THE POECILIID FISHES (CYPRINODONTIFORMES), THEIR STRUCTURE, ZOOGEOGRAPHY, AND SYSTEMATICS

DONN ERIC ROSEN AND REEVE M. BAILEY

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 126 : ARTICLE 1 NEW YORK : 1963

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 126, article 1, pages 1–176, text figures 1–61,
plates 1, 2, tables 1–3, maps 1–19

Issue December 6, 1963
Reprinted June 30, 1973
Price: $4.00 a copy

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INTRODUCTION

THE FAMILY POECILIIDAE AND COMMENTS ON THE GENERIC CONCEPT

THE MEMBERS OF THE order Cyprinodontiformes are cosmopolitan in tropical and temperate latitudes and are especially notable for the range of fresh-water and saline habitats that they occupy. The order is currently divided into seven families. Of these, four, the Poeciliidae, Anablepidae, Jenynsiidae, and Goodeidae, are endemic to the New World, and, with the exception of a single species, their members bear living young. The poeciliids are small fishes; none attains an over-all length of 200 mm., and most are less than half of that size. They form one of the dominant animal groups in the fresh and brackish waters of Middle America and the West Indies. Poeciliids include some of the smallest and also some of the most highly polymorphic of living vertebrates. The broad tolerance for salt and brackish environments of many of these chiefly fresh-water species makes them of particular interest in zoogeographic studies of over-water dispersal, and their considerable structural diversity marks them as important in evolutionary studies of adaptive specialization.

Poeciliids exhibit numerous secondary sexual modifications. In males, the anal fin, the internal anal-fin supports, and the overlying parts of the axial skeleton are substantially altered during sexual development to form a complex mechanism of bone, muscle, and connective tissue (the gonopodial system) that functions to transfer sperm bundles to the female genitalium. Some of the bony components of this mechanism have demonstrable importance for taxonomic studies at various levels of classification. At the same time, the group is unusual among fishes in having the majority of the taxonomically useful structures concentrated in the male. Although traits of the female have been less thoroughly explored than those of the male, still it is apparent that many of the relationships as we now understand them would be difficult or impossible to discern with the use of females alone. In contrast to most other fresh-water groups in which the sexes are not strikingly dimorphic and in which each sex has a more or less equal number of salient taxonomic features, in poeciliids the males of different species show large structural contrasts; the females, comparatively little. The differentiation of the Poeciliidae has emphasized the morphology of the reproductive system and breeding behavior, and it is to this system that we must turn in efforts to reconstruct the phylogeny of the group. In the early taxonomic history of the family, species known only from females were assigned to two or three large genera, as were even males before the significance of reproductive characters was realized. It is probably true, however, that in most other fish groups, structures of the male and female, whether dimorphic or not, are in the aggregate at least as effective taxonomically as are the wealth of specializations in the male poeciliid. Hence, we do not believe that a taxonomic assessment of the Poeciliidae requires methods or concepts of classification that differ in any respect from those applied to other families of marine or fresh-water fishes.

It has often been said that there are no objective criteria for genera. This is certainly true, but like so many aphorisms this statement is too cryptic to convey the full amplitude of the concept. As a consequence, refuge is often sought in the above statement to delimit genera without regard either to the pragmatic or philosophic needs of taxonomy. During the years before the objectives of modern systematics had begun to crystallize, ichthyologists were preoccupied with the essential task of describing the legion of previously unknown kinds of fishes. Emphasis was placed on points of difference in the seemingly endless procession of new forms, and the need for synthesis was not immediately apparent. It is hardly surprising, therefore, that with only scant knowledge of interrelationships there should have been a strong tendency toward smaller and smaller genera, until a point was reached at which many if not most genera were monotypic. Although faunal monographs are still appearing at a respectable rate, currently most students are applying themselves to the question of group

relationships, and the genus is naturally the first of the synthetic categories with which a peace must be made. In our view, it is the role of the genus in functional systematics that is at issue. Because the generic name is an integral part of the scientific name, stability in its use is much to be desired, but, even more important, the genus can and should serve to express relationships. Again, since it enters the scientific name, the genus can be employed more advantageously as a clue to affinity than can other supraspecific taxonomic categories (e.g., family, subfamily, and subgenus).

The primary criterion of genera that has been employed by most workers is degree of morphological difference. In the application of this criterion, species or groups of species that differ widely from other species are set apart generically. The measure of "wide separation" is determined by the personal judgment of the investigator. In this method, as far as it goes, there is no fault. That it goes not far enough is suggested by the failure of the mere gauging of degrees of difference to lead *a priori* toward a useful and internally consistent arrangement of genera within a family. The criterion of "wide separation" must therefore be applied within the framework of the family. Ideally, generic groups should be constructed on similar standards of morphological distinctiveness, just as families should be morphologically co-ordinate entities within an order. The fact that some genera may thus become immense and unwieldy (e.g., *Notropis*) interferes with their pragmatic value but enhances their philosophic usefulness by emphasizing the evolutionary potential of a group with a certain combination of features. A solution to problems of unwieldiness is available which restores the practical value of greater subdivision and retains the biological meaningfulness of the genus; this, of course, is the use of subgenera and species groups.

It is evident that the phylogenetic relationships between different species or between distinct groups of species are reflected in a host of features, some anatomical and behavioral, some physiological and biochemical, and some genetic and developmental—in short, in some features of all the major systems and processes that characterize organisms. Hence, investigators in the fields of comparative anatomy and comparative development, as well as many experimental biologists, may contribute directly and indirectly to systematic knowledge. For the nonsystematist, however, a classification consisting of too many small genera presents a major obstacle to his efforts at recognizing differences and similarities between related organisms that are worthy of study. In an earlier classification of the poeciliids, for example, two species now shown to be intimately related were placed in different genera because one of them possesses an asymmetrical external genitalium. Under this taxonomic arrangement, a developmental biologist interested in problems of asymmetry and hence in the asymmetric species would have difficulty identifying the symmetrical relative, the comparative study of which might be expected to yield important clues as to the origin of the asymmetric condition. The use of separate genera is usually, and justifiably, taken as a mark of the gross genetic incompatibility of the species thus separated taxonomically, and in the foregoing example may be expected to draw attention away from important biological properties common to both. It may even, at times, tend to prevent experimental workers from realizing that the comparative study of both species is appropriate. When a single genus is used for these species, the comparative materials are collected together, and the likelihood is increased that studies in other fields will be performed by investigators whose results are important to systematics. In general, the masking effects of an oversplit classification may be remedied by the use of comprehensive genera that assemble, and thereby underscore, some contrasting features as well as the many unifying characters to be found among intimately related organisms. The function of broad and co-ordinate genera, when data on complex and little-known groups are made available to non-systematists, is often overlooked by the taxonomist.

These remarks are especially appropriate in a taxonomic study of the Poeciliidae. Since the date of the last revision more than a quarter of a century ago, the poeciliids have been the subject of more than 1000 publica-

tions in the fields of taxonomy, ecology, zoogeography, embryology, physiology, behavior, genetics, and cytology. Although these fishes, unlike most, are adaptable to laboratory conditions, the interest they hold for systematists and non-systematists alike, and the stimulus they offer for future study, will depend heavily on the way they are classified. With these thoughts in mind we have attempted a revision of the subfamilies, tribes, and genera of the Poeciliidae as a first step toward a better classification of these fishes.

The present work, therefore, is an analysis of relationships and employs chiefly criteria that have a direct bearing on the generic, tribal, and subfamilial alignments. These principal criteria are osteological, for, as we hope to demonstrate, details of the skeleton provide the soundest framework for an enduring arrangement of the Poeciliidae. In keeping with this study's primary objective, the generic diagnoses are analytical statements of those combinations of characters that suggest affinities. Many individual features of the fins, skull, and axial skeleton that appear in the diagnoses are virtually the same in numerous genera. The common occurrence of certain details is, of course, most often encountered in the diagnoses of genera within a single tribe and less often in the diagnoses of genera within distinct but related tribes. The repetition of a character is then a partial indicator of relationship. Although these analytical diagnoses offer a convenient and concise method of indicating phyletic lines, they cannot be employed readily in routine identifications, because many of the phylogenetically significant details are entirely internal and are fully appreciated only with the aid of special methods of preparation. Some effort to defeat this shortcoming has been made by the inclusion of a summarizing table (table 3) that incorporates all those features which, in various combinations, permit the separation of the 19 genera of the Poeciliinae, the only one of the three subfamilies that is polytypic. As a further aid to the reader, a check list of the species and subspecies is provided, which contains basic synonymies, known geographical ranges, the probable species groups or subgenera, and nomenclatural and anatomical details that seem to the authors to be of importance.

MATERIALS AND METHODS

Material

The specimens of the Poeciliidae that were used or are mentioned in this study are from the collections of the institutions that are listed below:

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
B.M.N.H., British Museum (Natural History)
C.A.S., the California Academy of Sciences
C.N.H.M., Chicago Natural History Museum
C.U., Cornell University
L.R.R., Luis R. Rivas, private collection
L.S.U., Louisiana State University, Baton Rouge
M.C.Z., Museum of Comparative Zoölogy at Harvard College
M.N.H.N.P., Museum National d'Histoire Naturelle, Paris
S.M.M., Zoologischen Staatssammlung in München
S.U., Stanford University
T.N.H.C., University of Texas Natural History Collection, Austin
U.H.P.M., University of Havana, Poey Museum
U.M.I.M., University of Miami Ichthyological Museum
U.M.M.Z., Museum of Zoology of the University of Michigan, Ann Arbor
U.S.N.M., United States National Museum, Smithsonian Institution

Some aquarium specimens that represent other cyprinodontiform families have also been utilized. For each species of which preserved material was available, skeletons or radiographs (or both) of adult males and females were prepared and studied (see Rosen and Bailey, 1959, p. 3).

Diagnoses

Generic and subgeneric diagnoses incorporate chiefly osteological characters, since these alone are found to be entirely satisfactory for rigorous definition and separation of the many groups of poeciliids. Characters of lesser importance are discussed below each diagnosis. A diagnosis includes a unique com-

bination of characters in the skull, axial skeleton, and appendages, and is meant to stand on this combination rather than on any single character, however unusual that may be. Unless otherwise specified, skull characters are drawn from males and females; all other traits, from males only. Throughout the Poeciliidae an attempt is made to establish genera on a level of structural equivalence so that they are as nearly co-ordinate as possible, thus facilitating their use in zoogeographic and evolutionary interpretation.

Classification

As a historical aid to the reader, the broader groupings (genera and higher categories) of the classification proposed herein are contrasted, in tables 1 and 2, with those that were in general use prior to the initiation of the present series of studies (Rosen, 1952, 1960; Rosen and Bailey, 1959).

Types

In the compilation of the check list, an effort was made to locate the place of deposit of the types or type series of all forms for which distinctive specific and subspecific names have been proposed. Type materials were located for 80 per cent (207 of 259) of proposed names. Many of those not located are now or were previously in the Berlin Museum or in the Museo Poey of the University of Havana, Cuba. Still others, at one time in American museums, are now lost or misplaced. When known, the museum of deposit and the catalogue number of the holotype, lectotype, or syntypes are given following the type locality in the citation of the original description. Most of the types in the Academy of Natural Sciences of Philadelphia, the American Museum of Natural History, the Chicago Natural History Museum, the Museum of Comparative Zoölogy, the Museum of Zoology of the University of Michigan, Stanford University, and the United States National Museum have been examined by one or the other of the authors.

Anatomical Terms

The nomenclature of parts of the gonopodial system of the adult male (external genitalium and internal appendicular and axial supports) follows that proposed by Rosen and Gordon (1953; see also Rosen and

TABLE 1

Prior Classification of the Poeciliidae, as Compiled from the Works of Recent Authors, with the Present Reference of the Genera

Taxon	Authority	Present Reference of Genus
Poeciliidae	Hubbs *in* Kulkarni, 1940	
Gambusiinae	C. L. Hubbs, 1926	
Gambusiini	C. L. Hubbs, 1926	
Heterophallus	C. L. Hubbs, 1926	*Gambusia*
Gambusia	C. L. Hubbs, 1926	*Gambusia*
Belonesox	C. L. Hubbs, 1926	*Belonesox*
Hemixiphophorus	C. L. Hubbs, 1926	*Poeciliopsis*
Flexipenis	Hubbs *in* Rivas, 1963	*Gambusia*
Dicerophallini	Alvarez, 1952	
Dicerophallus	Alvarez, 1952	*Gambusia*
Heterandriini	C. L. Hubbs, 1926	
Brachyrhaphis	C. L. Hubbs, 1926	*Brachyrhaphis*
Plectrophallus	C. L. Hubbs, 1935a	*Brachyrhaphis*
Trigonophallus	C. L. Hubbs, 1926	*Brachyrhaphis*
Priapichthys	C. L. Hubbs, 1926	*Priapichthys*
Panamichthys	C. L. Hubbs, 1926	*Priapichthys*
Pseudoxiphophorus	C. L. Hubbs, 1926	*Heterandria*
Heterandria	C. L. Hubbs, 1926	*Heterandria*
Priapella	Alvarez, 1948a	*Priapella*
Allogambusia	C. L. Hubbs, 1926	*Neoheterandria*

TABLE 1—(*Continued*)

Taxon	Authority	Present Reference of Genus
Alloheterandria	C. L. Hubbs, 1926	*Priapichthys*
Neoheterandria	C. L. Hubbs, 1926	*Neoheterandria*
Pseudopoecilia	C. L. Hubbs, 1926	*Priapichthys*
Girardinini	Rivas, 1958	
Toxus	Rivas, 1958	*Girardinus*
Glaridichthys	Rivas, 1958	*Girardinus*
Allodontium	Rivas, 1958	*Girardinus*
Dactylophallus	Rivas, 1958	*Girardinus*
Girardinus	Rivas, 1958	*Girardinus*
Quintanini	Howell-Rivero and Rivas, 1944	
Quintana	C. L. Hubbs, 1934	*Quintana*
Cnesterodontini	C. L. Hubbs, 1926	
Darienichthys	C. L. Hubbs, 1926	*Priapichthys*
Diphyacantha	Henn, 1916	*Priapichthys*
Cnesterodon	C. L. Hubbs, 1924	*Cnesterodon*
Phalloceros	C. L. Hubbs, 1924	*Phalloceros*
Phallotorynus	C. L. Hubbs, 1924	*Phallotorynus*
Poeciliopsinae	C. L. Hubbs, 1936	
Poeciliopsis	C. L. Hubbs, 1936	*Poeciliopsis*
Poecilistes	C. L. Hubbs, 1936	*Poeciliopsis*
Aulophallus	C. L. Hubbs, 1936	*Poeciliopsis*
Carlhubbsia	Whitley, 1951	*Carlhubbsia*
Phallichthys	C. L. Hubbs, 1936	*Phallichthys*
Phalloptychus	C. L. Hubbs, 1936	*Phalloptychus*
Xenophallus	C. L. Hubbs, 1936	*Neoheterandria*
Xenodexiinae	C. L. Hubbs, 1950	
Xenodexia	C. L. Hubbs, 1950	*Xenodexia*
Poeciliinae	C. L. Hubbs, 1926	
Pamphoriini	C. L. Hubbs, 1924	
Pamphorichthys	C. L. Hubbs, 1924	*Poecilia*
Pamphoria	C. L. Hubbs, 1924	*Poecilia*
Xiphophorini	C. L. Hubbs, 1924	
Platypoecilus	C. L. Hubbs, 1924	*Xiphophorus*
Xiphophorus	C. L. Hubbs, 1924	*Xiphophorus*
Poeciliini	C. L. Hubbs, 1926	
Poecilia	C. L. Hubbs, 1926	*Poecilia*
Micropoecilia	C. L. Hubbs, 1926	*Poecilia*
Limia	C. L. Hubbs, 1926	*Poecilia*
Parapoecilia	C. L. Hubbs, 1926	*Poecilia*
Lebistes	C. L. Hubbs, 1926	*Poecilia*
Allopoecilia	C. L. Hubbs, 1926	*Poecilia*
Mollienesia	C. L. Hubbs, 1926	*Poecilia*
Curtipenis	Rivas and Myers, 1950	*Poecilia*
Alfarinae	Howell-Rivero and Hubbs, 1936	
Alfaro	Howell-Rivero and Hubbs, 1936	*Alfaro*
Furcipenis	Howell-Rivero and Hubbs, 1936	*Alfaro*
Tomeuridae	Hubbs *in* Kulkarni, 1940	
Tomeurus	Hubbs *in* Kulkarni, 1940	*Tomeurus*

SUMMARY

Families, 2
Subfamilies, 5
Tribes, 9
Genera, 52

TABLE 2

PROPOSED CLASSIFICATION OF THE POECILIIDAE, WITH EQUIVALENTS IN PRIOR CLASSIFICATION

Taxon	Equivalents in Prior Classification
Poeciliidae	
Tomeurinae	
Tomeurus	*Tomeurus*
Poeciliinae	
Poeciliini	
Alfaro	*Alfaro, Furcipenis*
Poecilia	*Pamphorichthys, Pamphoria, Poecilia, Micropoecilia, Limia, Parapoecilia, Lebistes, Allopoecilia, Mollienesia, Curtipenis*
Priapella	*Priapella*
Xiphophorus	*Platypoecilus, Xiphophorus*
Cnesterodontini	
Phallotorynus	*Phallotorynus*
Phalloceros	*Phalloceros*
Phalloptychus	*Phalloptychus*
Cnesterodon	*Cnesterodon*
Gambusiini	
Brachyrhaphis	*Brachyrhaphis, Plectrophallus, Trigonophallus*
Gambusia	*Heterophallus, Gambusia, Dicerophallus, Flexipenis*
Belonesox	*Belonesox*
Girardinini	
Girardinus	*Toxus, Glaridichthys, Allodontium, Dactylophallus, Girardinus*
Quintana	*Quintana*
Carlhubbsia	*Carlhubbsia*
Heterandriini	
Priapichthys	*Priapichthys, Panamichthys, Alloheterandria, Pseudopoecilia, Darienichthys, Diphyacantha*
Neoheterandria	*Allogambusia, Neoheterandria, Xenophallus*
Heterandria	*Pseudoxiphophorus, Heterandria*
Poeciliopsis	*Hemixiphophorus, Poeciliopsis, Poecilistes, Aulophallus*
Phallichthys	*Phallichthys*
Xenodexiinae	
Xenodexia	*Xenodexia*

SUMMARY

Families, 1
Subfamilies, 3
Tribes, 5
Genera, 21

Kallman, 1959; and Rosen and Bailey, 1959, pp. 10–12).

The nomenclature of parts of the skull derives from that employed by Starks (1904, 1926), Goodrich (1930), Gregory (1933), Ramaswami (1945, 1946), Kulkarni (1948), Rosen (1962a), and others; synonymic terms are given in parentheses.

There has been some uncertainty in the use of the terms "lateral ethmoid" and "prefrontal." Both have been employed to designate a membrane bone that arises lateral to the cartilage [of the lamina orbitonasalis. "Prefrontal" is employed herein to distinguish this characteristic bone from an endochondral or perichondral (or both) ossification that involves the lamina orbitonasalis, the "lateral ethmoid." A lateral ethmoid, *sensu stricto*, is infrequently well developed among cyprinodontiforms. Gregory (1933, p. 218, fig. 97A, B) mistakenly labeled the nasal as a "prefrontal."

The pterotic is a complex bone in all cyprinodontiform fishes, but there is considerable variation in the extent and development of the dermal component (dermopterotic or supratemporal). In some well-ossified forms (e.g., some fundulines and goodeids), this bone overlies part of the sphenotic, frontal, and parietal, often entirely covering the sphenotic-pterotic suture. More commonly the dermopterotic is much reduced and is confined to the area of the underlying autopterotic. In some forms (e.g., *Jenynsia maculata;* C.N.H.M. No. 295) the two conditions are present on opposite sides of the same individual.

In all cyprinodontiform fishes, a tiny bone is seated on or near the lateral process of the sphenotic and just behind the orbital extension of the frontal. It carries a short infraorbital extension of the supraorbital canal (pores 6 and 7 of Gosline, 1949, or their corresponding neuromasts if the canal is undeveloped). This bone (variously termed "dermosphenotic," "intertemporal," "postfrontal," "suborbital 5," "suborbital 6," or a "postorbital") carries the remnant posterior section of the infraorbital canal and is the last bone of the suborbital series. Except for the lachrymal (also called "preorbital" or "suborbital 1"), the intervening bones of the infraorbital ring together with their canal are absent in cyprinodontiforms. We follow Kulkarni (1948), Harrington (1955, pp. 285–286), and Norden (1961, p. 688) in applying the name "dermosphenotic" to this posterior bone in the ring, and interpret it as the homologue of suborbital 6 of fishes with a complete complement of suborbitals (Smith and Bailey, 1962).

Gregory (1933, p. 218, fig. 97C) mislabeled the maxilla as the "palatine," and on his page 217 (fig. 96A) the structure identified as "lachrymal" is actually two bones, the lachrymal and the prefrontal, which are joined by dried connective tissue.

We apply the name "intercalar" to the dermal bone that lies on the under side of the cranium in the vicinity of the epiotic-pterotic juncture and receives the bony or ligamentous lower arm of the posttemporal. Rayner (1951, p. 77) in fact regarded the intercalar as an ossification within the ligament attached to the shoulder girdle. Although enlarged in some teleosts, in cyprinodontiforms the intercalar is frequently absent and, where present, is minute. It has commonly been termed "opisthotic," as by Harrington (1955, p. 287) and Norden (1961, p. 690), but that name has also been employed, for example, by Gardiner (1960, p. 359), for an endochondral bone of the neurocranium that lies behind the prootic. It is not clear that the opisthotic of actinopterygian fishes is different from the autopterotic. If we accept the argument of De Beer (1937, p. 497), we may at present apply the term "opisthotic" with certainty only to a cartilage bone of tetrapods.

SECONDARY SEXUAL CHARACTERS, THEIR STRUCTURE, DEVELOPMENT, AND USE IN SYSTEMATICS

SEXUALLY DIMORPHIC MODIFICATIONS are exceptionally numerous in the Poeciliidae. Other than size, these involve the anal fin and anal-fin suspension, the pelvic and pectoral fins and to a lesser extent the dorsal and caudal fins, the mouth parts and dorsicranium, the pleural ribs, and color pattern. The anal fin (gonopodium, in male) and its suspension (gonopodial suspensorium, in male) are sexually dimorphic in all poeciliids and constitute the primary basis for the separation of tribes, genera, species, and, at least in some instances, subspecies (see Rosen, 1960). The gonopodial system, because of its great importance in taxonomic assessment, is discussed in some detail, even though accounts of gonopodial and suspensorial morphology and development are available elsewhere. The purpose here is to digest the published information that pertains to systematic problems and to add such original observations as seem relevant. Dimorphic structures other than those of the anal fin and its suspension are discussed separately in the systematic accounts of the tribes and genera.

The development of the gonopodial system marks the beginning of somatic sex differentiation in the male poeciliid. In the guppy, *Poecilia reticulata*, the average length of time that elapses after birth before onset of gonopodial development is about 100 days (Hopper, 1949). For the swordtail, *Xiphophorus helleri*, the first appearance of gonopodium formation requires 18 weeks (Sangster, 1948), although this period may vary considerably among the geographic races of *helleri*.

Changes in the testis may and probably do precede gonopodial morphogenesis in time. From a study of the gonads and internal skeletal elements in *Xiphophorus helleri*, Vivien and Mohsen (1951) concluded not only that gonadal development precedes skeletal changes, but that in the male morphogenetic changes in the suspensorial elements anticipate related changes in rays 3, 4, and 5 of the anal fin (gonopodium formation). In juvenile males of *X. helleri*, Essenberg (1923) found that tubule formation is definitely established at the inception of gonopodial morphogenesis.

The period of combined growth and differentiation of male secondary sexual structures varies in duration. *Gambusia affinis*, according to Turner (1947), requires about 50 days at room temperature to develop these structures fully, but a period three times as long appears to be normal for *X. helleri*. Sangster (1948) claimed that different structures require different periods of time to complete their development. He noted that the development of the caudal-fin extension, or "sword," in *X. helleri* not only begins later than that of the gonopodium but requires a longer period for its full expression.

The rate at which these changes take place has received comparatively little attention. Turner (1947) has shown that gonopodium development in *Gambusia affinis* follows a typical sigmoid growth curve which approaches an asymptote at approximately 50 days. The initial spurt of growth is a measure of the degree to which new tissue is being laid down in the fin during its elongation, whereas the leveling off reflects the increasing role played by differentiative processes during development.

GONOPODIUM

During the course of development of the gonopodium, certain phases can be arbitrarily distinguished. In *Xiphophorus maculatus*, Grobstein (1940) delimited three that correspond fairly well with the pattern of morphogenesis in other species studied: a preliminary phase, a growth phase, and a phase of differentiation.

In the preliminary phase the third ray thickens, while the fourth to seventh rays undergo primary bifurcation. The enlargement of the blood vessels and an increased flow of blood in the fin tissues, especially pronounced around the region of rays 3, 4, and 5, are also signs of the onset of anal-fin metamorphosis (Cummings, 1943). In the growth

phase, a rapid elongation of the third, fourth, and fifth rays occurs, to form a 3–4–5 complex. At the end of this phase the contour of the adult fin is foreshadowed. The various specialized segments that distinguish the mature gonopodium are differentiated during the third phase, after which the hypertrophied cutis shrinks and the gonopodium is mature. Approximately half to three-quarters of the total metamorphic period is spent in the third phase.

Probably a period of a week or 10 days elapses between the early thickening of the third ray and the beginning of elongation. During this period, early bifurcation of the fourth to seventh rays is usually under way. As the interradial tissue of the presumptive gonopodium grows out at the ends of rays 3, 4, and 5, fine calcified spicules (hyalin fibrils, of authors) extend out from the ends of the rays in the form of a partially opened fan. These spicules or fibrils, composed in part of dense collagenous ground substance, probably are homologous with the actinotrichia of the unmodified anal fin. As these spicules become longer, a fissure appears at right angles to their long axes. This gradually widens and becomes the boundary of a new segment. The spicules solidify to form an ossified unit like the preceding segments of the ray.

Rays 3, 4, and 5 approximately double or treble in length during the early growth phase. Growth occurs largely by the formation of new segments at the distal ends of the rays. The rate of segment formation in the third ray averages, according to species, 0.75 to 1.50 segments per day. Simultaneously the ray is rapidly thickened.

Apparently ray elongation may be influenced, at least indirectly, by the thyroid. Experiments involving the administration of thyroid hormone to *Poecilia reticulata*, *Xiphophorus maculatus*, and *Gambusia affinis* have been summarized by Pickford and Atz (1957, pp. 132, 138); they illustrate the capability of this hormone for inducing ray growth, even in young, sexually indifferent fish. Elongation of pectoral rays of the order of 10 per cent after 15 days of treatment was observed in one experiment, and, in another, anal rays grew beyond their normal limits. Hence a relatively uncomplicated physiological mechanism appears to be available to permit formation of a much longer gonopodium, the adaptive significance of which has been suggested by Rosen and Tucker (1961, p. 210).

As elongation proceeds, the contour of the developing fin is gradually altered. By the end of the growth phase, the tip of the developing gonopodium is smooth and approaches roundness. When rounding becomes clearly evident, various minor promontories or excrescences may appear at the penultimate region, their exact form depending upon species. At the end of the growth phase, the short brushes of refractory fibrillae are no longer clearly visible.

Initially rays 4, 5, and 6 contain the greatest number of segments. During development, rays 3, 4, and 5 elongate extensively, while the other rays lag behind, ultimately adding from one to at most 10 segments. The first new segments are just as long as, and in some cases longer than, the original segments, but those formed toward the end of morphogenesis are usually conspicuously shorter and more slender, causing the rays to taper toward their tips.

Local differentiation of the rays, involving modifications of the segments and the addition of new structures in the 3–4–5 complex, identifies the last, or differentiation, phase. There is usually some overlap with the preceding growth phase, for example, in *Xiphophorus maculatus* (Grobstein, 1940). Elongation continues unabated well into the differentiation phase in *Poecilia latipinna* (Cummings, 1943). In general, early differentiative changes appear before elongation is quite complete. During the period of differentiation, specific types of structure are produced, and functional relationships between two or more structures are established.

Allometry is characteristic of the growth phase in which a differential rate of growth is established between the rapidly developing 3–4–5 complex and the slower-growing rays 6 to 10. Even within the 3–4–5 complex, growth inequalities of the individual rays and their components lead to disparate lengths and number of segments. For example, in *Gambusia affinis* at about 20 days of metamorphosis, segment addition in ray 3 accelerates, while in ray 5 it continues at a uniform

pace. Before this difference in the rate of segment addition is established, ray 3 contains about 20 segments and ray 5 approximately 24; when morphogenesis has been completed, ray 3 has 34 to 40 segments and ray 5 only 30 to 33. In spite of having fewer segments, ray 5 is the longer, a fact explained by the development of long, slender segments in ray 5a and short, broad ones in ray 3. The long, slender, terminal segments in ray 5 form the distal segment arc—a unit of functional importance for successful copulations (Rosen and Gordon, 1953, p. 22, text fig. 12A).

So long as growth and segmentation proceed at the same rate, the segments are of uniform size (Turner, 1941). When an accelerating growth rate is combined with a steady segmentation rate, each successive segment becomes longer, as in the intermediate portion of ray 4. Inequality in segmentation of branches of rays in which the branches also are of unequal length suggests that both the segmentation and growth rates have been altered. Where different growth rates occur on opposite sides of a segment during its formation, the plane of segmentation becomes oblique, as seen in the intermediate segments of ray 3. Plotting segmentation rate against growth rate in a single ray should produce a straight line, if the two processes proceed at a constant rate. An isometric relation between the two is, however, not usual (Turner, 1941). The rapid rise in the segmentation curve of ray 3, for example, clearly results from a relative retardation of growth or a relative enhancement of the segmentation rate.

The relation of growth to segmentation is evidently a major factor in molding the gonopodium into a normal pattern. Apparently, however, this relation is influenced by the size that the fish attains at sexual maturity. Thus, in *Xiphophorus maculatus*, Gordon and Rosen (1951) found positive correlations between (1) the standard length of the fish and the length of the gonopodium, (2) the standard length and the number of segments in a specific area of the gonopodium, and (3) the gonopodial length and the average height of specific segments. Moreover, Turner (1941) showed that the inequalities of growth and segmentation in the various rays of the gonopodium differ in males of different size groups. Recall that ray 3, which begins its role in gonopodial morphogenesis with fewer segments than ray 5, concludes its development with an equal or greater number (in *Poecilia latipinna* and *Gambusia affinis*). When the developing male exceeds a certain critical size, however, ray 5 again outstrips ray 3 in the rate of segment formation, so that in large males one of the original relations between these two rays, as it was prior to morphogenesis, is finally restored.

It is clear, then, that there is an allometric relation between body growth and an increase in gonopodial length as reflected in the rate of segment addition to the rays. Superimposed on this primary allometry is the secondary inequality in the growth rates of rays 3, 4, and 5 versus those of rays 6 to 10. A further inequality is then impressed upon this secondary dichotomy, wherein each component of the 3–4–5 complex exhibits its own highly individual and changing rate of growth and segmentation.

During the differentiation phase of gonopodium development, the role of size-correlated factors is obscured by the complexity of developmental systems that influence the osteoblasts, and the interaction of adjoining morphogenetic fields.

The specialized terminal gonopodial structures are produced by specific fields (fig. 1) of osteogenic tissue. These fields have the following attributes: (1) they appear at different stages of development in a definite sequence and are therefore of different duration, since they do not disappear until the gonopodium is fully differentiated (synchrony and heterochrony); (2) their locations are specific and circumscribed; (3) they are of different sizes; (4) they are of different shapes and have a tendency to elongate along the axes of the rays; (5) their dimensional limits are defined by a complex vascular bed; and (6) they add new bone to the rays according to definite patterns that are foreshadowed by the particular arrangement of capillaries in the vascular bed.

As the vascular bed is being organized in relation to the presumptive differentiation areas, special morphogenetic patterns take form that later will influence the precise character of terminal structures. For example, in *Xiphophorus*, as the fifth ray

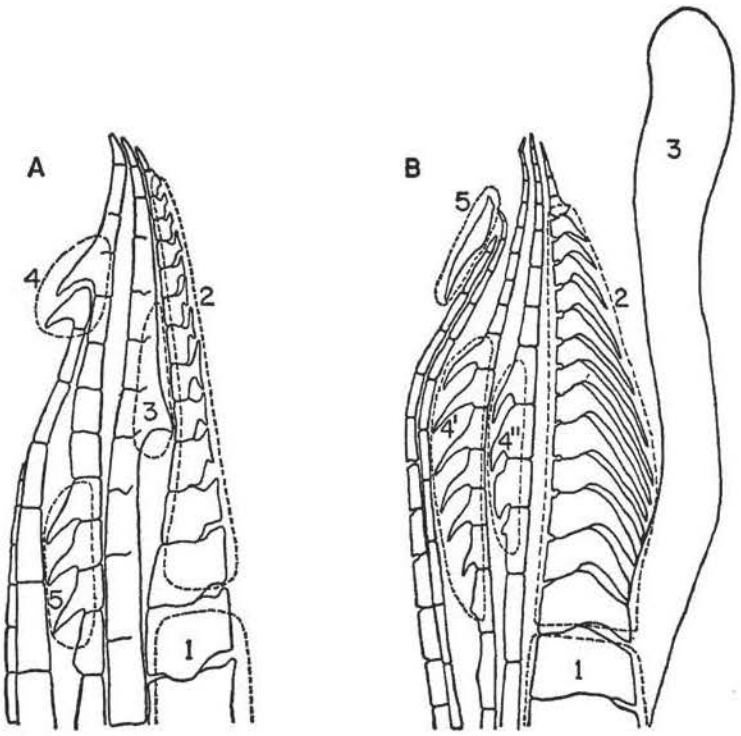


FIG. 1. Differentiation areas in the poeciliid gonopodium. A. *Gambusia affinis*, modified from Turner (1941). B. *Poecilia reticulata*, modified from Hopper (1949). Differentiation areas are numbered and enclosed by dashed line. The numbers from 1 to 5 represent the order in which the structures developed in these areas make their appearance.

lengthens it bends downward to make contact with the growing tip of ray 4. The intimate association of these two rays persists, so that in the mature gonopodium there are two sets (one from each ray) of clearly interrelated special structures. The fifth ray has developed a claw-like element just behind that point on ray 4 from which arises a series of tooth-like segments. Both structural units serve as holdfasts that secure the male to the female during copulation. Among the eight species of *Xiphophorus* a very precise inverse correlation exists between the size of the claw (ray 5) and the size and number of serrae (ray 4) (Rosen, 1960). Hence, *helleri*, the species with the largest claw, possesses the smallest and fewest serrae. At the other extreme, *maculatus* has the smallest claw and the largest and most numerous serrae. Rosen also noted several rare individuals of *maculatus* which developed a claw of the *helleri* type, which was in every case accompanied by a reduction in number of serrae. On the basis of these observations, we advance the hypothesis that the developing fifth ray inhibits the expression of fourth-ray serrae. The hypothesis was tested in *Xiphophorus* by the removal of the distal half of ray 5 during the growth phase of gonopodium development. Although the operated-on fifth ray regenerated rapidly, in most instances it lagged behind and failed to touch the penultimate segments of ray 4. The effects of experimental interference were dramatic; the region of ray 4 normally in contact with the claw of ray 5 bristled with serrae, adding as many as five additional elements to the typical complement of this ray (pl. 1, figs. 3–5). In possessing these supernumerary serrae, the experimental fins in *Xiphophorus* resemble the gonopodia of species of *Poecilia*. A relationship between the two genera has been sug-

gested (C. L. Hubbs, 1926; Rosen and Gordon, 1953).

On the strength of such experiments, it may be inferred that if, in *Xiphophorus*, a developmental block prevented the terminal portions of rays 5a, 5p, and 4p from growing outward to their normal limits, the remaining array of distal elements would show striking resemblances to those normally present in the gonopodium of *Priapella*. Deletions of this sort may have been a major source of the differences that now separate some poeciliid genera.

Heterochronous development also may strongly influence morphological patterns, perhaps even more than changing rates of ray growth and segment addition, by altering the time and changing the sequence of appearance of certain elements. In *X. maculatus* the spines of ray 3 and the proximal serrae of ray 4p appear synchronously, whereas in *P. latipinna* spines develop before proximal serrae are evident. Hence, the spines and serrae of *X. maculatus* lie in the same vertical section, whereas in *P. latipinna* the serrae are distal to the spines. Heterochrony also may contribute to differences in size and extension of the genital palp in *Poecilia*. In *P. reticulata* the palp is one of the first structures to appear and is quite long, extending out beyond the tip of the fin; in *P. latipinna* it arises later and is less developed.

In spite of differences in the length and details of terminal specialization, most poeciliid gonopodia function on almost identical mechanical principles (Rosen and Gordon, 1953). Gonopodial morphogenesis typically is directed toward the elaboration of a bilaterally symmetrical fin, with a built-in mechanism that allows the rotation and folding of one ray against the other as the gonopodium is swung forward. This folding of the uppermost, or fifth, ray against the lowermost, or third, results in the formation of a transitory groove along one side of the fin. Through this temporary channel spermatophores are transmitted to the terminal portion of the genitalium that is used in contact with the female.

The rotational centers that allow folding of the rays are built up into a functional mechanism long before the terminal specializations are differentiated. In certain species the rotational centers grow asymmetrically, so that the rays are actually folded during development, and a permanent groove is formed in the sinistral or dextral position. Such development is always accompanied by the loss of some intrinsic symmetry and the asymmetrical addition of new structures.

Permanent asymmetric folding of the gonopodium has arisen independently at least five times within this family (Rosen and Bailey, 1959). From a structural viewpoint the chief characteristic of these fins is not the folding itself but the accompanying great development of rami that abut directly on the groove formed by the permanently folded third and fifth rays. In fact, in the several types of asymmetric gonopodia, actual folding of the rays usually constitutes only a minor component of the total distortion to which the fin is subjected. In *Phallichthys* and *Neoheterandria umbratilis*, closure of the unilateral groove is minimal, but the marginal segments are still greatly enlarged. In *Quintana*, although the distal segments of ray 4p are slightly twisted sinistrally, the fin as a whole is symmetrical.

Perhaps the initial step in the evolution of asymmetric poeciliid genitalia was a slight unilateral asymmetry that resulted from a minor disturbance in some component of the developing system. The work of Dulzetto (1931) suggests how this may have come about. With appropriate staining, he showed that in *Gambusia affinis* the developing gonopodium is organized into two structural components, an outer and an inner matrix, at a time when new segments are still forming around the core of hyaline fibrils early in the growth phase. Each component consists partly of connective tissues that display a definite geometry in cross section. Actually the core or inner matrix of the fin is a long rod of closely packed reticular fibers. These form a well-defined net of crossing strands around the centrally located hyaline fibrils and segments. This internal rod of dense tissue is itself centrally situated within and parallel to the long axis of the cigar-shaped outer supporting matrix. The tubular form and concentric alignment of these two major components of the developing gonopodium provide an efficient supporting framework for the delicate, growing endoskeleton. If there were a displacement of the core away

from the geometrical center or some other unilateral distortion of the inner matrix, the embedded hyaline fibrils and developing segments might be forced over to one side by asymmetric growth of the enveloping reticular network and thus grow outward in a new plane. Bonner (1952, pp. 63–71) indicated that mechanical stresses set up in developing tissues may act as stimuli to growth in some relation to the direction of the applied force, much as the trabeculae in mammalian cancellous bone develop in accordance with the lines of compression and tension of a loaded structure (Thompson, 1952, pp. 975–980). Small developmental asymmetries probably are a normal occurrence in the gonopodial morphogenesis of all poeciliid species. Given the right combination of functional and structural circumstances, minor heritable asymmetries may confer a small selective advantage and hence be perpetuated. Permanent folding permits structural modification to enhance the effectiveness of a mechanism that is normally mechanically folded during use and clearly is potentially adaptive.

Permanent asymmetric folding of the rays is found only in species with relatively long gonopodia; it is universally absent in poeciliids with short genitalia. Furthermore the action of the short gonopodium during sperm transfer is assisted by complex bilateral accessory structures (modifications of the pectoral and pelvic fins) that are wanting in forms with long gonopodia. From this, Rosen and Tucker (1961) reasoned that the absence of gonopodial asymmetry in species with short gonopodia may indicate that their developmental pathways are so strongly canalized to produce complex accessory bilateral mechanisms that even slight asymmetric distortions would be inadaptive and therefore quickly eliminated.

Once the rotational mechanisms and terminal specializations have been laid down, there is a rapid reduction of the fleshy border of the fin, strikingly evident at the distalmost angle of the gonopodium. Actually, reduction of the fleshy cutis probably begins sometime during late differentiative processes when the distal tips of the rays are converging. The shrinkage does not become conspicuous, however, until quite late. The reduction is first emphasized when the tips of the terminal structures, previously buried deep in the cutis, are observed to be flush with the periphery. The process continues until the cutis is thin and translucent. In the adult, the cutis can hardly be noticed except along the anterior (ventral) border of the third ray and where it is stretched between the tips of rays 3, 4, and 5.

The increased flow of blood, apparent throughout the development of the gonopodium, gradually subsides, although the number of minor vessels has been markedly increased in the distal third of the fin. The vascular anatomy of the differentiated gonopodium was described by Rosen and Gordon (1953).

The addition of new terminal segments, which persists throughout life in the female, ceases altogether in the male after gonopodial differentiation. The anal fin of the male undergoes no further change after it attains its mature configuration.

GONOPODIAL SUSPENSORIUM

In morphogenesis of the gonopodial suspensorium, the following changes occur in the order of their appearance during metamorphosis:

1. Elongation of actinosts 2, 3, 4, and 5.
2. Dissolution of the hemal arch of the first hemal spine; gradual migration cephalad of the remnant of the first hemal, the "ligastyle," for a distance of from one to three vertebrae; gradual forward displacement of the anal fin to a position in which actinosts 3, 4, and 5 lie almost directly under the ligastyle; forward migration, by bending and the addition of new bone, of the tips of the shafts of the anterior hemal spines, the "gonapophyses," so that they maintain intimate contact with the actinosts; early formation in many species of paired uncini on the anterior gonapophyses.
3. Formation of the definitive features of the primary gonactinostal complex from actinosts 2, 3, and 4; beginning of fusion of the mesonosts with the bases of the gonactinosts to form the basal fossae and lateral

processes; final reorientation of the dorsal region of the 2–3–4 complex; formation of definitive uncini on the anterior gonapophyses.

4. Formation of uncini on the posterior gonapophysis.

In general, during normal development the anal-fin suspensorium passes through a period of histolysis that results in the gradual dissolution of the anterior hemal spines. In females, histolysis proceeds unchecked, and as many as four of the anterior hemal spines may be eliminated. In the maturing male, histolysis is counteracted by the rapid addition of bone, and typically not more than a single hemal is eliminated before osteogenesis sets in (fig. 2). Rosen and Kallman (1959) demonstrated that histolysis proceeds autonomously, but that in some cases the superimposed osteogenetic changes in the hemal spines are specifically induced by the developing underlying actinosts. This discovery tends to confirm Turner's (1942a) earlier hypothesis that the hemal and actinostal complexes develop as distinct (although sometimes interdependent) units within separate morphogenetic fields.

Accompanying the development of the bony suspensorial modifications are the reorganization of associated muscle masses (see Rosen and Gordon, 1953) and changes in nerve and vascular routes and supply. The related changes in the soft parts are, however, poorly known.

The development of some suspensorial structures appears to be controlled largely by body form and absolute size. Others transcend purely mechanical forces and retain a large measure of developmental independence. It is with the morphological details that show some developmental autonomy that the systematist is primarily concerned, for only such structures hold definite promise of aiding phylogenetic analysis.

Commenting on the relation between ligastyle size and body depth in *Phallichthys* and *Carlhubbsia*, Rosen and Bailey (1959) pointed out that in the slenderest species the ligastyle is reduced to a rudiment of bone embedded in the primary suspensory ligament, whereas in deep-bodied forms the ligastyle is a well-developed, long, bony rod. Similar relations prevail in other genera or species that differ radically in body depth, provided that orientation of the gonactinosts remains constant. In *Poecilia*, for example, in which the gonactinostal complex is well developed and the body is generally rather slender, often only a minute ligastyle is interpolated between the fin supports and the vertebral column and rarely is it reduced to a few fragments or is altogether absent. In *Xiphophorus* the gonactinosts are less developed, and the body may be extremely deep; in these fishes the ligastyle attains its maximum size in the family. In both genera the gonactinosts are inclined slightly forward.

In the slender-bodied *Cnesterodon* the ligastyle is typically well developed, and the gonactinosts are inclined backward. Here the ligastyle is the sole remnant of median axial support of the gonactinosts, for gonapophyses are absent. It appears, therefore, that interpretations based on ligastyle size alone cannot lead to a clear understanding of relationships in this family.

Much the same may be said of assessments that depend on an analysis of size or angular growth of the gonapophyses, for it is evident that these structures too respond to differences in body proportion quite independently of more fundamental features discussed below. In the slenderest species of *Gambusia*, for example, the gonapophyses are bent sharply forward, whereas in the deeper-bodied species and in the allied *Belonesox* these elements are much less sharply bent. In large examples of *Xiphophorus helleri* the gonapophyses are long, straight, and often vertical; in the smaller *X. pygmaeus* they are short, sinuous, and inclined forward.

Gonapophyseal form, in addition to being affected by size factors, is closely related to the relative position in the body of the underlying gonactinosts. Thus, a species in which the anal fin of the male is displaced far forward possesses more sharply bent gonapophyses than one with little or no forward displacement. In the most highly specialized poeciliids the developing gonopodium is displaced anteriorly to a point between the posterior limits of the primary shoulder girdles. Experiments reported by Rosen and Kallman (1959) involving extirpation and transplantation of the presumptive gonactinosts in the developing suspensorium suggest that in the more specialized poeciliids these

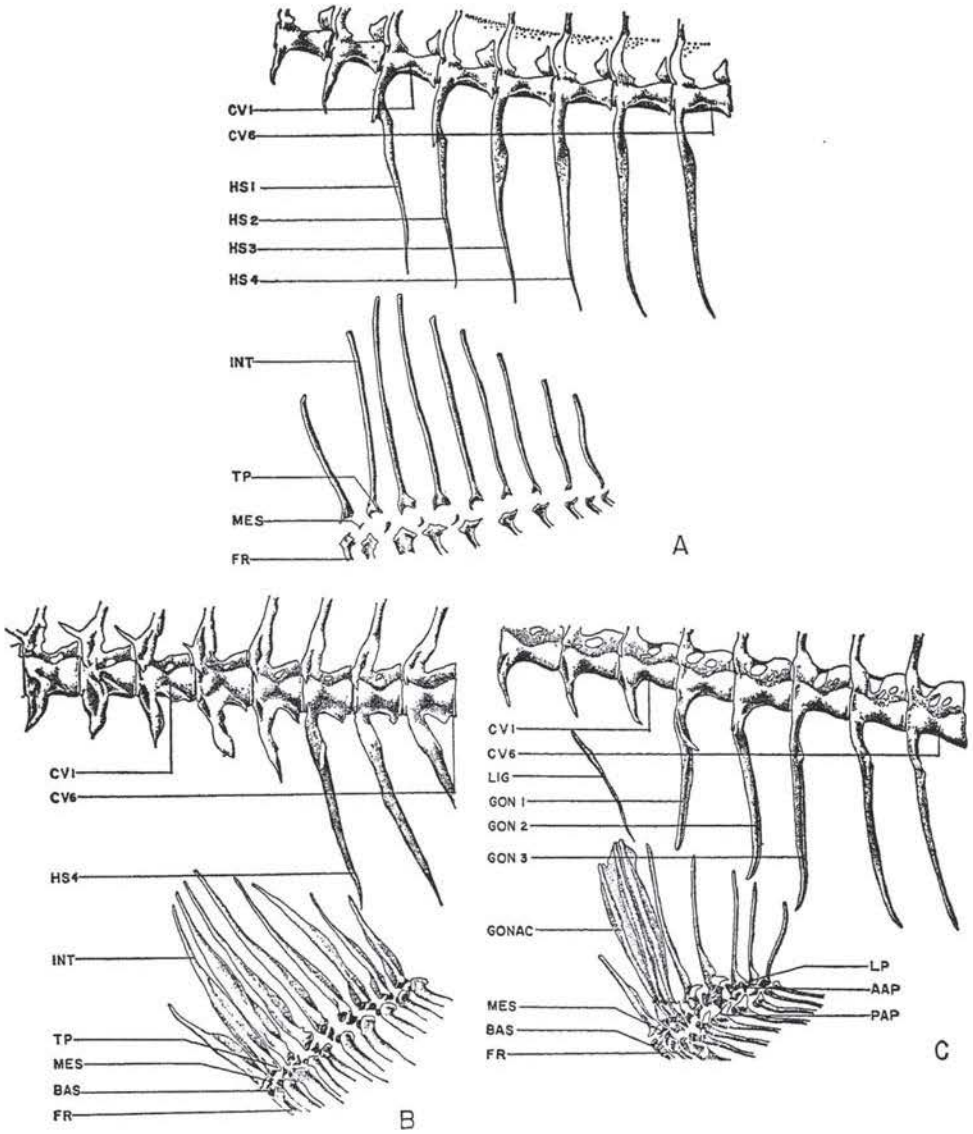


FIG. 2. Stages in the development of the anal-fin suspensorium in *Xiphophorus maculatus*. A. Juvenile. B. Female. C. Maturing male. From Rosen and Kallman (1959).

Abbreviations: aap, anterior articular process; bas, baseost; cv, caudal vertebra; fr, fin ray; gon, modified hemal spine or gonapophysis; gonac, modified actinosts or gonactinosts; hs, hemal spine; int, interhemal spine or actinost; lig, ligastyle; lp, lateral process; mes, mesonost; pap, posterior articular process; tp, transverse process. Drawn by Samuel B. McDowell, Jr.

elements provide an inductive stimulus essential for normal development of the overlying gonapophyses. In the more generalized forms this induction effect is not apparent. They also discussed evidence indicating that the origin of an inductive relationship between axial (gonapophyses) and appendicular (gonactinosts) elements paved the way for one of the major events in poeciliid evolution, involving a pronounced shift forward of the anal fin. In the poeciliids with the structurally most advanced suspensorial sys-

tem (*Cnesterodon, Tomeurus*), the anal fin is displaced so far forward that an inductive relationship depending partly on the proximity of axial and appendicular elements has apparently been lost secondarily; gonapophyses fail to develop. Rosen and Kallman speculated that *Poecilia* and those forms of *Gambusia* with two instead of the more usual three gonapophyses may represent species in the process of losing their gonapophyses. Mohsen (1960) recently discovered a strain of *Poecilia reticulata* with the third gonapophysis present. This exceptional occurrence may be construed as the reappearance of the ancestral condition for which developmental capabilities persist. Such capabilities appear also in *Poecilia amazonica* and *P. parae* in which we have identified individuals with a third gonapophysis (pl. 2, figs. 4–6). Rosen and Kallman postulated that even *Cnesterodon*, which lacks all gonapophyses, still possesses the developmental potentialities for elaborating these structures.

Developmentally, two kinds of gonapophyseal structures for the attachment of supporting connective tissues can be distinguished. The more usual type develops as a normal outgrowth of the posterior edge of a transforming hemal spine where much bone is being laid down within an anchoring ligament to strengthen a subdistal flexure point—a flexure point being a site of early active histolysis. Such outgrowths are termed "uncini." The second type of structure is formed in a quite different manner on gonapophyses that have a more proximal flexure point near the vertebral axis and that lack a subdistal anchoring ligament. In this case, the deposition of bone at the proximal flexure point of the spine and enlarged parapophyses that grow backward and downward toward the centers of active osteogenesis combine to reënforce the posterior edge of the spine.

What matters from the viewpoint of mechanical control is not, however, the embryological origin of such supporting structures or even the precise point at which these structures arise, but the total adaptation for the job of suspension. In a sense, all poeciliids can be said to have developed equally an effective suspensory apparatus. Some species have developed it in connection with a long gonopodium; others, with a short or an asymmetrical gonopodium; and still others have evolved a gonopodial system that operates in relation to specialized pelvic or pectoral fins. Hence, in spite of the fact that all poeciliids have developed a mechanism for gonopodial support with the same basic set of axial and appendicular structures and according to a common morphogenetic plan, each genus presents a relatively distinctive "total solution" to the problem of gonopodium suspension. With allowances for the influence of size on certain relations, the details of suspensorial morphology thus represent a primary source of taxonomic information in these fishes.

ADAPTIVE SIGNIFICANCE OF GONOPODIAL STRUCTURES

Kosswig (1948) suggested that the " . . . gonopodia of the Poeciliidae experienced during their evolution all possible permissible changes which, however, were of no adaptive significance."[1] This sweeping conclusion, which was again stated by him (1959) in essentially the same terms, was based on experiments conducted by Şengün that showed how male guppies with deformed, abnormally regenerated gonopodia were still capable of inseminating females. In Şengün's (1949) actual report, however, a lowered efficiency of the abnormal males as compared with normal controls was demonstrated. Clark and Rosen (*in* Rosen and Gordon, 1953) reported also that removal of one or the other of two assumed holdfasts from the tip of a swordtail gonopodium materially reduced the efficiency of the system, and that removal of both structures altogether prevented insemination. Actually the real problem is not that the varied terminal modifications in the gonopodia of poeciliids are indispensable for insemination. Some poeciliids altogether lack specialized terminal elements (some species of *Brachyrhaphis* and members of the Heterandriini), and the viviparous goodeids have no bony genitalia at all. The distal and subdistal gonopodial spines, hooks, claws, and serrae more probably enhance the

[1] A translation from the original German.

effectiveness of the really essential behavioral items that result in the precise juxtaposition of the fins and bodies of males and females during copulation, especially in groups (*Poecilia*, *Xiphophorus*, and *Gambusia*) in which mating is behaviorally rather complex (Rosen and Tucker, 1961). Moreover, Rosen and Gordon (1953) presented a considerable body of morphological and functional evidence of the definite role these structures play in copulation, especially relating to their holdfast and sensory functions. In a well-documented study of the comparative behavior of the species of *Xiphophorus*, Clark, Aronson, and Gordon (1954) indicated that a species with larger gonopodial holdfasts (*X. helleri*) has a longer copulatory contact than one (*X. maculatus*) in which they are less developed, and that copulations are terminated abruptly by a sharp break. They noted that some female swordtails bled from their genital openings following insertion and withdrawal of the gonopodial tip. Subsequently, Rosen (1960) pointed out that species of *Xiphophorus* with larger holdfasts inhabit more swiftly flowing waters.

VIVIPARITY

SCRIMSHAW (1945) BELIEVED that the developing embryos of many poeciliids utilize nourishment outside of that contained in the yolk. This conclusion was based on his measurements of the mean dry weights of the egg at fertilization, as compared with the mean dry weights of the embryo at birth, the two weights being approximately equal in 19 of the species studied. He reasoned that, since the food requirement of the embryo for maintenance metabolism must be considerable, the similarity in weight must mean that the parent contributed nutritive materials to the embryo and that the yolk supply alone was insufficient to sustain embryonic growth. In *Heterandria formosa* and *Poeciliopsis* (*Aulophallus*) *elongata* he found that the mean dry weight of the embryo at birth considerably exceeds the mean dry weight of the egg at fertilization. This is in accordance with Scrimshaw's (1944a) earlier discovery that in *Heterandria formosa* nearly all the nourishment for embryonic development is obtained from the mother.

Trinkaus and Drake (1952) removed embryos in various stages of development (some pre-blastula) from females of *Poecilia reticulata* and raised them in saline and saline-glucose solutions. They concluded from these experiments that (1) limited organogenesis of embryos of *Poecilia reticulata* may proceed *in vitro* independent of exogenous nutrients, but that it is augmented by the addition of glucose, and (2) embryos developing *in vivo* probably require little if any nutritional contribution from the mother. Sanders and Soret (1954) showed that embryos of *Gambusia affinis* also can be reared successfully in nutrient solutions, whereas, in contrast, Baker and Ferguson (1942) were able to raise embryos of *Xiphophorus maculatus* successfully in sterile, autoclaved tap and pond water. Moreover, Fontaine (1945) observed an exceptional female of *Poecilia reticulata* that under apparently normal conditions released 12 eggs which drifted down to the sandy bottom of the aquarium. Three days later these eggs hatched, and the young lived for 15 days, seemingly quite normal during the entire period. Houssay (1930) also observed females of the South American *Cnesterodon decemmaculatus* extruding eggs spontaneously, but he did not mention whether or not the eggs had been fertilized or if any embryos were hatched from them. [The results reported by Houssay in *Cnesterodon* may not be comparable with those in the exceptional female of *Poecilia*, for Hildebrand (1917) showed that females of *Gambusia affinis* that had wintered without males and that, therefore, contained no stored sperms, regularly discharged their unfertilized eggs.] The existing disagreement among the different reports may reflect, in part, an inherent variability in the requirements for exogenous nutrients by poeciliid embryos. Clearly, however, the embryos of many species are dependent on food materials supplied by the maternal environment.

Tomeurus apparently differs from all other poeciliids in possessing a chorionated egg and a facultative viviparity. Pope's observations (see Gordon, 1955) of a female of *Tomeurus* from Kartabo, British Guiana, showed that some members of this species are capable of maturing several ova at once and that these, once fertilized, may be retained within the body of the parent to accomplish most if not all of their embryonic growth. In our collections of preserved specimens of *Tomeurus* from British Guiana we found 15 extruded embryos in various stages of development. The containing eggs presumably were laid while the fish were still alive in transit to this country. Almost half of these embryos showed characteristics of advanced growth, and caudal fin rays were clearly discernible in four. The living pair of *Tomeurus* maintained under laboratory conditions, however, produced no more than two eggs at once, and these were extruded separately, presumably shortly after fertilization.

Many poeciliids undoubtedly are still in the process of evolving specialized reproductive patterns. Studies of superfetation in these fishes by Turner (1937, 1940a) and Scrimshaw (1944a, 1944b) suggest that those Poeciliidae with the highest degree of viviparity, *Poeciliopsis* (*Aulophallus*) *elongata* and *Heterandria formosa*, also show well-developed

superfetation. In some other poeciliids, superfetation is less common and is erratic; apparently it is not an important component of their methods of reproduction. Thus, Scrimshaw concluded that many poeciliids, though they probably show a tendency toward superfetation, do not make functional use of it in their normal reproductive cycles. Turner (1947) said, with reference to piscine reproduction in general, that there can be no sharp distinctions among the various types of reproduction, because in many instances an evolution is in progress from one type into another. Even among typically egg-laying cyprinodontiforms such as *Oryzias*, exceptional instances of internal fertilization and embryo retention are reported (Amemiya and Murayama, 1931; Yamamoto, 1961). There are examples among teleosts in which viviparity occurs normally in genera or species of families, the other members of which are oviparous. For example, in the family Zoarcidae, the European ocean pout, *Zoarces vivipara*, gives birth to broods of approximately 300 living young, and the closely allied American ocean pout, *Macrozoarces americana*, may lay as many as 4000 eggs on inshore beds of rocks or pebbles (Bigelow and Schroeder, 1953). Among viviparous fishes numerous intermediate stages occur between those in which embryos depend least and those in which embryos depend most on the parent for nutrients, even in species within a single genus (Turner, 1942b).

In temperate and subtropical zones, natural reproductive cycles in poeciliid fishes decline in late summer and fall and cease altogether in winter. Interruption of these cycles is attributed largely to seasonal fluctuations in daylight and mean temperature (Barney and Anson, 1921; Turner, 1938). Scrimshaw (1944b) found superfetation in poeciliids similarly sensitive to light in northern latitudes. The environmental factors are superimposed on and interact with basic physiological ones that control ovulation and birth. Turner (1942b) believed that in poeciliid fishes the postponement of ovulation after maturation and fertilization of the ovum (embryo retention) may indicate the attainment of a threshold level of the pituitary gonadotropins. Stimulation of the ovarian musculature and genital sphincter muscles at birth also may be under some form of pituitary control. Houssay (1930, 1931) was able to change the usual course of ovulation in the poeciliid *Cnesterodon decemmaculatus* by implantation of piscine pituitary. Chavin (1956) induced a hormonal imbalance in goldfish by raising the water salinity. Hence, it is possible that in euryhaline fishes such as poeciliids ecological preferences for fresh or salt water also are involved with the physiological requirements of reproduction.

A major selective advantage of embryo retention may be its involvement as an agent in dispersal (Rosen, 1962b). For example, a viviparous species is more readily capable of depositing a potential breeding population in fringing areas of its range. The oviparous species must depend on the uncertainties of wind and currents to carry young or on the chance that breeding males and females will arrive together in extraperipheral regions.

Hagan (1951) speculated that viviparity in insects might have begun as a heritable capacity for a slightly delayed deposition of eggs while the female sought favorable environments for them. This process, once begun, could have been prolonged under constant selection pressure until internal hatching (ovoviviparity) came to precede extrusion as a regular routine. Turner (1947) gave an excellent account of the possible physiological and structural transitions from oviparity to viviparity in fishes.

RELATIONSHIPS OF THE POECILIIDAE

IF, ON THE BASIS of its primitive egg structure and facultative viviparity, we regard *Tomeurus* as descended from an ancient and primitive stock of poeciliids, we may also assume that the gonopodium evolved in the Poeciliidae before viviparity was well established or even existent. By analogy, the Indian cyprinodontiform *Horaichthys setnai* certainly has evolved an elaborate gonopodium without losing its essentially oviparous method of reproduction.

The presence of a gonopodium in an oviparous species, of course, insures fertilization of the egg by restricting the process to the narrow confines of the gonaduct in the female. But such a mechanism is not necessarily more efficient than external fertilization of the egg, provided that specific mating behavior patterns and the environment are combined to favor this more usual method. For small fishes living under fluviatile conditions or in tidal embayments, however, the development of a specific structure to localize the flow of sperms to the egg would have adaptive value. If, for example, one such solution to the problem of fluviatile fishes was the ability to create a transitory concavity in the anal fin as it is brought forward and to one side, as do some species of *Aphyosemion* (Kosswig, 1948), and if the next step were the ability to raise the fin to a point under the genital pore of the female, it would be but another few short steps to the eventual evolution of a generalized type of gonopodium. Rosen and Gordon (1953) have detailed some possible intermediate conditions that could have led to the poeciliid genitalium.

The development of a complex external male genitalium in the Poeciliidae is paralleled by anal-fin modifications in the two New World cyprinodontiform genera *Jenynsia* and *Anableps* and by those in the Old World genus *Horaichthys*. Viviparity, which is only moderately developed in many poeciliids, is very elaborate in jenynsiids and anablepids, and in the goodeids of the Mexican plateau. Facultative viviparity, such as that found in the poeciliid genus *Tomeurus*, is approached by conditions in *Horaichthys* and *Oryzias* (Amemiya and Murayama, 1931; Rosen and Gordon, 1953; Yamamoto, 1961). All other groups of cyprinodontiforms, so far as known, are oviparous. Hence, an analysis of poeciliid relationships in the order would seem to hinge largely on the question of to which of the actually or potentially viviparous groups they are structurally closest. On general osteological grounds, however, poeciliids appear to be as closely allied to some oviparous cyprinodontiforms as to the viviparous ones. Obviously many transitional forms in the evolution of the viviparous genera are now extinct, and all the New World groups are now separated by rather abrupt gaps.

The anal-fin suspensory mechanism of poeciliids is more highly specialized than that of any other cyprinodontiform group, consisting as it does of elaborately modified elements of both axial and appendicular structures. The axial division of the system contributes the ligastyle (for the primary suspensory ligament) and two or three ornate gonapophyses (modified hemal spines). The appendicular system is unusually specialized and is divided into two parts, the anterior one developed from the consolidated actinosts 2, 3, and 4 (primary gonactinosts) which articulate with principal anal-fin rays 3, 4, and 5 that form the gonopodium proper.

In *Anableps*, the hemal spines are modified chiefly by distortion and some reduction, and five elements rather than three or four are involved. Actinosts 2 and 3 are incorporated into a simple anterior gonactinostal complex, and the gonopodium proper is developed from rays 2 to 9 [this enumeration differs somewhat from Turner's (1950), because he did not include the first small actinostal and lepidotrichial elements].

In *Jenynsia*, the whole system is still further simplified. The hemal spines are slightly bent forward but are essentially normal, and the anterior actinosts are unconsolidated and are little larger than in some oviparous genera. The gonopodium is like that of *Anableps;* in both, the many rays are twisted together to form an enclosure for an extension of the sperm duct. In poeciliids the sperm duct opens directly to the outside at the base of the gonopodium where it discharges

spermatophores into a cup formed by anal rays 6 to 9.

In *Horaichthys* the hemal spines are reduced to accommodate the subjacent actinosts; firm axial support is provided anteriorly by a pair of swollen pleural ribs. Primary actinostal support is developed by the fusion of elements 3 and 4 [called "basiradials" by Kulkarni (1940)], and the gonopodium proper, formed from anal rays 3, 4, and 5, is isolated by a wide gap from a series of more than 20 succeeding unmodified fin rays.

The viviparous goodeids have no gonopodium, although, according to Mohsen (1961a, 1961b), there are internal structures that may serve as such. The first few short anal rays of the male are merely separated by a notch from the larger elements that follow.

Gonadal adaptations for viviparity are equally variable. The simplest of these is exemplified by *Tomeurus* and *Horaichthys* in which a chorionated egg is first fertilized within the follicle or oviduct where it undergoes some or all of its development before being passed to the outside. Such eggs resemble those of oviparous cyprinodontiforms in possessing adhesive filaments. Probably in all poeciliids except *Tomeurus*, the egg is without a hard shell, and fertilization and embryogeny are intrafollicular; follicular rupture or degeneration just precedes parturition.

In some poeciliids and in *Anableps* the inner wall of the follicle becomes highly vascular and develops villi that lie against the yolk sac of the embryo to form what Turner (1939) terms "follicular pseudoplacentae." In the jenynsiids and goodeids, the fertilized egg is discharged from the follicle into the ovarian cavity at an early stage in its development, as in *Tomeurus*. In the goodeid *Ataeniobius*, the embryos remain in the oviduct, being nourished principally by a large yolk supply. The embryos of most goodeids, and of the jenynsiids, have much less yolk available and depend for their later growth on materials taken up via complex absorptive processes. In the goodeids, ribbon-shaped outgrowths, or trophotaeniae, develop from the rectal lip of the embryo. In *Jenynsia*, club-shaped vascular flaps grow out from the ovarian wall and extend into the branchial and mouth cavities of the embryo through an enlarged opercular opening (Turner, 1940c).

On the basis of gonopodial modifications, poeciliids are most like the Indian genus *Horaichthys*, whereas from the standpoint of their ovarian adaptations for viviparity they are closest to *Anableps*. In skull osteology, however, poeciliids do not closely resemble any of the above groups.

Cyprinodontiform fishes can be divided into four groups on the basis of their skull anatomy. By far the largest group consists of forms included by Myers (1931) in the Aplocheilini (=Rivulini) and the Aplocheilichthyini (his subfamily Fundulinae, in part). These fishes (e.g., *Aplocheilus*, *Aphyosemion*, *Rivulus*, *Aplocheilichthys*) are distinguished by the following partial list of characters: basicranium with one basioccipital and two exoccipital condyles; first vertebra with a closed neural arch and three facets for condylar articulation; foramen magnum bordered above by exoccipitals; basibranchials three or four in number; primary postcleithrum present.

A second major group is represented in part by Myers' tribe Fundulini [e.g., *Fundulus* (fig. 3A), *Lucania*] and differs from the above chiefly in having two rather than three or four basibranchials. A third group, represented in part by Myers' subfamily Cyprinodontinae (e.g., *Cyprinodon*, *Aphanius*), also has two basibranchials, but shows the following additional features: basicranium with a single occipital condyle (basioccipital); first vertebra with an open neural arch, the leading edges of the neural spines being joined firmly to the outer surface of the exoccipitals, and with a single articular facet; foramen magnum bordered above by a posterior extension of the supraoccipital between the exoccipitals (fig. 3B).

A fourth group, the Poeciliidae, also with two basibranchials, usually has the foramen magnum formed like that of the Fundulini, and the basioccipital region of the skull and first vertebra formed essentially like that of the Cyprinodontinae (although the neural spines tend to be free and to form an arch in carnivorous species). In addition, poeciliids altogether lack a primary postcleithrum (see p. 31), as do the Oryziatini (fig. 3C), the

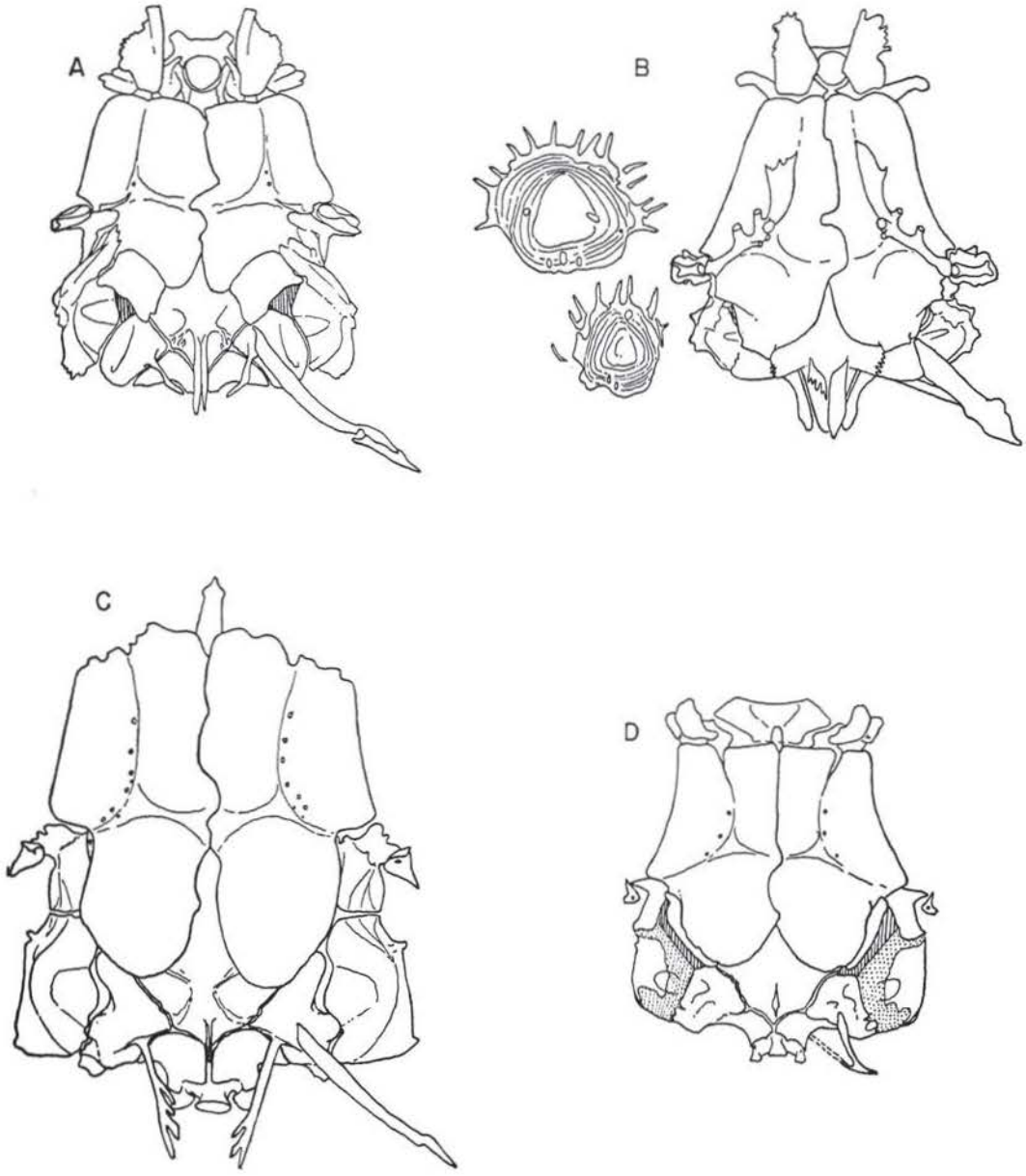


FIG. 3. Dorsicrania and head scales of cyprinodontiforms. A. *Fundulus heteroclitus*, Long Island Sound, New York. B. *Cyprinodon variegatus*, same locality; median head scales with calcified ctenii, and dorsicranium, all from same individual, an adult breeding male. C. *Oryzias latipes*, aquarium specimen. D. *Horaichthys setnai*, Bombay Province, India.

Horaichthyidae (fig. 3D), and apparently some of the Anablepidae (fig. 4A), although members of the last three groups have well-developed exoccipital condyles.

On the basis of this classification, the viviparous jenynsiids (fig. 4B) and goodeids (fig. 4C), and the oviparous Orestiatinae (fig. 4D) from the Peruvian Altiplano, are defined by a mixture of fundulin and cyprinodontine skull characters. The Anablepidae also have the triple basioccipital and first vertebra contact of the fundulins but are

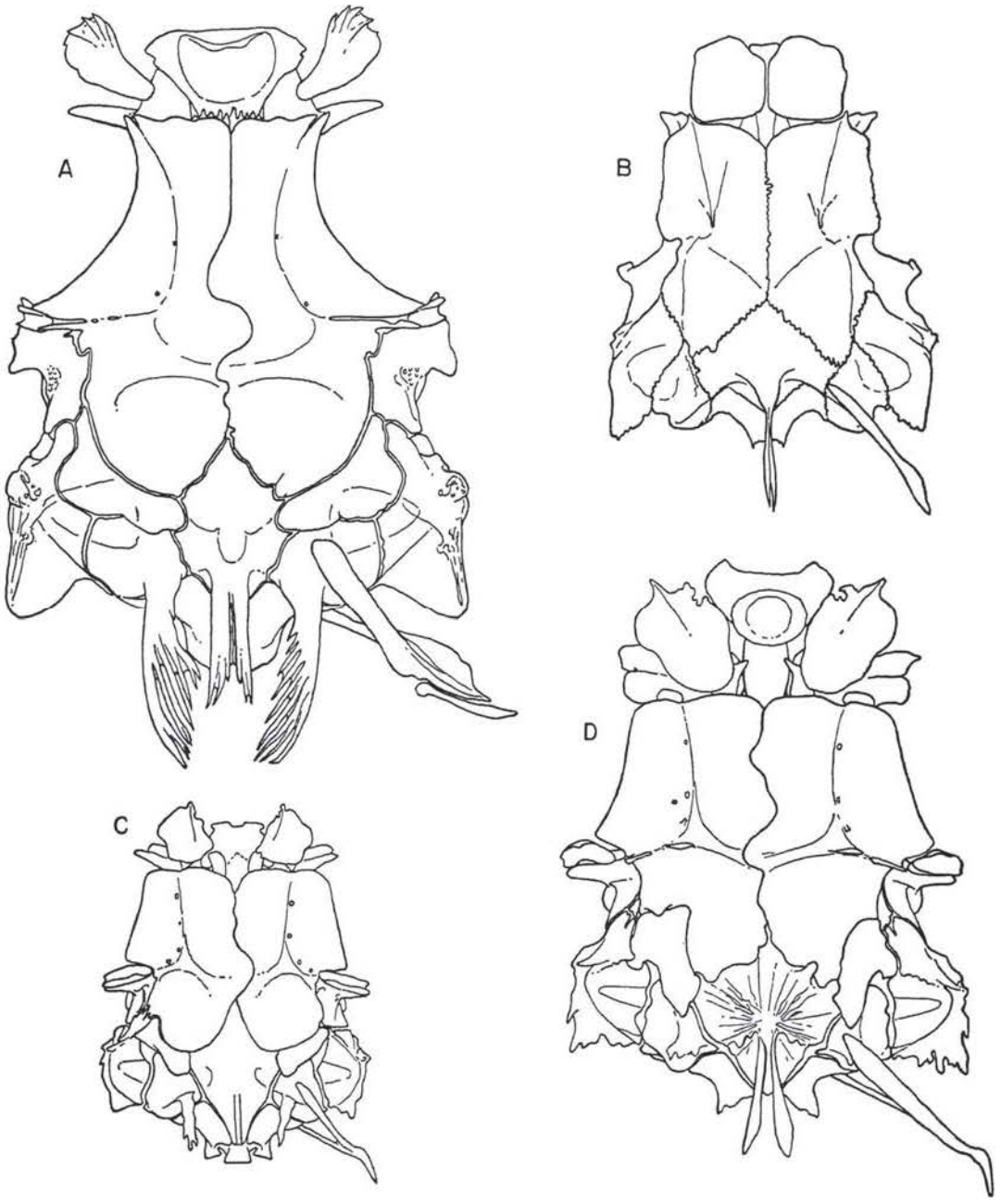


FIG. 4. Dorsicrania of cyprinodontiforms. A. *Anableps dowei*, southern Mexico. B. *Orestias pentlandi*, Lake Titicaca, Peru. C. *Jenynsia maculata*, C.N.H.M. No. 295. D. *Allophorus robustus*, S.U. No. 47627.

uniquely specialized in other respects. Despite the osteological distinctiveness of the Poeciliidae, some members of the probably primitive genus *Brachyrhaphis* are remarkably similar, in general form and the distribution of color patterns, to the Middle American fundulin genus *Profundulus*, and striking similarities in the dorsicranium of

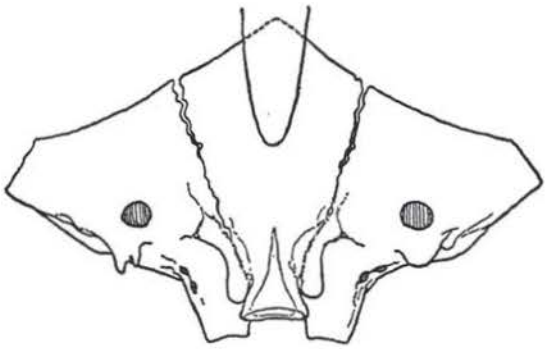


FIG. 5. Basioccipital region of *Tomeurus gracilis*. Note paired teardrop-shaped swellings along base of basioccipital condyle.

