
X. h. helleri	
Rio Jamapa (Veracruz, Mexico)	26 years
X. h. strigatus	
Rio Papaloapan (Veracruz, Mexico)	19 years
Rio Coatzacoalcos (Veracruz, Mexico)	10 years
X. h. guentheri	
Rio Grijalva (Chiapas, Mexico)	4 years
Rio Belize (British Honduras)	9 years
Rio Lancetilla (Honduras)	6 years

Types of Hybrid Produced	Number of Adult Hybrids
Rio Jamapa ♀ x Rio Papaloapan ♂	F_1 = 4
Rio Jamapa ♀ x Rio Coatzacoalcos ♂	F_1 = 50; F_2 = 18
Rio Jamapa ♀ x Rio Lancetilla ♂	F_1 = 22; F_2 = 35
Rio Coatzacoalcos ♀ x Rio Belize ♂	F_1 = 35
Rio Papaloapan ♀ x (Rio Jamapa-Rio Papaloapan F_1)	Backcross = 20
Rio Papaloapan ♀ x Rio Belize ♂	F_1 = 108
Rio Grijalva ♀ x Rio Lancetilla ♂	F_1 = 20
Rio Belize ♀ x Rio Lancetilla ♂	F_1 = 40; F_2 = 28

TABLE 26

VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus helleri* FROM DIFFERENT NATURAL POPULATIONS RAISED UNDER SIMILAR CONDITIONS IN THE LABORATORY

	11	12	13	14	15	(N)	Mean	S.E.
Rio Coatzacoalcos stock	1	12	3	1		(17)	12.24 ±	0.16
Belize River stock		2	18			(20)	12.90 ±	0.07
Honduras stock			3	7	1	(11)	13.82 ±	0.18

TABLE 27

Distribution and variation in the number of dorsal fin rays in *Xiphophorus helleri*

	11	12	13	14	15	16	17	(N)	Mean	S.E.
X. helleri helleri										
Rio Nautla		5	2					(7)	12.28	± 0.22
Rio Chachalacas										
Encero	4	82	7					(93)	12.03	± 0.04
Plan del Rio		6	6					(12)	12.50	± 0.15
Rio Antigua										
Jalapa	22	98	1					(121)	11.83	± 0.04
Rio Bejucos	8	91	11					(110)	12.03	± 0.04
Rio Jamapa										
L'Encero	4	52	6					(62)	12.03	± 0.05
Cordova	12	134	40	1				(187)	12.16	± 0.04
Boca del Rio	3	2						(5)	11.40	± 0.26
X. helleri strigatus										
Rio Papaloapan										
Orizaba	5	8	1					(14)	11.71	± 0.16
Otopa	1	2	8					(11)	12.64	± 0.20
Motzorongo		1	12	1				(14)	13.00	± 0.10
El Hule	2	45	32					(79)	12.38	± 0.06
Papaloapan	4	104	81	4				(193)	12.44	± 0.04
Obispo		16	8	3				(27)	12.52	± 0.13
Achotal	2	6						(8)	11.75	± 0.16
Rio Coatzacoalcos										
Almagres		9	9	1				(19)	12.58	± 0.14
Jesus Carranza	8	23	2					(33)	11.82	± 0.09
Minatitlan		4	2					(6)	12.33	± 0.24

TABLE 27 (continued)

DISTRIBUTION AND VARIATION IN THE NUMBER OF DORSAL FIN RAYS IN *Xiphophorus helleri*

	11	12	13	14	15	16	17	(N)	Mean	S.E.
X. helleri guentheri										
Rio Tonala			4	6	2			(12)	13.83	± 0.21
Rio Grijalva			14	20	2	1		(37)	13.72	± 0.11
Rio Usumacinta										
Upper Rio Usumacinta		2	4					(6)	12.67	± 0.21
Rio de la Pasion		2	32	33				(67)	13.46	± 0.07
Arroyo Xotal		1	24	90	14	1		(130)	13.92	± 0.05
Laguna de Zotz			3	18	3			(24)	14.00	± 0.10
Rio Hondo, Uaxactun			61	92	14			(167)	13.72	± 0.05
Belize River										
Benque Viejo		1	12	9				(22)	13.36	± 0.13
Rio Privacion		16	67					(83)	12.81	± 0.04
Rio Frio	1	3	67	48	1			(120)	13.38	± 0.05
Rio Grande (Brit. Hond.)			1	7	2			(10)	14.10	± 0.10
Rio Motagua	1	3	2					(6)	12.17	± 0.34
Rio Chamelecon		5	33	25	1			(64)	13.34	± 0.08
Rio Lancetilla			3	2	2			(7)	13.85	± 0.34
Rio San Juan					1			(1)	15	——
Rio Bonito				3	3	1		(7)	14.71	± 0.29
Estero Salado					9	2	1	(12)	15.33	± 0.19
X. helleri alvarezi								(21)	11.23	± 0.10
Rio Santo Domingo	16	5								

TABLE 28

DISTRIBUTION AND VARIATION IN THE NUMBER OF SCALES IN A LATERAL SERIES IN *Xiphophorus helleri*

	25	26	27	28	29	(N)	Mean	S.E.
X. helleri helleri								
Rio Nautla			1	6		(7)	27.85	± 0.14
Rio Antigua								
Jalapa			3	7		(10)	27.70	± 0.16
Bejucos			4	4		(8)	27.50	± 0.20
Rio Jamapa								
L'Encero			9	43	7	(59)	27.97	± 0.07
Boca del Rio		3	1			(4)	26.8	—
X. helleri strigatus								
Rio Papaloapan (Papaloapan)			2			(2)	27.0	—
Rio Coatzacoalcos								
Almagres		4	10	3		(17)	26.94	± 0.16
Jesus Carranza		6	15	13		(34)	27.21	± 0.13
Minatitlan			3	1		(4)	27.3	—
X. helleri guentheri								
Rio Tonala	2	2	4			(8)	26.25	± 0.32
Rio Grijalva	4	21	7			(32)	26.09	± 0.10
Rio Usumacinta								
Rio del la Pasion		2				(2)	26.0	—
Rio Hondo, Uaxactun	6	7	4			(17)	25.88	± 0.19
Belize River								
Benque Viejo	1	7	7			(15)	26.40	± 0.17
Rio Frio		10	1			(11)	26.09	± 0.09
Rio Grande (Brit. Hond.)	1	5	1			(7)	26.00	± 0.22
Rio Motagua		3	3			(6)	26.50	± 0.24
Rio Chamelecon	6	26	26	2		(60)	26.43	± 0.09
Rio Lancetilla	1		2	4		(7)	27.28	± 0.33
Rio San Juan			1			(1)	27.0	—
Rio Bonito		5	1			(6)	26.17	± 0.21
Estero Salado		3	7			(10)	26.70	± 0.16
X. helleri alvarezi								
Rio Santo Domingo		5	15		1	(21)	26.86	± 0.14

TABLE 29

DISTRIBUTION AND VARIATION OF RELATIVE LENGTH OF CAUDAL FIN IN *Xiphophorus helleri*

Subspecies and	Class Intervals																						
Drainage	2.6	.7	.8	.9	3.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	4.0	.1	.2	.3	.4	.5	(N)	Mean	S.E.
h. helleri																							
Rio Nautla							1	1	2	2	1			1							(8)	3.47	± 0.06
Rio Chachalacas						1		3	9	4	8	9	7	4	1	1	2				(49)	3.64	± 0.03
Rio Jamapa							1	3	10	13	14	14	10	12	12	13	7	3	1	2	(117)	3.80	± 0.03
h. strigatus																							
Rio Papaloapan			2	5	3	6	7	4	8	2	1										(38)	3.19	± 0.03
Rio Coatzacoalcos			1	5	9	11	9	2	6	4	2	1									(50)	3.18	± 0.01
h. guentheri																							
Rio Grijalva		2	1	5	2																(10)	2.87	± 0.04
Rio Usumacinta	1		8	4	8	9	2	2	1	1											(36)	3.01	± 0.03
Rio Hondo			3	8	3	2															(16)	2.92	± 0.02
Belize River			1	1	1	2	2	2	2												(11)	3.15	± 0.06
Rio Frio		1		1	6	2	2	2	5	1		1									(21)	3.19	± 0.05
Rio Polochic	2	6	9	1																	(18)	2.75	± 0.02
Independent Atlantic tributaries (Hond.)		2	3	6			1														(12)	2.87	± 0.04
h. alvarezi																							
Rio Santo Domingo				1																	(1)	2.9	—

TABLE 30

FREQUENCY DISTRIBUTION OF GONOPODIAL SEGMENTS IN *Xiphophorus helleri*

Subspecies	Distal serrae (ray 4p)					Subterminal segments (ray 3)							
	2	3	4	5	6	4	5	6	7	8	9	10	11
h. helleri													
Rio Nautla		2	1						2	1			
Rio Antigua	1	7	2				4	6					
Rio Jamapa	5	11	3				10	8	1				
h. strigatus													
Rio Papaloapan		7	9				2	3	8	3			
Rio Coatzacoalcos	1	9	9	1		1	7	5	6	1			
h. guentheri													
Rio Grijalva		6	10	2	1			3	3	5	3	4	1
Rio Hondo			11	8			4	3	7		4		
Rio Frio		4	5	1	1			6	4	1			
La Lima, Honduras				1								1	
h. alvarezi													
Rio Santo Domingo (Rio Usumacinta system)		1								1			

TABLE 31

VARIATION OF FIVE MORPHOMETRIC TRAITS IN TWO POPULATIONS OF *Xiphophorus helleri* [*]

	Laguna de Sontecomapan Veracruz, Mexico				Arroyo del Azufre Tabasco, Mexico			
	Min.-Max.	(N)	Mean	S.E.	Min.-Max.	(N)	Mean	S.E.
Dorsal fin rays	12-14	(25)	13.08	± 0.08	13-14	(15)	13.67	± 0.13
Scales in a lateral series	26-27	(24)	26.46	± 0.11	26-27	(15)	26.27	± 0.12
Greatest relative depth of body	2.5-2.9	(14)	2.67	± 0.03	2.7-3.3	(7)	2.89	± 0.09
Least relative depth of caudal peduncle	4.3-4.9	(14)	4.58	± 0.05	4.4-4.9	(7)	4.68	± 0.07
Relative length of caudal fin	2.7-3.2	(25)	2.90	± 0.03	3.1-3.6	(7)	3.41	± 0.08
Lateral striping	multiple red stripes and a diffuse, dusky midlateral band.				multiple red stripes and a distinct, black or dusky midlateral stripe.			

---

[*] All values for males, females, and subadults are combined.

DISTRIBUTION AND ECOLOGY OF *XIPHOPHORUS*

The principal features of the ecology of the eight species of *Xiphophorus* are outlined in table 32. Such tabulations, however, are but approximations of the complete ecologies of species. Year round regular and often drastic cyclic changes associated with seasonal and climatic fluctuations create diverse ecologic situations, particularly for organisms confined chiefly to the smaller streams and tributaries. Seasonal fluctuations, in turn, are modified by geographic position along the Atlantic coastal plain of Mexico and northern Central America in various climatic zones. According to hydrologic data given by Tamayo (1946), *Xiphophorus* occupies 22 primary and subsidiary drainage areas in Mexico alone, from Nuevo Leon and Tamaulipas southward to Tabasco and Chiapas. In the north rainfall is comparatively light, about 500 mm. per annum, while in the region including the Grijalva and Usumacinta river systems (*X. helleri* and *X. maculatus*), rainfall may reach 4500 mm. per annum. In the comparatively arid northern limits of the range of *Xiphophorus*, rivers are fewer and their basins are not as sprawling and complex as in moist tropical regions to the south. Other topographical features of the landscape may restrict the abundance of certain types of habitats and tend to reenforce or partially obliterate ecological distinctions between species.

Distribution Patterns of *Xiphophorus* in Relation to Habitat Preferences

Ecological Restrictions

The eight species of *Xiphophorus* may be separated imperfectly into two groups. One prefers clear, fast water over a rocky or sandy substrate; the other lives principally in standing or sluggish, clear or murky water, over a mud or silt bottom, amid dense stands of submerged aquatic or shoreline emergent vegetation (figs. 24-25). Average temperature differences between these two biotopes may or may not provide an additional distinction. In the torrential headwater

---

Figure 24. Restricted swordtail and platyfish habitats. Above, a swift, rocky stream near Jalapa, Veracruz, Mexico, in which the green swordtail, *X. helleri*, occurs, but no platyfishes. Below, a small, muddy, heavily overgrown and sluggish stream, tributary to the Rio Tonala, Tabasco, Mexico; the platyfish, *X. maculatus*, was common in the mud and among the dense rooted vegetation, a situation that is probably unsuitable for swordtails. Undated photographs from the collection of Myron Gordon.

TABLE 32

SYNOPSIS OF ECOLOGY OF EIGHT SPECIES OF *Xiphophorus*

Species	Water Color	Vegetation	Shore	Bottoms	Nature of Water Course	Occurrence
couchianus	clear and white	dense aquatics or emergents; rarely none	desert scrub or open	usually mud and clay; rarely rocky rubble	spring pools; rarely sluggish flowing streams	concentrated in spring pools, rare in main river channel
maculatus	clear and white to turbid and brown	dense aquatics or emergents; rarely none	jungle, wooded or open	mud and clay	spring pools, ditches and swamps; rarely sluggish flowing streams or ponds	concentrated in spring pools, ditches and swamps; rare in sluggish flowing streams and main river channels
variatus	clear and white to turbid and brown	dense aquatics or emergents; occasionally none	desert-scrub, wooded or open	usually mud and clay; rarely rocky rubble	spring pools, ditches and swamps; occasionally sluggish and rapid flowing streams	concentrated in spring pools, ditches and swamps; scattered in sluggish and rapid flowing streams and main river channels
milleri	clear and white	sparse green algae	jungle	sand and silt; sparse rocks	flowing, steep banked streams with slight current	known from a single stream, tributary to Laguna de Catemaco
montezumae	clear and white to slightly brown; rarely turbid	usually none; rarely sparse aquatics and algae	jungle, wooded or open	usually sand, gravel or rocks, rarely mud or clay	flowing streams, rarely ponds or ditches	concentrated in pools in stream bed along shore; scattered in main streams and lowland pools

TABLE 32 (continued)

SYNOPSIS OF ECOLOGY OF EIGHT SPECIES OF *Xiphophorus*

Species	Water Color	Vegetation	Shore	Bottoms	Nature of Water Course	Occurrence
pygmaeus	clear and white or faintly yellowish; never turbid	thick stands of sagittaria on undercut stream bank; rarely patches of submerged plants in shallows	jungle, wooded or open	sand, gravel and rocks	swiftly flowing streams	concentrated in dense submerged aquatics along undercut bank of swift streams; scattered in shallow shoreline areas; very rare in isolated pools
clemenciae	clear and white	none	jungle	mud, sand, and rocks	flowing, steep banked streams with slight to torrential current	known from a single headwater stream
helleri	clear and white to slightly brown; rarely turbid	usually none; rarely sparse aquatics and algae or partly submerged coarse shoreline grass	jungle growth; rarely wooded or open	usually sand, gravel or rocks; rarely mud or clay	flowing streams; rarely ponds or ditches	concentrated in pools in stream bed along shore; scattered in main streams and lowland pools and swamps

habitat of *pygmaeus nigrensis* where the Rio Choy emerges from a cave mouth at the base of a mountain, a water temperature of 76° F. was recorded in January 1957. The water temperature of the headwater habitat of *montezumae montezumae* adjoining the cataracts and rapids of the Rio Salto de Agua was recorded as 58° F. during the same period. Spring pools maintained throughout the year by seepage may remain quite cold although in other ways they are generally representative of a lowland ecology. The platyfishes *maculatus* and *couchianus* have been taken in such situations. In general, however, water temperatures of headland or stream habitats are lower than those of most lowland bodies of water. This undoubtedly represents a real average difference between lotic and lentic communities in the region being considered. [See Goldman (1951) for a discussion of the life zones and biotic provinces of Mexico.]

Xiphophorus helleri, X. clemenciae, X. montezumae, X. pygmaeus, and *X. milleri* are all typically representative of stream habitats. *X. helleri,* though primarily a species of lotic communities, is taken frequently in standing or sluggish water such as spring pools, lakes, swamps, or in sluggish meandering streams in the southern part of its range. Even in lagoons and lakes, however, it prefers cooler, clearer water over a sandy or gravel substrate. *X. montezumae,* also chiefly a fast water species, has been collected in numbers in spring pools and lagoons, but never in lakes or swamps. In flowing streams *pygmaeus* is generally confined to the faster waters of the undercut banks a few feet down amidst rooted vegetation or sheltering rocky ledges. Despite its rare occurrence in patches of vegetation or over sandy beaches on the slipoff slopes of flowing streams, it is even then confined to a broadly lotic habitat. *X. milleri* has been taken in a single upland tributary to Laguna Catemaco together with *helleri.* *X. clemenciae* is known only from a headwater tributary of the Rio Coatzacoalcos where it, too, occurs with *helleri.*

Xiphophorus variatus, X. maculatus and *X. couchianus* are primarily species of lentic communities. In the Rio Tecolutla and Rio Cazones, however, *variatus* occupies both headwater and lowland habitats. Some have taken in a torrential, boulder strewn headland tributary of the Rio Tecolutla, whereas in the Rio Axtla it occurs with *montezumae* in sandy or rocky pools in stream beds. *X. maculatus* is restricted almost entirely to spring pools (some with moderate turnover from ground seepage), lagoons, swamps, and lakes. Occasionally, it is taken along the banks of sluggish meandering streams and torrents of which the swordtails and *milleri* are characteristic.

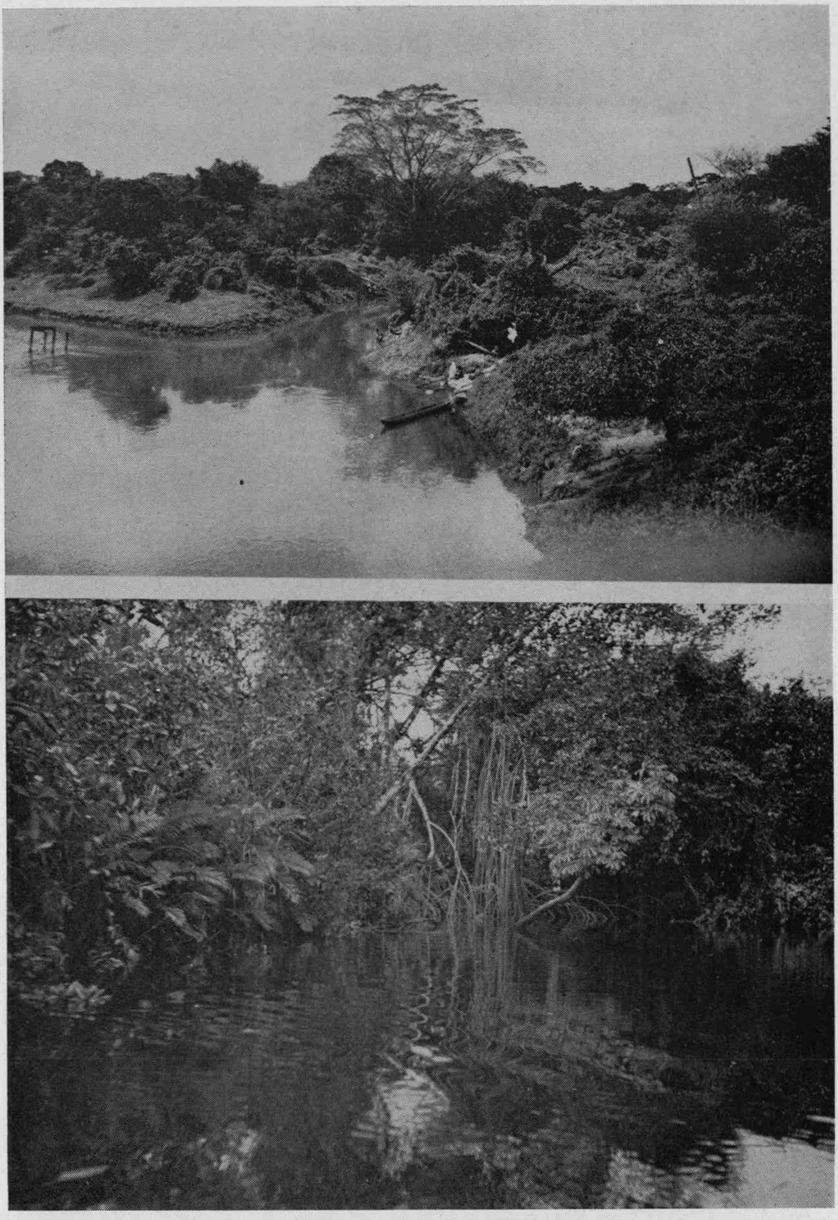


Figure 25. Unrestricted swordtail and platyfish habitats. Two situations in which *X. helleri* and *X. maculatus* live in close association. Above, the Rio Coatzacoalcos, near Jesus Carranza, Veracruz, Mexico. Below, a large tributary to the Rio Tonala, Tabasco, Mexico. In both places the platyfish, *X. maculatus*, has been taken among the rooted vegetation and in the mud along shore or in small backwaters, the swordtail over sandy or rocky patches, or in pools, farther from shore where there is a definite slight current. In the upper picture both species were taken in different sections of the tributary entering the main river at left center. Undated photographs from the collection of Myron Gordon.

During times of flash floods that scour out many of its lowland habitats, *maculatus* may be found widely dispersed in flooded pasture land and temporarily swollen streams. In dry seasons, this species, may be trapped in drying pools in stream beds. In such impermanent habitats the fish are quickly eliminated by predators or else killed by desiccation.

X. couchianus has been taken in large numbers in the Rio Santa Catarina in two spring pools that probably are maintained throughout the year by seepage. Like *maculatus*, a few individuals may be swept downstream during times of flood, thus accounting for the occasional specimens taken near Monterrey in larger bodies of moving water. The annual and in some cases total disruption of lowland habitats by flood waters makes existence hazardous for such species, and certainly eliminates vast numbers of platyfishes each year. At the same time the cyclic floods may wash large numbers of fish into main streams and rivers, where they probably serve as a reserve from which new local populations are reconstituted when the floods subside as well as a means for dispersing the species. Beyond any question, *maculatus* has fared well under these severe and continuing environmental pressures as evidenced by its great local abundance throughout a 600 mile range.

TYPES OF TOPOGRAPHICAL AND ECOLOGICAL ISOLATION

Isolation in different drainages has been the most important factor in bringing about raciation[3] and subspeciation in *Xiphophorus* in the recent past. The geographical races and subspecies of *helleri*, for example, are distributed in 17 distinct drainages, those of *variatus* in 7, and of *maculatus* in 8 (figs. 4, 10, 19).

Geographical isolation between populations also is operative within single river systems where each population is confined to the middle reaches of different major tributaries that have lowland or coastal estuarine confluences. In the Rio Panuco basin in northern Veracruz the subspecies of *montezumae* and *pygmaeus* are effectively isolated in northern and southern tributaries. In the swampy coastal region of Tabasco the large and complex Grijalva and Usumacinta-river systems come together in a network of canals, swamps and streams, which was possibly at some former time a confluence of estuarine proportions. These two major southern rivers contain distinctive populations of *X. h. guentheri*.

---

[3] Here used to mean the formation of microgeographic races.

Isolation in different lakes or between lakes and adjacent river systems, though rare, nevertheless separates some races of *maculatus* in the Peten District of northern Guatemala.

Within a single tributary altitudinal differences (table 33) constitute an effective topographical barrier. Distinct subspecies of *variatus* exist in the headwaters and lowlands of the Rio Tecolutla in northern Veracruz. The headland form is isolated by a series of cataracts at an altitude of approximately 4000 feet. It seems highly improbable that this population originated from the lowland Tecolutla form. More likely it was derived by headwater transfer (stream capture) from the form inhabiting the headwaters of the adjacent Rio Cazones. A distinct subspecies of *helleri* occurs at about 1500 feet in the headwaters of the Rio Usumacinta; in this instance the altitudinal barrier is reenforced by linear distance. This subspecies is separated by an airline distance of more than 100 miles from the lowland swordtail, and perhaps double or treble this distance by the tortuous river course.

The species of *Xiphophorus*, unlike the infraspecific units, are isolated both geographically and ecologically (Gordon, 1947a, 1953b). The three platyfish species are completely allopatric. One of them, *variatus*, occurs sympatrically in the same stream cross section (Rio Axtla) with *montezumae* and *pygmaeus*, both *variatus* and *montezumae* occupying an ecological niche distinct from that of *pygmaeus* but not from each other. In most other cases, *montezumae* and *variatus* occupy separate habitats.

