

FISHES FROM THE UPLANDS AND  
INTERMONTANE BASINS OF  
GUATEMALA: REVISIONARY STUDIES  
AND COMPARATIVE GEOGRAPHY

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## CONTENTS

Abstract . . . . .	271
Introduction . . . . .	271
Acknowledgments . . . . .	273
Methods and Concepts . . . . .	275
Species Concepts and Cladistic Recognition of Natural Hybridization . . . . .	275
Measurements, Anatomical Terms, and Counts . . . . .	278
Poeciliid Fishes of the Genus <i>Heterandria</i> . . . . .	278
General Anatomy and Relationships to Other Poeciliids . . . . .	278
Analysis of Selected Characters and Interrelationships of Species . . . . .	280
Gonopodial Suspensorium . . . . .	280
Gonopodium . . . . .	281
Meristic Characters . . . . .	287
Morphometric Characters . . . . .	288
Pigment Patterns . . . . .	293
Dentition . . . . .	297
Synapomorphy Scheme for the Species . . . . .	298
Analytical Key . . . . .	310
Systematic Account . . . . .	312
Genus <i>Heterandria</i> Agassiz . . . . .	312
Subgenus <i>Heterandria</i> . . . . .	312
<i>Heterandria formosa</i> Agassiz . . . . .	314
Subgenus <i>Pseudoxiphophorus</i> Bleeker . . . . .	315
<i>Heterandria attenuata</i> , New Species . . . . .	315
<i>Heterandria jonesi</i> (Günther) . . . . .	319
<i>Heterandria litoperas</i> , New Species . . . . .	320
<i>Heterandria obliqua</i> , New Species . . . . .	321
? <i>Heterandria obliqua</i> x <i>Heterandria bimaculata</i> . . . . .	322
<i>Heterandria anzuetoi</i> , New Species . . . . .	324
<i>Heterandria cataractae</i> , New Species . . . . .	328
<i>Heterandria dirempta</i> , New Species . . . . .	329
<i>Heterandria bimaculata</i> (Heckel) . . . . .	330
Poeciliid Fishes of the Genus <i>Xiphophorus</i> . . . . .	332
General Anatomy and Relationships to Other Poeciliids . . . . .	332
Analysis of Selected Characters and Interrelationships of Species . . . . .	334
Explanation of the Synapomorphy Scheme for the Species . . . . .	342
Synapomorphy Scheme . . . . .	347
Analytical Key . . . . .	350
Systematic Account . . . . .	353
Genus <i>Xiphophorus</i> Heckel . . . . .	353
<i>Xiphophorus couchianus</i> (Girard) . . . . .	353
<i>Xiphophorus gordonii</i> Miller and Minckley . . . . .	353
<i>Xiphophorus variatus</i> (Meek) . . . . .	353
<i>Xiphophorus xiphidium</i> (Gordon) . . . . .	354
<i>Xiphophorus evelynae</i> Rosen . . . . .	354
<i>Xiphophorus maculatus</i> (Günther) . . . . .	356
<i>Xiphophorus milleri</i> Rosen . . . . .	356

*Xiphophorus pygmaeus* Hubbs and Gordon . . . . . 356

*Xiphophorus nigrensis* Rosen . . . . . 356

*Xiphophorus montezumae* Jordan and Snyder . . . . . 357

*Xiphophorus cortezi* Rosen . . . . . 357

*Xiphophorus clemenciae* Alvarez . . . . . 357

*Xiphophorus alvarezi* Rosen . . . . . 357

?*Xiphophorus alvarezi* x *Xiphophorus helleri* . . . . . 361

*Xiphophorus* "PMH" . . . . . 361

*Xiphophorus helleri* Heckel . . . . . 362

*Xiphophorus signum* Rosen and Kallman . . . . . 364

Comparisons of *Heterandria* and *Xiphophorus* and General Summary . . . . . 365

Points of Geographic Similarity . . . . . 365

Points of Geographic Dissimilarity . . . . . 366

Congruent and Incongruent Cladistic Elements in Relation to Geography . . . . . 370

Literature Cited . . . . . 374



## ABSTRACT

Continuing studies of the fish fauna of the karst regions of Guatemala along the northern foothills of the sierras have revealed the presence of about two dozen species in thirteen genera and nine families in isolated basins with subterranean outlets. Eleven to thirteen of these species, mostly fishes of the family Poeciliidae, are endemic to the isolated basins; five have been described previously. Among poeciliid fishes, members of the genera *Heterandria* and *Xiphophorus* are best represented in the karst regions. Because of similarities in their geography the two genera are reviewed together: nine species of *Heterandria* are recognized, of which six are new (*H. attenuata*, *H. litoperas*, *H. obliqua*, *H. anzuetoi*, *H. cataractae*, *H. dirempta*); 15 species of *Xiphophorus* are recognized, of which none is new, although numerous taxa previously recognized as subspecies are treated here as species. Taxonomic decisions concerning recognized species of *Xiphophorus* are based on a reconsideration of various current species concepts from which it is concluded that the "biological species" should be rejected as a conceptual tool and the "subspecies" as a methodological one. Earlier taxonomic accounts of *Heterandria* and *Xiphophorus* by the author are found to be unacceptable because they were not rigorously and explicitly based on a search for shared derived characters (synapomorphies). Many of the subgroups recognized in those prior accounts are grade groups based merely on the failure of the included taxa to possess the derived defining characters of other subgroups, therefore suggesting, that they were, in fact, defined unacceptably by shared primitive characters (symplesiomorphies). As newly revised on the basis of proposed synapomorphy schemes, and the derivative cladograms of relationship, various members of *Heterandria* and *Xiphophorus* are shown to possess a number of cladistic similarities in relation to geography:

1. Mexican and Central American species together form a natural group separated from their sister group to the north by a gap, the southern boundary of which is somewhat to the north of Tampico, Mexico.

2. In Middle America the sister group of a group including many southern Mexican and Central American species is in the region around Tampico.

3. A relatively plesiomorphic species occupies two separate isolated karst basins along the western foothills of the sierras in Guatemala.

4. Less plesiomorphic forms occupy the two southernmost Guatemalan rivers that drain into the Gulf of Honduras as well as Atlantic coastal drainages of Honduras.

5. The most apomorphous sister pair of species includes a widespread species that extends along coastal regions of southern Mexico and parts of the Yucatan Peninsula and a species that is confined to an easterly karst basin.

6. Putative hybrids are present between the distributions of the westerly karst species and the widespread form. A discussion of cladistic theory in relation to hybridization suggests how the cladistic interrelationships of putative parents can resolve whether or not intergradation between species in nature is to be considered secondary (i.e., due to the effects of hybridization).

The geographic similarities between *Heterandria* and *Xiphophorus* are compared by converting their cladograms of taxa into cladograms of areas. In terms of probability theory, it is concluded that the congruence of their area cladograms at a very high confidence level indicates that the two genera shared, in part, a common history in Middle America.

## INTRODUCTION

Explorations between 1963 and 1974 of a series of isolated river basins in the Río Usamacinta watershed along the northern edge of the Sierra de Chamá and its westerly extension in Guatemala have uncovered numerous endemic fishes, some of which are related to species from other geographically remote areas

to the south (Rosen, 1967, 1970, 1972). Some of the endemic forms belong to two poeciliid genera, *Heterandria* and *Xiphophorus*, which have northerly distributions. It was found that the populations of *Heterandria* and *Xiphophorus* from some of the isolated basins associated with the two westerly tributaries of

the Río Usumacinta (the Río Lacantún and Río Salinas) are more closely related to each other than they are to the members of these two genera in the isolated basin associated with the eastern Usumacinta tributary (the Río de la Pasión). The historical implications of this coincident geographic pattern prompted the present detailed systematic analyses of the two genera, and the results of the systematic analyses of *Heterandria* and *Xiphophorus* have provided opportunities for a review of some aspects of congruence and vicariance theory in biogeography, species concepts and related taxonomic matters (Rosen, 1978, and comments below).

The northern foothills of the Sierras in Guatemala and in neighboring regions of Honduras and Mexico (Chiapas) are formed mainly of Cretaceous limestones that have been somewhat uplifted and then unevenly eroded during the Tertiary to form a complex karst topography of undulating hills, steep escarpments, collapsed ground surface, caves, and sink holes. A large but unknown percentage of the water is subterranean and the surface waters follow erratic courses in and around the more erosionally resistant limestone mounts. Some of the surface waters have become isolated from their parent rivers by the collapse of a part of their stream beds to form subterranean passages, in some cases followed by a reversal in the direction of water flow, or by the down-dropping of a whole block of land to separate upper and lower stream sections by cascades or ribbon falls. It is presumably the erosional processes, which have been going on since the appearance of major basement and surface folding of the land during the early Eocene orogenic phase of Middle American geohistory (De Cserna, 1960; Weyl, 1973; Anderson et al., 1973), that have created opportunities for the isolation and preservation of some old faunal elements. I say "old" because in the groups that have been studied cladistically, fishes in all but one of the isolated basins occupy plesiomorph positions, and those in the main river tributaries to the north, apomorph positions, in their cladograms of relationships. Another indication of considerable age for some of the intermontane isolates is the geographic re-

moteness of their nearest relatives—in the Great Lakes of Nicaragua and in South America.

Although a considerable effort has been made to explore the karst regions in Guatemala, it is evident from a brief report by Miller (1957) that similar areas of the neighboring mountains in Chiapas are both virtually unknown and clearly worth exploring. In that report Miller noted the presence, in an isolated laguna of 7 km. extent, of a peculiar and hitherto unknown poeciliid (still undescribed because of the lack of adult males); moreover, I have had an opportunity to study some more recently collected specimens of a swordtail (genus *Xiphophorus*) slightly different from, but apparently related to, those from the endemic upland fauna of Guatemala. Thus, the challenge to understand this probably relic karst fauna of nuclear Central America remains.

The fish fauna in the isolated basins of the Río Usumacinta watershed in Guatemala is known at present to include about two dozen species in 13 genera and nine families. Of these, two characids (*Bramocharax baileyi* Rosen and *B. dorioni* Rosen, which was originally described as a subspecies of *B. bransfordi* Gill) and seven poeciliids (*Scolichthys iota* Rosen and *S. greenwayi* Rosen; *Xiphophorus signum* Rosen and Kallman, originally described as a subspecies of *X. helleri* Heckel; and four species of *Heterandria* to be described below) are endemic to these basins. In addition, a distinct form of the characid genus *Astyanax* and other poeciliids of the genera *Poecilia* and *Xiphophorus*, may also prove on subsequent study to represent endemic taxa. In terms of numbers of taxa per family, the fauna consists of the following: Characidae (4 or 5), Ictaluridae (one reported but not collected), Pimelodidae (3), Cyprinodontidae (1), Poeciliidae (11 to 13), Atherinidae (1), Cichlidae (2; one of the two, *Cichlasoma champotonis*, is represented by a single specimen), Eleotridae (1), Synbranchidae (1).

Each of the three southern tributaries of the Río Usumacinta, the western Río Lanactún and Río Salinas (= Río Chixoy or Río Negro) and the eastern Río de la Pasión, has one or more isolated basins associated with its upper course



along the foothills of the Sierras in the departments of Huehuetenango, El Quiché or Alta Verapaz. In some instances, the point of subsidence of a basin is less than a kilometer distant from its presumed connection with a main Usumacinta tributary. Specimens that appear to be intergrades between an endemic isolate and a main river form in *Heterandria* and in *Xiphophorus* have been collected in the upper Río Lacantún and Río Salinas and just downstream of their isolated basins.

The fish fauna of the three main tributaries of the Usumacinta north of the subterranean passages that isolate them from the upland basins includes more than 50 species in 32 genera and 20 families, of which 17 (three undescribed) are cichlids and 10 (one undescribed) are poeciliids.

The principal isolated basins of Guatemala fall into several categories (figs. 1, 2): (1) a single large, western basin, the upper Río San Ramón, of Río Lacantún drainage; (2) a single, small eastern basin, the Río Chajmaic, of Río de la Pasión drainage; (3) a central series of three small and one large basin, the Río Dolores, of which the Río Dolores and one small basin of only a few hundred yards in extent have Río Salinas drainage and two small basins, the Río Chiaín and Río Candelaria Yalicar, within the same enclosed, oval Candelaria valley, have unknown drainage; (4) a series of one small and two moderate-sized basins that lie between the Candelaria valley and the Río de la Pasión and have a mixture of Río Dolores and Río de la Pasión faunal elements, and have Río de la Pasión drainage; (5) a small, headwater stream, the Río Sachicha, isolated by a long ribbon fall from water which flows into the Río Salinas and whose fauna is shared in part with the Río Dolores; (6) a series of still unexplored basins to the east associated with the Río de la Pasión, Río Sarstún and Río Polochic watersheds, and (7) the numerous streams, lakes, lagunas, and sink holes of the north in the department of El Petén some of whose water historically, and in some cases currently, and some of whose fauna is related to the drainages, and fauna, of Belize (British Honduras), particularly the Río Hondo, Río Belize and New River. This report is concerned

mainly with the endemic species of *Xiphophorus* and *Heterandria* in basins of the first six categories as well as their interrelationships with congeners that exist outside these basins from North America southeastward to Honduras and Nicaragua.

The plan of this paper is first to present a detailed cladistic review of *Heterandria*, followed by a reconsideration of the systematics of *Xiphophorus* incorporating new information and considerably modifying an earlier, and now unacceptable, taxonomic analysis of my own (Rosen, 1960). It concludes with a comparison of the two groups in relation to cladistic structure and geography.

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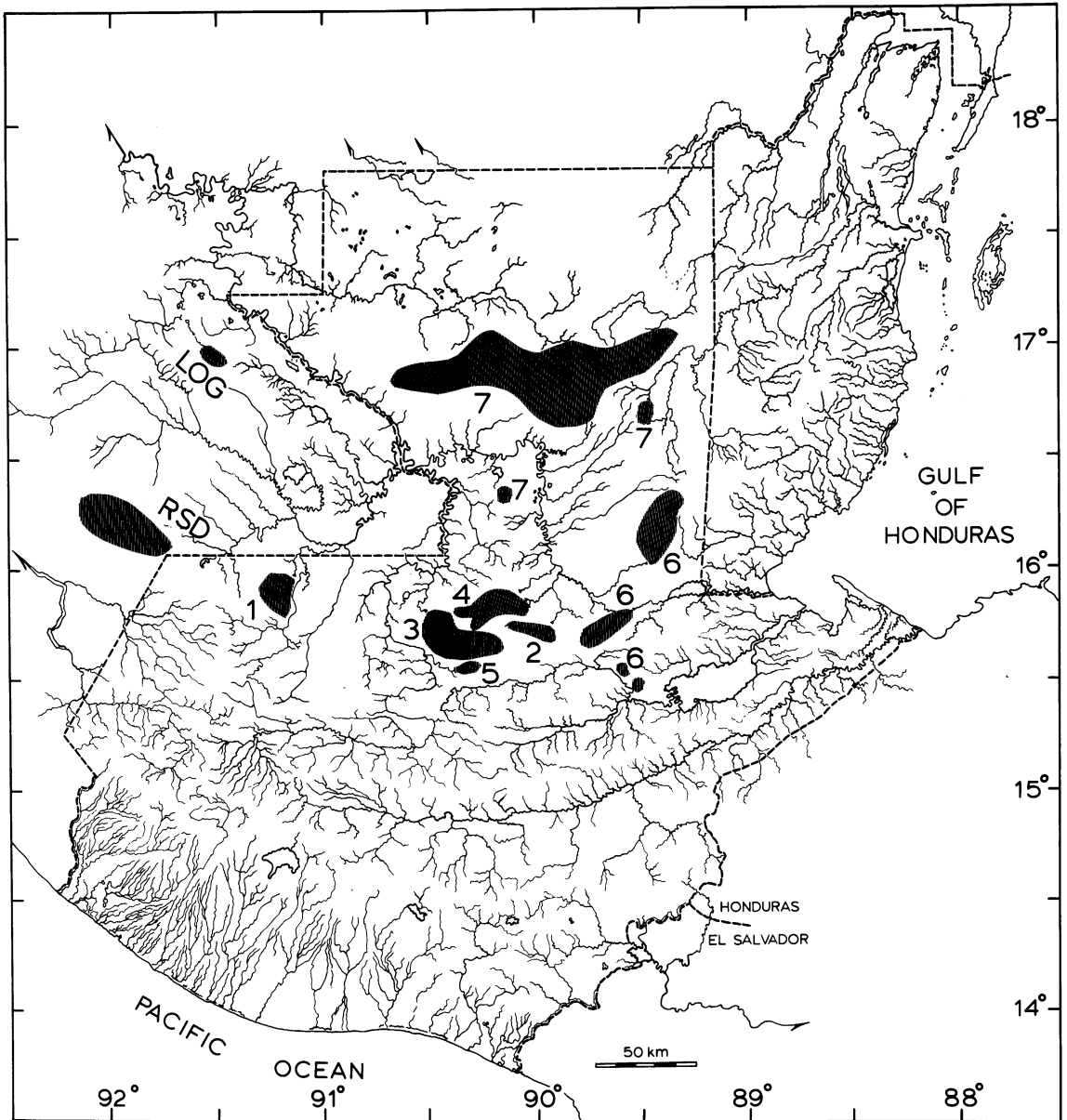


FIG. 1 Some major areas of isolated inland basins of northern Guatemala and neighboring Chiapas, Mexico. 1, upper Río San Ramón basin, Río Lacantún system, Río Usumacinta drainage. 2, Río Chajmaic basin, Río de la Pasión system, Río Usumacinta drainage. 3, Río Dolores basin (including a small surface stream at Cubilguitz, and, questionably, the Río Candelaria Yalcar and Río Chiaín), Río Salinas system, Río Usumacinta drainage (Río Candelaria Yalcar and Río Chiaín may possibly be of Río de la Pasión drainage). 4, Río Candelaria and Río San Simón basins, the latter in two sections, Río de la Pasión system, Río Usumacinta drainage. 5, Río Sachicha basin, Río Salinas (= Río Negro or Río Chixoy) system, Río Usumacinta drainage. 6, upper Río Sarstún basin, Río Sarstún drainage (6, center); Río Ixbobo basin, Río de la Pasión system, Río Usumacinta drainage (6, upper); two small basins (6, lower) associated with the Río Cahabón system, Río Polochic (Lago Izabal-Río Dulce) drainage. 7, lakes and streams of the Petén district (7, upper), of which the eastern ones (Lago Petén Itzá and Laguna Yaxjá) had a probable former surface drainage into the Río Hondo of northern Belize and the western ones a probable former drainage into the Río Usumacinta watershed; Laguna Las Pozas (7, left lower), Río de la Pasión system, Río Usumacinta drainage; upper isolated basins of the Río Mopán system (7, right lower), Río Belize drainage. In Chiapas, Mexico, LOG represents Laguna Ocotal Grande, RSD, Río Santo Domingo, and the shaded area to left of RSD a major isolated basin presumably associated with the Río Santo Domingo and the Río Lacantún system.



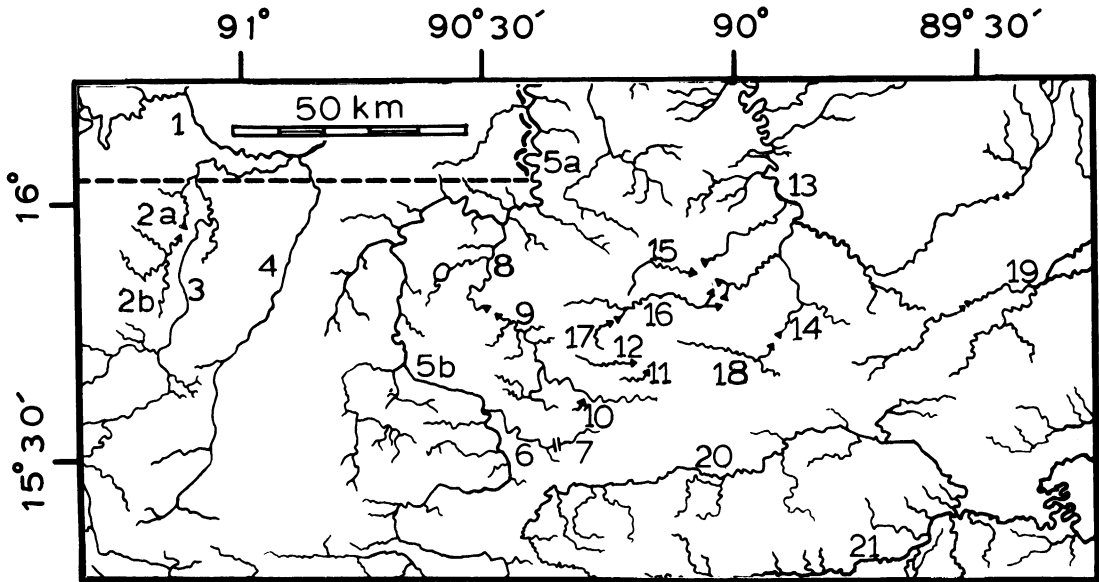


FIG. 2. Detail of the rivers and streams of the karst region of the departments of Huehuetenango, El Quiché, Alta Verapaz and Izabal in northern Guatemala. 1, Río Lacantún; 2a, lower Río San Ramón; 2b, upper Río San Ramón (isolated); 3, Río Ixcán; 4, Río Xalbal; 5a, Río Salinas; 5b, Río Chixoy or Negro; 6, Río Senizo; 7, Río Sachicha (isolated); 8, Río Ixvolay; 9, Río Dolores (isolated); 10, small stream at Cubilguitz (isolated); 11, Río Chiafín (isolated); 12, Río Candelaria Yalicar (isolated); 13, Río de la Pasión; 14, Río Sebol; 15, Río Candelaria (isolated); 16, lower Río San Simón (isolated); 17, upper Río San Simón (isolated); 18, Río Chajmaic (isolated); 19, Río Sarstún; 20, Río Cahabón; 21, Río Polochic.

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## METHODS AND CONCEPTS

### SPECIES CONCEPTS AND CLADISTIC RECOGNITION OF NATURAL HYBRIDIZATION

Repeated attempts over a 10-year period (1963-1973) to produce laboratory hybrids be-

tween a distinct form of the green swordtail (originally described by Rosen and Kallman, 1969, as *Xiphophorus helleri signum*) and swordtails from various other parts of Middle America failed, although the unsuccessful at-

tempts involved direct and reciprocal combinations offering only a choice of a heterotypic mate. These results were unexpected in view of the extensive possibilities of interspecific hybridization in the genus that had been demonstrated by the quarter-century of genetic experiments with these fishes by Myron Gordon (see list of known hybrid combinations in Rosen, 1960; and Atz, 1962). Subsequently Kallman (personal commun.) conducted sperm-competition experiments with the aim of deciding whether the failure to achieve the laboratory hybridization of *signum* could have been due to inadequate laboratory procedure or to inherent reproductive properties of *signum*. His experiments consisted of mixing the sperms of *signum* and another swordtail (*X. helleri*) and of introducing the mixture by micropipette into the urogenital orifice of females of each form. Only homotypic offspring were produced, i.e., the heterotypic sperm were rejected. Although unsuccessful laboratory hybridization experiments are always subject to the suspicion of failure of experimental design, these results appear to come as close as one can to demonstrating a real reproductive incompatibility: all fish were maintained under the same laboratory conditions, all stocks produced offspring through many generations, and the homotypic young produced by artificial insemination were normal in all known respects. In relation to a "biological species" concept, one might use the above results to argue that *signum* is a separate species.

Within the framework of the "biological species" concept, zones of secondary intergradation (hybridization) in nature between recognizably different natural populations have been taken by some taxonomists as *prima facie* evidence that the two populations represent only a single species (Mayr, 1969, p.195). In the upper parts of the Río Lacantún and Río Salinas drainages along the foothills of the Guatemalan Sierras, there appears to be such a zone of intergradation between distinct forms within both *Xiphophorus* and *Heterandria*. In cladograms of relationships for the Middle American representatives of each group (see below, pp. 308 and 348), the alleged intergradation occurs between forms separated in their

respective cladograms by two or three branch points (fig. 3). If the above *prima facie* reasons for species recognition are accepted, C and F in figure 3 are one species of *Xiphophorus* and D and H are a species of *Heterandria*. The implications of these conclusions are that, in *Xiphophorus*, E, as the sister group of F, and D, as the sister group of E plus F, are a part of species C-F and, for similar reasons, E, F, and G are part of species D-H in *Heterandria*. The results of laboratory hybridization experiments reject that conclusion for *Xiphophorus* since F (= *signum*) is reproductively incompatible with E (= *helleri*). Of course, one might argue that the cladograms are wrong, that, for example, C is the sister group of F in *Xiphophorus* and the D is the sister group of H in *Heterandria*. To so argue, however, requires that reproductive compatibility is evidence of relationship—and, moreover, evidence that transcends all other criteria of relationship in its biological impor-

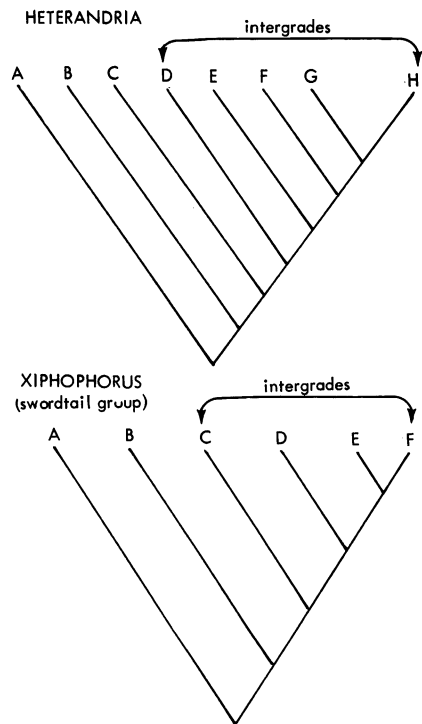


FIG. 3. Simplified cladograms derived from those in figures 48 and 49. Letters stand for taxa.



tance. But, within the history of any lineage, reproductive compatibility is an attribute of the members of the ancestral species of that lineage, an attribute which is gradually diminished and ultimately lost in its descendants during geographic differentiation. In other words, reproductive compatibility is a primitive attribute for the members of a lineage and has, therefore, no power to specify relationship within a genealogical framework. It is to be expected that reproductive compatibility, like other primitive traits, might be retained or altered in a mosaic pattern during evolution, an inference which is entirely consistent with the results of natural and laboratory mating patterns in *Xiphophorus*.

If, as it now appears, the "biological species" concept will lead to inferences that are in direct conflict with the avowed aims of systematics, viz., to reconstruct the genealogical history of lineages by a process of estimating a hierarchy of relationships, how are we to decide on the limits of species? Elsewhere (Rosen, 1978) I have argued that the "biological species" concept has other logical flaws associated with its criterion of sympatry to test for reproductive incompatibility, and I have suggested reasons for thinking that the "evolutionary species" concept is merely a decorative version of Regan's (1926) proposal that a species is what a competent taxonomist says it is. I have also argued that all populations or groups of populations that are distinguished by some definable apomorphy are potentially informative, whether they differ from other such populations qualitatively or only quantitatively (i.e., overlap in some derived traits but have different means). The specific reasons for this argument are that all populations defined by apomorphic traits can be incorporated into a cladistic hierarchy, and that this cladistic hierarchy forms the only logical basis for discussions of the history of organic change in time and space (the relevance of cladistic hierarchies to biogeography has been discussed by Platnick and Nelson, 1978; and Rosen, 1978). It seems evident, therefore, that if a "species" is merely a population or group of populations defined by one or more apomorphous features, it is also the smallest natural aggregation of individuals

with a specifiable geographic integrity that can be defined by any current set of analytical techniques. If a "subspecies" is, by definition, something less than a species, and yet a "species" is the smallest cluster of individuals in nature that can be defined, then subspecies are, also by definition, unobservable and undefinable. The idea of subspecies can thus be applied only if one employs criteria of species recognition other than those stemming from a search for derived characters to incorporate into a cladistic hierarchy. The only other such criterion of which I am aware is the potentially non-arbitrary reproductive property of "biological species" in nature, the search for which, however, is logically flawed (Rosen, 1978) and which implies, as an underlying premise, the use of a primitive character to specify relationships. I am, thus, compelled to reject both the "biological species" as a conceptual tool and the "subspecies" as a methodological one, and this argument constitutes my reason for now recognizing as species forms that were hitherto recognized as subspecies.

A final comment pertaining to the earlier discussion of natural hybridization is in order here, since there has been a long, and still active, discourse in systematics about how natural hybrids may be identified. The suggestions have included (1) observing intermediacy of characters; (2) observing that the suspected hybrids occur in a region where there is intergradation between the populations of other groups of organisms (i.e., they are in a zone of hybridization); (3) finding evidence that suspected hybrids are sterile; (4) experimentally duplicating the suspected hybrids by producing laboratory hybrids in cross-matings of the suspected parents, or (5) conducting various mathematical analyses designed to test for differences in variability between the suspected hybrids and parents. Still another suggestion is implicit in the cladograms of *Xiphophorus* and *Heterandria* discussed above. In each of these cases, the intergrades (putative hybrids) are between taxa that are separated by more than one branch point in the cladogram. The implication of this topology is that speciation events have occurred prior to the geographic overlap of the parental populations (two such events in

*Xiphophorus*, between D and E-F and between E and F, and three such events in *Heterandria*, between E and F-G-H, between F and G-H, and between G and H). A cladogram would not resolve instances of hybridization between sister species (e.g., between E and F in *Xiphophorus* or between G and H in *Heterandria*); but, then, this hardly seems important since intergrading sister-taxa are as easily interpreted as a single species which is undergoing subdivision as they are two species, still reproductively somewhat compatible, which have come together. Neither of these interpretations would conflict with the cladistic representation of such natural variation. Even a relatively lower fertility of the intergrades, usually considered the most crucial of the five criteria of hybridization above, would not resolve such interpretive problems: for example, in a U-shaped distribution in which the two ends of the distribution are biologically very different but in a region ecologically favorable for reproduction whereas the biologically intermediate midpoint of the distribution occurs in an ecologically unfavorable region that adversely affects gonad development, the result would be a primary intergradation accompanied by lowered fertility, as contrasted with a secondary intergradation (hybridization). I see no *a priori* reason why changes in intrapopulational variability might not also result from primary causes affecting different parts of a species' range, or even why such a species might not

develop geographic or ecophenotypic morphs (i.e., exhibit multi-modal character distributions). The simplest solution in such cases of intergradation would appear to be to treat the complex as one species, an action that would not conflict with any cladistic information. In contrast to the failure to resolve primary and secondary intergradation in cases of terminal sister species, the intergradation of species separated by one or more branch-points in their cladogram of relationships seems logically to call for the inference of hybridization. The more general conclusion that emerges, therefore, is that the suspicion of natural hybridization should be pursued within a framework of cladistic analysis of the two suspected parents and at least one other member of the group.

#### MEASUREMENTS, ANATOMICAL TERMS, AND COUNTS

In general, body and fin measurements and counts of numbers of scales, fin rays, and vertebrae follow standard practice in studying poeciliid fishes as given in Rosen and Bailey (1959). Some special measurements and counts of the external male genitalium (gonopodium) of poeciliids, not previously used elsewhere, are described in the text and footnotes to tabulated data. The nomenclature of parts of the gonopodial system follows Rosen and Bailey (1963), however.

### POECILIID FISHES OF THE GENUS *HETERANDRIA*

#### GENERAL ANATOMY AND RELATIONSHIPS TO OTHER POECILIIDS

Since the original proposal by Rosen and Bailey (1963) that *Pseudoxiphophorus bimaculatus* (Heckel) be included in *Heterandria* with *H. formosa* Agassiz, seven additional species, including those named here, have been added to the group, and the group has been subdivided by Miller (1974) into its original components, *Heterandria* and *Pseudoxiphophorus*, as subgenera. It is now appropriate,

therefore, to review Rosen and Bailey's reasons for the original merger of *H. formosa* and *P. bimaculatus* and to ask if present evidence agrees or disagrees with the proposal that *Heterandria* and *Pseudoxiphophorus* form a monophyletic assemblage. Before answering that question, it should be noted that the diagnoses of genera and other supra-specific groups in Rosen and Bailey were designed as phenetic statements of overall similarity. In short, little attention was paid to finding unique characters

for defining taxa and only an implicit effort was made to interpret the different states of a character as primitive or derived.

The various works of Willi Hennig (particularly 1966) and the many discussions of cladistic methodology during the last several years in *Systematic Zoology* have made it abundantly clear to me that phenetic measures of overall similarity are unable to provide a precise and repeatable basis for testing theories of phylogenetic relationship and comprise my reasons for adopting a cladistic methodology here. An example drawn from Rosen and Bailey will suffice: in their diagnosis of *Heterandria*, 19 characters are listed. Some are ambiguous, some are present in other groups of poeciliids of the tribe Heterandriini and may therefore be primitive for *Heterandria*, and only two can be shown to be unique derived characters known then in *formosa* and *bimaculata*. These two shared derived characters, or synapomorphies, concern the structure of the sixth gonactinost in the gonopodial suspensorium and the nature of the distal segments of gonopodial ray 3.

The structure of the sixth gonactinost noted by Rosen and Bailey refers to a winglike outgrowth that arises laterally near or at the dorsal tip of the gonactinost. Although these paired expansions of the dorsal tip of gonactinost 6 have been found to be well-developed in all the presently recognized forms of *Heterandria*, I have found similar but smaller expansions on this gonactinost in some other poeciliids, for example, in *Priapichthys annectens* and *P. pria*, and they may be present simply as a function of the width of the dorsal margin of the gonactinostal complex to which they are attached by ligaments. Hence, this character in *Heterandria* may be a highly derived state of a character that is a general synapomorphy for several groups of poeciliids (perhaps even the entire Heterandriini)—a possibility that could be decided only by reinvestigation of this problem.

The gonopodial character mentioned by Rosen and Bailey specifies that the subdistal segments of ray 3, normally seen in most poeciliids as spinelike elements, are represented instead by short clublike structures without free tips. Spines of this type are present, however, in some forms of *Brachyrhaphis* (tribe Gambu-

siini) and in *Priapichthys annectens* (tribe Heterandriini). In *Brachyrhaphis*, the character is probably primitive for the Gambusiini since it is also present in the sister group of *Gambusia*, *Belonesox belizanus*, and in *Gambusia vittata*, the sister group of other species of *Gambusia*.<sup>1</sup> In the heterandriin genus *Priapichthys*, the character is present only in *P. annectens*, the other members of the genus having well-formed spines. But whether the character is primitive or derived in *Heterandria* depends on knowing its probable sister group. If its sister group is, for example, *Neoheterandria* in which spines, though few in number, are present as small pointed elements subdistally on ray 3, the trait in *Heterandria* would be derived if the sister group of *Heterandria* plus *Neoheterandria* also had normal spines. Since in other heterandriins with symmetrical gonopodia (the species of *Priapichthys*), normal spines are present in all except *P. annectens*, it is most parsimonious to assume that clublike elements represent a derived character in *Heterandria*, and that such structures have been acquired independently in *P. annectens* and in the ancestor of the Gambusiini. Heterandriins with asymmetrical gonopodia (*Poeciliopsis* and *Phallichthys*) either have unmodified ray 3 segments or bluntly tipped spines with free tips (one species of *Phallichthys*).

In addition to the above two characters found by Rosen and Bailey, I have identified a skeletal character and some pigmentary features which help to define *Heterandria* as a monophyletic group. The skeletal character is a clublike swelling of the segments at the tip of ray 6 of the gonopodium. Swollen distal segments on gonopodial rays 6 and 7 are present in several other poeciliids, but uniquely in *Heterandria*, so far as I can find, the distal tip of the clublike part is elongated ventrally into a pointed

<sup>1</sup>Both *Belonesox belizanus* and *Gambusia vittata* lack many of the derived gonopodial features of other *Gambusia* and, instead, have gonopodia only slightly but similarly more derived than those of some *Brachyrhaphis*. *Gambusia vittata*, but not *Belonesox*, however, has a synapomorphy with all other *Gambusia*, namely, the development of a notch along the upper margin of the pectoral fin in the male.

process that extends toward ray 5 at a very shallow angle. The only comparable modification may be found, again, in the genus *Priapichthys* in which, in *P. annectens*, the ventral part of the swollen sixth ray bears a pointed process directed posteriorly rather than postero-ventrally. The pigmentary feature mentioned above is more a combination of features present in some manner in all species of *Heterandria*: a distinct basicaudal spot, a strong or diffuse lateral band, and basal pigment on the dorsal and anal fins.

The character which, traditionally, has been thought of as distinguishing the species of *Heterandria* is the presence of one or more segments at the tip of gonopodial ray 4a that enter a terminal membranous sheath and form a ventrally directed hooklike or finger-like appendage at the tip of the fin. Although a very similar structure is present in all known species of *Neoheterandria* (Rosen and Bailey, 1963, figs. 57d-f), the terminal hook in *Heterandria* is never arched upward as it is in *Neoheterandria* and appears to be a synapomorphy of *Heterandria*, as discussed below.

There are many resemblances between *Heterandria* and other heterandriin genera, some of which have been discussed above in relation to the characters of *Priapichthys* and *Neoheterandria*. The species of *Heterandria* also resemble members of the genera *Poeciliopsis* (in the form of gonapophyses of the gonopodial suspensorium; cf. figs. 4 and 5 with figs. 55 and 56 in Rosen and Bailey, 1963) and *Phallichthys* (a still undescribed Costa Rican form with a terminal hook on gonopodial ray 3 rather like that in *Heterandria*).

The conclusion reached from all these comparisons is that although the nearest relatives of *Heterandria* may lie somewhere within the Heterandriini, a precise sister group relationship cannot yet be specified. Partly, the problem arises from the fact that some of the heterandriins are not anatomically as well known as others. Partly, it arises from the fact that past accounts of heterandriins have been formulated with phenetic criteria of overall similarity and useful statements about apomorphic characters are difficult to extract from this literature.

Together, these two limitations make it difficult or even impossible, without much new study, to decide whether *Priapichthys*, for example, is a monophyletic group *sensu* Hennig (1966).

In order to proceed one must assume, therefore, that the present outgroup comparisons have been appropriate for assigning polarity to the different states of a character within a transition series and that certain enumerated traits of the species assigned to *Heterandria* are synapomorphic for the group. I have made these working assumptions and provisionally redefine *Heterandria* on the basis of five characters discussed above: the combined pigmentary features of the body and fins, the modification of the dorsal tip of gonactinost 6 in the gonopodial suspensorium of the male, the structure of the spines on gonopodial ray 3, the modifications of the distal half of gonopodial ray 6, and the one or more segments at the tip of gonopodial ray 4a that enter a decurved or hooked membranous sheath.

#### ANALYSIS OF SELECTED CHARACTERS AND INTERRELATIONSHIPS OF SPECIES<sup>1</sup>

**GONOPODIAL SUSPENSORIUM:** With respect to the form and orientation of the gonapophyses, there are two types of suspensoria among the species of *Heterandria* (figs. 4,5). In *formosa* (Rosen and Bailey, 1963, fig. 55A) and *attenuata*, the shaft of the third gonapophysis is nearly parallel with that of the second, and the uncini on all three gonapophyses originate nearer the base than the tip of the gonapophyseal shaft. In the other species, the shaft of the third gonapophysis is bent forward at a noticeable angle to the shaft of the second, and the uncini on the last two gonapophyses arise at the midpoint, or nearer the tip, of the gonapophyseal shaft. Within the Heterandriini, a bent third gonapophysis occurs in some but not all species of *Poeciliopsis* (compare figs. 55D, 56A,B with 56C,D in Rosen and Bailey, 1963) and where bent in *Priapichthys nigroventralis* the bent shaft of the third gonapophysis is parallel with the bent

<sup>1</sup>Other characters are discussed in the synapomorphy scheme for the nine species (pp. 298-310).



shaft of the first and second. In *Neoheterandria umbratilis* (fig. 54E, Rosen and Bailey, *op. cit.*) the third element is curved gently forward, parallel with the first, but not with the second, gonapophysis. In all other heterandriins (the other species of *Priapichthys*, and *Neoheterandria*, and in *Phallichthys*) the gonapophyseal shafts are nearly straight, bent slightly forward, or are decurved and are parallel, or at least the last two gonapophyses are so aligned. On the basis of the widespread occurrence of parallel gonapophyses within the Heterandriini (and in most other poeciliids as well) and the occurrence of non-parallel second and third elements in only some members of other presumed monophyletic groups, I tentatively conclude that the parallel condition (in *H. formosa* and *H. attenuata*) is primitive and the non-parallel condition derived.

With reference to the site of the uncini, the species of *Poeciliopsis* and *Phallichthys* (figs. 55C,D; 56 in Rosen and Bailey, 1963) have these processes arising on the last two gonapophyses at the midpoint (*Poeciliopsis*), or nearer the tip (*Phallichthys*), of the shaft as in *Heterandria jonesi*, *H. litoperas*, *H. obliqua*, *H. anzuetoi*, *H. cataractae*, *H. dirempta*, and *H. bimaculata*. In all other heterandriins (figs. 53, 54, 55A,B in Rosen and Bailey, *op. cit.*) they arise proximally on the last two gonapophyses as in *Heterandria formosa* and *H. attenuata*. In *Poeciliopsis* and *Phallichthys*, however, the uncini on the last two gonapophyses almost consistently arise farther out on the shaft than in any species of *Heterandria*, and from this, and the general distribution of proximal uncini in other heterandriins, as well as other poeciliids with long gonopodia (other possible sister-groups of *Heterandria*), I conclude that proximal uncini (as in *H. formosa* and *H. attenuata*) may be regarded as primitive for *Heterandria*.

**GONOPodium:** There are three segmental gonopodial characters that form transformation series among the species of *Heterandria*: (figs. 6,7) (1) the terminal one or two segments of the fourth anterior ray (4a) which enter a slightly to strongly decurved membranous envelope; (2) the number of short, penultimate segments on the same ray (4a); and (3) the

small, peglike processes that arise ventrally on those short, penultimate segments.

To understand the polarity of the transformation of the first character requires evidence that the different conditions of the character in *formosa* and the other taxa are different states of the same character, and that one or more of these states can be regarded as derived relative to the others. These conditions, in turn, depend on an interpretation of the terminal portion of ray 4a of *Heterandria* in relation to that of other poeciliids, particularly other heterandriins, among which a precise sister-group relationship of *Heterandria* is most likely to be discovered. Other heterandriins do in fact show some specialization of the tip of gonopodial ray 4a. Among fishes presently classified in *Priapichthys* all species, except for *P. nigroventralis*, have a slightly to strongly decurved ray 4a, but the segments at the tip of the ray are undifferentiated (figs. 32D-F; 35C,D in Rosen and Gordon, 1953; figs. 57A, B, C in Rosen and Bailey, *op. cit.*). In *P. nigroventralis* ray 4a is straight and is terminated by an elongate segment with an enlarged distal end. In *Neoheterandria* the entire distal part of the fourth ray is arched upward toward the fifth and at the gonopodial tip ray 4a, consisting of several ankylosed segments or of one crescentic segment, is strongly decurved (fig. 57D,E,F, in Rosen and Bailey, *op. cit.*). In *Phallichthys* and *Poeciliopsis* the gonopodium is permanently asymmetric and the tip of ray 4a is greatly reduced and twisted to one side; in one species of *Phallichthys* (to be described by W.A. Bussing), however, there is a somewhat enlarged and curved terminal segment on ray 4a. Of these various conditions, the distal part of ray 4a in *Heterandria* most resembles that of the species of *Priapichthys* (*nigroventralis* excluded) in not being arched upward (as in *Neoheterandria*) or asymmetric (as in *Phallichthys* and *Poeciliopsis*), but instead being decurved and having its ultimate and penultimate segments enter a terminal, membranous envelope. Assuming the validity of these comparisons, I infer that the relatively undifferentiated ray 4a of *Priapichthys* is primitive for the Heterandriini, that this ray in *Heterandria* is specialized only in having an elongate ultimate

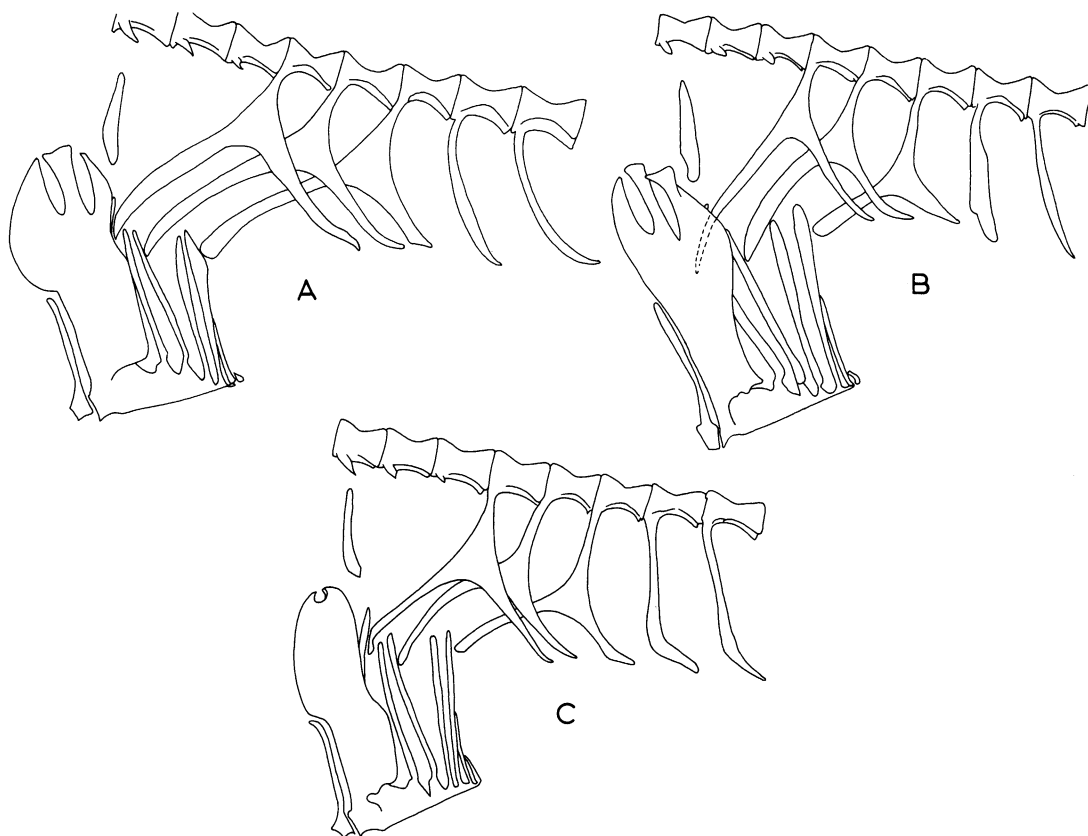


FIG. 4. Gonopodial suspensoria in *Heterandria* (simplified). A, *H. attenuata*, AMNH 36334. B, *H. jonesi*, UMMZ 187718. C, *H. litoperas*, AMNH 24492.

segment entering the decurved membranous envelope, and in having this ultimate segment preceded by one or more short segments and then more proximally by additional elongate elements.

Within *Heterandria*, the simplest explanations for the difference between *formosa* and the other species are that in *formosa* the ultimate and penultimate segments have become incorporated into an enlarged, decurved terminal envelope and that in the other species only the ultimate segment has been enlarged. Thus, the condition in *formosa* is primitive for all species and the condition in *attenuata* is derived relative to that in *formosa* and primitive relative to that in other species. This explanation is consistent with the frequency distribu-

tion in the number of penultimate short segments of ray 4a. In *formosa* there are one, or rarely two short segments; in *attenuata* and *jonesi* there are modally three or four; and, in the other species, there are modally more than four (table 1). Also consistent in polarity with this scheme is the frequency distribution in the number of ventral, peglike processes on the penultimate short segments: there are none in *formosa*, *attenuata*, and *jonesi*, two in *litoperas*, and more than two in the other taxa.

A summary of the argument that synthesizes anatomical data derived from the study of gonopodial ray 4a follows: *formosa* differs from the other species in having the penultimate short segments enter the decurved, terminal membranous envelope, in never having

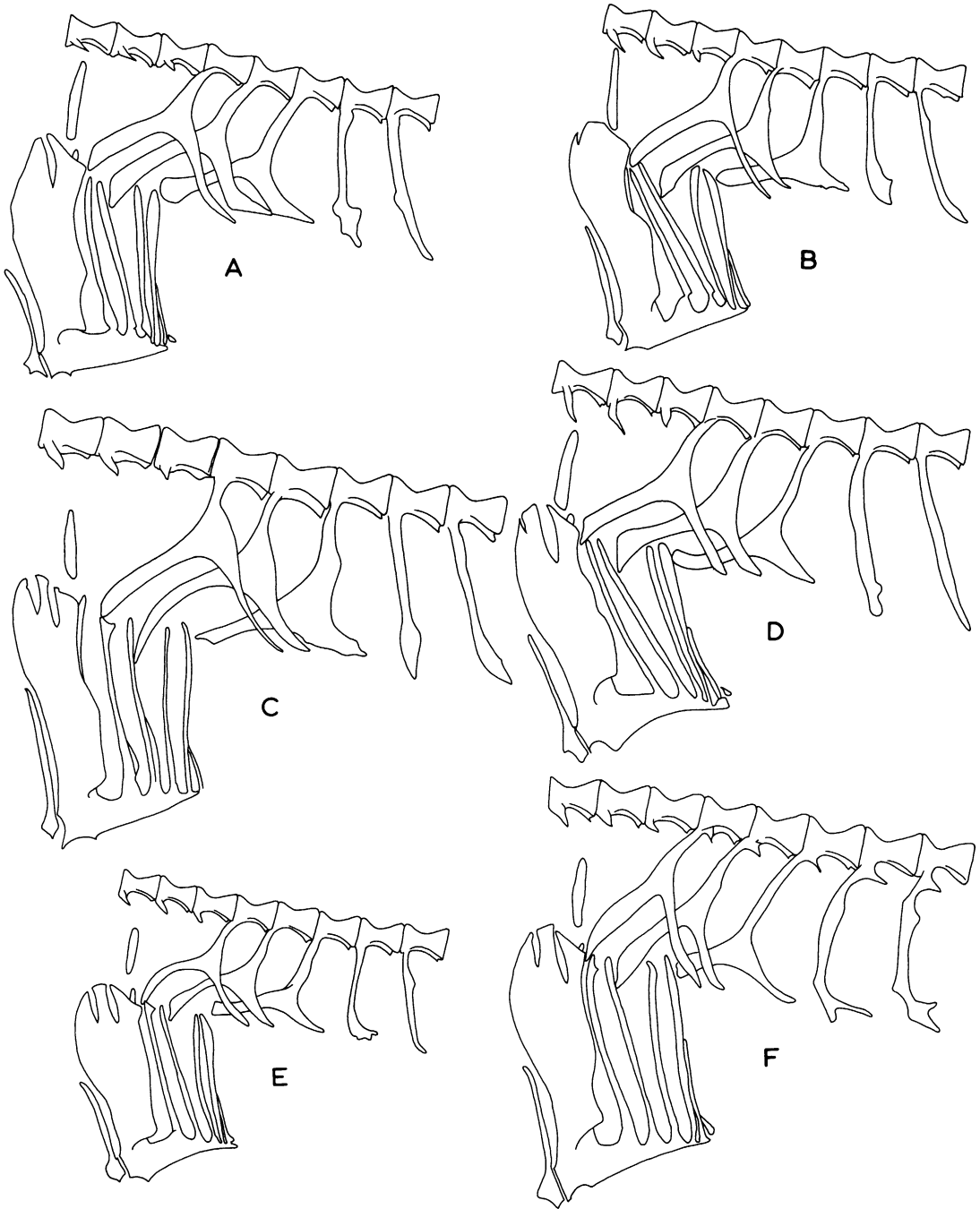


FIG. 5. Gonopodial suspensoria in *Heterandria* (simplified). A, *H. obliqua*, AMNH 36318. B, *H. anzueto*, AMNH 36326; C, same, AMNH 36325. D, *H. bimaculata*, AMNH 36338; E, same, AMNH 36347; F, same, AMNH 1377.

