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Systematics and Biogeography of the Genus *Gambusia* (Cyprinodontiformes: Poeciliidae)

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ABSTRACT

The systematic and biogeographic relationships of the poeciliid genus *Gambusia*, a monophyletic group of 45 species, are examined in detail. As it focuses primarily on the interrelationships of subgenera and species groups, this work is not intended as a formal revision of the genus; however, areas where revisionary work are needed are pointed out. The genus has a sister-group relationship with the genus *Belonesox*, and these two in turn are related to the genus *Brachyrhaphis*. *Gambusia vittata* and the members of the *rachowi* species group, each previously assigned to monotypic genera, do possess the synapomorphies described for the genus *Gambusia*, and are thus included. Three subgenera within *Gambusia* are diagnosed: the subgenus *Heterophallina*, the subgenus *Arthrophallus*, and the subgenus *Gambusia*. The subgenera *Arthrophallus* and *Gambusia* are sister groups. Within the subgenus *Heterophallina*, the *panuco* and *rachowi* species groups are more closely related to each other than either is to *G. vittata*. In the subgenus *Arthrophallus*, the *nobilis* and *senilis* species groups are sister taxa, and in the subgenus *Gambusia*, the *puncticulata* and *punctata* species groups are sister taxa. Relationships within species groups also are described. This scheme of relationships, and the new classification derived from it, is a product of cladistic analysis of morphological characters. A complete descriptive osteology

of *Gambusia hispaniolae* also is included, for comparison and reference.

Biogeographic analysis of the species groups of *Gambusia* concentrates on three areas. In southern Texas and northern Mexico, members of the *affinis*, *nobilis*, and *senilis* species groups overlap; their area cladograms are compared. The Río Pánuco basin of eastern Mexico is a meeting point for members of the subgenus *Heterophallina*, the *senilis* species group, and the *affinis* species group. A repeated pattern indicated a relationship between the Pánuco basin and the Cuatro Ciénegas basin of northern Mexico, with further ties to southern Mexico. Finally, links between Central America and the Greater Antilles are explored through the distribution patterns and area cladograms of the *nicaraguensis*, *puncticulata*, and *punctata* species groups. Repeated patterns include a relationship between Nuclear Central America (specifically Belize) and the Antilles, between Cuba and the Cayman Islands, and between eastern Cuba, Hispaniola, and the Bahamas. Whereas most of the Caribbean patterns do not strictly reiterate each other, the patterns are all consistent with each other. It is inferred that they represent different fragments of the complex history of Caribbean biogeography, and are compared with some published distributional information for other taxa.

INTRODUCTION

Much attention was drawn to the poeciliid genus *Gambusia* Poey, with around 45 species, in 1963, when two independent works were published dealing with the systematics, and to a lesser extent, the biogeography, of this group (Rivas, 1963; Rosen and Bailey, 1963). Since that time, the conflicts between the two schemes have never been resolved, and describers have had difficulty classifying their new *Gambusia* species (Miller, 1975). Systematic studies have emerged that focus on higher (Parenti, 1981) and lower (Rivas, 1969; Fink, 1971a, 1971b; Greenfield, 1985; Echelle and Echelle, 1986) systematic levels; this work aims to classify the entire genus, and to establish its close relatives, through the principles and methods of cladistic systematics. This paper is not intended as a formal revision of the genus, as it concentrates primarily on the subgenus and species group

levels; however, areas of the genus that are in need of revision are noted.

Poeciliid taxonomy traditionally has focused on the specialization of the male's anal fin, the gonopodium, often to the exclusion of other characters. In fact, detailed descriptions of other parts of the anatomy of any poeciliid generally are not available, with some notable exceptions, such as Ramaswami's 1945 description of the chondrocranium of *Gambusia affinis*, and Weisel's similar account of the guppy, *Poecilia reticulata*, in 1967. My osteological account of the members of the genus *Gambusia* uses a male *G. hispaniolae* as an exemplar, but discusses the range of variation in the genus for all characters. It will serve both as an introduction to the characters important for systematic analysis of the genus, and as a general reference for the complete osteology of a poe-

TABLE 1
Proposed Classification of *Gambusia*

Genus <i>GAMBUSIA</i> Poey, 1854
<i>Gambusia</i> Poey, 1854: 382 (type species <i>Gambusia punctata</i> Poey, by subsequent designation by Jordan and Copeland, 1876: 142)
<i>Heterophallus</i> Regan, 1914: 66 (type species <i>Heterophallus rachovii</i> , by monotypy)
<i>Flexipenis</i> Turner, 1940: 89 (nomen nudem for <i>Gambusia vittata</i> Hubbs, which was subsequently designated as the type species of <i>Flexipenis</i> , by C. L. Hubbs, in Rivas, 1963: 334)
<i>Dicerophallus</i> Alvarez, 1952: 95–97 (type species <i>Dicerophallus echeagayari</i> , by original designation)
Subgenus <i>Heterophallina</i> Hubbs, 1926: 26 (type species <i>G. regani</i> , by original designation)
<i>G. vittata</i> Hubbs, 1926
<i>panuco</i> species group:
<i>G. marshi</i> Minckley and Craddock, in Minckley, 1962
<i>G. panuco</i> Hubbs, 1926
<i>G. regani</i> Hubbs, 1926
<i>rachowi</i> species group:
<i>G. rachowi</i> (Regan, 1914)
<i>G. echeagayari</i> (Alvarez, 1952)
Subgenus <i>Arthrophallus</i> Hubbs, 1926 (type species <i>Heterandria patreulis</i> Baird and Girard, a subjective synonym of <i>Heterandria affinis</i> Baird and Girard; by original designation)
<i>affinis</i> species group:
<i>G. affinis</i> (Baird and Girard, 1854)
<i>G. holbrooki</i> Girard, 1859b
<i>G. speciosa</i> Girard, 1859c
<i>G. lemaitrei</i> Fowler, 1950
<i>G. aurata</i> Miller and Minckley, 1970
<i>nobilis</i> species group:
<i>G. nobilis</i> (Baird and Girard, 1854)
<i>G. heterochir</i> Hubbs, 1957
<i>G. krumholzi</i> Minckley, 1963
<i>G. georgei</i> Hubbs and Peden, 1969
<i>G. eurystoma</i> Miller, 1975
<i>G. sexradiata</i> Hubbs, 1936
<i>senilis</i> species group:
<i>G. senilis</i> Girard, 1859c
<i>G. gaigei</i> Hubbs, 1929
<i>G. alvarezi</i> Hubbs and Springer, 1957
<i>G. hurtadoi</i> Hubbs and Springer, 1957
<i>G. amistadensis</i> Peden, 1973b
<i>G. geiseri</i> Hubbs and Hubbs, in Hubbs and Springer, 1957
<i>G. longispinis</i> Minckley, 1962
<i>G. atrora</i> Rosen and Bailey, 1963
Subgenus <i>Gambusia</i>
<i>nicaraguensis</i> species group:
<i>G. nicaraguensis</i> Günther, 1866
<i>G. melapleura</i> (Gosse, 1851)

TABLE 1—(Continued)

<i>G. wrayi</i> Regan, 1913
<i>puncticulata</i> species group:
<i>G. yucatana</i> Regan, 1914
<i>G. hispaniolae</i> Fink, 1971b
<i>G. manni</i> Hubbs, 1927
<i>G. hubbsi</i> Breder, 1934
<i>G. bucheri</i> Rivas, 1944
<i>G. baracoana</i> Rivas, 1944
<i>G. monticola</i> Rivas, 1971
<i>G. puncticulata</i> Poey, 1854
<i>G. oligosticta</i> Regan, 1913
<i>G. caymanensis</i> Regan, 1913
<i>G. howelli</i> Rivas, 1944
<i>punctata</i> species group:
<i>G. luma</i> Rosen and Bailey, 1963
<i>G. beebei</i> Myers, 1935
<i>G. pseudopunctata</i> Rivas, 1969
<i>G. punctata</i> Poey, 1854
<i>G. rhizophorae</i> Rivas, 1969
<i>G. xanthosoma</i> Greenfield, 1983

ciliid, valuable for higher-level comparative work.

The species of *Gambusia* live in fresh and brackish water, and range from the eastern and southern United States through Mexico and Central America, with a single species along the South American coast. Particularly interesting are the 16 taxa found on islands in the West Indies. Speculations about how these fishes found their island homes, invoking phenomena such as land bridges, migration, and hurricanes, have abounded in the past, but subsequent developments in the science of biogeography have made it possible to critically assess hypotheses concerning distribution patterns. A necessary prerequisite for such a biogeographic analysis is a sound systematic hypothesis for the fishes involved. Only then can the nature of the relationship between the organisms and the areas they inhabit be determined. The major objective of this work, therefore, is to describe relationships within the genus, which are summarized in the proposed classification (table 1), and to discuss their biogeographic implications.

HISTORICAL REVIEW

The genus *Gambusia* was described by Poey in 1854. Although he realized that the two

TABLE 2
Classification of *Gambusia*, Based on
Rivas (1963)

Genus <i>Flexipenis</i>
<i>F. vittata</i>
Genus <i>Heterophallus</i>
<i>H. rachovii</i>
Genus <i>Dicerophallus</i>
<i>D. echeagayari</i>
Genus <i>Gambusia</i>
Subgenus <i>Orthophallus</i>
<i>G. lemaîtrei</i>
Subgenus <i>Arthropallus</i>
<i>G. affinis</i>
Subgenus <i>Heterophallina</i>
<i>G. panuco</i> <i>G. regani</i> <i>G. marshi</i>
Subgenus <i>Gambusia</i>
<i>senilis</i> species group:
<i>G. geiseri</i> <i>G. senilis</i> <i>G. gaigei</i>
<i>G. hurtadoi</i> <i>G. alvarezi</i> <i>G. longispinis</i>
<i>nobilis</i> species group:
<i>G. nobilis</i> <i>G. heterochir</i> <i>G. sexradiata</i>
<i>nicaraguensis</i> species group:
<i>G. melapleura</i> <i>G. nicaraguensis</i> <i>G. wrayi</i>
<i>G. gracilior</i> <i>G. dominicensis</i>
<i>puncticulata</i> species group:
<i>G. bucheri</i> <i>G. puncticulata</i> <i>G. howelli</i>
<i>G. baracoana</i> <i>G. manni</i> <i>G. hubbsi</i>
<i>G. oligosticta</i> <i>G. caymanensis</i> <i>G. yucatanana</i>
<i>punctata</i> species group:
<i>G. punctata</i> <i>G. beebei</i>

species he assigned to the genus (*G. punctata*, type species, and *G. puncticulata*) were poeciliids because of the presence of the male's gonopodium, he distinguished *Gambusia* from other genera of poeciliids that he encountered in his studies of Cuban fishes on the basis of body shape, tooth structure, and carnivorous habit. Many more species now referred to the genus *Gambusia* were described in the years that followed, but there was much confusion in generic assignment. It was Regan, in 1913, who realized that "differences in structure of the intromittent organ are of great systematic importance" (p. 978), and he described *Gambusia* as being characterized by the spines on ray 3, elbow in ray 4a, and hooks on rays 4p and 5a of the gonopodium. He listed 17 species, eight of which he described as new.

Hubbs (1924, 1926) was the first to subdivide the genus. By this time, the heavy emphasis placed upon gonopodial structure was

evinced by the names assigned to subgenera. Subgenera *Arthropallus* and *Schizophallus*, both monotypic, contained *G. patreulis* and *G. holbrooki*, respectively. Subgenus *Heterophallina* was created for three newly described species, *G. vittata*, *G. regani*, and *G. panuco*, and the remaining 11 species in the genus were placed in the subgenus *Gambusia*. Hubbs also created a tribe, the Gambusiini, to contain allied genera—the monotypic *Heterophallus* and *Belonesox*.

By the time of the next review of the genus (1963), 30 species bore the name *Gambusia*. Rivas (1963) removed Hubbs' *G. vittata* to a monotypic genus, *Flexipenis*, in the tribe Gambusiini, primarily because it lacks the distinctive elbow on ray 4a of the gonopodium. He also listed four subgenera; whereas he synonymized *Schizophallus* with *Arthropallus*, a new subgenus, *Orthophallus*, was created for *G. lemaîtrei*, from Colombia. Within the subgenus *Gambusia*, he described five species groups: the *senilis* species group, with 6 members; *nobilis*, 3 members; *nicaraguensis*, 5 members; *puncticulata*, 9 members; and *punctata*, 2 members (table 2). The criteria he employed in grouping were gonopodial characters and geographic distribution.

Also in 1963, Rosen and Bailey published a review of the Poeciliidae. Their tribe Gambusiini contained *Brachyrhaphis*, *Belonesox*, and *Gambusia*; their genus *Gambusia* listed 34 species, including two described as new. They also included *Flexipenis vittata* and *Heterophallus rachovii* in the genus *Gambusia*. While emphasizing the need for a thorough study of interrelationships in the genus, they recognized six species groups: *affinis* species group, 17 species; *punctata*, 4 species; *nobilis*, 7 species; *panuco*, 3 species; *vittata*, monotypic; and *rachowi*, 2 species (table 3). These groupings primarily were based on gonopodial specializations, but such characters as pigmentation, vertebral number, and body and fin configuration were also considered.

These two treatments in 1963 were concurrent and incongruent, both in delineation of groups and assignment to groups, and the overall status of relationships within the genus, or of generic limits, has not been addressed since.

Several studies have concentrated on relationships within species groups, following one scheme or the other. Rivas (1969) revised the *punctata* species group, describing two new species. Here he sharply disagreed with Rosen and Bailey's (1963) delineation of this group, and reiterated his belief that "only gonopodial characters (including the suspensorium) appear to be of value in recognizing and characterizing subgenera and species groups" (p. 779). In this revision, as in his 1963 work, Rivas did not explicitly describe relationships, although one is tempted to infer them from his classification.

Revisions of the *nicaraguensis* and *puncticulata* species groups, again as defined by Rivas, appeared in 1971 (Fink, 1971a, 1971b). These were detailed studies documenting the range of variation within each of these groups, particularly in reference to meristics and gonopodial features, but no schemes of relationships were presented.

Further work on the *puncticulata* species group (Greenfield et al., 1982; Greenfield and Wildrick, 1984; Greenfield, 1985) has included other types of characters, such as pigmentation, body proportions, and electrophoretic analysis. One of these studies (Greenfield and Wildrick, 1984) did present a branching diagram to summarize its results, and its implications are discussed in the Systematics section. Unfortunately, these workers lacked an overall scheme of relationships for the genus, necessary for outgroup comparisons, and their work has been criticized because of small sample sizes.

New species described since 1963 sometimes have been easy to classify, such as *G. xanthosoma* in the *punctata* species group (Greenfield, 1983) or *G. amistadensis* in the *senilis* species group (Peden, 1973b), but often, especially with taxa described from the southern Texas–northern Mexico area, the new species simply did not fit neatly into either of the Rivas or Rosen and Bailey schemes. Hubbs and Peden (1969) felt that *G. georgei* might lie either in the *affinis* or *nobilis* species group. Minckley's (1963) *G. krumholzi* showed characters both of the *nicaraguensis* species group and the *nobilis* species group, and Miller and Minckley's (1970) *G. aurata* also falls between the *affinis* and *nobilis* species groups. Miller, trying to

TABLE 3
Classification of *Gambusia*, Based on Rosen and Bailey (1963: 92–107)

Genus <i>Gambusia</i>	
<i>affinis</i> species group:	
<i>G. nicaraguensis</i>	<i>G. aestiputius</i> <i>G. lemaitrei</i>
<i>G. affinis</i>	<i>G. melapleura</i> <i>G. wrayi</i>
<i>G. gracilior</i>	<i>G. dominicensis</i> <i>G. myersi</i>
<i>G. yucatanana</i>	<i>G. puncticulata</i> <i>G. howelli</i>
<i>G. baracoana</i>	<i>G. bucheri</i> <i>G. manni</i>
<i>G. oligosticta</i>	<i>G. caymanensis</i>
<i>punctata</i> species group:	
<i>G. sexradiata</i>	<i>G. luma</i> <i>G. punctata</i>
<i>G. beebei</i>	
<i>nobilis</i> species group:	
<i>G. atrora</i>	<i>G. longispinis</i> <i>G. nobilis</i>
<i>G. senilis</i>	<i>G. gaigei</i>
<i>panuco</i> species group:	
<i>G. panuco</i>	<i>G. regani</i> <i>G. marshi</i>
<i>vittata</i> species group:	
<i>G. vittata</i>	
<i>rachowi</i> species group:	
<i>G. rachowi</i>	<i>G. echeagayari</i>

place *G. eurystoma* in either the *nobilis* or *punctata* group, suggested that "species groups of *Gambusia* be employed with caution until phyletic studies are completed" (1975: 1).

The taxonomic problems that need to be addressed include an assessment of the limits of the genus. C. L. Hubbs, and later Rivas, tended to remove any anomalous fish from the main body of the genus, either to a monotypic genus, as with *Flexipennis vittata*, *Heterophallus rachovii*, and *Dicerophallus echeagayari*, or to a monotypic or small subgenus, *Orthophallus* for *G. lemaitrei*, *Arthrophallus* for *G. affinis*, and *Heterophallina* for the three-member *panuco* group.

If classification is not necessarily meant to reflect relationship, this tactic of sequestering odd fishes is a convenient way to deal with them; however, I believe the most useful classifications are those that directly reflect ideas of relationship, and the sister-group relationships implied by that classification with the monotypic taxa have not been substantiated. Similarly, the delineation of subgenera and species groups should be arranged according to relationship, not convenience or geography.

The relationship of *Gambusia* to other poeciliids has not been addressed since 1963,

when Rosen and Bailey allied the genus with *Belonesox* and *Brachyrhaphis*. Beyond that, relationships among poeciliids are yet to be critically examined. The position of poeciliids within the order Cyprinodontiformes was recently reappraised by Parenti (1981), and her classification of the order is employed herein.

Interpretation of *Gambusia* distribution, particularly in the Caribbean, historically has been heavily influenced by a paper by Myers (1937) entitled "Fresh-water fishes and West Indian zoogeography." In this, he differentiated two kinds of freshwater fishes: primary-division fishes, such as ostariophysans, that are "very strictly confined to fresh water" due to "an ancient physiological inability to survive in salt sea water" (pp. 342-343), inferred because nearly all members of such groups are never found in even brackish water; and secondary-division fishes, including cyprinodontiforms, that are more tolerant to saltwater conditions. "It is evident that many species of this secondary group might easily survive a short sea journey. This is borne out by distributional fact" (p. 345). Regardless of the fact that these fishes do not habitually migrate from island to island, such "colonizing flights," of the type so maligned by Croizat (1964), are exactly the mechanism invoked to explain the distribution of poeciliids in the Greater Antilles, simply because some members of the family do not die in salt water.

Biogeography has often, until recently, been relegated to the last few pages of systematic revisions, and *Gambusia* revisers have tried to explain the distribution of the taxa based on their systematic conclusions (Hubbs and Springer, 1957; Rosen and Bailey, 1963; Rivas, 1963, 1969; Fink, 1971a, 1971b). Two obstacles have prevented this endeavor from being as fruitful as it might have been. First, because of the influence of Myers' judgment that random dispersal by poeciliids might not be that uncommon and of the prevailing notions of stabilist geography, related species were uncritically assumed to have achieved their current stations through migration. Secondly, oftentimes notions of "geographical cohesiveness" were used to justify certain systematic arrangements, i.e., using geographic proximity to indicate close systematic relationship. This obviously leads to

problems of circularity when one wishes to make general statements about biogeography based on systematics.

Croizat (1958, 1964) observed that groups of related organisms (even secondary-division freshwater fishes) generally are not distributed randomly; in fact, he documented an amazing degree of congruence in distribution patterns when surveying many groups. Rather than postulating that the distribution pattern of each group requires a separate explanation, as would be needed in a scenario based on chance dispersal, Croizat proposed that these congruent patterns (generalized tracks) have a single cause, that "life and earth evolve together." Rosen (1975) applied Croizat's method to the problem of Caribbean biogeography, and concluded that the distribution of *Gambusia* in the Antilles and Central America was but one example of a generalized track relating North America to the Caribbean.

Obviously, to discern the interdependence of organismic relationships and biogeographic relationships, the groups utilized must be natural units; that is, monophyletic groups. As expounded by Nelson and Platnick (1981), the employment of branching diagrams to portray levels of relationship is useful not only in systematics but also in biogeography. With such a tool, not only can one discern broad patterns of distributional congruence (Croizat's generalized tracks) but also finer patterns of congruence within the tracks, corresponding to the components of the cladograms. The classic example of this method is found in Rosen (1979), also discussed in Nelson and Platnick (1981), Humphries and Parenti (1986), and many other sources. The method is underutilized, mostly because of the prerequisite for resolved cladograms of related taxa that are endemic to certain areas. The ultimate purpose of this work is to provide such cladograms, to be used in biogeographic analysis, for monophyletic groups within *Gambusia*.

METHODS

The descriptive osteology follows the style of a similar work for a characin (Weitzman, 1962); thus I have chosen a single specimen, a mature male *Gambusia hispaniolae*, to il-

illustrate and describe. However, the description also is comparative, in the sense that those characters that vary in the genus also are discussed. The systematic implications of these characters are treated in the Systematics section.

With characters that do vary, I have tried to indicate the level of generality that they describe. For features that characterize higher groups that include *Gambusia*, I have relied on several sources—Rosen and Bailey (1963) for poeciliids, Rosen (1964) and Rosen and Parenti (1981) for atherinomorphs, and, particularly, Parenti (1981) for cyprinodontiforms. I also have noted where my observations conflict with the predictions of those works. These apparent contradictions are due, in large part, to the probably necessary, but unfortunately untrue, assumption that a few poeciliids, say, *Tomeurus* or *Xiphophorus*, are representative of all poeciliids. Although poeciliids certainly are well corroborated as a monophyletic group, there is a great deal of diversity among them.

As noted in the introduction, few osteological treatises on poeciliids have appeared. Rosen and Bailey (1963), of course, figured and discussed many gonopodia and gonopodial suspensoria. They also figured many dorsocrania and radiographs of whole fish, but left these undiscussed. The gonopodium has received much attention with regard to its structure, vascularization, innervation, functional morphology (Rosen and Gordon, 1953), behavior (Rosen and Tucker, 1961; Peden, 1972b), and development (Turner, 1941, 1942a) and similar attention has focused on the other sexually dimorphic systems of poeciliids, such as the gonopodial suspensorium (Turner, 1942b; Rosen and Kallman, 1959), pectoral fin (Turner, 1942c; Hubbs and Reynolds, 1957), and female genitalia (Peden, 1972a, 1973a). Other areas have received relatively little attention, the only exceptions as follows. Cranial development in *Gambusia affinis* was examined by Ramaswami (1945), and in *Poecilia reticulata* by Weisel (1967). Hollister (1940) described the caudal skeletons of *G. holbrooki* and *Poecilia latipinna*. And although de Beer (1937) included a figure of *G. affinis* and Gregory (1933) figures of *Belonesox belizanus* in their respective treatises on fish skulls, neither is

well described, nor, in Gregory's case, very accurate. Only works dealing with higher level groups have addressed other parts of the skeleton.

Osteological observations were made on cleared and stained specimens, following the method of Dingerkus and Uhler (1977), where bone is stained with alizarin red and cartilage stained with alcian blue. Numbers of specimens prepared per lot are listed in the Materials Examined section; in general two males, two females, two juveniles, and embryos taken from gravid females were prepared, collection size permitting. Several *Gambusia* species were raised in the lab to provide ontogenetic series. Drawings are ink tracings of pencil renderings, using a camera lucida attached to a Leitz binocular dissecting microscope. Meristic, pigmentary, and sensory canal characters were observed on well-preserved alcoholic specimens.

Systematic analysis of character distributions follows the method of Hennig (1966) as set forth by Nelson and Platnick (1981). The aim is to discover and describe monophyletic groups, and characterize them by synapomorphies. Groups characterized by primitive characters, or by the lack of derived characters, are disallowed. Determining the level of generality at which a particular character is to be considered derived, i.e., what group it is a synapomorphy of, is the most difficult and at the same time the most challenging part of systematics. Helpful in this effort are the techniques of outgroup comparison and ontogenetic investigation, both of which aid in discovering homologies (sensu Patterson, 1982). A common pitfall involves too heavy a reliance on a single outgroup, rather than surveying a wide range of taxa of ever-more-encompassing groups; I have tried to avoid this danger but undoubtedly have not escaped it completely.

Character distributions are not always congruent; parsimony is the criterion employed to choose between rival schemes, in that the most parsimonious diagram requires the fewest ad hoc assumptions. Parsimony analysis was aided by Swofford's PAUP program (version 2.4.1), run on an IBM-PC. The classification presented in this work is a direct reflection of the systematic conclusions based on parsimony analysis, such that all taxa are

monophyletic, and the convention of sequencing specifies interrelationships.

Biogeographic analysis uses the result of the systematics analyses, the cladograms of monophyletic taxa, as input data. Instead of simply implying relationships among taxa, these branching diagrams now also imply relationships among areas. A comparison of these area cladograms will reveal any congruence of distribution patterns among them, to the extent that the groups studied overlap in their areas of endemism. A simple interpretation is that congruence implies shared history, incongruence independent dispersal events. However, Rosen (1985) recently discussed the meaning of incongruence in area cladograms. If an area, such as the Caribbean, has had a complex history, more than one generalized track may reflect that history. In terms of area cladograms, there will be incongruent components that nevertheless reflect the same history; however, each shows just a part of the complete picture, a part that may be temporally and/or spatially displaced from other parts.

A fuller use of these area cladograms for biogeographic analysis of the regions occupied by *Gambusia* species, therefore, will only come when cladograms are available for many other taxa that also occupy those areas; this work is a step toward that end.

ABBREVIATIONS

Institutional:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
UMMZ	University of Michigan, Museum of Zoology
USNM	United States National Museum (National Museum of Natural History, Smithsonian Institution)

Anatomical:

AAR	Anguloarticular
ACC	Accessory cartilage
APL	Autopalatine
ASC	Ascending process of premaxilla
BB2,3	Basibranchial 2, 3
BH	Basihyal
BOC	Basioccipital
BSR	Branchiostegal rays
CB1-5	Ceratobranchials 1-5

CBB4	Cartilaginous basibranchial 4
CH	Ceratohyal
CL	Cleithrum
CLP	Cleithral process
CMK	Coronomeckelian bone
COR	Coracoid
DEN	Dentary
DOR	Dorsal process of maxilla
DR	Distal radial
DSP	Dermosphenotic
EB1-4	Epibranchials 1-4
ECT?	Ectopterygoid?
ELB	Elbow
END	Endopterygoid
EP	Epural
EPI	Epioccipital
EPiP	Epioccipital process
EPR	Epipleural rib
EXO	Exoccipital
FM	Foramen magnum
FR	Frontal
GP1-3	Gonapophyses 1-3
GPUN	Uncini of gonapophyses
GNA	Gonactinosts
HB1-3	Hypobranchials 1-3
HHC	Hypohyal cartilage
HYM	Hyomandibula
HYP	Hypural
HYPP	Hypural plate
IAC	Interarcual cartilage
IH	Interhyal
IOP	Interopercle
IPB2,3	Infrapharyngobranchials 2, 3
IPR	Inner process
LAC	Lacrimal
LET	Lateral ethmoid
LIG	Ligastyle
MAX	Maxilla
MES	Mesethmoid
MKC	Meckel's cartilage
MR	Medial radial
NAS	Nasal
NP	Neuropophysis
NS	Neural spine
OP	Opercle
PAR	Parietal
PAS	Parasphenoid
PC	Postcleithrum
PH	Parhypural
PMX	Premaxilla
POP	Preopercle
PQC	Palatoquadrate cartilage
PR	Pleural rib
PRO	Prootic
PRR	Proximal radial
PTT	Posttemporal
PU2	Preural centrum 2
Q	Quadrate

RAD	Radials
RAR	Retroarticular
SC	Scapula
SCF	Scapular foramen
SCL	Supracleithrum
SER	Serrae
SOC	Supraoccipital
SOCp	Supraoccipital process
SOP	Subopercle
SP	Spines
SPH	Sphenotic
SYM	Symplectic
THC	Terminal half-centrum
TP-IPB4	Fourth infrapharyngobranchial tooth-plate
UH	Urohyal
US	Urostyle
V	Vomer
VHH	Ventral hypohyal

MATERIALS EXAMINED

For species of *Gambusia* examined, locality information is provided and the species are arranged according to the new classification proposed herein. Other comparative material is arranged alphabetically within hierarchical groupings; i.e., other poeciliids, other cyprinodontiforms, other atherinomorphs. Locality information is not provided for these materials. Numbers of specimens are indicated in parentheses, first the number of cleared and stained specimens, followed by the total number in the lot. When only one number is given, the lot consists of only alcoholic specimens.

Gambusia:

Subgenus *Heterophallina*

G. vittata:

AMNH 32391 (1/12). Río Soto la Marina system, Tamaulipas, Mexico.

AMNH 38498 (1/5). Río Axtla, San Luis Potosí, Mexico.

UMMZ 202820 (126). Río Choy, San Luis Potosí, Mexico.

AMNH 75822 (3/50). Río Mante, Tamaulipas, Mexico.

AMNH 75754 (6/79). Río San Rafael, Tamaulipas, Mexico.

panuco species group

G. marshi:

AMNH 78130 (7/50). Cuatro Ciénegas, Coahuila, Mexico.

UMMZ 179167 (1) holotype. Río Salado, 2 mi south Hermanos, Coahuila, Mexico.

UMMZ 198934 (177). Río Mesquites, Cuatro Ciénegas, Coahuila, Mexico.

G. panuco:

AMNH 32390 (9/29). Río Soto la Marina system, Tamaulipas, Mexico.

AMNH 78131 (4/150). Río Coy, San Luis Potosí, Mexico.

UMMZ 198801 (143). Río Verde, San Luis Potosí, Mexico.

G. regani:

AMNH 78132 (7/100). Río Sabinas system, Tamaulipas, Mexico.

UMMZ 164734 (48). Arroyo del Encino, Encino, Tamaulipas, Mexico.

rachowi species group

G. rachowi:

AMNH 78133 (4/15). Mexico.

UMMZ 187761 (164). Río Chiquito, Tenochtitla, Veracruz, Mexico.

UMMZ 167098 (1) holotype of *G. atzi* (= *G. rachowi*). Jesús Carranza, Veracruz, Mexico.

G. echeagayari:

UMMZ 191731 (3/40). Palenque, Chiapas, Mexico.

Subgenus *Arthrophallus*

affinis species group

G. affinis:

UMMZ 122760 (3/349). Wheeler Reservoir, Alabama.

UMMZ 129784 (1580). Limola Lake, Brazos Co., Texas.

G. holbrooki:

AMNH 52245 (5/30). Green Cove Spring, St. John Co., Florida.

AMNH 16255 (1/3). Cochabamba, Bolivia.

UMMZ 163475 (61). Jackson Co., Florida.

G. speciosa:

AMNH 77947 (4/30). Melchor Musquiz, Río Grande drainage, Coahuila, Mexico.

UMMZ 120320 (684). Devils River, Verde Co., Texas.

UMMZ 196738 (177). Arroyo La Salada, Coahuila, Mexico.

G. aurata:

AMNH 75821 (7/62). Nacimiento del Río Mante, Tamaulipas, Mexico.

UMMZ 188736 (1) holotype. Río Mante, Tamaulipas, Mexico.

nobilis species group

G. nobilis:

AMNH 52233 (4/200). Dexter National Fish Hatchery, Eddy Co., Texas.

UMMZ 179801 (681). Phantom Cave, Jeff Davis Co., Texas.

UMMZ 132268 (27). Tunis Spring, Pecos Co., Texas.

G. krumholzi:

UMMZ 180322 (3/87) paratopotypes. Río de Mara, Coahuila, Mexico.

UMMZ 180320 (1) holotype. Nava, Coahuila, Mexico.

G. georgei:

UMMZ 187488 (3/43) paratopotypes. San Marcos River, Hays Co., Texas.

UMMZ 187447 (1) holotype. San Marcos River, Hays Co., Texas.

G. heterochir:

UMMZ 170937 (6) paratopotypes. Clear Creek, Menard Co., Texas.

UMMZ 170936 (1) holotype. Clear Creek, Menard Co., Texas.

G. eurystoma:

UMMZ 184717 (3/360) paratypes. Arroyo del Azufre, Teapa, Tabasco, Mexico.

UMMZ 197600 (1) holotype. Arroyo del Azufre, Teapa, Tabasco, Mexico.

G. sexradiata:

AMNH 24529 (17/122). Río de la Pasión, Alta Verapaz, Guatemala.

AMNH 25615 (1/13). Río de la Pasión, Peten, Guatemala.

AMNH 32025 (5/57). Río de la Pasión, Peten, Guatemala.

AMNH 24516 (4/31). Río de la Pasión, Alta Verapaz, Guatemala.

UMMZ 102989 (1) holotype (of *G. nicaraguensis sexradiata*). Río Papaloapan, Oaxaca, Mexico.

senilis species group*G. senilis*:

UMMZ 209026 (3/270). Rancho Houmigas, Chihuahua, Mexico.

UMMZ 166712 (135). Río San Juan, Río Concho, Chihuahua, Mexico.

G. cf. senilis:

UMMZ 211115 (3/891). Balnearia, San Diego, Chihuahua, Mexico.

G. gaigei:

UMMZ 84527 (1) holotype. Rio Grande at Boquillas, Brewster Co., Texas.

G. hurtadoi:

UMMZ 211112 (3/255). Ojo (Hacienda) Dolores, Chihuahua, Mexico.

UMMZ 168975 (1) holotype. Ojo (Hacienda) Dolores, Chihuahua, Mexico.

G. alvarezii:

AMNH 27492 (4/4). El Ojo de San Gregorio, Chihuahua, Mexico (cat. as *G. gaigei*).

UMMZ 211110 (3/295). El Ojo de San Gregorio, Chihuahua, Mexico.

UMMZ 168979 (1) holotype. El Ojo de San Gregorio, Chihuahua, Mexico.

G. amistadensis:

UMMZ 190407 (1) holotype. Goodenough Springs, Val Verde Co., Texas.

UMMZ 190408 (3/65) paratopotypes. Goodenough Springs, Val Verde Co., Texas.

G. geiseri:

UMMZ 120247 (3/130) paratypes. San Marcos River, Hays Co., Texas.

UMMZ 168974 (1) holotype. San Marcos River, Hays Co., Texas.

G. longispinis:

UMMZ 130382 (2/50). Cuatro Ciénegas, Coahuila, Mexico.