X. helleri occurs sympatrically with both *maculatus* and *variatus*, from which it is almost always ecologically distinct. For example, *helleri*, a fast-water species, is for the most part restricted to highlands, and *maculatus*, preferring a lentic environment, to lowland areas. In the Jamapa and Papaloapan river systems, headwater and lowland habitats are well separated by a comparatively steep gradient as the rivers course eastward from the mountains to the broad coastal plain. Immediately to the south in the Rio Coatzacoalcos the seaward gradient, though slight, is maintained to the river's mouth, and lotic and lentic situations are intermixed. Thus, in the Jamapa and Papaloapan systems the platyfish is restricted to coastal environments at elevations of 100 to 300 feet, the swordtail chiefly to higher elevations, 3000 to 4000 feet, and 15 to 20 miles farther inland. In the Rio Coatzacoalcos platyfish and swordtails, though still ecologically distinct for the most part occur side by side in the same region, either separated by only a few hundred feet or not at all, at elevations of

TABLE 33

Xiphophorus COLLECTING STATIONS WITH APPROXIMATE ALTITUDES

	Estimated Altitude[1]	Species Present[2]: *Xiphophorus* *couchianus*	*maculatus*	*variatus*	*milleri*	*montezumae*	*pygmaeus*	*clemenciae*	*helleri*
Rio Grande (Mexico)									
Santa Catarina	2,000	X							
4 miles west of Monterrey	1,800*	X							
Monterrey	1,700	X							
Rio Soto la Marina									
San Carlos	1,500**			X					
Rio Santa Lucia	1,500**			X					
Rio Purificacion	1,500**			X					
Rio Corona	1,500**			X					
Rio San Marcos	1,100			X					
Rio Tamesi									
Llera	500*			X					
Gomez Farias	500*			(X)		X			
Rio Panuco									
Rio Verde at Rascon	400*					X			
Rio Valles at Valles	400			X		X			
Rio Moctezuma at Tamazunchale	1,200*					X			
Rio Axtla	1,200*			X		X	X		
Rio Calaboza	1,000**			X		X			
Coastal	100**			X					
Estero Cucharas	200**			X					

TABLE 33 (continued)

	Estimated	Species Present[2]: *Xiphophorus*							
	Altitude[1]	*couchianus*	*maculatus*	*variatus*	*milleri*	*montezumae*	*pygmaeus*	*clemenciae*	*helleri*
Estero Tancochin	100**			X					
Rio Tuxpan				X					
Rio Cazones									
Arroyo Mariandrea	1,000**			X					
Tihuatlan	400**			X					
Rio Tecolutla									
Necaxa	4,000**			X					
Arroyo Sin Nombre	200*			X					
Rio Nautla									
Tlapacoyan	1,000**			X					X
Maria de la Torre	600**			X					
Rio Chachalacas									
Encero	3,000**								X
Plan del Rio									X
Rio Antigua									
Jalapa	5,000								X
Rio Bejucos									X
Rio Jamapa									
L'Encero	4,000**								X
Cordova	3,000								X
El Tijar	100**		X						
Boca del Rio	50**								X

TABLE 33 (continued)

	Estimated Altitude[1]	Species Present[2]: *Xiphophorus* *couchianus*	*maculatus*	*variatus*	*milleri*	*montezumae*	*pygmaeus*	*clemenciae*	*helleri*
Rio Papaloapan									
Orizaba	4,200								X
Otopa									X
Motzorongo	800								X
El Hule	200								X
Papaloapan	200		X						X
Obispo	300*		X						X
Cosamaloapan	100*		X						
Achotal	150*								X
Laguna Catemaco	1,000				X				X
Rio Coatzacoalcos									
Rio Sarabia	275							X	X
Almagres	150*		X						X
Jesus Carranza	300		X						X
Minatitlan	75		X						X
Rio Uxpanapa	100*		X						(X)
Coatzacoalcos	50		X						
Rio Tonala									
Huapacal	100**		X						
Tres Bocas	75**		X						
La Renal	50**		X						
La Venta	50**		X						X

TABLE 33 (continued)

	Estimated Altitude[1]	Species Present[2]: *Xiphophorus*							
		couchianus	*maculatus*	*variatus*	*milleri*	*montezumae*	*pygmaeus*	*clemenciae*	*helleri*
Rio Grijalva									
Teapa	800		(X)						X
Santa Anna ditch	600*								(X)
Arroyo Huasteca	500*								(X)
Villa Hermosa	300*		X						
Rio Usumactina									
Rio Santo Domingo	1,500								X
Rio de la Pasion	800**		X						
Arroyo Xotal	500**								X
Rio San Pedro de Martir	400**		X						
Laguna de Zotz	800**		X						X
Laguna de Eckixil	800**		X						X
Laguna de Peten	800**		X						
Rio Hondo, Uaxactun	800**		X						X
									X
Brook No. 1	25*		X						
Brook No. 2	25*		X						
Belize River									
Benque Viejo	550*								X
Rio Privacion	1,200**								X
Rio Frio	1,200**								X
Gabourel Creek	25*		X						

TABLE 33. (continued)

	Estimated	Species Present[2]: *Xiphophorus*							
	Altitude[1]	*couchianus*	*maculatus*	*variatus*	*milleri*	*montezumae*	*pygmaeus*	*clemenciae*	*helleri*
Rio Grande (British Honduras)	50*								X
Rio Motagua at Copan	1,995								X
Rio Chamelecon, Coastal	100**								X
Rio Lancetilla	100**								X
Rio San Juan	100**								X
Rio Bonito	100**								X
Estero Salado	100**								X

[1] Altitudes are given in feet. The approximate relative accuracies of the estimates are indicated by asterisks:
no asterisk: Altitude of locality given explicitly in one of the sources of data;
*one asterisk: Estimate based on altitudes given for nearby points and textual descriptions;
**two asterisks: Rough estimate based on general location in relation to points for which altitudes are given and on textual descriptions.

[2] Parentheses indicate very few fish of the species indicated were collected at the station, but that a larger sample was collected at a nearby point. Such small collections are not entered separately.

Sources of data are as follows:
Mexico: Goldman, 1951.
British Honduras: Survey Dept., wall map, published 1944.
Guatemala and Honduras: Lewis and Campbell, 1951.
Exceptions: Altitudes are given in the field descriptions of two stations, Rio Santo Domingo and Copan.

75 to 300 feet above sea level. Sympatricity of these two species is significantly higher in the Rio Coatzacoalcos (62 percent of the localities collected) than in the Rio Papaloapan (40 percent) or Rio Jamapa (1 percent). In the great majority of cases, sympatricity is accidental and impermanent, resulting from occasional waif swordtails being washed downstream into platyfish habitats and from both species being trapped together in drying pools in stream beds.[4]

In at least two or three places where *helleri* and *maculatus* occur together in the Rio Coatzacoalcos, the situation is one of permanent, established coexistence. Superficially there appears to be no ecological separation of the two species. These situations have not been studied critically, and microstratifications of currents around stones and crevices may permit two ecologically different species to exist in close association in what appears to be a relatively homogeneous environment.

However, *helleri* also occurs sympatrically with the very similar and closely related *clemenciae* in the Rio Coatzacoalcos, and here again there is at least no known major ecological separation. Indeed, because of their great similarity not only in coloration but in general body form, anything more than a microcosmic separation is difficult to imagine. Behavioral differences together with an incipient genetic isolation may reenforce minor discontinuities of habitat. In view of the relative ease with which interspecific hybrids are obtained among the members of this genus when they are subjected to heterotypic mating situations in the laboratory, it seems unlikely that genetic isolation is alone the determining factor in maintaining the integrity of *helleri* and *clemenciae*, or any other species of *Xiphophorus* in nature.

ADAPTIVE MODIFICATIONS TO THE ENVIRONMENT AND PATTERNS OF DISTRIBUTION

The geographical races and subspecies of *helleri* provide the best examples of correlation between types of biotic community and morphological specialization. The *helleri* that live at the highest altitudes in

---

[4] In order to define more precisely the different responses of *helleri* and *maculatus* to currents and other physical factors it would be helpful to be able to make reasonable estimates of the surface gradient in feet per mile as an index to average current conditions at various elevations. In Ohio Trautman (1942) found that distribution of bass and other fish was correlated with flow gradient. Smallmouth bass were found largely in stream sections having a gradient of 7 to 20 feet per mile; they were almost never collected where the gradient was below 3 or above 25 feet per mile. It is hoped to apply such quantitative methods to the ecology of *Xiphophorus* in the future.

rivers with the steepest gradients—Rio Nautla, Rio Chachalacas, Rio Antigua and Rio Jamapa—and thus are subject to the greatest velocity of current, exhibit the slenderest bodies, the shortest caudal fins, the fewest dorsal-fin rays, the most scales in a lateral series, and a unique combination of gonopodial traits. Reduction in body depth, and size of the dorsal and caudal fins in these swordtails may be interpreted as adaptive modifications that cut down resistance to water flow by smoothing the streamlines. Increase in scale number, perhaps by decreasing scale size, may also play a role in cutting down this resistance. The gonopodium of these swordtails shows a pronounced reduction in the number and size of the distal serrae and an enlargement of the functionally related dorsal claw. Clark, Aronson, and Gordon (1949) and Rosen and Gordon (1953) showed that both these specialized terminal gonopodial elements function as holdfasts that secure the male to the female during copulation. But the claw is larger, more pointed, and projects farther out than the serrae which originate on the fin ray beneath; it thus may serve as a more effective holdfast, perhaps functionally replacing the distal serrae in those fishes inhabiting turbulent waters.

As further evidence of the relationship of these modifications to physical conditions of the environment, the Rio Santo Domingo *helleri* is significantly more slender of body and averages 2 or 3 fewer dorsal fin rays than other swordtails living in the Rio Grijalva-Usumacinta system at approximately 1000 feet lower elevation. In addition, its gonopodium shows the same relationship of distal serrae to dorsal claw as in swordtails from the steeply descending northern rivers discussed above. Yet its pigmentary traits and geographic position show it clearly a derivative of the southern complex.

In *montezumae* and *milleri*, contrary to expectation for species of lotic communities, the gonopodial claw is severely reduced, sometimes obsolescent, and the distal serrae are as highly developed as in typically lowland species. The reproductive ecology of these species may not call for additional holdfasts, or perhaps their distal serrae have evolved in relation to other gonopodial traits that make them as effective as the alternative *helleri* mechanism. Nevertheless, *pygmaeus* and *clemenciae*, species entirely of lotic communities, have both slender bodies and well developed claw mechanisms in their gonopodia.

In general the characteristically stream-living species (*helleri, clemenciae, montezumae, pygmaeus, milleri*) are slender of body and have gonopodial claws. Platyfishes (*maculatus, variatus, couchianus*) are deep bodied and typically lack the claw. It is possible that the swordtail species and *milleri* may have had a common point of origin, perhaps in the Rio Panuco basin, the prototype evolving in a stream biota, while *maculatus* and *variatus* were derived from a lowland representative. Reasons for thinking that *couchianus* may have evolved separately from the other platyfishes are discussed below.

The region of Atlantic coastal Mexico from the Rio Nautla (northern Veracruz) north to the Rio Soto la Marina (southern Tamaulipas) includes 8 of the currently recognized 15 species and subspecies of *Xiphophorus*. Within the Rio Panuco system alone, in the center of this region, 5 of these forms occur, two endemically. South of the Rio Nautla *maculatus* and *helleri* have extended their ranges into northern Central America, while to the north of Rio Soto la Marina, only one species, *couchianus*, is to be found, in the Rio Grande system.

Because of the abundance of forms in the region of the Panuco system and the endemism exhibited by *montezumae* and *pygmaeus*, it is believed that the spatial origins of *Xiphophorus* must have centered in the great and complex river valleys of northern Veracruz and eastern San Luis Potosi. It is difficult to conceive of the numerous generalized forms in the north arising from a southern Mexican or northern Central American prototype of the most highly specialized form, *helleri*. If one regards the generalized *couchianus* in the Rio Grande system as a relict of a former center of southward dispersal, we are confronted with the complete absence of any species of *Xiphophorus* in the Rio San Fernando, the next major river basin to the south—a river close to the Rio Grande, yet about 100 miles from the next river to the south in which *variatus* is abundant. This absence is all the more compelling since poeciliid species such as *Mollienesia sphenops* that commonly live sympatrically with *Xiphophorus* elsewhere are plentiful in the Rio San Fernando.

The present distribution of species of *Xiphophorus* (figs. 4, 10, 19) may be accounted for primarily by their ecological specialization, and secondarily by past changes in hydrography or topographic coincidence. *X. helleri*, as a species that can adapt to a variety of lotic and lentic environments, is well suited to have penetrated as far south as Honduras where at present it occupies both pond and stream habitats. *X. maculatus*, on the other hand, while well suited to traversing sluggish coastal streams and meandering inland rivers, has extended its southern range only as far as northern British Honduras. Between that point and the coastal lowlands of Honduras the swift waters that descend from the Maya Mountains may well have checked its southward dispersal.

X. variatus, though perhaps restricted in the south by competition with *helleri* and *maculatus,* occupies a variety of habitats throughout the Rio Panuco basin and as far north as the Rio Soto la Marina.

The localization of *pygmaeus* in the Rio Panuco proper (excluding the Rio Tamesi) and of *milleri* in the Laguna Catemaco region may have been a result of their great specialization for stream habitats, while the less extreme localization of *montezumae* may have resulted from a combination of a preference for headwater environments and competition in the lowlands with the dominant and versatile *varitaus*. *X. montezumae* does, however, penetrate as far into the lowlands as the Rio Calaboza, but in this river *variatus* probably is the more abundant.

The disjunct geographical position of *couchianus* may represent an early and only partly successful attempt at northward expansion via coastal freshwater passageways.

The zoogeographic significance of the single known population of *clemenciae* is discussed below.

ROUTES OF DISPERSAL

Despite the importance of their ecological specializations in molding the distributional patterns of the species of *Xiphophorus,* certain topographic and hydrographic features of their environment have been instrumental in their dispersal. Details of the topographic and hydrographic changes in Mexico's Atlantic coastal plain through geologic time are virtually unknown. Such information is needed for a more well-rounded picture of the genus, as the concordance of geologic data with those derived from zoogeographic analysis is, in the absence of a fossil record, a critical test of the validity of any hypotheses regarding the group's evolutionary history.[5]

Species of *Xiphophorus* apparently have little or no tolerance for salt or brackish water environments. This is indicated by their conspicuous absence from brackish water deltas and by the notable distinctiveness of the many geographical races inhabiting adjacent rivers. Some of the races and subspecies of *Xiphophorus* live in rivers whose mouths are separated by less than 20 miles of coastline (e.g., New River–Rio Hondo–Belize River). The results of a few casual tests in the laboratory in which several groups of platyfish and swordtails

---

[5] I gratefully acknowledge that geological information in the following general discussion is based largely on correspondence received from W. Armstrong Price, Research Geological Oceanographer of the Texas Agricultural and Mechanical College, during 1954.

were subjected to a series of decreasing concentrations of seawater (pure seawater to slightly brackish) reaffirm the above conclusion; no group survived longer than one hour even in the lowest concentrations of seawater. This is in marked contrast to the ability of other poeciliid groups, such as the poeciliins and gambusiins, to occupy successfully a wide variety of brackish and marine environments.

This physiological restriction of *Xiphophorus*, except for the unlikely event that it may be a relatively recent development, must have limited its means of dispersal from one drainage area to another to three: 1) headwater transfer, the capture of the headwaters and associated fauna of one system by another through natural or man-made changes in landscape; 2) migration of a fauna via lowland or coastal confluences of coalescing freshwater deltas and bays; and 3) migration and/or transfer via periodically formed flood plains, and other effects of flooding or river and lake bed overflow. Though all three means have undoubtedly played a role in the spread northward and southward of *Xiphoporus*, present evidence indicates that migrations of these fishes via coastal estuarine confluences have been of primary importance. For example, we now have a huge area of confluences on the deltas of the Rio Grijalva, Rio Seco, Rio Teapa, Rio San Pedro, and Rio Usumacinta. In addition, a recent connection with the Rio Tonala is a strong probability. All but the Rio Seco and Rio San Pedro are known to contain a distinctive form (red-striped) of the green swordtail, *X. helleri*. The platyfish, *X. maculatus*, in this area differ significantly from all more northern populations in the frequencies of certain autosomal genes.

The Rio Tonala and Rio Coatzacoalcos (Rio Uspanapa) are so close that it is hard to see how a confluence at some time could have been avoided. A region of fairly high elevation separates them near the coast, but inland a connection may have occurred where the Uspanapa bends eastward, particularly if water levels were higher and this low divide assumed an estuarine character. There might also have been a headwater connection via lakes of the volcanic area. For example, a lake draining to the southeast might become blocked by lava and fill to overflow in some other direction, possibly to the west, thus sending the fish into a different system. But it is particularly the difference in elevation of the possible confluences between the Coatzacoalcos and Tonala, and between the Tonala and rivers to the east that is of greatest interest with reference to the fish distributions. This point at the Isthmus of Tehuantepec appears to be a region of marked transition between races and subspecies of *macu-*

latus and *helleri*. Confluences at higher elevations farther inland (Coatzacoalcos-Tonala) might have been most effective during periods of high seawater level, but their importance would dwindle with the receding waters only to give way to lower connections that were gradually being exposed (Tonala eastward to Usumacinta). Temporal changes of this sort would probably be sufficient to bring about isolation and divergence of the fish populations on either side of the divide.

In addition to relatively enduring confluences (swamps and other interlocking waterways) that develop directly on the coastal plain when mountain torrents send immense volumes of water to the lowlands where existing channels cannot contain them, offshore lagoons may play a significant role in fish distribution on a more intermittent basis. Goldman (1951) stated that along both coasts of the Mexican mainland, ". . . narrow, shallow lagoons, often of considerable length and varying character, occupy low-lying belts behind fringing sand dunes. These are usually located near or across the mouths of rivers. Through wave action along the shores, lines of sand dunes have gradually been thrown up as a barrier behind which the fresh-water drainage tends to spread parallel to the coast line."

There is also a probable stream capture at Acayucan (Coatzacoalcos) or at least in the stream that flows southeast past this village just to the west. Its headwaters might have once flowed into the San Juan branch of the Rio Papaloapan, via a creek entering it at Ixtampan. Possible connection between the Rio Papaloapan and Rio Jamapa would be most simply accomplished, as before, along the coastal lagoons, and this is precisely what is indicated by the similarity of the Boca del Rio swordtails (Jamapa) with those of the Papaloapan.

To the south in northern Central America, the best evidence at present favors the view that fish populations moved relatively freely across what is now the Peten lake district of northern Guatemala. The pattern of disjunct lakes and relict streams on this plateau suggests former headwater connections between the Rio Usumacinta system and the rivers of British Honduras. Platyfish populations in the three northern rivers of British Honduras may have reached there either by independent headwater entry, by mixing of waters via lowland confluences, or by both. The Hondo and New Rivers seem to be separated by a linear area of folded or faulted rocks. These rocks seem, from the drainage pattern, to have some appreciable elevation above present valley floors and flood plains. Hence land confluences seem unlikely during the immediate past, except for some capture among the minor headwaters. Confluence when the water was as little as 15 to 20 feet lower, possibly 6,000 to 10,000 years ago, seems almost a certainty. Almost certainly these rivers were similarly confluent with the Belize River. Below water all these rivers are tributary to a long narrow depression floored at 15 feet. Furthermore, the Belize is deltaic and might have been connected to the other rivers through a marsh or swamp (World Aeronautical Chart 645) at almost any precartographic date (200 to 5,000 years ago). Confluences between the Hondo and New Rivers, and possibly the Belize, are possible even today during the periodic floods that cause these rivers to overflow their banks and establish broad though shallow sheets of connecting waters.

RELATIONSHIPS WITHIN *XIPHOPHORUS*

ASSESSMENT OF CHARACTERS

GONOPODIUM.

A clawlike segment at the terminal region of ray 5a is among the important gonopodial characters that distinguish the species of *Xiphophorus*. The claw is an enlarged and highly modified terminal element that extends distally from base to tip and then curves upward or posteriorly to form a bony projection pointed away from the main axis of the gonopodium. The claw varies greatly in size between species, being largest in *helleri* and smallest in *montezumae*, *milleri* and the platyfishes.

In *helleri* the claw's most prominent characteristic is the curvature of the tip to form a large, pointed spine which projects through the epidermis. In this species its general appearance is that of a sickle; the distance from the base of the segment to the point of curvature is slightly less than that from the point of curvature to the projecting tip (fig. 20). In *pygmaeus* and *clemenciae* the claw has a more linear pattern; the base projects forward and the tip extends upward an equal distance at right angles to the base (figs. 11, 18). In *montezumae* and *milleri* the claw is much longer than high and rarely if ever greater in width than the segments on ray 5a preceding it; it is quite thin and turns up slightly at its tip to form a tiny protuberance that occasionally is lacking.

The progressive variation in size and shape of the claw from *helleri* to *milleri* corresponds to a change in the size and shape of the distal serrae in the fourth posterior ray (4p). In the generalized *Xiphophorus* gonopodium the distal serrae constitute a group of from

2 to 12 paired elements at the tip of ray 4p. They are laterally compressed and their bases are broad anteroposteriorly, tapering upward to a point. For purposes of comparison, the broad, anterior portion of a serra is called the *base,* the slender, tapering posterior portion the *shaft.*

In *helleri* and *maculatus* the heights of the shafts and the widths of the bases of the distal serrae are inherited independently (Gordon and Rosen, 1951). The critical dimension for comparing any two species is the average height of the serrae (shaft) referred to the degree of upward thrust of the tip of the claw.

In *helleri* the distal serrae number about 3 to 4 and are short and squat in lateral view. They vary in outline, some have broad bases and slightly developed shafts, others are almost triangular.

In *pygmaeus* the distal serrae usually number 4 to 5 and are typically slender with moderately developed shafts. The amount of variation in shaft height is equivalent to that found in *helleri;* the tallest serrae of *helleri* resemble the shortest ones of *pygmaeus.*

X. montezumae usually has 5 to 7 distal serrae. Their slender shafts are well developed, and their range of variability in height overlaps the range of those in *pygmaeus.*

Generally the heights of the shafts of the distal serrae are smallest in *helleri,* greatest in *montezumae,* and intermediate in *pygmaeus.* The number of distal serrae is least in *helleri,* greatest in *montezumae,* and intermediate in *pygmaeus.*

The claw on the 5th anterior ray shows just the reverse order of size from largest to smallest: *helleri* has the largest claw, *pygmaeus* one of intermediate size, *montezumae* the smallest. Apparently a strong inverse relationship exists between size of claw and height of distal serrae; *helleri,* the species with the largest and most strongly curved claw, has the smallest and most weakly expressed distal serrae. The interrelationships of claw size, distal serrae height, and distal serrae number are as follows:

	Size of claw	Height of distal serrae	Average number of distal serrae
helleri	large	low	3.06
pygameus	intermediate	intermediate	4.50
montezumae	small	high	4.70

Similar relationships occur within a single species. For example, the L'Encero swordtails (*helleri*) have gonopodia with large claws and three small serrae. Those of Almagrez have relatively smaller claws and their four distal serrae are proportionally larger, and usually have longer and more slender shafts.

The *helleri* gonopodium is further distinctive in its large, angular ramus at the terminus of ray 4a, and a consistently small and crescent-shaped hook on ray 3 (fig. 20). This condition is closely approached in the gonopodium of *clemenciae*. In the other species the rami are only slightly curved and weakly expressed, and the hooks are long and scythe-shaped.

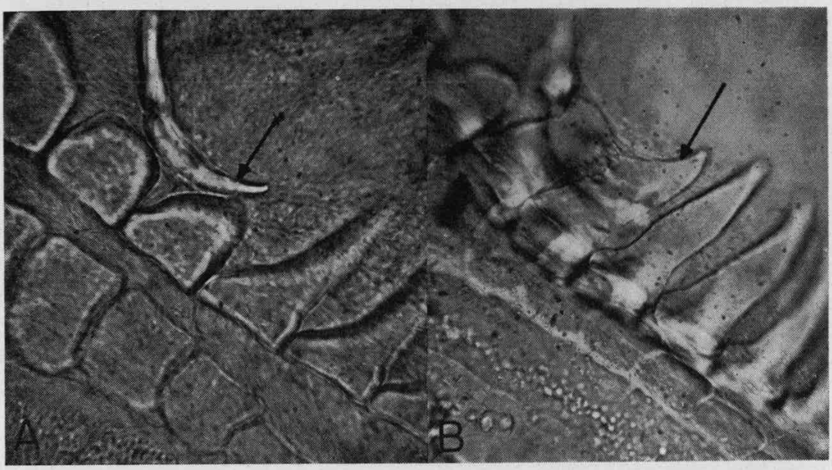


Figure 26. Two types of gonopodial claws identified in wild caught *X. maculatus*. A. The typical platyfish claw, formed entirely by modification of the terminal segment of ray 5a. B. Claw formed by the fusion of the terminal segment of ray 5a with the shaft of a serra on ray 4p to produce a dorsal holdfast of the swordtail type (see text).

In the platyfishes (*maculatus*, *variatus*, and *couchianus*) the terminal segment on ray 5a is generally a small, unmodified element, rounded at its tip. It is located just behind and slightly dorsal to the distal serrae, the area occupied by the claw in the swordtail gonopodium. As a rule this terminal element in the platyfish gonopodium shows some tendency to enlarge and occasionally to curve, so that it is morphologically different from any of the preceding elements on ray 5a. While this terminal segment tends to differentiate in the platyfish, it rarely becomes specialized except in size. However, in 9 out of 20 gonopodia from the platyfish (*maculatus*) of the Rio Jamapa system, the terminal element on ray 5a was unmistakably differentiated into a claw (fig. 26a). When these claws do appear in platyfish they are usually comparable in form to the claws of *montezumae*.

The essential contrast in the claw between *maculatus* and *montezumae* is the difference in its frequency. It is present virtually always in *montezumae*, but seldom in *maculatus*.

Two types of claws have been identified in *maculatus*. Type I, mentioned above, is small, crescent-shaped, and only slightly pointed as in *montezumae* and *milleri*. Type II was found in the gonopodia of platyfishes from the Rio Coatzacoalcos drainage system near Jesus Carranza, Veracruz (fig. 26b). Three out of seven mature males had gonopodia with large, well-formed claws of the swordtail type. In each the claw appears to have been formed from embryonic elements of both rays 4p and 5a. In each case the proximal region of the claw is articulated with ray 5a, and a small portion of the basal region seems to be a continuation of this ray. The sharp and angular end piece, which points posteriorly away from the axis of the fin, is intimately associated with the 6th member of the distal serrae of ray 4p and, in two out of three cases, with the 1st member of the subterminal segments. The terminal element of ray 5a apparently has pirated the pointed tip of the shaft of the 6th serra on ray 4p. This interpretation accounts for the incomplete separation of the claw from the distal members of the 4th ray, and is strengthened by the correspondence in height between the distal serrae of ray 4p and the end piece of the claw segment.

There seems little doubt that these two types of claws are distinct. The typical platyfish claw, type I, has its origin at the terminal region of ray 5a. Type II (the swordtail type) probably has a more complex origin with two developmental loci, one at ray 5a and the other at ray 4p, combining to produce the differentiated segment. Thus the underlying serrae and subterminal segments of ray 4 may in some way be related to claw development.