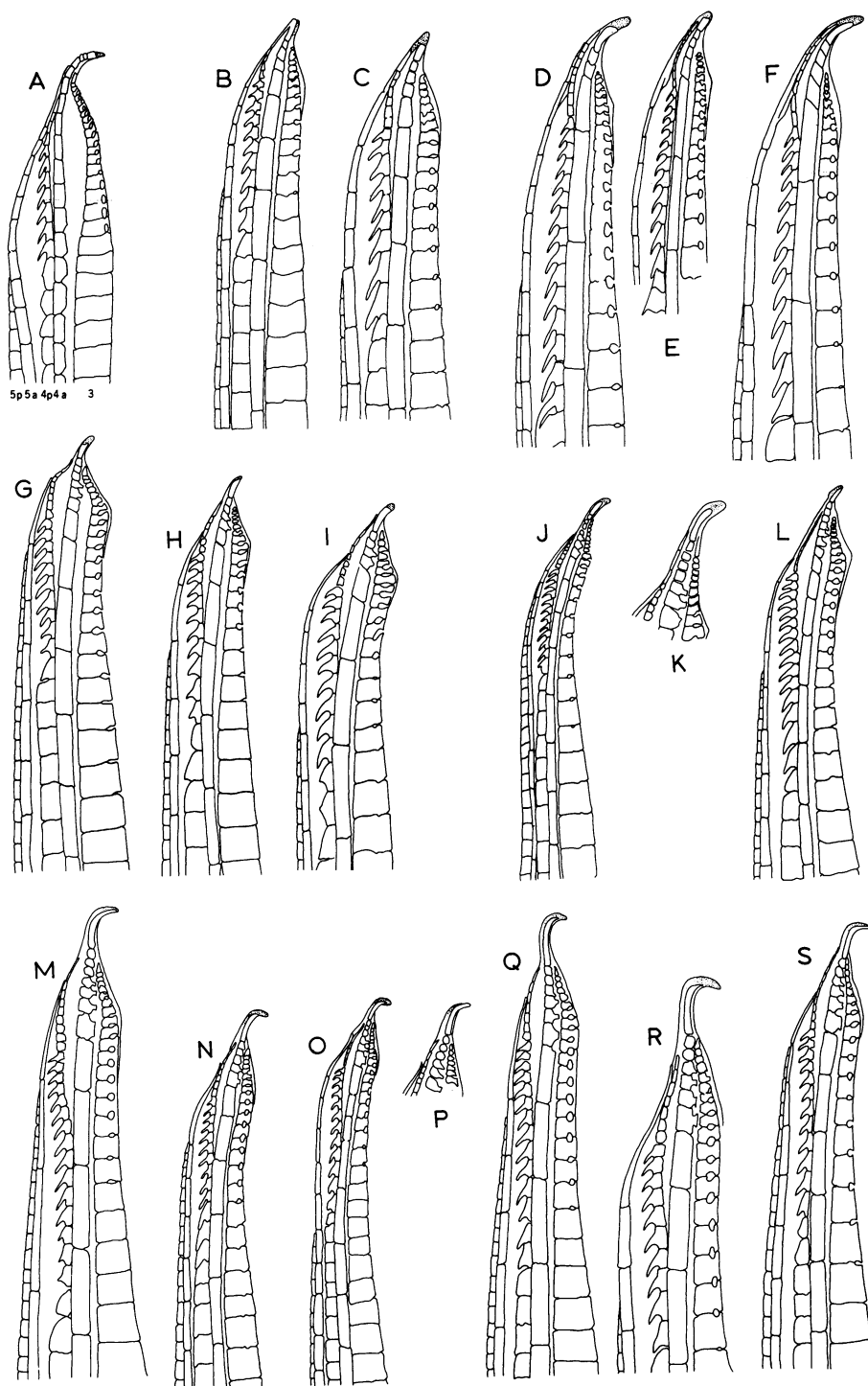


FIG. 6. Tips of gonopodia in *Heterandria* (continuous line around extreme tip of fin represents soft tissue within which stippling indicates optically dense tissue). A, *H. formosa*, UMMZ 158154. B and C, *H. attenuata*, AMNH 36334. D, *H. jonesi*, UMMZ 183887; E, same, AMNH 36336; F, same, UMMZ 186474. G, *H. litoperas*, AMNH 35003; H, same, AMNH 36331; I, same, UMMZ 146107. J and K, *H. obliqua*, UMMZ 190768; L, same, Río San Ramón laboratory stock. M-S, *H. anzueto*: M, AMNH 35150; N, UMMZ 190806; O, UMMZ 190800; P (distal tip only), AMNH 36326; Q and R, UMMZ 173305; S, UMMZ 173328.



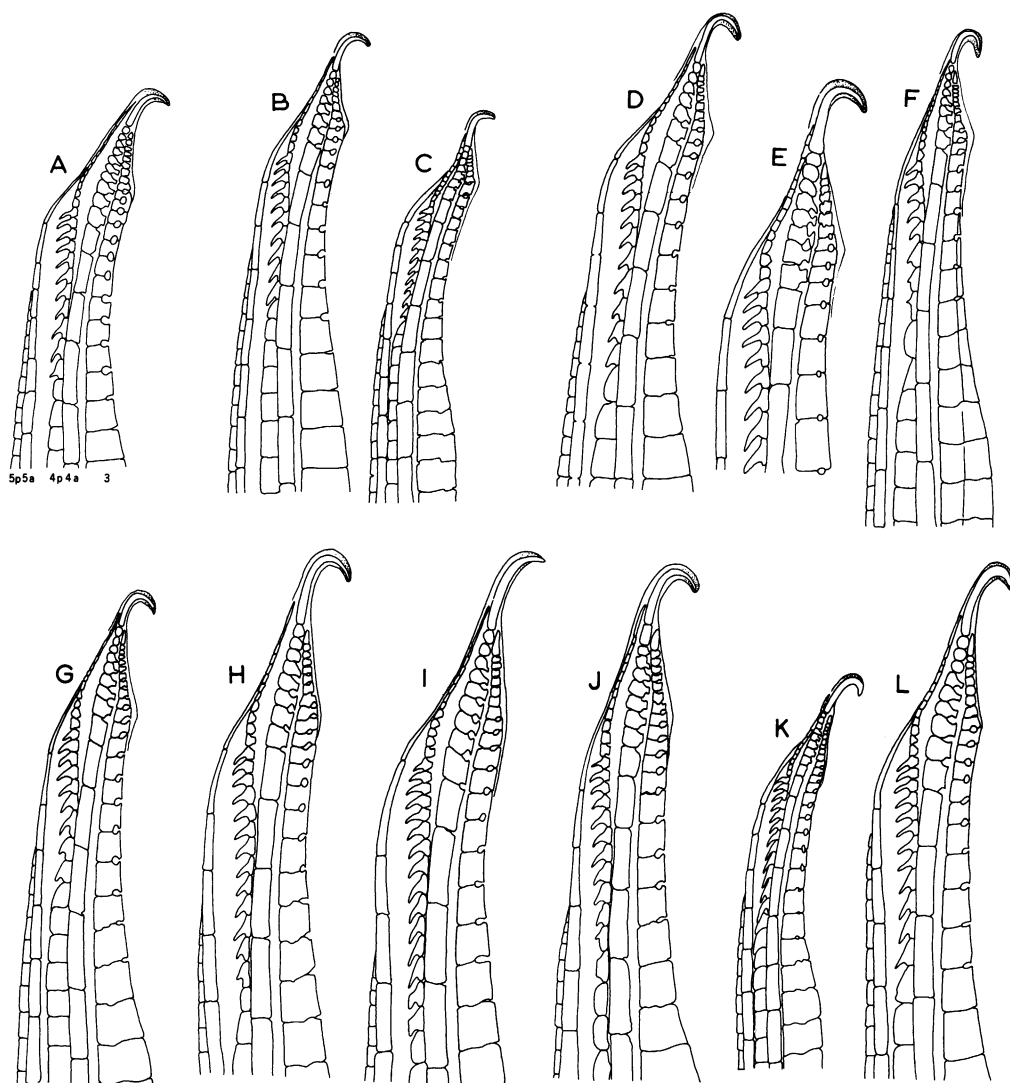


FIG. 7. Tips of gonopodia in *Heterandria* (continuous line around extreme tip of fin represents soft tissue within which stippling indicates optically dense tissue). A, *H. cataractae*, AMNH 24486. B, *H. dirempta*, AMNH 36362; C, same, UMMZ 187934. D-L, *H. bimaculata*: D, AMNH 36353; E, UMMZ 190441; F and G, AMNH 36346; H and I, AMNH 36352; J, AMNH 36341; K, UMMZ 190698; L, UMMZ 193827. The tip of I is anomalous, the only *bimaculata* like it in many hundreds of males collected, but the configuration of other structures (apart from the absence of a recurved hook) is normal for the species.

more than two penultimate short segments and in lacking ventral, peglike processes on these short segments. All or some of the other eight species possess the alternatives to these character states and these alternative states are considered derived and therefore evidence of

relationship, as follows: in all of these species the penultimate short segments are withdrawn into the gonopodial tip, i.e., are not present within the terminal, membranous envelope. This membranous envelope shows a progressive increase in length and curvature corresponding

TABLE 1  
Frequency Distribution of Number of Subdistal Short Segments on Ray 4a  
of Gonopodium in Male *Heterandria*

	Number of segments										
	1	2	3	4	5	6	7	8	9	10	11
<i>Heterandria formosa</i>											
North Carolina	3	—	—	—	—	—	—	—	—	—	—
Florida	14	—	—	—	—	—	—	—	—	—	—
<i>Heterandria attenuata</i>											
Río Candelaria Yalicar	—	2	7	3	2	—	—	—	—	—	—
<i>Heterandria jonesi</i>											
Mexico	—	3	26	15	—	—	—	—	—	—	—
<i>Heterandria litoperas</i>											
Río Cahabón	—	—	—	—	5	5	1	—	—	—	—
Río Polochic	—	—	1	4	6	1	1	—	—	—	—
Río Amatillo	—	—	—	—	2	4	—	—	—	—	—
<i>Heterandria obliqua</i>											
Cubilguitz	—	—	—	—	—	—	—	—	1	—	—
Río Dolores (Combined)	—	—	—	—	—	1	8	2	5	1	—
Río San Ramón (Combined)	—	—	—	—	2	8	14	7	1	—	—
<i>Heterandria anzuetoi</i>											
Río Motagua (Combined)	—	—	—	1	18	17	6	1	—	—	—
Río Lempa	—	—	—	1	2	5	3	—	—	—	—
Honduras (Combined)	—	—	2	6	17	28	6	3	—	—	—
Nicaragua (No Males)	—	—	—	—	—	—	—	—	—	—	—
<i>Heterandria cataractae</i>											
Río Sachicha	—	—	—	—	—	—	—	—	7	12	2
<i>Heterandria dirempta</i>											
Río Chajmaic	—	—	—	—	5	11	14	6	—	—	—
<i>Heterandria bimaculata</i>											
Mexico (Combined)	—	—	—	—	—	5	6	5	4	1	—
Río Lacantún	—	—	—	—	—	—	2	2	1	—	—
Río Salinas	—	—	—	—	—	—	6	4	3	1	—
Río de la Pasión	—	—	—	—	—	—	13	10	9	1	—
Belize drainages	—	—	—	—	—	—	2	9	6	2	—
Río Sarstún	—	—	—	—	—	—	6	9	7	—	—
Lower Río Polochic (No Males)	—	—	—	—	—	—	—	—	—	—	—
Lower Río Motagua	—	—	—	—	1	—	1	3	2	1	—
Honduras (Ceiba)	—	—	—	—	—	—	—	—	1	—	—

with an increase in length and curvature of the elongate, ultimate segment in each species from the relatively undifferentiated condition of these structures in *attenuata*. Within this group of species (i.e., all except *formosa*), *attenuata* and *jonesi* have the lowest number of penultimate short segments, specifying that *litoperas*, *obliqua*, *anzuetoi*, *cataractae*, *dirempta*, and *bimaculata* are more closely interrelated than any of them is related to *attenuata* or *jonesi*.

Ventral, peglike processes on the penultimate short segments are present in increasing number in each of these species except *attenuata* and *jonesi*, again specifying that they are all more closely interrelated than is any to *attenuata* or *jonesi*. Within the subgroup including *litoperas*, *obliqua*, *anzuetoi*, *cataractae*, *dirempta*, and *bimaculata* other hierarchical relationships are indicated by other sequential states of these same and other characters, as discussed below

under the species accounts and summarized in the character-state tree (fig. 20). Several gonopodial characters occur that are unique to one species (i.e., are autapomorphous) and thus serve to define that taxon. Autapomorphous character states are given in the formal diagnosis of each species.

**MERISTIC CHARACTERS:** Four meristic traits were analyzed: number of vertebrae, lateral-line scales, pectoral and dorsal fin rays. Modal number of vertebrae (table 2) is 33 in *attenuata* and 31 or 32 for the other species: *formosa* (32), *jonesi* (32), *litoperas* (31 or 32), *obliqua* (32), *anzuetoi* (31 or 32), *cataractae* (32), *dirempta* (32), *bimaculata* (31 or 32). The range in number of vertebrae is generally 30 to 33 (2 individuals of Floridian *formosa* have 34). Except for *attenuata* and *cataractae*, there is a range of three or four vertebrae for the number of vertebrae recorded in any one recognized taxon. Thus, vertebral number is of interest only insofar as it sets *attenuata* apart from the other species, but because there is neither adequate information on vertebral number in outgroups nor a precise theory of the sister group relationships of *Heterandria*, it is not possible to say whether the high number in *attenuata* is autapomorphous or the alternative, that the lower count is a synapomorphy of the other species.

The number of lateral line scales (table 3) has more general interest than vertebral number. Here modal number is 29 for *formosa* and two samples of *bimaculata* (from Belize and the lower Río Motagua). It is 30 in some *obliqua*, *cataractae*, and *bimaculata* from the Río Sarstún; 31 in *attenuata*, *jonesi*, *litoperas*, some *obliqua*, *anzuetoi*, *dirempta* and some *bimaculata*.

Number of pectoral fin rays (table 3) separates *formosa* from the other forms of *Heterandria* (modally 11 versus modally 13 or 14). Within the non-*formosa* group (subgenus *Pseudoxiphophorus*) a mode of 13 separates *attenuata* and one population of *obliqua* (Cubilguitz) from the other taxa. Other heterandriins have pectoral ray counts ranging from 10 to 15, exactly the span seen in *Heterandria*. Again, given the amount of outgroup variation, the absence of a precise sister

group position for *Heterandria* makes it impossible to decide unambiguously whether the low count of *formosa* is autapomorphous or the high count is a synapomorphy of the other species. The consistency of the lateral line scale counts, pectoral ray counts and anal fin ray counts (see below) with other characters suggests their probable value even though some ambiguity remains in establishing their polarity.

Unlike the other meristic traits, the number of dorsal fin rays (table 4) is both diagnostic of the subgroups of *Heterandria* and has an implied primitive-derived polarity. For example, *formosa* is sharply separated from the other species in having 6 or 7 (modally 7) dorsal rays, as compared with a range of 9 to 18 rays in the other species. Other heterandriins have counts ranging from about 6 to 10, the dorsal fin always being small and compact and higher than its base length, as in *formosa*. The non-*formosa* members of *Heterandria* have modal counts starting at 11, and the fin is low with a relatively long base. Modal counts are highest (15 or 16) in some *litoperas*, some *bimaculata*, and in *cataractae*. Given the polarity specified above from low (plesiomorphous) to high (apomorphic) counts, the non-*formosa* species form a subgroup (*Pseudoxiphophorus*) and the non-*attenuata* species form a subgroup of *Pseudoxiphophorus* (all those species with modal counts over 11). Within this secondary subgroup, differences in modal counts are characteristic of the different populations and taxa, as follows: *jonesi* (taken as a whole) and some *obliqua* (Cubilguitz), are modally 12; some *obliqua*, some *anzuetoi* (Honduras), and *dirempta* are modally 13; some *anzuetoi* and some *bimaculata*, modally 14; some *litoperas*, *cataractae*, and some *bimaculata*, modally 15; and some *litoperas* modally 16. In general, within this secondary subgroup, and at the level of recognizable taxa, *jonesi*, *obliqua*, and *dirempta* have the lowest average counts, *anzuetoi* has intermediate counts, and *litoperas*, *cataractae*, and *bimaculata* have the highest average counts. The differences among them are relatively slight, however, when the ranges of values are taken into account and when one considers that some of the taxa are geographically restricted to a single locality and others

TABLE 2  
Frequency Distribution of the Number of Vertebrae in *Heterandria*

	Vertebral Number				
	30	31	32	33	34
<i>Heterandria formosa</i>					
North Carolina	—	3	9	8	—
Florida	3	13	17	14	2
<i>Heterandria attenuata</i>					
Río Candelaria Yalicar	—	—	7	14	—
<i>Heterandria jonesi</i>					
Mexico	—	2	70	23	—
<i>Heterandria litoperas</i>					
Río Cahabón	3	18	22	—	—
Río Polochic	2	15	12	—	—
Río Amatillo	1	16	18	—	—
<i>Heterandria obliqua</i>					
Cubilguitz	—	1	10	—	—
Río Dolores (Combined)	—	2	46	6	—
Río San Ramón (Combined)	—	1	20	1	—
<i>Heterandria anzuetoi</i>					
Río Motagua (Combined)	—	4	116	1	—
Río Lempa	—	1	19	1	—
Honduras (Combined)	2	69	69	—	—
Nicaragua	—	—	1	—	—
<i>Heterandria cataractae</i>					
Río Sachicha	—	—	16	10	—
<i>Heterandria dirempta</i>					
Río Chajmaic	—	3	50	1	—
<i>Heterandria bimaculata</i>					
Mexico (Combined)	2	18	62	11	—
Río Lacantún	—	5	43	1	—
Río Salinas	—	10	29	—	—
Río de la Pasión	1	12	125	13	—
Belize drainages	1	34	14	—	—
Río Sarstún	1	6	27	2	—
Lower Río Polochic	—	2	8	1	—
Lower Río Motagua	—	1	10	2	—
Honduras (Ceiba)	—	2	2	—	—

are widely distributed in a great variety of ecologically and physiographically different habitats. At best, dorsal fin ray data suggest that the Middle American species form one monophyletic group (subgenus *Pseudoxiphophorus*) and that the Middle American forms can be further subdivided into *attenuata* and a monophyletic group (all other species) with modal counts of 12 or more. At the level of the taxa recognized here (i.e., the combined values of all populations or samples for each taxon), the

pattern produced by dorsal fin ray number is consistent with the less decisive data provided by the number of vertebrae, lateral line scales and pectoral fin rays.

**MORPHOMETRIC CHARACTERS:** An initial survey was made of 20 body measurements<sup>1</sup> (in-

<sup>1</sup>Standard length, greatest depth of body, least depth of caudal peduncle, distance from snout to dorsal fin origin, distance from tip of mandible to anal fin origin, distance from dorsal fin origin to caudal fin base, distance from anal



TABLE 3  
Frequency Distribution of the Number of Pectoral Fin Rays and  
Lateral Line Scales in *Heterandria*

	Pectoral Fin Rays						Lateral Line Scales				
	10	11	12	13	14	15	28	29	30	31	32
<i>Heterandria formosa</i>											
Florida	1	15	1	—	—	—	5	9	3	—	—
<i>Heterandria attenuata</i>											
Río Candelaria Yalicar	—	—	—	68	5	—	—	—	2	15	1
<i>Heterandria jonesi</i>											
Mexico	—	—	—	—	18	2	—	—	5	15	—
<i>Heterandria litoperas</i>											
Río Cahabón	—	—	—	—	25	2	—	—	10	16	—
Río Polochic	—	—	—	—	9	—	—	—	3	6	—
Río Amatillo	—	—	—	—	23	9	—	—	—	—	—
<i>Heterandria obliqua</i>											
Cubilguitz	—	—	—	7	1	—	—	—	—	8	—
Río Dolores (Combined)	—	—	—	13	56	4	2	16	27	22	—
Río San Ramón (Combined)	—	—	—	1	9	8	—	3	14	1	—
<i>Heterandria anzueto</i>											
Río Motagua (Combined)	—	—	—	—	27	25	1	6	4	38	1
Río Lempa	—	—	—	1	37	2	—	—	3	14	1
<i>Heterandria cataractae</i>											
Río Sachicha	—	—	—	4	36	—	—	1	12	7	—
<i>Heterandria dirempta</i>											
Río Chajmaic	—	—	—	8	59	2	—	—	9	40	—
<i>Heterandria bimaculata</i>											
Mexico (Combined)	—	—	—	—	9	6	—	—	3	11	1
Río Lacantún	—	—	—	1	32	3	—	2	11	22	—
Río Salinas	—	—	—	4	43	5	—	1	11	14	1
Río de la Pasión	—	—	1	4	62	14	1	8	31	54	—
Belize drainages	—	—	—	1	13	12	2	13	9	1	—
Río Sarstún	—	—	—	—	38	8	5	6	39	20	1
Lower Río Polochic	—	—	—	1	9	1	—	—	5	5	—
Lower Río Motagua	—	—	—	1	10	8	1	7	6	—	—

cluding standard length). Of these, 14 were discarded as having shown little or no comparative value in relation to two of the superficially most divergent taxa, *attenuata* and *litoperas*. Those retained, and expressed in thousandths of standard length, are (1) length of the dorsal fin

fin origin to caudal fin base, head length, head width, snout length, width of orbit, postorbital length of head, distance from orbit to preopercular angle, interorbital bony width, mouth width, length of dorsal fin base, length of depressed anal fin, caudal fin length, pectoral fin length, pelvic fin length.

base (tables 5,6); (2) distance from origin of the dorsal fin to the caudal fin base (tables 7,8); (3) length of the anal fin in the female (table 9); (4) head width in the female (table 10; males of all species become highly compressed laterally at maturity, a change which adversely affects the utility of this trait); and (5) least depth of the caudal peduncle (tables 11,12).

The first two measurements, length of dorsal fin base and dorsal origin to caudal base, give results that are virtually identical with those obtained by using dorsal fin ray counts (compare table 4 with tables 5-8). The similarity is

TABLE 4  
Frequency Distribution of the Number of Dorsal Fin Rays in *Heterandria*

	Ray Number													
	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>Heterandria formosa</i>														
North Carolina	5	14	—	—	—	—	—	—	—	—	—	—	—	
Florida	1	28	—	—	—	—	—	—	—	—	—	—	—	
<i>Heterandria attenuata</i>														
Río Candelaria Yalicar	—	—	—	—	35	44	—	—	—	—	—	—	—	
<i>Heterandria jonesi</i>														
Mexico <sup>a</sup>	—	—	—	1	3	277	358	110	38	6	—	—	—	
<i>Heterandria litoperas</i>														
Río Cahabón	—	—	—	—	—	—	—	—	18	31	11	1	—	
Río Polochic	—	—	—	—	—	—	—	—	—	5	13	12	3	
Río Amatillo	—	—	—	—	—	—	—	—	5	23	22	2	—	
<i>Heterandria obliqua</i>														
Cubilguitz	—	—	—	—	1	6	36	5	—	—	—	—	—	
Río Dolores (Combined)	—	—	—	—	—	2	23	52	2	—	—	—	—	
Río San Ramón (Com- bined)	—	—	—	—	—	—	8	19	2	—	—	—	—	
<i>Heterandria anzuetoi</i>														
Río Motagua (Combined)	—	—	—	—	—	—	2	63	120	45	3	—	—	
Río Lempa	—	—	—	—	—	—	1	19	58	13	1	—	—	
Honduras (Combined)	—	—	—	—	—	2	55	117	100	11	—	—	—	
Nicaragua	—	—	—	—	—	—	—	1	—	1	—	—	—	
<i>Heterandria cataractae</i>														
Río Sachicha	—	—	—	—	—	—	—	—	16	20	3	—	—	
<i>Heterandria dirempta</i>														
Río Chajmaic	—	—	—	—	—	—	25	73	1	—	—	—	—	
<i>Heterandria bimaculata</i>														
Río Papaloapan and north <sup>a</sup>	—	—	—	—	—	—	9	84	159	44	3	—	—	
Río Coatzacoalcos <sup>a</sup>	—	—	—	—	—	—	—	—	13	26	17	1	—	
Río Lacantún	—	—	—	—	—	—	—	2	16	19	1	—	—	
Río Salinas	—	—	—	—	—	—	1	3	9	26	15	1	—	
Río de la Pasión	—	—	—	—	—	—	—	—	29	61	10	—	—	
Lake Petén region	—	—	—	—	—	—	—	5	28	25	2	—	—	
Belize drainages	—	—	—	—	—	—	—	—	6	24	10	—	—	
Río Sarstún	—	—	—	—	—	—	—	—	25	41	16	—	—	
Lower Río Polochic	—	—	—	—	—	—	—	5	22	16	—	—	—	
Lower Río Motagua	—	—	—	—	—	—	1	3	20	10	3	1	—	
Honduras (Ceiba)	—	—	—	—	—	—	—	1	3	—	—	—	—	

<sup>a</sup>Counts of Mexican fish from Miller (1974).

especially striking between dorsal fin ray number and the two morphometric traits in males. The conclusion to be reached here is that the two types of measurements and the count of ray number are merely three different ways of looking at the same character, which is the anteroposterior size of the dorsal fin. Moreover,

the results obtained from the dorsal-origin to caudal-base measurement suggest that fin size has been increased at the anterior end. Thus, taken together, the three sets of data indicate that the larger dorsal fin is a synapomorphy of non-*formosa* members of the genus (subgenus *Pseudoxiphophorus*), that the non-*attenuata*

[illegible]

TABLE 6  
Frequency Distribution of Length of Dorsal Fin Base in Female *Heterandria*  
(Expressed in thousandths of standard length.)

	Class Intervals														
	060 -079	080 -099	100 -119	120 -139	140 -159	160 -179	180 -199	200 -219	220 -239	240 -259	260 -279	280 -299	300 -319	320 -339	340 -359
<i>Heterandria formosa</i>															
Florida	4	6	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Heterandria attenuata</i>															
Río Candelaria															
Yalícar	—	—	—	—	—	5	4	1	—	—	—	—	—	—	—
<i>Heterandria jonesi</i>															
Mexico	—	—	—	—	—	—	2	7	1	—	—	—	—	—	—
<i>Heterandria litoperas</i>															
Río Cahabón	—	—	—	—	—	—	—	—	—	—	—	—	9	6	—
Río Polochic	—	—	—	—	—	—	—	—	—	—	—	—	1	4	3
Río Amatillo	—	—	—	—	—	—	—	—	—	—	—	2	3	5	1
<i>Heterandria obliqua</i>															
Cubliguitz	—	—	—	—	—	—	—	—	1	8	6	—	—	—	—
Río Dolores (Com- bined)	—	—	—	—	—	—	—	—	—	13	22	5	—	—	—
Río San Ramón (Combined)	—	—	—	—	—	—	—	—	—	2	8	—	—	—	—
<i>Heterandria anzuetoí</i>															
Río Motagua (Com- bined)	—	—	—	—	—	—	—	—	—	1	19	36	6	—	—
Río Lempa	—	—	—	—	—	—	—	—	—	—	3	13	2	2	—
Honduras (Combined)	—	—	—	—	—	—	—	—	—	20	53	29	2	—	—
Nicaragua	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—
<i>Heterandria cataractae</i>															
Río Sachicha	—	—	—	—	—	—	—	—	—	—	—	4	15	1	—
<i>Heterandria dirempta</i>															
Río Chajmaic	—	—	—	—	—	—	—	—	1	10	20	4	—	—	—
<i>Heterandria bimaculata</i>															
Mexico (Combined)	—	—	—	—	—	—	—	—	—	—	—	—	7	2	1
Río Lacantún	—	—	—	—	—	—	—	—	—	—	1	6	9	4	1
Río Salinas	—	—	—	—	—	—	—	—	—	—	—	11	9	1	—
Río de la Pasión	—	—	—	—	—	—	—	—	—	—	5	15	21	13	2
Belize drainages	—	—	—	—	—	—	—	—	—	—	—	—	4	9	1
Río Sarstún	—	—	—	—	—	—	—	—	—	—	1	10	22	10	1
Lower Río Polochic	—	—	—	—	—	—	—	—	—	—	1	3	6	—	—
Lower Río Motagua	—	—	—	—	—	—	—	—	—	—	1	2	5	2	—
Honduras (Ceiba)	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—

depth of caudal peduncle (tables 11,12) give results different from the above, but results that are congruent with each other. Both types of measurements show only that *attenuata* is a more slender fish than other members of the genus, i.e., it is autapomorphous for slenderness of body.

Lastly, it appears from all the morphometric data that, on average, *litoperas* is slightly heavier-bodied and *obliqua* on average slightly more slender-bodied than other members of the subgroup including *jonesi*, *litoperas*, *obliqua*, *anzuetoí*, *cataractae*, *dirempta*, and *bimaculata*. It is undesirable to attach too much





TABLE 8  
**Frequency Distribution of Distance from Dorsal Fin Origin to Caudal Base in Female *Heterandria***  
**(Expressed in thousandths of standard length.)**

	Class Intervals									
	380 -399	400 -419	420 -439	440 -459	460 -479	480 -499	500 -519	520 -539	540 -559	560 -579
<i>Heterandria formosa</i>										
Florida	1	7	2	—	—	—	—	—	—	—
<i>Heterandria attenuata</i>										
Río Candelaria Yalicar	—	2	8	—	—	—	—	—	—	—
<i>Heterandria jonesi</i>										
Mexico	—	1	—	4	4	1	—	—	—	—
<i>Heterandria litoperas</i>										
Río Cahabón	—	—	—	—	—	1	5	9	—	—
Río Polochic	—	—	—	—	—	—	3	4	1	—
Río Amatillo	—	—	—	—	1	4	2	3	—	1
<i>Heterandria obliqua</i>										
Cubilguitz	—	—	—	3	7	5	—	—	—	—
Río Dolores (Combined)	—	—	—	—	21	15	3	—	—	—
Río San Ramón (Combined)	—	—	—	—	2	7	1	—	—	—
<i>Heterandria anzuetoii</i>										
Río Motagua (Combined)	—	—	—	—	7	35	18	2	—	—
Río Lempa	—	—	—	—	1	11	7	—	1	—
Honduras (Combined)	—	—	6	29	42	21	8	—	—	—
Nicaragua	—	—	—	—	—	2	—	—	—	—
<i>Heterandria cataractae</i>										
Río Sachicha	—	—	—	—	—	—	8	10	2	—
<i>Heterandria dirempta</i>										
Río Chajmaic	—	—	—	2	19	12	2	—	—	—
<i>Heterandria bimaculata</i>										
Mexico (Combined)	—	—	—	—	—	1	6	2	—	1
Río Lacantún	—	—	—	—	1	2	10	7	1	—
Río Salinas	—	—	—	—	—	8	8	5	—	—
Río de la Pasión	—	—	—	—	—	13	38	4	1	1
Belize drainages	—	—	—	—	—	4	9	1	—	—
Río Sarstún	—	—	—	—	—	7	26	8	3	—
Lower Río Polochic	—	—	—	—	—	3	5	2	—	—
Lower Río Motagua	—	—	—	—	—	4	5	—	1	—
Honduras (Ceiba)	—	—	—	—	1	2	—	—	—	—

strongly developed and extending from the basicaudal spot to the snout; and (4) the crosshatching vague and feebly developed dorsally and virtually absent below the midlateral stripe. In contrast, the other species of *Heterandria* have (1) the dorsal fin pigment present as two or more discrete rows of spots on the interrational membrane along the basal third to half of the fin and the anal fin pigment as irregular dusky markings and darker streaks

paralleling the rays in the interrational membrane; (2) the basicaudal spot larger than one scale width in height (sometimes spanning the caudal base), discrete in small juveniles and usually with diffuse or broken margins in adults, confined to the caudal peduncle only in some populations of *H. jonesi* (figs. 15C,F) and overlapping the caudal fin base in other populations of *H. jonesi* (fig. 15E) and in the remaining species, and almost always most strongly

expressed slightly or well above the midlateral position; (3) the midlateral stripe extremely diffuse, moderately to feebly developed on the caudal peduncle or trunk but never on both and never on the snout; and (4) the crosshatching present as a crisp, in some cases bold, pattern on the upper and lower sides.

In addition to these basic patterns vertical bars are evident, though weakly, in some indi-

viduals or populations of all species, and in all species except *H. formosa*, dark flecks or vertical dashes are irregularly scattered or form complete or broken rows along the side associated with the nodes in the pattern of crosshatching.

Of the four main patterns listed above, each of the conditions found in *H. formosa* may be found also in other poeciliids, although no

TABLE 9  
Frequency Distribution of Anal Fin Length in Female *Heterandria*  
(Expressed in thousandths of standard length.)

	Class Intervals													
	180 -189	190 -199	200 -209	210 -219	220 -229	230 -239	240 -249	250 -259	260 -269	270 -279	280 -289	290 -299	300 -309	
<i>Heterandria formosa</i>														
Florida	2	4	4	—	—	—	—	—	—	—	—	—	—	
<i>Heterandria attenuata</i>														
Río Candelaria Yalicar	—	2	3	4	—	—	—	—	—	—	—	—	—	
<i>Heterandria jonesi</i>														
Mexico	1	1	4	3	1	—	—	—	—	—	—	—	—	
<i>Heterandria litoperas</i>														
Río Cahabón	—	—	—	—	—	1	1	3	4	5	1	—	—	
Río Polochic	—	—	—	1	1	—	3	1	1	1	—	—	—	
Río Amatillo	—	—	—	—	2	7	2	—	—	—	—	—	—	
<i>Heterandria obliqua</i>														
Cubilguitz	—	—	—	1	4	2	4	3	1	—	—	—	—	
Río Dolores (Combined)	—	—	—	2	7	3	14	8	5	1	—	—	—	
Río San Ramón (Com- bined)	—	1	2	5	1	1	—	—	—	—	—	—	—	
<i>Heterandria anzuetoi</i>														
Río Motagua (Combined)	—	3	7	8	6	13	9	9	5	2	—	—	—	
Río Lempa	—	—	4	2	6	4	2	2	—	—	—	—	—	
Honduras (Combined)	—	—	—	1	5	12	15	31	19	14	2	4	1	
Nicaragua	—	—	—	—	—	—	—	—	1	—	1	—	—	
<i>Heterandria cataractae</i>														
Río Sachicha	—	—	1	2	3	7	3	3	1	—	—	—	—	
<i>Heterandria dirempta</i>														
Río Chajmaic	—	—	1	1	2	—	1	8	12	6	4	—	—	
<i>Heterandria bimaculata</i>														
Mexico (Combined)	—	—	—	—	—	2	2	5	1	—	—	—	—	
Río Lacantún	—	1	4	4	6	3	1	2	—	—	—	—	—	
Río Salinas	—	—	—	4	1	4	4	5	2	1	—	—	—	
Río de la Pasión	—	1	3	6	11	12	8	9	5	1	—	—	1	
Belize drainages	—	—	—	—	4	1	3	5	—	1	—	—	—	
Río Sarstún	—	—	5	6	6	8	9	9	1	—	—	—	—	
Lower Río Polochic	—	—	—	—	2	5	2	—	—	1	—	—	—	
Lower Río Motagua	—	—	—	—	—	2	3	2	2	1	—	—	—	
Honduras (Ceiba)	—	—	—	—	—	1	1	—	1	—	—	—	—	

TABLE 10  
Frequency Distribution of Head Width in Female *Heterandria*  
(Expressed in thousandths of standard length.)

	Class Intervals													
	140 -144	145 -149	150 -154	155 -159	160 -164	165 -169	170 -174	175 -179	180 -184	185 -189	190 -194	195 -199	200 -204	205 -209
<i>Heterandria formosa</i>														
Florida	—	—	—	—	—	—	—	—	2	4	3	—	1	—
<i>Heterandria attenuata</i>														
Río Candelaria Yalicar	1	—	2	3	1	3	—	—	—	—	—	—	—	—
<i>Heterandria jonesi</i>														
Mexico	—	—	—	—	—	—	1	2	1	5	1	—	—	—
<i>Heterandria litoperas</i>														
Río Cahabón	—	—	—	—	—	—	1	4	6	2	1	1	—	—
Río Polochic	—	—	—	—	—	—	—	2	2	2	1	1	—	—
Río Amatillo	—	—	—	—	—	—	2	2	2	—	—	—	—	—
<i>Heterandria obliqua</i>														
Cubilguitz	1	—	—	2	3	5	3	1	—	—	—	—	—	—
Río Dolores (Combined)	—	—	—	2	2	6	13	7	1	7	1	—	1	—
Río San Ramón (Com- bined)	—	—	—	—	1	1	4	4	—	—	—	—	—	—
<i>Heterandria anzuetoii</i>														
Río Motagua (Com- bined)	—	3	10	8	3	4	5	10	11	3	3	1	—	—
Río Lempa	—	—	—	—	—	1	4	6	4	2	1	2	—	—
Honduras (Combined)	2	4	7	14	20	18	17	10	6	7	—	—	—	—
Nicaragua	—	—	—	—	—	—	—	—	1	—	1	—	1	—
<i>Heterandria cataractae</i>														
Río Saohicha	—	—	—	—	—	2	5	5	4	3	1	—	—	—
<i>Heterandria dirempta</i>														
Río Chajmaic	—	—	—	—	—	2	3	3	14	8	4	—	—	1
<i>Heterandria bimaculata</i>														
Mexico (Combined)	—	—	—	—	—	—	—	1	2	2	3	1	1	—
Río Lacantún	—	—	—	—	2	7	1	6	3	2	—	—	—	—
Río Salinas	—	—	—	—	—	1	7	6	6	1	—	—	—	—
Río de la Pasión	—	—	—	—	—	2	13	20	10	10	1	1	—	—
Belize drainages	—	—	—	—	—	—	—	2	5	6	1	—	—	—
Río Sarstún	—	—	—	1	2	6	6	8	14	5	—	2	—	—
Lower Río Polochic	—	—	—	—	—	1	3	4	2	—	—	—	—	—
Lower Río Motagua	—	—	—	—	—	—	1	2	1	3	2	1	—	—
Honduras (Ceiba)	—	—	—	—	—	—	2	—	1	—	—	—	—	—

other poeciliid species outside of *Heterandria* includes all of them in combination. Two of the four main patterns, the weak midlateral stripe and bold crosshatching, as seen in the other species of *Heterandria*, also are known in other poeciliid species; the other two main patterns in these species, a large basicaudal spot mostly or entirely above the midlateral scale row and the distinctive pattern of spotting on

the dorsal fin (in which the spots of one row are staggered in relation to the position of those in the adjoining row), are unusual among poeciliids—at least I know of no other exactly comparable pattern expressions. Coupled with the ontogenetic evidence that shows these two patterns to be present in the juveniles of all species as they are in the adults of *H. formosa*, their uniqueness within the family suggests that

[illegible]

TABLE 12  
Frequency Distribution of Least Depth of Caudal Peduncle in Female *Heterandria*  
(Expressed in thousandths of standard length.)

	Class Intervals									
	120 -129	130 -139	140 -149	150 -159	160 -169	170 -179	180 -189	190 -199	200 -209	210 -219
<i>Heterandria formosa</i>										
Florida	—	—	1	5	4	—	—	—	—	—
<i>Heterandria attenuata</i>										
Río Candelaria Yalicar	1	8	1	—	—	—	—	—	—	—
<i>Heterandria jonesi</i>										
Mexico	—	—	—	1	8	1	—	—	—	—
<i>Heterandria litoperas</i>										
Río Cahabón	—	—	1	8	4	2	—	—	—	—
Río Polochic	—	—	—	3	5	—	—	—	—	—
Río Amatillo	—	—	5	6	—	—	—	—	—	—
<i>Heterandria obliqua</i>										
Cubilguitz	—	—	12	3	—	—	—	—	—	—
Río Dolores (Combined)	—	—	16	21	3	—	—	—	—	—
Río San Ramón (Combined)	—	—	8	2	—	—	—	—	—	—
<i>Heterandria anzueto</i>										
Río Motagua (Combined)	—	15	15	17	13	2	—	—	—	—
Río Lempa	—	4	4	10	5	1	—	—	—	—
Honduras (Combined)	—	6	12	27	31	21	7	2	—	—
Nicaragua	—	—	—	2	—	—	—	—	—	—
<i>Heterandria cataractae</i>										
Río Sachicha	—	3	15	2	—	—	—	—	—	—
<i>Heterandria dirempta</i>										
Río Chajmaic	—	—	2	15	15	3	—	—	—	—
<i>Heterandria bimaculata</i>										
Mexico (Combined)	—	—	—	2	4	3	1	—	—	—
Río Lacantún	—	1	5	6	8	1	—	—	—	—
Río Salinas	—	—	2	13	5	1	—	—	—	—
Río de la Pasión	—	—	4	31	18	4	—	—	—	—
Belize drainages	—	—	—	1	8	4	1	—	—	—
Río Sarstún	—	1	13	16	4	—	6	3	—	1
Lower Río Polochic	—	—	—	5	4	—	1	—	—	—
Lower Río Motagua	—	—	—	—	3	5	2	—	—	—
Honduras (Ceiba)	—	—	—	1	—	1	—	—	1	—

genus *Pseudoxiphophorus*, the jaw dentition is characterized by having an inner row of enlarged teeth behind (interior to) a more usual dentitional pattern of a row or band of small teeth and an outer row of larger teeth. No pattern like that of *Pseudoxiphophorus* is known to me in any other poeciliid. Only *Belonesox belizanus* of the tribe Gambusiini has enlarged inner teeth, but in this case all the enlarged inner teeth are larger than those of the outer tooth row. Thus, the dentition of the

species of *Pseudoxiphophorus* appears to be derived relative to that of *formosa* and other heterandriin species.

#### SYNAPOMORPHY SCHEME FOR THE SPECIES

Figure 20

Synapomorphies between *formosa* and the group including *attenuata*, *jonesi*, *litoperas*, *obliqua*, *anzueto*, *cataractae*, *dirempta*, and *bimaculata*.

1. Pigment patterns including a basicaudal spot,

basal pigment on the dorsal and anal fins, and, possibly, a midlateral stripe. It is not clear, however, that this last feature forms in the same way in *formosa* and the other species because, in the latter, the stripe is always rather diffuse and does not extend forward to the lips, and because, in at least some of the latter, the stripe condenses out of vertical bars as the fish matures (viz., *anzuetoi*). In *formosa*, vertical bars are present together with a midlateral stripe.

2. A posteroventrally directed spur distally on gonopodial ray 6. A similar spur occurs in some other heterandriin species as well, but in these the spur is not directed ventrally.
3. Segments at tip of gonopodial ray 4a elongate subdistally and comprising one or more penultimate short segments and a longer ultimate segment that enters a terminal membranous envelope. This ray is not arched upward but its tip and the membranous envelope are always slightly to strongly decurved.

4. Spines on gonopodial ray 3 peglike.

5. A pair of lateral triangular flanges distally on gonactinost 6 of the gonopodial suspensorium. Smaller flanges occur in some species of other heterandriin genera so that this trait may be a derived state of a more general heterandriin character. However, such structures are apparently absent in *Neoheterandria*, the most probable sister group of *Heterandria*, suggesting that the occurrence of this feature outside *Heterandria* is independent.

Synapomorphies between *attenuata* and the group including *jonesi*, *litoperas*, *obliqua*, *anzuetoi*, *cataractae*, *dirempta*, and *bimaculata*.

6. Basicaudal spot in adults partly or wholly above midlateral line and extending onto caudal base. The spot is restricted to the caudal peduncle in juveniles, a feature retained in some populations of *jonesi*.
7. Dorsal fin melanophores forming two or more rows of discrete spots and anal fin

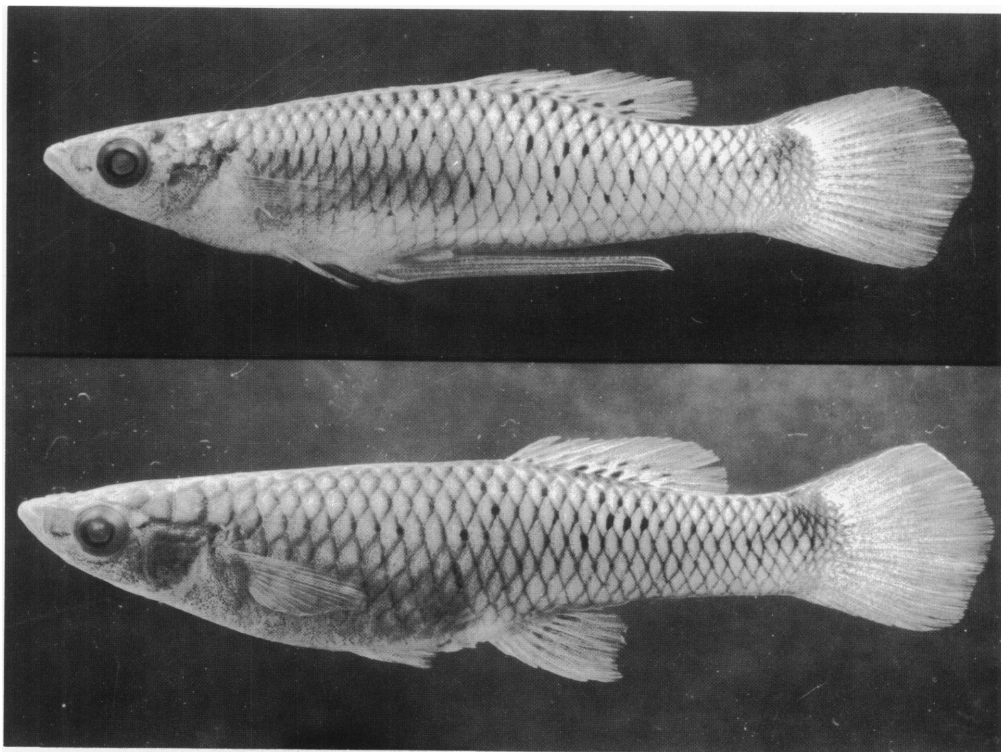


FIG. 8. *Heterandria attenuata*, new species. Typical pigment patterns. Above, male, 38.5 mm. standard length. Below, female, 62 mm. standard length. AMNH 36334.

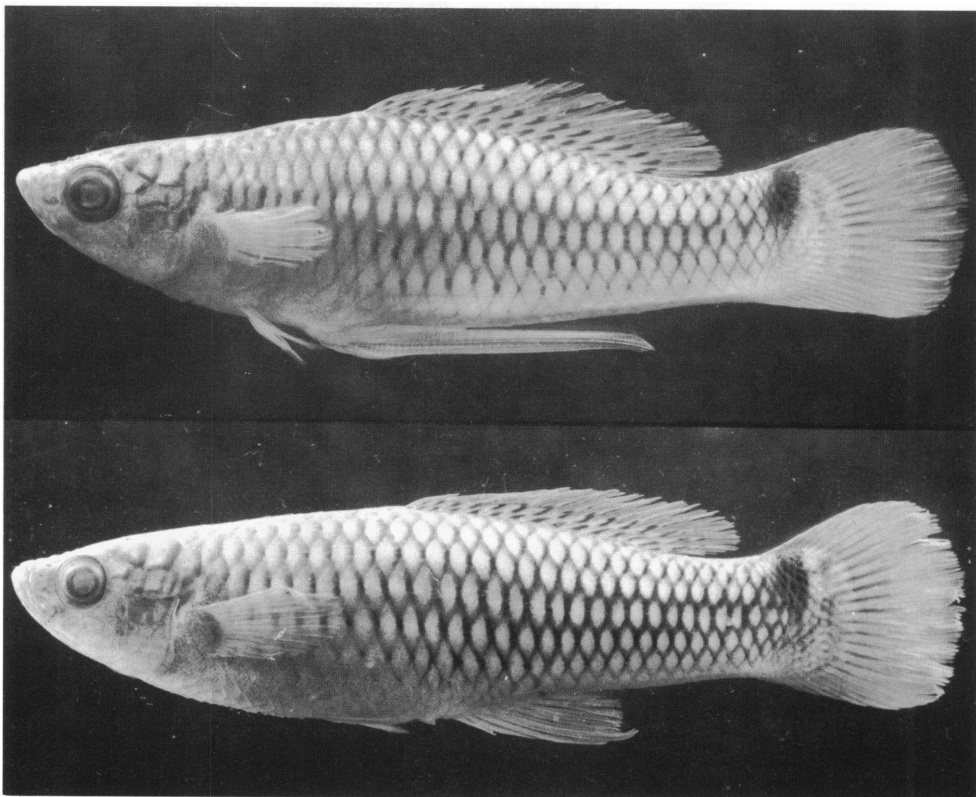


FIG. 9. *Heterandria litoperas*, new species. Typical pigment patterns. Above, male, holotype, 33.5 mm. standard length. AMNH 36328. Below, female, 58 mm. standard length. AMNH 24492.