UMMZ 179620 (2) holotype. Cuatro Ciénegas, Coahuila, Mexico.

G. atrora:

AMNH 40812 (30/728). Río Axtla, San Luis Potosí, Mexico.

UMMZ 179990 (1) holotype. Río Axtla, San Luis Potosí, Mexico.

Subgenus *Gambusia**nicaraguensis* species group*G. nicaraguensis*:

AMNH 20849 (10/64). Great Corn Island, Nicaragua.

AMNH 18830 (2/7). Guatemala.

AMNH 28612 (2/8). Río Chagres, Panama.

UMMZ 199461 (73). Port Royal, Honduras.

G. melapleura:

USNM 205559 (372). Shrewsberry River, Jamaica.

USNM 205555 (242). Bluefields River, Jamaica.

G. wrayi:

USNM 104338 (1/12). Roaring stream, Jamaica.

AMNH 74080 (8/104). Kingston Lagoon, Jamaica.

UMMZ 196801 (4). 30 mi east of Montego Bay, Jamaica.

USNM 205578 (193). Patterson Spring, Kingston, Jamaica.

G. gracilior:

USNM 206286 (36). Stony River, Chapelton, Jamaica (cat. as *G. wrayi*).

puncticulata species group*G. yucatana*:

AMNH 32261 (9/79). Laguna Yaxja, Peten, Guatemala.

AMNH 32364 (1/4). Naranjal Reservoir, Peten, Guatemala.

AMNH 32389 (1/38). Laguna Yaxja, Peten, Guatemala.

G. hubbsi:

AMNH 12455 (8) paratypes. South Andros Island, Bahamas.

AMNH 12979 (1/89). Long Island, Bahamas (cat. as *G. puncticulata*).

G. manni (AMNH lots cat. as *G. manni*, but more probably *G. hubbsi*):

AMNH 28804 (10/142). Grand Bahama, Bahamas.

AMNH 28680 (1/10). Berry Island, Bahamas.

AMNH 12459 (1/3). Andros Island, Bahamas.

AMNH 34353 (1/3). Conception Island, Bahamas.

UMMZ 64246 (5). Lake Kilkarney, New Providence Island, Bahamas.

UMMZ 72183 (1) holotype. New Providence Island, Bahamas.

G. hispaniolae:

AMNH 37344 (8/37). Between Port-au-Prince and Lake Miragôane, Haiti.

UMMZ 136377 (11) paratypes. Locality mislabeled as Cuba.

AMNH 78134 (1/1). Source Trou Caiman, Haiti. Exemplar used in descriptive osteology.

AMNH 78135 (6/16). Aquarium material, descendants of fishes caught at Source Trou Caiman, Haiti.

AMNH 37346 (2/11). East of Port-au-Prince, Dominican Republic.

USNM 204865 (1) holotype. Source Trou Caiman, Haiti.

G. bucheri:

UMMZ 143373 (3/6) paratypes. Río Jicotea, Moa system, Oriente, Cuba.

USNM 203149 (1) holotype. Río Jicotea, Moa system, Oriente, Cuba.

G. baracoana:

UMMZ 143375 (3/6) paratypes. Río Miel, Baracoa, Oriente, Cuba.

USNM 203150 (1) holotype. Río Miel, Baracoa, Oriente, Cuba.

G. puncticulata:

AMNH 9192 (2/2). Santa Clara, Cuba.

UMMZ 103336 (191). Artemisa, Piñar del Río, Cuba.

USNM 204402 (41). Río Jaimanitas, Havana, Cuba.

USNM 167691 (50). Cienfuegos Soledad, Santa Clara, Cuba.

G. oligosticta:

USNM 104339 (2/8). Spanish Town, Jamaica.

UMMZ 190129 (92). Port Henderson, Jamaica (cat. as *G. puncticulata*).

G. caymanensis:

USNM 089789 (2/7). Grand Cayman Island, British West Indies.

UMMZ 213615 (20). Grand Cayman Island,

British West Indies (cat. as *G. puncticulata*).

G. howelli:

UMMZ 143374 (9) paratypes. Punta del Este, Isla de la Juventud, Cuba (cat. as *G. puncticulata*).

punctata species group

G. luma:

AMNH 35161 (3/5). Río Sarstún system, Izabal, Guatemala.

AMNH 35096 (1/29). Río Dulce, Izabal, Guatemala.

UMMZ 143565 (1) holotype. Puerto Barrios, Izabal, Guatemala.

G. beebei:

USNM 203162 (163). Lake Miragôane, Haiti.

USNM 203161 (1) neotype. Lake Miragôane, Haiti.

G. pseudopunctata:

AMNH 78136 (1/1). Les Cayes, Haiti.

ANSP 158843 (31). Stream 2 km west Les Cayes, Haiti.

UMMZ 208139 (25) paratypes. Roseaux, Dept. de Sud, Haiti.

USNM 203163 (1) holotype. Roseaux, Dept. de Sud, Haiti.

G. punctata:

AMNH 3081 (1/2). Santa Clara, Cuba.

USNM 203165 (1) neotype. Havana, Cuba.

G. xanthosoma:

UMMZ 210200 (1) paratype. West Bay, Grand Cayman Island, British West Indies.

UMMZ 213616 (17). Grand Cayman Island, British West Indies.

G. rhizophorae:

AMNH 55239 (1/3). Crawl Key, Monroe Co., Florida.

UMMZ 213650 (100). Monroe Co., Florida.

USNM 203223 (1) holotype. Dade Co., Florida.

Other Poeciliids

Alfaro cultratus (Regan, 1908) – AMNH 10589 (2/6)

Brachyrhaphis cascajalensis (Meek and Hildebrand, 1913) – AMNH 37810 (1/43); AMNH 28591 (4/12)

Brachyrhaphis episcopi (Steindachner, 1878) – AMNH 20592 (4)

Brachyrhaphis terrabensis (Regan 1907) – AMNH 20503 (3/9)

Belonesox belizanus Kner, 1860 – AMNH 32027 (1/22); AMNH 27493 (5/5)

Carlhubbisia stuarti Rosen and Bailey, 1959 – AMNH 35103 (6/83)

Cnesterodon sp. – AMNH 35367 (4/30)

Girardinus uninotatus Poey, 1860 – AMNH 37749 (1/4)
Heterandria attenuata Rosen and Bailey, 1979 – AMNH 32911SW (4/76)
Heterandria jonesi (Günther, 1874) – AMNH 36781SW (4/4)
Limia nigrofasciata Regan, 1913 – AMNH 37349 (6/82)
Neoheterandria umbritalis (Meek, 1912) – AMNH 37665 (4/20)
Phallichthys amates (N. Miller, 1907) – AMNH 20593 (2/6)
Poecilia caucana (Steindachner, 1880) – AMNH 28137 (19/99)
Poecilia latipinna (LeSueur, 1821) – AMNH 51452 (6/82)
Poecilia minor (Garman, 1895) – AMNH 35359 (3/11)
Poeciliopsis gracilis (Heckel, 1848) – AMNH 24462 (3/20)
Priapella intermedia Alvarez, 1952 – AMNH 78021 (5/40)
Priapichthys dariensis (Meek and Hildebrand, 1913) – AMNH 28601 (3/28)
Scolichthys greenwayi Rosen, 1967 – AMNH 32887 (5/108)
Tomeurus gracilis Eigenmann, 1909 – AMNH 72910 (5/31)
Xenodexia ctenolepis Hubbs, 1950 – AMNH 24578 (5/187)
Xiphophorus alvarezi Rosen, 1960 – AMNH 36800SW (4/148)
Xiphophorus couchianus (Girard, 1859) – AMNH 22644 (14/14)
Xiphophorus milleri Rosen, 1960 – AMNH 27486 (15/15)

Other Cyprinodontiforms

Adinia xenica (Jordan and Gilbert, 1882) – AMNH 21836SW (2/2)
Aphanius ginaonis (Holly, 1929) – AMNH 28677SW (2/2)
Aplocheilichthys johnstoni (Günther, 1893) – AMNH 41591 (20)
Aplocheilus panchax (Hamilton-Buchanan, 1822) – AMNH 21957 (4/4)
Cubanichthys cubensis (Eigenmann, 1903) – ANSP 60286 (1/1)
Cynolebias adloffii Ahl, 1922 – AMNH 22148SW (1/1)
Cynolebias whitei Myers, 1942 – AMNH 22168 (3/3)
Cyprinodon variegatus Lacepede, 1803 – AMNH 28100 (1/1)
Fundulus grandis Baird and Girard, 1854 – AMNH 21915 (1/1)

Girardinichthys viviparus (Bustamante, 1837) – UMMZ 192379 (55/55)
Kosswigichthys asquamatus Sözer, 1942 – ANSP 89883 (1/1)
Megupsilon aporus Miller and Walters, 1972 – AMNH 38405SW (2/10)
Orestias forgeti Lauzanne, 1981 – AMNH 52113SW (1/4)
Pantanodon madagascarensis (Arnoult, 1963) – AMNH 20526 (1/4)
Profundulus labialis (Günther, 1866) – AMNH 24567 (2/2)
Profundulus punctatus (Günther, 1866) – AMNH 24432 (2/2)
Rachovia sp. – AMNH 22477 (3/3)
Rivulus hartii (Boulenger, 1890) – AMNH 8354 (2/2)
Skiffia bilineata (Bean, 1887) – UMMZ 189050 (42/42)

Other Atherinomorphs

Dermogenys sumatranus (Bleeker) – AMNH 9584 (2/2)
Menidia beryllina (Cope) – AMNH 35721SW (4/12)
Menidia menidia (Moenkhaus) – AMNH 55066SW (2/2)
Oryzias latipes (Temminck and Schlegel) – AMNH 57106SW (8/8)
Parexocoetys brachypterus (Richardson) – AMNH 14133SW (1/2)
Strongylura timucu (Walbaum) – AMNH 27409 (1/1)

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OSTEOLOGY

The following descriptive osteology is based on AMNH 78134, a mature male *Gambusia hispaniolae*, standard length 32.0 mm, and all illustrations in this section are of this specimen except where noted. Comments on variability of characteristics refer to variability within the species or among the species within the genus; the groups delineated by systematically important variabilities are specifically noted.

CRANIUM (figs. 1, 2, 3)

The large, cartilaginous mesethmoid block fills the front of the skull; a small disclike ossification can be seen within. The paired lateral ethmoid bones are affixed to the lateral edges of the cartilage block. Dorsally, the cartilage projects anteriorly under the nasals and posteriorly along the underside of the roofing bones (frontals) at midline. Ventrally, the cartilage extends posteriorly on the dorsal border of the parasphenoid. Anteriorly, the ventral surface of the cartilage is covered by the vomer. The edentulous vomer is triangular, and although broad, the ossification is quite thin.

The lateral ethmoids are twisted, complex bones. On each, the posterodorsal extension meets the anterior edge of the supraorbital section of the frontal, curving underneath it. This section medially attaches to the mesethmoid block. An anteromedial projection of the lateral ethmoid, again along the me-

dian cartilage, serves as articulation point for the autopalatine. Two wings of each lateral ethmoid expand anterolaterally, although these two are sometimes not separated completely.

The only elements corresponding to an infraorbital series in *Gambusia* are the lacrimal (infraorbital 1) and the dermosphenotic (infraorbital 6). The lacrimal is found lateral and anterior to the lateral ethmoid. Sensory nerve foramina are seen in its lateral surface; sometimes a distinct canal is present too. On its medial surface is a small transverse shelf, and posteromedially a small knob. The lateral posterior border attaches to tissues covering the eye. This border sometimes is broken into several sections.

The dermosphenotic is small and teardrop-shaped. It is found posterior to the posterolateral edge of the frontal, which ends in a notch, and anterior to a lateral projection of the sphenotic.

The skull is roofed by three pairs of dermal bones, the nasals, frontals, and parietals, and the median supraoccipital. The nasals are broad, flat, and roughly triangular. Nerve foramina can be seen along a median crest.

The frontals are very large, covering more than half of the skull. They overlap irregularly at midline, until they are separated by the supraoccipital. A bony tube, representing the sensory canal, runs in an anterior-posterior direction, dividing the anterior portion of the frontal into lateral (supraorbital) and medial sections. This bony tube also has nerve foramina piercing the frontal associated with it, just lateral to the tube on the supraorbital side. The lateral portion of the frontal is the dorsal border of the orbit; anterior to it is the lateral ethmoid, posterior the dermosphenotic. A large notch in the posterior section of the frontal accommodates the dermosphenotic. The bony tube and associated foramina are deflected from their straight path toward the dermosphenotic. Although the tube does not continue onto the dermosphenotic, more foramina are seen on this bone.

Parietals come and go among poeciliids; however, all species of *Gambusia* examined possess these thin, elongate bones. Incidentally, *Belonesox* also has well-developed parietals, although they are quite odd in form,

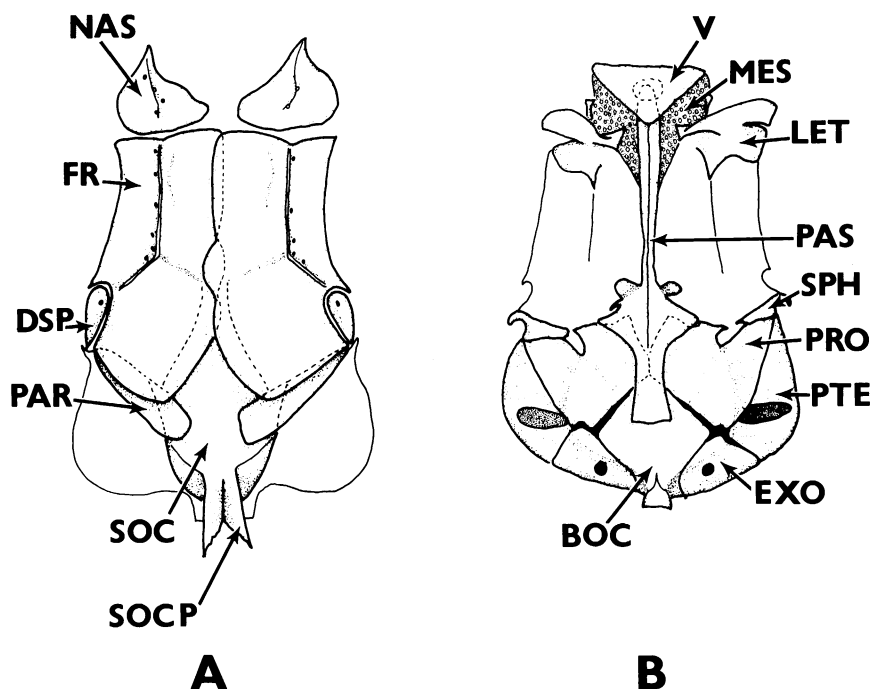


Fig. 1. Cranium of *Gambusia hispaniolae*. A. Dorsal view. B. Ventral view.

being dumbbell-shaped. *Gambusia* parietals are found at the posterior edge of the frontals, which overlie their anterior edge. Medially, the parietals extend further than the frontals, onto the supraoccipital.

The supraoccipital dorsally covers the posterior half of the skull. Its anterior edges are underneath the frontals. Short processes of the supraoccipital project laterally at the anterior edges of the parietals, again ventral to the frontals. Two winglike supraoccipital processes, joined medially, project posteriorly over the end of the skull. The posterolateral extension of the supraoccipital contacts the epioccipital, and, although the supraoccipital does not participate in the border of the foramen magnum, a thin vertical plate extends down from the supraoccipital processes to contact the exoccipitals at the top of the foramen magnum.

The epioccipitals also send off elongate posterior processes, paralleling the supraoccipital processes but slightly below them. The epioccipital bulges posterolaterally, then slopes back in to contact the pterotic anteroventrally, the parietal anterodor-

sally, and the exoccipital ventrally and posteriorly. The upper arm of the posttemporal contacts the epioccipital near the lateral edge of the base of the epioccipital process.

The pterotic (autopterotic; there is no dermal component) forms a lateral shelflike bulge. It is bordered anterolaterally by the sphenotic, anteromedially by the parietal, posteromedially by the epioccipital, and posteroventrally by the exoccipital in dorsal view. In ventral view, most of its medial border contacts the prootic. As a lateral shelf, the pterotic creates a shallow, open fossa above it and a deeper, also open, fossa below it. An elliptical autopterotic fossa, the thin flange of bone separating the course of the horizontal semicircular canal, conspicuously traverses the pterotic also. Laterally, the posterior fork of the hyomandibula contacts the pterotic. The anterior arm of the hyomandibula touches the sphenotic, which is wedged between the pterotic, parietal, dermosphenotic, and frontal dorsally; in ventral view, the sphenotic is just anterior and lateral to the prootic.

The exoccipitals form most of the border of the foramen magnum, excluded only from

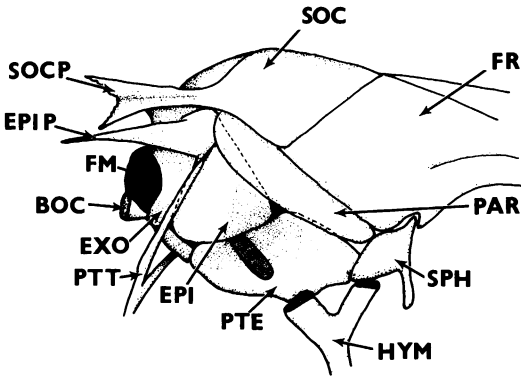
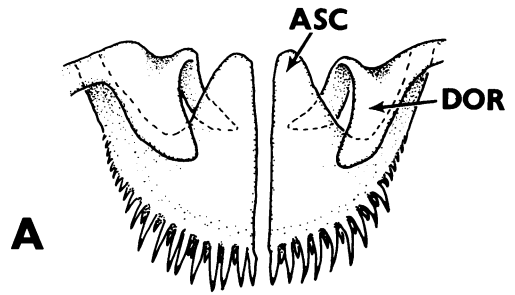


Fig. 2. Oblique dorsolateral posterior view of the cranium of *G. hispaniolae*.

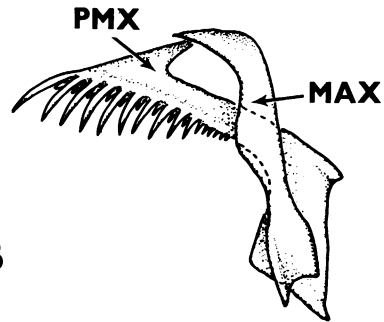
the ventral portion at the basioccipital condyle. Ventrally, the exoccipitals are medially bordered by the basioccipital, laterally by the pterotics, and anteriorly by the prootics. A large jugular foramen is visible. There are no exoccipital condyles; however, the neurapophyses of the first vertebra attach laterally to the exoccipitals at the edges of the foramen magnum (see separate discussion of vertebrae).

The basioccipital ends posteriorly in a centrumlike condyle, which serves as articular point for the first vertebra and, in ventral view, is seen to narrow to a point anteriorly. The basioccipital forms a ventral dome for the basicranium. Its anterior edge is covered by a posterior extension of the parasphenoid.

The prootics are large domed bones, forming much of the floor of the basicranium. Ventrally, they contact each other postero-medially, but are covered and anteriorly separated medially by the parasphenoid. The an-



A



B

Fig. 4. Upper jaw of *G. hispaniolae*. A. Dorsal view. B. Ventral view.

terior edge of each prootic is riddled with small notches and bridges of bone. On each side, the prootic laterally contacts the sphenotic and pterotic, posteriorly the exoccipital, and posteromedially the basioccipital.

The parasphenoid ventrally covers the median part of the basioccipital and prootics. Just anterior to the prootics, two small lateral tabs project dorsally. Anterior to this point, the parasphenoid is a thin median bar that angles dorsally to contact the mesethmoid block anterior to the lateral ethmoid, medial to the lacrimal, and just ventral to the nasals. This long, anterior extension of the parasphenoid has a thin vertical laminar flange.

UPPER JAW (fig. 4)

Two paired bones comprise the upper jaw, the maxillae and premaxillae. These overlap in both their dorsal and lateral aspects. Dorsally the ascending processes of the premaxillae are fairly long, broad, and triangular.

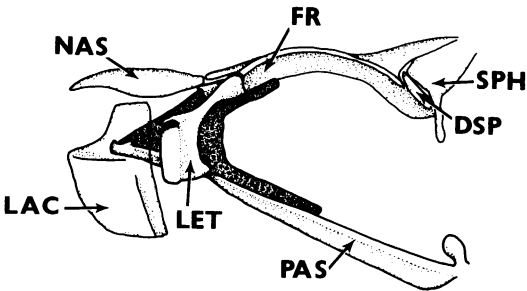


Fig. 3. Lateral view of the ethmoid and orbital regions of *G. hispaniolae*.

They parallel each other along the midline; in most species each ascending process ends in a pointed tip. Some variation is seen, however; the ascending processes may be rounded, squared, or medially pointed. Rounded ascending processes are seen in *Brachyrhaphis* and *Heterandria* (*Belonesox*, because of its elongate jaws, is quite apomorphic for premaxilla structure, and is not particularly useful as an outgroup for this character).

Capping the ascending process is the dorsal process of the maxilla, which has both dorsal and ventral components. The dorsal component is a thumb-shaped laminar sheet of bone, anteromedially directed, that usually partly covers the ascending process. The ventral component runs below the ascending process, is much narrower than the dorsal component, and usually more medially directed, approaching its fellow along the midline. The posteromedial junction of the dorsal and ventral components forms a large bump; just lateral to this bump is a depression, and just lateral to the depression, on the posterior side of the maxilla, one head of the autopalatine articulates. No rostral cartilage was seen in any poeciliid examined.

The thumb-shaped dorsal process of the maxilla is a characteristic of the superfamily Poecilioidea. This group is part of a larger group, Sept. 2 characterized in part by short and narrow ascending processes (see table 5, from Parenti, 1981). Although some poeciliids do have short and narrow ascending processes (e.g., *Xiphophorus*), all *Gambusia* species have ascending processes that are well developed.

In lateral view, the alveolar process of the premaxilla bears teeth back to the level where the maxilla crosses it. Posteroventral to this point, the premaxilla is roughly rectangular, varying from this shape sometimes to form an S-shape (thought to be primitive for cyprinodontoids; Parenti, 1981) by drawing out the posterodorsal corner posteriorly, the posteroventral corner ventrally, and the anteroventral corner curving anterodorsally.

The maxilla laterally covers the premaxilla. It varies from being a straight bar at two points. First, where it crosses the end of the tooth-bearing portion of the premaxilla, there is an anterior swelling, usually rounded in profile but sometimes pointed. Ventral to this

swelling, the maxilla narrows again, until it crosses the ventral margin of the premaxilla. Here there is another widening, more pronounced in some species than in others. The anteroventral tip is usually drawn out ventrally to a point. The dorsal extension of the maxilla also is said to characterize the superfamily Poecilioidea (Parenti, 1981).

Upper jaw teeth consist of an outer row of large recurved teeth and several inner rows of smaller pointed teeth. They are found on the premaxilla from the anterior edge back along the alveolar process to just where the maxilla laterally crosses the premaxilla. Tooth structure is constant for the genus and immediate outgroups, although a wide range of tooth morphologies is observed among poeciliids.

LOWER JAW (fig. 5)

The lower jaw is quite robust, consisting of dentary, anguloarticular, retroarticular, and coronomeckelian (sesamoid articular) bones. Two areas of Meckel's cartilage are prominent; the long thin mentomeckelian cartilage, surrounded by the dentary anteriorly and the anguloarticular posteriorly; and the cone-shaped articular cartilage, mostly surrounded by the retroarticular but dorsally covered by the anguloarticular. The articular ossification of Meckel's cartilage is presumed to be fused to the angular, as is general for clupeocephalans (Nelson, 1973), hence the name anguloarticular. Within the retroarticular, the cartilage is usually completely replaced with ossified tissue, leaving a hollow cone in the bone. Sometimes, however, a cone of cartilage persists in the adult.

The dentary bears teeth quite similar to the upper jaw teeth: an outer row of large recurved teeth and several irregularly spaced inner rows of smaller teeth. Teeth continue posteriorly on the dentary to the beginning of the coronoid process, which reaches posteriorly nearly to the posterior border of the premaxilla, which overlies it laterally. A prominent foramen is seen just below the tooth row, and a sensory canal runs below the level of Meckel's cartilage. A small posterior projection of the dentary carries the sensory canal posteriorly, between the two limbs of the anguloarticular. Below the sen-

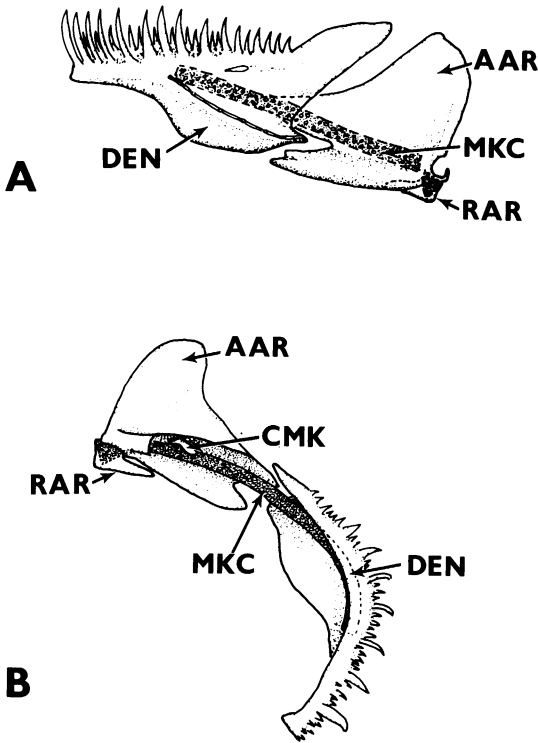


Fig. 5. Lower jaw of *G. hispaniolae*. A. Lateral view (anterior to left). B. Medial view (anterior to bottom right corner).

sory canal, the dentary is angled medially. In a medial view (fig. 5A), it can be seen that this ventral portion of the dentary forms a fossa into which Meckel's cartilage neatly fits. In this view it can also be seen that the dentary expands slightly at the anterior midline symphysis.

The anguloarticular dorsally reaches as high as the coronoid process on the dentary. Anteriorly it is forked; the dorsal, larger limb runs medial to the dentary, and it is this limb that surrounds the mentomeckelian cartilage. A smaller ventral limb also extends toward the medial process of the dentary, but is not overlain by it. The ventral portion of the anguloarticular also angles medially, similar to the dentary, continuing the fossa for Meckel's cartilage. The posteroventral corner of the anguloarticular forms a fossa for the articulation with the condylar head of the quadrate. The retroarticular is not involved in the joint surface, but the dorsal edge of the articular cartilage abuts the ventral margin of the joint.

In medial view, the posterior end of the

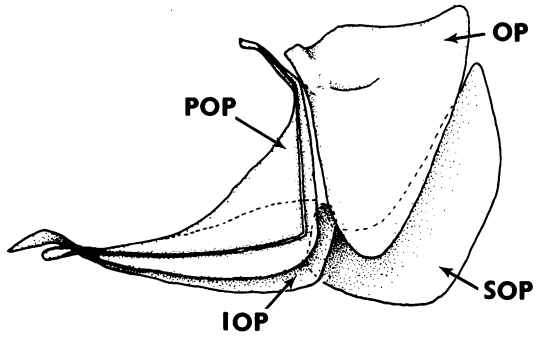


Fig. 6. Opercular apparatus of *G. hispaniolae*, lateral view.

mentomeckelian cartilage is surrounded by a cup of bone, an anteromedial extension of the anguloarticular. Just anterior to this cup is a small sesamoid bone, the coronomeckelian, that lies dorsally on the mentomeckelian cartilage.

The retroarticular, as noted above, ossifies about the ventral portion of the articular cartilage. It is wedge-shaped, fitting into the posteroventral corner of the anguloarticular, and is moderately sized.

OPERCULAR APPARATUS (fig. 6)

The opercle is a large, fairly flat bone with no spines or serrations. It articulates with the lateral side of the hyomandibula, just below the posterior fork on the dorsal part of that bone. The articulation is effected by a raised knob on the opercle.

Lying ventral and medial to the opercle is the subopercle, which projects beyond the limits of the opercle in both its posterior and ventral aspects. It also is a flat, unserrated bone.

The dorsal limit of the preopercle is near the anterior fork of the hyomandibula. Its posterior margin parallels the anterior margin of the opercle, and then it swings forward, narrowing anteriorly. Its anterior extension fits into the medial face of the quadrate, just short of the quadrate-anguloarticular joint. The preopercle also has an entire margin, and carries a distinct sensory canal, running dorsoventrally near the posterior margin of the bone, then turning at a right angle to run anteriorly to the end of the preopercle.

The interopercle is found closely appressed to the medial side of the preopercle, although

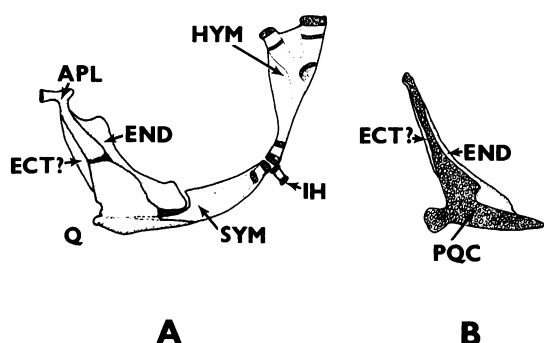


Fig. 7. A. Jaw suspensorium of *G. hispaniolae*, lateral view. B. Embryonic view of anterior half of jaw suspensorium.

it slightly exceeds the borders of the preopercle in its posterior and ventral aspects. Anteriorly, the interopercle narrows, crosses the preopercle dorsomedially, and via ligament is connected to the retroarticular.

JAW SUSPENSORIUM (fig. 7)

The palatoquadrate cartilage of the embryo ossifies in two centers, the autopalatine dorsally and the quadrate ventrally. The dorsal end of the autopalatine is hammerhead-shaped. The large anterior projection of the hammerhead is cartilage-capped and articulates with the maxilla. The hammerhead is somewhat twisted in the middle, so that the posterior head also faces slightly medially. It articulates with a facet on the lateral ethmoid. This facet either lies against the lateral edge of the cartilaginous mesethmoid, or is a small lateral projection from the same position.

There is no dermopalatine, and according to many authors there is no ectopterygoid (Ramaswami, 1945; Parenti, 1981); however, there is a laminar extension of bone along the anterior edge of the palatoquadrate arch, running from the dorsal tip of the arch ventrally to cover most of the anterior surface of the autopalatine and quadrate. This is considered to be an extension of the autopalatine by Parenti (1981), a characteristic of cyprinodontoids. This anterior flange of bone, however, does not preform in cartilage (determined by examination of cleared and stained embryos); its development mirrors that of the endopterygoid; however, whether this flange of bone represents an ectoptery-

goid closely appressed, ankylosed, or fused to the autopalatine (a line between them is visible, but they are neither separable nor independently movable), or whether it represents a laminar perichondral ossification of the autopalatine could not be determined.

The endopterygoid (= mesopterygoid) begins at the posterior head of the autopalatine, and runs along the posterior edge of the palatoquadrate cartilage, investing far into the medial face of the quadrate. A projection of the endopterygoid just ventral to the autopalatine heads is connected via ligamentous tissue to the lateral ethmoid. At its posteroventral edge, the endopterygoid is expanded, projecting past the quadrate to the symplectic.

The quadrate has two sections, the dorsal part that ossifies in the palatoquadrate cartilage, reaching toward the autopalatine, and a ventral section that extends posteriorly under the symplectic. The anteroventral corner of the quadrate forms a condylar head, articulating with the anguloarticular. The anterior ends of the symplectic and preopercle, both rodlike, terminate along the medial face of the ventral part of the quadrate. Ossification of the palatoquadrate cartilage is never complete; in adults, cartilage still can be seen between the autopalatine and the quadrate, as well as between the quadrate and the symplectic.

The hyosymplectic cartilage ossifies into two bones, the hyomandibula and the symplectic; no dermal bones are associated with this region of the suspensorium. The symplectic, as mentioned above, ends in a rodlike, cartilage-capped terminus along the medial face of the quadrate, near the articular condyle. Posterior to the quadrate and endopterygoid, a thin dorsal flange is developed on the symplectic, narrowing again as it approaches the cartilage-capped junction with the hyomandibula. Also articulating at this hyosymplectic juncture is the interhyal.

At its ventral edge, the hyomandibula also bears a cartilage-capped head to articulate with the symplectic and interhyal. Dorsally, the hyomandibula is forked, again with two cartilage-capped heads. The anterior head articulates with the sphenotic, the posterior with the pterotic. A facet to receive the operculum is ventral to the posterior fork.

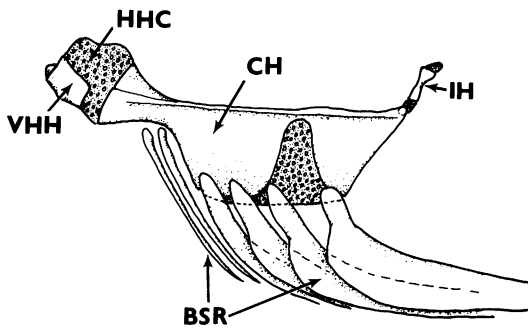


Fig. 8. Lateral view of hyoid arch of *G. hispaniolae*.

HYOID ARCH (figs. 8, 9)

The small ossified interhyal is connected via cartilage tips to the hyomandibula dorsally and to the posterior end of the ceratohyal ventrally. The large ceratohyal can be visualized in two parts, anterior and posterior. The posterior section (posterior ceratohyal; posterohyal of Nelson, 1969; epihyal of many authors, including Rosen, 1964, and Weitzman, 1962) serves as the attachment site for the last of the branchiostegal rays along its lower lateral surface. It is separated from the anterior section (anterohyal of Nelson, 1969; ceratohyal of many authors) by a deep, cartilaginous intrusion. Dorsally, however, the anterior and posterior sections of the ceratohyal are firmly joined by a bridge of bone. The anterior section of the ceratohyal is discussed in two sections. Its posterior half is wide, and bears the branchiostegal rays along its lateral surface. The third of these rays actually articulates sometimes on the cartilage that separates the anterior and posterior sections of the ceratohyal. The anterior half of the anterior section of the ceratohyal narrows sharply, then widens to form a cup around the cartilage of the hypohyal. Two slender branchiostegals articulate medially along this narrowed section; sometimes they merely approach the anterior ceratohyal at its ventral margin, articulating neither medially nor laterally.