In general, few serrae are associated with many subterminal segments and vice versa, and both are related to claw size. These relationships are illustrated as follows:

In *Xiphophorus helleri* (claw large) from the Rio Coatzacoalcos, near Jesus Carranza

Number of distal serrae	Number of subterminal segments	Total number of segments
4	5	9
3	6	9
4	5	9
4	5	9

In *Xiphophorus pygmaeus* (claw intermediate) from a laboratory reared stock.

Number of distal serrae	Number of subterminal segments	Total number of segments
6	4	10
4	6	10
5	5	10
5	5	10
5	5	10
5	5	10

In *Xiphophorus maculatus* (claw small, when rarely present) from the Rio Coatzacoalcos, near Jesus Carranza.

Number of distal serrae	Number of subterminal segments	Total number of segments
6	3	9
6	3	9
5	4	9
6	3	9
6	3	9
7	2	9

These data suggest that in normal development of the gonopodium definite restraints are placed on the number and size of the distal serrae laid down within circumscribed limits—in this case, the tip of ray 4p. If the claw of ray 5a is, in part, embryologically homologous with the shaft of a distal serra, as indicated above, then perhaps during gonopodial morphogenesis the developing tip of ray 5a provides the restraining influence on serrae growth. In other words, the greater the influence of the claw "field," the greater the suppression of serrae development in both size and number. Turner (1941) described such embryonic "field" effects in the gonopodium of the poeciliid *Gambusia affinis*. Accordingly, gonopodia having numerous well-developed serrae and small or no claws (*montezumae, milleri, maculatus, variatus, couchianus*) may be interpreted as representing a primitive condition, while gonopodia having fewer and smaller serrae and larger claws (*helleri, pygmaeus, clemenciae*), a more specialized one. In this regard it may be significant that *montezumae,* obviously allied to *clemenciae, pygmaeus* and *helleri* in many important features, nonetheless typically has a small type I claw at the tip of ray 5a. Perhaps the type I (platyfish) and type II (swordtail) claws, though morphologically distinct, are inseparably related phylogenetically, the existence of type I being requisite for the evolution of type II.

PIGMENTATION

The principal pigmentary characteristic of *Xiphophorus* is the occurrence of a small type of melanophore in the integument. Gordon (1927) called these cells micromelanophores and distinguished them from the larger cells known as macromelanophores, which are structurally and genetically different. Micromelanophores are found in the following regions.

Integument: Dermis, epidermis.
Perineural tissues: Brain, spinal cord.
Perivascular tissues: Principal blood vessels, intermuscular blood vessels.
Eye.
Peritoneal linings: Parietal peritoneum, pericardial peritoneum.

The dermal micromelanophores of *Xiphophorus* measured by the cytoplasmic melanin average individually about 1.5 mm when melanin is dispersed and 0.3 mm when it is completely constricted. These cells have a definite arrangement on the body. The middorsal region from the tip of the snout to the end of the caudal peduncle is heavily pigmented. On the sides of the animals these melanophores show a graded distribution, becoming less abundant ventrally. The midventral line anteriorly is practically devoid of pigment and shows silvery gray where the whitish peritoneum shines through the thin muscular wall of the belly. Along the anterior lateral region posterior to the head, the micomelanophores are arranged in a netlike pattern. This reticulum resembles the arrangement of scales, but does not follow the scale margins. The melanophores defining the reticulations actually line the scale pockets. It is the reticular network that gives rise to or influences all the basic body patterns, stripes, symmetrical blotching, or bars.

Another series of melanophores, the scale melanophores, does not participate directly in producing a special pigment pattern. The smallest and least pigmented of the chromatophores in these fishes, these cells apparently are distinct from the pattern micromelanophores. Gordon (1927) found that when the scales were removed from their dermal pockets, these melanophores adhered to the scale substance and the well developed, fully pigmented micromelanophores remained intact with the dermis. The scale melanophores are present as a fine dusting over the entire body surface. Their presence accentuates micromelanophore patterns and in combinations with other types of chromatophores gives a characteristic body "tone" that may be referred to as the underlying ground color.

When scale and micromelanophores are combined with xanthophores, erythrophores and guanophores (iridiocytes), the general ground color is olivaceous. (Goodrich, Hill, and Arrick (1941) found that *maculatus* and *helleri* possess the same three pigments for yellow and red or orange coloring—lutein, zeaxanthin, and erythropterin.) Microscopic scrutiny of fresh integumentary tissue resolves this hue into the individual chromatophore components. When, for any reason, the scale and micromelanophores are diminished or the individual melanophores are contracted, the ground color appears golden. Both golden and olivaceous ground coloring have been found in a single population of *Xiphophorus pygmaeus* from the Rio Axtla. In this instance, golden coloring is thought to be due to a genetically controlled reduction in the number of melanophores.

There is some question whether the faint even wash of fin melanophores in otherwise immaculate fins is due to the presence of scale type or micromelanophores. In such cases the fin melanophores, which are small and weakly pigmented, appear to be continuous in distribution with the scale melanophores at the fin base. Where bold, vivid patterns mark the fins, the cells composing them are discrete, larger, more heavily pigmented, and are of the micromelanophore type.

In addition to the genetic factors that are known to determine intra- and interspecific pattern differences, some of which may be large, special environmental conditions may initiate profound changes in both underlying ground color and superimposed patterns.

Sumner and Wells (1933), Sumner and Doudoroff (1938) and Sumner (1943, 1945) showed that *Gambusia affinis* may undergo color changes of at least two kinds: a) rapid and quickly reversible changes of appearance in response to change in the background, nervous stimuli or intense physiological stimuli; and b) more enduring changes resulting from prolonged exposure to a nonfluctuating background shade. Confirmatory findings were reported by Breder (1947b). These authors demonstrated that the rapid and quickly reversible changes are due to the shifting of pigment particles within the integumentary chromatophores, that either spread out these particles into full view or partly withdraw them from sight. The more enduring changes, resulting from longer subjection to the visual stimuli, are due to the actual production of new pigment or pigment cells, or to the loss of pigment previously present. Such changes affect all patterns regardless of position, though certain pattern components may respond more readily or more fully than others. Pierce (1941) has also shown that in *Mollienesia latipinna* changes in temperature as well as illumination produce generalized changes in pigmentation by temporarily altering the distribution of the melanin granules within the cells.

As the species of *Xiphophorus* live in a wide variety of environmental situations, some constantly shifting, possibly many of the pattern differences noted in preserved specimens reflect differences in habitat. Observations of living *Xiphophorus* under laboratory condititons show conclusively that the expression of all basic patterns is subject to great fluctuations with light, temperature, and state of activity. Some patterns may fade so that their presence can only be detected with the aid of a microscope.

With respect to the basic melanophore patterns on the body, the differences between species are more a matter of degree than of kind. In view of the diverse factors that bring about involuntary color change in nature, circumspection is required in using pigment patterns for taxonomic assessments. Nevertheless, contrast among the species of *Xiphophorus* is sometimes sizeable, in striping for example. No amount of color change in an individual or local population could possibly bridge the gap between two species with fundamentally different striped patterns. Even subspecies of *X. helleri* may be imperfectly separated using this basic pattern.

For the most part, the total pigmentary differences among species of *Xiphophorus,* including tail patterns, fin markings, and the nonmelanic coloring, serve an extremely useful role in taxonomic interpretation and provide as many unifying bonds between species as any other group of characters so far examined.

Metamerism and Body Form in Relation to Habitat

Dorsal Fin Ray, Lateral Scale, and Vertebral Number. The mathematical relationship between geography and values for dorsal fin ray and scale number in *X. helleri, X. variatus* and *X. maculatus* is discussed in Appendix 1. Values for altitude (table 33) are associated statistically with those for these two metameric traits. In all cases for which calculations were made, it was found that the effect of going north, as reflected in a change in fin ray or scale counts, is equivalent to the effect of going to a higher altitude. The resemblance of northern populations to those at higher altitudes suggests a relationship with temperature. It is assumed provisionally that temperature differences may actually have produced the effects noted, such that:

The number of dorsal fin rays decreases with temperature in *X. variatus* and in *X. maculatus,* increases with temperature in *X. helleri,* and

The number of scales in a lateral series increases with temperature in *X. maculatus,* decreases with temperature in *X. helleri.*

Counts made on laboratory reared descendants of the river populations of *X. helleri* and *X. variatus* support the view that the temperature-correlated differences are actually of a genetic nature. The offspring derived from natural populations with low, medium, and high fin ray counts each maintain their counts under laboratory conditions (table 26).

A number of important exceptions suggest that temperature is not alone responsible or even the most important factor for producing the alleged environmentally influenced variations. Most significant is the fact that the form of *variatus* (*v. evelynae*) having the highest fin ray count (table 9) lives at about 4000 feet, considerably higher than all other members of this species (table 33). Equally conflicting are the variations in vertebral number among the eight species (table 3). Whereas *X. helleri* has a higher vertebral count in the north than in the south, the mountain derivative of *X. helleri guentheri, X. helleri alvarezi* from Chiapas, resembles the northern form in many ways but has the low count characteristic of members of the southern complex. Similarly, *X. variatus evelynae* (4000 feet), and *X. variatus xiphidium* (1500 feet) have lower vertebral counts than at least four populations of *X. variatus variatus* (200-1200 feet). The two subspecies of *X. pygmaeus* that occur in similar habitats appear to have different vertebral counts.

This information suggests that metamerism, though certainly influenced by temperature, is also subject to other factors under natural conditions. Whereas environmentally influenced variation may become hereditary through the action of natural selection (Waddington, 1957: 162-187, "genetic assimilation of adaptive characters"), in some cases counter selection may neutralize or even reverse these effects—and at present we have no way of sorting out these two possibilities and of assessing the value of each. Because of this, arguments (see Hubbs and Gordon, 1943) using metameric traits to determine interspecific relationships in *Xiphophorus* appear to be unsound.

BODY PROPORTIONS AND ALLOMETRIC GROWTH. Gordon and Gordon (1954) found statistically significant differences among *X. macu-*

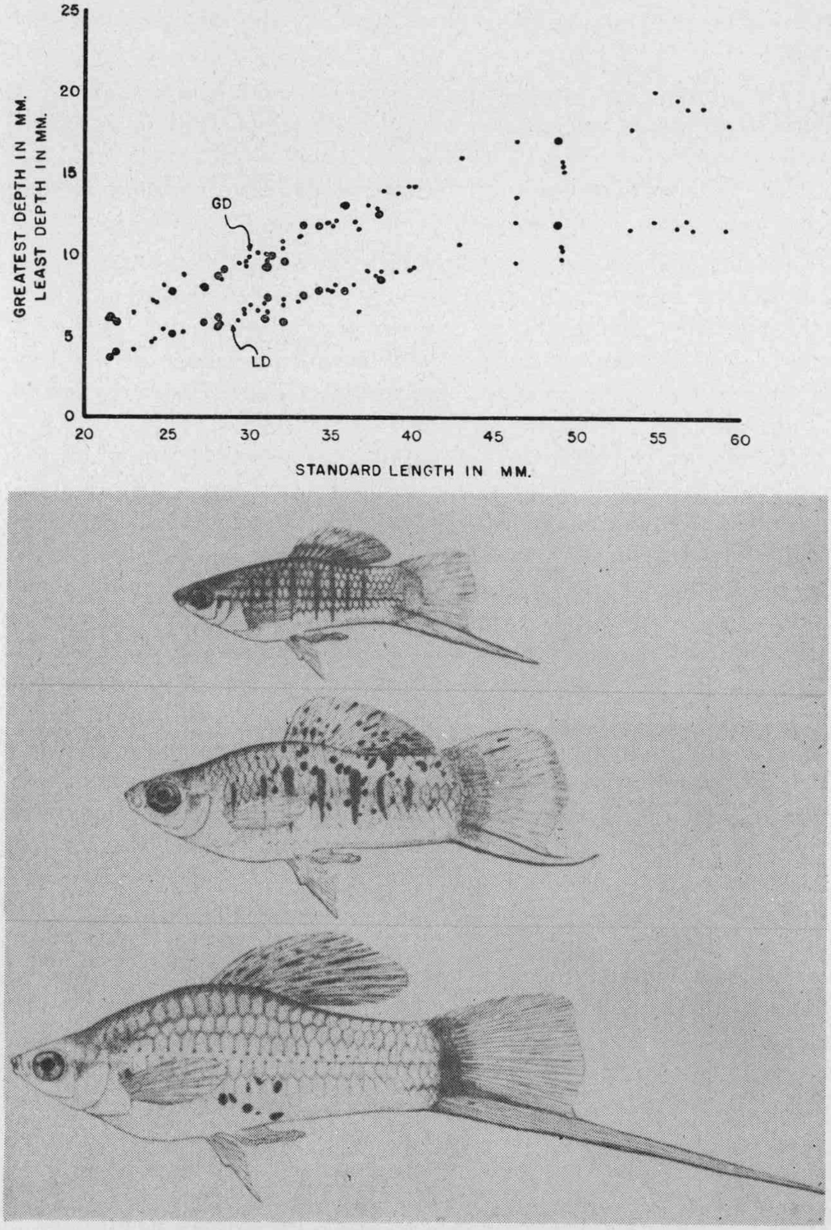


Figure 27. Graphic and pictorial representation of the unequal rates of growth of two vertical body dimensions in male *Xiphophorus montezumae* attaining different absolute sizes at sexual maturity. In the graph the large dots represent paired values of greatest depth (GD) and least depth (LD) of body in

latus taken on different days from the same collecting point with respect to a) the depth index (standard length/body depth), b) the length of the caudal peduncle index (standard length/length of caudal peduncle), and c) absolute length. Though the samples were all from the same population and the morphometric differences do not reflect genetic differences within the population, the effects of predation and other factors are sufficient to bring about appreciable changes in the indices for a population within a week.

The findings that fish taken on different days from the same locality not only are of different absolute sizes but have different relative proportions emphasizes a common difficulty in the use of body measurements. This involves the unequal rates of growth of different regions of the body as the animal increases in size. When greatest depth of body and least depth of caudal peduncle in four samples of *X. montezuma* are plotted together against standard length, two distinct growth lines are obtained (fig. 27). Standard length ranges approximately from 20 mm to 60 mm and, as all values fall along the same growth lines, each sample differs from the others only with respect to the distribution of its values along these lines. For example, *montezumae montezumae* from the Rio Tamesi is confined to the lower end of the distribution, *montezumae montezumae* from the Rio Salto de Agua occupies an intermediate position, the Rio Verde swordtail, *montezumae montezumae,* is found at the upper end, and the Rio Moctezuma swordtail, *montezumae cortezi,* extends from the lower end almost to the upper end of the distribution. The growth trends of the two vertical dimensions (body depth and caudal peduncle

---

individuals of *X. montezumae cortezi.* Small dots represent these two paired measurements in individuals of *X. montezumae montezumae.* Note that all points fall along two imaginary straight lines that diverge at a constant rate with increase in standard length of body. The upper fish is an adult male *X. montezumae montezumae* from the Rio Tamesi approximately 30 mm in standard length. In the center is an adult male of *X. montezumae cortezi* from the Rio Axtla, 37 mm in standard length. The lower fish is the holotype of this species described by Jordan and Snyder in 1899, and is approximately 55 mm in standard length. Despite striking differences in body form, all specimens are represented within the two trend lines in the graph.

X. montezumae cortezi (large dots); Rio Axtla—14 paired values from fish 22 mm to 48 mm in standard length.

X. montezumae montezumae (small dots): Rio Tamesi—13 paired values from fish 23 mm to 35 mm in standard length; Rio Salto de Agua—14 paired values from fish 26 mm to 46 mm in standard length; Rio Verde—11 paired values from fish 36 mm to 59 mm in standard length.

depth) are both essentially linear, but their rates of increase differ, as indicated by differences in slope of the two trend lines, body depth increasing at a greater rate than caudal peduncle depth. It is also clear from the slope of these lines that standard length increases at a greater rate than either vertical body dimension. The net result of these differences in terms of growth and body form is that as the animal matures and grows larger, it becomes progressively less deep bodied, while the caudal peduncle becomes more and more slender in relation to depth of the anterior trunk region. Thus, the small Rio Tamesi swordtails are rather stout with about equally deep trunk and peduncle; the large Rio Verde swordtails are comparatively slender, though the anterior trunk region is distinctly gibbous and the peduncle rather sharply tapering and shallow. These distinctive differences in body form apparently are due largely to the effects of allometric growth on animals confined to opposite ends of an unusually large size gradient.

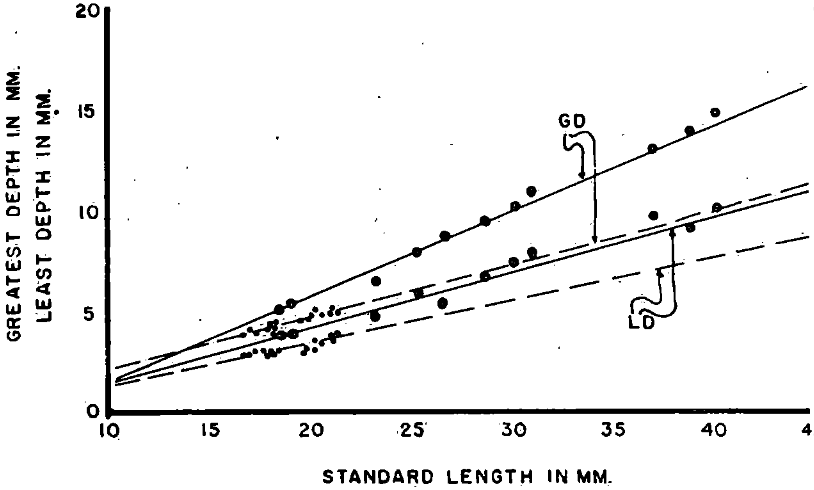


Figure 28. Graphic representation of the unequal rates of growth of two vertical body dimensions in male *Xiphophorus pygmaeus* attaining different absolute sizes at sexual maturity. The large dots represent paired values of greatest depth (GD) and least depth (LD) of body in individuals of *X. pygmaeus nigrensis*. Small dots represent those of the nominate form. The trend lines representing these distributions for *X. p. nigrensis* are solid, and dashed for the nominate form, *X. p. pygmaeus*.

A comparable situation occurs within a single population of *X. pygmaeus nigrensis* from the Rio Choy. Here two distinctive male body forms exist at opposite ends of a size gradient, where adult size ranges from 18.5 mm to 40 mm (fig. 28). Relative body depth and caudal peduncle depth allow the smallest males of *pygmaeus nigrensis* to be readily distinguished from the customarily small males of *pygmaeus pygmaeus* because the two subspecies have distinctly different growth lines. On the other hand, *montezumae cortezi* (Rio Moctezuma) is not separable from *montezumae montezumae* (Rio Tamesi, Rio Salto de Agua, Rio Verde) in this way.

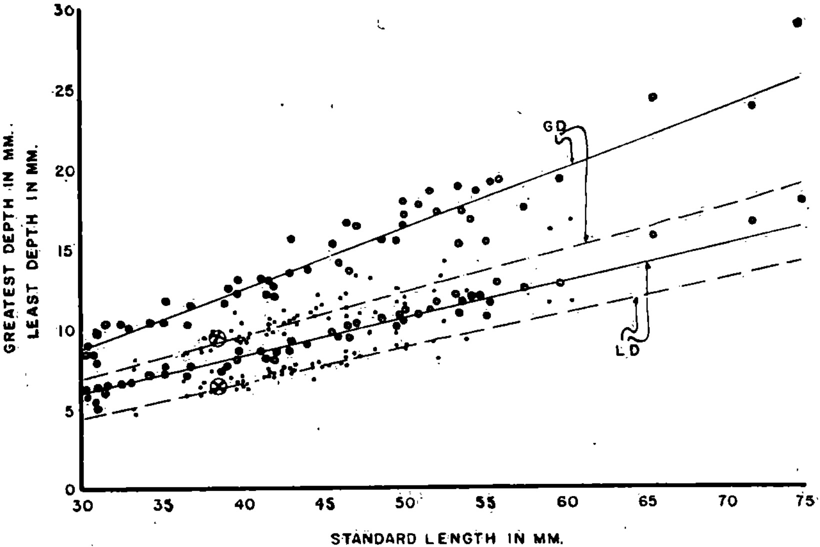


Figure 29. Graphic representation of the unequal rates of growth of two vertical body dimensions in male *Xiphophorus helleri* attaining different absolute sizes at sexual maturity. The large dots represent paired values of greatest depth (GD) and least depth (LD) of body in individuals of *X. helleri guentheri* from six rivers (Grijalva, Polochic, Lancetilla, Frio, de la Pasion, and Xotal). Small dots represent those of the nominate form from three systems (Nautla, Antigua, Jamapa). The two open circles with X's represent the paired values of a single specimen of *X. h. alvarezi*. The trend lines representing these distributions are solid for *X. h. guentheri*, and dashed for the nominate form, *X. h. helleri*. See text.

The four subspecies of *X. helleri* illustrate how both situations may occur within a single species (fig. 29). In *helleri* body depth tends to increase from north to south. When the paired values for two body proportions are plotted as above, two distinct sets of trend lines are obtained, one set representing samples of *helleri guentheri* from five geographical populations, and the other samples of *helleri helleri* from three. Comparable values obtained from samples of *helleri strigatus* may fall between those of *helleri helleri* and *helleri guentheri*, but many approximate those of *helleri guentheri* so closely that *strigatus* and *guentheri* are not clearly separable on the basis of these two body measurements and both may be conveniently described by a single set of trend lines. The single pair of values obtained for *alvarezi* closely approximates the lines of best fit for *helleri*. *X. h. helleri* and *alvarezi*, although both attaining a comparatively large size, are consistently more slender than are *strigatus* and *guentheri* of the same size. As this relationship persists in laboratory reared descendants of wild-caught swordtails, fixed proportional differences of this kind are manifestly due to inherent differences in the growth patterns.

Because many *helleri* and *alvarezi* are mountain forms and *guentheri* and *strigatus* lowland ones, differences in their allometries may reflect differences in their habitats. But environment does not explain the differences between *pygmaeus pygmaeus* and *pygmaeus nigrensis*, whose habitats are not notably unlike. Also difficult to correlate with habitat are the similar patterns of growth in four populations of *montezumae*, two of which (from the Rio Verde and Rio Salto de Agua) occur in torrential headland tributaries. How then are we to compare the different species with respect to body growth and form and make such comparisons meaningful in phylogenetic analysis? Although this question cannot yet be answered satisfactorily, it seems reasonable that interspecific comparisons of metamerism and body form in *Xiphophorus* are less important phylogenetically than are the ecological preferences that are correlated with them.

COMPARATIVE BEHAVIOR

Differences in the sensory apparatus of *X. maculatus* and *X. helleri* are indicated by the work of Crozier, Wolf, and Zerrahn-Wolf (1937 a, b, c) and Crozier and Wolf (1939a, b, c, d). They found that the curves representing the relationship between flicker frequency and mean critical illumination for response to a moving stripe pattern exhibit marked differences in both form and proportions in the two species. This is interpreted as having a genetic basis, reflected in the physiological activity of the retinal elements and central nervous system.

The observations of Clark, Aronson, and Gordon (1954) as well as my own knowledge of these species' behavior indicate that swordtails are more excitable than platyfish. In aquaria swordtails are easily disturbed, platyfish rarely are. The general behavior patterns of both groups are most probably closely tied to their ecological specializations. The excitable swordtail species occupy a headwater habitat where quick responses and the ability to swim strongly and perhaps jump are needed to overcome turbulent currents. The more placid platyfish frequent quiet shores and waters heavily grown with aquatic vegetation in lowland reaches.

Clark, Aronson, and Gordon (1954) discovered several qualitative and quantitative differences between the sexual behavior of *X. maculatus* and *X. helleri.* Whereas several types of behaviors, namely copulation, gonopodial thrusting and swinging, sidling, quivering, and nipping, were observed during courtship in both species, two behavior patterns typically shown by courting male platies, pecking and retiring, were not recorded for swordtails, and male swordtails showed exaggerated backing and nibbling actions not seen in platyfish.

Quantitatively the two species differ in the mean duration of copulation, rapidity with which copulations initially occurs during the observation periods, frequency of copulations, and number of inseminations resulting from copulations.

How useful these various behavioral differences may prove in a sytematic evaluation of the genus is still conjectural. The exaggerated backing movements of swordtails may be related to the presence of the long, brilliantly marked caudal appendage that the platyfish lack. Other quantitative differences may be closely interwoven with the ecological differences separating the species in nature.

SKELETAL ELEMENTS

In addition to the features discussed above, three other groups of structures were examined which, because of their relative constancy in this group of fishes, appear to be most significant from the standpoint of generic definition. They are the gonopodial suspensorium, the head skeleton, and the pectoral girdle. A few differences were noted at the specific level.