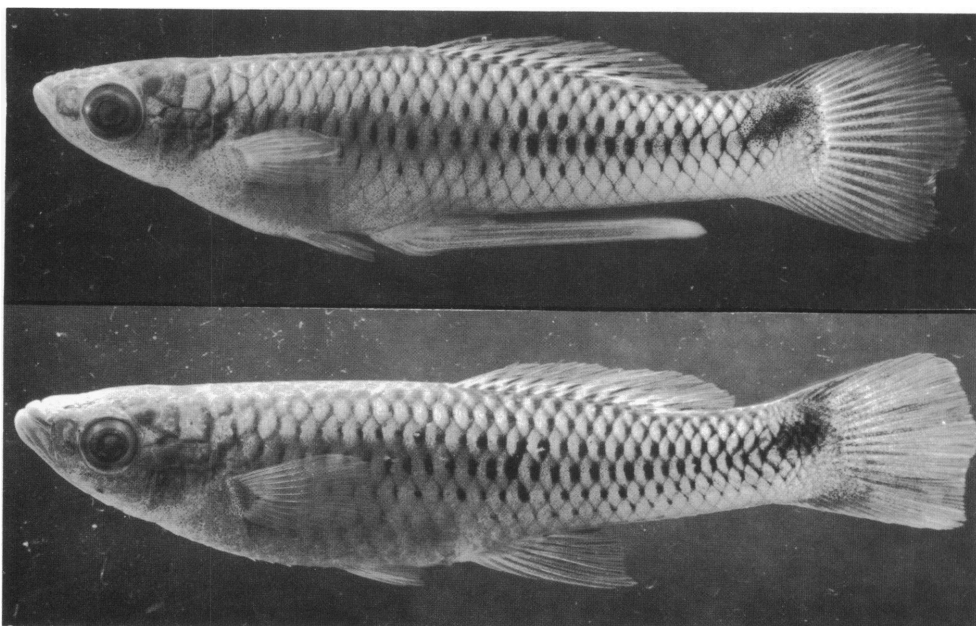


FIG. 10. *Heterandria obliqua*, new species. Typical pigment patterns. Above, subadult male, 35 mm. standard length. Below, female, 62 mm. standard length. AMNH 36316.



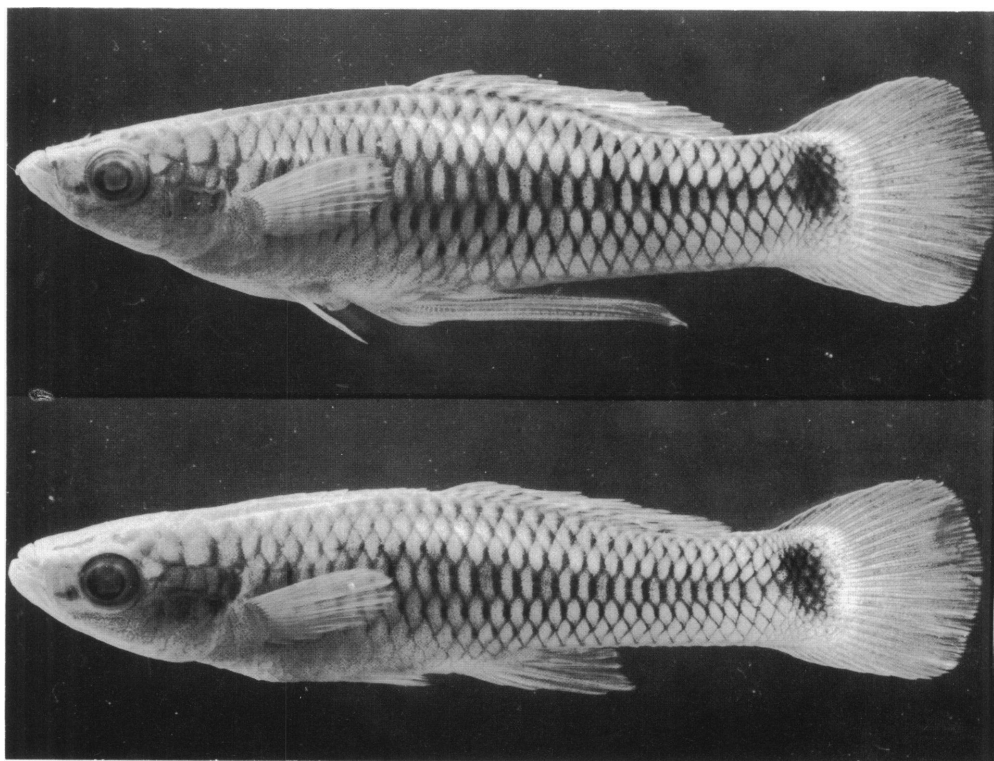


FIG. 11. *Heterandria anzuetoii*, new species. Typical pigment patterns. Above, male, 39 mm. standard length. Below, female, 39 mm. standard length. AMNH 36324.

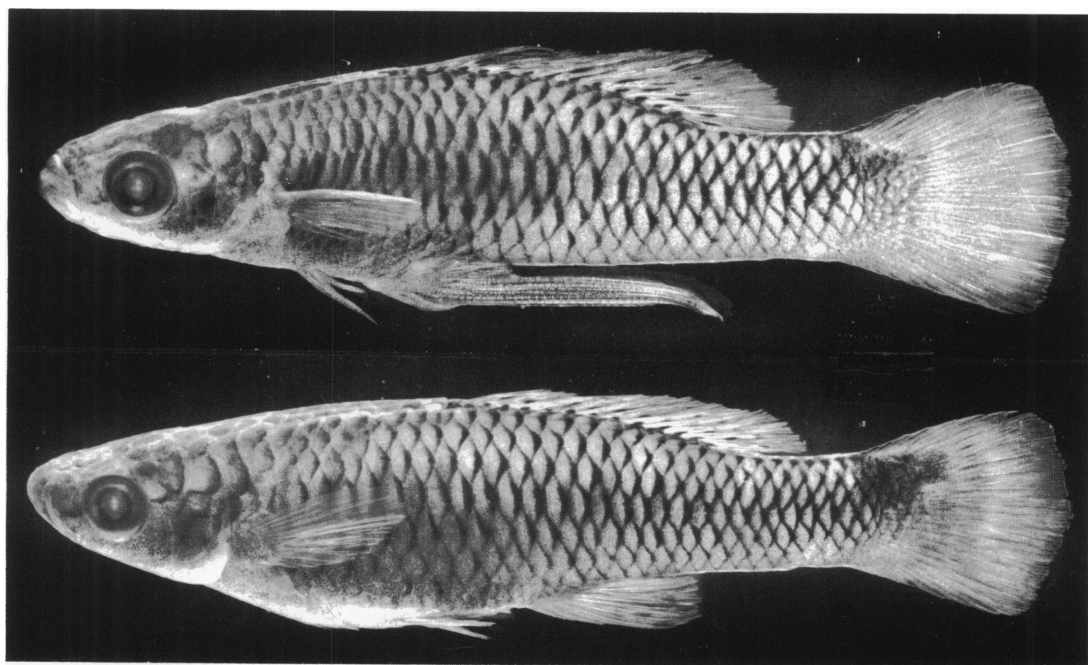


FIG. 12. *Heterandria cataractae*, new species. Typical pigment patterns. Above, male, holotype, 36.4 mm. standard length. AMNH 36381. Below, female, 60 mm. standard length. AMNH 24486.

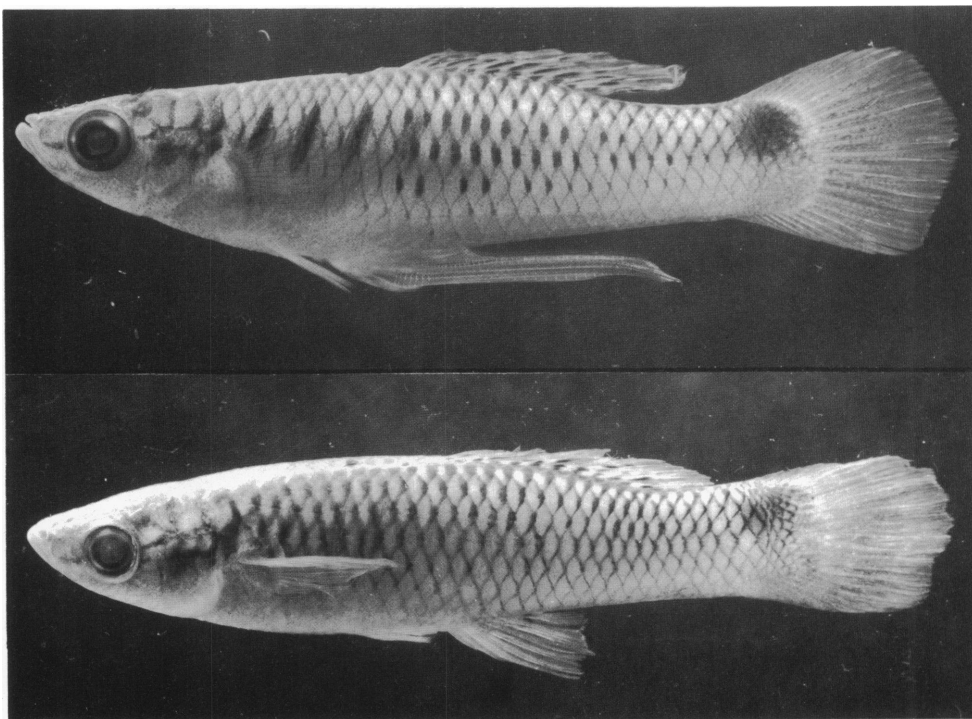


FIG. 13. *Heterandria dirempta*, new species. Typical pigment patterns. Above, male holotype, 31 mm. standard length. AMNH 36380. Below, female, 64 mm. standard length. AMNH 24564.

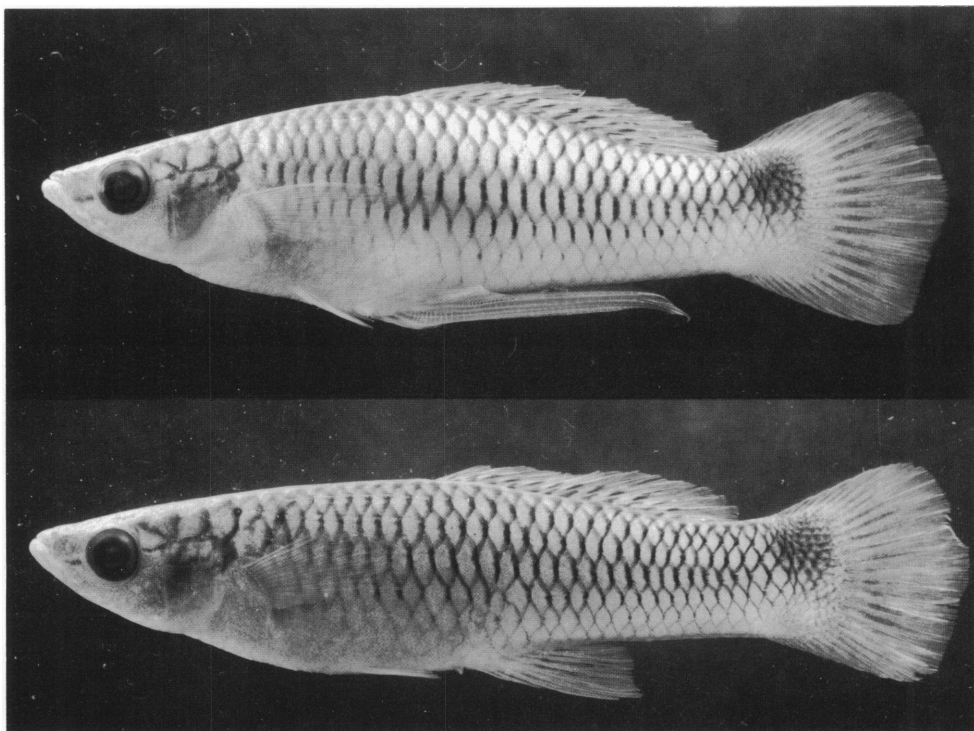


FIG. 14. *Heterandria bimaculata*. Typical pigment patterns. Above, male, 48 mm. standard length. Below, female, 66 mm. standard length. AMNH 24643.

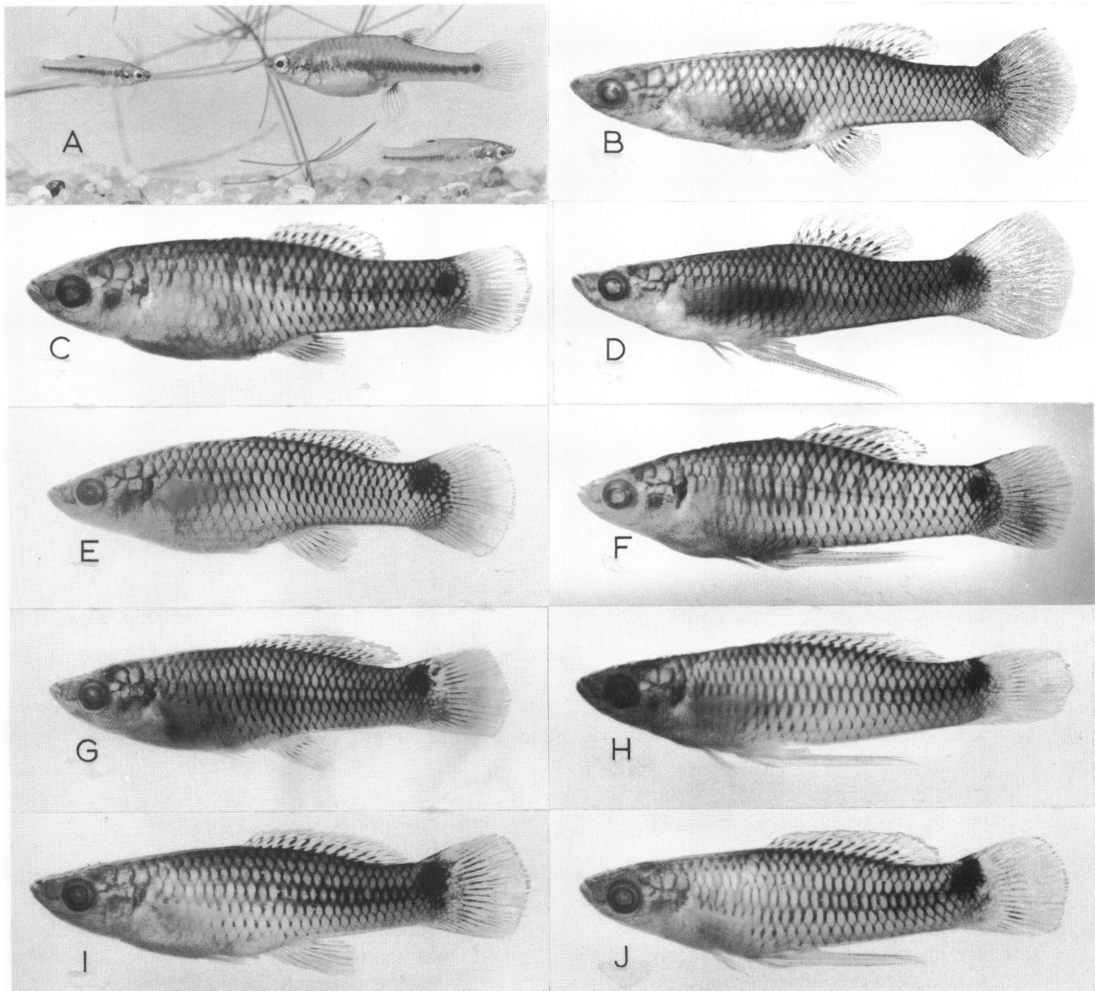


FIG. 15. Some variations in pigment patterns in species of *Heterandria*. A, *H. formosa*, laboratory strain from Florida; smaller fish, males. B, *H. attenuata*, female (60 mm. standard length); D, same, male (36.5 mm.), laboratory strain, Río Candelaria Yalicar. C, *H. jonesi*, female (36.5 mm.; UMMZ 187718); E, same, female (44 mm.; AMNH 36337); F, same, male (31.5 mm.; UMMZ 187718). G, *H. litoperas*, female (41.5 mm.; AMNH 36331); H, same, male (32 mm.; AMNH 36331); I, same, female (41.5 mm.; AMNH 35003); J, same, male (30.5 mm.; AMNH 35003).

- melanophores extending distally from anal fin base as streaks in interradyal membrane.
- 8. Pigment of scale pockets forming a strong reticular network along sides.
- 9. Dentition in jaws including an inner row of enlarged teeth behind band of small teeth and an outer row of larger teeth. The inner row is absent in *formosa*.
- 10. More than seven dorsal fin rays.
- 11. More than 28 scales in the lateral line (polarity ambiguous).

- 12. More than 12 pectoral fin rays (polarity ambiguous).
- 13. Eleven, rather than 10, anal fin rays.
- 14. Gonopodial ray 4p as long as, or longer than, ray 5a, excluding the latter from direct contact with ray 4a.
- 15. Penultimate short segments on gonopodial ray 4a withdrawn from base of terminal membranous envelope and two or more in number.
- 16. Ventral (anterior) profile of gonopodium

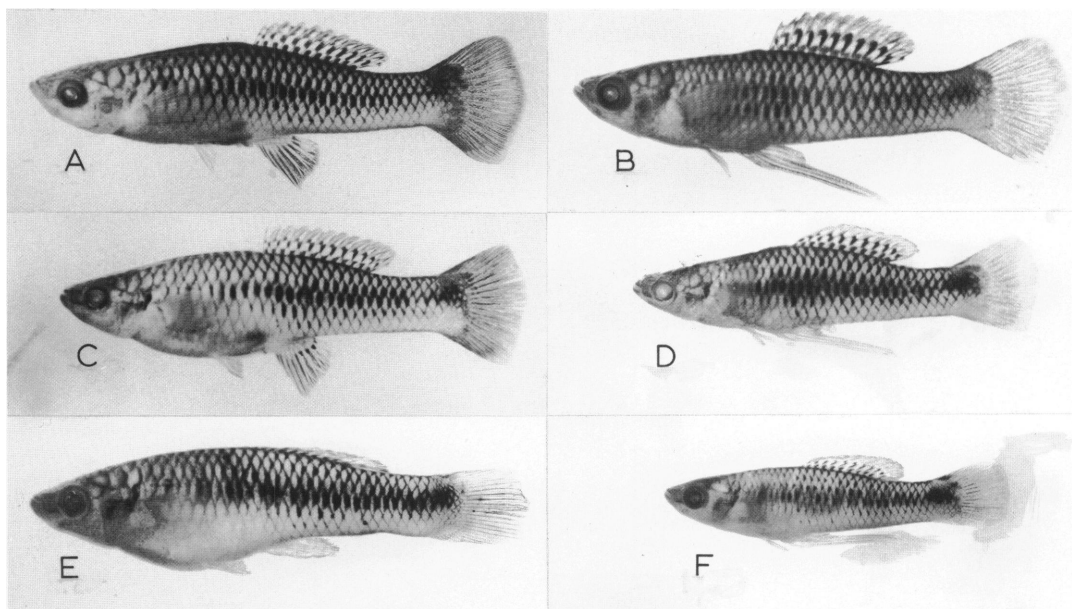


FIG. 16. Some variations in pigment patterns in *Heterandria obliqua* from upper Río San Ramón basin (cf. fig. 10). A-D from main stream of Río San Ramón, E-F from a tributary, the Río Chancolín. B, holotype, male, 31 mm. standard length, AMNH 36311. A, C, D, AMNH 36312: A, female, 62 mm.; C, female, 59 mm.; D, male, 39 mm.. E, female, 47.5 mm.; F, male, 30 mm., both AMNH 32909.

slightly to strongly concave behind distal spines of ray 3 (fig. 21).

Synapomorphies between *jonesi* and the group including *litoperas*, *obliqua*, *anzuetoi*, *cataractae*, *dirempta*, and *bimaculata*.

17. In ventral profile of body, a poorly defined transition between abdomen and caudal peduncle (as compared with an abrupt transition in *formosa*, *attenuata* and the species of *Neo-heterandria*).
18. Dorsal fin origin level with or anterior to anal fin origin and with modally more than 11 fin rays.
19. Pectoral fin rays modally 14 or 15, as compared with modally 13 in *attenuata*. The single exception to this statement is the presence of a modal number of 13 in the *obliqua* from Cubilguitz, a small population whose other characteristics clearly align it with the widespread *obliqua*.
20. Distal half of shaft of third gonapophysis in gonopodial suspensorium bent forward, not parallel with shaft of preceding element.

Synapomorphies between *litoperas* and the group in-

cluding *obliqua*, *anzuetoi*, *cataractae*, *dirempta* and *bimaculata*.

21. Length of depressed anal fin of adult females modally more than 22 percent of standard length.
22. Subdistal short segments on gonopodial ray 4a more than four in number and bearing ventral (anterior) peglike processes.
23. Subdistal spines on gonopodial ray 3 enlarged ventrally to form a slight bulge (elbow) along the ventral profile of the ray. This bulge occurs in the region occupied by a ventral fleshy swelling in *attenuata*, *jonesi*, and in this and the other species besides *formosa* (character 16).

Synapomorphy between *obliqua* and the group including *anzuetoi*, *cataractae*, *dirempta*, and *bimaculata*.

24. Distal fourth of gonopodium with an increased ventral (anterior) flexure of its rays and moderately to strongly concave along ventral profile behind enlarged spines of ray 3 (fig. 21).

Synapomorphy between *anzuetoi* and the group including *cataractae*, *dirempta*, and *bimaculata*.

25. Terminal segment on gonopodial ray 4a forming large decurved hook that is six times or more as long as high from base to tip.

Synapomorphy between *cataractae* and the group including *dirempta* and *bimaculata*.

26. Large decurved terminal hook on gonopodial ray 4a L-shaped or in form of open-J (as opposed to gently curved or sickle-shaped in *anzuetoi*).

Synapomorphy between *dirempta* and *bimaculata*.

27. Basicaudal spot large, spherical, dusky, filling area between midlateral line and dorsal margin of caudal peduncle.

Autapomorphous characters of the nine species.

*H. formosa*

28. Minute body size (male, 14 mm.; female 24 mm. standard length).

29. Superfoetation.

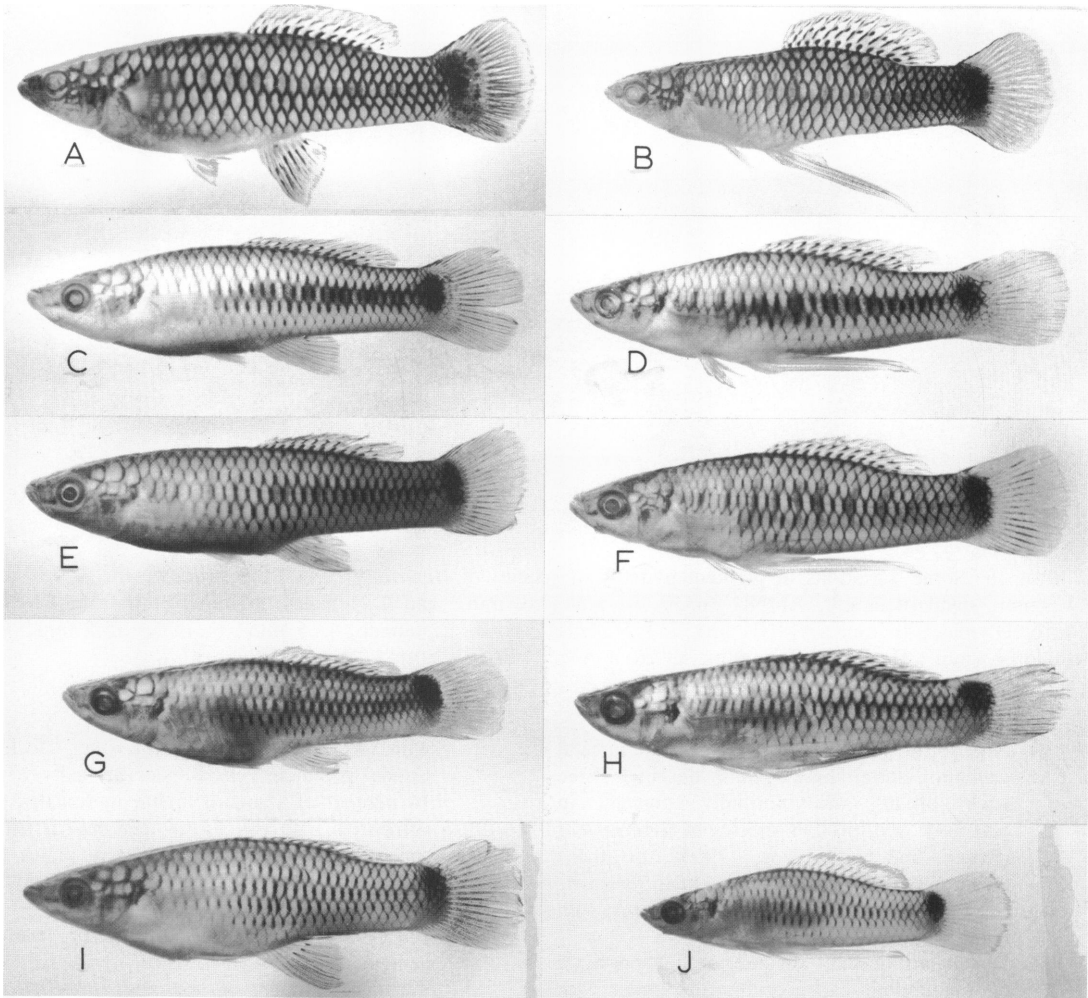


FIG. 17. Some variations in pigment patterns in *Heterandria anzuetoi* from Guatemala and Honduras. A-D from Río Motagua drainage, Guatemala; E, F from Río Lempa drainage, Guatemala; G and H from department of Atlantida, Honduras and I and J from department of Cortés, Honduras. A, female, 68.5 mm. standard length, and B, male, 41.5 mm., both from a laboratory strain from Gualán. C, female, 46 mm., and D, male, 36.5 mm. from Río Trimcheras, AMNH 35150. E, female, 46 mm., and F, male, 37 mm., AMNH 36327. G, female, 43.5 mm., UMMZ 173188. H, male, 30.5 mm., UMMZ 173207. I, female, 49 mm., and J, male, 33 mm., both from UMMZ 173305.



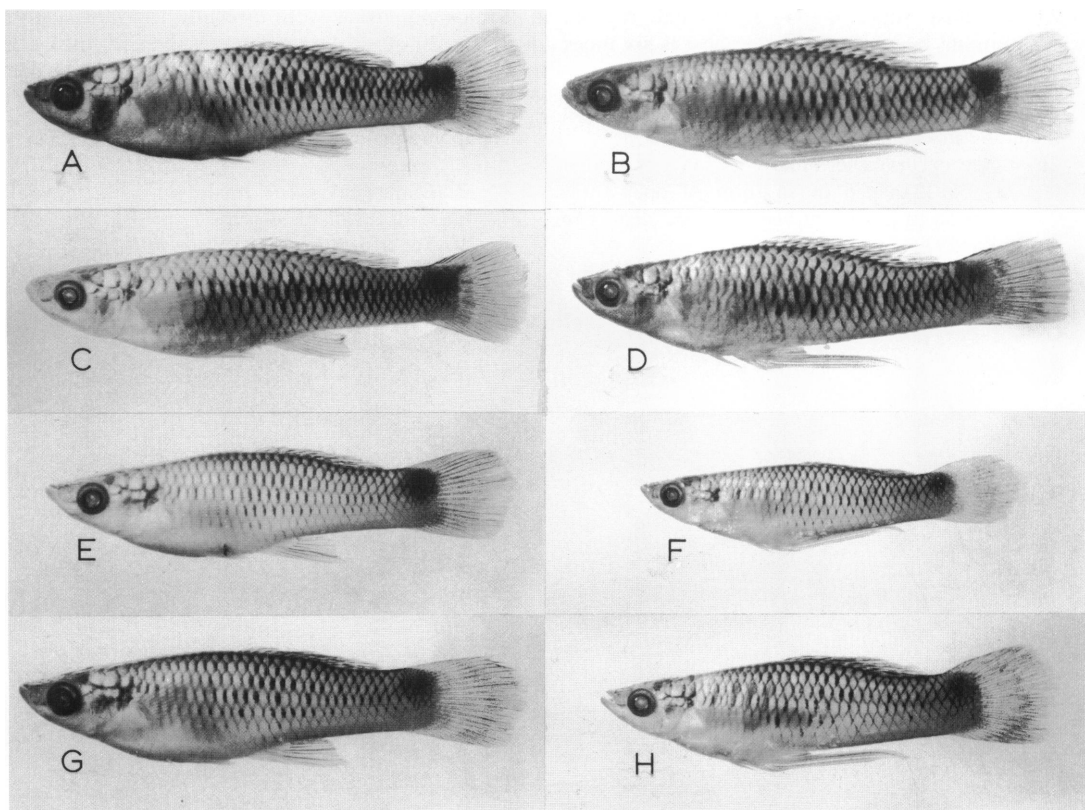


FIG. 18. Some variations in pigment patterns in species of *Heterandria*. A-D, *H. cataractae*: A, female, 44.5 mm. standard length, AMNH 36357. B, male, 40 mm., and C, female, 56 mm., both from AMNH 24486. D, male, 46 mm., AMNH 36357. E-H, *H. dirempta*: E, female, 43.5 mm.; F, male, 35.5 mm.; G, female, 43 mm.; H, male, 40.5 mm.; all from AMNH 36363.

30. Anteriormost pit organ of the supraorbital cephalic lateral line system absent. Three such organs are normally present in poeciliids and in other species of *Heterandria* (Rosen and Mendelson, 1960); of these three, it is the first that is absent in *formosa*.
31. Ray 5p below ray 6 of gonopodium with denticulate or serrate segments.
32. Distal half of shaft of anterior gonapophysis of gonopodial suspensorium subparallel with vertebral axis.
33. Ligastyle in gonopodial suspensorium reduced to a tiny ossicle.

*H. attenuata*

34. Head width of adult female averaging about 15 percent of standard length as compared

- with 17 to 19 percent for the other species.
35. Caudal peduncle very slender, modally 13 to 14 percent of standard length in females (as compared with 14 to 18 percent in other species), and 14 to 15 percent in males (as compared with 15 to 18 percent in other species).
36. Basicaudal spot diffuse and pale, or obsolescent in adults.
37. Terminal segment of gonopodial ray 4a ankylosed or joined by dense membranous tissue with tip of ray 5a.

*H. jonesi*

38. Tip of gonopodial ray 5a with a low, ventral flange that is seated between the paired halves of the underlying ray 4p.

39. Serrae of gonopodial ray 4p not arched away from the segments of ray 4a.
40. Subdistal segments of gonopodial ray 4a much elongated, the segments being equal in length to the combined bases of five to eight of the serrae above them on ray 4p.
41. First gonapophysis in gonopodial suspensorium longer and extending ventrally further than succeeding gonapophyses.

*H. litoperas*

42. Basicaudal spot barlike, extending from the upper caudal base to slightly below the mid-lateral scale row, bordered posteriorly by a sparsely pigmented area (white in life) which itself is bordered posteriorly by a slender, jagged line of dark pigment that lies across the upper caudal fin ray bases.
43. Subdistal spines of gonopodial ray 3 dis-

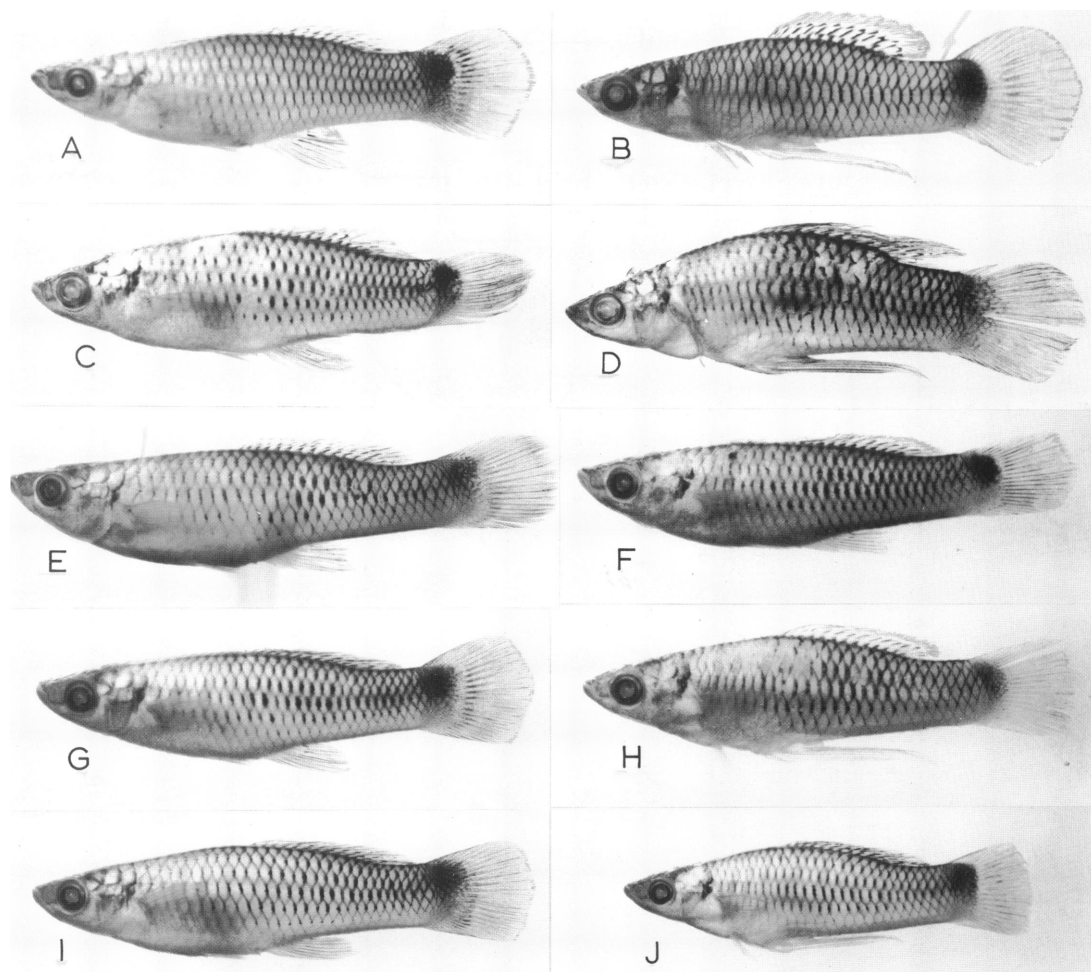


FIG. 19. Some variations in pigment patterns in *Heterandria bimaculata*. A and B, Río Motagua drainage, Guatemala. C and D, Ceiba, Atlantida, Honduras. E-J, Río Salinas system, Río Usumacinta drainage, Guatemala. A, female, 58.5 mm. standard length, and B, male, 31 mm., both AMNH 36342. C, female, 38 mm. and D, male, 47 mm., both UMMZ 193827. E and F, females, 53 mm. and 36.5 mm., respectively, and H, male, 31.5 mm., all from AMNH 25409. G and I, females, 39 mm. and 50.5 mm., respectively, and J, male, 40 mm., all from AMNH 25261.



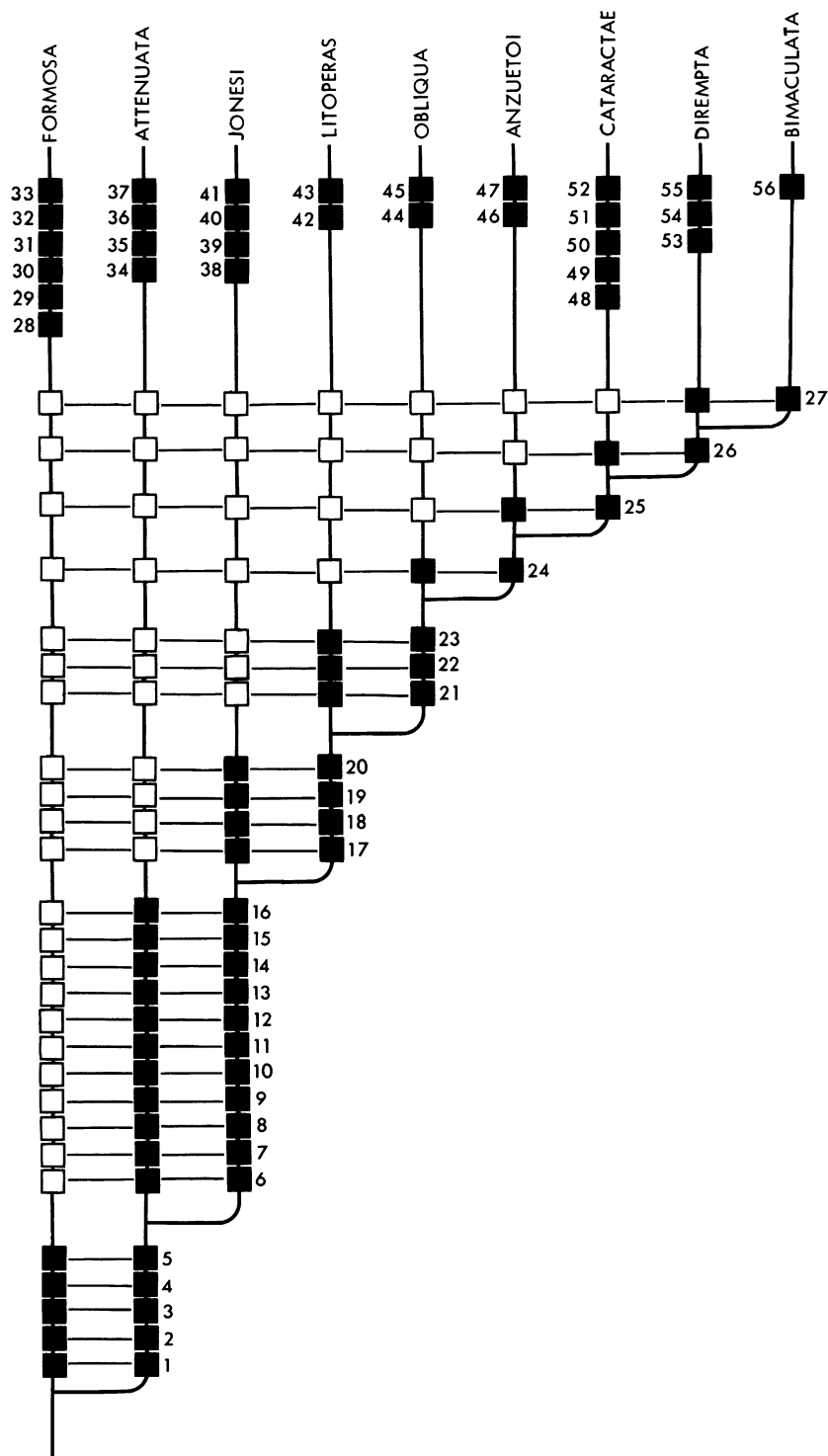


FIG. 20. Synapomorphy diagram for the species of *Heterandria*. Synapomorphies: black squares joined to open squares (the primitive states of a character), numbers 1-27. Autapomorphies: the unique defining properties of the taxa represented by numbers 28-56. Numbers 1-56 refer to numbered items of the synapomorphy scheme in text, pp. 298-310.

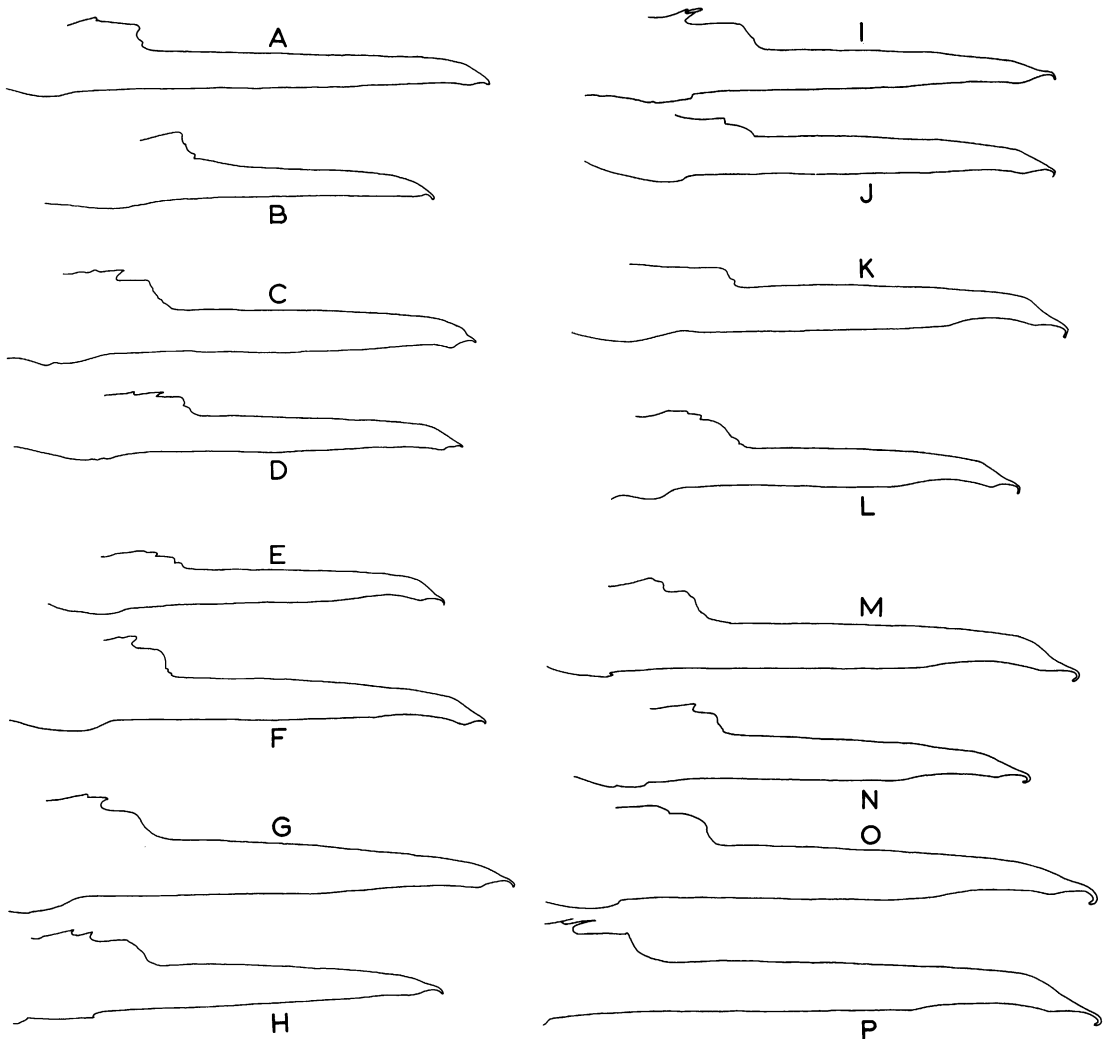


FIG. 21. Gonopodial outlines of the species of *Heterandria*. Note that the ventral profiles of A and B are more or less straight and that the tips of A to D are little extended. In E to P the ventral profile is distinctly concave and the tips are progressively extended, distinctly decurved in K to P, and recurved in M to P. A, *H. attenuata*, AMNH 36334. B, *H. jonesi*, UMMZ 183887. C and D, *H. litoperas*, AMNH 35003 and 36331, respectively. E and F, *H. obliqua*, UMMZ 190768 and AMNH laboratory strain from Río San Ramón, respectively. G to J, *H. anzuetoi*: G, Río Motagua drainage, Guatemala, AMNH 35150; H, Río Lempa drainage, Guatemala, AMNH 36326; I, Cortés, Honduras, UMMZ 173305; J, Ceiba, Atlantida, Honduras, UMMZ 173328. K, *H. cataractae*, AMNH 24486. L, *H. dirempta*, AMNH 36362. M to P, *H. bimaculata*: M, AMNH 36353; N, AMNH 36346; O, AMNH 36341; P, UMMZ 193827. G and O are from the Río Motagua in Guatemala, and J and P are from near Ceiba, Atlantida, Honduras.

tinctly enlarged to form a prominent elbow-like swelling. The similar structure in *obliqua*, *anzuetoi*, *cataractae*, *dirempta* and *bimaculata* is less well-developed.

*H. obliqua*

44. Basicaudal spot oblique and longer than high

in adults, its lower end merging anteriorly with midlateral pigment.

45. Sides with numerous black flecks, especially on caudal peduncle, and on midlateral scale row where they are aligned to form an interrupted midlateral stripe which overlies a diffuse, dusky band of pigment.

*H. anzuetoi*

46. Basicaudal spot a dark bar more than half the least depth of caudal peduncle that inclines slightly forward at its upper edge (a variant of this pattern is discussed in the species account).
47. Reticular pattern (crosshatching) along sides well-developed and accentuated above and below midlateral scale row and along the scale row by a series of short, broad bars and some dusky pigment.

*H. cataractae*

48. Caudal peduncle slender (14 to 15 percent of standard length). Convergent in this character with *attenuata*, but not quite as slender (see character 35).
49. Distance from dorsal fin origin to caudal base, as a percent of standard length, longer than in any species of *Heterandria* and matched by only two of three populations of *litoperas*. This character, which normally corresponds directly with dorsal fin ray number, is exceptional in *cataractae* in having as high a value as some *litoperas* without having as many fin rays as those populations (table 7).
50. Basicaudal spot elongate and confined to upper half of caudal peduncle and caudal fin base; the pattern is ragged posteriorly where it extends out onto the upper caudal fin ray bases.
51. Sides with black flecks forming one to three interrupted rows at midside. This character is very similar to that in *obliqua* where the midlateral row is more consistently developed. Such patterns, however, are both modifications of a feature present in all species of the subgenus *Pseudoxiphophorus*, namely,

the presence of comma-shaped or rectangular black flecks at the nodes of the crosshatching along the sides. These flecks tend to be slightly to well-organized into rows in all species except *attenuata* in which they have a scattered and random distribution.

52. Subdistal short segments on gonopodial ray 4a very numerous (9 to 11, modally 10).

*H. dirempta*

53. Anal fin of female long (modally 26 to 27 percent of standard length). This high value is matched by only a single population of *litoperas*.
54. Dorsal fin rays relatively few (modally 13). The modal value is lower than that for *litoperas*, for all but the combined sample of *anzuetoi* from Honduras, for *cataractae* and for all populations of *bimaculata*. The counts of *dirempta* are slightly higher (modally, one fin ray) than the combined counts for *obliqua* and *jonesi*. If this character in *dirempta* is convergently low, as suggested by several other congruent lines of evidence which place *dirempta* within a group of fishes (including *cataractae* and *bimaculata*) with high fin ray counts, it can be treated as an autapomorphic defining character.
55. A series of several, short, dark bars on the upper sides above the pectoral fins separated, in life, by iridescent green interspaces. The pattern fades in formalin preservation and is not, for this reason, incorporated in the diagnosis of this species (see discussion under species account of *dirempta*).

*H. bimaculata*

56. Terminal segment (hook) on gonopodial ray 4a very long and strongly and tightly recurved (retrorse).

## ANALYTICAL KEY

- A. Adult body size minute (males *ca.* 10-14 mm., females *ca.* 20-25 mm. standard length); supraorbital division of cephalic lateral line with two pit organs; dorsal fin rays 6 or 7; segments of midsection of gonopodial ray 5 ankylosed; ligastyle in gonopodial suspensorium a minute ossicle not much longer than wide; gestation superfoetatus<sup>1</sup>; Southeastern United States . . . . . *Heterandria formosa*
- AA. Smallest adult body size greater than 25 mm. standard length; supraorbital division of cephalic lateral line with three pit organs; dorsal fin rays more than 8; segments of midsection of gonopodial ray 5 not ankylosed; ligastyle prominent, distinctly rodlike; gestation of single large broods only . . . . . B
  - B. Body slender, least depth caudal peduncle modally 14 percent or less of standard length; head width modally 16 percent of standard length; dorsal fin origin behind anal origin; vertebrae modally

<sup>1</sup>Stearns, (1978) has found that some females of *Neo-heterandria tridentiger* are superfoetatus. Since *tridentiger*, like *formosa*, is the smallest member of its genus, and both are very small in absolute size, superfoetation in *formosa* is as easily interpreted as a reproductive au-

tapomorphy associated with its small body size as a possible synapomorphy with other superfoetatus heterandrii (*N. tridentiger* and the species of *Poeciliopsis* and *Phallichthys*).