Xenodexia and Cyprinodontinae are noted (p. 142).

Which of these sets of correlates has the greatest importance in the determination of relationships and origins of the poeciliid fishes will depend heavily on what eventually is uncovered in the fossil record. Rosen and Gordon (1953) believed that the hemal spines and actinosts in the anal-fin suspensorium of Cope's reputedly cyprinodontiform fossil, *Proballostomus longulus*, from the Ree Hills, South Dakota, are specialized in the direction of the poeciliid suspensorium. However, reëxamination of the type specimen by Dr. Teruya Uyeno and us reveals that this fish is referable to the Cyprinidae.

The possibility exists that the over-all similarities between *Tomeurus* and *Horaichthys* have resulted from common ancestral connections and not from convergence. Although *Tomeurus* lacks the exoccipital condyles found in *Horaichthys*, there is present on the ventral extremity of each of its exoccipitals a distinct internal tubular swelling with a hollow core (fig. 5) that may reasonably be interpreted as the structural base of a condylar head which has been secondarily lost.

A major objection to the inference of a distant alliance between *Tomeurus* and *Horaichthys* was raised by Hubbs (*in* Kulkarni, 1940) who stated that (1) the " . . . long posterior portion of the anal fin of . . . [*Horaichthys*] . . . is represented in *Tomeurus* by a sharp keel formed from the scales," and that (2) this difference " . . . assumes particular significance when we recall that practically all American Cyprinodonts of all families have a short-based and generally few rayed anal fin, whereas the old world types tend to run to long anal fins."

Differences in fin structure between these genera may be related chiefly to differences in the timing of fin-ray formation. The larvae of *Tomeurus* and *Horaichthys*, which are strikingly similar at first, become radically different when the anterior anal rays make their first appearance. In *Tomeurus* these elements grow quickly outward, giving rise to a small prominence that is set off from the remaining fin fold by a shallow notch (fig. 6). In *Horaichthys* anal-fin rays first develop along the length of the fold, and it is only in the late larva that a promontory appears anteriorly (Kulkarni, 1940, p. 419). In *Tomeurus* the anterior anal rays continue to grow, and the notch deepens, but fin rays do not appear in the posterior section of the ventral fold, although the fold itself persists throughout life. Later, this fleshy ridge becomes covered with scales, giving rise to the scaly keel of the post-larva and adult. Although the adults differ significantly in anal-fin structure, the nature of the developmental origin of the differences does not preclude the possibility that the poeciliids evolved from a prototype with a much longer anal fin through an intermediate stage such as that seen in *Horaichthys*.

The significance of the fact that virtually all New World and comparatively few Old World cyprinodontiforms have a short-based and few-rayed anal fin is twofold. On the one hand, it could mean that the fishes thus modified developed separately and convergently in the two hemispheres, and that at least all American forms are related, which would imply derivation of the poeciliids and other specialized groups from more generalized American families. It could also mean that the evolution of the primary groups with short-based anal fins from those with long-based anal fins and their subsequent radiation took place in the Old World and that these then migrated from some central position west to Europe, western Asia, and the Near East (*Aphanius*, *Anatolichthys*, *Tellia*,

Valencia, and others) and east to the Americas where they underwent an explosive secondary radiation.

In conclusion, present evidence for the affinities of the Poeciliidae with other Old World or New World cyprinodontiforms is equivocal. The possibility of their common descent from a group that gave rise to the similarly specialized Old World genus *Horaichthys*, and perhaps also to *Oryzias*, has not been ruled out. Other New World viviparous groups (the Jenynsiidae-Anablepidae, and the Goodeidae) may have evolved independently from the Poeciliidae.

ANALYSIS OF SUPRASPECIFIC GROUPINGS AND CHECK LIST OF SPECIES

FAMILY POECILIIDAE

DEFINITION: Prefrontal in some cases connected by ossified bridge (ossified lateral ethmoids) with prevomer (vomer) ventrally and mesethmoid cartilage dorsally, each lateral ethmoid with anterior articular facet for ethmopalatine process of autopalatine; supraethmoid (ethmoid) bone developed as thin, circular, scale-like plate that is bent down to form a seat for ascending premaxillary processes, in many cases a smaller, ventrally situated disc of bone just above prevomer; two rarely ossified anterior myodomes mesially in region of lamina orbitonasalis; prevomer without teeth. Frontal extensive and with three regions: supraorbital, interorbital, and sphenoidal; nasal bone usually subtriangular in outline and covering part of mesethmoid cartilage, prefrontal, lateral ethmoid, lachrymal, and maxilla; lachrymal mostly lateral to nasal, forming anterior boundary of orbit; dermosphenotic small and rolled up along both edges, situated in notch formed by supraorbital extension of frontal and sphenotic; parietals highly variable in size, position, and form, absent from many; two disc-like sclerotic bones in sclerotic cartilage of each eye. Three paired, prominent otic bullae, each corresponding in size and position with overlying otoliths (see Frost, 1926); intercalar not well defined, if present only imperfectly separated from or fused with exoccipital; sphenotic and pterotic each with distinct, elevated socket for receiving one of two heads of hyomandibular; parasphenoid with lateral process that joins prootic at lateral commissure, and highly variable dorsal arm that (1) joins directly with pterosphenoid (pleurosphenoid or alisphenoid), (2) joins it indirectly with intervention of dorsal arm of prootic that rises out of trigemino-fascialis chamber, or (3) lies free posteriorly in orbital chamber (conditions 1 and 2, only, lead to formation of a definitive posterior myodome); basisphenoid absent. Foramen magnum enclosed by basioccipital and exoccipitals, exoccipitals separated by supraoccipital only in *Xenodexia;* posttemporal bone simple or forked, lower fork frequently unossified or represented by relict ossifications in ligament; basioccipital condylar articulation in many cases reënforced by insertion of free edges of exoccipitals firmly between broad and flaring neurapophyses of first vertebra; exoccipital condyles absent. In upper jaw pterygoquadrate cartilage invested mesially by mesopterygoid (entopterygoid or endopterygoid); mesopterygoid distinct but firmly joined along its leading edge to inner posterior face of autopalatine; ectopterygoid small; metapterygoid absent; symplectic separate and greatly expanded, articulating with mesopterygoid; hyomandibular Y-shaped, with two distinct articular facets dorsally; premaxilla and dentary each with two bands of teeth, outer teeth usually larger, inner ones obsolescent in some cases. In branchial skeleton, pharyngeum superius consisting of three plates of bone that are associated with pharyngobranchials 2, 3, and 4; teeth on superior pharyngeal plates in rows, small, slender, and oar-shaped or spatulate, or larger and recurved conical, or, when mixed, larger teeth arising mesially on bony plates; superior plates constantly united suturally or ankylosed into single element; pharyngeum inferius of variable size, rarely reduced and approximating normal ceratobranchial, with teeth as in superior elements; two ossified

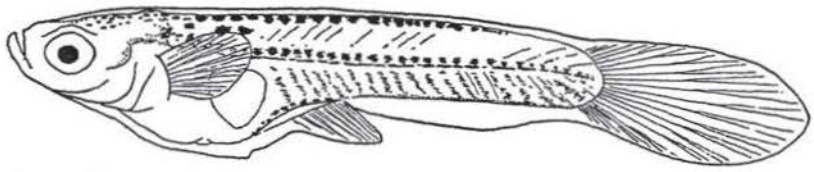


FIG. 6. Twenty-six-day-old larva of *Tomeurus gracilis*, aquarium reared. Scales and pelvic and dorsal fins are undeveloped.

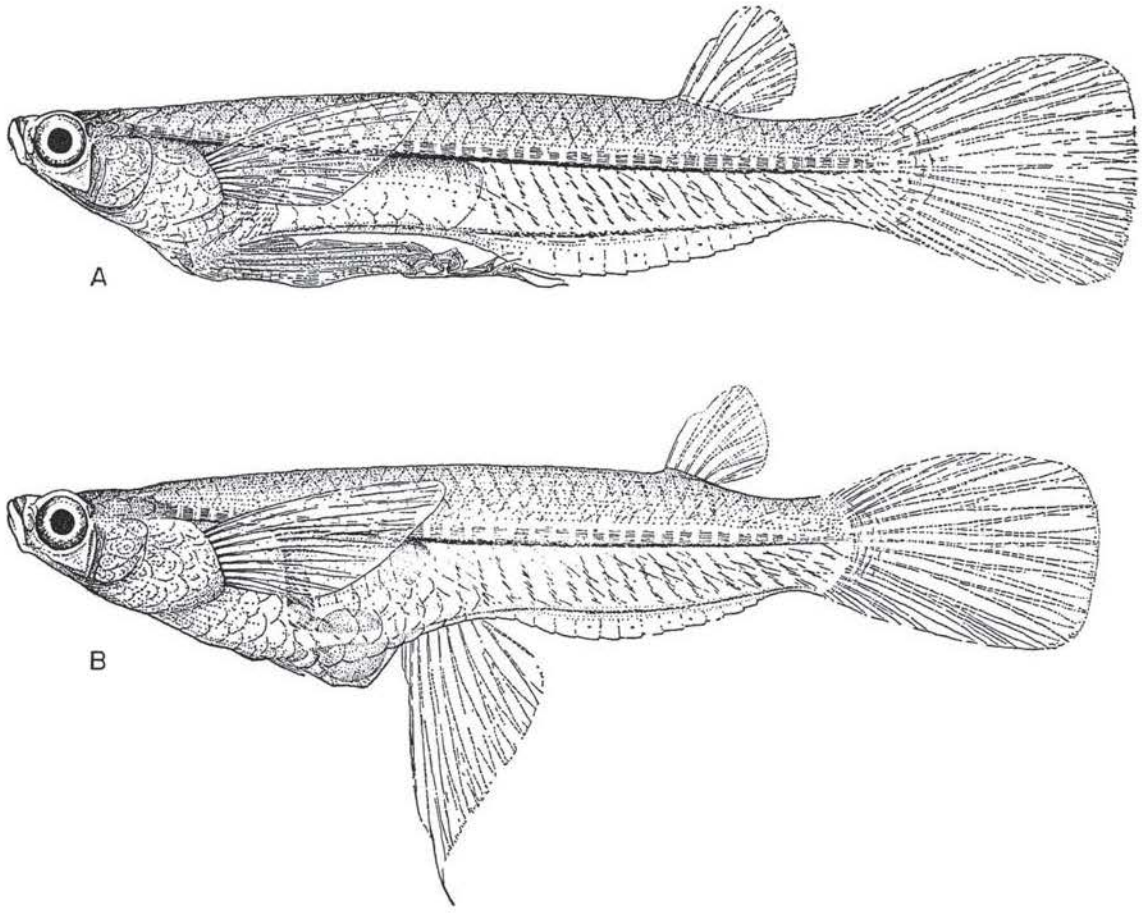


FIG. 7. *Tomeurus gracilis.* A. Male. B. Female. The single large egg can be seen faintly through the body wall of the female.

basibranchials; branchiostegals five or six, typically five; interhyal invariably present, lying just mesial to hyosymplectic juncture.

Primary postcleithrum absent. Single postcleithral bone lying on inner side of scapula and coracoid and having no articulation with cleithrum; interpreted as secondary postcleithrum.

Neurapophyses of first vertebra spread apart, in contact or co-ossified with outer posterior face of exoccipitals, or joined at tips to form neural canal and lacking exoccipital contact.

Axial skeletons of females and males sexually modified. In female, first two or three hemal spines (counting backward) completely or partially histolyzed, remaining anterior one or two bent backward against unmodified elements in series with them. In male, first one to four, rarely five, hemal spines completely or partially histolyzed, first usually remaining as bony relict (ligastyle) lying free in primary suspensory ligament of anal fin, remaining anterior two or three, rarely four, modified hemal spines (gonapophyses) usually greatly enlarged, thickened, inclined forward, and commonly possessing paired posterior outgrowths (uncini) to which connective tissues attach. Actinosts of anal fin of male sexually modified as gonactinosts; actinost 1 modified as thick, club-like, bony stay; actinosts 2, 3, and 4 fused to form bony complex with winged plates posteriorly that flare backward and outward away from midline or turn inward to form tubular column of bone around cen-

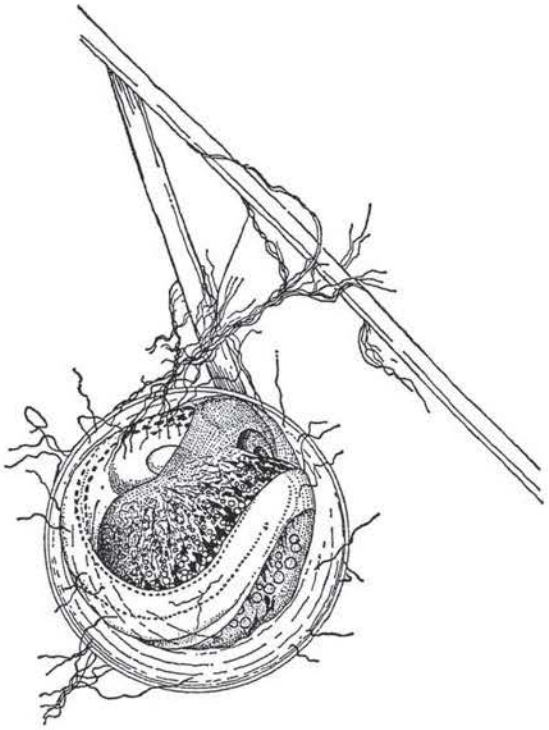


FIG. 8. Egg and advanced larva of *Tomeurus gracilis* shown with its adhesive threads twined about two strands of *Nitella* in an aquarium.

tral complex (gonactinosts 1–4 forming primary gonactinostal complex for gonopodial erector muscles); actinost 5 long and slender, usually nestled within plate-like outgrowths of primary gonactinostal complex; actinosts 6 to 9 long and slender, either converging at tips or spread apart and interdigitating with gonapophyses (modified hemal spines); actinosts 10 and 11, if present, small or obsolescent, in many cases fused into single element, or, if separate, grouped together and lying against base of actinost 9 (gonactinosts 5–9 and, when present, 10 and 11 forming secondary gonactinostal complex for gonopodial depressor muscles); mesonosts in male much enlarged and fused with bases of modified actinosts (gonactinosts), with variety of lateral processes that are effective in controlling muscle action (lateral processes)

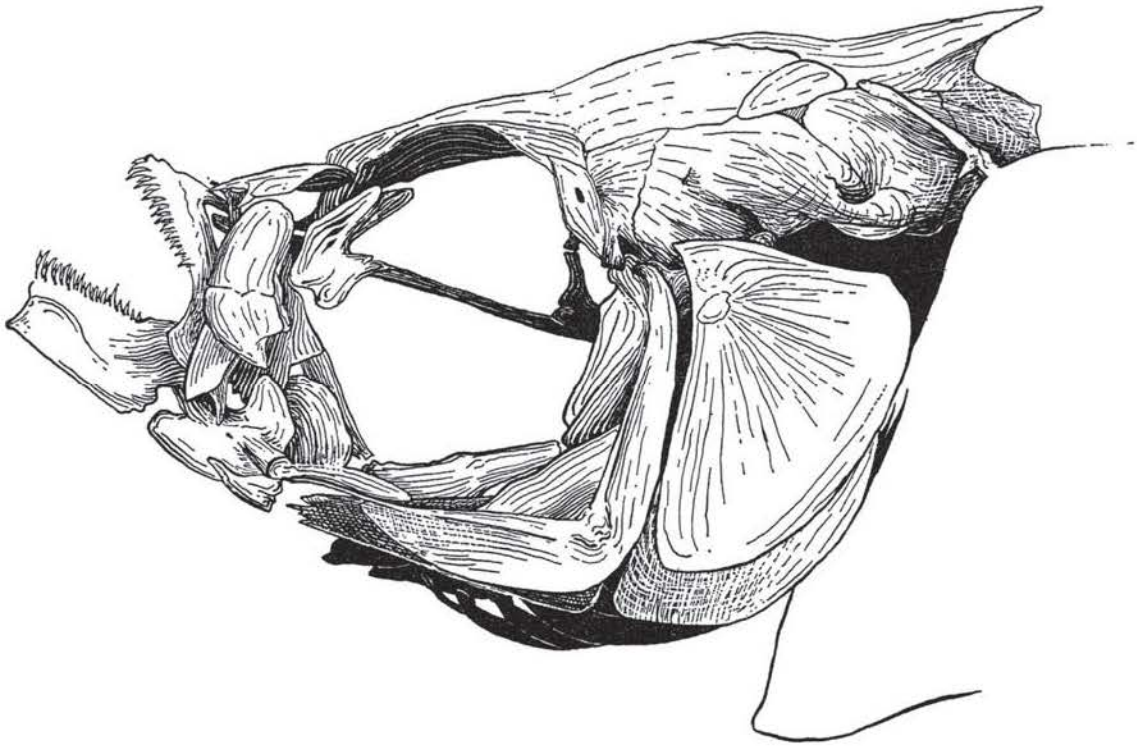


FIG. 9. Syncranium of *Tomeurus gracilis*, lateral view. Outline of pectoral girdle at right.

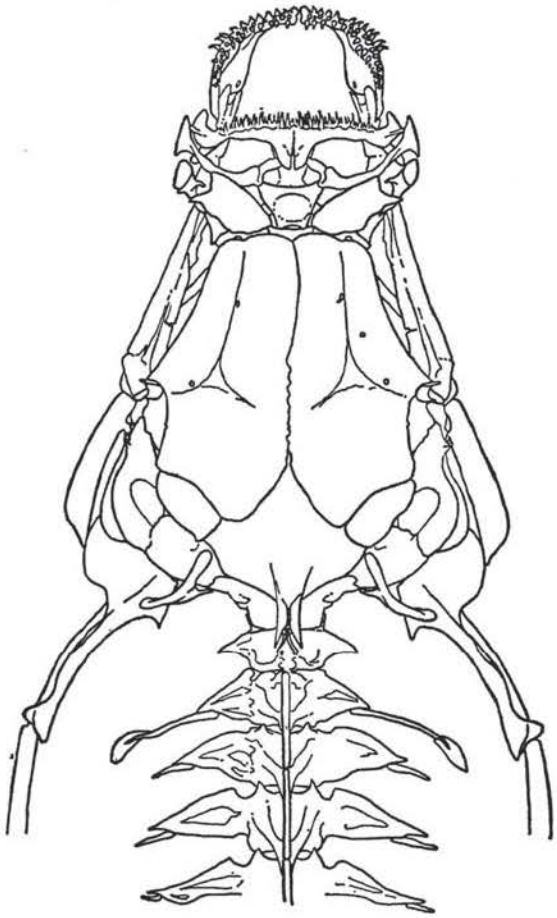


FIG. 10. Syncranium and anterior vertebrae of *Tomeurus gracilis*, dorsal view.

and in bracing baseosts (ventral processes), and forming deep sockets for receiving much-enlarged and strengthened lepidotrichial baseosts; anal-fin rays modified to serve as external genitalium (gonopodium); rays 1 and 2 small and slender, lying close against base of ray 3; rays 3, 4, and 5, much enlarged and strengthened, arranged symmetrically in one plane, or rays 3 and 5 permanently folded to one side, forming partially closed tube, or, rarely, all three rays folded and twisted to produce helical structure; gonopodium usually with series of spines, hooks, and serrae on or near tips of one or more rays and, in some cases, fleshy subradial processes that project downward and forward from free edge of ray 3; rays 5, 6, 7, 8, and 9 (10 and 11 when present) variously modified but invariably grouped together in cluster and joined by elastic interradial membrane to form cup below genital opening when gonopodium is swung forward and out to one side. First few pectoral-fin rays in some cases sexually modified in male. Pelvic fins well developed and sexually modified in male, or small and obsolescent; in males, first few pelvic rays in many cases sexually modified,

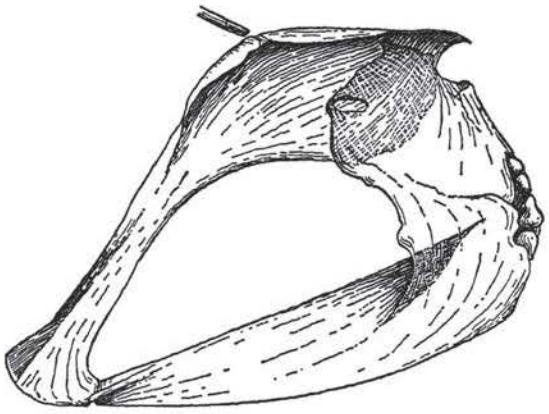


FIG. 12. Right pectoral girdle of *Tomeurus gracilis*, medial view.

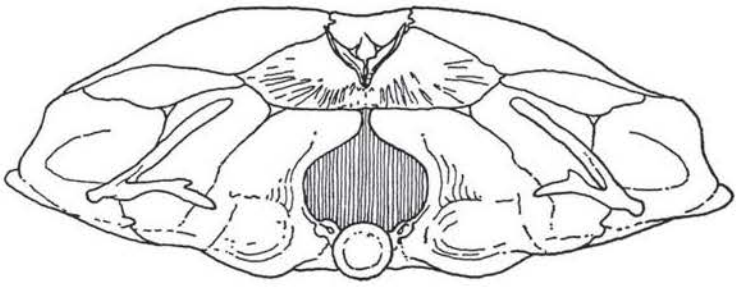


FIG. 11. Neurocranium and posttemporal bones of *Tomeurus gracilis*, posterior view.

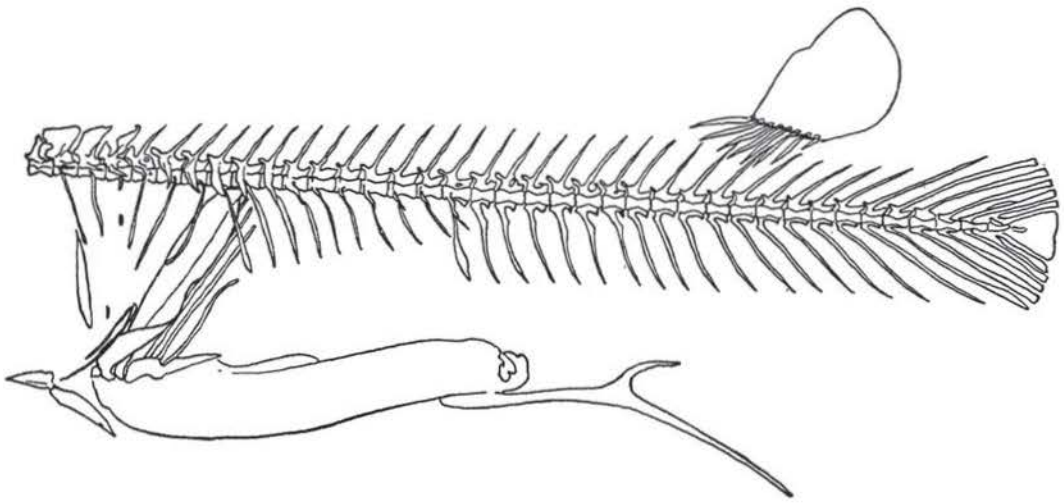


FIG. 13. Axial skeleton, dorsal, anal, and pelvic fins of adult male of *Tomeurus gracilis*.

with fleshy swellings or terminal hyaline prolongations.

Ventral musculature in male reoriented to accommodate sexually modified anal fin (gonopodium) (Rosen and Gordon, 1953, pp. 13–17): actinost 1 with small erector, erector analis minor; actinosts 2, 3, and 4 (gonactinostal complex) with large composite muscle, erector analis major; actinosts 5 to 9 each with smaller depressor analis muscles; a retractor analis inserting laterally on fascia of erector and depressor series that acts to modify orientation of erectors for greater leverage during fin movement; a retractor

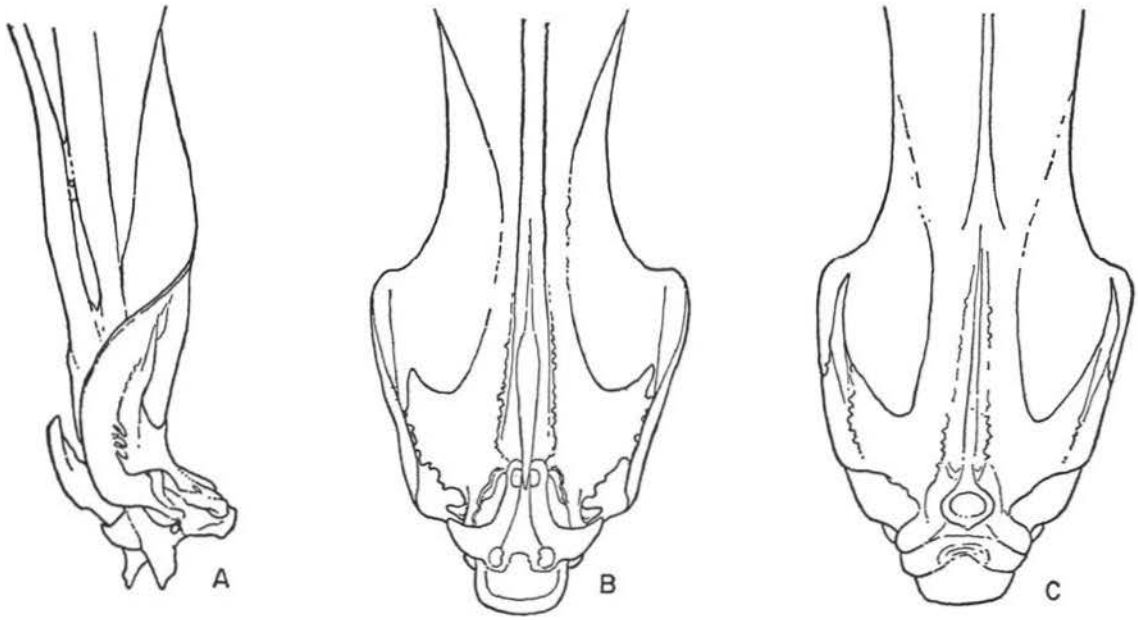


FIG. 14. Basal part of primary gonactinostal complex of adult male *Tomeurus gracilis*. A. Lateral view, anterior to left; the small gonactinost 1 can be seen to left of main complex formed from ankylosed actinosts 2, 3, and 4 (2–3–4 complex). B. Anterior view of 2–3–4 complex. C. Posterior view of same. A free fifth element, not shown, fits snugly against posterior surface of 2–3–4 complex as in other poeciliids.

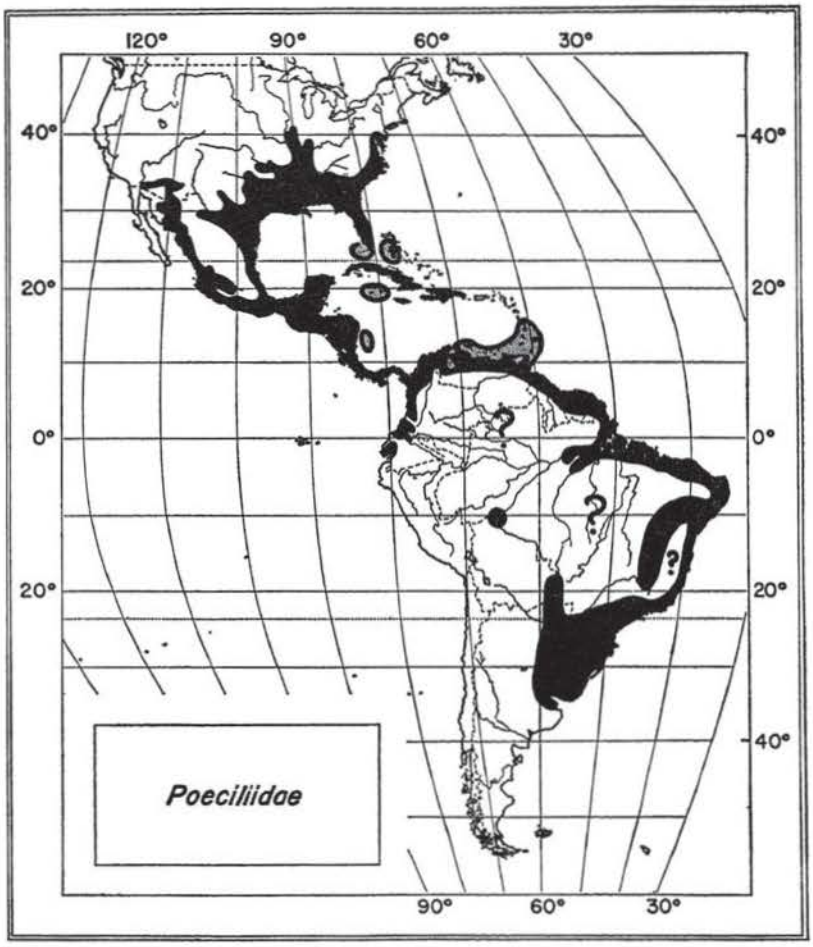
ischii serving principally as a protractor analis that, when acting unilaterally, facilitates lateral rotation of gonopodium; a series of inclinator analis muscles converging on bases of gonopodial rays that supplement action of protractor analis but act largely in role of tensors to steady fin and maintain maximum fin erection.

Paired ovaries fused into single, median, sac-like structure; embryos usually developing intrafollicularly and lining central excavation that leads directly to oviduct, or embryos developing within follicle for a variable time and then, following follicular rupture, being passed down oviduct to outside where their development is completed; egg typically without chorion, rarely with a dense chorion having numerous adhesive filaments. Paired testes fused into single, median, tubular structure; sperms massed together into tiny oval, unencapsulated spermatophores, their heads embedded in outer gelatinous matrix and their tails extending into lumen of spheroid; sperm duct leading into chamber of variable complexity, thence opening to outside near anal-fin origin.

REMARKS: The Poeciliidae are New World fishes that center in Middle America, both on the mainland and in the Antilles, with lesser representation north to central United States and south to northern Argentina (map 1). In this review the family is classified in three subfamilies, two of which are monotypic, five tribes, 21 genera, and 138 species.

SUBFAMILY **TOMEURINAE** EIGENMANN

DIAGNOSIS: Egg with tough, membranous covering that is continuous with ooplasm and



MAP 1. Distribution of the Poeciliidae.

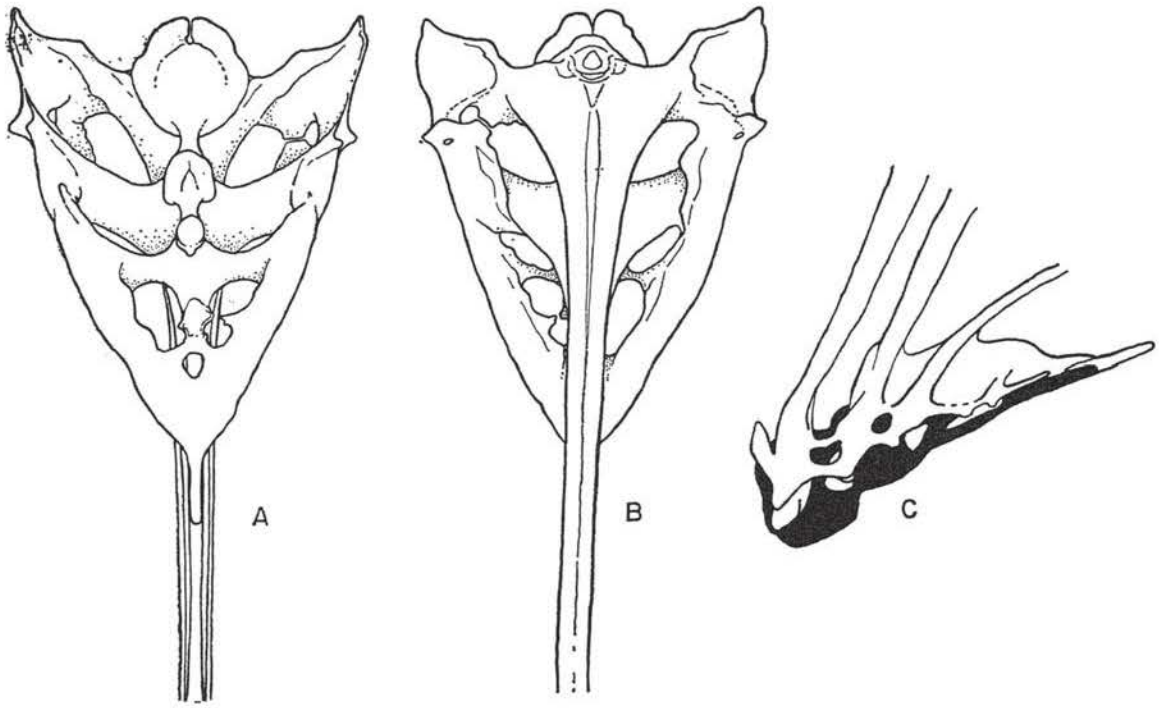


FIG. 15. Basal part of secondary gonactinostal complex of *Tomeurus gracilis*. A. Ventral view. B Dorsal view. C. Diagrammatic mid-sagittal section through complex, anterior to left; lateral structures of right side in solid black.

has numerous adhesive filaments. Dorsal aspect of head with row of median, unpaired scales between supraorbital and postorbital sections of cephalic canal system. Pelvic fin with four or fewer rays. Frontal bones without subrectangular posterior processes, having no contact with epiotics. Nasal bones not meeting at midline, in only a few cases reaching lateral margins of median ethmoid plate, and loosely joined posteriorly to lateral ethmoids via fibrous connective tissues or narrow columns of cartilage. Supraoccipital bone not approaching foramen magnum. Mesonosts of gonactinosts 6 to 9 in gonopodial suspensorium co-ossified. Actinost 1 of gonopodial suspensorium rather small and slender, not more than two-thirds as tall as primary gonactinostal complex, and lacking bony collar at distal tip. Vertebrae 38 or 39. Distal tips of sexually modified pleural ribs of male interrupted to form disjunct ossifications. No epipleural ribs. No unilateral pectoral clasper.

REMARKS: This subfamily is represented by a single genus and species, *Tomeurus gracilis* Eigenmann. Nikol'skii (1954 [1961]) proposed that the nominal family Tomeuridae and the Indian family Horaichthyidae be grouped as a superfamily Tomeuroidea. Similarities between the members of these monotypic families were attributed by Hubbs (*in* Kulkarni, 1940) to convergence. Kulkarni (1948) believed that in osteological characters *Horaichthys* most closely approaches the fishes of the cyprinodontid genus *Oryzias*.

GENUS TOMEURUS EIGENMANN

Text figures 5–16

Tomeurus.—EIGENMANN, 1909, p. 53 (type species, by monotypy, *Tomeurus gracilis* Eigenmann).

DIAGNOSIS: In addition to features presented in the subfamily diagnosis, others in the gonopodium and its suspensorium can be considered.

In gonopodium a broad ridge on ventrolateral margin of ray 3 and much-elevated

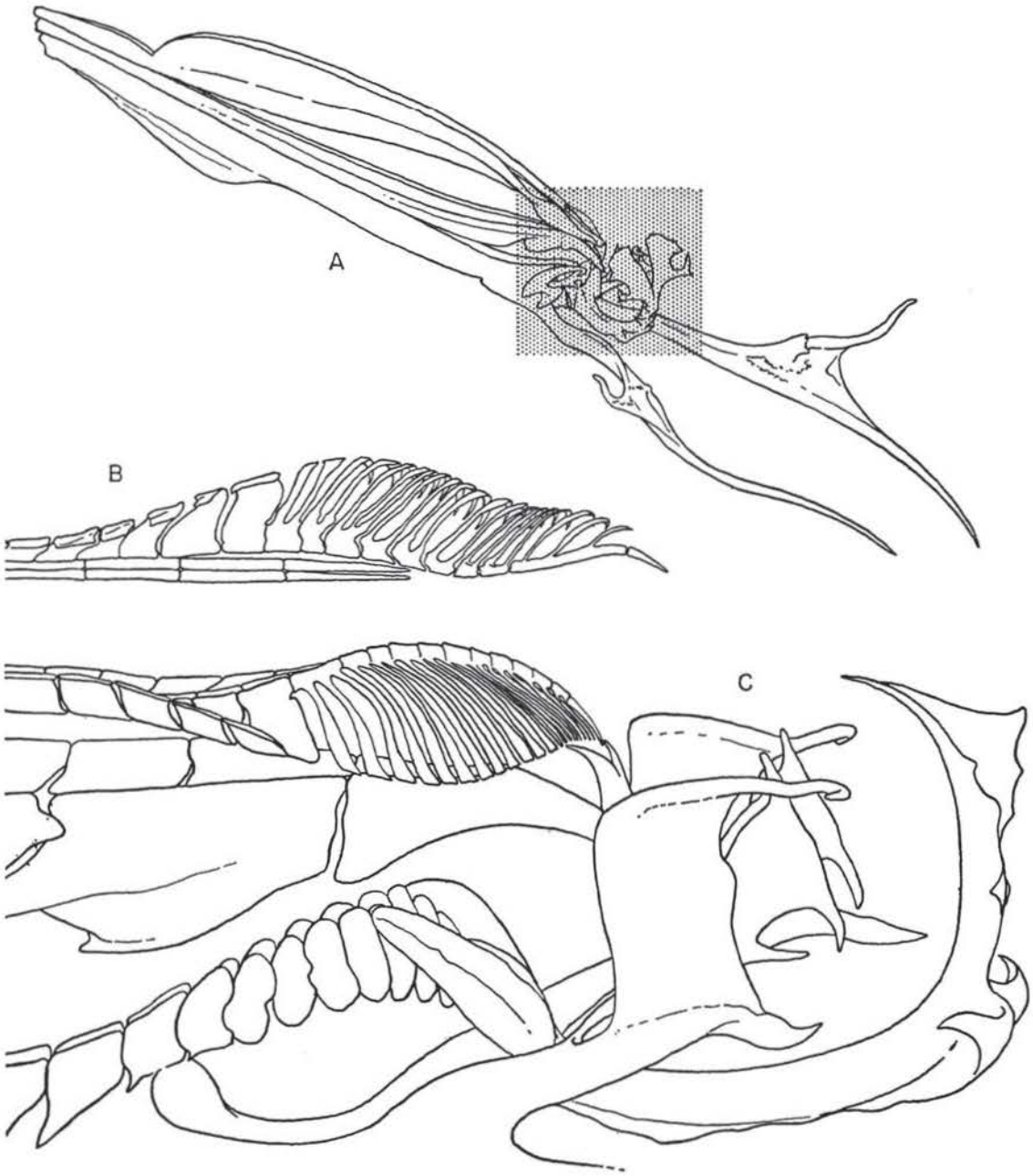


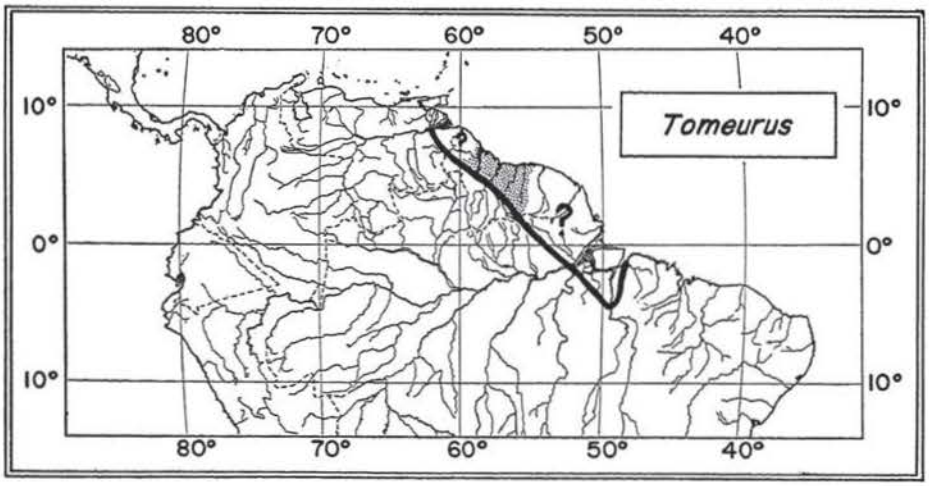
FIG. 16. Gonopodium of *Tomeurus gracilis*. A. Diagrammatic drawing of main part of gonopodium, segments omitted; shaded area enlarged in B and C. B. Dorsal view of right half of tip of posterior branch, and right and left halves of tip of anterior branch, of fifth ray. C. Tip of gonopodium as indicated by shading in A.

segments of ray 5p, suggesting that fin can be folded into transitory gonopodial trough for transmission of spermatophores. Basal rays (6 to 9) modified to form distensible sac or receptacle when fin is swung forward. Notable reduction of segmentation in central part of fin. Terminally on ray 5p, inflorescence of slender, delicately curved slivers of bone arranged symmetrically around pair of bony styles, whole structure having appearance of drooping palm leaf. Columnar elements of ray 4p resting on broad, flat, laterally expanded segments of 4a. Elbow-like structure situated ventrally on ray 4a resembling comparable elements in gonopodia of *Gambusia* and *Neoheterandria*. Ray 4 terminating in claw that overlaps tip of third ray. Ray 3 completely segmented except in region of eccentric ventrolateral groove near its basal third. Distally segments modified as spines that project downward and forward in manner of reduced spines of *Gambusia affinis*. At tip of ray 3, a plate-like bone from which arises a long, tubular, crescentic arm with concave face up in resting fin. From distal end of this arm triangular plates diverging; each scalloped dorsally and serrate laterally. Originating in region of spines of ray 3 are a pair of gristly, antler-like processes that extend beyond tip of fin by half of length of bony genitalium, joining ray 3 on broad peduncle at level of spines.

In most poeciliids the internal bony support of the gonopodium is accomplished with the supporting role of specialized portions of the anteriormost hemal spines; in *Tomeurus* gonapophyses are absent and gonactinosts 2, 3, and 4 have a broad ligamentous attachment (without ligastyle) to the vertebral axis. In *Cnesterodon*, in which gonapophyses are similarly lacking, a well-developed ligastyle is interposed between gonactinosts and vertebrae. In some species of *Poecilia* a ligastyle is absent, but gonapophyses are well developed in every case.

REMARKS: *Tomeurus* has many apparently fundamental similarities to other poeciliid fishes. Attention is called to the inferred relationship by joining them together in a single family. Hence, the monotypic family Tomeuridae is rejected and *Tomeurus gracilis* Eigenmann is returned to Eigenmann's (1912) original position as the subfamily Tomeurinae within the Poeciliidae. For accounts of the characteristics and taxonomic status of *Tomeurus*, see Eigenmann (1909, 1912), Regan (1913b), C. L. Hubbs (1926; *in* Kulkarni, 1940; 1941), Myers (1947), Kulkarni (1948), Rosen (1952), Rosen and Gordon (1953), Nikol'skii (1954 [1961]), Gordon (1955), Rosen and Kallman (1959), Rosen and Tucker (1961), and Mohsen (1962).

RANGE AND SPECIES COMPOSITION: The single species occurs in northeastern South America (map 2).



MAP 2. Distribution of *Tomeurus*.

Tomeurus gracilis Eigenmann

Tomeurus gracilis.—EIGENMANN, 1909, p. 53 (original description; Mud Creek in Aruka and Wismar, British Guiana; holotype, C.N.H.M. No. 53541).

MATERIAL: Region surrounding Georgetown, British Guiana; U.M.M.Z. Nos. 167944, 177382, 177383.

RANGE: Eastern Venezuela, British Guiana, and Surinam, to the Río Tocantins, Pará, Brazil (see R. von Ihering, 1931; Myers, 1947; Boeseman, 1952).

SUBFAMILY **POECILIINAE** GARMAN

DIAGNOSIS: Egg without tough, membranous covering or adhesive filaments. Dorsal aspect of head with alternating paired and unpaired scales between supraorbital and postorbital sections of cephalic canal system. Pelvic fin with more than four rays. Frontal bones without subrectangular posterior processes, covering only small anterior parts of epiotic bones or having no contact with them. Nasal bones not meeting at midline, in only a few cases reaching lateral margins of median ethmoid plate, and loosely joined posteriorly to lateral ethmoids via fibrous connective tissues or narrow columns of cartilage. Supraoccipital bone not approaching foramen magnum. Mesonosts of gonactinosts 6 to 9 in gonopodial suspensorium firmly joined together by anterior and posterior articular processes but not co-ossified. Actinost 1 of gonopodial suspensorium rather small and slender, not more than two-thirds as tall as primary gonactinostal complex, and lacking bony collar at its distal tip. Vertebrae 26 to 35. Distal tips of sexually modified pleural ribs of male not interrupted. Epipleural ribs present. No unilateral pectoral clasper.

REMARKS: The 19 genera herein admitted to the Poeciliinae can be grouped into five tribes. We start the sequence with the wide-ranging Poeciliini in which the gonopodial suspensorium is only moderately specialized and the gonopodium is relatively short. In the South American Cnesterodontini the gonopodium is shifted far forward, with necessary suspensorial modification, and the gonopodium is elongate. The three remaining tribes are more closely interrelated. All are largely Middle American and all have well-developed uncini on the gonapophyses. The least specialized are the carnivorous Gambusiini, with the gut short and the gonopodium short or moderate. The Girardinini have the gut long and coiled, and the gonopodium long and complexly modified. The Heterandriini have comparable modifications, although the gonopodial tip is usually simpler, and they are unified by common suspensorial specializations. Table 3 summarizes the more important distinguishing structural features in the subfamily.

TRIBE **POECILIINI**

All members of this tribe have comparatively short gonopodia and well-developed pelvic fins. In the suspensorium the gonapophyses lack uncini and are mostly rather simple, although large suspensorial parapophyses are present in many cases. Other similarities follow.

Poecilia and *Alfaro* possess the same type of gonopodial palp, and *Xiphophorus* (but not *Priapella*) has the comparable subradial gonopodial tissues slightly swollen. Histologically these structures in *Poecilia* and *Xiphophorus* are strikingly similar in appearance (see Rosen and Gordon, 1953). The pelvic fins are well developed in all, and those of *Xiphophorus* and *Poecilia* possess definite fleshy promontories. The pelvic fins in *Xiphophorus* and *Poecilia* have similar, if not, in some instances, identical, functions during courtship and copulation (see Clark and Kamrin, 1951, and Rosen and Tucker, 1961). The gonopodium of *Xiphophorus* could be converted into that of *Priapella* by simple reduction of the tips of rays 4p and 5a. The existing similarities appear far to outweigh the differences.

The entire suspensorial mechanism is similar in *Xiphophorus* and *Priapella*. The suspensorial gonapophyses of *Alfaro* resemble those of *Priapella* and *Xiphophorus* in being little modified and nearly vertical. There are two, rarely three, gonapophyses in *Poecilia*. In *Alfaro* there may be two, three, or four, all scarcely modified, the last gonapophysis in some cases not specialized for anal-fin support.

Adult males of *Poecilia* and *Xiphophorus* may develop brilliantly colored fin ornaments and typically show a high degree of polymorphism in color pattern.

The parietal bones are typically present,

TABLE 3

SUMMARY OF STRUCTURAL CHARACTERS FOR IDENTIFICATION OF THE GENERA OF THE POECILIINAE

	Poeciliini	*Alfaro*	*Poecilia*	*Priapella*	*Xiphophorus*	Cnesterodontini	*Phallotorynus*	*Phalloceros*	*Phalloptychus*	*Cnesterodon*	Gambusiini	*Brachyrhaphis*	*Gambusia*	*Belonesox*	Girardinini	*Girardinus*	*Quintana*	*Carlhubbsia*	Heterandriini	*Priapichthys*	*Neoheterandria*	*Heterandria*	*Poeciliopsis*	*Phallichthys*
GONOPODIUM																								
Gonopodial length																								
Less than ⅓ standard length		x[a]	x	x	x		—	—	—	—		o	o	x		—	—	—		—	—	—	—	—
More than ⅓ standard length		—	—	—	—		x	x	x	x		o	o	—		x	x	x		x	x	x	x	x
Subdistal segment ankylosis																								
Ray 3		—	—	—	—		x	—	—	—		—	—	—		o	—	—		—	—	—	o	—
Ray 4		—	—	—	—		—	—	x	x		—	—	—		o	—	—		—	—	—	—	—
Ray 5		—	—	—	—		—	—	—	—		—	—	—		o	—	—		—	—	—	—	—
Unisegmented or multisegmented subdistal swelling																								
Ray 3		—	—	—	—		x	—	—	—		—	—	—		—	—	—		—	—	—	—	—
Ray 4a		—	—	—	—		—	—	—	—		o	x	x		—	x	x		—	x[b]	—	—	—
Ray 5		—	—	—	—		—	—	—	—		—	—	—		o	x	—		—	—	—	—	—
Claws																								
Ray 4		—	—	—	—		—	—	—	—		—	x	x		—	—	—		—	—	—	—	—
Ray 5		—	o	—	o		—	—	—	x		—	x	x		—	—	—		—	—	—	—	—
Recurved hook																								
Ray 3		—	—	x	x		—	—	—	—		—	—	—		—	—	—		—	—	—	—	—
Ray 4		—	—	—	—		—	—	—	—		—	—	—		—	—	—		—	x	x	—	—
Serrae, ray 5		—	—	—	—		—	—	—	—		—	—	—		x	x	x		—	—	—	—	—
Processes on ray 3																								
Palp		x	o	—	—		—	—	—	—		—	—	—		—	—	—		—	—	—	—	—
Paired membranous cirri		—	—	—	—		—	—	—	—		—	—	—		x	—	—		—	—	—	—	—
Paired bony cirri		—	—	—	—		x	x	—	x		—	—	—		—	—	—		—	—	—	—	—
Simple cirrus		—	—	—	—		—	—	—	—		—	—	—		—	—	—		—	o	—	—	—
Bilaterally symmetrical		x	x	x	x		x	x	—	x		x	x	x		x	—	—		x	o	x	—	—
Sinistrally asymmetrical		—	—	—	—		—	—	x	—		—	—	—		—	x[c]	—		—	o	—	x	o
Dextrally asymmetrical		—	—	—	—		—	—	—	—		—	—	—		—	—	x		—	o	—	—	o
GONOPODIAL SUSPENSORIUM																								
Number of gonapophyses																								
None		—	—	—	—		—	—	—	x		—	—	—		—	—	—		—	—	—	—	—
Two		o	o	—	—								o											
Three or more		o	o	x	x		x	x	x	—		x	o	x		x	x	x		x	x	x	x	x
Ligastyle																								
Minute or absent		x	x	—	—		—	—	—	o		—	o	—		—	—	—		—	—	—	—	—
Moderately or well developed		—	—	x	x		x	x	x	o		x	o	x		x	x	x		x	x	x	x	x

TABLE 3—(*Continued*)

	Poeciliini	*Alfaro*	*Poecilia*	*Priapella*	*Xiphophorus*	Cnesterodontini	*Phallotorynus*	*Phalloceros*	*Phalloptychus*	*Cnesterodon*	Gambusiini	*Brachyrhaphis*	*Gambusia*	*Belonesox*	Girardinini	*Girardinus*	*Quintana*	*Carlhubbsia*	Heterandriini	*Priapichthys*	*Neoheterandria*	*Heterandria*	*Poeciliopsis*	*Phallichthys*
Paired processes																								
Parapophyses (i.e., originating on vertebrae)		x	x	x	x		x	x	x	—		—	—	—		—	—	—		—	—	—	—	—
Uncini (i.e., originating on gonapophyses)		—	—	—	—		—	—	—	—		x	x	x		x	x	x		x	x	x	x	x
Gonactinosts 2, 3, 4																								
Columnar		—	—	—	—		—	—	—	—		—	x	x		—	—	—		—	—	—	—	—
Plate-like anteriorly		x	x	x	x		x	x	x	x		x	—	—		x	x	x		x	x	x	x	x
Gonactinosts 8–10 with paired wing-like plates		—	—	—	—		—	—	—	—		—	—	—		—	—	—		x	o	—	o	—
RIBS																								
Pleural ribs (adult male)																								
Abruptly curved forward and produced		—	—	—	—		x	x	x	x		—	—	—		o	—	—		o	x	—	o	—
Expanded		—	—	—	—		—	—	—	—		—	—	—		—	—	—		—	x	—	—	—
PAIRED FINS AND SUSPENSORIUM																								
Posttemporal																								
Simple		—	—	—	—		x	x	x	x		—	—	—		—	o	o		—	—	x	—	—
Bifid		x	x	x	x		—	—	—	—		x	x	x		x	o	o		x	x	—	x	x
Modified paired fins of male																								
Tip of pectoral bent upward		—	—	—	—		—	—	—	—		—	x	—		—	—	—		—	—	—	—	—
Tip of pelvic swollen or elongate or both		—	x	—	x		—	—	—	—		—	—	—		—	—	—		—	—	—	—	—
JAW TEETH																								
Marginal																								
Compressed		—	x	—	x		x	x	—	x		—	—	—		x	x	x		o	—	o	o	x
Conical, cylindrical, or club-like		x	—	x	—		—	—	x	—		x	x	x		—	—	—		o	x	o	o	—
Inner larger than marginal teeth		—	—	—	—		—	—	—	—		—	—	x		—	—	—		—	—	—	—	—
SCALES																								
Lateral series more than 45		—	—	—	—		—	—	—	—		—	—	x		—	—	—		—	—	—	—	—

[a] *Symbols:* x, invariable; o, variable.
[b] Poorly developed in *Neoheterandria elegans.*
[c] Only the serrae on 4p are twisted sinistrally in *Quintana.*

although variably developed, and the posttemporal bone is strongly bifid in all. *Alfaro* and *Priapella* possess large jaws and large, recurved, conical teeth, whereas *Poecilia* and *Xiphophorus* possess smaller jaws, with delicate compressed teeth.

Genus **ALFARO** Meek

Text figures 17, 21A, B, 23A, B, 25A

Petalosoma.—Regan, 1908, p. 462 (type species, by monotypy, *Petalosoma cultratum* Regan; preoccupied by *Petalosoma* Lewis, 1903, in Coleoptera).

Alfaro.—Meek, September, 1912, p. 72 (type species, by monotypy, *Alfaro acutiventralis* Meek, a subjective synonym of *Alfaro cultratus*).

Petalurichthys.—Regan, November, 1912, p. 494 (substitute for *Petalosoma*, preoccupied).

Furcipenis.—C. L. Hubbs, 1931, pp. 1–3 (type species, by original designation, *Priapichthys huberi* Fowler).

Diagnosis: In skull, parietals present and well developed, extending along posterolateral borders of frontal and generally quite broad medially; epiotic and supraoccipital processes very well developed; posttemporal forked; marginal jaw teeth recurved, conical. Posterior pleural ribs not sexually dimorphic. Gonopodial suspensorium with 3, rarely 2 or 4, scarcely differentiated gonapophyses that are more or less vertical, in some cases inclined slightly forward or backward, and lacking uncini; all gonapophyses, as well as two or three following, unmodified hemal spines, with large, sinuous parapophyses; ligastyle minute, irregular, and applied closely to dorsal margin of gonactinostal complex; gonactinostal complex slightly notched dorsally, both superior and inferior lateral wings developed, but inferior wings only produced prominently outward from medial bony plate. Gonopodium bilaterally symmetrical; eccentric grooves on ray 3 extremely well developed and supporting membranous genital palp; spines 15 to 20 in number, developed distally on ray 3, larger ones each with horizontal plate extending outward at right angles to long axis of spines, these plates together forming bony ledge that lies directly on top of upper surface of genital palp; subdistally on ray 4p, four or five segments with obsolescent serrae, or serrae wanting. Pelvic fin well developed, first principal ray with terminal prolongation.

Range and Species Composition: Atlantic coastal drainage of Central America from southern Guatemala to western Panama (map 3). Two species.

Alfaro cultratus (Regan)

Text figures 17A, 21A, 23A, 25A

Petalosoma cultratum.—Regan, 1908, p. 462 (original description; Río Iroquois, Costa Rica;

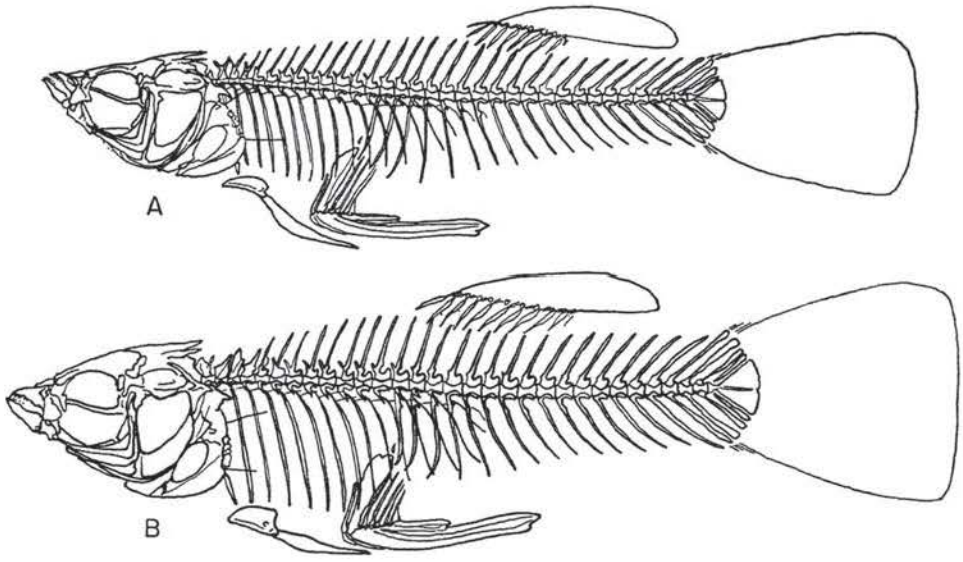
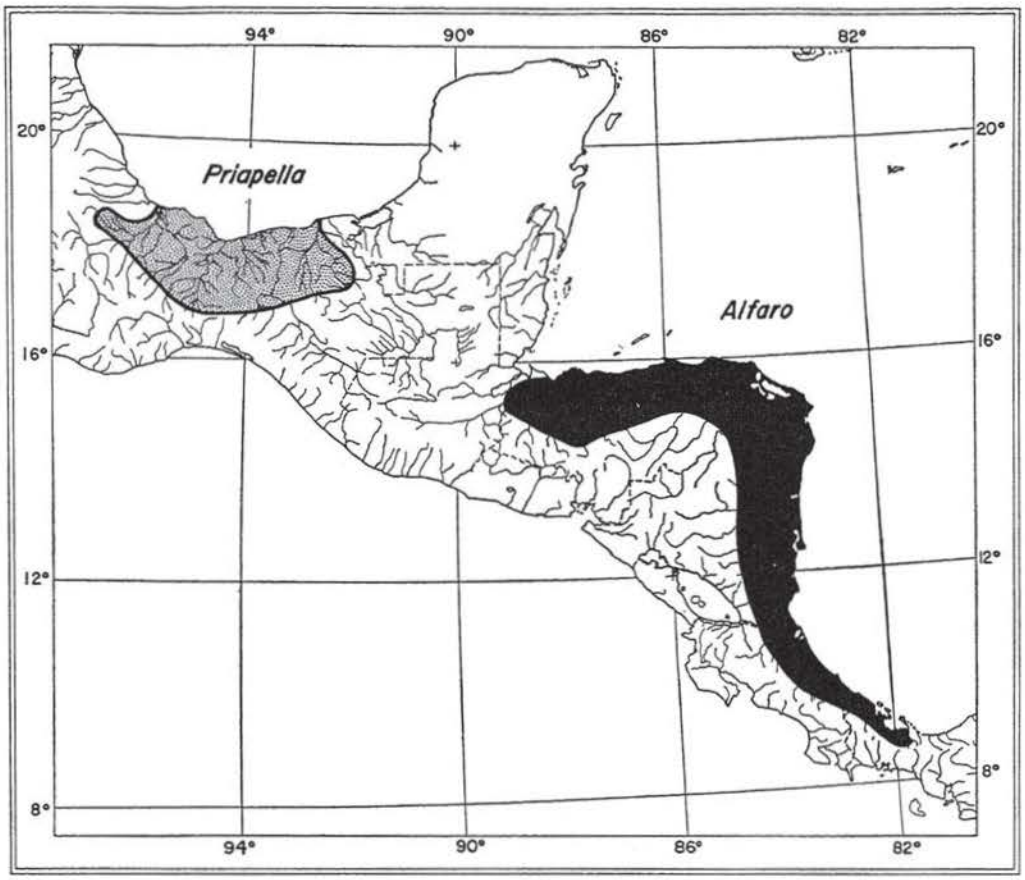


Fig. 17. Skeletons of adult males of *Alfaro*, composite drawings. A. *A. cultratus*. B. *A. huberi*.



MAP 3. Distribution of *Alfaro* and *Priapella*.

holotype, B.M.N.H.). *Petalurichthys cultratus.*—REGAN, 1912, p. 494. *Alfaro cultratus.*—REGAN, 1913b, p. 981.

Alfaro acutiventralis.—MEEK, 1912, p. 72 (original description; Guapilis [Limón], Costa Rica; holotype, C.N.H.M. No. 7679, as corrected by Grey, 1947, pp. 112–113). *Alfaro acutiventris.*—JORDAN, EVERMANN, AND CLARK, 1930, p. 193 (*lapsus* for *acutiventralis*).

Petalosoma amazonum.—REGAN, 1911b, p. 659 (original description; Amazon River at Óbidos, Brazil, presumably erroneous locality; syntypes, B.M.N.H.). *Petalurichthys amazonum.*—REGAN, 1912, p. 494. *Alfaro amazonum.*—REGAN, 1913b, p. 981.

MATERIAL: Siquirres, Costa Rica; U.M.M.Z. No. 159157. La Castilla, Panama, and lower Río Reventazon, Costa Rica; S.U. No. 32202.

RANGE: Atlantic drainage of western Panama and Costa Rica to Río Huahuasán, Zelaya, Nicaragua (specimens in the University of Michigan Museum of Zoology).

Alfaro huberi (Fowler)

Text figures 17B, 21B, 23B

Priapichthys huberi.—FOWLER, 1923, p. 27 (original description; Marceligo Creek, Tunky River, Miranda, Nicaragua; holotype, A.N.S.P. No. 51220). *Furcipenis huberi.*—C. L. HUBBS, 1931, pp. 1–3. *Alfaro huberi.*—ROSEN, 1952, pp. 151–156.

MATERIAL: Río Armenta, north of San Pedro Sula, Cortés, Honduras; U.M.M.Z. No. 173163.

RANGE: Atlantic drainage from southern Guatemala to Nicaragua.

GENUS **POECILIA** BLOCH AND SCHNEIDER

Plate 2, figures 4–6; text figures 18, 19, 21C, D, 22, 23C, D, 25B–F

Poecilia.—BLOCH AND SCHNEIDER, 1801, p. 452

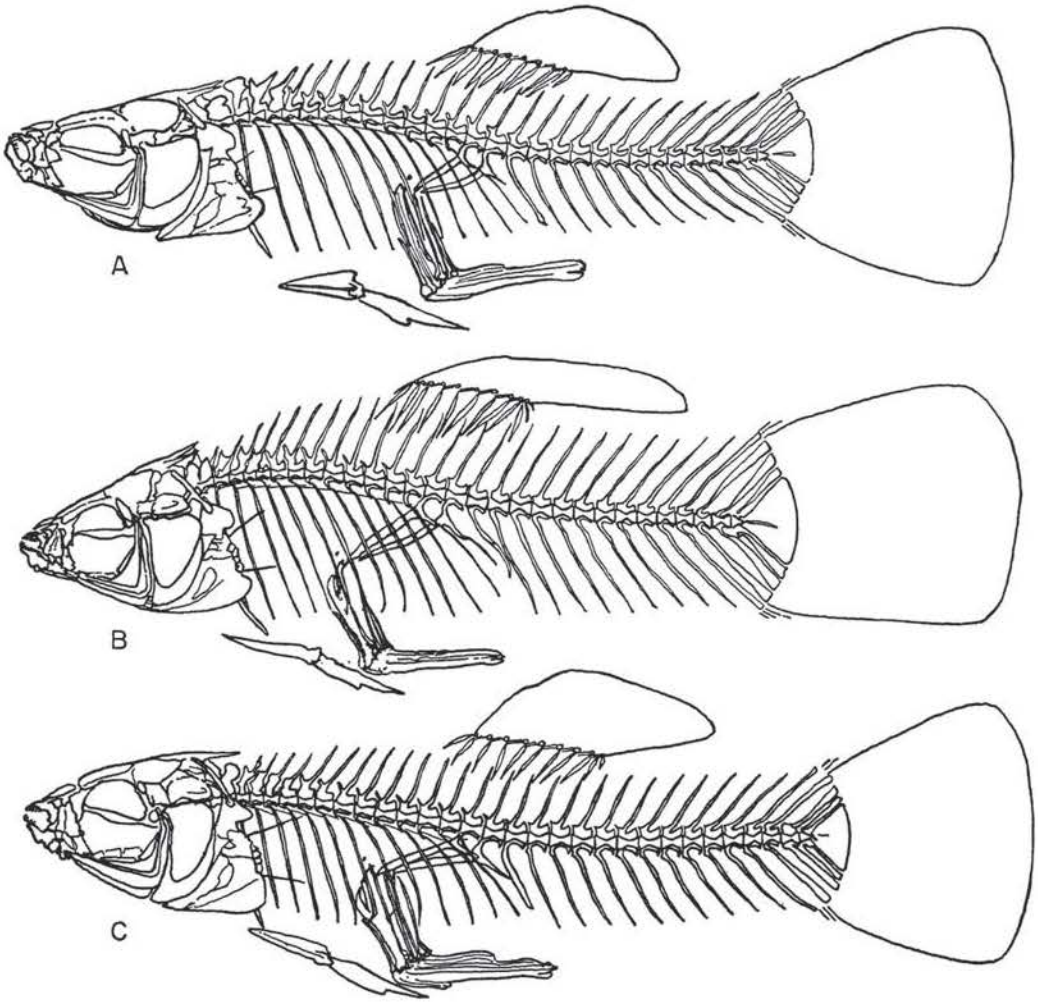


FIG. 18. Skeletons of adult males of *Poecilia*, composite drawings and tracing from radiograph. A. *P. sphenops*. B. *P. sphenops* (holotype, A.N.S.P. No. 71750, of *P. veti-providentiae* Fowler). C. *P. elegans*.

(type species, by monotypy, *Poecilia vivipara* Bloch and Schneider).

Mollienesia.—LESUEUR, 1821, p. 3 (type species, by monotypy, *Mollienesia latipinna* LeSueur). On the orthography of *Mollienesia*, see Bailey and Miller, 1950.

Alazon.—GISTL, 1848, p. ? (substitute for *Poecilia* Bloch and Schneider, thought to be preoccupied).

Limia.—POEY, 1854, pp. 381, 389–390 (type species, by monotypy, *Limia cubensis* Poey, a subjective synonym of *Poecilia vittata*).

Lebistes.—DE FILIPPI, 1861, p. 70 (type species, by monotypy, *Lebistes poeciloides* de Filippi, a subjective synonym of *Poecilia reticulata* and a secondary homonym of *Limia poeciloides* Girard = *Poecilia latipinna*).

Acropoecilia.—HILGENDORF, 1889, p. 52 (subgenus of *Poecilia;* type species, by monotypy, *Poecilia tridens* Hilgendorf, probably a subjective synonym of *Poecilia versicolor*).

Acanthophacelus.—EIGENMANN, 1907, p. 426 (type species, by original designation, *Poecilia reticulatus* Peters).

Pamphorichthys.—REGAN, 1913b, p. 1003 (type species, by monotypy, *Heterandria minor* Garman).

?*Pamphoria.*—REGAN, 1913b, p. 1003 (type species, by monotypy, *Cnesterodon scalpridens* Garman).

Neopoecilia.—C. L. HUBBS, 1924, p. 11 (type species, by original designation, *Neopoecilia holacanthus*, a subjective synonym of *Poecilia vivipara*).

Parapoecilia.—C. L. HUBBS, 1924, p. 11 (type species, by original designation, *Limia hollandi* Henn).

Allopoecilia.—C. L. HUBBS, 1924, p. 11 (type species, by original designation, *Girardinus caucanus* Steindachner).

Micropoecilia.—C. L. HUBBS, 1926, p. 73 (type species, by original designation, *Poecilia vivipara parae* Eigenmann).

Psychropoecilia.—MYERS, 1935, p. 310 (subgenus of *Mollienesia*; type species, by original designation, *Platypoecilus dominicensis* Evermann and Clark).

Lembesseia.—FOWLER, 1949, p. 267 (type species, by original designation, *Lembesseia parvianalis* Fowler, a probable synonym of *Poecilia sphenops*).

Curtipenis.—RIVAS AND MYERS, 1950, pp. 289–290, 294 (type species, by original designation, *Mollienisia elegans* Trewavas).

Recepoecilia.—WHITLEY, 1951, p. 68 (substitute name to replace *Micropoecilia* C. L. Hubbs, regarded as a homonym of *Micropoecila* Kraatz, 1880, in Coleoptera).

DIAGNOSIS: In skull, parietals, where present, extremely small and confined to posterior region of frontal adjacent to or overlying supraoccipital and epiotic; epiotic and supraoccipital processes present and well developed, or latter variably developed or obsolescent; posttemporal forked; marginal jaw teeth compressed. Posterior pleural ribs in male not curved, extending obliquely backward, rarely two or three with their tips bent slightly forward. Gonopodial suspensorium with two well-developed gonapophyses bent sharply

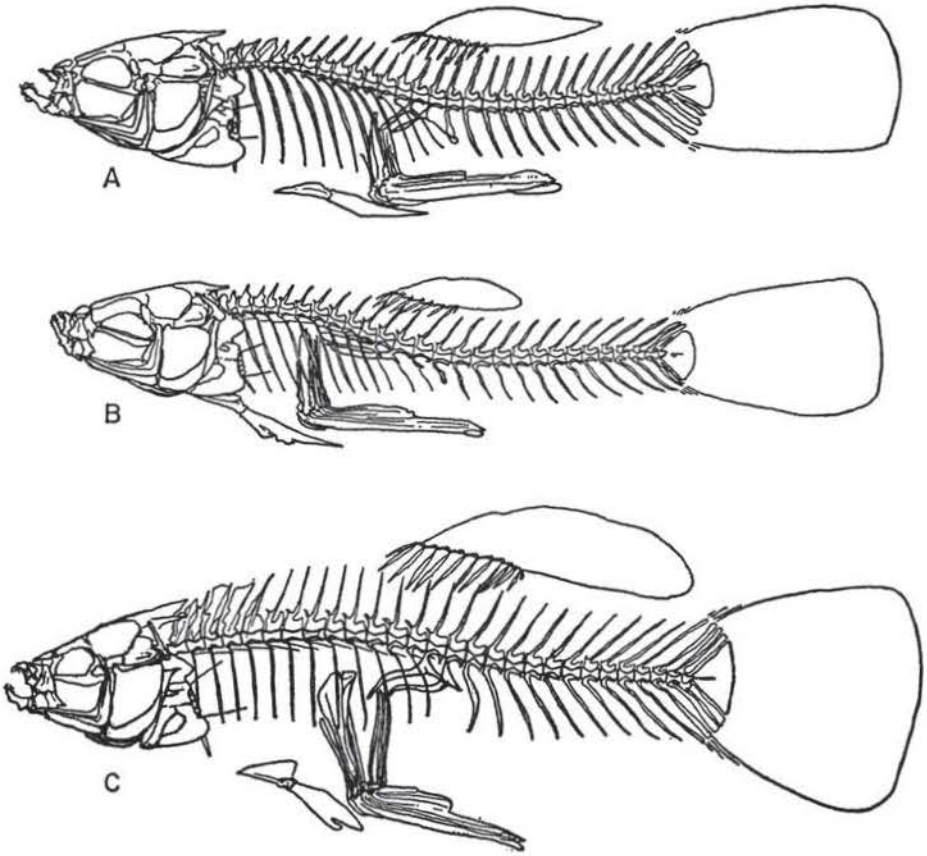
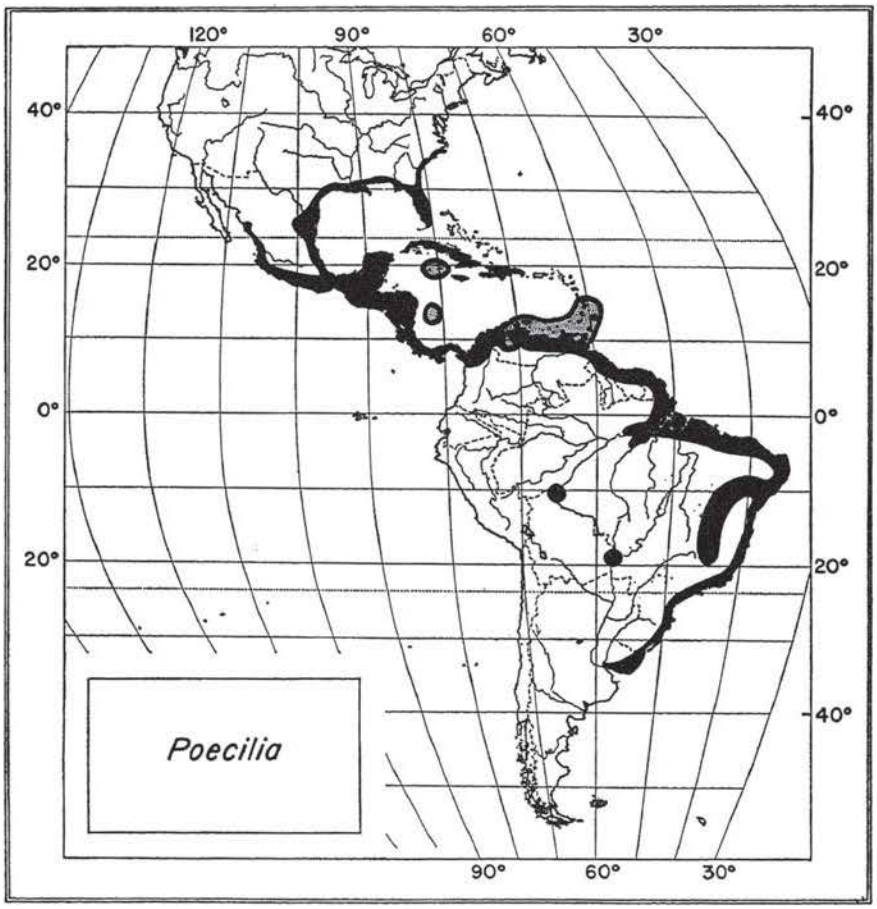


FIG. 19. Skeletons of adult males of *Poecilia*, composite drawings. A. *P. reticulata*. B. *P. hollandi*. C. *P. ornata*.

forward and lacking uncini; each gonapophysis with pair of large parapophyses near its base, a third gonapophysis present as individual variation in *Poecilia reticulata*, *P. parae*, and *P. amazonica;* primary gonactinostal complex much compressed anteroposteriorly, anterior part (incorporated elements 2 and 3) in many cases separated from posterior section (element 4 and superior and inferior lateral wings) by very large and distinct notch that extends downward from dorsal margin for one-fifth to one-fourth of height of complex; ligastyle variably developed, generally quite small and delicate or present as one or two, rarely three, tiny ossicles, in some cases absent. Gonopodium bilaterally symmetrical; from ventral surface of ray 3, large, fleshy palp usually arising that may envelop ventral half of gonopodium, this palp wanting in *P. heterandria* and minute in *P. elegans;* ray 3 with or without series of spinous processes distally or subdistally; ray 4a rarely with a few subdistal serrae; 4p typically with 10 or more subdistal serrae; ray 5 frequently terminated by small, backward-projecting, bony claw that is joined to underlying segments by intervening connective tissues. Pelvic fin highly modified, specializations typically involving rays 1, 2, and 3, rarely rays 4 and 5, ray 2 typically the longest and with dentate, serrate, or crenulate leading margin, and showing extensive ankylosis of basal segments.