GONOPODIAL SUSPENSORIUM. Gordon and Benzer (1945) studied and reviewed the literature on the gonopodial suspensorium of *Xiphophorus* and gave a brief account of the morphological differences among the six then-known species. Their efforts to define phyletic lines within *Xiphophorus* from the information gained by their study of the suspensoria revealed only a mosaic of interrelationships. Many of the difficulties they encountered in their original work are now partly resolved by study of several hundred additional specimens, both cleared and stained material as well as radiographs. Some generalizations may now be made on features common to the suspensoria of all of the species of *Xiphophorus*:

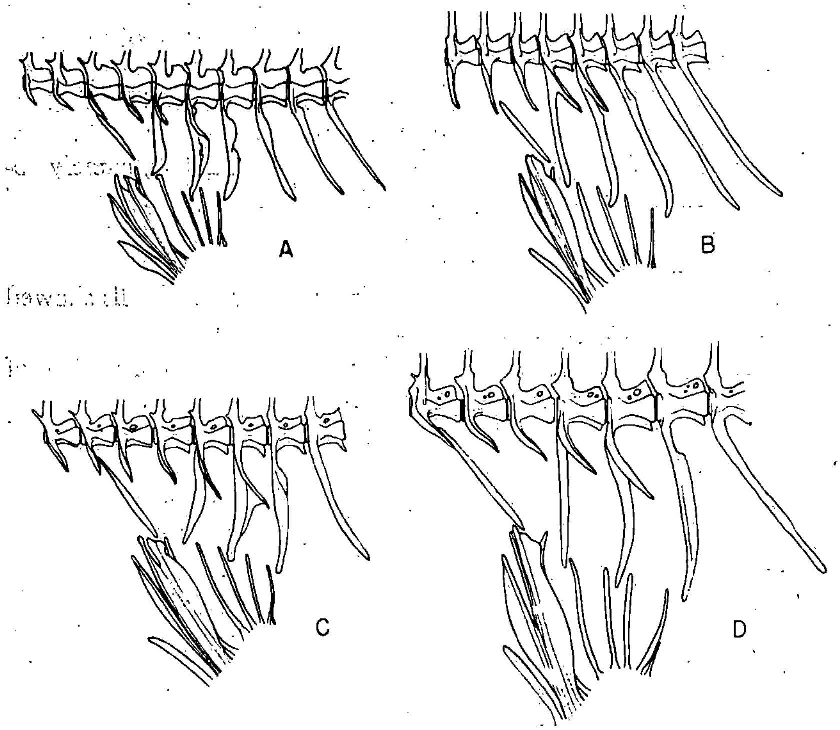


Figure 30. Gonopodial suspensoria in platyfishes. A. *X. couchianus* (Girard) (UMMZ: 97571). B. *X. maculatus* (Guenther) (UMMZ: 124255). C. *X. variatus xiphidium* (Gordon) (UMMZ: 124416). D. *X. variatus variatus* (Meek) (UMMZ: NYZS-GL, Rio Nautla).

1) The bony elements of the gonopodial suspensorium (figs. 30-31) are among the most conservative and least variable characters used in taxonomic studies of these fishes at the species level.

2) Consistent differences in suspensoria between even the most diverse species are small.

3) Intrinsic intraspecific variability in the suspensorial elements frequently is sufficient to obscure what differences do exist. What Gordon and Benzer viewed as anomalies of development have now been found frequently enough to be regarded as structural modifications within the range of normal variability.

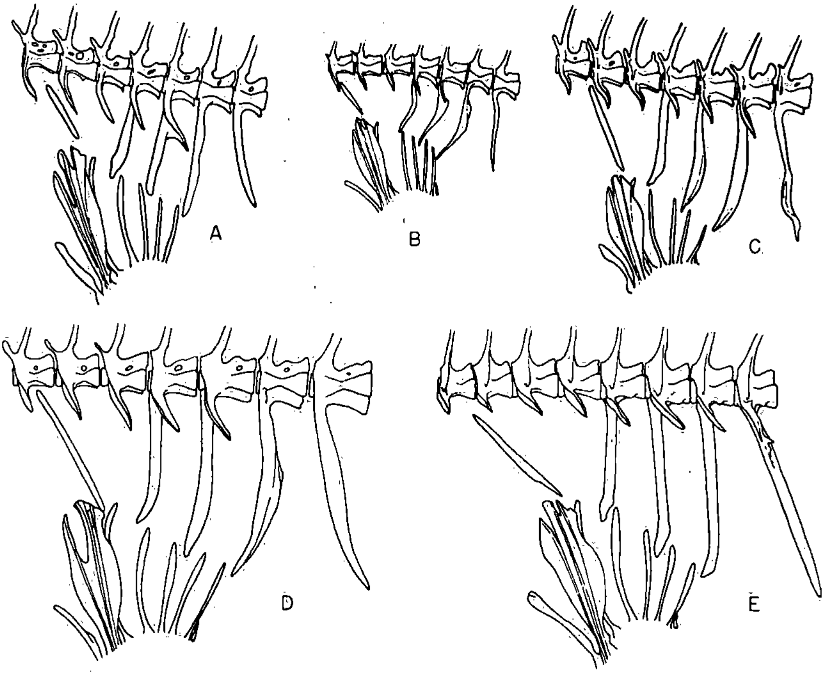


Figure 31. Gonopodial suspensoria in swordtails and *X. milleri.* A. *X. milleri,* n. sp. (UMMZ: 177310). B. *X. pygmaeus pygmaeus* Hubbs and Gordon (UMMZ: 124366). C. *X. montezumae montezumae* Jordan and Snyder (SU: 6146). D. *X. montezumae cortezi,* n. ssp. (UMMZ: 124374). E. *X. helleri guentheri* Jordan and Evermann (UMMZ: 143769).

4) The basic architecture of the suspensorial elements in *Xiphophorus* is considerably simpler than previously thought. Gordon and Benzer show figures of four species bearing uncinatoid processes on the posterior faces of their gonapophyses. It is now apparent that uncini do not occur regularly in any species. Gordon and Benzer's "uncini" are undoubtedly parapophyses that have become elongate and appressed to the shafts of the sexually modified hemal spines.

HEAD SKELETON AND DENTITION. The morphological units of the skull have been given scant attention in the taxonomy of poeciliid fishes. This has resulted, in part, from early recognition of and emphasis on the readily accessible sexually dimorphic traits by those who laid the foundations of modern poeciliid classification. To the present, the complex secondary sexual characters of the adult male poeciliid continue to provide fish taxonomists with the most precise means of assessing relationships of the genera and species. Hubbs

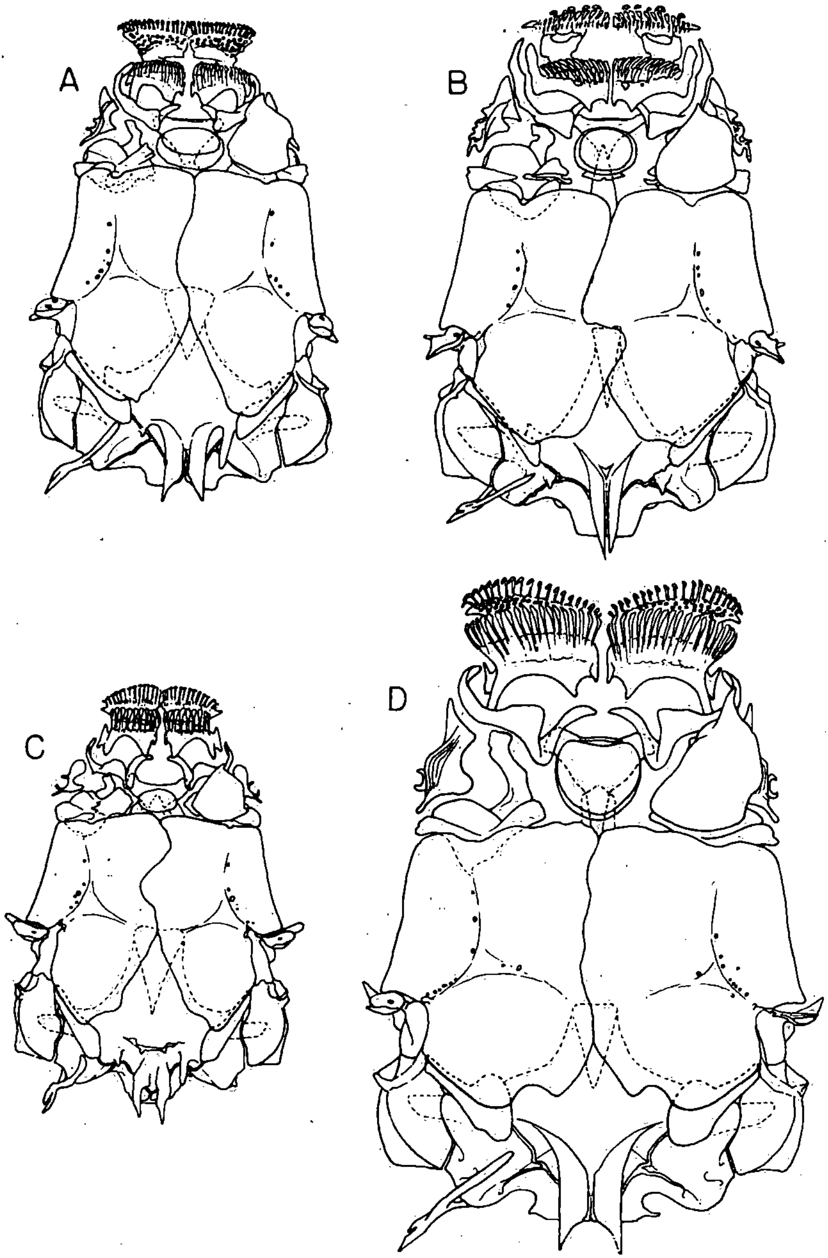


Figure 32. Dorsal views of the skulls of platyfishes. A. *X. couchianus* (Girard) (UMMZ: 97571). B. *X. maculatus* (Guenther) (UMMZ: 124255). C. *X. variatus xiphidium* (Gordon) (laboratory stock). D. *X. variatus variatus* (Meek) (UMMZ:NYZS-GL, Rio Nautla).

and Turner (1939) declared that since the identification and classification of the poeciliids depends chiefly on gonopodial characters of adult males, taxonomic evaluation "remains a guess when such males are not at hand, except in genera and higher groups which may be recognized definitely on the basis of very superficial, at times almost subjective, characters."

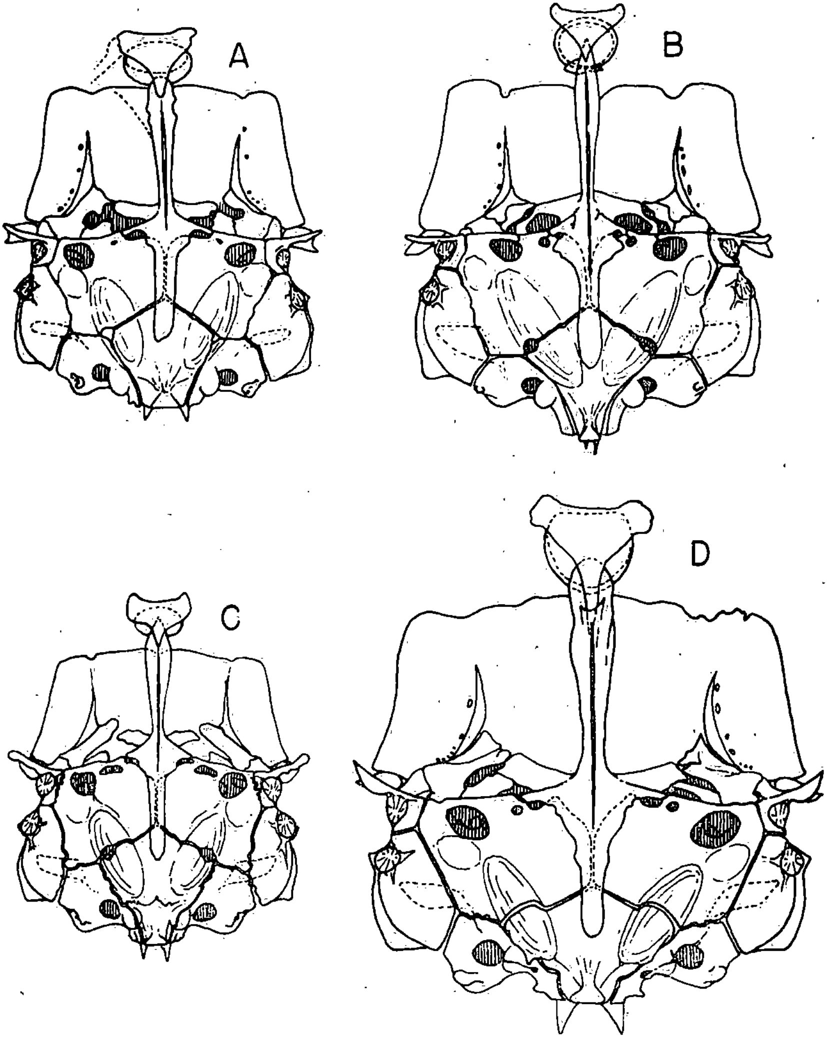


Figure 33. Ventral views of the crania of platyfishes. A. *X. couchianus* (Girard) (UMMZ: 97571). B. *X. maculatus* (Guenther) (UMMZ: 124255). C. *X. variatus xiphidium* (Gordon) (laboratory stock). D. *X. variatus variatus* (Meek) (UMMZ:NYZS-GL, Rio Nautla).

Prior to Regan's rediscovery of the importance of genitalic characters, some skull characters, particularly the dentition, was employed extensively in poeciliid classification, with questionable results. Dentitional characters were reserved mainly for defining taxa at the generic level and above. Garman's (1895) work is outstanding as the only major effort to utilize the detailed structure of the teeth as well as tooth arrangement in an analysis of the poeciliids and other cyprinodont species. Garman correctly illustrated that placing too much reliance on dentitional characters, particularly in categories above the species, may lead to an unnatural arrangement of these fishes. This view was reiterated recently by Rosen and Bailey (1959: 32, 35), and it is adhered to here.

The adult osteocranium of *Xiphophorus* (figs. 32-37) shows little phylogenetically significant variation among the eight species. Allometric changes in dimensions and the relative proportions of certain structures that accompany growth of the individual are more or less uniform throughout the genus. In the posterior region of the skull, however, some minor bones and accessories, chiefly those serving as points of muscle attachment, show some degree of interspecific variation. These are the parietal bones, the pterotic processes, the supraoccipital processes, and the epiotic processes.

The parietal bones vary from long, slender, well-ossified bones, extending from the pterotic-sphenotic junction to the supraoccipital, to one or more poorly ossified remnants distributed irregularly along the posterolateral margins of the frontals. Epiotic processes are either well developed (in which case their bases may extend medially onto the supraoccipital) or they are altogether wanting. Pterotic processes may be broad and winglike with retrorse elements, or they may be simple narrow flanges that follow the posterior curve of the cranium. The supraoccipital processes are either set high on the skull with long and slender posterior extensions, or they are flattened down to the cranial vault and their posterior elements are broad and terminate abruptly with short, blunt, chisellike extensions.

Xiphophorus helleri, for example, is distinguished by having well developed parietals, broad, hooked pterotic processes, and long, slender, well-developed processes on both supraoccipital and epiotic bones. *X. pygmaeus*, on the other hand, shows less well-developed, sometimes fragmented parietals, extremely reduced pterotic wings, long and slender supraoccipital processes, and no epiotic processes. These differences are not due solely to differences in size between the species, for *X. montezumae*, a species which may exceed *X. helleri* in

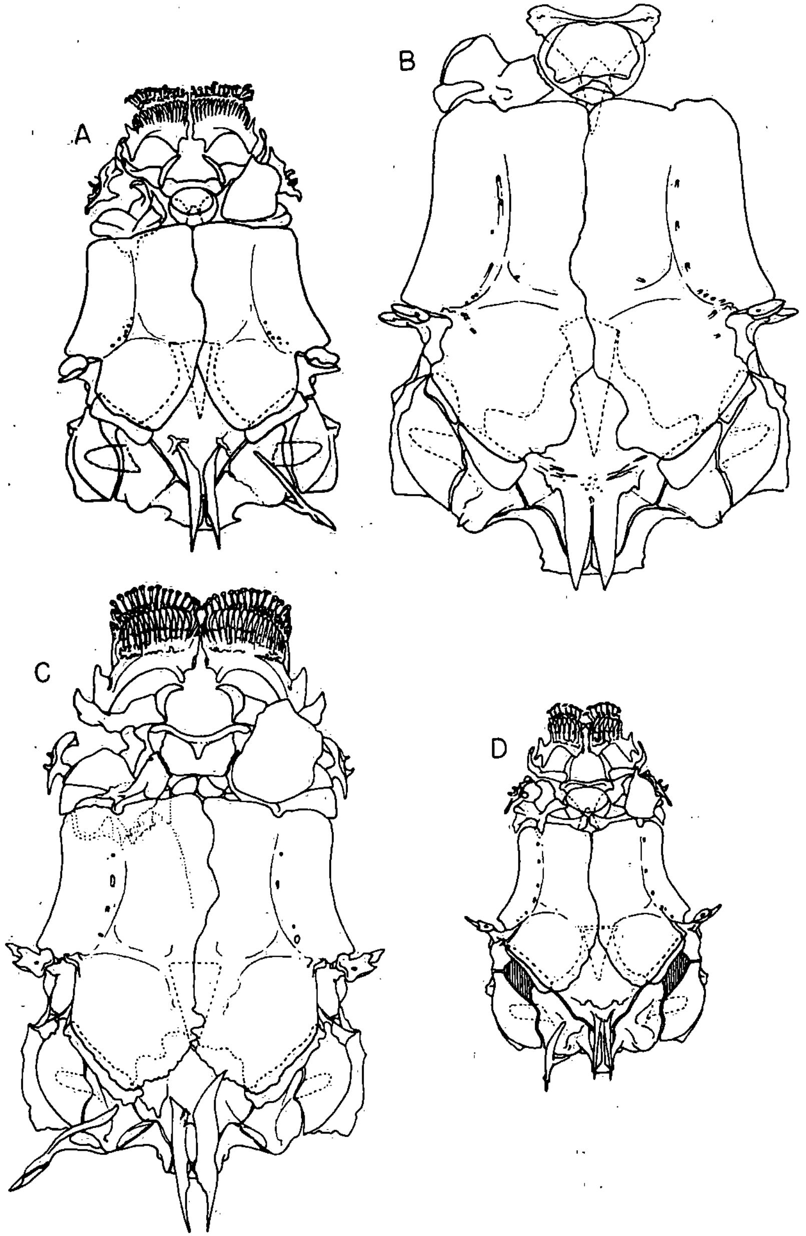


Figure 34. Dorsal views of the skulls of *X. milleri*, *X. montezumae* and *X. pygmaeus*. A. *X. milleri*, n. sp. (UMMZ: 177310). B. *X. montezumae montezumae* Jordan and Snyder (SU: 6146). C. *X. montezumae cortezi*, n. ssp. (laboratory stock). D. *X. pygmaeus pygmaeus* Hubbs and Gordon (laboratory stock). A posttemporal bone is shown in C. In B, mouth parts are not illustrated.

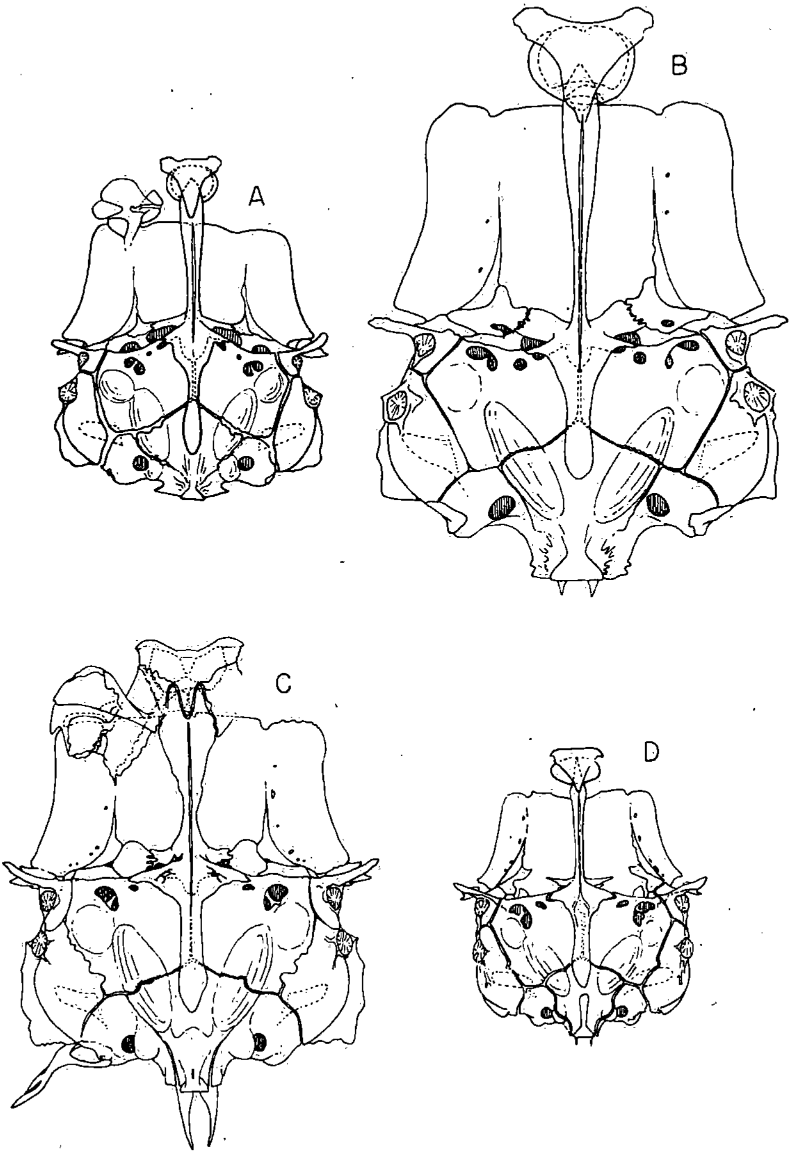


Figure 35. Ventral views of the crania of *X. milleri*, *X. montezumae*, and *X. pygmaeus*. A. *X. milleri*, n. sp. (UMMZ: 177310). B. *X. montezumae montezumae* Jordan and Snyder (SU: 6146). C. *X. montezumae cortezi*, n. ssp. (laboratory stock). D. *X. pygmaeus pygmaeus* Hubbs and Gordon (laboratory stock). A lateral ethmoid is shown in A and C, and a posttemporal bone in C.

length, shows characters that ally it with *X. pygmaeus.* The parietals are poorly developed, sometimes in two separate fragments, the pterotic processes are only moderately developed, the supraoccipital processes are broad and blunt, and the epiotic processes are either lacking or are represented by tiny irregular nubbins where their bases would normally be. The shape of the parietals in the three species of platyfishes also may be of significance; in all they are noticeably spatulate and flare laterally to form moderate to broad disclike elements.

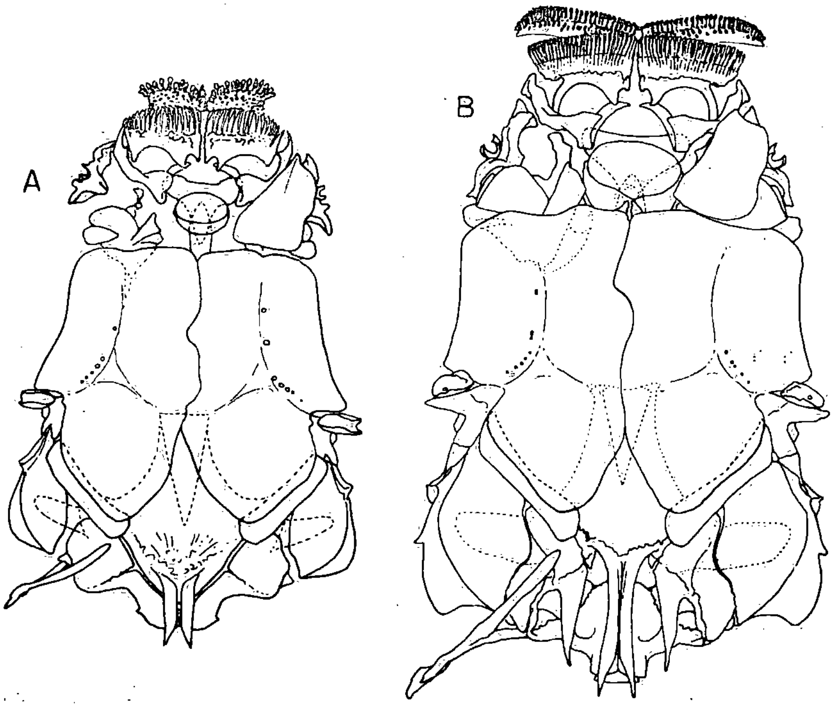


Figure 36. Dorsal views of the skulls of *X. clemenciae* and *X. helleri.* A. *X. clemenciae,* Alvarez (UMMZ: M57-55). B. *X. helleri guentheri* Jordan and Evermann (UMMZ: 143769).

Pectoral Girdle. Of the three major elements of the girdle, the cleithrum, scapula and coracoid, only the coracoid shows significant variation in *Xiphophorus* (figs. 38-39). The coracoid extends cephalad in a broad, subtriangular anterior process to join the cleithrum at its anteroventral limit. Posteriorly, below the recess which receives the two inferior actinosts, the coracoid sends out a flat, spatulate process that extends backward beyond the origin of the pectoral fin base. Laterally this process serves as the point of origin for the posterior slips of the abductor pectoralis profundus muscles, while medially it seats a tough ligament that runs obliquely upward across the adductor profundus to form an aponeurosis with the anterior portions of the adductor superior. It is interesting and perhaps significant that the posterior coracoid process is present and usually well-developed in most species of *Xiphophorus,* whereas in *couchianus,* and in some specimens of *variatus xiphidium,* the lower edge of the coracoid is gently and evenly sloped upward posteriorly to meet the recess for the actinosts.