- 33; lateral line scales modally 31; pectoral rays modally 13; basicaudal spot diffuse, pale, or obsolescent in adults of both sexes; uncini of gonopodial suspensorium arising nearer base than midpoint of shaft of gonapophysis; shaft of third gonapophysis parallel with shaft of second; terminal segment of gonopodial ray 4a coalesced, or joined by dense, granular tissue, with tip of ray 5, not more than three times as long as high and not decurved. Río Candelaria Yalicar, Alta Verapaz, Guatemala ..... *Heterandria attenuata*
- BB. Body robust, least depth caudal peduncle modally more than 14 per cent of standard length; head width modally more than 16 percent of standard length; dorsal fin origin directly over or in advance of anal origin; vertebrae modally 31 or 32; lateral line scales modally 28 or 29; pectoral rays modally 14 or 15; basicaudal spot strongly developed in adult females and most adult males; uncini of gonopodial suspensorium arising nearer midpoint than base of shaft of gonapophysis; distal half of shaft of third gonapophysis bent forward, not parallel with shaft of second gonapophysis; terminal segment of gonopodial ray 4a not coalesced, or joined by dense, granular tissue, with tip of ray 5, three or more times as long as high and decurved or not ..... C
- C. In gonopodium: tip of ray 5a with low ventral flange; serrae of ray 4p not arched away from ray 4a; subdistal small segments (segment length less than 1½ times height) on ray 4a modally 3 and without ventral peglike processes; central spines on ray 3 not enlarged to form elbow. Atlantic slope of Mexico north of Veracruz ..... *Heterandria jonesi*
- CC. In gonopodium: tip of ray 5a without flange; serrae of ray 4p arched away from ray 4a; subdistal small segments on ray 4a modally more than 3 and with ventral peglike processes; central spines on ray 3 enlarged to form elbow ..... D
- D. Basicaudal spot large, barlike, extending only slightly below lateral line, sloped backward dorsally, bordered posteriorly by a clear area and by broken dark pigment and, in most cases, extending dorsally to upper margin of caudal peduncle; dorsal fin rays 14 to 18, modally 15 or 16; height of gonopodial tip 80 to 110 percent of its length; terminal segment of gonopodial ray 4a about three times as long as high, not decurved; subterminal short segments of ray 4a three to seven in number, rarely more than six, modally five or six. Basin of the Río Polochic, Guatemala ..... *Heterandria litoperas*
- DD. Basicaudal spot, when barlike, extending below lateral line, not sloped backward or ocellated posteriorly, not extending to dorsal midline, or not barlike; dorsal fin rays 10 to 17, modally 12 to 15; height of gonopodial tip 60 to 100 percent of its length, only rarely more than 90 percent; terminal segment of gonopodial ray 4a three or more times as long as high, slightly to strongly decurved; subterminal short segments of ray 4a three to 11 in number, always more than six, modally five to 10 ..... E
- E. Basicaudal spot elongate, extending obliquely between upper caudal fin base and midlateral scale row of caudal peduncle where it merges with diffuse band of dusky pigment and a row of close-set, vertical, black dashes; terminal segment of gonopodial ray 4a three to five times as long as high, very slightly to slightly decurved. Isolated basins of the Río Chixoy (Salinas) and Río Lacantún in the Sierra de Chamá and its westerly extension, Guatemala ..... *Heterandria obliqua*.
- EE. Basicaudal spot extending below midlateral scale row of caudal peduncle; terminal segment of gonopodial ray 4a more than five times as long as high, this segment, and/or its membranous envelope, moderately to strongly decurved ..... F
- F. Basicaudal spot barlike and sloping forward, extending well below midlateral line, or a vertically elongate oval centered on and extending above and below midlateral line; midlateral scale row dusky posteriorly and bordered above and below by zigzag lines formed from the conjoined, darkened elements of the reticular network; terminal segment of gonopodial ray 4a and/or its membranous envelope gently curved or sickle-shaped, but never recurved; subterminal short segments of ray 4a three to eight in number, modally five or six. Río Lempa drainage, Guatemala, and the highlands and Atlantic versant of Honduras, southward to the Nicaraguan lowlands ..... *Heterandria anzuetoi*.
- FF. Basicaudal spot developed mainly above midlateral scale row and with comet-tail like ventral or posterior extensions; midlateral scale row not emphasized by zigzag melanophore patterns; terminal segment of gonopodial ray 4a and its membranous envelope always strongly decurved or recurved (L-shaped or J-

shaped); subterminal short segments of ray 4a five to 11 in number, modally seven, eight or 10 .....G

G. Basicaudal spot irregular, horizontally elongated, not extending below mid-lateral scale row, in most cases with wispy, streaklike posterior extensions onto upper caudal fin base; sides coarsely reticulated with large, interlocking, black crescents; caudal peduncle slender, modally 14 to 15 percent of standard length in females; distance from dorsal origin to caudal base modally 52 to 54 percent of standard length in females; subterminal short segments on gonopodial ray 4a nine to 11 in number, modally 10. Arroyo Sachicha, Alta Verapaz, Guatemala ..... *Heterandria cataractae*.

GG. Basicaudal spot large and almost perfectly round, only very slightly ovoid in a few cases, and in some cases with a dusky, taillike ventral extension; reticulum on sides not forming large crescents; caudal peduncle generally less slender, modally more than 15 percent of standard length in females; distance from dorsal origin to caudal base modally less than 52 percent of standard length in females; subterminal short segments on gonopodial ray 4a five to 10 in number, modally seven or eight (possibly more in Honduras *bimaculata*, but presently known population includes only a single male) .....H

H. Dorsal fin relatively short, base length modally 26 to 30 percent of standard length in males, 24 to 28 percent in females; dorsal fin rays 12 or 13, rarely 14, modally 13; terminal segment on gonopodial ray 4a strongly decurved (L-shaped or in form of open-J); subterminal short segments on ray 4a five to eight in number, mean number less than seven. Río Chajmaic, Alta Verapaz, Guatemala.....

..... *Heterandria dirempta*  
HH. Dorsal fin longer, base length modally more than 30 percent of standard length in males, more than 28 percent in females; dorsal fin rays 12 to 17, modally 14 or 15; terminal segment on gonopodial ray 4a long and strongly and tightly recurved (retrorse); subterminal short segments on ray 4a six to 10, rarely five, in number, mean number more than seven. Southeastern Mexico to Ceiba, Honduras, mostly in lowlands ..... *Heterandria bimaculata*

## SYSTEMATIC ACCOUNT

### GENUS *HETERANDRIA* AGASSIZ

**DEFINITION:** Poeciliid fishes with a basicaudal spot; a discrete to obsolescent band of dark pigment at midside; dusky or dark pigment along the basal third of dorsal and anal fin; a downturned membranous sheath at the tip of the gonopodium that incorporates the distal part of ray 4a; gonopodial ray 3 falling short of tip of fin and bearing blunt, peglike, ventral spines distally; a series of from seven to 15 serrae subdistally on ray 4p; ray 6 of gonopodium swollen and ankylosed distally and with a strong distal spur directed obliquely toward base of ray 5; in gonopodial suspensorium gonapophyses with large recurved uncini arising within basal half of shaft, with tip of shaft curving downward and tip of uncinus curving posteriorly.

**REMARKS:** Rosen and Bailey (1963) pre-

sented a generic synonymy and an expanded definition of the group. The taxonomic history of the genus was discussed by Rosen and Bailey (*op. cit.*), who recognized two species (*formosa* and *bimaculata*) and more recently by Miller (1974), who redescribed a third (*jonesi*). The present account describes six additional species as new. Miller (*op. cit.*) subdivided the genus into two subgenera, an action followed here.

**RANGE AND SPECIES COMPOSITION:** Nine species in Atlantic drainages from North Carolina southward to Nicaragua, one of which is also present in a single Pacific drainage in southeastern Guatemala (figs. 22,23).

### SUBGENUS *HETERANDRIA* AGASSIZ

**DIAGNOSIS:** Body size minute, about 14 mm. (male) and 24 mm. (female) in standard length; length of dorsal fin base 6 to 10 percent of



FIG. 22. Distribution of *Heterandria* in North and Middle America.

standard length; reproductively superfoetatus; supraorbital division of cephalic lateral-line system with only two pit organs present; basicaudal spot about one scale wide, midlateral in position, and confined to caudal peduncle; reticular network of scale pocket pigment feebly developed; distinct dark or dusky midlateral stripe present from snout to basicaudal spot; numerous vertical bars along sides of adults; basal markings on dorsal and anal fin present as a continuous band of dark pigment; lateral line scales 28 to 30, usually 29; pectoral fin rays 10 to 12, usually 11; anal rays 9 or 10; dorsal rays

6 or 7; jaw dentition including an outer row of large teeth and an inner band, two teeth wide, of much smaller teeth; in gonopodium of male, ray 5a longer than ray 4p, some segments of ray 5p below ray 6 differentiated into serrae-like elements, an elongate terminal element and the one penultimate short segment of ray 4a entering downturned membranous envelope, ventral (anterior) profile of gonopodium convex; in gonopodial suspensorium, anterior gonapophysis subparallel with vertebral axis, uncini on gonapophyses arising proximally on gonapophyseal shaft just below vertebral col-



FIG. 23. Locations of the mouths of some major river basins referred to in this study.

umn, ligastyle reduced to an ossicle that appears no higher than wide in lateral view.

**SPECIES COMPOSITION:** A single species, *H. formosa*, as given below.

*Heterandria formosa* Agassiz  
Figures 6A, 15A

**DIAGNOSIS AND REMARKS:** Diagnosis as for the subgenus. A synonymy for this species is given in Rosen and Bailey (1963).

**MATERIAL:** *North Carolina:* USNM 94332 (29 hf.-gr. to ad. males and females, 11-26 mm.), Lower Burnt Mill Creek, Wilmington, New Hanover County. *South Carolina:* AMNH 18655 (1 ad. male, 13.5 mm.), freshwater tributary to Santee River. *Florida:* AMNH 36309 (7 ad. males and females, 13-21 mm.), River Styx at Cross Creek Rd., Alachua Co.; AMNH 37278 (30 ad. males and females, 16-22.5 mm.), Lakeland, Polk Co.; USNM 133265 (197



ad. males and females, 13-29 mm.), St. John's River, Crows Bluff near De Land, Volusia County.

**GEOGRAPHY:** Southeastern North Carolina, south through eastern and southern Georgia and peninsular Florida, west near the Gulf Coast to New Orleans, Louisiana (fig. 22). The only species of *Heterandria* in North America.

#### SUBGENUS *PSEUDOXIPHOPHORUS* BLEEKER

**DIAGNOSIS:** Adult body size greater than 25 mm. in standard length; length of dorsal fin base 16 to 40 percent of standard length; gestation of single large broods only; supraorbital division of cephalic lateral line system with three pit organs; basicaudal spot in adults more than one scale wide, extending slightly or significantly above midlateral scale row and onto caudal fin ray bases (in at least some representatives of all species); reticular network of scale pocket pigment well developed; midlateral stripe when present diffuse, never extending onto snout; vertical bars when present in adults few, broad, confined mostly to trunk region above midlateral scale row; dorsal fin with more than one row of discrete dark spots on interradi al membrane (one row near fin base), anal fin with dark pigment radiating from a dense proximal blotch into basal third or half of fin along interradi al membrane; lateral line scales 28 to 32, usually 30 or 31; pectoral fin rays 12 to 15, usually 13 or 14; anal rays 11; dorsal rays 9 to 18; jaw dentition including an outer and inner row of large teeth separated by a narrow band of smaller teeth; in gonopodium of male, ray 5a shorter than 4p, segments of ray 5p below ray 6 not denticulate or serrate, downturned membranous envelope at tip of ray 4a containing only the elongate terminal segment of that ray, the 2 to 11 penultimate short segments withdrawn into tip of gonopodium proximal to terminal membranous envelope, ventral (anterior) profile of distal third or fourth of gonopodium weakly to strongly concave; in gonopodial suspensorium, anterior gonapophysis at angle of about 45° to vertebral axis, uncini on posterior gonapophyses arising near midpoint or beyond on gonapophyseal shaft, ligastyle rodlike in lateral view.

**REMARKS:** The several species described

here as new are represented by informal designations in Rosen (1978), as follows: *attenuata* = species A; *litoperas* = species B; *obliqua* = species C; *anzuetoi* = species D; *cataractae* = species E; *dirempta* = Chajmaic *bimaculata*.

**RANGE AND SPECIES COMPOSITION:** Eight species from Atlantic slope of Mexico and northern Central America. One population in Pacific drainage (Río Lempa) of Guatemala (figs. 22-25).

#### ***Heterandria attenuata* Rosen and Bailey, new species**

Figures 4A; 6B, C; 8; 15 B,D; 21A; 24; 26

**DIAGNOSIS:** A slender, sharply-snouted species with a short-based dorsal fin (18 to 22 percent of standard length in adult males, as compared with 22 to 40 percent in the other species of the subgenus) originating behind a vertical from the anal fin origin, and a narrow head (table 10) and short anal fin (table 9) in adult females; ventral profile of adult females showing abrupt transition between abdomen and caudal peduncle; vertebrae 32 or, modally, 33 (modally less than 33 in other species); dorsal fin rays 10 or 11 (table 4); pectoral fin rays 13, rarely 14; lateral line scales 31, rarely 30 or 32; sides with sparsely scattered vertical black spots one scale width or less in height, basicaudal spot diffuse and pale, or obsolescent in adults (well-developed and punctate in juveniles); in gonopodium of male, short, blunt terminal segment of ray 4a ankylosed or joined by dense membranous tissue with tip of ray 5a, subdistal short segments 2 to 5, modally 3, short membranous envelope at fin tip only little downturned, ventral profile of subdistal region of gonopodium very slightly concave behind a fleshy swelling below the penultimate segments of ray 3, height-length ratio of gonopodial tip 1.0 or greater (i.e., as high as, or higher than, long); in gonopodial suspensorium, uncini arising much nearer base than tip of anterior gonapophyses, and shaft of third gonapophysis distal to uncini parallel with shafts of first and second gonapophyses.

**DESCRIPTION AND REMARKS:** Additional meristic and morphometric characters of *attenuata* are given in tables 1 to 12, and figures

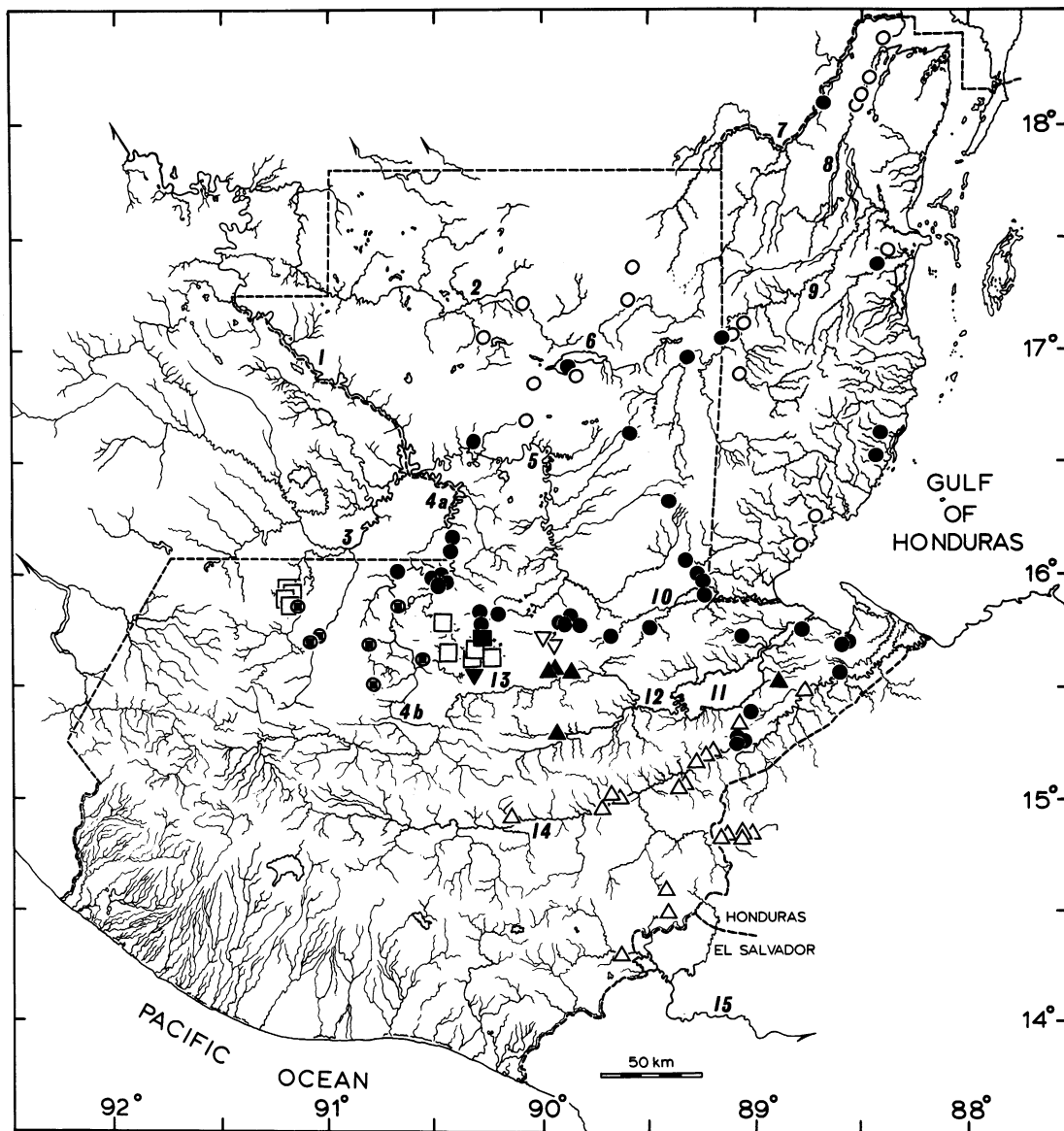


FIG. 24. Distribution by record stations of the species of *Heterandria* in Guatemala; Copán, Honduras; and Belize. Dot, *H. bimaculata* included in tabular data; open circle, *H. bimaculata* examined but not included in tabular data; open square, *H. obliqua*; solid square, *H. attenuata*; solid inverted triangle, *H. cataractae*; open inverted triangle, *H. dirempta*; solid triangle, *H. litoperas*; open triangle, *H. anzuetoi*; open circle with solid square, putative hybrids between *H. obliqua* and *H. bimaculata*. 1. Río Usumacinta. 2. Río San Pedro de Martír. 3. Río Lacantún. 4a. Río Salinas. 4b. Río Chixoy or Negro. 5. Río de la Pasión. 6. Lago Petén Itzá. 7. Río Hondo. 8. New River. 9. Belize River. 10. Río Sarstún. 11. Lago Izabal. 12. Río Polochic. 13. Río Cahabón. 14. Río Motagua. 15. Río Lempa.

8 and 15 B,D. These data are summarized by the following general statements:

1. In the relative length of the depressed

anal fin, females of *attenuata* may be separated from all species except *jonesi*.

2. In the relative distance from the dorsal

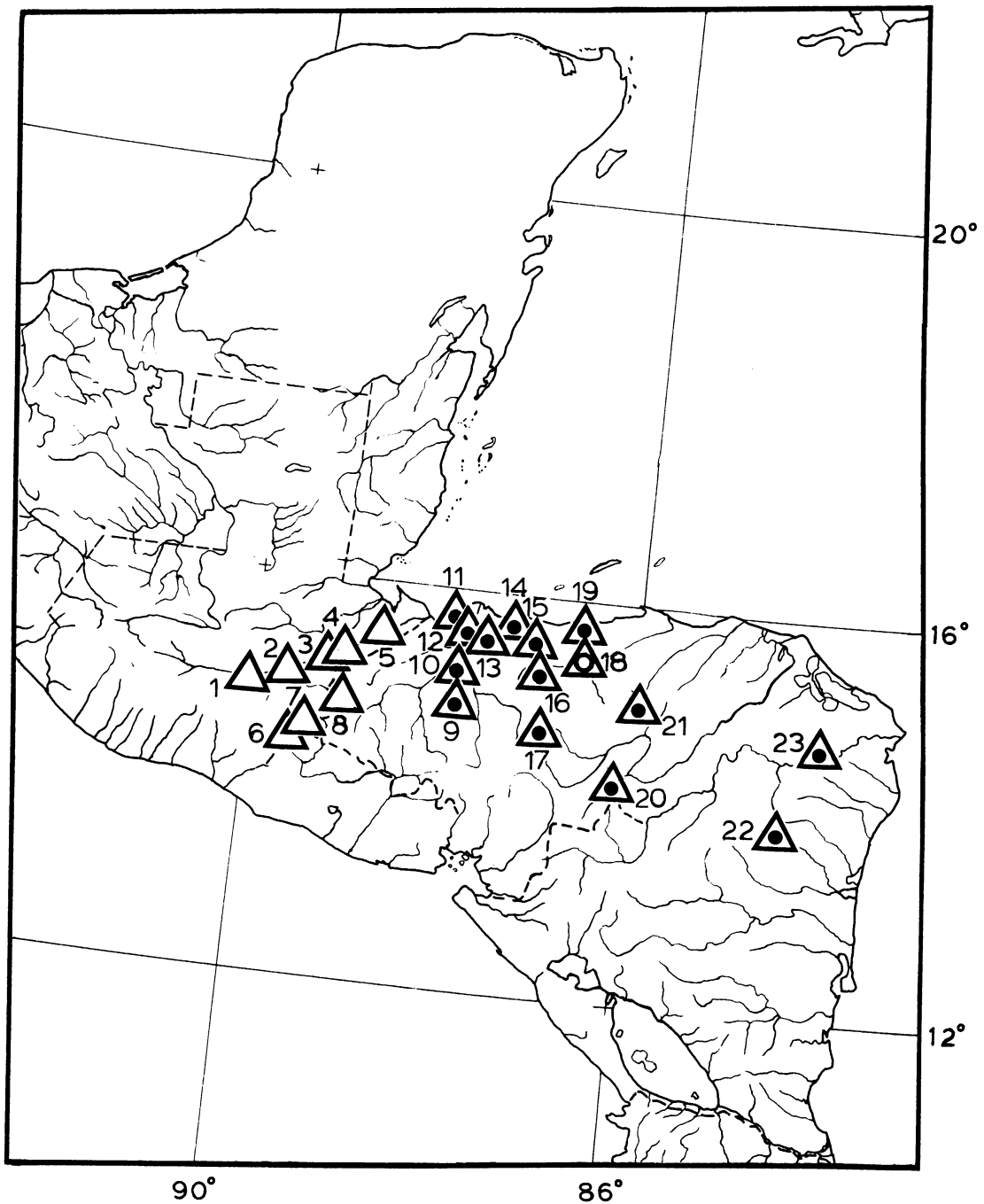


FIG. 25. Distribution by record stations of *Heterandria anzuetoi*. Open triangle, Río Motagua; triangle plus dot, Honduras and Nicaragua; triangle plus open circle, literature record only. 1. AMNH 36323, USNM 114529, UMMZ 193876. 2. AMNH 36325, UMMZ 190576, UMMZ 190813, AMNH 36322, 36324, USNM 134583, 134584. 3. AMNH 1416, USNM 73972, UMMZ 65258, AMNH 36319 holotype, 36320, 36321, UMMZ 193976, AMNH 35138, UMMZ 197288. 4. AMNH 35145, UMMZ 197298, AMNH 35149, 35150. 5. AMNH 35177, UMMZ 197330. 6. AMNH 35215, UMMZ 197389. 7. AMNH 36327, UMMZ 190806, UMMZ 163807, AMNH 36326, USNM 114517, UMMZ 190800. 8. LACM 32393, 32395, 32396, 32474. 9. LACM 32340, 32401, 32436. 10. LACM 32379, 32380. 11. LACM 32385, 32467, 32464; UMMZ 173271, 173287,

origin to the caudal base, females of *attenuata* can be separated from females of all species except *jonesi*, although the mean values for *attenuata* are lower than those for *jonesi*.

3. In the relative length of the dorsal fin base, males of *attenuata* differ from all other species in this subgenus, and females of *attenuata* differ from all except females of *jonesi*.

4. In the relative distance from the dorsal fin origin to the snout, females of *attenuata* may be separated from all species except females of *jonesi*.

5. In relative head width, females of *attenuata* have a lower mean than all other species although there is considerable overlap in the range of values.

6. In relative greatest depth of body, females of *attenuata* differ from all other species

in mean value except for a population of *bimaculata* from the upper Río Sarstún.

7. In relative least depth of caudal peduncle, males and females of *attenuata* differ from all other species of the subgenus in having lower mean values.

The slenderness of body in this species is accentuated by the posterior origin of the short-based dorsal fin and by the relatively short dorsal and anal fin rays.

*Heterandria attenuata* also has, on average, fewer pectoral fin rays (13) and more vertebrae (33) than other species (tables 2, 3).

In pigmentation, both living and preserved specimens of *attenuata* are rather pale, and somewhat translucent in life. The reticular network on the side of the body forms a delicate pattern of thin, intersecting, sigmoid lines,

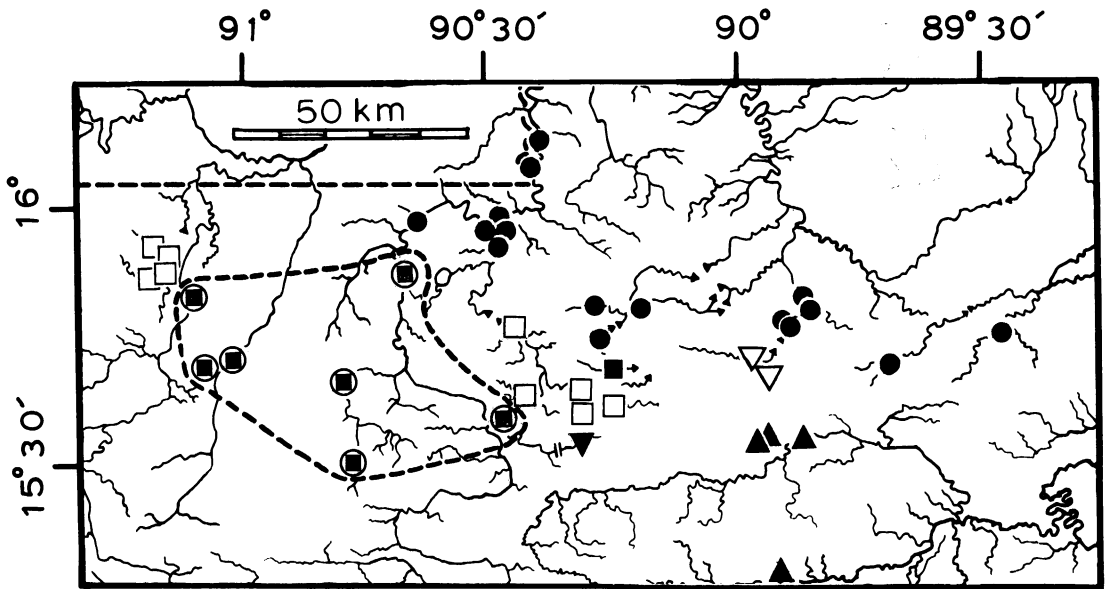


FIG. 26. Distribution by record stations of the species of *Heterandria* in the karst regions of Huehuetanango, El Quiché and Alta Verapaz, Guatemala. Detail of figure 24. Symbols as in figure 24. The area circumscribed by the dashed line represents a region of intergradation, here interpreted as hybridization between *H. obliqua* (open squares) and *H. bimaculata* (dots).

173305, 173257, 173279. 12. LACM 32374, 32376, 32377; UMMZ 173161, 173148, 173155, USNM 101781. 13. LACM 32451, 32410, 32454, 32453, 32450, 32411, 32452. 14. ANSP 81642, LACM 32435, UMMZ 189564, 173200, 173178, 173188, 173207, 173348. 15. UMMZ 173365, 173223, 173227. 16. LACM 32372, 32368, 32371. 17. UMMZ 188108. 18. USNM 163678. 19. LACM 32462, 32471, UMMZ 173328. 20. LACM 32298, 32299. 21. LACM 32306, 32305. 22. ANSP 65156-7.

which is interrupted at the nodes of intersection here and there by small, dark, vertical dashes. Two rows of dorsal fin spots are present but the upper row is much less developed than the lower one and in many cases is interrupted by gaps of unpigmented interradiation membrane. The basicaudal spot is distinct, almost perfectly round, entirely above the midlateral scale row, and only about 25 to 30 percent of the depth of the caudal base in juveniles and young fish. In adults, the basicaudal spot fades to a diffuse blotch near the upper caudal base and occupies 40 to 60 percent of the caudal peduncle depth. In some adult specimens, especially males, the spot is so faint that it is barely detectable. Adult females have the lower sides dusky in front of the anal fin and possess periproctal pigment consisting of one or two very dark, punctate spots on each side of the urogenital region. The median fins (especially the caudal), tend to be dusky near their margins, and the basal pigment on the anal fin, characteristic of all species of *Heterandria* is well developed in the female and young. Adult males show a broad band of dusky pigment at midside between the pectoral base and the area above the gonopodial base. In life, the median fins of adults contain pale yellow or orange pigment, and the dorsal fin has opaque white spots associated with the basal rows of black spots. The upper gill cover is iridescent bluish green.

**MATERIAL:** Holotype (AMNH 36332), an adult male, 37.9 mm. in standard length, collected in the Río Candelaria Yalcar about halfway between source and mouth, Río Usumacinta system via an unknown subterranean connection, Alta Verapaz, Guatemala, on April 4, 1974, by Reeve M. Bailey, Donn E. Rosen, Richard P. Vari, Roderico Anzueto, and René Debroy. Taken with the holotype were 67 half-grown to adult males and females (AMNH 32911), 29-53 mm.; and UMMZ 197097. Additional paratypes are: AMNH 36334 (23 hf.-gr. to adult males and females, 30-59 mm.), and UMMZ 190491, Río Candelaria Yalcar at Candelaria; AMNH 36333 (45 laboratory-reared young to adult males and females, 17-70 mm.) from the type locality.

**GEOGRAPHY:** Known only from the Río Candelaria Yalcar, an east-west stream about 7

miles long with a subterranean outlet from the Candelaria Valley, Alta Verapaz, Guatemala (figs. 24,26). Neither sympatric nor syntopic with other forms of *Heterandria*.

**ETYMOLOGY AND AUTHORSHIP:** The trivial name *attenuata*, an adjective, refers to the slender body form of this species. The description of this species is based, in part, on data gathered jointly by me and Dr. Reeve M. Bailey, and should be jointly attributed.

*Heterandria jonesi* (Günther)

Figures 4B; 6D-F; 15 C, E, F

**DIAGNOSIS:** a robust species with a relatively short dorsal fin (18 to 24 percent in adult females, tables 5,6) originating slightly anterior to a vertical from the anal fin origin, and a relatively short anal fin in females (table 9); basicaudal spot small, discrete, confined to caudal peduncle, or larger, diffuse and overlapping bases of upper caudal rays; dorsal fin rays 9 to 15, modally 12; in gonopodium of male, tip of ray 5a with a low ventral flange that is seated between the paired halves of the underlying ray 4p, serrae of ray 4p not arched away from the segments of 4a which are much elongated, each elongated segment being equal in length to the combined bases of 5 to 8 of the serrae on 4p, terminal element on 4a gently decurved, comma-shaped, preceded by 2 to 4, modally 3, penultimate short segments; in the gonopodial suspensorium, first gonapophysis longer and extending ventrally farther than succeeding elements.

**REMARKS:** Miller (1974) has discussed the taxonomic history of this species and has given a synonymy.

**MATERIAL:** *Mexico (Veracruz):* AMNH 36335 (43 half-grown to adult males and females, 27-58 mm.), Río Atoyac, 2 km. north-northwest of Potrero; UMMZ 187718 (476 young to adult males and females, 13-49 mm.), Rancho Sierra de Agua, about 12 miles west of Orizaba; ANSP 23145-174 (30 adult males and females, 25-72 mm.), ANSP 24169 (1 adult female, 52 mm.), Orizaba?; ANSP 15884-896 (13 adult males and females, 29-71 mm.), Orizaba. (*Puebla*): AMNH 36336 (17 young to adult males and females, 17-43 mm.), AMNH

36337 (17 half-grown to adult males and females, 23-63 mm.), both from small tributaries to Río Zoyoquila, but separated by falls, 10 and 9 km., respectively, north-northwest of Rancho Las Margaritas, Huetamalco. (*San Luis Potosí*): ANSP 91265 (2 yg. to half-grown., 18-24 mm.).

**GEOGRAPHY:** Río Guayalejo (Río Tamesí basin) of southeastern Tamaulipas southward to the Río Nautla and Río Atoyac, Veracruz, Mexico. *Heterandria jonesi* overlaps the northern tip of the range of *H. bimaculata* in southern Mexico where a single case of sympatry between them has been reported (Miller, 1974; fig. 4) in the upper Río Atoyac due west of Veracruz.

***Heterandria litoperas*** Rosen and Bailey, new species

Figures 4C; 6 G-I; 9; 15 G-J; 21 C, D; 24

**DIAGNOSIS:** a species of *Heterandria* with a long dorsal fin (14 to 18 rays, modally 15 or 16 and tables 5,6) that in females originates well in front of the anal fin origin, a strongly developed reticular pattern on the sides that forms hexagonal elements along the midlateral scale row, and a basicaudal spot in adults that is barlike, extends from the upper caudal base to slightly below the midlateral scale row and is bordered posteriorly by a sparsely pigmented area (opaque white in life) that is itself bordered posteriorly by a slender, somewhat jagged line of dark pigment that lies on the fin ray bases; in gonopodium of male, terminal segment of ray 4a only slightly projecting beyond tip of fin and only slightly or not at all bent downward and preceded by 3 to 7, modally 5 or 6, penultimate short segments with ventral, peglike processes, central spines near tip of ray 3 enlarged to form a distinct elbow that very noticeably enters the ventral profile of the gonopodium; tip of gonopodium, on average, as high as long.

**DESCRIPTION:** The meristic and morphometric data contained in tables 1 to 12 and figures 9 and 15 G-J may be summarized by the following general statements:

1. With respect to measurements of the length of the depressed anal fin in females,

head width in females, distance from dorsal origin to caudal base, length of dorsal fin base, and least depth of caudal peduncle, *litoperas* is sharply separated only from *formosa*, *attenuata* and *jonesi*. Relative to the other forms of *Heterandria* its values tend to be consistently high although not diagnostic. Its most striking difference from *obliqua*, *anzuetoi* and *bimaculata* occurs in the length of dorsal fin base in males, which is higher in mean value except for Belize *bimaculata*. In addition, one population of *litoperas*, from the Río Cahabón, has females with a higher mean value of depressed anal fin length than all other forms of *Heterandria*.

2. In vertebral number *litoperas* has a lower mean number than all populations except specimens from Honduras (see discussion under *bimaculata*).

3. Dorsal fin ray number in *litoperas* includes some of the highest counts for the genus, 10 individuals having 17 rays and two having 18. Of several hundred *bimaculata* counted, only three specimens had 17 rays and none had 18. The lowest count in *litoperas* is 14 rays (23 individuals) as compared with the lowest counts in *obliqua* (10), *anzuetoi* (12), and the forms here grouped as *bimaculata* (11 in one individual from Honduras; 12 in several populations from throughout the range).

4. In the number of short subterminal segments on gonopodial ray 4a, *litoperas* has a mean number distinctly different from those of *obliqua* and non-Honduras *bimaculata*, but similar to those of *anzuetoi*.

**MATERIAL:** Holotype (AMNH 36328), an adult male, 33.5 mm. in standard length, collected from a tributary to Río Cahabón, 1 km. north-northwest of Lanquín, Río Polochic system, Alta Verapaz, Guatemala, on March 13, 1963, by Donn E. Rosen and Klaus Kallman. Taken with the holotype were 33 young to adult males and females (AMNH 24492), 16-56 mm. Additional paratypes are as follows:

*Río Polochic system (Alta Verapaz):* AMNH 36331 (16 young to adult males and females, 14-54 mm.), bypass of Polochic 1.5 km. west of Pancajché, and UMMZ 190753; AMNH 24489 (9 young to adult males and females, 19-37 mm.), small branch of river emerging

from Lanquín cave, tributary to Río Cahabón; UMMZ 146106-07 (35 young to adult males and females, 17-53 mm.) Río Cahabón, 6 km. west of Cahabón; USNM 114258 (3 half-grown, to adult female, 22-45 mm.), tributary to Río Polochic, 14 miles west of Panzós; USNM 134585 (38 young to adult males and females, 10-70 mm.) spring-fed creek into large tributary to Polochic, about 4 km. west of Panzós; USNM 134586 (154 young to adult males and females, 11.5-51 mm.), tributary to Polochic about 6 km. west of Pancajché. AMNH 37666 (19 half-grown to adult males and females, 23.8-62.5 mm.), tributary to Río Boca Nueva, 5-10 km. east of Senahú. (*Izabal*): AMNH 36330 (1 half-grown, 25 mm.), spring inlet from north to Río Tatin, about 500 m. upstream of junction with Río Dulce, 7 km. southwest of Livingston; AMNH 36329 (1 young, 1 adult male, 14 and 24 mm., respectively), Río Amatillo, tributary to Lago Izabal, at highway bridge at Benque, and UMMZ 190586; AMNH 35003 (59 young to adult males and females, 9-60 mm.), spring tributary to Río Amatillo at Benque, and UMMZ 197134.

**GEOGRAPHY:** Basin of the Río Polochic, including both the Río Polochic and Río Cahabón as far east as streams flowing into Lago Izabal, departments of Alta Verapaz and Izabal, Guatemala (fig. 24). *Heterandria bimaculata* also occurs in the Polochic system, but in low-land streams that empty into more easterly parts of the basin (Río Dulce and El Golfete).

**ETYMOLOGY AND AUTHORSHIP:** the trivial name *litoperas*, a noun in apposition, is from the latinized Greek roots *litos*, an adjective meaning smooth or plain, and *peras*, a neuter noun meaning end, in reference to the simple terminal segment in the gonopodium of the male. The description of this species is based, in part, on data gathered jointly by me and Dr. Reeve M. Bailey, and should be jointly attributed.

***Heterandria obliqua*, new species**

Figures 5A;6J-L;10;16;21E,F;24;26

**DIAGNOSIS:** a moderately slender-bodied species with a dorsal fin base of intermediate

length (22 to 31 percent of standard length and 10 to 14 fin rays, modally 12 or 13); basicaudal spot oblique and longer than high in adults, its lower end merging anteriorly with midlateral pigment; sides with numerous black flecks, especially posteriorly and on midlateral scale row where they are aligned to form an interrupted midlateral stripe which overlies a diffuse, dusky band of pigment; in gonopodium of male, terminal element of ray 4a three to five times longer than high, slightly to moderately decurved and preceded by numerous subdistal short segments (6 to 9, rarely 5 or 10) bearing ventral peglike processes; ventral profile of gonopodium below ray 3 moderately concave; in gonopodial suspensorium, uncini of second and third gonapophyses angulate along the anteroventral margin and bent upward so that they point posteriorly.

**DESCRIPTION:** Meristic and morphometric data are given in tables 1 to 12 and figures 10 and 16. These data, which fail to separate *obliqua* sharply from succeeding taxa, show nevertheless that it is a relatively slender-bodied, slender-headed fish with a relatively short dorsal fin and relatively few pectoral fin rays. The primary superficial distinguishing characters of this species are in the gonopodium of the male and in body pigmentation. The gonopodium is characterized both by the downward curvature of its distal fifth or sixth, emphasized by the noticeable concavity along the ventral margin below ray 3, and by the short to very short terminal segment on ray 4a. The distinguishing pigmentary features are concentrated along the midlateral scale row: a rather diffuse, dusky stripe that, in most individuals, extends forward from the caudal base almost to the pectoral base; a series of very dark rectangles or crescents at the internodes of the reticular pattern where it coincides with the dusky lateral stripe; and the basicaudal spot which, in adults, merges with and becomes incorporated into the dusky and reticular pigment of the midlateral scale row. This basicaudal spot undergoes a series of ontogenetic changes, beginning in the youngest fish as a round spot which, in adults, merges with and becomes incorporated into the dusky and reticular pigment of the midlateral scale row. This

round spot of youngest fish extends only from the midlateral scale row dorsally to just short of the middorsal line. With increasing size of fish, the ventral margin of the spot develops an anterior extension along the midlateral scale row at the same time as the anterodorsal margin of the spot becomes ragged and poorly defined; at this stage the basicaudal spot has an elongated, somewhat oblique shape, extending anteriorly from the upper caudal base to the last two or three pitted scales of the midlateral scale row. As the fish reaches maturity, the spot darkens, especially where it overlaps the midlateral scales, and its anteriormost part becomes indistinguishable from the darkening pigment of the reticular internodes and dusky, midlateral stripe. The stripe itself has an ontogenetic history of interest because it begins as a series of broad vertical bars which gradually condense onto the midlateral scale region and become interconnected by new pigment cells to produce a continuous dusky band.

**MATERIAL:** Holotype (AMNH 36311), an adult male, 31.0 mm. in standard length, collected in upper Río San Ramón basin, 2-3 km. (by air) above subterranean channel, Río Lacantún drainage, Río Usumacinta system, Huehuetenango, Guatemala, on March 29, 1973, by Reeve M. Bailey, Donn E. Rosen, and party. Taken with the holotype were 21 young to adult males and females, (AMNH 36313), 12-54 mm., and UMMZ 193935. Additional paratypes are as follows:

**RÍO USUMACINTA SYSTEM: Río Salinas—Río Icvolay (Río Dolores basin) drainage (Alta Verapaz):** AMNH 36314 (43 young to adult males and females, 17-57 mm.), pools in small tributary of lower Río Dolores at Finca Agua Blanca, and UMMZ 193911; AMNH 36316 (17 young to adult males and females, 14-64 mm.), Río San Vicente Chitacal, near mouth in Río Dolores at San Vicente, and UMMZ 190507; AMNH 36317 (7 half-grown to adult males and females, 21-44 mm.), outlet of laguneta between Río Rocía Pemec and Río Canillá due west of Finca Taque Canguinic, and UMMZ 190768; AMNH 36318 (13 half-grown to adult males and females, 24-53 mm.), along shore of the Dolores, at Yaxcabnal; AMNH 36315 (113 half-grown to adult males and females, 25-64

mm.), Arroyo Devasilá, tributary to Río Choctún, and UMMZ 193893; AMNH 24638 (11 young to adult males and females, 18-52 mm.), tributary to Dolores at Cubilguitz, and UMMZ 188010.

**Río Lacantún—Río San Ramón (Upper Río San Ramón basin) drainage (Huehuetenango):** AMNH 32909 (124 young to adult males and females, 12-66 mm.), Río Chancolín, about midway along course, and UMMZ 197079; AMNH 32915 (10 half-grown to adult males and females, 29-44 mm.), junction Río Espíritu and Río Negro, and UMMZ 197073.

**GEOGRAPHY:** Known only from the Río Dolores system (with a subterranean connection to the Río Salinas), department of Alta Verapaz, and Río San Ramón system (with a subterranean connection to the Río Ixcán-Río Lacantún), department of Huehuetenango, both part of the Río Usumacinta basin in Guatemala (figs. 24,26). *Heterandria bimaculata* occurs on the downstream side of the subterranean passages both in the Río Salinas and Río Ixcán-Río Lacantún. The shortest distance between the Río Dolores and Río San Ramón is at least several hundred kilometers via the connection of their parent streams, the Salinas and Lacantún, with the Río Usumacinta.

**ETYMOLOGY:** the trivial name *obliqua*, an adjective, refers to the oblique orientation of the caudal blotch in half-grown and adult fish.

*?Heterandria obliqua* x *Heterandria bimaculata*

Figures 24, 26-28

In seven sites in the upper parts of the Río Lacantún and Río Salinas drainages in Alta Verapaz, El Quiché, and Huehuetenango, specimens of *Heterandria* were taken that could not readily be assigned to any known taxon. Some of their characters were those of *obliqua*, others seemed to be more like those of *bimaculata*, and still others were intermediate. All the fish are rather slender-bodied like *obliqua* and, also like that species, the caudal blotch is rather elongated horizontally in many cases and, in a very few examples, even has an anterior extension that ends on the midlateral scale row (figs. 27D,F). Lateral pigmentation on the sides of the body is also similar to that seen in *obliqua*:



in some individuals dark vertical dashes which form at the nodes of the reticular pattern are not only lined up in definite rows, but form a continuous series on the midlateral scale row (figs. 27A,D). Neither the caudal blotch nor the rows of dashes are a consistent feature of these samples, however. In some cases the caudal blotch is round or oval as in *bimaculata* (figs. 27A,E) and, in most examples, the dashes form discontinuous rows or are scattered. Meristic and morphometric data have not helped decisively in understanding these samples since, in such features, *obliqua* and *bimaculata* do not differ greatly from one another over their ranges and these two classes of data are in general rather variable. In gonopodial features, however, these upland samples are intermediate between *obliqua* and *bimaculata* in the length and curvature of the terminal hook on ray 4a. Both hook length and curvature are somewhat variable (fig. 28), but never as short and straight as in *obliqua* or as strongly curved as in *bimaculata*. A presumption that these vari-

able upland samples might be secondary intergrades (between *obliqua* and *bimaculata*—the only other *Heterandria* present in this region) seems reasonable since the same upland region is also an area of apparent intergradation between species of *Xiphophorus* (*X. alvarezi* and *X. helleri*). As is the case in *Xiphophorus*, the intergrades in *Heterandria* are between forms separated by one or more branch points (speciation events) in their cladogram of relationships, a topology that logically requires an interpretation of the intergradation as secondary (i.e., as hybridization; see discussion above under Methods, Species Concepts, and see also discussion on pages 338-342).

**MATERIAL:** *Río Lacantún drainage* (*El Quiché*): AMNH 24568 (61 young to adult males and females, 16-61 mm.), *Río Xalbal*, 1 km. south of Ixcán; AMNH 24584 (20 half-grown to adult males and females, 23-57 mm.), large jungle stream (*Río Negro*), tributary to *Río Xalbal* just north of Ixcán. (*Huehuetenango*): AMNH 36360 (1 half-

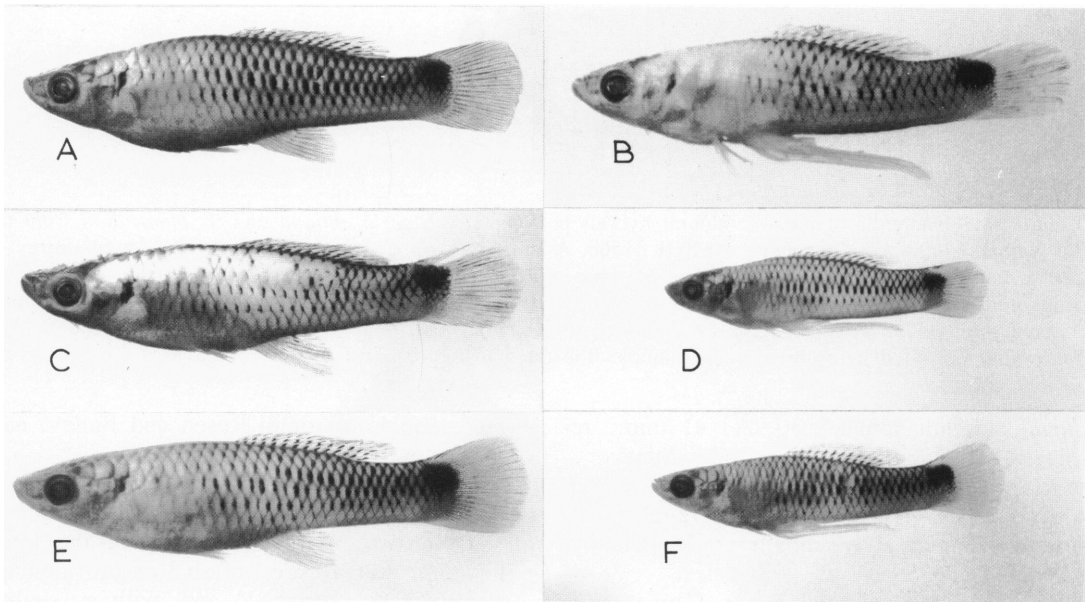


FIG. 27. Putative natural hybrids involving *Heterandria obliqua* and *H. bimaculata* from the Río Salinas-Río Chixoy (or Negro) system, A-C, and the Río Lacantún system, D-F. A, female, 43.7 mm. standard length, and B, male, 28 mm. from Arroyo Batzulup, AMNH 25478. C, female, 38 mm., Río Senizo, AMNH 36359. D, male, 29.5 mm., Río Ixcán, AMNH 36360. E, Female, 48 mm., and F, male, 31.5 mm., Río Xalbal, AMNH 24568. Note variability in caudal blotch and lateral spotting.

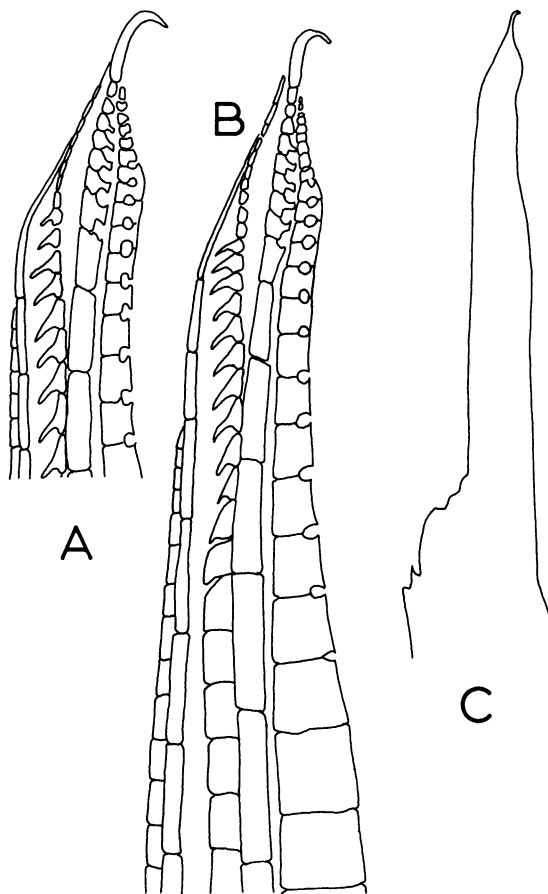


FIG. 28. Gonopodia of putative natural hybrids between *Heterandria obliqua* and *H. bimaculata* from the Río Xalbal, El Quiché, Guatemala, AMNH 24568. A and B, gonopodial tips showing terminal hook on ray 4a intermediate in length and curvature between those of *H. obliqua* and *H. bimaculata*. C shows outline of an entire gonopodium which is comparable in ventral profile and development of decurved tip with the most extreme form of *H. obliqua* (fig. 21E), although its terminal hook is developed as shown in A and B. The gonopodia illustrated here are from the sample illustrated in figure 27E,F.

grown, 1 adult female, 30 and 41 mm., respectively), Río Ixcán above Todos Santos.

*Río Salinas drainage (Alta Verapaz):* AMNH 25478 (11 young to adult, 12-42 mm.), Arroyo Batzulup, above mouth into Río Chixoy; AMNH 36359 (2 females, 38-64 mm.), Río Senizo at Finca Temal. (*El Quiché*): AMNH 36358 (3 young, 15-23 mm.), Río Copón, near Finca San Pedro Copón; UMMZ 131143 (21 young to adult, 27-54 mm.), Río Tesoro, 42 km. east north-east of Nebaj.