RANGE AND SPECIES COMPOSITION: Southeastern United States and throughout most of Middle America and the West Indies to north, north-central, and eastern South America as far south as Río de la Plata (map



MAP 4. Distribution of *Poecilia*.

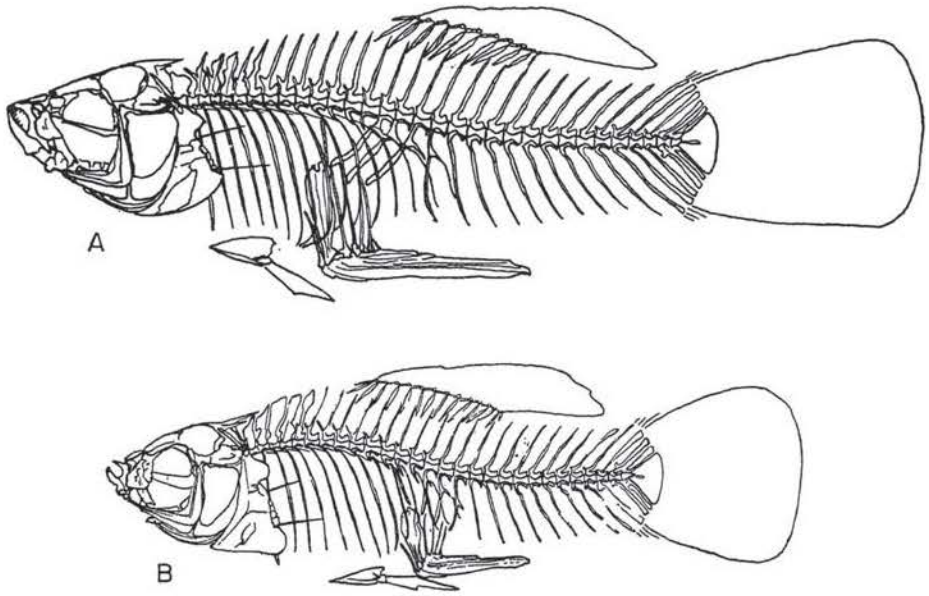


FIG. 20. Skeletons of adult males of the Poeciliini, composite drawings. A. *Priapella intermedia.* B. *Xiphophorus variatus evelynae.*

4). The 32 species listed, including some of doubtful validity, are provisionally arranged in four subgenera.

SUBGENUS **POECILIA** BLOCH AND SCHNEIDER

DIAGNOSIS: Gonopodium typically with rather short, retrorse, or erect spines developed to within one to three segments of tip of ray 3; usually with small retrorse claw at tip of ray 5a and tough, membranous, or bony hook projecting downward from tip of ray 3; edentate distal segments of ray 4p of variable height but in only few cases higher than long; distal segment arc of ray 5 curved gently downward toward ray 4p; ray 5p extending distally to within two or three segments of tip of ray 5a. Pelvic fin of adult male with variably developed fleshy swelling distally on ray 1 and a long, fleshy, finger-like extension of tip of ray 2; ray 2 thickened subdistally, in many cases joining distinct bony prominence that may enter or make contact with terminal fleshy swelling on ray 1; rays 1 and 2 joined by dense connective tissue and usually separated from rays 3 to 5 by distinct notch; ray 3 rarely with slight fleshy swelling at tip; rays 3 to 5 separated from each other by deep or shallow notches in interradial membrane or joined by smooth, uninterrupted membrane. Pelvic insertion of adult male at level of fourth to sixth pleural ribs.

RANGE AND SPECIES COMPOSITION: The distribution is approximately that of the genus. There are 11 species, only three of which enter the Antilles; in South America the species occur along the coast.

Poecilia caucana (Steindachner)

Text figures 21C, 22G, 23C, 25B

Girardinus caucanus.—STEINDACHNER, 1880, pp. 87, 93 (original description; Cáceres, Colombia). *Poecilia caucana.*—GARMAN, 1895, p. 68. *Mollienisia caucana.*—HENN, 1916, pp. 136–137 (gonopodium). *Allopoecilia caucana.*—C. L. HUBBS, 1924, pp. 11, 30 (gonopodium).

MATERIAL: Río Camarones at Arroyo de Arena, Colombia; U.M.M.Z. No. 55052. Río Aruza, Aruza, Darién, Panama; C.A.S. No. 14041.

RANGE: Pacific drainage of Darién, Panama, to the Río Cauca, Antioquia, Colombia, and Lago de Maracaibo, Venezuela.

REMARKS: A moderately high ridge arises laterally along the edge of gonactinost 2 in the gonactinostal complex. Specimens from the Río Camarones (U.M.M.Z. No. 55052) have eight gonactinosts and a basal plate for

the ninth. In the gonopodium subdistally on ray 4a, a slender ridge laterally merges insensibly with the segments of the proximal third of the fin. A few small serrae are commonly found along the midportion of ray 5p, and the terminal segments of 4p are higher than long.

Poecilia elegans (Trewavas)

Text figures 21D, 23D, 25C

Mollienisia elegans.—TREWAVAS, 1948, p. 409 (original description; Jarabacoa, Dominican Republic; holotype, B.M.N.H.). *Curtipenis elegans.*—RIVAS AND MYERS, 1950, pp. 289–290, 294.

MATERIAL: Río Yuna, north of Monseñor Noel, La Vega, Dominican Republic; U.M.M.Z. No. 160661, and specimens in the University of Miami Ichthyological Museum.

RANGE: Northern drainage of Dominican Republic.

REMARKS: In this species and in *Poecilia montana*, both from Hispaniola, the gonopodial spines (ray 3) are rather reduced, and in the male all the pelvic rays are separated from one another by deep incisions in the interradial membrane. These forms are probably closely related and have presumably differentiated on the island. Osteologically they are not unlike *P. caucana*, two small undescribed forms collected by L. P. Schultz in Venezuela (U.S.N.M. Nos. 121669–121673, 121675, 121683, 161595), and the smaller members of the *P. sphenops* complex, although in none of these mainland forms are the gonopodial spines so reduced or the pelvic membranes so deeply notched. We do not think that the differences between the island and mainland forms, which are of degree rather than of kind, deserve subgeneric recognition. Should future study indicate that *elegans* and *montana* merit subgeneric (or generic) status, *Psychropoecilia* Myers (1935) is available and has priority over *Curtipenis* Rivas and Myers, 1950.

In the skull the intercalar is developed as a well-defined disc, and parietals are lacking.

Poecilia montana, new name

Platypoecilus dominicensis.—EVERMANN AND CLARK, 1906, p. 852 (original description; San Francisco Mountains, Santo Domingo, 40 miles from Santo Domingo City, Hispaniola; holotype, U.S.N.M. No. 53277). *Limia dominicensis.*—REGAN, 1913b, p. 1015 (in part; excluding description and all of synonymy save reference to Evermann and Clark). *Mollienisia dominicensis.*—MYERS, 1931, p. 2 (distribution). *Mollienisia (Psychropoecilia) dominicensis.*—MYERS, 1935, pp. 310–312 (diagnosis and history).

Limia caudofasciata (not of Regan).—NICHOLS AND MYERS, 1923, p. 2.

MATERIAL: Río Camis, 9 kilometers west of La Vega, La Vega, Dominican Republic; in the University of Miami Ichthyological Museum.

RANGE: Northern drainage of Dominican Republic.

REMARKS: With the reduction of *Limia* to subgeneric rank and its consolidation with *Mollienesia* in the genus *Poecilia*, *Platypoecilus dominicensis* Evermann and Clark (1906) becomes a junior secondary homonym of *Poecilia dominicensis* Valenciennes (*in* Cuvier and Valenciennes, 1846). Evermann and Clark's form is therefore redesignated; the name *montana* is an allusion to the "... clear mountain torrents which are the habitat of the species" (Myers, 1935, p. 311).

PLATE 1

1, 2. Gonopodial tip in *Neoheterandria umbratilis*, U.S.N.M. No. 74244, illustrating fleshy contours. 1. Lateral view of right side. 2. Lateral view of left side.

3. Gonopodial tip of normal *Xiphophorus maculatus*, Río Jamapa laboratory strain.

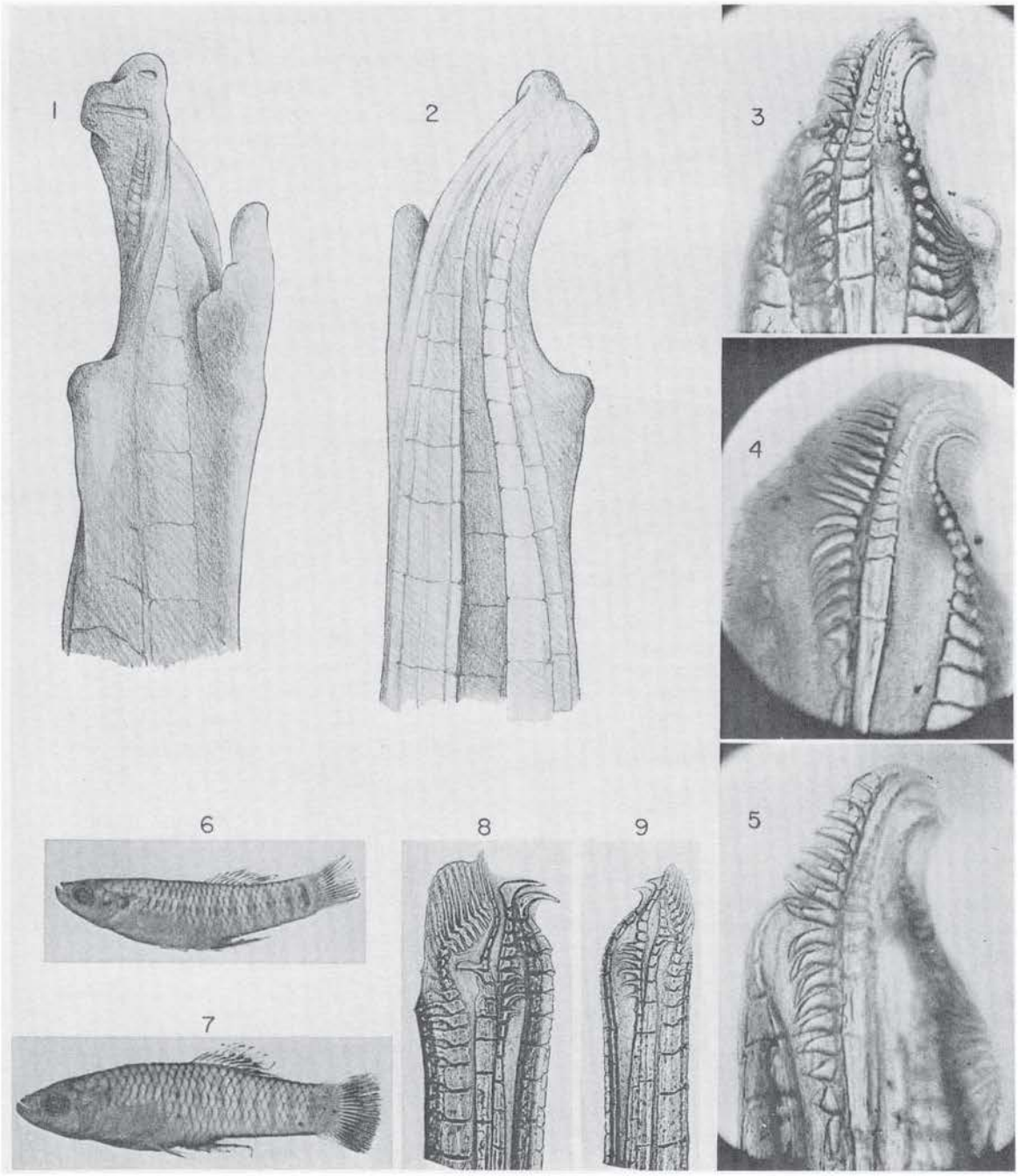
4, 5. Gonopodial tips of experimental *Xiphophorus maculatus*, Río Jamapa laboratory strain. The growing tip of ray 5 had been removed during gonopodial morphogenesis, after which the fins completed their development, with the results illustrated. In neither case does the regenerated ray 5 approach as closely as in the normal fin (3) to ray 4p which now has supernumerary serrae in the position of normal ray-5 contact. See text.

6. *Brachyrhaphis rhabdophora*, adult male, U.S.N.M. No. 94196.

7. *Brachyrhaphis rhabdophora* (holotype of *Panamichthys tristani* Fowler, A.N.S.P. No. 53935).

8. Gonopodial tip of *Gambusia punctata* Poey, syntype, M.C.Z. No. 6393, Havana, Cuba. Right side. Photomicrograph by L. Howell-Rivero.

9. Gonopodial tip of *Gambusia puncticulata* Poey, syntype, M.C.Z. No. 6391, Havana, Cuba. Left side. Photomicrograph by L. Howell-Rivero.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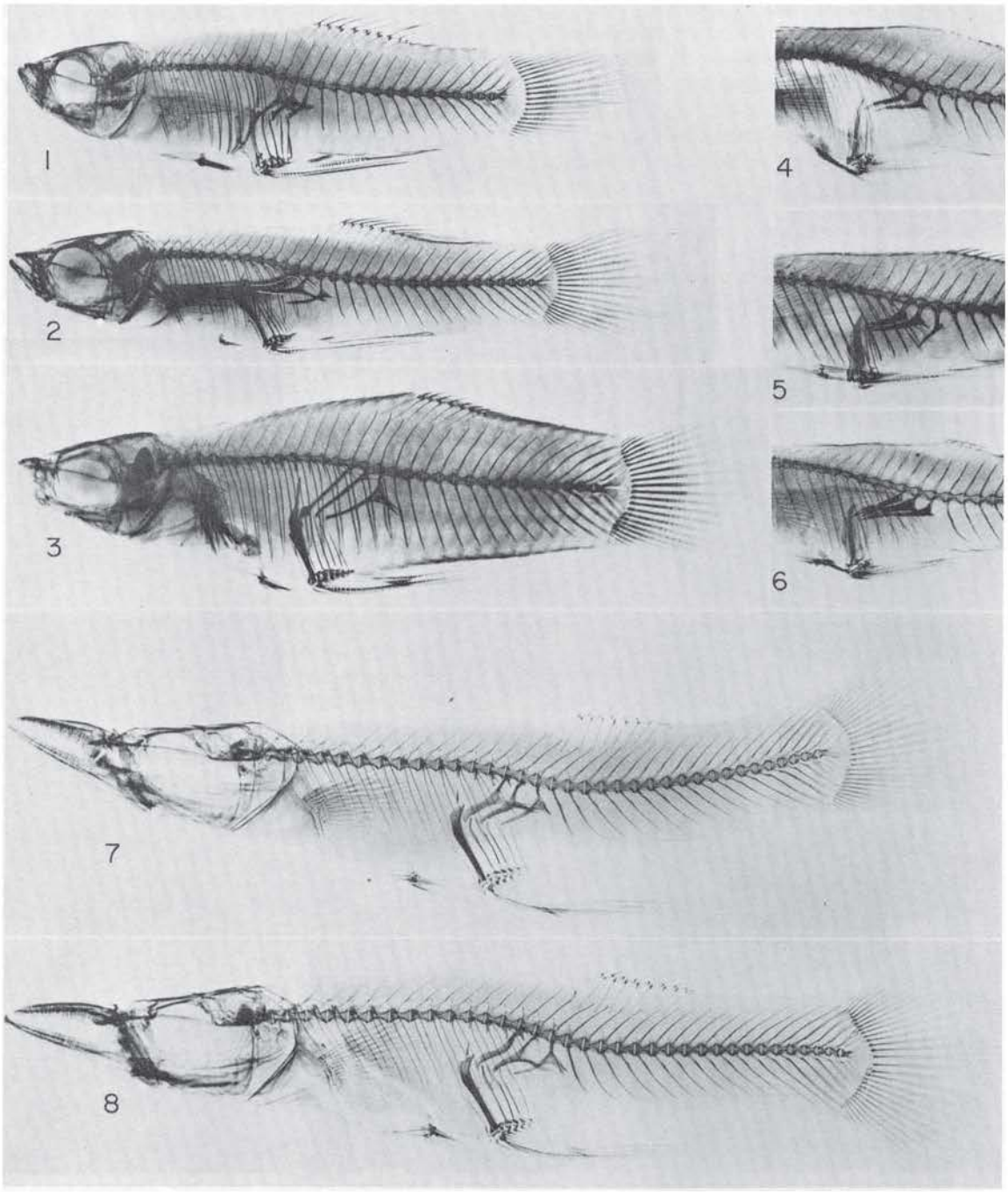
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U.S.N.M. No. 53277 (see above) becomes the holotype of *Poecilia montana*.

Poecilia vivipara Bloch and Schneider

Text figure 22D

Poecilia vivipara.—BLOCH AND SCHNEIDER, 1801, p. 452 (original description; Surinam).

Poecilia schneideri.—HUMBOLDT AND VALENCIENNES, 1821, p. 159 (original description; Surinam).

Poecilia surinamensis.—HUMBOLDT AND VALENCIENNES, 1821, pp. 157–159, 216 (original description; Surinam; syntypes, M.N.H.N.P. Nos. B.932 [Surinam], B.931 [Baía, Brazil], 4391 [Cayenne, French Guiana]). *Molinesia surinamensis*.—MÜLLER AND TROSCHEL, 1844, p. 36. *Mollienisia surinamensis*.—BLEEKER, 1860, p. 485.

Poecilia unimaculata.—HUMBOLDT AND VALENCIENNES, 1821, p. 158 (original description; Rio de Janeiro, Brazil; syntypes, M.N.H.N.P. Nos. B.933, B.934). *Poecilia unimacula*.—BLEEKER, 1860, p. 486.

Neopoecilia holacanthus.—C. L. HUBBS, 1924, p. 11 (original description; fresh-water streams of Puerto Rico [an introduced stock]). *Poecilia holacanthus*.—FOWLER, 1943, p. 2.

MATERIAL: Fajardo, Puerto Rico; C.A.S. No. 9405 (*Neopoecilia holacanthus*). Ceará-Mirim, Brazil; S.U. No. 22119. Santos, Brazil; S.U. Nos. 32098, 31759. Curaçao, Netherlands Antilles; A.N.S.P. No. 65069–95. Aquarium stock; U.M.M.Z. No. 102073.

RANGE: Aruba, Curaçao, Bonaire, and the Venezuelan islands, Trinidad and the Leeward Islands north to Martinique, and western Venezuela coastwise to Río de la Plata, Argentina; introduced in Puerto Rico.

Poecilia sphenops Valenciennes

Text figures 18A, B, 22E, F

?Molinesia fasciata.—MÜLLER AND TROSCHEL, 1844, p. 36 (original description; Mexico). *Mollienisia fasciata*.—BLEEKER, 1860, p. 485. *Poecilia fasciata*.—EIGENMANN, 1893, p. 57.

Poecilia sphenops.—VALENCIENNES, *in* Cuvier and Valenciennes, 1846, p. 130 (original description; Veracruz, Mexico; syntypes, M.N.H.N.P. No. B.930). *Mollienisia sphenops*.—REGAN, 1913b, p. 1012.

Poecilia mexicana.—STEINDACHNER, 1863, p. 178 (original description; Orizaba, Mexico). *Mollienisia mexicana*.—C. L. HUBBS, 1961, pp. 8, 12.

Poecilia thermalis.—STEINDACHNER, 1863, p. 181 (original description; warm springs in Central America).

Xiphophorus Gillii.—KNER AND STEINDACHNER, 1864, p. 25 (original description; Río Chagres, Panama). *Poecilia gillii*.—GÜNTHER, 1868, pp. 395, 406, 485.

Gambusia plumbea.—TROSCHEL, 1865, p. 106 [640] (original description; Mexico).

Gambusia modesta.—TROSCHEL, 1865, p. 105 [639] (original description; Mexico).

Poecilia chisoyensis.—GÜNTHER, 1866, p. 342 (original description; Río Chisoy, Alta Vera Paz, Guatemala; syntypes, B.M.N.H.).

Poecilia petenensis.—GÜNTHER, 1866, pp. 342–343 (original description; Lake Petén, Guatemala; syntypes, B.M.N.H.).

Poecilia dovii.—GÜNTHER, 1866, p. 344 (original description; Lake Nicaragua; Lake Amatitlán, Mexico; syntypes, B.M.N.H.).

Poecilia spilurus.—GÜNTHER, 1866, p. 345 (original description; Central America; holotype, B.M.N.H.).

Platypoecilus mentalis.—GILL, 1876, p. 335 (original description; Isthmus of Panama; holotype, U.S.N.M. No. 16675).

Poecilia Boucardi.—STEINDACHNER, 1878, p. 386 (original description; Colón, Panama; syntypes, M.C.Z. No. 32959).

Poecilia Vandepolli.—VAN LIDTH DE JEUDE, 1887, p. 137 (original description; Curaçao, Netherlands Antilles). *Girardinus vandepolli*.—MEEK, 1909, p. 209.

Poecilia arubensis.—VAN LIDTH DE JEUDE, 1887, p. 138 (original description; Aruba, Netherlands Antilles).

PLATE 2

1. Radiograph of *Brachyrhaphis hartwegi*, new species, holotype, U.M.M.Z. No. 179539.

2. Radiograph of *Gambusia atrora*, new species, holotype, U.M.M.Z. No. 179999. Gonapophyses of gonopodial suspensorium retouched.

3. Radiograph of *Gambusia luma*, new species, holotype, U.M.M.Z. No. 143565.

4–6. Radiographs of adult males of *Poecilia parae*, U.M.M.Z. No. 108895. 4. Two gonapophyses in gonopodial suspensorium. 5. Two normal gonapophyses and a third one partly developed in the gonopodial suspensorium. 6. Three normal gonapophyses in the gonopodial suspensorium.

7. Radiograph of adult male of *Belonesox belizanus*, aquarium specimen, showing first gonapophysis of gonopodial suspensorium, with well-developed uncini.

8. Radiograph of adult male of *Belonesox belizanus*, aquarium specimen, showing first gonapophysis of gonopodial suspensorium, without uncini.

Poecilia butleri.—JORDAN, 1889, p. 330 (original description; Río Presidio, near Mazatlán, Sinaloa, Mexico; syntypes, U.S.N.M. No. 37158).

Poecilia cuneata.—GARMAN, 1895, p. 62 (original description; Turbo, Gulf of Darién [Panama]; syntypes, M.C.Z. No. 6458, U.S.N.M. No. 120285). *Mollienisia cuneata*.—MEEK AND HILDEBRAND, 1916, pp. 326, 329.

Poecilia reticulata.—GARMAN, 1895, p. 62 (reference to *vandepolli* and *arubensis*).

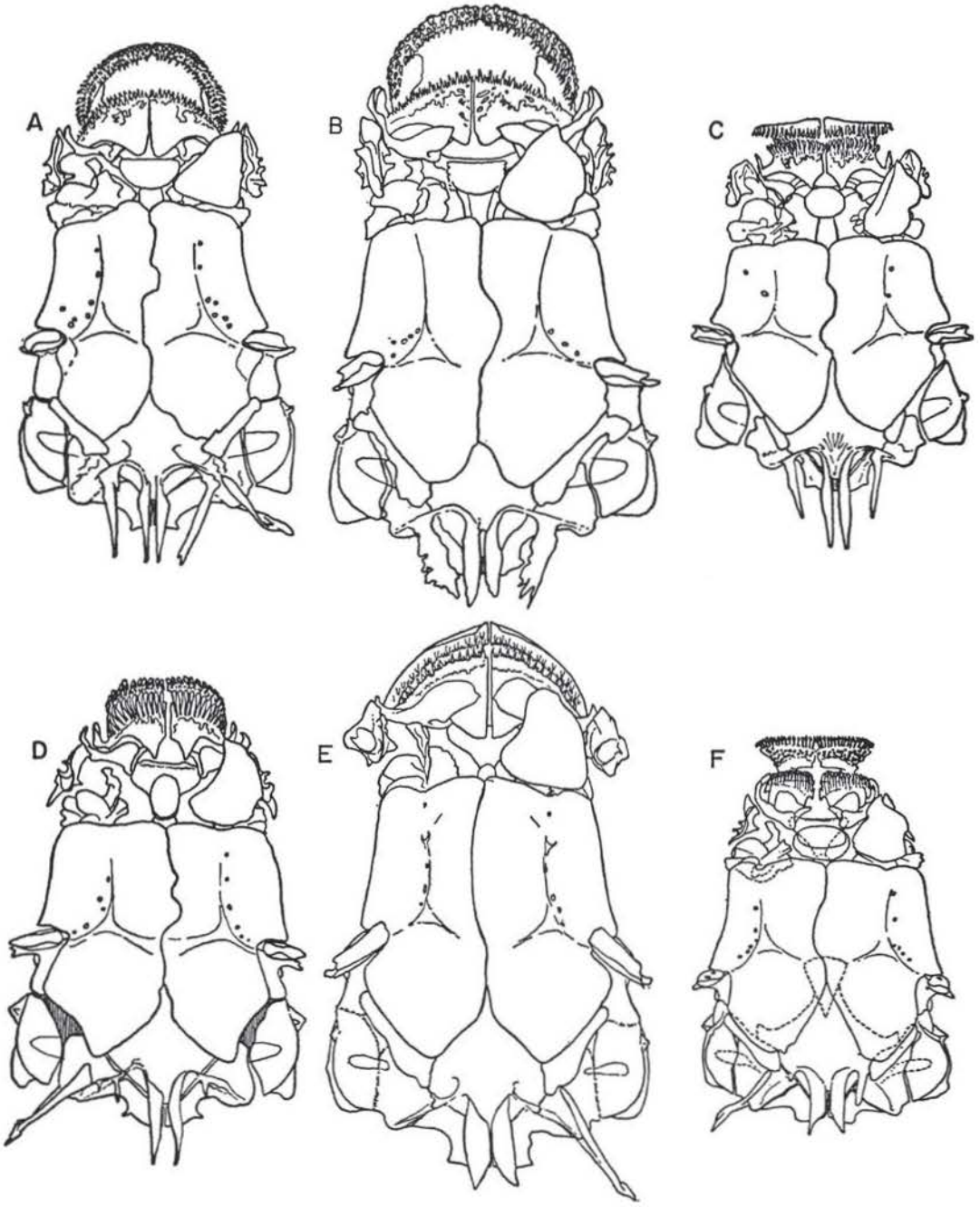


FIG. 21. Dorsicrania of the Poeciliini. A. *Alfaro cultratus*, male, U.M.M.Z. No. 159157. B. *Alfaro huberi*, male, U.M.M.Z. No. 173163, Honduras. C. *Poecilia caucana*, female, U.M.M.Z. No. 55052. D. *Poecilia elegans*, female, U.M.M.Z. No. 160661. E. *Priapella compressa*, male, A.M.N.H. No. 20440. F. *Xiphophorus couchianus*, from Rosen (1960).

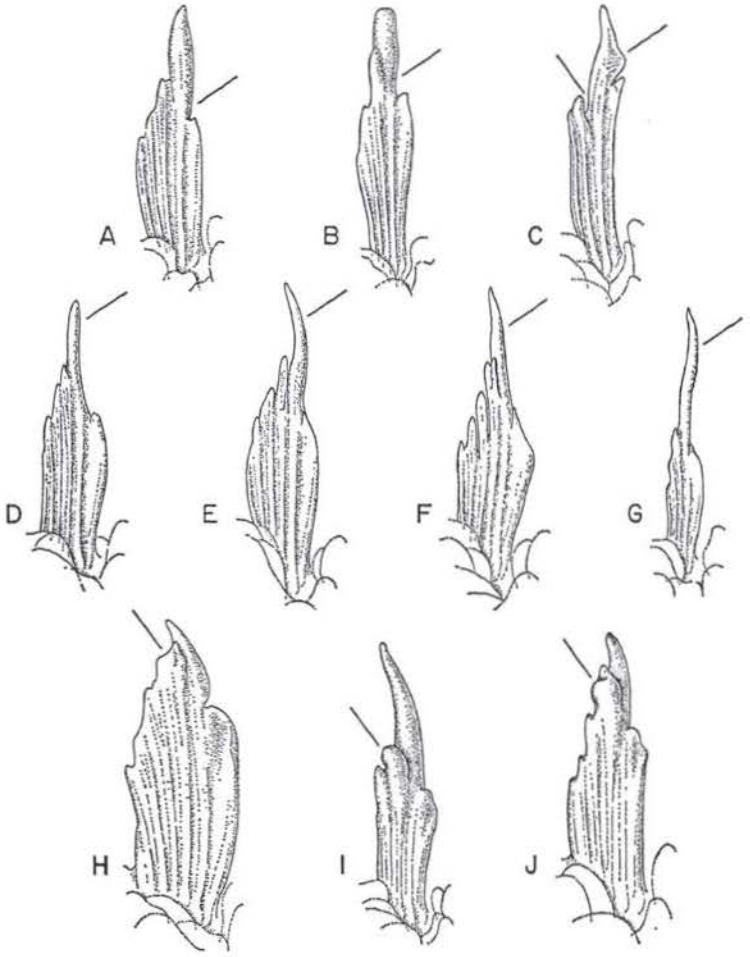


FIG. 22. Ventral view of the right pelvic fin in adult males of representative species of *Poecilia*. Diagnostic features are indicated by sloping line. A. *P.* (*Lebistes*) *reticulata*, U.M.M.Z. No. 158721, Río Macarapana, 5 kilometers southeast of Carupano, Venezuela. B. *P.* (*Lebistes*) *picta*, U.M.M.Z. No. 147008, Morawhanna, Northwest District, British Guiana. C. *P.* (*Pamphorichthys*) *hollandi*, U.M.M.Z. No. 179890, Lagôa de Olaria, Pirapora, Minas Gerais, Brazil. D. *P.* (*Poecilia*) *vivipara*, U.M.M.Z. No. 102073, aquarium stock, E, F. *P.* (*Poecilia*) *sphenops*, U.M.M.Z. No. 171988, Río Tuxpan, Nayarit, Mexico. G. *P.* (*Poecilia*) *caucana*, U.M.M.Z. No. 55052, Río Camarones, Arroyo de Arena, Colombia. H. *P.* (*Limia*) *nigrofasciata*, U.M.M.Z. No. 167223, Étang Saumâtre, Haiti. I. *P.* (*Limia*) *vittata*, U.M.M.Z. No. 61464, Calabazar, Cuba. J. *P.* (*Limia*) *melanonotata*, U.M.M.Z. No. 167231, Trau Caiman, Haiti.

Poecilia limantouri.—JORDAN AND SNYDER, 1900, pp. 116–117, 129–131 (original description; Río Tamesoe [Tamesí], near Tampico, Tamaulipas, Mexico; holotype, S.U. No. 6165).

Platypoecilus nelsoni.—MEEK, 1904, pp. 145, 147 (original description; Río Balsas, Guerrero, Mexico; holotype, U.S.N.M. No. 51484).

Platypoecilus tropicus.—MEEK, 1907, pp. 145–147 (original description; Turrialba, Costa Rica; holotype, C.N.H.M. No. 6027). *Poecilia tropica*.—REGAN, 1908, pp. 459–460. *Mollienisia sphenops tropica*.—FOWLER, 1916a, p. 392.

Poecilia salvatoris.—REGAN, 1907a, p. 65 (original description; San Salvador, El Salvador; syntypes, B.M.N.H.).

Poecilia tenuis.—MEEK, 1907, p. 146 (original description; Tiribi, Costa Rica; holotype, C.N.H.M. No. 6028).

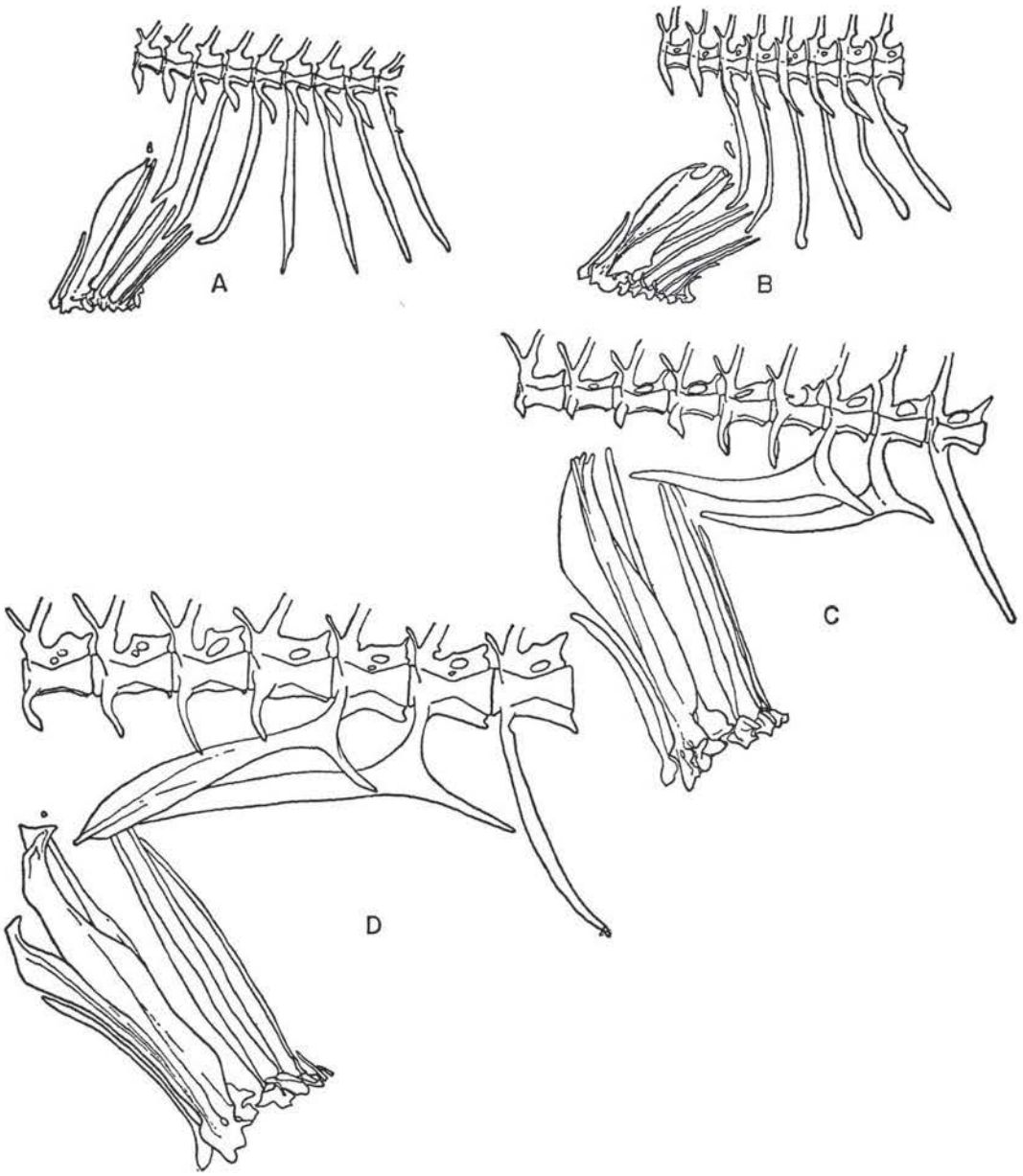


FIG. 23. Gonopodial suspensoria in the Poeciliini. A. *Alfaro cultratus*, U.M.M.Z. No. 159157. B. *Alfaro huberi*, U.M.M.Z. No. 173163, Honduras. C. *Poecilia caucana*, U.M.M.Z. No. 55052. D. *Poecilia elegans*, U.M.M.Z. No. 160661.

Poecilia spilonota.—REGAN, 1908, p. 460 (original description; San José, Costa Rica, syntypes, B.M.N.H.). *Platypoecilus spilonotus.*—EIGENMANN, 1910, p. 459.

Poecilia caudata.—MEEK, 1909, pp. 209–210 (original description; Turrubares, Costa Rica; holotype, C.N.H.M. No. 6360).

Mollienisia gracilis.—REGAN, 1913b, p. 1012 (original description; replacement name for *Poecilia petenensis* Günther, not *Mollienisia petenensis* Günther; Lake Petén, Guatemala; syntypes, B.M.N.H.).

Mollienisia sphenops vantynei.—C. L. HUBBS, 1935b, pp. 11–12 (original description; hydrographic basin of Río Hondo, Uaxactún, Petén, Guatemala; holotype, U.M.M.Z. No. 97874).

Mollienisia sphenops macrura.—C. L. HUBBS, 1935b, pp. 12–13 (original description; Río San Pedro de Mártir [Río Usumacinta system], at El Paso de los Caballos, Petén, Guatemala; holotype, U.M.M.Z. No. 95516).

Mollienisia sphenops altissima.—C. L. HUBBS, 1936, pp. 242–245 (original description; Miramar Spring, near Talcha, Yucatán, Mexico; holotype, U.M.M.Z. No. 102127).

Mollienisia sphenops melanistia.—C. L. HUBBS, 1937, p. 296 (*nomen nudum;* Arroyo Marmolejo, tributary to Arroyo San Carlos, at La Morita ranch, Río Soto la Marina system, Tamaulipas, Mexico). *Mollienisia sphaenops melanistica.*—WICKBOM, 1943, pp. 5–18.

Poecilia orri.—FOWLER, 1943, pp. 1–3 (original description; Bonacca Island, Bay Islands, off northern Honduras; holotype, A.N.S.P. No. 70158).

Mollienisia sphenops pallida.—DE BUEN, 1943a, pp. 251–259 (original description; La Bocana del Río Marqués [tributary to Río Balsas, Michoacán], Mexico).

Lembesseia parvianalis.—FOWLER, 1949, pp. 267–269 (original description; Oka, Congo system, Africa; undoubtedly introduced; holotype, A.N.S.P. No. 71924).

Poecilia veti-providentiae.—FOWLER, 1950, pp. 76–77 (original description; Old Providence, Colombian West Indies; holotype, A.N.S.P. No. 71750).

Mollienesia sphenops petersi.—SCHINDLER, 1959, pp. 1–6 (original description; Lago Yojoa, Honduras; holotype, S.M.M. No. 15639).

MATERIAL: British Honduras; U.M.M.Z. No. 159299. Panama; S.U. Nos. 6943–6944 (*boucardi*). Piscadera Bay, Curaçao, Netherlands Antilles (*vandepolli*). Río Tamesí, Tampico, Mexico; S.U. No. 6165 (*limantouri*). Río Tuxpan, Nayarit, Mexico; U.M.M.Z. No. 171988. Río Verde, Rascón, Mexico; S.U. No. 6169 (*limantouri*). Huffingtons Creek at watering place ¼ mile south of Ironwood Hill, Old Providence Island, Colombian West Indies; A.N.S.P. Nos. 71750, 71751–66 (*vetiprovidentiae*).

RANGE: Río San Juan, northeastern Mexico, and southern Sonora, Mexico (U.M.M.Z. No. 161553), southward along both coasts of Middle America to the Caribbean slope of Colombia and the Netherlands and Colombian West Indies.

REMARKS: *Molinesia fasciata* Müller and Troschel, when referred to *Poecilia* by Eigenmann (1893, p. 57), became a junior secondary homonym of *Poecilia fasciata* Bloch and Schneider, a synonym of *Fundulus heteroclitus* (Linnaeus). Had this homonymy been noted and *Molinesia fasciata* Müller and Troschel rejected prior to 1960, that name would now be unavailable (Stoll and others, 1961, p. 57). Because apparently no such action was taken, we assume that the name is nomenclaturally available. As noted by Garman (1895, p. 60), however, the original description is so sketchy as to be of uncertain application. Furthermore, even if the name applies to a species of the *sphenops* complex, the general type locality "Mexico" indicates that either *sphenops* or *mexicana* (see below) could be involved. We therefore regard *Molinesia fasciata* as unidentifiable unless the type material be located.

The *sphenops* complex is widely distributed, and it is not now certain whether all the above-named forms should be regarded as members of a single species, *Poecilia sphenops*. C. L. Hubbs (1961) has expressed the opinion that sympatric species occur from Veracruz to Costa Rica. *Poecilia sphenops* is said to have tricuspid inner jaw teeth; *P. mexicana*, to have these teeth unicuspid. These species are apparently interfertile under laboratory conditions. Should these findings be corroborated, it will be necessary to allocate the many synonyms listed above to their proper species. Various subspecies of *sphenops* have been recognized, some of which are rather well defined. If there are proved to be two, or more, species, either or both may be polytypic. The *sphenops* complex is subject to great regional variations, and careful study, preferably with laboratory experimentation, is essential to a lucid comprehension of the problem.

The above synonymy is designed only to bring together the various nominal references. Some forms in addition to *mexicana*, e.g., *vandepolli* (and *arubensis* which it probably includes), may eventually be referred to distinct species.

On the basis of Fowler's account of its structure and coloration, *Lembesseia parvianalis* is probably some form of *P. sphenops* that has been introduced into Africa. It is known only from a single female.

Poecilia sphenops is probably represented as a fossil in sub-Recent, fresh-water, diatomaceous deposits of El Salvador (see comments below under *Poeciliopsis maldonadoi*).

Poecilia formosa (Girard)

AMAZON MOLLY

Limia formosa.—GIRARD, 1859c, p. 115 (original description; Paolo Alto, Mexico). *Gambusia formosa.*—BLEEKER, 1860, p. 485. *Mollienesia formosa.*—GÜNTHER, 1866, p. 349.

Mollienisia latipinna (in part; misidentification).—GARMAN, 1895, p. 50.

MATERIAL: Olmito, 6 miles southeast of San Benito, Cameron County, Texas; U.M.M.Z. No. 157340.

RANGE: The southern tip of Texas, south to the Río Papaloapan system, Veracruz, Mexico.

REMARKS: This species, described originally from a male and female, has since been known largely from females, most of which under laboratory conditions reproduce by gynogenesis. Kallman (1962) summarized what is known of this fish as an experimental animal. His historical review can be paraphrased as follows: Gynogenesis, in which the spermatozoon does not contribute any genetic material to the zygote but provides the activating stimulus for the egg, is believed to occur regularly in this species (C. L. Hubbs, 1955; Hubbs and Hubbs, 1932, 1946). When mated to males of *P. sphenops*, *P. latipinna*, or a number of other species of *Poecilia*, *P. formosa* females have been reported to produce all-female offspring that are phenotypically indistinguishable from their mother. When such "hybrids" were backcrossed for as many as 20 generations to males of other species, no introgression of any of the characters of these species was noticeable in the offspring. Of the more than 8000 fish so produced, each was a female closely resembling the original *formosa* progenitor (Hubbs and Hubbs, 1946).

Females of this species occur in southern Texas together with *latipinna* and in northeastern Mexico with *sphenops* (Hubbs and Hubbs, 1932). In appearance *formosa* is intermediate between *sphenops* and *latipinna*, both of which are bisexually reproducing species. Presumably *formosa* maintains itself in nature gynogenetically, utilizing *sphenops* or *latipinna* males. In the laboratory, mature females of *formosa* do not reproduce when isolated or when separated from males of *sphenops* or *latipinna* by a glass plate, thus ruling out parthenogenesis (Meyer, 1938).

It is not known whether females of *formosa* reproduce gynogenetically when mated to the supposed males of this species. Such males are exceedingly rare and are not yet available for genetic or histologic analysis. Among several thousand specimens of *formosa* collected in their natural habitat, there were only four supposed males (Hubbs, Drewry, and Warburton, 1959; and unpublished).

Haskins, Haskins, and Hewitt (1960) reported that females of *formosa* rarely produce conventional hybrids with males of *Poecilia vittata*, as they may also with males of *sphenops* (Kallman, personal communication).

Poecilia latipinna (LeSueur)

SAILFIN MOLLY

Mollienesia latipinna.—LESUEUR, 1821, p. 3 (original description; Lake Pontchartrain, New Orleans, Louisiana; syntypes, M.N.H.N.P. No. B.929). *Mollinesia latipinna.*—STORER, 1846, pp. 182–183.

Poecilia multilineata.—LESUEUR, 1821, p. 4 (original description; New Orleans, Louisiana).

Limia poeciloides.—GIRARD, 1859a, p. 70 (original description; Indianola, Texas). *Gambusia poecilioides.*—BLEEKER, 1860, p. 485. *Poecilia poeciloides.*—GARMAN, 1895, p. 65.

Poecilia lineolata.—GIRARD, 1859a, p. 70 (original description; Rio Grande, near Brownsville, Texas). *Limia lineolata.*—GIRARD, 1859c, pp. 114–115. *Gambusia lineolata.*—BLEEKER, 1860, p. 485.

Limia matamorensis.—GIRARD, 1859c, p. 117 (original description; Matamoras, Mexico; syntypes, U.S.N.M. No. 3509). *Gambusia matamorensis.*—BLEEKER, 1860, p. 485.

MATERIAL: Florida; U.M.M.Z. No. 138424. Apalachee Bay, St. Marks bird refuge, Walkulla County, Florida; U.M.M.Z. No. 163388. Guadelupe River, Guadelupe County, ¾ mile south of Seguin, Texas; A.N.S.P. No. 73667. Matamoros; U.S.N.M. No. 3509 (*matamorensis*).

RANGE: Southeastern North Carolina, southward along the coast, throughout peninsular Florida and the Florida Keys, westward along the Gulf coastal United States, and southward in Atlantic coastal Mexico to Yucatán where it probably " . . . occupies the coastal region along the northwest side of the basal half of the Yucatán Peninsula" (C. L. Hubbs, 1936, pp. 246–247). Coastal fresh water, brackish, and salt water.

REMARKS: The International Commission on Zoological Nomenclature, using its plenary powers, has accorded precedence to the name *latipinna* over *multilineata* of identical date

(International Commission on Zoological Nomenclature, 1959).

This form and the two following ones, *petenensis* and *velifera*, may be members of a single polytypic species. They are all allopatric, are similar in appearance, and differ in minor characters.

Poecilia petenensis (Günther)

Mollienesia petenensis.—GÜNTHER, 1866, p. 348 (original description; Lake Petén, Guatemala; syntypes, B.M.N.H.).

MATERIAL: Arroyo de Puebla Nueva tributary to Lake Petén, Petén, Guatemala; U.M.M.Z. No. 143634.

RANGE: Río Usumacinta drainage and nearby lakes, Petén, Guatemala.

REMARKS: Günther (1866) assigned the specific name *petenensis* to two species. One he called *Poecilia petenensis* (p. 342); the other, *Mollienesia petenensis* (p. 348). These species are very different, as can be seen by the illustrations of Günther (1868, pls. 85, 86). Regan (1913b, p. 1012) recognized that the two species were congeneric and, because of the homonymy, proposed for *Poecilia petenensis* the substitute name *Mollienisia gracilis*. This species is treated by us in the synonymy of *Poecilia sphenops*. *Poecilia* Bloch and Schneider (1801) has priority over *Mollienesia* LeSueur (1821). *Mollienesia petenensis* Günther is therefore transferred to *Poecilia*, where it is confronted with *Poecilia petenensis* Günther. Two courses of action seem open to resolve this confusion. The name *petenensis* of the combination *Mollienesia petenensis* could be replaced by a substitute. This solution has the disadvantage that both of Günther's original names would be supplanted, and we therefore reject it. The second course was made possible by Regan who, as first reviser, decided which of the two names should be suppressed. Hence we transfer *Mollienesia petenensis* to *Poecilia*. *Poecilia petenensis* (Günther) is intimately related to and allopatric with *Poecilia latipinna* and eventually may find a place in the synonymy of that species.

Poecilia velifera (Regan)

YUCATÁN SAILFIN

Mollienisia velifera.—REGAN, 1914a, p. 338 (original description; Progreso, Yucatán, Mexico; syntypes, B.M.N.H.).

Mollienisia vivipara (misidentification).—SCRIMSHAW, 1945, p. 242.

MATERIAL: El Río o Ciénaga, south of Progreso, Yucatán, Mexico; U.M.M.Z. No. 143099.

RANGE: Coastal waters of the outer part of the Yucatán Peninsula, Mexico (C. L. Hubbs, 1936, p. 248).

Poecilia latipunctata Meek

Poecilia latipunctata.—MEEK, 1904, pp. 150–151 (original description; Río Pánuco Basin, Forlón, Tamaulipas, Mexico; holotype, C.N.H.M. No. 4484). *Mollienisia latipunctata.*—C.L. HUBBS, 1933, pp. 266–268.

MATERIAL: Mexico; M.C.Z. No. 39586.

RANGE: Río Tamesí system of the Río Pánuco basin, Tamaulipas, Mexico.

Poecilia sulphuraria (Alvarez)

Mollienisia sulphuraria.—ALVAREZ, 1948b, pp. 276, 279–280 (original description; Baños del Azufre, Tabasco, Mexico; holotype in collection of José Alvarez).

MATERIAL: Twenty-nine specimens from the type series, see synonymy above; U.M.M.Z. No. 172504.

RANGE: Baños del Azufre, Tabasco, Mexico.

SUBGENUS **LEBISTES** DE FILIPPI

DIAGNOSIS: Gonopodium typically with prominent, comma-shaped, retrorse spines developed to within one to five segments of tip of ray 3; in some cases with small retrorse claw at tip of ray 5a; without membranous or bony hook at tip of ray 3; edentate distal segments of ray 4p longer than high; distal segment arc of ray 5 curved gently downward (or buckled outward and then downward) toward ray 4p; ray 5p extending forward to within two or three segments of tip of ray 5a. Pelvic fin of adult male with slightly developed, fleshy swelling distally on ray 1, and long, fleshy, finger-like extension of tip of ray 2; ray 2 slightly thickened near base and without bony prominence; rays 1 and 2 firmly joined with dense connective tissue except where pointed tip of ray 1 is set apart by shallow notch; ray 3 without fleshy swellings; rays 3 to 5 united by smooth, uninterrupted membrane. Pelvic insertion of adult male at level of fourth to sixth pleural ribs.

Differing further from *Poecilia* in high degree of color polymorphism of adult males.

RANGE AND SPECIES COMPOSITION: Northern and northeastern South America and the Lesser Antilles. Six species.

Poecilia reticulata Peters

GUPPY

Text figures 19A, 22A, 25D

Poecilia reticulata.—W. PETERS, 1859, p. 412 (original description; Caracas, Venezuela; types, formerly Berlin Museum, B.M.N.H.). *Girardinus reticulatus.*—GÜNTHER, 1866, p. 352. *Poeciloides reticulatus.*—JORDAN AND GILBERT, 1883, p. 344. *Acanthophacelus reticulatus.*—EIGENMANN, 1907, pp. 426–427. *Lebistes reticulatus.*—REGAN, 1913b, p. 1008. *Glaridichthys (Girardinus) reticulatus.*—MILEWSKI, 1920, p. 624.

Lebistes poeciloides.—DE FILIPPI, 1861, p. 70 (original description; Barbados). *Girardinus poeciloides.*—E. G. BOULENGER, 1912, p. 906. *Poecilia poeciloides.*—LANGER, 1913, p. 200.

Girardinus guppii.—GÜNTHER, 1866, p. 353 (original description; Trinidad, Venezuela; syntypes, B.M.N.H.). *Heterandria guppii.*—JORDAN, 1887, p. 563. *Acanthophacelus guppii.*—EIGENmann, 1910, p. 458.

Girardinus vandepolli (misidentification).—MEEK, 1909, p. 209 (Curaçao; see Henn, 1916, p. 134).

MATERIAL: Río Poolamar at El Valle, Isla de Margarita; U.M.M.Z. No. 58706. Georgetown trenches, British Guiana; C.A.S. No. 12072. Río Bue, Maracay, Venezuela; C.A.S. No. 15149. Barbados, the West Indies; C.A.S. Nos. 12073–12074. Río Macarapana, 5 kilometers southeast of Carupano, Venezuela; U.M.M.Z. No. 158721.

RANGE: The Netherlands Antilles and the Venezuelan islands, Trinidad, the Windward (Barbados) and Leeward (St. Thomas and Antigua) Islands, and from Yaracuy Province, western Venezuela, in coastal rivers and streams east to British Guiana. Records from the Lesser Antilles may be due to introductions. The guppy has been widely distributed as an aquarium fish, and feral populations can be anticipated in any climatically suitable area. We know or have heard of such established stocks in Brazil (São Paulo), Costa Rica, India, Italy, Madagascar, Marshall Islands, Mexico, and West Africa.

Poecilia parae Eigenmann

Plate 2, figures 4–6

Poecilia vivipara parae.—EIGENMANN, 1894, p. 628 (original description; Ruadas, Mongubas, Pará, Brazil; syntypes, C.A.S. No. 22552). *Poecilia parae.*—REGAN, 1913b, p. 1006. *Micropoecilia parae.*—C. L. HUBBS, 1926, p. 74.

Acanthophacelus bifurcus.—EIGENMANN, 1909, pp. 51–53 (original description; Christianburg, Wismar, British Guiana; holotype, C.N.H.M. No. 53539). *Micropoecilia bifurca.*—C. L. HUBBS, 1926, p. 74.

Acanthophacelus melanzonus.—EIGENMANN, 1909, pp. 51–52 (original description; Georgetown trenches, British Guiana; holotype, C.N.H.M. No. 52717; in part, male only). *Poecilia melanzona.*—HENN, 1916, p. 132. *Micropoecilia melanzona.*—C. L. HUBBS, 1926, p. 74.

Lebistes reticulatus (misidentification).—REGAN, 1913b, pp. 1007–1008 (reference to type of *melanzona*).

MATERIAL: Christianburg Pond, British Guiana; C.A.S. Nos. 11763–11764 (*bifurcus*). Christianburg Canal, British Guiana; C.A.S. Nos. 11765–11766 (*bifurcus*). Demarara River, Christianburg, British Guiana; S.U. No. 21930 (*bifurcus*). Wismar, British Guiana; U.M.M.Z. No. 108900 (*bifurcus*). Yarakita River, British Guiana; U.M.M.Z. No. 147004 (*bifurcus*). Georgetown, British Guiana; U.M.M.Z. No. 110154 (*parae*). Georgetown, British Guiana; U.M.M.Z. No. 108895 (*parae*). Río (?Rua) das Mongubas, Pará, Brazil; C.A.S. No. 5079 (*parae*).

RANGE: British Guiana, coastwise to the mouth of the Amazon River, Brazil; reported to occur in Trinidad (Stoye, 1935, p. 67).

REMARKS: Living adult males and females of this species from the vicinity of Georgetown, British Guiana, were maintained for a period of two years in the laboratory. Sixty-six young from laboratory bred and reared adults were obtained. Of 34 females, all were identical and of the *parae* type. Of 32 males, seven were of the *melanzona* type, five of the *parae* type (two of which had a light ventral as well as a strong dorsal emargination on the caudal fin and were therefore of the *bifurca* type), and 20 were without markings other than a "shoulder spot." Only a single female bore young that were of all three basic types. Most broods consisted of unmarked fish with one or two of the *melanzona* type. Brood size never exceeded 10 individuals and was usually four or five.

The three polymorphs do not differ in morphometric traits or gonopodial characters.

Poecilia picta Regan

Text figure 22B

Poecilia picta.—REGAN, 1913b, p. 1007 (original description; Demerara, British Guiana; syntypes, B.M.N.H.). *Micropoecilia picta.*—C. L. HUBBS, 1926, p. 74.

Acanthophacelus melanzonus.—EIGENMANN, 1909, p. 51 (in part; females only).

Lebistes reticulatus (misidentification).—FOWLER, 1954, p. 236 (figure of male and female only).

MATERIAL: Georgetown trenches, British Guiana; C.A.S. No. 11762. Morawhanna, Northwest District, British Guiana; U.M.-M.Z. No. 147008.

RANGE: British Guiana and Trinidad, coastwise to Pará, Brazil.

Poecilia branneri Eigenmann

Poecilia branneri.—EIGENMANN, 1894, p. 629 (original description; Santarem, Pará, Brazil; syntypes, S.U. No. 2158, C.A.S. Nos. 22550, 22551). *Micropoecilia branneri*.—C. L. HUBBS, 1926, p. 75.

Poecilia heteristia.—REGAN, 1909, p. 235 (original description; Pará, Brazil; syntypes, B.M.N.H.).

MATERIAL: Brazil; S.U. No. 2158. Also seen were specimens collected by C. P. Haskins in Belém, Brazil.

RANGE: Pará, Brazil.

REMARKS: Mayer (1948) gave a brief account of courtship behavior in this species that calls to mind the sexual display of our laboratory-reared *P. picta*. Both species are heavily barred with dusky pigment and are alike in gonopodial characters. They may be closely related. *Poecilia branneri* is the southernmost representative of this subgenus, being common in the lower Amazon. There is a yet undescribed form of the *picta-branneri* complex from Venezuela (specimens in the Museum of Zoology of the University of Michigan). It is much like *picta* in fin structure and coloration, but is distinct in having the tip of gonopodial ray 5 slightly buckled outward.

Poecilia amazonica Garman

Poecilia amazonica.—GARMAN, 1895, p. 64 (original description; Santa Cruz, Pará, Brazil; syntypes, M.C.Z. Nos. 27573A, 27573; U.S.N.M. No. 120286).

MATERIAL: Type material.

RANGE: Santa Cruz, Pará, Brazil.

REMARKS: The type material includes at least two specimens with three gonapophyses in their gonopodial suspensoria. This observation is exceptionally important in the light of Mohsen's (1960) discovery of three elements in a domesticated strain of *P. reticulata*. It provides support for the idea that the mechanism in *Poecilia* was derived from a more normal system with three supports, as was previously suggested by Rosen and Kallman (1959). Hence, *P. amazonica* may be a form in which gonapophyseal number has not yet been stabilized. Almost all specimens of *amazonica* (96 fish in M.C.Z. No. 27573A, some of which are quite mutilated and faded) possess square or rectangular shoulder bars that are edged on both sides by clear areas and dark lines. One female and two juvenile males have an oval caudal spot of dusky color, and one of these males also has a large postanal blotch that is similar to the flank markings of some examples of *P. picta*. Because of the absence of definitive gonopodia, these three fish cannot be certainly assigned but may be *branneri*, *picta*, or a form of *reticulata*. *Poecilia amazonica*, which is certainly not closely related to *P. vivipara*, can be treated provisionally as a distinct species allied to *branneri* (which also lives at Pará and has a caudal blotch).

Poecilia scalpridens (Garman)

Cnesterodon scalpridens.—GARMAN, 1895, p. 45 (original description; Amazon basin, Santarém, Óbidos, Tapajos, Villa Bella, Trombetas; syntypes, M.C.Z. No. 6839). *Pamphoria scalpridens*.—REGAN, 1913b, p. 1003.

RANGE: Amazon basin, Santarém, Óbidos, Tapajos (River), Trombetas (River), Pará, Brazil; Villa Bella, Mato Grosso, Brazil.

REMARKS: We have not seen Garman's male type of this form, but from his figure and diagnosis we suspect that it is unrelated to *Pamphorichthys minor* (see Regan, 1913b) and should be placed provisionally in the subgenus *Lebistes*. This form is of small size (about 1 inch) and does not have the advanced pelvic insertion of *P. minor*.

SUBGENUS **PAMPHORICHTHYS** REGAN

DIAGNOSIS: Gonopodium typically without definitive spines on ray 3 except penultimately where a few segments may develop minute prominences; without claw at tip of ray 5a or membranous or bony terminal hook on ray 3; edentate distal segments of ray 4p higher than long; distal segment arc of ray 5 curving downward just perceptibly toward ray 4p; ray 5p extending forward to within two to six segments of tip of ray 5a. Pelvic fin of adult male with moderately developed, fleshy swelling distally on ray 1, separated by

deep notch from ray 2[1]; ray 2 very long, thickened, usually with series of large, spinous, bony processes (a comb) arising on leading margin of ray between its distal end and tip of ray 1; entire distal half of ray 2 enveloped by fleshy tissues; ray 2 separated from rays 3 to 5 by deep notch; ray 3 distally with slight fleshy swelling; rays 3 to 5 held closely together and united at tips by smooth, uninterrupted membrane. Pelvic insertion of adult male at level of first or second pleural rib.

RANGE AND SPECIES COMPOSITION: Northern, north-central, and northeastern South America. Four species.

Poecilia minor (Garman)

Text figure 25E

Heterandria minor.—GARMAN, 1895, p. 92 (original description; Villa Bella, Brazil; syntypes, M.C.Z. No. 6254, U.S.N.M. No. 120268). *Pamphorichthys minor.*—REGAN, 1913b, p. 1003.

MATERIAL: Villa Bella, Brazil; M.C.Z. No. 6254.

RANGE: Villa Bella, Mato Grosso, Amazon basin, Brazil.

REMARKS: We have seen Garman's types, and the adult males are extremely small, averaging about 10 mm. in total (not standard) length. *Poecilia minor* differs from *hollandi* in being smaller, having the comb-like modification of pelvic ray 2 less developed, and in two gonopodial characters. In *minor*, the penultimate four segments on ray 3 have antrorse dorsal and ventral prominences, whereas in *hollandi* the penultimate six or seven segments are modified as minute spines without any dorsal outgrowths. In *hollandi* the subdistal segments of ray 5a project downward toward the serrae on ray 4p; in *minor* they rarely do so to any marked degree.

Poecilia hollandi (Henn)

Text figures 19B, 22C

Limia hollandi.—HENN, 1916, pp. 95, 104, 138 (original description; Penedo, Río São Francisco, Brazil; holotype, C.N.H.M. No. 55861). *Parapoecilia hollandi.*—C. L. HUBBS, 1926, p. 75. *Poecilia (Parapoecilia) hollandi.*—R. VON IHERING, 1931, p. 271.

MATERIAL: Boqueiras Río Grande, Río São Francisco, Brazil; C.N.H.M. No. 55858. Santa Rita de Río Preto, Río São Francisco, Brazil; C.N.H.M. No. 55859. Lagôa de Porto, Brazil; C.N.H.M. No. 47302. Lagôa da Olaria, Pirapora, Minas Gerais, Brazil; U.M.M.Z. No. 179890.

RANGE: Brazil: basin of Río São Francisco; Río Itapicurú, Baía; and coastal streams near Santos, São Paulo.

Poecilia hasemani (Henn)

Heterandria hasemani.—HENN, 1916, pp. 116–117 (original description; Puerto Suarez, Río Paraguay basin, Bolivia; holotype, C.N.H.M. No. 55874 [dry], three paratopotypes, C.N.H.M. No. 55875 [fair condition]).

RANGE: Puerto Suarez, Río Paraguay basin, Bolivia (Henn, 1916, p. 116).

REMARKS: This form is known only from the four female types. Henn's (1916) figure and description suggest that it is a species of *Poecilia*, especially as judged from the great length of the pelvic fins. He remarked that " . . . this species may possibly be a member of *Pamphorichthys* Regan."

Poecilia heterandria (Regan)

Limia heterandria.—REGAN, 1913b, p. 1017 (original description; La Guaira, Venezuela; syntypes, B.M.N.H.).

MATERIAL: All from Venezuela, and all in the Museum of Zoology of the University of Michigan. Río Guaiguaza, 3 kilometers west of Puerto Cabello. "Bajo seco," east side of Puerto Cabello in brackish water. Lagoon 2 kilometers northwest of Ocumare on flats near mouth of Río Cumboto. Río Barburata, at mouth, 3 kilometers east of Puerto Cabello, at Guañango. Río Alpargaton, 5 kilometers north of Morón. Boca Yaracuy, 4 kilometers northwest of Puerto Cabello. Lagoons, Tucacas, 60 kilometers northwest of Puerto Cabello. Río Noguera, at Noguera.

RANGE: Venezuela.

REMARKS: Myers (1931) thought that *Heterandria zonata* Nichols and *Limia heterandria* Regan were the same, that Regan's record was probably erroneous, and that the species is confined to Hispaniola (Samaná Peninsula, Dominican Republic). Recently *heterandria* was re-collected (see above), and it is now evident that Regan's original record is valid, and that the species is Venezuelan and not West Indian. The question of its

[1] Hubbs and Hubbs's (1945) figure 2 of the pelvic fin of *P. minor* does not show the notches.

alignment in the genus is less clear; in the bony details of the gonopodium *P. heterandria* is closest to *minor* and *hollandi* of this subgenus. It is unique in the genus, however, in lacking all trace of a gonopodial palp, and in most features of the pelvic fins it resembles members of the subgenus *Lebistes*. As in *Pamphorichthys*, the pelvic-fin insertion of *heterandria* is more advanced than in members of the other subgenera but somewhat less so than in *minor* or *hollandi*.

SUBGENUS **LIMIA** POEY

DIAGNOSIS: Gonopodium without spines on ray 3; no claw at tip of ray 5a; a tough, membranous, or bony hook projecting downward from tip of ray 3; edentate distal segments on ray 4p in every case higher than long; distal segment arc of ray 5 bending abruptly downward toward ray 4p; ray 5p extending distally to within 10 to 15 segments of tip of ray 5a. Pelvic fin of adult male with small to moderate fleshy swelling distally on ray 1 and long finger-like extension of tip of ray 2; ray 2 not much thickened and rarely with bony prominence; rays 1 and 2 joined firmly with dense connective tissue and separated from rays 3 to 5 by distinct notch (in *caudofasciata* inner portion of notch secondarily covered by delicate membrane); a variably developed fleshy thickening at tip of ray 3; rays 3 to 5 joined distally by uninterrupted membrane that may be smooth, slightly crinkled, or heavily folded. Pelvic insertion of adult male at level of fourth to sixth pleural ribs.

Caudal fin in some members of subgenus, particularly males, possessing angulate upper margin from which posterior margin of fin extends obliquely downward and forward.

RANGE AND SPECIES COMPOSITION: Eleven species confined to the Greater Antilles.

Poecilia vittata Guichenot

Text figures 22I, 25F

Poecilia vittata.—GUICHENOT, 1853, pp. 2, 146; 1855, atlas, pl. 5, fig. 1 (original description; Cuba; syntypes, M.N.H.N.P. No. 4398). *Limia vittata*.—POEY, 1854, pp. 381, 389–390. *Gambusia vittata*.—BLEEKER, 1860, p. 485.

Limia cubensis.—POEY, 1854, pp. 381, 388, 390 (original description; Havana, Cuba; syntypes, M.C.Z. No. 6403, A.N.S.P. No. 6814, U.S.N.M. No. 120419). *Gambusia cubensis*.—BLEEKER, 1860, p. 485. *Poecilia cubensis*.—GÜNTHER, 1866, p. 340.

Limia pavonina.—POEY, 1876, p. 142 (original description; Havana, Cuba; syntypes, M.C.Z. No. 6400).

MATERIAL: All from Cuba: A.N.S.P. Nos. 6815–6817. San Cristobal; U.M.M.Z. No. 65257. Guanimar; A.N.S.P. Nos. 37135–37139. Streams of central highway, 19 kilometers west of Victoria de las Quinas, Oriente; in the University of Miami Ichthyological Museum. Pinar del Río; C.A.S. No. 9711. Calabazar; U.M.M.Z. No. 61464.

RANGE: Cuba.

Poecilia perugiae (Evermann and Clark)

Platypoecilus perugiae.—EVERMANN AND CLARK, 1906, pp. 851, 853 (original description; San Francisco Mountains, Santo Domingo; holotype, U.S.N.M. No. 53278). *Limia perugiae*.—JORDAN, EVERMANN, AND CLARK, 1930, p. 191.

RANGE: Dominican Republic.

Poecilia melanonotata (Nichols and Myers)

Text figure 22J

Limia melanonotata.—NICHOLS AND MYERS, 1923, p. 1 (original description; Las Lajas, on Étang Saumâtre, Santo Domingo [Haiti]; holotype, A.M.N.H. No. 8220).

MATERIAL: Spring at Dessalines, l'Artibonite, Haiti; in the University of Miami Ichthyological Museum. Trou Caiman, Haiti; U.M.M.Z. No. 167231.

RANGE: Haiti.

Poecilia nigrofasciata (Regan)

Text figure 22H

Limia nigrofasciata.—REGAN, 1913b, p. 1015 (original description; Miragoâne, Haiti; syntypes, B.M.N.H.).

Limia arnoldi.—REGAN, 1913b, p. 1016 (original description; Miragoâne, Haiti; syntypes, B.M.N.H.).

MATERIAL: Étang Saumâtre, Haiti; U.M.M.Z. No. 167223. Lake Miragoâne, north end of lake, Departement du Sud, Haiti; in the University of Miami Ichthyological Museum.

RANGE: Haiti.

Poecilia ornata (Regan)

Text figure 19C

Limia ornata.—REGAN, 1913b, p. 1016 (original description; Haiti; syntypes, B.M.N.H.).

MATERIAL: Lake Miragoâne, southwest end of lake, Departement du Sud, Haiti; in the University of Miami Ichthyological Museum.

RANGE: Haiti.

Poecilia melanogaster Günther

Poecilia melanogaster.—GÜNTHER, 1866, pp. 345–346 (original description; locality unknown but possibly Jamaica; syntypes, B.M.N.H.). *Limia melanogaster.*—MYERS, 1935, pp. 313–314.

Limia caudofasciata tricolor.—STOYE, 1933, pp. 12–14 (original description; small stream near Kingston, Jamaica; location of types unknown, said by Myers, 1935, p. 314, to have been deposited by Stoye in the Museum of Zoology of the University of Michigan). *Limia tricolor.*—STOYE, 1935, pp. 65–66.

RANGE: Jamaica.

Poecilia caudofasciata (Regan)

Limia caudofasciata.—REGAN, 1913b, p. 1017 (original description; Jamaica; syntypes, B.M.N.H.).

MATERIAL: Black River, spa spring at Black River town (200 yards from sea), Jamaica; in the University of Miami Ichthyological Museum. Jamaica; A.N.S.P. No. 6-288-90.

RANGE: Jamaica.

Poecilia dominicensis Valenciennes

Poecilia dominicensis.—VALENCIENNES, *in* Cuvier and Valenciennes, 1846, p. 131 (original description; Haiti, Santo Domingo; syntypes, M.N.H.N.P. Nos. 1893, 4390; syntypes, B.M.N.H.). *Limia dominicensis.*—REGAN, 1913b, p. 1015.

MATERIAL: Riviere Grise at bridge of road from Port-au-Prince to St. Marc, about 5 miles northeast of Port-au-Prince, Haiti; in the University of Miami Ichthyological Museum. Jeremie, Haiti; M.C.Z. No. 1417.

RANGE: Hispaniola.

Poecilia zonata (Nichols)

Heterandria zonata.—NICHOLS, 1915, p. 603 (original description; Samaná Peninsula, Santo Domingo; holotype, A.M.N.H. No. 5232).

RANGE: Samaná Peninsula, Dominican Republic.

REMARKS: See comments under *P. heterandria* (Regan).

Poecilia nicholsi (Myers)

Heterandria versicolor.—NICHOLS, 1915, p. 603 (not of Günther; description and figures; San Juan River at Samaná, Santo Domingo; holotype, A.M.N.H. No. 5239a).

Limia nicholsi.—MYERS, 1931, p. 1 (renamed from Nichols' material).

MATERIAL: Río Camir, 9 kilometers west of La Vega, La Vega, Dominica; in the University of Miami Ichthyological Museum.

RANGE: San Juan River, Samaná, Dominican Republic.

Poecilia versicolor (Günther)

Girardinus versicolor.—GÜNTHER, 1866, p. 352 (original description; Santo Domingo; types, B.M.N.H.). *Limia versicolor.*—REGAN, 1913b, p. 1017.

?Poecilia dominicensis.—GÜNTHER, 1866, p. 346 (not of Valenciennes; in part; Santo Domingo; excluding Barbados material).

?Poecilia (Acropoecilia) tridens.—HILGENDORF, 1889, p. 52 (original description; Port-au-Prince, Haiti).

MATERIAL: Río Yaguajal at Santiago Rodriguez, Monte Cristi, Dominican Republic; in the University of Miami Ichthyological Museum. Dominican Republic; U.S.N.M. No. 89002.

RANGE: Hispaniola.

REMARKS: We follow Myers (1935) on the synonymy of this form.

GENUS **PRIAPELLA** REGAN

Text figures 20A, 21E, 24A, 25H

Priapella.—REGAN, 1913b, p. 992 (type species, by monotypy, *Gambusia bonita* Meek).

DIAGNOSIS: In skull, parietals well developed, extending along lateral posterior margin of frontal, becoming spatulate medially; epiotic processes small or obsolescent; supraoccipital processes well developed, broad and spatulate; posttemporal forked; marginal jaw teeth recurved, conical. Distal tips only of posterior pleural ribs in male bent sharply forward and converging. Gonopodial suspensorium with three long, slender gonapophyses that lack uncini and are inclined moderately or slightly forward, each with pair of small curvilinear parapophyses originating near its base; frequently with pair of parapophyses on first unmodified hemal spine, as in *Alfaro;* ligastyle long, slender, and rod-like, rarely

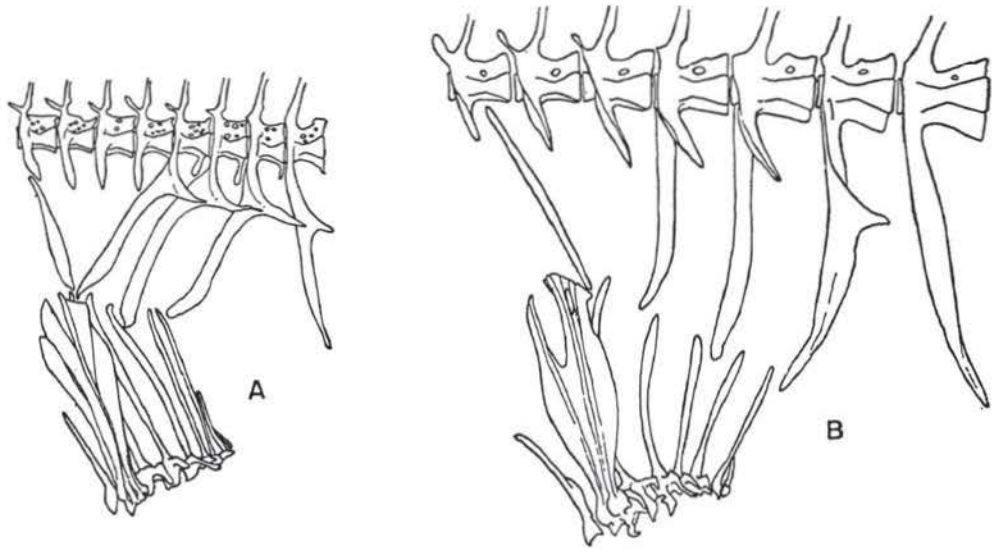


FIG. 24. Gonopodial suspensoria in the Poeciliini. A. *Priapella compressa*, A.M.N.H. No. 20440. B. *Xiphophorus montezumae*, U.M.M.Z. No. 124374.

with two ventral rami; primary gonactinostal complex like that of *Xiphophorus*, moderately dilated anteroposteriorly, inclined slightly forward, upper edge deeply notched. Gonopodium bilaterally symmetrical; ray 3 terminating in long, bony hook that is followed by three to five simple oblong segments and a series of from 10 to 20 spines; thin crescent of tough membranous tissue dorsally on terminal hook of ray 3 that is similar to but smaller than blade in *Xiphophorus*, distal ramus of ray 4a curving downward over this membranous covering; rays 4p and 5 stopping abruptly 10 to 12 segments proximal to tip of 4a; 4p subdistally with approximately 10 paired, retrorse serrae; ray 5 without terminal modifications. Pelvic fin rather large but without terminal modification.