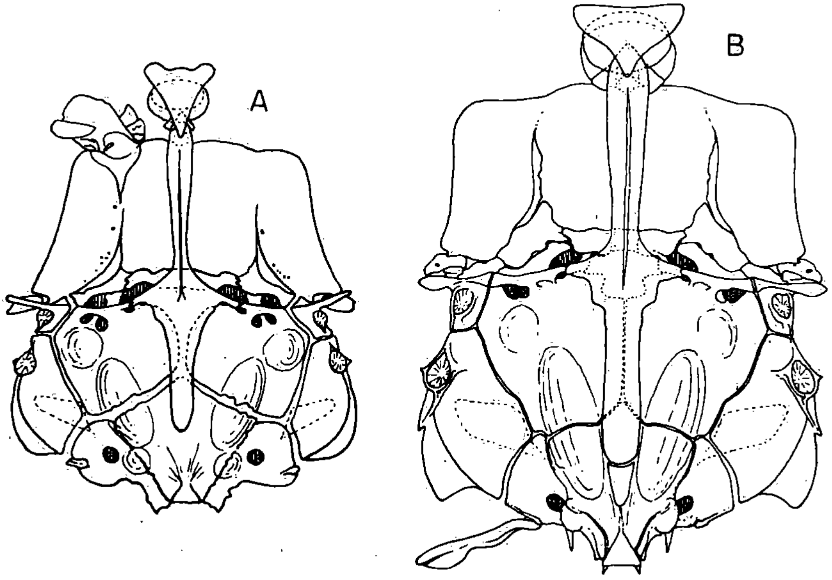


Figure 37. Ventral views of the crania of *X. clemenciae* and *X. helleri.* A. *X. clemenciae* Alvarez (UMMZ:M57-55). B. *X. helleri guentheri* Jordan and Evermann (UMMZ: 143769). A posttemporal bone is shown in B, and a lateral ethmoid in A.

The pectoral girdle has two fenestrations, a large interosseous space between the cleithrum and the coracoid, and a scapular foramen. Some specific differences were noted in the size and form of both openings, which may prove to be no more than ontogenetic variations when a larger series of skeletons is examined. The actinosts also show some variations, especially in shape and the extent of fusion between either the scapular pair or the inferior pair within the coracoidal recess. These differences are also probably chiefly ontogenetic in origin.

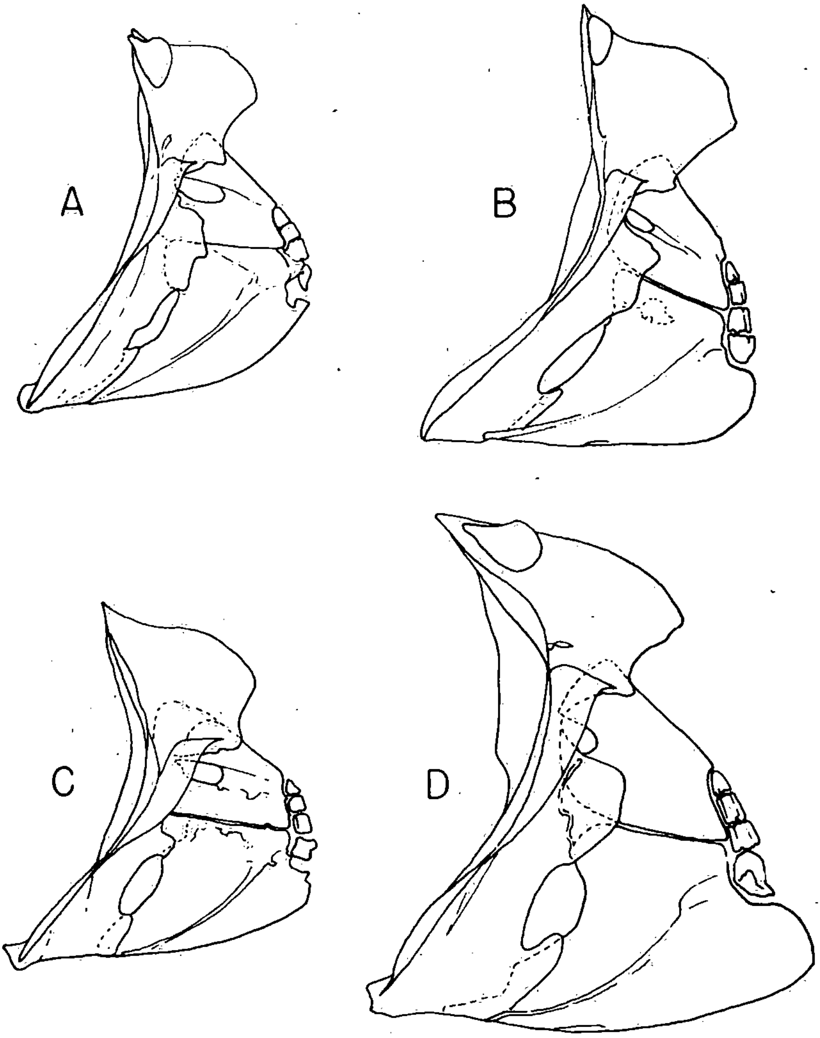


Figure 38. Left primary shoulder girdle in four forms of platyfishes. A. *X. couchianus* (Girard) (UMMZ: 97571). B. *X. maculatus* (Guenther) (UMMZ: 124255). C. *X. variatus xiphidium* (Gordon) (laboratory stock). D. *X. variatus variatus* (Meek) (UMMZ:NYZS-GL, Rio Nautla). The supracleithrum is shown in A, B, and D.

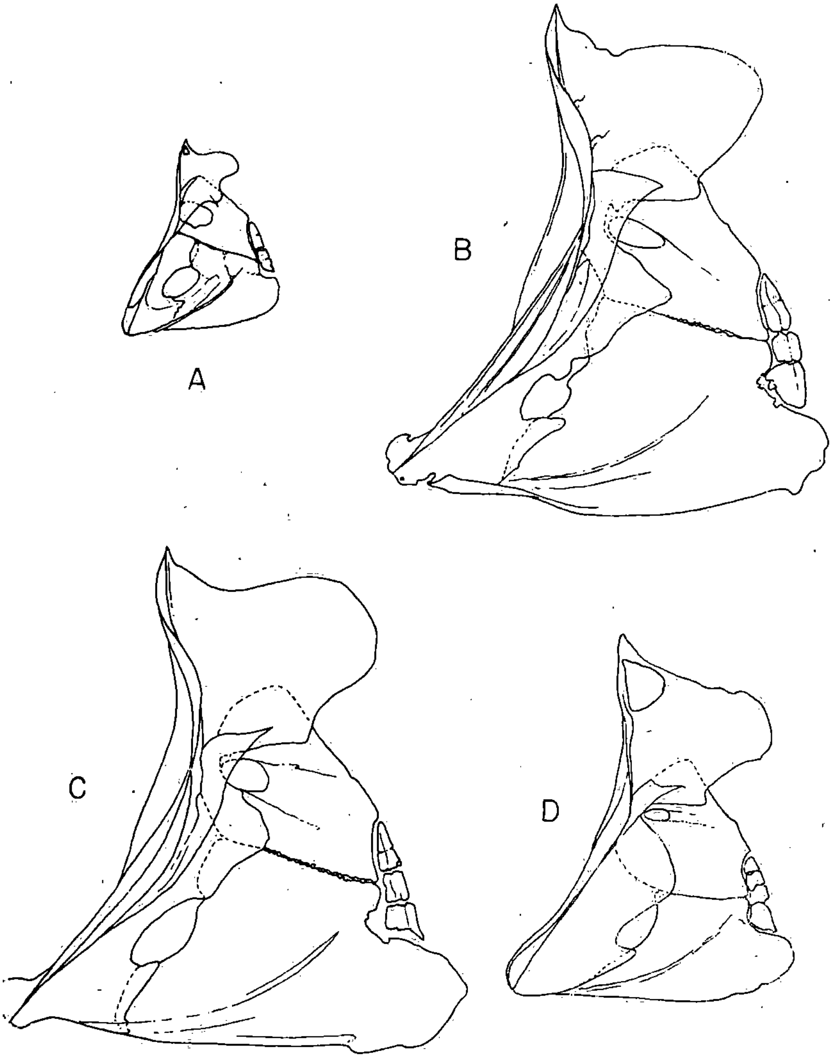


Figure 39. Left primary shoulder girdle in four forms of swordtails. A. *X. pygmaeus pygmaeus* Hubbs and Gordon (laboratory stock). B. *X. montezumae cortezi,* n. ssp. (laboratory stock). C. *X. montezumae montezumae* Jordan and Snyder (SU: 6146). D. *X. helleri guentheri* Jordan and Evermann (UMMZ: 143769). The supracleithrum is shown in A and D.

VIABILITY, DEVELOPMENT, AND MORPHOLOGY OF INTERSPECIFIC HYBRIDS AS SYSTEMIC CRITERIA IN *Xiphophorus*.

The species of *Xiphophorus* may be hybridized with comparative ease in the laboratory when offered only the choice of a heterotypic mate. No hybrid *Xiphophorus* has yet been found in the many thousands of specimens thus far collected in the field, although all but *couchianus* occur sympatrically with at least one other member of the genus, and *helleri* occurs sympatrically with four. Nevertheless, it has been possible to induce experimentally at least 47 qualitatively different hybrids involving 6 of the 8 known species.

All the hybrids at hand were obtained during genetic studies of normal and atypical pigment cell growth (Gordon, 1927-1957). Each mating was established to test the genetic behavior of various micro- or macromelanophore markings. This resulted in a great emphasis on obtaining certain hybrids, such as *maculatus-helleri* and *montezumae-helleri* crosses, and in lesser emphasis on others. Therefore the frequency with which certain interspecific combinations are known is not to be interpreted as an indication of the facility with which such combinations can be obtained under laboratory conditions.

A tabulation of interspecific hybrids of *Xiphophorus* is given in table 34. Intraspecific matings of *variatus variatus* with *variatus xiphidium* are included because heretofore these two forms were regarded as distinct species. Their new taxonomic position is discussed below in relation to the effects of hybridization.

The cytology of the *Xiphophorus* species is known only from the studies of Friedman and Gordon (1934), and Wickbom (1943). According to these authors in *helleri, montezumae, pygmaeus, maculatus, variatus,* and *couchianus,* the diploid number of chromosomes is 48. Friedman and Gordon found a small additional element in the nominate form of *varitaus,* and regarded it as a univalent, while in *variatus xiphidium* the number, as above, is 48. Wickbom also noted an "unusual" element in *variatus variatus,* but because of great technical difficulties encountered in making accurate counts, he reserved final judgment on its possible status as a univalent. It is concluded that as yet no known mechanical barrier exists that would prevent the chromosomes of hybrid zygotes from synapsing normally.

EMBRYONIC DEVELOPMENT, FERTILITY, AND SEXUALITY OF INTERSPECIFIC HYBRIDS IN RELATION TO THEIR GENETIC BACKGROUND

The degree of sterility in the hybrids between *maculatus* and *helleri* depends upon the type of mating, the genotype of the hybrid,

TABLE 34

HYBRIDS OF *Xiphophorus* PRODUCED EXPERIMENTALLY IN THE LABORATORY

P_1		F_1			F_2		
Female	Male	Males	Females	Young	Males	Females	Young
X. helleri strigatus	*X. montezumae cortezi*[*]	5					
ditto	*X. maculatus*[*]	98	99				
ditto	*X. variatus variatus*	1	1	1			1
ditto	*X. couchianus*	20	12	17			
X. montezumae cortezi	*X. helleri strigatus*[*]	26	11	46	3	28	14
ditto	*X. maculatus*	40	1				
ditto	*X. variatus variatus*	7	9	21			
X. pygmaeus pygmaeus	*X. montezumae cortezi*	3	5	1	2		
ditto	*X. variatus variatus*	1					
ditto	*X. variatus xiphidium*	27	38				
X. maculatus	*X. helleri strigatus*[*]	10	94		109	305	
ditto	*X. montezumae cortezi*	4	6				
ditto	*X. variatus variatus*	3					
ditto	*X. variatus xiphidium*	39	31	29			
ditto	*X. couchianus*	14	23	78			
X. variatus variatus	*X. pygmaeus pygmaeus*	11	16				
ditto	*X. variatus xiphidium*	6	9		21	13	40
ditto	*X. couchianus*	61	60		16	1	34
X. variatus xiphidium	*X. maculatus*	10	10				
ditto	*X. variatus variatus*	20	30	33	2	2	1
X. couchianus	*X. maculatus*	51	22	21	14	8	19
ditto	*X. variatus variatus*	5		12			

P_1		F_3, F_4, F_5, backcross and complex hybrids		
Female	Male	Males	Females	Young
p. pygmaeus-v. xiphidium	*p. pygmaeus*	13		3
maculatus-couchianus	*couchianus*	9	1	1
couchianus	*maculatus-couchianus*	11		2

TABLE 34 (continued)

P_1		F_3, F_4, F_5, backcross and complex hybrids		
Female	Male	Males	Females	Young
couchianus	*couchianus-(maculatus-couchianus)*	10	3	
(maculatus-couchianus)-couchianus	*couchianus*	2	1	1
v. variatus-v. xiphidium	*maculatus*	9	6	7
v. variatus	*maculatus-v. variatus*	50	41	3
maculatus-v. xiphidium	*v. xiphidium*	6	35	
v. xiphidium-v. variatus	*maculatus—v. xiphidium*	16	6	59
F_2 [*v. xiphidium-v. variatus)-(maculatus-v. xiphidium)*]	*v. variatus-(maculatus—v. variatus)*	4	5	
m. cortezi-h. strigatus	*m. cortezi*[*]	3	18	11
h. strigatus	*m. cortezi—h. strigatus*[*]	9	2	
(m. cortezi-h. strigatus)-h. strigatus	*h. strigatus*[1]	12	23	47
h. strigatus	*(m. cortezi-h. strigatus)—h. strigatus*[*]	41	27	
h. strigatus-(m. cortezi-h. strigatus)	*h. strigatus-(m. cortezi—h. strigatus)*[*]	4	3	
(m. cortezi-h. strigatus)-h. strigatus	*(m. cortezi—h. strigatus)—h. strigatus*[*]	18	32	9
F_2 *m. cortezi-h. strigatus*	F_2 *m. cortezi—h. strigatus*	16	8	
F_3 *m. cortezi-h. strigatus*	F_3 *m. cortezi—h. strigatus*			
F_4 *m. cortezi-h. strigatus*	F_4 *m. cortezi—h. strigatus*			
F_2 *h. strigatus-(m. cortezi-h. strigatus)*	*h. strigatus*	60	64	31
v. variatus-v. xiphidium	*couchianus-maculatus*	27	9	11
couchianus-maculatus	*v. xiphidium—x. variatus*	6	7	43
maculatus-h. strigatus	*h. strigatus*[*]	310	604	
maculatus	*maculatus—h. strigatus*[*]	20	141	
h. strigatus	*h. strigatus—maculatus*[*]	43	100	
h. strigatus-maculatus	*h. strigatus*[*]	17	30	
(h. strigatus-maculatus)-h. strigatus	*h. strigatus*[*]	20	54	

[*] Many of the multiple backcross hybrids that originally involved matings of *montezumae-helleri* and *maculatus-helleri* are not listed, but are discussed elsewhere fully by Gordon and his coworkers. The grouping of hybrids by male, female and young is, in many instances, arbitrary as it is known that in some hybrids that appear superficially as females no gonads are present, while in others known to be genetically male either gonads or secondary sex characters are not found or both. The above arrangements are based largely on external appearance of the fish.

and particularly the presence or absence of the Y chromosome of the platyfish parent (or, at least, genes present on this differentiated platyfish sex chromosome). For example, when *maculatus* from the Rio Jamapa is the female parent (XX), the sex ratio among their hybrids (XX′)[6] is approximately 90 percent female and 10 percent male, according to Gordon (1948b). Such a mating can be studied genetically by having the platyfish sex chromosomes "marked" with appropriate genes. Gene markers commonly used in these matings are Sp, representing irregular macromelanophore spotting on the flanks of the platyfish, Sd, representing macromelanophore spotting on the dorsal fin, and Sr, representing striped macromelanophore markings along the sides.

Tavolga (1949) showed that for such matings involving the Sp gene, 33 platyfish-swordtail female hybrids (XX′) tested for fertility yielded only two hybrids that were completely sterile, and three with significantly low productivity that produced aberrant broods, each of which contained over 30 percent anomalous embryos.

Of 34 female hybrids (XX′) involving the Sd gene, 15 were completely sterile, 11 produced aberrant broods, and 8 produced normal broods. Four out of 5 male hybrids (XX′) carrying the Sd gene, and 4 or 5 male hybrids (XX′) carrying the Sp factor, when tested with virgin female *maculatus, helleri* or their hybrids, proved fertile.

If the *helleri* from the Rio Papaloapan is the female parent (X′X′) and the stripe-sided (Sr), spotted-dorsal (Sd) *maculatus* from the Rio Jamapa is the male (XY), the sex ratios are quite different; 50 percent of the hybrids (XX′) carried the Sr gene and were mostly fertile; 3 percent that had the probable chromosomal constitution (YX′) carried the Sd gene, were functional females, but proved only partially fertile; 2 percent of the spotted-dorsal hybrids (YX′) were fertile males; 45 percent of the Sd hybrids (YX′) failed to differentiate sexually. Most of these latter hybrids had no visible gonads, and they attained a greater body size than did the other hybrids.

In the platyfish-swordtail hybrids the gonadal abnormalities are probably related to certain incompatibilities resulting from the chance union of dissimilar chromosomes and their genes. The interspecific mating between *maculatus* and *helleri* shows the X chromosome of the platyfish to be fairly compatible with its theoretical counterpart,

---

[6] The X′ chromosome of the swordtail is the *theoretical* counterpart of the heterochromosome of platyfish; it has never actually been identified in genetic tests. The swordtail has an unknown, though labile, sex-determining mechanism.

the X′ chromosome of the swordtail, but the platyfish Y chromosome is usually incompatible with the swordtail X′.

Apart from gross defects in gonadal development in these hybrids, inviability or failure to undergo maturation division of the male and female reproductive cells are additional causes of platyfish-swordtail hybrid infertility. Berg and Gordon (1953) determined that about half of all the adult hybrid fish have normal gonads; the others have either atrophic gonads or none. Gonadal abnormalities in the male hybrids, they found, are usually associated with processes after the completion of spermatogenesis, whereas those in females are usually related to processes during early oogenesis. Some of the embryonic lethal effects noted by Tavolga (1949) may owe their origin to gametic abnormalities of hybrids containing the platyfish Y chromosome.

Some of the abnormalities that developed spontaneously in the testes of platyfish-swordtail hybrids resemble testicular abnormalities in other poeciliid fishes treated experimentally with sex steroids. This suggested to Berg and Gordon how a disturbance in the endocrine balance of the hybrid fishes may have brought about abnormal testicular development. Testicular abnormalities resembling those produced by the administration of sex hormones were described by Gordon and Aronowitz (1951) in an untreated functional male *maculatus* that had the genetic constitution of a female (XX). This sex-reversed platyfish was fertile for a short time only, after which it became sterile. Histological examination of its sterile testis revealed many functional and structural abnormalities. It was suggested that the premature sterility of the sex-reversed male was due to a hormonal imbalance, brought about by androgenic agents acting upon a genetically constituted female.

PIGMENT CELL ABNORMALITIES IN HYBRIDS

Hybridization in many instances leads to abnormal cellular behavior not only in the reproductive cells but also in the pigment cells, particularly the macromelanophores. Under conditions of hybridization a transformation takes place in the phenotypic expression of the macromelanophore genes when the spotting factor, Sp, of *maculatus* is brought into association with the modifying factors of *helleri*. A rapid multiplication of macromelanophores results. The hybrid may become melanotic, and in some individuals a true neoplasm, a melanoma, develops as a direct result of this combination of genotypes.

The appearance of lethal melanotic tumors in some hybrids has been suggested as a physiological isolating mechanism which at one time may have prevented gene interchange between the platyfish and swordtail when they occurred sympatrically. However, it can be shown that 1) only about 20 percent of the platyfish, *maculatus,* in the rivers and streams of Mexico and Central America carry factors for macromelanophore spotting, 2) the two species are sympatric in something less than 10 percent of the localities where they have been collected, and 3) when the platyfish and swordtail do occur sympatrically, usually the swordtails constitute 1 percent or less of the total mixed swordtail-platyfish population. Most sympatric situations are transient ones resulting from swordtails being washed downstream into platyfish territory; the two species are eventually concentrated in pools in stream beds and shortly thereafter are killed by predators or desiccation. Females of both species that are brought together by flood waters probably already carry homotypic sperm that may compete successfully with heterotypic sperm and cause a female to be unreceptive to courting males. These facts, in addition to total absence of natural hybridization, make it extremely unlikely that macromelanophore genes ever contributed to the building up of isolating mechanisms in this genus.

The significance for systematic studies of the appearance of melanotic or melanomatous growths in the platyfish-swordtail hybrids thus is not as an isolating mechanism, but as a measure of the degree of genetic diversity between the two species when subjected to special conditions in the laboratory. Gordon (1947b), Gordon and Rosen (1951), and Clark, Aronson, and Gordon (1954) have indicated that in nature geographical, ecological, and physiological isolating mechanisms effectively protect the species against gene interchange. Under laboratory conditions, with the breakdown of the natural isolating mechanisms when homotypic matings are prevented, the platyfish and swordtail hybridize readily. It is only then that we are made aware of their many genetic and physiological incompatibilities of which the degree of atypical pigment cell growth is but one measure.

When a platyfish, *maculatus,* carrying the sex-linked dominant macromelanophore factor, Sp, for spotting, is mated with each of the other species of *Xiphophorus,* their first generation hybrids all show atypical, rapid multiplication of the macromelanophores along the sides and flanks. In some of the F_1 hybrids from matings of *maculatus* with *helleri, montezumae, pygmaeus,* or *couchianus,* the atypical pigment cell growth results in the production of melanoma. In matings of spotted *maculatus* with *variatus,* the first generation hybrids show a moderate to severe melanosis, but never melanoma. A mating of *maculatus* with the nominal species *xiphidium* (= *variatus xiphidium*) gives essentially the same results, melanosis, but no melanoma.

Gordon (1951b,c) showed that in atypical macromelanophore growth no fundamental difference exists between interspecific hybrids and intraspecific ones involving two geographical populations. This conclusion was based upon an analysis of the genetic behavior of a macromelanophore gene, Sd, for irregular spotting in the dorsal fin of the platyfish, *maculatus*. By mating a Rio Jamapa female platyfish with a Rio Coatzacoalcos spotted dorsal male platyfish, F_1 interriver hybrids were obtained that showed varying intensities of dorsal fin pigmentation. Some had no dorsal pigment while others had intensely black dorsal fins, yet all of the individuals carried the Sd gene. The genetic analysis of the process by which a dominant gene for macromelanophore production shifts from no macromelanophore formation in interriver platyfish hybrids to the development of melanomas in interspecific platyfish-swordtail hybrids showed that several types of modifying genes are involved.

The members of the various natural populations of the platyfish apparently have many polygene modifiers, some of which increase and others decrease the expressivity of the Sd gene. These effects are small compared to the modifying effects of swordtail genes, even though a condition approaching melanosis of the dorsal fin was obtained in the interriver platyfish hybrids. The difference in macromelanophore growth between intra- and interspecific matings thus is primarily one of degree and not of kind, as Gordon indicated. As a corollary, the considerably less severe nature of the atypical pigment cell growth in the interriver platyfish hybrids, as compared with this response in species hybrids, is a measure of their much greater genetic and physiological compatibility, which is our primary concern in systematic studies of these fishes. This is why the relatively mild macromelanophore response in *maculatus-variatus* F_1 hybrids is considered consistent with a close historical relationship between these two species.

It must be pointed out that in the foregoing discussion *maculatus* had been used as a base or test species, for it is only the macromelanophore genes of this form that yield consistent results of the sort outlined above. Macromelanophore genes of many of the other species have such variable and inconsistent expressions in hybrids that application of the results is not yet possible. Atz (MS) has summarized and discussed these experiments.

It may be concluded tentatively that evidence adduced from genetic and correlated studies of the response of *maculatus* pigment cell genes in hybrids of *Xiphophorus*, although certainly not substantiating, is at least consistent with the proposed status of *helleri, montezumae, pygmaeus, couchianus*, and *maculatus* as good species.

ABNORMALITIES OF THE EXTERNAL GENITALIA OF HYBRIDS

DESCRIPTION AND INTERPRETATION OF SOME SPECIFIC ANOMALIES. Among the diverse effects of interspecific hybridization in *Xiphophorus* are those concerned with the development of the external male genitalium, or gonopodium. The gonopodia of male hybrids, in general, display a spectrum of abnormalities ranging all the way from those that never complete morphogenesis to those that develop fully but contain a number of minor or drastic structural defects. Most anomalous fins in male hybrids fail to develop fully and show no differentiation of terminal specialized bony elements (hooks, spines, serrae). Such fins resemble the gonopodia of normal male *Xiphophorus* during the early stages of sexual differentiation. The gonopodia are long with blunt, rounded tips. Segmentation appears to have proceeded at a normal rate, the individual rays being elongate and considerably thickened, but no terminal specializations have appeared. Failure of these fins to differentiate may result from endocrinological disturbances of the hybrids that may hold in check some of the processes necessary for complete sexual differentiation.

The absence of relatively large numbers of male hybrids for morphometric analyses is a common difficulty in studies of interspecific hybridization. Dobzhansky (1941) stated that "interspecific hybrids in which a straight-forward genetic analysis can be made constitute . . . only a residue left after the elimination of the sterile and chromosomally abnormal hybrids." Among 301 F_1 platyfish-swordtail hybrids, only 8 males had gonopodia sufficiently well formed for genetic analysis (Gordon and Rosen, 1951; and see table 34). Of well over 400 F_2 hybrids only 108 males had gonopodia that could be analyzed. Similar difficulties were encountered in studying the gonopodia of many backcross hybrids.

The results of two independent studies (Sengun, 1950, and Gordon and Rosen, 1951) suggest that the mode of inheritance of the distal serrae (ray 4p), spines (ray 3), and claw (ray 5a) in interspecific hybrids may be explained tentatively as follows:

a. The pattern of inheritance of spines (ray 3) and claws (ray 5a) is based on a small number of independently assorting multiple factors.

b. The pattern of inheritance of distal serrae (ray 4p) indicates that these structures cannot be evaluated as a single unit, and that the variables, basal width and shaft height, react independently. Each appears to have a polygenic mode of inheritance similar to other gonopodial structures.