***Heterandria anzuetoi* Rosen and Bailey, new species**

Figures 5B,C;6M-S;11;17;21G-J;24;25

**DIAGNOSIS:** A robust species with the dorsal fin origin well forward of anal origin (although slightly less advanced, and with a slightly smaller relative base length and number of fin rays than in *bimaculata*); basicaudal spot in form of a dark bar more than half the least depth of caudal peduncle and that inclines slightly forward (but see below for a variant of

this pattern); reticular pattern (cross-hatching) along sides well-developed and accentuated above and below the midlateral scale row and along this scale row by a series of short, broad bars (about one scale width in height) and some dusky pigment; in gonopodium of male, terminal segment of ray 4a somewhat elongate, six or more times as long as high, gently decurved to sickle-shaped, and, in most cases, not entirely filling terminal membranous envelope which is more strongly decurved than the enclosed segment and reinforced by dense granular tissue; tip of ray 5a, in most cases, terminating posterior to the base of terminal segment of ray 4a; subdistal short segments on ray 4a 3 to 8, modally 6, and bearing ventral peglike processes; central spines near tip of ray 3 enlarged to form a distinct elbow; gonopodial tip not quite as high as long (higher than in *jonesi*, *obliqua*, *cataractae*, *bimaculata* and *dirempta*); ventral profile of gonopodium below ray 3 moderately concave proximal to elbow.

**DESCRIPTION:** This species closely resembles *bimaculata* and is inseparable from it in most meristic and morphometric data (tables 1 to 12). The two forms are most easily told apart in the Río Motagua where they are sympatric (but not syntopic) in that river's lower reaches (fig. 24). In this region three gonopodial characters and three pigmentary characters distinguish them. In *anzuetoi* the terminal segment on gonopodial ray 4a is sickle-shaped and is followed by relatively few short segments (in *bimaculata* the terminal segment is hook-shaped and is followed by more numerous subdistal short segments) (table 1 and figs. 6M-S). The two differ also in the height/length ratio of the gonopodial tip, the gonopodial tip of *anzuetoi* being relatively higher and shorter. In pigmentary characters, the two differ in the extent of development of the reticulum, the development of midlateral pigment, and the formation of the basicaudal spot. *Heterandria anzuetoi* has the reticulum well-developed to very heavily developed; in *bimaculata* it is slightly to moderately developed (figs. 11,14,17,19). In *anzuetoi* short vertical bars separated by lighter interspaces are concentrated all along the midlateral scale row which is bounded above and below by a zigzag border formed from especially dense reticular

components; in adult *bimaculata*, vertical bars are confined to the upper sides of the trunk and the midlateral scale row is not bordered. The basicaudal spot in newborn *bimaculata* is large and round (in some cases with an anterior peak) and occupies a position that is always more dorsal than midlateral, a location that becomes accentuated by the addition of melanophores posterodorsally during development; the end result is usually a quite round or somewhat elongate dorsal spot that overlaps the upper peduncular base and the upper caudal fin base. In *anzuetoi* the spot first appears in newborn young as a diamond-shaped pattern, the anterior angle of which overlies the last, pitted, midlateral scale on the caudal base; the spot is thus located midlaterally or only very slightly dorsally. During development, the basicaudal spot of *anzuetoi* elongates first dorsally and then posteroventrally and the anterior and posterior angles of the original pattern disappear; the adult pattern is thus barlike, vertical but inclined slightly forward and is either entirely confined to the caudal fin base or, rarely, very slightly overlapping the upper caudal peduncle base.

These pigmentary features are especially characteristic of *anzuetoi* from the Río Motagua basin in Guatemala and Honduras and the upper Río Lempa basin in Guatemala. In the other drainages of Honduras, *anzuetoi* is more variable and therefore more difficult to define and to distinguish from *bimaculata* with which, until now, it has been considered conspecific. For comparison of Honduras *anzuetoi* with *bimaculata*, the latter species is presently known only from a single locality on the north coast of Atlantida, Honduras, and the sample is small and includes only one male. This male (fig. 19D), however, shows the gonopodial features typical of Mexican and Guatemalan *bimaculata* (figs. 7L,21P), especially the strongly curved terminal hook on ray 4a. Although this element is never recurved in Honduras *anzuetoi*, it varies from being sickle-shaped to strongly decurved; in the latter condition, *anzuetoi* resembles certain other forms discussed below, including *bimaculata*, in which, very rarely, the terminal hook on ray 4a lacks a recurved tip. Even those specimens with a decurved ter-

minimal element, however, have the diagnostically low number of subterminal short segments. Compare, for example, the modal values for these segments in *anzuetoi* and *bimaculata* and the range of values for Honduras *anzuetoi* with the count for the single male of *bimaculata* from Honduras (table 1). Variability in gonopodial traits in Honduras *anzuetoi* is matched by that shown by pigmentation. In general Honduras *anzuetoi* do not exhibit the very heavy reticulum present in specimens from the Río Motagua, but most individuals from any region of that country have concentrated barlike pigment on the midlateral scale row and have this row bordered above and below by components of the reticular network. The basicaudal spot in Honduras *anzuetoi* is also variable. In some it is clearly barlike, not differing in any noticeable way from the pattern of Motagua and Lempa fish. Other Honduras examples seem to have retained the juvenile pattern of a diamond-shaped spot centered on the last pitted scale of the midlateral sensory line, and still others have a spot somewhere between this and the bar patterns. Always there is less pigment from the basicaudal spot overlapping the upper base of the caudal peduncle than in *bimaculata*, so that with some study, or with a moderate sample, the *anzuetoi* and *bimaculata* patterns can be distinguished clearly.

Finally, because Honduras *anzuetoi* differs from the Río Motagua and Río Lempa fish in reticulum development and in the constancy of the midlateral pigment and the full bar pattern on the caudal base, it is possible that the two kinds of fish represent differentiated populations that other characters may be found to define more sharply. At present, the simpler solution of considering them all as one species sympatric with *bimaculata* is adopted here. In addition, the two Nicaraguan fish, neither of which are males nor have well-preserved pigment patterns, are simply being treated provisionally as *anzuetoi*; a similar action is being taken, and for the same reasons, with regard to a small sample from Francisco Morazan.

**MATERIAL:** Holotype (AMNH 36319), an adult male, 42.6 mm. in standard length, collected in Río Achuelo, south side of Gualán, Río Motagua drainage, Zacapa, Guatemala, on

April 5, 1973, by Reeve M. Bailey, Donn E. Rosen, and party. Taken with the holotype were 16 young to adult males and females (AMNH 36321), 9-48 mm., and UMMZ 193976. Additional paratypes are as follows:

*Río Motagua drainage, Guatemala (Zacapa):* AMNH 36322 (1 young, 1 adult female, 16 and 47 mm., respectively), Río Teculután at highway CA 9, 1 km. west of Teculután; AMNH 36324 (1 young, 14 mm.), Río Pasabien, upstream of Santa Cruz; AMNH 36325 (50 young to adult males and females, 11-57 mm.), cascade of Río Pasabien between Teculután and Río Hondo, and UMMZ 190576, 190813; AMNH 35138 (99 young to adult males and females, 12-68 mm.), Río Matasano at CA 9, km. 17, and UMMZ 197288; AMNH 35145 (91 young to adult males and females, 16-65 mm.), Quebrada Juilín at CA 9 crossing, and UMMZ 197298; AMNH 35149 (8 young to half-grown, 15-27 mm.), Riachuelo Mestizo at CA 9 crossing; AMNH 1416 (7 young to adult males and females, 12-38 mm.), USNM 73972 (5 half-grown to adult males and females, 25-41 mm.), irrigation ditch west of Gualán; USNM 134583 (44 young to adult males and females, 12-53 mm.), Riachuelo near Teculután. (*El Progreso*): AMNH 36323 (1 half-grown, 32 mm.), Río Morazan at bridge on Salama Road, and UMMZ 193876; USNM 114529 (9 young to adult females, 19-51 mm.), Río Morazan; USNM 134584 (4 half-grown to adult males, 29-34 mm.), Río Hato west of San Agustín Acasaguastlán. (*Izabal*): AMNH 35150 (79 young to adult males and females, 12-72 mm.), tributary to Río Trimcheras at Aldea Campo Dos; AMNH 35177 (20 young to adult males and females, 18-54 mm.), Riachuelo Las Cruces at Morales-Flores Road, km. 249, and UMMZ 197330. (*Chiquimula*): AMNH 36327 (26 half-grown to adult males and females, 19-58 mm.), Río La Conquista at Quetzaltepeque, and UMMZ 190806. *Honduras (Copán)*: LACM 32390 (1 adult male, 29 mm.), Quebrada Otuta, 2.2 miles east of El Jaral; LACM 32393 (6 half-grown to adults males and females, 27-51 mm.), Quebrada Ticocla, 0.5 km. southeast of El Jaral; LACM 32395 (80 young to adult males and females, 19-68 mm.), Quebrada Ayagua, 0.5 mile east of

Copán; LACM 32396 (1 adult female, 45 mm.), 2.1 miles west of Copán; LACM 32474 (1 adult female, 46 mm.), tributary to Río Amarillo, 12.8 km. east-northeast of Copán.

*Río Lempa drainage, Guatemala (Chiquimula)*: AMNH 36326 (56 young to adult males and females, 11-58 mm.), Río Atulapa, tributary to Río San Juan, 3 miles southeast of Esquipulas, highway CA 10, and UMMZ 190800; USNM 114517 (41 young to adult males and females, 13-61 mm.), Río Atulapa, Esquipulas; UMMZ 163807 (one young, 25 mm.) 3 km. north of Esquipulas, on upper tributary of Río Olopa. (*Jutiapa*): AMNH 35215 (67 half-grown to adult males and females, 21-64 mm.), unnamed tributary to Río Ostúa, 75 km. southeast of Asunción Mita, and UMMZ 197389.

*Honduras (Cortés)*: LACM 32340 (37 young to adult males and females, 18-35 mm.), Quebrada Agua Amarilla, 6 km. west of Santa Cruz de Yojoa; LACM 32376 (32 young to adult males and females, 18-50 mm.), Río Piedras, 1.6 miles north of San Pedro Sula; LACM 32377 (66 adult males and females, 27-51 mm.), Río Bermejo, 2.2 miles north of San Pedro Sula; LACM 32379 (3 half-grown, 29-38 mm.), Quebrada Maracana, 0.5 mile north of Maracana; LACM 32380 (1 young, 13 mm.), Quebrada Caracol at Aldea Caracol; LACM 32385 (1 adult male, 1 adult female, 26, 29 mm., respectively), unnamed stream 6 km. west of Puerto Cortés; LACM 32401 (1 half-grown, 1 ad. male, 19, 24 mm., respectively), Laguna del Monte, 6.4 km. east on Santa Cruz de Yojoa Highway from junction San Pedro Sula-Tegucigalpa Highway; LACM 32436 (1 young, 1 adult female, 17 and 30 mm., respectively), Quebrada La Curva, 8.1 km. south of Peña Blanca; LACM 32464 (1 half-grown, 31.5 mm.), Quebrada Dieciocho, 3.7 km. northeast of Omoa; LACM 32467 (3 half-grown to adult female, 24-44 mm.), Río Chivana, 6.3 km. northeast of Omoa; UMMZ 173305 (51 young to adult males and females, 15-51 mm.), second Río Tulian at Tulian; UMMZ 173271 (6 young to adult males, 16-28 mm.), brook at Veracruz; UMMZ 173287 (5 half-grown to adult males and females, 19-44 mm.), Río Masca at Masca; UMMZ 173155 (11

half-grown to adult males and females, 18-38 mm.), Agua Priete, north of San Pedro Sula, Choloma Rd.; UMMZ 173148 (1 adult male, 32 mm.), Río Bermeja, tributary to Río Chamelecón, north of San Pedro Sula; UMMZ 173161 (1 half-grown, 22 mm.), Río Armenta, north of San Pedro Sula, Choloma Rd.; UMMZ 173279 (8 young to adult females, 14-35 mm.), Río Mapache at Masca; UMMZ 173257 (9 young to adult males and females, 14-39 mm.), stream at Campo Verde, Omoa. (*Atlántida*): LACM 32374 (1 adult female, 57 mm.), unnamed stream 28.6 miles northeast of El Progreso, 9.2 miles southwest of Tela; LACM 32435 (5 half-grown to adult males and females, 27-50 mm.), unnamed stream, 13.7 km. southwest of Tela; LACM 32453 (1 adult female, 54 mm.), unnamed stream, 0.3 km. northeast of Campo Las Mujerlas, 22.4 km. northeast of Toyos; LACM 32454 (2 half-grown, 26-35 mm.), Río San Alejo at Campo Las Mujerlas; LACM 32462 (1 half-grown, 28 mm.), Río Cangrejal, 4.8 km. southeast of Barrio La Isla (La Ceiba); LACM 32471 (3 adult females, 44-55 mm.), Río Piedra Pintada, 10.4 km. east of La Ceiba; ANSP 81642 (1 adult female, 62.5 mm.), ANSP 81641 (21 half-grown to adult males and females, 17-49.5 mm.), UMMZ 173207 (11 half-grown to adult males and females, 18-35 mm.), Lancetilla; UMMZ 173348 (31 young to adult males and females, 16-59 mm.), 48.5 km. west of La Ceiba, near San Juan Benque; UMMZ 173178 (1 adult female, 40 mm.), tributary to Río Lancetilla, 1 mile south of Tela; UMMZ 189564 (7 young to adult females, 13-61 mm.), Río Lancetilla at Lancetilla; UMMZ 173365 (1 adult female, 39 mm.), Río Cuero near La Masca; UMMZ 173200 (2 young, 16 mm.), UMMZ 173188 (7 young to adult males, 14-43 mm.), tributary to Río Lancetilla at Lancetilla; UMMZ 173223 (13 young to adult males and females, 17-41 mm.), ditch to Río San Alejo (Santiago branch); UMMZ 173227 (1 adult female, 31 mm.), ditch, African Oil Palm Plantation, San Alejo; UMMZ 173328 (6 young to adult male, 12-30 mm.), Sambo Creek, 18.3 km. east of La Ceiba. (*Yoro*): LACM 32368 (1 adult female, 43 mm.), Río Aguan, 4.6 miles west of Yoro; LACM 32371 (10 half-grown to adult males

and females, 26-67 mm.), Quebrada "Panca," 2 miles west of Yoro; LACM 32372 (11 young to adult males and females, 17-39 mm.), Río Puente Grande, 0.6 mile northeast of Aldea Puente Grande; LACM 32410 (5 half-grown to adult females, 21-39 mm.); unnamed stream 5 km. south of El Progreso; LACM 32411 (15 half-grown to adult males and females, 20-42 mm.), Quebrada San Antonio de Norte, 14 km. south of El Progreso; LACM 32450 (1 adult male, 41 mm.), Quebrada Colorado, 53 km. south of Toyos; LACM 32451 (5 half-grown to adult females, 27-41 mm.), Quebrada Camalote, 3.5 km. northeast of El Progreso. (*Olancho*): LACM 32305 (1 half-grown, 25 mm.), Río San Carlín, 5.6 miles east of Escuela Nacional Agricultura, Catacamas; LACM 32306 (2 adult females, 30-34 mm.), Río Guingle, 4.3 miles east of the Escuela. (*El Paraíso*): LACM 32298 (7 half-grown to adult males and females, 20-58 mm.), first small tributary to Río Guayambre, 1 mile north of Santa María; LACM 32299 (5 half-grown to adult female, 25-37 mm.), small tributary to Río Guayambre, 0.9 mile south of Santa María. (*Cabo Gracias á Dios*): LACM 32459 (1 adult female, 35 mm.), Quebrada de Aeropuerto, 1.6 km. north of Leimos. (*Francisco Morazán*) (questionably *anzuetoi*): UMMZ 188108 (10 half-grown to adult females, 26-49 mm.), stream between Las Flores and Guaimaca.

*Nicaragua* (questionably *anzuetoi*): ANSP 65156-7 (2 adult females, 48-50 mm.), Marceligo Creek, tributary to Río Tunkú at Miranda.

**GEOGRAPHY:** Basin of the Río Motagua in the departments of El Progreso, Zacapa, Chiquimula, and Izabal, Guatemala, and Copán, Honduras, and basin of the Río Lempa in the departments Chiquimula and Jutiapa, Guatemala (and presumably in neighboring departments of El Salvador through which the Río Lempa flows) (figs. 24,25). In the Motagua basin, *anzuetoi* extends downstream to within about 100 km. (following the river bed) of the mouth of the Motagua into the Gulf of Honduras. Although it penetrates into the river's lowland region, *anzuetoi* continues to occupy clear, flowing, rocky streams there, as it does

in its habitats farther upstream in El Progreso and Zacapa. In the department of Izabal, *anzuetoi* overlaps *bimaculata* which penetrates up into the Motagua basin as far west as Los Amates. The two species overlap for a distance of 40 km. but they have never been taken together (i.e., appear not to be syntopic). In the area of sympatry, *bimaculata* occurs only in the muddier, more sluggish streams or parts of streams that are tributary to the river's main channel. Below the region of overlap (to the east), *bimaculata* is widespread in the lowlands.

**ETYMOLOGY AND AUTHORSHIP:** the trivial name *anzuetoi* commemorates my deep appreciation of, and affection for, my good friend and frequent field companion in Guatemala, Roderico Anzueto. The description of this species is based, in part, on data gathered jointly by me and Dr. Reeve M. Bailey, and should be jointly attributed.

#### ***Heterandria cataractae*, new species**

Figures 7A; 12; 18 A-D; 21K; 24; 26

**DIAGNOSIS:** A slender species (caudal peduncle 14 or 15 percent of standard length) with a long, many-rayed dorsal fin (14 to 16, modally 15, rays) of advanced position; dorsal fin origin to caudal base modally 56 to 58 percent of standard length in males and 52 to 54 percent in females, as compared with 50 to 52 and 46 to 48 in *dirempta* and 54 to 58 and 50 to 52 in *bimaculata*; basicaudal spot elongate and ragged posteriorly and confined entirely to upper half of caudal peduncle and caudal fin base; sides coarsely reticulated with large, interlocking, black crescents; in gonopodium of male, terminal segment of ray 4a more than six times as long as high and L-shaped or in form of open-J and preceded by numerous subdistal short segments with ventral pegs (9 to 11, modally 10); ventral profile of gonopodium below ray 3 strongly concave.

**DESCRIPTION:** Meristic and morphometric data are given in tables 1 to 12; those data of comparative relevance are noted in the diagnosis. *Heterandria cataractae*, like the other two forms with a consistently strongly decurved terminal segment on gonopodial ray 4a, also

has the distal fifth or sixth of the gonopodial tip long and slender and the ventral margin of the distal fourth of the gonopodium below ray 3 strongly concave.

In pigmentation, *cataractae* resembles *dirempta* and some populations of *bimaculata* and, to some extent, *obliqua* in having dark markings at the internodes of the reticulum in several rows along the posterior sides, but these markings are decidedly coarser, more strongly crescentic, and more evenly distributed on the entire body, save the ventral part of the caudal peduncle, in *cataractae*. Its basicaudal spot is most like that of *dirempta* and *bimaculata* in having, ontogenetically, a dorsal nucleus that is initially almost perfectly round; in developing adults, this marking is modified by the addition of melanophores posteriorly to produce a horizontally elongated blotch that covers and even extends beyond the basal scale sheath of the caudal fin. Unlike the pattern in *dirempta* and *bimaculata*, however, this spot remains almost wholly confined above the midlateral scale row. This posteriorly elongated marking complements the slender caudal peduncle to give the posterior part of the body an extremely attenuated aspect.

**MATERIAL:** Holotype (AMNH 36381), an adult male, 36.4 mm. in standard length, collected in a large jungle stream, the Arroyo Sachicha (tributary to, but isolated above a ribbon fall from, the Río Senizo), about 20 km. northwest of Cobán and 6-8 km. north of Cancal, Río Salinas drainage, Río Usumacinta system, Alta Verapaz, Guatemala, on March 12, 1963, by Donn E. Rosen, Klaus Kallman, Tilo Cámara, and Filedelfo Monteroso. Taken with the holotype were 93 young to adult males and females (AMNH 24486), 12-63 mm.. Additional paratypes are: AMNH 36357 (105 young to adult males and females, 12-64 mm.), same locality, and UMMZ 193888.

**GEOGRAPHY:** Known only from the Arroyo Sachicha, one of two tributaries to the Río Senizo which flows into the upper Río Chixoy (Río Salinas) at Chamá, Alta Verapaz, Guatemala (figs. 24, 26), and isolated from all other flowing water by a downstream ribbon fall perhaps 30 meters or more in height.

**ETYMOLOGY:** the trivial name *cataractae*, a

noun in apposition, refers to the isolation above a ribbon fall of the stream section in the Arroyo Sachicha where this species occurs.

### ***Heterandria dirempta*, new species**

Figures 7 B,C; 13; 18 E-H; 21 L; 24; 26

**DIAGNOSIS:** A species of *Heterandria* similar to *cataractae* and *bimaculata* in always having the terminal segment on gonopodial ray 4a strongly decurved, to *cataractae* in having this segment L-shaped or in the form of an open-J, and to *bimaculata* in having the basicaudal spot large, occupying the area from just below the dorsal midline to the level of the ventral margin of the midlateral scale row, almost perfectly round, and overlapping the base of the caudal peduncle by about one scale width but mostly on the caudal fin base, but differing from *cataractae* and *bimaculata* in having relatively few dorsal fin rays (12 to 14, modally 13) and a short dorsal fin base (tables 5, 6), a relatively posterior dorsal fin origin (tables 7, 8), a relatively long anal fin in the female (table 9), and a relatively low number of subterminal short segments with ventral pegs on gonopodial ray 4a (5 to 8, modally 6 or 7; 9 to 11, modally 10 in *cataractae*; 5 to 10, modally 7 to 9 in *bimaculata*) (table 1), and from *bimaculata* in not having the terminal segment of gonopodial ray 4a strongly and tightly recurved (retrorse); ventral profile of gonopodium below ray 3 strongly concave.

**DESCRIPTION:** Meristic and morphometric data are given in tables 1 to 12; data of comparative relevance are noted in the diagnosis. Another significant feature of *dirempta*, not noted elsewhere, is the development, especially in adult males, of a series of a few short vertical bars anteriorly on the upper sides in the supra-axillary region. In life, these bars are often very strongly expressed, more so, in fact, than in any other population of *Heterandria* seen by me. These bars are also, probably uniquely, separated by iridescent green interspaces. Like so many other of the many complex pigment patterns in these fishes, they often, if not usually, fade somewhat during initial preservation, perhaps changing their expression as a result of stress. The supra-axillary

bars of *dirempta* are shown, in the common, somewhat diminished expression of preserved material in figure 13.

**MATERIAL:** Holotype (AMNH 36380), an adult male, 31.0 mm. in standard length, collected in a clear meandering tributary to Río Chajmaic, 15 km. (by road) south of Sebol, Río de la Pasión drainage, Río Usumacinta system, Alta Verapaz, Guatemala, on March 16, 1963, by Donn E. Rosen and Klaus Kallman. Taken with the holotype were 12 half-grown to adult males and females (AMNH 24564), 25-38 mm.. Additional paratypes are as follows:

*Río de la Pasión drainage (Alta Verapaz):* AMNH 24501 (4 young to half-grown, 13-30 mm.), Río Semococh tributary to Río Chajmaic, 0.5 km. from its mouth in the Pasión, and UMMZ 187950; AMNH 36361 (16 half-grown to adult males and females, 28-71 mm.), second arroyo above mouth of Río Semococh in the Chajmaic; AMNH 36362 (76 half-grown to adult males and females, 21-67 mm.), meandering tributary to Río Chajmaic 15 km. (by road) south of Sebol; UMMZ 187934 (91 young to adult males and females, 23-71 mm.), Arroyo Salaguna, first stream below Río Semococh, 6 km. southeast of Sebol; AMNH 36363 (102 half-grown to adult males and females, 19-48 mm.), woodland pool, 13 km. southeast of Sebol, and UMMZ 187940.

**GEOGRAPHY:** Known only from the Río Chajmaic, an intermontane basin of about 22 km. in length, connected by subterranean passage with the Río Sebol (upper Río de la Pasión), Alta Verapaz, Guatemala (figs. 24, 26).

**ETYMOLOGY:** the trivial name *dirempta* is a Latin adjective meaning separate or isolated in reference to the physical isolation of the Río Chajmaic to which this species is endemic.

*Heterandria bimaculata* (Heckel)

Figures 5 D-F; 7 D-L; 14; 19; 21 M-P; 24; 26

**DIAGNOSIS:** A robust and morphometrically and meristically variable species (tables 1-12); basicaudal spot large, round and somewhat diffuse, mostly confined to, as well as almost filling, the area above the midlateral scale row (as in *dirempta*), and almost always with a

diffuse ventral extension below the midlateral line in large individuals; in gonopodium of male, terminal segment on ray 4a almost completely filling a retrorsely hooked membranous sheath and preceded by 6 to 9, rarely 5 or 10, and modally 7 to 9 subdistal short segments with ventral pegs; ventral profile of gonopodium below ray 3 strongly concave.

**MATERIAL:** *Mexico (Tabasco):* AMNH 20388 (5 half-grown to adult females, 19-43 mm.), entrance to cave, head Arroyo del Solpho, Tapijulapa; AMNH 20401 (48 young to adult males and females, 11-61 mm.), 1 mile downstream from same cave. (*Chiapas*): AMNH 24649 (1 half-grown 23 mm.), sulfur stream at Baños del Azufre. (*Veracruz*): AMNH 20500 (9 young to half-grown, 16-30 mm.), Río Santecomapan, Santecomapan; UMMZ 187689 (36 young to adult males and females, 15-62 mm.), La Zanja La Sol, off Mesa San Lorenzo about 3 km. south-southwest of Tenochtitlán; USNM 55761 (36 half-grown to adult males and females, 25-51.5 mm.), Jalapa; USNM 214147 (47 young to adult males and females, 14-51 mm.), Río Puente Chica, 21.2 miles east of Jalapa; USNM 214151 (119 young to adult males and females, 14-65.5 mm.), Arroyo Escuinopan, tributary to Laguna Catemaco; ANSP 15920-26 (7 adult females, 34-52 mm.), ANSP 23175-203 (22 adult males and females, 28.5-54 mm.), ANSP 15897-908 (14 adult males and females, 30-72 mm.), Orizaba.

*Guatemala, Río Usumacinta System: Río de la Pasión drainage (Alta Verapaz):* AMNH 24526 (6 young to adult females, 18-38 mm.), west-flowing tributary to the Pasión, 8 km. downstream from Sebol; AMNH 24561 (1 half-grown, 26 mm.), Río Sebolita (small stream), 1 km. south of Sebol; AMNH 24544 (1 adult male, 45 mm.), tributary to the Pasión, 8 km. east of Sebol; AMNH 36353 (89 half-grown to adult males and females, 24-69 mm.), swamp west of Sebol near banks of the Pasión; AMNH 24643 (27 young to adult males and females, 15-68 mm.), upper Río San Simón, 1000 m. north of Chisec; AMNH 36338 (131 young to adult males and females, 16-75 mm.), Río San Simón, 6 km. due west of Chisec; AMNH 36339 (21 young to adult males and females,



12-69 mm.), main isolated section Río San Simón, 7 km. northeast of Chisec. (*Petén*): AMNH 25167 (1 adult female, 48 mm.), Arroyo Yaxtunilá, 8 km. from the Pasión; AMNH 36347 (9 half-grown to adult males and females, 24-54 mm.), Río Bulbul, north fork of Río Santa Isabel; AMNH 36350 (91 young to adult males and females, 17-55 mm.), Arroyo La Puente, 42 km. north-northwest of Poptún on Flores Road.

*Río Salinas drainage (Petén)*: AMNH 25244 (46 half-grown to adult males and females, 21-51 mm.), unnamed stream 44 km. upstream of Laguna Ronpiro; AMNH 25513 (2 adult females, 38-43 mm.), Arroyo Caribe, 250 m. above mouth in the Salinas. (*Alta Verapaz*): AMNH 25261 (10 half-grown to adult males and females, 27-50 mm.), rock pools in rapids Río Icvolay; AMNH 25264 (35 young to adult males and females, 12-57 mm.), Arroyo Chiquibul, tributary to Río Icvolay; AMNH 25329 (8 young to adult males and females, 12-37 mm.), Arroyo de Laguneta Río Viejo from Laguneta to Río Chixoy. (*El Quiché*): AMNH 25282 (9 half-grown to adult males and females, 25-31 mm.), Río Lechugal, below mouth of Icvolay in Río Chixoy; AMNH 25409 (67 young to adult females, 15-55 mm.), Arroyo de Dante, tributary to upper Chixoy.

*Río Motagua drainage, Guatemala (Izabal)*: AMNH 31661 (3 adult females, 36-60 mm.), Río Tenedores, km. 270 at highway CA9, 2 km. north of Tenedores; AMNH 36341 (2 adult males, 29-31 mm.), AMNH 36342 (21 young to adult males and females, 19-64 mm.), Río La Vegega at CA9 crossing below road to Los Amates; AMNH 1377 (6 adult males and females, 39-67 mm.), Los Amates; AMNH 1406 (1 half-grown 1 adult male, 26 and 28 mm., respectively), USNM 73933, 73934 (7 adult males and females, 29-62 mm.), pond east of Los Amates. (*Zacapa*): AMNH 35154 (14 yg. to adult males and females, 14-57 mm.), Río Trimcheras at km. 218, CA9 crossing downstream of Aldea Campo Dos.

*Bahía de Amatique drainage, Guatemala (Izabal)*: AMNH 1335 (5 adult females, 40-57 mm.), AMNH 1389 (1 adult female, 53 mm.), swampy streams 1 and 2 miles west of Puerto Barrios, respectively; USNM 73992, 73993 (6

half-grown to adult males and females, 37-52 mm.), Puerto Barrios.

*Río Moho drainage, Guatemala (Petén)*: AMNH 35051 (10 half-grown to adult males and females, 20-41 mm.), Río Pusilá at Balam, 6 km. east of Poptún Road at Muquilá.

*Río Sarstún drainage, Guatemala (Alta Verapaz)*: AMNH 36344 (44 half-grown to adult males and females, 22-68 mm.), AMNH 36356 (8 adult females, 58-80 mm.), Río Chiyú, 19 km. (by air) northeast of Cahabón, 14 km. west-southwest of Chajal; AMNH 36345 (15 young to adult males and females, 17-44 mm.), Río Chajal near Finca Sesincheu, 40 km. (by air) northeast by east of Cahabón, Alta Verapaz-Izabal border. (*Petén*): AMNH 36346 (169 young to adult males and females, 8-69 mm.), stream 35 km. south-southeast of San Luis, about km. 153 on Flores-Sarstún Road; AMNH 36349 (8 young to adult females, 16-44 mm.), Quebrada Seca, below Flores-Sarstún Road, 56 km. south-southeast of Poptún; AMNH 36352 (57 adult males and females, 34-74 mm.), stream on Sarstún Island between Río San Pedro and Río Sarstún.

*Laguna de Petén drainage, Guatemala (Petén)*: AMNH 36348 (1 adult female, 69 mm.), *Vallisneria* beds on Flores Island.

*Lower Río Polochic drainage, Guatemala (Izabal)*: AMNH 36351 (10 young to adult females, 14-59 mm.), deep isolated pool in stream bed, 12 miles from Río Dulce ferry, San Felipe-Sarstún Road.

*Río Belize drainage, Guatemala (Petén)*: AMNH 36340 (6 adult males and females, 33-49 mm.), Río Mopán at Melchor; AMNH 36343 (35 young to adult males and females, 17-72 mm.), Arroyo Sal Si Puedes above mouth in Río Mopán; AMNH 36354 (13 young to half-grown 16-31 mm.), Río Santo Domingo, about 10 miles southeast of Santo Toribio.

*Belize*: AMNH 24587 (7 young to adult males and females, 12-56 mm.), small tributary to Mango Creek, about 5 miles (by river) from coast, Toledo District; AMNH 24606 (7 half-grown to adult females, 27-70 mm.), southeast of Waha Leaf, in Waha Leaf Creek, Stann Creek District; AMNH 28602 (8 young to adult males and females, 14-31 mm.), San Antonio Lagoon to east branch Río Hondo, Orange

Walk Distr.; AMNH 36355 (16 half-grown to adult males and females, 29-56 mm.), small tributary to Río Sibun, on Gracie Rock Road.

*Honduras (Atlántida)*: UMMZ 193827 (4 adult males and females, 38.5-49 mm.), 20 km. east of La Ceiba.

**GEOGRAPHY:** Southern Veracruz and Oaxaca, Mexico southeastward in lowland and some higher elevation localities (in the Río Usumacinta and Río Grijalva systems), along the northwestern margins of the Yucatan Penin-

sula, in northern El Quiché and Alta Verapaz (Guatemala) and neighboring regions of Mexico, throughout much of the Petén and Izabal departments of Guatemala as far east as Puerto Barrios, and throughout Belize (fig. 24). Sympatric (but not syntopic) with *anzuetoi* in the lower Río Motagua and coastal Honduras (Ceiba), and syntopic at a single known locality in the northern part of its range (Río Atoyac) with *jonesi* (Miller, 1974).

## POECILIID FISHES OF THE GENUS *XIPHOPHORUS*

### GENERAL ANATOMY AND RELATIONSHIPS TO OTHER POECILIIDS

*Xiphophorus* is one of the best defined groups of poeciliid fishes, mainly because of the complexity of the external male genitalium (gonopodium) and associated modifications of the male pelvic fins. All the known species are united by the presence in the gonopodium (figs. 29-31) of a large decurved hook followed by a series of simple segments and a series of elongate, ventrally directed and converging spines distally on ray 3; a large, laterally compressed and calcified mass of granular tissue (the blade) arising from the dorsal margin of the ray 3 terminal hook; the distal ramus of ray 4a curving down around, and conforming to the shape of, the blade; two series of serrae separated by undifferentiated segments distally on ray 4p; ray 5a turning down toward ray 4p and contacting the undifferentiated segments of 4p just proximal to the distalmost serrae of that ray; and rays 6 and 7 swollen and clublike distally. During copulation the gonopodium is swung forward and to one side and placed against the erected pelvic fin of that side (Clark and Kamin, 1951; Clark, Aronson and Gordon, 1954; Rosen and Tucker, 1961). The pelvic fin is modified by the enlargement of the tip of the first ray and the elongation of the second and third rays.

As in the case of *Heterandria*, earlier definitions of the group (Rosen, 1960; Rosen and

Bailey, 1963) included many features that most probably are plesiomorphous for poeciliids and even for more inclusive groups (e.g., the forked posttemporal which is plesiomorphous for cyprinodontoids, the only slightly bent tips of the posterior pleural ribs of the male, the little modified gonopodial suspensorium, etc.). Nevertheless, its sister group relationship to *Priapella*, as proposed by Rosen and Bailey (1963), is probably soundly based. This relationship is predicated mainly on shared special similarities in gonopodial structure. In the gonopodium of *Priapella*, ray 3 carries a distal, slightly decurved, hook bearing a dorsal covering of dense, calcified, granular tissue (a kind of primitive blade) to which the downturned distal ramus of ray 4a conforms. The terminal hook of ray 3 is followed by a few undifferentiated segments and a series of somewhat elongate but peglike spines that do not converge. Serrae are also present on ray 4p in the position of the proximal series of serrae on ray 4p in *Xiphophorus*. Distal serrae are not present on this ray since, in *Priapella*, this ray and ray 5a end abruptly just beyond the proximal serrae.

Although the relationship between *Priapella* and *Xiphophorus* is supported, their inclusion together with *Alfaro* and *Poecilia* in a tribe (Poeciliini) is not. All the putative defining characters of the Poeciliini presented by Rosen and Bailey (1963) are almost certainly either

plesiomorphous for poeciliids, ambiguous, or irrelevant. Nevertheless, many of the characters of *Priapella* can be used to provide a polarity for different states of these characters in *Xiphophorus* because they are either absent in other poeciliids or occur only as autapomorphies of species in other groups. For example, the species of *Xiphophorus* have delicate, flattened, depressible teeth on rather small, lightly built jaws. In *Priapella* the teeth are large, conical and fixed in large, robust jaws. In the

interrelated genera, *Alfaro* and *Poecilia*, the former has a dentition like that in *Priapella*, whereas *Poecilia* has teeth like those in *Xiphophorus*. All members of the Gambusiini (*Brachyrhaphis*, *Belonesox*, *Gambusia*) have fixed, conical teeth, and all the Heterandriini, save *Phallichthys* and some species of *Poeciliopsis*, have fixed conical teeth. Moreover, the sister group of the entire subfamily Poeciliinae (all other poeciliids but one), *Tomeurus gracilis*, has robust jaws and fixed

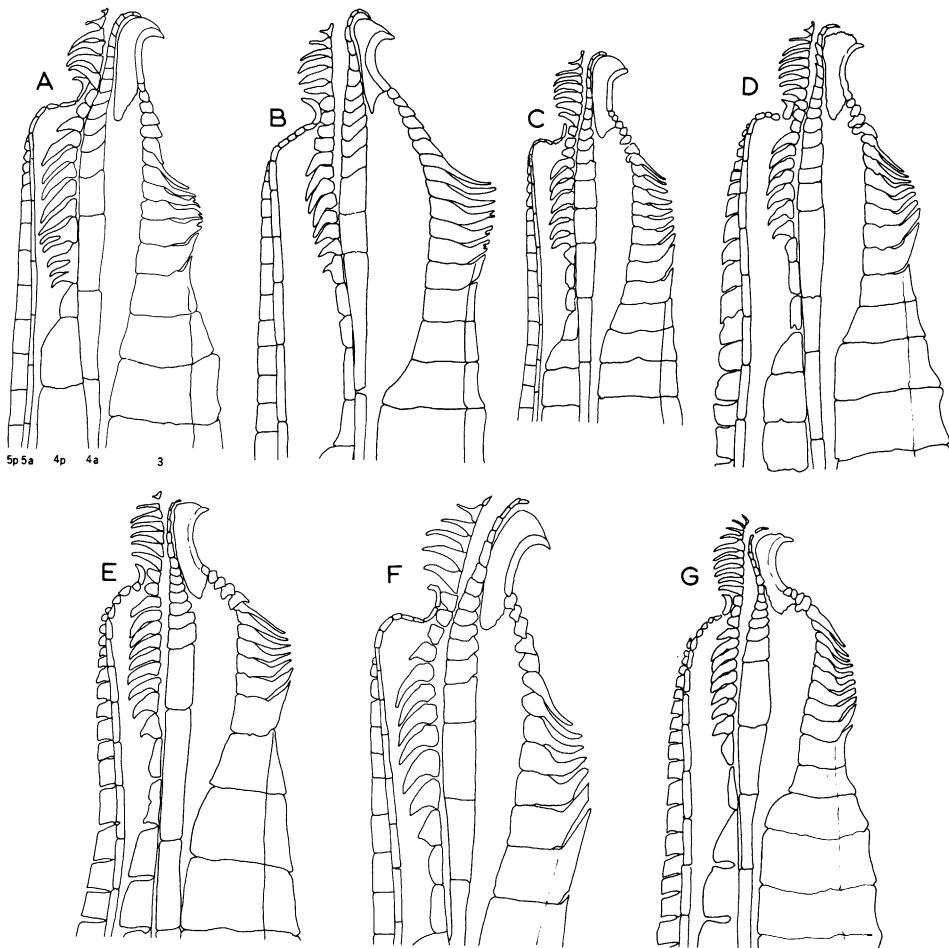


FIG. 29. Tips of gonopodia in species of *Xiphophorus*. A, *X. couchianus*. B, *X. gordonii*. C, *X. variatus*. D, *X. evelynae*. E, *X. xiphidium*. F, *X. maculatus*. G, *X. milleri*. B is from AMNH 20448. Others, after Rosen (1960). Each figure shows the maximum claw development on the tip of ray 5a known for the species. Claw development is a rare occurrence in all, however.

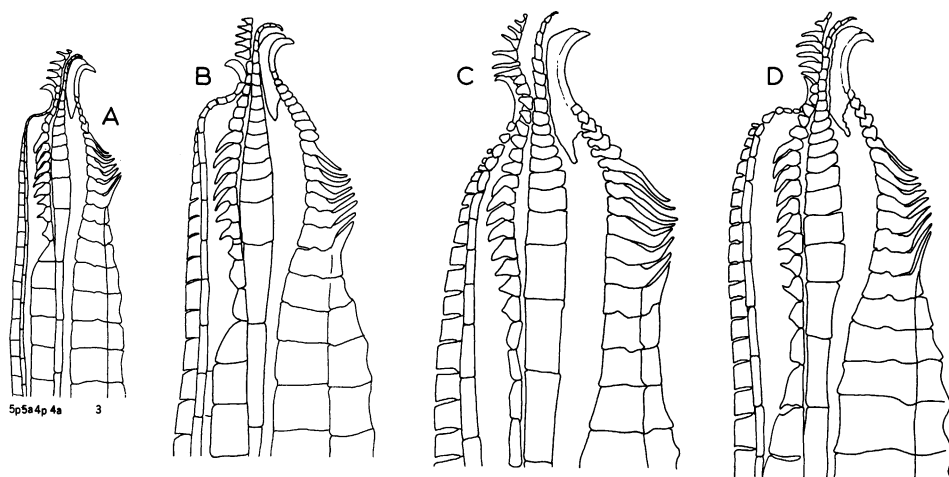


FIG. 30. Tips of gonopodia in species of *Xiphophorus*. A, *X. pygmaeus*. B, *X. nigrensis*. C, *X. montezumae*. D, *X. cortezi*. After Rosen (1960).

conical teeth. It seems reasonable to infer, therefore, that delicate, compressible teeth might be a synapomorphy of the species of *Xiphophorus* and that this condition has evolved elsewhere independently several times.

In summary, the species of *Xiphophorus* presently are united by five synapomorphies of gonopodial structure, one involving the pelvic fins of the male, and one involving dentition. *Xiphophorus* in turn is united in a monophyletic group with *Priapella* by five gonopodial synapomorphies, three of which (the blade, hook and spines of ray 3) in *Priapella* are in a different, probably more primitive state than the comparable features of *Xiphophorus*. The curved ramus of gonopodial ray 4a and the proximal serrae of ray 4p which are shared by, and are apparently indistinguishable in, *Priapella* and *Xiphophorus*, therefore, cannot be included as defining characters of *Xiphophorus*.

#### ANALYSIS OF SELECTED CHARACTERS AND INTERRELATIONSHIPS OF SPECIES

The last general theory of relationships among the species of *Xiphophorus*, by Rosen (1960), proposed three groups of unspecified relationship to one another. The first of these groups, listed in the order given in that publica-

tion, consists of five taxa: *couchianus*, *variatus variatus*, *v. xiphidium*, *v. evelynae*, and *maculatus*. The second group also includes five taxa: *pygmaeus pygmaeus*, *p. nigrensis*, *montezumae montezumae*, *m. cortezi*, and *milleri*. The last group, again of five taxa, contains *clemenciae*, *helleri helleri*, *h. strigatus*, *h. guentheri*, and *h. alvarezii*. Since 1960 two more taxa have been added: *gordoni* by Miller and Minckley (1963) and said to be related to *variatus*, but later shown by Rosen and Kallman (1969) to be very close to *couchianus*, and *helleri signum* (Rosen and Kallman, 1969). After restudy of this problem and review of some new and old material, I have found no reason to add named taxa to the genus, although for reasons discussed above under Species Concepts and below in the ensuing discussion, the 17 named taxa are treated as 15 taxa at the specific level. Ample reason has been found, however, to disagree strongly with Rosen's (1960) proposal of interrelationships among the species-level groups. Two of the groups recognized by Rosen (*couchianus*, *gordoni*, *xiphidium*, *variatus*, *evelynae*, *maculatus* and *pygmaeus*, *nigrensis*, *montezumae*, *cortezi*, *milleri*) are grade groups assembled largely on phenetic criteria of overall similarity and defined principally by means of primitive char-

acters. Thus the first, or platyfish group, was assembled mainly because its members lacked swordtail characteristics. The second group, consisting of four swordtails and *milleri* was assembled mainly because its members lacked the more derived genitalic features of the third group, *clemenciae*, *alvarezi*, *helleri* (including *strigatus* and *guentheri*), and *signum*.

Because the genus has been extensively studied by many workers over a long period of

time and because the various characters that have been used to diagnose species and populations of *Xiphophorus* have been treated in detail elsewhere, problems in the use of any character can be dealt with relatively simply and are discussed individually in relation to appropriate parts of the synapomorphy scheme of species presented below. Most of the evidence in this part of the review, however, pertains to the swordtail species and populations, particularly

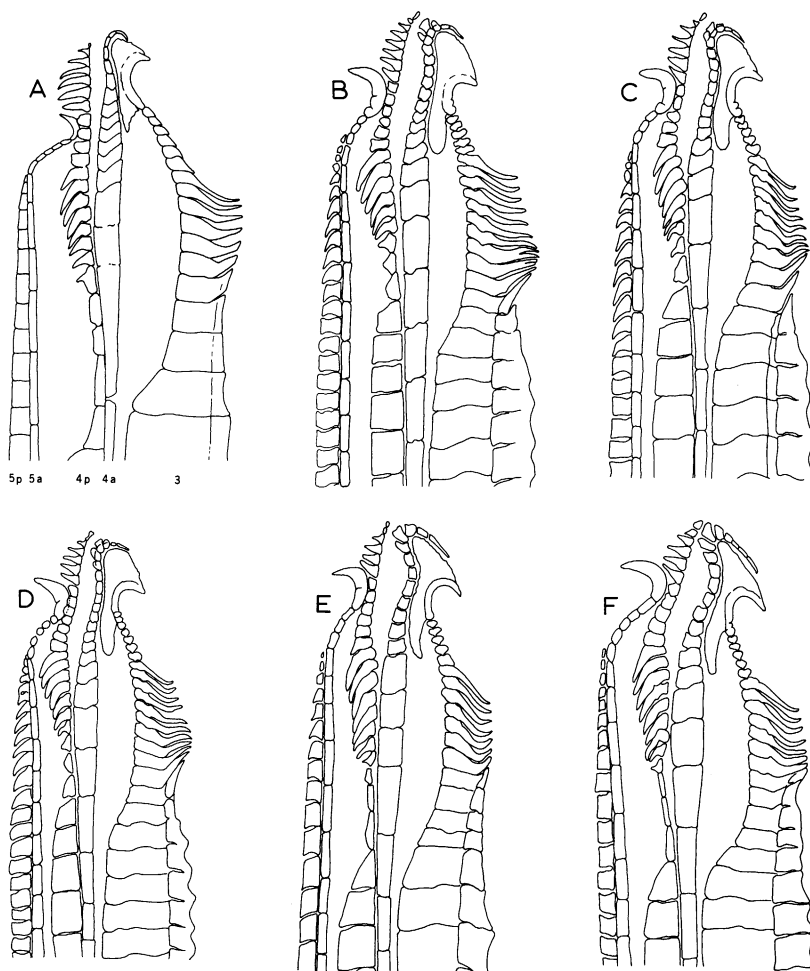


FIG. 31. Tips of gonopodia in species of *Xiphophorus*. A, *X. clemenciae*, after Rosen and Kallman (1969). B-D, *X. alvarezi* from Río Candelaria Yalcar, Alta Verapaz, Guatemala, AMNH 36798. E and F, *X. helleri* from Río San Simón, Alta Verapaz, Guatemala, AMNH 36790. The two localities in B to F are only a few kilometers apart, and are shown as localities numbered 12 and 17 in figure 2.

those from Guatemala and Honduras. As the result of extensive and now more informative collections of swordtails in the intermontane basins and uplands of Atlantic slope Guatemala as well as the discovery of two gonopodial characters not previously used in studying these animals, some discussion of these characters in relation to swordtail interrelationships are presented now.

The characters in question are (1) the blade of dense, calcified, granular tissue that is dorsal (posterior) to, and fused with, the terminal hook on gonopodial ray 3, and (2) the distal ramus of ray 4a that lies over, and conforms in shape with, the blade on ray 3. Some background is first necessary. The blade, as noted above, is present in all species of *Xiphophorus* and in its sister group, *Priapella*. In *Priapella*, the blade conforms entirely to the convex side of the hook on ray 3 and in *Xiphophorus couchianus* and other platyfishes (fig. 29), and in swordtails such as *montezumae*, *pygmaeus* (fig. 30), and *clemenciae* (fig. 31A), the blade conforms to the hook and is bluntly rounded distally where it extends only to about the level of the tip of the underlying hook on ray 3 or slightly forward of the hook. This, therefore, appears to be the primitive condition of the blade in *Xiphophorus*. In a group of species including *alvarezi*, *helleri* (figs. 31 B-F) and *signum* the blade is elongated distally and the underlying hook is foreshortened, so that the blade extends well beyond the tip of the hook. In *helleri* and *signum*, the blade is further modified by being pointed distally. Corresponding with these differences in blade shape and hook length is a change in the distal ramus of ray 4a, which is more strongly decurved over the blade in *alvarezi*, *helleri*, and *signum* than in the other species. In *alvarezi*, *helleri*, and *signum* the segments of the ramus are also enlarged where the ramus curves downward over the tip of the blade. In other species, the distal ramus of ray 4a consists of slender segments, longer than high. In *alvarezi*, the ray 4a segments dorsal to the blade are almost invariably slender, much longer than high, as compared with the much heavier segments in *helleri* and *signum*, and the two or three corner segments have small to moderate dorsal processes. In

*helleri* and *signum*, the corner segments of the ray 4a ramus have moderate to large dorsal processes which, in most cases, are flared, and the segments themselves are heavier than in *alvarezi*. Conforming with the shape of the blade below, the distal ramus of 4a in *helleri* and *signum* curves sharply downward and backward (is recurved) over the blade's pointed tip.