RANGE AND SPECIES COMPOSITION: Streams from the Río Papaloapan to the Río Grijalva, tributary to the Gulf of Campeche, southeast Mexico (map 3). Three species.

Priapella bonita (Meek)

Gambusia bonita.—MEEK, 1904, p. 132 (original description; Refugio, Veracruz, Mexico; types, C.N.H.M. No. 4630, two adult females, 33.5 and 42.0 mm. in standard length). *Priapella bonita.*—REGAN, 1913b, p. 993.

RANGE: Refugio and Motzorongo, upper reaches of the Río Tonto, Río Papaloapan system, Veracruz, Mexico.

Priapella intermedia Alvarez

Text figure 20A

Priapella intermedia.—ALVAREZ, 1952a, pp. 284–286, 289 (original description; Santa Maria Chimalapa, in Arroyo El Zacatal, Oaxaca, Mexico; holotype in collection of José Alvarez).

MATERIAL: Topotypic material; U.S.N.M. No. 162502, S.U. No. 17486.

RANGE: Upper reaches of the Río Coatzacoalcos system, Oaxaca, Mexico.

Priapella compressa Alvarez

Text figures 21E, 24A, 25H

Priapella compressa.—ALVAREZ, 1948a, pp. 334-335, 338–340 (original description; Palenque ruins, Chiapas, Mexico; holotype in collection of José Alvarez).

MATERIAL: Topotypic material; A.M.N.H. No. 20440.

RANGE: Palenque ruins, Río Grijalva system, Chiapas, Mexico.

GENUS **XIPHOPHORUS** HECKEL

Plate 1, figures 3–5; text figures 20B, 21F, 24B, 25G

Xiphophorus.—HECKEL, 1848, p. 291 (type species, by subsequent restriction of Günther,

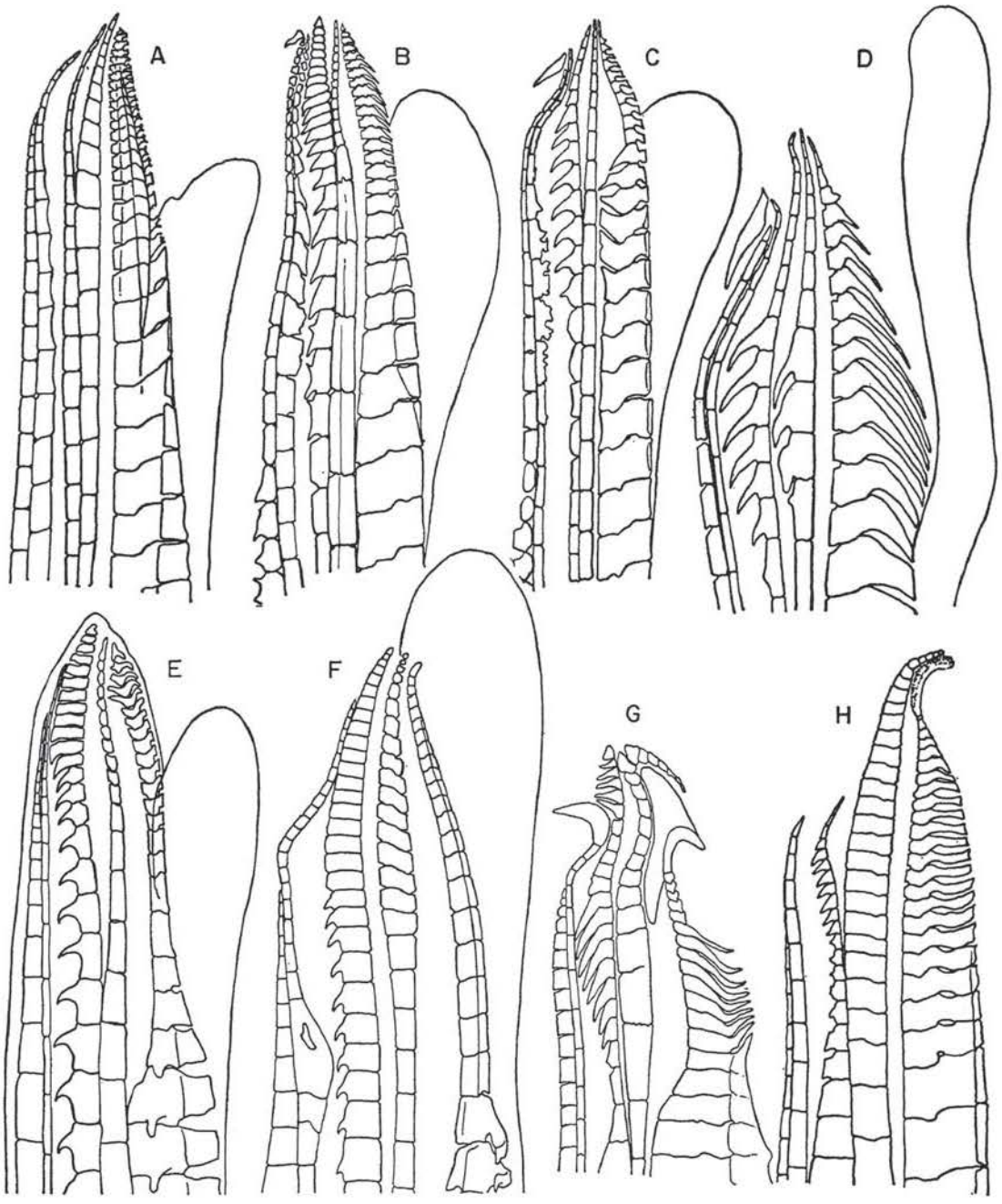


FIG. 25. Gonopodia in the Poeciliini. A. *Alfaro cultratus*, U.M.M.Z. No. 159157. B. *Poecilia caucana*, U.M.M.Z. No. 155052. C. *Poecilia elegans*, U.M.M.Z. No. 160661. D. *Poecilia reticulata*, aquarium specimen. E. *Poecilia minor*, from Rosen and Gordon (1953). F. *Poecilia vittata*, same source. G. *Xiphophorus helleri*, from Rosen (1960). H. *Priapella compressa*, A.M.N.H. No. 20440.

1866, pp. 349–350, *Xiphophorus Hellerii* Heckel).

Platypoecilus.—GÜNTHER, 1866, pp. 350–351 (type species, by monotypy, *Platypoecilus maculatus* Günther).

DIAGNOSIS: In skull, parietals very small, in some cases each subdivided into two or three separate ossifications, or very large and extending from epiotic processes laterally to cover a portion of sphenotic-pterotic commissure; supraoccipital processes well developed, epiotic processes strongly or weakly developed, or absent; posttemporal forked; marginal jaw teeth compressed. Distal tips only of posterior pleural ribs in males of some species bent slightly forward. Gonopodial suspensorium with three erect, more or less linear gonapophyses that lack uncini; parapophyses present and well developed on first and second gonapophyses, variously developed or absent on third; irregular osseous thickenings or nubbins rarely visible at locus of uncini; ligastyle long and rod-like, almost as long as first gonapophysis; primary gonactinostal complex moderately dilated anteroposteriorly, inclined slightly forward, upper edge deeply notched. Gonopodium bilaterally symmetrical; ray 5a forming broad, lanceolate platform that is flanked by erect, ridge-like elements of 5p; whole framework forming long, shallow, trough-like area; ultimate segment of 5a usually modified as claw or hook; ray 4p terminated by erect distal and retrorse subdistal serrae, two series separated by several simple oblong or cuboidal segments; proximal portion of 4p developed as compressed ridge of raised, slender segments directly beneath lanceolate platform of ray 5a; ray 4a simple, except distally where it is modified as ramus that arches or hooks ventrally (anteriorly); well-developed hook at terminus of ray 3, followed by several irregularly oval or cuboidal subterminal segments and series of large, more or less erect spines with angulated shafts; dense blade of tough, membranous tissue separating tips of rays 3 and 4a, its anterior edge merging with hook (ray 3), its posterior edge following contour of terminal ramus (ray 4a); posterior margin of ray 3 proximal to spines raised to meet anterior margin of ray 4a; tips of rays 6 and 7 swollen and club-shaped. Pelvic fin of male with fleshy appendage developed along distal third of first short, unbranched ray, second and third rays somewhat prolonged.

REMARKS: Many of the species in this genus have the lower caudal fin rays developed into a pointed, pigmented appendage, the "sword."

RANGE AND SPECIES COMPOSITION: Atlantic coastal drainages from northern Mexico southeast to northern Honduras (map 5). *Xiphophorus* was reviewed by Rosen (1960), who recognized eight species and 15 forms. These were arranged in three species groups, as follows: the *maculatus* species group: *couchianus*, *maculatus*, and *variatus* (the last two regarded as a well-defined superspecies); the *montezumae* species group: *milleri*, *montezumae*, and *pygmaeus;* and the *helleri* species group: *clemenciae* and *helleri*.

Xiphophorus couchianus (Girard)

NORTHERN PLATYFISH

Text figure 21F

Limia couchiana.—GIRARD, 1859c, p. 116 (original description; Monterrey). *Gambusia couchiana*.—BLEEKER, 1860, p. 485. *Mollienesia couchiana*.—JORDAN AND COPELAND, 1876, p. 143. *Poecilia couchiana*.—JORDAN AND GILBERT, 1883, p. 348. *Platypoecilus couchianus*.—REGAN, 1913b, pp. 1003–1004. *Xiphophorus couchianus*.—ROSEN AND GORDON, 1953, p. 23. ROSEN, 1960, pp. 66–69 (characters; distribution).

Poecilia couchii.—GÜNTHER, 1866, p. 347 (emendation of *couchiana*).

Platypoecilus variatus.—RACHOW, 1936, sheets 145–146 (in part; erroneous synonymic reference).

Xiphophorus gordoni.—MILLER AND MINCKLEY, 1963, pp. 540–548 (original description; outlet of Laguna Santa Tecla, about 10 miles south-southeast of El Candido, Coahuila, Mexico; holotype, U.M.M.Z. No. 179866).

RANGE: Río Grande basin in Coahuila (A.M.N.H. No. 20448) and Nuevo León, Mexico.

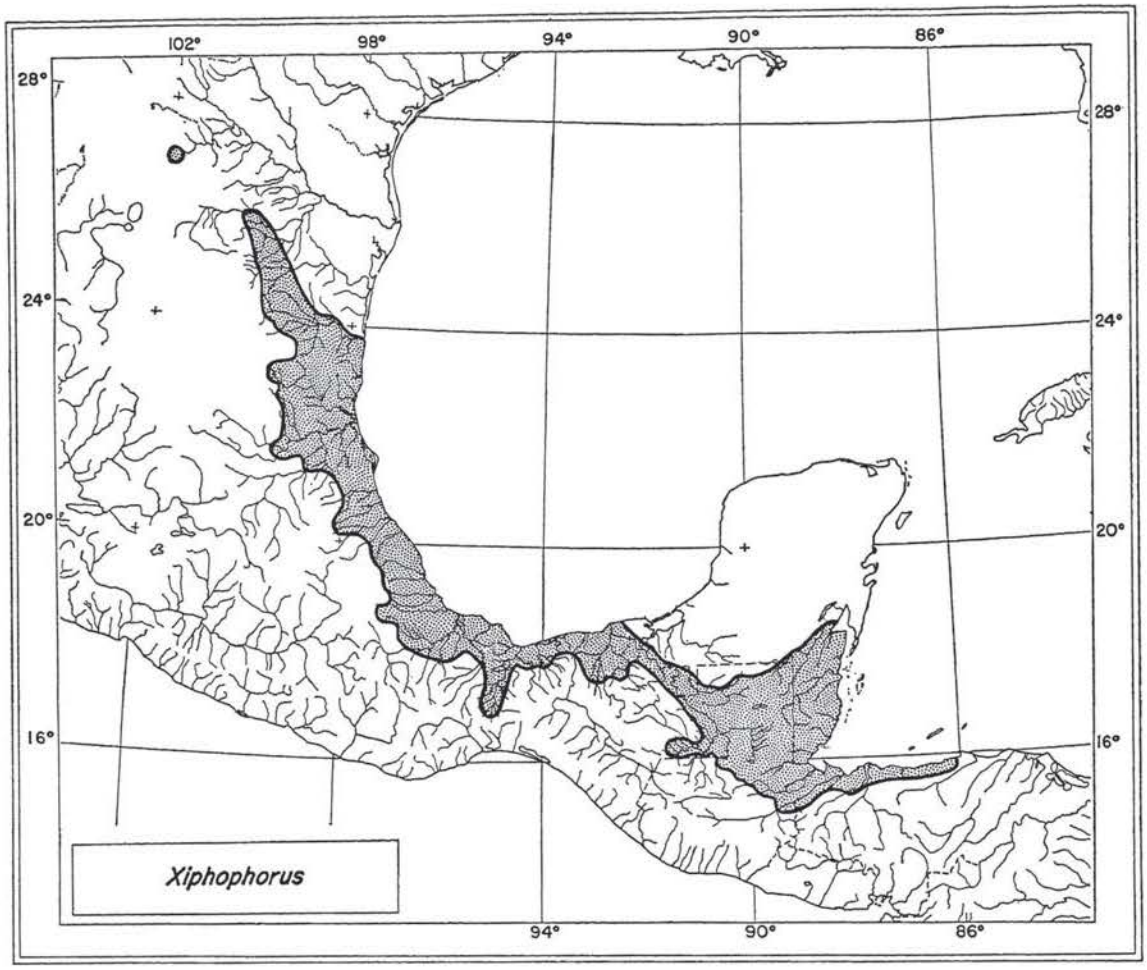
REMARKS: Two subspecies can be recognized: *X. c. gordoni* Miller and Minckley, Coahuila; and *X. c. couchianus* (Girard), Nuevo León (Kallmann and Rosen, MS).

Xiphophorus maculatus (Günther)

SOUTHERN PLATYFISH

Plate 1, figures 3–5

Platypoecilus maculatus.—GÜNTHER, 1866, pp. 350–351 (original description; Mexico; syntypes, B.M.N.H.). *Poecilia maculata*.—REGAN, 1906–



MAP 5. Distribution of *Xiphophorus*.

1908, p. 105 (in part). *Platypoecilia maculata.*—TAUBLES, 1916, p. 16. *Xiphophorus* (*Platypoecilus*) *maculatus.*—GORDON, 1952, p. 91. *Xiphophorus maculatus.*—GORDON, 1953, p. 192. ROSEN, 1960, pp. 69–78 (characters; distribution).

Platypoecilus nigra.—BRIND, 1914, p. 22 (original description; southern Mexico). *Platypoecilus maculata nigra.*—BRIND, 1919, p. 167. *Platypoecilus maculatus niger.*—MYERS, 1922, p. 15. *Platypoecilus maculatus nigra.*—STOYE, 1935, p. 51.

Platypoecilus pulchra.—BRIND, 1914, p. 22 (original description; as aquarium fish). *Platypoecilus maculatus pulcher.*—MYERS, 1922, p. 15. *Platypoecilus maculatus pulchre.*—TROEMNER, 1943, pp. 1–3.

Platypoecilus rubra.—BRIND, 1914, p. 22 (original description; as aquarium fish). *Platypoecilus maculatus ruber.*—MYERS, 1922, p. 15.

Platypoecilus maculatus immaculatus.—MYERS, 1922, p. 15 (original description; as aquarium fish).

Platypoecilus maculatus cyanellus.—MEINKEN, 1934, pp. 261–263 (original description; as aquarium fish).

Platypoecilus maculatus aurata.—STOYE, 1935, p. 51 (original description; as aquarium fish).

Platypoecilus maculatus sanguinea.—STOYE, 1935, p. 51 (original description; as aquarium fish).

RANGE: Veracruz, Mexico, to northern British Honduras, usually at low elevations.

REMARKS: The several names based on aquarium varieties (see synonymy) are not represented by name-bearing types.

Xiphophorus variatus (Meek)

VARIABLE PLATYFISH

Text figure 20B

Platypoecilus variatus.—MEEK, 1904, pp. 146–

147 (original description; Valles, San Luis Potosí, Mexico; holotype, C.N.H.M. No. 4501). *Platypoecilus variatus variatus.*—GORDON, 1940, p. 172. *Xiphophorus (Platypoecilus) variatus.*—ARONOWITZ, NIGRELLI, AND GORDON, 1951, pp. 239–240. *Xiphophorus variatus.*—ROSEN, 1960, pp. 78–79 (characters; distribution). *Xiphophorus variatus variatus.*—ROSEN, 1960, pp. 84–87.

Poecilia maculata.—REGAN, 1906–1908, p. 105 (in part). *Platypoecilus maculatus.*—REGAN, 1913b, p. 1004 (in part).

Mollienisia formosa (misidentification, not *Limia formosa* Girard).—RACHOW, 1932, p. 705. *Mollienesia formosa* (misidentification).—WHEELER AND INGLE, 1953, p. 266.

Platypoecilus xiphidium.—GORDON, 1932a, p. 287 (original description; locality given in 1932b, p. 89, as Río Soto la Marina; lectotype, designated by Rosen, 1960, p. 83, U.M.M.Z. No. 97573). *Platypoecilus xiphodium* (misspelling).—NEEDHAM, 1942, p. 387. *Platypoecilus xiphidinus* (*lapsus* for *xiphidium*).—MAYR, 1942, p. 171. *Xiphophorus xiphidium.*—ROSEN AND GORDON, 1953, pp. 23, 47. *Xiphophorus variatus xiphidium.*—ROSEN, 1960, pp. 81–84.

Platypoecilus variatus dorsalis.—STOYE, 1933, pp. 306–307 (*nomen nudum*).

Xiphophorus variatus evelynae.—ROSEN, 1960, pp. 87–89 (original description; Tepexic, Puebla, Mexico; holotype, U.M.M.Z. No. 177306).

RANGE: Atlantic slope of eastern Mexico, from southern Tamaulipas, eastern San Luis Potosí, and northern Veracruz, at elevations of 100 to 4000 feet.

REMARKS: Rosen (1960) recognized three subspecies: *X. v. xiphidium* (Gordon), Río Soto la Marina system, Tamaulipas; *X. v. variatus* (Meek), Río San Rafael, Tamaulipas, to Río Nautla system, Veracruz; and *X. v. evelynae* Rosen, Río Tecolutla system, Puebla.

Xiphophorus milleri Rosen

CATEMACO LIVEBEARER

Xiphophorus milleri.—ROSEN, 1960, pp. 89–92 (original description; Laguna Catemaco, Veracruz, Mexico; holotype, U.M.M.Z. No. 177308).

RANGE: Laguna Catemaco, Veracruz, Mexico.

Xiphophorus montezumae Jordan and Snyder

MONTEZUMA SWORDTAIL

Text figure 24B

Xiphophorus montezumae.—JORDAN AND SNYDER, 1900, pp. 131–133 (original description; Río Verde, near Rascón, San Luis Potosí; holotype, S.U. No. 6145). ROSEN, 1960, pp. 92–98 (characters; distribution). *Xiphophorus montezumae montezumae.*—ROSEN, 1960, pp. 93–96.

Platypoecilus variatus (misidentification).—C. H. PETERS, 1933, p. 9.

Xiphophorus montezumae cortezi.—ROSEN, 1960, pp. 96–98 (original description; Comoca, Río Panuco basin, San Luis Potosí, Mexico; holotype, U.M.M.Z. No. 177302).

RANGE: Río Tamesí and Río Panuco basins, Tamaulipas and San Luis Potosí, Mexico.

REMARKS: Rosen (1960) recognized two subspecies: *X. m. montezumae* Jordan and Snyder, drainages of the Río Tamesí, Tamaulipas, and the Río Salto of the Río Panuco system, San Luis Potosí; and *X. m. cortezi* Rosen, drainage of the Río Moctezuma of the Río Panuco system, San Luis Potosí.

Xiphophorus pygmaeus Hubbs and Gordon

PYGMY SWORDTAIL

Xiphophorus pygmaeus.—HUBBS AND GORDON, 1943, pp. 31–33 (original description; Río Axtla, San Luis Potosí, Mexico; holotype, U.M.M.Z. No. 124365). ROSEN, 1960, pp. 98–103 (characters; distribution). *Xiphophorus pygmaeus pygmaeus.*—ROSEN, 1960, pp. 102–103.

Xiphophorus pygmaeus nigrensis.—ROSEN, 1960, pp. 100–102 (original description; Río Choy, San Luis Potosí, Mexico; holotype, U.M.M.Z. No. 177301).

RANGE: Río Panuco basin, San Luis Potosí, Mexico.

REMARKS: Rosen (1960) recognized two subspecies: *X. p. nigrensis* Rosen, Río Choy, Río Panuco system; and *X. p. pygmaeus* Hubbs and Gordon, drainage of the Río Axtla, Río Panuco system.

Xiphophorus clemenciae Alvarez

YELLOW SWORDTAIL

Xiphophorus clemenciae.—ALVAREZ, 1959, pp. 69–71 (original description; Río Sarabia, Oaxaca, Mexico; holotype, in collection of José Alvarez). ROSEN, 1960, pp. 104–106 (characters; distribution).

RANGE: Río Sarabia, Río Coatzacoalcos system, Oaxaca, Mexico.

Xiphophorus helleri Heckel

GREEN SWORDTAIL

Text figure 25G

Xiphophorus hellerii.—HECKEL, 1848, p. 291 (original description; "in einem klaren Bache des

Gebirges Orizaba in Mexico"). *Xiphophorus helleri.*—MEEK, 1904, p. 157. ROSEN, 1960, pp. 106–127 (characters; distribution). *Xiphophorus helleri helleri.*—DEL CAMPO, 1938, p. 226. ROSEN, 1960, pp. 116–118 (characters; distribution). *Xiphophorus hellerii hellerii.*—HUBBS AND GORDON, 1943, p. 32.

Xiphophorus guentheri.—JORDAN AND EVERMANN, 1896 (1896–1900), p. 702 (original description; Río Chisoy, Guatemala). *Xiphophorus hellerii guntheri.*—C. L. HUBBS, 1935b, pp. 10–11. *Xiphophorus helleri guentheri.*—ROSEN, 1960, pp. 122–126 (characters; distribution).

Xiphophorus jalapae.—MEEK, 1902, p. 107 (original description; Jalapa, Veracruz, Mexico; holotype, C.N.H.M. No. 3724).

Xiphophorus strigatus.—REGAN, 1907a, p. 65 (original description; Veracruz and Oaxaca). *Xiphophorus helleri strigatus.*—DE BUEN, 1940, p. 44. ROSEN, 1960, pp. 118–122 (characters; distribution). *Xiphophorus hellerii strigatus.*—HUBBS AND GORDON, 1943, p. 32.

Xiphophorus brevis.—REGAN, 1907a, p. 65 (original description; Stann Creek, British Honduras; syntypes, B.M.N.H.). *Xiphophorus hellerii brevis.*—HUBBS AND GORDON, 1943, p. 32.

Xiphophorus rachovii.—REGAN, 1911a, p. 373 (original description; Puerto Barrios, Guatemala; syntypes, B.M.N.H.).

Xiphophorus helleri alvarezi.—ROSEN, 1960, pp. 126–127 (original description; Río Santo Domingo, Río Usumacinta system, Chiapas, Mexico; holotype, U.M.M.Z. No. 177304).

RANGE: Atlantic drainage from Río Nautla, Veracruz, southward to northern Honduras.

REMARKS: Rosen (1960) recognized four subspecies: *X. h. helleri* Heckel, drainages of the Río Nautla, Río Chachalacas, Río Antigua, and Río Jamapa, Veracruz, Mexico; *X. h. strigatus* Regan, drainages of the Río Papaloapan and Río Coatzacoalcos, Veracruz, Mexico; *X. h. guentheri* Jordan and Evermann, Laguna de Sontecomapan, Veracruz, Mexico, to Atlantida, northern Honduras; and *X. h. alvarezi* Rosen, Río Jatate drainage, Chiapas, Mexico.

TRIBE CNESTERODONTINI

The four genera of this tribe are confined to eastern South America. They apparently lack typical parietal bones and have an unforked posttemporal bone. The gonopodium is long in all genera. *Cnesterodon*, *Phalloceros*, and *Phallotorynus* possess a unique type of bony style at the tip of the gonopodium, to which is affixed a membranous growth. The gonopodium of *Phalloptychus* is asymmetrical and shows considerable reduction of all terminal ornaments except the serrae on ray 4p. In all genera the pleural ribs are sexually dimorphic; in adult males several from the third to the tenth are curved forward along their lengths, with elongate distal extensions that converge on or approach the pelvic girdle.

Phalloceros, *Phallotorynus*, and *Phalloptychus* possess three long, rather straight suspensorial gonapophyses, each with a pair of long, pointed parapophyses near its attachment to a vertebra. *Cnesterodon* typically lacks gonapophyses in its gonopodial suspensorium, axial support being accomplished primarily via the ligastyle. Philippi (1909), however, noted the rare occurrence of small, abnormally developed gonapophyses in this genus. Rosen (1958) speculated that the more anterior position of the anal fin in *Cnesterodon* as compared with its position in the other three genera is related to absence of the modified hemals. A hypothesis was offered suggesting a possible developmental relationship to account for the missing structures, viz., that the developing appendicular elements may in some way determine the presence or absence of, and growth and form of, neighboring axial structures. Rosen and Kallman (1959) demonstrated that removal of the anal fin and actinosts prior to the onset of gonopodial morphogenesis results in the loss of gonapophyses or the formation of much-reduced and rather abnormal gonapophyses in *Poecilia reticulata* and *Phalloceros caudimaculatus*. In gonopodial structure, *Cnesterodon* and *Phalloceros* are quite similar.

We find no close relatives for this probably autochthonous South American tribe. Although their morphological and zoogeographic integrity is readily demonstrable, the genera are well differentiated. Hence, the group may be rather old.

GENUS PHALLOTORYNUS HENN

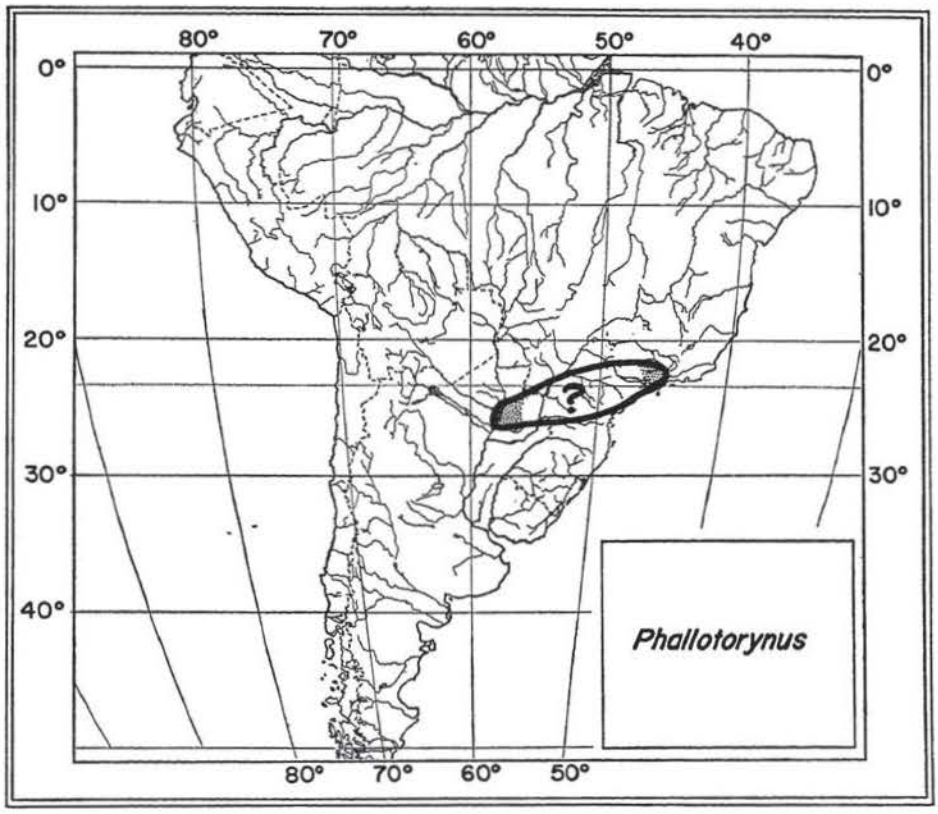
Text figures 26A, 27A, B, 29A, 31A, B

Phallotorynus.—HENN, 1916, pp. 95, 129 (type species, by original designation, *Phallotorynus fasciolatus* Henn).

DIAGNOSIS: In skull, parietals typically absent in adult females, frontal, however, extending backward over area normally occupied by parietals as bluntly triangular plate;

in male, two small, oval bones (parietals?) overlie part of supraoccipital, epiotic, and pterotic and are overlain by frontals which in this sex are evenly rounded posteriorly and not triangular; no epiotic processes; supraoccipital processes moderately developed, in some cases with small additional prongs near their bases in large adults; posttemporal not forked; marginal jaw teeth compressed. Fifth to tenth pleural ribs in male curved forward along their lengths, sixth to ninth or tenth ribs with elongate distal extensions that converge on or fall just short of pelvic girdle. Gonopodial suspensorium with three well-developed, long, slender, and sinuous gonapophyses that lack uncini and are bent sharply forward and downward toward appendicular elements; gonapophyses I, II, and III with paired, slender, and pointed parapophyses that extend outward and backward from base of shaft of spine; ligastyle well developed and rod-like or slightly bifid ventrally; primary gonactinostal complex variably notched dorsally, its superior and inferior lateral wings very broad and extending backward beyond tip of gonactinost 6. Gonopodium bilaterally symmetrical; ray 3 consisting mostly of ankylosed segments subdistally and forming near tip of fin massive, bony, elbow-like ventral prominence; at terminus of ray 3, which consists of series of minute subrectangular ossicles, a long, slender, antrorse, bony pedicel, composed of fused, paired elements, that supports a massive, largely membranous, backward-projecting flanged structure; bony pedicel at tip of ray 3 joined via connective tissues with ventral surface of tip of ray 4a; penultimately on ray 4p a series of five to eight retrorse serrae; on ray 5a, distal to underlying serrae of ray 4, bony segments bend downward at midline toward ray 4, exposing their strongly incised medial edges.

RANGE AND SPECIES COMPOSITION: Para-



MAP 6. Distribution of *Phallotorynus*.

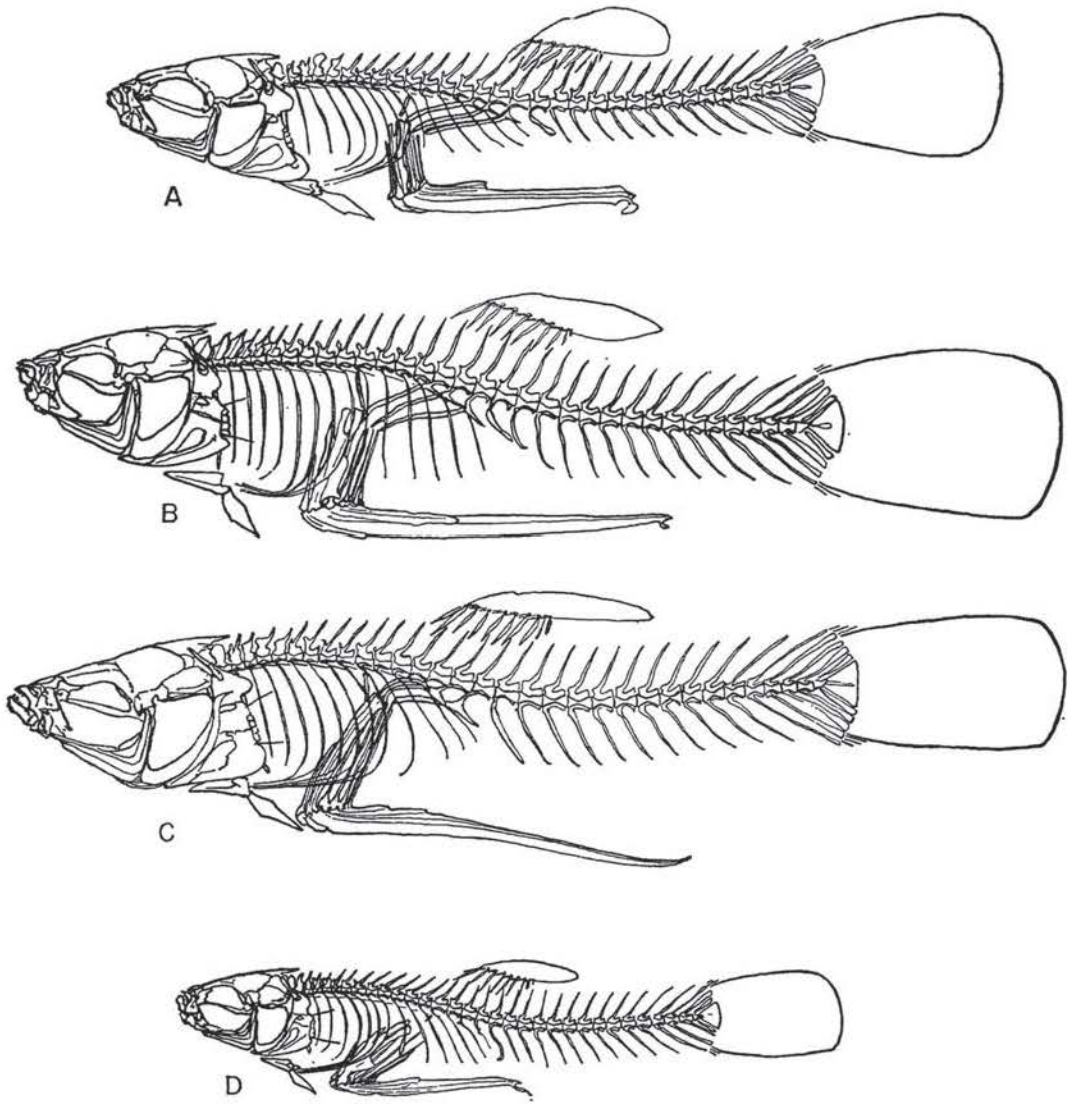


FIG. 26. Skeletons of adult males of the Cnesterodontini, composite drawings. A. *Phallotorynus jucundus*. B. *Phalloceros caudimaculatus*. C. *Phalloptychus januarius*. D. *Cnesterodon carnegiei*.

guay and southeastern Brazil (map 6). Two species.

Phallotorynus fasciolatus Henn

Text figures 27A, 29A, 31A,B

Phallotorynus fasciolatus.—HENN, 1916, pp. 95, 129 (original description; Jacarehy, São Paulo, Brazil; holotype, C.N.H.M. No. 55061). C. L. HUBBS, 1924, p. 9. R. VON IHERING, 1931, pp. 248, 267–268, 277. ROSEN AND GORDON, 1953, p. 28. FOWLER, 1954, p. 239.

MATERIAL: Jacarehy, São Paulo, Brazil; C.A.S. No. 13315, C.N.H.M. No. 55062.

RANGE: Basin of Río Paraíba, 1 mile north of Jacarehy, São Paulo, Brazil (Henn, 1916, p. 129).

Phallotorynus jucundus von Ihering

Text figure 26A

Phallotorynus jucundus.—R. VON IHERING, 1930, pp. 98–99 (original description; Corrego de Rinçao, São Paulo, Brazil). GUIMARAES, 1930, p. 783. R. VON IHERING, 1931, pp. 248, 267–268, 277. *Phallotorynus jacundus*.—FOWLER, 1954, p. 240 (*lapsus* for *jucundus*).

MATERIAL: Vicinity of Asunción, Paraguay; A.M.N.H. No. 20441.

RANGE: Basin of Río Paraná, São Paulo, Brazil, and Central, Paraguay.

GENUS **PHALLOCEROS** EIGENMANN

Text figures 26B, 27C, D, 29B, C, 31C, D

Phalloceros.—EIGENMANN, 1907, p. 431 (type species, by monotypy, *Girardinus caudimaculatus* Hensel).

DIAGNOSIS: In skull, parietals typically absent in adult females, frontal, however, extending backward over area normally oc-

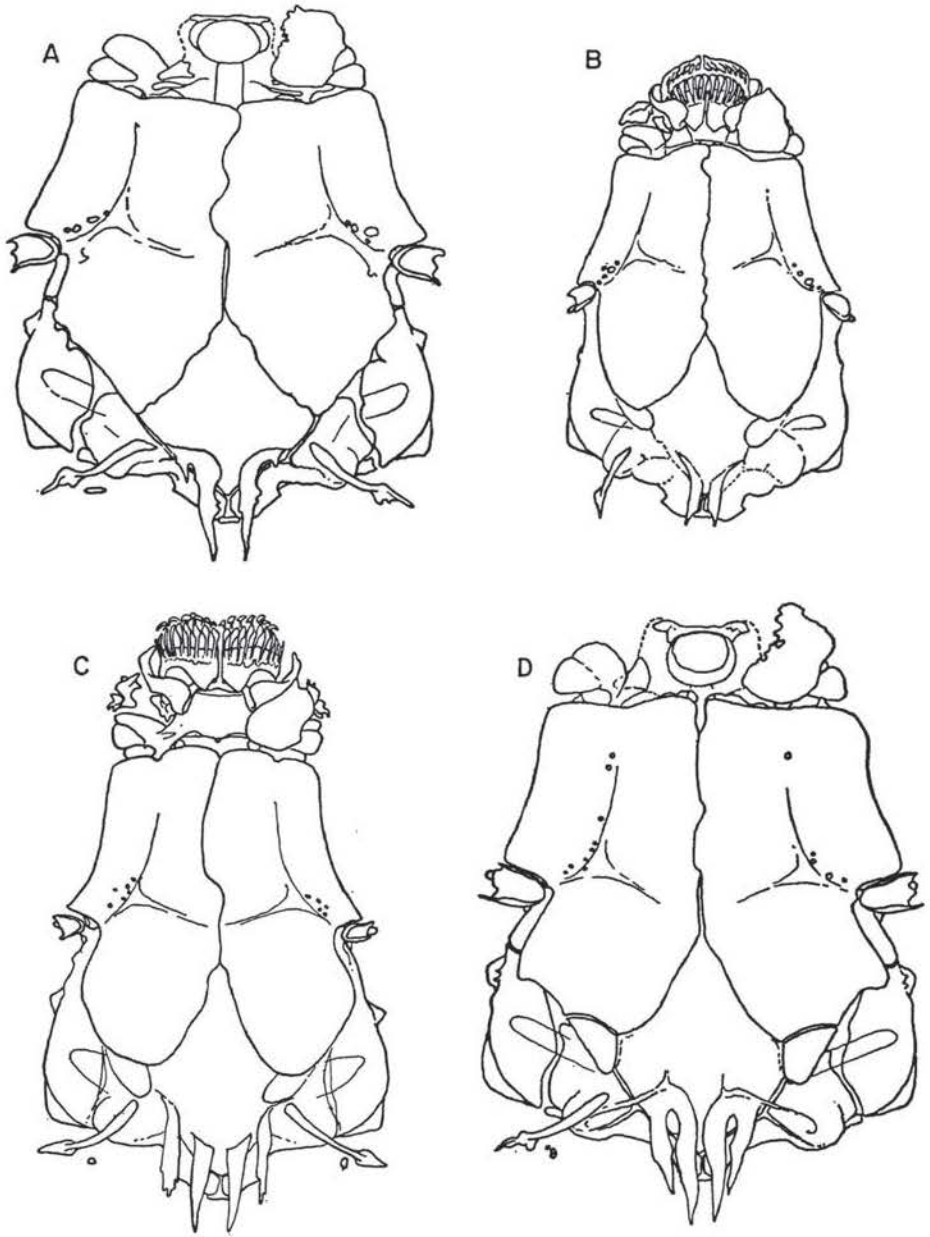


FIG. 27. Dorsicrania of the Cnesterodontini. A. *Phallotorynus fasciolatus*, female. B. Male of same. Both C.N.H.M. No. 55062. C. *Phalloceros caudimaculatus*, male. D. Female of same. Both C.N.H.M. No. 55886.

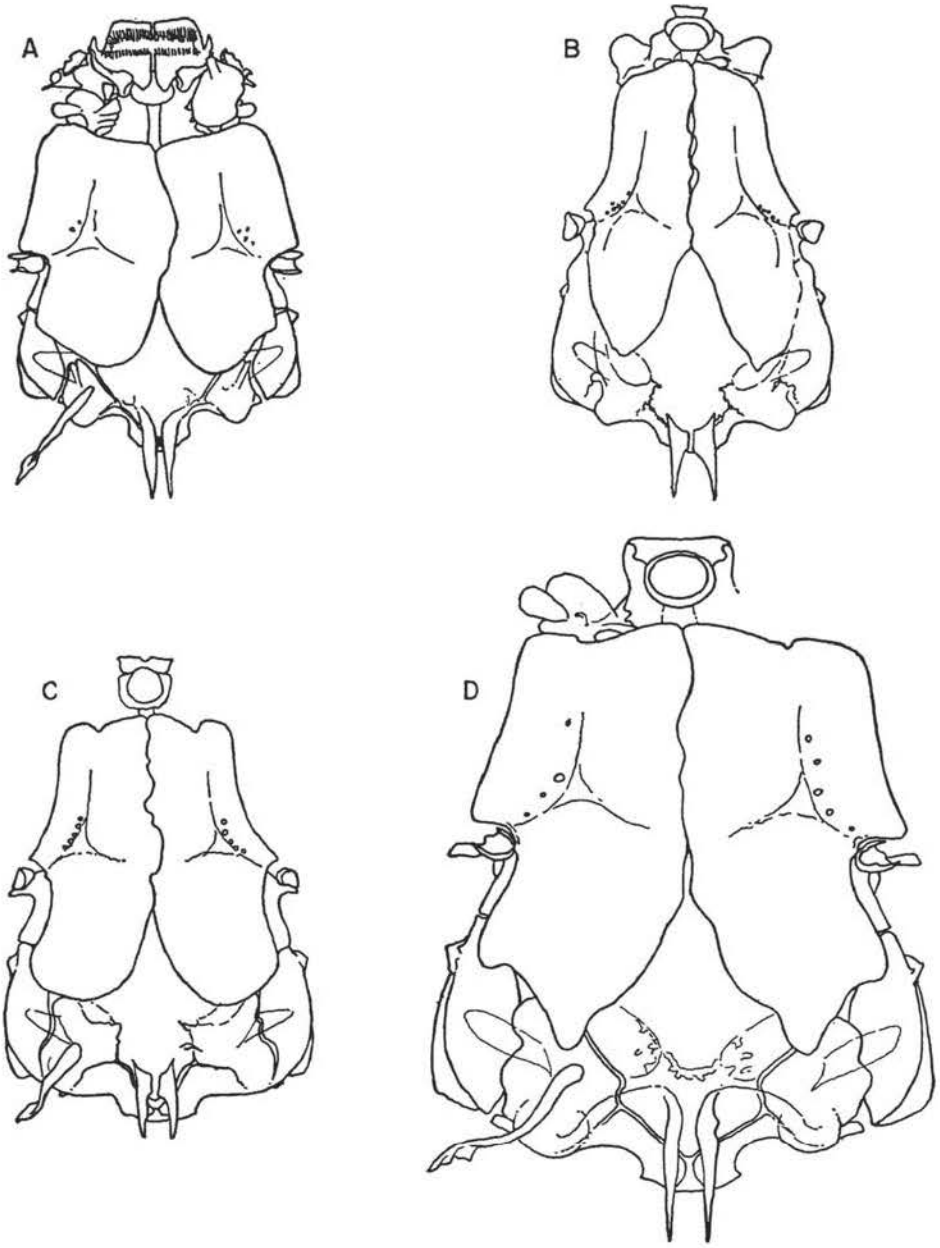


FIG. 28. Dorsicrania of the Cnesterodontini. A. *Phalloptychus eigenmanni*, female, C.N.H.M. No. 55877. B. *Cnesterodon decemmaculatus*, male, U.S.N.M. No.87826. C. *Cnesterodon carnegiei*, male. D. Female of same. Both C.N.H.M. No. 54248.

cupied by parietals as bluntly triangular plate, in many cases separated from main section by oblique, slightly arched, smooth suture line; in male, two small, oval bones (parietals?) overlying part of supraoccipital, epiotic, and pterotic and overlain by frontals which in this sex are evenly rounded posteriorly and not triangular; no epiotic processes; supraoccipital with two well-developed, paired processes, inner ones longer; posttemporal not forked but frequently with one or more minute, irregular, relict ossifications in ventral

ligament; marginal jaw teeth compressed. Fifth to tenth pleural ribs in male curved forward along their lengths, sixth to ninth ribs with elongate distal extensions that converge on or fall just short of pelvic girdle. Gonopodial suspensorium with three long, slender, slightly sinuous gonapophyses that lack uncini and are bent sharply forward; gonapophysis I bent downward at tip in long acinar process; gonapophyses I, II, and III with paired, slender, and pointed parapophyses that extend outward and backward from base of shaft of spine; ligastyle quite long and rod-like; primary gonactinostal complex typi-

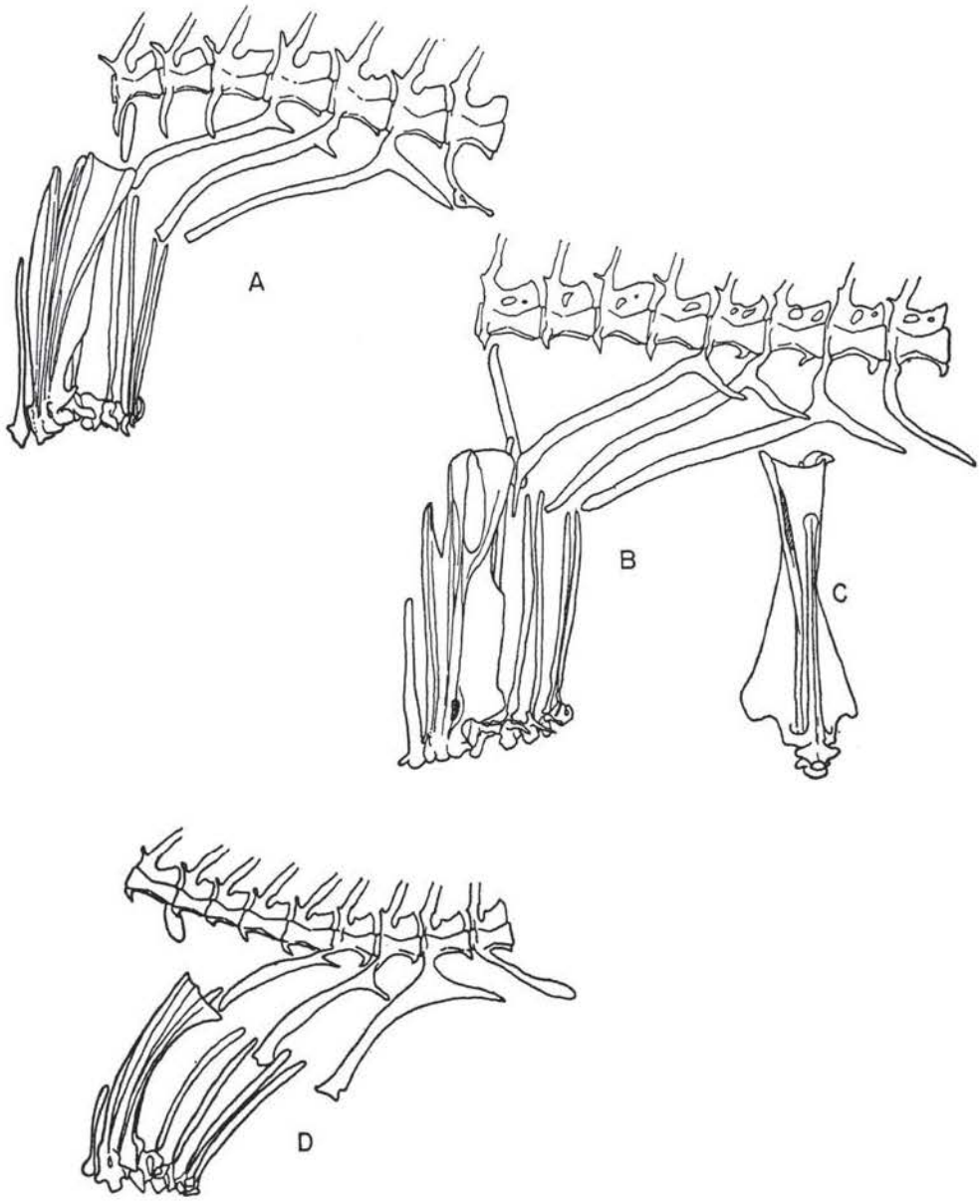
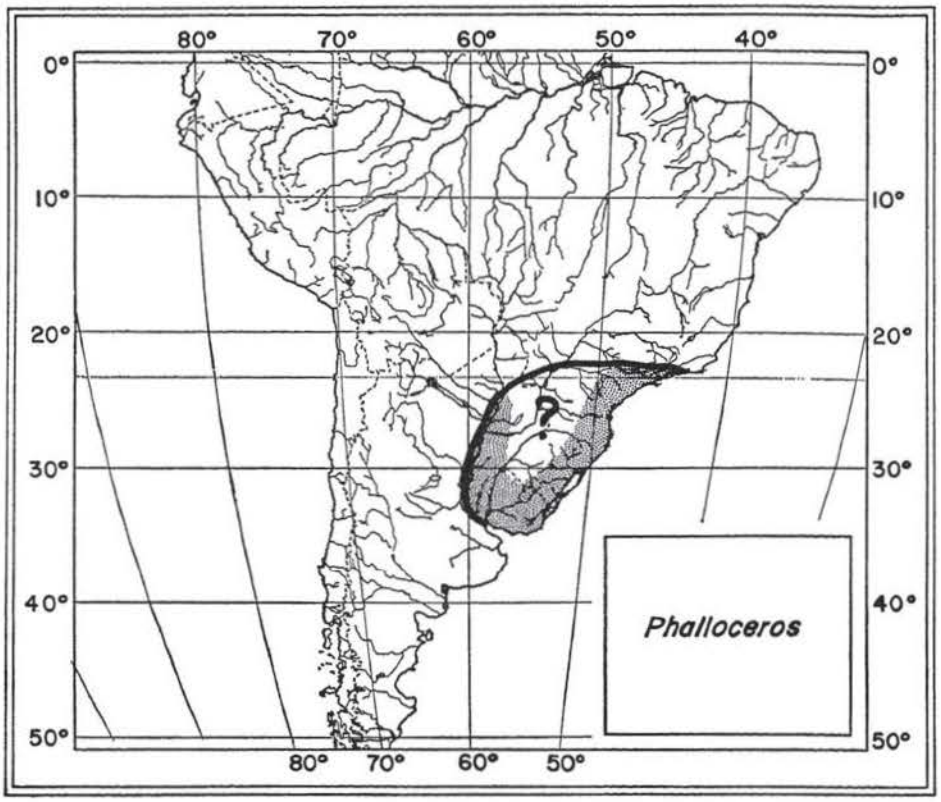


FIG. 29. Gonopodial suspensoria in the Cnesterodontini. A. *Phallotorynus fasciolatus*, C.N.H.M. No. 55062. B. *Phalloceros caudimaculatus*. C. Frontal three-quarter view of 2–3–4 complex of same. Both C.N.H.M. No. 55886. D. *Phalloptychus eigenmanni*, C.N.H.M. No. 55877.



MAP 7. Distribution of *Phalloceros*.

cally with two deep notches dorsally, one between incorporated elements 2 and 3 and other between last element and superior lateral wings; lateral wings well developed, upper elements extending backward, lower ones backward and outward away from midline. Gonopodium bilaterally symmetrical; ray 3 moderately ankylosed and without spinous processes; at tip of this ray, which consists of series of minute, subrectangular bony ossicles, a pair of long, slender, antrorse segments of general form and orientation of pedicel of *Phallotorynus;* these stylar segments, which join via connective tissues with ventral portion of tip of ray 4a, differing from those of *Phallotorynus* in having one or more minute denticles or spines ventrally and compressed, obovate end piece that is invested with large flap of membranous tissue; tips of rays 4a and 4p entering inflated membranous structure from which arises single, unpaired, inverted-teardrop-shaped bone; ray 4p subdistally with series of 10 to 15 weakly to moderately developed erect to retrorse serrae.

RANGE AND SPECIES COMPOSITION: Southeastern South America (map 7). Monotypic.

Phalloceros caudimaculatus (Hensel)

Text figures 26B, 27C, D, 29B, C, 31 C, D

Girardinus caudimaculatus.—HENSEL, 1868, p. 362 (original description; Río Grande do Sul). H. VON IHERING, 1883, pp. 468–469. EIGENMANN AND EIGENMANN, 1891, p. 65. COPE, 1894, p. 102. EIGENMANN AND NORRIS, 1900, p. 361. *Poecilia caudomaculatus.*—EIGENMANN, 1894, p. 636. *Glaridichthys caudimaculatus.*—PHILIPPI, 1904, p. 197. *Phalloceros caudomaculatus.*—EIGENMANN, 1907, p. 431; 1910, p. 458. REGAN, 1913b, p. 999. HENN, 1916, pp. 94, 99, 100–102, 104, 127. HILDEBRAND, 1917, pp. 6, 8. *Phalloceros caudimaculatus.*—FOWLER, 1916b, p. 437. R. VON IHERING, 1931, pp. 246, 267–268, 271, 274, 276–277.

Glaridodon januarius (misidentifications, not of Hensel).—GARMAN, 1895, p. 42. BERG, 1897, p. 289. SCHREINER AND MIRANDA RIBEIRO, 1903, p. 100. *Glaridichthys januarius* (misidentifica-

tions).—PHILIPPI, 1906, pp. 229–230; 1909, pp. 1–94. LANGER, 1913, pp. 195, 206, 227, 230, 232, 234, 261–263.

MATERIAL: Jacarehy, Río Paraíba, Brazil; C.N.H.M. No. 55886. Santa Anna, Brazil; M.C.Z. Nos. 6844, 6846.

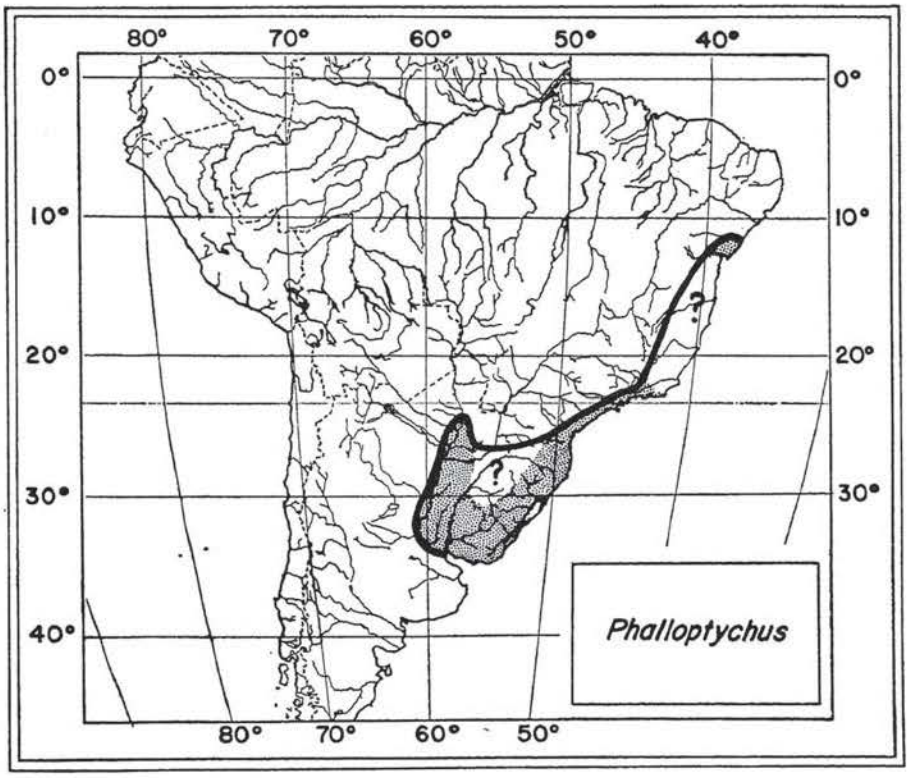
RANGE: Río de Janeiro to Uruguay and Paraguay (Henn, 1916, p. 125).

GENUS **PHALLOPTYCHUS** EIGENMANN

Text figures 26C, 28A, 29D, 31E

Phalloptychus.—EIGENMANN, 1907, p. 430 (type species, by monotypy, *Girardinus januarius* Hensel).

DIAGNOSIS: In skull, parietals absent, frontals not extending backward over area normally occupied by parietals and with smoothly rounded posterior margin; no epiotic processes; supraoccipital processes well developed; posttemporal not forked; marginal jaw teeth very small and numerous, rather cylindrical and bluntly pointed. Fifth to ninth or tenth pleural ribs in male curved forward along their lengths, sixth to ninth ribs with elongate distal extensions that converge on or fall just short of pelvic girdle. Gonopodial suspensorium with three long, slender, slightly sinuous gonapophyses that lack uncini and are bent sharply forward; gonapophyses I and II turned slightly downward at tips; gonapophyses II and III with heavy, terminal, knob-like structures; gonapophyses I, II, and III with paired, slender, and pointed parapophyses that extend outward and backward from the base of shaft of spine; ligastyle short and massive, loaf-shaped; primary gonactinostal complex rather compressed anteroposteriorly, incorporated elements curving backward toward gonapophysis I; dorsal margin of primary complex flat and entire; superior and inferior lateral wings moderately developed, extending laterally and slightly backward. Gonopodium sinistrally asymmetrical; segments of ray 3 not ankylosed and without spinous processes; segments of ray 4a ankylosed distally; ray 4p terminated by series of large, pointed, paired, retrorse serrae; tips of rays 4a and 4p invest-



MAP. 8. Distribution of *Phalloptychus*.

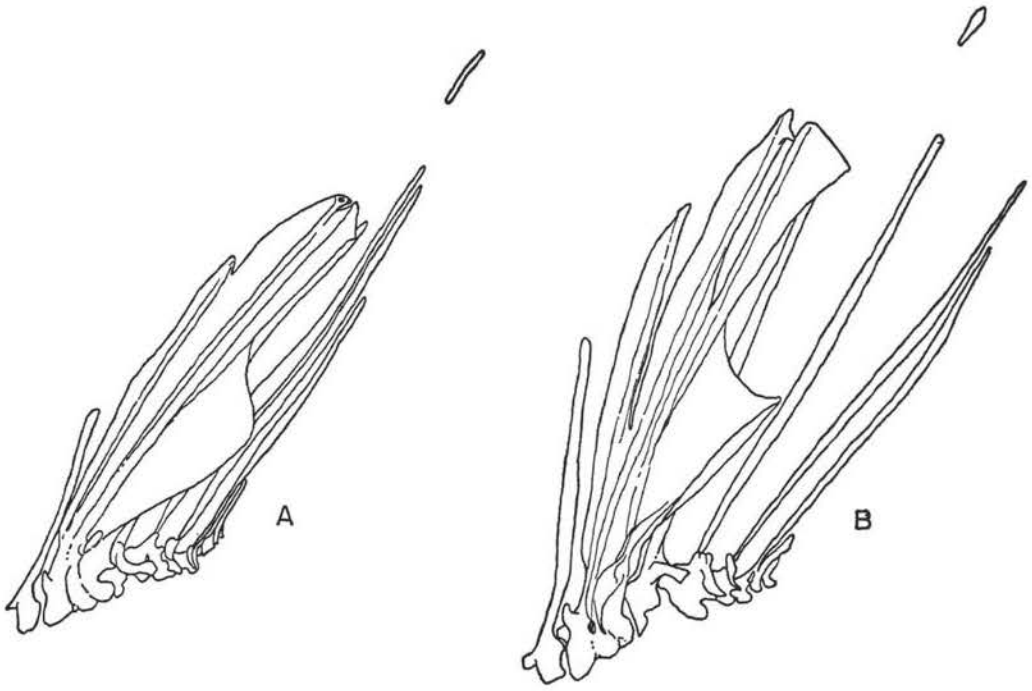


FIG. 30. Gonopodial suspensoria in *Cnesterodon*. A. *C. decemmaculatus*, U.S.N.M. No. 87826. B. *C. carnegiei*, C.N.H.M. No. 54248.

ing bluntly pointed terminal development of tough membranous tissue.

RANGE AND SPECIES COMPOSITION: Southeastern Brazil, eastern Paraguay, and Uruguay (map 8). Two species.

Phalloptychus januarius (Hensel)

Text figure 26C

Girardinus januarius.—HENSEL, 1868, p. 360 (original description; Rio de Janeiro). EIGENMANN AND EIGENMANN, 1891, p. 65. MIRANDA-RIBEIRO, 1905, p. 178. *Poecilia januarius.*—EIGENMANN, 1894, pp. 636–637. *Phalloptychus januarius.*—EIGENMANN, 1907, pp. 430–431; 1910, p. 458. LANGER, 1913, p. 208 (copy of Eigenmann's figure only). REGAN, 1913b, p. 999. HENN, 1916, pp. 94, 121–122. C. L. HUBBS, 1926, p. 71. R. VON IHERING, 1931, pp. 253, 267–268.

Girardinus iheringii.—G. A. BOULENGER, 1889, p. 266 (original description; Río Grande do Sul, Brazil; syntypes, B.M.N.H.). EIGENMANN AND EIGENMANN, 1891, p. 65.

MATERIAL: Río Grande do Sul, Brazil; C.A.S. Nos. 4899, 1132.

RANGE: Río de Janeiro to Río Grande do Sul, Brazil, eastern Paraguay, and Uruguay.

Phalloptychus eigenmanni Henn

Text figures 28A, 29D, 31E

Phalloptychus eigenmanni.—HENN, 1916, pp. 95, 121 (original description; Alagoínhas, Río Catu, Baía, Brazil; holotype, C.N.H.M. No. 55876). GEISER, 1924, table. C. L. HUBBS, 1926, p. 71. FOWLER, 1954, p. 238. *Phalloptychus januarius eigenmanni.*—R. VON IHERING, 1931, p. 253.

MATERIAL: Río Catu, Alagoínhas, Baía, Brazil; C.N.H.M. No. 55877.

RANGE: Río Catu, Alagoínhas, Baía, Brazil (Henn, 1916, p. 121).

REMARKS: The posttemporal bone in our specimens of *eigenmanni* is twisted about 90 degrees along its length.

GENUS **CNESTERODON** GARMAN

Text figures 26D, 28B–D, 30, 31F, G

Cnesterodon.—GARMAN, 1895, p. 43 (type species, by original designation, *Poecilia decemmaculata* Jenyns).

Gulapinnus.—LANGER, 1913, pp. 208, 230, 234, 258, 264 (type species, by monotypy, *Poecilia decem-maculata* Jenyns).

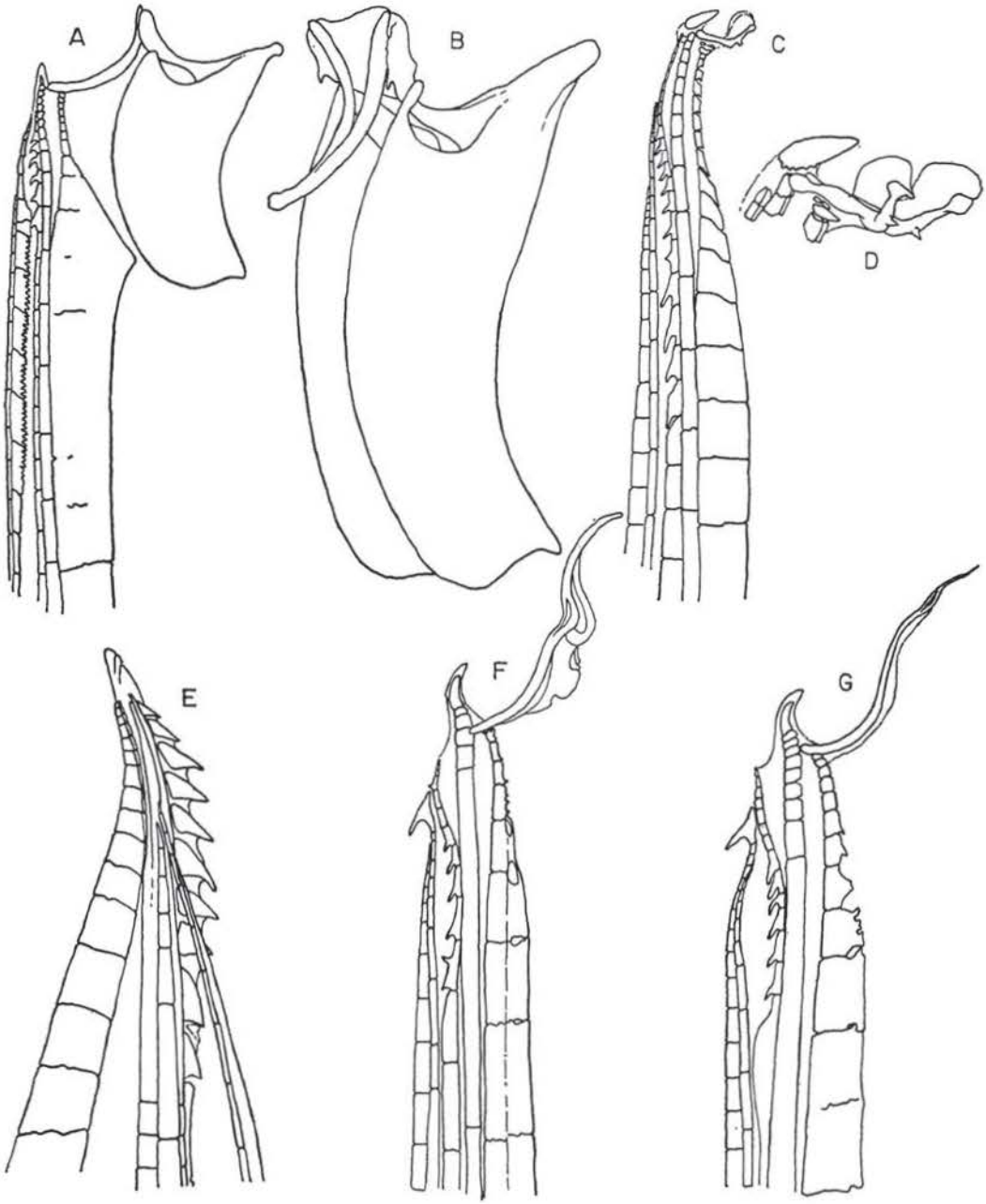
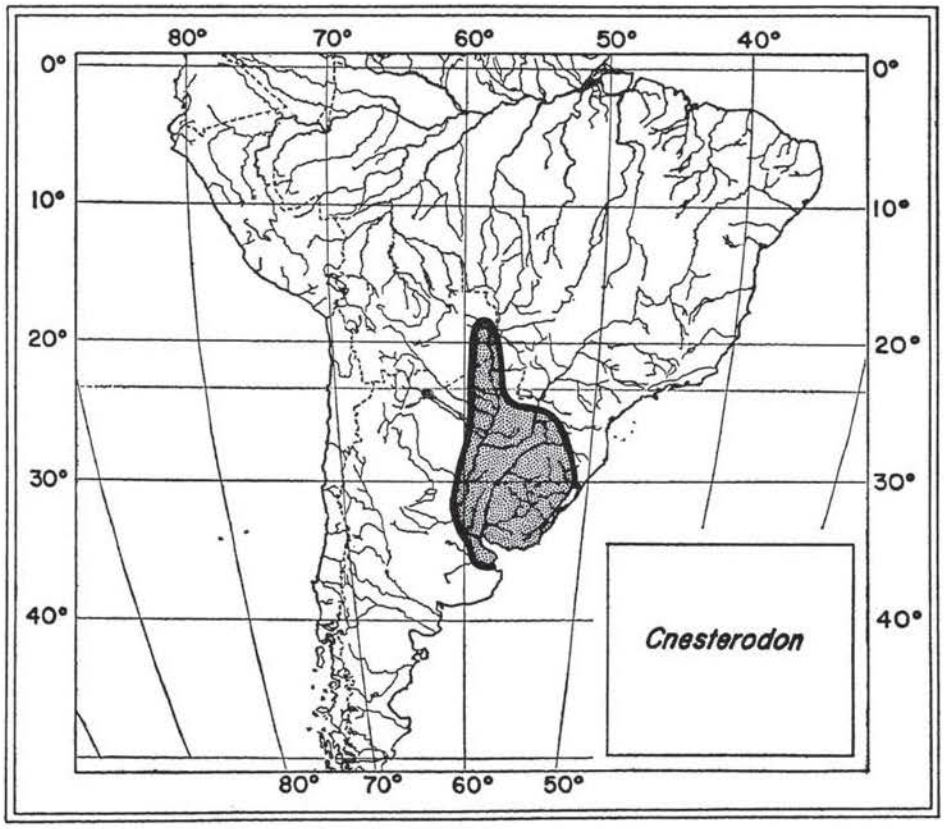


FIG. 31. Gonopodia in the Cnesterodontini. A. *Phallotorynus fasciolatus*. B. Dorsal three-quarter view, enlarged, of complex terminal structure of same. Both C.N.H.M. No. 55062. C. *Phalloceros caudimaculatus*. D. Ventral three-quarter view, enlarged, of complex terminal structure of same. Both C.N.H.M. No. 55886. E. *Phalloptychus eigenmanni*, C.N.H.M. No. 55877. F. *Cnesterodon decemmaculatus*, U.S.N.M. No. 87826. G. *Cnesterodon carnegiei*, C.N.H.M. No. 54248.

DIAGNOSIS: In skull, parietals typically absent in adult females, frontal, however, extending backward over area normally occupied by parietal as bluntly triangular plate; in male, small, oval bone (parietal?) overlying part of supraoccipital, epiotic, and pterotic and overlain by frontal which in this sex is evenly rounded posteriorly and not triangular; no epiotic processes; supraoccipital processes well developed; posttemporal not forked; marginal jaw teeth compressed. Third to eighth pleural ribs in male bent forward along their lengths, fifth to eighth ribs with elongate distal extensions that converge on pelvic girdle. Gonopodial suspensorium without gonapophyses or rarely with remnants of one or two modified hemal spines with parapophyses that are closely applied to vertebral base but have no direct contact with other suspensorial elements; gonactinostal complex situated far forward near posterior limits of shoulder girdle, inclined steeply backward, rounded dorsal surface of gonactinostal complex in some cases slightly to deeply notched; superior and inferior lateral wings very well developed, particularly latter which extends mostly backward as thin plate of bone overlapping bases of gonactinost 5, in some cases 6 and 7, and in many instances is turned slightly forward at its edges; distal tip of gonactinost 3 of primary complex with pair of variably developed, pointed, bony processes; ligastyle small to moderate, rod or loaf-shaped. Gonopodium bilaterally symmetrical; one or two segments subdistally on ray 3, in many cases each with up to three minute denticles; at tip of this ray, which consists of three to five moderately developed subrectangular ossicles, a long, slender, sinuous, antrorse, bony style formed by fusion of paired elements that gives rise ventrally to complex investment of more or less rigid membranous tissue; proximal end of stylar bone joined by connective tissues with vent-



MAP 9. Distribution of *Cnesterodon*.

ral surface of tip of ray 4a; ray 4a largely consolidated subdistally and terminated by claw-shaped, median ossicle that invests a membranous, bluntly pointed, terminal structure; ray 4p subdistally with continuous or discontinuous series of minute, sharply pointed, erect or retrorse serrae; ray 5a terminated by well-developed retrorse claw, with antrorse prolongation of its base.

RANGE AND SPECIES COMPOSITION: Southeastern South America (map 9). Two species.

Cnesterodon decemmaculatus (Jenyns)

Text figures 28B, 30A, 31F

Poecilia decem-maculata.—JENYNS, 1843, pp. 115–116 (original description; Maldonado, Uruguay; syntypes, B.M.N.H.). BLEEKER, 1860, p. 486. HOLMBERG, 1884, p. 103. EIGENMANN, 1894, p. 637. *Cnesterodon decem-maculatus.*—GARMAN, 1895, p. 44. BERG, 1897, p. 290. EIGENMANN, 1907, p. 431; 1910, p. 458. REGAN, 1913b, p. 1000. HENN, 1916, pp. 94, 99–101, 104, 130. HILDEBRAND, 1917, p. 8. *Girardinus decemmaculatus.*—GÜNTHER, 1866, p. 355. HENSEL, 1868, p. 364. EIGENMANN AND EIGENMANN, 1891, p. 65. PERUGIA, 1891, p. 653. LAHILLE, 1895, p. 273. G. A. BOULENGER, 1897, p. 4. ZOLOTNISKY, 1901, pp. 65–71. WICHAND, 1906, pp. 463–465. *Glaridichthys decem-maculatus.*—PHILIPPI, 1906, pp. 229–230; 1909, pp. 1–94. *Gulapinnus decemmaculatus.*—LANGER, 1913, pp. 208, 230, 234, 258, 264.

Poecilia gracilis.—VALENCIENNES, *in* Cuvier and Valenciennes, 1846, pp. 133–134 (original description; Montevideo, Uruguay; syntypes, M.N.H.N.P. No. B. 939). *?Gambusia gracilis.*—PERUGIA, 1891, p. 652.

MATERIAL: Montevideo, Uruguay; U.S.-N.M. No. 87826.

RANGE: Bolivian Chaco to Río Grande do Sul, Brazil, eastern Paraguay, Uruguay, and Buenos Aires, Argentina.

REMARKS: Our specimens of *decemmaculatus* differ from those of *carnegiei* in a number of features. In *decemmaculatus* the spines on gonopodial ray 3 are obsolescent; in *carnegiei* they are small but distinct. The complex bony cirrus at the gonopodial tip in *decemmaculatus* is invested with more membrane and the bony style is itself more bent than in *carnegiei*. *Cnesterodon decemmaculatus* possesses a tiny prong on a subterminal segment of ray 4p that is lacking in *carnegiei*. Striking differences in the form of suspensorial gonactinosts are illustrated in figure 30.

Cnesterodon carnegiei Haseman

Text figures 26D, 28C, 30B, 31G

Cnesterodon carnegiei.—HASEMAN, 1911, pp. 385–386 (original description; Serrinba Paraná, Río Iguassú; paratypes, C.A.S. No. 22553).

Cnesterodon decemmaculatus.—HENN, 1916, pp. 130–131 (in part; Haseman's paratypic material only).

MATERIAL: Porto Uniao da Victoria, Brazil; C.N.H.M. No. 54248. Porto Unios, Río Iguassú, Brazil; C.N.H.M. No. 56349.

RANGE: Southeastern Brazil and Uruguay.

TRIBE **GAMBUSIINI**

The members of this tribe are active, carnivorous, usually streamlined fishes that are alike in numerous features of body and fin pigmentation, gonopodium, and gonopodial suspensorium. The intimacy of relationship between *Gambusia* and *Belonesox* has long been recognized, for example, in C. L. Hubbs's (1926) arrangement. Less commonly noted but no less impressive is the evident alliance of *Brachyrhaphis* and *Gambusia*, commented on by Hildebrand (1938, p. 296).

Brachyrhaphis and *Gambusia* are especially similar in the distribution of the fin pigment. Commonly these genera have a distal and subdistal zone of melanophores on the dorsal and caudal fins, and in some species of each there is a dark blotch or streak on or near the bases of the middle rays of the anal fin. This particular arrangement of dorsal, anal, and caudal fin markings occurs in no other members of the family. Also, many species of *Brachyrhaphis* and *Gambusia* have a supraaxillary blotch, and the members of these two genera and *Belonesox belizanus* commonly possess a midlateral dark or dusky stripe.