According to Parenti (1981), cyprinodontoids have no dorsal hypohyal, and no ossified dorsal hypohyal was found in poeciliid materials examined; however, the hypohyal region is occupied by a large block of cartilage that is posteriorly delimited by the anterior

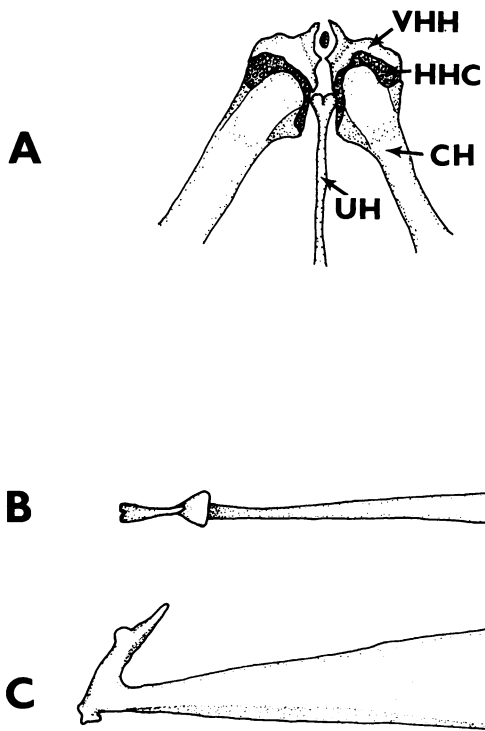


Fig. 9. A. Anterior part of the hyoid arch of *G. hispaniolae*, ventral view. B. Urohyal of *G. hispaniolae*, dorsal view. C. Urohyal of *G. hispaniolae*, lateral view.

ceratohyal. An ossification around the anterior, anteroventral, anteromedial, and anterolateral aspects of this cartilage is interpreted as the ventral hypohyal. Among *Gambusia* species, the extent of the ventral hypohyal ossification is variable. Some species show the ventral hypohyal ossification covering most of the ventral surface, meeting the anterior ceratohyal in a relatively straight line; fishes of the subgenera *Heterophallina* and *Arthrophallus* show this condition. In other species, it is the anterior ceratohyal that covers most of the ventral surface of the hypohyal cartilage, projecting an anteriorly directed ventrolateral lobe and a smaller anteromedially directed lobe. This bilobed head of the anterior ceratohyal is a more conventional arrangement, reminiscent of the situation in many other fishes, where the anteromedially directed lobe contacts the dorsal hypohyal. However, these fishes have no dorsal hypohyal. The dorsal aspect of this region reveals a large expanse of cartilage with

only the anteromedial portion ossified as the medial section of the ventral hypohyal. When the anterior ceratohyal extends forward thus, the ventral hypohyal is sometimes reduced to a triangular shape, not covering the anterolateral corner of the hypohyal cartilage. This condition typifies the *nicaraguensis* species group. Other members of the subgenus *Gambusia* have the ventral hypohyal covering the anterolateral corner of the cartilage.

A group containing poeciliids, procato-pines, *Fluviphylax*, and *Pantanodon* is described by Parenti (1981) as having the ventral hypohyal form a cap of bone over the end of the anterior ceratohyal (see her fig. 28C, p. 399). This condition is found in *Tomeurus*; however, *Gambusia* and other poeciliids examined possess cartilage where the dorsal hypohyal would be, so that the ossifications appear more similar to her figure 28B, the condition found in most cyprinodontoids.

In ventral view, the ventral hypohyals face each other anteromedially in distinct cup-shaped condyles. These are connected to each other by tough connective tissue in which a median ovoid cartilage or ossified bone sometimes appears. This is most probably an adventitious structure, as its appearance is not constant within species, and it is seen on occasion throughout cyprinodontiforms.

The anterior end of the urohyal lies between the posterior ends of the two hypohyals, and is somewhat expanded relative to its posterior shaft. The anterior head varies from being broadly triangular to more commonly being slightly cleft, with a median keyhole and two slightly angled heads, each ligamentously connected to a ventral hypohyal. Posteriorly, the urohyal extends to the level of basibranchial 4. Thin laminar plates extend slightly in a lateral plane.

Laterally the urohyal is seen as a broad median plate, wider posteriorly. Anteriorly is a posterodorsally directed spike, with a small knob that approaches the anterior end of basibranchial 2, and a usually spatulate extension posterior to that knob that runs under basibranchial 2 and is approached by the anterior forks of the first hypobranchials. In some *Gambusia* species, this extension is bifid, each side associated with its respective hypobranchial 1 anterior fork.

The basihyal is a long, triangular bone, comparable in length to the sum of the rest of the basibranchial series. Its narrow posterior end articulates with basibranchial 2, and it is ossified for only one-third to one-half of its length, the broader anterior end remaining cartilaginous.

The branchiostegal rays, as alluded to earlier, are consistently six in number, with two thin anterior rays that attach to (or approach) the narrow part of the anterior ceratohyal, and four larger rays attached to the lateral face of the wide part of the ceratohyal. Although the dorsal heads of these four rays are roughly identical, the rays expand in width ventral to those heads, appearing to have an anterior bulge. This is slight in the first of these rays and most pronounced in the more posterior rays.

DORSAL GILL ARCHES (fig. 10)

There are no suprapharyngobranchials, as is true of most modern teleosts. There also is no first infrapharyngobranchial; its absence is the general condition for Division II atherinomorphs—Beloniformes and Cyprinodontiformes (Rosen and Parenti, 1981). Infrapharyngobranchials 2 and 3 are ossified and have toothplates fused to them. There is no fourth infrapharyngobranchial in atherinomorphs, but there is a fourth infrapharyngobranchial toothplate.

Infrapharyngobranchial 2, with its associated toothplate, is rather small, partially overlain by infrapharyngobranchial 3. It has two cartilage-tipped articular heads, one on the lateral side that is approached by epibranchial 2, and an usually larger one on the anterolateral corner of infrapharyngobranchial 2, which is approached by a similar process on infrapharyngobranchial 3. The recurved teeth of the infrapharyngobranchial 2 toothplate face slightly more anterior than those of the infrapharyngobranchial 3 toothplate, which are more ventrally directed.

The large infrapharyngobranchial 3's and their toothplates are the major elements in the dorsal gill arches. Infrapharyngobranchial 3 has three cartilage-tipped articular heads. Anteriorly, one approaches its counterpart on infrapharyngobranchial 2. Near the posterolateral edge of infrapharyngobranchial 3, a small articular head contacts epibranchial 3.

Finally, the posterior edge of infrapharyngobranchial 3 is dominated by a broad articular head that receives the equally broad epibranchial 4. On the infrapharyngobranchial 3 toothplate, the large teeth curve medially. In *Gambusia*, but not in immediate outgroups, these teeth are bicuspid or serrate along their inner edge. The medial teeth in members of the subgenus *Heterophallina* are exaggeratedly deformed from a simple curve cone; they have a serrate bump or pad along the medial side of the tooth.

The infrapharyngobranchial 4 toothplate is fairly small, beginning at the posterior edge of infrapharyngobranchial 3 and extending just slightly beyond epibranchial 4. Its teeth are smaller than those associated with infrapharyngobranchial 3.

There are four epibranchials. Generally in cyprinodontiforms, epibranchial 1 has no distinct uncinatous process (Parenti, 1981). Rather, the base of this element is broadened, and its posterior edge serves as articular point for the interarcual cartilage. This type of epibranchial 1 is seen in outgroups studied and many *Gambusia* species as well. However, members of the subgenus *Heterophallina* and of the *nobilis* species group of the subgenus *Arthrophallus* regularly have uncinatous processes on their first epibranchials. Other members of the subgenus *Arthrophallus* usually do not have such an uncinatous process. And, more confusingly, whereas most members of the subgenus *Gambusia* do not typically have these uncinatous processes, they occasionally do, even varying from the left and right sides of the same fish. A distinct uncinatous process on epibranchial 1, leading to the interarcual cartilage, can be considered a derived condition at this level, but the character is variable in the subgenus *Gambusia*. The orientation of epibranchial 1 is interesting also. It does not run parallel to the other epibranchials, but points almost directly anteriorly. This condition is common to many cyprinodontiforms.

The interarcual cartilage, when present, arises near the posteromedial edge of epibranchial 1 when epibranchial 1 has no uncinatous process, or near the uncinatous process of epibranchial 1 when present. The general acanthomorph condition is for the interarcual cartilage to run from the uncinatous process of epibranchial 1 to the cartilage-tipped

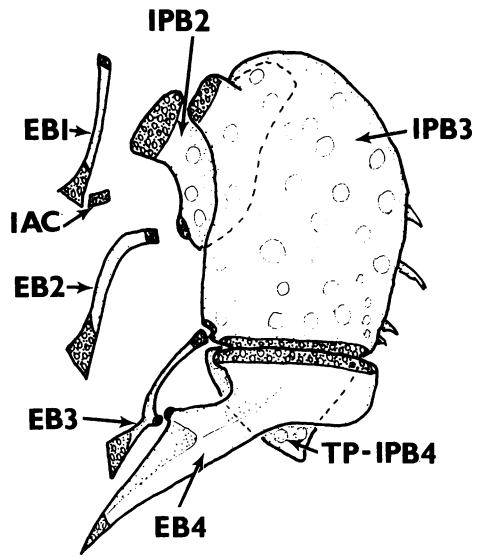


Fig. 10. Dorsal gill arches of *G. hispaniolae*, dorsal view, right side only.

process of infrapharyngobranchial 2. In cyprinodontoids, the interarcual cartilage is reduced in size, and rarely approaches infrapharyngobranchial 2. In *Gambusia*, the maximum length of interarcual cartilage seen is roughly one-third of the length of epibranchial 1. Often it is reduced to a small ball of cartilage, and sometimes it is absent altogether.

Epibranchial 2 is a slender, slightly twisted bone that medially approaches infrapharyngobranchial 2. It never has an uncinatous process in *Gambusia*; the generality of that lack is unclear, as it is absent in cyprinodontiforms and some other atherinomorphs, but not in beloniforms.

Epibranchial 3 is similarly slender, but it does bear an uncinatous process, fairly close to its base. (In fact, this bone looks quite similar to epibranchial 1 when it bears an uncinatous process.) The medial tip of epibranchial 3 contacts a small cartilage-tipped process on infrapharyngobranchial 3. The uncinatous process, directed posterodorsally, approaches the uncinatous process of epibranchial 4.

Epibranchial 4 is much larger than the other epibranchials, forming the major support for the dorsal gill arch elements, as is the general condition for atherinomorphs (Rosen and Parenti, 1981). Its broad medial head contacts infrapharyngobranchial 3 and the toothplate of infrapharyngobranchial 4. The

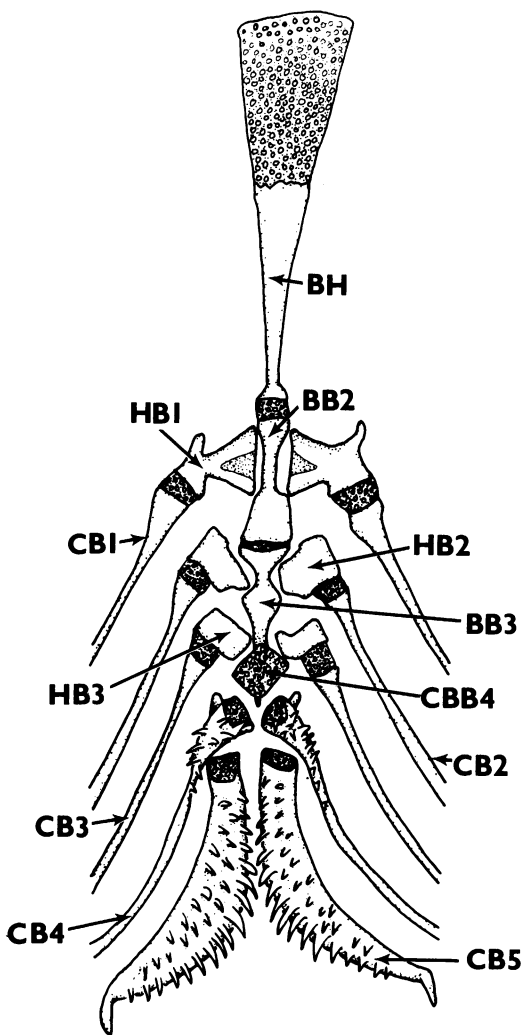


Fig. 11. Ventral gill arches of *G. hispaniolae*, dorsal view.

uncinate process arises from the anterior side of the bone, pointing dorsolaterally toward the uncinate process of epibranchial 3. Lateral to the uncinate process, the bone extends a thin flange, then tapers to contact the ceratobranchials.

VENTRAL GILL ARCHES (fig. 11)

Ceratobranchials 1, 2, and 3 are slender, rodlike elements running from their respective hypobranchials ventrally to their respective epibranchials dorsally. They are heavily adorned with gill rakers.

Ceratobranchial 4 contacts epibranchial 4

dorsally, but as there is no hypobranchial 4, ventrally it approaches the cartilaginous fourth basibranchial. The medial head of ceratobranchial 4 is cartilage-tipped. Just distal to this is an anterolaterally directed flange. In all species of *Gambusia* examined as well as *Belonesox*, *Brachyrhaphis*, and some other poeciliids, there are teeth on ceratobranchial 4, most heavily concentrated near the medial head but extending along one-third of the bone's length. These teeth have been hypothesized to represent fused gill rakers (Gosline, 1963; Nelson, 1969). This a character of spotty distribution within poeciliids, within cyprinodontiforms, and within atherinomorphs.

Ceratobranchial 5 is a much larger bone, bearing only teeth, no gill rakers. Anteriorly, the cartilage-tipped head approaches the medial head of ceratobranchial 4. The two ceratobranchial 5's are triangular-shaped and, although they are separate bones, they are close together along the midline, until each curves dorsolaterally toward its respective side. Ceratobranchial 5 is covered with small to moderately sized conical teeth, and larger, somewhat recurved teeth are found along the inner curve of the bone. Posteriorly, ceratobranchial 5 tapers to a cartilage-tipped point that approaches epibranchial 4. On the medial side of this point is a posteriorly directed process, shaped like a shark's tail. Ventrally, each ceratobranchial 5 has a large median flange, extending directly ventrad, with a hook at the anterior end.

There are three pairs of hypobranchials. There is a good deal of variability in the form of hypobranchial 1. It can be described as having two parts: a medial triangular part that points laterally so that the broad flat base of the triangle articulates with a narrow part of basibranchial 2, and lateral to this triangle, a square or diamond-shaped base. Such a form of hypobranchial 1 is found in many species of *Brachyrhaphis* and *Heterandria*. Other species of these genera, as well as most species of *Gambusia*, have hypobranchial 1 modified in that the triangular part is medially cleft, resulting in a forked hypobranchial 1 with two medial articular heads. The posterior, usually wider, head articulates with the constricted part of basibranchial 2. The anterior head is angled somewhat ventrally,

and approaches the dorsal, ventrally directed flange of the urohyal. Variation occurs with respect to the depth of the cleft, the degree of separation of the two heads, and the relative sizes of the two heads, compared to each other.

In addition, there is variation in the lateral part of hypobranchial 1. Some species of *Gambusia* (particularly those in the subgenus *Gambusia*) have an anteriorly directed process along the lateral edge of hypobranchial 1. In other species, and outgroups examined, this process is indistinct or absent.

Forked first hypobranchials are not unique to *Gambusia* or its close relatives. Some, but not all, poeciliids have them, and I have noticed the character in some other cyprinodontoids (*Aphanius*, *Cubanichthys*; *Orestias*, in Parenti, 1984), some aplocheloids (*Rachovia*, *Rivulus*), and atherinoids such as *Atherinella* (Chernoff, 1986); however, the forked hypobranchial 1 with a distinct lateral process seems to be unique to *Gambusia*.

Hypobranchial 2 is similarly composed of a lateral box and a medial triangle, but these shapes are less distinct, and the element is neither forked nor does it have a lateral process. Hypobranchial 2 medially articulates with a constricted part of basibranchial 3.

Hypobranchial 3 is closer to being a simple rectangle in shape. Medially it articulates with a second narrowing in basibranchial 3 at the end of its ossified portion. All three pairs of hypobranchials primarily stain blue, although clear red ossified portions are seen along the lateral and anterior edges.

Cyprinodontoids have two ossified basibranchials. Parenti (1981) hypothesized that this represents a loss of basibranchial 1, rather than a fusion event. Therefore, basibranchial 2 anteriorly contacts the basihyal, and is posteriorly flared where it contacts basibranchial 3. Similarly, the anterior head of basibranchial 3 is flared, then the bone narrows at the spot where the second hypobranchials articulate with it. Just beyond that point, the bone flares out laterally, forming wings. These wings are a characteristic of the subgenus *Gambusia*; other subgenera in the genus have a relatively straight basibranchial 3. Posterior to its articulation with hypobranchial 3, basibranchial 3 extends further back, ventral to basibranchial 4 and cerato-

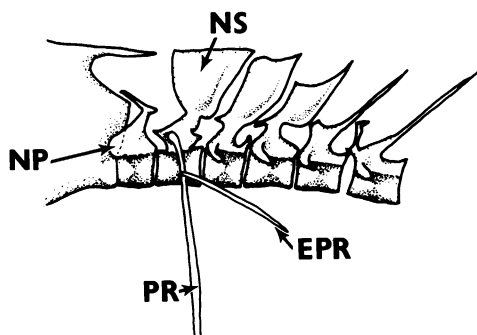


Fig. 12. Lateral view of the anterior vertebrae of *G. hispaniolae*. Only the first pleural and epi-pleural ribs are shown.

branchial 4, but is only cartilaginous in this region.

A cartilaginous basibranchial 4 occupies a central position to the third hypobranchials anteriorly and the fourth ceratobranchials posteriorly. Its shape is variable among species, ranging from diamond to hexagon to octagon to spade. Dense, blue-staining connective tissue often connects the two third hypobranchials, basibranchial 4, and the two fourth ceratobranchials into one unit.

VERTEBRAE (figs. 12, 13, 17A, 18)

Total vertebral number in the genus ranges from 29 to 33, usually 30 or 31, with 12 to 14 precaudal vertebrae and 15 to 19 caudal vertebrae (not counting the terminal half-centrum of the caudal skeleton).

The centrum of the first vertebra fits neatly against the centrumlike basioccipital condyle; like other poeciliids, *Gambusia* has no exoccipital condyles. The neurapophyses of the first vertebra are applied to the lateral sides of the skull near the centrum. As the neural arch continues dorsally, the neurapophyses of each side retreat from the skull, meeting at midline. Once joined, the neural arch is now directed sharply forward, pointing anterodorsally, to again contact the skull. This projection of the first neural arch lies on top of the exoccipitals at the dorsal border of the foramen magnum. This intriguing form of the first vertebra is found in all members of the tribe Gambusiini and some of the Heterandriini; however, other groups of poeciliids have a completely different form of the first vertebra.

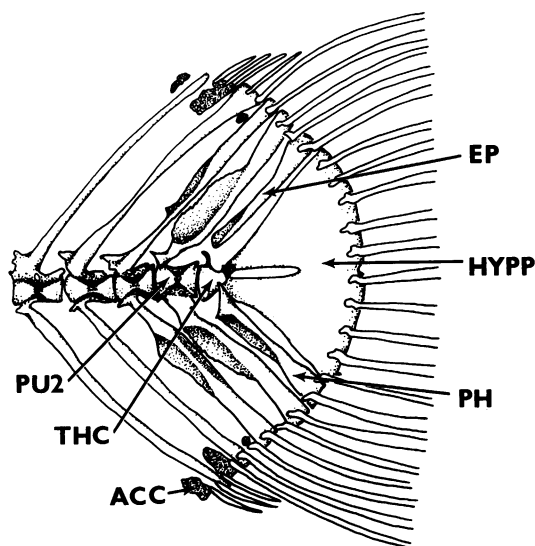


Fig. 13. Caudal skeleton of *G. hispaniolae*, lateral view. Only the right halves of the fin rays are shown.

The second, third, and fourth vertebrae have neural spines that are greatly expanded in the anterior-posterior plane. The parapophyses are found rather high on these anterior vertebrae, although the parapophyses gradually move to a more ventral position in subsequent vertebrae. A pleural rib articulates along the posterior edge of each parapophysis. The first pleural rib is borne upon the second vertebra, a distinctive feature of cyprinodontiforms (Rosen, 1964; Parenti, 1981). Epipleural ribs, extending posterolaterally from each pleural rib, also begin here, and are found through to about the ninth or tenth vertebra.

The neural arch of the fifth vertebra is sometimes slightly expanded, but usually it and always the sixth vertebra assume a more conventional form, seen throughout the pre-caudal vertebrae. The neural prezygapophyses rise anterodorsally and meet in midline, forming a complete arch. The elongate neural spine, angled posteriorly, forms when neural arch material from each side of the centrum extends dorsally to midline, then lengthens as a single unit. A small neural postzygapophysis usually is present also.

A few anterior caudal vertebrae, i.e., those vertebrae bearing hemal arches (and spines, here), also bear pleural ribs. In males, these

vertebrae are modified for gonopodial support. In females, these vertebrae also are unconventional; they are discussed in conjunction with the female anal fin.

The form of the caudal vertebrae posterior to the anal fin can be seen in figure 13. The neural arches and spines are generally as described for pre-caudal vertebrae, although the neural prezygapophyses usually do not extend far enough to meet in midline; rather, they approach the postzygapophyses of the preceding vertebra. The hemal arch and spine mirror the neural side, although with smaller zygapophyseal processes. A hemal canal, beginning at the first caudal vertebra (not before) runs through the hemal arches.

CAUDAL FIN (fig. 13)

The terminal half-centrum, representing the first preural centrum plus the first two ural centra, is fused to the single hypural plate, which is a fusion of hypurals 1–5. The half-centrum curves dorsally, and in some small specimens it extends a short way along the dorsal edge of the hypural plate. There seems to be some neural arch material (presumably of the first ural vertebra) incorporated here at the posterodorsal edge of the half-centrum in embryos; this suggests possible homology with the urostyle of many other fishes (also noted by Hollister, 1940). However, in most fully formed adults, the “urostyle” material is completely incorporated into the hypural plate, and the half-centrum ends abruptly, with a small hook projecting posterolaterally on each side. Anteriorly on the half-centrum, neural arch material (presumably of the first preural vertebra) forms a dorsal projection on each side; these usually meet at the midline. No extension into a neural spine is seen.

All hypurals arise from the half-centrum. Varying degrees of fusion of the hypurals are seen in the genus; however, within any particular species, the pattern observed is fairly constant. *Belonesox belizanus* has two symmetrical hypural plates, the lower plate presumed to represent hypurals 1 and 2, the upper hypurals 3, 4, and 5. The medial edges of the two plates are straight and parallel. *Gambusia luma* exhibits a pattern common in the genus, where there are two hypural plates, as in *Belonesox*, but their medial edges

are not straight. Instead, there is an indented notch, starting at the half-centrum and extending about two-thirds of the length of the hypural plate. These symmetrical notches look like a keyhole. The two plates are separate distal to the keyhole. This pattern is typical of most of the subgenus *Gambusia*, but appears occasionally elsewhere in the genus. *Gambusia hispaniolae* shows the other popular pattern for *Gambusia*. Here, the keyhole notch is present, but the hypurals are fused distal to the keyhole, forming a single hypural plate with a hole in it. Sometimes there is a small notch in the posterior edge of the plate, directly distal to the keyhole. The size of the keyhole also varies. The final pattern seen occasionally in *Gambusia* has no keyhole at all; instead a solid hypural fan is fused to the half-centrum. This is found only in several derived members of the *senilis* species group.

Although these varying degrees of fusion might easily be envisioned as a transformation series, the polarity of such a series is not clear. All four states described above are found throughout the Poeciliidae, and though *Belonesox* has the unfused state, species of *Brachyrhaphis* exhibit all states of fusion. Ontogeny offers some help, as embryos generally have two separate hypural plates. The shape of these two early plates (e.g., see fig. 44D) is common to most species of *Gambusia*, but does not represent any of the adult stages. No species has been observed to pass through several different stages to reach the adult state; instead, the adult state is formed directly from the embryonic state.

The parhypural articulates with the terminal half-centrum, but is not fused with it. It ends posterodorsally with the hypurapophysis.

The single epural dorsally mirrors the position of the parhypural; however, it does not articulate with the terminal half-centrum. The form and development of this epural suggest that it represents a detached neural spine, presumably of the first preural vertebra, serially homologous to the neural spines (not arches) of preceding centra. A similar relation between the parhypural and the preceding hemal spines is also suggested, although the fate of the hemal arch material for the first preural vertebra is unclear.

Preural vertebra 2 bears a full neural arch and spine, as well as a full hemal arch and spine. The neural and hemal spines of the second and third preural vertebrae have thin laminar extensions, as do the epural and parhypural.

Principal caudal fin rays are borne on the hypural plate, the epural, the parhypural, and the neural and hemal spines of the second, third, and often fourth preural vertebrae. The neural and hemal spines of the fourth and fifth preural vertebrae also are involved in the support of procurrent fin rays. Lying between the distal tips of the hemal spines of the sixth and fifth, fifth and fourth, and fourth and third preural vertebrae are small blocks of accessory cartilages that also are involved in fin-ray support. Three blocks of accessory cartilage also are found between the distal tips of the neural spines of the same vertebrae.

DORSAL FIN (fig. 14)

The number of rays in the dorsal fin ranges from 7 to 10 in the genus. In a young specimen, each fin ray is supported by a long proximal radial and a small round distal radial. In the adult fish, a medial radial has separated off from the distal end of each of the proximal radials except the first. The proximal and medial radials often remain connected by intervening cartilage.

The proximal radials extend between the neural spines, sometimes abutting their dorsal tips. When this happens, the dorsal part of the neural spine often becomes cup-shaped, sometimes with a median hole in the cup.

The first proximal radial has an enlarged anterior keel. Subsequent proximal radials have thin laminar flanges also, but not as extensive as the first.

There is an extra element at the posterior end of the dorsal fin (the "end piece" of Weitzman, 1962). Rarely does it completely ossify. Its proximal end is fingerlike, mimicking a small proximal radial. It is found close to the medial radial of the last dorsal fin ray; sometimes it is inseparable from it. Its serial homology is unknown.

Gambusia, and all other cyprinodontoids, have no rudimentary rays anterior to the first dorsal fin ray; i.e., anterior to the ray that is associated with the first proximal and distal

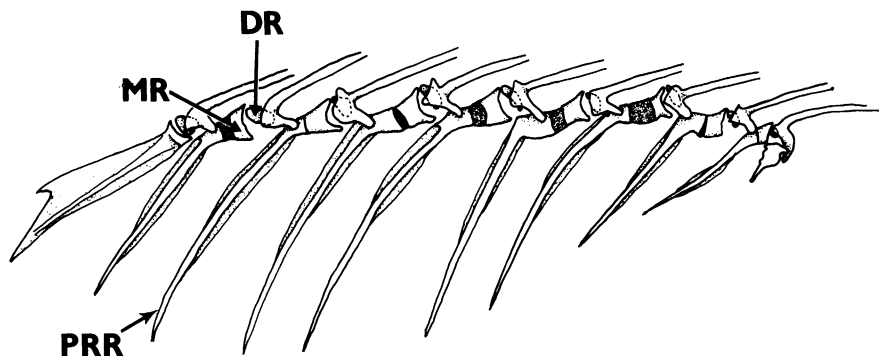


Fig. 14. Dorsal fin skeleton of *G. hispaniolae*, lateral view. Only the proximal ends of the right halves of the fin rays are shown.

radials. Parenti (1981) calls this character "loss of first dorsal fin ray"; strictly speaking, the character should be "loss of ray(s) anterior to the first dorsal fin ray"; although the groups described by these two characters are the same.

PECTORAL GIRDLE AND FIN (fig. 15)

The posttemporal is forked. The longer dorsal arm contacts the epioccipital anteriorly; the lower arm, that points anteroventrally, is about half the length of the upper arm, and does not contact the skull. The lower arm is often reduced or fragmented, but always present in this genus. The ventral base of the posttemporal laterally covers the dorsal part of the supracleithrum.

The small supracleithrum is shaped like an upside-down teardrop, and is sandwiched between the posttemporal laterally and the cleithrum medially.

The cleithrum consists of an anterior face, a lateral wing, a medial wing, and a medial face. The anterior face is roughly diamond-shaped. The lateral and medial edges of the anterior face are raised and thickened, and the ventral extension of this face meets its counterpart at the midline. The lateral wing begins dorsally at the top of the anterior face, and extends laterally almost to the scapular foramen. It narrows abruptly ventral to the scapula. The medial wing mirrors the lateral wing but extends further—dorsally to the posttemporal and supracleithrum, and ventrally to the coracoid. The medial face is firmly affixed to the medial side of the scapula and upper part of the coracoid, and together

with the scapula it forms most of the border of the scapular foramen. The dorsal extension of this face meets the dorsal part of the medial wing, the supracleithrum, and the posttemporal. Posteriorly, the dorsal edge of the medial face forms a thumb-shaped projection.

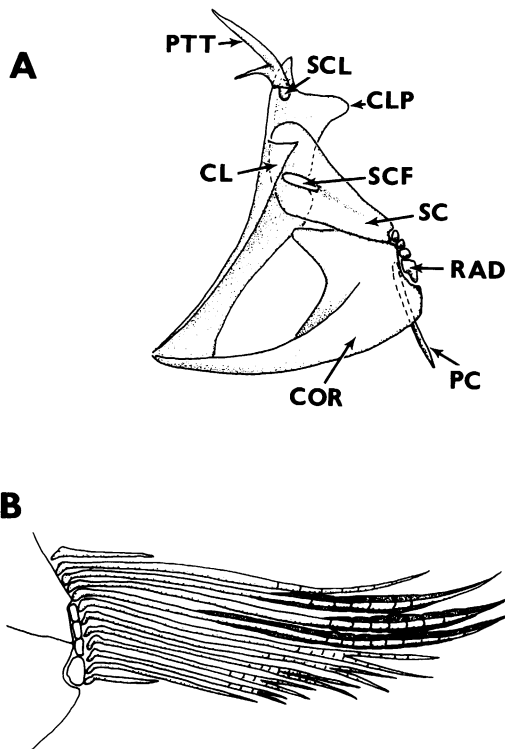


Fig. 15. Pectoral girdle and fin of *G. hispaniolae*. **A.** Lateral view, fin removed. **B.** Pectoral fin, lateral view. Modified extension on rays 3–5 are stippled darkly.

This is similar in shape and position to the "scapular process" of *Cyprinodon*, although not as large. Similar projections are seen in *Profundulus*, some aplocheiloids, and most poeciliids. This cleithral projection is particularly elongate in the *rachowi* species group, of the subgenus *Heterophallina*.

The scapula is anteriorly affixed to the lateral edge of the medial face of the cleithrum. It is a roughly triangular flat bone, its most acute angle posteriad. The scapular foramen is oval, with its long axis running anterior-posterior. When the pectoral girdle is fully formed, the scapular foramen is confined to the anterior third of the scapula; however, in juveniles, the foramen more closely resembles a cleft, running posteriorly almost to the border of the scapula. The medial face of the cleithrum also participates in the border of the scapular foramen; this usually signals the posterior limit of the cleithrum.

Ventrally, the scapula is bordered by the coracoid. Its major flat surface is comma-shaped, running from the scapula to meet the ventral tip of the cleithrum. A second surface, projecting laterally, runs from the anteroventral edge, about three-quarters of the way up along the coracoid.

Four radials fit neatly into a recess in the posterior edge of the borders of the scapula and coracoid. The dorsal three radials are roughly cube-shaped; the fourth is somewhat larger than the others and more irregularly shaped.

An elongate postcleithrum arises along the medial side of the coracoid, just anterior and ventral to the radials. Parenti (1981) labeled this as postcleithrum 3, following Weitzman (1962). It tapers posteroventrally, often abutting the first rib. There is no first postcleithrum in poeciliids, although most other cyprinodonts have this scale-shaped bone just posterior to the thumb-shaped process of the cleithrum. No cyprinodont has a bone in the position of Weitzman's (1962) postcleithrum 2, and, as is true for all neoteleosts, there is no mesocoracoid.

The pectoral fin of females is quite conventional, with 12 to 14 pectoral fin rays, the top three and bottom three unbranched. In males, however, the second, third, fourth, fifth, and sometimes sixth pectoral fin rays are modified, presumably to support the gon-

opodium during copulation (Hubbs and Reynolds, 1957). The second, third, fourth, and fifth fin rays, particularly, are elongated, and their distal third curves upwards. This curve becomes quite pronounced in some species, most spectacularly in *G. heterochir*. There is a bit of variation in the degree of modification along these rays, but the basic pattern is for each segment in the middle third of the fin ray to thicken and produce a laminar dorsal extension. Sometimes the extension of each segment is kept separate, giving the fin ray a scalloped appearance; other times, these extensions, and sometimes the segments themselves, anastomose. Turner (1942c) described the morphogenesis of the pectoral fin modification in the male of *Gambusia affinis*, as well as partial induction of the character in females when treated with androgenic hormones. This pectoral fin modification is seen in all species of *Gambusia*, including *G. vittata*, although its development is very weak in *G. luma*. It is not seen in any other poeciliid. According to Turner (1942c), the final length of the elongated pectoral fin rays 2, 3, 4, and 5 is dependent at least in part on the length of time that male reproductive hormones are maintained at proper concentrations. This, in turn, depends on the size at which the fish matures, more rapidly at a small size or more slowly at a larger size.

PELVIC GIRDLE AND FIN (fig. 16)

The two pelvic bones lie parallel, with their posteromedial extensions overlapping. In ventral view, the long anterior extension of the bone has a bony tube in its center. A vertical flange projects ventrally from this tube on the anterior third of the bone. At the posterior terminus of the tube is a tablike projection, near which the ventral half of the lateralmost pelvic ray articulates. The dorsal half of that ray articulates near a notch in the posterolateral border of the bone. The other five pelvic fin rays articulate along the posterior border of the bone; this area is angled slightly dorsally. No radials were observed, nor was a significant ischial process noted.