In order to obtain a quantitative estimate of the differences in blade, hook, and ramus shape in these swordtails, a form-index was derived for the blade by measuring in micrometer units the length of the blade distal to the curved tip of the hook on ray 3 and the height of this part of the blade halfway between its distal tip and the curved tip of the ray 3 hook. This index clearly distinguishes between *alvarezi*, on the one hand, and *signum* and most populations of *helleri*, on the other (table 13). One population of *helleri* from northern Huehuetenango in Guatemala (Laguna Yalnabaj, AMNH 32107) resembles *alvarezi* in its blade height-length index, although the blade itself retains the sharply pointed distal tip characteristic of *helleri* and *signum*. These swordtails are of exceedingly small body size; all the males are 25 mm. in standard length or less, and are smaller than the adults of any other swordtail population known to me. In order to determine if the height-length ramus index values of the Yalnabaj sample, which are entirely within the range of those of *alvarezi*, are high because of small body, a brood of laboratory-born swordtails (*helleri*) from the Río Sarabia (Río Coatzacoalcos drainage of southern Mexico) were stunted so that some of the Sarabia males were in the size range of the Yalnabaj males. The Sarabia males that overlapped Yalnabaj males in absolute body size had correspondingly high height-length index values, whereas those larger than 25 mm. had lower values approaching or coinciding with, the values of wild-caught Sarabia males (table 14). Hence, except in cases of extremely small body size, the height-length index satisfactorily reflects the qualitative differences in several gonopodial traits between *alvarezi* and swordtails of the *helleri* group. When *alvarezi* and *helleri* are raised under more or less uniform laboratory conditions, the two are sharply separated in

height-length index values, whereas wild-caught males of *alvarezi* and *helleri*, maturing under more variable natural conditions, show a slight overlap in values (table 15). Three samples from the *helleri* group (table 13), from the Río Polochic, Río Motagua, and Honduras drainages, all of which are large fish (some Honduras fish being the largest of all known swordtails) appear to show a slight, though

real, increase in index values, and these slightly higher values are correlated with a slightly less pointed blade and less sharply curved distal ramus on ray 4a; their ray 4a segments are nonetheless heavy and as high as, or higher than, long with the corner segments greatly elevated, as in *helleri* (figs. 32 A-E). In a theory of relationships based on these gonopodial features, *alvarezi* is therefore the

TABLE 13  
Frequency Distribution of Height/Length Ratios of Tip of  
Blade on Gonopodial Ray 3 in *Xiphophorus helleri* Species Complex

	Class Intervals											
	3.0- 3.4	3.5- 3.9	4.0- 4.4	4.5- 4.9	5.0- 5.4	5.5- 5.9	6.0- 6.4	6.5- 6.9	7.0- 7.4	7.5- 7.9	8.0- 8.4	8.5- 8.9
<i>Xiphophorus alvarezi</i>												
Chiapas, Mexico												
Laguna Ocotál Grande	—	—	—	—	—	—	—	—	—	—	—	1
Río Santo Domingo	—	—	—	—	—	—	1	1	1	—	—	—
Huehuetenango, Guatemala												
Río San Ramón	—	—	—	—	—	1	3	8	11	4	4	1
El Quiché, Guatemala												
Río Xalbal - Ixcán	—	—	—	—	—	—	—	1	3	1	1	—
Alta Verapaz, Guatemala												
Río Dolores	—	—	—	—	—	1	2	2	13	4	—	—
Cubilguitz	—	—	—	—	—	—	—	—	3	4	1	—
Río Candelaria Yalcar	—	—	—	—	—	—	1	7	11	5	3	—
<i>Xiphophorus helleri</i>												
Northern Mexico												
Orizaba	—	2	3	7	—	—	—	—	—	—	—	—
Río Atoyac	2	3	2	2	—	—	—	—	—	—	—	—
Southern Mexico												
Río Papaloapan	—	—	1	1	—	—	—	—	—	—	—	—
Laguna Catemaco	—	—	—	—	2	—	—	—	1 <sup>a</sup>	—	—	—
Río Coatzacoalcos	2	2	9	3	—	1	—	—	—	—	—	—
Río Grijalva	1	2	4	1	—	—	—	—	—	—	—	—
Guatemala												
Río Salinas	—	2	—	1	1	—	—	—	—	—	—	—
Río de la Pasión	—	1	7	10	6	1	—	—	—	—	—	—
Río Sarstún	1	4	24	4	3	—	—	—	—	—	—	—
Belize (combined)	—	3	18	13	5	3	—	—	—	—	—	—
<i>Xiphophorus</i> "P-M-H"												
Río Polochic	—	—	—	3	1	—	—	—	—	—	—	—
Río Motagua	—	—	—	3	5	4	2	—	—	—	—	—
Honduras	—	1	—	—	1	2	2	—	—	—	—	—
<i>Xiphophorus signum</i>												
Río Chajmaic	—	3	13	3	—	—	—	—	—	—	—	—

<sup>a</sup>Individual possibly abnormal, but all three individuals with short gonopodial tip; may represent a relic or differentiated population.

TABLE 14  
**Frequency Distribution of Height/Length Ratios of Tip of Blade on  
 Gonopodial Ray 3 in a Natural Population of Dwarf *Xiphophorus*  
*helleri* Compared With Ratios of Normal *Xiphophorus helleri* and Stunted  
 Laboratory-reared *Xiphophorus helleri***

	Class Intervals								
	3.5 -3.9	4.0 -4.4	4.5 -4.9	5.0 -5.4	5.5 -5.9	6.0 -6.4	6.5 -6.9	7.0 -7.4	7.5 -7.9
Dwarf form, Laguna Yalnabaj, Huehuetenango, Guatemala, AMNH 32107	—	—	—	—	—	1	3	6	1
Stunted Lab.-reared descendants from Río Sarabia stock	—	1	—	—	1	1	1	1	1
Wild-caught fish, Río Sarabia, Oaxaca, Mexico. UMMZ 180631	1	4	1	—	—	—	—	—	—
	standard length more than 25 mm.					standard length, 25 mm. or less			

sister group of the other members of this swordtail assemblage and the Polochic-Motagua-Honduras swordtails are the sister group of the species pair, *helleri* and *signum*.

One other set of height-length indices is of interest here, for it is almost exactly intermediate between those of Guatemalan *helleri* and Guatemalan *alvarezi* (Mexican samples of *alvarezi* are too small to analyze). The interest in these intermediates stems from the facts that (1) these fish occur geographically between the isolated upland *alvarezi* and the main-river *helleri*; (2) their gonopodial morphology is intermediate between the two and rather variable (comparable with the variability of all southern *helleri* combined, table 15), and (3) they occupy the same region where, in *Heterandria*, there exists a variable and morphologically intermediate population between an upland (*obliqua*) and main-river (*bimaculata*) form (figs. 24, 26, 33). With the thought that these naturally occurring intermediates might be intergrades, laboratory hybrids were produced between *alvarezi* (Río Candelaria Yalcar population) and a Guatemala-type *helleri* (Belize population); the results are shown in table 15 and compared with wild-caught *alvarezi*, *helleri*, and the suspected intergrades. Except for the fact that each laboratory sample has a slightly higher mean than its comparable wild-caught sample (some-

thing that has proved generally true of laboratory reared swordtails with respect to the height/length index), the results are closely similar and the variety of blade shapes in the known hybrids corresponds well with the naturally occurring intermediate sample. Because all the *alvarezi* in Guatemala are confined to isolated basins and are sharply separated from *helleri* even where the two live in close proximity but in separate basins (e.g., *alvarezi* from the Río Candelaria Yalcar are less than a kilometer of ground surface distant from typical *helleri* in the upper Río San Simón), there seem to be three possible interpretations of these intergrades: (1) they represent another species; (2) they represent a primary morphocline in which an upland *alvarezi* ecophenotype has not yet become isolated from a lowland *helleri* ecophenotype, or (3) they represent a secondary morphocline (i.e., hybrids). The first possibility is rejected because the population lacks definable characteristics and its individuals are morphologically variable with respect to the relevant gonopodial characteristics. Objections to the second possibility that the morphocline is primary and induced ecophenotypically are that a type of blade somewhat more primitive than that of *helleri* occurs in both upland and lowland fish from Río Polochic, Río Motagua and Honduras drainages,



that the more derived *helleri* condition occurs at both high and low altitudes in Mexico (Rosen, 1960) and Guatemala, and that even if the morphocline is not associated with altitude, one must accept the contrived explanation that the factors causing it in *Xiphophorus* have also caused a morphocline in pigmentary and gonopodial characters in *Heterandria* in this

one region of Guatemala. The third possibility, that the morphocline is secondary rather than primary, depends on the acceptability of the theory of relationships posed above (and see fig. 37) in which *alvarezi* is the sister group of Polochic-Motagua-Honduras (PMH) swordtails plus the species pair, *helleri* and *signum*: if the forms that intergrade are separated from each

TABLE 15  
Frequency Distribution of Height/Length Ratios of Tip of Blade on Gonopodial Ray 3 in Laboratory-reared and Wild-caught Representatives of *Xiphophorus helleri* Species Complex and Their Laboratory and Putative Natural Hybrids

	Class Intervals														
	3.0- 3.4	3.5- 3.9	4.0- 4.4	4.5- 4.9	5.0- 5.4	5.5- 5.9	6.0- 6.4	6.5- 6.9	7.0- 7.4	7.5- 7.9	8.0- 8.4	8.5- 8.9	9.0- 9.4	9.5- 9.9	10.0 10.4
Lab.-reared descendants of natural populations															
<i>Xiphophorus alvarezi</i>															
Río San Ramón	—	—	—	—	—	—	—	—	2	8	5	5	—	—	—
Cubilguitz	—	—	—	—	—	—	—	—	—	—	1	1	2	1	1
Río Candelaria															
Yalicar	—	—	—	—	—	—	—	1	8	5	3	2	1	—	—
<i>Xiphophorus helleri</i>															
Río Papaloapan	—	—	—	5	9	5	—	—	—	—	—	—	—	—	—
Río Grijalva	—	1	5	1	—	—	—	—	—	—	—	—	—	—	—
<i>Xiphophorus</i> "P-M-H" Honduras															
	—	—	1	2	4	2	—	—	—	—	—	—	—	—	—
Lab.-reared descendants and their hybrids (m̄ = arithmetic mean)															
<i>Xiphophorus alvarezi</i> (combined)															m̄
	—	—	—	—	—	—	—	1	10	13	9	8	3	1	1 8.04
<i>X. alvarezi</i> × <i>X. helleri</i> (F <sub>1</sub> + F <sub>2</sub> ) <sup>a</sup>															
	—	—	—	—	1	8	7	6	3	1	—	—	—	—	6.30
<i>Xiphophorus helleri</i> (combined)															
	—	1	5	6	9	5	—	—	—	—	—	—	—	—	4.93
Wild-caught fish and their putative hybrids															
<i>Xiphophorus alvarezi</i> (combined)															
	—	—	—	—	—	2	7	19	42	18	9	2	—	—	7.22
Natural intergrades (upper Río Salinas)															
	—	—	—	1	4	2	1	2	2	—	—	—	—	—	5.91
<i>Xiphophorus helleri</i> , Río Papaloapan to Río Sarstún (combined)															
	2	12	53	29	15	4	—	—	—	—	—	—	—	—	4.44

<sup>a</sup>Río Candelaria Yalicar ♂ (*alvarezi*) × Belize River ♀ (*helleri*).

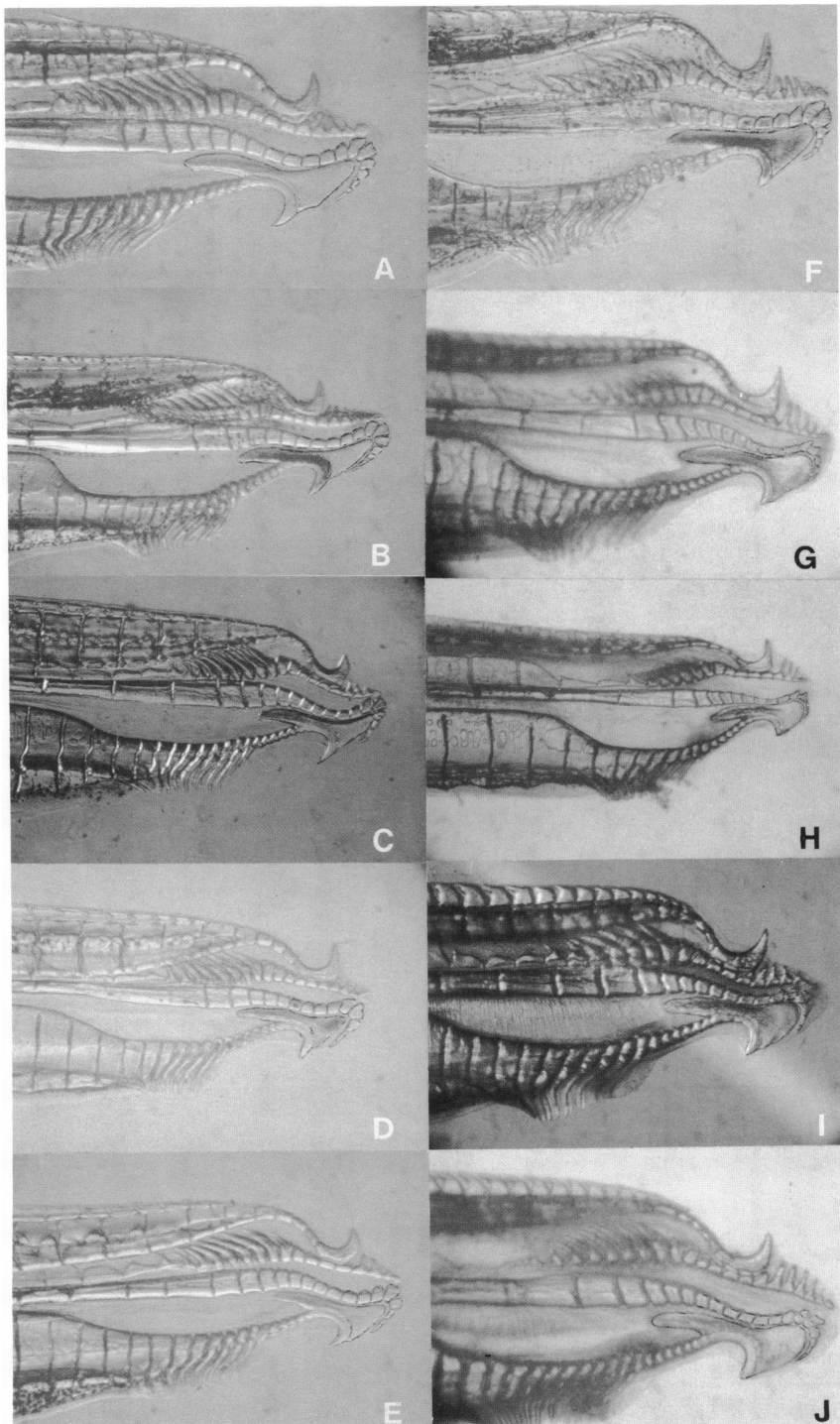


FIG. 32. Photomicrographs of tips of gonopodia in species of *Xiphophorus*. A-E, *X. helleri*. F, *Xiphophorus* "PMH." G-J, *X. alvarezii*. A, Río Hondo, Belize, UMMZ 97871. B, Belize River, Belize, UMMZ 159294. C, Río Coatzacoalcos, lab. strain. D, Río Papaloapan, lab. strain. E, Río Antigua, just north of Río Jamapa, UMMZ 97579. F, La Lima, Atlantida, Honduras, laboratory strain. G and H, Río Espiritu, upper Río San Ramón basin, AMNH 32916. I, Cubilguitz, Río Dolores basin, AMNH 24637. J, Río Dolores near subterranean terminus (Agua Blanca), AMNH 32124. For localities in A-E, see figure 23; for those in G-J, see figure 2, numbers 2b, 10, and 9; for F, see easternmost limit of range in Honduras in figure 40. Note differences in blade (ray 3) and ramus (ray 4a) shape in the three forms.

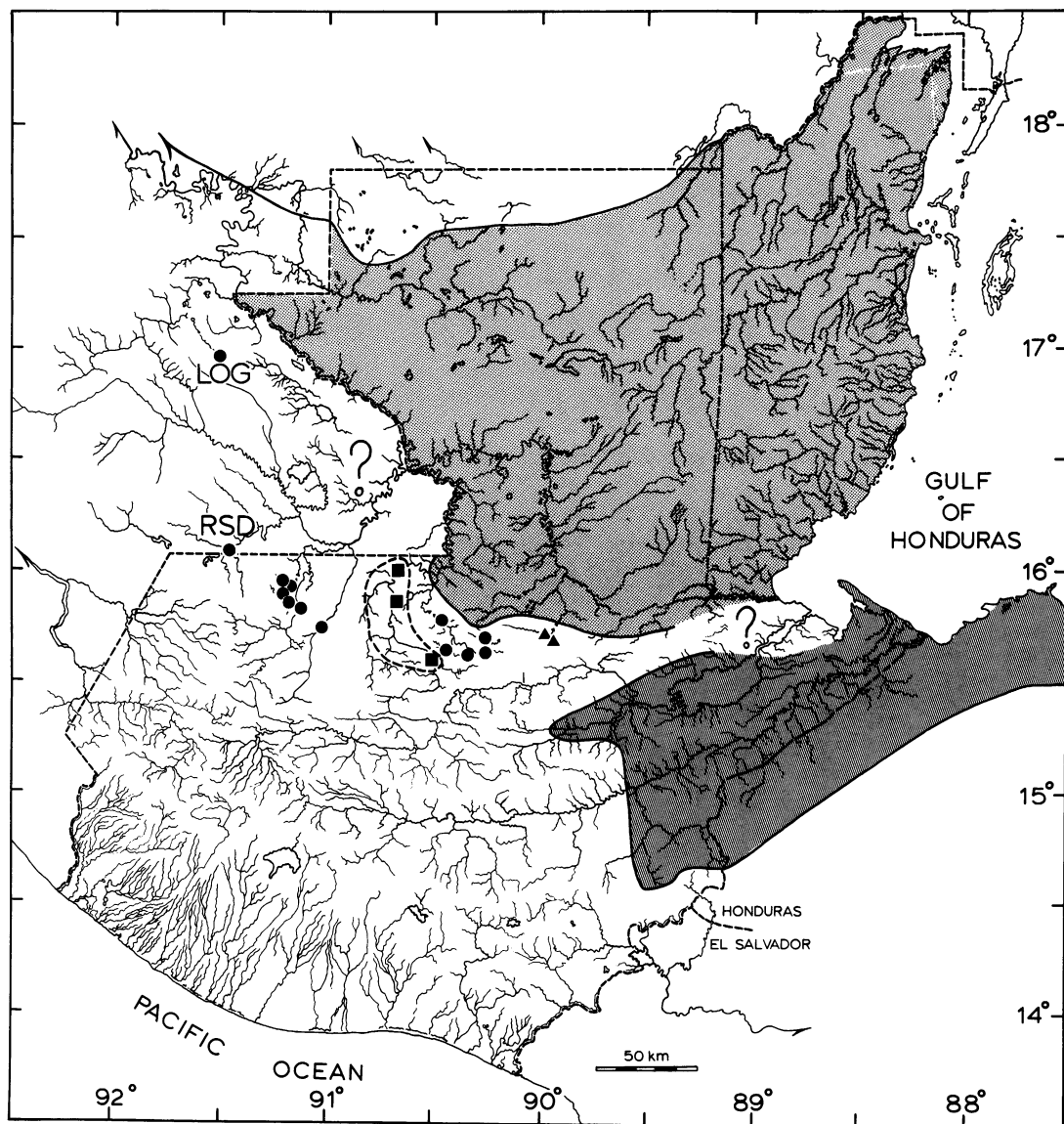


FIG. 33. Distribution by record stations of the upland swordtail species of *Xiphophorus* in Guatemala and Chiapas, Mexico in relation to the range of *X. helleri* (upper, lightly shaded region) and *Xiphophorus* "PMH" (lower, darker shaded region). Dots, *X. alvarezi*; triangles, *X. signum*; squares enclosed by dashed line, putative hybrids between *X. alvarezi* and *X. helleri*. LOG, Laguna Ocotal Grande. RSD, Río Santo Domingo. Two question marks identify insufficiently studied regions.

other historically by one or more speciation events (= branch points) in their phylogeny (= cladogram of relationships), the hybrid status of the intergrades is a logical inference (see section on Methods). This is the inference made here, since *alvarezi* is separated from *helleri* by two speciation events (or one event if the PMH swordtails are included in *helleri*) and since intergrades in *Heterandria* in the same region are between two forms, *obliqua* and *bi-maculata*, separated by three speciation events. Given the logical requirements of the cladistic argument and the coincident geography of the intergrades, two geographical facts stand out: *Xiphophorus alvarezi* and *Heterandria obliqua* both have distributions confined to the Sierran foothills of Guatemala which, at least for *alvarezi*, may even extend into central Chiapas, and this distribution is interrupted at one point by intergrades in a region that lacks barriers to fish movement up and down stream. The simplest apparent explanation of this pattern is that an old fauna, which extended across the Sierran foothills from the Río Dolores basin northward perhaps as far as Chiapas, has been preserved by the formation of solution caves and the isolation of headwater streams in some regions and is being replaced or at least degraded by newer faunal elements in regions where subterranean barriers have not formed.

Working with previously published data from Rosen (1960), Miller and Minckley (1963), Kallman and Atz (1967), Rosen and Kallman (1969), Kallman (1971, 1975), and Schreibman and Kallman (1977), as well as the new data presented above, the following synapomorphy scheme is proposed and illustrated in the cladogram in figure 37.

#### EXPLANATION OF THE SYNAPOMORPHY SCHEME FOR THE SPECIES

1. *Xiphophorus couchianus* and *X. gordonii* possess all the defining genitalic, pelvic, and dentitional characters with other members of the genus. With each other they share a strongly bicolored body pigmentation (darkly pigmented above the midlateral line and much paler below), deep-lying (subdermal), dashes of

very dark pigment laterally, spines of gonopodial ray 3 with divided distal tips and with distal serrae on gonopodial ray 4p that converge at their tips.

2. A group including *variatus*, *evelynae*, *xiphidium*, *milleri*, and *maculatus* differs from *couchianus* and *gordonii*, but resembles other groups of *Xiphophorus*, in having micromelanophore tail patterns and pigment patterns made up of large, specialized melanophores (macromelanophores) and in showing some degree of development of a caudal appendage (prolongation of the ventral-most principal caudal fin rays in adult males). The argument favoring recognition of this group is somewhat complex: all members of this group except *evelynae* possess a series of special autosomal pigment patterns in the tail region made up of small melanophores (micromelanophores), and all of them possess various macromelanophore and non-melanic patterns that are sex-linked (associated with a sex chromosome, as opposed to the micromelanophore patterns which are controlled autosomally). Within the group, *milleri* has three tail patterns belonging to a simple, dominant, autosomal allelic series, of which two have been shown by morphological study and inferred from related genetic experiment (Kallman and Atz, 1967; Kallman, 1975) to be the same as two patterns of *maculatus*. Within this group, *variatus*, *evelynae*, and *xiphidium* also are united by various unique pigment patterns (see below, pp. 354-355) not associated with the tail patterns or sex-linked macromelanophore patterns (Rosen, 1960). Of the two subsections of this group (*variatus*, *evelynae*, *xiphidium* and *milleri*, *maculatus*), a caudal appendage ("sword") is a characteristic feature in one species (*xiphidium*) of one subsection and has been induced experimentally in both species (*maculatus* and *milleri*) of the other subsection (Zander and Dzwillo, 1969) (see remarks below on body size in relation to sword development). The implication of these occurrences is that "sword genes" are present but usually unexpressed in this section of the genus.

3. A group including all swordtail species differs from the preceding ones in having the caudal sword consistently present and black-

edged in all but one case and in having the tip of gonopodial ray 5a always differentiated into a clawlike segment. Within this swordtail group:

a. *Xiphophorus pygmaeus* and *X. nigrensis* have the defining synapomorphies of the group but none (except two problematic features) with any other member of the group. One of these problematic features is an oval pigment blotch on the caudal base of some adult males of *nigrensis* (but not *pygmaeus*) that is found also in some *montezumae* and *cortezii*. The expression of this blotch (Kallman, personal commun.), which is made up of micromelanophores, is both size-related (poorly expressed in smaller individuals) and responsive to social conditioning (melanophores punctate in non-dominant males). The other problematic feature concerns the presence of yellow pigment patterns in *pygmaeus*, *nigrensis*, *cortezii*, and *montezumae* and the presence of both red and yellow in the other species. G-xanthophores are responsible for yellow color and G-xanthophores plus a set of modifier genes, which cause them to develop as xanthoerythrophores, are responsible for red color (see Kallman, 1975). Pure yellow patterns, apparently composed of unmodified G-xanthophores, are also present in some populations of *X. maculatus* and *X. milleri* in which, in being sex-linked, their genetic control is quite different (Kallman, 1975, pp. 107-108). Moreover, a red dorsal fin pattern has recently been found in *X. montezumae* (Kallman, personal commun.). Thus, only the caudal blotch might be used to argue for common ancestry of the *pygmaeus-nigrensis* and *montezumae-cortezii* species pairs by assuming an independent loss of the caudal blotch in *pygmaeus*. The two pigmy swordtails, *pygmaeus* and *nigrensis*, are united with each other, however, by various unique pigment patterns of the dorsal fin and body (especially the pale space between the dorsal body pigment and the midlateral stripe) and a gonopodial trait.

b. *Xiphophorus montezumae* and *X. cortezii* differ from the preceding and resemble the other swordtails in the development of a double-margined, caudal sword with yellow pigment between the black margins. The two species are united by unique body pigment pat-

terns (see Rosen, 1960; Rosen and Kallman, 1969) and by a tendency of the caudal sword to curve upward.

c. *Xiphophorus clemenciae* differs from the preceding species and resembles other swordtails in the presence of a midlateral band of dark pigment that is continuous with the dorsal pigment margin of the caudal sword and the presence of two or more stripes of red pigment following the scale rows on the sides (but see comments below, under *signum*).

d. *Xiphophorus alvarezi* (fig. 31B-D) differs from the preceding but resembles *helleri* (fig. 31 E, F) and *signum* (Rosen and Kallman, 1969, fig. 4B) in having the terminal hook on gonopodial ray 3 shortened and strongly decurved and recurved in some cases, the blade above this hook elongated distally, the corner segments somewhat enlarged at the point of downward curvature of the ray 4a distal ramus, and the distal claw on ray 5a greatly enlarged, sharply pointed and extending upward well above the tips of the distal serrae on ray 4p. As in most populations of *helleri*, this species has two irregular rows of red spots on the dorsal fin (but see below, under *signum*) and its various isolated populations are united by the consistent presence of two red stripes bordering the midlateral (pitted) scale row with a band of sky blue refractive pigment between them, by the development, especially in older adult males (and females in some instances) of intense yellow or red pigment, or both, on the lower sides from below the pectoral fin to the caudal fin base, and by the greater width of the median scale between the supraorbital sections of the cephalic lateral-line system (figs. 35, 36).

e. *Xiphophorus helleri* (here including *strigatus* and *guentheri*) differs from *alvarezi* and resembles *signum* in having the blade above the hook on gonopodial ray 3 sharply to bluntly pointed and the distal ramus of ray 4a with greatly enlarged corner segments where it turns sharply downward and backward to conform with the bluntly or sharply pointed blade. Actually, within a transition series involving the degree of pointedness of the gonopodial blade, three geographic units may be separated off from *helleri*: in populations from the Río Polochic, Río Motagua, and Honduras (the

southeastern extremity of its range, see figure 33), the blade is always rather bluntly pointed, less pointed than in more northwesterly *helleri* but more pointed and with larger corner segments on ray 4a than in *alvarezi*. Because of the variability of the southeasterly populations and the geographic heterogeneity of *helleri* to the northwest, recognition of another distinct taxon for the southeastern populations would be difficult and inconvenient by current standards of taxonomic practice (type designation, precise diagnosis, etc.). Nevertheless, to follow a consistent cladistic methodology in dealing with the aforementioned character states, these populations, assuming they represent a cryptic though monophyletic group, should precede *helleri* in the cladogram and they are so included as "*Xiphophorus* populations PMH" (Polochic, Motagua, Honduras).

f. *Xiphophorus signum* differs from all other *Xiphophorus* in being a uniform green-gold color, in having a high, somewhat falcate dorsal fin, in having a black spot on the base of the lower caudal fin rays in all half-grown individuals and adult females, and in having the cranial canals of the cephalic lateral-line system very wide and completely enclosed. This species in some ways resembles northernmost

*helleri*, some populations and individuals of which have also lost the red striping and red dorsal fin spotting and are a uniform iridescent green in color. To assume that the absence of red striping is primary in *signum* and some northern *helleri*, would require the unpar-simonious inference that red striping has appeared independently in *clemenciae*, *alvarezi*, "*Xiphophorus* populations PMH," and most populations of *helleri*, and that red dorsal fin spotting arose independently in *alvarezi*, some *helleri*, and in the southern "PMH" populations.

There is still another transition series involving *alvarezi*, *helleri*, and *signum* that concerns the development of the cephalic lateral-line canals (as noted above), head width, and the shape of the median scale between the supra-orbital sections of the cephalic lateral-line. In a comparison of males of exactly the same standard length (fig. 34), the head of *alvarezi* is the widest and *signum* the narrowest, and the median scale is correspondingly wider and shorter. A comparison of scales removed from this position on the head in various populations of *alvarezi* (fig. 35) and *helleri* (fig. 36) shows that there is a real average difference between the median scales of even adjoining members

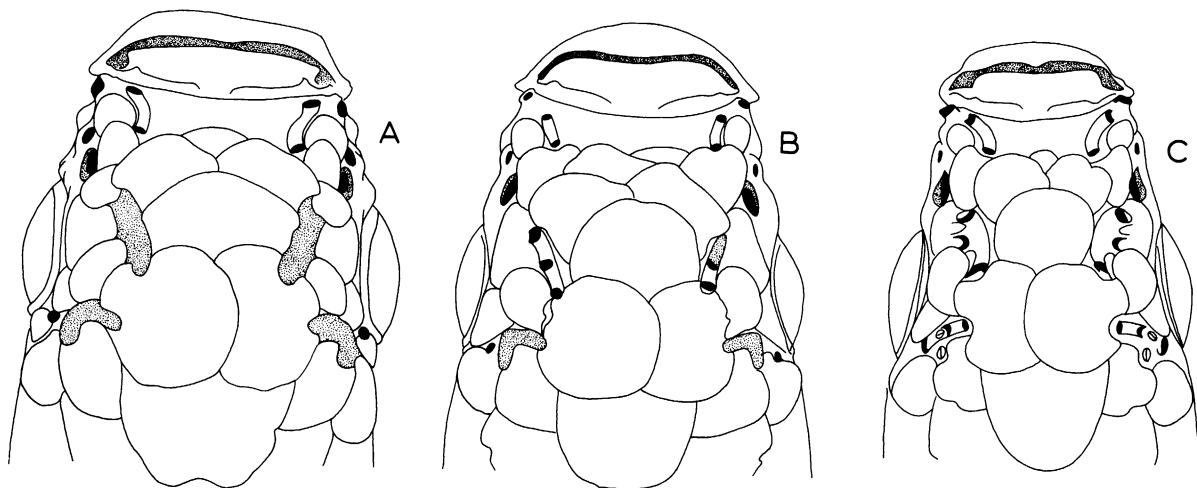


FIG. 34. Patterns of dorsal, cephalic lateral-line system and head squamation in three species of *Xiphophorus*. A, *X. alvarezi*, Río Dolores basin, AMNH 32124. B, *X. helleri*, upper Río San Simón basin, AMNH 36790. C, *X. signum*, Río Chajmaic basin, AMNH 27671. All drawings from specimens exactly 60 mm. in standard length.

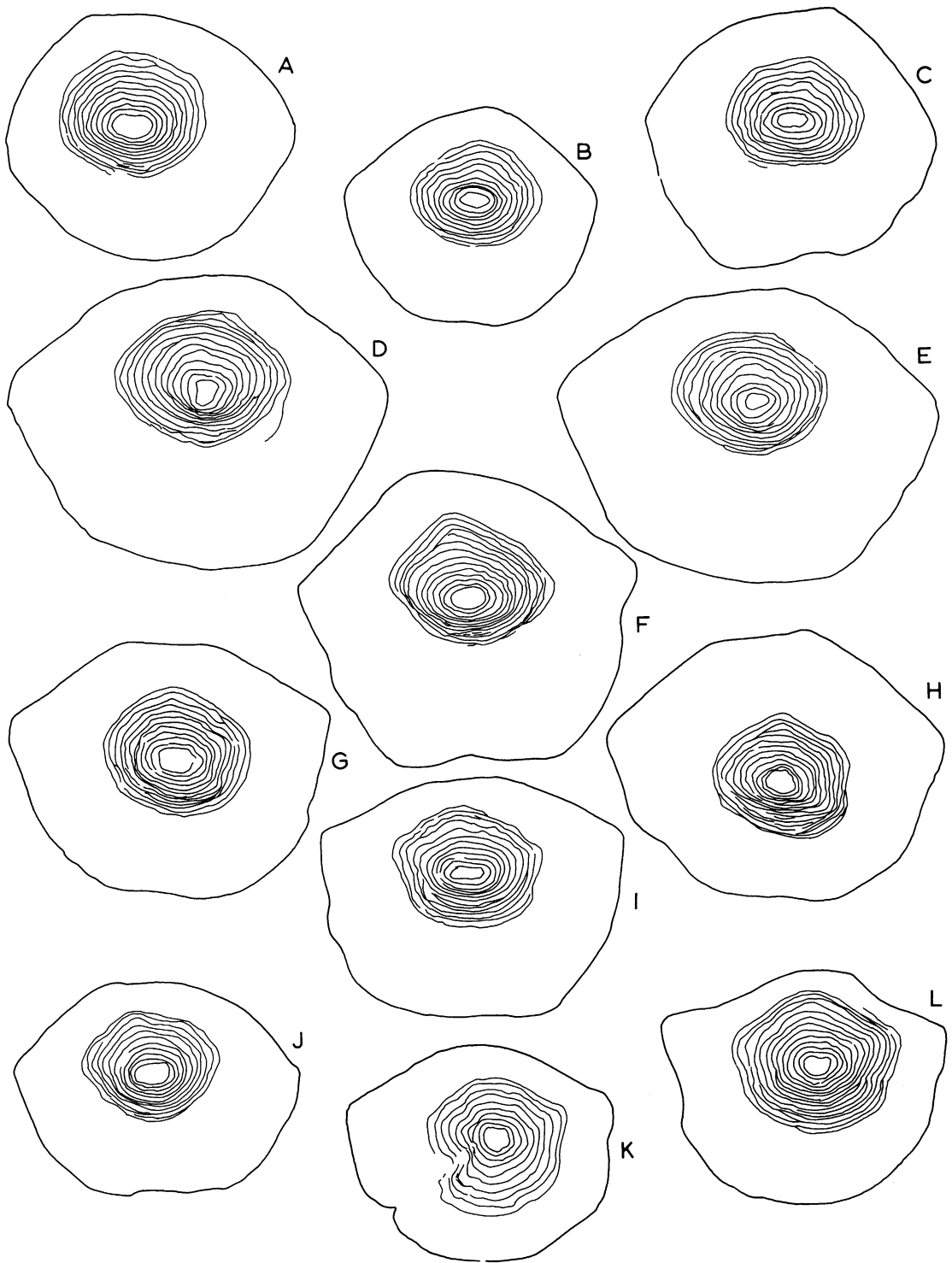


FIG. 35. Median head scale from between supraorbital sections of cephalic lateral-line system (only inner circulae, nucleus and scale outline shown) in *Xiphophorus alvarezii*. A-C, Cubilguitz, AMNH 24637. D-E, Río Candelaria Yalicar, AMNH 36798. F-H, Río Dolores at Agua Blanca, AMNH 32124. I-L, Río Espiritu, upper Río San Ramón basin, AMNH 32916. For localities, see figure 2.

of the series. This character has not been thoroughly surveyed, however, because of the

specimen mutilation required to represent it accurately. Correlated with these differences in

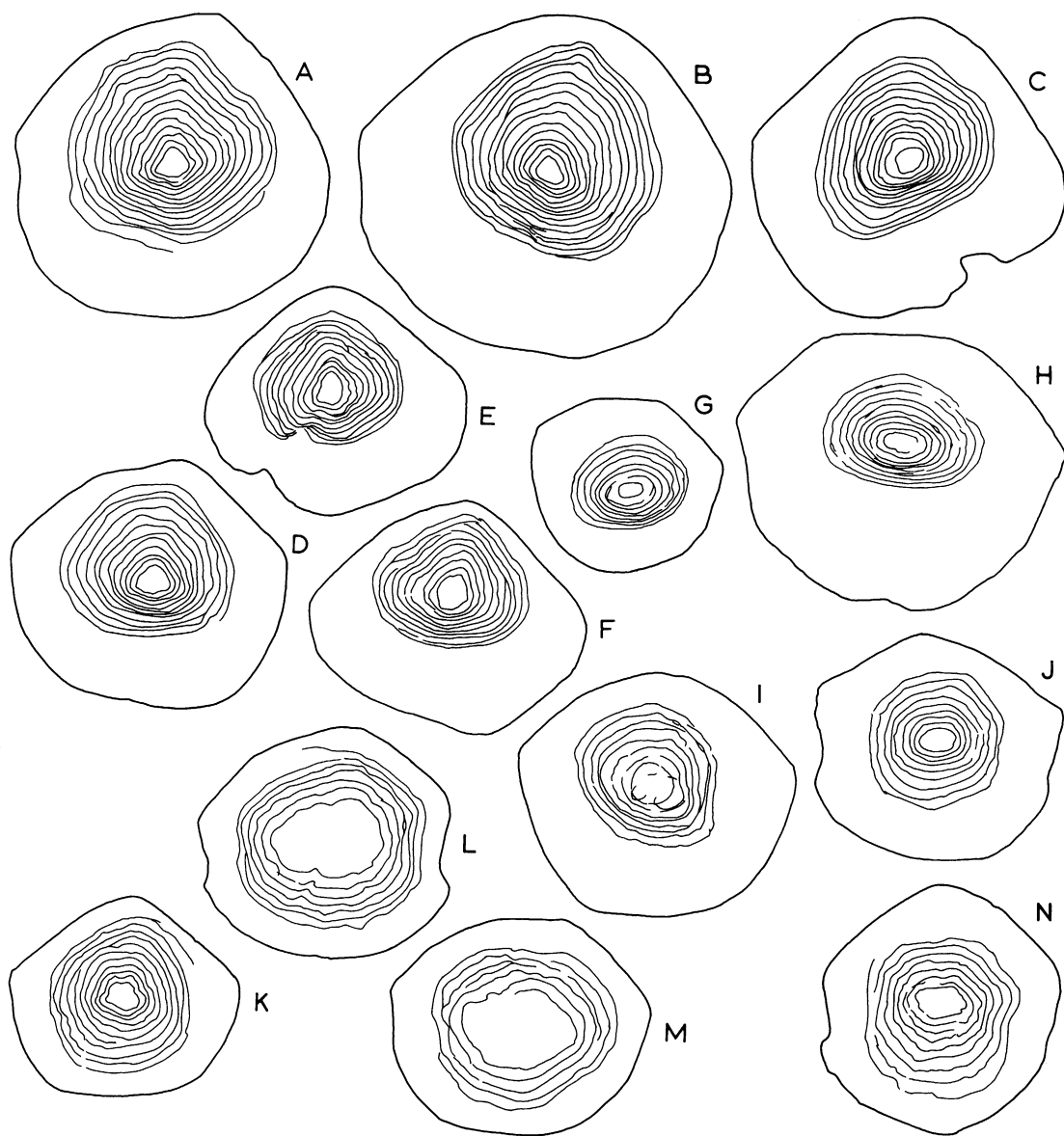


FIG. 36. Median head scale from between supraorbital sections of cephalic lateral-line system (only inner circulae, nucleus and scale outline shown) in Guatemalan *Xiphophorus helleri*. A-D, upper Río San Simón basin, AMNH 36790. E and F, El Petén, AMNH 32074. G-J, Río Sebol, AMNH 27696. K-N, Río Ixvolay, AMNH 25281. For localities, see figure 2.



head and scale width are average differences in the extent of closure of the interorbital sections of the cephalic lateral-line canal. It is mostly open in *alvarezii*, closed or open in *helleri*, and closed in *signum*. In *signum*, even part of the supratemporal canal, internal to the canal of the dermosphenotic, is partly closed over. Whether these several traits are independent or part of a single complex character is undetermined. Although not used in the formal synapomorphy scheme for want of a thorough survey of these traits in the numerous populations of *alvarezii*, *helleri* and the Polochic-Motagua-Honduras fish, it is worth noting that to the extent they are presently understood they are entirely compatible with the cladistic relationships of these fishes based on other characters.

### SYNAPOMORPHY SCHEME

Figure 37

Synapomorphies of *couchianus* and *gordoni* with all other species.

1. Pelvic fin of male with fleshy appendage developed along distal third of first short, unbranched ray, second and third rays somewhat prolonged.
2. Outer jaw teeth depressable, compressed distally and spatulate to ob lanceolate.
3. Gonopodium of male with blade of dense granular tissue along inner margin of terminal hook on ray 3 greatly enlarged.
4. Gonopodium of male with a subdistal series of greatly enlarged, angulate spines on ray 3.
5. Gonopodium of male with a distal series of serrae on ray 4p.

Synapomorphies between *couchianus* and *gordoni*.

6. Body pigmentation strongly bicolored, darkly pigmented above the midlateral line and much paler below.
7. Deep-lying (subdermal) dashes of very dark pigment laterally.
8. Spines of gonopodial ray 3 with distal tips scalloped or deeply indented.
9. Distal serrae on gonopodial ray 4p converging at their tips (a character poorly developed, but present, in many individuals of *gordoni*).

Synapomorphies of a group including *variatus*, *evelynae*, *xiphidium*, *milleri*, and *maculatus* with the swordtail species.

10. Micromelanophore tail patterns and macromelanophore body and fin patterns (and see discussion above).

11. Prolongation of the ventralmost principal caudal fin rays in adult males (and see discussion above).

Synapomorphies of the group including *variatus*, *evelynae* and *xiphidium*, with *maculatus* and *milleri*.

12. Specialized series of autosomal, micromelanophore tail patterns (Kallman and Atz, 1967).
13. Specialized series of sex-linked macromelanophore patterns (Kallman and Atz, 1967).
14. Specialized series of sex-linked red and yellow patterns [known for the *variatus* complex and *maculatus* and inferred for *milleri* based on field reports by R. R. Miller of bright yellow males (Rosen, 1960, p. 91)].

Synapomorphies among *variatus*, *evelynae*, and *xiphidium*.

15. Vertical bars very well developed in some adult males of each species, and extending almost from dorsal to ventral margins of body in trunk region and anterior part of caudal peduncle (Rosen, 1960, figs. 6,7).
16. Two or more variably complete zigzag black midlateral stripes from opercular membrane to base of caudal peduncle, best developed in females.
17. Two or more oblique black lines extending downward from midlateral stripe just behind pectoral base.

Synapomorphy between *maculatus* and *milleri*.

18. Identity of two tail-pattern alleles (Kallman and Atz, 1967; Kallman, 1975).

Synapomorphies of *pygmaeus* and *nigrensis* with other swordtail species.

19. Ventral principal caudal fin rays noticeably prolonged in male to form a "sword" in all but one species (*pygmaeus*) in which the sword is present but short (see character 20).
20. Sword of male black edged in all but *pygmaeus* and the dwarf form of *nigrensis* [Kallman, personal commun., has found that sword development is suppressed in the rapidly differentiating (small) morph of *nigrensis* and that the black pigment present in the sword of the large morph is also suppressed; he has proposed that the absence of black pigment in the sword of its consistently small sister species, *pygmaeus*, is similarly explained].
21. Bony claw at tip of gonopodial ray 5a consistently present and, in most species, larger than those which appear sporadically in the

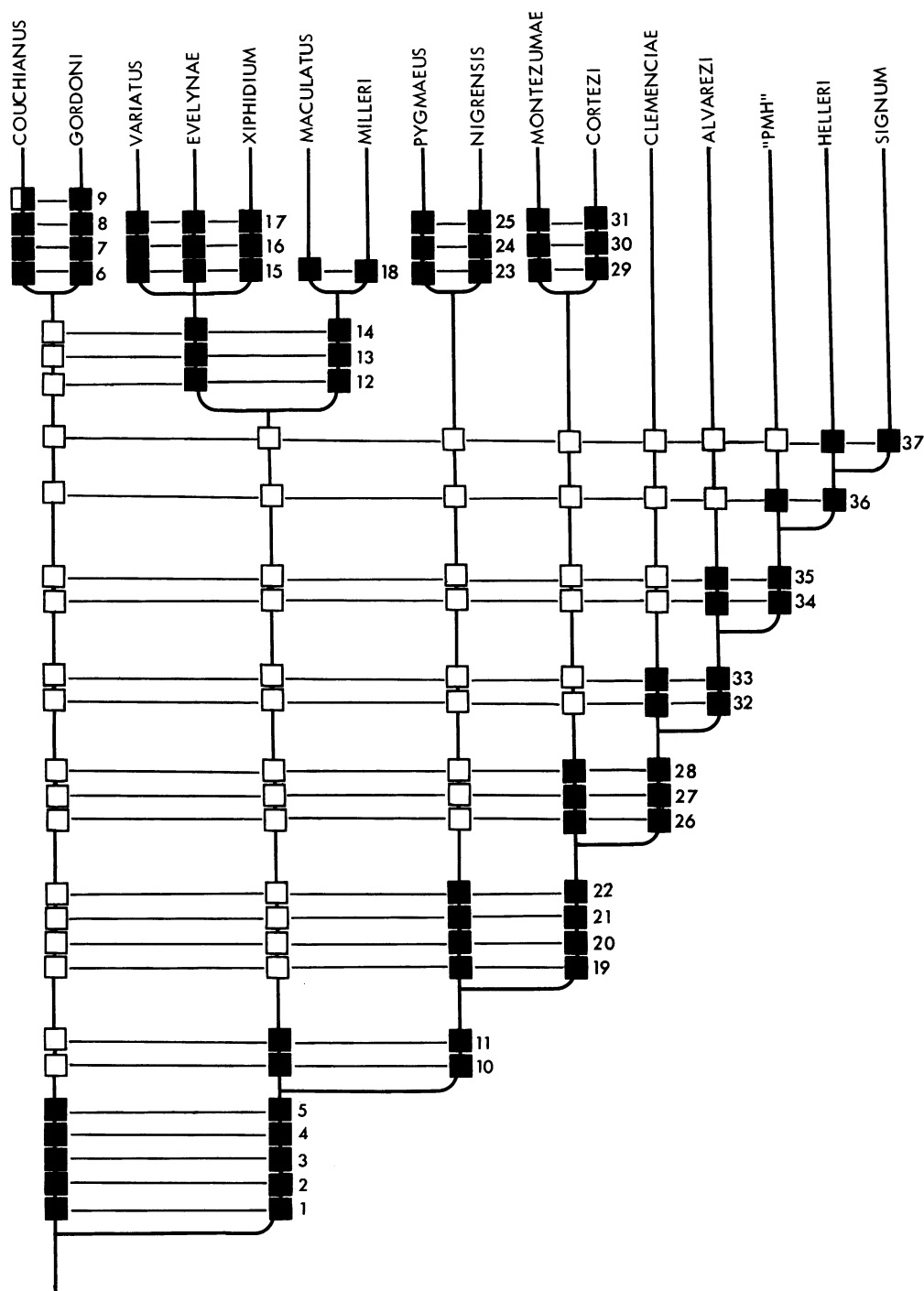


FIG. 37. Synapomorphy diagram for the species of *Xiphophorus*. Open squares represent the primitive states of a character (not indicated for some secondary and all tertiary branch points). The half-blackened square for character 9 indicates a somewhat ambiguous synapomorphy. Numbers 1-37 refer to numbered items of the synapomorphy scheme in text, pp. 347-350. Autapomorphies (unique defining characters of species) not shown here, but given in diagnoses of species in text.

preceding forms [compare figure 3 (in Rosen, 1960), figure 13 (in Rosen and Kallman, 1969), and figure 29 with figures 30 and 31 in this paper].

22. High mean lateral-line scale number (consistently 26.5 and over, as compared with 26.0 or less in other species).

Synapomorphies between *pygmaeus* and *nigrensis*.

23. Sides with a broad dark band or stripe from snout to caudal fin base separated by a clear space from an irregular row of dark blotches just below middorsal line.
24. Dorsal fin with a distinct narrow line of marginal dark pigment and a subbasal row of dark spots on the interradial membrane.
25. Claw at tip of gonopodial ray 5a small but sharply upturned distally and with its long axis extending obliquely away from the axis of ray 4p.

Synapomorphies of *montezumae* and *cortezii* with *clemenciae*, *alvarezi*, *helleri*, and *signum*.

26. Generally large body size (attaining a maximum standard length of 60 to 75 mm. as compared with a maximum of 40 to 45 mm. in all other species; Rosen, 1960, and see figures 27 to 29).
27. Caudal fin sword of male usually rather long and broad at its base, the sword length commonly more than half of the standard length of body and as long as the body in a few cases.
28. Caudal fin sword margined with black pigment above as well as below and, in most cases, strongly pigmented with yellow between the black margins.

Synapomorphies between *montezumae* and *cortezii*.

29. Caudal fin sword slightly to strongly turned up in most cases (figs. 38, 39).
30. Reticular pattern on sides well-developed above lateral line, poorly developed or absent below, and forming one or more strongly developed zigzag horizontal stripes bordering a scale row (figs. 38, 39).
31. Dorsal fin with two rows of dark spots on interradial membrane of proximal half of fin, the spots of the lower row streaklike and in some cases fusing with those of upper row (fig. 38; in figure 39 the upper row of spots is faded).

Synapomorphies of *clemenciae* with *alvarezi*, *helleri* and *signum*.

32. Midlateral band of dark or dusky pigment that is continuous with the dark dorsal pigment of the caudal fin sword in males.
33. Two or more stripes of red pigment following the scale rows on sides (red striping is interpreted as secondarily lost in *signum* and reduced in some of the northern populations of *helleri*).