The gonactinostal part of the gonopodial suspensorium of *Gambusia* and *Belonesox* is highly specialized, and it is characterized by one of the most distinctive structural modifications in the subfamily Poeciliinae. In these genera, in contrast to all others, elements 2 and 3 of the primary gonactinostal complex are so closely appressed to each other and to element 4 that no space is left between them for the elaboration of an intervening bony plate. In consequence, the whole structure has the form of a long column of bone, with the pointed tips of the incorporated elements

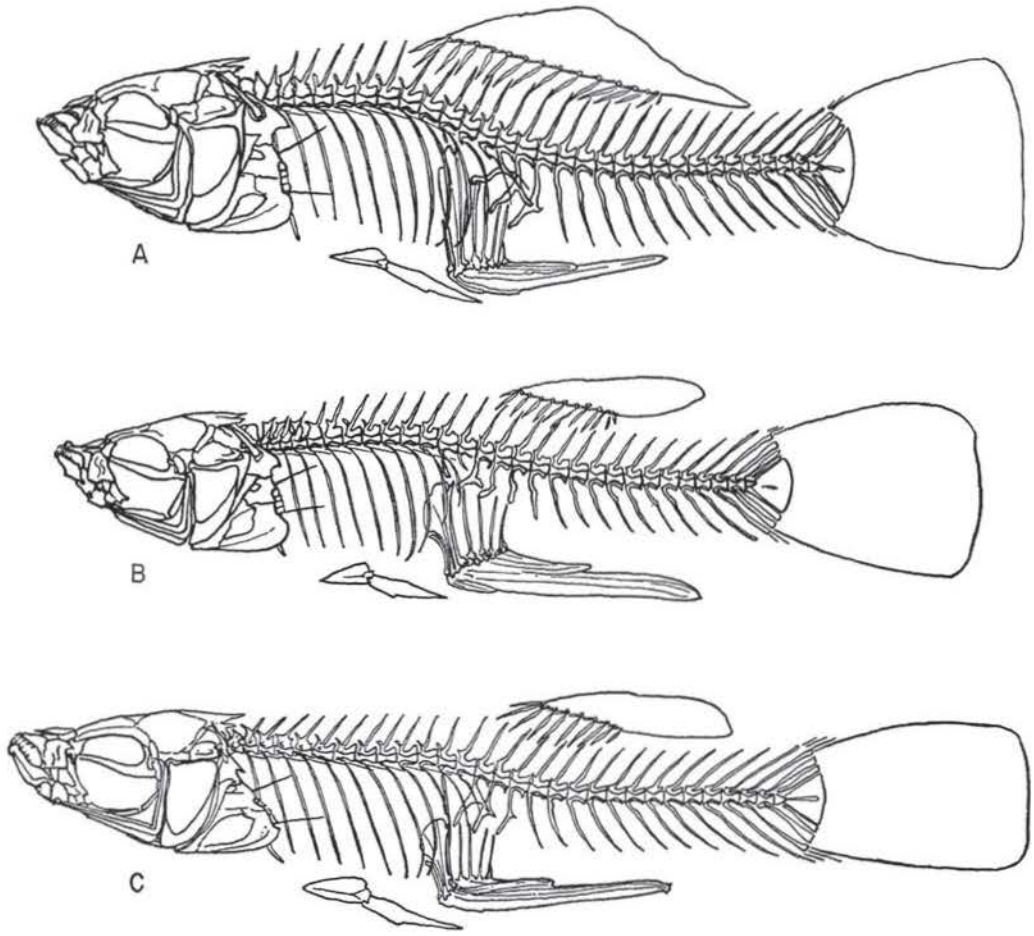


FIG. 32. Skeletons of adult males of *Brachyrhaphis*, composite drawings. A. *B. terrabensis*. B. *B. episcopi*. C. *B. cascajalensis*.

just visible dorsally. The columnar aspect of the structure is enhanced by the development on each gonactinost of lateral ridges of bone (the equivalent of the inferior lateral wings) that grow outward and backward together and fuse into a single mass, leaving only a slight groove where they fail to meet posteriorly on the midline. Gonactinost 5 fits snugly against this groove, and its tip is bounded laterally or is even partially encircled by the hypertrophied superior lateral wings of the primary complex. The flaring expansion thus formed has a wide, ventrally directed surface, on which the massive erector analis major muscle originates.

Although the primary gonactinostal complex of *Brachyrhaphis* has a plate-like anterior section, as in other poeciliines, it nonetheless incorporates some features that point toward the *Gambusia-Belonesox* system. The unifying features, especially in the form and position of the superior lateral wings, can be appreciated from a posterior view of the complex (fig. 38D, E). Also shown are rather striking resemblances between *Belonesox* and *Brachyrhaphis cascajalensis* in the form and orientation of the ligastyle and the three well-developed gonapophyses with uncini.

Apparently Regan (1913b) appreciated the similarities in gonopodial structure of *Brachyrhaphis rhabdophora*, *Belonesox*, and some species of *Gambusia*, the illustrations of which he combined in a single comparative figure. We note further resemblances, particularly between *Gambusia vittata* and the *Gambusia*-like species of *Brachyrhaphis* (*parismina* and

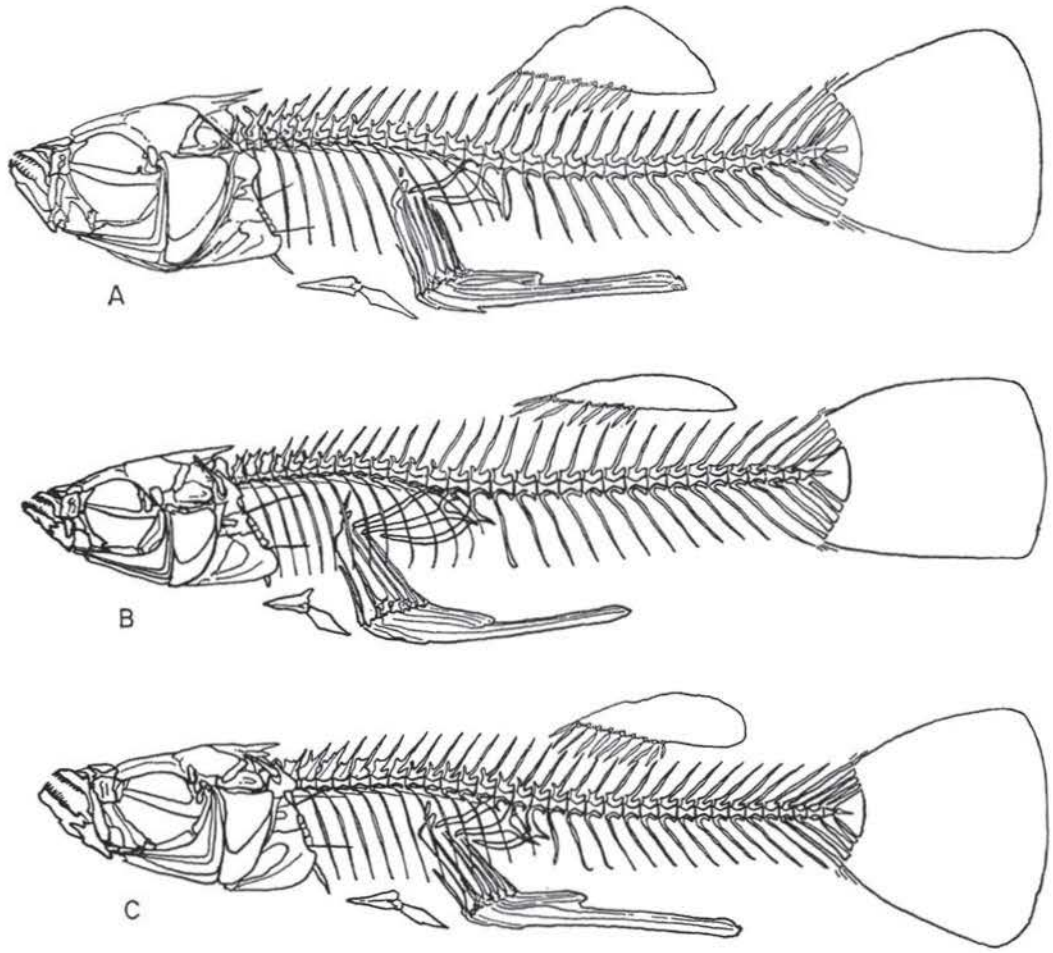


FIG. 33. Skeletons of adult males of *Gambusia*, composite drawings and tracing from radiograph. A. *G. nobilis*. B. *G. lemaitrei* (paratype, A.N.S.P. No. 71939). C. *G. beebei*.

cascajalensis). In each of these species, and to some extent in *Belonesox*, the penultimate part of the gonopodium is bent downward and then upward at the very tip, the small or obsolescent spine-bearing segments on ray 3 stop well short of the gonopodial tip, and the distal segments of ray 4a near the second or upward flexure of the ray are rather heavy and are suggestive of "elbow" formation at this point. The upturned tips of rays 4p and 5a in *Brachyrhaphis* are formed from long but simple segments, whereas in *G. vittata* the upturned terminal segments are modified into small but definite claw-like structures.

Additional support of the basic similarity in the gonopodia of *Gambusia* and *Brachyrhaphis* can be adduced from the discovery of atypical representatives of two species of *Gambusia*, *affinis* and *geiseri*. In a single unusually large, perhaps late-developing male of *affinis*,[1] the gonopodium (fig. 39I), although in all respects well formed, lacks the elbow and claws that are diagnostic of *Gambusia*. It resembles in considerable detail the gonopodia of some species of *Brachyrhaphis*. Geiser (1923, p. 188) illustrated a specimen of *geiseri* (as *G. senilis*) that shows no trace of the elbow.

There are of course many differences among these genera, as noted in the diagnoses,

[1] Taken by C. P. Haskins and party in 1949 in an independent coastal drainage along U. S. Route 98 between the towns of Mary Esther and Fort Walton, Okaloosa County, Florida.

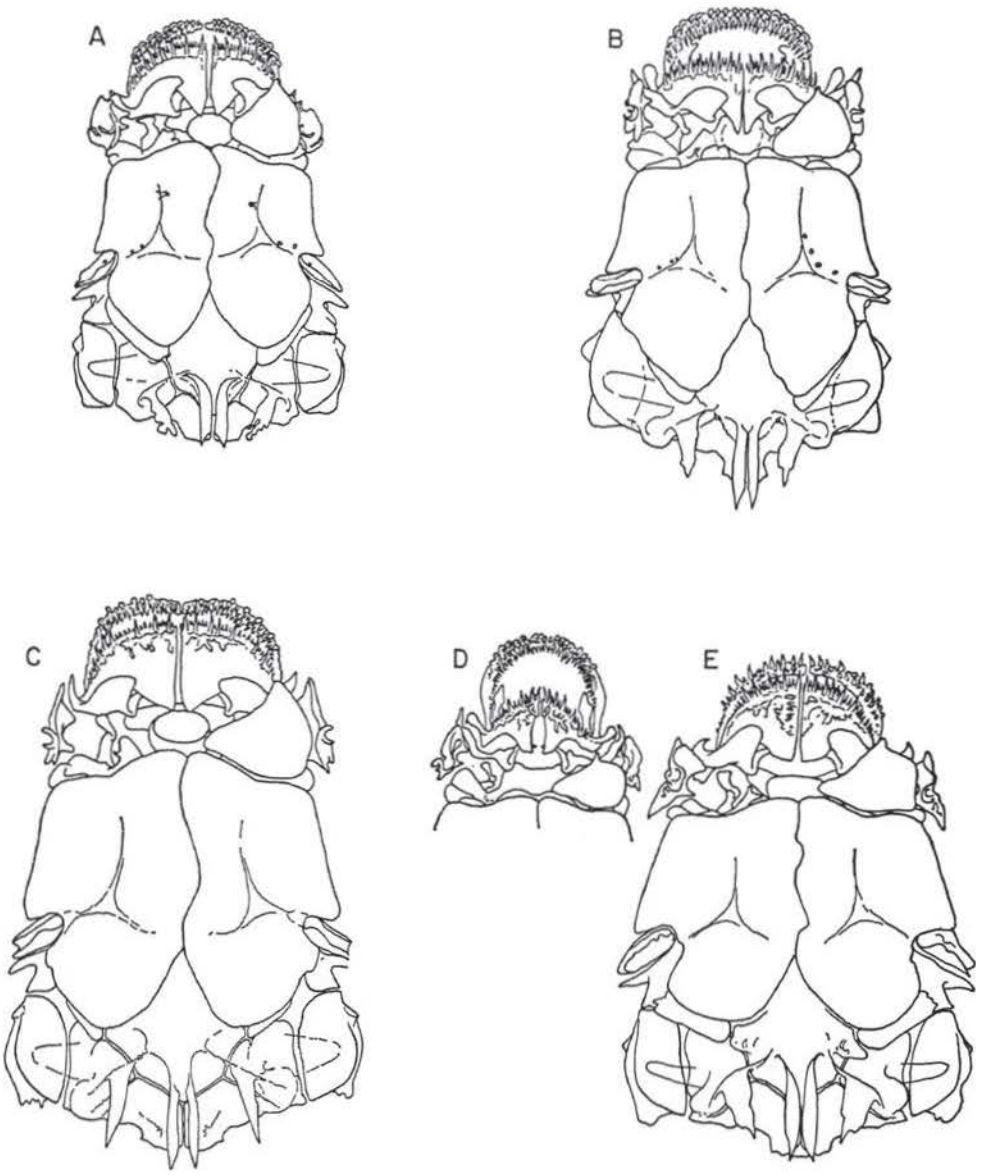


FIG. 34. Dorsicrania of *Brachyrhaphis*. A. *B. terrabensis*, male, U.M.M.Z. No. 72592. B. *B. rhabdophora*, male, U.S.N.M. No. 92154. C. *B. cascajalensis*, female, U.M.M.Z. No. 72596. D. *B. episcopi*, male, mouth parts only to show bony knob at premaxillary symphysis, C.U. No. 13141. E. Female, same data.

but it appears that their interrelationships are indeed real. In this realignment, we suggest that *Brachyrhaphis* is closest to the ancestral gambusiins and that a form resembling *cascajalensis* gave rise to the prototype of *Gambusia* and *Belonesox*. Since it appears likely that both of these genera arose in Atlantic coastal Mexico, *Brachyrhaphis* may once have been more widespread than it is today. Of *Gambusia* and *Belonesox*, the latter is closer to *Brachyrhaphis* in gonapophyseal, gonopodial, and pectoral-fin characters. Evidently, the common ancestral form evolved the columnar primary gonacti-

nostal complex, since this specialization is present and virtually identical in *Gambusia* and *Belonesox*. Presumably this ancient stock split and the two genera then arose. One branch early developed the upturned, anterior, pectoral-fin rays that are unique and are found in mature males of all forms of *Gambusia*, including *vittata*. Gonopodial structures of the earliest forms of *Gambusia* probably were still of a generalized *Brachyrhaphis* type.

The presumptive center of differentiation and dispersal of *Gambusia* in the region surrounding and including the Río Panuco basin and its subsequent spread to the north and south finds a parallel in *Xiphophorus* of the Poeciliini (see Rosen, 1960, and discussion below, p. 148). Unlike the strictly freshwater habits of the species of that largely Mexican genus, many forms of *Gambusia* are tolerant of salt and brackish water and have been capable of rapid extension of range. *Gambusia* has not only a wide distribution on the mainland, but occupies most of the Greater Antilles and the Bahamas as well. Euryhalinity is found also in some species of *Brachyrhaphis* and in *Belonesox*, so that it has probably long been characteristic of *Gambusia*.

Genus **BRACHYRHAPHIS** Regan

Plate 1, figures 6, 7; plate 2, figure 1; text figures 32, 34, 37, 38A, D, 39A–E, 41

Brachyrhaphis.—Regan, 1913b, p. 997 (type species, by monotypy, *Gambusia rhabdophora* Regan).

Trigonophallus.—C. L. Hubbs, 1926, p. 48 (type species, by original designation, *T. punctifer* C. L. Hubbs).

Plectrophallus.—Fowler, 1932, p. 384 (subgenus of *Panamichthys;* type species, by original designation, *Panamichthys tristani* Fowler, an abnormal specimen of *Brachyrhaphis rhabdophora*).

Diagnosis: In skull, parietals variably developed but present in all adults; supraoccipital processes rather broad and well developed in adults, epiotic processes large, irregularly branched, and variably notched distally; posttemporal forked; marginal jaw teeth recurved, conical. Posterior pleural ribs in male in only a few cases much modified, in some turned slightly forward at tips. Gonopodial suspensorium with three rather short and irregular gonapophyses that usually are but little bent forward; gonapophysis I usually heavy and inclined forward or with shaft nearly vertical and tip bent sharply forward, with variably developed but usually massive uncini that arise nearer

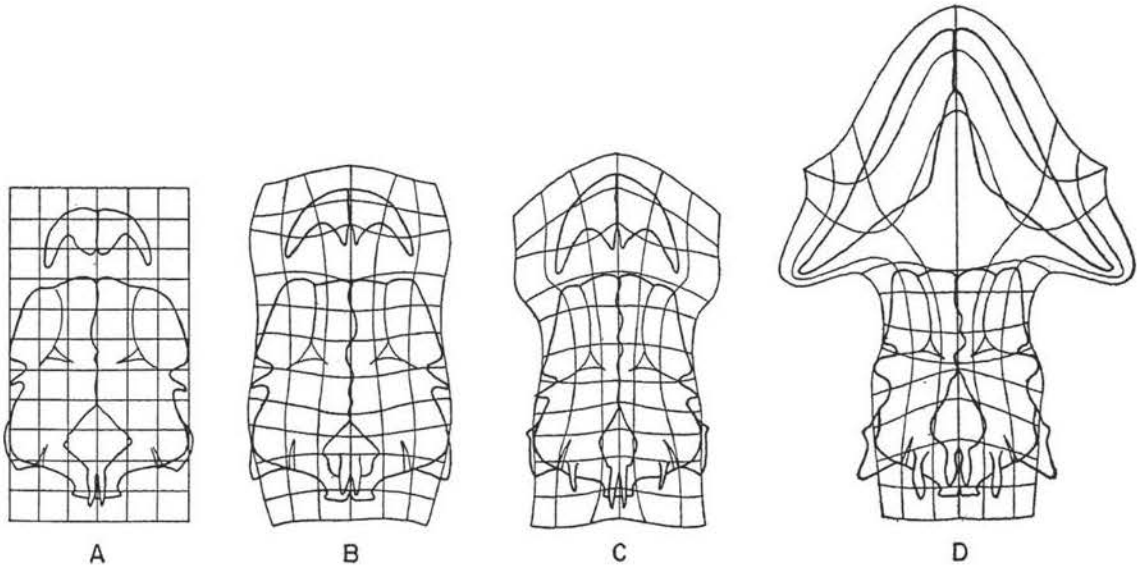


Fig. 35. Distortion grid diagrams, showing differences in skull proportions in four gambusiin species with different sizes of the premaxillary bones. A. *Gambusia affinis*. B. *Gambusia manni*. C. *Gambusia beebei*. D. *Belonesox belizanus*.

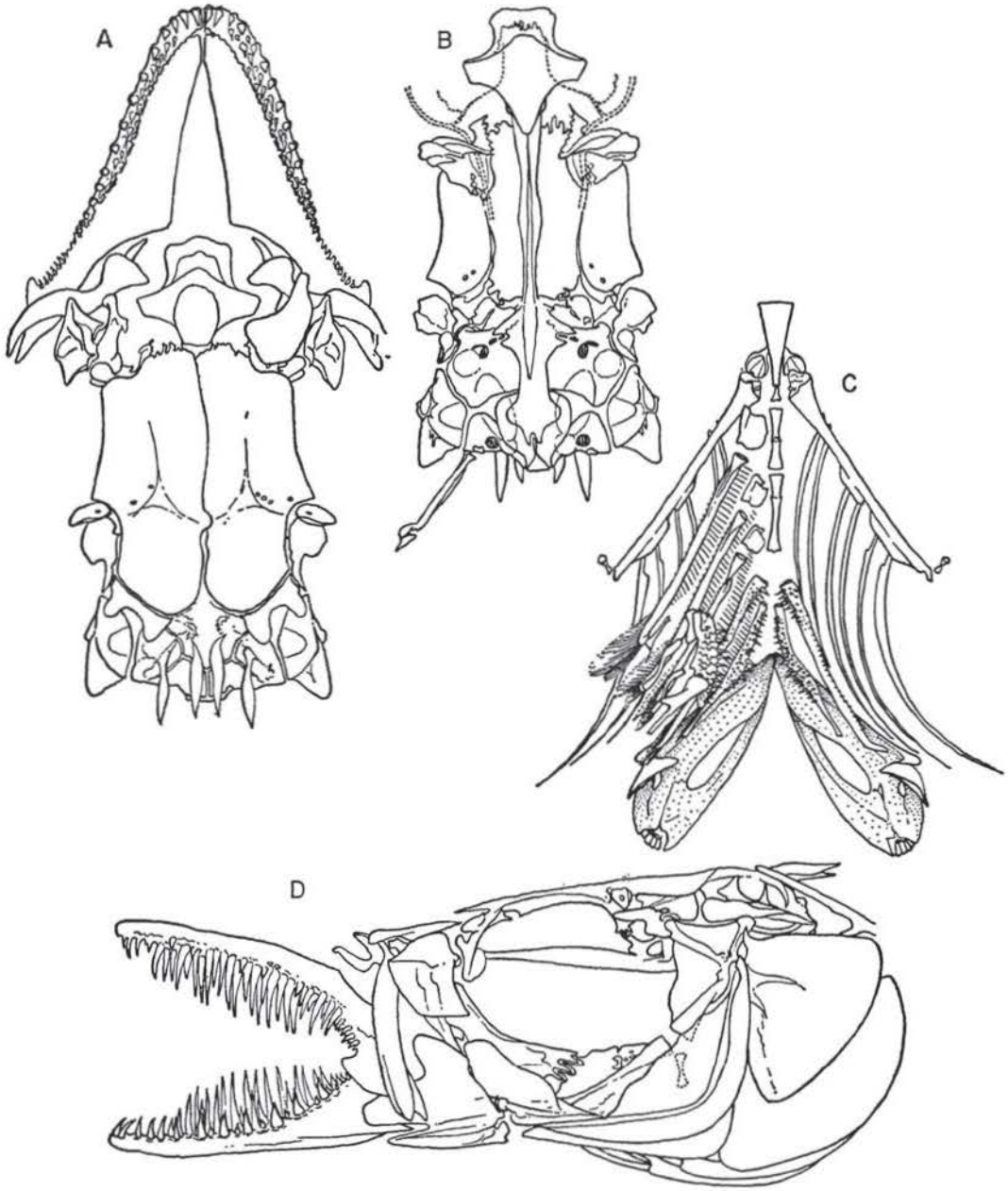


FIG. 36. Skull anatomy of *Belonesox belizanus*, aquarium specimen. A. Dorsal view of skull. B. Basicranium. C. Pharyngobranchial apparatus and shoulder girdles. D. Lateral view of skull.

tip than base of gonapophysis and have blunt or knobbed tips; gonapophysis II rarely much bent, but usually rather irregular in outline, and with variably developed uncini that usually arise nearer its tip than base; gonapophysis III usually oriented vertically, little modified, and rarely with definitive uncini; ligastyle usually short and massive; primary gonactinostal complex variably developed, in some cases with a recess anteriorly for gonactinost 1 and with gonactinosts 2 and 3 in many cases flaring upward and outward away from element 4; gonactinosts 5 to 11 rarely with specialized, wing-like,

bony plates. Gonopodium bilaterally symmetrical, in many cases with a pair of gristly processes at extreme tip that arise laterally and extend outward at right angles to long axis of fin or curve slightly backward; ray 3 terminating somewhat short of other rays, with series of small or incipiently developed spines distally; ray 4p with well-developed subdistal serrae that merge with several small, unspecialized, distal segments; rays 4 and 5 in some cases bent upward at their tips. Pectoral fin rays not sexually dimorphic.

Nasal bone very broad and distinctly triangular; upper part of cleithrum typically bent strongly inward; and usually a distinct black blotch at bases of first three or four anal-fin rays in males, females, and young.

In most slender-bodied species, *B. cascajalensis* and *B. parismina*, dorsal-fin insertion rather far back (above seventeenth vertebra), and suspensorium containing well-formed, inclined gonapophyses with large, pointed uncini. In more deep-bodied forms, dorsal insertion rather far forward (*episcopi*, above fifteenth or sixteenth vertebra; *terrabensis*, above eleventh vertebra), and axial support of anal actinosts in some cases developed from combination of greatly enlarged parapophyses (fig. 37B, C), much-reduced and modified hemal spine, and incipient uncini (gonapophysis I), fairly normal element with small uncini (gonapophysis II), and hardly modified hemal spine with incipient or no uncini (gonopophysis III). In many cases spine that encloses hemal arch on gonapophysis I abruptly bent forward, reduced to short, club-like prominence, or absent.

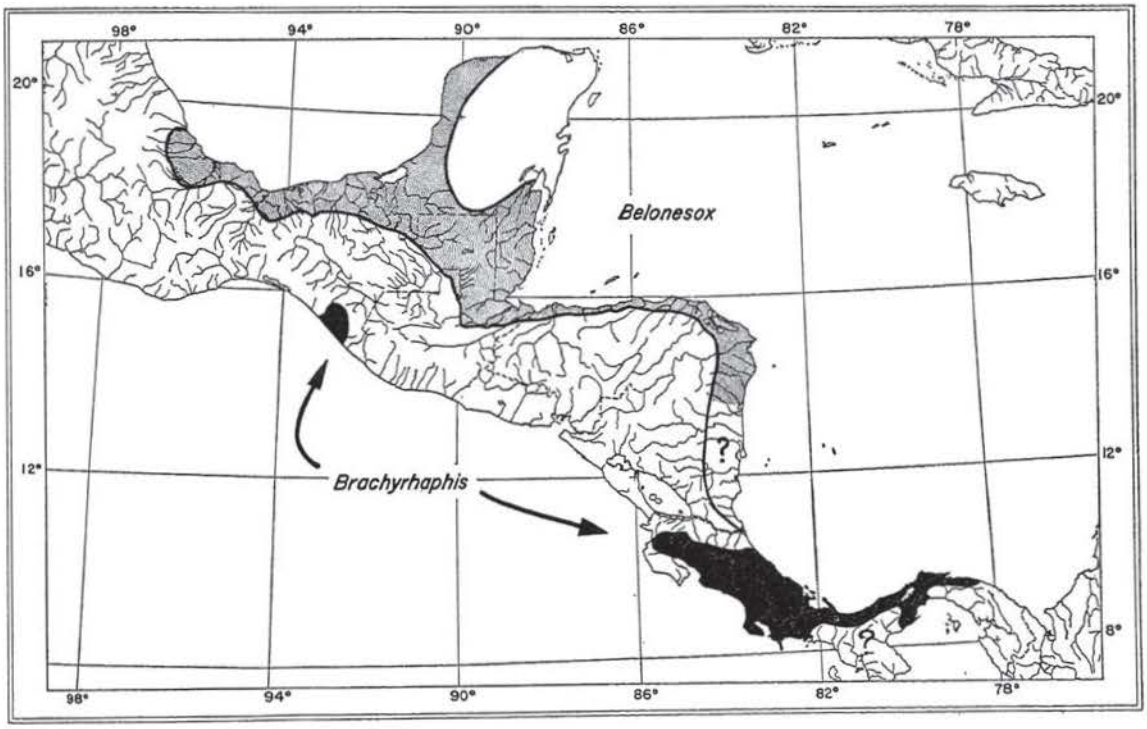
Adult males of *B. episcopi* having ascending processes of premaxillae developed into large, knobby outgrowths. In females and young, premaxillae normal.

RANGE AND SPECIES COMPOSITION: Pacific drainage, Soconusco District, Chiapas, Mexico, and Atlantic and Pacific slopes of Costa Rica and western and central Panama (map 10). Seven species.

Brachyrhaphis terrabensis (Regan)

Text figures 32A, 34A, 37A, 39A

Gambusia terrabensis.—REGAN, 1907b, p. 260



MAP 10. Distribution of *Brachyrhaphis* and *Belonesox*.

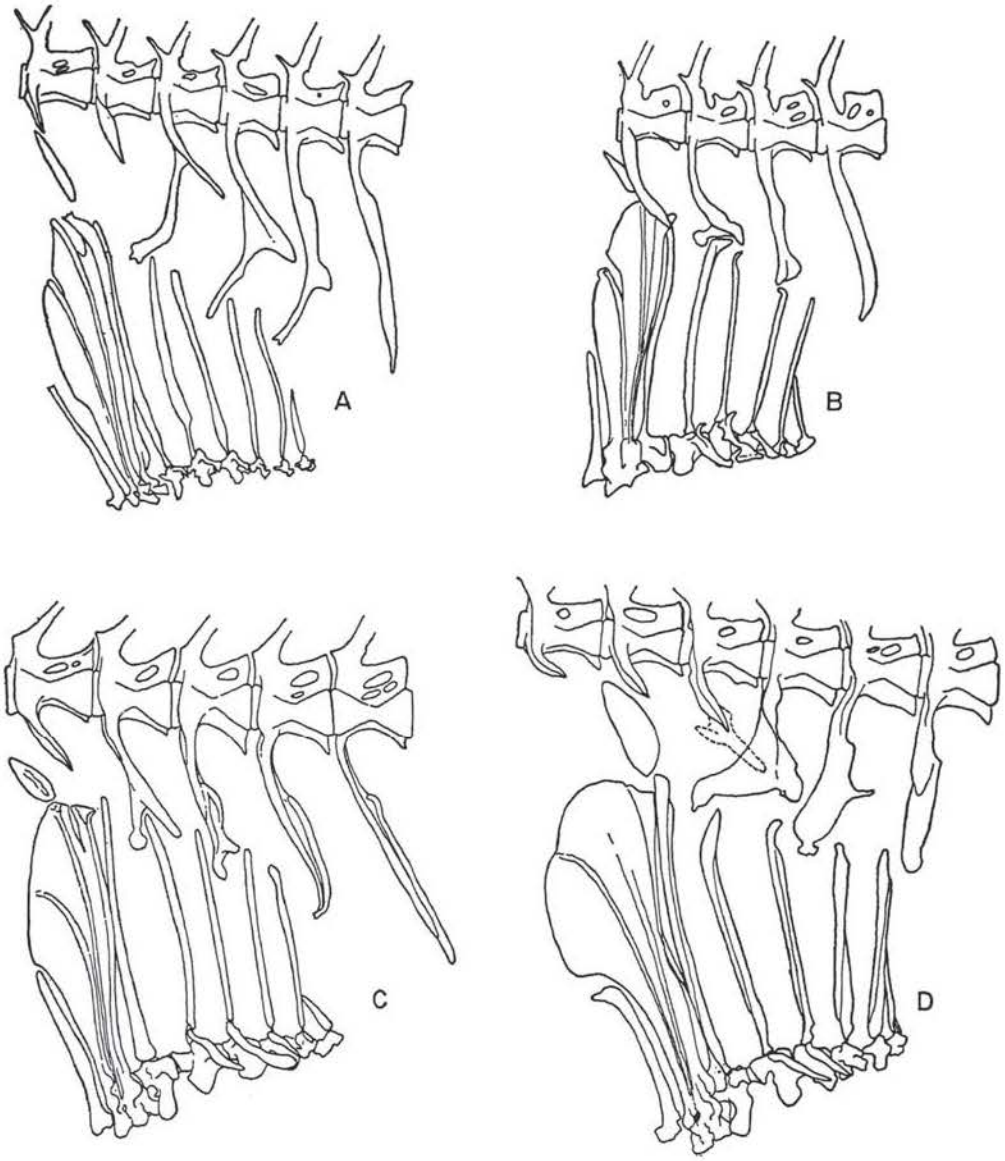


FIG. 37. Gonopodial suspensoria in *Brachyrhaphis*. A. *B. terrabensis*, U.M.M.Z. No. 72592. B. *B. rhabdophora*, U. S.N.M. No. 94196. C. The same, but the form known formerly as *olomina*, U.S.N.M. No. 92151. D. *B. episcopi*, C.U. No. 13141.

(original description; Río Grande de Tèrraba [Puntarenas], Pacific slope of Costa Rica; syntypes, B.M.N.H.). *Pseudoxiphophorus terrabensis*.—REGAN, 1913b, p. 993. *Brachyrhaphis terrabensis*.—C. L. HUBBS, 1926, pp. 43–46.

MATERIAL: Quebrada Copera, Panama; U.M.M.Z. No. 72592. Panama; U.S.N.M. No. 88868.

RANGE: Pacific slope of southern Costa Rica (Puntarenas) and western Panama (Chiriquí), at higher elevations.

REMARKS: Some specimens of *terrabensis* (U.M.M.Z. No. 170962) lack the dark blotch at the anal-fin base. Adult males of this species possess an irregular fleshy swelling in the interradial membrane between pelvic rays 1 and 2, but closer to the tip of the first ray. Although less developed, this modification

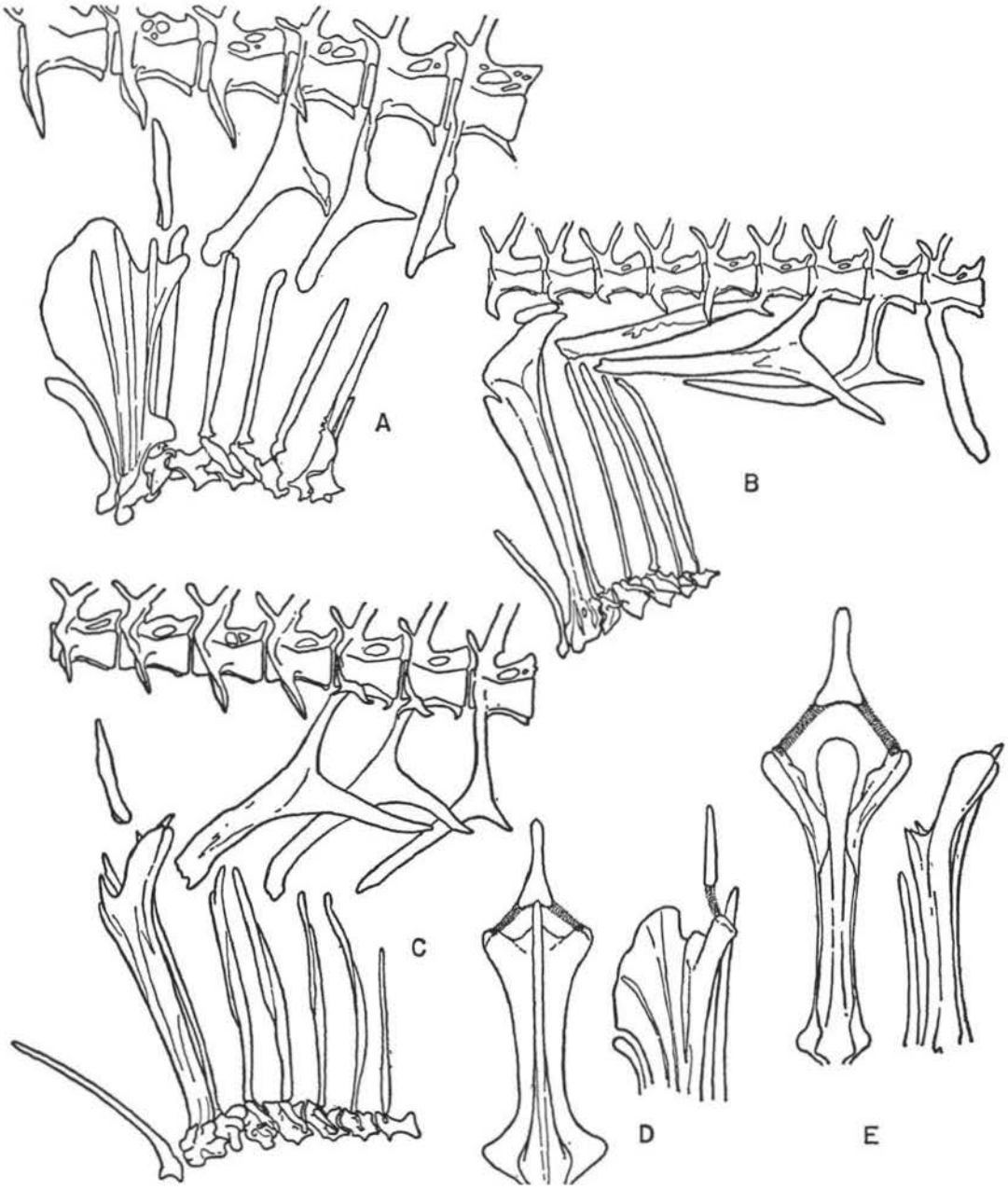


FIG. 38. Gonopodial suspensoria in the Gambusiini. A. *Brachyrhaphis cascajalensis*, U.M.M.Z. No. 72596. B. *Gambusia affinis*, U.M.M.Z. No. 163655. C. *Belonesox belizanus*, aquarium specimen. D. *Brachyrhaphis cascajalensis*, U.M.M.Z. No. 72594; posterior view, left, and lateral view of 2–3–4 complex and ligastyle. E. The same for *Belonesox belizanus*, U.M.M.Z. No. 143524.

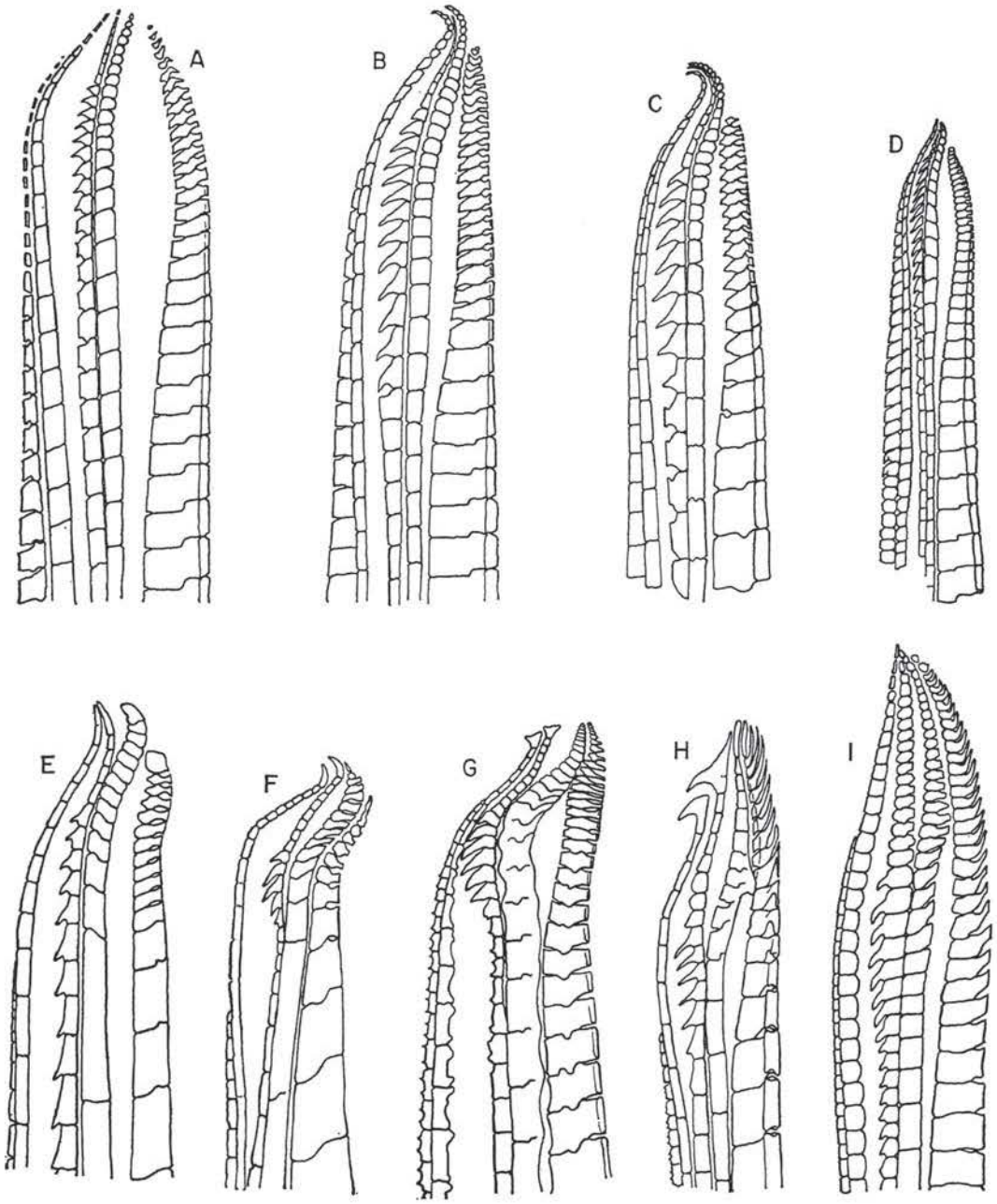


FIG. 39. Gonopodia of the Gambusiini. A. *Brachyrhaphis terrabensis*, U.M.M.Z. No. 72592. B, C. *Brachyrhaphis rhabdophora*. B. U.S.N.M. No. 94195. C. U.S.N.M. No. 92151, formerly classified as the form *olomina*. D. *Brachyrhaphis episcopi*, C.U. No. 13141. E. *Brachyrhaphis cascajalensis*, U.M.M.Z. No. 72594. F. *Gambusia vittata*, U.M.M.Z. No. 169501. G. *Belonesox belizanus*, aquarium specimen. H. *Gambusia aestiputius*, holotype, A.N.S.P. No. 71772. I. *Gambusia affinis*, atypical male, Florida (see text).

calls to mind the similar fleshy pad in the pelvic fin of *hartwegi*.

Brachyrhaphis hartwegi, new species

Plate 2, figure 1; text figure 41

MATERIAL: The holotype (U.M.M.Z. No. 179539) is an adult male, 23.9 mm. in standard length, seined in a stream tributary to the Río Jalapa, which in turn flows into an independent Pacific drainage, the Río Zintalapa, at Finca Esperanza, 450 feet in elevation, longitude 92° 36′ W., latitude 15° 20′ N., about 6 kilometers north-northeast of Escuintla, Soconusco District, Chiapas, Mexico, on August 18, 1937, by Norman Hartweg and Pierce Brodkorb. Taken with the holotype were 61 young to adult males and females, 9.0 to 30.7 mm. in standard length (U.M.M.Z. No. 168918). Other specimens from the same locality are three adult females, 20.0 to 25.0 mm. in standard length, taken by Hartweg and Brodkorb, July 11, 1937 (U.M.M.Z. No. 168904); nine young to adult females and one immature male, 11.0 to 32.0 mm. in standard length, collected by Brodkorb and A. E. Staebler, March 3, 1939 (U.M.M.Z. No. 169069); 52 young to adult males and females, 12.0 to 23.0 mm. in standard length, captured by Brodkorb and Staebler, March 13, 1939 (U.M.M.Z. No. 169071). The site of capture was described by Brodkorb and Staebler as: water, clear; vegetation, sparse; bottom, mud and gravel; shoreline, muddy; current, slow to rather swift; depth of water and depth of capture, 1–10 inches. The stream, according to Norman Hartweg, was not over 6 feet wide.

DIAGNOSIS: Small, slender-bodied species of *Brachyrhaphis*, with 10 to 15 moderately developed, dusky bars on side, eight or nine dorsal-fin rays (counting last ray as double at base), 28 scales in midlateral series, distinct, fleshy, bean-shaped pad on inner surface of tip of first short, unbranched pelvic ray, and without black or dusky blotch at anal-fin base. Dorsal and caudal fins with proximal row of long, dark streaks in interradial membranes and narrow distal band of dark or dusky pigment. Gonopodium with pair of small, fleshy, pointed processes projecting laterally from extreme tip. Gonopodial suspensorium with three well-developed gonapophyses, each with pair of large, pointed uncini that arise midway along gonapophyseal shaft. Ground color of body variable, but frequently consisting of distinct, net-like pattern that fades out on lower trunk and belly, and that, in females, is interrupted by dark or dusky midlateral stripe. Predorsal length of body 53 to 69 per cent of standard length. Premaxillary symphysis of males without bony knob.

DESCRIPTION: Dorsal-fin rays 8 (4), 9 (11); anal-fin rays 8 (1), 9 (9); sum of left and right pectoral fin rays 26 (13); scales in lateral series 28 (11); scale rows around caudal peduncle 14 (11); vertebrae 30 (16), 31 (1). Measurements for males and females separately are expressed as thousandths of the standard length; a range in values for the series is followed by the value in parentheses of the holotype.

Males: Greatest depth of body, 246–291 (285); least depth of caudal peduncle, 171–196 (192); dorsal origin to snout tip, 526–630 (569); anal origin to mandibular symphysis, 462–490 (490); dorsal origin to caudal base, 402–457 (439); anal origin to caudal base, 558–617 (582); head length, 283–293 (293); head width, 158–172 (172); snout length,[1] 083 (084); orbit length,[1] 083 (084); interorbital bony width,[1] 126 (121); mouth, over-all width,[1] 087 (096); dorsal fin, depressed length,[1] 283 (305); gonopodial length, 418–463 (418); caudal-fin length, 265–291 (280); pectoral-fin length, 189–209 (201); pelvic-fin length, 120–135 (126).

Females: Greatest depth of body, 235–280; least depth of caudal peduncle, 165–178; dorsal origin to snout tip, 613–690; anal origin to mandibular symphysis, 549–596; dorsal origin to caudal base, 333–405; anal origin to caudal base, 410–473; head length, 261–299; head width, 174–200; snout length, 074–098; orbit length, 078–095; interorbital bony width, 108–135; mouth, over-all width, 087–106; dorsal fin, depressed length, 221–266; anal fin, depressed length, 212–275; caudal-fin length, 246–302; pectoral-fin length, 154–244; pelvic-fin length, 091–124.

The above measurements are based on 10 adult females, 19.5 to 30.7 mm. in standard

[1] Only one specimen, in addition to the holotype, was measured.

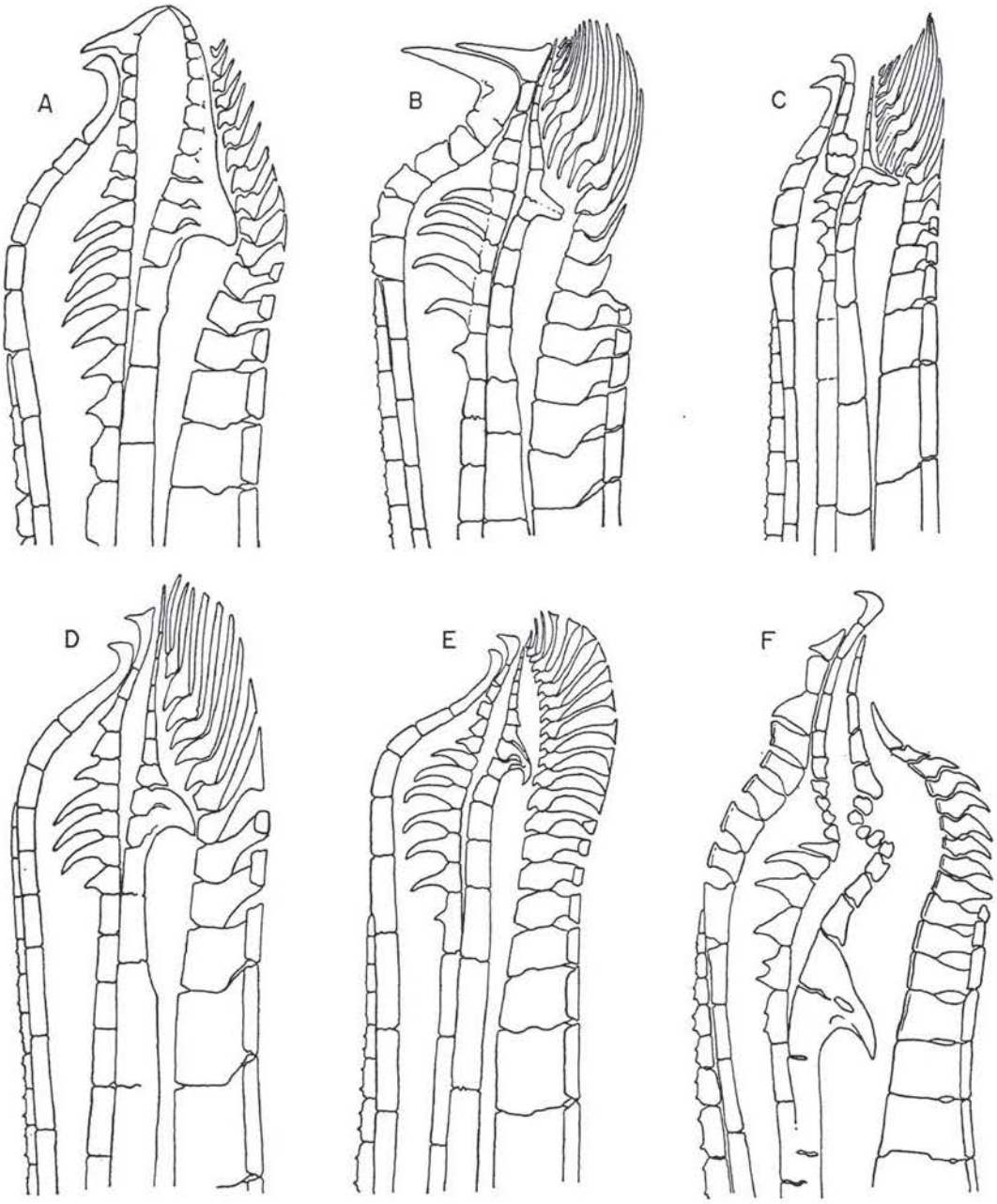


FIG. 40. Gonopodia in *Gambusia*. A. *G. myersi*, U.M.M.Z. No. 103332. B. *G. luma*, holotype, U.M.M.Z. No. 143565. C. *G. atrora*, holotype, U.M.M.Z. No. 179999. D. *G. nobilis*, U.M.M.Z. No. 120356. E. *G. regani*. U.M.M.Z. No. 162149. F. *G. rachowi*, after Rosen and Gordon (1951).

length, and five adult males, 17.5 to 23.9 mm., all from the type series.

In the largest females the mandibular canal of the cephalic lateralis system is represented by deep grooves and small segments of a closed canal. The preorbital and preopercular canals also are represented by grooves and canal sections. All other head canals are represented entirely by distinct grooves.

RELATIONSHIPS: *Brachyrhaphis hartwegi* is a typical but well-marked species of its genus. In possessing the fleshy thickenings at the tip of its gonopodium, *hartwegi* resembles *punctifer*, *episcopi*, and *rhabdophora*. In having a bean-shaped fleshy pad near the tip of the first pelvic ray, *hartwegi* shows alliance with *terrabensis*, with some specimens of which it agrees further in lacking a dark blotch at the anal-fin base. We are inclined to regard the resemblance between *hartwegi* and *terrabensis* as indicative of particularly close relationship.

RANGE: Structurally *B. hartwegi* is distinctive but not distinguished among its congeners. Geographically, however, it is notable. It is known only from the Pacific drainage of Chiapas (map 10). All other known species of *Brachyrhaphis* are confined to Costa Rica and Panama. Despite rather careful collecting in the intervening region, especially in Guatemala, El Salvador, and the Choluteca drainage of Honduras, the genus is unknown there.

ETYMOLOGY: Named for Dr. Norman Hartweg, Curator of Herpetology of the Museum of Zoology, the University of Michigan, who secured the first known examples of this new species and who has long been an enthusiastic and active student of the biota of Mexico.

Brachyrhaphis rhabdophora (Regan)

Plate 1, figures 6, 7; text figures 34B, 37B, C, 39 B, C

Gambusia terrabensis (misidentification, not of Regan).—MEEK, 1907, p. 146.

Gambusia rhabdophora.—REGAN, 1908, p. 457 (original description; Volcano of Tenorio and Río Grande de Tèrraba [Puntarenas], Pacific slope of Costa Rica; syntypes, B.M.N.H.). *Brachyrhaphis rhabdophora*.—REGAN, 1913b, p. 997.

Priapichthys olomina.—MEEK, 1914, pp. 112, 114 (original description; Río Grande deTárcoles, Orotina [Alajuela], Costa Rica; holotype, C.N.H.M. No. 7827). *Brachyrhaphis olomina*.—C. L. HUBBS, 1924, p. 22.

Panamichthys tristani.—FOWLER, 1932, p. 384 (original description; Escobal, Costa Rica; holotype, A.N.S.P. No. 53935). *Plectrophallus tristani*.—C. L. HUBBS, 1935a, p. 3.

MATERIAL: All from Costa Rica; Siquirres, Limón; U.M.M.Z. No. 138245. Liberia, Guanacaste; U.M.M.Z. No. 159155. Orotina; U.S.N.M. No. 94196; U.M.M.Z. No. 162477. Escobal; A.N.S.P. No. 53935. Costa Rica; U.S.N.M. No. 92154. Tilarán, Río Santa Rosa [Guanacaste]; S.U. No. 32202.

RANGE: Atlantic and Pacific slopes of Costa Rica.

REMARKS: This species and *Priapichthys olomina*, previously separated but indicated by C. L. Hubbs (1926, p. 46) to be questionably distinct, are treated as conspecific. They are not separable on the basis of fin-ray and scale counts or body proportions. Regan (1908), however, gave only a sketchy account of the coloration of *rhabdophora*, and we have not examined the types. *Panamichthys tristani* Fowler corresponds in counts, measurements, and color pattern with Meek's (1914) description and our paratypes (U.S.N.M. No. 92151; U.M.M.Z. No. 162477) of *olomina*, and its peculiar gonopodial features have almost certainly resulted from abnormal growth, owing probably to injury during development.

Brachyrhaphis episcopi (Steindachner)

Text figures 32B, 34D, 37D, 39D

Gambusia episcopi.—STEINDACHNER, 1878, p. 387 (original description; Obispo [Canal Zone], Panama). *Priapichthys episcopi*.—REGAN, 1913b, p. 992. *Brachyrhaphis episcopi*.—C. L. Hubbs, 1926, p. 47.

Gambusia latipunctata.—MEEK AND HILDEBRAND, 1913, p. 87 (original description; Arrijan, Panama; holotype, C.N.H.M. No. 7595).

MATERIAL: All from Panama: Albrook Field, Canal Zone; C.U. No. 13123. Barro Colorado Island, Canal Zone; C.U. No. 13141, U.M.M.Z. No. 92127. Atlantic slope; U.S.N.M. No. 148676. Barro Colorado, Gatún Lake; S.U. No. 24287. Allee Creek, Barrow; A.N.S.P. No. 67664–83.

RANGE: Both slopes of central Panama, but not in brackish coastal waters.

Brachyrhaphis punctifer (Hubbs)

Trigonophallus punctifer.—C. L. HUBBS, 1926, p. 49 (original description; Río Cricamola, Atlantic slope of western Panama; holotype, U.M.M.Z. No. 72573).

MATERIAL: Nomonuen Creek, Río Cricamola, Panama; U.M.M.Z. No. 72574.

RANGE: Río Cricamola and western river systems, Caribbean slope, Panama (C. L. Hubbs, 1926, p. 49).

REMARKS: *Brachyrhaphis punctifer*, like *episcopi*, has the subtriangular thickening at the tip of the gonopodium well developed.

Brachyrhaphis cascajalensis
(Meek and Hildebrand)

Text figures 32C, 34C, 38A–D, 39E

Gambusia cascajalensis.—MEEK AND HILDEBRAND, 1913, p. 86 (original description; Río Cascajal, Porto Bello [Colon], Atlantic slope of Panama; holotype, C.N.H.M. No. 7594). *Brachyrhaphis cascajalensis.*—C. L. HUBBS, 1926, pp. 47–48.

MATERIAL: All from Panama: Quebrada Nigra, tributary to Almirante Bay; U.M.M.Z. No. 72596. Albrook Field, Canal Zone; C.U. No. 13124. Monte Liria, Canal Zone; U.S.N.M. No. 78769. Cativá; U.S.N.M. No. 109079.

RANGE: Atlantic slope from southeastern Costa Rica (Behre, 1928, p. 315) east to Río Nargana, 40 miles east of Carti, San Blas, Panama. Said by Hildebrand (1938) to have been taken in the Pacific drainage of central Panama. It commonly associates with *Gambusia nicaraguensis*, and it occurs at times in brackish water (Hildebrand, 1938, pp. 296, 300).

REMARKS: This species is most closely related to *B. parismina*, with which it agrees in gonopodial and suspensorial characters and in the short dorsal fin that is placed well back on the body. *Brachyrhaphis parismina* possesses a large black blotch on the caudal base that *cascajalensis* lacks.

Brachyrhaphis parismina (Meek)

Gambusia parismina.—MEEK, 1912, p. 71 (original description; Parismina [Limón], Costa Rica; holotype, C.N.H.M. No. 7678). *Priapichthys parismina.*—REGAN, 1913b, p. 992. *Brachyrhaphis parismina.*—C. L. HUBBS, 1926, p. 48.

RANGE: Atlantic coastal lowland of Costa Rica.

REMARKS: C. L. Hubbs (1926) first called attention to the close relationship of *parismina* to *cascajalensis*.

GENUS **GAMBUSIA** POEY

Plate 1, figures 8, 9; plate 2, figures 2, 3; text figures 33, 35A–C, 38B, 39F, H, I, 40, 42, 43

Gambusia.—POEY, 1854, pp. 376, 380, 384, 390 (type species, by subsequent designation by Jordan and Copeland, 1876, p. 142, *Gambusia punctata* Poey). On official list of generic names in zoology.

Paragambusia.—MEEK, 1904, p. 133 (type species, by monotypy, *Gambusia nicaraguensis* Günther).

Heterophallus.—REGAN, 1914, p. 66 (type species, by monotypy, *Heterophallus rachovii* Regan).

Heterophallina.—C. L. HUBBS, 1926, p. 26 (subgenus of *Gambusia;* type species, by original designation, *Gambusia regani* Hubbs).

Arthrophallus.—C. L. HUBBS, 1926, p. 38 (subgenus of *Gambusia*; type species, by original designation, *Heterandria patruelis* Baird and Girard, a subjective synonym of *Heterandria affinis* Baird and Girard).

Schizophallus.—C. L. HUBBS, 1926, p. 40 (subgenus of *Gambusia;* type species, by original designation, *Gambusia holbrookii* Girard, a subjective synonym of *Heterandria affinis* Baird and Girard).

Flexipenis.—TURNER, 1940a, p. 89 (*nomen nudum* for *Gambusia vittata* Hubbs, which was subsequently designated formally as type of *Flexipenis* by C. L. Hubbs, *in* Rivas, 1963, p. 334).

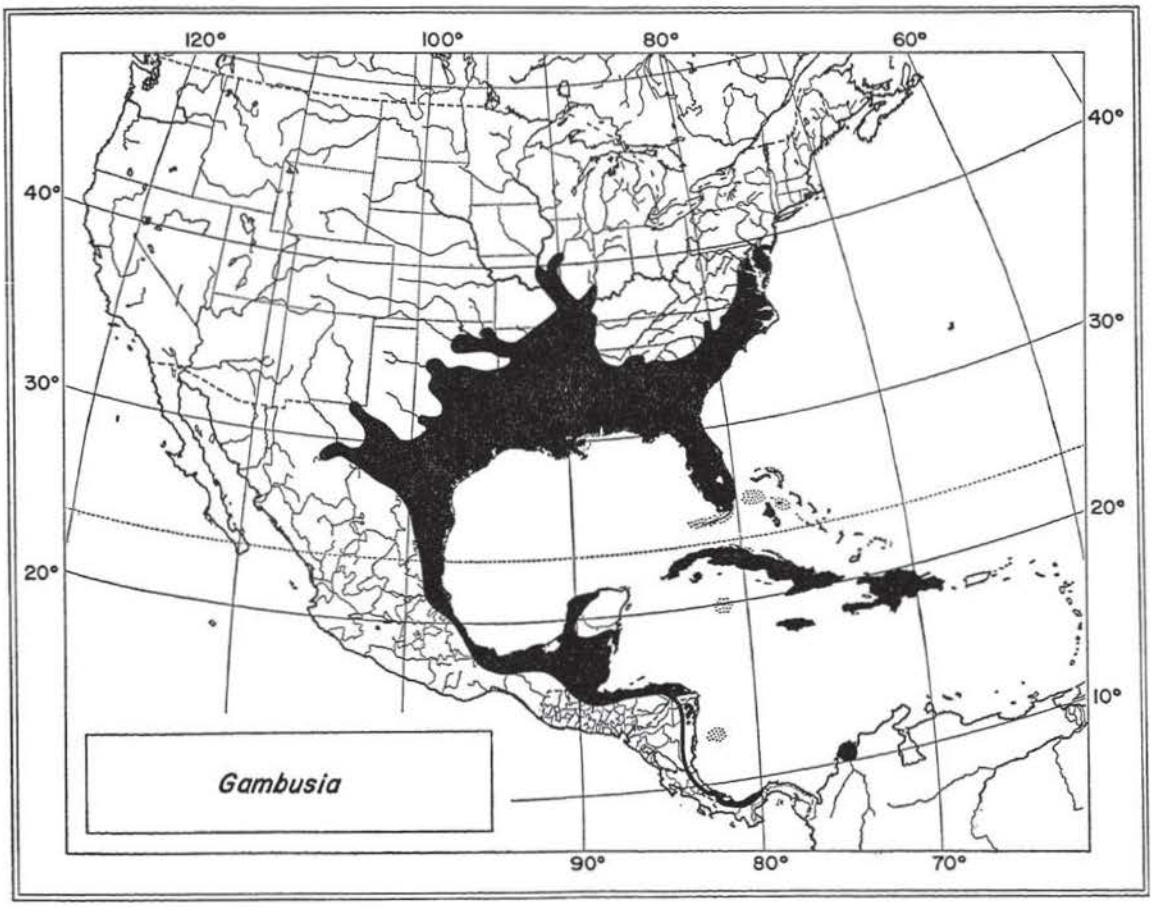
Dicerophallus.—ALVAREZ, 1952b, pp. 95–97 (type species, by original designation, *Dicerophallus echeagarayi* Alvarez).

Orthophallus.—RIVAS, 1963, p. 339 (subgenus of *Gambusia;* type species, by original designation, *Gambusia lemaitrei* Fowler).

DIAGNOSIS: In skull, parietals typically well developed, broad, in some cases sinuous, broadest medially, and extending from pterotic-sphenotic juncture medially and backward to cover part of epiotic-supraoccipital commissure; supraoccipital processes moderately developed; epiotic processes variably developed or absent; posttemporal forked; marginal jaw teeth recurved, conical. Pleural ribs typically not sexually dimorphic, rarely distal tips of posterior elements bent slightly forward in male. Gonopodial suspensorium with two or three well-developed gonapophyses; if three, numbers II and III inclined

sharply forward, in many cases bent forward so that they parallel vertebral axis; tips of gonopophyses I and II straight or arched gently downward, of III, if present, either straight or bent slightly upward toward ventral surface of II; gonapophyses II and III typically with well-developed, long, pointed uncini; gonapophysis I rarely with uncini, gonapophysis II rarely without uncini; ligastyle present, variable in development, in many cases with rugose surface, rarely with two ventral rami; primary gonactinostal complex typically long, slender, and tubular, incorporated gonactinosts 2, 3, and 4 crowded together and grown over by bone derived partly from inferior lateral wings, superior lateral wings having grown outward and backward from gonactinost 4 to form bony, collar-like enclosure for tip of gonactinost 5 (of secondary gonactinostal complex). Gonopodium bilaterally symmetrical; distal elements of ray 3 variably developed as spines; ray 4a with ventral, elbow-like, bony, subdistal growth that may be associated with lateral fleshy outgrowths, elbow poorly developed in *vittata;* rays 4p and 5a terminated by variably developed claws; with proximal serrae on ray 4p at or proximal to level of elbow on 4a; dorsal surfaces of elements of 5p typically with denticles or minute serrations.

REMARKS: The configuration of the pectoral fin of adult males of *Gambusia* constitutes a unifying character that emphasizes the integrity of the group. The upper four to six pectoral rays are usually distinctly thickened and typically curved upward just distal to their middle to form a bow or notch



MAP 11. Distribution of *Gambusia*.

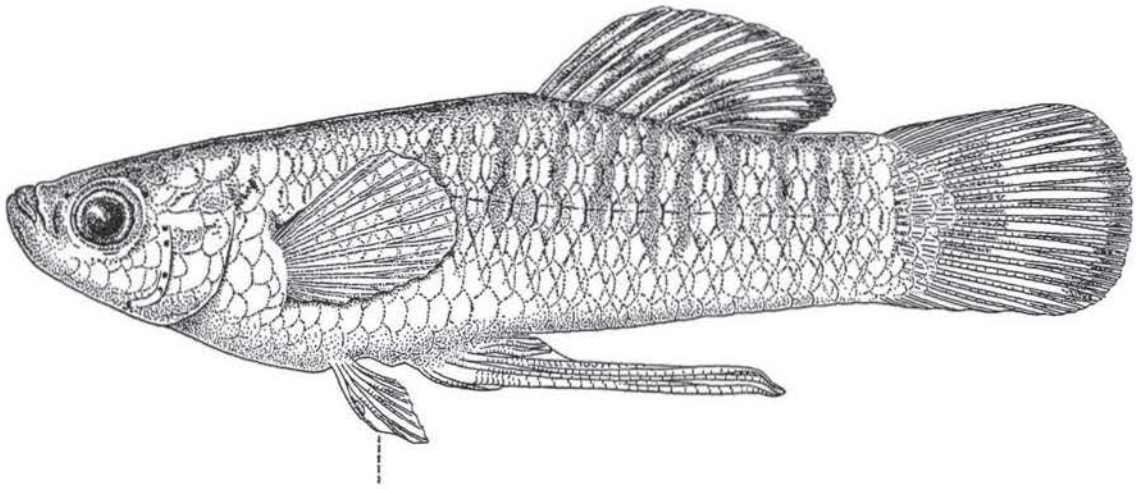


FIG. 41. Holotype of *Brachyrhaphis hartwegi*, new species, U.M.M.Z. No. 168918. Drawn by S. Runyan.

on the leading edge of the fin. This feature is unique; it is lacking in *Brachyrhaphis* and *Belonesox*. In most species of *Gambusia*, this sexually dimorphic feature is evident though unspectacular. The minimal development observed is in *G. luma*, in which the upper rays are not thickened and only slightly upturned. But in *G. heterochir* the modification is unusually well developed, forming a deep concavity on the upper edge of the fin (C. Hubbs, 1957, fig. 5).

RANGE AND SPECIES COMPOSITION: Atlantic drainage from the eastern and southern United States southward in Middle America to northern Colombia, and in the Greater Antilles east to Hispaniola and the Bahamas (map 11). Thirty-four species.

CLASSIFICATION OF *Gambusia*

A thorough revisionary study is needed for an assessment of the interrelationships and a reconstruction of the phylogeny of the species of *Gambusia*. We have examined all the mainland species and feel fairly confident of their status. For the closely related forms of the Antilles, however, additional material and more thorough analysis are required for a delimitation of species and subspecies and to assure confidence in relationships.

All students of *Gambusia* emphasize gonopodial differences in classification; some even restrict characterization of groups to such features (e.g., Rivas, 1963). We find that variations in the gonopodial suspensorium, in pigmentation, in vertebral number, and in body and fin configuration are also useful, and we suspect that more penetrating analyses will reveal additional characters.

The 34 species listed are arranged in a number of more or less sharply defined groups. Some of these groups are so distinctive that genera have previously been erected for them; others merge so imperceptibly that lines for separation are arbitrary. We emphasize the common origin and over-all unity of the group by the recognition of a single genus, as defined above. Most of the constituent groups are less well defined than, for example, the subgenera of *Poecilia*. Therefore, at least until better understood, we withhold subgeneric division and recognize six species groups. With few exceptions, chiefly imperfectly known forms on Cuba and Jamaica, the nominal species in any one group are allopatric, but representatives of two or more species groups commonly occur together.

Among poeciliids, well-developed antrorse spines on ray 3 of the gonopodium are found only in *Gambusia*. In species in which ray 3 is shorter than ray 4, however, these spines are poorly developed or are perpendicular to the ray; such species are regarded as unspecialized in this feature. Contrariwise, long spines and long internal bases for the spines are thought to be specializations. Similarly, rather straight, unmodified rays in the

gonopodium are assumed to be ancestral; abrupt curves, elbows, notably projecting fleshy horns, and enlarged bony claws are subsequent specializations. Another important modification in *Gambusia* involves the relatively advanced anal fin of the male and the attendant changes in the suspensorium. In related but more generalized *Brachyrhaphis* and *Belonesox* there are three gonapophyses, all of which usually bear uncini, but those on the first are in some cases missing (pl. 2, figs. 7, 8). In *Gambusia* the first gonapophysis lacks uncini except as an infrequent individual variation; the second may lack the uncinus on one or both sides (usually has no uncinus in *luma*), and the third gonapophysis, if developed, is highly variable. Most species of *Gambusia* have regular rows or scattered dark spots or speckles on the body and fins, but they are lacking in two species groups. Similarly a dusky lateral stripe is present in some species groups but not in others. A dark subocular bar is characteristic of some species and is uniformly absent in others, but variations within and between species in this feature limit its usefulness.

The six species groups that we recognize do not seem to fall into a simple linear sequence. Each group has both generalized and specialized characters for the genus. We start the sequence with the largest and most wide-ranging group, from the ancestors of which most of the others are probably derived.

affinis Species Group

Diagnosis: Gonopodium acute to moderately broad, spines of ray 3 antrorse, short to moderate in length, about eight to 11, their tips falling short of or slightly exceeding tip of ray 4a, internal bases wanting or poorly developed; ray 4a with well-defined elbow that is opposite or, in most cases, distal to outer serrae on ray 4p, elbow composed of two or more segments, in some as many as eight or nine distal ones joined along ventral edges (this character unique to this species group), distal part of ray straight or gently curved; ray 4p with four to seven weak or strong serrae that are more or less retrorse or perpendicular to shaft, terminal segment a well-formed, in some cases compound, claw that usually has acute, distal apex; ray 5a with well-formed claw that is usually J-shaped: suspensorium involving two or, usually, three gonapophyses; dorsal fin variable in position, with five to 11 rays, usually six to eight; subocular dark bar usually present and well marked; body with spots, either scattered or in rows; caudal peduncle without broad lateral stripe (a narrow axial streak may be present). Middle rays of anal usually dark, much as in *Brachyrhaphis*.

Remarks: *Gambusia nicaraguensis* and *G. affinis*, the most widespread mainland forms, are closely related and share the weak development of spines on gonopodial ray 3. *Gambusia yucatana* has longer spines on ray 3 and a more strongly marked series of dark spots on the body and fins.

Range and Species Composition: Atlantic drainage from northern Colombia to New Jersey, West Indies east to the Bahamas and Hispaniola. Seventeen species.

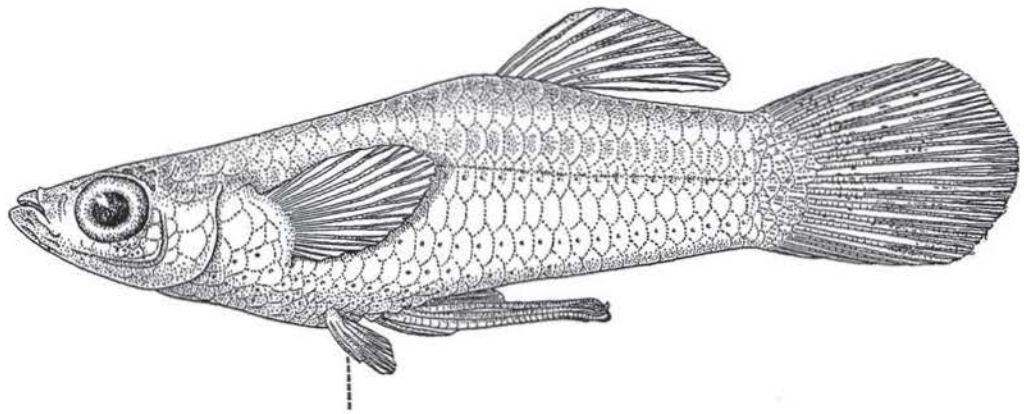


Fig. 42. Holotype of *Gambusia luma*, new species, U.M.M.Z. No. 143565. Drawn by S. Runyan.

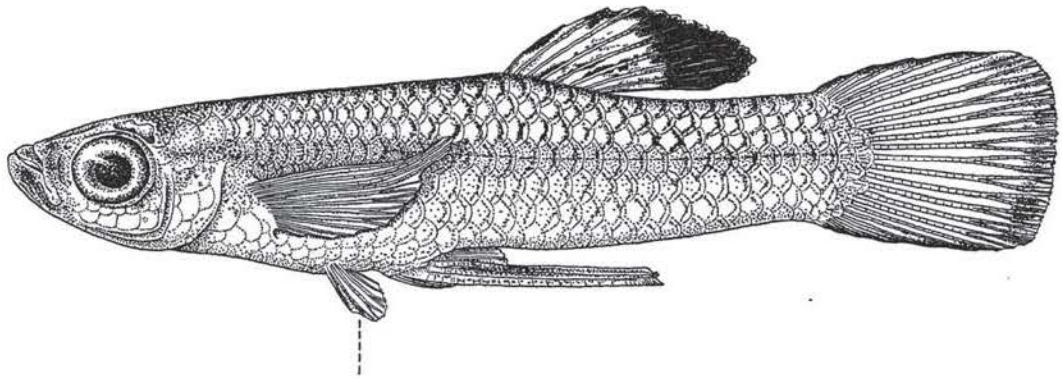


FIG. 43. Holotype of *Gambusia atrora*, new species, U.M.M.Z. No. 179999. Drawn by S. Runyan.

Gambusia nicaraguensis Günther

Gambusia nicaraguensis.—GÜNTHER, 1866, pp. 336–337 (original description; Lake Nicaragua, Nicaragua; syntypes, B.M.N.H.). *Gambusia nicaraguensis nicaraguensis.*—C. L. HUBBS, 1936, pp. 225–226 (in part, material from Puerto Barrios, Guatemala, and Tela, Honduras). *Paragambusia nicaraguensis.*—MEEK, 1904, p. 133 (in part, type material only).

Gambusia dovii.—REGAN, 1913b, p. 986 (original description; Lake Nicaragua, Nicaragua; holotype, B.M.N.H.).

?Gambusia mcneili.—FOWLER, 1916b, p. 433 (original description; Panama; holotype, A.N.S.P. No. 6818).

Gambusia affinis speciosa (misidentification, not Girard).—BREDER, 1933, p. 567 (Barro Colorado Island, Canal Zone; see Hildebrand, 1938, pp. 297–298).

MATERIAL: Gatún Lake, Barro Colorado, Panama; U.M.M.Z. No. 92126.

RANGE: Lago de Izabal (U.S.N.M. No. 134591) and Puerto Barrios, Guatemala, south in Atlantic coastal drainages to Gatún Lake, Panama. Occasionally in brackish or salt water (Hildebrand, 1938, p. 297). The original Lake Nicaragua records are doubtful, since recent collections have not confirmed its presence in the lake.

REMARKS: The range of *nicaraguensis* apparently does not overlap that of *sexradiata* or in fact that of any other species of *Gambusia* except *luma*.

Gambusia aestiputius Fowler

Text figure 39H

Gambusia aestiputius.—FOWLER, 1950, p. 87 (original description; San Andres Island, Colombian West Indies; holotype, A.N.S.P. No. 71772).

MATERIAL: San Andres Island, Colombian West Indies; A.N.S.P. Nos. 71772, 71773–71775.

RANGE: San Andres Island, Colombian West Indies.

REMARKS: This form is apparently closely related to and perhaps conspecific with *Gambusia nicaraguensis*.

Gambusia lemaitrei Fowler

Text figure 33B

Gambusia lemaitrei.—FOWLER, 1950, p. 2 (original description; Totuma Lake, Colombia [presumably Cienega del Totumo, at Totumo, 30 miles northeast of Cartagena, Atlantico, latitude 10° 43′ N., longitude 75° 14′ W.]; holotype, A.N.S.P. No. 71938). *Gambusia (Orthophallus) lemaitrei.*—RIVAS, 1963, p. 339.

MATERIAL: Paratopotype, A.N.S.P. No. 71939.

RANGE: Cienega del Totumo, Atlantico, Colombia.

Gambusia affinis (Baird and Girard)

MOSQUITOFISH

Text figures 25A, 38B, 39I

Heterandria affinis.—BAIRD AND GIRARD, 1853, p. 390 (original description; Rio Medina and Rio Salado [San Antonio River drainage, Texas]; syntypes, A.N.S.P. Nos. 6974–6975). *Gambusia affinis.*—GIRARD, 1859a, p. 72; 1859c, p. 120. *Gambusia affinis affinis.*—LINDBERG, 1934, pp. 351–367.