In lateral view, the posterodorsal portion of the bone rises in a dorsal process. The shape of this process is variable, sometimes

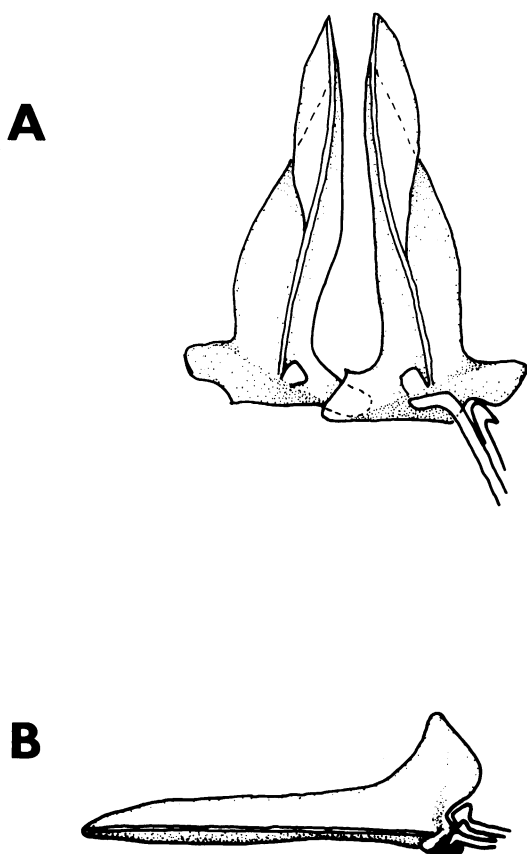


Fig. 16. Pelvic girdle of *G. hispaniolae*. A. Ventral view. Only the outer two fin rays are shown. B. Lateral view.

angled anteriorly or posteriorly, sometimes flat or squared. The aforementioned tab also is evident in this view, at the posteroventral corner.

FEMALE ANAL FIN (fig. 17)

The proximal radials of the first five anal-fin rays are anterior to and lean on the hemal arch and spine of the 14th vertebra. This vertebra also bears a parapophysis and pleural rib. The next caudal vertebra also bears a parapophysis; sometimes a small rib articulates with it too. Parenti (1981) noted that many poeciliids and some of their relatives show this condition.

There are 11 anal-fin rays. Except for the first and last, each is supported by proximal, medial, and distal radials. The proximal and distal radials are always joined by a large ball of cartilage; the medial radial never completely separates off. The ventral ends of the proximal radials often develop small anterior and posterior wings to grab the cartilage. The distal radial is a small ball of cartilage that has not been seen ossified. It is at least partly obscured by the anal-fin ray, as it is held between the anterodorsal tips of the two halves of the fin ray.

The first anal-fin ray lacks any ossification of a medial radial, as does the last. The proximal radial of the last anal-fin ray is reduced,

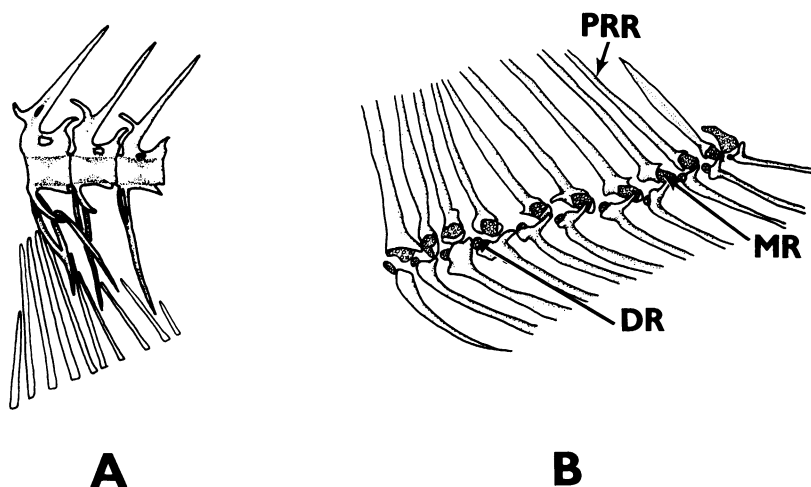


Fig. 17. Anal fin skeleton of a female *G. hispaniolae*. A. Lateral view of hemal spines and proximal anal radials. B. Closer lateral view of proximal, medial, and distal anal radials. Right side only shown for proximal radials and fin rays.

irregular in shape, and often not completely ossified.

GONOPODIAL SUPPORT (fig. 18)

The skeletal support of the gonopodium involves modification of two types of bones. The hemal arches and spines of the 14th, 15th, and 16th vertebrae are changed into gonapophyses, and the anterior proximal radials of the anal fin are modified into the gonactinostal complex.

The first gonapophysis projects anteroventrally from the anteroventral edge of the centrum of the 14th vertebra at approximately a 45° angle. Near the base of the first gonapophysis, a small parapophysis extends backwards, almost always bearing a small rib. The first gonapophysis extends anteriorly the length of three centra, where it meets the gonactinostal complex. This gonapophysis is sometimes thickened along its posteroventral edge, and sometimes bowed.

The second gonapophysis extends forward just behind the first. It often has a small parapophysis, but usually does not bear a rib. In *Gambusia luma*, the second gonapophysis is identical to the first, but in all other species, the second gonapophysis develops posteriorly directed uncini on each side. (The lack of such an uncinate process on the first gonapophysis is a synapomorphy of the genus.) The ventral outline of the second gonapophysis, from the anterior extension to the end of the uncini, varies from being softly rounded to almost horizontal. In some taxa, particularly in *G. hispaniolae*, the posterior ends of the uncini are slightly forked.

Some *Gambusia* species usually have only these two gonapophyses; this condition unites the *nobilis* and *senilis* species groups. Most, however, develop a third, again with uncini, although the uncini of the third gonapophysis are usually not as long as those of the second. The anterior projection of the third gonapophysis is bowed slightly dorsally, whereas the first and second gonapophyses are bowed slightly ventrally. The third gonapophysis does not generally bear parapophyses.

Turner (1942b) described the formation of the gonapophyses in development, and the partial induction of gonapophyses in females following hormone treatment. Rosen and

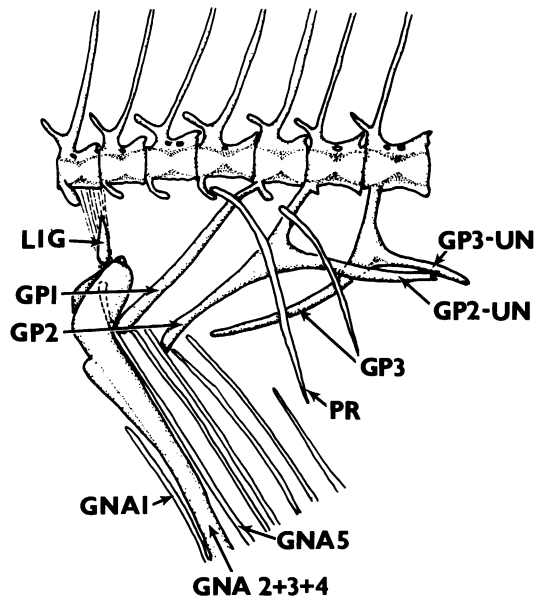


Fig. 18. Gonopodial suspensorium of *G. hispaniolae*, lateral view.

Kallman (1959), in a series of experiments, investigated the possibility of an inductive relationship between the gonactinosts and gonapophyses.

The gonactinostal complex is of constant form in the genus and in its sister taxon, *Belonesox*. The first proximal anal radial is not involved and rather reduced. The second, third, and fourth proximal anal radials grow together and elongate, forming a column. The column has a small anterior wing, and expands dorsally to form a cup, open at the top. The fifth proximal anal radial also is elongate but separate. It lies along the posterior edge of the column, and projects into the dorsal cup. In other poeciliids, the fifth proximal anal radial is incorporated into the gonactinostal complex and does not stand freely.

From the dorsal tip of the fifth radial, a ligament connects the gonactinostal complex to the ventral side of the tenth vertebra (the fourth vertebra anterior to the first gonapophysis). In this ligament is a small bone called the ligastyle, that varies from being a long thin splint, to a teardrop, to a round ball, or it may be absent altogether.

Turner (1942b) has shown that the 13th vertebra is, in fact, the first caudal vertebra, upon which a hemal arch and spine form. The hemal arch is subsequently histolyzed,

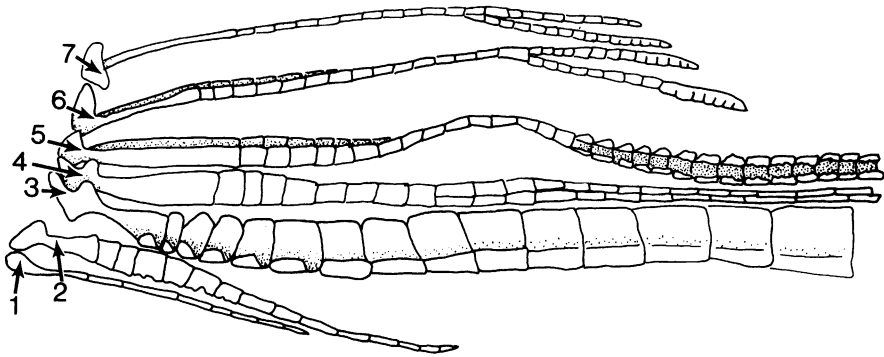


Fig. 19. Lateral view of the proximal part of the anal fin of *G. hispaniolae*, rays 1–7.

and the hemal spine of the 13th vertebra becomes associated with the ligament that attaches to the anterior vertebra as the ligastyle. He showed that the same process of histolysis of the first hemal arch occurs in females also, and a small remnant of the hemal spine is sometimes seen in small females; however, the female “ligastyle” never becomes associated with a suspensory ligament or migrates forward, and in larger females, it too is completely histolyzed.

The sixth and seventh proximal anal radials parallel the gonactinostal complex, but are dorsally limited by the first gonapophysis. Similarly, the second gonapophysis provides the dorsal border for the eighth and ninth proximal anal radials.

The medial radials of the anal fin also are modified for gonopodial support. The medial radials of the second, third, and fourth anal-fin rays are fused to the proximal radials, as part of the columnar gonactinostal complex. The medial radials of the fifth, sixth, and seventh anal-fin rays, however, are separate units and highly developed. Each produces an anterior spike, and expanded lateral processes, facing posterodorsally.

GONPODIUM (figs. 19, 20)

The main units of the gonopodium are anal-fin rays 3, 4, and 5, which, at the onset of sexual maturity, elongate, thicken, and differentiate. The first anal-fin ray is reduced to a small splint, and the second, although thickened at its base, also is relatively short. The thickening at the base of ray 2, however, is unique to *Gambusia*. The sixth, seventh, and,

to a lesser degree, eighth anal-fin rays, while they do not elongate, are specialized at their distal tips. These branched rays become thickened and swollen, due to increased segmentation distal to the branching point. There is sometimes a bit of anastomosis of these segments, making these fin ray tips look scalloped or paddlelike.

The third ray is very thick, from its base to just before the terminal specializations. This is not a branched fin ray. At the distal

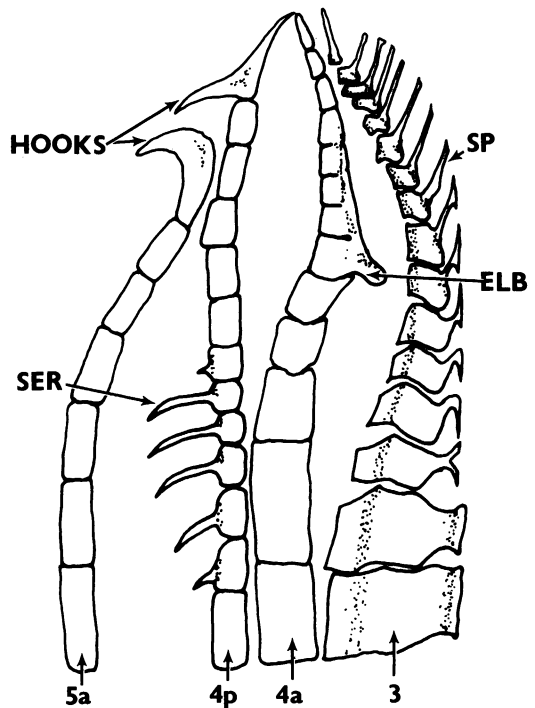


Fig. 20. Gonopodium of *G. hispaniolae*.

tip of the gonopodium, segments of the third ray develop spines along the lateral (anterior) edge. (A note on directional terminology: when the gonopodium is being used, the male swings it around so that ray 3 is relatively anterior, ray 5 posterior. This anterior-posterior labeling is used in differentiating positions on the gonopodium, whether it is in use or resting.) The number of spines varies from 8 to 17; high spine number characterizes the *panuco* species group, whereas very low spine number is a feature of the *senilis* species group. The length of the spines also varies, from quite short and stubby to long and thin, or long and straplike. In most groups, these spines are directed primarily toward the distal tip, with only the *panuco* and *rachowi* species groups possessing many recurved spines. In all species, however, the most proximal spine may be recurved. The outline of the spines, and thus the anterior outline of the gonopodium, varies among the species groups: fanlike (*panuco* species group); pointed mediolaterally (*vittata*, *affinis* species group, *nicaraguensis* species group); rounded (*nobilis* and *puncticulata* species groups); pointed anterodistally (*senilis* species group); or lobelike (*punctata* species group).

The segments of ray 3 that bear spines may be further modified to develop proximally directed inner processes along their posterior (medial) edges. Inner processes most often are associated with long spines, as in the *nobilis* and *senilis* species groups of the subgenus *Arthrophallus*, and the *puncticulata* and *punctata* species groups of the subgenus *Gambusia*.

The fourth anal-fin ray is relatively unmodified near the base, but the termini of its two branches (ray 4a and ray 4p) are highly specialized. Ray 4a has an anterior swelling, termed the elbow, that is possessed by all *Gambusia* species except *G. vittata* and by no other poeciliid; *G. vittata* and *Belonesox belizanus* do exhibit a swollen, ankylosed ray 4a that is bent anteriorly at the spot where an elbow would be, and this is interpreted as being homologous to the elbow, characteristic of the genera *Gambusia* and *Belonesox*. The shape of the elbow varies among groups; it is most commonly falcate; the subgenus *Gambusia* is distinguished by a triangular el-

bow, and the *punctata* species group of that subgenus modifies the simple triangle into a spatulate form. It may be composed of a single segment, or up to eight segments. It often has small lateral processes arising from its sides (in the *affinis* and *puncticulata* species groups). Distal to the elbow, ray 4a sometimes is quite constricted, sometimes foreshortened, such that ray 4a does not reach the end of the gonopodium, or sometimes rather curved, due to an increased number of segments distal to the elbow. Proximal to the elbow, ray 4a also is constricted sometimes, forming a distinct notch in the ray (in the *nobilis* and *senilis* species groups).

Ray 4p has segments that bear posteriorly directed serrae. Serrae on ray 4p are common to most poeciliids. Characteristics of the serrae vary within the genus, however. The number varies from as few as three to as many as eight. High serrae numbers are found in the *panuco* species group, and unusually low serrae numbers in the *senilis* species group. Their position relative to the elbow varies—distal, opposite, or proximal; generally among poeciliids, the serrae are not very close to the distal tip, therefore, species with serrae opposite the elbow (the *nobilis* species group) or distal to the elbow (the *rachowi* species group, and within the *affinis* species group) are considered to be specialized in this trait. The shape of the serrae in most poeciliids is for them to be pointing sharply proximally. This general shape is modified in some groups to serrae that project horizontally from the segment (such as in the *puncticulata* species group) to highly antrorse recurved serrae (as seen in *G. sexradiata* and *G. eurystoma* of the *nobilis* species group).

Just distal to the serrae on ray 4p, some groups in *Gambusia* are characterized by a large segment or two, as seen in the *puncticulata* and *senilis* species groups. Beyond this, the ray is narrow, with small segments. Distally, a hooked terminus is common to the genus. It may end in a rounded hook, curved posteriorly, that is composed of a single element. It sometimes is distinguished further by being either a rather weak hook, pointing posterodistally, or by being enlarged and claw-shaped. Alternatively, the terminal modification of ray 4p might be acuminate, the

anterior point reaching toward (or even touching) the distal tip of ray 4a, and the posterior tip hooked toward ray 5a. Acuminate hooks are found in the subgenera *Arthrophallus* and *Gambusia*, although some members of those groups have the more general rounded hooks. The sharpness of the distal point varies; it might be softened, and in *G. wrayi* is recurved. The acuminate tip of ray 4p often is multisegmented; hooks with several distinct segments are found in the *affinis* species group, and some members of the *puncticulata* species group.

Ray 5 also is a branched ray, but ray 5p does not extend all the way to the tip of the gonopodium, and therefore is not involved in the terminal specializations. At the proximal end of the anal fin, ray 5 has a prominent bulge, characteristic of this genus alone. Distal to this bulge, ray 5 is split open posteriorly, with serrate edges. Ray 5p ends just before the level of the serrae on ray 4p. Ray 5a continues, often rather straight but sometimes curving sharply anteriorly, to end in a posteriorly directed hook, found also in the sister group to the genus, *Belonesox*. Like the hook on ray 4p, this may be rather weak, pointing posterodistally, or enlarged and clawlike. Most often, however, it is simply rounded, although a small knob sometimes appears on its anterodorsal edge. The terminal segment of ray 5a sometimes has a long base, suggesting that it has fused with the penultimate segment. The spotty distribution of this character, however, has limited its usefulness.

The interpretation of gonopodial characters is discussed in the systematic section. In general, outgroup comparison is less helpful here than with other types of characters because outgroups simply do not possess comparable specializations. Ontogenetic criteria can be employed, but with a degree of caution. Turner (1941) described the morphogenesis of the gonopodium of *Gambusia affinis*, concentrating on a comparison of segmentation, bifurcation, growth, and ankylosis of segments between males and females. In a later work (1942a), he described gonopodial formation in terms of developmental fields, with a growth period followed by a differentiation period. During the growth period, fields corresponding to the special-

izations of rays 6, 7, and 8, the proximal bulge of ray 5, and the thickening of ray 3 are active, followed by the appearance of spines on ray 3. In the differentiation period, first the serrae of ray 4p appear, followed by the terminal hooks of ray 4p and ray 5a, and lastly, the elbow. This order of appearance seems stereotyped in the genus, as I observed the same thing in many species. Beyond this ordering, the gonopodium, like most fin rays, develops along a proximal-to-distal gradient. Therefore, although it is observed that, in the hook at the end of ray 4p, for example, the single-segment, posteriorly directed hook ontogenetically precedes the multisegment, anteriorly directed part of the acuminate hook, this simply may be a consequence of the fact that the anteriorly directed hook is distal to the posteriorly directed hook. A similar discussion can be construed for the single-segment elbow versus the multisegment elbow. I have considered ontogenetic information where possible, given this caveat, and ultimately incorporated it into an overall parsimony argument.

SYSTEMATICS

In the discussion of characters pertinent to the study of relationships that follows, each character is followed by a number in brackets []. The systematic results of each section are summarized with branching diagrams containing character numbers. These cladograms were derived using PAUP; the character matrices (using the same numbering system for the characters) and tree statistics are included in the Appendix.

OUTGROUP RELATIONSHIPS (fig. 21)

Tables 4, 5, and 6 show the placement of *Gambusia* within a hierarchical classification. Following Rosen and Parenti (1981), atherinomorphs are the sister group to the other group of acanthopterygians, the percomorphs. The Series Atherinomorpha contains two divisions. It is within Division II that the order Cyprinodontiformes lies, with the order Beloniformes as its sister group. Parenti's (1981) classification of the order

TABLE 4
Classification of Atherinomorphs, from Rosen
and Parenti (1981: 23)

Series Atherinomorpha
Division I
Family Atherinidae
Family Bedotiidae
Family Isonidae
Family Melanotaeniidae
Family Phallostethidae
Family Telmatherinidae
Division II
Order Cyprinodontiformes (see table 5 for classification of this order)
Order Beloniformes
Suborder Adrianichthyoidei
Family Adrianichthyidae
Suborder Exocoetoidei
Superfamily Exocoetoidea
Family Hemiramphidae
Family Exocoetidae
Superfamily Scomberesocidea
Family Belonidae
Family Scomberesocidae

TABLE 5
Classification of Cyprinodontiformes, from
Parenti (1981: 462–463)

Order Cyprinodontiformes
Suborder Aplocheiloidei
Family Aplocheilidae
Family Rivulidae
Suborder Cyprinodontoidei
Section 1
Family Profundulidae
Section 2
Division 1
Family Fundulidae
Division 2
Sept 1
Family Valenciidae
Sept 2
Superfamily Poecilioidea
Family Anablepidae
Subfamily Anablepinae
Subfamily Oxyzygonectinae
Family Poeciliidae
Subfamily Poeciliinae
Subfamily Fluviphylacinae
Subfamily Aplocheilichthyinae
Superfamily Cyprinodontoidea
Family Goodeidae
Family Cyprinodontidae

TABLE 6
Classification of Poeciliids, from Rosen and Bailey
(1963: 10) with the Addition of *Scolichthys* from
Rosen (1967)

Family Poeciliidae (= Subfamily Poeciliinae of Parenti, 1981)
Subfamily Tomeurinae
<i>Tomeurus</i>
Subfamily Poeciliinae
Tribe Poeciliini
<i>Alfaro Priapella</i>
<i>Poecilia Xiphophorus</i>
Tribe Cnesterodontini
<i>Phallotorhynchus Phalloptychus</i>
<i>Phalloceros Cnesterodon</i>
Tribe Gambusiini
<i>Bachyrhaphis Gambusia</i>
<i>Belonesox</i>
Tribe Girardiini
<i>Girardinus Quintana</i>
<i>Carlhubbisia</i>
Tribe Heterandriini
<i>Priapichthys Heterandria</i>
<i>Neoheterandria Poeciliopsis</i>
<i>Phallichthys</i>
Tribe Scolichthyini
<i>Scolichthys</i>
Subfamily Xenodexinae
<i>Xenodexia</i>

Cyprinodontiformes is presented in table 5. Following convention, I refer to members of the order vernacularly as cyprinodontiforms, and of the suborder Cyprinodontoidei as cyprinodontoids. Parenti expanded the membership of the family Poeciliidae to include procatopines, *Fluviphylax*, and *Pantanodon*, and the fishes vernacularly referred to as poeciliids now constitute the subfamily Poeciliinae, as it was originally defined by Regan (1913). Although I accept her classification, I have continued to use the vernacular term poeciliid to refer to members of this subfamily.

A classification of poeciliids is presented in table 6, based primarily on Rosen and Bailey (1963) with the addition of a more recently described tribe (Rosen, 1967). Although this classification does not imply sister-group relationships as the two previous tables do, there is evidence that the tribe Gambusiini is a monophyletic group. Its sis-

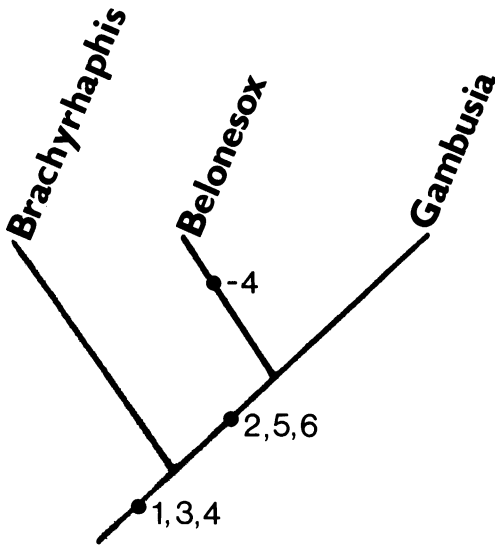


Fig. 21. Cladogram depicting interrelationships in the tribe Gambusiinae.

ter group, however, remains unknown. Members of the tribe Gambusiini are similar in many ways to some members of the tribe Heterandriini, but it has not been determined if these similarities are primitive or derived.

Members of the tribe Gambusiini—*Brachyrhaphis*, *Belonesox*, and *Gambusia*—share specializations of the gonactinostal complex. In figure 22A, *Heterandria jonesi* shows the general condition for many poeciliids. The first five gonactinosts are united by a laminar plate in the anterior-posterior plane. The gonactinosts are spread out on this plate like spokes in a fan. The plate divides and curves posterior to the fourth gonactinost, extending as lateral wings. In *Brachyrhaphis cascajalensis* (fig. 22B), the anterior part of the plate is somewhat reduced but still present. The lateral wings are modified toward embracing gonactinost 5. Gonactinost 5 stands freely, rather than being incorporated into the plate, and projects dorsally through the lateral wings [1]. *Belonesox belizanus* (fig. 22C) and all *Gambusia* species (*G. holbrooki* in fig. 22D; also see *G. hispaniolae* in fig. 18) also have a free gonactinost 5, projecting dorsally through the modified superior lateral wings. In these two genera, the anterior plate is much reduced, and gonactinosts 2, 3, and 4 form a column. The dorsal part of this column (the “collar” of

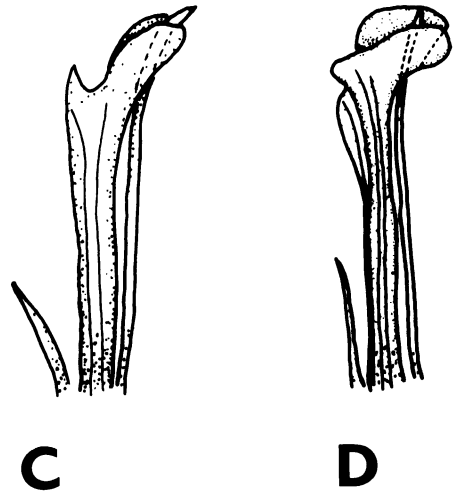
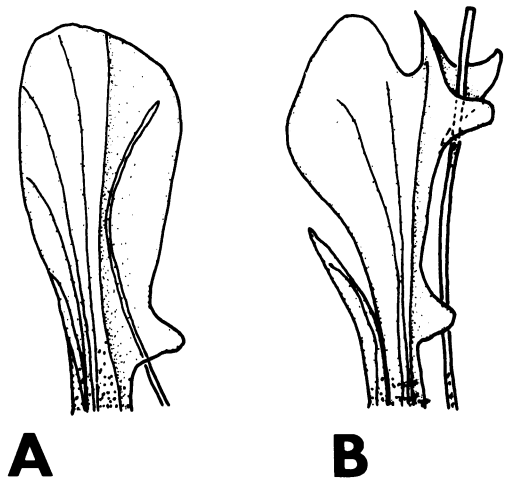


Fig. 22. Lateral view of the gonactinostal complex of: A. *Heterandria jonesi*, B. *Brachyrhaphis cascajalensis*, C. *Belonesox belizanus*, D. *Gambusia holbrooki*.

Turner, 1942b) represents the lateral wings, that are expanded to form a cup [2]. This distinctive form of the gonactinostal complex is quite consistent in *Belonesox* and all of *Gambusia*; it is known nowhere else.

These three genera share some pigmentation characters, particularly an axillary blotch, anterodorsal to the pectoral fin insertion [3]. Hildebrand (1938) and Rosen and Bailey (1963) have commented on the striking re-

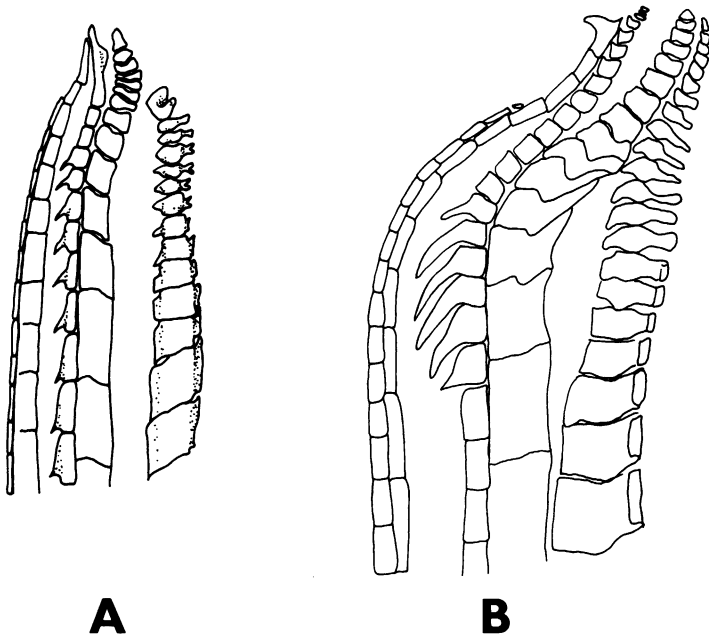


Fig. 23. Gonopodia of: **A.** *Brachyrhaphis cascajalensis*, **B.** *Belonesox belizanus*.

semblance in body form and pigmentation that exists between *Brachyrhaphis* and *Gambusia*, particularly in the anal-fin area of the female. *Brachyrhaphis* species have a very dark band of pigment at the base of the anal fin. Anal-fin pigment is not quite as dark in *Gambusia*; it ranges from very dusky to very faint, usually heaviest on the first few rays. Females in both genera have dark pigment around the genital opening, its expression varying from species to species and dependent on the female's physiological state [4]. *Belonesox* shows no anal pigment, either around the genital opening or on the anal fin, and these pigments are seen only rarely elsewhere in the subfamily.

Gambusia and *Belonesox* share some gonopodial features, in particular, a well-formed hook on ray 5a [5] (fig. 20; see also fig. 23). Although the termini of rays 4p and 5a do curve over in some *Brachyrhaphis* species, no hook is formed. The pointed anterior tip of the *Belonesox* hook is seen in several *Gambusia* species (see *G. nobilis*, fig. 40A) although most are more rounded. *Belonesox* does not have an elbow on ray 4a; however, this ray is modified from the straight ray that is seen in *Brachyrhaphis*, to be thickened, somewhat coalesced, and with a sharp an-

terior bend where the elbow would be [6]. The same sort of ray 4a is seen in *Gambusia vittata* (see fig. 33A); all the other *Gambusia* species, although they have well-formed elbows, also show these coalesced segments and anterior bending to some degree.

DIAGNOSIS OF THE GENUS *GAMBUSIA*

The genus *Gambusia*, as described here, includes *G. vittata*, *G. rachowi*, and *G. echeagayari*, fishes that have each been assigned to monotypic genera by some authors. A series of derived characters places these species within *Gambusia*, and therefore their banishment from the genus is unwarranted, as that classification would not reflect sister-group relationships.

Males of all species of *Gambusia* have modified pectoral fins [7], as described in the Osteology section (fig. 15B), and, contrary to the claims of Hubbs and Reynolds (1957) and others, this modification is not seen, to any degree, in *Belonesox*, or, in fact, any other poeciliid. Details of this modification and its degree of development vary within the genus.

The proximal part of the male anal fin (fig. 19) shows two synapomorphies for the genus, a thickening of ray 2 at its base [8], and a

prominent bump in ray 5 [9]. Again, these characters are consistent within the genus, and not found elsewhere.

In the gonopodial suspensorium, there are several reductive trends in the form of the gonapophyses. Although there are some poeciliids that have no gonapophyses at all, the most common condition is for there to be three gonapophyses, each with full uncinat processes. Within the genera *Gambusia* and *Poecilia*, there are subgroups that have only two gonapophyses; on all other bases, these two genera do not seem to be very closely related. In all members of *Gambusia*, there is no uncinat process on the first gonapophysis [10]. This process is quite prominent in *Belonesox* and *Brachyrhaphis*; however, as with the reduction in number of gonapophyses, this reductive character is seen in some distantly related poeciliids.

In the gonopodium, all *Gambusia* species except *G. vittata* have an elbow in ray 4a [11]. Because *G. vittata* does possess the other synapomorphies for the genus [7–10] and those for its subgenus, its lack of a well-formed elbow implies the retention of a primitive character, not a basis for grouping.

DIAGNOSES OF SUBGENERA

As shown in table 1, I recognize three subgenera—*Heterophallina*, *Arthrophallus*, and *Gambusia*. Each of these names has been proposed for a subgenus before, by Hubbs in 1926. Note, however, that although the designated type species for each subgenus, of course, remains within it, the constituency of each subgenus is changed from that originally proposed.

Heterophallina: Hubbs (1926) used this name for a new subgenus to include three newly described species, *G. vittata*, *G. panuco*, and *G. regani*, designating *G. regani* as the type species. At the time, he knew *G. vittata* only from females, and when he later obtained *G. vittata* males, he removed it from *Gambusia* altogether (in Rivas, 1963). However, I have reinstated *vittata* to *Gambusia*, and placed it in the subgenus where it was originally described. In addition to *G. vittata*, this subgenus also includes two species groups—*panuco* and *rachowi*. Rivas (1963) used the subgenus name *Heterophallina* only

for members of the *panuco* species group. *Gambusia rachowi*, of the *rachowi* species group, has often been assigned to a monotypic genus, *Heterophallus*. The subgenus name, *Heterophallina*, was chosen by Hubbs to indicate some degree of affinity between the groups.

Gambusia vittata and the members of these two species groups share a gonopodial specialization (see fig. 33). The hooks on rays 4p and 5a are distinctively shaped [12]. They are rounded anteriorly, and the posterior point does not hook over completely but rather points at an angle. The hooks are also small, each consisting of only a single segment. This distinctive shape is considered a derived condition for this subgenus, rather than a primitive state, because the hooks of *Belonesox* show a different shape, tending toward anterior points. The hypothesis that the *Belonesox* state is primitive for the genus is supported by the fact that it does appear occasionally in some members of the other subgenera of *Gambusia*.

A unique morphology of the median teeth of the toothplate of the third infrapharyngobranchial also characterizes this group [13]. These large teeth are recurved at their tips, as they are in several species of *Gambusia*, but on the medial surface, below the tip, is a serrate lump or pad (fig. 24). In other subgenera, these median teeth are usually smooth along their inner borders, or have just a slight hint of a shoulder along the medial edge.

Arthrophallus: Hubbs (1926) created this subgenus for *G. patreulis*, a name often synonymized with *G. affinis* (see discussion by Geiser, 1923, and in the footnote about the confusion over these names²). *Arthrophallus*

² A nomenclatural digression is necessary to clarify the status of some of the members of this group. Baird and Girard (1854) described two Texas mosquitofishes as *Heterandria affinis* and *H. patreulis*, which differ slightly in head shape and dorsal-fin ray number. After Poey's 1854 description of the genus *Gambusia*, Girard (1859a) referred these two species to the new genus, adding *G. holbrooki* of Florida (1859b), which he cited as being described by Agassiz in the genus *Heterandria*, and later *G. speciosa* of the Río San Juan in Nuevo Leon and *G. gracilis* of Matamoras (1859c). Jordan and Copeland (1876) listed *G. holbrooki* and *G. affinis* as valid, with *patreulis*, *gracilis*, and *speciosa* as doubtful species. How-

has page priority over *Schizophallus*, another Hubbs (1926) subgenus, this one created for *G. holbrooki*, which is also often synonymized with *G. affinis*. Rivas (1963) retained *Arthrophallus* as a monotypic subgenus.