Synapomorphies of *alvarezi* with *helleri* and *signum*.

34. In gonopodium, hook on ray 3 shortened and strongly decurved and recurved in some cases, the blade of granular tissue on inner side of hook elongated distally, the segments of the distal ramus of ray 4a somewhat enlarged at the point of the downward curvature over the blade on ray 3 (there appear to be two, or perhaps three, distinct traits involved here, but which are treated together as a single decisive synapomorphy).

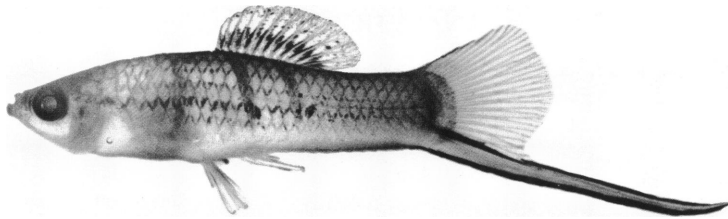


FIG. 38. Laboratory-reared male of *Xiphophorus montezumae* from the Río Salto de Agua, Río Panuco drainage, showing long, broad-based, double-margined sword with upturned tip, interlocking double row of spots on proximal half of dorsal fin, heavy reticulum on upper sides, and zigzag midlateral stripe (cf. fig. 39).

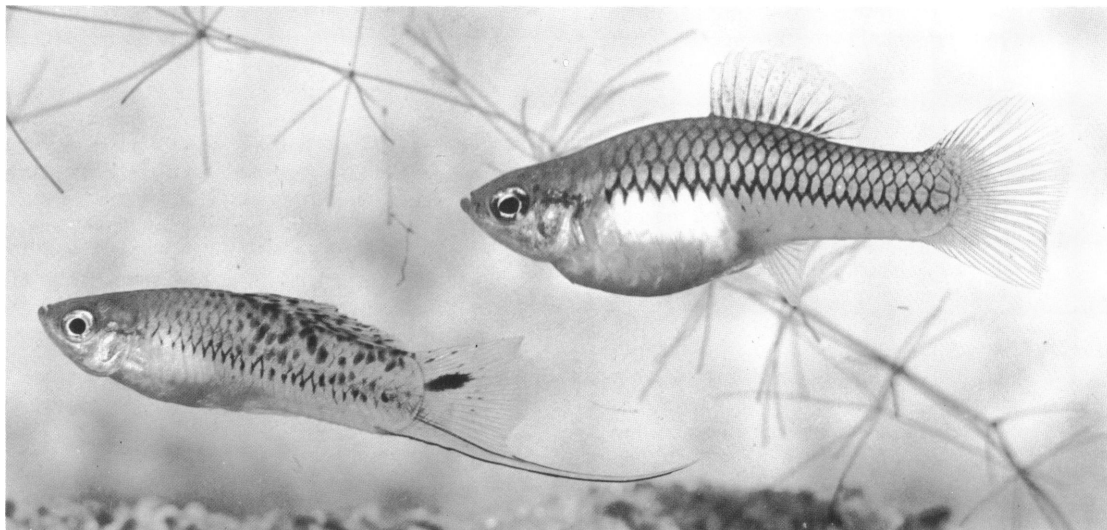


FIG. 39. Laboratory-reared male and female of *Xiphophorus cortezi* (cf. fig. 38). In dorsal fin of female, the upper of the two proximal rows of spots is poorly expressed but present.

35. Claw at tip of gonopodial ray 5a greatly enlarged, sharply pointed and extending well beyond tips of distal serrae on ray 4p.

Synapomorphy of swordtails of *helleri* type (identified below as "PMH," meaning from the Río Polochic, Río Motagua and Honduras) with *helleri* and *signum*.

36. Subdistal segments of downturned ramus of gonopodial ray 4a greatly enlarged and flared, and ramus somewhat angulate over bluntly pointed blade on ray 3 (fig. 32F).

Synapomorphy between *helleri* and *signum*.

37. Blade above hook on gonopodial ray 3 sharply pointed distally, and the overlying

ramus of ray 4a strongly angulate where it conforms with the pointed tip of the blade [as compared with the rounded ramus and bluntly rounded blade of *alvarezi* (figs. 32 G-J) and the somewhat angulate ramus and bluntly pointed blade of "PMH" swordtails (fig. 32F)].

Autapomorphous characters of the species.

These defining traits have been presented elsewhere in some detail (Rosen, 1960), and are not here included in the character-state tree (fig. 34). They are incorporated in abbreviated form in the key and species diagnoses which follow.

#### ANALYTICAL KEY

- A. Body distinctly bicolored, dark above and pale below midlateral line; without micromelanophore tail patterns or a caudal appendage or sword; with deep-lying (subdermal) dark dashes on sides; in gonopodium distal serrae on ray 4p converge at their tips and tips of spines on ray 3 are notched or denticulate.
- a. Vertebrae 28, rarely 27 or 29; dorsal fin rays 9, rarely 8 or 10; scales in lateral series 26, rarely 25 or 27; gill rakers on first arch 13 to 17, modally 15; distal serrae on gonopodial ray 4p strongly converging at their tips; Huasteca Canyon, Nuevo Leon, Mexico ..... *Xiphophorus couchianus* (Girard)
  - aa. Vertebrae 29, rarely 30; dorsal fin rays 11, rarely 10 or 12; scales in lateral series 26 or 27; gill rakers on first arch 15 to 19, modally 16 or 17; distal serrae on gonopodial ray 4p only slightly converging at their tips (Miller and Minckley, 1963, fig. 3B); Cuatro Ciénegas, Coahuila, Mexico ..... *Xiphophorus gordonii* Miller and Minckley
- AA. Body not strongly bicolored; with either micromelanophore tail patterns or macromelanophore fin and body patterns or both; with or without a caudal appendage; without subdermal dark markings on sides;

- in gonopodium, distal serrae of 4p erect, not converging, and tips of spines of ray 3 not notched (three or four proximal spines notched in *clemenciae*) .....B.
- B. With an array of polymorphic autosomal micromelanophore tail patterns or sex-linked macromelanophore fin and body patterns or both in all species; caudal fin in adult male rounded (with a small, pigmentless, ventral appendage in one species); in gonopodium, terminal segment on ray 5a simple .....b.
- b. Dorsal fin long-based, of 9 to 14, usually 10 to 12, rays .....b.1.
- b.1. Adult male with about five, very broad vertical bars on trunk and a short, spikelike, unpigmented caudal appendage; Río Soto la Marina, Tamaulipas, Mexico .....*Xiphophorus xiphidium* (Gordon).
- b.2. Adults with two or more zigzag black midlateral stripes and a few short, pale, vertical bars, or none; Río Panuco basin, Tamaulipas, south to Río Nautla, northern Veracruz, Mexico .....*Xiphophorus variatus* (Meek).
- b.3. Adult male with 8 to 12 close-set, slender, dusky to black, vertical bars along sides; depressed dorsal fin of male reaching almost to caudal base; headwaters above and below fall line of Río Tecolutla system, Puebla, Mexico .....*Xiphophorus evelynae* Rosen
- bb. Dorsal fin short-based, of 7 to 11, usually 9 or 10, rays .....bb.1.
- bb.1. Caudal peduncle deep; body robust and stocky; sides without prominent reticular network; ventral margin of caudal peduncle without black pigment; Río Jamapa, Veracruz, Mexico, southeastward through northern Guatemala to Belize *Xiphophorus maculatus* (Günther).
- bb.2. Caudal peduncle slender; body rather slender and attenuate; upper and lower sides with a prominent reticular network; ventral margin of caudal peduncle with a thin line of deep-lying dark pigment; Laguna Catemaco, Veracruz, Mexico *Xiphophorus milleri* Rosen.
- BB. Micromelanophore tail patterns monomorphic when present; caudal appendage (sword) present in adult male; a bony claw present on terminus of gonopodial ray 5a (when bony claw poorly developed in some individuals, caudal appendage large; when caudal appendage poorly developed in some very small individuals, a distinct bony claw present on gonopodial ray 5a) .....C.
- C. Caudal appendage (sword) of adult male variably developed and present in all but a few very small individuals, without a dorsal black margin; tip of small claw on gonopodial ray 5a turned strongly upward; dark pigment of upper sides separated by a clear area from midlateral dark band .....c.
- c. Caudal appendage (sword) of adult male, when present, small, colorless and spikelike; vertebrae 28, rarely 29; scales in lateral series 25 to 26, usually 26; dorsal fin rays 9 to 12, usually 11; Río Axtla, San Luis Potosí, Mexico .....*Xiphophorus pygmaeus* Hubbs and Gordon.
- cc. Caudal appendage (sword) always present in males; in small slender males spikelike and in some cases colorless and in larger deep-bodied males extending well beyond posterior margin of caudal fin and always bordered below by black pigment; vertebrae 29; scales in lateral series 25 to 28, usually 27; dorsal fin rays 11 to 14, usually 12; Ríos Choy and Coy, San Luis Potosí, Mexico .....*Xiphophorus nigrensis* Rosen
- CC. Caudal appendage (sword) of adult male always present and consistently two or more times the length of caudal fin rays immediately above sword, bordered above and below by black pigment .....D
- D. Reticular network always well-developed on sides; midlateral dark stripe, when present, not merging with black dorsal border of sword in adult .....d.
- d. Dorsal fin of adult male with a distinct median row of black spots on the interradial membrane; reticular network on sides forming darker, horizontal, zigzag lines; Río Tamesí, Tamaulipas and Río Salto de Agua (Río Panuco basin), San Luis Potosí, Mexico .....*Xiphophorus montezumae* Jordan and Snyder
- dd. Dorsal fin of adult male without a median row of black spots; reticular network on sides evenly developed, forming a darker zigzag line only at midside below lateral-line scales; Río Moctezuma (Río Panuco basin), Hidalgo and San Luis Potosí, Mexico .....*Xiphophorus cortezi* Rosen

- DD. Reticular network never well-developed on sides, never visible to the unaided eye as a distinct, prominent pattern; a dark or dusky midlateral stripe merging with black dorsal border of sword in adult male and one to several red stripes alternating with iridescent blue or green areas alongside (when red stripes are absent, the body is greenish or greenish gold and the midlateral dark stripe is present).....E.
- E. Dorsal fin with row of triangular black or dusky markings on the interradi al membrane of the proximal third of fin; caudal fin base with three to six red or orange spots; in adult male, a brownish or dusky stripe extending forward from ventral dark margin of sword across belly to below pectoral fin base; tips of proximal three or four spines on gonopodial ray 3 blunt, in some cases notched; dorsal fin rays 10 to 13, usually 11 or 12; Río Sarábia (Río Coatzacoalc os basin), Oaxaca, Mexico .....*Xiphophorus clemenciae* Alvarez
- EE. Dorsal fin with one, two or, rarely, three rows of red and black spots on interradi al membrane (except in *signum*); tips of spines on gonopodial ray 3 pointed; blade over hook on ray 3 extending well forward of decurved tip of hook; distal ramus of ray 4a with one or two enlarged corner segments where ray turns down around blade; a large clawlike segment terminating ray 5a, rising above level of tips of adjacent distal serrae on ray 4p; dorsal fin rays 11 to 17, usually 12 to 14 .....F.
- F. Blade over hook on gonopodial ray 3 broadly rounded; corner segments of distal ramus of ray 4a averaging about twice as high as long and well separated from bases of distal serrae on ray 4p; distal ramus of ray 4a gently curved around tip of blade; diffuse red or yellow pigment developing below midlateral scale row on belly and caudal peduncle of large adult males (red pigment is size-related in this and the following species); width of median scale between the supraorbital sections of the cephalic lateral-line system one-half or more the distance from anterior margin of this scale to posterior margin of next posterior median head scale; uplands of the Río Lacantún basin in Chiapas, Mexico, and El Quiché and Huehuetenango, and the Río Dolores of the Río Salinas basin and Río Candelaria Yalicar in Alta Verapaz, Guatemala .....*Xiphophorus alvarezii* Rosen
- FF. Blade over hook on gonopodial ray 3 sharply or bluntly pointed; corner segments of distal ramus of ray 4a more than twice as high as long and approaching closely or abutting distal serrae of ray 4p; distal ramus of ray 4a strongly hooked around tip of pointed blade; width of median scale between the supraorbital sections of the cephalic lateral-line system less than one half the distance from anterior margin of this scale to posterior margin of the next posterior median head scale .....G.
- G. Body color iridescent greenish gold, with a dark midlateral stripe but no red stripes; dorsal fin with a dusky bar across proximal third and without red or black spots; bases of second and third branched caudal rays (counting from bottom) with a distinct black mark in half-grown and adult females; dorsal fin noticeably higher in front, the upper surface of fin slightly concave; scales in lateral series 28; canals of cephalic lateral-line system on top of head very broad and completely enclosed; Río Chajmaic (Río de la Pasión system), Alta Verapaz, Guatemala .....*Xiphophorus signum* Rosen and Kallman
- GG. Body bluish or greenish with one or more red stripes (lacking in some northern populations), and with a dark or dusky midlateral stripe (often faint in forms heavily striped with red); dorsal fin with rows of black or red spots or both (greatly reduced as an individual variation); young and females without spot on caudal fin base; anterior and posterior dorsal fin rays subequal, (the posterior ones the longer in some adult males) and the dorsal border of the fin straight or convex; scales in a lateral series 26 to 28, rarely 25; canals of the cephalic lateral line system on top of head narrow, only the interorbital ones membrane-enclosed in many cases, but the postorbital section always open; Río Nautla, Veracruz, Mexico south-

eastward through northern Guatemala and Belize to Atlantic coastal Honduras ..... *Xiphophorus helleri* Heckel

## SYSTEMATIC ACCOUNT

### GENUS *XIPHOPHORUS* HECKEL

**DIAGNOSIS:** Poeciliid fishes less than 100 mm. in standard length showing a high degree of pigment polymorphism in often sex-linked (macromelanophore) and autosomal (micro-melanophore) body and fin patterns; marginal jaw dentition consisting of a row of delicate, depressible teeth with anteroposteriorly flattened distal halves; pelvic fin of male with fleshy appendage developed along distal third of first short, unbranched ray and second and third rays somewhat prolonged; in gonopodium of male (figs. 29-31), ray 3 terminated by a large, decurved hook supporting, and fused with, a bladelike structure of dense, calcified, granular tissue, and followed by a series of ovoid ossicles of subequal size and another series of sinuous or angulate ventrally directed spinelike segments; ray 4p of gonopodium terminated by two to eight upright (dorsally directed) serrae that are preceded by a series of cuboidal ossicles and, more proximally, by another longer series of slightly recumbent serrae.

**REMARKS:** The above diagnosis includes only derived characters that distinguish *Xiphophorus* from *Priapella* and other poeciliids (cf. more elaborate phenetic characterizations in Rosen, 1960; and Rosen and Bailey, 1963). The elaborate synonymies presented in those two publications are not repeated here, but, because most of the subspecies formerly recognized are here treated as species, basic synonymies are presented citing the original description of all trivial names.

**RANGE AND SPECIES COMPOSITION:** Fifteen species along the Atlantic slope of Middle America from the Río Grande basin southeast to Honduras (fig. 40).

#### *Xiphophorus couchianus* (Girard)

*Limia couchiana* Girard, 1859, p. 116 (Monterrey, Nuevo Leon, Mexico).

**DIAGNOSIS:** A strongly bicolored species (a dark reticulum above and no reticulum below the midlateral scale row); with a moderately developed zigzag midlateral stripe; short, heavy

vertical bars at midside; a variable number of deep-lying black spots in one to three rows on the caudal peduncle and flank where the myomeres are abruptly bent; the tips of some or all the proximal spines on gonopodial ray 3 notched; the distal serrae on gonopodial ray 4p strongly converging at their tips; vertebrae 27 to 29, modally 28; dorsal fin rays (last two counted as one) 8 to 10, modally 9; scales along midlateral scale row 25 to 27, modally 26; gill rakers on first arch 13 to 17, modally 15.

**GEOGRAPHY:** Springs, lagunas, and streams tributary to the Río San Juan (Río Grande basin) in the Huasteca Canyon near Santa Catarina and at Monterrey, Nuevo Leon, Mexico.

#### *Xiphophorus gordonii* Miller and Minckley

*Xiphophorus gordonii* Miller and Minckley, 1963, p. 538 (Cuatro Ciénegas basin, Coahuila, Mexico).

**DIAGNOSIS:** Body pigmentation and spines on gonopodial ray 3 as in *couchianus*, but distal serrae on gonopodial ray 4p converging or not at their tips (cf. Rosen, 1960, fig. 3A; Miller and Minckley, 1963, fig. 3; Rosen and Kallman, 1969, fig. 13); vertebrae 29 or 30, modally 29; dorsal fin rays 10 to 12, modally 11; scales along midlateral scale row 26 or 27; gill rakers on first arch 15 to 19, modally 16 or 17.

**REMARKS:** There are also some slight differences between *couchianus* and *gordonii* in pigmentation and the structure of the pectoral girdle, as discussed by Miller and Minckley (see also comparisons in Rosen and Kallman, 1969, and their figures 11 and 12, in which *gordonii* is regarded as a subspecies of *couchianus*).

**GEOGRAPHY:** Known only from the type locality.

#### *Xiphophorus variatus* (Meek)

*Platypoecilus variatus* Meek, 1904, pp. 146-147 (Valles, Río Panuco basin, San Luis Potosí, Mexico).

**DIAGNOSIS:** A species with a well-developed

reticular network both above and below midlateral scale row, two or more zigzag midlateral dark stripes, several vertical bars ("parr marks") when present about the width of two or three scale rows in height and one scale width in breadth, and with numerous polymorphic pigment patterns involving yellow dorsal and yellow, orange, and red caudal fins and micromelanophore and macromelanophore body and fin patterns; vertebrae 28 to 30, modally 28 or 29; dorsal fin rays 9 to 14, modally 11; mean head length of adults (measured from lower jaw tip to end of opercular membrane) more than 3.3 times in standard length; mean caudal peduncle length of adult females less than 2.6 times in standard length; mean caudal fin length more than 3.0 times in standard length.

**REMARKS:** As the trivial name implies, this is a variable taxon both because of the polymorphism within populations and because of differences in meristic, morphometric, and pigmentary features among the numerous allopatric populations along the considerable expanse of the Atlantic slope of Mexico from north of Tampico south to the middle latitude of Veracruz (Rosen, 1960). Its inter-river phenotypic variability is equaled only by that of *helleri*. Subsequent study may provide a basis for subdividing this taxon. Like almost all pigmentary features in *Xiphophorus*, the primary defining feature of populations referred here to *variatus* (the two or more zigzag midlateral dark stripes) is subject to some individual variation: (1) in some physiological states associated with a general paling of all melanophore patterns, the stripes may be difficult to detect, and (2) in the presence along the sides of intense macromelanophore spotting, the stripes, and all other melanophore patterns as well, are not expressed.

**GEOGRAPHY:** Independent Atlantic tributaries south of the Río Soto la Marina, Tamaulipas south to the Río Nautla in Veracruz at both high and low elevations.

*Xiphophorus xiphidium* (Gordon)

*Platyopocilus xiphidium* Gordon, 1932a, p. 287 (first mention of small caudal fin appendage or "sword"); 1932b, p. 89 (Río Soto la Marina).

**DIAGNOSIS:** A consistently deep-bodied species with the abdomen distinctly rounded in profile; zigzag midlateral striping when present pale and variably developed or replaced by a diffuse dusky band, and middle sides and caudal peduncle in many cases with irregular black speckling; older adult males in many cases with four or five broad blue-black vertical bars (two scales in width) extending from back halfway or more down abdomen or to ventral margin of peduncle below dorsal fin; adult males with a short, broad, pointed appendage ("sword") developed from the ventral angle of the caudal fin; vertebrae 27 or 28, usually the latter; dorsal fin rays 9 to 11, modally 10; mean head length of adults more than 3.3 times in standard length.

**GEOGRAPHY:** Río Soto la Marina, Tamaulipas, Mexico.

*Xiphophorus evelynae* Rosen

*Xiphophorus variatus evelynae* Rosen, 1960, p. 87 (Río Tecolutla system, Puebla, Mexico).

**DIAGNOSIS:** A species with a consistently present, but moderately developed reticular network along sides and in adults, with 8 to 12 slender, sharply delineated, close-set vertical bars extending from the back to ventral profile in anterior half of body; dorsal fin consistently with a basal row of dark spots on interradiation membrane; vertebrae 27 or 28, usually the latter; dorsal fin rays 11 to 14, modally 12 or 13; mean head length of adults less than 3.3 times in standard length; mean caudal peduncle length of adult females more than 2.6 times in standard length; mean caudal fin length less than 3.0 times in standard length.

**REMARKS:** Among platyfish species, *evelynae* is unique in lacking autosomal micromelanophore tail patterns. It has a speckled pattern along the sides composed of macromelanophores, however (Rosen, 1960). Its relationship to *variatus* and *xiphidium* is indicated by the development of strong, discrete vertical bars that anteriorly extend most or all of the distance across the sides. In *variatus*, strong bars are seldom present, but male individuals in some populations possess a few strong, wide bars of about three scale rows in height, and



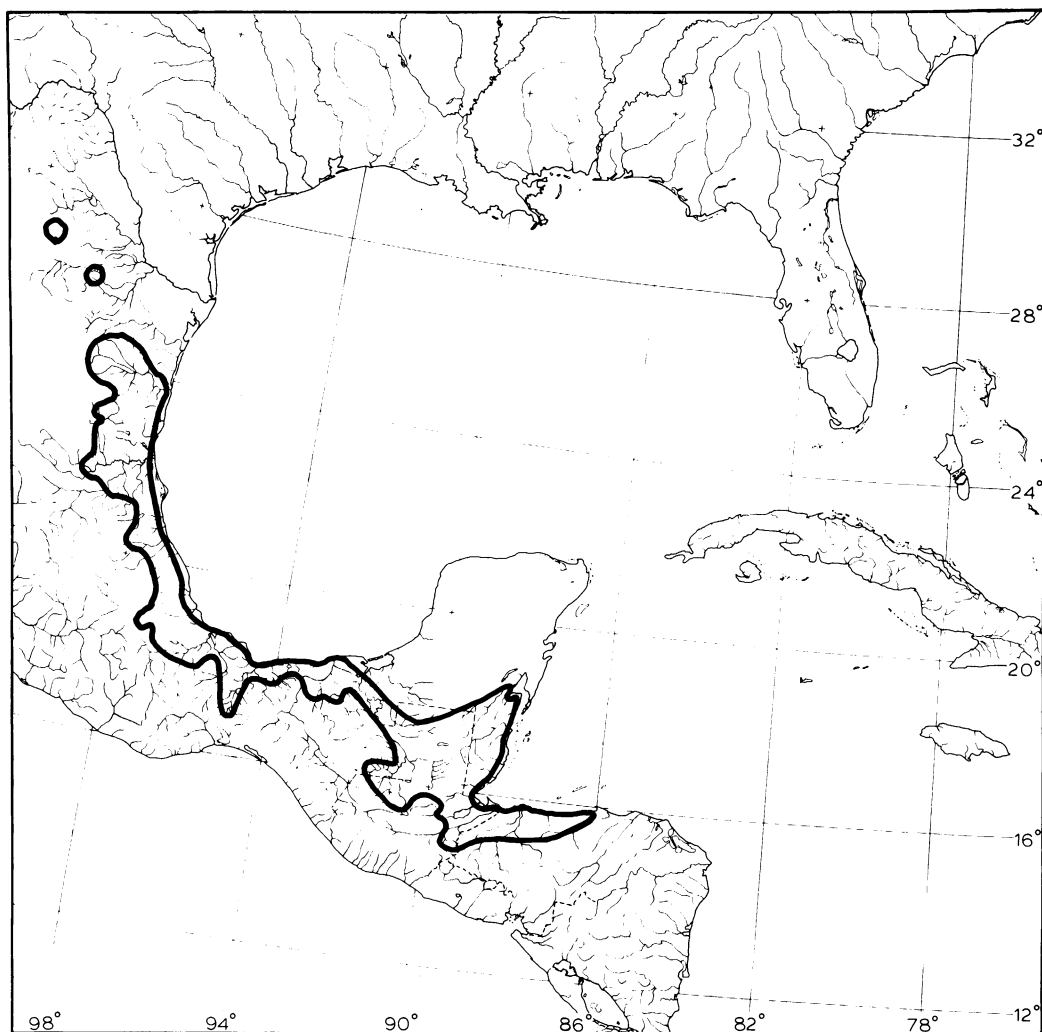


FIG. 40. Distribution of *Xiphophorus* in Río Grande and Middle American drainages.

many older males of *xiphidium* have a few even stronger, higher bars. Such bars occur elsewhere in the genus only in some *X. nigrensis*, but they are most strongly developed anteriorly in *variatus*, *xiphidium*, and *evelynae* and posteriorly in *nigrensis*. All these forms, formerly grouped within *variatus*, have a relatively high modal dorsal fin ray number among platyfishes (9 in *couchianus*, *gordoni*, and most populations of *maculatus*; 10 in *xiphidium*, 11 in

*variatus* and 12 or 13 in *evelynae*). *X. variatus* and *xiphidium* are, in turn, united by the presence of a small series of unique micromelanophore tail patterns (Rosen, 1960, p. 80), and *variatus* and *evelynae* are united by the presence in many individuals of intense yellow or yellow-orange pigment in the caudal fin, especially in its proximal half.

**GEOGRAPHY:** Known only from the type locality.

*Xiphophorus maculatus* (Günther)

*Platypoecilus maculatus* Günther, 1866, pp. 350-351 (Mexico).

**DIAGNOSIS:** A small, deep-bodied species with a faintly developed reticular pattern and no midlateral stripe, a more or less uniform dusky ground color, and a great variety of polymorphic macromelanophore and micromelanophore body and fin patterns; vertebrae 26 to 28, modally 27 or 28 (28 or 29 in other platys); dorsal fin rays 7 to 11, modally 9 or 10; lateral-line scales 22 to 25 (modally 26 in other platys); mean least depth of caudal peduncle less than 5.0 times in standard length (more than 5.0 times in other platys).

**GEOGRAPHY:** Río Jamapa basin, Veracruz, Mexico, southward at lower elevations to Belize and Guatemala.

*Xiphophorus milleri* Rosen

*Xiphophorus milleri* Rosen, 1960, p. 89 (Laguna Catemaco, Río Papaloapan basin, Veracruz, Mexico).

**DIAGNOSIS:** A small species with a slender, laterally compressed caudal peduncle, a reticular pattern well-developed on the trunk (except for the lower abdomen) and caudal peduncle, 6 to 8 dusky stripes along sides that follow the scale rows, a deep-lying ridge of black pigment midventrally on caudal peduncle, and a dorsal fin as high as long with a broad dusky band of marginal pigment and subbasal row of distinct black dashes paralleling the fin rays in the interradial membrane; distal serrae on gonopodial ray 4p large and numerous, 8 to 11 in number (as compared with a maximum of 8 in other platys and 6 in swordtails); vertebrae 28, rarely 29; dorsal fin rays 9 to 11, modally 10; lateral-line scales 25 to 27, modally 26.

**REMARKS:** The evidence regarding shared derived pigmentary and genetic characters in *milleri* and *maculatus* is discussed above in the synapomorphy scheme.

**GEOGRAPHY:** Known only from the type locality.

*Xiphophorus pygmaeus* Hubbs and Gordon.

*Xiphophorus pygmaeus* Hubbs and Gordon, 1943, pp. 31-33 (Río Axtla, Río Panuco basin, San Luis Potosí, Mexico).

**DIAGNOSIS:** A very small, slender species of swordtail (males 20 to 28 mm. in standard length) with a weakly developed male caudal appendage ("sword"), a striking pigment pattern on the sides consisting of a broad, dark band or stripe from snout to caudal fin base separated above by a clear space from an irregular row of dark blotches just below the mid-dorsal line, dorsal fin with a distinct narrow line of marginal dark pigment and a subbasal row of dark spots on the interradial membrane, a line of deep-lying dark pigment midventrally on the caudal peduncle; in gonopodium, 4 or 5 rather short, subtriangular distal serrae on ray 4p and a small, sharply upturned claw distally on ray 5a that extends slightly above the level of the tips of the adjacent distal serrae on ray 4p; vertebrae 28, rarely 29; dorsal fin rays 9 to 12, modally 10 or 11; lateral-line scales 25 or 26, modally 26.

**GEOGRAPHY:** Río Axtla, Río Moctezuma drainage, Río Panuco basin, San Luis Potosí, Mexico.

*Xiphophorus nigrensis* Rosen

*Xiphophorus pygmaeus nigrensis* Rosen, 1960, p. 100 (Río Choy, Río Panuco basin, San Luis Potosí, Mexico).

**DIAGNOSIS:** A species similar to *pygmaeus* but larger (20 to 42 mm. in standard length) and deeper bodied, male with a distinct caudal appendage equal to the caudal fin in length and bordered below by a line of black pigment, dark pigment on upper sides above clear area not forming a blotchy, irregular row and midlateral band dusky rather than dense (in dominant males all dark body pigment fades which brings out a brilliant blue iridescence); vertebrae 29; dorsal fin rays 11 to 14, modally 12; lateral-line scales 25 to 28, modally 27; mean greatest depth of body less than 4.0 times in standard length (instead of more than 4.0); mean least depth of caudal peduncle of males less than 5.0 times in standard length (instead of more); mean least depth of caudal peduncle in females less than 6.0 times in standard length (instead of more).

**REMARKS:** Males of this species show a great range in absolute size, the larger sibs (diagnosed above) averaging about 30 mm.

standard length and the smaller (described here) averaging about 20 mm.. The small males are similar to the above but have a short, spikelike sword in some cases without ventral pigment and are less deep bodied (as in *pygmaeus*). All pigmentary, gonopodial, and meristic traits are the same in both types of males except that dominant small males develop less blue iridescence, and that a micromelanophore tail pattern, caudal blotch, when genetically present in small males, is phenotypically poorly expressed.

Populations of *nigrens* from the Río Coy have distinctive males. Although indistinguishable from Río Choy fish in body proportions, metamerism and pigment patterns as given above, all Río Coy males also have a dark pigment spot behind and above the pectoral fin base and larger males have numerous, elongate, dark vertical bars along the sides. Additional study of these fish may reveal other differences between females from the Choy and Coy populations that would warrant the formal taxonomic recognition of another pygmy swordtail.

**GEOGRAPHY:** Río Choy and Río Coy and related northern tributaries of the Río Panuco basin, San Luis Potosí, Mexico.

*Xiphophorus montezumae* Jordan and Snyder

*Xiphophorus montezumae* Jordan and Snyder, 1900, pp. 131-133 (Río Verde near Rascon, San Luis Potosí, Mexico).

**DIAGNOSIS:** A species of swordtail with a strongly developed reticulum that forms several zigzag horizontal stripes above or below a scale row, the striping best developed below the midlateral scale row; male with a long caudal appendage ("sword") longer than the caudal fin in all but the smallest males, sword green or yellow, bordered above and below by black pigment and slightly upturned in some cases; dorsal fin with two rows of dark spots on interradial membrane of proximal (basal) half of fin.

**GEOGRAPHY:** Río Tamesí basin and northern tributaries of Río Panuco basin, San Luis Potosí, Mexico.

*Xiphophorus cortezi* Rosen

*Xiphophorus montezumae cortezi* Rosen, 1960, p. 96 (Río Moctezumae, Río Panuco basin, San Luis Potosí, Mexico).

**DIAGNOSIS:** A species similar to *montezumae* but with never more than one zigzag lateral stripe below the midlateral scale row and with the noticeably upturned "sword" in the male always delicate and very slender and only faintly black-edged above where it extends beyond caudal fin margin. In the samples studied by Rosen (1960), it is slightly longer headed than *montezumae* (table 17 in that report).

**GEOGRAPHY:** Southern tributaries of the Río Panuco basin, Hidalgo and San Luis Potosí, Mexico.

*Xiphophorus clemenciae* Alvarez

*Xiphophorus clemenciae* Alvarez, 1959, pp. 69-71 (Río Sarabia, Río Coatzacoalcos basin, Oaxaca, Mexico).

**DIAGNOSIS:** A small to moderate swordtail species with a well-developed yellowish caudal appendage that is conspicuously edged with black dorsally and ventrally, two continuous solid red lateral stripes extending from caudal base to opercle, a small black band between front of eye and lips, a well-developed dusky stripe in male extending from ventral margin of pectoral base posteriorly along belly to base of gonopodium or beyond, 3 to 6 small salmon-colored spots on scaled part of caudal fin base, dorsal fin with a row of triangular black or dusky markings on interradial membrane along its proximal third and a diffuse band of dusky pigment along its distal third; distal ramus of gonopodial ray 4a slender, but definitely hooked backward over bluntly pointed blade, extending slightly beyond tip of ray 4p; vertebrae 29, rarely 28; dorsal fin rays 10 to 13, modally 11 or 12; lateral-line scales 26 or 27, modally 27.

**GEOGRAPHY:** Known only from the Río Sarabia, the type locality.

*Xiphophorus alvarez* Rosen

Figures 31B-D, 32G-J, 33, 34A, 35, 41A, 42, 43

*Xiphophorus helleri alvarez* Rosen, 1960, p. 126 (Río Santo Domingo, Río Usumacinta basin, Chiapas, Mexico).

**DIAGNOSIS:** A swordtail species with a broad head and the supraorbital and postorbital sec-

tions of the cephalic lateral-line system forming broad, open troughs (fig. 34), two or more solid red lateral stripes along sides, the two midlateral stripes that border the lateral-line scales always present and separated by a band of turquoise blue in both sexes, the lower sides of abdomen and caudal peduncle of older males and females yellow or orange-yellow, dorsal fin with two rows of bright red spots on proximal and distal thirds of interradial membrane and caudal appendage as in *clemenciae*, *helleri*, and *signum*; ray 5a of gonopodium tipped by large clawlike element that rises well above the 3 to 5 short slender-tipped distal serrae on ray 4p, segments of distal ramus of ray 4a longer than high except where ramus curves down and back over elongate rounded blade on ray 3 below, the two or three corner segments at point of curvature with dorsal processes (table 13).

REMARKS: The Guatemalan populations, when first collected, were thought to represent an undescribed form, but they can not be

clearly separated from Chiapas specimens from the Río Santo Domingo previously described by me as *alvarezi*. The Río Santo Domingo sample contains only a few fish of relatively small size which are slender as compared with most Guatemalan individuals (fig. 42). Detailed laboratory comparisons have shown that some of the smaller specimens from the Río San Ramón and Río Dolores drainages in Guatemala are comparably slender. Nothing is known, however, about the life colors of Río Santo Domingo fish so that the present identification of Guatemalan material (fig. 41A) as *alvarezi* is only a best current estimate to be reviewed when more Mexican material comes to hand. A similar argument is used to include in *alvarezi* a male and three females from Laguna Ocotol Grande, also in Chiapas. The males from all these samples exhibit the same relatively primitive gonopodial characters of the ray 3 blade and ray 4a distal ramus (fig. 43) as given in the diagnosis and discussed above (pp. 336-338). The

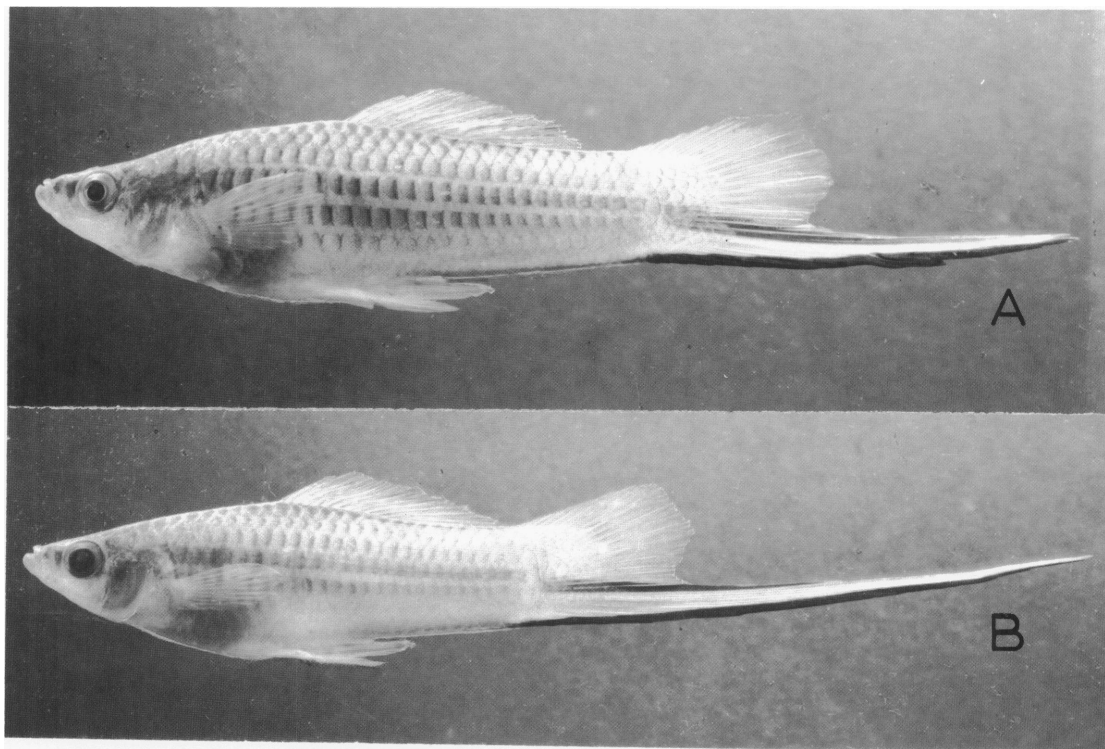


FIG. 41. Comparison of the generally short-sworded, multistriped *Xiphophorus alvarezi*, A, with the longer-sworded, fewer-striped *Xiphophorus helleri*, B. A, 59 mm. standard length, Río Candelaria Yalicar, AMNH 32912, and B, 55 mm., from the nearby upper Río San Simón, AMNH 36790. For localities, see figure 2.

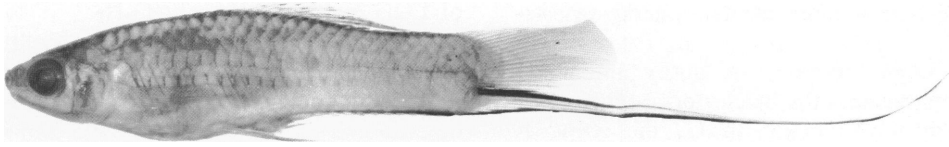


FIG. 42. Holotype of *Xiphophorus alvarezi*, UMMZ 177304, 39 mm. in standard length, from the Río Santo Domingo, Chiapas, Mexico.

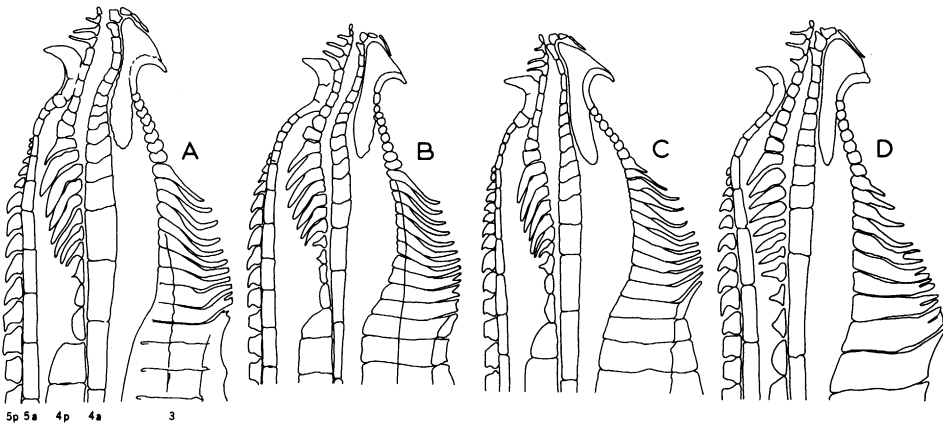


FIG. 43. Tips of gonopodia of *Xiphophorus alvarezi* from type series (A-C), Río Santo Domingo, compared with that of a male from Laguna Ocotol Grande (D), all from Chiapas, Mexico. A, holotype, UMMZ 177304. B, paratype, BMNH 12. 12. 1-2. C, paratype, UMMZ 160727. D, UMMZ 194965.

autapomorphic features that define the Guatemalan populations as a recognizable entity are pigmentary features (the midlateral blue band bordered by two red stripes and the development of yellow or orange coloring on the lower sides of older fish), and these features are unknown for both Chiapas samples. Both Chiapas localities are within the Río Lacantún system (tributary to the Río Usumacinta) as are the Río San Ramón samples from Guatemala. The Río Dolores samples in Guatemala are within the Río Salinas system and those from Río Candelaria Yalicar are either within the Río Salinas or Río de la Pasión systems (fig. 33). Eventual separate recognition of any of these populations would not alter the basic outlines of the proposed cladistic relationships since their gonopodial features are all more derived

than those of *clemenciae* and less so than those of *helleri* and *signum*, below.

That Mexican and Guatemalan samples might be found to represent recognizably different forms is indicated by the following 10 observations, based on the many (G) Guatemalan samples, the four fish from (LOG) Laguna Ocotol Grande (UMMZ 194965), and the five specimens from the (RSD) Río Santo Domingo (UMMZ 160727, 177304; BMNH 1950.12.12.1-2; 16 additional specimens are in a private collection as indicated in Rosen, 1960, p. 126).

1. In LOG, the body is darkly pigmented with melanophores and the reticulum is relatively well-developed, even below the midlateral scale row. In G and RSD, the body is lightly pigmented with melanophores and, al-

though the reticulum is not clearly evident, on each scale between the dorsum and the scale row below the midlateral one there is a broad, dusky crescent of pigment that is darkest posteriorly.

2. In LOG, there is a dusky midlateral stripe merging with the black dorsal pigment of the sword in the male. In G, the stripe is present or absent and in RSD it is absent.

3. In LOG, the supraorbital canals of the cephalic lateral-line system are only partially enclosed posteriorly by slender bridges of tissue, in G the canals are open in most cases, and in RSD they are open.

4. In LOG, the snout and head are very short (especially in the male); the head is longer but the snout is quite short in RSD, and both are longer in G. However, the LOG specimens are laboratory grown, although wild-caught as juveniles, and a foreshortened snout or pug-nosed condition is not rare in laboratory-reared fish. Moreover, both LOG and RSD are small as compared with most G and the possibility of size-related allometry in head proportions has not been investigated.

5. In RSD and G, the dorsal fin has distinct rows of spots and dusky marginal pigment, whereas in LOG the dorsal fin is darkly pigmented all over and shows only a faint indication of spotting. Some swordtail (*X. helleri*) populations, e.g., in the Río Coatzacoalcos in southern Mexico, lack dorsal fin spotting, however, and the dark ground color of the fin in LOG, as well as the relatively dark body pigment and strong midlateral stripe, may simply be indications that the fishes were maintained under laboratory conditions that enhanced all melanophore pigmentation.

6. In LOG, the first pelvic fin ray is as long as the second, whereas in RSD it is only half as long and in G one half to a third as long as the second.

7. In the gonopodium of LOG and RSD (fig. 43), the claw at the tip of ray 5a is relatively low and the distal serrae on ray 4p are three in number, short and have uniformly slender shafts arising from broad bases, whereas in most G the claw on ray 5a is high and the serrae on ray 4p are more numerous (4 or 5) and have heavy, tapering shafts (figs. 31

B-D, 32 G-J). Small specimens of G from the Río San Ramón system, however, have gonopodial claws and serrae resembling those of LOG and RSD (fig. 32 G-H).

8. The caudal appendage or "sword" in the male of LOG is twice as long as the caudal fin, is rather broad and tapers abruptly to a blunt tip. In G, the "sword" is also broad and abruptly tapering, but is two to three times as long as the caudal fin (fig. 41A). In RSD, however, the "sword" is four times the length of the caudal fin, very slender and tapers very gradually to a sharply-pointed, almost hairlike tip (fig. 42).

9. The dorsal fin rays (the last two rays counted as one) are 11 or 12 in RSD and LOG, and usually 13 in G.

10. The lateral-line scales (pitted scales of the midlateral scale row from the upper opercular margin to the end of the hypural plate in the caudal fin skeleton) are 26 or 27, usually 27, in RSD, and 27 or 28 in LOG and G.

Only additional specimens of RSD and LOG will make it possible to decide whether the above differences are consistent and representative of distinct natural populations or whether some or all are individual variations, or have been induced by very local environmental conditions (in the case of RSD) or laboratory conditions (in the case of LOG).

**MATERIAL:** *Río Usumacinta System, Mexico and Guatemala:*

*Río Lacantún drainage (Chiapas):* UMMZ 177304, Holotype *Xiphophorus helleri alvarezii* Rosen, 1960 (1 adult male, 39 mm.), UMMZ 160727 (2 adult male and female, 37-40 mm.), BMNH 1950.12.12. 1-2 (2 adult male and female, 42.5-43 mm.), Río Santo Domingo, 90 km. east of Comitán; UMMZ 194965 (4 adult male and females, 38-45 mm.), Laguna Ocotol Grande. (*Huehuetenango*): AMNH 32916 (143 young to adult males and females, 14-57 mm.), AMNH 36799, 36799SW (160 laboratory-reared young to adult males and females, 15.5-59 mm.), junction Río Espíritu and Río Negro into upper isolated section of Río San Ramón; AMNH 32141 (4 half-grown, to adult male and female, 30-44.5 mm.), Río San Ramón about 2-3 km. by air above subterranean channel; AMNH 32910 (1320 young to

adult males and females, 12-52 mm.), about midway along course of Río Chancolín, into upper isolated section of Río San Ramón; AMNH 32131 (3 subadult males to adult female, 42-49 mm.), UMMZ 193929 (2 adult male and female, 49-53 mm.), Río Ixcán, channel on east side of island above Finca Todos Santos, 18 km. east-northeast of Barillas. (*El Quiché*: AMNH 24570 (31 half-grown to adult male and females, 21-52 mm.), Río Xalbal, 1 km. south of Ixcán; AMNH 24583 (27 half-grown to adult male and females, 27-62 mm.), Río Negro into Río Xalbal, north of Ixcán.

*Río Candelaria Yalicar drainage, Guatemala (Alta Verapaz)*: AMNH 32912 (217 young to adult males and females, 13-61 mm.), Río Candelaria Yalicar, about midway along course; AMNH 36800, 36800 SW (148 laboratory-reared young to adult males and females, 7-59 mm.), about 2 km. upstream of Candelaria; AMNH 36798, 36798SW (100 young, to adult males and females, 12-67.5 mm.), at Candelaria.

*Río Salinas drainage, Guatemala (Alta Verapaz)*: AMNH 32124, 32124SW (213 young to adult males and females, 16-71 mm.), tributary of lower Río Dolores at Finca Agua Blanca; AMNH 36797 (31 half-grown to adult males and females, 24-59 mm.), outlet of small lagoon between Río Rociá Pemec and Río Canillá, due west of Finca Taquec Canguinic; AMNH 36796 (16 half-grown to adult males and females, 35.5-69.5 mm.), Río San Vicente Chitacal, near mouth in Río Dolores at San Vicente; AMNH 36801, 36801SW (46 laboratory-reared half-grown to adult males and females, 27.5-59 mm.), AMNH 24637 (327 young to adult males and females, 10-64 mm.), spring origin of isolated tributary with underground connection to Río Dolores at Cubilguitz.

**GEOGRAPHY:** Intermontane and upland basins of the Sierras in Chiapas, Mexico and Huehuetenango, El Quiché and Alta Verapaz, Guatemala of the Río Usumacinta watershed.

*?Xiphophorus alvarezii x Xiphophorus helleri*

**REMARKS:** Several samples (table 15; fig. 33) are interpreted here as representing secondary

intergrades between these two swordtails for the reasons discussed above (pp. 277-278 and 338-342)

**MATERIAL:** *Guatemala, Río Usumacinta System, Río Salinas drainage (Alta Verapaz)*: AMNH 25471 (1 female, 40 mm.), Arroyo Batzulup about 200 m. above mouth in Río Chixoy, 2 km. upstream of Rubelolom, lower end Islote Quita Camiso; AMNH 36795 (1 subadult male, 36 mm.), Río Senizo at Finca Temal. (*El Quiché*): AMNH 25354 (1 adult male, 36 mm.), Río Chixoy, behind island; AMNH 25407 (141 half-grown to adult males and females, 20-54 mm.), Arroyo de Dante, into upper Río Chixoy.

**LABORATORY HYBRIDS:** AMNH 36794 [40 laboratory hybrids, F<sub>1</sub> generation of *alvarezii* male (*Río Candelaria Yalicar drainage, Alta Verapaz*) x *helleri* female (*Belize River, Belize*), half-grown to adult males and females, 24.5-56 mm.].

#### *Xiphophorus* "PMH"

**REMARKS:** As discussed above (pp. 337-338) these fishes from the Río Polochic, Río Motagua and Honduras drainages (fig. 33) are clearly allied with *helleri* and *signum* in having the derived state of one gonopodial character (the distal ramus of ray 4a) but are more primitive than both in another (the height-length index of the blade on ray 3) (fig. 32 F; table 13). Additional samples, especially from Honduras, might clarify their status as a possibly separate entity from *helleri*.

**MATERIAL:** *Río Polochic drainage, Guatemala (Alta Verapaz)*: AMNH 31689 (2 subadult male and female, 33-36 mm.), bypass of the Polochic, 1.5 km. west of Pancajche; AMNH 36803 (3 subadult to adult males, 53-56 mm.), Río Juaquitún into Río Secón, 45 km. northeast of Panzós. (*Izabal*): AMNH 31603 (17 half-grown to adult males and females, 26-56 mm.), pool 12 miles from Río Dulce ferry, San Felipe-Sarstún Road.

*Lake Izabal drainage, Guatemala (Izabal)*: AMNH 31578 (1 half-grown, 34 mm.), Río Amatillo at Benque; AMNH 35001 (6 young, to adult male and female, 15-47 mm.), spring tributary to Río Amatillo at Benque.