Heterandria patruelis.—BAIRD AND GIRARD, 1853, p. 390 (original description; hydrographic

basin of Rio Nueces, Rio Sabinal, Rio Leona, Rio Nueces, Elm Creek, Texas; syntypes, M.C.Z. No. 1300). *Gambusia patruelis.*—GIRARD, 1859a, pp. 72–73; 1859c, pp. 120–121. *Zygonectes patruelis.*—BLEEKER, 1860, p. 486.

Gambusia speciosa.—GIRARD, 1859c, p. 121 (original description; Río San Diego, San Juan drainage, near Cadereita, Nuevo Leon, Mexico). *Zygonectes speciosa.*—BLEEKER, 1860, p. 486. *Gambusia affinis speciosa.*—KRUMHOLZ, 1948, p. 5.

Gambusia holbrooki.—GIRARD, 1859b, pp. 61–62 (original descripton; Palatka, Florida, and South Carolina; syntypes, A.N.S.P. Nos. 6976–6977, U.S.N.M. No. 8301). *Gambusia affinis holbrookii.*—HARLEMAN, 1916–1917, p. 99.

Gambusia gracilis.—GIRARD, 1859c, p. 121 (original description; Matamoras [Tamaulipas], Mexico; syntypes, A.N.S.P. No. 6973). *Zygonectes gracilis.*—BLEEKER, 1860, p. 486.

Gambusia humilis.—GÜNTHER, 1866, p. 335 (substitute for *Gambusia gracilis* Girard, 1859c, preoccupied in *Gambusia* by *Xiphophorus gracilis* Heckel, 1848 [Bleeker, 1860, p. 485]).

Haplochilus melanops.—COPE, 1870, p. 457 (original description; Neuse River, North Carolina; syntypes, A.N.S.P. Nos. 7143–7159). *Zygonectes melanops.*—JORDAN, 1878, p. 52.

Zygonectes atrilatus.—JORDAN AND BRAYTON, 1878, p. 84 (original description; Neuse River, Goldsboro, North Carolina).

Zygonectes brachypterus.—COPE, 1880, p. 34 (original description; Trinity River at Fort Worth [Texas]; holotype, A.N.S.P. No. 20446).

Zygonectes inurus.—JORDAN, 1883, p. 143 (original description; Cache Creek, southern Illinois).

Gambusia nobilis (misidentification).—JORDAN AND EVERMANN, 1896 (1896–1900), p. 682 (account, in part).

MATERIAL: Clear Creek, 10 miles west of Menard, Menard County, Texas; T.N.H.C. No. 4653. Roadside ditch on U. S. 90, Gentilly Road, New Orleans, Orleans Parish, Louisiana; U.M.M.Z. No. 163655. Near San Juan, Mexico; U.S.N.M. No. 117533. Val Verde County, Texas; U.S.N.M. No. 117535. Blue Springs, about 5 miles northeast of Marianna, Jackson County, Florida; U.M.M.Z. No. 163475. Río Axtla at ferry to Xilitla, San Luis Potosí, Mexico; L.S.U. No. 6313.

RANGE: Southern tip of New Jersey (Fowler, 1920, p. 154) southward along Atlantic coastal plain, throughout peninsular Florida, along Gulf coastal plain, and northward in Mississippi Valley to southern Illinois and Indiana, south in Mexico to the Río Pánuco basin, northern Veracruz. Frequently in brackish water.

REMARKS: From the time of their simultaneous description by Baird and Girard in 1853, *affinis* and *patruelis* were treated as distinct species until 1894 when Evermann and Kendall (p. 107) united them and, as first revisers, selected the name *affinis* (Krumholz, 1948, p. 4). These two names were based on the same species, widely known under the name *affinis* by recent authors. As was noted by C. Hubbs and Springer (1957, p. 291), the species called *G. affinis* by C. L. Hubbs (1926) is that currently called *G. geiseri* Hubbs and Hubbs. The erroneous use of the name *patruelis* for the mosquitofish persists in some quarters, presumably because that name rather than *affinis* was employed by Jordan, Evermann, and Clark (1930, p. 185).

The two presently recognized subspecies intergrade in the area between southern Mississippi and the Florida panhandle. They are distinct in gonopodial characters; *holbrooki* has a series of prominent denticles on the posterior surface of ray 3 and a rather short, unsegmented bony claw on 4p, whereas *affinis* lacks the denticles and has a longer, segmented claw. The dorsal rays characteristically number seven in *holbrooki*, six in *affinis*.

Gambusia a. affinis (Baird and Girard) occurs in the Río Pánuco basin, northern Veracruz, Mexico, northward to southern Indiana and eastward to southern Alabama; it is widely introduced elsewhere.

Gambusia a. holbrooki Girard ranges from southern Alabama and Florida northward on the coastal plain to southern New Jersey.

Gambusia melapleura (Gosse)

Poecilia melapleura.—GOSSE, 1851, pp. 84–85 (original description; Jamaica; syntypes, B.M.N.H.). *Gambusia melapleura.*—JORDAN, 1887, p. 564. *Fundulus melapleurus.*—JORDAN AND EVERMANN, 1896, p. 659.

Poecilia melanopleura.—BLEEKER, 1860, p. 486 (emended spelling). *Haplocheilus melanopleurus.*—GÜNTHER, 1866, p. 317. *Gambusia melanopleura.*—GARMAN, 1895, p. 88.

MATERIAL: Shrewsberry River, headwater springs, about 8 miles northeast of Jaranna

la Mar, Westmoreland, Jamaica; in the University of Miami Ichthyological Museum.

RANGE: Jamaica.

REMARKS: We are uncertain of the status of this species and of the next two, but we doubt that all are valid.

Gambusia wrayi Regan

Gambusia wrayi.—REGAN, 1913b, p. 988 (original description; Jamaica; syntypes, B.M.N.H.).

MATERIAL: Silver Springs at road from Sayana la Mar to Green Island Harbor, Jamaica; in the University of Miami Ichthyological Museum.

RANGE: Jamaica.

Gambusia gracilior Regan

Gambusia gracilior.—REGAN, 1913b, p. 989 (original description; Jamaica; syntypes, B.M.N.H.).

MATERIAL: Jamaica; S.U. No. 16775. Jamaica; S.U. No. 24179. Stony River north of Aispelton, Jamaica; in the University of Miami Ichthyological Museum. Puerto Rico (locality perhaps erroneous); U.S.N.M. No. 86545. Jamaica; U.S.N.M. No. 104338.

RANGE: Jamaica.

Gambusia dominicensis Regan

Gambusia dominicensis.—REGAN, 1913b, p. 989 (original description; Haiti; syntypes, B.M.N.H.).

MATERIAL: Cadion de Papito at road from Barahona to Cabral, near Laguna de Cabral (Rincon), Barahona, Dominican Republic; in the University of Miami Ichthyological Museum. Haiti; U.S.N.M. No. 78247. Trou Caiman Springs, Haiti; S.U. No. 39325.

RANGE: Hispaniola.

Gambusia myersi Ahl

Text figure 40A

Gambusia modesta.—AHL, 1923, p. 220 (original description; Mexico; ? types in Zoological Museum of Berlin).

Gambusia Myersi.—AHL, 1925, p. 36 (substitute for *modesta*, preoccupied in *Gambusia* by *Gambusia modesta* Troschel, 1865, a subjective synonym of *Poecilia sphenops* Valenciennes).

Gambusia sp.—DARNELL, 1962, p. 333 (Río Tamesí, Mexico; said by C. L. Hubbs not to be *G. myersi*).

MATERIAL: Canal, 5 miles south of Limón, Tamaulipas, Mexico; U.M.M.Z. No. 97546.

RANGE: Río Tamesí basin, Mexico.

REMARKS: In the Río Tamesí drainage of Tamaulipas a very distinctive species of *Gambusia* occurs that has not been generally recognized except by Darnell (1962), who quoted Carl L. Hubbs's opinion that this species is not the one originally named *G. modesta* Ahl, for which *G. myersi* Ahl is a replacement name. Ahl's description, in rough translation, is as follows: "Body structure resembling that of *Gambusia affinis*. Proportions: Female length is 4 times height (without caudal fin); male length is $4\frac{1}{2}$ times height. Head length $3\frac{1}{2}$–$3\frac{3}{5}$ into body length. Eye 3–$3\frac{1}{4}$. Interorbital width slightly over two (2) into head. Snout little less than diameter of eye. Scales 29–30 in longitudinal row. Dorsal of 6–7 rays; in female it begins directly over end of anal and is equidistant between opercular margin and base of caudal fin. In dorsal fin of male the longest ray is $\frac{1}{2}$ head length and originates exactly between base of caudal and middle of operculum. Anal fin of female with 7–8 rays and with first ray the longest and $\frac{2}{3}$ head length. Gonopodium of male $\frac{1}{3}$ body length, rather slender at the point and not conspicuously widened; the distal segments of the first prolonged ray not drawn out into very long continuations (just like those of *G. holbrookii*); elbow of preceding branch of the second ray only weak, the main part of the protuberance lies rather close to the first ray and reaches to the tip of the gonopodium: between the anterior and posterior branch of the second ray there is a relatively large space; the barbed hooks of the second ray are as long as those of the third ray. Pectorals $\frac{2}{3}$ of the head length. Ventrals do not reach anal. Least height of caudal peduncle is $\frac{1}{2}$ head length. Color of female (in alcohol) yellow-olive, each scale darkly edged; below midline the sides of the body are dark till [?] the gravid spot; with a dark suborbital bar; with a fine stripe from below the dorsal at mid-body to beginning of tail; occasionally with very fine black spots on back of caudal peduncle; dorsal and caudal with black spots arranged in rows. Male like female only the dark side zones extend farther onto the caudal peduncle so that the back appears light in comparison; dorsally with a few fine speckles;

dorsal and caudal with dark spots arranged in rows.

"The type specimens of this species are in the Zoological Museum of Berlin; 5 males 26–31 mm., 3 females 34–39 mm. Habitat Mexico, gifts of Mrs. B. Kuhnt. Closely related to *G. affinis* from which it differs, however, in a whole series of characters."

The description of the gonopodium fits that of the Tamesí species (fig. 40A) better than that of any other species of *Gambusia;* especially to be noted are the references to the distinctive configuration of ray 4 (second ray of Ahl) and the pigmentation.

Complete confidence in allocation of the name *myersi* must perhaps await examination of Ahl's type material. Nonetheless, the description, which obviously applies to the *affinis* species group, not only agrees well with that of the present species, but does so much better than with that of the other Mexican species (*affinis* and *yucatana*). We therefore tentatively assign Ahl's name *myersi* to this species.

Gambusia myersi can be described as follows: Ray 3 of gonopodium slightly bowed downward opposite elbow, with about 10 short antrorse spines, the last exceeded by one or two terminal segments of ray 4a; ray 4a with a low, blunt elbow that extends outward and involves nine or 10 segments; shoulder of elbow opposite two distal serrae of ray 4p; ray 4a widely diverging from 4p distally, tips of two rays arching toward and then touching each other; ray 4p with seven long, curving, retrorse serrae; strong, retrorse claw of ray 4p with long, downward-pointing apex, that of 5a elongate and J-shaped; two gonapophyses, the first without uncini, its shaft forming angle of about 40 or 45 degrees with vertebral column, the second straight, with well-developed uncini; third caudal vertebra with normal hemal spine and no uncinus; dorsal rays 7; origin of dorsal 1.6 to 1.7 times in predorsal length in males, 2.2 in female; body depth, 3.8 in standard length in males; distance from tip of snout to origin of anal, 2.1 in standard length; rays 2 to 5 of pectoral fin in adult males notably upturned distally, more expanded than lower rays; subocular dark bar downward and backward from eye; dorsal with narrow dusky margin and four series of discrete dark spots on membranes of fin; caudal with narrow dusky margins and with two or three rather vertical series of spots, series distal to middle of fin especially well marked, basal third of fin with scattered spots; anal fin immaculate in male, with faint dusky edge in female; predorsal streak moderately wide; postanal streak narrow, faint; lateral axial streak on body well developed; lateral dark stripe faint or obsolete anteriorly, undeveloped posteriorly; dark cross hatching of scale edges pronounced, extending over lower side of caudal peduncle, upper side, and back; body with as many as six more or less regular series of lateral, dark spots, these chiefly at junctions of cross hatching; periproct not darkened in female; lower lip rather dark in male, less so in female.

Gambusia yucatana Regan

Gambusia yucatana.—Regan, 1914b, p. 67 (original description; Progreso, Yucatán, Mexico; syntypes, B.M.N.H.).

Material: All from Mexico: El Río o La Cienaga, 200 feet south of lagoon bridge on Progreso-Merida road, Yucatán; U.M.M.Z. No. 156710. One kilometer south of Coatzacoalcos, Veracruz; U.M.M.Z. No. 146143. Progreso, Yucatán; M.C.Z. No. 33969.

Range: From near Coatzacoalcos, Veracruz, Mexico, to the outer part of the Yucatán Peninsula, the Petén Lake district of Guatemala, and northern British Honduras.

Remarks: The range of *yucatana* overlaps that of *sexradiata* in southern Mexico, the Yucatán Peninsula, and in Petén, Guatemala.

Gambusia puncticulata Poey

Plate 1, figure 9

Gambusia puncticulata.—Poey, 1854, pp. 381, 386, 390 (original description; Havana, Cuba; syntypes, M.C.Z. Nos. 6391, 6397, 6401, U.S.N.M. No. 120259).

Gambusia picturada.—Poey, 1868, p. 410 (original description; Cuba). *Gambusia picturata.*—Poey, 1876, p. 141.

Gambusia nigropunctata.—Regan, 1913b, p. 987 (original description; Fermina, Bemba, Cuba; syntypes, B.M.N.H.).

Gambusia melanosticta.—Regan, 1913b, p. 987 (original description; Cuba; syntypes, B.M.N.H.).

Material: Preston near Nipe Bay, Cuba; M.C.Z. No. 33740.

Range: Cuba.

Gambusia howelli Rivas

Gambusia howelli.—RIVAS, 1944a, pp. 41, 44, 46 (original description; Punta del Este, Isle of Pines; holotype, U.H.P.M. No. 454).

MATERIAL: Brackish water lagoon near Punta del Este, Isle of Pines; U.M.M.Z. No. 143374.

RANGE: Isle of Pines, Cuba.

Gambusia baracoana Rivas

Gambusia baracoana.—RIVAS, 1944a, p. 46 (original description; Río Miel, Baracoa, Oriente Province, Cuba; holotype, L.R.R. No. 134).

MATERIAL: Fresh-water pond near mouth of Río Miel, Baracoa, Oriente, Cuba; U.M.M.Z. No. 143375.

RANGE: Río Miel, Oriente, Cuba.

Gambusia bucheri Rivas

Gambusia bucheri.—RIVAS, 1944a, pp. 42, 44–45 (original description; Río Jicotea, between Aserrio de Moa and Punta Gorda, Oriente Province, Cuba; holotype, L.R.R. No. 132).

MATERIAL: Río Jicotea (Moa system) at bridge between Asserio de Moa and Punta Gorda, Oriente, Cuba; U.M.M.Z. No. 143373.

RANGE: Río Jicotea, Oriente, Cuba.

Gambusia manni Hubbs

Text figure 35B

Gambusia manni.—C. L. HUBBS, 1927, pp. 62, 64 (original description; New Providence, Bahamas; holotype, U.M.M.Z. No. 72183).

Gambusia hubbsi.—BREDER, 1934, pp. 1, 3 (original description; South Andros Island, Bahamas, the West Indies; holotype, A.M.N.H. No. 12454).

MATERIAL: Mangrove swamp, east of Bimini Island, Bahamas, the West Indies; U.M.M.Z. No. 167453.

RANGE: All Bahamas, the West Indies: New Providence, Andros, Green Turtle Cay, San Salvador Islands, Bimini.

REMARKS: We have compared materials in the Museum of Zoology from New Providence, North and South Andros Islands, and Bimini and are unable to distinguish more than a single species.

Gambusia oligosticta Regan

Gambusia oligosticta.—REGAN, 1913b, p. 988 (original description; Jamaica; syntypes, B.M.N.H.).

MATERIAL: Milk River at road from Alley to Rest, Jamaica; in the University of Miami Ichthyological Museum. Jamaica; S.U. No. 24178. Jamaica; U.S.N.M. No. 104339.

RANGE: Jamaica and Haiti.

Gambusia caymanensis Regan

Gambusia caymanensis.—REGAN, 1913b, p. 990 (original description; Grand Cayman; syntypes, B.M.N.H.).

MATERIAL: Grand Cayman; U.S.N.M. No. 89789.

RANGE: Grand Cayman Island.

punctata SPECIES GROUP

DIAGNOSIS: Gonopodium broad and bluntly rounded distally, spines of ray 3 antrorse, long, 10 to 13, terminal in fin or subequal with ray 4a, internal bases long; ray 4a with slender elbow that is slightly distal to or opposite outer serrae of ray 4p, elbow consisting of one to three segments that are commonly discrete, ray not constricted proximal to elbow, distal part of ray straight or gently curved downward at elbow or at tip, with six to eight segments, slender and tapering; ray 4p with four to six short or long, antrorse or retrorse serrae, distally with four to six mostly squarish segments, the last a strong, curved claw that may have a short distal apex; ray 5a moderately to broadly bowed upward opposite serrae of ray 4p; terminal segment a strong claw that is longer than serrae on 4p; gonactinostal complex remote from vertebral column, ligastyle long; three gonapophyses, anterior two projecting away from vertebral axis at angle of 50 degrees or more; uncini on second gonapophysis present or absent, those on third well developed; dorsal fin rays six to 10; subocular bar in most cases strong (weak or absent in *punctata*); body in many cases with prominent dark spots; caudal peduncle without broad dusky stripe; females with much dark pigment in anal fin.

RANGE AND SPECIES COMPOSITION: Atlantic drainage from Río Nautla, Veracruz, Mexico, to Puerto Barrios, Guatemala; Cuba, southern Florida, and Hispaniola. Four species.

Gambusia sexradiata Hubbs

Gambusia nicaraguensis sexradiatus.—C. L. HUBBS, 1936, pp. 225–226 (original description;

Río Papaloapan, at Papaloapan, Oaxaca, Mexico; holotype, U.M.M.Z. No. 102989). *Gambusia sexradiata.*—Rivas, 1962, p. 154 (Río de la Pasión, Sayaxché, Guatemala).

Gambusia nicaraguensis nicaraguensis.—C. L Hubbs, 1936, pp. 225–226 (in part, excluding material from Puerto Barrios, Guatemala, and Tela, Honduras).

Material: Laguna de Petén at Flores Island, Petén, Guatemala; U.M.M.Z. No. 143587. Río Chajmajic, Alta Vera Paz, Guatemala; U.M.M.Z. No. 143613. Río Piedra, on road to Alvarado, Veracruz, Mexico; U.M.M.Z. No. 164742.

Range: Río Nautla, Veracruz, Mexico, south to the Yucatán Peninsula, and in the Río Usumacinta basin, Guatemala.

Remarks: The figures by C. L. Hubbs (1926, pl. 2) and by Rosen and Gordon (1953, text fig. 31C) labeled *G. nicaraguensis* apply properly to *Gambusia sexradiata.* These species were confused also by C. L. Hubbs (1936, table 29); counts attributed to *G. n. nicaraguensis* include both of these allopatric species. Both *G. nicaraguensis* and *G. sexradiata* exhibit geographic gradients in dorsal-ray count, whether modally six or seven. These gradients remain to be analyzed, but the variations in ray counts should not mask the sharp differences between these representatives of different species groups.

Gambusia sexradiata is discussed further under *G. nicaraguensis*, *G. yucatana*, and *G. luma.*

Gambusia luma, new species

Plate 2, figure 3; text figures 40B, 42

Material: The holotype (U.M.M.Z. No. 143565) is an adult male, 32 mm. in standard length, seined at Puerto Barrios, Izabal, Guatemala, on May 3, 1935, by Carl L. Hubbs.[1] Taken with the holotype were 43 juveniles and adult males and females 13–42 mm. long (U.M.M.Z. No. 143566). Additional specimens are as follows: Female, 32 mm., Río Polochic at the "playa," 0.5 kilometer east of Panzos, Alta Vera Paz, Guatemala, collected by L. C. Stuart, March 6, 1940 (U.M.M.Z. No. 144087); immature male and two adult females, 26–35 mm., Río Polochic, Panzos, Guatemala, collected by Robert Rush Miller, April 30, 1946 (U.S.N.M. No. 134592); 11 immature adults, 23.5–30 mm., Río Sauce, about 2 miles southwest of El Estor, at mouth (in Lago de Izabal), collected by Miller, April 27, 1947 (U.S.N.M. No. 114276); three adults, males and female, 25.5–34.5 mm., northeast corner, Lago de Izabal, Guatemala, collected by Miller, April 6, 1946 (U.S.N.M. No. 134588); two adults, male and female, 27 and 30.5 mm., tributary to Lago de Izabal at northeast end, Guatemala, collected by Miller, April 6, 1946 (U.S.N.M. No. 134589); three females, 31–33 mm., Lago de Izabal at Paraiso, Guatemala, collected by Miller, April 7, 1946 (U.S.N.M. No. 134590); one male and four females, 24–30 mm., Lago de Izabal at Río Polochic, Guatemala, collected by Miller, April 7–8, 1946 (U.S.N.M. No. 134591); nine immature males and adult females, 20–38.5 mm., Río Dulce at San Felipe, Guatemala, collected by Miller and Mendizabal, April 5, 1946 (U.S.N.M. No. 134587); 24 immature to adult males and females, 16–28.5 mm., Río Sarstún, about 20 miles above mouth, Guatemala and British Honduras, collected by Miller, April 29–30, 1947 (U.S.N.M. No. 114321); 15 immature to adult males and females, 17–34 mm., Jicotea Creek, tributary to Río Sarstún, Guatemala, collected by Miller, April 30, 1947 (U.S.N.M. No. 114343); one male and four females, 25 to 34 mm., Belize River, vicinity of El Cayo, British Honduras, collected by L. E. Hopun, (?) 1937 (U.M.M.Z. No. 167687; not paratypes).

Diagnosis: Member of *punctata* species group of *Gambusia*, with serrae of ray 4p in gonopodium very long and curved, flaring backward and upward, then upward and forward, claws on rays 4p and 5a tremendously enlarged and straight, directed upward, elbow of ray 4a consisting of one or two segments; gonapophysis of second caudal vertebra of adult male typically with uncini undeveloped or rudimentary; color plain, fins with mere traces of diffuse dark spots; body not definitely spotted; lower side of chin and lower jaw notably dusky; upper pectoral rays of adult males scarcely upturned.

Description: Dorsal-fin rays 6 (2), 7 (17); anal-fin rays 10 (19); sum of left and right

[1] C. L. Hubbs, who collected the type series, was the first to recognize the species as distinct; he separated it from the sympatric *Gambusia nicaraguensis.*

pectoral rays 28 (9), 29 (4), 30 (5); scales in lateral series 29 (18), 29 (1); scale rows around caudal peduncle 16 (19); vertebrae 30 (1), 31 (29), 32 (4). Measurements for males and females expressed as thousandths of the standard length; a range in values for the series is followed by the value, in parentheses, of the holotype.

Males: Greatest depth of body, 265–299 (295); least depth of caudal peduncle, 183–198 (194); dorsal origin to snout tip, 664–687 (667); anal origin to mandibular symphysis, 504–536 (514); dorsal origin to caudal base, 347–376 (365); anal origin to caudal base, 508–556 (556); head length, 282–304 (283); head width, 169–180 (178); snout length, 90–102 (102); orbit length, 102–124 (105); interorbital bony width, 124–133 (133); mouth, over-all width, 103–134 (124); dorsal fin, depressed length, 295–333 (333); gonopodial length, 320–345 (333); caudal-fin length, 352–389 (362); pectoral-fin length, 232–246 (—); pelvic-fin length, 128–139 (130).

Females: Greatest depth of body, 297–355; least depth of caudal peduncle, 165–187; dorsal origin to snout tip, 686–720; anal origin to mandibular symphysis, 591–611; dorsal origin to caudal base, 310–339; anal origin to caudal base, 433–471; head length, 267–306; head width, 166–184; snout length, 86–104; orbit length, 98–112; interorbital bony width, 131–149; mouth, over-all width, 117–132; dorsal fin, depressed length, 257–306; anal fin, depressed length, 301–360; caudal-fin length, 346–384; pectoral-fin length, 251–281; pelvic-fin length, 142–160.

The above measurements are based on nine adult males, 23.0 to 31.5 mm. in standard length, and 10 adult females, 24.2 to 38.6 mm. long, from Puerto Barrios and Lago de Izabal and its confluents.

The gonopodium (fig. 40B) together with that of *G. sexradiata* (Rosen and Gordon, 1953, text fig. 31C) is distinctive in the configuration of the five or six serrae of ray 4p. In both species ray 5a is bowed up more steeply over these serrae, and ray 3 is bent down less notably opposite the elbow, than in *punctata*. The claws of rays 4p and 5a exceed those of *sexradiata* in length and development, making them the strongest of any known species of *Gambusia*.

In radiographs and cleared material of 21 maturing or adult males studied, none has uncini on the first gonapophysis, 14 lack uncini on the second gonapophysis, five have mere nubbins or none or two short uncini, and only two have well-developed uncini. All have three gonapophyses, with well-developed uncini, on the third. In one dissected specimen there is a long uncinus on one side of the second gonapophysis, none on the other. Parapophyses on the second caudal vertebra are usually well developed.

Modification of the pectoral fin of adult males is minimal for the genus. The upper rays are not thickened, as is common, and the upward bend in the distal part of the rays is so slight as to be easily overlooked. It is interesting to speculate whether *luma* preserves the ancestral unmodified condition or has nearly lost it secondarily.

Gambusia luma is the plainest species known to us in *Gambusia*. There is a well-marked dark bar extending down and back from the eye on the cheek only. The dorsal is generally light, with some concentration of melanophores near the margin and diffuse traces of one or two rows of spots. There are some melanophores above the fin base. The caudal fin is light, with melanophores near the posterior margin and along the edges of and on the rays. These denote the position of spots which are clearly evident in many species but obsolescent in *luma*. In the anal fin both sexes have a heavy suffusion of melanophores in rays 3 to 8 and their membranes; the anterior and posterior rays are lighter, but in females the leading edge is not clear white. The body, too, is plain, with a dark axial streak but no broader dark lateral stripe. There is no clear pattern of cross hatching, and there are no developed spots. Faint longitudinal streaks are visible along the centers of the scale rows in the dorsolateral region; these lie in the position of conspicuous rows of dark spots in *G. punctata*. A narrow postanal streak is present. Predorsal and postdorsal streaks are narrow, equally strong and dark, but not black. The lower lip and the front of the gular membrane are decidedly dark.

RELATIONSHIP: *Gambusia luma* is most closely related to *G. sexradiata*. So far as known these species are allopatric. It will be of interest to determine the status of this

complex in the poorly collected area between the known range of *sexradiata* and that of *luma*.

ETYMOLOGY: The substantive *luma* (Latin, thorn) is employed in reference to the striking character of the terminal claw on ray 5 of the gonopodium (fig. 40B).

RANGE: Known from brackish and fresh waters from Puerto Barrios, Guatemala, to the Belize River, British Honduras.

Gambusia punctata Poey

Plate 1, figure 8

Gambusia punctata.—POEY, 1854, pp. 376, 380, 384, 390 (original description; Havana, Cuba; syntypes, M.C.Z. Nos. 6393, 6394, 6424, U.S.N.M. Nos. 4867, 120411, A.N.S.P. No. 9678).

Gambusia punctata punctulata.—GARMAN, 1895, p. 87 (original description; Remedios, Cuba; syntypes, M.C.Z. Nos. 1409, 1410).

Gambusia finlayi.—SANTA MARIA, 1956, p. 96 (*nomen nudum*; figure only; Cuba).

MATERIAL: All from Cuba: Soledad, Santa Clara; M.C.Z. No. 33992. Stream 4 kilometers west of Nueva, Isle of Pines; M.C.Z. No. 33701. Havana; S.U. No. 2477. Palacios; S.U. No. 8499. Río Almendares; S.U. No. 1539. Arroyo los Gansos, San Juan de los Yeros, Santa Clara; S.U. No. 32020.

RANGE: Florida Keys (U.M.M.Z. No. 145059), and Cuba, including the Isle of Pines.

Gambusia beebei Myers

Text figures 33C, 35C

Gambusia beebei.—MYERS, 1935, pp. 305, 307–310 (original description; Lake Miragoâne, Haiti; holotype formerly No. 7168 of the Department of Tropical Research, New York Zoological Society, present location unknown; topotypes in U.M.I.M.).

MATERIAL: Southwest end of Lake Miragoâne, Departement du Sud, Haiti; in the University of Miami Ichthyological Museum.

RANGE: Lake Miragoâne, Haiti.

nobilis SPECIES GROUP

Hubbs and Springer (1957) recognized as members of this group *nobilis*, *senilis*, *geiseri*, *gaigei*, *hurtadoi*, and *alvarezi*. Of these only *nobilis* and *geiseri* are now sympatric. Tabulating Hubbs and Springer's data, we find three subgroups that have reasonably sharp boundaries, particularly in gonopodial structures, one consisting of *nobilis* and *senilis*, another of *geiseri*, and a third of *gaigei*, *hurtadoi*, and *alvarezi*. In the *nobilis-senilis* subgroup the elbow on gonopodial ray 4a is large, consolidated, and made up of two to four, in most cases three, fused segments, the serrae on ray 4p are rather large, and the claws on rays 4p and 5a are smoothly curved upward. In *gaigei*, *hurtadoi*, and *alvarezi* the elbow is of intermediate size, composed of either one or two segments, the serrae on ray 4p are moderately developed, and the claws on 4p and 5a are without the additional bony prominence that characterizes *geiseri*.

The *nobilis-senilis* subgroup is the most widespread, with *nobilis* in northern, and *senilis* chiefly in southern, tributaries to the Rio Grande. In *nobilis* ray 4a is equal to or exceeds 4p instead of being much shorter, and the two forms differ in pigmentation. *Gambusia geiseri* is now sympatric, perhaps through introduction, with the northern representative of that group (*nobilis*) and also occurs to the east in the Guadalupe drainage. The members of the subgroup that includes *gaigei*, *hurtadoi*, and *alvarezi*, although not taken with *senilis*, overlap that form in a southern tributary to the Rio Grande, and in a broad sense are now or in the past certainly have been sympatric with it. The forms of this subgroup share a common gonopodial structure and have at most minor differences in dorsal count and pigmentation. Thus, subgroup I consists of two allopatric populations (*nobilis* in the north and *senilis* in the south); subgroup II (*geiseri*) is sympatric with *nobilis* (perhaps through introduction); and subgroup III (*gaigei-hurtadoi-alvarezi*) is broadly sympatric with or overlaps *senilis*.

All the above forms are set apart from other mainland species of *Gambusia* except *G. heterochir*, *G. longispinis*, *G. myersi*, and *G. yucatana* in typically having only two gonapophyses in their gonopodial suspensoria. The third caudal vertebra has a normal or somewhat ill-formed hemal spine that does not participate in support of the anal fin. On the basis of its gonopodial and suspensorial characters, *G. heterochir*, also from Texas, clearly belongs in the *nobilis* group rather than being closely allied to *nicara-*

guensis, as contended by C. Hubbs (1957). *Gambusia heterochir*, although allied to *nobilis* and a member of the *nobilis* group, is distinct in gonopodial and pectoral-fin structure. In addition, *G. atrora* and the recently described *G. longispinis* also belong to the expanded *nobilis* species group, which is defined below.

DIAGNOSIS: Gonopodium acute distally, spines of ray 3 antrorse, about six to 11, middle or distal ones longest and terminal in fin, internal bases moderate to very long; ray 4a with well-defined elbow that is opposite or somewhat distal to outer serrae of ray 4p, elbow composed of one to four separate or consolidated segments, distal part of ray straight, consisting of three to eight slender, discrete segments that taper to tip, ray 4p with four to six weak to strong serrae that are retrorse or perpendicular to shaft, with four to six distal segments, last a simple claw that varies from smoothly curved to an angulate distal apex; ray 5 gently to strongly bowed above serrae of ray 4p, distal segment strongly recurved, J-shaped claw; gonactinostal complex rather narrowly separated from vertebral column, ligastyle short, gonapophyses 1 and 2 almost straight, extending abruptly forward at angle of about 15 to 45 degrees from vertebral axis, uncini of second long, projecting backward in line with lower part of shaft; gonapophyses usually two, but three in *atrora* and *longispinis;* dorsal fin rather well forward, with seven to 10 rays; subocular dark bar usually absent (in some cases faint but well developed in *heterochir*); body commonly with some scattered dark specks or spots; side of body usually with broad, though diffuse, dusky to black lateral stripe; anal fin without dark blotch near base.

RANGE AND SPECIES COMPOSITION: Atlantic drainage from central Texas to the Panuco River system, Mexico. Seven species.

Gambusia atrora, new species

Plate 2, figure 2; text figures 40C, 43

MATERIAL: The holotype (U.M.M.Z. No. 179999) is an adult male, 23.5 mm. in standard length, seined from ferry across Río Axtla to a shallow area 150 yards upstream, Xilitla, San Luis Potosí, Mexico, on December 31, 1951, by Malcolm S. Gordon and W. Z. Lidicker, Jr. Taken with the holotype were 537 juvenile to adult males and females, 13–30 mm. long (U.M.M.Z. No. 169499). Additional specimens are as follows: one male, 20 mm., Río Axtla, Axtla, San Luis Potosí, Mexico, collected by Myron Gordon and James Atz on January 14, 1939 (U.M.M.Z. No. 124172); five adult males and females, 19–22 mm., same locality, collected by Myron Gordon and party on April 14, 1939 (U.M.M.Z. No. 124361); one adult male, 27 mm., and seven adult females, 26–40 mm., Río Matlapa, at Matlapa, 13 miles north of Tamazunchale, San Luis Potosí, Mexico, by Myron Gordon and party on April 14, 1939 (U.M.M.Z. No. 124335); 13 half-grown to adult males and females, 16–36 mm., Arroyo Plan de Jalpilla, 18 miles north of Tamazunchale, San Luis Potosí, Mexico (U.M.M.Z. Nos. 124348–124349).

DIAGNOSIS: Member of *nobilis* species group of *Gambusia*, with three gonapophyses in gonopodial suspensorium, second and third with well-developed uncini; middle spines of anal ray 3 much longer than those proximal or distal, forming acute tip of gonopodium and separated by notch at end of short, weak ray 4a from claws of rays 4p and 5a, which strongly enter profile; elbow slender, erect, often formed of one segment but commonly buttressed by adjacent segments; serrae of ray 4p three or four, short and slightly retrorse, next two distal segments enlarged, cuboidal; dorsal rays usually eight; suborbital bar undeveloped; conspicuous, broad, black border posteriorly and marginally on dorsal fin; scale borders dark-edged, dusky lateral stripe, scattered dark spots and scales on dorsolateral surface; pectoral fin of adult male turned abruptly upward distally, upper rays enlarged but not grossly distorted.

DESCRIPTION: Dorsal fin rays 8 (19); anal-fin rays 10 (14), 11 (1); sum of left and right pectoral rays 24 (8), 25 (2), 26 (2); scales in lateral series 30 (1), 31 (6), 32 (9), 33 (3); scale rows around caudal peduncle 16 (20); vertebrae 33 (5), 34 (12). Measurements for males and females expressed as thousandths of the standard length; a range in values for the series is followed by the value, in parentheses, of the holotype.

Males: Greatest depth of body, 214–240 (234); least depth of caudal peduncle, 152–169 (166); dorsal origin to snout tip, 562–591

(583); anal origin to mandibular symphysis, 448–489 (489); dorsal origin to caudal base, 418–458 (443); anal origin to caudal base, 554–575 (570); head length, 260–286 (260); head width, 144–157 (149); snout length, 93–107 (106); orbit length, 93–106 (106); interorbital bony width, 95–111 (111); mouth, over-all width, 93–107 (106); dorsal fin, depressed length, 239–264 (264); gonopodial length, 317–333 (328); caudal-fin length, 247–286 (281); pectoral-fin length, 230–277 (277); pelvic-fin length, 80–93 (85).

Females: Greatest depth of body, 224–250; least depth of caudal peduncle, 131–145; dorsal origin to snout tip, 599–658; anal origin to mandibular symphysis, 523–585; dorsal origin to caudal base, 356–408; anal origin to caudal base, 447–481; head length, 259–291; head width, 151–169; snout length, 96–106; orbit length, 84–106; interorbital bony width, 100–116; mouth, over-all width, 100–122; dorsal fin, depressed length, 212–232; anal fin, depressed length, 200–227; caudal-fin length, 227–261; pectoral-fin length, 202–231; pelvic-fin length, 99–118.

The above measurements are based on 10 adult males, 21.7 to 25.0 mm. in standard length, and 10 adult females, 24.5 to 30.4 mm. long, from the type locality.

The upper pectoral-fin rays of adult males are somewhat thickened and the upper four or five are turned upward in their distal fourth.

No definite suborbital bar is developed, but a few melanophores in many cases are scattered on the cheek below and behind the eye. The dorsolateral body scales are marked with pronounced dark edging, with few melanophores elsewhere; below the dusky lateral stripe the scales have melanophores throughout, and the scale edges are scarcely darker. Black spots are scattered irregularly on the side, mostly above the axial stripe. The margin of the dorsal is dark in males, notably so in the distal third; in females the edge is dusky, there is also a dark bar near the dorsal base, stronger in males; the caudal is clear except that the margin is dark, especially in males, and there may be one or a few macromelanophores near the base; the anal fin of females has some melanophores over the fin, concentrated in the basal two-thirds of rays 4 to 7, in males melanophores are concentrated on the upper part of the gonopodium, especially rays 4, 5, and 6, of which ray 5 is darkest. In females the periproct has a wedge-shaped border, dark anteriorly and laterally, or on the sides only.

RELATIONSHIP: *Gambusia atrora* is perhaps most closely related to *G. longispinis*. Unlike other species of the *nobilis* group, these two have three gonapophyses in contact with the gonactinosts, either directly or by tendinous extension of the third gonapophysis. The two species differ markedly in pigmentation. *Gambusia atrora*, by comparison, has more conspicuously bicolored dorsal and caudal fins, the midaxial and subpeduncular streaks better developed and darker, the scale borders more clearly outlined with dark, the lower jaw dusky, and contrasting dark spots scattered on the side. In the gonopodium of *atrora* (compare fig. 40C, with Minckley, 1962, fig. 1), the elbow of ray 4a consists chiefly of a single segment rather than three or four fused elements, and the distal part of the ray is much reduced rather than subequal to ray 4p; the serrae of ray 4p are fewer and shorter, and the segments distal to them are cuboidal and much higher than the terminal segments.

ETYMOLOGY: The substantive *atrora* (Latin *ater*, black, and *ora*, a border or edge) has reference to the striking dark pigment on the distal margins of the dorsal and caudal fins.

RANGE: Known from the Río Axtla and Río Matlapa, San Luis Potosí, northeastern Mexico.

Gambusia longispinis Minckley

Gambusia longispinis.—MINCKLEY, 1962, pp. 391–393, figs. 1–3 (original description; marsh adjacent to Langostura Canal, about 4 miles south and 6 miles west of Cuatro Ciénegas, Coahuila, Mexico; holotype, U.M.M.Z. No. 179620).

MATERIAL: About 4 miles south-southwest of Cuatro Ciénegas, Coahuila, Mexico; U.M.M.Z. No. 130382.

RANGE: Cuatro Ciénegas basin, Coahuila, Mexico.

Gambusia nobilis (Baird and Girard)

Text figures 33A, 40G

Heterandria nobilis.—BAIRD AND GIRARD, 1853, p. 390 (original description; Leona and Comanche Springs, valley of the Rio Grande del Norte,

Texas; lectotype, M.C.Z. No. 1455, designated by Hubbs and Springer, 1957, p. 297). *Gambusia nobilis.*—GIRARD, 1859a, pp. 71–72; 1859c, p.120.

MATERIAL: Phantom Lake and ditch, Jefferson Davis County, Texas; U.M.M.Z. No. 120344. Comanche Springs at Fort Stockton, Pecos County, Texas; U.M.M.Z. No. 120356. Phantom Lake, Toyahvale, east side of Davis Mountains, Texas; S.U. No. 35962.

RANGE: Western tributaries to the Pecos River in Texas and New Mexico (Hubbs and Springer, 1957, p. 294).

Gambusia senilis Girard

Gambusia senilis.—GIRARD, 1859c, p. 122 (original description; Chihuahua River, Río Grande drainage, Mexico). *Zygonectes senilis.*—BLEEKER, 1860, p. 486.

MATERIAL: Sauz, Mexico; S.U. No. 24665. Río Chihuahua, Chihuahua, Mexico; S.U. No. 9401. Tributary to Río Conchos, ¼ mile south of Mesqui, Mexico; U.M.M.Z. No. 166721.

RANGE: Devils River, Texas (C. Hubbs, 1958, p. 239), and Río Conchos and tributaries, Chihuahua and Durango, Mexico (Hubbs and Springer, 1957, p. 299).

REMARKS: This form is allopatric with but distinct from *Gambusia nobilis*, its closest relative (see p. 101).

The gonopodial characters that separate *senilis* from *nobilis* are less well marked than those that distinguish the subspecies of *Gambusia affinis* (*affinis* and *holbrooki*).

Gambusia gaigei Hubbs

Gambusia gaigei.—C. L. HUBBS, 1929, pp. 3–6, 8, 10 (original description; Rio Grande at Boquillas, Brewster County, Texas; holotype, U.M.M.Z. No. 84527).

Gambusia alvarezi.—HUBBS AND SPRINGER, 1957, pp. 279–321 (original description; El Ojo de San Gregorio, Chihuahua, Mexico; holotype, U.M.M.Z. No. 168979).

Gambusia hurtadoi.—HUBBS AND SPRINGER, 1957, pp. 279–321 (original description; El Ojo de la Hacienda Dolores, Chihuahua, Mexico; holotype, U.M.M.Z. No. 168975).

MATERIAL: Spring at Boquillas along Rio Grande, Texas; U.M.M.Z. No. 84528. El Ojo de San Gregorio, Chihuahua, Mexico; T.N.H.C. No. 4207. El Ojo de la Hacienda Dolores, Chihuahua, Mexico; T.N.H.C. No. 4205.

RANGE: Graham Ranch Warm Spring and Boquillas Spring near Boquillas Canyon, Brewster County, Texas, El Ojo de San Gregorio and El Ojo de la Hacienda Dolores, Chihuahua, Mexico (Hubbs and Springer, 1957).

REMARKS: The three forms treated as distinct species (*gaigei*, *alvarezi*, *hurtadoi*) by Hubbs and Springer (1957) differ only in average meristic, morphometric, and pigmentary characters, and we prefer to treat them as conspecific.

Gambusia geiseri Hubbs and Hubbs

Gambusia geiseri.—HUBBS AND HUBBS, *in* Hubbs and Springer, 1957, pp. 279–324 (original description; San Marcos River, San Marcos, Texas; holotype, U.M.M.Z. No. 168974).

MATERIAL: San Marcos River, 1 mile east of San Marcos, Hays County, Texas; U.M.M.Z. No. 166018. Comanche Springs at Fort Stockton, Pecos County, Texas; U.M.M.Z. No. 120358.

RANGE: Confined to Texas: upper Guadalupe River system; apparently introduced in South Concho River, Devils River, irrigation ditch in Reeves County, Comanche Springs, and Tunis Springs (Hubbs and Springer, 1957, pp. 289–291).

Gambusia heterochir Hubbs

Gambusia heterochir.—C. HUBBS, 1957, pp. 3–16 (original description; Clear Creek, Menard County, Texas; holotype, U.M.M.Z. No. 170936).

MATERIAL: Clear Creek, 10.4 miles west of Menard, Menard County, Texas; T.N.H.C. No. 4652.

RANGE: Headsprings of Clear Creek, Menard County, Texas (C. Hubbs, 1957, p. 8).

panuco SPECIES GROUP

This small group of species is closely related to the *nobilis* assemblage, but is clearly set off by the characteristic modification of the spines on gonopodial ray 3, which are arranged like the stays of a fan. Because of this easily noted feature, the group has been treated by some authors as a subgenus, *Heterophallina*. To impose this rank on all comparable structural modifications in *Gambusia* would, we believe, unnecessarily en-

cumber classification and restrict its utility. *Gambusia panuco* and its allies can be defined as follows.

DIAGNOSIS: Gonopodium broadly rounded distally, spines of ray 3 long (except for distal one or two), proximal ones curved and retrorse, those distad becoming progressively straight and vertical and then, near tip, slightly curved upward and in line with axis of gonopodium; spines numerous, about 12 to 15, terminal in fin, and with internal bases poorly developed; ray 4a almost straight, with retrorse elbow composed of three or four discrete or imperfectly fused segments, elbow opposite distal first to third serrae of ray 4p; straight distal part of ray 4a with six to 10 slender, discrete segments, tip falling just short of to slightly beyond tip of ray 4p; ray 4p with six to eight rather long, straight or curved, retrorse serrae, distal to which are about five or six rectangular segments, claw at tip of ray 4p rather weak and evenly curved upward, distal tip not angulate; ray 5a notably bowed upward over serrae on 4a, terminal segment long, with bluntish, upturned claw; gonactinostal complex rather close to vertebral column, ligastyle short; three gonapophyses, anterior two parallel and projecting away from vertebral axis at angle of about 30 to 45 degrees; uncini typically present on second and third gonapophyses; dorsal-fin rays seven to nine (11); no dark subocular bar; body and fins with some scattered dark spots; dusky to black lateral stripe.

RANGE AND SPECIES COMPOSITION: Atlantic drainage of northeastern Mexico from the Río Panuco to the Río Salado basin. Three species.

Gambusia panuco Hubbs

Gambusia panuco.—C. L. HUBBS, 1926, pp. 22, 30–32 (original description; Río Valles, Valles, San Luis Potosí, Mexico; holotype, C.N.H.M. No. 14060).

MATERIAL: All from Mexico: Flats and pool 64 miles south of Tampico on coastal road, 52 miles north of Alamo ferry, Veracruz; U.M.M.Z. No. 167529. Tributary to Estero Tancochin, east of Naranjos, Veracruz; U.M.M.Z. No. 97537. Rascón, San Luis Potosí; L.S.U. No. 6298. Laguna Cerro la Pez near Ebano, San Luis Potosí; in the Louisiana State University.

RANGE: Río Panuco system, Atlantic drainage of Mexico.

REMARKS: This species and *regani* are allopatric in the northern and southern tributaries of the Río Panuco system. Their differences are not so great as those that separate the subspecies of *Xiphophorus montezumae* and *X. pygmaeus* within the same drainage (see Rosen, 1960). Future study may show that *panuco* and *regani* are conspecific.

Gambusia regani Hubbs

Text figure 40E

Gambusia regani.—C. L. HUBBS, 1926, pp. 22, 28–29 (original description; Río Forlón, Forlón, Tamaulipas, Mexico; holotype, C.N.H.M. No. 14033).

MATERIAL: Río Caballero, 729 kilometers north of Mexico City, Tamaulipas, Mexico; U.M.M.Z. No. 162149.

RANGE: Río Panuco system, Atlantic drainage of Mexico.

Gambusia marshi Minckley and Craddock

Gambusia marshi.—MINCKLEY AND CRADDOCK, *in* Minckley, 1962, pp. 392–396, figs. 2–6 (original description; Río Salado de los Nadadores near junction with Río Salado de Monclova, 1 mile south of Hermanas, Coahuila, Mexico; holotype, U.M.M.Z. No. 179167).

MATERIAL: Laguna Churince, 12.2 miles south-southwest of Cuatro Ciénegas, Coahuila; U.M.M.Z. No. 179196.

RANGE: Río Sabinas de Coahuila, Río Salado, and Río Salado de los Nadadores and tributaries, Coahuila, Mexico.

vittata SPECIES GROUP

The end of the gonopodium of *Gambusia vittata* is bent downward, as in *Belonesox belizanus* (fig. 39F, G). Whether the similarity in gonopodial morphology reflects common retention of ancestral characters or convergence is uncertain, but flexure is associated with surprising agreement in structure. In this respect *G. vittata* is distinctive in its genus, but in over-all morphology, including the suspensorium and the sexual modification of the pectoral fin, relationship to the *nobilis* group is suggested. In pigmentation *vittata* is very similar to two sympatric species, *Gambusia atrora* and *Xiphophorus pygmaeus*.

Gambusia vittata has been described as lacking an elbow in the gonopodium. The segments of ray 4a at the locus of the elbow are elevated, however, as are those distal to it in the ray. The structure here and in *Belonesox* could aptly be described as an elongate elbow similar to that seen in the anomalous *G. affinis* gonopodium described above (fig. 391). *Gambusia vittata* can be diagnosed as follows.

DIAGNOSIS: Gonopodium rather blunt, bent downward at level of spines on ray 4p, extreme tip turned upward; spines of ray 3 obsolescent or ill-formed, distal end exceeded by one to four segments of ray 4a; ray 4a with sigmoid flexure, proximal to which, segments largely ankylosed and without constriction, without usual elbow; about eight to 11 much-elevated, discrete segments that largely fill space between rays 3 and 4a; ray 4p very slender proximal to posterior serrae; serrae four or five, straight or slightly curved, retrorse; segments distal to serra 8 or serra 9, angled downward, last a weak convex claw that is directed upward and backward; ray 5a with abrupt downward flexure proximal to which segments ankylosed, and distal to which are about seven short segments, last a finger-like, posteriorly directed claw; gonactinostal complex lying close to vertebral column, suspensory ligament and ligastyle short; three gonapophyses, third bent upward and forward, its tip continued to gonactinosts as strong ligament; gonapophyses 2 and 3 with long uncini; dorsal fin rather far forward, with eight rays; no subocular dark bar; body and fins without dark spots, conspicuous dark lateral stripe on body; lips and mandible notably darkened.

RANGE AND SPECIES COMPOSITION: Río Panuco basin, eastern Mexico. One species.

Gambusia vittata Hubbs

Text figure 39F

Gambusia vittata.—C. L. HUBBS, 1926, pp. 22, 26–27 (original description; Río Forlón, Forlón, Tamaulipas, Mexico; holotype, C.N.H.M. No. 14046). *Flexipenis vittata.*—TURNER, 1940a, p. 89; 1940b, p. 73. *Flexipenis vitta.*—SCRIMSHAW, 1944b, p. 181 (*lapsus* for *vittata*). *Flexipenis vittatus.*—C. L. Hubbs, *in* Rivas, 1963, p. 334.

MATERIAL: Río Choy at Rancho Colandria, 2 miles west of Tamuin, San Luis Potosí, Mexico; L.S.U. No. 6323. Río Valles at Valles, San Luis Potosí, Mexico; U.M.M.Z. No. 97513. Arroyo Plan de Jalpilla, 18 miles north of Tamazunchale, San Luis Potosí, Mexico; U.M.M.Z. No. 124352.

RANGE: Río Pánuco basin from Ciudad Victoria, Tamaulipas, to northern Veracruz, Mexico.

REMARKS: *Gambusia vittata* C. L. Hubbs, 1926, is a junior secondary homonym of *Poecilia vittata* Guichenot, 1853, a species that Bleeker (1860, p. 485) placed in *Gambusia*. Bleeker's referral has not been followed by others, and *vittata* Guichenot is now assigned to *Poecilia* (in the subgenus *Limia*). Hence, no confusion results from the secondary homonymy. Since *Gambusia vittata* C. L. Hubbs was not, prior to 1960, replaced on grounds of homonymy, the name is to be retained under terms of Article 59 of the International Code of Zoological Nomenclature (Stoll and others, 1961, p. 57).

rachowi SPECIES GROUP

Two species, each assigned by some authors to monotypic genera because of gonopodial specialization, share on the one hand several distinctive features not found in other poeciliids and on the other possess fundamental attributes of the genus *Gambusia*. These species are therefore associated as a species group that is regarded as a specialized complex in *Gambusia* but one that retains some generalized features. It can be characterized as follows.

DIAGNOSIS: Gonopodium acute distally, with broad subterminal bulge formed by ray 3; ray 3 with six or seven short spines without internal processes, distal ones retrorse, others erect; two or three distal segments without spines, tip of ray 3 exceeded by two or more segments of ray 4a; ray 4a slender proximal to strongly retrorse elbow, which is composed of one to three discrete or partly coalesced segments; tip of elbow opposite two most proximal serrae of ray 4p; just distal to elbow ray 4a contorted, from this point a fleshy pair of lateral, horn-like projections emerging; distally, slender elements of ray 4a end opposite, or segment short of, tip of ray 4p; ray 4p with four or five short, straight or scarcely curved, erect serrae; distally ray 4p bent slightly downward, very slender, with

about 10 to 13 segments, distal ones longer, and terminating in weak claw that is directed upward; ray 5 slightly to moderately bowed above serrae on ray 4p, distal one to three or four segments with weak upward-directed claws; gonactinostal complex rather well separated from vertebral column; ligastyle very small and slender; three gonapophyses, the first without uncini, forming angle of about 35 to 45 degrees with vertebral column, second and third parallel, converging on tip of first, both continuous to gonactinost, each with straight well-developed uncini and straight or moderately curved shaft; dorsal placed far back, distance from its origin to caudal base 1.9 to 2.3 in predorsal length in males, 2.2 to 2.4 in females; dorsal rays six; no subocular dark bar; body and fins without dark spots; dark axial streak prominent but no broad lateral stripe; middorsal and subpeduncular streaks dark, rather broad; females with some dusky pigment on membranes of anterior six rays of anal fin; caudal fin with long dark streak on center of each interradial membrane.

RANGE AND SPECIES COMPOSITION: Atlantic slope of southern Mexico, Veracruz to Chiapas. Two species.

Gambusia rachowi (Regan)

Text figure 40F

Heterophallus rachovii.—REGAN, 1914b, p. 66 (original description; Veracruz, Mexico; types, B.M.N.H.). *Heterophallus rachowi.*—ROSEN AND GORDON, 1953, p. 25.

Gambusia atzi.—ROSEN AND GORDON, 1951, pp. 267–269, 272 (original description; "Laguna de la Sapote," 1 kilometer northwest of Jesús Carranza, Veracruz, Mexico; holotype, U.M.M.Z. No. 167098).

MATERIAL: Jesús Carranza, Veracruz, Mexico; U.M.M.Z. No. 167099 (*atzi*).

RANGE: Veracruz, Mexico.

Gambusia echeagarayi (Alvarez)

Dicerophallus echeagarayi.—ALVAREZ, 1952b, pp. 95–97 (original description; Río Michol, Palenque, Chiapas, Mexico; holotype in collection of José Alvarez).

RANGE: The type locality.

GENUS **BELONESOX** KNER

Plate 2, figures 7, 8; text figures 35D, 36, 38C, E, 39G

Belonesox.—KNER, 1860, p. 419 (type species, by monotypy, *Belonesox belizanus* Kner).

DIAGNOSIS: Skull like that of *Gambusia* except for premaxillae and dentaries which are much strengthened and enlarged to form prominent, pointed beak; teeth of inner series two or three times as large as those of outer series which are recurved, conical. Ribs like those of *Gambusia.* Gonopodial suspensorium like that of *Gambusia* except gonapophysis I typically having pair of large uncini. Gonopodium like that of *Gambusia vittata*, elbow on ray 4a and terminal claws on rays 4p and 5a poorly developed. Pectoral in adult male with first few rays unmodified and without a notch.

REMARKS: The scales are minute and numerous. The size attained is the largest in the family.

RANGE AND SPECIES COMPOSITION: A single species inhabiting the Atlantic lowlands of southern Mexico and northern Central America (map 10). In fresh and brackish water.

Belonesox belizanus Kner

PIKE KILLIFISH

Plate 2, figures 7, 8; text figures 35D, 36, 38C, 39G

Belonesox belizanus.—KNER, 1860, pp. 419–422 (original description; Belize, British Honduras).

Belonesox belizanus maxillosus.—C. L. HUBBS, 1936, pp. 228–230 (original description; 3 kilometers south of Progreso, Yucatán, Mexico; holotype, U.M.M.Z. No. 102137).

MATERIAL: Lake Petén around shores of Flores Island, Petén, Guatemala; U.M.M.Z. No. 144173. El Río o la Cienega, south of Progreso, Yucatán, Mexico; U.M.M.Z. No. 143090. Río Polochic, Panzos, Alta Vera Paz, Guatemala; U.M.M.Z. No. 146076.

RANGE: Río Antigua system, Veracruz, Mexico, south to Yucatán, Guatemala, British Honduras, and Atlantic drainages of Honduras and Nicaragua (map 10). A stock originating in Progreso has been successfully introduced into southern Florida (U.M.M.Z. No. 178973).

REMARKS: C. L. Hubbs (1936, pp. 229–230) treated this species as a complex of two subspecies: *Belonesox b. belizanus* Kner, from most of the range of the species; and *B. b. maxillosus* Hubbs, from Yucatán.

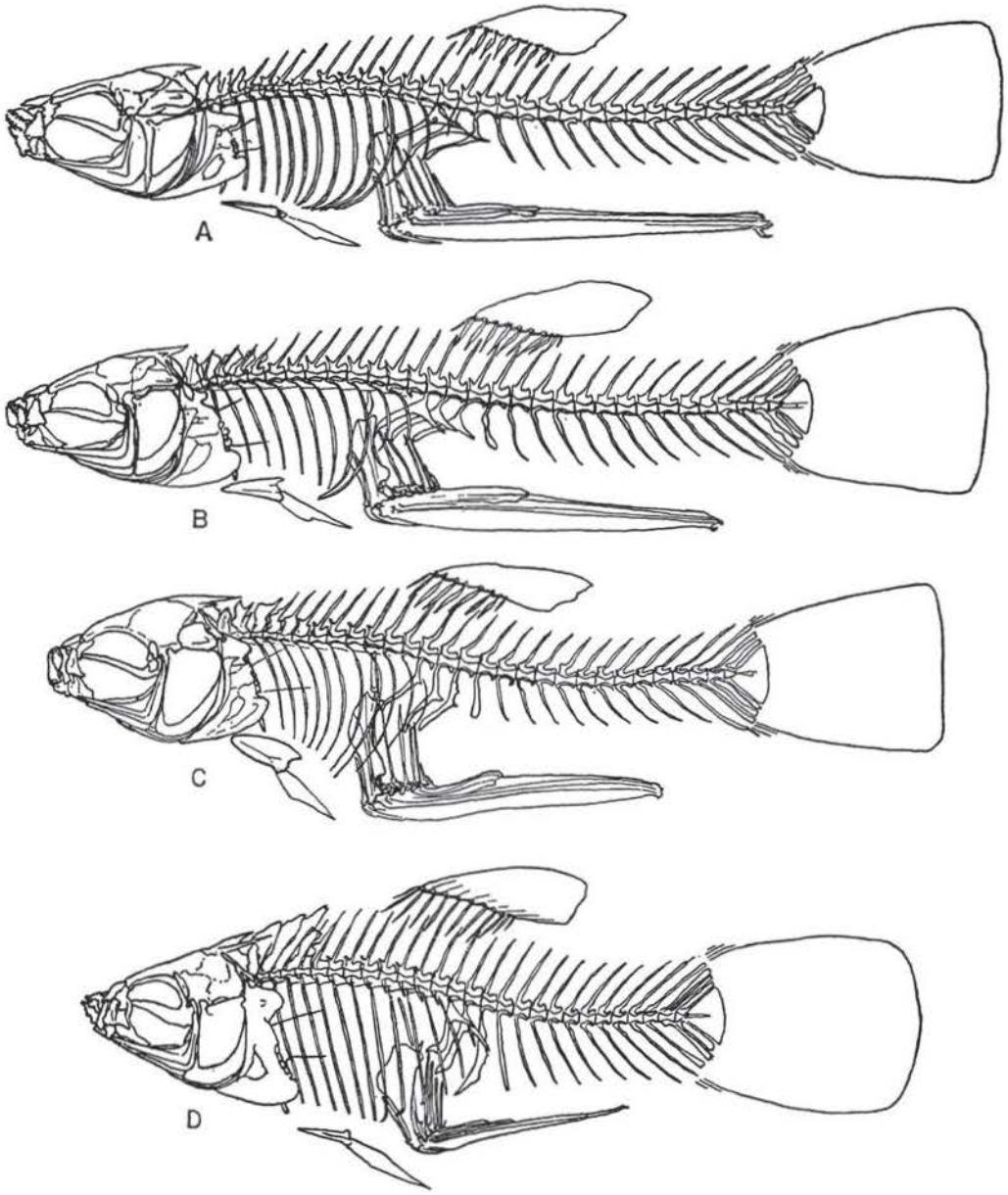


FIG. 44. Skeletons of adult males in the Girardinini, composite drawings. A. *Girardinus cubensis*. B. *Girardinus denticulatus*. C. *Quintana atrizona*. D. *Carlhubbsia stuarti*, from Rosen and Bailey (1959).

TRIBE GIRARDININI

The endemic Cuban genera *Girardinus* and *Quintana* and the Middle American *Carlhubbsia* possess well-developed serrae distally on ray 5p of the gonopodium, a feature not occurring in other members of the family. Other structures that demonstrate the integrity of the group were discussed by Rosen and Bailey (1959, pp. 35–41). The application of the tribal name Girardinini to this group of three genera thus gives it limits expanded from those of previous classifications, in which the term was equivalent to *Girardinus* of this paper. *Girardinus*, *Quin-*

tana, and *Carlhubbsia* share the following: dorsal and anal fins that tend to be sharply pointed and even falcate; three suspensorial gonapophyses, each with a pair of variably developed, slender, pointed uncini; uncini on first two gonapophyses emerging nearer base than tip of spine, those on third emerging midway along spine; uncini of all gonapophyses overlapping, when present and well-developed, but arising and produced within an uncinar plane that extends backward and slightly downward; minute recurved terminal hook on ray 3 of gonopodium, weak retrorse serrae on ray 4p, and, as noted above, moderately to well-developed serrae on ray 5p. In some other details of the gonopodium, *Quintana* shows relationships to *Carlhubbsia* on the one hand and to *Girardinus* on the other, according to Rosen and Bailey (1959, pp. 35–37). They regarded it as likely that the ancestors of the Cuban genera came from Middle America. In contrast to the Gambusiini, the Girardinini have the gut long and coiled and the marginal jaw teeth compressed.

Rivas (1958) suggested that *Girardinus* (=Girardinini of Rivas) is most closely allied to *Allogambusia* (lower Central America) and *Phalloceros* (eastern South America). He did not mention *Quintana* in this connection. On the basis of numerous cranial, suspensorial, and gonopodial characters *Phalloceros* is clearly integrated into the Cnesterodontini (pp. 66–73), and *Allogambusia* (now included with *Xenophallus* in *Neoheterandria*) is placed in the Heterandriini, partly on the basis of the plate-like modifications of the posterior gonactinosts in its gonopodial suspensorium (pp. 116–128).

Genus GIRARDINUS Poey

Text figures 44A, B, 45A, 46A, 47A

Girardinus.—Poey, 1854, p. 383 (type species, by monotypy, *Girardinus metallicus* Poey).

Glaridodon.—Garman, 1895, p. 40 (not *Glaridodon* Seeley; type species, by original designation, *Girardinus uninotatus* Poey; Jordan, Evermann, and Clark, 1930, p. 188, mistakenly listed the type as *Glaridodon latidens* Garman [=*Poeciliopsis latidens*]).

Glaridichthys.—Garman, 1896, p. 232 (substitute for *Glaridodon* Garman, preoccupied).

Toxus.—Eigenmann, 1903, p. 226 (type species, by original designation, *Toxus riddlei* Eigenmann).

Dactylophallus.—Howell-Rivero and Rivas, 1944, p. 15 (type species by original designation, *Girardinus denticulatus* Garman).

Allodontium.—Howell-Rivero and Rivas, 1944, p. 17 (type species, by original designation, *Heterandria cubensis* Eigenmann).

Diagnosis: In skull, parietals small, ovate, narrower end lying underneath frontal, broader end extending toward midline and lying over or co-ossified with parts of supraoccipital and epiotic bones; supraoccipital processes moderately to well developed, epiotic processes reduced or absent; posttemporal bone forked; marginal jaw teeth compressed. Posterior pleural ribs in male curved gently forward along their lengths. Gonopodial suspensorium with three well-developed gonapophyses that are inclined only slightly forward; each gonapophysis with pair of long, slender, pointed uncini; uncini on gonapophyses I and II emerging nearer base than tip of spine, those on III emerging midway along spine; uncini of all gonapophyses overlapping, always arising and produced within uncinar plane that extends backward and slightly downward; ligastyle bifid ventrally, in frontal view appearing as slightly distorted, acute equilateral triangle; inferior lateral wings of primary gonactinostal complex greatly expanded and projecting backward to or beyond level of gonactinost 5. Gonopodium bilaterally symmetrical; ray 3 variably consolidated and terminated by pair of minute, pointed, diverging, retrorse, bony hooks, penultimately with series of minute oval or subrectangular segments that is followed by cluster of two to five spinules, with paired, antrorse, membranous appendages arising ventrally at level of spinules; ray 4a variably consolidated, without enlarged subdistal segments; ray 4p variably consolidated, subdistally with series of minute or obsolescent retrorse serrae; ray 5a variably consolidated, in some cases with four or five penultimate segments enlarged and projecting ventrally to form elbow-like structure; ray 5p with distal or subdistal five to 20 segments modified as prominent retrorse serrae.

Remarks: The above generic synonymy was first proposed by Rosen and Bailey (1959, p. 35). Rivas (1958) reviewed the group and recognized eight species of *Girardinus* (as here restricted). There appear to be three subgroups (*serripenis-creolus; uninotatus-*

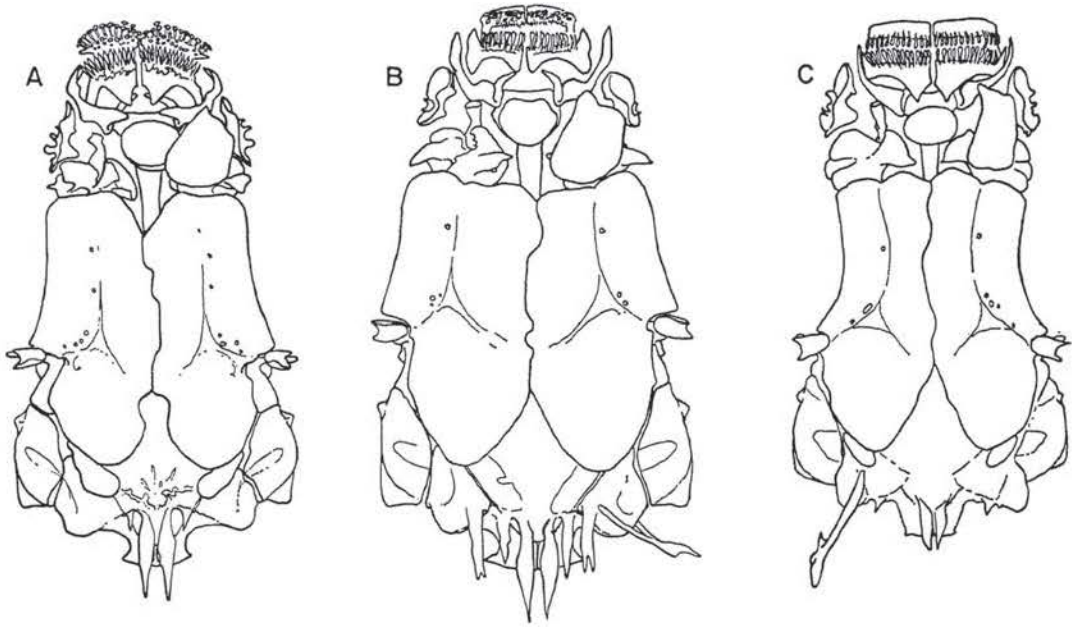


FIG. 45. Dorsicrania of the Girardinini. A. *Girardinus cubensis*, female, U.M.M.Z. No. 146704. B. *Quintana atrizona*, female, aquarium specimen. C. *Carlhubbsia kidderi*, female, U.M.M.Z. No. 144213.

falcatus; microdactylus-metallicus) in which one member typically occurs at higher altitudes in faster waters. The highland and lowland members in each case seem to be allopatric, although Rivas' distributional data are not sufficiently detailed to permit a positive conclusion in this regard. The members of at least two of the pairs seem to differ mostly in average characters (particularly the gonopodial ones) and in these cases the highland forms and the lowland forms may prove to be ecotypes and not distinct species.

In support of his policy of recognizing eight species, Rivas claimed (his p. 290) that gonopodial characters are not " . . . correlated with ecological conditions and therefore may be considered as not directly adaptive" and that " . . . gonopodial differentiation does not proceed below the species level." There is, however, much indirect evidence that some gonopodial structures may be ecologically correlated and that terminal ornaments in general are highly adaptive (see Clark, Aronson, and Gordon, 1949, 1954; Rosen and Gordon, 1953; Rosen, 1960; Rosen and Tucker, 1961; and discussion on pp. 20–21). Furthermore, diagnostic differences in gonopodial structure are demonstrable at the subspecific level in *Xiphophorus* (Rosen, 1960) and in *Gambusia affinis*, and the form of *Poecilia sphenops* from Aruba and Curaçao (*vandepolli*) lacks the claw on gonopodial ray 5 that is found well developed in typical *sphenops* from the mainland.

RANGE AND SPECIES COMPOSITION: Cuba and the Isle of Pines (map 12). Eight species.

Girardinus serripenis (Rivas)

Toxus serripenis.—RIVAS, 1958, pp. 283, 286–287, 289 (original description; Río Taco Taco at Rangel, Pinar del Río Province, Cuba; holotype, U.M.I.M., formerly L.R.R. No. 69).

MATERIAL: Río Taco Taco at Rangel, Pinar del Río, Cuba; in the University of Miami Ichthyological Museum (not the holotype).

RANGE: Upper reaches of Río Taco Taco, Rangel, Pinar del Río, Cuba (Rivas, 1958, p. 287).

Girardinus creolus Garman

Girardinus creolus.—GARMAN, 1895, p. 47 (original description; Cuba; syntypes, M.C.Z. No.

6399). *Toxus creolus.*—HOWELL-RIVERO AND RIVAS, 1944, p. 17.

Toxus riddlei.—EIGENMANN, 1903, p. 226 (original description; San Cristobal, Cuba; allotype, an adult male, C.N.H.M. No. 3915, location of holotype unknown).

MATERIAL: Stream at village of Lunidero, Pinar del Río, Cuba; in the University of Miami Ichthyological Museum. Jardin de Blain, Aspiro Station, Cruz de los Piños, Pinar del Río, Cuba; U.M.M.Z. No. 146705. Santa Cruz River, Cuba; U.S.N.M. No. 7745.

RANGE: Highland streams of southern drainage of Sierra de los Organos, Pinar del Río, Cuba (Rivas, 1958, p. 287).

Girardinus uninotatus Poey

Girardinus uninotatus.—POEY, 1860, p. 309 (original description; Río Taco Taco, Pinar del Río Province, Cuba; syntypes, M.C.Z. No. 6405, U.S.N.M. No. 120264). *Glaridodon uninotatus.*—GARMAN, 1895, p. 41. *Glaridichthys uninotatus.*—EIGENMANN, 1903, pp. 223–224.

Glaridichthys torralbasi.—EIGENMANN, 1903, pp. 225–226 (original description; Pinar del Río, Cuba; holotype, M.C.Z. No. 32957).

MATERIAL: Río Taco Taco, Pinar del Río, Cuba; U.M.M.Z. No. 103345. Tributary to Río Taco Taco at Jardin de Blain, Pinar del Río, Cuba; in the University of Miami Ichthyological Museum. San Cristobal, Cuba; S.U. No. 8502. Pinar del Río, Cuba, U.S.N.M. No. 100678.

RANGE: Highland streams of southern and northwestern drainages of Sierra de los Organos, Pinar del Río, Cuba (Rivas, 1958, p. 288).

REMARKS: Rivas (1958, p. 288) recognized two subspecies: *Girardinus u. uninotatus* Poey, from the Río Guamá system eastward; and *G. u. torralbasi* (Eigenmann), from the Río Guamá system westward.

Girardinus falcatus (Eigenmann)

Glaridichthys falcatus.—EIGENMANN, 1903, p. 224 (original description; San Cristobal [Pinar del Río], Cuba; holotype, C.A.S. No. 22548). *Girardinus falcatus.*—ROSEN AND BAILEY, 1959, p. 39.

Glaridichthys atherinoides.—RIVAS, 1944b, p. 3 (original description; Arroyo Blanco, Camagüey Province, Cuba; holotype, U.M.I.M., formerly L.R.R. No. 130).

MATERIAL: Old river channel near Río San Cristobal, Pinar del Río, Cuba; in the University of Miami Ichthyological Museum. Arroyo Blanco, Mabuya, Camagüey, Cuba; in the University of Miami Ichthyological Museum. Laguna La Canoa, Pinar del Río, Cuba; U.M.M.Z. No. 103342. Cuba; U.M.-M.Z. No. 146975. Laguna La Canoa, Artemisia, Pinar del Río, Cuba; S.U. No. 32023. San Cristobal, Pinar del Río, Cuba; S.U. No. 8500.

RANGE: Ponds, lakes, and lowland streams of central and western Cuba (Rivas, 1958, p. 288).

Girardinus cubensis (Eigenmann)

Text figures 44A, 45A, 46A, 47A

Heterandria cubensis.—EIGENMANN, 1903, p. 227 (original description; Los Palacios, Pinar del Río, Cuba; holotype, M.C.Z. No. 32958). *Toxus cubensis.*—C. L. HUBBS, 1926, p. 58. *Allodontium cubense.*—HOWELL-RIVERO AND RIVAS, 1944, pp. 12–18. *Girardinus cubensis.*—ROSEN AND BAILEY, 1959, p. 39.

MATERIAL: Jardin de Blain, Aspiro Station, Cruz de los Piños, Pinar del Río, Cuba; U.M.M.Z. No. 146704.

RANGE: Ponds, lakes, and streams of southern drainage of Sierra de los Organos, Pinar del Río, Cuba (Rivas, 1958, p. 288).

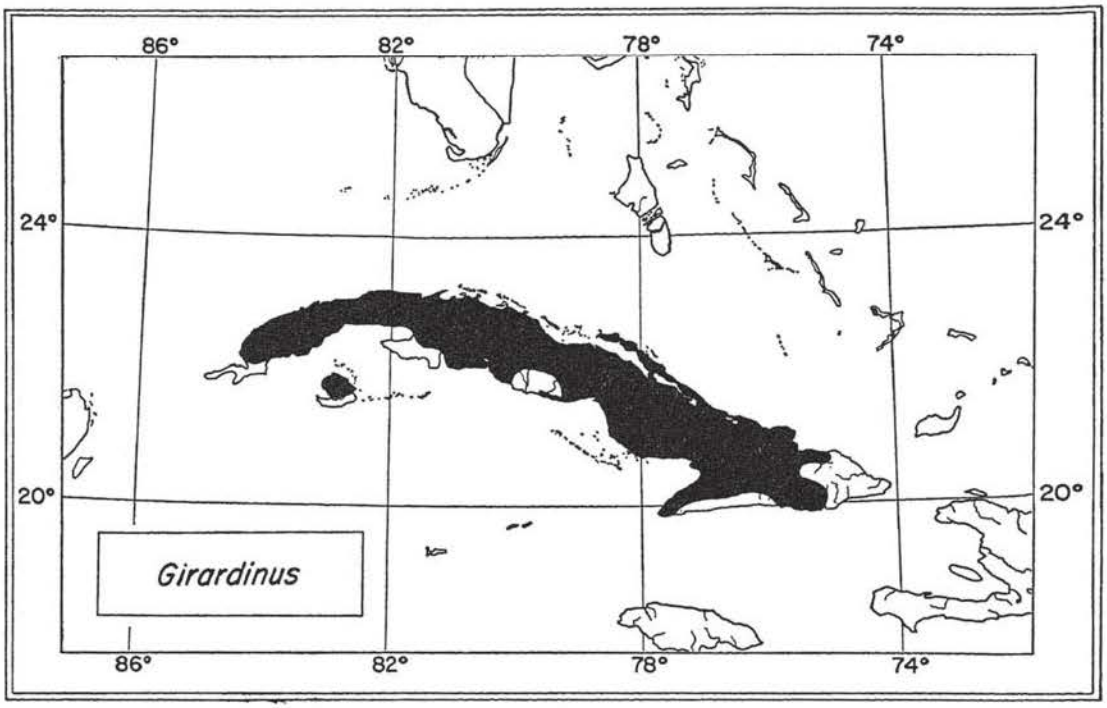
Girardinus denticulatus Garman

Text figure 44B

Girardinus denticulatus.—GARMAN, 1895, p. 47 (original description; Remedios, Cuba; syntypes, M.C.Z. No. 1412). *Dactylophallus denticulatus.*—HOWELL-RIVERO AND RIVAS, 1944, pp. 15–17.