As described below, the subgenus *Arthrophallus* is not monotypic; rather, it contains three species groups—*affinis* (including, among others, both *G. affinis* and *G. holbrooki*), *nobilis*, and *senilis*. The cephalic sensory canal system provides a consistent synapomorphy for this subgenus [14]. Rosen and Mendelson (1960) surveyed cephalic sensory canals in a range of poeciliids, noting that the carnivorous top-feeding species, e.g., *Brachyrhaphis*, *Belonesox*, and *Gambusia*, have open grooves rather than closed canals, with the following sets of neuromasts: supraorbital (1,

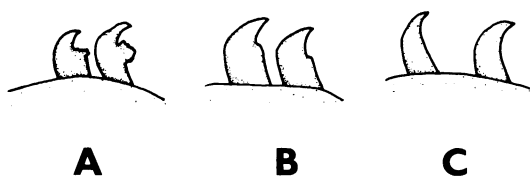


Fig. 24. Median teeth of third pharyngobranchial toothplate: A. *Gambusia vittata*, B. *Gambusia yucatana*, C. *Gambusia luma*.

2a; 2b, 3, 4a), infraorbital, posterior section only (4b, 5, 6a; 6b, 7), preopercular (7 neuromasts), preorbital (7 neuromasts), and mandibular (4 neuromasts). Of interest here is the infraorbital section. In all members of the subgenus *Arthrophallus*, there is a distinct break in this canal, leaving two discontinuous grooves (4b, 5, 6a; 6b, 7) (fig. 25A). In

ever, Jordan and Gilbert (1886) recognized *G. patreulis* with *G. gracilis* now synonymized under this name. Evermann and Kendall (1894), however, synonymized *G. patreulis*, *G. gracilis*, and *G. speciosa* under the name *G. affinis*, and in 1896, *G. holbrooki* was also placed in this synonymy (Jordan and Evermann, 1896–1900).

However, Regan (1913) recognized three valid species, *G. holbrooki*, *G. patreulis*, and *G. affinis*, the latter containing *speciosa* as well, differentiated again by slight variations in dorsal-fin ray number. Geiser (1923) demonstrated that *G. holbrooki* is gonopodially distinct from all other species under question, being the only species in the genus to have denticulations on the posterior edges of the ray three segments proximal to the spines. He recommended full species status for *holbrooki*, with all other forms named *affinis*.

Adding to the confusion, Hubbs (1926) decided to limit the name *G. affinis* to a new species, related to *G. senilis*, from San Marcos, Texas, and to use the name *G. patreulis* for the widespread species usually called *affinis*. Under *G. patreulis*, he included *G. speciosa*, *G. modesta*, and *G. myersi* (the latter two names proposed by Ahl for a fish of the Pánuco region in eastern Mexico). As a separate subgenus, Hubbs recognized *G. holbrooki*, following Geiser. Hubbs and Springer (1957), after examining the co-types for *Heterandria affinis*, described the San Marcos mosquitofish as *G. geiseri*, and the widespread fish was again renamed *G. affinis*, this time the name *G. patreulis* finally disappearing.

Krumholz (1948), C. L. Hubbs (1955), C. Hubbs (1957), and Hubbs and Springer (1957) have all cited two unpublished manuscripts that reported natural introgression between *G. affinis* and *G. holbrooki*, and therefore have recognized these forms as only subspecifically different. (Hubbs et al., 1953, also listed *G. affinis speciosa*, from Comal Springs.)

However, the ability to interbreed is a primitive character (Rosen, 1979), and shared primitive characters are not valid for describing groups, even if the level of the group is a single species. Secondly, all *affinis* × *holbrooki* hybrids are not viable; a chromosomal difference involving female heterogameity in one form (*holbrooki*) but not the other results in only the offspring of *holbrooki* males with *affinis* females surviving (Black and Howell, 1979). Furthermore, natural hybridization occurs elsewhere in the genus: between *G. nobilis* and *G. affinis* (Hubbs, 1955); *G. heterochir* and *G. affinis* (Hubbs, 1957); *G. georgei* and *G. affinis*, *G. nobilis* and *G. geiseri*, and *G. hurtadoi* and *G. heterochir* (the last in artificial pools) (Hubbs and Peden, 1969). Clearly if the interbreeding criterion does not apply in these cases, it need not apply in the *affinis-holbrooki* case either. Like any symplesiomorphy, the ability to interbreed is certainly indicative of relationship at some (higher) level. All reported cases of natural hybridization occur within the subgenus *Arthrophallus*, and therefore this ability, although apparently lost in some apomorphic taxa, may characterize this large group. Finally, Wooten et al. (1988) have recently examined the *affinis-holbrooki* matter biochemically, and have found the two taxa to be electrophoretically distinct. They also recommend the recognition of *G. holbrooki* as a valid species.

Gambusia speciosa, as a valid species, has appeared on two recent checklists, without comment as to its status (Miller, 1986; Smith and Miller, 1986). I have examined some new material, from Melchor Musquiz, Mexico, and have found it to be gonopodially distinct from other forms of *Gambusia*, and therefore provisionally treat it as a full species. However, I have not yet been successful in locating the type material; this will be necessary for full resolution of this problem, which clearly needs further investigation.

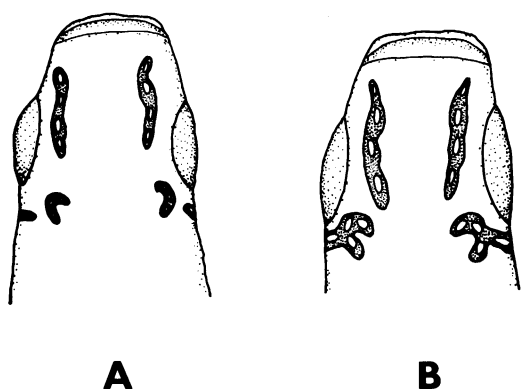


Fig. 25. Dorsal views of the cephalic sensory canal systems of: A. *Gambusia senilis*, B. *Gambusia pseudopunctata*.

Brachyrhaphis, *Belonesox*, and *gambusiini* in the subgenera *Heterophallina* and *Gambusia*, the two sections of this canal are joined into one continuous groove (fig. 25B). At this level, disjunct canals must be considered a synapomorphy of the subgenus *Arthrophallus*; it is consistent within the group. The generality of this character—continuous versus discontinuous—above this level, for example, among all poeciliids, was not examined. It was not discussed by Rosen and Mendelson (1960), and unfortunately their figures do not consistently distinguish the two conditions.

Karyotypes are known for several members of this subgenus (*G. affinis* of the *affinis* species group, *G. nobilis* of the *nobilis* species group, and *G. hurtadoi* of the *senilis* species group, for examples) (Campos and Hubbs, 1971; Chen and Ebeling, 1968). The species mentioned have a diploid number of 48, with a moderate to large metacentric chromosome in females only [59]. This karyotype is different from that known for *Belonesox*, for members of the subgenus *Gambusia* (*G. luma*, *G. rhizophorae*, *G. xanthosoma*—Wildrick et al., 1985), and for members of the subgenus *Heterophallina* (*G. vittata*, *G. regani*; *G. marshi* is autapomorphic with a reduced number of chromosomes). Except for the subgenus *Arthrophallus*, the general karyological condition seems to be a diploid number of 48, with no metacentric chromosomes.

A subgroup of the *punctata* species group, in the subgenus *Gambusia*, has a different karyotype, with one pair of metacentric chromosomes in both sexes, but this is inferred

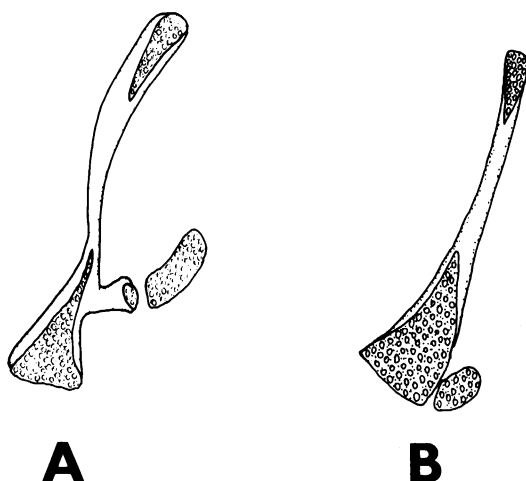


Fig. 26. Epibranchial 1: A. *Gambusia regani*, B. *Gambusia pseudopunctata*.

to be a separate character. The metacentric chromosome in females only is inferred to be a synapomorphy of the subgenus *Arthrophallus*, but this is only tentative, and must be tested by karyotyping more species.

Gambusia: Seven characters [15–21] describe the subgenus *Gambusia*. The only gonopodial character refers to the shape of the elbow of ray 4a. In the other two subgenera, the elbow is distinctly falcate and hooked. In the subgenus *Gambusia*, the proximal surface of the elbow is flat; rather than falcate, the elbow is triangular in shape [15]. In the *punctata* species group, the triangular shape is further modified to a more spatulate outline; these fish still have a flat, unarched, proximal surface to the elbow.

In the dorsal gill arches, the first epibranchial has no uncinat process for species of this subgenus [16] (fig. 26). Although this represents a reversion to the condition general for atherinomorphs, the rest of the genus does have such a process. In the ventral gill arches, the members of the subgenus *Gambusia* possess very well-developed anteriorly directed lateral prongs on the first hypobranchials [17] (fig. 27). Such processes are sometimes seen in *Heterophallina* and *Arthrophallus*, but merely as thickenings, not prongs. The third basibranchial also is modified in this group from the relatively straight rod that is seen in the other two subgenera to an hourglass-shaped bone (fig. 27). The bone is slender at

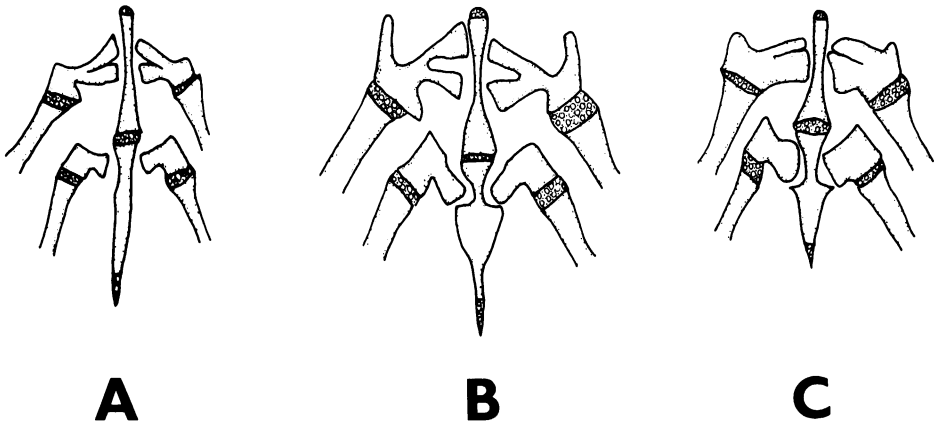


Fig. 27. Anterior part of ventral gill arches, dorsal view: **A.** *Gambusia panuco*, **B.** *Gambusia yucatana*, **C.** *Gambusia puncticulata*.

the point where the two second hypobranchials articulate with it, but just posterior to this point the bone flares out in lateral wings [18].

The ventral aspect of the ventral hypohyal is distinctive in this group as well. As discussed earlier (p. 20), a group containing poeciliids is described in part by a ventral hypohyal that contacts the anterior ceratohyal squarely, in a straight line. This condition is seen in the other two subgenera. In the subgenus *Gambusia*, the anterior ceratohyal has an anterior lobe that invades much of the space of the ventral hypohyal; therefore, the juncture between these two bones is not at all square [19] (fig. 28).

The pattern of hypural fusion in the genus is complex. Generally, adults of *Heterophallina* and *Arthrophallus* have a single hypural

plate, usually with a keyhole near the base. Most members of the subgenus *Gambusia* have two hypural plates, as shown for *G. luma* (see fig. 44), also with a keyhole opening [20]. This condition is seen occasionally in the other subgenera, for example the *rachowi* species group, but best characterizes this level.

Another character that fits best at this level but is not completely consistent has to do with pigment patterns on the dorsal and caudal fins. Most but not all members of *Heterophallina* and *Arthrophallus* have a basal row of spots on these fins, with dusky to very dark fringe at the edge of the fins. In the subgenus *Gambusia*, the fin pattern consists of three or four rows of spots (fig. 29). This spotted pattern is seen occasionally in the other subgenera (e.g., *G. holbrooki* of *Arthrophallus*, and *G. panuco* of *Heterophallina*) [21].

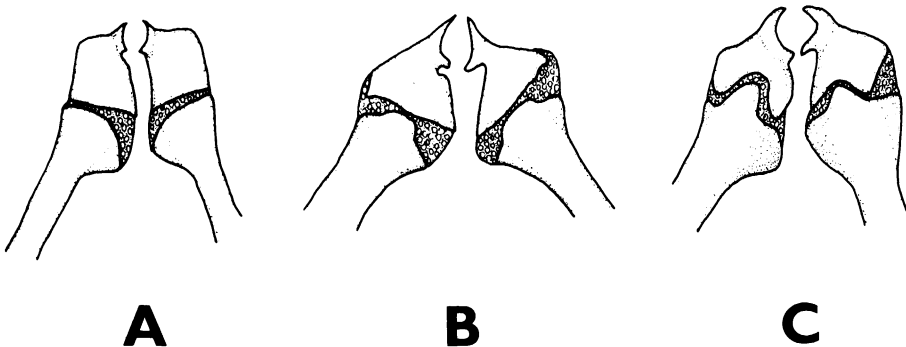


Fig. 28. Ventral hypohyal and anterior ceratohyal, ventral view: **A.** *Gambusia panuco*, **B.** *Gambusia wrayi*, **C.** *Gambusia punctata*.

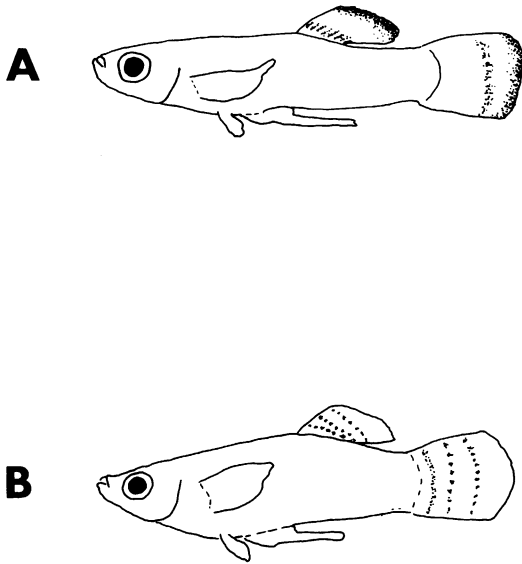


Fig. 29. Dorsal and caudal fin patterns: **A.** *Gambusia alvarezii*, **B.** *Gambusia pseudopunctata*.

RELATIONSHIPS AMONG
SUBGENERA (fig. 30)

The subgenera *Arthrophallus* and *Gambusia* are sister groups, with the subgenus *Heterophallina* as the sister group to that assemblage. Members of both *Arthrophallus* and *Gambusia* have a suborbital bar [22] that

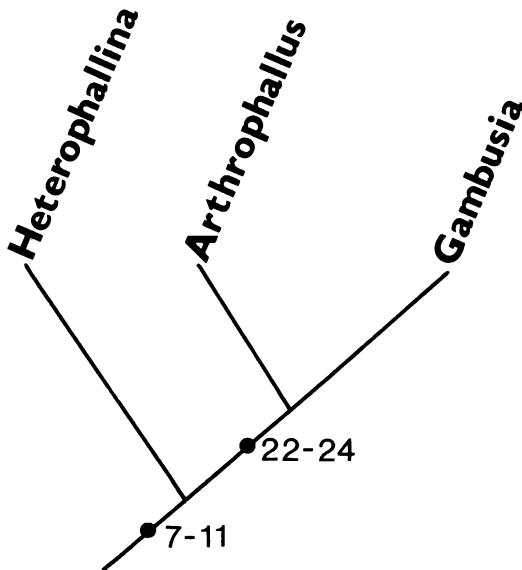


Fig. 30. Cladogram depicting relationships among subgenera.

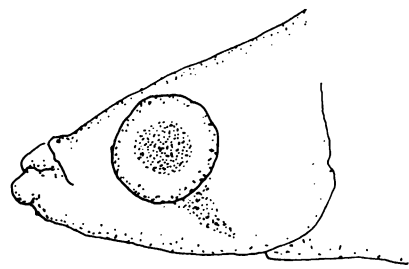


Fig. 31. Suborbital bar, shown on *Gambusia holbrooki*.

varies from being just a few melanophores running in a curved line below the eye to a very dark streak in the same location (fig. 31). The degree of expression of the suborbital bar also varies, depending on the age, sex, and physiological state of the organism. In the gonopodium, members of these two subgenera develop an acuminate terminal hook on ray 4p, drawn out distally and sometimes arching anteriorly [23]. In many cases, the acuminate hook is multisegmented. This condition is thought to be more specialized than the single-segment, rounded hook because during the morphogenesis of the gonopodium, the proximal segment of the hook forms first, and it much resembles a rounded hook; it is not yet acuminate. The distal portion is next formed, producing the acuminate tip. This ontogenetic sequence, however, also

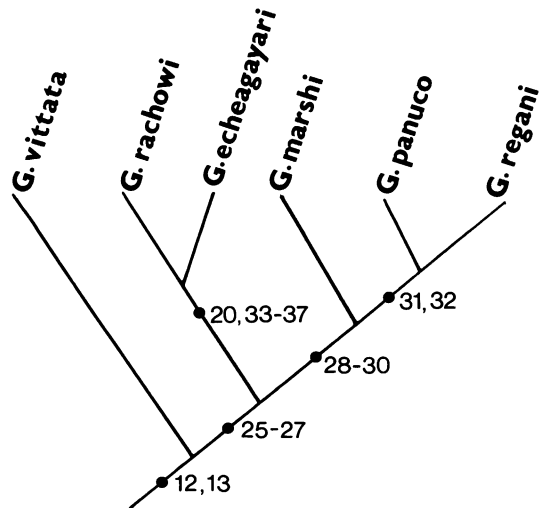


Fig. 32. Cladogram depicting relationships in the subgenus *Heterophallina*.

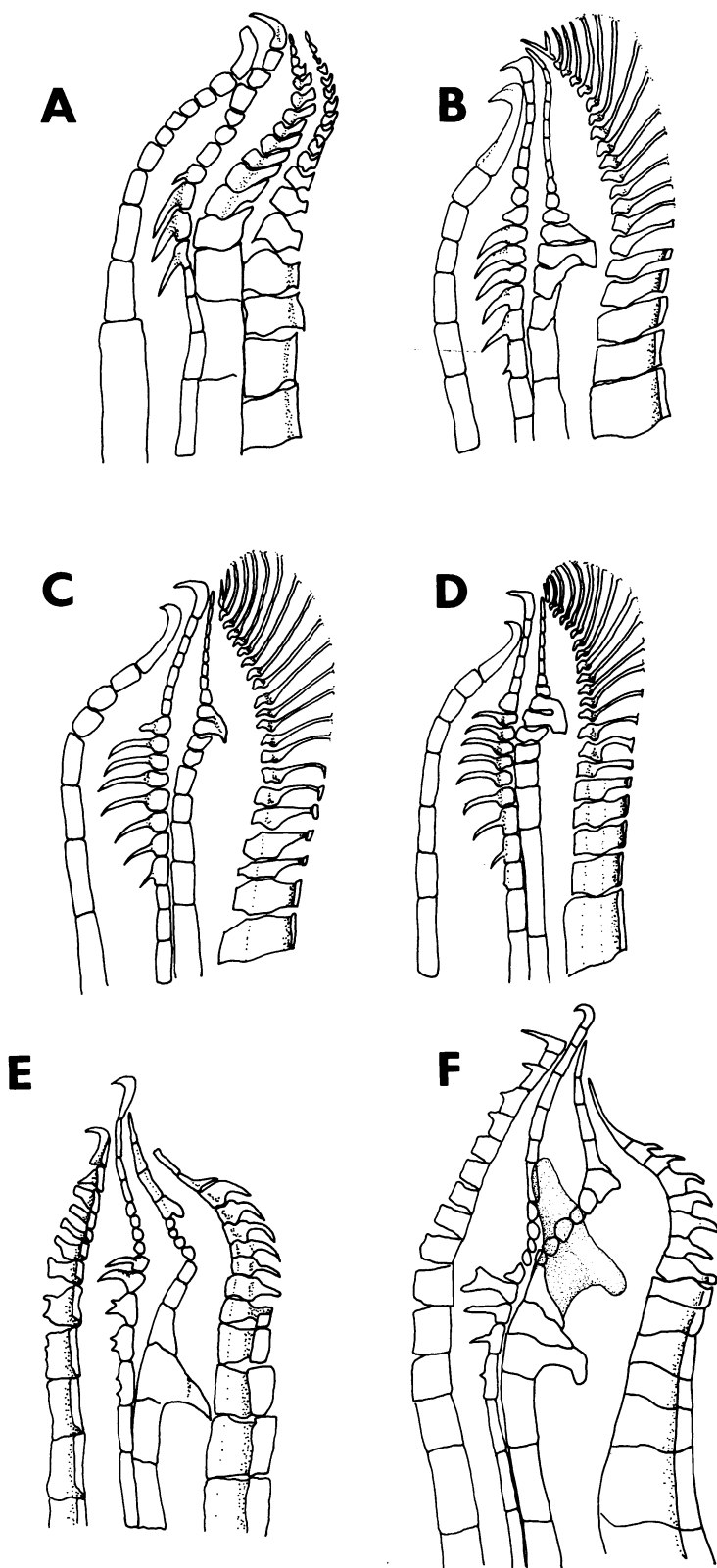


Fig. 33. Gonopodia of members of the subgenus *Heterophallina*: **A.** *Gambusia vittata*, **B.** *Gambusia marshi*, **C.** *Gambusia panuco*, **D.** *Gambusia regani*, **E.** *Gambusia rachowi*, **F.** *Gambusia echeagayari*.

reflects the general proximal-to-distal direction of specialization.

Peden (1973a) described some differences among species in the form of the anal spot in the female. Members of the *panuco* species group, as well as *Brachyrhaphis* species, have a median anal spot. Members of the subgenera *Arthrophallus* and *Gambusia* that he described have paired crescent-shaped spots around the anus and genital pore instead [24], except for three members of the *senilis* species group, whose median spots are considered derived at that level. Although this synapomorphy seems straightforward enough based on Peden's work, the character could not be examined in the many species that he did not cite, because, as he pointed out, the anal spot is often not seen well in preserved specimens (his observations were of live material).

RELATIONSHIPS WITHIN THE SUBGENUS *HETEROPHALLINA* (fig. 32)

The *panuco* and *rachowi* species groups together form a monophyletic group. Three gonopodial peculiarities unite them (fig. 33): retrorse spines on ray 3, as opposed to all spines basically pointing forward [25]; an increase in the number of segments to six or more in ray 4a distal to the elbow, with a concomitant reduction in size [26]; and a similar increase in the number of segments distal to the serrae of ray 4p often up to nine or more [27]. The normal range in the number of these segments in the genus is from four to eight, usually four or five.

G. vittata: As noted earlier, this species lacks the well-formed elbow on ray 4a of the gonopodium. It also is remarkable in that it is the only *Gambusia*, of those for which stomach content analyses have been performed, that is reported to eat much algae (specifically filamentous *Spirogyra*), which accounted for up to 50 percent of the stomach contents. The remainder consisted of arthropod parts, a more conventional diet for a *Gambusia* (Darnell, 1962).

***panuco* species group:** The three members of the *panuco* species group, *G. marshi*, *G. panuco*, and *G. regani*, have a distinctive gonopodium (fig. 33B–D); this group has been recognized at some level as a cohesive unit by all previous students of the genus. There

is a high number of slender spines on ray 3, typically 14–17 [28]; the number of spines in other groups usually ranges from 8 to 13. Some members of the *punctata* species group have up to 15 spines, but these are broad and straight with long inner processes. In the *panuco* species group, the spines curve like a fan, and their distal tips do not end pointedly, but gently merge into the membrane of the gonopodial margin [29]. Spines in other groups have distinct pointed edges. The terminal segment of ray 5a in this group, that bears the hook at its distal tip, is proximally elongated, covering the distance of two segments [30]. The terminal segment may have fused with the penultimate one; however, no evidence of fusion was seen. This particular character is found occasionally in other groups in the genus.

Within the *panuco* species group, *G. panuco* and *G. regani* are more closely related to each other than either is to *G. marshi*. *Gambusia marshi*, however, is polymorphic with regard to pigmentation patterns and morphometrics (Minckley, 1962 and personal commun.); it may represent a complex of species, but variation at that level was not investigated here. The gonopodia of *G. panuco* and *G. regani* have more serrae on ray 4p than any others in the genus [31]. These two species have eight or nine serrae, *G. marshi* usually five, the *rachowi* species group and *G. vittata* two to four, and other groups in the genus typically four to six. These serrae extend directly perpendicular from ray 4p [32]. This modification is seen again in some other groups (see the *puncticulata* species group, and within the *nobilis* species group) but must be considered a more advanced condition than the retrorse serrae that are common not only in the genus but to most poeciliids. *Gambusia panuco* and *G. regani* can be distinguished from each other on meristic (*G. regani* has fewer dorsal-fin rays) and pigmentary (*G. regani* has no spotting on the body) grounds. Otherwise, these sister species are very similar.

***rachowi* species group:** This group contains two species that previously have been assigned to two monotypic genera. *Heterophallus rachovii* was inadvertently redescribed as *Gambusia atzi* by Rosen and Gordon (1951); while recognizing its differ-

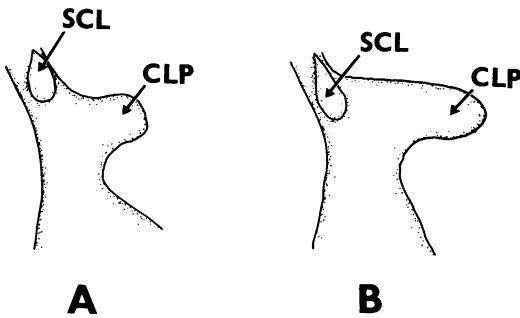


Fig. 34. Cleithral process: A. *Gambusia luma*, B. *Gambusia echeagayari*.

ences from the other members of *Gambusia*, they stressed commonalities, especially the elbow of ray 4a in the gonopodium. When describing *Dicerophallus echeagayari*, Alvarez (1952) had not seen any material of *G. rachowi*; the two species are actually quite close and do not belong in separate genera. Rosen and Bailey (1963), following Rosen and Gordon (1951), retained both of these species within *Gambusia*, as the *rachowi* species group, as I have done here. Rivas (1963), however, recognized the monotypic taxa and described them as "allied genera."

These two species do have a very strange gonopodium that clearly distinguishes them as a monophyletic group (fig. 33E, F). There are no forward-pointing spines on ray 3 [33]. There is an odd buckling of ray 4a [34], distal to the elbow, that results in the elbow, which is quite prominent and falcate, being displaced proximally. A fleshy palp grows laterally from the gonopodium between rays 3 and 4a, just distal to the elbow [35]. Present in both species, this palp is developed to a greater degree in *G. echeagayari*. Both species are very slender fish, as are all members of this subgenus, but these two narrow to a steep ventral keel; all other species are more rounded ventrally [36]. Additionally, these two fishes have a caudal-fin skeleton that consists of two unfused hypural plates [20]. Within this subgenus, all other fishes have hypurals fused into one plate, with a keyhole in the middle. This condition is not unique within the genus, however; the subgenus *Gambusia* also is characterized by two unfused hypurals in the caudal skeleton. Finally, these two species have a cleithral process that extends further posteriorly than in any other species

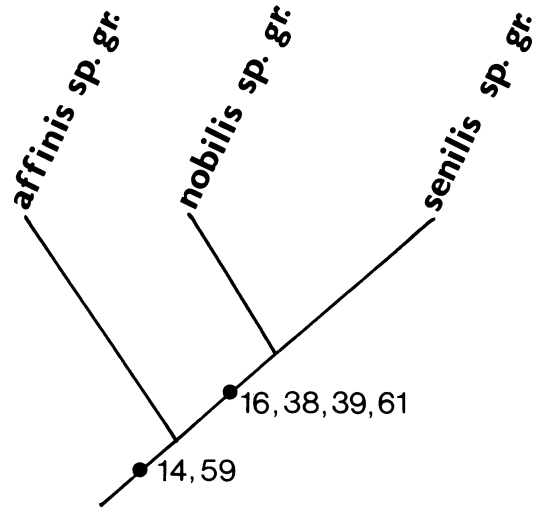


Fig. 35. Cladogram depicting relationships in the subgenus *Arthrophallus*.

of the genus (or allied genera) (fig. 34). Rather than being a simple, rounded process, it is more like a drawn-out ellipse.

RELATIONSHIPS WITHIN THE SUBGENUS *ARTHROPHALLUS* (fig. 35)

The *nobilis* and *senilis* species groups form a monophyletic unit. In their gonopodium, ray 4a has a distinct notch proximal to the elbow [38]. Although obviously all species with elbows narrow in ray 4a just proximal to the elbow, in these groups this narrowing soon widens and ray 4a resumes its normal width, with the transition from narrow to wide being rather abrupt. In other groups, ray 4a also widens, but does so gradually, with no noticeable demarcation of narrow and wide zones (compare figs. 41 and 43 with those of other groups, e.g., figs. 33, 47, 49, 51). These two groups also share long spines on ray 3, with well-developed inner processes [39]. This particular character, as just described, also will characterize a monophyletic subunit of the subgenus *Gambusia* (see p. 49); however, the width, shape, and outline of the spines and inner processes are different in the two groups. Most members of these two species groups typically have only two gonapophyses (fig. 37), instead of the more general number of three, often with a slight swelling on the third hemal spine being the only indication of a third gonapophysis [61]. Also, the mem-

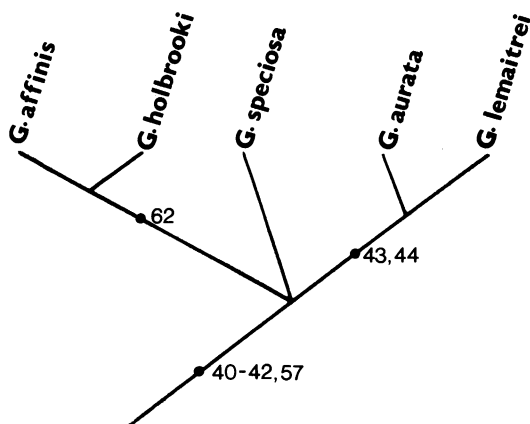


Fig. 36. Cladogram depicting relationships within the *affinis* species group.

bers of these groups have no uncinat process on the first epibranchial [16]. The difficulty in interpreting the generality of this character was discussed earlier (p. 21); although the character may not be a synapomorphy, it does describe the condition found in these two subgroups and is congruent with other synapomorphies.

***affinis* species group** (fig. 36): This constitution of this group is the most novel proposition of this work. Although Rosen and Bailey (1963) designated an "*affinis* species group," theirs was a rather uncharacterizable assemblage of some fishes not only of this subgenus but also some of the subgenus *Gambusia*. The group as here described contains five members, sharing the following specializations (fig. 38). The elbow of ray 4a of the gonopodium consists of many segments, up to ten, which are coalesced along their anterior borders [40]. Elbows in other groups are most often unisegmental, or consist of at most three segments. The spines of ray 3 are small and stout, and their distal tips are bifid [41]. The small size might be considered a retention of the condition found in *Belonesox* and *Brachyrhaphis*, whose spine-bearing segments of ray 3 do not have true spines but are slightly drawn out anteriorly; however, these "spines" are not bifid. A further peculiarity of this group is a lateral bulge at the anteroproximal tip of the elbow [42]. It is usually more pronounced on one side of the gonopodium than the other, so that in the resting gonopodium, ray 4a is displaced

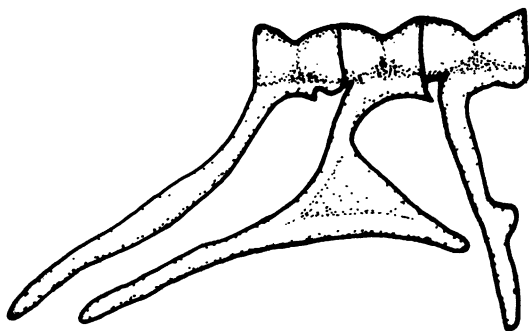


Fig. 37. Gonopodial suspensorium of *Gambusia georgei*. Compare with fig. 18.

slightly toward one side. A lateral projection from the gonopodium is seen in the *rachowi* species group, but the projection is a large, fleshy palp, dissociated from (or not associated with, at any rate) the elbow. In the *affinis* species group, the lateral projection is a bony prominence on the elbow. Finally, these fishes all have a particularly impressive pectoral fin in males, with a unique modification [57]. The fifth pectoral ray has a distinct scalloped portion near its distal tip, something more than the blade that is developed above this ray in most species of the genus (fig. 39). Except for the autapomorphic *G. heterochir* of the *nobilis* species group, this group has the most pronounced pectoral-fin modifications in the genus.

Gambusia aurata and *G. lemaitrei* both have very high serrae on ray 4p of the gonopodium, extending to distal to the elbow [43]. In these two species, ray 3 is somewhat foreshortened, such that it does not reach the distal tip of the gonopodium [44]. And in *G. affinis* and *G. holbrooki*, the gonopodia are exaggeratedly drawn out at their distal tips, coming to a much more acute point than in any other species in the genus [62].

***nobilis* species group** (fig. 40): A group with this name was implied in a key by Hubbs in 1926, and in 1929 he formalized it with the description of *G. gaigei*. He grouped *G. nobilis*, *G. senilis*, and "*G. affinis*" with this new species, but the characters describing the group are actually applicable to larger groups in *Gambusia*. Hubbs and Springer (1957) clarified that the "*G. affinis*" of Hubbs (1926, 1929) was not *G. affinis*, but a new species, *G. geiseri*. They added another two species to the group, *G. alvarezi* and *G. hurtadoi*.