The independence of base and shaft of serrae is precisely what might be expected if, as discussed above, the shaft of a serra alone can become incorporated as a separate entity into the terminal complex of ray 5a to form a claw without disturbing the topographical or developmental relationships of its basal section. It is of interest that most of the structural anomalies found in gonopodia of species of *Xiphophorus* and their hybrids occur in the region of the claw on ray 5a. More than half of the interspecific platyfish hybrids and many platyfish-swordtail hybrids show ray 5 anomalies, perhaps indicating that genetic and developmental stability of the claw "field" has not yet been achieved in most *Xiphophorus*. From an evolutionary viewpoint the definitive claw may therefore represent a relatively recent innovation (also see above).

The data on the frequency of occurrence of gonopodial anomalies in the interspecific hybrids, to be presented elsewhere in detail, may be summarized as follows:

a. The gonopodia of hybrids resulting from matings of *couchianus* and any other species of *Xiphophorus* show a high percentage of anomalous structures. Of four basic types of anomalies thus far detected all have been found in these hybrids.

b. The gonopodia of hybrids resulting from matings of *maculatus* with subspecies of *variatus* show a high percentage of anomalies. This percentage is somewhat lower than in matings involving *couchianus*. In *maculatus-variatus* hybrids, three of the four known types of anomalies occur.

c. The gonopodia of hybrids resulting from matings of *montezumae* with *variatus* and *helleri* and of *maculatus* with *helleri* show the lowest percentage of anomalous structures. Only one of the four known types of anomalies occur in these hybrids.

d. The most frequent anomaly in the gonopodia of hybrids derived from both direct and reciprocal matings of *maculatus* with *helleri* involves failure of the gonopodium to differentiate fully.

e. No significant anomalies were discovered in the gonopodia of the 23 adult male *v. variatus-v. xiphidium* hybrids or interspecific hybrids between *pygmaeus* and *montezumae* (4 adult males) and *variatus* (10 adult males).

f. The most severe anomalies occur in hybrids derived from matings of *couchianus* with *variatus*, and *couchianus*, *variatus* and *maculatus* with *montezumae*.

The gonopodial anomalies resulting from matings of *montezumae-couchianus*, *montezumae-variatus*, and *montezumae-maculatus* are of a highly specific sort and are virtually identical in all three hybrids. Of all the gonopodial anomalies encountered in this study, none is more remarkable nor more specific than these. Of the four adult male *montezumae-variatus* hybrids, three had anomalous fins, and of the four adult male *maculatus-montezumae* hybrids, as well as the only surviving *montezumae-couchianus* male hybrid, all had anomalous fins.[7] In all but one case the anomaly involves simultaneously rays 3, 4a, and 4p, so that there appears to be considerable developmental correlation within the fin as a whole (fig. 40a-c).

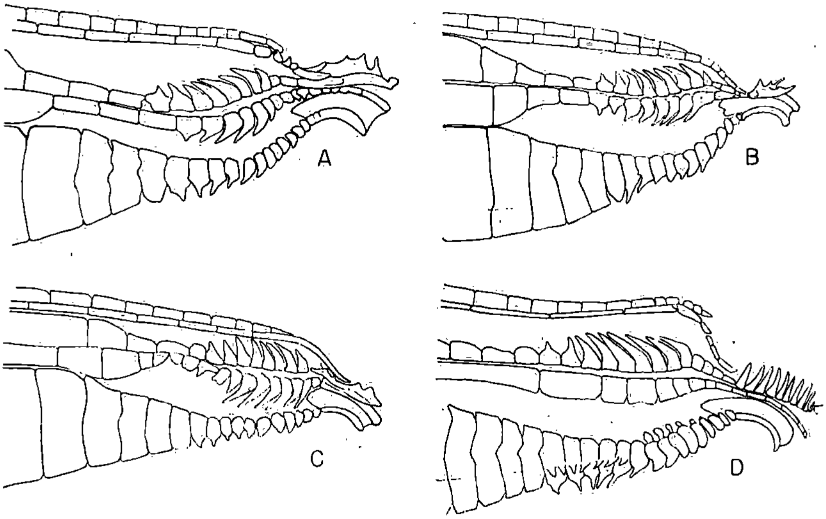


Figure 40. Distal tips of anomalous gonopodia of male F₁ hybrids. A. *X. montezumae cortezi* ♀ x *X. variatus variatus* ♂. B. *X. maculatus* ♀ x *X. montezumae cortezi* ♂. C. *X. montezumae cortezi* ♀ x *X. couchianus* ♂. D. *X. montezumae cortezi* ♀ x *X. variatus variatus* ♂.

Apart from fragmentation of many of the gonopodial elements and some atypical growth of others, the principal abnormalities are 1) the

---

[7] Eleven of the 12 male F₁ hybrids (*montezumae cortezi* ♀—*couchianus* ♂) died during sexual differentiation. Hybridization experiments with these two forms are still in progress.

mirror-image duplication of ray 4p in the area normally occupied by 4a, and 2) the almost total reduction of the spines' shafts subdistally on ray 3. Despite a slight tendency toward differentiation of distal serrae on the "true" 4p, the similarity between the two rami is nonetheless remarkable in terms of symmetry and morphological details. Even more remarkable is the fact that this group anomaly, virtually identical in all principal features, appeared in all three types of hybrids.

Two lines of evidence indicate that this situation cannot be explained adequately by assuming that *montezumae,* the species common to all of these matings, contributes to any type of interspecific hybrid a small but potent genic complex that controls the development of elaborate "group effects" in the presence of foreign genotypes. For example, group anomalies of the sort described have not occurred in the gonopodia of hybrids between *montezumae* and *helleri* (and these are plentiful, see table 34) or between *montezumae* and *pygmaeus,* despite the fact that the gonopodia of *montezumae-helleri* hybrids show many less specific abnormalities. Moreover, of the anomalous fins in the three *montezumae-variatus* hybrids, one did not show the complete "group effect." Instead only the ray 3 reduction occurred in this fin and the ray developed precisely as in the other anomalous fins; the ray 4 complex was undisturbed, giving no indication of duplication or other structural abnormality (fig. 40d). If we assume that many genes are involved in these reactions, then the genotypes of *couchianus, maculatus,* and *variatus* must have in common a number of homologous genes controlling segment form that yield the peculiar group anomalies when combined with the *montezumae* genotype. Genetic experiments indicate that a considerable number of autosomal and sex linked genes controlling the expression of melanophore patterns are homologous at least in *variatus* and *maculatus* (Atz, Ms.)

General Significance of Gonopodial Anomalies in Hybrids and Conclusions. Gordon presented evidence in several papers to show that one of the important effects of interspecific mating is a hormonal imbalance in the hybrids. To some extent this imbalance is reflected in failure of the gonads to develop normally or to produce viable gametes. A hormonal imbalance can be induced experimentally in poeciliids by administration of sex steroids. This may result not only in gonadal abnormalities but also in poorly formed, defective gonopodia. The strong influence of sex hormones upon normal growth and differentiation of the poeciliid gonopodium has been indicated by many workers. Turner (1942) assumed that in gonopodium development of the normal male the direction of development and level of tissue susceptibility in each differentiation area is under genetical control, and that the amount of hormone output by the developing testis (and, it should be pointed out, possibly other tissues, as well) controls the rate and completeness of gonopodial development.

It is inferred that abnormalities of the gonopodia of interspecific hybrid fish result from 1) the fortuitous combination of incompatible genetic systems that establish the developmental limitations of specific differentiation areas, such as in spines, hooks, serrae, and 2) an endocrine imbalance that may cause or be caused by failure of the gonad to develop normally. It is possible, therefore, that the type and degree of atypical gonopodium development in interspcific male hybrids is a meaure of the biological gap that separates the parent species, in exactly the manner that the degree of atypical pigment cell growth reflects genetic and physiological diversity.

The data on gonopodial anomalies in *Xiphophorus* hybrids and other effects of interspecific hybridization support the arrangement of the species based on morphological considerations. Furthermore the status of *helleri, montezumae, couchianus, variatus*, and *maculatus* as valid species is consistent with the occurrence of large numbers of severe developmental anomalies in the gonopodia of their interspecific hybrids. That such anomalies are not found in hybrids between *pygmaeus* and *montezumae* or *variatus* may reflect the relatively small number of such adult male hybrids obtained (4 *pygmaeus-montezumae* and 10 *pygmaeus-variatus* hybrids). Other evidence indicates that *montezumae* and *pygmaeus* are closely related. The occurrence of virtually identical "group anomalies" in the gonopodia of hybrids between *montezumae* and *couchianus*, *montezumae* and *maculatus*, and *montezumae* and *variatus* is interpreted as indicating a closeness of relationship among the three platyfish species. The absence of significant anomalies in 26 adult male hybrids from direct and reciprocal matings of *variatus* with the nominal species, *xiphidium*, is in line with the view expressed earlier that these two forms are not separable specifically. Apparently *v. variatus-v. xiphidium* hybrids are as vigorous and fertile as interriver hybrids of the southern platyfish, *maculatus*.

SPECIES GROUPS IN *Xiphophorus*

Some of the geographical units of *helleri* and *variatus* have been regarded as full species. It has also been suggested that *variatus*, *maculatus*, *couchianus*, and the nominal species *xiphidium* constitute members of a single polytypic species (see Dobzhansky, 1941; Mayr, 1942). The green swordtail, *helleri*, has been divided into as many as six nominal species because of what were believed to be not only clear cut but sizeable morphological differences among members of different allopatric populations. In the platyfish species it was argued that though morphologically distinct, 1) as a group they are more similar to one another than to any of the swordtail species, 2) they are all allopatric, and 3) they hybridize readily in the laboratory with the production of some fertile offspring and are therefore potentially not reproductively isolated. The error in trying to split the swordtails and lump the platyfishes arose with the belief that 1) the swordtails constituted a distinct genus, and 2) unawareness that the sympatric platy and swordtail species, *maculatus* and *helleri*, though reproductively isolated in nature, nevertheless produce considerable numbers of fertile F_1, F_2 and backcross hybrids in the laboratory.

Rigid use of the terms polytypic and monotypic to characterize species that do or do not consist of two or more distinctive geographical populations tends to confuse the taxonomic assessment of *Xiphophorus*. *X. helleri*, for example, may be regarded as a polytypic species because it consists of four definable subspecies that differ morphologically by sizeable gaps. The numerous geographic populations of *maculatus* are characterized by the frequencies of their micro- and macromelanophore patterns, but differ in no other way; here subspecific boundaries have no usefulness. Yet Gordon (1947a) and Gordon and Gordon (1950, 1957) showed that many populations of *maculatus* differ genetically not only with respect to frequency and presence or absence of genes controlling melanophore spotting, but also in their genetic sex determining mechanisms. Members of different geographical populations of *maculatus* when mated together produce hybrids with unusual sex ratios, or in which the combination of foreign genotypes results in abnormal macromelanophore development (Gordon, 1951b). Interriver *helleri* hybrids show no such abnormalities. None of the data derived from intraspecific laboratory matings in *maculatus* and *helleri* indicate greater genetic diversity within either species. Physiological differences in the races of *maculatus* may be as great or greater than the morphological ones in subspecies of *helleri*.

Despite these difficulties, the *concept* of the polytypic species as it is generally understood today has served as an essential guide in this revisional study. In the case of sympatric species, complete reproductive isolation under conditions in nature establishes for us the limits of our morphological species. As discussed hereinafter, experimental evidence adduced from laboratory crossmatings of the species of *Xiphophorus* is useful in assessing the degree of relationship between species units, as indicated by the effects of hybridization on reproductive potential, development, physiology and morphological correlation. This evidence, combined with morphological, distributional, and ecological data, provides the basis for the following suggested divisions of the genus.

I. THE *maculatus* SPECIES GROUP (*couchianus, maculatus* AND *variatus*)

Xiphophorus couchianus stands somewhat apart from the other two platyfish species. In a sense, it is certainly the least specialized member of the genus, for it lacks not only the caudal "sword," the swordtail type of gonopodial claw, and a midlateral black stripe, but also the tail patterns and macromelanophore markings found in most of the other species. It has a number of distinctive features: the distal serrae on ray 4p of its gonopodium converge at their tips and the posterior edges of the proximal spines on ray 3 are distinctly scalloped; in its pectoral girdle the coracoid is smoothly rounded posteriorly (at least in the 10 animals skeletonized) and lacks the spatulate process that provides additional surface for anchoring the abductor pectoralis profundus muscle in the other species; and finally it is always sharply bicolored—dark above and pale below—because of an intensification of the entire dorsal reticulum.

Though *couchianus* lacks macromelanophore spotting, it carries genes that interact with a *maculatus* macromelanophore pattern to produce a typical melanotic growth in F_1 hybrids—a reaction as severe as that obtained in the more intensively studied *maculatus-helleri* hybrids. This stands in strong contrast to the comparatively mild influence on macromelanophore development initiated in matings between the much more closely allied *maculatus* and *variatus*. Many severe gonopodial anomalies occur in hybrids between *couchianus* and *variatus*.

If it is agreed that *couchianus* is a relatively unspecialized member of the genus, then it seems probable that its penetration of the Rio Grande drainage, the northern outpost of *Xiphophorus*, may represent one of the earliest attempts by *Xiphophorus* to establish itself outside the region surrounding and including the great Panuco basin. If so, it was not a particularly successful invasion, for *couchianus* is restricted entirely to the region around Monterrey in the Rio Santa Catarina, and no other form like it, or indeed any *Xiphophorus*, has ever been taken in the next major independent drainage to the south, the Rio San Fernando.

The evidence for grouping together *couchianus* with *maculatus* and *variatus* is mostly indirect, deriving from genetic experiments designed primarily to study pigmentary abnormalities of hybrids. Nevertheless, Atz (Ms.) concluded from a survey of available material that the three species have genetically compatible sex determining mechanisms, and evidence presented above suggests a possible genetic homology of several differentiation areas on rays 3, 4a, and 4p of their gonopodia. In addition, these three species are alike ecologically, preferring regions of sluggish waters in dense aquatic vegetation, muddy undercut banks, or shallow pools away from riffles. This ecological specificity, in turn, is reflected in their comparatively robust, deep-bodied form.

The two completely allopatric species, *maculatus* and *variatus*, display many features that establish their close relationship. Their uniting characters include more or less erect distal serrae on ray 4p and antrorse proximal spines on ray 3, a wide variety of morphologically similar and genetically homologous micromelanophore tail patterns and macromelanophore spotted patterns, and similar genetic sex-determining mechanisms, except in the extreme south of the range of *maculatus* where the two species are separated by more than 500 miles.

Despite the obvious intimacy of relationship between these allopatric species, laboratory produced hybrids show a high percentage of anomalous structures in their gonopodia. When the spot-sided gene of *maculatus* is involved in such matings, the hybrids may show moderate to severe melanosis. Morphologically *maculatus* is unexpectedly uniform throughout its range, *variatus* tremendously variable and separable into three distinct morphological units. Furthermore *maculatus* is highly specialized ecologically, while *variatus* has more generalized requirements. Because of the consistency of these species over their considerable ranges with respect to a combination of morphological, physiological, and ecological factors, they are here treated as distinct. However, they are regarded as constituting a well defined superspecies to emphasize their close affinities.

Why *maculatus* should be morphologically comparatively uniform over a coastal range of nearly 600 miles and *variatus* so tremendously variable, within a region half this size, may be related to differences 1) in the selective agencies operating on them in different geographic and perhaps biotic zones, and 2) in their relative ages and rates of evolution along different lines.

X. maculatus may have been moving southward during the time of the Pleistocene glaciation when water levels were lower and more of the coastal plain was exposed. Progress southward probably was facilitated by the existence of extensive coastal canal systems and interlocking deltas (Price, 1942). Under these conditions opportunities for gene flow to have occurred may have been sufficient to neutralize or at least obscure the establishment of local genetic fluctuations affecting morphological traits, while at the same time selection may have helped to stabilize a body form preeminently suited to traversing the sluggish waters of coastal estuaries and bays.

X. variatus, on the other hand, in penetrating the complex Pañuco basin and the mountainous regions immediately to the south, has come to occupy a wide variety of ecological surroundings in each of which selection may have made new demands on body form, size of dorsal fin, and other traits.

II. THE *montezumae* SPECIES GROUP (*milleri, montezumae,* AND *pygmaeus*)

This division of the genus is rather diffuse; some of its uniting features show similarities to the highly specialized green swordtail (*X. helleri*) and others to the superspecies including *maculatus* and *variatus.* Despite its somewhat ambiguous position, much indirect evidence favors its erection, especially as it shows a number of structural grades intermediate between *helleri* and *maculatus* and *variatus.* Nor can the uniting morphological features of the group be stated simply, since no one diagnosis is completely restrictive for all of the three species. Pigmentary patterns illustrate this point.

The development of the black reticulum including the midlateral band on the sides and flanks is strikingly similar in *milleri* and *montezumae montezumae,* and in adult males only of *montezumae cortezi* and *pygmaeus nigrensis.* Dorsal fin patterns are alike in all except *montezumae cortezi,* but similar ones are found also in *variatus.* A bar-like micromelanophore tail pattern occurs only in *milleri,* both subspecies of *montezumae,* and *pygmaeus nigrensis,* but one additional tail pattern in *milleri* strongly resembles that of *variatus* and another in *montzumae montezumae* shows some similarities to a pattern found only in *maculatus.* Two macromelanophore spotted patterns of *milleri* are like those in *montezumae montezumae,* one of which also occurs in both *maculatus* and *variatus.* Each member of this division has a well developed, deep-lying ridge of black pigment midventrally on the caudal peduncle, but so do *helleri* and *clemenciae.* Only the subspecies of *montezumae* and *pygmaeus nigrensis* possess a well-developed, pigmented caudal appendage, as do *helleri* and *clemenciae*; the small colorless "sword" of *pygmaeus pygmaeus* is comparable with that of *variatus xiphidium*; *milleri* has none at all.

Some features of the gonopodia and gonopodial suspensoria of *milleri*, *pygmaeus*, and *montezumae* also cross divisional boundaries. The small claw at the tip of gonopodial ray 5a that characterizes somewhat less than 80 percent of available samples of *milleri* and *montezumae* occurs in about 10 percent of the *variatus* and 2 percent of the *maculatus* that have been examined. Other gonopodial features of *milleri* and *montezumae* are not distinctively different from those of the platyfishes. The claw and distal serrae in the gonopodium of *pygmaeus* are always readily identified. In the suspensorium the axial portion of the system (gonapophyses, parapophyses, ligastyle) of *montezumae* is like that of *helleri*; these elements are similar in *milleri* and *variatus xiphidium*, and in *pygmaeus* the structures are variable and not distinctive. Perhaps more than anything else these facts constitute the most direct evidence of the generic integrity of the platyfishes and swordtails that heretofore were accorded successively generic and subgeneric separation.

Nevertheless, all members of this division are typically inhabitants of stream communities and this ecological specificity is probably of some significance historically, as discussed above.

Adult females of *milleri* and *montezumae montezumae* are strikingly similar in general form and, particularly, in the complex development of the reticulum and banding along the sides and other pigment patterns. This is interpreted as at least presumptive evidence of a close relationship. Although a closeness of relationship between *montezumae* and *pygmaeus* seems strongly indicated, each has followed separate courses morphologically, the former in the great development of the caudal "sword" (as in *m. montezumae*) and the latter in de-emphasis of the distal serrae type of dorsal gonopodial holdfast in favor of the more specialized swordtail claw type (see above). Their close relationship was never before suspected, and the problem of their affinities is for the first time brought clearly in focus by the discovery of the new pygmy swordtail, *X. pygmaeus nigrensis*. This subspecies is remarkable in two ways. It is infinitely more swordtaillike than the nominate form, which now appears as a rather specialized poor relation. It is no wonder Hubbs and Gordon (1943) found difficulty in choosing between *Xiphophorus* and *Platypoecilus* as its place of final rest. Large adult males of *pygmaeus nigrensis* bear a striking resemblance to the often silvery blue males of *montezumae cortezi,* not only in general coloration, but in size, body proportions, shape and development of dorsal fin, and coloration and extent of development of the caudal appendage. In addition, a highly distinctive rectangular micromelanophore tail pattern occurs in *pygmaeus nigrensis* and *montezumae montezumae,* and rarely in *m. cortezi,* as discussed above. The relationships would not be at all apparent in the nominate forms of each species as in many respects *m. montezumae* and *p. pygmaeus* have diverged widely. It may be significant that in the 10 osteocrania of each that have been examined, the parietals exhibit a characteristic reduction and/or fragmentation.

The specific rank assigned to *montezumae* and *pygmaeus* depends upon their complete reproductive isolation in northern and southern tributaries of the Rio Panuco drainage. The coordinate status of *milleri* is inferred from the many and constant morphological features that make this form so distinctive. Its disjunct geographical position and apparently restricted distribution in the basin of Laguna Catemaco (Rio Papaloapan system) may perhaps result from competition with the ecologically similar and dominant swordtail, *helleri,* with which it occurs sympatrically.

III. THE *helleri* SPECIES GROUP (*clemenciae* AND *helleri*)

This group is characterized by the presence in adult males of a uniformly well developed and pigmented caudal appendage, a high, posteriorly pointed dorsal fin, one or more well-developed red lateral stripes running from base of caudal peduncle to opercle (a black stripe in many northern *helleri*), a black horizontal stripe running forward from eye to lips, a black or dusky axillary stripe running from pectoral base posteriorly along belly (absent in southern *helleri*), and a ridge of deep-lying black pigment along ventral edge of caudal peduncle. Their gonopodia have a claw constantly developed at tip of ray 5a; distal tip of ray 4a moderately to strongly hooked, underlying blade (ray 3) moderately to strongly pointed, and hook on ray 3 short and sickle-shaped. Though rarely taken directly in the current, these two swordtail species are confined mostly to headwater areas or regions adjoining swiftly flowing waters in potholes and shoreline eddies.

Of the eight species of *Xiphophorus, helleri* and *clemenciae* are the most highly specialized with reference to gonopodial characters and extent of development of lateral striping. These two forms may have split off from the main stem of a group antecedent to this and the previous division. Geographically this probably occurred some-where south of the Rio Panuco drainage area. The localized geographical position far south of Tampico and the somewhat more generalized gonopodium of *clemenciae* open up the possibility that it, not *helleri,* may have been the original swordtail invader of the southern Atlantic drainages of Mexico, only later to be replaced by *helleri* that had evolved in isolation farther north. That *helleri* undoubtedly had already attained essentially its present form in the north before entering upon the great southerly extension of its range is indicated by the north-south clinal nature of its morphological change. A morphologically less stabilized species undertaking such an extensive emigration might be expected to leave behind a less coherent record.

The status of these two forms as valid biological species is established by their complete reproductive isolation in the upper part of the Rio Coatzacoalcos, to which *clemenciae* is apparently restricted.

SUMMARY AND CONCLUSIONS

Drawing upon information from the present studies of the comparative and functional morphology, distribution, and ecology of *Xiphophorus* and those made during the last quarter of a century on their genetics, cytology, embryology, endocrinology, and ethology, the species are arranged and classified in a manner that is believed indicative of their phylogenetic relationships.

Descriptive Basis of Classification

Sixteen morphological features are considered in relation to 1) variations in their expressions corresponding with differences in size, age, or sex, 2) amounts and kinds of variability at the population, race, subspecies, and species levels, and 3) their probable adaptive significance. The morphological details found to be of primary importance in defining the species and subspecies are 1) bony elements at the tip of the adult male's external genitalium (gonopodium), 2) pigmentary patterns, both basic patterns and individual melanophore markings, and 3) presence, absence or extent of development of the caudal fin appendage or "sword." Traits having secondary taxonomic importance or that are more meaningful at supraspecific levels are: 1) gonopodial suspensorium, 2) head skeleton, including dentition and osteocranium, 3) pectoral girdle, 4) number of dorsal fin rays and lateral scales, 5) number of vertebrae, and 6) six relative body measurements. An analysis of these morphological details in the members of 124 natural populations of *Xiphophorus* indicates that the genus may be conveniently divided into 8 species and 11 subspecies, as contrasted with the 7 species and 6 informally listed subspecies of previous classifications.

EXPERIMENTAL BASIS OF CLASSIFICATION

The taxonomic divisions based on morphological criteria are evaluated from the standpoint of the developmental and functional disturbances that have been detected in 47 different types of laboratory-produced hybrids between morphologically distinct forms. The hybrid abnormalities considered fall under the general headings of sterility, embryonic lethality, endocrine imbalance, atypical pigment-cell growth, and anomalies of the external genitalium. Many of these defects are traceable directly or indirectly to the union of incompatible genetic systems. Two lines of evidence suggest that the degree of atypical pigment cell growth and the severity of structural anomalies in the gonopodia of hybrids may be used as measures of the degree of genetic relationship between the parental forms. Such information has provided one basis for assessing the status of these forms as valid biological species. Data presented in this study and reported by others on the effects of hybridization are consistent with the systematic portrayal of the genus based upon morphological considerations. The following taxa are recognized:

Xiphophorus couchianus (Girard)

Xiphophorus maculatus (Guenther)

Xiphophorus variatus (Meek)
  Xiphophorus variatus variatus (Meek)
  Xiphophorus variatus xiphidium (Gordon)
  Xiphophorus variatus evelynae, new subspecies

Xiphophorus milleri, new species

Xiphophorus montezumae Jordan and Snyder
  Xiphophorus montezumae montezumae Jordan and Snyder
  Xiphophorus montezumae cortezi, new subspecies

Xiphophorus pygmaeus Hubbs and Gordon
  Xiphophorus pygmaeus nigrensis, new subspecies
  Xiphophorus pygmaeus pygmaeus Hubbs and Gordon

Xiphophorus clemenciae Alvarez

Xiphophorus helleri Heckel
  Xiphophorus helleri helleri Heckel
  Xiphophorus helleri strigatus Regan
  Xiphophorus helleri guentheri Jordan and Evermann
  Xiphophorus helleri alvarezi, new subspecies

ZOOGEOGRAPHY AND EVOLUTION OF THE GENUS

The behavior and ecological specializations of the species and subspecies are examined with reference to kinds of geographical or topographical isolation that in the evolution of the genus may have given rise to 1) the present day geographical distribution of the genus as a whole, and 2) the biological isolating mechanisms that prevent hybridization in nature between species now living sympatrically. Their mechanisms and routes of dispersal along the Atlantic coast of Mexico and northern Central America are considered in relation to what is known of the geologic history of this region. Reasons are advanced for suggesting that the spatial origins of *Xiphophorus* may have had as a focal point the great and complex river valleys of northern Veracruz and eastern San Luis Potosi.