Dactylophallus ramsdeni.—RIVAS, 1944a, p. 48 (original description; Río Guaso, Guantánamo, Oriente Province, Cuba; holotype, U.M.I.M., formerly L.R.R. No. 73).

MATERIAL: Río Rancho Nuevo north of Central Baguanos, Oriente, Cuba; U.M.M.Z. No. 146695. Lake formed by Río Pedro Sanchez at Central Baguanos, Oriente, Cuba; in the University of Miami Ichthyological Museum. Río Guaso, at Guantánamo, Oriente, Cuba; U.M.M.Z. No. 143371. Cuba; U.S.N.M. No. 130217. Monte Verde Spring, Cuba; U.S.N.M. No. 15041. Cuba; U.S.N.M. No. 130031. Río Guaso, at Guantánamo, Oriente, Cuba; in the University of Miami Ichthyological Museum. Arroyo los Guansos, San Juan de los Yeros, Santa Clara, Cuba; S.U. No. 32025.



MAP 12. Distribution of *Girardinus*.

RANGE: Ponds, lakes, and streams of central and eastern Cuba (Rivas, 1958, p. 289).

REMARKS: Rivas (1958, p. 289) recognized two subspecies: *Girardinus d. denticulatus* Garman, central and eastern Cuba, except Río Guaso and Yateras systems; and *G. d. ramsdeni* (Rivas), the Río Guaso and Río Yateras systems, southeastern drainage of Sierra Maestra, Province of Oriente, eastern Cuba.

Girardinus microdactylus Rivas

Girardinus microdactylus.—RIVAS, 1944a, p. 51 (original description; Río Taco Taco, Jardin de Blain, Pinar del Río Province, Cuba; holotype, U.M.I.M., formerly L.R.R. No. 110).

MATERIAL: San Cristobal, Cuba; S.U. No. 41659. Río Taco Taco, Rangel, Pinar del Río, Cuba; S.U. No. 32024. Spring-fed creek, tributary to Río Taco Taco (San Cristobal system), Jardin de Blain, Pinar del Río; U.M.M.Z. No. 143372. Arroyo del Jardin de Blain, Aspiro, Pinar del Río, Cuba; in the University of Miami Ichthyological Museum. Cuba; U.S.N.M. Nos. 92188, 130216.

RANGE: Highland streams of southern drainage of Sierra de los Organos, Pinar del Río, Cuba, and Isle of Pines (Rivas, 1958, p. 289).

Girardinus metallicus Poey

Girardinus metallicus.—POEY, 1854, p. 387 (original description; Jardin Botanico, Habana Province, Cuba; syntypes, M.C.Z. No. 6414, A.N.S.P. No. 6871, U.S.N.M. No. 120263).

Girardinus garmani.—EIGENMANN, 1903, p. 226 (original description; Los Palacios, Pinar del Río, Cuba; holotype, M.C.Z. No. 32780).

Girardinus pygmaeus.—RIVAS, 1944a, p. 49 (original description; Río Hatiguanico, Matanzas Province, Cuba; holotype, U.M.I.M., formerly L.R.R. No. 128).

MATERIAL: Arroyo los Gansos, San Juan de los Yeros, Santa Clara, Cuba; U.M.M.Z. No. 108685. San Cristobal, Cuba; S.U. No. 8506. Pinar del Río, Cuba; S.U. No. 8507. Cuba; U.S.N.M. No. 55699.

RANGE: Ponds, lakes, and streams throughout all but easternmost Cuba (Rivas, 1958, p. 289).

GENUS **QUINTANA** HUBBS

Text figures 44C, 45B, 46B, 47B

Quintana.—C. L. HUBBS, 1934, pp. 1–8 (type species, by original designation, *Quintana atrizona* C. L. Hubbs).

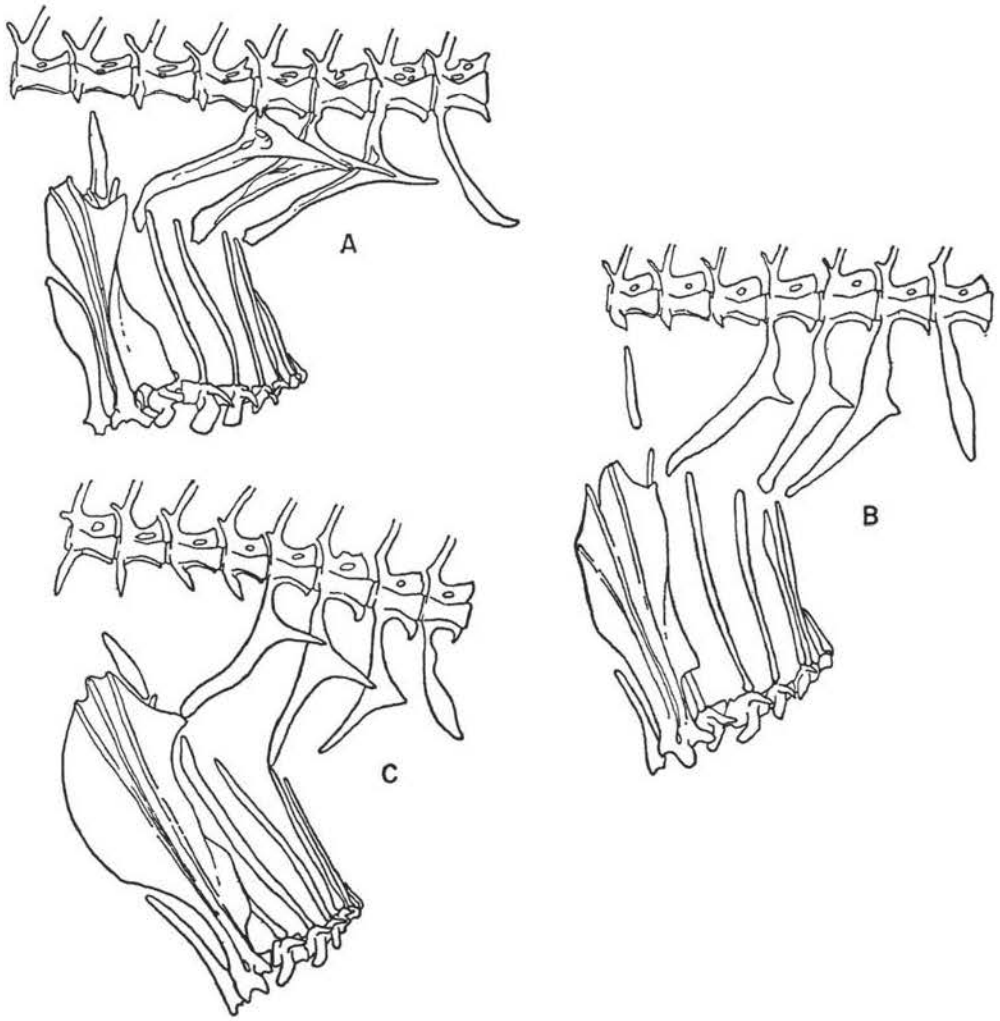


FIG. 46. Gonopodial suspensoria in the Girardinini. A. *Girardinus cubensis*, U.M.M.Z. No. 146704. B. *Quintana atrizona*, U.M.M.Z. No. 106460. C. *Carlhubbsia kidderi*, U.M.M.Z. No. 144213.

DIAGNOSIS: In skull, parietals small and ovate, or irregular and co-ossified with parts of supraoccipital and epiotic bones, or absent; supraoccipital processes moderately developed, epiotic processes moderately developed, small, or absent; posttemporal forked, or lower arm incompletely developed; marginal jaw teeth compressed. Posterior pleural ribs in male curved gently forward along their lengths. Gonopodial suspensorium with three well-developed gonapophyses that are inclined only slightly forward; uncini of all gonapophyses little developed or obsolescent, in some cases absent, slender and pointed when present, those on gonapophyses I and II emerging nearer base than tip of spine, those on III emerging midway along spine; uncini of all gonapophyses arising and produced within uncinar plane that extends backward and slightly downward; ligastyle bifid ventrally, in frontal view appearing as slightly distorted, acute, equilateral triangle; inferior lateral wings of primary gonactinostal complex greatly expanded and projecting backward to or beyond level of gonactinost 5. Gonopodium with rays 3, 4a, and 5 bilaterally symmetrical, ray 4p sinistrally asymmetrical; ray 3 terminated by pair of minute, blunt-tipped, retrorse, bony hooks, penultimately with large, irregular, in some cases ovate bony

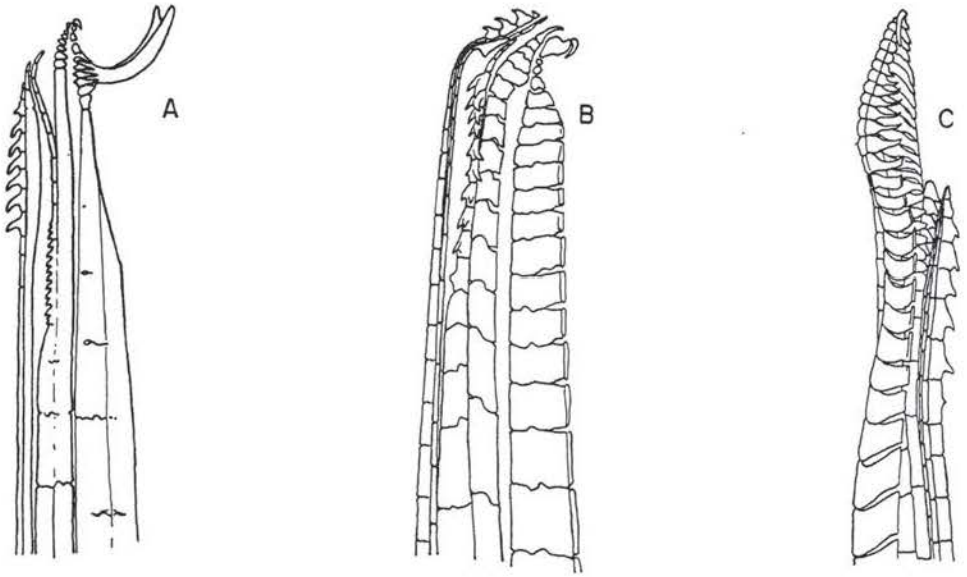


FIG. 47. Gonopodia in the Girardinini. A. *Girardinus cubensis*, U.M.M.Z. No. 146704. B. *Quintana atrizona*, after Rosen and Bailey (1959). C. *Carlhubbsia kidderi*, after Rosen and Bailey (1959).

segment that is separated from long series of tall, narrow, plate-like segments by three or four tiny ossicles; ray 4a with subdistal 4 or 5 segments much expanded and forming ventral, elbow-like, bony prominence; ray 4p subdistally with series of minute, retrorse serrae, those on right half standing erect, those on left half tilted to left; ray 5a typically with moderately developed, consolidated, subdistal element that projects ventrally to form elbow-like structure; ray 5p terminated by three or four paired, retrorse serrae.

RANGE AND SPECIES COMPOSITION: A single species apparently confined to western Cuba (map 13).

Quintana atrizona Hubbs

Text figures 44C, 45B, 46B, 47B

Quintana atrizona.—C. L. HUBBS, 1934, pp. 1–8 (original description; "Baracoa," Cuba; holotype, U.M.M.Z. No. 106459). ROSEN AND BAILEY, 1959, pp. 35–40 (figures, gonopodium, gonopodial suspensorium; characters).

MATERIAL: Reputedly vicinity of Baracoa, Cuba—aquarium-bred from Everglades Aquatic Nursery; U.M.M.Z. No. 106460.

RANGE: Western Cuba (Rivas, 1958, p. 305); types reported to have come from Havana and Baracoa (Oriente), Cuba (C. L. Hubbs, 1934).

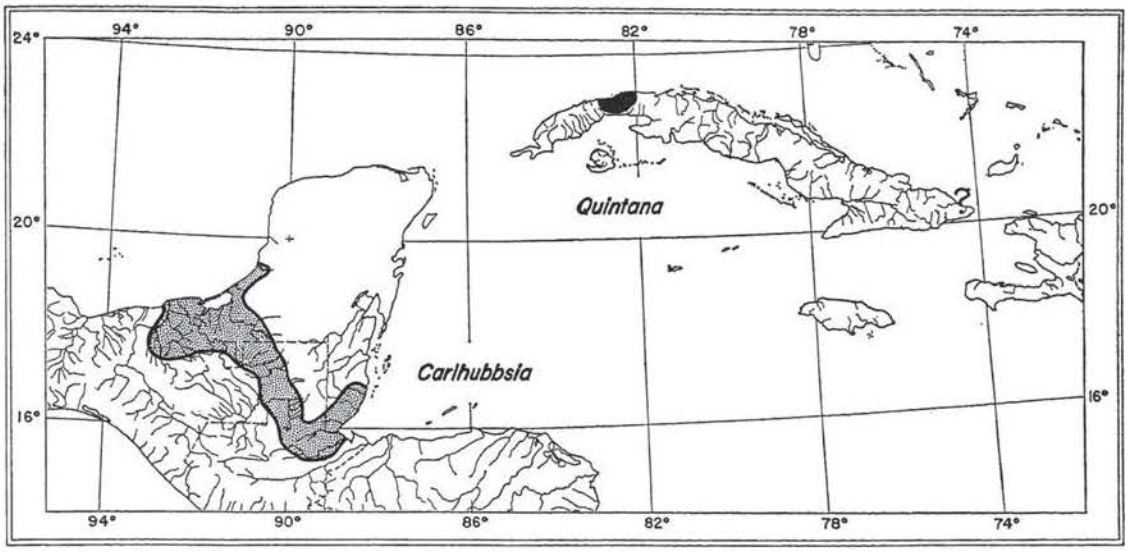
GENUS CARLHUBBSIA WHITLEY

Text figures 44D, 45C, 46C, 47C

Allophallus.—C. L. HUBBS, 1936, p. 232 (type species, by original designation, *Allophallus kidderi* Hubbs).

Carlhubbsia.—WHITLEY, 1951, p. 67 (replacement synonym for *Allophallus* Hubbs, a name that is preoccupied by *Allophallus* Dziedzicki, 1923, in Diptera).

DIAGNOSIS: In skull, parietals small, ovate, narrower end overlapped by frontal, broader end extending inward away from frontal and overlapping supraoccipital-epiotic commissure; supraoccipital processes very large, epiotic processes moderate or very large, in many cases longer than supraoccipital processes; posttemporal forked, or lower arm incompletely developed; marginal jaw teeth compressed. Posterior pleural ribs in male curved slightly forward along their lengths and then abruptly forward at their tips. Gonopodial suspensorium with three gonapophyses that are inclined slightly forward and often downward at their tips; uncini on gonapophyses I and II emerging nearer base than tip of spine, not curved, moderately slender,



MAP 13. Distribution of *Quintana* and *Carlhubbsia*. The reported occurrence of *Quintana* in eastern Cuba needs verification.

and sharply pointed; uncini on gonapophysis III, if present, generally small, emerging midway along spine, not curved downward, moderately thickened, rarely slender; uncini of all gonapophyses overlapping, forming uncinar plane that extends slightly downward and backward; ligastyle present in all species but variably developed; dorsal half of primary gonactinostal complex greatly dilated anteroposteriorly, upper edge of complex slightly notched or entire. Gonopodium dextrally asymmetrical; single series of flat, irregular, unpaired serrae on right half of ray 5p extending eight to 20 segments beyond tip of ray 6; single series of unpaired serrae distally on lateral margin of left half of ray 5a; single series of unpaired serrae originating distally on left half of ray 4p, tightly grouped into cluster, distal and subdistal elements of ray 4p that lack serrae extremely slender, reduced or obsolescent; terminal segments of ray 4a widened transversely; ray 3 terminated by minute bony or membranous hook, without consolidated terminal or subterminal segments, right half of ray with row of unpaired broad and flat spines that form ventral wall of gonopodial groove, left half with minute denticles on subdistal elements; segments of distal half of ray 6 swollen, transversely thickened, those of basal half asymmetrical, paired elements not side by side; rays 7 and 8 simple, distinctly separated, not converging or in contact.

RANGE AND SPECIES COMPOSITION: A narrow band of lowlands across the base of the Yucatán Peninsula, Atlantic drainage of Mexico and Guatemala (map 13). Two species.

Carlhubbsia stuarti Rosen and Bailey

Text figure 44D

Carlhubbsia stuarti.—ROSEN AND BAILEY, 1959, pp. 5–8 (original description; Río Polochic at the "playa," about 0.5 kilometer east of Panzós, Alta Vera Paz, Guatemala; holotype, U.M.M.Z. No. 146084).

RANGE: Río Polochic drainage and Laguna Izabal, Guatemala (Rosen and Bailey, 1959, p. 8).

Carlhubbsia kidderi (Hubbs)

Text figures 45C, 46C, 47C

Allophallus kidderi.—C. L. HUBBS, 1936, pp. 232–238 (original description; Río Champotón, Campeche, Mexico; holotype, U.M.M.Z. No. 102199). *Aulophallus kidderi*.—SCRIMSHAW, 1945, pp. 239–241. *Carlhubbsia kidderi*.—WHITLEY, 1951, p. 67. ROSEN AND BAILEY, 1959, pp. 8–16 (figures, gonopodium, gonopodial suspensorium; characters).

RANGE: Río Champotón, Campeche, Mexico, and the drainages of Río San Pedro de

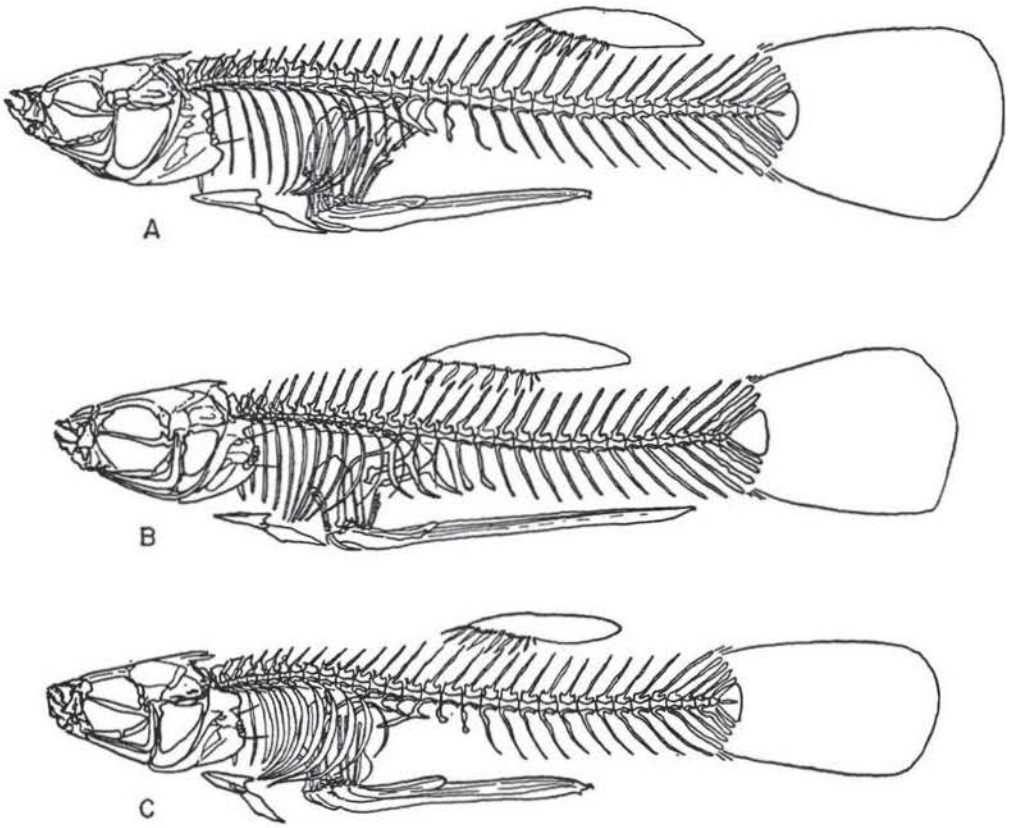


FIG. 48. Skeletons of adult males in the Heterandriini, composite drawings. A. *Priapichthys darienensis*. B. *Priapichthys nigroventralis*. C. *Neoheterandria tridentiger*.

Mártir, El Petén, and Río de la Pasión, El Petén and Alta Vera Paz, Guatemala (Rosen and Bailey, 1959, p. 13).

TRIBE HETERANDRIINI

Poeciliopsis and *Heterandria* have in common the following features in their gonopodial suspensoria: three well-developed gonapophyses that typically project downward for about half of their lengths and then turn abruptly forward and again downward at their tips; gonapophyses I and II each with a pair of sinuous uncini that arise from broad bases at the first gonapophyseal flexure and describe a complete or nearly complete sigmoid curve; gonapophysis III frequently with a pair of short, pointed uncini (rarely with longer, sinuous elements) that arise from broad bases at the first gonapophyseal flexure. In these two genera the gonopodium is quite long, extending to or nearly to the caudal base, and has comparatively few ornaments. These consist largely of a row of well-developed, paired serrae on ray 4p, reduced or obsolescent spines on ray 3, and a bony hook joined to the tip of ray 4a or lying free in a terminal enlargement of connective tissue. In the subgenus *Poeciliopsis* and in *Heterandria formosa*, the leading margin of the primary gonactinostal complex is excavated to receive gonactinost 1. This anterior margin is typically unexcavated in *Heterandria bimaculata* and in *Aulophallus*, a subgenus of *Poeciliopsis*. The incorporated gonactinosts of the primary complex (2, 3, and 4) arch gently backward in *Poeciliopsis* and *Heterandria*. The phenomenon of superfetation, although not restricted to these groups, is most characteristic of *H. formosa* and the species of *Poeciliopsis*. These same groups are distinct further in that the young are larger at birth than are the unfertilized eggs (see p. 22).

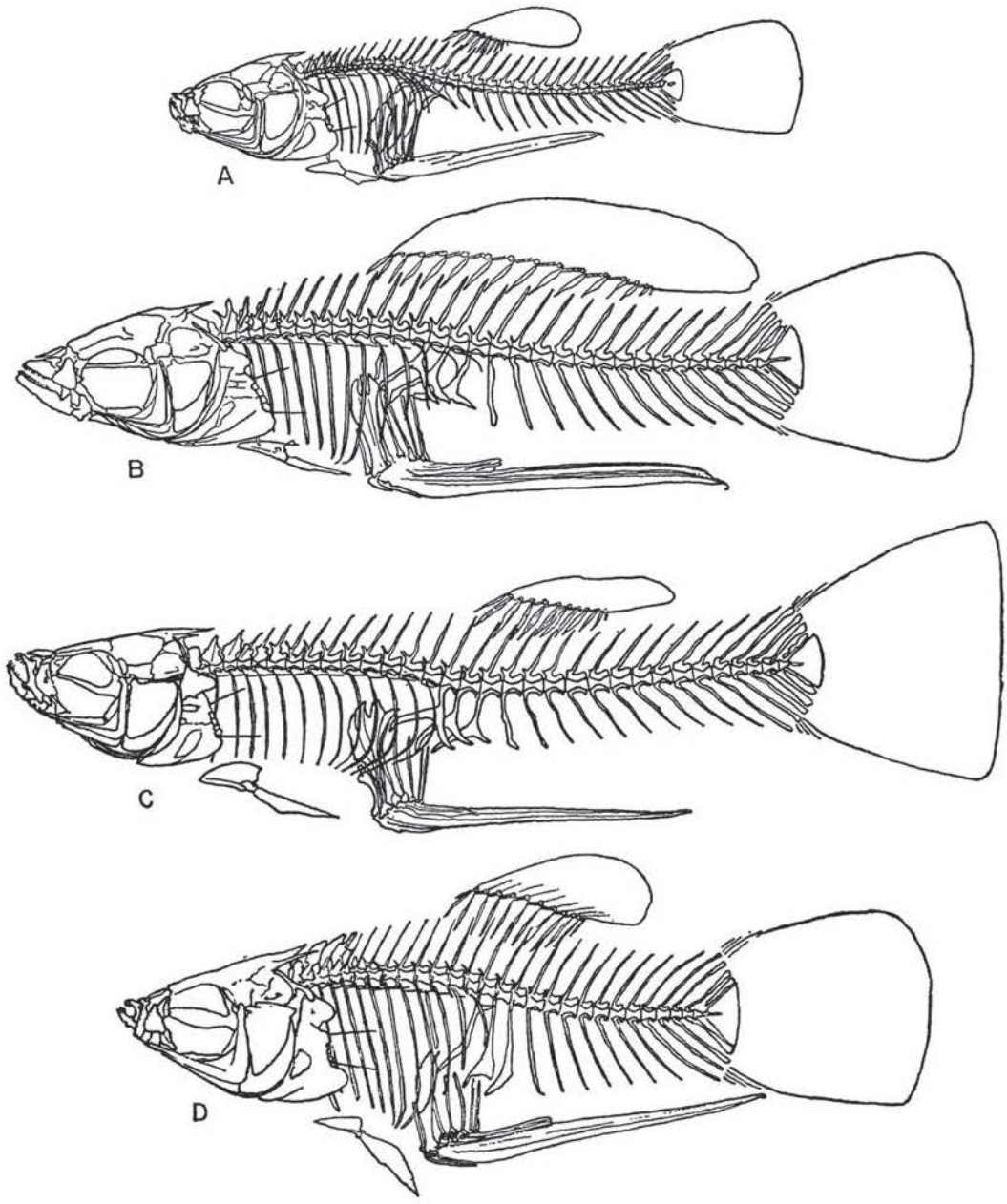


FIG. 49. Skeletons of adult males in the Heterandriini, composite drawings. A. *Heterandria formosa*. B. *Heterandria bimaculata*. C. *Poeciliopsis lucida*. D. *Phallichthys fairweatheri*, after Rosen and Bailey (1959).

There is a tenuous morphological basis for an alliance of *Phallichthys* with *Poeciliopsis* (Rosen and Bailey, 1959). Specific points of similarity between these genera could well have been independently derived. Another fact rendering uncertain the present association of genera in the Heterandriini is the presence of a simple posttemporal bone in *Heterandria* and a forked one in the other genera. We do not regard dentitional differences among these genera as a basis for tribal separation (see table 3).

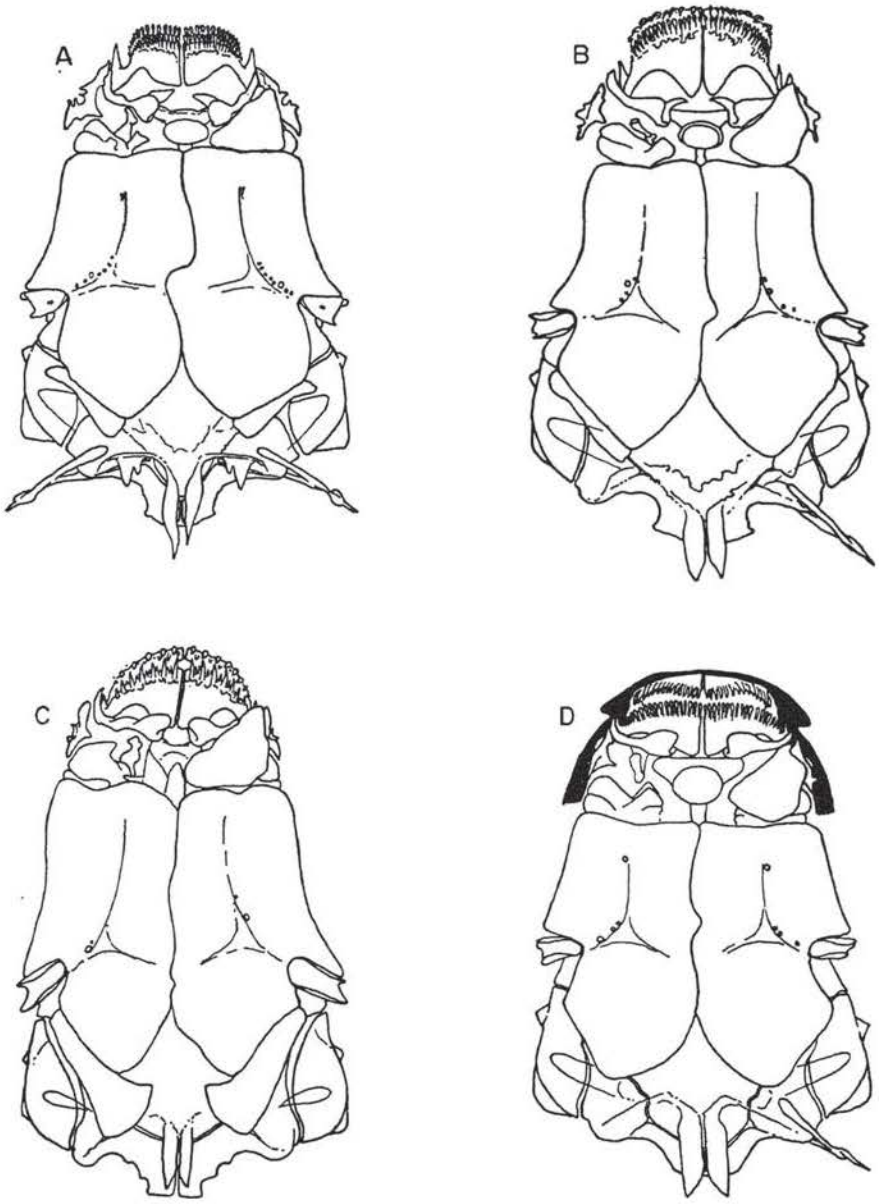


FIG. 50. Dorsicrania in *Priapichthys*. A. *P. darienensis*, female, U.S.N.M. No. 128482. B. *P. chocoensis*, male, C.N.H.M. No. 57009. C. *P. nigroventralis*, female, C.N.H.M. No. 57719. D. *P. fria*, female, U.S.N.M. No. 83519.

Despite these divergences, suspensorial features of heterandriins set them apart from other poeciliids. All genera except *Heterandria* and *Phallichthys* may have one or more pairs of plate-like outgrowths on secondary gonactinosts 8 to 10, structures not developed in other members of the family, and all heterandriin genera have much in common morphologically and zoogeographically.

Within the tribe, *Neoheterandria* and *Priapichthys* constitute a closely knit natural assemblage that contributes a major element of the diversified tropical American poeciliid fauna. These genera are known from Ecuador

northward along the northwest slope of South America to Panama and Costa Rica. The naturalness of the subgroup within the tribe is underscored by the presence in the gonopodial suspensorium of prominent paired outgrowths (versus smaller ones in *Poeciliopsis*) of gonactinosts 8 to 10 and upon the distributional integrity of its members.

C. L. Hubbs (1926) separated *Priapichthys*, *Panamichthys*, *Alloheterandria*, and *Pseudopoecilia* partly on the basis of differences in gonopodial structure and dorsal-fin position. At this time, however, Hubbs apparently was unaware of these fishes' suspensorial modifications and of their close relationship to *Diphyacantha* and *Darienichthys*

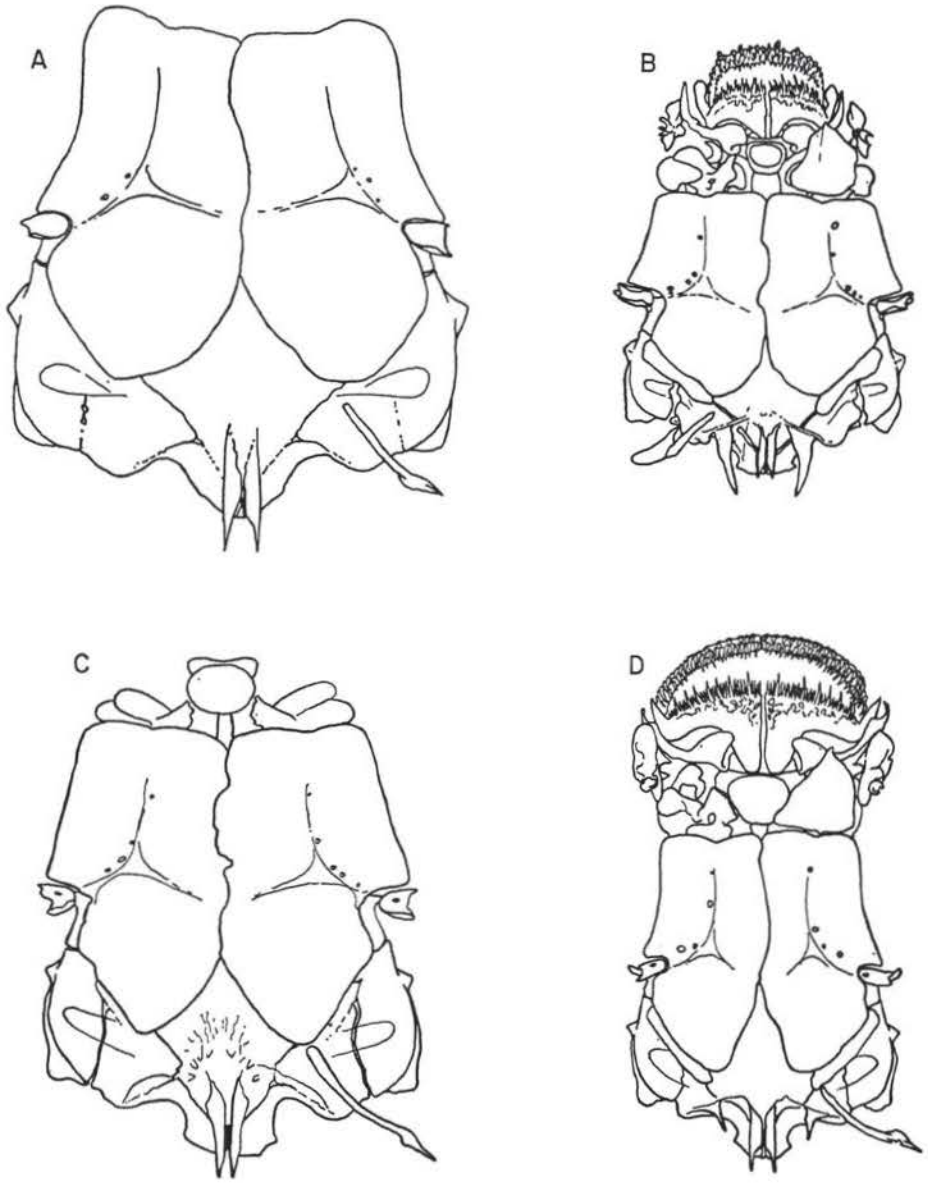


FIG. 51. Dorsicrania in the Heterandriini. A. *Neoheterandria elegans*, female, C.N.H.M. No. 57008. B. *Neoheterandria tridentiger*, female, U.M.M.Z. No. 115776. C. *Heterandria formosa*, female, U.M.M.Z. No. 155309. D. *Heterandria bimaculata*, male, A.M.N.H., uncatalogued, Mexico.

(then placed by him in the Cnesterodontini). We are unable to accept differences in dorsal-fin position, *per se*, as indicative of generic differentiation in a family in which the position and size of this fin vary widely between closely related species, e.g., *Brachyrhaphis terrabensis-B. episcopi* and *Poecilia latipinna-P. sphenops*. Differences in gonopodial structure among most of these nominal genera are more of degree than of kind. In *annectens* rays 3 and 4a merge at their tips and together turn gently downward into a terminal membranous swelling. In *panamensis* these rays not only turn downward but are hooked slightly backward, and the distal segments of ray 3 are consolidated into a single stylus within a terminal envelope of membranous tissue. In *chocoensis* and *darienensis* the bony style at the tip of ray 3 is separated from the tip of ray 4a by a notch, although this latter ray still remains bent downward as in *annectens* and *panamensis*. "*Alloheterandria*" *nigroventralis* can be separated from the other species of *Priapichthys* by slight differences in gonopodial structure and its highly ornate suspensorial uncini, and "*Pseudopoecilia*" is distinguished by its club-like or columnar marginal jaw teeth and the presence of but a single pair of gonactinostal plates. All but one species of *Priapichthys* possess some form of distinctive, paired, plate-like growths emerging from the shafts of the posterior or secondary suspensorial gonactinosts, however, and despite slight dentitional differences the premaxillary bones in all species are remarkably similar, being very massive and having the teeth firmly rooted.

The members of the genus *Neoheterandria* were formerly separated widely and allocated in distinct subfamilies, the Gambusiinae and Poeciliopsinae, by C. L. Hubbs (1924, 1926). All are now shown to share such an extensive list of fundamental structural similarities as to make separation at the generic or higher taxonomic levels imprudent. They share the same skull structure, the expanded pleural ribs, and striking similarities in the architecture of the primary gonactinostal complex and suspensorial gonapophyses, and have gonopodia that are virtually identical except in symmetry. Furthermore, *N. umbratilis* and *N. tridentiger* are remarkably alike in general appearance, particularly in the blunt head and other body proportions, and in the distribution of body and fin pigment. In *umbratilis* there are approximately 10 dark vertical bars along the flank, and a dark blotch or band of pigment basally and a lighter more diffuse one distally on the dorsal fin. In *tridentiger* the vertical bars on the side may number as high as 15 and the dorsal-fin markings are somewhat less developed. Although *N. elegans* lacks well-developed dorsal-fin pigment, it and *tridentiger* are similar in the development of vertical barring and in the common occurrence of a rectangular dusky blotch at midside. The bilateral gonopodial symmetry of *tridentiger* and *elegans* and the sinistral or dextral asymmetry of *umbratilis* represent the only instance among vertebrates known to us in which a fundamental anatomical system is bilaterally symmetrical in one or more species of a genus and is extensively and normally asymmetrical in another.

Through *Neoheterandria* the correct alignment of *Poeciliopsis* in the Heterandriini can be demonstrated. In *N. elegans*, *tridentiger*, and *umbratilis*, gonopodial rays 7 and 8 merge or are co-ossified distally. In the gonopodial suspensorium of *umbratilis* gonactinost 1 shows a distinct subdistal swelling, and the incorporated actinosts 2, 3, and 4 of its primary gonactinostal complex curve gently backward and are separated at their tips by excavations in the intervening bony plate. These three gonopodial and suspensorial features of *Neoheterandria* (as here restricted) are among those diagnostic of the subgenus *Poeciliopsis* (genus *Poeciliopsis*).

Genus PRIAPICHTHYS Regan

Text figures 48A, B, 50, 53, 54A, 57A–C

Priapichthys.—Regan, 1913b, p. 991 (type species, by subsequent designation by Henn, 1916, p. 115, *Gambusia annectens* Regan).

Pseudopoecilia.—Regan, 1913b, p. 995 (type species, by monotypy, *Poecilia festae* Boulenger).

Diphyacantha.—Henn, 1916, p. 113 (type species, by monotypy, *Diphyacantha chocoënsis* Henn).

Panamichthys.—C. L. Hubbs, 1924, p. 8 (type species, by original designation, *Priapichthys panamensis* Meek and Hildebrand).

Darienichthys.—C. L. Hubbs, 1924, p. 8 (type species, by original designation, *Gambusia darienensis* Meek and Hildebrand).

Alloheterandria.—C. L. Hubbs, 1924, p. 9 (type

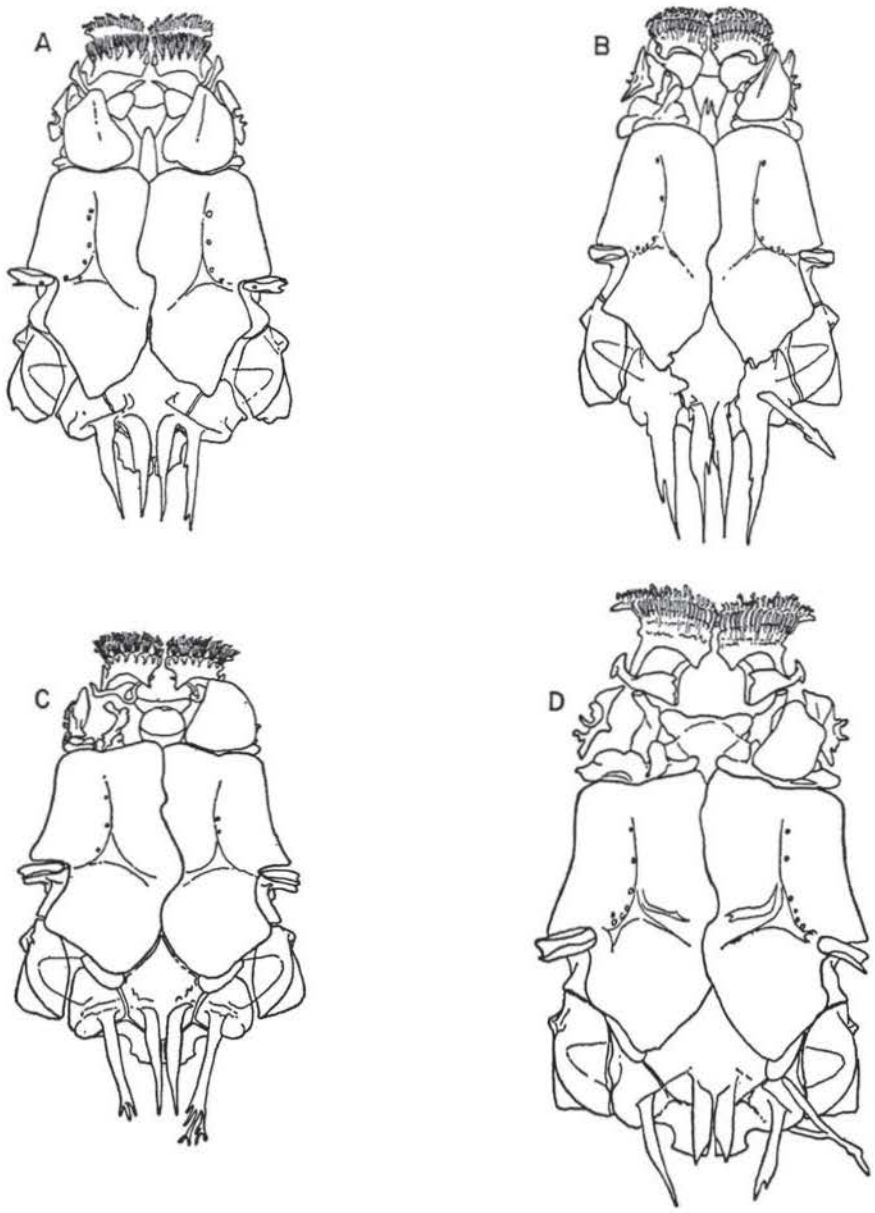


FIG. 52. Dorsicrania in the Heterandriini. A. *Poeciliopsis presidionis*, female, U.M.M.Z. No. 164662. B. *Poeciliopsis infans*, female, U.M.M.Z. No. 108649. C. *Poeciliopsis elongata*, male, U.S.N.M. No. 78846. D. *Phallichthys amates*, male, U.M.M.Z. No. 173280, Honduras.

species, by original designation, *Gambusia nigroventralis* Eigenmann and Henn).

DIAGNOSIS: In skull, parietals present or absent, if present, large, subrectangular, flaring broadly at midline; supraoccipital processes moderately to well developed; epiotic processes small, obsolescent, or absent; posttemporal forked; marginal jaw teeth recurved, conical, or somewhat flattened and bluntly pointed. Posterior pleural ribs in male curved gently forward along their lengths. Gonopodial suspensorium with three well-

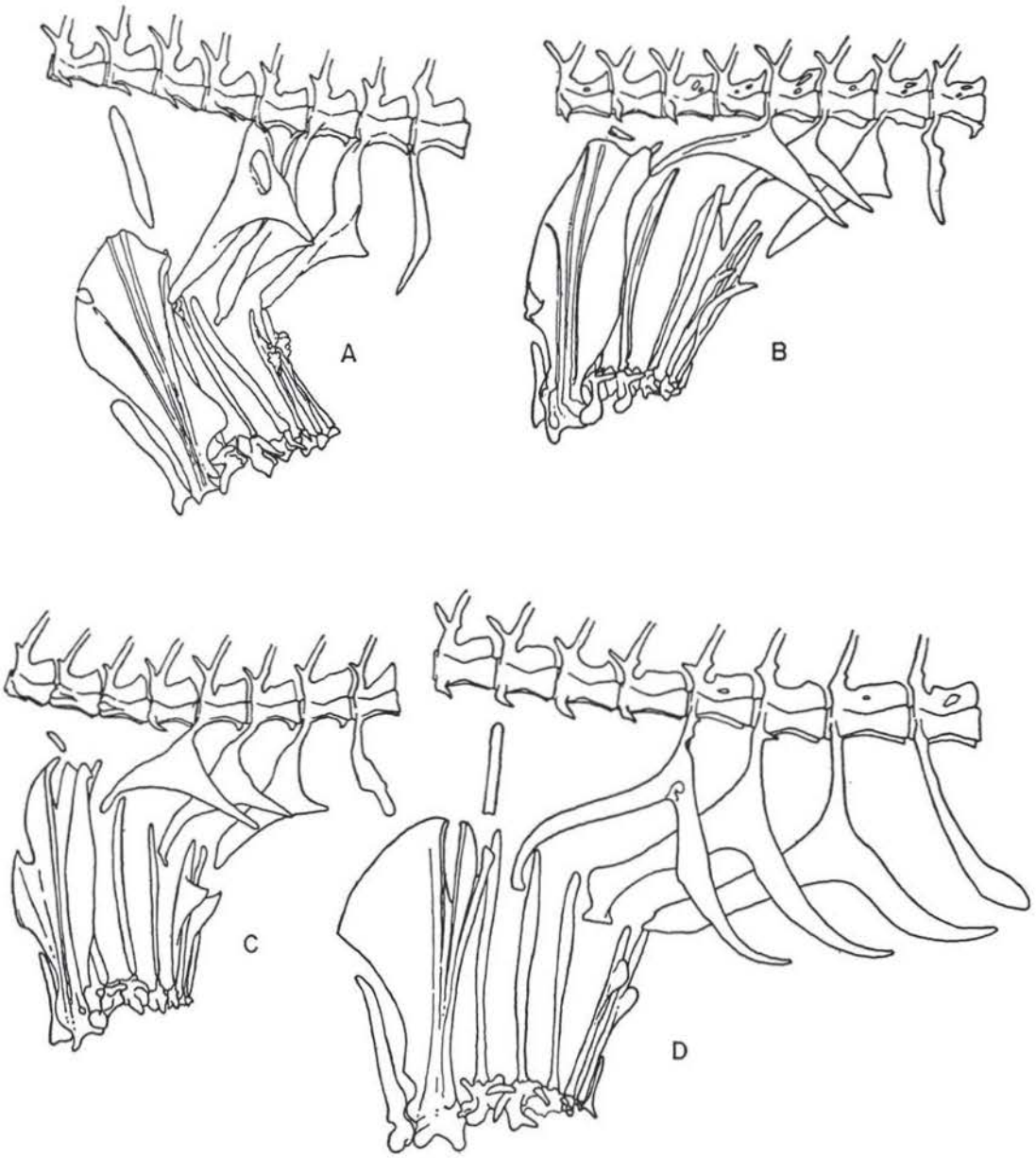
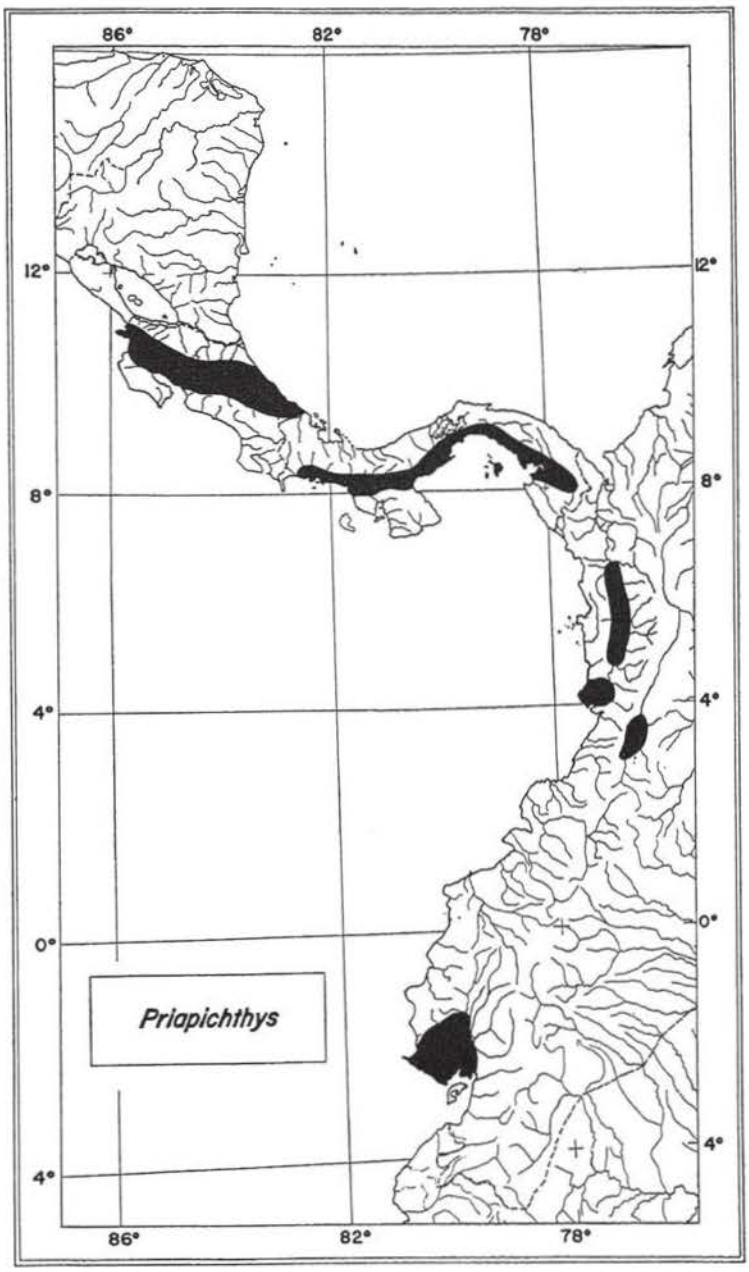


FIG. 53. Gonopodial suspensoria in *Priapichthys*. A. *P. annectens*, A.N.S.P. No. 45379. B. *P. darienensis*, U.S.N.M. No. 128482. C. *P. chocoensis*, C.N.H.M. No. 57009. D. *P. nigroventralis*, C.N.H.M. No. 57719.

developed, in many cases sinuous, gonapophyses that are bent moderately to sharply forward, each with a pair of long, broad-based, sharply pointed, in many cases backward-curving, uncini that arise nearer base than tip of shaft; gonactinostal complex usually recessed anteriorly to receive gonactinost 1, upper angle of recess in many cases bordered by pair of pointed, plate-like outgrowths; superior and inferior lateral wings moderately to well developed, inferior ones very broad and extensive, superior ones usually confined and rather pointed, but larger than inferior wings in *nigroventralis;* dorsal margin

of complex moderately or strongly notched or entire; incorporated elements 2, 3, and 4 in many cases extending upward and backward as in *Poeciliopsis;* ligastyle variable and present either as rod or ossicle; midsections of gonactinosts 8 and 9, rarely 9 or 10, or both, with pair of plate-like outgrowths that are sharply pointed dorsally, rounded, or nubbly at their outer edges. Gonopodium bilaterally symmetrical; ray 3 with subdistal series of approximately 10 moderately or poorly developed spinous processes, in some cases obsolescent, followed by two to eight simple elements and in many cases termi-



MAP 14. Distribution of *Priapichthys.*

nated by drop-shaped, pointed, or L-shaped segment; distal ramus of ray 4a curving gently downward over tip of ray 3 or not curved downward and terminated by rather long consolidated segment that is swollen distally; ray 4p with eight to 20 moderately developed proximal serrae; except in *annectens*, tip of ray 5a falling short of tip of underlying ray 4p which it touches; ray 5a rarely terminated by rather heavy consolidated element.

RANGE AND SPECIES COMPOSITION: Both slopes of Costa Rica, the Pacific slope of Panama, the Río Atrato and upper Cauca drainages of Colombia, thence south in the Pacific drainage to Guayas, Ecuador (map 14). In fresh and brackish water. Eight species.

Priapichthys annectens (Regan)

Text figure 53A

Gambusia annectens.—REGAN, 1907b, p. 259 (original description; Carrillo and Juan Venas, Irazu, Costa Rica; syntypes, B.M.N.H.). *Priapichthys annectens.*—REGAN, 1913b, p. 992.

Priapichthys annectens hesperis.—C. L. HUBBS, 1924, pp. 22–23 (original description; Río María Aguilar, upper tributary to Río Grande de Tárcoles, San José, Costa Rica; holotype, C.N.H.M. No. 14106).

MATERIAL: Guapiles [Limón], Costa Rica; A.N.S.P. No. 45379–90.

RANGE: Atlantic and Pacific drainages of Costa Rica (map 14).

REMARKS: C. L. Hubbs (1924, 1926) recognized two subspecies, *P. a. annectens* (Regan) from lowland streams of the Atlantic drainage and *P. a. hesperis* Hubbs from the Río Grande de Tárcoles of the Pacific slope. The differences between the forms do not appear to be great, and some populations were found to be variously intermediate.

Priapichthys panamensis Meek and Hildebrand

Priapichthys panamensis.—MEEK AND HILDEBRAND, 1916, pp. 322–323 (original description; Chame Point, Panama; holotype, C.N.H.M. No. 8950). *Panamichthys panamensis.*—C. L. HUBBS, 1924, p. 8.

MATERIAL: Chame Point, Panama; U.S.N.M. No. 78858, C.A.S. No. 14049.

RANGE: Pacific drainage of Panama; in fresh and brackish water.

Priapichthys darienensis (Meek and Hildebrand)

Text figures 48A, 50A, 53B, 57A

Gambusia darienensis.—MEEK AND HILDEBRAND, 1913, p. 88 (original description; Río Capetí [Darien], Panama; holotype, C.N.H.M. No. 7597). *Priapichthys dariensis.*—MEEK AND HILDEBRAND, 1916, pp. 229, 231–232, 320–321. *Darienichthys dariensis.*—C. L. HUBBS, 1924, p. 18.

MATERIAL: Pearl Islands, Panama; U.S.N.M. No. 128482 (locality perhaps erroneous). Panama Canal Zone; U.S.N.M. No. 109085.

RANGE: Pacific slope of the eastern half of Panama.

Priapichthys chocoensis (Henn)

Text figures 50B, 53C, 57B

Diphyacantha chocoënsis.—HENN, 1916, pp. 95, 104–105, 114–115 (original description; Río Calima, Chocó, Colombia; holotype, C.A.S. No. 22547).

MATERIAL: Creek near mouth of Río Calima, Colombia; C.N.H.M. No. 57009.

RANGE: Río Calima, tributary to the lower Río San Juan, Pacific drainage, Chocó, Colombia (Henn, 1916, p. 114).

Priapichthys nigroventralis (Eigenmann and Henn)

Text figures 48B, 50C, 53D, 57C

Gambusia nigroventralis.—EIGENMANN AND HENN, *in* Eigenmann, 1912, p. 26 (original description; Istmina, San Juan Basin, Colombia; holotype, C.N.H.M. No. 56045). *Priapichthys nigroventralis.*—REGAN, 1913b, p. 992. *Alloheterandria nigroventralis.*—C. L. HUBBS, 1924, p. 9.

Gambusia caudovittata.—REGAN, 1913a, p. 471 (original description; Río Condoto, western Colombia; holotype, B.M.N.H.).

MATERIAL: Raspadura, Colombia; C.N.H.M. No. 57719, C.A.S. No. 13616. Tambo, Colombia; C.N.H.M. No. 57718.

RANGE: Río Atrato and Río San Juan systems, Colombia (Henn, 1916, p. 116).

Priapichthys caliensis (Henn)

Gambusia caliensis.—HENN, 1916, pp. 95, 113 (original description; Cali, Colombia; holotype, C.N.H.M. No. 57721). *Alloheterandria caliensis.*—C. L. HUBBS, 1926, p. 57.

MATERIAL: Near Cartago, upper Cauca,

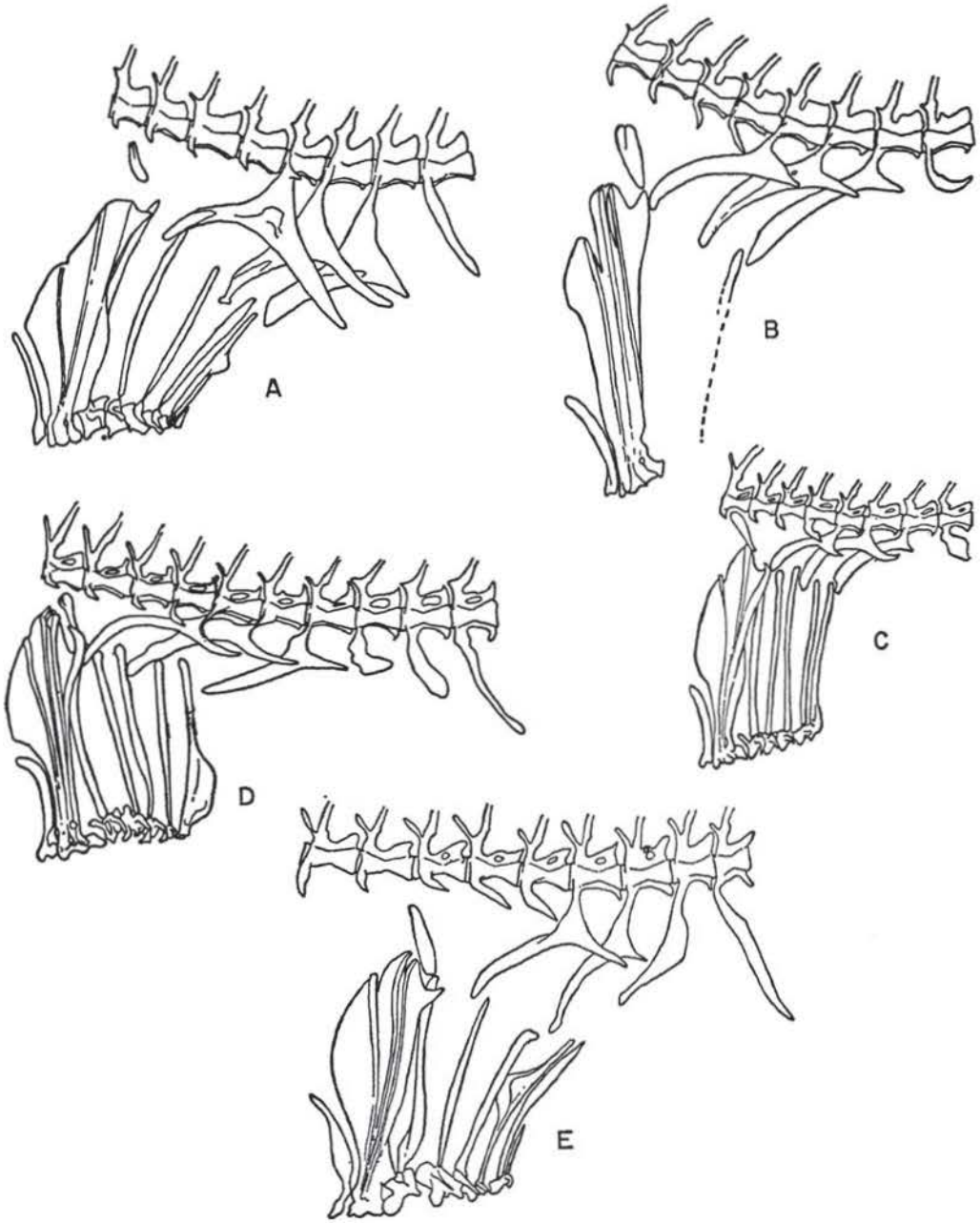


FIG. 54. Gonopodial suspensoria in the Heterandriini. A. *Priapichthys fria*, U.S.N.M. No. 83519. B. *Neoheterandria elegans* (mutilated), C.N.H.M. No. 57008. C. Same, S.U. No. 13612. D. *Neoheterandria tridentiger*, U.M.M.Z. No. 115776. E. *Neoheterandria umbratilis*, U.S.N.M. No. 74244.

Colombia; in the British Museum (Natural History). Cali, Colombia; A.M.N.H. No. 20443.

RANGE: Cali, Colombia (Henn, 1916, p. 113), and Alto Cauca, Distrito del Bolo and la Quebrada de las Cruces (Miles, 1943, p. 62).

REMARKS: This species was described originally from females. Miles (1943) figured the gonopodium of a form identified by him as

caliensis, but this illustration apparently is of an immature male in which the gonopodial tip had not differentiated fully. Specimens collected by Miles [in the British Museum (Natural History)] near Cartago, upper Cauca, differ slightly from those obtained by R. Socolof (A.M.N.H. No. 20443; one male, and two females) from a collector in Cali, the type locality, but not enough to necessitate the description of the Cartago form as new. The gonopodium of *caliensis* can be distinguished from that of *nigroventralis* by the fact it turns upward at the tip. In suspensorial features, *caliensis* is distinct in lacking the wing-like outgrowths of the posterior gonactinosts that are well developed in *nigroventralis*. In other details of the gonopodial system, the two species are virtually the same. The single male from Cali, first seen by us some hours after it had died, showed the following color pattern: ground color yellowish olive, side with eight broad, well-defined, dusky bars, scales on dorsum and upper part of side darkly edged, margin of dorsal fin and subdistal part of caudal fin with a band of dusky and black pigment, gonopodium jet black except for the extreme distal and proximal ends which are clear, pectoral and pelvic fins and posterior margin of caudal fin clear, the proximal two-thirds of the dorsal and caudal fins and the base and ventral margin of the caudal peduncle bright orange-red. The two adult females lack orange or red coloring, and the dark margins on the dorsal and caudal fins are dusky rather than black. Socolof informs us that not all males from Cali have a black gonopodium. Specimens from Cartago also show the dusky margin on the dorsal fin of males and females as well as faint bars on the side, and the gonopodium is without black pigment. Miles, in his description of *caliensis*, noted that the margin of the dorsal fin and that of the caudal fin are yellow.

Priapichthys festae (Boulenger)

Poecilia festae.—G. A. BOULENGER, 1898, p. 13 (original description; San Vicente, Santa Elena, Ecuador; syntypes, B.M.N.H.). *Pseudopoecilia festae.*—REGAN, 1913b, p. 996.

RANGE: Hot springs (35° C.), San Vicente, Santa Elena, Ecuador (Eigenmann, Henn, and Wilson, 1914, p. 14).

Priapichthys fria (Eigenmann and Henn)

Text figures 50D, 54A

Poecilia fria.—EIGENMANN AND HENN, *in* Eigenmann, Henn, and Wilson, 1914, pp. 13–14 (original description; Vinces, Ecuador; holotype, C.A.S. No 22549). *Pseudopoecilia fria.*—HENN, 1916, pp. 95, 104–105, 119.

MATERIAL: Vinces, Ecuador; C.A.S. (I.U.M. No. 13107). Ecuador; U.S.N.M. No. 83519. Forest pools, Vinces, Ecuador; C.N.H.M. No. 56604. Occidente, Santo Domingo de los Colorados, Ecuador; U.S.N.M. No. 183040.

RANGE: Vinces, Ecuador.

REMARKS: Further study will likely show that this species is a synonym of *Priapichthys festae*. We assign the specimens from Santo Domingo de los Colorados to *fria* on the basis of their close correspondence in color pattern with Eigenmann and Henn's description.

GENUS **NEOHETERANDRIA** HENN

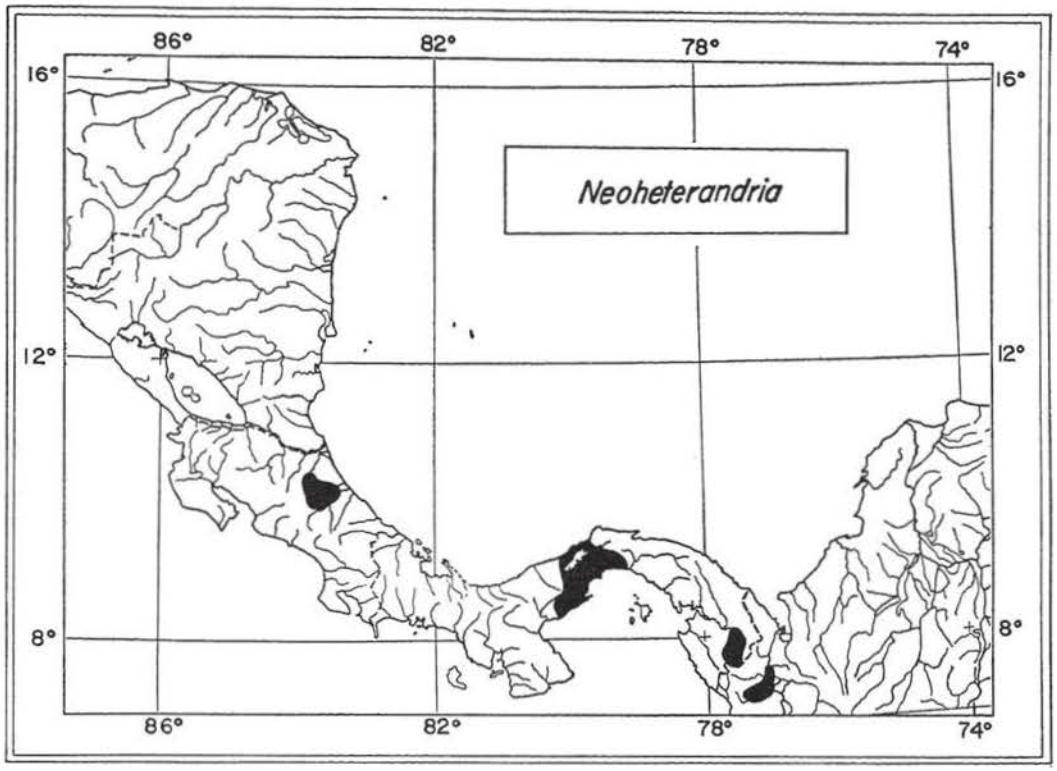
Plate 1, figures 1, 2; text figures 48C, 51B, 54B–E, 57D–F

Neoheterandria.—HENN, 1916, p. 117 (type species, by monotypy, *Neoheterandria elegans* Henn).

Allogambusia.—C. L. HUBBS, 1924, p. 8 (type species, by original designation, *Gambusia tridentiger* Garman).

Xenophallus.—C. L. HUBBS, 1924, p. 10 (type species, by original designation, *Gambusia umbratilis* Meek).

DIAGNOSIS: In skull, parietals present or absent, where present, broadest medially, spatulate in many cases; supraoccipital and epiotic processes present, variably developed; posttemporal forked, but lower limb in many cases plate-like and not co-ossified with upper limb; marginal jaw teeth recurved, conical. Posterior pleural ribs in male bent sharply forward along their lengths, their tips nearly in contact with pelvic girdle, their midsections much dilated anteroposteriorly. Gonopodial suspensorium with three well-developed gonapophyses that are inclined sharply forward and bear small, pointed, in many cases upturned uncini near their bases; gonapophyses I and II sinuous, III in some cases nearly straight; ligastyle moderately developed, its dorsal margin in some cases bifid; primary gonactinostal complex dilated anteroposteriorly, in some cases recessed an-



MAP 15. Distribution of *Neoheterandria*.

teriorly to receive gonactinost 1, superior lateral wings well developed and giving rise to tubular, sharply or bluntly pointed, posterodorsal prolongation; gonactinosts 8 or 9 in many cases with plate-like outgrowths near their bases. Gonopodium bilaterally symmetrical or dextrally or sinistrally asymmetrical; ray 3 typically with cluster of minute spinules subdistally from which (except in *elegans*) an unpaired, subradial fleshy outgrowth emerges; ray 4a with variably developed, subdistal, bisegmental, ventral prominence terminated by extremely long, consolidated bony rod that projects forward and downward, usually into finger-like investment of membranous tissue; in many cases with several small to moderate serrae subdistally on ray 4p; rays 7 and 8 in close apposition distally or along middle of their lengths or co-ossified at their tips.

REMARKS: *Neoheterandria elegans* can be distinguished from *N. tridentiger*, *N. cana*, and *N. umbratilis* by the absence of a subradial outgrowth of tough membranous tissue below gonopodial ray 3, by the larger plates on the secondary gonactinosts of its gonopodial suspensorium, and by color characters that are mentioned above in the discussion of the tribe. In the suspensorium of *umbratilis* gonactinost 8 has a pair of large bony plates that project outward and forward from its mid-section; these apparently are developed asymmetrically in accordance with the direction of asymmetry of the gonopodium. The gonopodium of *umbratilis* is dextrally or sinistrally asymmetrical; the gonopodia of *elegans*, *tridentiger*, and *cana* are bilaterally symmetrical.

RANGE AND SPECIES COMPOSITION: Atlantic drainage of Costa Rica, both slopes of central Panama, Pacific slope of eastern Panama, and Atlantic drainage of northwestern Colombia (map 15). Four species.

Neoheterandria elegans Henn

Text figures 51A, 54 B, C, 57D

Neoheterandria elegans.—HENN, 1916, p. 118 (original description; Río Truando, Colombia; holotype, C.N.H.M. No. 57007).

MATERIAL: Truando, Colombia; C.N.H.M. No. 57008, S.U. No. 13612.

RANGE: Río Truando, tributary to lower Río Atrato, Colombia (Henn, 1916, p. 118).

Neoheterandria tridentiger (Garman)

Text figures 48C, 51B, 54D, 57E

Gambusia tridentiger.—GARMAN, 1895, p. 89 (original description; Panama; syntypes, M.C.Z. No. 6389, U.S.N.M. No. 120260). *Priapichthys tridentiger.*—REGAN, 1913b, p. 992. *Allogambusia tridentiger.*—C. L. HUBBS, 1924, p. 8.

MATERIAL: Stream south of Toro Point, Fort Sherman, Canal Zone, Panama; S.U. No. 19240. Madden Dam, Chagres River, Panama; S.U. No. 24775. Panama; U.M.M.Z. No. 115776. Río Chame at Chame, Panama; C.A.S. No. 14050. Arrijan, Panama; C.A.S. No. 14051.

RANGE: Both slopes of central Panama and Taboga Island (Meek and Hildebrand, 1916, p. 321).

REMARKS: This and the following form may be conspecific (see Meek and Hildebrand, 1916).

A radiograph of 10 males and 10 females from U.M.M.Z. No. 115776 indicates that there may be sexual dimorphism in vertebral number in this species. Among them, three counts of 31 (two males and one female) are regarded as atypical, because in each the thirtieth vertebra has two neural or two hemal spines and is thus complex. Of the remainder, all eight males have 32 vertebrae (13 precaudal and 19 caudal); eight females have 31 vertebrae; only one has 32.

Neoheterandria cana (Meek and Hildebrand)

Gambusia cana.—MEEK AND HILDEBRAND, 1913, p. 87 (original description; Río Satiganti, Cana [Darién], Panama; holotype, C.N.H.M. No. 7596). *Allogambusia cana.*—C. L. Hubbs, 1924, p. 8. *Priapichthys tridentiger cana.*—MEEK AND HILDEBRAND, 1916, pp. 231–232, 320–321.

MATERIAL: Río Satigante, Cana, Darién, Panama; C.N.H.M. Nos. 8654–8677.

RANGE: Known only from the type locality.

REMARKS: As noted above, this form and *tridentiger* may be indistinguishable.

Neoheterandria umbratilis (Meek)

Plate 1, figures 1, 2; text figures 54E, 57F

Gambusia umbratilis.—MEEK, 1912, p. 70 (original description; Guapilis [Limón], Costa Rica; holotype, C.N.H.M. No. 7684). *Brachyrhaphis umbratilis.*—MEEK, 1914, p. 115. *Xenophallus umbratilis.*—C. L. HUBBS, 1924, p. 10.

Poeciliopsis maculifer.—FOWLER, 1916a, pp. 390–392 (original description; Río Guapilis at Guapilis [=Guapiles], Costa Rica; holotype, A.N.S.P. No. 45391).

MATERIAL: Guapilis, Daplo, Limón, Costa Rica; U.M.M.Z. No. 162479, U.S.N.M. No. 74244.

RANGE: Atlantic drainage of Costa Rica.

REMARKS: The figure and description of *Poeciliopsis maculifer* Fowler agree well with those of *Gambusia umbratilis* Meek; the types of both nominal forms are from the same locality.

GENUS **HETERANDRIA** AGASSIZ

Text figures 49A, B, 51C, D, 55A, B, 58A

Heterandria.—AGASSIZ, 1853, p. 135; 1855, p. 135 (type species, by designation under the plenary powers, *Heterandria formosa* Agassiz). On official list of generic names in zoology.

Pseudoxiphophorus.—BLEEKER, 1860, p. 482 (type species, by monotypy, *Xiphophorus bimaculatus* Heckel).

Poeciloides.—STEINDACHNER, 1863, p. 176 (type species, by monotypy, *Poeciloides bimaculatus* Steindachner).