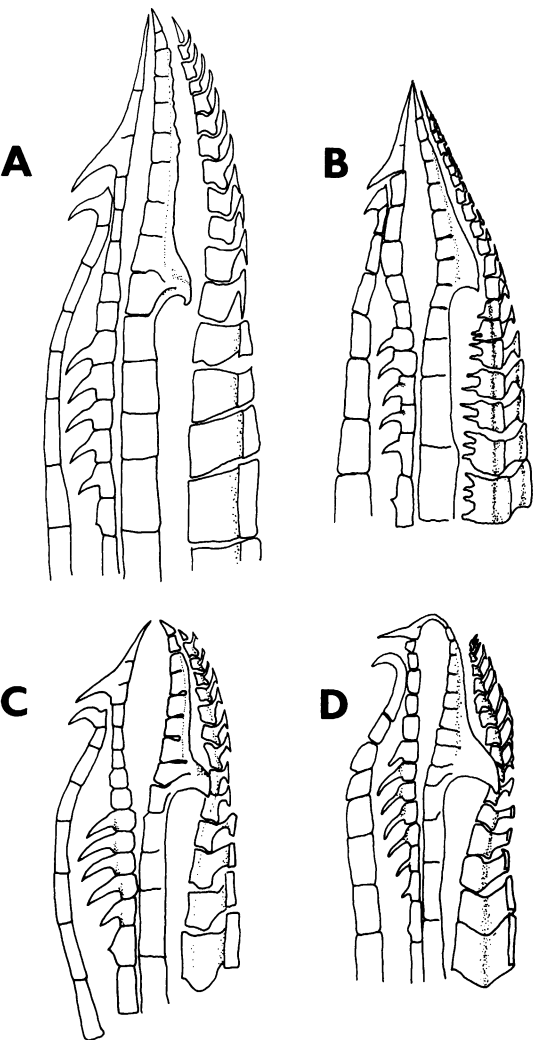


Fig. 38. Gonopodia of members of the *affinis* species group: **A.** *Gambusia affinis*, **B.** *Gambusia holbrooki*, **C.** *Gambusia speciosa*, **D.** *Gambusia aurata*. Note: *G. lemaitrei* also belongs to this group. See Rivas (1963) for a figure of its gonopodium.

Their group definition again consisted primarily of primitive characters, although the composition corresponds roughly to the combination of the *nobilis* and *senilis* species groups as described herein. The same applies to the Rosen and Bailey (1963) *nobilis* species group; they also added *G. heterochir*, *G. longispinis*, and *G. atrora*. Rivas (1963) did distinguish the *nobilis* and *senilis* species groups; however, his *nobilis* species group is again not characterized by derived traits, but rather

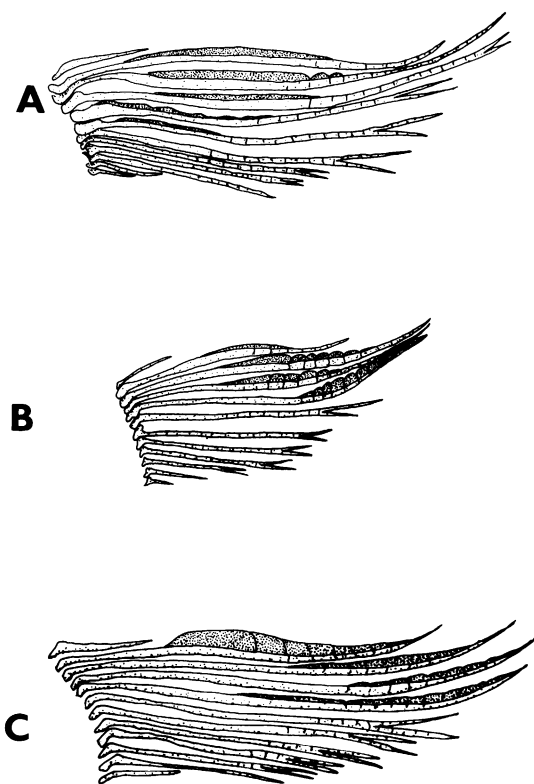


Fig. 39. Male pectoral fins. Modified parts of pectoral fins are stippled darkly: **A.** *Gambusia vittata*, **B.** *Gambusia holbrooki*, **C.** *Gambusia pseudopunctata*. Note: Compare with fig. 15B for *G. hispaniolae*.

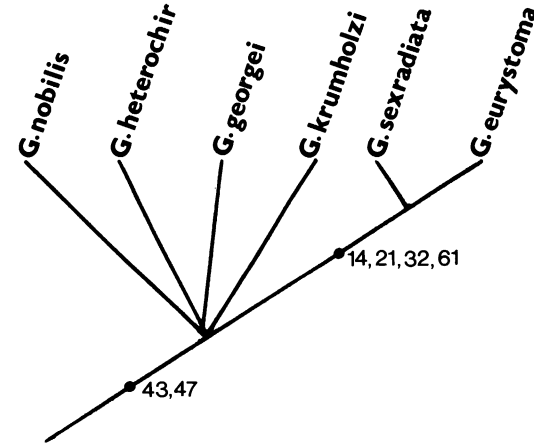


Fig. 40. Cladogram depicting relationships within the *nobilis* species group.

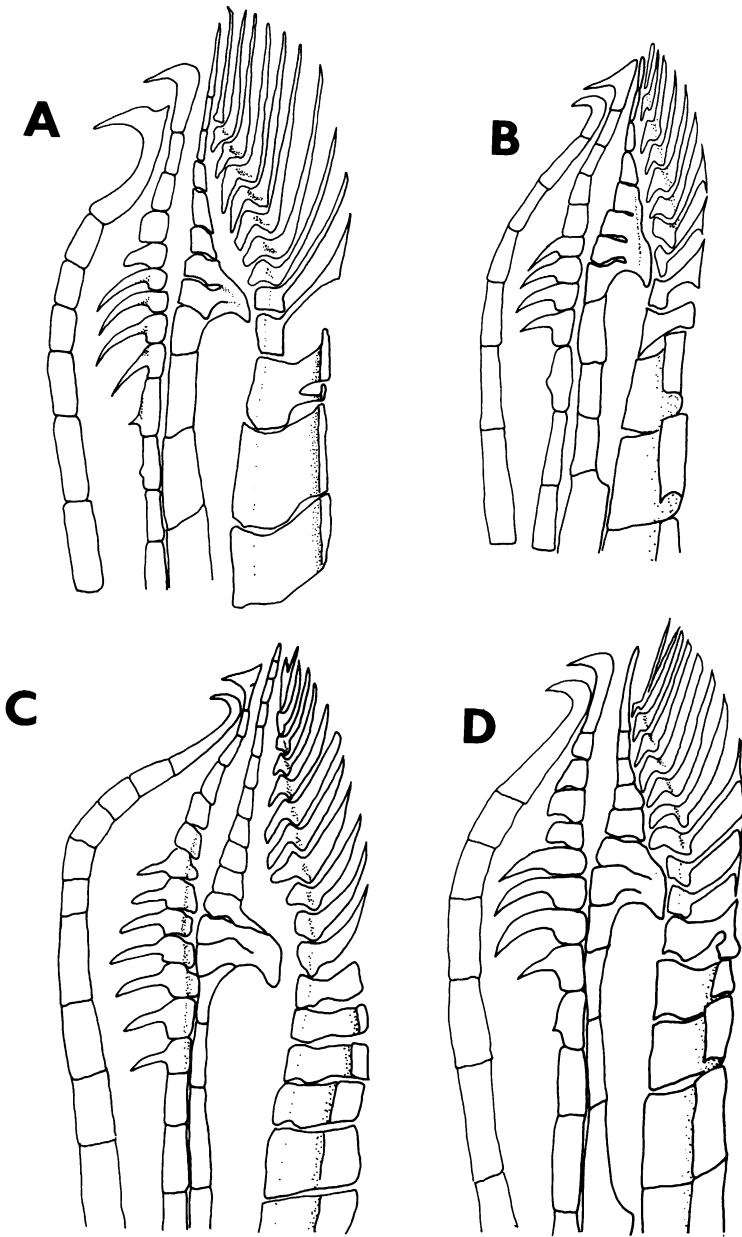


Fig. 41. Gonopodia of members of the *nobilis* species group: **A.** *Gambusia nobilis*, **B.** *Gambusia georgei*, **C.** *Gambusia heterochir*, **D.** *Gambusia krumholzi*, **E.** *Gambusia eurystoma*, **F.** *Gambusia sexradiata*.

by the lack of the derived traits of the *senilis* species group.

Indeed, members of the *nobilis* species group do share several derived characters with the *senilis* species group, indicating a sister-group relationship (see p. 43); however, the *nobilis* species group can be characterized by the position of the serrae on ray 4p, being

opposite the elbow rather than proximal to it [43], and by the rounded gonopodial outline [47], unique to this group within the subgenus (fig. 41).

Gambusia nobilis, *G. heterochir*, *G. georgei*, *G. krumholzi*, *G. eurystoma*, and *G. sexradiata* comprise this species group. *Gambusia eurystoma* and *G. sexradiata* clearly are

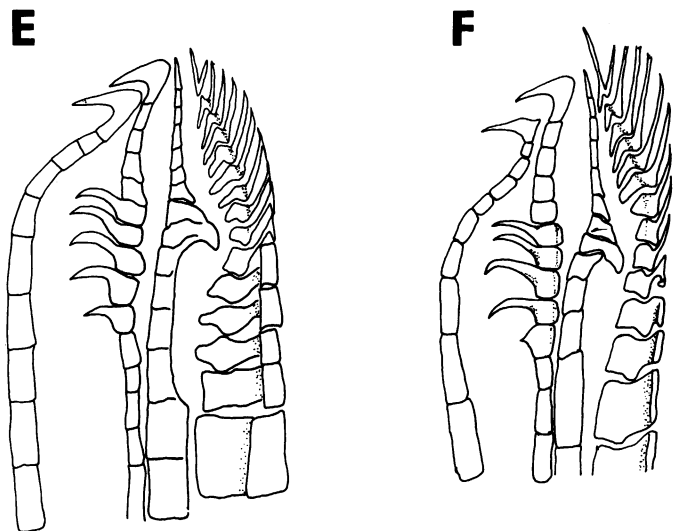


Fig. 41—Continued.

sister taxa, sharing recurved serrae on ray 4p of the gonopodium [32], spotted dorsal and caudal fins [21], continuous grooves in the posterior section of the infraorbital latero-sensory canals [14], and three gonapophyses [61]. No other resolution of relationships within this group was possible, however. Each of the four remaining species has certain autapomorphies, for example the exaggerated pectoral-fin modification of *G. heterochir* males, but no synapomorphies uniting any subgroup of these were discernable.

senilis species group (fig. 42): The *senilis* species group was first proposed by Rivas (1963), to contain *G. senilis*, *G. geiseri*, *G. gaigei*, *G. alvarezi*, and *G. hurtadoi*. To his list I add *G. longispinis* of his *nobilis* species group, *G. atrora*, and *G. amistadensis*. Three gonopodial features distinguish this group (fig. 43). Ray 4a is foreshortened distal to the elbow, such that it does not extend to the end of the gonopodium [45]. Consequently, there are very few segments in ray 4a distal to the elbow. There also is a reduced number of spines on ray 3, typically eight [46]. Finally, these fishes have a very distinctive gonopodial outline [47]; the furthest extension of the gonopodial tip is drawn out to a point on the anterior edge, and the medial distal edge actually dips a little proximally before being drawn out to that tip.

This group can be divided into two monophyletic subgroups. One, containing *G. se-*

nilis, *G. gaigei*, *G. alvarezi*, *G. hurtadoi*, and *G. amistadensis*, is characterized by a median anal spot in females (Peden, 1973a), rather than the paired crescents more common in the subgenera *Arthrophallus* and *Gambusia* [24], and a transversely enlarged segment on ray 4a distal to the serrae [48]. Transversely enlarged segments also are seen in the *puncticulata* and *punctata* species groups of the subgenus *Gambusia*, but in those fishes, the segments extend primarily toward ray 4a, and in the members of the *senilis* species group, the extension is toward ray 5a only. Fur-

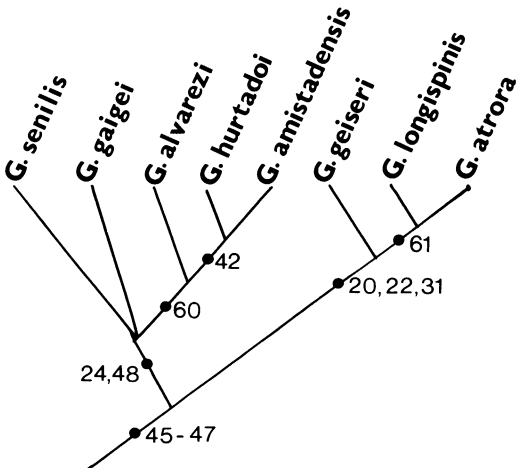


Fig. 42. Cladogram depicting relationships within the *senilis* species group.

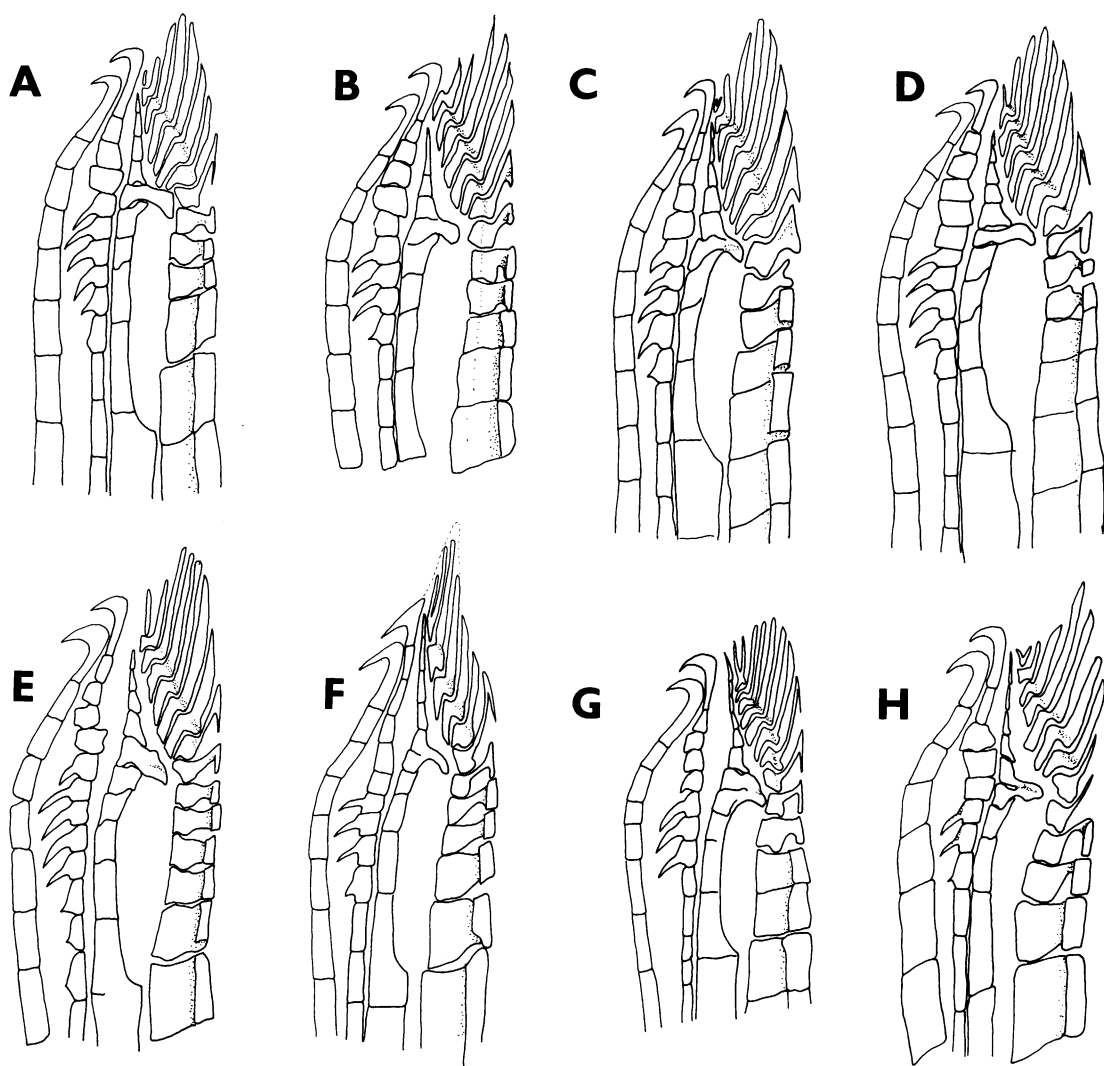


Fig. 43. Gonopodia of members of the *senilis* species group: **A.** *Gambusia senilis*, **B.** *Gambusia gaigei*, **C.** *Gambusia alvarezi*, **D.** *Gambusia hurtadoi*, **E.** *Gambusia amistadensis*, **F.** *Gambusia geiseri*, **G.** *Gambusia longispinis*, **H.** *Gambusia atrora*.

thermore, these *senilis*-type species usually have only one expanded segment, with an abrupt transition to more narrow segments just distal to it. In the *puncticulata* and *punctata* species groups, there often are two, three, or four expanded segments that gradually narrow distally. Within this small group, *G. hurtadoi* and *G. amistadensis* share a small lateral projection on the elbow of ray 4a [42], and *G. alvarezi* shares with these two a similar hypobranchial 1 shape [60]; however, it

should be emphasized that all five members of this clade are quite similar.

The sister clade to this group consists of *G. geiseri*, *G. longispinis*, and *G. atrora*. These three are united by a reduction in the number of serrae on ray 4p, to fewer than four [31], no suborbital bar [22], and a form of hypural fusion unique within the genus (fig. 44). There is only one hypural plate, a complete fusion of the hypural elements into a fan, with no keyhole remaining [20]. *Gambusia atrora* and

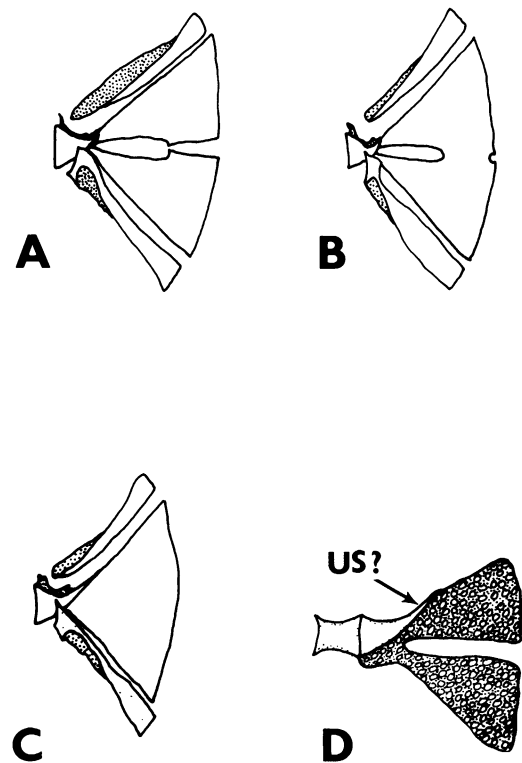


Fig. 44. Caudal fin skeletons of: A. *Gambusia luma*, B. *Gambusia hispaniolae*, C. *Gambusia atrora*, D. embryonic caudal skeleton of *G. hispaniolae*.

G. longispinis are sister species within this clade, as these two species have three gonapophyses, whereas other members of the *nobilis* and *senilis* species groups typically have only two [61].

RELATIONSHIPS WITHIN THE SUBGENUS *GAMBUSIA* (fig. 45)

Within this subgenus, a group consisting of the *puncticulata* and *punctata* species groups can be described. These fishes share several synapomorphies in gonopodial structure. In ray 4p, just distal to the serrae, one or two segments (or more) are transversely enlarged [48] in all species except *G. luma*. As in the *nobilis* and *senilis* species groups, the spines of ray 3 are elongate and develop inner processes [39]; however, the inner processes of this group are wider and flatter at their proximal edges. In the *nobilis* and *senilis* species groups, the inner processes tend to

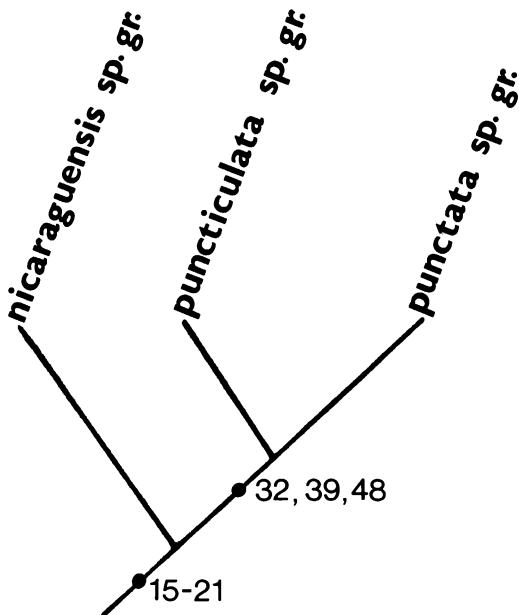


Fig. 45. Cladogram depicting relationships among species groups in the subgenus *Gambusia*.

curve anteriorly as they extend proximally, and they narrow to fingerlike proximal edges. Similarly, the shapes of the spines, and particularly the outline of the gonopodia as formed by the spines, are distinctive for each

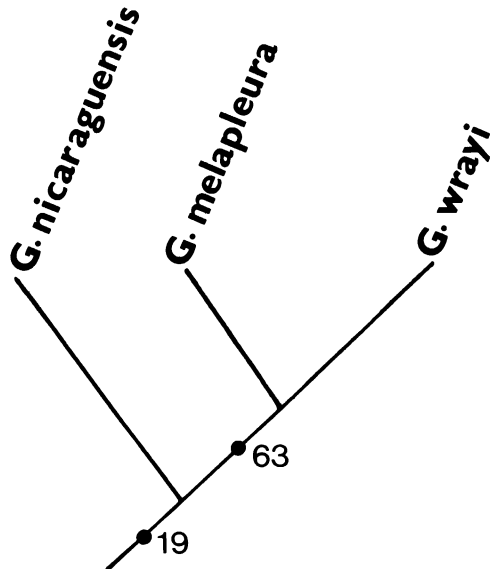


Fig. 46. Cladogram depicting relationships within the *nicaraguensis* species group.

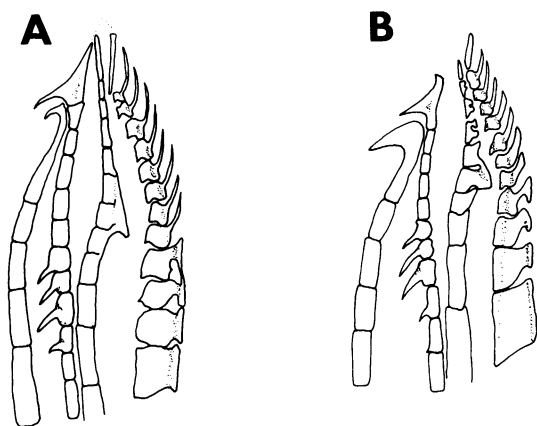


Fig. 47. Gonopodia of members of the *nicaraguensis* species group: **A.** *Gambusia nicaraguensis*, **B.** *Gambusia wrayi*. Note: *Gambusia melapleura* also belongs to this group; see Fink (1971b) for a figure of its gonopodium.

species group. These two groups are further separated from the *nicaraguensis* species group by the fact that their serrae on ray 4p are straight, not retrorse [32].

***nicaraguensis* species group** (fig. 46): Rivas (1963) described a *nicaraguensis* species group to contain *G. nicaraguensis*, *G. wrayi*, *G. melapleura*, *G. gracilior*, and *G. dominicensis*, but did not use derived characters for its description. Fink (1971b) revised Rivas' group, adding *G. hispaniolae*. He also discussed the status of *G. dominicensis*, described by Regan from "Haiti," which has never been subsequently collected there or anywhere. I have not examined Regan's syntypes, but Fink's figures clearly indicate that the common *Gambusia* of Hispaniola, which is often identified as *G. dominicensis*, is actually *G. hispaniolae*, and that, as Fink suggests, Regan's locality information for *G. dominicensis* is probably incorrect. Fink (1971b) also synonymized *G. gracilior* under *G. wrayi*, after examining Regan's syntypes of both and concluding that the proportional differences cited by Regan (1913) were indistinct. Not having examined these syntypes myself, I accept the synonymy, but cautiously. Material I have examined of *G. wrayi* shows a dimorphism in gonopodial structure, with a unique recurved form of the terminal hook on ray 5a, and also a distinctive pelvic girdle in these same samples. This particular gonopodial in-

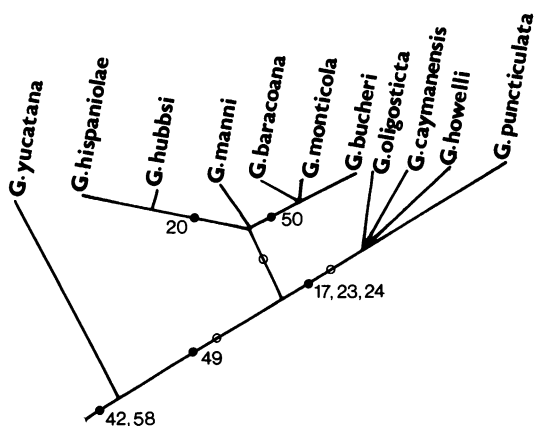


Fig. 48. Cladogram depicting relationships within the *puncticulata* species group.

novation is not shown in either Fink's (1971b) or Regan's (1913) figures. This is one of several areas in the genus where additional taxonomic work at the alpha level would be fruitful.

The *nicaraguensis* species group, as herein diagnosed, contains *G. nicaraguensis*, *G. wrayi*, and *G. melapleura*; present evidence places *G. hispaniolae* in the *puncticulata* species group (fig. 47).

These fishes have a more triangular ventral hypohyal than that found elsewhere in the genus [19]. In figure 28, different conditions of the ventral aspect of the ventral hypohyal are portrayed. The general condition for the genus is for the ventral hypohyal to be roughly square, meeting the anterior ceratohyal in a straight line. In the subgenus *Gambusia*, the anterior ceratohyal has an anterior lobe, so that the connection of the two bones is no longer square. In the *puncticulata* and *punctata* species groups, however, the anterolateral edge of the ventral hypohyal is still squared. In the *nicaraguensis* species group, the anterolateral corner of the ventral hypohyal is no longer squared; rather, the edge of the bone cuts directly from the antero-medial edge to the posterolateral edge, resulting in a triangular bone.

Gambusia wrayi and *G. melapleura* have odd segments in ray 4a distal to the elbow, each with two or three serrations in its anterior edge [63].

***puncticulata* species group** (fig. 48): The *puncticulata* species group of Rivas (1963)

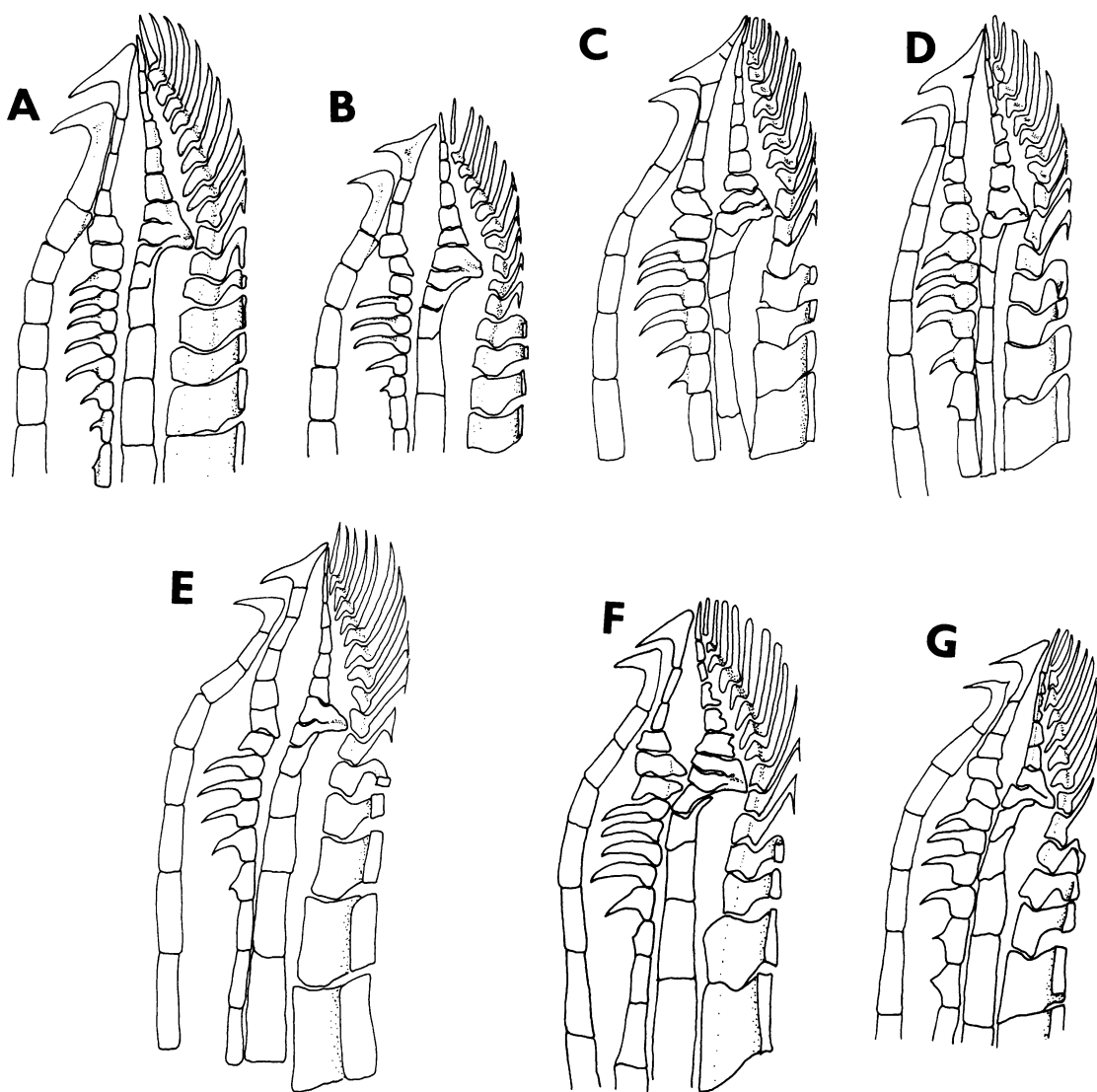


Fig. 49. Gonopodia of members of the *puncticulata* species group: A. *Gambusia yucatana*, B. *Gambusia hubbsi*, C. *Gambusia baracoana*, D. *Gambusia bucheri*, E. *Gambusia puncticulata*, F. *Gambusia oligosticta*, G. *Gambusia caymanensis*. Note: *G. manni*, *G. monticola*, and *G. howelli* also belong to this group, but are not figured. See Fink (1971a) for some of these figures. See fig. 20 for *G. hispaniolae*.

was revised by Fink (1971a). In that work, he synonymized the eight forms in the group under the name *G. puncticulata*, with *G. puncticulata puncticulata* representing the former *G. puncticulata*, *G. oligosticta*, *G. caymanensis*, *G. hubbsi*, and *G. howelli*. *Gambusia manni*, *G. bucheri*, *G. baracoana*, and *G. yucatana* were reduced to subspecific status, along with *G. puncticulata monticola*. This study was primarily based on meristics,

pigmentation, and gonopodial counts and measures, and the rationalization for combining all these forms under one species name was that they were not gonopodially distinct. Additionally, the forms combined in the nominal subspecies had overlapping ranges for all of the characters studied.

Greenfield and Wildrick (1984) reexamined the group, using additional characters including electrophoretic analysis. They pro-

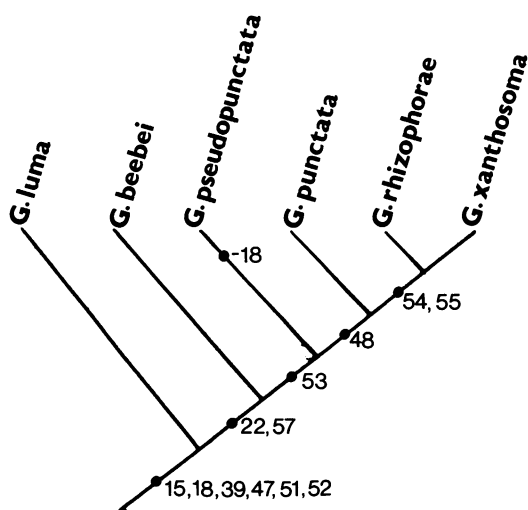


Fig. 50. Cladogram depicting relationships within the *punctata* species group.

posed that *G. yucatanana* be reinstated to full species rank and be the sister group to the other members of the group. In fact, subspecies *G. yucatanana yucatanana* and *G. yucatanana australis* were later described (Greenfield, 1985). The island members of the species group were divided into two sections: one containing *G. puncticulata* from Cuba, *G. howelli*, *G. caymanensis*, and *G. oligosticta*; the other with *G. puncticulata* from the Bahamas (= *G. hubbsi*), *G. manni*, *G. bucheri*, *G. baracoana*, and *G. monticola*. These groups were found to be electrophoretically distinct from each other and from *G. yucatanana*.

Clearly, further alpha-level work needs to be done to address the species problems in this group. It is beyond the scope of the current work to evaluate the relative merits of these two studies; however, it is my intent to try to determine which taxa form groups, and which groups are related to which. Although specimens of some of the endemic taxa are quite scarce, I have chosen to include all nominal forms in the analysis; taxa shown to form a monophyletic group might at some later point be synonymized if their differences prove to be inconsequential. Furthermore, I wish to have all the taxa available for use in the biogeographic analysis.

As described herein, the members of the *puncticulata* group (fig. 49) have a lateral thickening along the proximal base of the el-

bow in ray 4a of the gonopodium [42], reminiscent of the lateral knob of the *affinis* species group; however, in that group, the lateral projection is a knob projecting from the anteroproximal tip of the elbow, while in this group the thickening is along the flat proximal edge, seeming more like a shelf than a knob. The members of this species group also share a somewhat different pectoral-fin modification. In other groups, the blades on rays 2 through 5 are developed primarily on the dorsal side of the ray. In this group (fig. 39), the blades are equally well developed on both the dorsal and ventral sides [58].

Greenfield and Wildrick (1984) united all species in the group except *G. yucatanana* by several electrophoretic characters. They also noted that all island species of this group show red and yellow coloration in the dorsal and caudal fins, especially in breeding males [49]. *Gambusia yucatanana* shows no such colors. Another character they use at this level is the longer serrae on ray 4p possessed by the island species as compared to *G. yucatanana*; although this is true, the sister group of the *puncticulata* species group, the *punctata* species group, also has long serrae.