On the basis of the combined evidence from 1) descriptive morphological studies, 2) experimental studies of the effects of hybridization on reproductive potential, development, physiology, morphological integration, and behavior, and 3) distributional and ecological analysis, three phyletic lines are defined, as:

I. THE *maculatus* SPECIES GROUP (*couchianus, maculatus, variatus*). The unifying features of these three platyfish species are identified chiefly in their overall ecological specializations for sluggish waters, general build, and gonopodial traits, and by the fact that available experimental evidence indicates the presence in all of genetically compatible sex determining mechanisms and genetic homology of several differentiation areas in their gonopodia (external male genitalia). Because of the consistency of these allopatric species throughout their known ranges in a combination of morphological, physiological, and ecological factors, they are here treated as distinct. However *maculatus* and *variatus* are regarded as constituting a well-defined superspecies to emphasize their very close affinities.

II. THE *montezumae* SPECIES GROUP (*milleri, montezumae, pygmaeus*). This division of the benus is rather diffuse, as some of its uniting features show similarities to the highly specialized green swordtail (*helleri*) and others to the superspecies including *maculatus* and *variatus*. Despite its somewhat ambiguous position, much indirect evidence is presented for the erection of this division, especially as it shows a number of structural grades intermediate between the most and least specialized members of the genus. In addition to many similarities in body and fin pigmentation, all members of this division are typically inhabitants of stream communities. This ecological specificity is thought to be of some significance phylogenetically. The specific rank assigned to *montezumae* and *pygmaeus* depends upon their complete reproductive isolation in nature under conditions of sympatricity. The coordinate status of the allopatric *milleri* is inferred from its many and constant distinctive morphological features.

III. THE *helleri* SPECIES GROUP (*clemenciae, helleri*). This group is set apart from the others by the high degree of specialization of pigmentary and gonopodial features. Though these two forms are superficially very similar in appearance, their status as valid biological species is established by their complete reproductive isolation in the upper part of a single river to which *clemenciae* is restricted. It is suggested that *clemenciae* may have been the original swordtail invader of the southern Atlantic drainages of Mexico, only later to be replaced by *helleri* that had evolved in isolation farther north.

It is further suggested that 1) members of divisions II and III, the swordtail species, were all derived from a common prototype that evolved in a headland stream biota, but that the highly specialized members of division III may have split off early from the main stem, 2) members of division I, the platyfishes, probably were derived from a lowland form that was characteristic of lentic environments, and 3) the center of adaptive radiation of the genus may have been in the region surrounding and including the Rio Panuco basin.

APPENDIX 1

NOTES ON MERISTIC CHARACTERS [1]

Method

An attempt was made to study the relationship between the geographical location of a station and the values observed at that station for the meristic characters. In order to put geographic location into a numerical form, certain approximations were necessary.

The river systems in which *Xiphophorus* has been collected are arranged in the order of their common Atlantic Ocean drainage, determined by the position of each river's mouth. The correlation between the position of a river system and the meristic characters of the fish in it was studied. Each river system, and consequently each station, was assigned a numerical value in relation to each species found in it, by numbering consecutively the river systems in which each particular species is found, beginning with the northern most. While this procedure is somewhat artificial, it has the advantage of being simple and definite.

Another numerical value associated with each station is its altitude. It was found profitable to use the best available estimates of station altitudes, though some of these may be inaccurate (see table 33). The correction between meristic characters and altitudes is probably underestimated because of the inaccuracies; it is unlikely to be overestimated. Thus, while better values of the altitudes would be helpful in the present analysis, they are not essential.

Each station was treated as providing a single set of observations; no attempt was made to allow for sample sizes except that stations from which five or fewer specimens were available have been disregarded. A few stations that could not be located precisely when the calculations were made were not included in the calculations. The one or two stations that were omitted for any one species, could hardly affect the results substantially. Wherever a sufficient number of stations was available, total, partial, and multiple correlation coefficients and partial regression coefficients, were calculated (see table 35).

---

[1] The arranging of the data for analysis and their mathematical treatment are gratefully credited to Hugh Gordon, Department of Mathematics, Harvard College, Cambridge, Massachusetts. The author, however, assumes full responsibility for all biological conclusions drawn from this analysis.

Analysis

The accompanying table gives values for certain correlation coefficients. In particular, $r_{13 \cdot 2}$ measures the correlation between north-south position and meristic characters, and $r_{23 \cdot 1}$ measures that between altitude and the meristic characters. In three cases, one of these coefficients differs significantly from zero. The number of dorsal fin rays decreases from north to south and increases with altitude in *Xiphopohrus maculatus.* The number of dorsal fin rays decreases from north to south in *X. helleri.* Consideration of the multiple correlation coefficient indicates some relation between either north-south position, or altitude and number of scales in the lateral series in *X. helleri.* Probably this number decreases from north to south and increases with altitude. Certain other correlations also appear probable from the table.

Discussion

In all five cases for which calculations were made the correlations are such that the effect of increasing latitude is equivalent to that of increasing altitude. Some of the correlations involved are small. The resemblance of northern populations to those at high altitudes suggests a relationship with temperature. Assuming that temperature differences actually produce the effects noted, and that the correlation coefficients correctly reflect the real correlation despite the effects of chance:

The number of dorsal fin rays decreases with temperature in *X. variatus* and in *X. maculatus.*

The number of dorsal fin rays increases with temperature in *X. helleri*;

The number of scales in the lateral series increases with temperature in *X. maculatus*;

The number of scales in the lateral series decreases with temperature in *X. helleri.*

It should be noted that even the portion of the variation in the number of fin rays that is correlated with temperature may be genetic, rather than environmental in character. The data on laboratory-reared *X. helleri* support this view. Considering their small size, the laboratory populations would not be expected to give exactly the same values for the mean number of fin rays as the wild populations from which they are derived, even if environment had no influence on that number. For this reason it is not worth while to compare wild

TABLE 35

VARIANCES, CORRELATION COEFFICIENTS, AND REGRESSION COEFFICIENTS FOR MERISTIC CHARACTERS AS RELATED TO GEOGRAPHICAL LOCATION IN *Xiphophorus*

	Dorsal fin rays			Scales in lateral series	
Species	*variatus*	*maculatus*	*helleri*	*maculatus*	*helleri*
N	11	21	31	11	17
$\sigma^2{}_3$	.25	.10	1.00	.02	.41
$\sigma^2{}_{3\cdot 1}$	.24	.10	.46	.02	.27
$\sigma^2{}_{3\cdot 2}$	.17	.06	.80	.01	.27
$\sigma^2{}_{3\cdot 12}$	.17	.04	.43	.01	.23
r_{13}	.14	—.24	.73	.22	—.59
r_{23}	.57	.66	—.45	—.61	.57
$r_{13\cdot 2}$	—.08	—.52	.68	.03	—.42
$r_{23\cdot 1}$	.56	.75	—.26	—.59	.40
$\mathbf{r}_3({}_{12})$	.58	.77	.76	.64	.67
$b_{31\cdot 2}$	—.014	—.062	.154	.001	—.053
$b_{32\cdot 1}x10^3$	.37	.95	—.14	—.81	.17
a	11.02	9.39	11.79	23.35	27.06
$z_{13\cdot 2}$	—.08 .34	—.59 .24	.83 .38	.03 .38	—.44 .28
$z_{23\cdot 1}$	.65 .38	.97 .24	—.27 .19	—.67 .38	.42 .28
$N\mathbf{r}_3({}_{12})$	3.64	12.41	17.67	4.53	7.60
$P(z_{13\cdot 2})$	.8	.014	.000012	.9	.11
$P(z_{23\cdot 1})$	.09	.00005	.16	.08	.13
$P(\mathbf{r}_3({}_{12}))$	.17	.002	.00015	.11	.02

1 (as a subscript) has the following significance. For each species, the river systems in which that species is found are numbered consecutively from north to south. 1 refers to these numbers.

2 (as a subscript) refers to the altitude in feet.

3 (as a subscript) refers to the number of dorsal fin rays or of scales in the lateral series as indicated at the tops of the columns.

variance: $\sigma^2{}_3$

residual variances: $\sigma^2{}_{3\cdot 1}$, $\sigma^2{}_{3\cdot 2}$, $\sigma^2{}_{3\cdot 12}$

correlation coefficients: r_{13}, r_{23}, $r_{13\cdot 2}$, $r_{23\cdot 1}$, $z_{13\cdot 2}$, $z_{23\cdot 1}$, $\mathbf{r}^2{}_3({}_{12})$

regression coefficients: $b_{31\cdot 2}$, $b_{32\cdot 1}$. The "best linear estimate" of either meristic character on the basis of location is given by: $B_{31\cdot 8}X+b_{32\cdot 1}Y+a$ where X is the number of the river system (see above) and Y is the altitude in feet.

tests of significance: Standard errors are given for $z_{13\cdot 2}$ and $z_{23\cdot 1}$. $N\mathbf{r}^2{}_3({}_{12})$ may be regarded as a value of X^2 with two degrees of freedom for the purpose of determining whether $\mathbf{r}^2{}_3({}_{12})$ is significantly greater than zero.

probabilities: $P(z_{13\cdot 2})$, $P(z_{23\cdot 1})$ and $P(\mathbf{r}_3({}_{12}))$ are the probabilities of values as great as those obtained here for each respective correlation coefficient arising by chance in the absence of the particular correlation that coefficient measures.

with laboratory populations to any great extent. Table 26 shows that a population of *X. helleri* with a low fin ray count, one with a medium count, and one with a high count each maintain their counts, with minor changes, in the laboratory. Thus the temperature-correlated variation appears to be in part, hereditary in *X. helleri.*

APPENDIX 2

KEY TO SPECIES OF *Xiphophorus*

1a. Without a distinct ridge of black pigment midventrally on caudal peduncle.

  2a. Distal serrae on ray 4p of gonopodium of male converging at their tips (fig. 3a). Both sexes usually sharply bicolored, dark above and pale below, except in faded specimens in which only the midlateral section of the reticular pigment is apparent; frequently with 1 to 3 broken rows of deep-lying black dashes along caudal peduncle; without micromelanophore tail patterns or superficial macromelanophore spotted patterns. Rio Grande Basin, Nuevo Leon Mexico . . . . *Xiphophorus couchianus*

  2b. Distal serrae on ray 4p of gonopodium of male not converging at their tips, spread apart like fingers on a hand (fig. 3b-j). Both sexes rarely sharply bicolored; without deep-lying black dashes along caudal peduncle; frequently with micromelanophore tail patterns and/or superficial macromelanophore spotted patterns (fig. 5).

    3a. Reticular pigment developed into an indistinct netlike pattern above and below midside; without horizontal zigzag stripe at midside. Dorsal fin rays 7 to 11, usually 9 or 10. Scales in a lateral series 22 to 25, usually 23 or 24. Atlantic coastal streams and rivers from Veracruz, Mexico, to northern British Honduras . . . . *Xiphophorus maculatus*

    3b. Reticular pigment developed into a distinct netlike pattern above midside; with one or two midlateral zigzag black or dusky stripes that are best developed anteriorly. Dorsal fin rays 9 to 14, usually 25 to 27. (A minute, unpigmented caudal appendage in male, Rio Soto la Marina system only.) Atlantic coastal streams and rivers of southern Tamaulipas, eastern San Luis Potosi, northern Veracruz, and eastern Puebla, Mexico . . . . *Xiphophorus variatus*

1b. With a definitive, superficial and/or deep-lying ridge of black pigment midventrally on caudal peduncle. (Occasionally partially obscured by overlying scales or heavy deposition of fatty tissue as in *X. montezumae cortezi,* in which the apparent pigment is restricted to the base of the caudal peduncle as a small, black streak.)

4a. Terminal portion of ray 4a of gonopodium of male arched slightly downward but never hooked sharply backward; blade blunt, rounded (figs. 9, 11). Reticular pigment developed into a distinct netlike pattern, or modified as a series of dusky or brown blotches on the upper sides. Ventral rays of caudal fin of male variably produced as a pointed appendage that may be with or without marginal black pigment, or caudal appendage wanting. Both sexes with 1 to 6 solid or zigzag black or dusky (never red) horizontal stripes on sides.

5a. Claw at tip of ray 5a of gonopodium of male small or obsolescent, always longer than high when present (fig. 11a-d). Without a series of dusky or brown blotches on the upper sides separated from the midelateral stripe by a clear area. Dorsal and caudal fin without a distinct thin line of marginal pigment.

6a. Male without pointed caudal appendage. In both sexes, standard length 5.6 to 6.7 times least depth of caudal peduncle, not under 5.6 in male. Dorsal fin rays 9 to 11, usually 10. Laguna Catemaco basin, Veracruz, Mexico . . . *Xiphophorus milleri*

6b. Male with pointed caudal appendage edge with black above and below. In both sexes standard length 3.8 to 6.3 times least depth of caudal peduncle, not over 5.5 in male. Dorsal fin rays 10 to 14, usually 11 or 12. Rio Panuco basin, San Luis Potosi and Veracruz, Mexico . . . *Xiphophorus montezumae*

5b. Claw at tip of ray 5a of gonopodium of male as high as long, with a distinct though small terminal cusp (fig. 11e-f). With a series of dusky or brown blotches on the upper sides separated from the midlateral black or brown stripe by a clear area. Dorsal and caudal fin of male frequently with a distinct thin line of black marginal pigment. (Caudal appendage of male variably produced, sometimes with a ventral margin of black pigment.) Rio Panuco basin, San Luis Potosi, Mexico . . . . *Xiphophorus pygmaeus*

4b. Terminal portion of ray 4a of gonopodium of male distinctly hooked or curved backward over sharply or bluntly pointed blade (figs. 18, 20). Reticular pigment not developed into a distinct netlike pattern above midside. Ventral rays of caudal fin of male produced as a pointed appendage edged with black above and below. Both sexes with a single solid or zigzag, black or dusky horizontal stripe, or one or more red stripes. (Red stripes appear paler than the surrounding integument in alcohol.)

7a. Terminal portion of ray 4a of gonopodium of male slender, the bony segments regular in outline and longer than high; claw at tip of ray 5a variably developed, not higher than distal serrae on ray 4p. Both sexes constantly with 2 or more horizontal red stripes at midside. Adult male constantly with a dusky stripe that extends backward from axillary region to a point above or just beyond anal base. Dorsal fin with a black or dusky bar nearer base than tip. Dorsal fin rays 10 to 13, usually 11 or 12. Upper Rio Coatzacoalcos basin, Oaxaca, Mexico . . . . *Xiphophorus clemenciae*

7b. Terminal portion of ray 4a of gonopodium of male heavy, the bony segments irregular in outline and frequently as high or higher than long; claw at tip of ray 5a constantly higher than distal serrae on ray 4p. Both sexes with a single, horizontal black or 1 to 6 red stripes on sides. Axillary stripe of adult male occurring together only with single black or dusky midlateral stripe, never with multiple red stripes. Dorsal fin without pigment, or with one or two irregular rows of black or red spots. Dorsal fin rays 11 to 17, usually 12 to 14. Atlantic coastal streams and rivers from Veracruz, Mexico, to northwestern Honduras . . . . . *Xiphophorus helleri*

LITERATURE CITED

Anonymous

1937. Platy map of Mexico from map by Gordon giving results of present work. Home Aquar. Bull., *In* All-Pets Mag., vol. 9, p. 46.

Arnold, J. P.

1914. Die Namenanderungen der labengebarenden Zahnkarpfen: Die Gattung *Xiphophorus.* Wochenschrift für Aquarien- und Terrarienkunde, vol. 11, no. 7, pp. 125-126.

Aronowitz, O., R. F. Nigrelli, and M. Gordon

1951. A spontaneous epithelioma in the platyfish, *Xiphophorus* (*Platypoecilus*) *variatus.* Zoologica, vol. 36, no. 4, pp. 239-242.

Atz, J. W.

[MS.] Morphological and genetic studies on the pigmentary patterns of xiphophorin fishes and their hybrids. Ph.D. thesis 1959, on file New York University.

Bailey, R. M., H. E. Winn, and C. L. Smith

1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci. Philadelphia, vol. 106, pp. 109-164.

Baker, J. A., and M. S. Ferguson

1942. Growth of platyfish (*Platypoecilus maculatus*) free from bacteria and other microorganisms. Proc. Soc. Exp. Biol. Med., vol. 52, no. 301, pp. 116-119.

Bayliss, E. C.

1929. Comments on platies. Fish Culturist, vol. 8, no. 7, pp. 76-78.

1943. Comments on platies. *Ibid.*, vol. 22, pp. 73-75 (reprinted from March 1929 number).

Bean, B. A.

1898. Notes on a collection of fishes from Mexico, with description of a new species of *Platypoecilus.* Proc. U.S. Natl. Mus., vol. 21, no. 1159, pp. 539-542.

Beldt, O. C.

1917. The origin of the red *helleri.* Aquatic Life, vol. 9, pp. 17-18.

Bellamy, A. W.

1922. Sex-linked inheritance in the teleost, *Platypoecilus maculatus.* Anat. Rec., vol. 24, no. 6. pp. 419-420.

1924. Bionomic studies on certain teleosts (Poeciliinae). I. Statement of problems, description of material and general notes on life histories and breeding behavior under laboratory conditions. Genetics, vol. 9, pp. 513-529.

1928. [Same title]. II Color pattern inheritance and sex in *Platypoecilus maculatus*. *Ibid.*, vol. 13, no. 3, pp. 226-232, 2 figs.

1936. Interspecific hybrids in *Platypoecilus*, one species ZZ-ZW, the other XY-XX. Proc. Natl. Acad. Sci., vol. 22, no. 9, pp. 531-536.

Berg, O., and M. Gordon

1953. Relationship of atypical pigment cell growth to gonadal development in hybrid fishes. *In* Gordon, Pigment Cell Growth. Academic Press, New York, pp. 43-72.

Bleeker, P.

1859-1860. Conspectus systematis cyprinorum. Natuurwetenschappelijk tijdschrift voor Nederlandsch-Indie, 20, pp. 421-441.

1860. Ichthyologiae Archipelagi Indici Prodromus, II. Cyprini. K. Natuurkundige vereeniging en Nederlandsche-Indie, Batavia, Verhandelengen, vol. 7, pp. 1-492, i-xiv.

Breder, C. M., Jr.

1932. A new department at Aquarium. Bull. N. Y. Zool. Soc., vol. 35, pp. 3-10.

1947a. An analysis of the geometry of symmetry with especial reference to the squamation of fishes. Bull. Amer. Mus. Nat. Hist., vol. 88, art. 6, pp. 325-412.

1947b. A note on protective behavior in *Gambusia*. Copeia, 1947, no. 4, pp. 223-227.

Breider, H.

1938. Die genetischen, histologischen und zytologischen Grundlagen der Geschwulstbildungung nach Kreuzung verschiedener Rassen und Arten lebengebarender Zahnkarpfen. Zeitschrift für Zellforschung und Mikroskopische Anatomie, vol. 28, no. 5, pp. 784-828.

Brind, W. L.

1914. Domesticated fish. Part 2. Privately printed, New York, pp. 16-22.

1919. *Platypoecilus maculatus*. Aquatic Life, vol. 4, pp. 167-168.

1938. The encyclopedia of tropical fishes. Home Aquar. Bull. *In* All-Pets Mag., vol. 9, no. 10, pp. 42-45; vol. 9, no. 11, pp. 39-41.

Buen, F. de

1940. Lista de peces de agua dulce de México. En preparación de su catálogo. Trabajos estación limnologica de Patzcuaro. Patzcuaro, Michoacan, vol. 2, pp. 1-66 (published in four parts).

Champy, C.

1924. Sexualité et hormones. Paris.

Chavin, W., and M. Gordon

1951. Sex determination in *Platypoecilus maculatus*. I. Differentiation of the gonads in members of all-male broods. Zoologica, vol. 36, no. 2, pp. 135-145.

Clark, E., L. R. Aronson, and M. Gordon

1949. The role of the distal tip of the gonopodium during the copulatory act of the viviparous teleost *Platypoecilus maculatus.* Anat. Rec., vol. 105, p. 506. [Abstract]

1954. Mating behavior patterns in two sympatric species of xiphophorin fishes: their inheritance and significance in sexual isolation. Bull. Amer. Mus. Nat. Hist., vol. 103, art. 2, pp. 135-226.

Crozier, W. J., and E. Wolf

1939a. The flicker response contours for genetically related fishes, II. Jour. Gen. Physiol., vol. 22, no. 4, pp. 463-485.

1939b. Temperature and critical intensity for response to visual flicker. III. On the theory of the visual response contour and the nature of the visual duplexity. Proc. Natl. Acad. Sci., vol. 25, pp. 171-175.

1939c. Temperature and critical illumination for reaction to flickering light. V. *Xiphophorus, Platypoecilus* and their hybrids. Jour. Gen. Physiol., vol. 23, No. 2, pp. 143-153.

1939d. Specific constants for visual excitation. IV. On the nature of genetic differences. Proc. Natl. Acad. Sci., vol. 25, no. 4, pp. 176-179.

Crozier, W. J., E. Wolf, and G. Zerrahn-Wolf

1937a. Critical illumination and flicker frequency in related fishes. Jour. Gen. Physiol., vol. 21, no. 1, pp. 17-56.

1937b. Intensity and critical frequency of visual flicker, I. *Ibid.*, vol. 21, no. 2, pp. 203-221.

1937c. Specific constants for visual excitation, I. Proc. Natl. Acad. Sci., vol. 23, no. 9, pp. 516-520.

Darwin, C.

1871. Descent of man and selection in relation to sex. C. Appleton and Co., New York, vol. 1, 409 pp.; vol. 2, 436 pp.

Dobzhansky, Th.

1941. Genetics and the origin of species, 2nd ed. Columbia Univ. Press, New York, 364 pp.

Eigenmann, C. H.

1893. Catalogue of the fresh-water fishes of Central America and southern Mexico. Proc. U.S. Natl. Mus., vol. 16, pp. 53-60.

Essenberg, J. M.

1923. Sex differentiation in the viviparous teleost *Xiphophorus helleri* Heckel. Biol. Bull., vol. 45, no. 1, pp. 44-96.

Evermann, B. W., and H. W. Clark

1906. New fishes from Santo Domingo. Proc. U.S. Natl. Mus., vol. 30, pp. 851-855.

Evermann, B. W., and W. C. Kendall

1894. The fishes of Texas and the Rio Grande Basin, considered chiefly with reference to their geographic distribution. Bull. U.S. Fish Comm., vol. 12 (1892), pp. 57-121.

Friedman, B., and M. Gordon

1934. Chromosome numbers in xiphophorin fishes. Amer. Nat., vol. 68, no. 7/8, pp. 446-455.

Gabriel, M. L.

1944. Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*. Jour. Exp. Zool., vol. 95, no. 1, pp. 105-147.

Garman, S.

1895. The cyprinodonts. Mem. Mus. Comp. Zool., vol. 19, no. 1, pp. 1-179.

Gerlach, G.

1909. Neuere lebengebärende Zahnkarpfen. VIII. *Platypoecilus maculatus*. Wochenschrift für Aquarien- und Terrarienkunde, vol. 6, no. 3, pp. 25-27.

Gerschler, M. W.

1914. Über alternative Vererbung bei Kreuzung von Cyprinodontidengattungen. Zeitschrift für Induktive Abstammungsund Vererbungslehre, vol. 12, no. 2, pp. 73-96.

Gill, T.

1876. Notes on fishes from the Isthmus of Panama, collected by Dr. J. F. Bransford, U.S.N. Proc. Acad. Nat. Sci. Philadelphia, vol. 28, pp. 335-336.

Girard, C.

1859. Ichthyological notices, 41-59. Proc. Acad. Nat. Sci. Philadelphia, no. 11, pp. 113-122.

Goldman, E. A.

1951. Biological investigations in Mexico. Smithsonian Misc. Coll., no. 115, pp. 1-476.

Goldschmidt, R.

1937. A critical review of some recent work in sex determination. I. Fishes. Quart. Rev. Biol., vol. 12, no. 4, pp. 429-439.

Goldsmith, E. D., R. F. Nigrelli, A. S. Gordon, A. H. Charipper, and M. Gordon

1944. Effect of thiourea upon fish development. Endocrinology, vol. 35, pp. 132-134.

Goodrich, H. B.

1929. Mendelian inheritance in fish. Quart. Rev. Biol., vol. 4, pp. 83-99.

1939. Chromatophores in relation to genetic and specific distinctions. Amer. Nat., vol. 73, no. 746, pp. 198-207.

Goodrich, H. B., G. A. Hill, and M. S. Arrick

1941. The chemical identification of gene-controlled pigments in *Platypoecilus* and *Xiphophorus* and comparisons with other tropical fishes. Genetics, vol. 26, no. 6, pp. 573-586.

Gordon, Hugh, and M. Gordon

1950. Colour patterns and gene frequencies in natural populations of a platyfish. Heredity, vol. 4, pp. 61-73.

1954. Biometry of seven natural populations of the platyfish, *Xiphophorus maculatus* from Central America. Zoologica, vol. 39, no. 2, pp. 37-59.

1957. Maintenance of polymorphism by potentially injurious genes in seven natural populations of the platyfish, *Xiphophorus maculatus*. Jour. Genetics, vol. 55, no. 1, pp. 1-44.

Gordon, Myron

1927. The genetics of a viviparous top-minnow *Platypoecilus*; the inheritance of two kinds of melanophores. Genetics, vol. 12, pp. 253-283.

1928. Pigment inheritance in the Mexican killifish. Interaction of factors in *Platypoecilus maculatus*. Jour. Heredity, vol. 19, no. 12, pp. 551-556.