*Bahía de Amatique drainage, Guatemala*

(*Izabal*): AMNH 1411 (1 half-grown 31 mm.), swamp stream 1 mile west of Puerto Barrios; AMNH 1392 (1 adult female, 59.5 mm.), sulphur river 3.5 miles west of Puerto Barrios.

*Río Motagua drainage, Guatemala (Izabal)*: AMNH 1400 (1 half-grown male, 25 mm.), AMNH 1403 (2 subadult to adult males, 37.5-51 mm.), AMNH 1436 (5 half-grown to adult female, 29.5-51.5 mm.), pond, swamp, and brook east of Los Amates; AMNH 32184 (27 young to adult males and females, 17-78 mm.), Río LaVegega at highway CA9 crossing, below Los Amates Rd.; AMNH 35151 (11 young to half-grown 9-32 mm.), stream at Aldea Campo Dos, Río Trimcheras. (*Chiquimula*): AMNH 36802 (17 young to adult males and females, 14.5-57 mm.), Río La Conquista at Quetzaltepeque. (*Zacapa*): AMNH 35140 (14 young to adult males and females, 19-61 mm.), Quebrada Juilín at highway CA9 crossing; AMNH 35153 (3 adult males and female, 43-52 mm.), downstream from Aldea Campo Dos, Río Trimcheras, at CA9 crossing, Km 218; AMNH 35128 (10 young to half-grown, 16-34 mm.), Río Matasano at CA9, Km 17. *Honduras (Copán)*: UMMZ 188159 (6 half-grown to adult male and females, 27-49 mm.), Río Copán below ruins.

*Río Chamelecon drainage, Honduras (Cortés)*: UMMZ 189556 (2 adult male and female, 63-76 mm.), Río Armenta, north of San Pedro Sula, Choloma Road.

*Gulf of Honduras drainage, Honduras (Cortés)*: UMMZ 189559 (67 half-grown to adult male and females, 22-52 mm.), brook at Veracruz.

*Río Lancetilla drainage, Honduras (Atlántida)*: UMMZ 189558 (4 adult males and female, 66-80 mm.), AMNH 36804 (3 adult male and females, 36.5-72 mm.), ANSP 85046 (1 adult male, 39.5 mm.), pond at Lancetilla, 5 km. south of Tela.

*Xiphophorus helleri* Heckel

Figures 31 E, F; 32 A-E; 33; 34 B; 36; 41 B

*Xiphophorus helleri* Heckel, 1848, p. 291 (Orizaba, Veracruz, Mexico).

**DIAGNOSIS:** A species similar to *alvarezii*, but with a slightly narrower head and with the

supraorbital section of the cephalic lateral-line system less broad and canal-enclosed in most cases (fig. 34), without a blue band on the midlateral scale row bordered above and below by red stripes in females and without the consistent development of yellow or orange pigment on the lower sides in older fish; the distal ramus of gonopodial ray 4a consistently with heavy, flared corner segments and, in most cases with the more proximal segments as high as long and the distal end of the elongate blade on ray 3 distinctly pointed (table 13).

**REMARKS:** As noted by Rosen (1960), this species, now excluding *alvarezii* and possibly also the populations of the Río Polochic, Río Motagua and Honduras, shows striking geographic variation from north (in the Río Nautla) southward to Guatemala. Some of the geographic variation was previously used to define taxa (Rosen, 1960): *helleri helleri*, Río Nautla south to Río Jamapa, Veracruz, Mexico (defined by a black or dusky, rather than red, midlateral stripe, an axillary stripe on the lower abdomen, a short caudal fin, few distal serrae on gonopodial ray 4p, and relatively high vertebral and scale counts); *helleri strigatus*, Río Papaloapan and Río Coatzacoalcos, Veracruz and Oaxaca, Mexico (defined by a dark red stripe at midside and several short vertical bars); and *helleri guentheri*, Río Grijalva and Río Usumacinta in southern Mexico and Guatemala and the rivers of Belize (defined by multiple red stripes on the side and a higher average dorsal fin ray count). Review of collections made since 1960 has shown that some of the defining characters of these groups are not diagnostic of all the populations included in each taxon and that the geographic boundaries between taxa may not be as precise as understood formerly. Of the defining features listed above, I would expect only some of the ones that are characteristic of the northern samples (*helleri helleri*) to remain valid (caudal fin length and high vertebral and lateral-line scale number). The problem needs further study, however, and this is outside the objectives of the present review. Since available evidence nevertheless indicates that all populations are in some manner interrelated, they are treated here as a single operational taxon, *helleri*.



**MATERIAL:** *Río Atoyac-Río Jamapa drainage, Mexico (Veracruz):* UMMZ 183897 (39 young to adult males and females, 12-61 mm.), Río Sinvato above Estación Tezonapa, south-east of Orizaba; UMMZ 196676 (70 half-grown to adult males and females, 20-60 mm.), tributary to Río Metlac, near north edge of Fortín; UMMZ 181308 (173 young to adult males and females, 12-62 mm.), creek at Naranja Shangrila, west edge of Cordoba; UMMZ 183895 (178 young to adult males and females, 12-74 mm.), Río Atoyac at Atoyac.

*Lago Santecomapan drainage, Mexico (Veracruz):* AMNH 20499 (10 young to subadult female, 14.5-34 mm.), Río Santecomapan, Santecomapan, 10 miles by road east of Catemaco.

*Laguna Catemaco drainage, Mexico (Veracruz):* UMMZ 184555 (41 half grown to adult males and females, 23-67 mm.), tributary to west side of the lagoon, 1.5 miles south of Catemaco.

*Río Papaloapan drainage, Mexico (Veracruz):* UMMZ 196672 (25 young to adult males and females, 17-53 mm.), Arroyo Obispo, route 147, 7 miles southeast of turnoff from Tuxtepec-Oaxaca Hwy.; UMMZ 183893, AMNH 36793SW (106 half-grown to adult males and females, 21-56 mm.), irrigation ditch at Rancho Sierra de Agua, southwest of Orizaba. (*Oaxaca*): UMMZ 124253 (7 subadult to adult male and females, 33-57 mm.), lagoon beside Río Papaloapan, 3 km. north of San Bartolo; UMMZ 124236 (60 half-grown to adult male and females 21-72.5 mm.), lagoon and pool 4 km. south of Papaloapan at Km 149 on railroad; UMMZ 124217 (19 half-grown to adult male and females, 26-50 mm.), Arroyo Zacatispan and lagoon, 4.5 km. south of Papaloapan.

*Río Coatzacoalcas drainage, Mexico (Oaxaca):* UMMZ 183912, 183913 (20 half-grown to adult male and females, 32-49 mm.), small tributary to Río Sarabia, 67 miles south of Acayucan, Veracruz; UMMZ 180631, AMNH 36791SW (42 half-grown to adult males and females, 21-52 mm.), Río Sarabia and small tributary on Trans-Isthmian Hwy., about 75 miles south of Acayucan.

*Río Grijalva drainage, Mexico (Tabasco):* UMMZ 202384, AMNH 36792SW (97 young

to adult males and females, 19-54.5 mm.), spring at Teapa; UMMZ 202386 (4 half-grown to adult males, 22-45 mm.) Arroyo Huasteca, 28 km. from Villahermosa to Teapa; UMMZ 202385 (1 adult male, 54 mm.), Hacienda de Santa Ana, ditch 39 km. from Villahermosa to Teapa. (*Chiapas*): AMNH 24650 (3 young 12-16 mm.), sulfur stream at Baños del Azufre.

*Río Usumacinta System, Río de la Pasión drainage, Guatemala (Alta Verapaz):* AMNH 36790, 36790SW (63 young to adult males and females, 14-68 mm.), upper isolated section of Río San Simón, 6 km. due west of Chisec; AMNH 32127 (44 young to adult male and females, 10-66 mm.), main isolated section of Río San Simón, 7 km. northeast of Chisec; AMNH 24642 (9 young to adult males and females, 14-50 mm.), upper isolated section of Río San Simón, 1 km. north of Chisec; AMNH 27672 (8 half-grown to adult females, 21-47 mm.), arroyo 8 km. east of Sebol; AMNH 27673 (3 half-grown to adult females, 21-41 mm.), westward flowing tributary 8 km. downstream of Sebol; AMNH 27676, 27676SW (94 young to adult males and females, 17-51 mm.), swamp west of Sebol, near banks of the Pasión; AMNH 27674 (3 half-grown to subadult males, 26-42 mm.), tributary to Río Chajmaic Cajbón 0.5 km. from junction with the Pasión. (*Petén*): AMNH 18833 (19 young to adult male and females, 19-35.5 mm.), spring tributary at Santo Toribio; AMNH 36789 (35 young to subadult male, 17-32.5 mm.), Arroyo La Puente, 42 km. north-northwest of Poptún on Flores Rd.; AMNH 36788 (27 half-grown to adult males and females, 20-39 mm.), Arroyo Boca del Monte, 18 km. north of Poptún on Flores Rd.; AMNH 32394 (47 young to adult males and females, 12-40 mm.), spring 2 km. east of Santo Toribio; AMNH 25616 (2 adult females, 39-40 mm.), Arroyo El Porvenir, 8 km. above mouth in the Pasión. *Río Salinas drainage, Guatemala (Alta Verapaz):* AMNH 25267 (19 half-grown to adult males and females, 22-48 mm.), Arroyo Chiquibul, downstream from campsite on the Río Ixvolay; AMNH 25327 (17 half-grown to adult males and females, 23-46 mm.), Arroyo de Laguneta Río Viejo from the Laguneta to the Río Chixoy. (*Petén*): AMNH 25246 (22 half-grown

to subadult, 18-34 mm.), arroyo 44 km. upstream of Laguna Ronpiro, on Mexican side of river; AMNH 25515 (2 half-grown 23-28 mm.), Arroyo Caribe, 250 m. above mouth in the Salinas. (*El Quiché*): AMNH 25281 (67 half-grown to adult male and female, 22-44 mm.), Arroyo Lechugal, below mouth of Río Icvolay on Río Chixoy; AMNH 25445 (1 half-grown 23 mm.), Arroyo Cancaná, about 1 km. above mouth in Río Chixoy.

*Laguna Yalnabaj drainage, Guatemala (Huehuetenango)*: AMNH 32107 (107 young to adult males and females, 10-36 mm.), southeast corner of the lagoon.

*Río Hondo drainage, Guatemala (Petén)*: AMNH 32365 (4 subadult males, 38-50 mm.), Naranjal Reservoir, Tikal.

*Belize River drainage, Guatemala (Petén)*: AMNH 32393 (80 young to adult males and females, 13-40 mm.), Río Santo Domingo, about 10 miles southeast of Santo Toribio; AMNH 32277 (2 half-grown male and female, 31-36 mm.), Arroyo Sal Si Puedes, above mouth into Río Mopán on turnoff from Flores-Melchor Road.

*Gulf of Honduras drainage, Belize (Stann Creek Distr.)*: AMNH 24602 (25 young to adult males and females, 17-75 mm.), southeast of Waha Leaf, in Waha Leaf Creek; (*Toledo Distr.*): AMNH 24596 (33 young to adult males and females, 19-62 mm.), stream tributary to Mango Creek, about 5 miles by river from coast.

*Río Moho drainage, Guatemala (Petén)*: AMNH 35053 (1 half-grown male, 42 mm.), Río Pusilá at Balam, 6 km. east of Poptún Rd., Muquilá.

*Río Sarstún drainage, Guatemala (Petén)*: AMNH 32074 (338 young to adult males and females, 8-62 mm.), arroyo 35 km. south-southeast of San Luis, Km 153 on Flores-Sarstún Rd.; AMNH 36787 (2 half-grown to subadult, 21-38 mm.), Quebrada Seca below Flores-Sarstún Rd., Km 155, 56 km. south-southeast of Poptún; AMNH 31593, 31593SW (98 subadult to adult males and females, 40-73 mm.), arroyo on Sarstún Island between Río San Pedro and Río Sarstún, on Poptún-Morales Road. (*Izabal*): AMNH 35060 (1 half-grown, 20 mm.), Río Nimblaja, 1 km. above mouth in the Sarstún.

**GEOGRAPHY**: Río Nautla, Veracruz, Mexico, south to Belize at high and low elevations.

*Xiphophorus signum* Rosen and Kallman

Figures 33, 34C, 44

*Xiphophorus helleri signum* Rosen and Kallman, 1969, p. 5 (Río Chajmaic, Río de la Pasión basin, Alta Verapaz, Guatemala).

**DIAGNOSIS**: a species similar to *helleri*, but with a narrower head and the cephalic lateral-line system usually entirely canal-enclosed (fig. 34C), a high, triangular dorsal fin in which the anterior rays are much longer than posterior ones to give the fin a falcate appearance when not fully erect, a shorter and more spikelike caudal appendage ("sword") in male, a uniform greenish gold ground color, a dark brown to dusky midlateral stripe, an elongate black spot on lower caudal fin base in female and half-grown individuals that corresponds in position with a broad posterodorsal black margin on the "sword" of the male, dorsal fin color pattern consisting of a row of vertical dusky markings on interradiial membrane of proximal third of the fin and a broad marginal band of dusky pigment; dorsal fin rays 12 or 13 (instead of modally 13 or 14 as in southern *helleri*); lateral-line scales 28 (instead of modally 26 or 27 as in southern *helleri*).

**MATERIAL**: *Río Usumacinta System, Río de la Pasión drainage, Guatemala (Alta Verapaz)*: AMNH 27675, Holotype *Xiphophorus helleri signum* Rosen and Kallman, 1969 (1 adult male, 63.2 mm.), AMNH 27671, 27671SW, Paratypes *X. helleri signum* (413 young to adult males and females, 9.5-70 mm.), AMNH 35802 (153 laboratory-reared, young to adult males and female, 14-63.5 mm.), tributary to Río Chajmaic, 15 km. by road south of Sebol; AMNH 27677, Paratypes *X. helleri signum* (18 young to half-grown 19-37 mm.), second arroyo above mouth Río Semococh into Río Chajmaic; AMNH 27678, Paratypes *X. helleri signum* (551 young to half-grown, 14-35 mm.), pool about 13 km. southwest of Sebol.

**GEOGRAPHY**: Known only from the type locality (fig. 33).

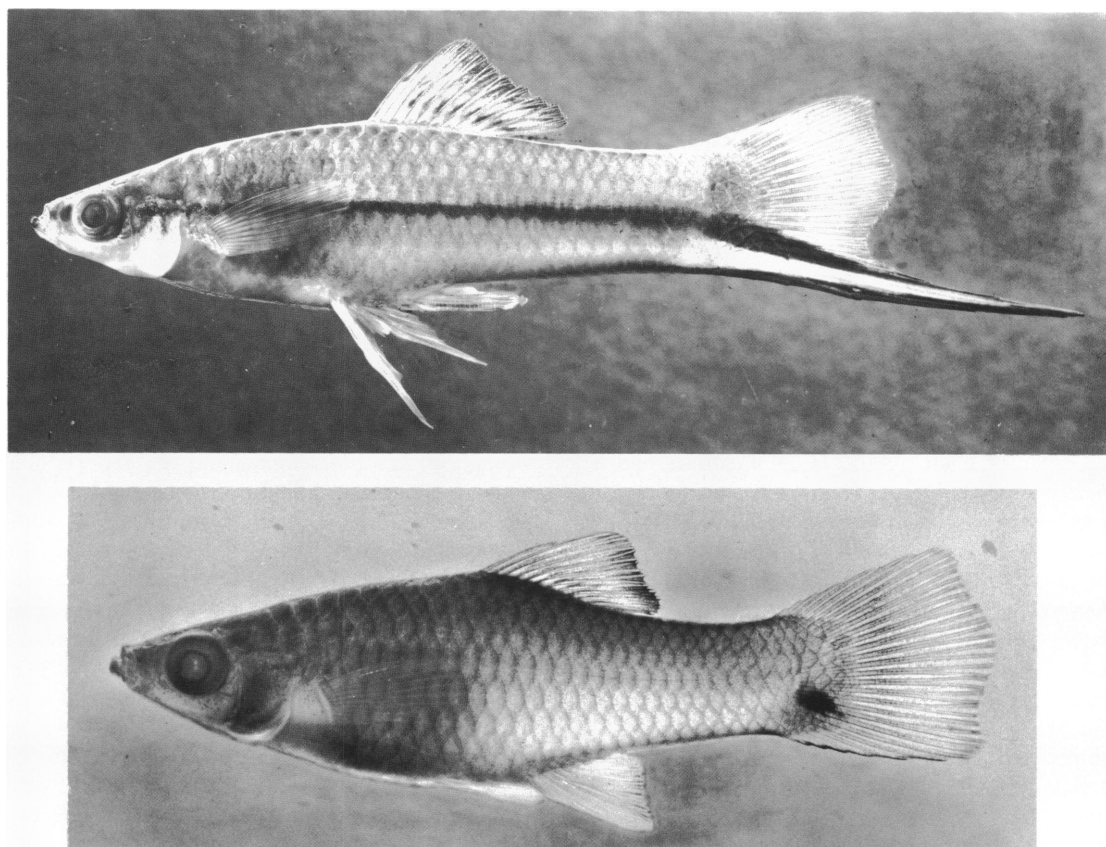


FIG. 44. Male, above, and female, below, of *Xiphophorus signum*. Laboratory reared.

## COMPARISONS OF *HETERANDRIA* AND *XIPHOPHORUS* AND GENERAL SUMMARY

### POINTS OF GEOGRAPHIC SIMILARITY

(1) *Taxa in isolated karst basins (Río Usamacinta watershed) of the Sierran foothills of Guatemala.* Each genus has a species present in the western karst basins, the Río San Ramón (Río Lacantún drainage) and Río Dolores (Río Salinas drainage): *Heterandria obliqua* (figs. 24, 26) and *Xiphophorus alvarezi* (fig. 33). Populations in the karst region of Chiapas, Mexico, tentatively considered conspecific with Guatemala *X. alvarezi*, are in the Río Santo Domingo (the type locality of *alvarezi*) and Laguna Ocotol Grande. The latter locality apparently is an isolated lake (Paynter, 1957) and

the former is a high elevation tributary, 1500 feet above sea level (Rosen, 1960) that may be isolated by rapids from the main river (World Aeronautical Chart, Operational Navigation Chart J-25); both are within the Río Lacantún drainage area. A small stream of a few hundred yards extent at Cubilguitz, Alta Verapaz, Guatemala, is surrounded by other streams of the Río Dolores complex, but is isolated from them by a subterranean digression only another few hundred yards from the mainstream of the Río Dolores; it contains both *H. obliqua* and a slightly differentiated population of *X. alvarezi*. Northwest of the mainstream of the Río Dolo-

res, but within the latitudinal and longitudinal limits of the latter, there is an oval Candelaria valley containing a small, shallow, muddy, meandering southern stream of about 1 mile in extent, the Río Chiaín (not collected) and the larger, northern stream of about 7 miles in length, the Río Candelaria Yalicar, from which have been collected *X. alvarezi* and another very distinct form, *H. attenuata* (the plesiomorph sister group of all other Middle American *Heterandria*). Both genera also have endemic species in a more easterly basin, the Río Chajmaic (Río de la Pasión drainage): *H. dirempta* and *X. signum*. These two forms are most closely related to the most widespread member of each genus, *H. bimaculata* and *X. helleri*, respectively. Apparently, secondary intergrades (hybrids) occur in the upper Río Salinas (=Chixoy or Negro) between *H. bimaculata* and *H. obliqua* and between *X. helleri* and *X. alvarezi*. All the isolated karst basins so far mentioned have subterranean digression; another isolated stream in the karst region of Alta Verapaz, Guatemala, the Río Sachicha, is separated from its effluent into the upper Río Salinas (the Río Senizo) by a ribbon fall of 80 to 100 m. in height and has an endemic *Heterandria*, *H. cataractae*, but no *Xiphophorus*. *Heterandria*, thus, has two unique elements, endemic taxa in the Río Candelaria Yalicar and Río Sachicha, but both *Heterandria* and *Xiphophorus* have the populations in the isolated and, from each other, geographically remote basins of the two main western Río Usumacinta tributaries (Río Lacantún and Río Salinas) more closely related to each other than either is to the endemic representatives in the isolated basin of the eastern tributary, the Río de la Pasión.

(2) *Endemic taxa in other, non-karst, regions of North and Middle America*. Both genera have one or more distinct forms north of the Río San Fernando in Tamaulipas and Nuevo Leon, Mexico: *Heterandria* has a minute representative, *H. formosa*, that is widespread in the southeastern United States (fig. 22), and *Xiphophorus* has a species pair, *X. couchianus* and *X. gordonii*, from the Río Grande watershed in northern Mexico (fig. 40).

*X. couchianus* is confined to spring-fed pools near Monterrey (Nuevo Leon), and *X. gordonii* is confined to the isolated lagunas of the intermontane Cuatro Ciénegas basin (Coahuila). Both *H. formosa* and the *Xiphophorus* species pair are the plesiomorph sister group of all other members of their respective genera. Both genera also have one or more endemic taxa in the Río Panuco watershed and in waters somewhat north and south of it (fig. 45): *H. jonesi* and *X. xiphidium*, *X. variatus*, *X. evelynae*, *X. pygmaeus*, *X. nigrensis*, *X. montezumae*, and *X. cortezi*. Just south of these taxa and slightly overlapping them in distribution, each genus is represented by a widespread species (or species complex), *H. bimaculata* and *X. helleri*, that extends along the Atlantic versant of Mexico to the base of the Yucatan Peninsula in Mexico, Guatemala and Belize (a few specimens of *H. bimaculata* have also been taken in northwestern Honduras) (figs. 45-47). Finally, both genera have differentiated forms in the rivers that drain into the Gulf of Honduras (Bay of Amatique): within *Heterandria*, two species are recognized, one from the Río Polochic watershed area, *H. litoperas*, and another from the Río Motagua (and Río Lempa, see below) and Atlantic streams and rivers of Honduras and Northern Nicaragua, *H. anzuetoii* (figs. 25, 46); within *Xiphophorus* (figs. 33, 47), the populations from the Río Polochic, Río Motagua, and northern Honduras are slightly different from, but are most closely related to the species pair, *X. helleri* and *X. signum*, and are described above as *Xiphophorus* "PMH." The possibility is suggested that *H. anzuetoii* populations might ultimately be divisible into two entities, those from the Río Motagua (and Río Lempa) and those from Honduras and Nicaragua.

#### POINTS OF GEOGRAPHIC DISSIMILARITY

(1) *Northernmost elements north of Río San Fernando*. Although the Río San Fernando seems to mark a boundary between North and Middle American distributions, the North American representative of *Heterandria*, as noted above, is confined to the eastern United

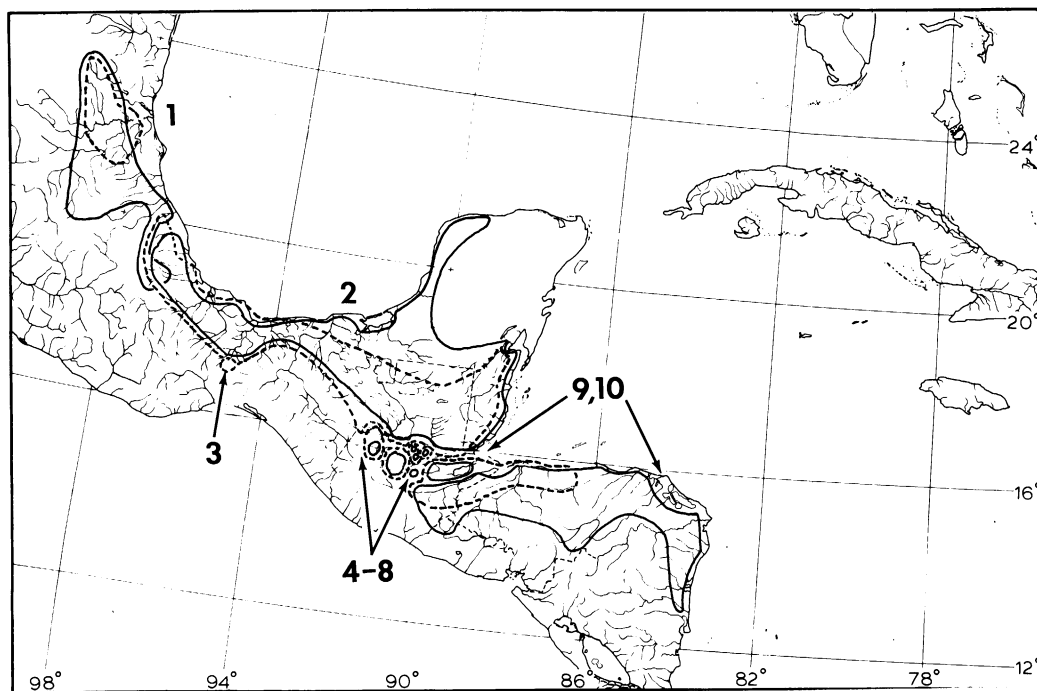


FIG. 45. Comparison of the distributions of species of *Xiphophorus* (dashed; swordtails only) and *Heterandria* (solid) in Middle America. Numbers refer to regions defined by the occurrence of taxa. See text.

States and the northern species pair of *Xiphophorus* to the west on the Mexican side of the Río Grande watershed.

(2) *Two distinct, overlapping sections of genus south of Río San Fernando.* In *Xiphophorus*, the two major lineages, of platyfishes (*xiphidium*, *evelynae*, *variatus*, *maculatus*, *milleri*) and swordtails (*pygmaeus*, *nigrensis*, *montezumae*, *cortezi*, *clemenciae*, *alvarezi*, *signum*, *helleri*), have roughly coincident distributions although platyfishes occur somewhat farther north in the Río Soto la Marina (*xiphidium*) and swordtails somewhat farther south in Honduras (*Xiphophorus* "PMH") (Rosen, 1960, figs. 4, 10, 19). The only aspect of *Heterandria* somewhat comparable with this is the occurrence of *H. attenuata*, the sister taxon to all other Middle American *Heterandria*, within the distributional limits of, and surrounded by, several other congeners in the Sierran foothills of Guatemala (fig. 26).

The difference between the two genera in this regard is that *H. attenuata* is entirely allopatric to other species and, within *Xiphophorus*, the platyfishes and swordtails, as two integral groups of many species, are broadly sympatric. Taken at face value, these two situations seem to call for two different explanations: a persistent history of allopatry in *Heterandria* and a history of sympatry resulting from dispersal of one species ancestral to the platyfishes and another ancestral to the swordtails prior to the differentiation of each into its numerous descendant species.

(3) *Number of recognized species in the region around and including the Río Panuco basin.* Only a single species of *Heterandria*, *H. jonesi*, is known so far, whereas seven are known for *Xiphophorus* of which five occur within the Río Panuco watershed itself (see above).

(4) *Endemic taxa in Río Papaloapan and*

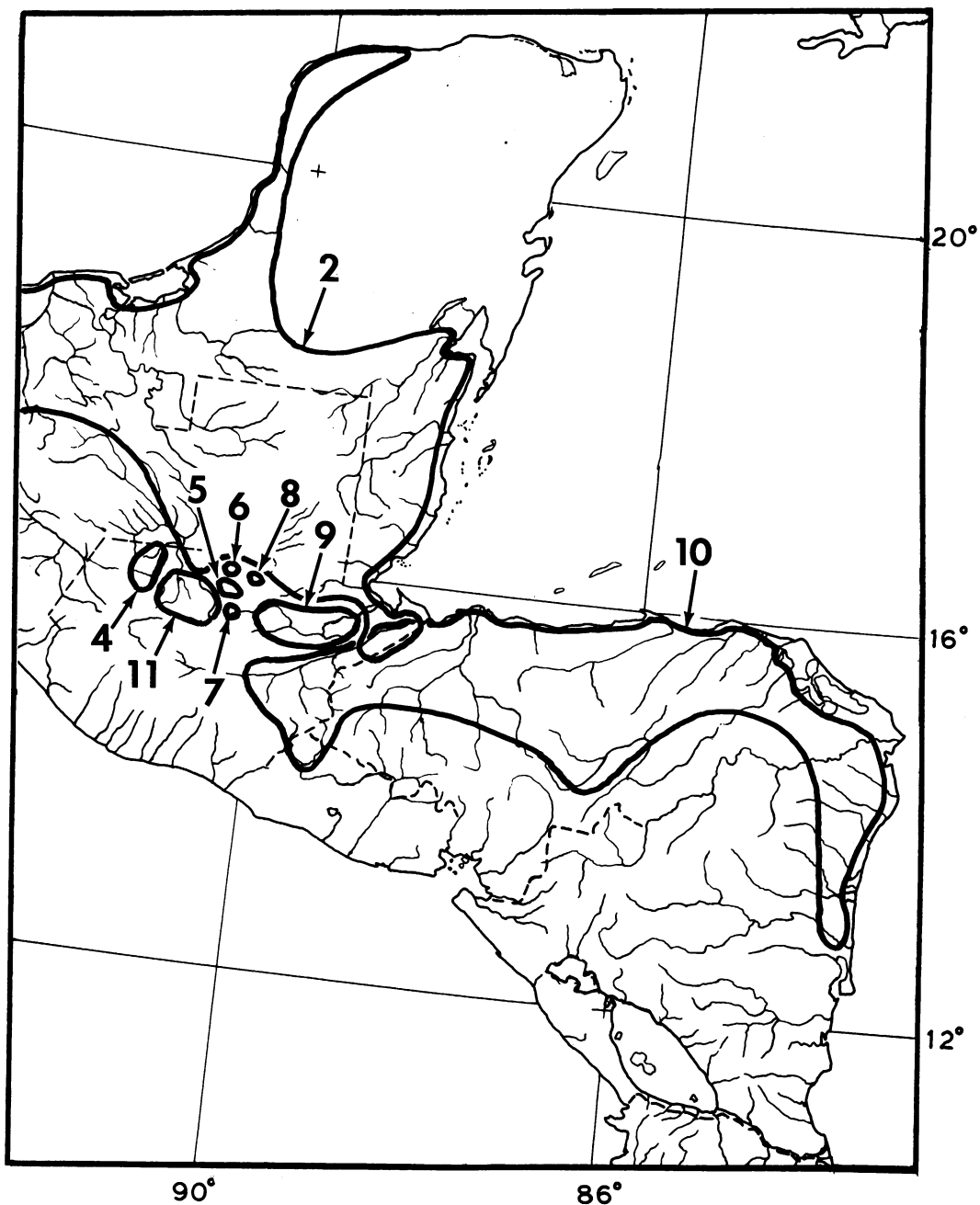


FIG. 46. Detail of the distributions of species of *Heterandria* in southern Mexico and northern Central America.

*Río Coatzacoalcas watersheds.* Within the area spanned by these two major rivers near the

Isthmus of Tehuantepec, *Heterandria* is represented at present only by the widespread spe-

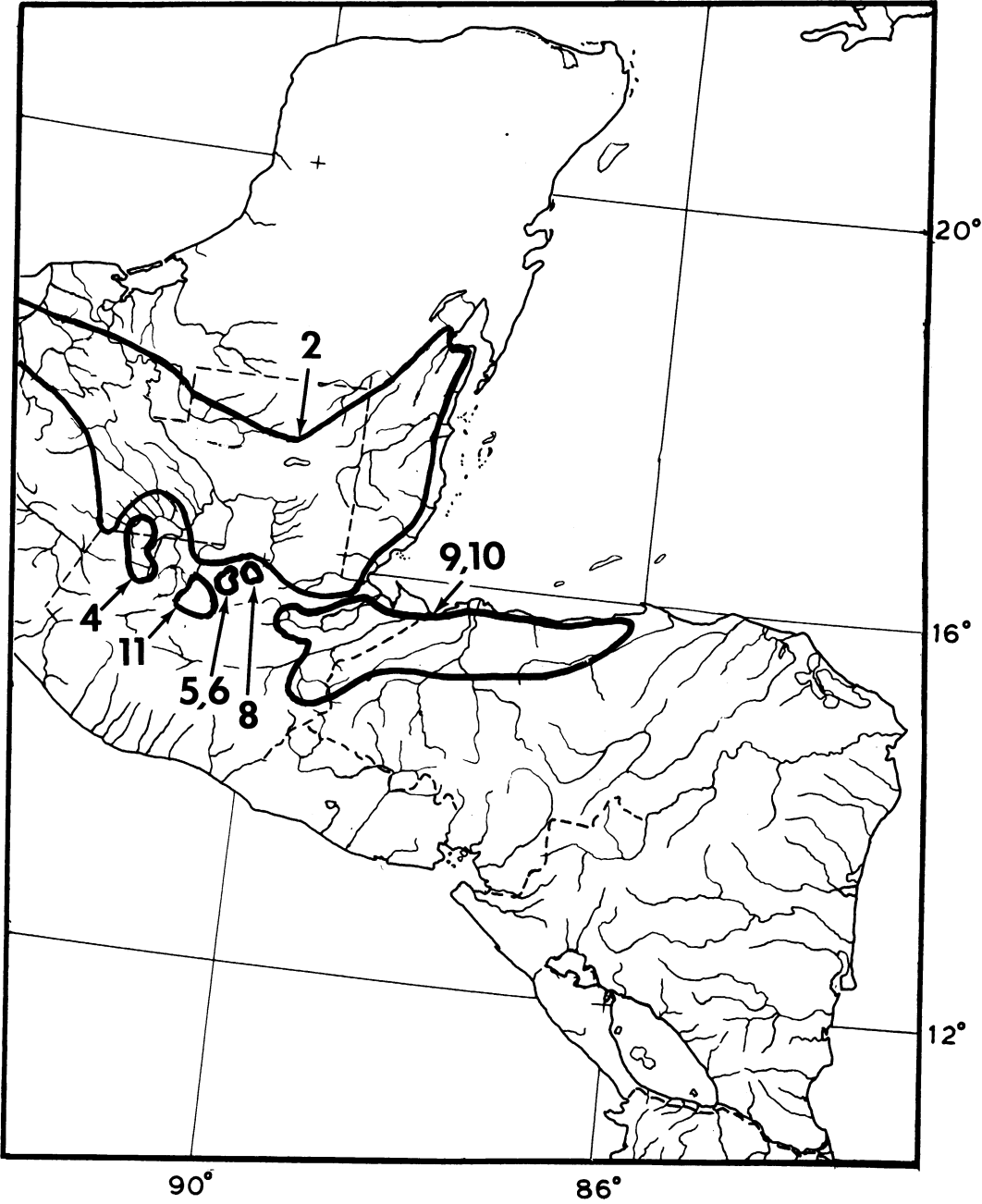


FIG. 47. Detail of the distributions of swordtail species of *Xiphophorus* in southern Mexico and northern Central America.

cies (or species complex), *H. bimaculata*. In *Xiphophorus*, there is an endemic form, *X. mil-*

*leri*, coastward in the Río Papaloapan region (in Laguna Catemaco), and there is an endemic

species of swordtail, *X. clemencia* (area 3, fig. 45), sympatric and syntopic with the widespread swordtail species (or species complex), *X. helleri*, in the upland portions of the Río Coatzacoalcos (in the Río Sarabia).

(5) *Endemic taxa in the Río Candelaria Yalicar, Río Sachica, and Río Polochic.* As noted above, only *Heterandria* has endemic forms in these waters.

(6) *Distributions of widespread taxa.* In each genus, there is a widespread species ranging from somewhat south of the Río Panuco region to the Yucatan Peninsula in Mexico, Guatemala, and Belize, *H. bimaculata* and *X. helleri*, of which *bimaculata* has the wider occurrence, especially in the northern half of the Yucatan Peninsula. To the east, *H. anzueto* is also more wide-ranging in Honduras and Nicaragua than the *Xiphophorus* populations "PMH" which occur only as far east as central northern Honduras.

(7) *Representation in Pacific coastal drainages.* Of all species in both genera, only *H. anzueto* has a Pacific slope occurrence which, so far as known, includes only the headwater streams of the Río Lempa watershed in Guatemala and its border with El Salvador in Lago Guija (fig. 25).

#### CONGRUENT AND INCONGRUENT CLADISTIC ELEMENTS IN RELATION TO GEOGRAPHY

The foregoing geographic summaries have been given primarily to illustrate that, for these two groups of poeciliid fishes, there exists an obvious geographic coincidence at the most general level of comparison (a disjunction between North and Middle American taxa north of the Río San Fernando, in which the North American elements are plesiomorph sister groups to all Middle American forms), and, at the more detailed level of comparison, some additional points of geographic coincidence as well as some points of geographic discordance. If it is true that scientific explanation depends on the discovery of some generality in nature (i.e., a pattern) about which theories can be made, it is evident that the present comparisons must include the expectation that, in the sum of

the observed coincidences and discordances, the similarities have not arisen by chance. In other words, it must be shown that the cases of distributional congruence add up to a statement of generality greater than mere geographic coincidence. To qualify as having some significant generality, a geographic relationship must also, therefore, be tied to the biological properties of organisms that make up the distributions. These properties might, of course, be ecological—properties that will somehow show us that organisms coexisting in the same narrow corner of the earth have similar ways of coping with their special province. But such correlations will be disappointing because, while perhaps telling us something about why two (or more) organisms can coexist in some special circumstance of nature, they tell us nothing of how they or their ancestors came to be where they are and what relationship their history has to the history of other members of their parent group in another geographic and ecologic context. In short, ecological comparisons, although of inherent interest from the standpoint of ecological theory, do not include information relative to the history of the patterns of coincidence. A more general method of comparison is therefore required that will lead to inference about whether all of the cases of coincidence can be attributed to common historical elements, inferences that will therefore include historical explanations of common ecologies. An ecology is, after all, the sum total of interactions of all the organisms that have come to live together in a particular geographic setting. The most general property of organisms that ties them to historical concepts is the property of kinship, and the discovery of this property is achieved by a method which has variously been called phylogeny reconstruction, genealogical analysis or cladistic analysis. The purpose of the following discussion will therefore be to examine the extent to which the known cases of geographic coincidence of the species and recognizable populations of *Heterandria* and *Xiphophorus* are correlated with their cladograms or relationship.

The cladistic configurations for *Heterandria* and *Xiphophorus* shown in figures 48 and 49 are derived from the primary synapomorphy



schemes and character state trees discussed earlier (pp. 298-310, 347-350, figs. 20, 37) and include nine and 15 taxa, respectively. These

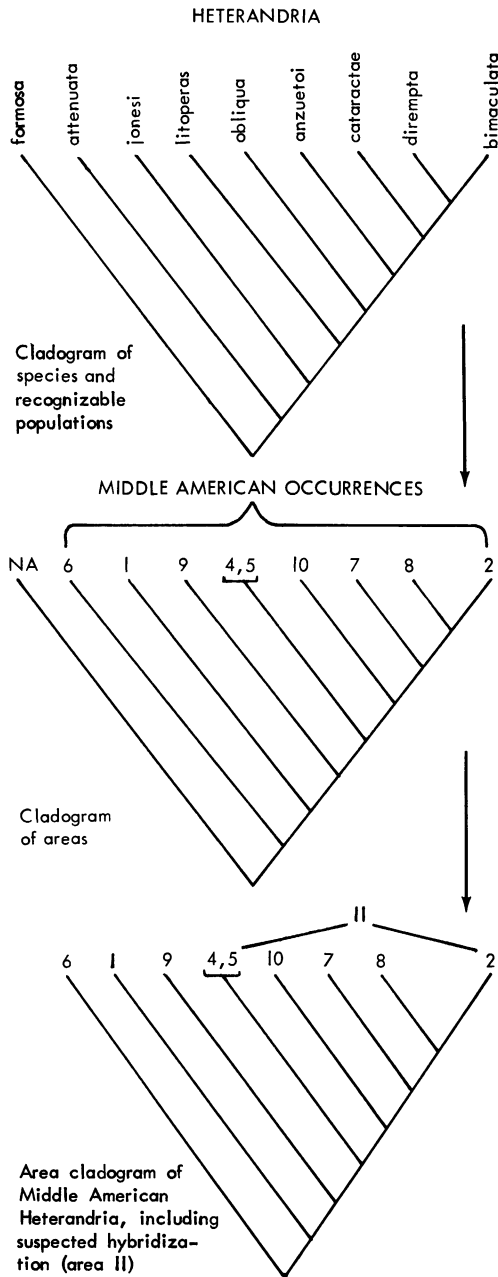
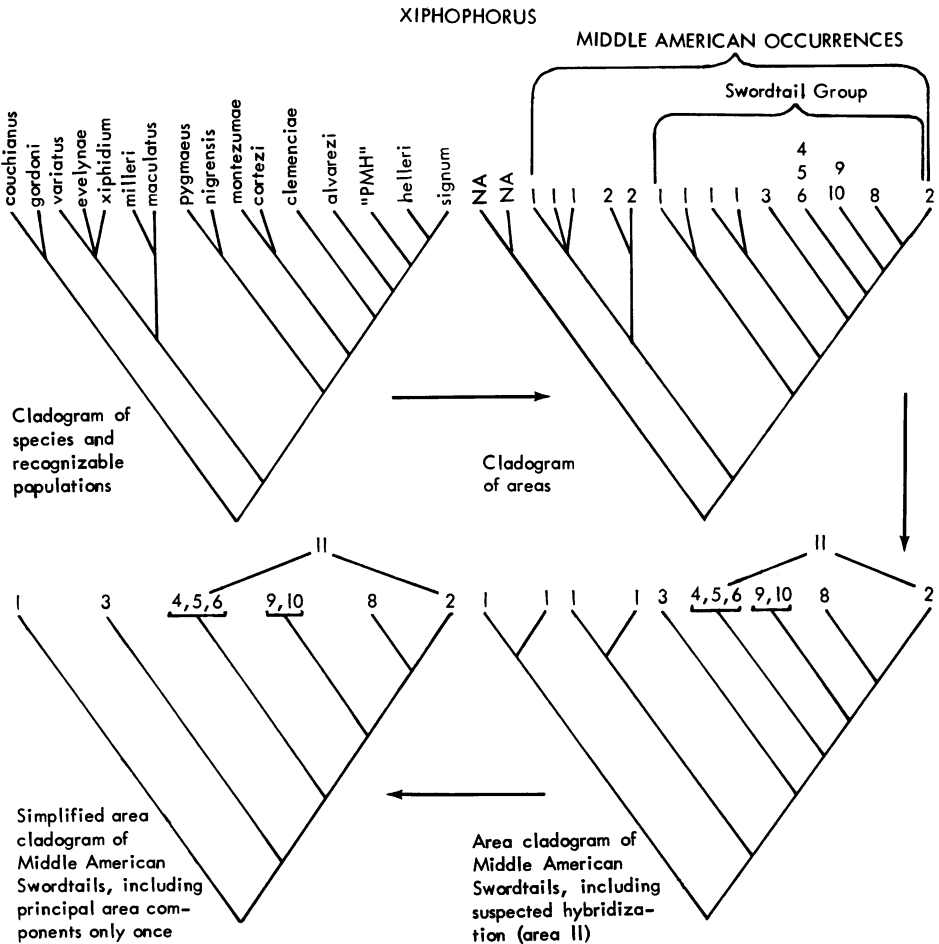


FIG. 48. Species and area cladograms for *Heterandria*.

cladograms may be compared with geographic information by replacing the named taxa and recognizable populations with geographic terms, i.e., by converting the cladograms of taxa into cladograms of areas. For this purpose, the geographic areas represented by the biological distributions are identified by letter and numeral designations (figs. 45-47): NA, North America; 1, Río Panuco region; 2, Atlantic slope Mexico from south of the Río Panuco region to the base of the Yucatan Peninsula north of the Sierras; 3, Río Sarabia; 4, Río San Ramón (isolated section); 5, Río Dolores; 6, Río Candelaria Yalicar; 7, Río Sachicha; 8, Río Chajmaic; 9, Río Polochic (including Laguna Izabal region); 10, Río Motagua, Río Lempa, the Atlantic slope of Honduras and northeastern Nicaragua. An area 11 is also designated (figs. 46, 47), representing the region in the upper Río Salinas and Río Lacantún, in which inferred secondary intergradation has been found among members of each genus.

Since geographic discordances between *Heterandria* and *Xiphophorus*, involving the occurrences of endemic species geographically unique with reference to the specified areas, are found only among Middle American taxa, and because the North American taxa in the two genera are so widely separated as to raise questions about the significance of their co-occurrence in such a large region, attention will be focused now on the Middle American distributions (fig. 45). In Middle America there are three relevant kinds of distributions; the species of *Heterandria* (subgenus *Pseudoxiphophorus*) and the platyfish and the swordtail sections of Middle American *Xiphophorus*. Platyfishes are relatively uninformative with respect to this problem however, because of their confinement to only two of the 11 areas specified by this problem (fig. 49); in other words, their distributions are of a very low level of significance from the standpoint of either coincidence or discordance. The problem may, therefore, be simplified to a comparison of *Heterandria* (*Pseudoxiphophorus*) with the swordtail section of *Xiphophorus*, both of which are represented in 10 of the 11 specified areas (figs. 48, 49). And the cladistic statement of the problem may be further simplified by noting that, from the

FIG. 49. Species and area cladograms for *Xiphophorus*.

standpoint of geographic relationships, the two most positionally plesiomorphic branches of the swordtail cladogram represent four taxa in area 1 and that they contain no more information about the relationships of areas than a single branch representing area 1: the swordtail cladogram is accordingly, reduced to the simpler form (fig. 49, lower left) to facilitate comparison.

With the problem reduced to its simplest and yet most informative elements, it is evident that the area cladograms for *Heterandria* and *Xiphophorus* differ with respect to four areas: area 3 (the Río Sarabia) which has an endemic swordtail, *X. clemenciae*, but no endemic *Heterandria* (fig. 45); and areas 6 (the Río

Candelaria Yalicar), 7 (the Río Sachicha) and 9 (the Río Polochic) which have endemic species of *Heterandria* (*H. attenuata*, *H. cataractae* and *H. litoperas*, respectively) but no endemic species of swordtail (figs. 46, 47). These four areas represent unique components of the two area cladograms and, as such, do not specify any general problem. Any attempt at their explanation must therefore involve unique explanations of unique events, at least insofar as the present problem is concerned. In contrast to these unique elements, the remaining areas are represented by endemic taxa or recognizable populations in both groups, and the most significant observation that can be made about them is that the area cladograms remaining af-

ter being further simplified by the deletion of unique components are congruent, i.e., they show the same areas in the same cladistic sequence (fig. 50). Not only is this true with regard to geographically and biologically recognizable entities, but it is also true of the inferred secondary intergradation (hybridization) in area 11, involving areas 4, 5, and 2 (figs. 48-50).

The general problem may now be stated: what is the significance of finding two geographically congruent, five-term area cladograms derived from the more complete biological and area cladograms containing some incongruent elements? The problem may be viewed thus: for any five taxa, there are 105 possible dichotomous configurations (i.e., 105 possible solutions to the problem of their interrelationships as determined by a random search

for synapomorphies such that only one topology will ultimately be found to be a most parsimonious character state tree and a best current estimate of the single real phylogeny of a group), and for six taxa (if one includes the reticulate element represented by area 11 as a separate and distinct historical event) there are 945 possible configurations (Schlee, 1971). Geographical congruence between any two such cladograms could therefore, be expected to occur only once in 105 or 945 cases of geographical coincidence if the cladistic congruence had been ruled by chance. Moreover, if one were to add the North American taxon of each genus, which increases the congruence to include seven terms, the unlikelihood of duplicating a given cladistic topology by chance alone is staggering. The nature of probability estimates derived from this type of reasoning about

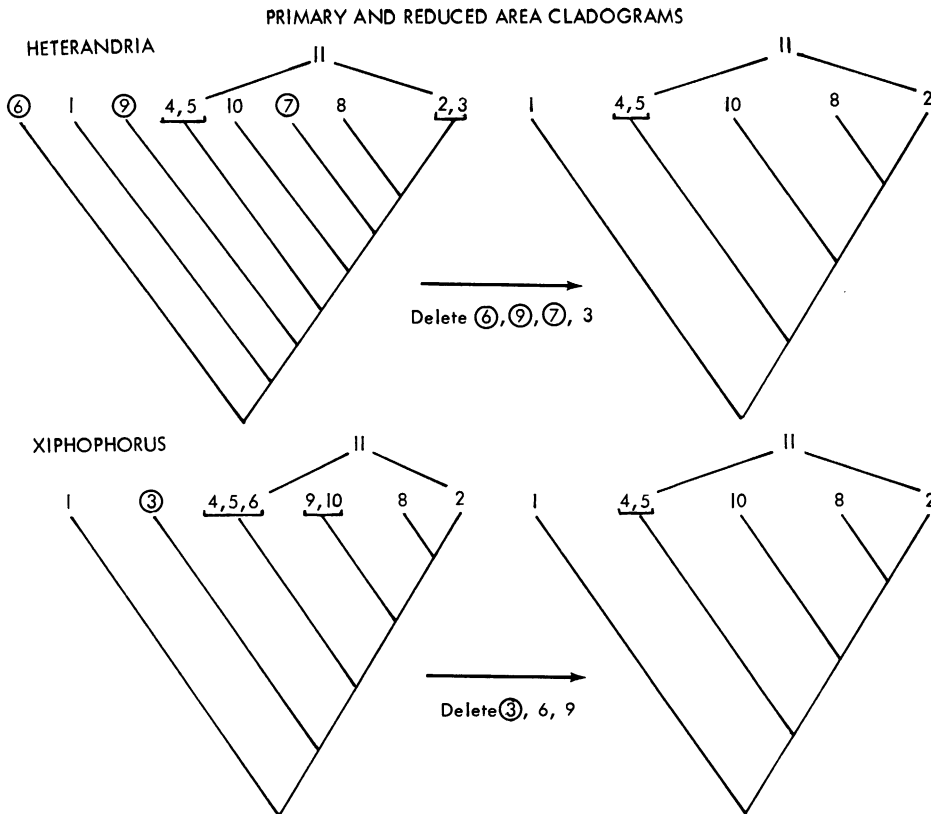


FIG. 50. Comparison of area cladograms for *Heterandria* and the swordtail species of *Xiphophorus* and their simplification by the deletion of incongruent geographic components.

cladistic congruence and the way in which it may be associated with historical explanation has been considered in more detail elsewhere (Rosen, 1978), but for our purposes here, it seems justified to conclude that (1) the con-

gruence between *Heterandria* and *Xiphophorus* in North and Middle America has resulted from their sharing, in part, a common history, and (2) to the extent that incongruent elements are present their histories have diverged.

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