Gambusia hubbsi, *G. manni*, *G. hispaniolae*, *G. baracoana*, *G. bucheri*, and *G. monticola* constitute a monophyletic group, corresponding (except for the addition of *G. hispaniolae*) to the "hubbsi group" designated by Greenfield and Wildrick (1984). Within the group, *G. hubbsi* and *G. hispaniolae* have hypurals fused into a single hypural plate, with a keyhole [20]. *Gambusia bucheri*, *G. baracoana*, and *G. monticola* share an increased number of lateral-line scales and vertebrae [50]; Fink (1971a) documented the range of variation in these meristic characters for the species group.

In Greenfield and Wildrick's (1984) "*puncticulata* group," consisting of *G. puncticulata*, *G. oligosticta*, *G. caymanensis*, and *G. howelli*, the anteriorly directed lateral prongs of the first hypobranchials in the ventral gill arches, characteristic of the subgenus *Gambusia*, are reduced to very small bumps [17] (fig. 26C). This group also is characterized by a permanent median anal spot in the females; Greenfield and Wildrick (1984) reported no anal spot either in *G. yucatanana* or in the *hubbsi* forms, although Peden (1973a) indicated

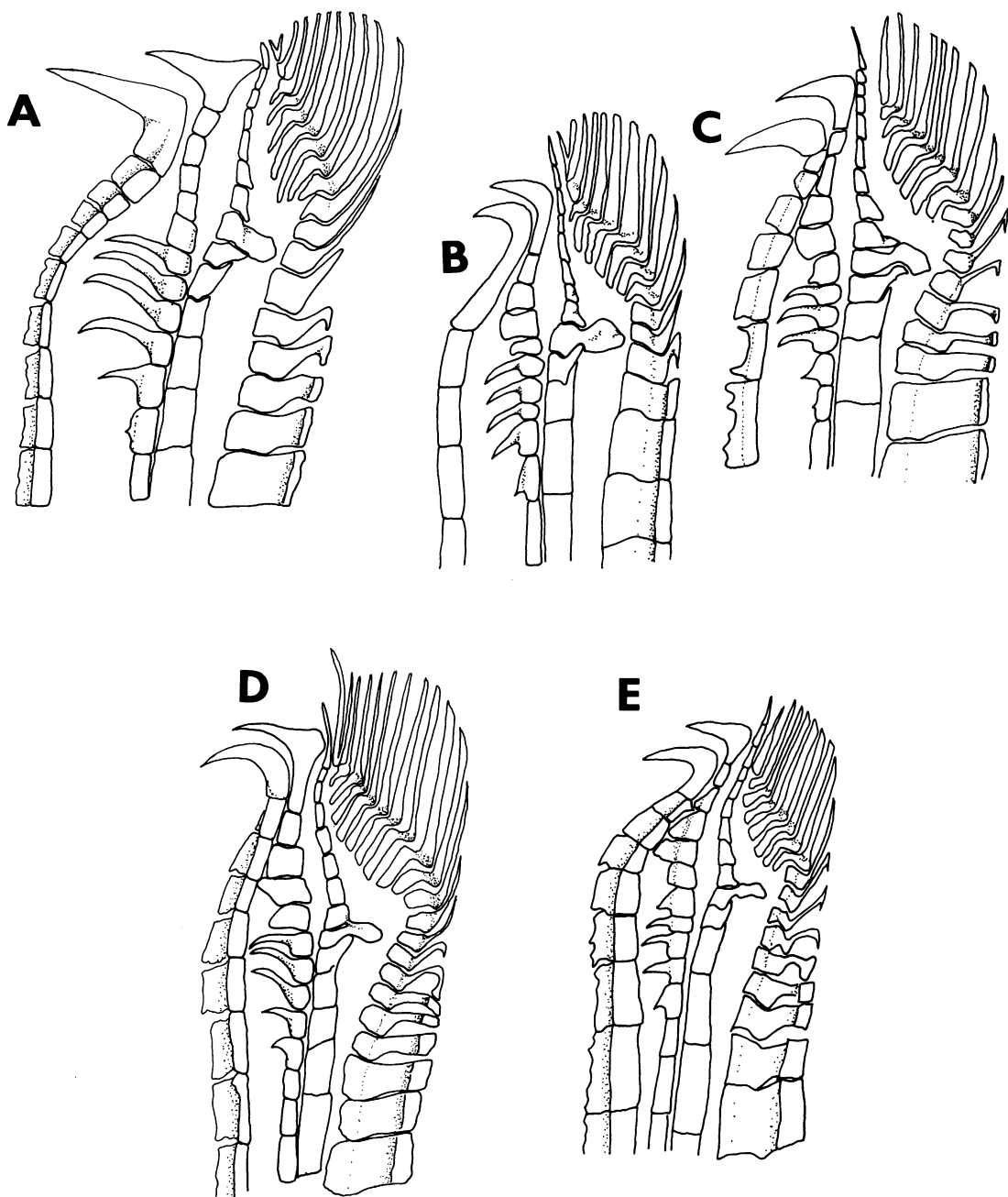


Fig. 51. Gonopodia of members of the *punctata* species group: A. *Gambusia luma*, B. *Gambusia pseudopunctata*, C. *Gambusia punctata*, D. *Gambusia rhizophorae*, E. *Gambusia xanthosoma*. Note: *G. beebei* also belongs to this group. See Rivas (1969) for a figure of its gonopodium.

that some of these forms have paired crescents.

***punctata* species group** (fig. 50): This species group was recognized by both Rivas and Rosen and Bailey, although these authors disagreed with a few members. The gonopodium is quite distinctive (fig. 51), with a spatulate elbow [15]. The hooks on both rays 5a [51] and 4p [52] are enlarged and scythelike. The spines on ray 3 are very long and straplike [39], as are their inner processes, which reach far in, almost touching ray 4a. These spines form a lobelike outline to the gonopodium, not pointed at all [47]. In the ventral gill arches, the wings on the third basibranchial are reduced [18] in all species examined except *G. pseudopunctata*; this character was not examined in *G. xanthosoma* or *G. beebei*.

As diagnosed above, this species group includes six members: *G. luma*, *G. beebei*, *G. pseudopunctata*, *G. punctata*, *G. xanthosoma*, and *G. rhizophorae*. All of these species except *G. luma* have the suborbital bar reduced or absent [22], and several morphometric and meristic characters described by Greenfield (1983) apply at this level, such as a more anterior placement of the dorsal fin and higher dorsal-fin ray counts. All members of this species group except *G. luma* have a unique pectoral-fin modification [57] in males, where the blade on ray 2 thickens abruptly near its proximal end, and the segments are anastomosed in this area. *Gambusia luma* does not have the transversely enlarged segments on ray 4p just distal to the serrae, but otherwise its placement in this group is obvious, contrary to the arguments of Rivas (1969).

Except for the suborbital bar of *G. luma* and the postocular bar that is prominent in all species of this group, pigmentation is very plain in *G. luma* and *G. beebei*. The other four species of the group are united by a well-developed pigmentation pattern, of four to six rows of large dark spots along the sides of the body [53], a striking pattern that earned *G. punctata* its name.

Gambusia punctata, *G. xanthosoma*, and *G. rhizophorae* have especially pronounced enlargements of the posterior edges of the segments just distal to the serrae on ray 4p of the gonopodium. These extensions fill the

space between ray 4p and ray 5a, sometimes with small anterior projections from ray 5a filling in the gaps [48].

Gambusia xanthosoma and *G. rhizophorae* share a unique karyotype, reported by Wildrick et al. (1985). One pair of metacentric chromosomes and two pairs of submetacentric chromosomes are found in both sexes [54]. *Gambusia luma* also was karyotyped by the same authors; it has no metacentrics or submetacentrics in either sex, inferred to be the general condition for the genus (see discussion, p. 38). *Gambusia beebei*, *G. pseudopunctata*, and *G. punctata* were not tested, so it is unclear how large a group this character might specify. In the gonopodium of *G. xanthosoma* and *G. rhizophorae*, ray 4a distal to the elbow curves in an S-shape anteriorly over the first of the ray 3 spines [55]. These two species also share a pigmentation character, the development of a distinct midlateral stripe, and they are both the normal small size of most gambusias. Other members of this species group attain large sizes, with *G. beebei* at up to 59 mm standard length (Rivas, 1969) being the largest species of the genus. *Gambusia rhizophorae* and *G. xanthosoma* are the only species of the group that thrive in brackish water; they are both found associated with mangrove swamps.

BIOGEOGRAPHY

Distributional information presented herein is compiled from various sources, including the materials examined, the original descriptions of the species, Geiser (1923), Hubbs and Springer (1957), Rosen and Bailey (1963), Rivas (1963, 1969, 1971), Fink (1971a, 1971b), and Greenfield et al. (1982), as well as other sources mentioned below.

DISTRIBUTION OF THE SUBGENUS *HETEROPHALLINA* (fig. 52)

Members of this subgenus are known only from strictly freshwater habitats, most often the headwaters and swiftly flowing streams that drain the Sierra Madre Oriental.

***Gambusia vittata*:** This species is limited to the Río Pánuco and Río Tamesí systems of Tamaulipas and San Luis Potosí, Mexico. It is sympatric with *G. aurata* and *G. affinis*

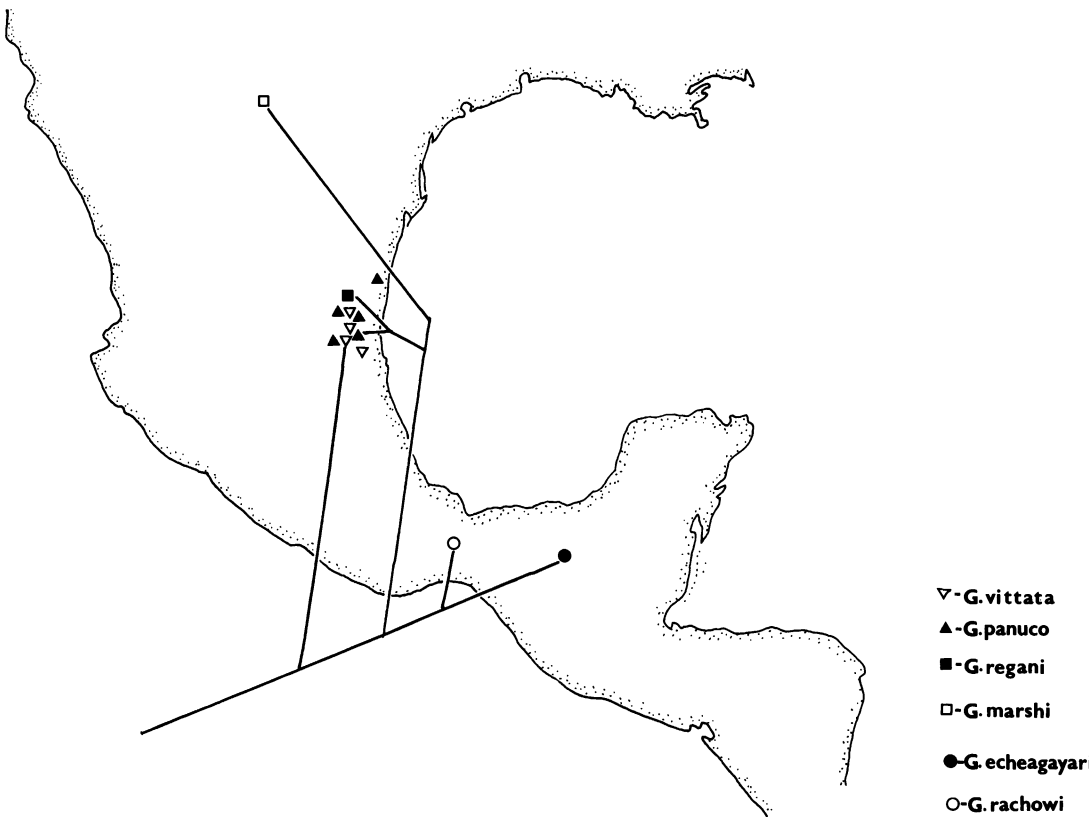


Fig. 52. Distribution of members of the subgenus *Heterophallina*.

in the Río Mante, and with *G. atrora* in the Río Axtla system. It also is sympatric with *G. panuco* throughout much of its range; although *G. vittata* is not found in the Río Ojo Frío system, it is found in Pánuco tributaries further east and south than *G. panuco* (such as the Río Atlapexco). It may extend south into the Río Tuxpan system.

panuco species group: Two of the species of this group are confined to the Río Pánuco and Río Tamesí systems; the third is isolated from them in northern Mexico. All three species in this group are allopatric with respect to one another.

Gambusia marshi is widespread in the Río Salado system and in parts of the Cuatro Ciénegas basin in Coahuila, Mexico. It shares the Cuatro Ciénegas area with *G. longispinis*, and may be sympatric in part of the Salado drainage with *G. speciosa*.

Gambusia panuco, as described above under *G. vittata*, is widespread throughout the

Pánuco valley. It is found in the Río Tamesí system, except at the extreme headwaters of the Río Sabinas, where it is replaced by *G. regani*. In the Río Pánuco system, it is the only *Gambusia* in the Río Ojo Frío system, and it coexists with both *G. vittata* and *G. atrora* in the Río Axtla. It is found as far south as the Río Calabozo, but drops out after that. It also is found in headwater areas of the Río Soto La Marina, to the north.

Gambusia regani is confined to the headwaters of the Río Sabinas system, Río Tamesí drainage, Tamaulipas, Mexico. Although some other localities in the Tamesí and Soto La Marina systems are cataloged in some collections as *G. regani*, these are in fact *G. panuco*.

rachowi species group: Each of the two species of this small group is known only from the area of the type locality, both in southeastern Mexico. Both are sympatric with *G. sexradiata*.

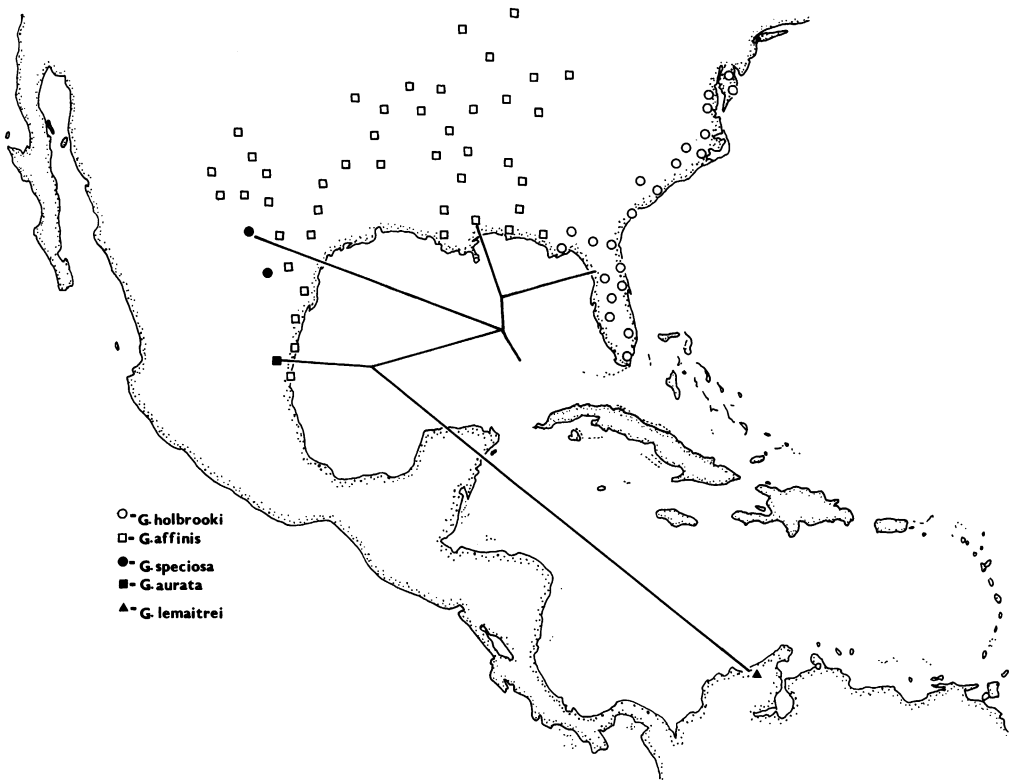


Fig. 53. Distribution of members of the *affinis* species group.

Gambusia rachowi is found at Jesus Caranza, Veracruz, in the Río Coatzacoalcos system.

Gambusia echeagayari inhabits a small stream near the town of Palenque, Chiapas, which drains into the Río Usumacinta system.

DISTRIBUTION OF THE SUBGENUS *ARTHROPHALLUS*

This subgenus is distributed over continental and coastal habitats, from eastern North America to southern Mexico, with a single species in South America. It has no members either in lower Central America or the Antilles; the greatest diversity of taxa occurs in Texas and northern Mexico.

***affinis* species group** (fig. 53): This species group is the most far-ranging of the genus, both as a group, from New Jersey to Colombia, and as individual species, as *G. affinis* and *G. holbrooki* are quite widespread. These two species have been introduced worldwide to control mosquitos. These efforts have had

some limited success; *Gambusia* apparently prefers to eat larval fish when available, and the introduction of these species has often had devastating effects on the native fish fauna, including other species of *Gambusia*. It is difficult to know certainly the natural ranges of these two taxa, but careful compilations and record-keeping allow a reasonable approximation.

Gambusia holbrooki is found in fresh water along the Eastern Seaboard of the United States, from the southern tip of New Jersey through to the Florida Keys, and in western drainages from Georgia into the Gulf of Mexico. It is replaced by *G. affinis* further west; the exact dividing line or the nature of a zone of intergradation was not studied here. It is broadly sympatric with *G. rhizophorae* in extremely southern Florida.

Gambusia affinis, in addition to the Gulf drainages of Louisiana, Alabama, Mississippi, and Texas, ranges further north in the United States (to Illinois) and is common throughout the Río Grande and Pecos River

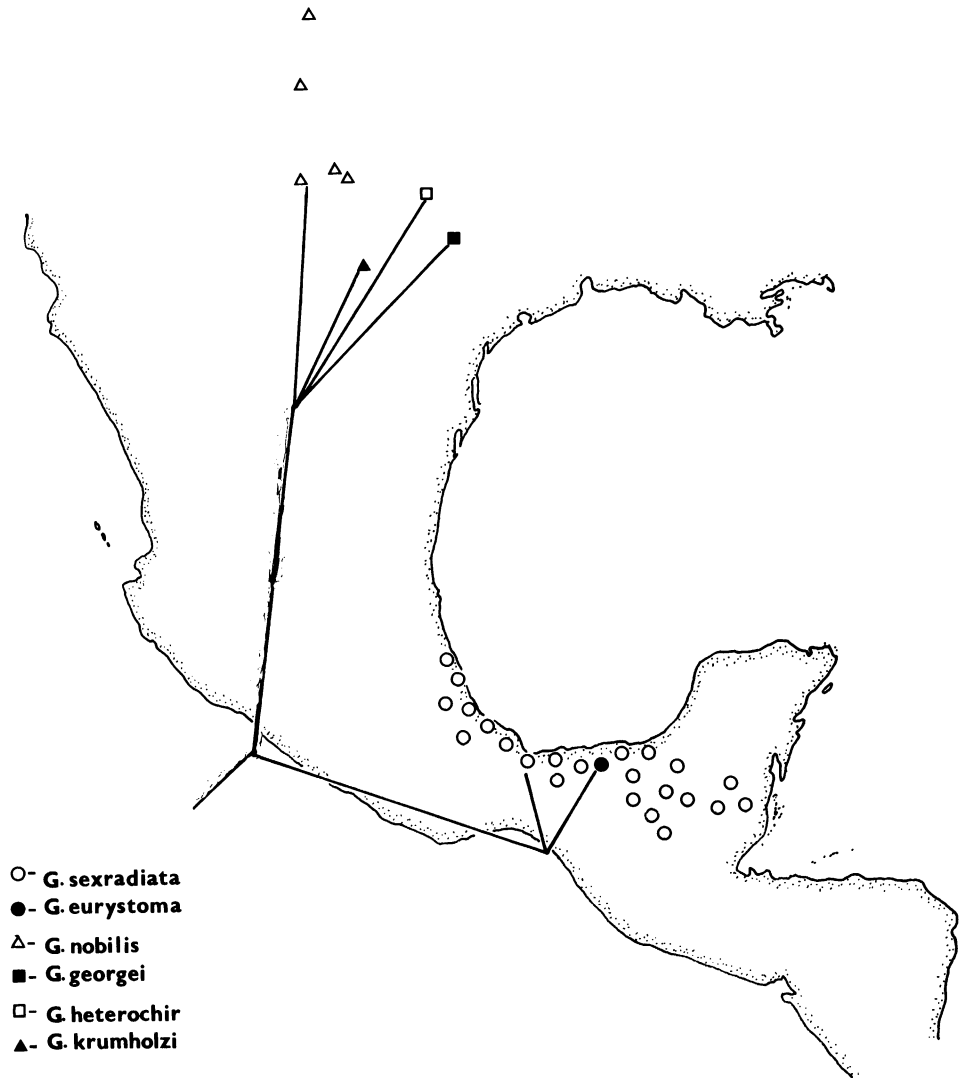


Fig. 54. Distribution of members of the *nobilis* species group.

drainages. It also is reported to occur in Gulf drainages along the east coast of Mexico as far south as Tampico. However, such reports were not checked by the author, and many of these southern localities may be referable to *G. speciosa*. In Texas, *G. affinis* is sympatric (but seldom syntopic) with many members of the *nobilis* and *senilis* species groups.

Gambusia speciosa was described from the Río San Juan, in Nuevo Leon, and a population recently has been found at Melchor Musquiz, in a stream of the Río Salada-Río Grande drainage, in Coahuila. Clark Hubbs

(personal commun.) also reports it from the Devil's River, Texas. The full extent of the range of this species also needs further study. As with *G. affinis* and *G. holbrooki*, locality records for this species are confusing because of the years of nomenclatural confusion.

Gambusia aurata resides in the Río Mante, of Río Tamesí drainage, in Tamaulipas, Mexico. It has been taken, both in the nacimiento and canals through Ciudad Mante, with three other *Gambusia* species: *G. affinis*, *G. panuco*, and *G. vittata*. Darnell (1962) and Miller and Minckley (1970) described the microhabitats of these sympatric species.

Gambusia lemaitrei offers the oddest distributional note. Known only from Totumo, Colombia, it is the only South American representative of the genus. However, it is not well collected, and no further details of its distribution are available.

***nobilis* species group** (fig. 54): Most of the species of this group are endemic to freshwater springheads. The precarious nature of these habitats, in the face of development, has warranted three of these species to be federally listed as endangered: *G. nobilis*, *G. heterochir*, and *G. georgei*. The Mexican *G. krumholzi* is limited to a small area, but is not threatened; *G. eurystoma* also is a strict endemic whose status is still safe. Only *G. sexradiata* of this group has a widespread distribution at present, and it is the only member found in other than a strictly freshwater situation.

Gambusia nobilis is endemic to the Pecos River drainage in Texas and New Mexico, found primarily in small springs and sinkholes. Geographic variation among the isolated springhead populations was recently studied by Echelle and Echelle (1986), who concluded that subspecific designations were unwarranted. Historical records indicate that the species was previously both more abundant and widespread, and C. Hubbs (personal commun.) reports hybridization of this species with *G. affinis*.

Gambusia georgei, of the upper San Marcos River, Hays County, Texas, is sympatric with *G. geiseri*, of the *senilis* species group, and *G. affinis*, of the *affinis* species group. According to Hubbs and Peden (1969), these three species partition the environment, with *G. geiseri* most common in midwater, *G. affinis* in shallow vegetated areas, and *G. georgei* restricted to shallow areas with no vegetation. This rare (and possibly extinct) species also hybridizes somewhat with *G. affinis*, reported by Hubbs and Peden (1969).

Gambusia heterochir is restricted to the headwaters of Clear Creek, Menard County, Texas. Clear Creek flows into the San Saba River, where *G. affinis* occurs, and hybridization between the two species, in Clear Creek, has been reported by Hubbs (1957).

Gambusia krumholzi is known only from the type locality, the Río de Nava, which is

a small stream in the Río Grande drainage, of Coahuila, Mexico.

Gambusia eurystoma was described from a sulfurous, spring-fed stream, Arroyo del Azufre, at Baños de Azufre, 10 km west of Teapa, Tabasco, Mexico, and is found only at that locality (Miller, 1975).

Gambusia sexradiata, first described as a subspecies of *G. nicaraguensis*, inhabits the coastal drainages of Mexico from the Río Nautla south to the Yucatan peninsula. It also is found throughout the Usumacinta drainage of Guatemala. In these areas, it is primarily a freshwater form. In Belize, however, Greenfield et al. (1983) reported that it also is found in brackish and sea water. In Belize, *G. sexradiata* shares its habitat with *G. luma* and *G. yucatanana*.

***senilis* species group** (fig. 55): As with the *nobilis* species group, many members of this group are strictly limited to small, threatened springhead habitats. *Gambusia gaigei* and *G. amistadensis* are listed as endangered; *G. amistadensis* is reported to be extinct.

Gambusia senilis is most common in the Río Conchos system of Chihuahua and Durango, Mexico; it also occurred in the Devil's River of Texas, but is now extinct there. It inhabits clear springs, turbid water, and irrigation ditches, and although widespread, much of its habitat dries up periodically.

Gambusia gaigei, the Big Bend *Gambusia*, was described from Boquillas Spring, Río Grande drainage, Brewster County, Texas. Hubbs and Brodrick (1963) report that the population was extirpated at the type locality, but that the fish was introduced into Croton Springs, is in Graham Ranch Springs, and is found in an artificial pool in Big Bend National Park.

Within the range of *G. senilis* are two isolated areas, each containing an endemic species. *Gambusia alvarezi* is known only from El Ojo de San Gregorio (a warm spring) and adjacent creeks. *Gambusia hurtadoi* is described from El Ojo de la Hacienda Dolores, another warm spring, and associated irrigation ditches. Both are in Chihuahua, Mexico.

Gambusia amistadensis was described from Goodenough Spring and its outflow to the Río Grande in Val Verde County, Texas (Pe-

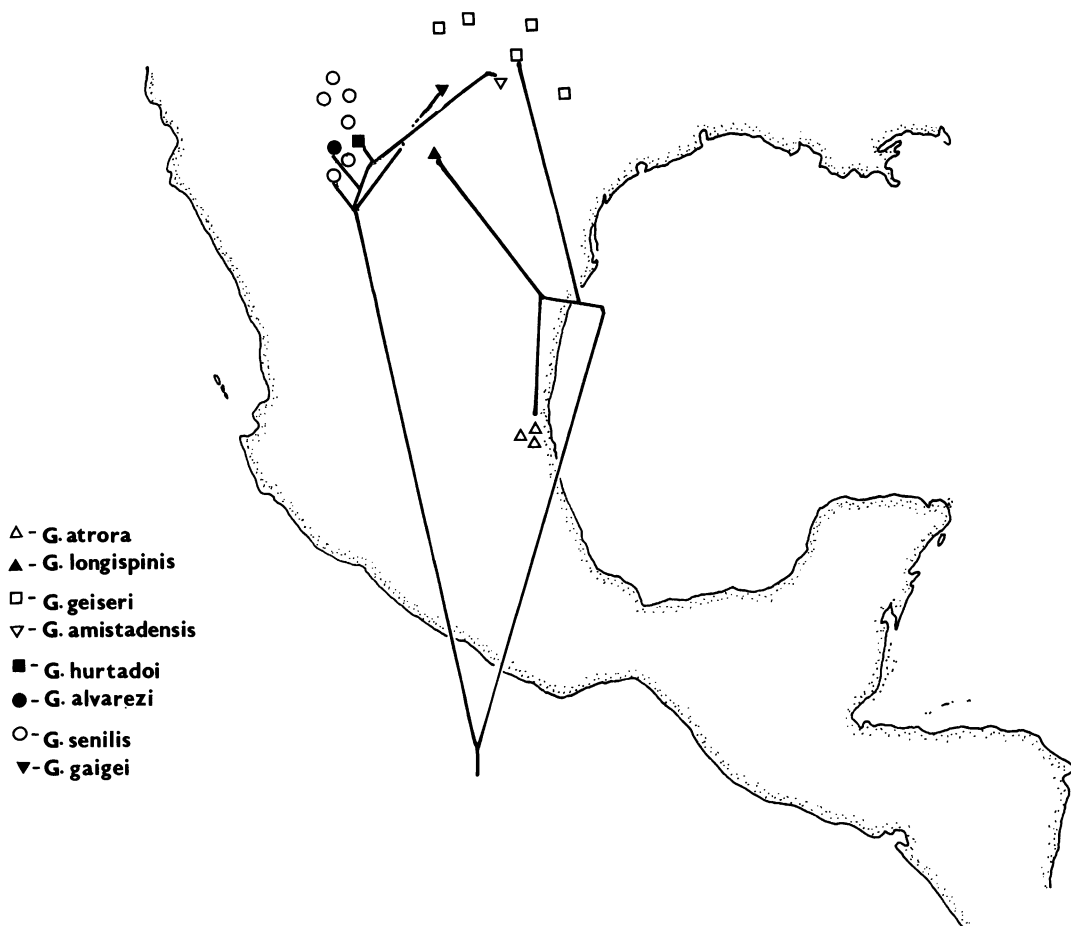


Fig. 55. Distribution of members of the *senilis* species group.

den, 1973b), based on material collected in April 1968. In July of that same year, the construction of the Amistad Reservoir caused permanent flooding of the spring, destroying the habitat necessary for this species. Although some stocks were maintained in artificial aquaria, Peden (1973b) surmised that the indigenous population of this species is extinct.

Gambusia geiseri is found in several systems in Texas, always near the emergence of cold, clear springs. It occurs in the San Marcos, Guadalupe, Conchos, and Devil's rivers, and is sympatric with *G. affinis*. Hubbs and Springer (1957) suspected that it is native only to the San Marcos Springs and Comal Springs and introduced at the other Texas springs, based on earlier collection records.

Gambusia longispinis is restricted to the Cuatro Ciénegas basin of Coahuila, Mexico. *Gambusia marshi*, of the subgenus *Heterophallina*, is more widespread, occurring in parts of the Río Salado system.

Gambusia atrora is rather far removed from the remainder of the species group. It is found in the Río Axtla and its tributaries, in the Río Pánuco drainage, San Luis Potosí, Mexico. It is sympatric here with *G. panuco* and *G. vittata*.

DISTRIBUTION OF THE SUBGENUS *GAMBUSIA*

Each of the species groups in this subgenus is primarily Caribbean, but each also has one mainland member, in Central America.

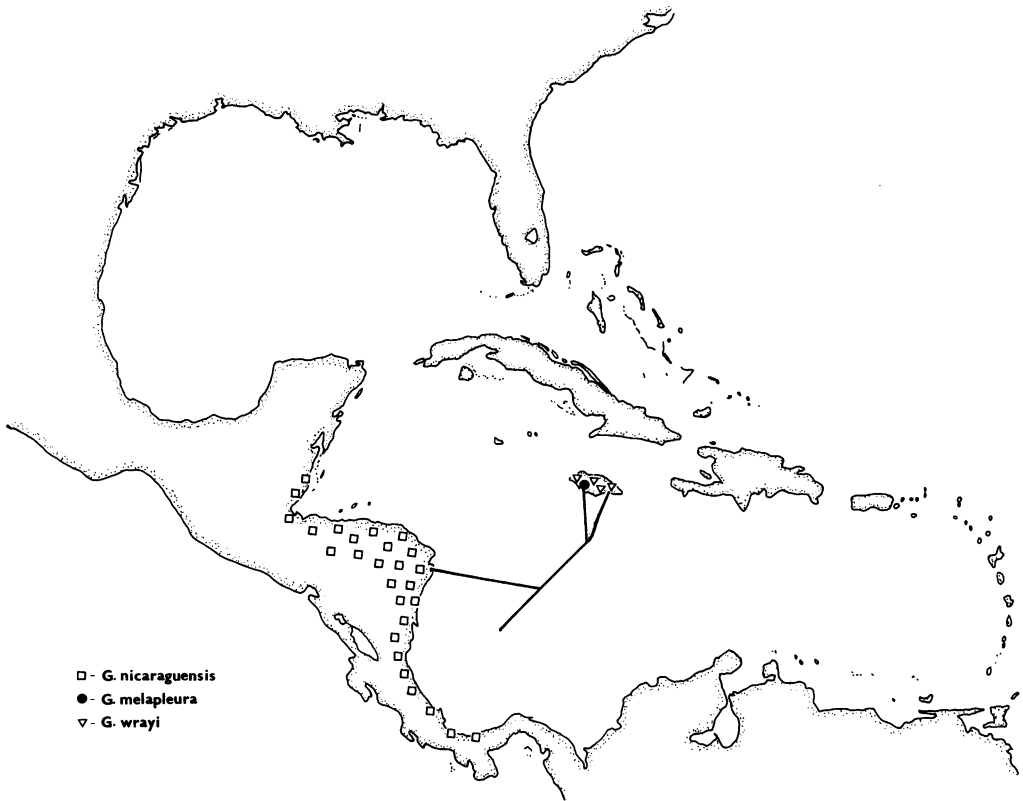


Fig. 56. Distribution of members of the *nicaraguensis* species group.

***nicaraguensis* species group** (fig. 56): *Gambusia nicaraguensis* is found in Atlantic Coast drainages of Central America, as far south as the Río Chagres, Panama. It generally is found in fresh water in lower Central America, where it is the only *Gambusia* present, although *Belonesox* and *Brachyrhaphis* are common here; in the northern extremity of its range, in Belize, it is most often found in high-salinity river mouths or in full strength sea water. In Belize, it is sympatric with *G. luma*, but *G. luma* prefers less saline waters; in saline waters, *G. nicaraguensis* sometimes occurs with *G. yucatanana*. As with *G. yucatanana* (see below), slender- and deep-bodied forms can be described, with deeper-bodied forms occurring at more inland, freshwater localities (Greenfield et al., 1982).

Gambusia wrayi, as redescribed by Fink (1971b), is common in the freshwater drainages of Jamaica, most populous in the southern drainages. In brackish and salt waters, it is replaced by the *G. oligosticta* form of the *puncticulata* species group.

Gambusia melapleura is restricted to the type locality, freshwater springs of the Shrewsbury River, Bluefields, Jamaica.