1931a. Morphology of the heritable color patterns in the Mexican killifish *Platypoecilus*. Amer. Jour. Cancer, vol. 15, no. 2, pp. 732-787.

1931b. Hereditary basis of melanosis in hybrid fishes. *Ibid.*, vol. 15, no. 3, pp. 1495-1523.

1932a. Dr. Myron Gordon going on expedition. Aquatic Life, vol. 15, pp. 287-288.

1932b. Expedition for aquarium fishes in Mexico. Fish Culturist, vol. 12, pp. 3-5.

1932c. How fishes get their names. *Ibid.*, vol. 12, pp. 87-92.

1933a. The catching of the swordtailed platyfish and the climb to the Mexican Plateau. *Ibid.*, vol. 12, no. 6, pp. 143-146.

1933b. To the natural habitat of the new Moctezuma platyfish and the true Montezuma swordtail. Aquatic Life, vol. 16, pp. 518-522; vol. 17, pp. 4-6.

1933c. Natural polymorphism in related species of Mexican fishes. Amer. Nat., vol. 67, no. 708, pp. 77-78. [Abstract]

1934a. Von naturlichen Fundort und Fang des neuen *Platypoecilus variatus* und des echten *Xiphophorus montezumae*. Blätter für Aquarien- und Terrarienkunde, vol. 45, pp. 107-110.

1934b. A history of the common platyfish in aquaria from the earliest times. Fish Culturist, vol. 14, pp. 79-92.

1935a. Platyfish geography. Home Aquar. Bull., vol. 5, pp. 7-10.

1935b. The Monterrey platyfish and their molly companions. Home Aquar. Bull., vol. 5, pp. 185-188.

1935c. Heckel, the man behind the name *Xiphophorus hellerii*. Canadian Aquaria, vol. 3, pp. 50-51, 60.

1937. Genetics of *Platypoecilus*. III. Inheritance of sex and crossing over of the sex chromosomes in the platyfish. Genetics, vol. 22, pp. 376-392.

1938. The genetics of *Xiphophorus hellerii:* Heredity in Montezuma, a Mexican swordtail fish. Copeia, 1938, pp. 19-29.

1940a. The fish that was jungle born and city bred. Nat. Hist., vol. 45, pp. 96-106.

1940b. Back to nature platyfish. Aquarium, vol. 9, pp. 3-5.

1940c. Black wagtail platy. *Ibid.*, vol. 9, pp. 22-24.

1940d. Black wagtail platies. *Ibid.*, vol. 9, pp. 63-64.

1940e. The ecological isolation factor involved in the failure of *Platypoecilus* and *Xiphophorus* to hybridize in nature. Anat. Rec., vol. 78, no. 4, pp. 171-172. [Abstract]

1941a. *In* Reports of Investigators. Ann. Rept. Biol. Lab., Long Island Biol. Assoc., 1941, pp. 38-39. [Abstract]

1941b. Hybridization in seven species of Mexican fishes following removal of the geographical factors of isolation. Anat. Rec., vol. 81, (4th suppl.), pp. 112-113. [Abstract]

1942a. Mortality of albino embryos and aberrant Mendelian ratios in certain broods of *Xiphophorus hellerii.* Zoologica, vol. 27, pp. 73-74.

1942b. The true montezumae swordtails tenth year in the aquarium. Aquarium, vol. 10, pp. 196-197.

1942c. Frequencies of seven dominant genes in natural populations of *Platypoecilus maculatus* and experimental evidence of multiple allelic series. Rec. Gen. Soc. Amer., vol. 11, p. 76. [Abstract]

1943a. Black topper platy. Aquarium, vol. 12, pp. 71-72.

1943b. *In* Reports of Investigators. Ann. Rept. Biol. Lab. Long Island Biol. Assoc. (1942), pp. 27-28. [Abstract]

1943c. Genetic studies of speciation in the swordtail-platyfish group and of the experimentally produced hybrids. Trans. N. Y. Acad. Sci., ser. 2, no. 5, pp. 63-71.

1946a. The three to one ratio in genetic sex determination. Rec. Gen. Soc. Amer., vol. 15, pp. 51-52.

1946b. Interchanging genetic mechanisms for sex determination in fishes under domestication. Jour. Heredity, vol. 37, no. 10, pp. 307-320.

1946c. Genetics of ocular-tumor development (preliminary report). Jour. Natl. Cancer Inst., vol. 7, pp. 87-92.

1946d. Introgressive hybridization in domesticated fishes. I. The behavior of Comet a *Platypoecilus maculatus* gene in *Xiphophorus hellerii.* Zoologica, vol. 31, no. 2, pp. 77-88.

1947a. Speciation in fishes. Distribution in time and space of seven dominant multiple alleles in *Platypoecilus maculatus.* Advances in Genetics, vol. 1, pp. 95-132.

1947b. Genetics of *Platypoecilus maculatus.* IV. The sex determining mechanism in two wild populations of the Mexican platyfish. Genetics, vol. 32, pp. 8-17.

1948a. Effects of five primary genes on the site of melanomas in fishes and the influence of two color genes on their pigmentattoin. Biology of Melanomas, Special Publ. N. Y. Acad. Sci., vol. 4, pp. 216-268.

1948b. Review of the genetic factors in melanotic tumor development in fishes. Acta, vol. 6, no. 1, pp. 254-261.

1950a. Fishes as laboratory animals. *In* E. J. Farris (ed.), The Care and Breeding of Laboratory Animals. John Wiley and Co., New York, chap. 14, pp. 345-449.

1950b. The origin of modifying genes that influence the normal and atypical growth of pigment cells in fishes. Zoologica, vol. 35, pp. 19-20. [Abstract]

1950c. Heredity of pigmented tumours in fish. Endeavour, vol. 9, no. 33, pp. 26-34.

1951a. Genetics of *Platypoecilus maculatus*. V. Heterogametic sex-determining mechanism in females of a domesticated stock originally from British Honduras. Zoologica, vol. 36, no. 2, pp. 127-134.

1951b. The variable expressivity of a pigment cell gene from zero effect to melanotic tumor induction. Cancer Res., vol. 11, no. 9, pp. 676-686.

1951c. Genetic and correlated studies of normal and atypical pigment cell growth. Growth, Symposium 10, pp. 153-219.

1952a. Sex determination in *Xiphophorus* (*Platypoecilus*) *maculatus*. III. Differentiation of gonads in platyfish from broods having a sex ratio of three females to one male. Zoologica, vol. 37, no. 2, pp. 91-100.

1952b. Hereditary influences in melanoma development. Texas Rept. Biol. Med., vol. 10, no. 4, pp. 987-995.

1953a. The use of fishes in the evaluation of heredity in atypical pigment cell growth. Trans. N. Y. Acad. Sci., ser. 2, vol. 15, pp. 192-195.

1953b. The ecological niche of the pygmy swordtail, *Xiphophorus pygmaeus*, in the Rio Axtla, Mexico. Copeia, 1953, no. 3, pp. 148-150.

1953c. The influence of the mating system upon normal and atypical pigment cell growth. Acta, vol. 9, no. 4, pp. 787-793.

Gordon, M., and O. Aronowitz

1951. Sex determination in *Platypoecilus maculatus*. II. History of a male platyfish that sired all-female broods. Zoologica, vol. 36, no. 2, pp. 147-153.

Gordon, M., and P. Benzer

1945. Sexual dimorphism in the skeletal elements of the gonopodial suspensoria in xiphophorin fishes. Zoologica, vol. 30, pp. 57-72.

Gordon, M., H. Cohen, and R. F. Nigrelli

1943. A hormone-produced taxonomic character in *Platypoecilus* diagnostic of wild *P. xiphidium*. Amer. Nat., vol. 77, pp. 569-572.

Gordon, M., and F. Flathman

1943. The genetics of melanoma in fishes. VI. Mendelian segregation of melanophore reaction types in embryos of a melanomatous mother. Zoologica, vol. 28, no. 2, pp. 9-12.

Gordon, M., and A. C. Fraser

1931. Pattern genes in the platyfish. Inheritance of naturally occurring color pattern variations in the Mexican killifish, *Platypoecilus maculatus.* Jour. Heredity, vol. 22, pp. 168-185.

Gordon, M., and W. Lansing

1943. Cutaneous melanophore eruptions in young fishes during stages preceding melanotic tumor formation. Jour. Morph., vol. 73, pp. 231-245.

Gordon, M., and D. E. Rosen

1951. Genetics of species differences in the morphology of the male genitalia of xiphophorin fishes. Bull. Amer. Mus. Nat. Hist., vol. 95, art. 7, pp. 409-464.

Gordon, M., and G. M. Smith

1938a. The production of a melanotic neoplastic disease in fishes by selective matings. IV. Genetics of geographical species hybrids. Amer. Jour. Cancer, vol. 34, pp. 543-565.

1938b. Progressive growth stages of a heritable melanotic neoplastic disease in fishes from the day of birth. Amer. Jour. Cancer, vol. 34, no. 2, pp. 255-272.

Grobstein, C.

1940a. Endocrine and developmental studies of gonopod differentiation in certain poeciliid fishes. I. The structure and development of the gonopod in *Platypoecilus maculatus.* Univ. California Publ. Zool., vol. 47, no. 1, pp. 1-22.

1940b. Effect of testosterone propionate on regenerating anal fin of adult *Platyoecilus maculatus* females. Proc. Soc. Exp. Biol. Med., vol. 45, no. 283, pp. 484-486.

1942a. Effect of various androgens on regenerating anal fin of adult *Platypoecilus maculatus'* females. *Ibid.*, vol. 49, no. 297, pp. 477-478.

1942b. Endocrine and developmental studies of gonopod differentiation in certain teleosts. II. Effect of testosterone propionate on the normal and regenerating anal fin of adult *Platypoecilus maculatus* females. Jour. Exp. Zool., vol. 89, no. 2, pp. 305-328.

Grobstein, C., and A. W. Bellamy

1939. Some effects of feeding thyroid to immature fishes (*Platypoecilus*). Proc. Soc. Exp. Biol. Med. vol. 41, no. 233, pp. 363-365.

Gunther, A.

1866. Catalogue of the Physostomi . . . . Cat. Fishes Brit. Mus., vol. 6, pp. 1-368.

1869. An account of the fishes of the states of Central America, based on collections made by Capt. J. M. Dow, F. Godman, Esq., and O. Salvin, Esq. Trans. Zool. Soc. London, vol. 6, pp. 377-494.

Heckel, J.

1848. Eine neue Gattung von Poecilien mit rochenartigen Anklammerungsorgane. Sitzungsberichte der K. Akademie der Wissenschaften, Vienna, vol. 1, pp. 289-303.

Hubbs, C. L.

1924. Studies of the fishes of the Order Cyprinodontes, I-IV. Misc. Publ. Mus. Zool., Univ. Michigan, no. 13, pp. 1-31.

1935. Fresh-water fishes collected in British Honduras and Guatemala. *Ibid.*, no. 28, pp. 1-22.

1937. Fishes from San Carlos Mountains. Univ. Michigan Studies Sci. Ser., vol. 12, pp. 293-297.

Hubbs, C. L., and M. Gordon

1943. Studies of cyprinodont fishes. XIX. *Xiphophorus pygmaeus*, new species from Mexico. Copeia, 1943, pp. 31-33.

Hubbs, C. L., and C. L. Turner

1939. Studies of the fishes of the Order Cyprinodontes. XVI. A revision of the Goodeidae. Misc. Publ. Mus. Zool., Univ. Michigan, no. 42, pp. 7-80.

Jordan, D. S.

1878. A catalogue of the fishes of the fresh waters of North America. Bull. U.S. Geol. and Geogr. Surv., vol. 4, pp. 407-442.

1885. A catalogue of the fishes known to inhabit the waters of North America, north of the Tropic of Cancer, with notes on the species discovered in 1883 and 1884. Rept. U.S. Comm. Fish and Fish., vol. 13, pp. 789-973.

Jordan, D. S., and H. E. Copeland

1876. Check list of the fishes of the fresh waters of North America. Bull. Buffalo Soc. Nat. Sci., vol. 3 (1877), pp. 133-164.

Jordan, D. S., and B. W. Evermann

1896-1900. The fishes of North and Middle America. Bull. U.S. Natl. Mus., vol. 47 (4 pt.), pp. 1-3313.

Jordan, D. S., and C. H. Gilbert

1883. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus., vol. 16, pp. i-lvi, 1-1018.

Jordan, D. S., and J. O. Snyder

1900. Notes on a collection of fishes from the rivers of Mexico, with descriptions of twenty new species. Bull. U.S. Fish. Comm. (1899), pp. 115-147.

Kosswig, C.

1935. Die Kreunzung zweier XX-bzW., XY-Geschlechter miteinander und der Ersatz eines Y-Chromosoms einer Art durch das X-Chromosom einer anderen. Der Zuchter, vol. 7, no. 2, pp. 40-48.

1937. Genotypische und phanotypische Geschlechtsbestimmung bei Zahnkarpfen. VII. Kreuzungen mit *Platypoecilus xiphidium*. Archiv für Entwicklungsmechanik der Organismen (Wilhelm Roux), vol. 136, pp. 491-528.

Langer, W. F.

1913. Beitrage zur Morphology der viviparen Cyprinodontiden. Morphologische Jahrbuche, vol. 47, pp. 193-307.

Levine, M., and M. Gordon

1946. Ocular tumors with exophthalmia in xiphophorin fishes. Cancer Res., vol. 6, no. 4, pp. 197-204.

Lewis, C., and J. D. Campbell (ed.)

1951. The American Oxford Atlas. Oxford Univ. Press, New York, pp. 1-80, maps I-XXVI, 1-98.

Martin del Campo, R.

1938. Nota acera de algunos peces del Lago de Catemaco. Anales de Instituto Biologicas Mexicana, vol. 9, pp. 225-226.

Mayr, E.

1942. Systematics and the origin of species. Columbia Univ. Press, New York, 334 pp.

Meek, S. E.

1902. A contribution to the ichthyology of Mexico. Field Columbian Mus. Publ. 65, zool. ser., vol. 3, no. 6, pp. 63-128.

1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec. *Ibid.*, vol. 5, pp. i-lxiii, 1-252.

1907. Notes on fresh water fishes from Mexico and Central America. *Ibid.*, Publ. 124, vol. 7, pp. 133-157.

Meinken, H.

1933. Über einige, in letzter Zeit eingeführte Fische III. 3. *Platypoecilus variatus* S. E. Meek. Blätter für Aquarien- und Terrarienkunde, vol. 44, no. 6, pp. 89-92.

1934. [Same title]. 9. *Platypoecilus maculatus* Gunther var. *cyanellus* n. var. Der "Blanue Platy." *Ibid.*, vol. 45, no. 14, pp. 261-263.

Miller, R. R.

1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool., Univ. Michigan, vol. 68, pp. 1-155.

Myers, G. S.

1922a. The aquarium and its denizens. Hudson County Aquar. Soc., pp. 1-22.

1922b. A recently described aquarium fish. Copeia, no. 113, p. 89.

1932. The two Chinese labarinth fishes of the genus *Macropodus*. Lingnan Sci. Jour., vol. 11, no. 3, pp. 385-403.

1935. An annotated list of the cyprinodont fishes of Hispaniola, with descriptions of two new species. Zoologica, vol. 10, no. 3, pp. 301-316.

Needham, J.

1942. Biochemistry and morphogenesis. Cambridge Univ. Press, Cambridge, 787 pp.

Nigrelli, R. F., and M. Gordon

1944. A melanotic tumor in the silverside, *Menidia beryllina peninsulae* (Goode and Bean). Zoologica, vol. 29, no. 1, pp. 45-48.

1951. Spontaneous neoplasms in fishes. V. Acinar adenocarcinoma of the pancreas in a hybrid platyfish. *Ibid.*, vol. 36, no. 2, pp. 121-125.

Nigrelli, R. F., S. Jakowska, and M. Gordon

1951. The invasion and cell replacement of one pigmented neoplastic growth by a second, and more malignant, type in experimental fishes. Brit. Jour. Cancer, vol. 5, pp. 54-68.

Peters, C. H.

1933. *Platypoecilia variatus* variations. Home Aquar. Bull., vol. 2, no. 12, pp. 9-10.

Pierce, M. E.

1941. The activity of the melanophores of a teleost, *Mollienisia latipinna*, to light, heat and anesthetics. Jour. Exp. Zool., vol. 87, pp. 1-12.

Potts, H. E.

1942. The anatomy and morphology of the hypophysis of several species of ovo-viviparous poeciliids. Zoologica, vol. 27, no. 2, pp. 85-96.

Price, W. A.

1942. Migration of fresh-water biota via stream confluences of coalescing deltas. Jour. Geomorph., vol. 5, no. 2, pp. 167-170.

Rachow, A.

1932. *Mollienisia formosa* (Girard). Wochenschrift für Aquarien- und Terrarienkunde, vol. 29, no. 45, pp. 705-707.

1936. Fam. Poeciliidae Unterfam.: Poeciliinae *Platypoecilus variatus* S. E. Meek. Die Aquarienfische in Wort und Bild, lief. 13-14, sheets 145-146 (18C, c. 16), 1 fig.

Ralston, E. M.

1933. The chromosomes of *Xiphophorus*, *Platypoecilus* and their hybrids during maturation stages. Science, new ser., vol. 78, no. 2015, pp. 124-125.

1934. A study of the chromosomes of *Xiphophorus*, *Platypoecilus* and of *Xiphophorus-Platypoecilus* hybrids during spermatogenesis. Jour. Morph., vol. 56, no. 3, pp. 423-433.

Ramaswami, L. S.

1946. A comparative account of the skull of *Gambusia*, *Oryzias*, *Aplocheilus* and *Xiphophorus* (Cyprinodontes: Teleostomi). Spolia Zeylanica, vol. 24, no. 3, pp. 181-192.

Regan, C. T.

1906-1908. Pisces. Biol. Centrali-Americana; pp. i-xxxiii, 1-203.

1907. Diagnoses of new Central-American freshwater fishes of the families Cyprinodontidae and Mugilidae. Ann. Mag. Nat. Hist., 7th ser., vol. 19, pp. 64-66.

1911. On some fishes of the family Poeciliidae. *Ibid.*, 8th ser., vol. 8, pp. 373-374.

1913. A revision of the cyprinodont fishes of the subfamily Poeciliinae. Proc. Zool. Soc. London, vol. 4, pp. 977-1018.

Regnier, M.

1938. Contribution a l'etude de la sexualite des cyprinodontes vivipares (*Xiphophorus helleri, Lebistes reticulatus*). Bulletin biologique de la France et de la Belgique, vol. 72, pp. 385-493.

Rivero, L. H., and C. L. Hubbs

1936. Studies of the fishes of the Order Cyprinodontes. XV. The characters and relationships of *Furcipenis huberi* and *Alfaro cultratus*. Occ. Papers Mus. Zool., Univ. Michigan, no. 339, pp. 1-11.

Rosen, D. E., and R. M. Bailey

1959. Middle-American poeciliid fishes of the genera *Carlhubbsia* and *Phallichthys*, with descriptions of two new species. Zoologica, vol. 44, pt. 1, pp. 1-44.

Rosen, D. E., and M. Gordon

1953. Functional anatomy and evolution of male genitalia in poeciliid fishes. Zoologica, vol. 38, pt. 1, pp. 1-47.

Roth, A.

1932. *Mollienisia formosa* Girard from Tampico. Aquatic Life, vol. 16, no. 6, p. 249.

Rubin, A. A., and M. Gordon

1953. Effects of alpha-estradiol benzoate and methyl testosterone upon the platyfish *Xiphophorus maculatus* skeleton. Proc. Soc. Exp. Biol. Med., vol. 83, pp. 646-648.

Rust, W.

1939. Mannliche oder weibliche Heterogametie bei *Platypoecilus variatus*. Zeitschrift für Induktive Abstammungsund Vererbungslehre, vol. 77, no. 1, pp. 172-176.

Schauenburg, E.

1920. Beobachtungen an *Xiphophorus helleri* (hahnenfedrige Weibchen).—Aus der Heimat des Schwertträgers. Blätter für Aquarien und Terrarienkunde, vol. 31, no. 17, pp. 260-261.

Schreitmüller, W.

1910a. *Platypoecilus* sp. Blätter für Aquarien und Terrarienkunde, vol. 21, pp. 177-178.

1910b. Über *Platypoecilus maculatus* Gunther und *Platypoecilus* spec.? *Ibid.*, vol. 21, no. 36, pp. 573-576.

Sengün, A.

1950. Beiträge zur Kenntnis der erblichen Bedingtheit von Formünterschieden der Gonopodien lebendgbärender Zahnkarpfen. Revue de la Faculté des Sciences de l'Université d'Istanbul, ser. B, vol. 15, no. 2, pp. 110-133.

Shaw, G.

1932. The effects of biologically conditioned water upon rate of growth in fishes and amphibians. Ecology, vol. 13, no. 3, pp. 263-278.

Steindachner, F.

1863. Beiträge zur Kenntniss der Sciaenoiden Brasiliens und der Cyprinodonten Mejicos. Sitzungsberichte der K. Akademie der Wissenschaften, Vienna, vol. 48, pt. 1, no. 13, pp. 162-185.

Stoye, F. H.

1933. Einige neueingeführte Zahnkarpfen, I. Blätter für Aquarien- und Terrarienkunde, vol. 44, no. 18, pp. 305-309.

1934. The Mexican swordtails and platies. Aquarium, vol. 3, no. 4, pp. 84-86.

1935. Tropical fishes for the home: their care and propagation, 2nd ed. Carl Mertens, New York, 284 pp.

Sumner, F. B.

1943. A further report upon the effects of the visual environment on the melanin content of fishes. Biol. Bull., vol. 84, no. 2, pp. 195-205.

1945. The cause must have had eyes. Sci. Monthly, vol. 60, pp. 181-186, (March).

Sumner, F. B., and P. Doudoroff

1938. Some effects of light intensity and shade of background upon the melanin content of *Gambusia*. Proc. Natl. Acad. Sci., vol. 24, no. 10, pp. 459-463.

Sumner, F. B., and N. A. Wells

1933. The effects of optic stimuli upon the formation and destruction of melanin pigment in fishes. Jour. Exp. Zool., vol. 64, pp. 379-403.

Tamayo, J. L.

1946. Datos para la hidrología de la República Mexicana. Publication 84, Instituto Panamericano de Geografia e Historia, Mexico, 448 pp.

Taubles, J.

1916. Community aquaria. Aquatic Life, vol. 2, p. 16.

Tavolga, W. N.

1949. Embryonic development of the platyfish (*Platypoecilus*), the swordtail (*Xiphophorus*) and their hybrids. Bull. Amer. Mus. Nat. Hist., vol. 94, art. 4, pp. 165-229.

Trautman, M. B.

1942. Fish distribution and abundance correlated with stream gradients as a consideration in stocking programs. Trans. 7th North Amer. Wildlife Conf., vol. 7, pp. 221-223.

Troemner, J. L.

1943. Notes. Fish Culturist, vol. 23, no. 1, pp. 1-3.

Turner, C. L.

1940. Pseudoamnion, pseudochorion and follicular pseudoplacenta in poeciliid fishes. Jour. Morph., vol. 67, no. 1, pp. 58-89.

1941. Gonopodial characteristics produced in the anal fin of *Gambusia affinis affinis* by treatment with ethynyl testosterone. Biol. Bull., vol. 80, no. 3, pp. 371-383.

1942. A quantitative study of the effects of different concentrations of ethynyl testosterone in the production of gonopodia in females of *Gambusia affinis*. Physiol. Zool., vol. 15, no. 3, pp. 263-280.

1947. The rate of morphogenesis and regeneration of the gonopodium in normal and castrated males of *Gambusia affinis*. Jour. Exp. Zool., vol. 106, no. 2, pp. 125-143.

Waddington, C. H.

1957. The strategy of the genes. Macmillan Co., New York, 262 pp.

Weyenburgh, H.

1874. Bijdrage tot de kennis van het Visschengeschlacht *Xiphophorus* Heck. Verslagen en Mededeelingen K. Akademie van Wetenschappen, vol. 8, pp. 291-308.

Wheeler, A. C., and R. W. Ingle

1953. Fishes of the genus *Mollienesia*. Water Life, pp. 264-266, (October).

Wickbom, T.

1943. Cytological studies on the family Cyprinodontidae. Hereditas, vol. 29, pp. 1-24.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the Caribbean area are solicited especially.

Manuscripts should be of medium length—12 to 200 printed pages. Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges only. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this, fifty copies are furnished the author without cost.

PREPARATION OF MANUSCRIPT

Highly recommended as a guide is the "Style sheet for the scientific serial publications of the American Museum of Natural History," second edition, revised, 1953.

Manuscripts should be typewritten with double spacing, with ample margins, and on only one side of the paper. The author should keep a copy; the copy submitted must be the original. Tables, legends of figures, and all footnotes should be assembled separate from the text. Several legends or footnotes may be placed on a single sheet.

Illustrations, including maps and photographs, should be referred to as "figures" wherever possible. All illustrations are reduced to a maximum of 4¼ by 7⅛ inches. The scales, wherever it is necessary, should be incorporated into the figure.

All references to literature should conform with the bibliographic style used in recent numbers of the BULLETIN. Spell out in full the titles of non-English serials.

Footnote material should be kept to a minimum. However, provide copy for a footnote detailing the title, affiliations, and address of the author (see recent numbers of the BULLETIN).

Manuscripts must be accompanied by a synopsis—a brief and factual summary (not a mere description) of the contents and conclusions, which points out the presence of any new information and indicates its relevance. In it list all new organisms described and give their ranges; indicate all taxonomic changes proposed. The synopsis, written in full sentences, should be concise, but completely intelligible in itself without reference to the paper, thereby enabling the busy reader to decide more surely than he can from the title alone whether the paper merits his reading. The synopsis will be published with the paper, hence it does not replace the usual conclusions or summary sections. It will also serve as copy for the abstracting services.

Manuscripts and all editorial matters should be addressed to:

Editor of the BULLETIN
Flint Hall
University of Florida
Gainesville, Florida