***puncticulata* species group** (fig. 57)³: *Gambusia yucatanana*, the only mainland member of this species group, is found in Mexico, Guatemala, and Belize. Greenfield (1985) distinguished two subspecies, *G. yucatanana yucatanana* from the northern Yucatan peninsula, and *G. yucatanana australis* further south, based on multivariate analysis of morphometric data. The species dwells in a variety of habitats, from inland freshwater lakes to brackish coastal streams to nearly full-

³ As noted on p. 52, I have not made any formal recommendations as to the status of the taxa in the *puncticulata* species group. Recent workers (Fink, 1971a; Greenfield and Wildrick, 1984) disagree as to the number of species-level taxa in this group. Not having looked at enough material to make alpha-level decisions, I have simply included all the named taxa *provisionally*, in order that statements about relationships and biogeography could be made.



Fig. 57. Distribution of members of the *puncticulata* species group.

strength sea water. Greenfield (1985) also noted that, in both subspecies, the freshwater inland forms are more slender-bodied than their coastal counterparts. *Gambusia yucatanana* is sympatric with members of three other species groups, *G. luma*, *G. nicaraguensis*, and *G. sexradiata*.

The group corresponding to Greenfield and Wildrick's (1984) "*puncticulata* group" has members throughout Cuba and the Isla de la Juventud (Isle of Pines), Grand Cayman Island and Cayman Brac, and Jamaica. *Gambusia puncticulata* (sensu stricto) is quite common across Cuba, sympatric with both *G. punctata* and *G. rhizophorae*, but *G. puncticulata* prefers more brackish water than *G. punctata*. *Gambusia howelli*, the form from the Isla de la Juventud, is not readily distinguishable from the species of the main island based on materials available, and should probably remain in synonymy with *G. puncticulata*. *Gambusia caymanensis* is the form found on Grand Cayman, Little Cayman, and Cayman Brac. *Gambusia oligosticta*, the Ja-

maican form, is occasionally found with *G. wrayi*, but in general *G. oligosticta* occupies brackish water and *G. wrayi* fresh. As with *G. howelli*, however, it must be emphasized that the taxonomic distinction of *G. oligosticta* and *G. caymanensis* from *G. puncticulata* is not clear at this point.

The "*hubbsi* group" also has members in Cuba, but these are restricted to purely freshwater habitats, narrowly endemic to localities on the extreme east end of the island. Other members are found in the Bahamas and Hispaniola. In Cuba, *G. monticola* inhabits a swift mountain stream, the Río Yao, Río Cauto system, Province of Oriente; *G. baracoana* is described from a freshwater pond at the mouth of the Río Miel, near Baracoa, Oriente; and *G. bucheri* is found in Jicotea Creek, Moa system, also in the Province of Oriente. Each of these is known only from the type locality. Another narrow endemic in this group is *G. manni*, whose distribution Fink (1971a) described as limited to two freshwater lakes on New Providence Island

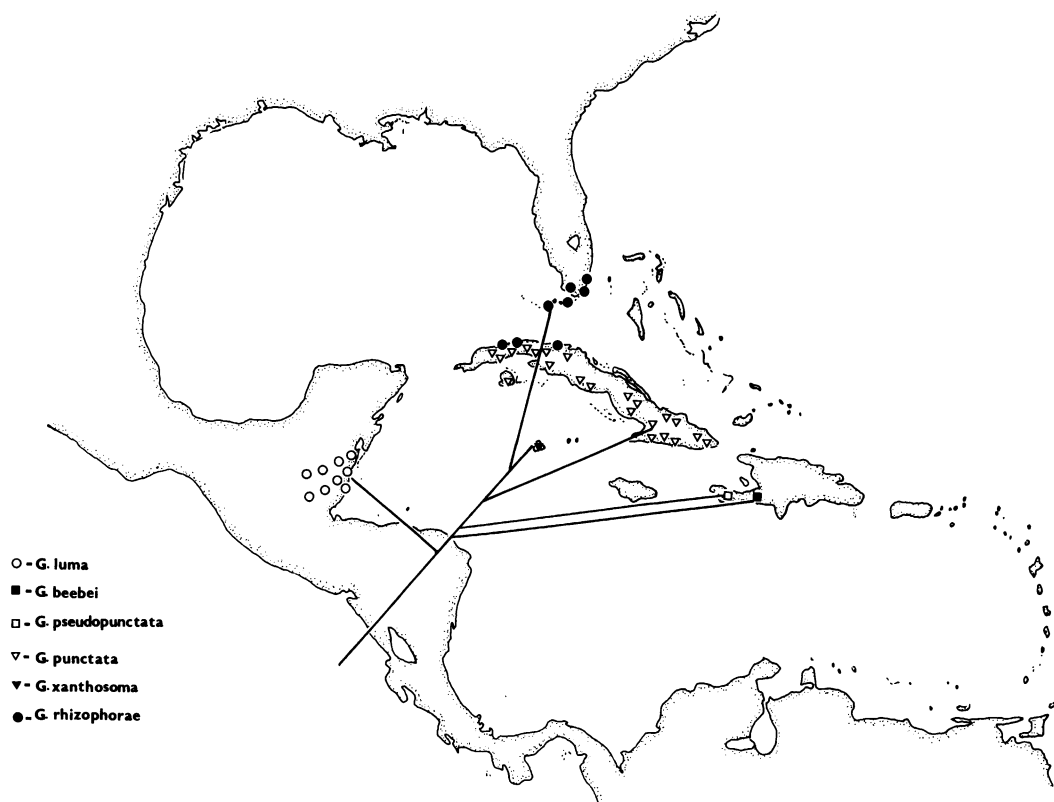


Fig. 58. Distribution of members of the *punctata* species group.

in the Bahamas, Lake Cunningham and Lake Kilkarney. Other Bahamian *Gambusia* specimens are often referred to as *G. manni* in many collections, but Fink (1971a) relegated the much more common Bahamian form to *G. puncticulata puncticulata*, which was originally known as (and herein referred to as, at least provisionally) *G. hubbsi*. Rosen and Bailey (1963), feeling that populations from South Andros Island, from where *G. hubbsi* was described (Breder, 1934), and populations from other Bahamian islands were indistinguishable, synonymized *G. hubbsi* under the name *G. manni*. However, if the name *G. manni* applies only to the fishes of the two lakes of New Providence Island, the name *G. hubbsi* should be used for the other Bahamian populations.

Gambusia hispaniolae is common in both fresh and brackish water habitats throughout Haiti and the southern Dominican Republic. Fink (1971b) called it the dominant *Gambusia* of the island; it has been taken sym-

patrically with introduced *G. holbrooki*, but otherwise its widespread distribution does seem to restrict the other *Gambusia* species of the island, which are narrowly endemic (*G. pseudopunctata*), rarely caught (*G. beebei*), or virtually unknown except for the type species (*G. dominicensis*).

***punctata* species group** (fig. 58): *Gambusia luma* ranges through Belize and Guatemala, from Río Hondo in the north to Puerto Barrios and the Belize River in the south; it is primarily coastal but is found inland throughout Lago de Izabal. It is both sympatric and syntopic with *G. sexradiata* throughout the northern part of the range; *G. luma*, however, prefers rivers and streams whereas *G. sexradiata* is more likely to be found in standing water. When together, *G. luma* is often in the middle of streams, in open water, and *G. sexradiata* is near shore, amid vegetation (Greenfield et al., 1983). In southern Belize, *G. luma* is sympatric with *G. nicaraguensis*, but *G. nicaraguensis* is usu-

ally in more brackish water. In the northern part of its range, a similar relationship exists with *G. yucatana*, which may be found occasionally in full-strength sea water (Greenfield et al., 1982). Although not commonly found in salty waters, Carter (1981) has shown that *G. luma* does have the physiological tolerance to adapt to saline conditions.

Gambusia beebei is endemic to Lake Miragôane, Haiti, on the Tiburon peninsula. Apparently a rare fish, it is known in U.S. collections only from the neotype and "neoparatype" series designated by Rivas in 1969. Several recent collections in Haiti have recovered only *G. hispaniolae* from Lake Miragôane; however, a more thorough study of that lake is needed to assess the status of this species.

Gambusia pseudopunctata is also endemic to Haiti, again on the Tiburon peninsula. It is known from the type locality springs at Roseaux, as well as several nearby springs, but it is not widespread. As Fink (1971b) speculated, *G. hispaniolae* may well have confined both *G. beebei* and *G. pseudopunctata* to their limited ranges.

Gambusia punctata is known from many localities across Cuba and the Isla de la Juventud; it is common and abundant, and may be found up to elevations of 2000 ft (Rivas, 1969). The type locality is from the moats of the Jardín Botánico in the city of Havana. As is true also for *G. beebei* and *G. pseudopunctata*, *G. punctata* is not at all salt tolerant; in brackish areas it is replaced by *G. punctulata*. It is sympatric but not syntopic with *G. rhizophorae* along the northwest coast of the island.

Gambusia rhizophorae, unlike the previous species, shows a great deal of salt tolerance. As the trivial name implies, it lives in mangrove swamps, sometimes in full-strength sea water. It occurs only in such swamps, along the northwest coast of Cuba, extreme southern Florida, and the Florida Keys.

Gambusia xanthosoma, a distinctive yellow species, is confined to Grand Cayman Island, which it shares with a member of the *punctulata* species group, *G. caymanensis*. The type locality is a brackish-water mosquito control ditch, adjacent to a mangrove swamp.

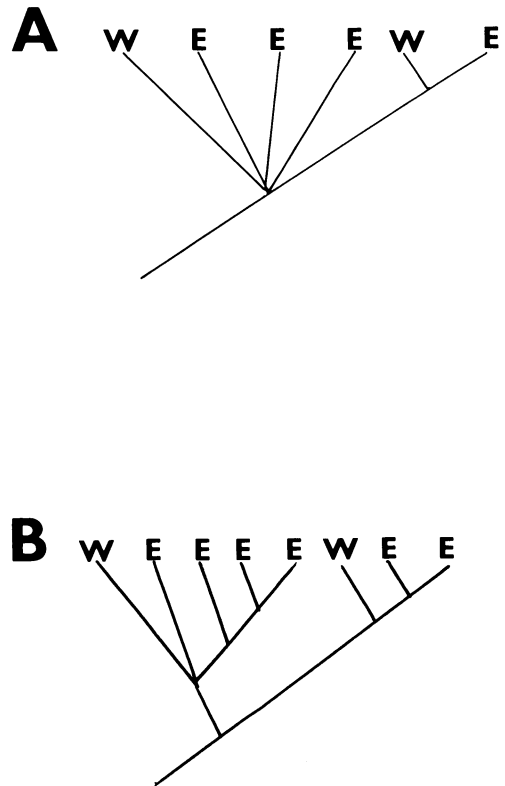


Fig. 59. Area cladograms for groups found in Texas and northern Mexico: A. *nobilis* species group, B. *senilis* species group. Legend: W = widespread, E = endemic.

GEOGRAPHIC AREAS

Texas and Northern Mexico (fig. 59): Members of the *nobilis* and *senilis* species groups overlap in this area, although they occupy different areas of endemism, making direct comparison of their distribution patterns impossible. In each of these groups, however, one species is fairly widespread (*G. nobilis* in the *nobilis* species group, although its range is currently limited and diminishing; *G. senilis* and *G. geiseri* in each of the subclades of the *senilis* species group), and all others are restricted to endemic habitats, usually springheads. The recurrent pattern finds the widespread species unresolved with respect to some of the endemic members of the clade. In other words, a widespread species does not appear to be more closely related to a particular endemic species than to the other endemic species of the group. Hubbs and Springer (1957) have suggested that the en-

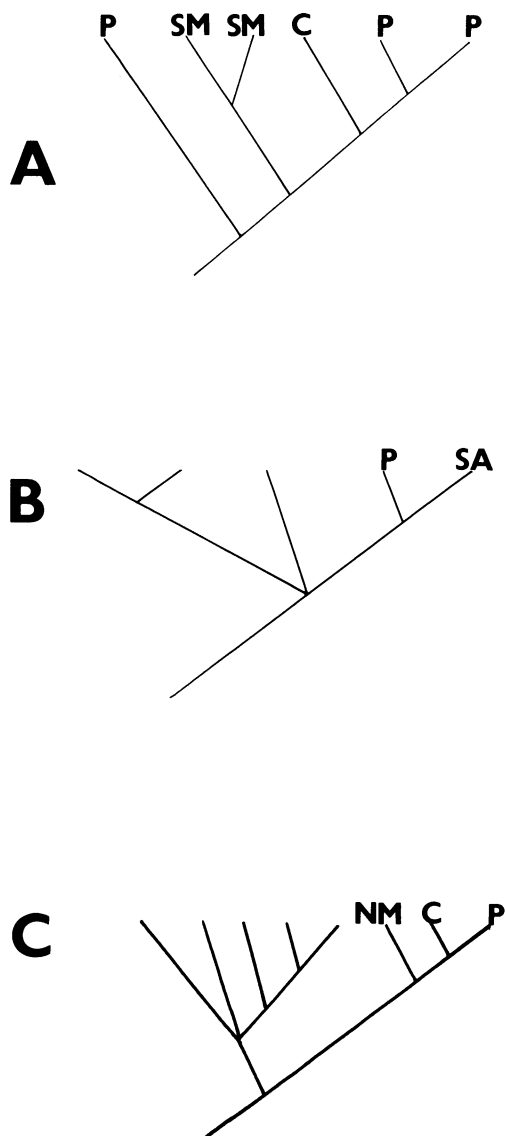


Fig. 60. Area cladograms for groups found in the Río Pánuco basin: A. subgenus *Heterophallina*, B. *affinis* species group, C. *senilis* species group. Legend: P = Pánuco basin, C = Cuatro Ciénegas basin, SM = Southern Mexico, NM = Northern Mexico, SA = South America.

demic species of these groups are differentiated relicts of formerly widespread species, isolated due to desert conditions and competition with *G. affinis*. The cladograms for these groups, superimposed with distributional information, do not contradict the interpretation of Hubbs and Springer (1957), as, in each case, endemics are (often derived)

members of a group that includes a widespread member. Such a scheme of peripheral isolation might also account for the lack of resolution in these groups.

Río Pánuco Basin, Mexico (fig. 60): Although physically not very different from similar river basins in eastern Mexico, the Río Pánuco basin is something of a focal point in *Gambusia* biogeography, as members of three species groups, and *G. vittata*, overlap there. Two sister species of the *panuco* species group, *G. panuco* and *G. regani*, are endemic there, with *G. panuco* being fairly widespread in the system and *G. regani* endemic in a northern tributary. These two taxa are, in turn, related to *G. marshi*, of the Cuatro Ciénegas basin. A relationship between the Pánuco basin and Cuatro Ciénegas area is repeated in the *senilis* species group, where *G. atrora* (Río Axtla-Río Pánuco) and *G. longispinis* are sister species. These two, however, are related to *G. geiseri*, of central Texas. The *panuco* group is related to the *rachowi* group, which inhabits drainages further south in Mexico (Río Coatzacoalcos, Río Usumacinta). The sister group to that entire assemblage, *G. vittata*, is again a Pánuco endemic.

A very similar track is exhibited by the poeciliid genus *Xiphophorus*, which has members in Cuatro Ciénegas and northern Mexico, much diversification in the Pánuco basin, and representatives southwards, through the drainages mentioned above to Guatemala. Cladistic relationships within the genus have been proposed (Rosen, 1979) and are in the process of being updated, with the incorporation of newly discovered taxa; when complete, the degree of congruence between *Gambusia* and *Xiphophorus* patterns can be explored.

A most curious member of the Pánuco basin fauna is *G. aurata*, endemic to the Río Mante, in the northern Tamesí drainage, which also is the home of another endemic poeciliid, *Poecilia latipunctata*. *Gambusia aurata* is a member of the *affinis* species group, whose namesake, *G. affinis*, is a widespread species that reaches just to the Pánuco basin; however, by virtue of gonopodial evidence, *G. aurata* seems to be most closely related not to *G. affinis* but to another member of the species group, *G. lemaitrei*, from northern Colombia! The affinities of the Pánuco basin,

which seemingly relate to three habitats—to Cuatro Ciénegas, northern Mexico, and Texas, to Cuatro Ciénegas and points south in Mexico, and to South America—are complex. Seemingly unintelligible tracks, however, should not be dismissed simply because they do not agree with a priori notions, and simply because there is incongruence does not mean that these tracks are uninformative. They do imply that the Pánuco basin is a much more complex area than one might expect at first glance, and, as in the Caribbean, no one group of species will provide the entire story. This area will be an exciting one for future research; in addition to *Gambusia*, *Xiphophorus*, and *Poecilia*, already mentioned, groups of minnows and cichlids also show endemic patterns in the Pánuco basin.

Central America and the Antilles (fig. 61): Perhaps the most interesting generalizations about biogeographic patterns within *Gambusia* might be drawn from an examination of the tracks of the three species groups that have members in the West Indies and a comparison of those tracks to each other and to other published distributional records. The *nicaraguensis* species group, although it contains three members, is of limited usefulness here as an area cladogram. *Gambusia wrayi* and *G. melapleura* are sister species, and because they both inhabit the island of Jamaica, the area cladogram for the *nicaraguensis* species group is reduced to a two-taxon statement: a relationship between Central America, specifically the area from Belize to Costa Rica, and Jamaica; however, it is intriguing to note that one of the generalized tracks documented by Croizat in the Caribbean portrays the same relationship. His figure 110 (p. 782, 1958, I) summarizes the distributions of the bird genera *Mimus* and *Nesomimus*, stretching from Central America, at the Honduras–Nicaragua bulge, to Jamaica. Some of the taxa he included in this generalized track also have representatives in the Galapagos.

The other two species groups of the subgenus *Gambusia*, the *puncticulata* and *punctata*, offer more detailed information about the interrelationships among the Antillean islands and Central America. Within the *puncticulata* species, a sister-group relationship between *G. yucatanana* and all other members

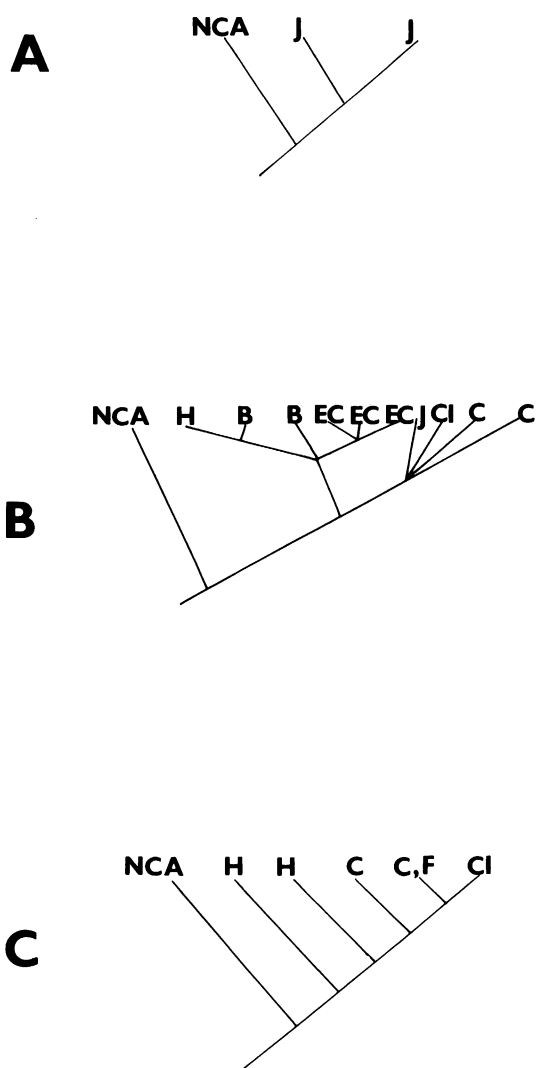


Fig. 61. Area cladograms for groups found in Central America and the Caribbean: **A.** *nicaraguensis* species group, **B.** *puncticulata* species group, **C.** *punctata* species group. Legend: NCA = Nuclear Central America, J = Jamaica, H = Hispaniola, B = Bahamas, EC = Eastern Cuba, CI = Cayman Islands, C = Cuba, F = Florida.

of the group implies the same relationship between Nuclear Central America (specifically the Yucatan Peninsula, Guatemala, and Belize; Rosen, 1975) and the major Antillean islands. Within the Antillean clade are two monophyletic subgroups. The “*puncticulata* forms,” which include many of the taxa synonymized by Fink (1971a), show a relationship between Cuba, the Isla de la Juventud,

the Cayman Islands, and Jamaica. (Relationships within this clade were not resolved, however; perhaps the synonymy of these under the name *G. puncticulata* would be appropriate.) The second Antillean clade, the "hubbsi forms," shows a different pattern, with a greater degree of resolution. The members of this clade inhabit the Bahamas, eastern Cuba, and Hispaniola. The three Cuban taxa, *G. monticola*, *G. bucheri*, and *G. baracoana*, forming a monophyletic group, are each confined to restricted habitats on the extreme portion of Cuba. These taxa are part of a group encompassing the Bahamas (*G. hubbsi* and *G. manni*) and Hispaniola (*G. hispaniolae*). Within this group, evidence suggests that *G. hispaniolae* and *G. hubbsi* are closely related, implying the same relationship between the Bahamas and Hispaniola, with these two related to eastern Cuba.

The *puncticulata* species group, therefore, lends some support to the notion of a hybrid Cuba, as the extreme eastern part of the island acts as a separate area of endemism, different from the actions of the species widespread throughout the island and its western adjunct (Isla de la Juventud).

The distribution of *G. puncticulata* across Cuba is repeated by *G. punctata*, which also is widespread in Cuba and the Isla de la Juventud. Another repeated pattern is the sister-group relationship between a species inhabiting Guatemala and Belize (*G. luma*) and the species in the Antilles. Details of the relationships within the Antilles for the *punctata* species group, however, reveal another facet of the complex story of Caribbean biogeography. *Gambusia punctata*, *G. rhizophorae*, and *G. xanthosoma*, a monophyletic clade, depict the relationship between Cuba (with the Isla de la Juventud), the Florida Keys, and Grand Cayman Island. This is reminiscent of the relationship portrayed by the "*puncticulata* forms," particularly in terms of the affinities of the Cayman Islands. The next two sister taxa for this group, *G. pseudopunctata* and *G. beebei*, indicate a relationship between the areas just mentioned above and southwestern Hispaniola (the Tiburon Peninsula), to which these two strictly endemic species are confined. Such a relationship can be interpreted in two ways. On one hand, this pattern is not incongruent with

the pattern described by the *puncticulata* species group, where a group with Cuba-Cayman Island members is related to a group including a Hispaniolan species. Following this view, one would predict that any member of the *punctata* species group discovered in the future in extreme eastern Cuba or the Bahamas might be likely to be more closely related to the Hispaniolan species than to *G. punctata* and its close associates. On the other hand, the distributional data for the Hispaniolan *Gambusia* species also support the possibility of a hybrid Hispaniola. The two members of the *punctata* species group are only found on the Tiburon Peninsula, whereas the *puncticulata* species group representative seems to be widespread across the island. Biogeographic patterns, therefore, can be proposed as evidence for certain scenarios of historical geology.

One place to compare the patterns displayed by *Gambusia* is in the compendia of Croizat (1958, 1964). His figure 37 (p. 146, 1964) of the distribution of certain liverworts indicates two tracks: one connecting Jamaica with Cuba (as in the *puncticulata* species group); and a separate track uniting Belize with southeastern Hispaniola (as in the *punctata* group). And, his figure 96 (p. 687, 1958, I) portrays a relationship between Hispaniola and the Bahamas (as in the *puncticulata* species group) for a lizard genus, *Aristelliger*, and a passeriform, *Loxigilla*. This relationship is again reflected in his figure 35 (p. 141, 1964) for the genus *Lycium*. Finally, the relationship between Cuba, the Cayman Islands, and the Florida Keys is reiterated in his figure 86 (p. 633, 1958, I) for species of the bird genus *Columba*. This selective list of examples is provided merely to testify to the fact that distribution patterns of *Gambusia* in the Caribbean are not peculiar simply to *Gambusia*, but are merely instances in a larger scheme.

Rosen (1985), in an attempt to synthesize current ideas of historical biogeography in the Caribbean, derived a series of four-taxon area cladograms that would be consistent with that history. He predicted that groups of organisms with Antillean endemics should produce area cladograms congruent with his derived from geology. The close relationship of the *puncticulata* species group members of

Hispaniola, eastern Cuba, and southern Bahamas is evident in his scheme, as is the relationship between Cuba and Jamaica. By examining predicted relationships based on progressive slices of geological time, he showed that 18 different four-taxa statements are consistent with this historically complex area. As other groups are studied, their information will add, as that of *Gambusia* has done, to a greater understanding of the area.

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APPENDIX

In the following character list, each character is merely summarized and abbreviated here; the discussion of the full nature of each character and its level of generality is found in the text. Most characters listed are scored absent = 0, present = 1. Scoring for multistate characters is given in the list.

1. Gonactinost 5 stands freely.
2. Gonactinosts 2, 3, and 4 fuse into a column.
3. Axillary blotch.
4. Female anal pigment.
5. Hook on ray 5a.
6. Ray 4a with coalesced segments, bent anteriorly.
7. Male pectoral fin modification.
8. Thickened ray 2, proximally.
9. Bump in ray 5 proximally.
10. No uncinat process on gonapophysis 1.
11. Elbow in ray 4a.
12. Hooks on rays 4p and 5a pointing upwards.
13. IPB3 teeth with medial serrate pad.
14. Disconnected infraorbital sensory canals.
15. Elbow shape: falcate = 0; triangular = 1; spatulate = 2.
16. No uncinat process on EP1.
17. Lateral prong on HB1.
18. Wings on BB3.
19. Shape of VHH: flat = 0; with central processes = 1; triangular with central processes = 2.
20. Hypurals: unfused = 0; fused, with keyhole = 1; fused completely = 2.
21. Spotted fin patterns.
22. Suborbital bar.
23. Ray 4p hook: round = 0; acuminate = 1; multisegmented acuminate = 2.
24. Anal spots: none = 0; median = 1; paired crescents = 2.
25. Retrorse spines on ray 3.
26. High number (more than 5) of segments distal to the elbow on ray 4a.
27. High number (up to 9 or more) of segments distal to the serrae on ray 4p.
28. High number (16 or more) of spines on ray 3.
29. Ray 3 spines fanlike, not pointed.
30. Terminal segment of ray 5a with long base.
31. High number (8 or more) of serrae on ray 4p.
32. Serrae on ray 4p: pointing proximally = 0; perpendicular = 1; reaching distally and recurved = 2.
33. No forward-directed spines on ray 3.
34. Buckling in ray 4a, with displaced elbow.
35. Lateral palp on gonopodium.
36. Body with ventral keel.
37. Elongate cleithral process.
38. Notch proximal to elbow.
39. Long ray 3 spines, with long inner processes.
40. Multisegmented elbow (to 7 segments).
41. Small bifid ray 3 spines.
42. Lateral projection on elbow.
43. Serrae on ray 4p: proximal to elbow = 0; opposite elbow = 1; distal to elbow = 2.
44. Ray 3 foreshortened.
45. Ray 4a foreshortened.
46. Eight or fewer ray 3 spines.
47. Gonopodial outline: median pointed = 0; rounded = 1; lobelike = 2 within subgenus *Gambusia*; pointed at anterolateral edge = 2 within subgenus *Arthrophallus*.
48. Transversely enlarged segment(s) distal to serrae on ray 4p = 1; same segments greatly enlarged, filling gaps between ray 4p and 5a = 2.
49. Electrophoretic characters; red and yellow caudal and dorsal fins (Greenfield et al., 1982).
50. High meristic characters (Fink, 1971a).
51. Ray 5a hook large, scythelike.
52. Ray 4p hook large, scythelike.
53. Body with 4–6 rows of large spots.
54. One pair metacentric and two pairs submetacentric chromosomes in both sexes.
55. Ray 4a S-shaped, curving back over ray 3 spines.
56. Pectoral ray 5 with distal scallop.
57. Pectoral ray 2 with enlarged blade proximally.
58. Pectoral rays with both dorsal and ventral blades.
59. One pair of large metacentric chromosomes in female only.
60. Shape of medial part of HB1: square, no cleft = 0; with shallow cleft not split = 1; deep cleft, not split = 2; forked, widely split = 3.
61. Number of gonapophyses: three = 0; sometimes or always two = 1.
62. Exaggerated distal point of gonopodium.
63. Serrated segments on ray 4a distal to elbow.

The following character matrices were used as PAUP input. The analyses were performed on an IBM-PC, which has a limit of 100 equally parsimonious trees. Because of the lack of resolution in several areas of the cladogram, this limit was quickly exceeded when all taxa and all characters were run together. Therefore, I chose to subdivide the data set into the following matrices, using only the characters relative to that particular level and group. The following options were used: MISSING = 9, SW = GL, MULPARS, MAXTREE = 100, ROOT = OUTGROUP, OPT = FARRIS.

1. For figure 21. Outgroup relationships.

CHAR. NO.	1	2	3	4	5	6
OUTGROUP	0	0	0	0	0	0
BRACHYRH	1	0	1	1	0	0
BELONESO	1	1	1	0	1	1
GAMBUSIA	1	1	1	1	1	1

One tree was found.
Length = 7.000
Consistency Index = 0.857

2. For figure 30. Subgeneric relationships.

CHAR. NO.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HETEROPH	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1
ARTHROPH	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	1	2
GAMBUSIA	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1

One tree was found.
Length = 20.000
Consistency Index = 0.950

3. For figure 32. Relationships within the subgenus *Heterophallina*.

CHAR. NO.	12	13	20	21	25	26	27	28	29	30	31	32	33	34	35	36	37
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VITTATA	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MARSHI	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0
PANUCO	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0
REGANI	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0
RACHOWI	1	1	1	0	1	1	1	0	0	0	0	1	1	1	1	1	1
ECHEAGAY	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	1

One tree was found.
Length = 20.000
Consistency Index = 0.850

4. For figures 35, 36, 40, and 42. Relationships within the subgenus *Arthrophallus*.

CHAR. NO.	14	16	17	18	20	21	22	23	24	30	31	32	38	39	40	41	42	43	44	45	46	47	48	57	60	61	62
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AFFINIS	1	0	0	0	1	1	1	2	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	2	0	1
HOLBROOK	1	0	0	0	1	1	1	2	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1
SPECIOSA	1	0	0	0	0	1	0	2	9	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	3	0	0
AURATA	1	0	1	0	1	1	1	2	9	1	0	0	0	0	1	1	0	2	1	0	0	0	0	1	3	1	0
LEMAITRE	1	0	9	0	9	1	9	2	9	1	0	0	0	0	1	1	0	2	1	0	0	0	0	9	9	9	0
NOBILIS	1	1	0	0	0	0	1	0	2	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0
GEORGEI	1	1	0	0	0	0	1	1	2	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0
KRUMHOLZ	0	1	0	0	0	0	0	0	9	1	0	1	1	1	0	0	0	1	0	0	0	1	0	0	3	1	0
HETEROCH	1	9	0	1	9	0	1	1	2	1	2	1	1	1	0	0	0	2	0	0	0	1	0	0	9	9	0
EURYSTOM	0	9	0	0	0	1	1	1	9	0	0	2	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0
SEXRADIA	0	1	0	0	0	1	1	0	9	0	0	2	1	1	0	0	0	1	0	0	0	1	0	0	2	0	0
SENILIS	1	1	0	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	2	1	0	1	1	0
GAIGEI	1	1	0	0	9	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	2	1	0	3	1	0
GEISERI	1	1	0	0	2	0	0	1	2	1	1	0	1	1	0	0	0	0	0	1	1	2	0	0	3	1	0
ALVAREZI	1	1	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	1	2	1	0	0	1	0
HURTADOI	1	1	0	0	1	0	1	0	1	0	0	0	1	1	0	0	1	0	0	1	1	2	1	0	0	1	0
LONGISPI	1	1	0	0	2	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	1	2	0	0	1	0	0
AMISTADE	1	1	0	0	1	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	1	1	0
ATRORA	1	1	0	0	2	0	0	0	2	0	1	0	1	1	0	0	0	0	0	1	1	2	1	0	0	0	0

15 trees were found.
Length = 71.000
Consistency Index = 0.507

Figures 35, 36, 40, and 42 represent parts of the strict consensus tree of the 15 trees found.

5. For figures 45, 46, 48, and 50. Relationships within the subgenus *Gambusia*.

CHAR. NO.	15	16	17	18	19	20	21	22	23	24	30	32	39	42	47	48	49	50	51	52	53	54	55	59	60	61	63
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NICARAGU	1	0	0	1	2	0	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WRAYI	1	1	1	1	2	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
MELAPLEU	1	9	1	1	2	9	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0
YUCATANA	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	3	0
HISPANIO	1	0	1	1	1	1	1	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0
MANNI	1	9	1	1	1	1	1	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	9	0
HUBBSI	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1
MONTICOL	1	9	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	9	0
BUCHERI	1	9	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1
BARACOAN	1	9	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	9	0
PUNCTICU	1	1	1	1	1	0	1	1	2	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	2	1
OLIGOSTI	1	1	1	1	1	0	1	1	2	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	9	1
CAYMANEN	1	9	1	1	1	0	1	1	2	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	9	1
HOWELLI	1	9	1	1	9	0	1	1	2	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	9	1
LUMA	2	0	1	0	0	0	1	1	0	0	0	2	1	0	2	0	0	0	1	1	0	0	0	0	0	1	0
BEEBEI	2	0	1	1	1	0	1	0	0	0	1	1	1	0	2	9	0	0	1	1	0	9	0	0	9	0	0
PSEUDOPU	2	0	1	1	1	0	1	0	0	0	1	1	1	0	2	1	0	0	1	1	1	9	0	0	3	0	0
PUNCTATA	2	0	1	1	1	0	1	0	0	0	0	1	1	0	2	2	0	0	1	1	1	9	0	0	2	0	0
RHIZOPHO	2	1	1	0	1	0	1	0	0	0	0	2	1	0	2	2	0	0	1	1	1	2	1	0	2	0	0
XANTHOSO	2	9	1	9	1	0	1	0	0	0	0	1	1	0	2	2	0	0	1	1	1	2	1	0	9	0	0

For relationships among species groups in the subgenus, and for relationships within the *nicaraguensis* and *punctata* species groups, *G. oligosticta*, *G. caymanensis*, and *G. howelli* were dropped (except for missing data, these taxa are coded identically to *G. puncticulata*, and to each other). This produced 80 trees.

Length = 62.000

Consistency Index = 0.613

Figures 45, 46, and 50 are parts of a strict consensus tree of the 80 equally parsimonious trees found.

For relationships within the *puncticulata* species group, the deleted taxa were restored and members of other species groups deleted. This produced 45 trees.

Length = 32.000

Consistency Index = 0.812

Figure 48 is a strict consensus tree of the 45 equally parsimonious trees found.

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