DIAGNOSIS: In skull, parietals strongly or weakly developed and bordering posterior margin of frontals or partially fused with frontals and epiotics; epiotic processes present or absent, supraoccipital processes present and well developed; posttemporal unforked; marginal jaw teeth slightly compressed and pointed, lanceolate or recurved and conical. Posterior pleural ribs in male curved gently forward along their lengths, in many cases bent sharply forward at their tips. Gonopodial suspensorium with three long, slender gonapophyses that are bent moderately or sharply forward and then downward at their tips (except last which may be straight); pair of long, slender, in some cases sinuous, and in all cases pointed, gonapophyseal uncini arising near base or midsection of each gonapophysis and extending backward and slightly downward; ligastyle slightly longer than wide, not rod-like; primary gonactinostal complex usually with recess anteriorly for gonactinost 1; gonactinost 6 with pair of small, wing-like processes near its tip. Gonopodium bilaterally symmetrical, without fleshy appendages; rays 3 and 5 extending to

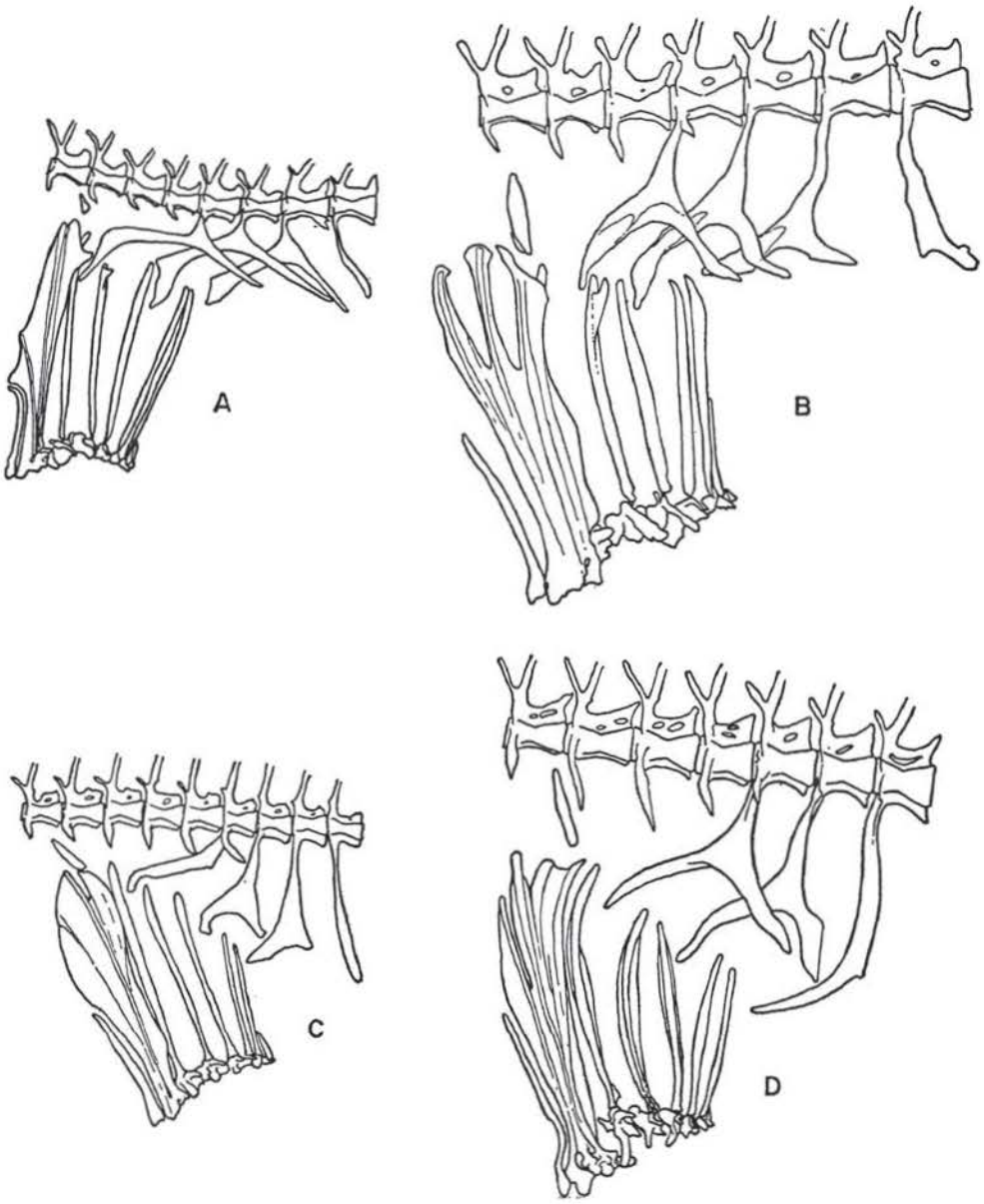
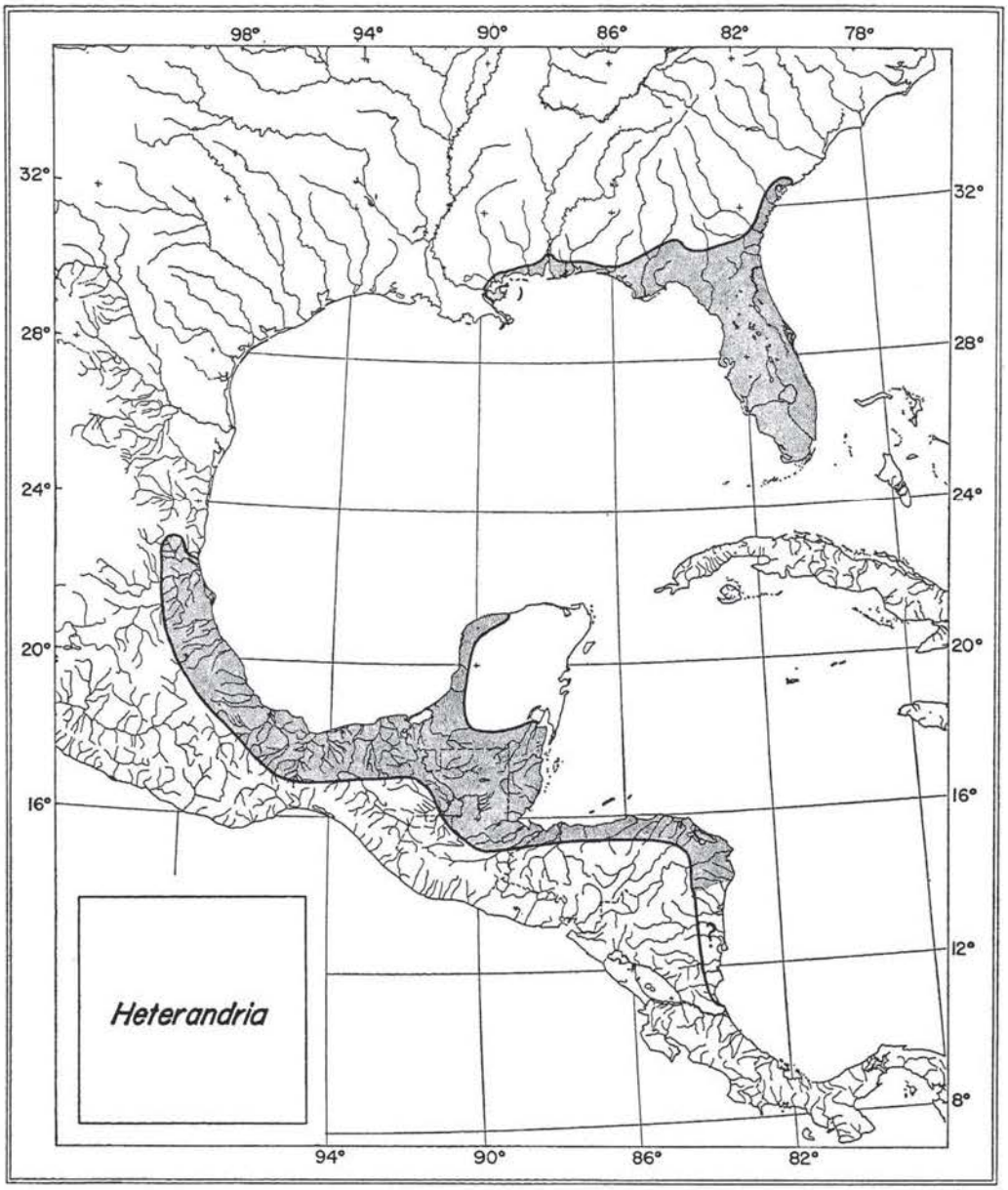


FIG. 55. Gonopodial suspensoria in the Heterandriini. A. *Heterandria formosa*, U.M.M.Z. No. 155309. B. *Heterandria bimaculata*, A.M.N.H., uncatalogued, Mexico. C. *Phallichthys amates pittieri*, after Rosen and Bailey (1959). D. *Poeciliopsis elongata*, U.S.N.M. No. 78846.

tip of membranous portion of gonopodium; ray 3 with five to 10 rudimentary spinous processes distally; ray 4a projecting beyond membranous tip as hook composed of single, or three or more, in many cases ankylosed elements; ray 4p with seven to 10 or more subdistal serrae; distal portion of ray 5 segmented or not, curving gently downward and forward adjacent to terminal elements of ray 4.

RANGE AND SPECIES COMPOSITION: Two species, one in Florida and near the coast from



MAP 16. Distribution of *Heterandria*.

South Carolina to Louisiana, the other from the Atlantic slope of Middle America from Río Tamesí, Mexico, to Nicaragua (map 16).

Heterandria formosa Agassiz

LEAST KILLIFISH

Text figures 49A, 51C, 55A, 58A

Heterandria formosa.—AGASSIZ, 1855, p. 136 (original description; locality given as Mobile, New Orleans, and Gulf states, in 1853, p. 135). *Heterandria* (=*Girardinus*) *formosa*.—JORDAN, 1885, p. 323. *Girardinus formosus*.—GIRARD, 1859b, p. 62. *Gambusia formosa*.—BLEEKER, 1860, p. 485.

MATERIAL: Overflow of creek, 7.5 miles southeast of Slidell, 0.2 mile north of junction with U. S. 90, St. Tammany Parish, Louisiana; U.M.M.Z. No. 155309.

RANGE: Berkeley County, South Carolina (U.M.M.Z. No. 143227), south through eastern and southern Georgia and peninsular Florida, west near the Gulf coast to New Orleans, Louisiana; in lowland fresh and brackish waters.

Heterandria bimaculata (Heckel)

Text figures 49B, 51D, 55B

Xiphophorus bimaculatus.—HECKEL, 1848, p. 296 (original description; Orizaba Mountains, Mexico). *Pseudoxiphophorus bimaculatus.*—BLEEKER, 1860, p. 485. *Gambusia bimaculata.*—REGAN, 1906–1908, p. 98. *Gambusia (Pseudoxiphophorus) bimaculatus.*—REGAN, 1907b, p. 260. *Pseudoxiphophorus bimaculatus bimaculatus.*—C. L. HUBBS, 1924, p. 18.

Poeciloides bimaculatus.—STEINDACHNER, 1863, p. 176 (original description; Tepeaca (Tepeyacac), later corrected [Steindachner, 1864, p. 74] to Teapa, on the boundary between Chiapas and Tabasco, Mexico). Preoccupied by *Xiphophorus bimaculatus* Heckel.

Pseudoxiphophorus reticulatus.—TROSCHEL, 1865, p. 104 (original description).

Mollienisia jonesii.—GÜNTHER, 1874, p. 371 (original description; Alcohuaca, near Huanmantla, Mexico; syntypes, B.M.N.H.). *Gambusia jonesii.*—REGAN, 1907b, p. 260. *Pseudoxiphophorus jonesii.*—REGAN, 1913b, p. 993. *Pseudoxiphophorus bimaculatus jonesii.*—C. L. HUBBS, 1924, p. 17.

Pseudoxiphophorus pauciradiatus.—REGAN, 1904, p. 256 (original description; Río Blanco, Orizaba, Mexico; types, B.M.N.H.).

Pseudoxiphophorus bimaculatus taeniatus.—REGAN, 1905, p. 303 (original description; Río Tanto and San Domingo de Guzman, Mexico).

Pseudoxiphophorus bimaculatus peninsulae.—C. L. HUBBS, 1936, pp. 157–165, 230 (original description; Progreso, Yucatán, Mexico; holotype, U.M.M.Z. No. 102078).

MATERIAL: Laguna de Petenxil, Petén, Guatemala; U.M.M.Z. No. 144225. Río Cahabón, about 6 kilometers west of Cahabón, Alta Vera Paz, Guatemala; U.M.M.Z. No. 146106.

RANGE: Atlantic drainage, from Río Tamesí, southern Tamaulipas, Mexico, to Nicaragua (Río Tunky, Miranda [Zelaya]; Fowler, 1923, p. 28).

REMARKS: This species has been treated by C. L. Hubbs (1924, 1926, 1936) as a complex of four subspecies that differ chiefly in average dorsal-ray counts (there being fewer at higher elevations and in the north), body form, and in pigmentation. The characters are apparently clinal and grade imperceptibly from one race to another: *Heterandria b. jonesi* (Günther), higher mountain streams and lakes of east-central Mexico; Río Tamesí to Río Tecolutla; *H. b. bimaculata* (Heckel), lower, warmer waters at moderate elevations behind Veracruz, from Río Chalchalacas to the Río Papaloapan; *H. b. peninsulae* (Hubbs), near Progreso, Yucatán; and *H. b. taeniata* (Regan), lowlands of the Isthmus of Tehuantepec, Veracruz, Mexico, to Guatemala, British Honduras, Honduras, and Nicaragua.

GENUS **POECILIOPSIS** REGAN

Text figures 49C, 52A–C, 55D, 56, 58B, C, 59

Hemixiphophorus.—BLEEKER, 1859, p. 440 (no species listed; type species, by subsequent restriction of Bleeker, 1860, p. 485, *Xiphophorus gracilis* Heckel).

Poeciliopsis.—REGAN, 1913, p. 996 (type species, by subsequent designation of Henn, 1916, p. 119, *Poecilia presidionis* Jordan and Culver). Placed on official list of generic names in zoology.

Leptorhaphis.—REGAN, 1913, p. 998 (type species, by monotypy, *Gambusia infans* Woolman).

Poecilistes.—C. L. HUBBS, 1926, p. 68 (type species, by original designation, *Heterandria lutzi* Meek).

Aulophallus.—C. L. HUBBS, 1926, p. 69 (type species, by original designation, *Poecilia elongata* Günther).

NOMENCLATURE: *Hemixiphophorus* Bleeker, based on *Xiphophorus gracilis* Heckel, 1848, has been regarded by past authors as a synonym of *Gambusia* (e.g., Garman, 1895, p. 85), as a subgenus of *Gambusia* (e.g., Jordan, Evermann, and Clark, 1930, p. 185), as a doubtful genus (e.g., C. L. Hubbs, 1926, pp. 41–42), or has been overlooked or disregarded (Günther, 1866; Regan, 1913b), although the latter authors included Heckel's species (*gracilis*) in *Gambusia*. Two adult males 30 and 31 mm. long in the Naturhistoriches Museum, Vienna, were made available through the courtesy of Dr. Paul Kahsbauer. They are labeled *Gambusia gracilis* Heckel, Orizaba, 1847, C. Heller, and are presumably part of Heckel's type series. A reconsideration of the original account and figures of *Xiphophorus gracilis* (Heckel, 1848, pp. 300–302, pl. 9, figs.

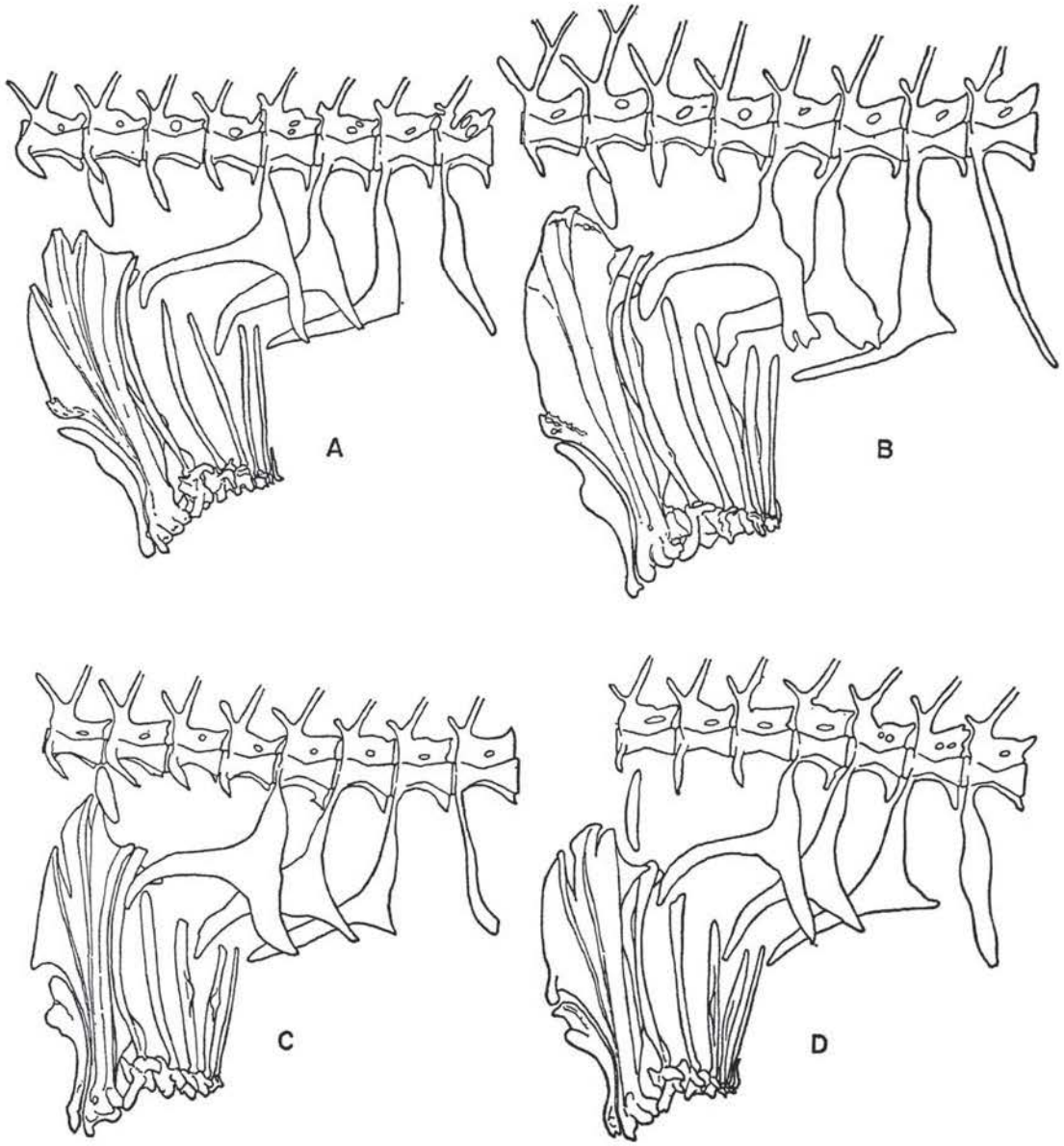


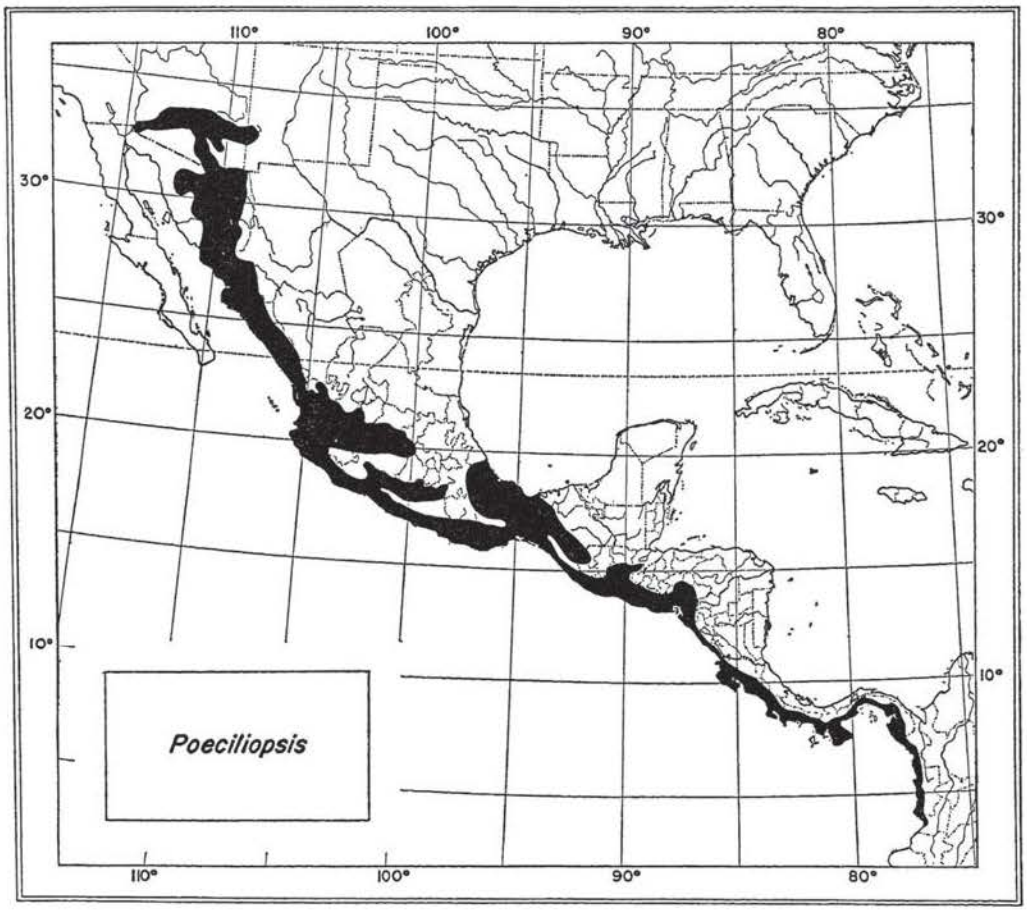
FIG. 56. Gonopodial suspensoria in *Poeciliopsis*. A. *P. presidionis*, U.M.M.Z. No. 164662. B. *P. gracilis*, U.M.M.Z. No. 161518. C. *P. infans*, U.M.M.Z. No. 108649. D. *P. occidentalis*, S.U. No. 3359.

3d, e, f, 4) and study of the available syntypes make it evident to us that they apply to a species of the genus currently known as *Poeciliopsis*. The only species of that genus known from near the type locality of *gracilis*, a clear brook in the Orizaba Mountains [Veracruz], Mexico, is *Poeciliopsis pleurospilus* (including *Heterandria lutzi* Meek). Heckel's diagnosis, freely translated from the German, is as follows: "*Xiphophorus gracilis* Heckel. *Male*. Dorsal fin base short, originating toward the middle of the body; upper inclined edge of fin truncated. Anal fin with the entire base situated in front of the dorsal fin; the sword [gonopodium] slender, twice as long as the head. A longitudinal black stripe from

over the operculum to the base of the caudal fin; a long black line on [the ventral edge of] the caudal peduncle to the caudal fin; all fins unmarked. *Female.* Dorsal and anal fins originating at the same level toward the middle of the body; each with a short base and with the inclined edge truncated. Coloration as in the male. Pectoral rays 1/11. Pelvic rays 1/5. Dorsal rays 2/6. Anal rays 2/6 (♀ 3/6). Caudal rays 7/14/7. Scales 3/29/3 and 2–3."

Especially to be noted is the great length of the gonopodium, which alone is sufficient reason to reject placement in or near *Gambusia*. The black lateral stripe is frequently encountered in "*lutzi*" from Veracruz, but is not characteristic of any species of *Gambusia* found south of the Panuco basin. The syntypes have the black lateral stripe broken into a series of large roundish spots, as is usual in *P. pleurospilus*. The body configuration points clearly to a species of *Poeciliopsis*. We therefore regard *Hemixiphophorus* as a senior synonym of *Poeciliopsis*, but do not admit it as the valid name of the genus because *Poeciliopsis* is on the official list of generic names in zoology (as name number 901) of the International Commission on Zoological Nomenclature. *Xiphophorus gracilis* Heckel, 1848, however, has priority over *Girardinus pleurospilus* Günther, 1866, and replaces it.

DIAGNOSIS: In skull, parietals small and obsolescent or wanting; supraoccipital processes present and typically well developed; epiotic processes usually well developed, occasionally much reduced; posttemporal forked; marginal jaw teeth distributed evenly along jaws if recurved and conical, or grouped



MAP 17. Distribution of *Poeciliopsis*.

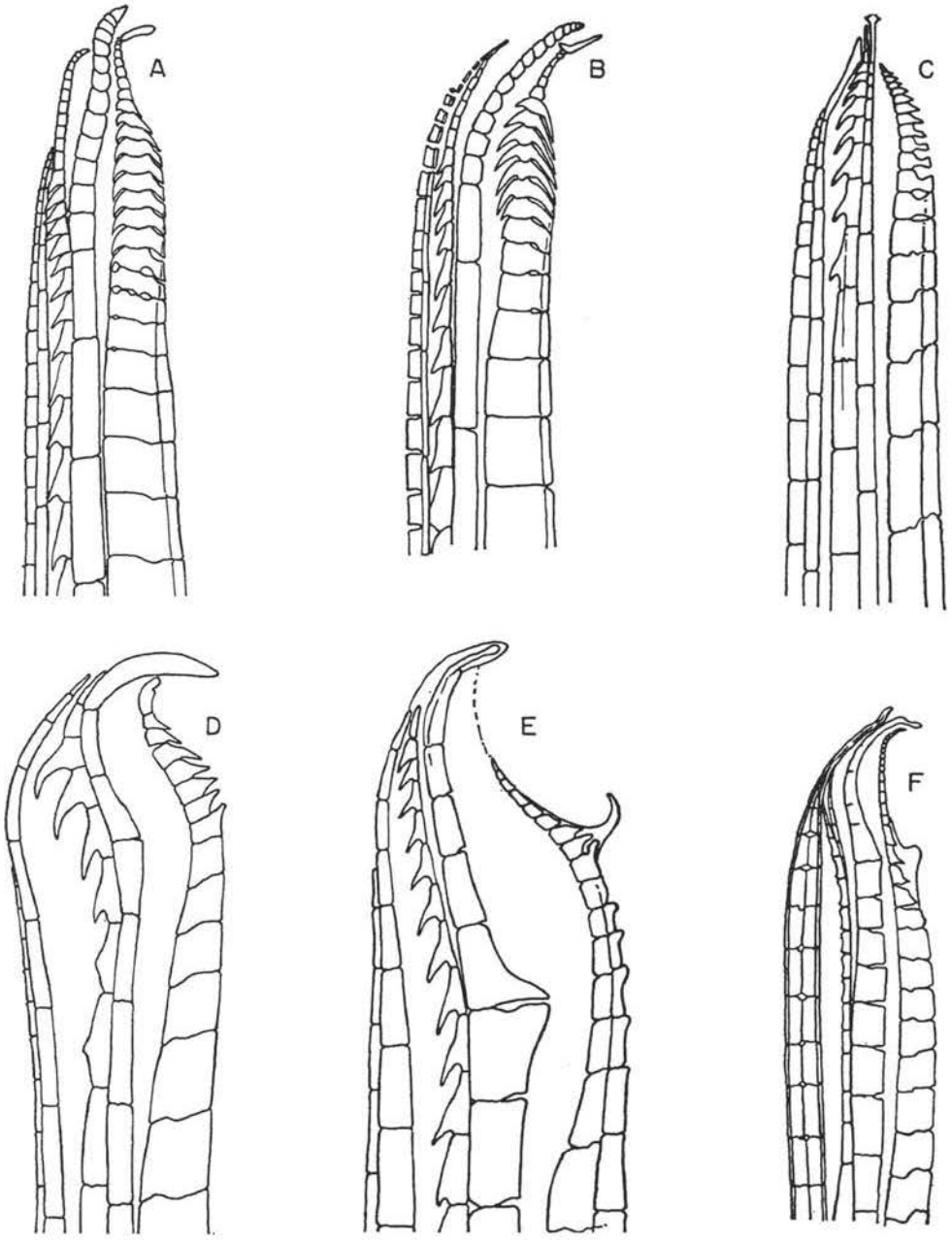


FIG 57. Gonopodia in the Heterandriini. A. *Priapichthys darienensis*, U.S.N.M. No. 109085. B. *Priapichthys chocoensis*, C.N.H.M. No. 57009. C. *Priapichthys nigroventralis*, C.N.H.M. No. 57719. D. *Neoheterandria elegans*, after Henn (1916). E. *Neoheterandria tridentiger*, U.M.M.Z. No. 115776. F. *Neoheterandria umbratilis*, U.S.N.M. No. 74244.

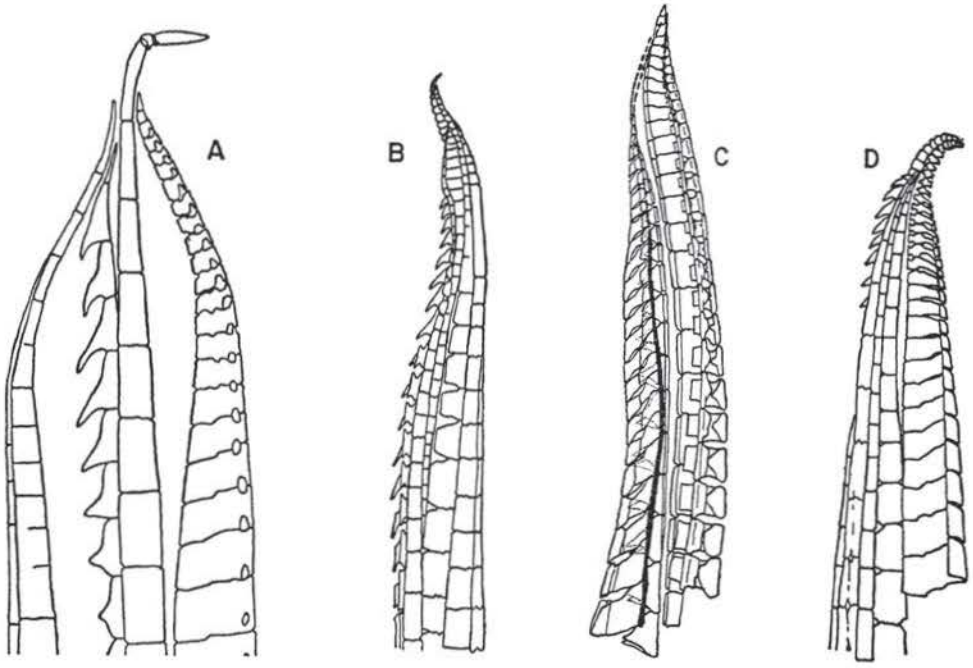


FIG. 58. Gonopodia in the Heterandriini. A. *Heterandria formosa*, aquarium specimen. B. *Poeciliopsis presidionis*, U.M.M.Z. No. 164662. C. *Poeciliopsis elongata*, U.S.N.M. No. 78846. D. *Phallichthys amates*, after Rosen and Bailey (1959).

in clusters of five or six if compressed or hair-like. Distal half of posterior pleural ribs inclined sharply forward. Gonopodial suspensorium with three, rarely four, well-developed gonopophyses typically bent sharply forward, sinuous, curving downward at tips, and possessing heavy, bluntly or sharply tipped sinuous uncini that arise about midway along gonapophyseal shaft (in smaller species, e.g., *prolifica*, last gonapophysis not curved downward at tip, and uncini in many cases broad-based and not sinuous); uncini on gonapophysis I in every case projecting more sharply downward than those on gonapophysis II; ligastyle invariably present, usually short and massive, in some cases delicate and rod-like, especially in smaller species; in most cases primary gonactinostal complex with distinct recess anteriorly for gonactinost 1, with well-developed superior and inferior lateral wings, larger superior ones extending outward and backward in bluntly or sharply pointed process, with incorporated gonactinosts 2, 3, and 4 rising upward and then curving backward (elements 2 or 3 rarely more or less erect in smaller species), and separated at their tips by distinct notches; in most cases gonactinost 1 with bony knob that projects forward at or just below its distal tip; in some cases gonactinost 7, in others gonactinost 8, in still others both gonactinosts, with paired, shallow, plate-like processes that extend laterally from their mid-section. Gonopodium sinistrally asymmetrical, rays 3, 4, and 5 folded inward to form closed or partly closed trough or twisted into helical structure; ray 3 subdistally showing varying degrees of ankylosis; ray 4p with either paired symmetrical serrae subdistally or unicuspid serrae on one branch and bicuspid serrae on other; rays 7 and 8 in close apposition distally or along middle of their lengths.

RANGE AND SPECIES COMPOSITION: Pacific drainage from southwestern United States to Colombia and in some Atlantic streams of southeastern Mexico, Guatemala, and Honduras (map 17). Fifteen species.

SUBGENUS POECILIOPSIS REGAN

DIAGNOSIS: Gonactinost 1 of gonopodial suspensorium with pronounced, anterior, subdistal swelling. Subdistal segments of both

halves of gonopodial ray 3 variably ankylosed into single long segment, segments on right half of this ray not modified as separate spines, but joined end to end and rolled upward to form a continuous bony ridge; series of asymmetrically paired serrae distally on ray 4p; subdistal segments of gonopodial ray 5p longer than high, not forming definitive bony ridge over dorsal wall of gonopodial groove.

RANGE AND SPECIES COMPOSITION: Range as for genus. Thirteen species.

Poeciliopsis turrubarensis (Meek)

Gambusia fasciata (not *Gambusia fasciata* Meek, 1904).—MEEK, 1907, p. 137 (material from Guatemala).

Gambusia turrubarensis.—MEEK, 1912, p. 71 (original description; Turrubares [San José], Costa Rica [Pacific slope]; holotype, C.N.H.M. No. 7676). *Priapichthys turrubarensis.*—REGAN, 1913b, p. 992. *Poeciliopsis turrubarensis.*—C. L. HUBBS, 1926, p. 67. ALVAREZ AND AGUILLAR, 1957, p. 165.

Heterandria colombianus.—EIGENMANN AND HENN, *in* Eigenmann, 1912, p. 27 (original description; Río Dagua, Colombia; holotype, C.N.H.M. No. 56047). *Poeciliopsis colombiana.*—HENN, 1916, p. 120. *Poeciliopsis colombianus.*—MEEK AND HILDEBRAND, 1916, p. 325.

Priapichthys fosteri.—HILDEBRAND, 1925, p. 260 (original description; Río Lempa, San Marcos, El Salvador; holotype, U.S.N.M. No. 87263, male, 58 mm. in total length).

MATERIAL: Río Choluteca, near Choluteca, Pacific drainage of Honduras; U.M.M.Z. No. 147185.

RANGE: Pacific coast from Jalisco, Mexico (U.M.M.Z. No. 178375), to Río Dagua, Colombia; in fresh, brackish, and salt water.

Poeciliopsis maldonadoi Alvarez and Aguillar

Text figure 59

Poeciliopsis maldonadoi.—ALVAREZ AND AGUILLAR, 1957, pp. 167–168 (original description; fossil; Zanjon de Tzitzimicu, El Salvador; holotype in collection of José Alvarez).

REMARKS: One of us (Rosen) has examined and reworked much of the original material on which this fossil species is based. It is all in a powdery, fresh-water diatomite of unknown age. Careful preparation has exposed the gonopodium of one specimen almost intact to its tip. The paired serrae on ray 4p are clearly visible (fig. 59). The serrae on each half of this ray are of approximately the same size, the proximal members of the left half being strongly bifid. Such a pattern is precisely that of serrae in the gonopodium of *Poeciliopsis turrubarensis*, which is common in the Lempa drainage of El Salvador today. In the other living Salvadoran species, *P. gracilis*, the paired serrae are distinctly subequal, especially near the tip of the fin, and the proximal members are seldom strongly bifid. Another reworked specimen proves to be of the genus *Poecilia* (*?sphenops*), since it clearly shows the characteristic suspensorial features of that group. These two forms are common poeciliids in El Salvador today. Hence, this fossil deposit (possibly a lake or swamp) is perhaps of Recent or sub-Recent date. We suspect that *P. maldonadoi* should be referred to the synonymy of *P. turrubarensis*.

Poeciliopsis presidionis (Jordan)

Text figures 52A, 56A, 58B

Poecilia presidionis.—JORDAN, 1895, pp. 412–414 (original description; Río Presidio, Sinaloa, Mexico; syntypes, S.U. No. 2687). *Girardinus presidionis.*—REGAN, 1906–1908, p. 99. *Poeciliopsis presidionis.*—REGAN, 1913b, p. 996.

MATERIAL: Río Presidio, Sinaloa, Mexico; S.U. No. 2687.

RANGE: Río Sinaloa, Sinaloa, to vicinity of San Blas, Nayarit, Pacific drainage of Mexico; near the coast but not entering salt water.

Poeciliopsis gracilis (Heckel)

Text figure 56B

Xiphophorus gracilis.—HECKEL, 1848, pp. 300–302, pl. 9, figs. 3d, e, f, 4 (original description; Orizaba Mountains [Veracruz], Mexico; syntypes, Naturhistorisches Museum, Vienna, two adult males, 30 and 31 mm.).

Gambusia Heckeli.—BLEEKER, 1860, p. 485 (substitute name for *Xiphophorus gracilis* Heckel [preoccupied by *Gambusia gracilis* Girard]).

Girardinus pleurospilus.—GÜNTHER, 1866, pp. 353–354 (original description; Lake of Dueñas, Guatemala; syntypes, B.M.N.H.). *Heterandria pleurospilus.*—JORDAN AND EVERMANN, 1896 (1896–1900), p. 148. *Poeciliopsis pleurospilus.*—REGAN, 1913b, p. 997. *Poecilistes pleurospilus.*—C. L. HUBBS, 1926, p. 68. *Poecilistes pleurospilus pleurospilus.*—C. L. HUBBS, 1950, pl. 4.

Heterandria lutzi.—MEEK, 1902, p. 106 (original description; Río Quiotepec, Cuicatlán, Oaxaca,

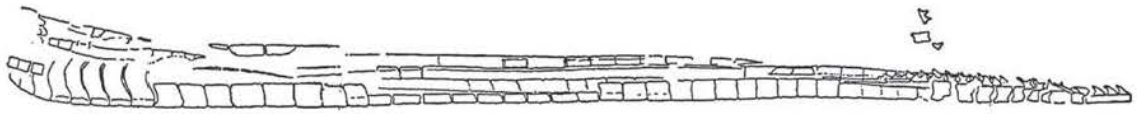


FIG. 59. Gonopodium of the fossil poeciliid *Poeciliopsis maldonadoi*, A.M.N.H. No. 20498

Mexico; holotype, C.N.H.M. No. 3718). *Girardinus lutzi.*—REGAN, 1906–1908, p. 99. *Poeciliopsis lutzi.*—REGAN, 1913b, p. 996.

Priapichthys letonai.—HILDEBRAND, 1925, p. 258 (original description; Río San Miguel, San Miguel, El Salvador; holotype, U.S.N.M. No. 87251, male 42 mm. in total length).

NOMENCLATURE: As indicated on pages 131–133, the species long known as *P. pleurospilus* had previously been named by Heckel which necessitated the adoption of the name *gracilis*.

MATERIAL: Lake Amatitlán, Guatemala; A.N.S.P. Nos. 64788–64817. Bay or "laguna" in Río Tehuantepec, Oaxaca, Mexico; U.M.M.Z. No. 161518. Cuicatlán, Mexico; C.A.S. No. 10991.

RANGE: Southern Mexico to Honduras: on the Atlantic slope from Río Chachalacas, Veracruz (U.M.M.Z. No. 97569), to the Río Grijalva basin of Guatemala, also in upper Río Motagua drainage of Guatemala and Río Humuya, Comayagua, Honduras (U.M.M.Z. No. 155877); on the Pacific slope from Río Mitla, Río Verde drainage, 3 miles south of Oaxaca, Oaxaca, Mexico (U.M.M.Z. No. 178577), to Río Choluteca, Honduras (Carr and Giovannoli, 1950, pp. 15–16).

Poeciliopsis infans (Woolman)

Text figure 56C

Gambusia infans.—WOOLMAN, 1894, pp. 56, 62 (original description; Río Lerma, Mexico; lectotype, U.S.N.M. No. 45570, a female, designated by Jordan and Evermann, 1896 [1896–1900], p. 680). *Leptorhaphis infans.*—REGAN, 1913b, p. 998 (Río Lerma record only). *Poeciliopsis infans.*—C. L. HUBBS, 1926, p. 65.

Gambusia affinis (not *Heterandria affinis* Baird and Girard).—PELLEGRIN, 1901, p. 205.

Poeciliopsis porosus.—DE BUEN, 1943b, pp. 268, 273–277, figs. 9–11 (original description; Lago de Camécuaro [about 5 kilometers south of Zamora], Michoacán, Mexico).

MATERIAL: Río Grande de Santiago near Ocotlán, Mexico; U.M.M.Z. No. 108649. "El Canal de la Presa de Lagado," 12 miles south of Guadalajara on Jalisco highway 35, Jalisco, Mexico; S.U. No. 47631. Lake San Anton, southwest of Zamora, Michoacán; U.M.M.Z. No. 173625.

RANGE: Highlands (above 3000 feet) of the basins of Río Grande de Santiago (chiefly in the Río Lerma basin) and Río Ameca, Jalisco and Michoacán, Mexico.

REMARKS: According to Jordan and Evermann [1896 (1896–1900, p. 680)], the type series of *infans* contains only males. R. R. Miller (personal communication) informs us that Jordan and Evermann's subsequently designated lectotype is, in fact, a female, as noted above.

Since we are unable to distinguish specimens taken in Lake San Anton, near Zamora (U.M.M.Z. No. 173625), close to the type locality of *Poeciliopsis porosus* de Buen, from *P. infans* collected in Lake Chapala and elsewhere in the range of the species, we place *porosus* in the synonymy of *infans*.

Poeciliopsis lucida Miller

Text figure 49C

Poeciliopsis lucida.—R. R. MILLER, 1960, pp. 2–3 (original description; tributary to Río Mocorito, north of San Benito, Sinaloa, Mexico; holotype, U.M.M.Z. No. 177266).

RANGE: Río Mocorito, Río Sinaloa, and Río del Fuerte, from northwestern Sinaloa to extreme southeastern Sonora (R. R. Miller, 1960, p. 3).

Poeciliopsis occidentalis (Baird and Girard)

GILA TOPMINNOW

Text figure 56D

Heterandria occidentalis.—BAIRD AND GIRARD, 1853, p. 390 (original description; Rio Santa Cruz near Tucson, Rio Gila, Arizona; syntype, A.N.S.P. No. 6972). *Girardinus occidentalis.*—GIRARD, 1859a, p. 73. *Poecilia occidentalis.*—GARMAN, 1895, p. 71. *Mollienisia occidentalis.*—REGAN, 1913b, p. 1013. *Poeciliopsis occidentalis.*—C. L. HUBBS, 1926, p. 65.

Girardinus sonoriensis.—GIRARD, 1859c, p. 120 (original description; San Bernardino Creek, Mexico).

MATERIAL: Eastern spring tributary to Tanque Verde Creek, Santa Cruz River basin, near Tucson, Pima County, Arizona; U.M.M.Z. No. 141726.

RANGE: Basin of the Gila River in New Mexico (Koster, 1957, p. 86) and Arizona southward through coastal rivers of Sonora.

REMARKS: We are informed by R. R. Miller that *sonoriensis* is intimately related to and likely conspecific with *occidentalis;* his investigation of the status of these forms is being continued.

Poeciliopsis viriosa Miller

Poeciliopsis viriosa.—R. R. MILLER, 1960, pp. 4–5 (original description; creek southwest of Las Palmas, Ixtapita, Jalisco, Mexico; holotype, U.M.M.Z. No. 177270).

RANGE: Río Ameca basin of northern Jalisco and southern Nayarit to the Río Mocorito, Sinaloa, Mexico (R. R. Miller, 1960, p. 5).

Poeciliopsis monacha Miller

Poeciliopsis monacha.—R. R. MILLER, 1960, pp. 3–4 (original description; Arroyo San Benito, Sonora, Mexico; holotype, U.M.M.Z. No. 177268).

RANGE: A few small streams in the vicinity of Rancho Guirocoba, in extreme southeastern Sonora, Mexico (R. R. Miller, 1960, p. 4).

Poeciliopsis balsas Hubbs

Gambusia gracilis (misidentification, not *Xiphophorus gracilis* Heckel).—MEEK, 1902, p. 99.

Gambusia infans (misidentification, not of Woolman).—REGAN, 1906–1908, p. 96 (in part; Río Balsas record only). *Leptorhaphis infans* (misidentification).—REGAN, 1913b, p. 998.

Poeciliopsis balsas.—C. L. HUBBS, 1926, p. 66 (original description; Río Balsas, Guerrero, Mexico; holotype, C.N.H.M. No. 3702).

Poeciliopsis anonas.—DE BUEN, 1943b, pp. 263–270, 281–283, figs. 1–7 (original description; Arroyo Anonas, Río Marqués [tributary to Río Balsas, Michoacán], 406 meters, Mexico).

MATERIAL: Río Aguililla at Aguililla, Michoacán, Mexico; U.M.M.Z. No. 178412. Puente de Ixtla, Mexico; C.A.S. No. 10984. Arroyo Cancita, about 9 miles east of Apatzingan, Michoacán, Mexico; U.M.M.Z. No. 178415.

RANGE: Pacific slope of Mexico, basin of the Río Balsas and two small streams, Río Arteaga and Río Aguililla, in Michoacán.

REMARKS: The synonymy follows that of C. L. Hubbs (1926), to which we add *Poeciliopsis anonas* de Buen. We have not seen specimens from the precise type locality of *anonas*, but a fine series (U.M.M.Z. No. 178415) is available from the Río Marqués drainage. These fish agree well with *P. balsas* from elsewhere in the Balsas basin and with the illustrations and description of the holotype (a female) of *anonas*. The figured male of *anonas* has the caudal peduncle slightly deeper than in our specimens, but we attach no systematic significance to this. De Buen emphasized the high dorsal-ray count of *anonas* (eight) in contrast to that of *balsas*. It is probable that de Buen counted all dorsal elements; we count seven dorsal rays in *P. balsas* and treat the last ray as double at the base.

Poeciliopsis fasciata (Meek)

Gambusia fasciata.—MEEK, 1904, p. 129 (original description; San Geronimo, Tehuantepec, Oaxaca, Mexico; holotype, C.N.H.M. No. 4715). *Heterandria fasciata.*—REGAN, 1913b, p. 995. *Poeciliopsis fasciata.*—C. L. HUBBS, 1926, p. 67.

RANGE: Fresh and brackish waters of the Pacific slope of Mexico from Laguna Coyuca near Acapulco, Guerrero (U.M.M.Z. No. 173520) to Río Pijijiápan, Tonalá, Chiapas (U.M.M.Z. No. 169075); Atlantic drainage headwaters of Río Coatzacoalcos, Oaxaca, Mexico (U.M.M.Z. No. 178523).

Poeciliopsis latidens (Garman)

Glaridodon latidens.—GARMAN, 1895, p. 42 (original description; Chihuahua, Mexico; syntypes, M.C.Z. No. 1307). *Glaridichthys latidens.*—REGAN, 1906–1908, p. 99. *Poeciliopsis latidens.*—C. L. HUBBS, 1926, p. 66. HUBBS AND MILLER, 1954, pp. 1–12 (synonymy; characters; comparisons).

RANGE: Pacific coastal lowlands of Mexico from Río del Fuerte, southern Sonora, to near San Blas, Nayarit; in fresh, brackish, and salt water.

Poeciliopsis prolifica Miller

Poeciliopsis prolifica.—R. R. MILLER, 1960, pp. 5–6 (original description; Arroyo Sonolona, Sinaloa, Mexico; holotype, U.M.M.Z. No. 177272).

RANGE: Lower Río Yaqui, Sonora, south-

ward along the coastal plain to San Blas, Nayarit, Mexico (R. R. Miller, 1960, p. 6); enters brackish water.

SUBGENUS **AULOPHALLUS** HUBBS

DIAGNOSIS: Gonactinost 1 of gonopodial suspensorium without anterior subdistal swelling. Subdistal segments of right half of gonopodial ray 3 not ankylosed, developed as broad flat spines, with pointed tips that curve upward to form ventral wall of gonopodial groove, enclosing much-reduced, long, and slender elements of left half of this ray; series of symmetrically paired or unpaired serrae distally on ray 4p; subdistal segments of right half of gonopodial ray 5p developed as long, very thin parallelograms of bone that are higher than long, these, with underlying elements of 5a, forming continuous ridge that serves as dorsal wall of gonopodial groove.

RANGE AND SPECIES COMPOSITION: Pacific slope of Costa Rica and western and central Panama. Two species.

Poeciliopsis elongata (Günther)

Text figures 52C, 55D, 58C

Poecilia elongata.—GÜNTHER, 1866, p. 342 (original description; Panama; holotype, B.M.N.H.). *Mollienisia elongata.*—REGAN, 1913b, p. 1013. *Poeciliopsis elongatus.*—MEEK AND HILDEBRAND, 1916, p. 324. *Poeciliopsis elongata.*—EIGENMANN, 1922, p. 181. *Aulophallus elongatus.*—C. L. HUBBS, 1926, p. 69.

MATERIAL: Corozal, Panama; U.S.N.M. No. 78846.

RANGE: Pacific coast of Costa Rica and western and central Panama (Hildebrand, 1938, p. 309). We are unable to locate the source of the Costa Rican report.

REMARKS: The largest female seen measures 13.3 cm., and the largest male 4 cm., in standard length.

In the gonopodium of this species there are large, paired serrae distally on ray 4p. In *retropinna* (below) these serrae are smaller and are unpaired.

Poeciliopsis retropinna (Regan)

Poecilia retropinna.—REGAN, 1908, p. 458 (original description; Costa Rica; holotype, B.M.N.H.). *Poeciliopsis retropinna.*—REGAN, 1913b, p. 997. *Aulophallus retropinna.*—C. L. HUBBS, 1926, p. 69.

MATERIAL: Quebrada Copera, into Río Chiriquí del Tire, Pacific slope, Panama; U.M.M.Z. No. 72578.

RANGE: Costa Rica and Río Chiriquí del Tire, western Panama, both on the Pacific slope.

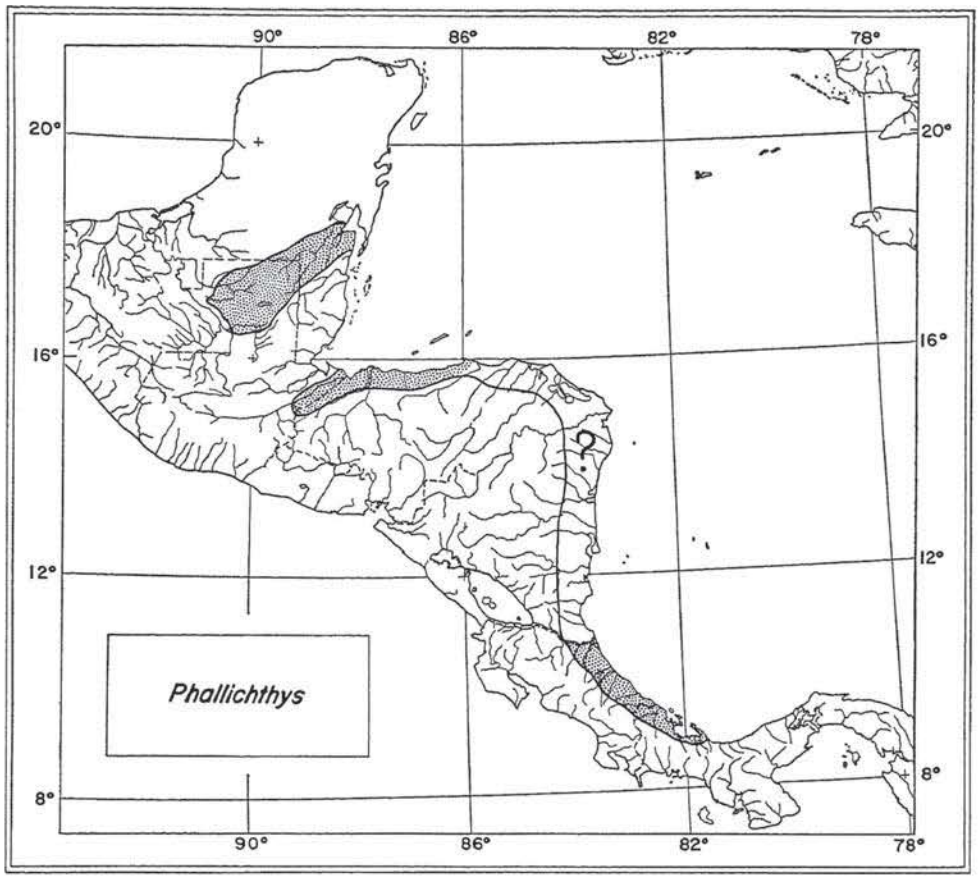
GENUS **PHALLICHTHYS** HUBBS

Text figures 49D, 52D, 55C, 58D

Phallichthys.—C. L. HUBBS, 1924, p. 10 (type species, by original designation, *Poeciliopsis isthmensis* Regan, a subjective synonym of *Phallichthys amates pittieri* Meek).

DIAGNOSIS: In skull, parietals small, ovate, with narrower end overlapped by frontal and broader end extending inward away from frontal and overlapping supraoccipital-epiotic commissure; supraoccipital processes well developed; epiotic processes small to well developed; posttemporal forked; marginal jaw teeth compressed. Posterior pleural ribs in male curved gently forward along their lengths. Gonopodial suspensorium with three gonapophyses that are nearly vertical or inclined slightly forward and turned downward at their tips; uncini on gonapophysis I, if present, emerging near base of spine just below vertebral centrum; uncini of gonapophyses II and III situated distally on spines to form broad swellings, tips arching ventrally; ligastyle present but variably developed; primary gonactinostal complex long, slender, narrow anteroposteriorly. Gonopodium dextrally or sinistrally asymmetrical; ray 5p modified as laterally compressed, knife-like ridge forming dorsal wall of gonopodial groove on left (in sinistral species) or right (in dextral species) half; ray 4p high, laterally compressed and ridge-like proximally, with row of unpaired distal serrae on right (in sinistral species) or left (in dextral species) half, with five or six minute serrae on right half in dextral species; ray 3 with row of unpaired, broad, flat, and moderately incurved spines forming ventral wall of gonopodial groove on left (in sinistral species) or right (in dextral species) half, without consolidated terminal or subterminal segments; segments of distal half of ray 6 swollen, transversely thickened, those of basal half asymmetrical, paired elements not side by side; rays 7 and 8 distinctly separated, not converging or in contact.

RANGE AND SPECIES COMPOSITION: Two species in Atlantic drainage from British



MAP 18. Distribution of *Phallichthys*.

Honduras and northern Guatemala to Costa Rica and western Panama (map 18).

Phallichthys amates (Miller)

Text figures 52D, 55C, 58D

Poecilia amates.—N. MILLER, 1907, p. 108 (original description; Los Amates, Guatemala; paratypes, C.N.H.M. No. 56168, C.A.S. No. 22554). *Poeciliopsis amates.*—HENN, 1916, p. 120. *Phallichthys amates.*—C. L. HUBBS, 1924, p. 10. ROSEN AND BAILEY, 1959, pp. 18–24 (figures of gonopodium, gonopodial suspensorium; characters).

Poecilia pittieri.—MEEK, 1912, pp. 71–72 (original description; La Junta [Limón], Costa Rica; holotype, C.N.H.M. No. 7680). *Poeciliopsis pittieri.*—REGAN, 1913b, p. 997. *Phallichthys pittieri.*—C. L. HUBBS, 1924, p. 10.

Poeciliopsis isthmensis.—REGAN, 1913b, p. 997 (original description; Colón, Panama; syntypes, B.M.N.H.). *Phallichthys isthmensis.*—MYERS, 1925, p. 370.

RANGE: Atlantic coastal lowland of the Motagua River system, Guatemala, southeast to the Caribbean slope of Costa Rica and western Panama (Rosen and Bailey, 1959, pp. 22, 24).

REMARKS: Rosen and Bailey (1959) treated *amates* and *pittieri* as subspecies, saying that these forms " . . . are well separated geographically but are strikingly similar in general appearance and in most diagnostic characters." The area of Atlantic coastal Nicaragua intervening between their known ranges is as yet largely uncollected. The subspecies are: *Phallichthys a. amates* (Miller), Atlantic slope of southern Guatemala and northern Honduras; and *P. a. pittieri* (Meek), Atlantic slope of Costa Rica and western Panama; Río

Huahuasán, Zelaya, Nicaragua (U.M.M.Z. No. 180639).

Phallichthys fairweatheri Rosen and Bailey

Text figure 49D

Dextripenis evides.—TURNER, 1940a, p. 89 (*nomen nudum*).

Phallichthys fairweatheri.—ROSEN AND BAILEY, 1959, pp. 24–29 (original description; Río San Pedro de Mártir, El Petén, Guatemala; holotype, U.M.M.Z. No. 172456).

RANGE: Río Hondo and New River systems, northern British Honduras, and Río de la Pasión and Río San Pedro de Mártir systems, northern Guatemala (Rosen and Bailey, 1959, p. 29).

SUBFAMILY **XENODEXIINAE** HUBBS

DIAGNOSIS: Egg without tough, membranous covering or adhesive filaments. Dorsal aspect of head with alternating paired and unpaired scales between supraorbital and postorbital sections of cephalic canal system. Pelvic fin with more than four rays. Frontal bones with subrectangular posterior extensions that overlie anterior part of epiotics. Nasal bones extremely large and meeting at midline, covering almost entire ethmoid region. Posterior extension of supraoccipital bone forming small segment of dorsal wall of foramen magnum. Mesonosts of gonactinosts 6 to 8 in gonopodial suspensorium firmly joined together by anterior and posterior articular processes but not co-ossified.[1] Actinost 1 of gonopodial suspensorium extremely large, almost as large as primary gonactinostal complex, and having bony collar at distal tip.[1] Vertebrae 34. Distal tips of sexually modified pleural ribs of male not interrupted. Epipleural ribs present. Right pectoral fin of adult male with elaborate clasper (C. L. Hubbs, 1950).

REMARKS: C. L. Hubbs (1950) classified *Xenodexia ctenolepis* in a separate subfamily, the Xenodexiinae, chiefly because of the presence in the only adult male (holotype) of a dextral pectoral clasper in combination with a dextrally asymmetrical gonopodium. Hubbs thought that the unilateral pectoral modification served a clasping function because it appears to have a definite morphology consonant with use during courtship. It was inferred that both dextrally asymmetric structures act in concert during copulation.

While this paper was in press, Klaus Kallman and Rosen collected a large series of a species of *Xenodexia* in Río Xalbal, just south of Ixcán, El Quiche, Guatemala. All males have a dextral gonopodium and a unilateral (dextral) pectoral clasper. The holotype of *X. ctenolepis* is therefore not anomalous or teratological in displaying these features.

A second feature of the Xenodexiinae emphasized by Hubbs and regarded by him as unique involves the presence of ctenoid scales. The ctenii are loosely joined to the scale margin, most of them in connective tissue, and do not make contact with underlying scale substance. They are calcified structures, but in general are similar in size, distribution, and attachment to the transitory contact structures that occur in many cyprinodontiform fishes. Myers (1931, p. 11) noted the presence of ctenoid scales in the African cyprinodontid *Lamprichthys tanganicanus* (Boulenger). We have seen them also on the head and nape of *Cyprinodon variegatus* (see fig. 3B), and R. J. Schultz has called our attention to their occurrence on the head in *Poeciliopsis*. Thus, ctenoid scales, though probably not general,

[1] Based on a radiograph of the holotype of *Xenodexia ctenolepis*.

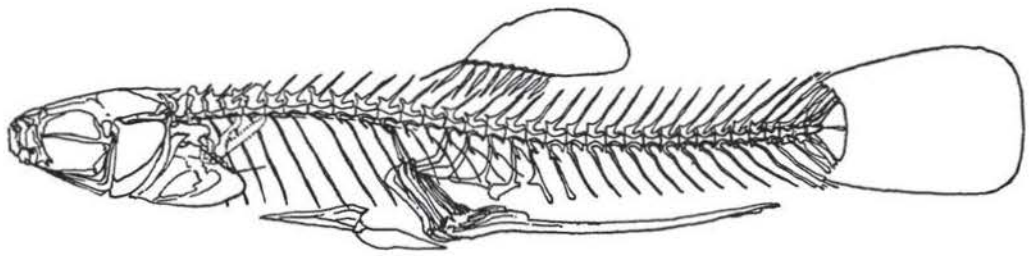


FIG. 60. Skeleton of adult male *Xenodexia ctenolepis*, holotype, U.M.M.Z. No. 105460.

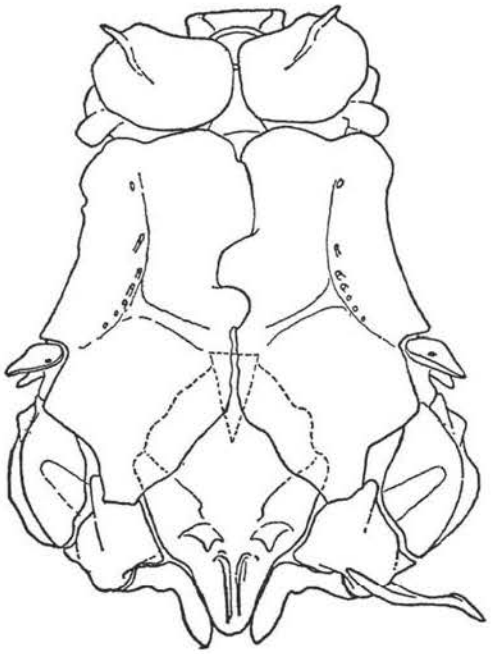


FIG. 61. Dorsicranium of *Xenodexia ctenolepis*, female, U.M.M.Z. No. 105459.

are more or less randomly distributed in the order. Their appearance in *Xenodexia* carries less weight than formerly.

GENUS XENODEXIA HUBBS

Text figures 60, 61

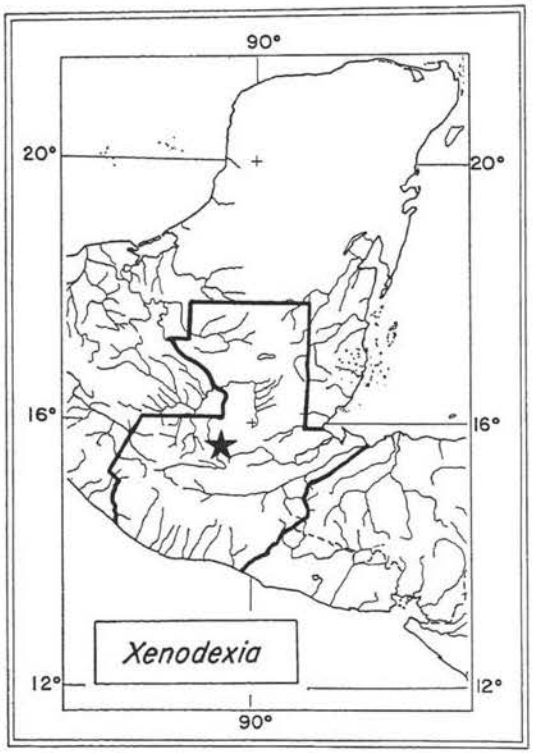
Xenodexia.—C. L. HUBBS, 1950, p. 8 (type species, by original designation, *Xenodexia ctenolepis* Hubbs).

Although a rigid diagnosis of this genus is not possible without study of additional adult males, some information has been pieced together from radiographs of the adult male holotype (e.g., R. R. Miller, 1957, fig. 2) and skeletons of adult females. On the basis of what can be gathered from these sources it appears that, in addition to its dextral pectoral clasper and ctenoid scales, *Xenodexia ctenolepis* possesses unique features in the skull and gonactinosts of its gonopodial suspensorium (fig. 60).

DIAGNOSIS: In skull, frontals unusually extensive, reaching well back over parts of supraoccipital and epiotic bones, terminating posteriorly in flat, subrectangular plates in region normally occupied by parietals. No parietals. Posttemporal forked. Supraoccipital bone rather confined laterally, posteriorly developing tongue of bone that penetrates between exoccipitals to form small part of dorsal wall of foramen magnum.

These details of the posterior dorsicranium vividly call to mind the typical condition in the oviparous Cyprinodontinae (e.g., *Cyprinodon*, *Floridichthys*).

Anteriorly in the skull, the nasal bones of *Xenodexia* are tremendously enlarged, and are similar to those in some species of the cyprinodontid genus *Orestias* (prefrontals of Gregory, 1933, p. 218). The nasals meet at the midline and completely cover the ethmoid complex and all but the tiny lateral outgrowths of the prefrontals; posteriorly they are solidly hinged to the lateral ethmoids via an extensive band of cartilage. The underlying double-laminar ethmoid ossification is typical of that in poeciliids generally, and a small prevomer is present. In the gonopodial suspensorium of *Xenodexia*, gonactinost 1 is almost as massive as the primary gonactinostal complex and appears to have a large dorsal



MAP. 19. Guatemala, showing the single known locality for *Xenodexia*.

collar. The complex itself is difficult to interpret on the radiograph but seems to be asymmetrically distorted and long and tubular. As in other poeciliids, gonactinost 1 articulates with gonopodial rays 1 and 2, and the primary complex (co-ossified actinosts 2, 3, and 4) articulates with principal gonopodial rays 3, 4, and 5. The ligastyle is long and rodlike. There are four gonapophyses; these extend downward from the vertebral axis and then bend abruptly forward. Gonapophyses II and III appear to be dilated distally, and numbers III and IV have short uncini at the points of flexure.

The dextrally asymmetrical gonopodium was described by C. L. Hubbs (1950). It appears to lack the assortment of terminal serrae and spines present in most other poeciliids. Correlated with the dextral asymmetry of the gonopodium is a thickened fleshy ridge along the ventromesial edge of the proximal third of the outer ray of the right pelvic fin.

REMARKS: On the basis of the above unique combination of skull characters and those in the gonactinostal elements of the gonopodial suspensorium, as well as the presence in the adult male of a dextral pectoral clasper, this genus is tentatively regarded as representing a distinct subfamily of the Poeciliidae, the Xenodexiinae. Despite certain superficial similarities and the common developmental trait of superfetation, we regard as improbable the suggestion that *Xenodexia* may be allied to *Poeciliopsis*. *Xenodexia* appears to be distinctly set apart from other Recent poeciliids.

RANGE AND SPECIES COMPOSITION: A single described species from central Guatemala (map 19).

Xenodexia ctenolepis Hubbs

Xenodexia ctenolepis.—C. L. HUBBS, 1950, pp. 1–28 (original description; Río Seniso [properly Cenizo, or Río Salbá], Finca Chamá, Alta Vera Paz, Guatemala; holotype, U.M.M.Z. No. 105460).

MATERIAL: Type locality; U.M.M.Z. No. 105459.

RANGE: Finca Chamá, 30 kilometers northwest of Cobán, Alta Vera Paz, in the Río Salbá, tributary to the Río Negro (Río Chixoy) which lower down becomes the Río Salinas of the Río Usumacinta basin, Guatemala.

ZOOGEOGRAPHY

MAINLAND DISTRIBUTION

THE POECILIID FISHES are native to the New World, where their distribution is principally tropical. Only 11 representatives from four genera have colonized the southern frontiers of the United States. One of these, *Gambusia affinis*, has spread throughout Florida and wide areas of the coastal plain and as far north as southern New Jersey and Illinois. The Cnesterodontini make up an apparently autochthonous South American tribe that at present occupies a broad band along the southeast slope of Brazil, Uruguay, and parts of Paraguay and Argentina. This region is largely savanna, with some deciduous, pine, and palm forest, and a narrow coastal strip of tropical rain forest. The other principal tribes either occur chiefly in regions of tropical rain or deciduous forest (Heterandriini and Gambusiini) or at least have their probable centers of radiation and dispersal situated in such regions (Verdoorn, 1945, vegetation map of Latin America). In the one instance of a sizable poeciliid penetration of North America (*Gambusia*), a secondary center of radiation apparently has formed in a region of desert scrub and thorn forest that is comparatively impoverished biotically. Although this is seemingly at variance with the more lush habitats in tropical lowlands occupied by the probably older southern species aggregates, the gambusias live for the most part in spring waters that furnish an equable environment.

An outstanding distributional feature of poeciliids is their dominance and ubiquity throughout tropical Middle America, as compared with their peripheral character on the continents, where they constitute a fringing fauna that is commonly well developed only in or near brackish water. Thus in extensive continental faunas they are well adapted to environments that are inhospitable to the more strictly fresh-water and marine fishes.

If we assume that the center of origin of a tribe is in the region where it is represented by the largest concentration of genera, or at least where the genera seem to converge, the picture is as follows. The Heterandriini, with five genera, originated in southern Central America and northern Colombia. They show evidence of a former more widespread occurrence, since *Heterandria formosa* from Florida and nearby states is now shown to be intimately related to *Heterandria* (formerly *Pseudoxiphophorus*) *bimaculata* from Middle America. The Gambusiini, with three genera, of which the largest is *Gambusia*, appear to have diversified chiefly in Mexico, with representation in the United States, Central America, Colombia, and the West Indies, but the more generalized *Brachyrhaphis* represents a secondary but perhaps older center, principally in Costa Rica and Panama. The Girardinini, with one northern Central American genus and two genera from Cuba, appear to be most closely related to the Gambusiini. The Cnesterodontini, with four genera, are confined to southeastern Brazil and surrounding countries, and they appear not to have really close relatives. The cnesterodontins are highly specialized and may be rather old. Of all the Poeciliidae, the Poeciliini, here grouped in four genera, are the most perplexing, and the tribe, as here defined, may eventually prove to be a complex assemblage. *Poecilia* is most diversified in South America (13 species) and the West Indies (16 species), and has a smaller center in Mexico (about six species). Through a mosaic of characters *Poecilia* appears to be related to *Alfaro* (Central American) and *Priapella* and *Xiphophorus* (chiefly Mexican). The apparently simple explanation that the poeciliin genera had an ancient center in lower Middle America from which their ancestors were largely displaced by other groups may be challenged because of the uncertainty of their relationships. Nevertheless, as these genera now stand, all but *Poecilia* seem to be descended from a Central American stock. If *Poecilia* also originated in Central America, it may have sent out three offshoots radially from this center, one to Mexico, another to the West Indies, and a third to South America. But there has been much obfuscating secondary intermingling of the different members of the

genus. For example, the West Indies contain elements of two subgenera, *Limia* and *Poecilia*, and *Poecilia sphenops* (belonging to the Mexican complex), or forms very much like it, has penetrated most of Central America and parts of northern South America where it overlaps the subgenera *Lebistes* and *Pamphorichthys*. An old or secondary center in northern South America could have contained the ancestors of both subgenera *Pamphorichthys* and *Limia*, the latter colonizing the West Indies from a South American rather than a Central American vantage point.

The Xenodexiinae, apparently with but one genus and species from central Guatemala, are very incompletely known.

The subfamily Tomeurinae, also with one genus and species, is confined to northern South America and shows some primitive reproductive features.

Of the Poeciliinae, *Brachyrhaphis* seems to have anatomical features that are generalized. This genus apparently is largely restricted to the region of the isthmian bridge, as already indicated.

In summary, the poeciliids have radiated principally from Central America, with lesser centers in the extreme northern Andean region (the Heterandriini), the Guianas (the Tomeurinae and some of the Poeciliini), the Brazilian region (the Cnesterodontini), and in Mexico, from which a few species have filtered over to the subtropical and temperate United States.

WEST INDIAN ENDEMISM

Although the view has been repeatedly expressed that poeciliids and other cyprinodontiforms reached the West Indies by essentially fortuitous means (Myers, 1938; Darlington, 1957), Rivas (1958) suggested that *Girardinus* [=his Girardinini], one of the two endemic and probably old Antillean genera, utilized former land connections to arrive in Cuba from Yucatán during Miocene-Pliocene times (also see above, pp. 108–109, and Rosen and Bailey, 1959).

Rivas believed that *Girardinus* must have used a land bridge with fresh-water drainage because " . . . poeciliid fishes originated [in] and have remained confined to fresh water until comparatively recent times when a few forms have partially succeeded in adapting themselves to the coastal marine habitat." In the present family structure, however, species in each of the five tribes of the Poeciliinae are either characteristically euryhaline or can adapt to salt water. It is not clear, therefore, on what evidence Rivas based his statement. His attempt to show that the ancestors of *Girardinus* were as rigidly confined to fresh water as is *Girardinus* today rested on the proposition that adaptation to salt or fresh water requires a long time to be acquired or lost. This idea is inadmissible as evidence, if poeciliids have always been salt-tolerant, as we believe they have (in common with the other major groups of cyprinodontiform fishes), and is a gratuitous argument to use for a family that is virtually unknown in the fossil record. Furthermore, in recent experiments[1] we have succeeded in step-by-step transfers of *Girardinus uninotatus* and *Quintana atrizona* to full-strength sea water.

A species even partially adapted to a brackish environment might be able to negotiate short stretches of salt water. Once colonization of an island is effected, such a species could either preserve its previously acquired osmoregulatory mechanism (as *G. uninotatus* and *Quintana atrizona* seem to have done) or lose it in favor of one more suited to the sweeter waters of a new habitat. A similar point is raised by Bond (1962) in reference to Rivas' argument for continental

[1] During the period April 11 to May 2, 1962, at laboratory temperatures ranging from 27.0° C. to 30.5° C., a juvenile specimen of *Girardinus uninotatus* originally in fresh water was acclimatized to a solution of artificial sea salts equal to a salinity of 37.6 parts per thousand. The gradual transfer was accomplished by the daily addition of enough sea salts to raise the hydrometer level by approximately 0.002 points of the apparent specific gravity reading. The fish remained in this solution for 26 days, in apparently good health, and then died on May 28. During the period January 4 to January 21, 1963, at temperatures ranging from 22.0° C. to 26.5° C., a male and female of *Quintana atrizona* were acclimatized to a salinity of 34.4 parts per thousand. The male died on January 24, but the female is still alive and in apparently good health at the present writing (February 11, 1963). The experiments were conducted in a one-gallon covered aquarium containing an airstone and bottom filter.

land connections to the West Indies. Moreover, we know of no basis for estimating the time required to alter osmoregulatory mechanisms, but the time needed to evolve an endemic genus (or two) would perhaps permit considerable adjustment.

The greatest mainland concentration of poeciliid species that occur in brackish or marine habitats is to be found in Middle America; at least 17 species from seven genera enter or live in saline waters from Mexico to Colombia. The coasts of North and South America combined accommodate only eight species from four genera. The ancestral Central American poeciliids presumably lived under ecological restrictions essentially similar to those of modern species, and they were probably well represented in brackish situations. If Central America served as a principal source of the West Indian poeciliid fauna, then it is reasonable to suppose that the colonizing species, like modern ones, were somewhat salt-tolerant.

As preface to a discussion of the poeciliid fauna of the Greater Antilles, it is desirable to mention certain peripheral and adventitious forms which are of secondary concern. Three species of *Poecilia* have entered the West Indian fauna from northern South America: *P. vivipara* lives on the Netherlands and Venezuelan islands, Trinidad, and the Leeward Islands north to Martinique, and it is also the only poeciliid that occurs on Puerto Rico, where it was likely introduced by man (Myers, 1938). *Poecilia reticulata* occurs on the Netherlands and Venezuelan islands, Trinidad, Barbados, St. Thomas, and Antigua. *Poecilia sphenops* occurs on the Netherlands and Colombian West Indies. These species are probably relatively recent invaders of the West Indies, perhaps owing their presence there to transfer by human agency (Myers, 1938), and (except perhaps for the last) have differentiated little if at all from mainland stocks. *Gambusia aestiputius* from San Andres Island in the Colombian West Indies is close to or identical with *G. nicaraguensis* on the adjacent mainland of Central America.

With the above exceptions, all West Indian poeciliids occur on the Bahamas, Cuba and the Isle of Pines, Hispaniola, Grand Cayman, or Jamaica. All species (except *Gambusia punctata*; see below) and two of the four genera present are endemic. Thirty-five species are listed from these islands, but it is likely that future study will result in reduction, especially on Cuba, Jamaica, and Hispaniola.

The extent of intermingling of the West Indian poeciliid island faunas is not well known, but there is circumstantial evidence that a small amount of faunal exchange does take place. Some species of *Gambusia* show a significant ability to withstand transport from one island to another. *Gambusia punctata*, for example, occurs in Cuba and in the southern tip of Florida. *Gambusia manni* occurs on several Bahamian islands and keys, and *G. oligosticta* is reported from both Jamaica and Hispaniola. Thirteen species of *Poecilia* appear to be island endemics, as are also the eight species of *Girardinus*, and *Quintana atrizona*.

The high endemism of the poeciliid faunas of the West Indies provides a measure of the effectiveness of the salt-water barrier to crossing by these fishes. Nevertheless, an explanation of this endemism does not require land bridges with fresh-water drainage. It should be noted here that chance colonization by live-bearing species is mathematically far more probable than for bisexual, oviparous forms. Successful arrival of a single pregnant female sets the stage for establishment of a new colony. The reality of such chance crossing of formidable barriers of sea water by poeciliids is vividly documented by the presence of *Gambusia punctata* in southern Florida, which it obviously reached by crossing the Gulf Stream from Cuba, possibly via hurricanes which commonly follow this route. Another bit of evidence argues strongly against the necessary existence of a late land bridge connecting Yucatán with Cuba. No species of the subgenus *Poecilia* occurs on Cuba despite abundant representation of this euryhaline group along the mainland coasts of the Gulf of Mexico. The apparent failure of establishment in this situation provides a striking illustration of the vagaries of filter-bridge colonization.

If zoogeographic significance may be deduced from the endemism and distinctiveness of the West Indian poeciliids it is that, although powerfully held by permanent land,

their colonization of the islands was probably gradual and via the adventitious means available to waifs. The most highly differentiated poeciliid faunas in the West Indies are found in islands that are closest to the mainland. There are, for example, four genera of poeciliids in Cuba, two in Jamaica and Hispaniola, and one in the Bahamas. This situation, which at first may seem to reflect the decreasing chances of survival of waif populations that were being moved passively farther and farther from their mainland sources of origin in actuality is probably related chiefly to the size and environmental diversity of the islands colonized and when, in relative time, the different colonizing groups arrived. Cuba and the Isle of Pines support 15 recognized species belonging to *Gambusia* (five species), *Poecilia*, subgenus *Limia* (one), *Girardinus* (eight), and *Quintana* (one). The two last-named genera are known only from these islands. Hispaniola, next in size to Cuba, supports 13 listed species—three in *Gambusia* and 10 in *Poecilia* (subgenera *Poecilia* and *Limia*, with two and eight nominal species, respectively). Jamaica has two species of *Limia* and four of *Gambusia*, one of which is shared with Hispaniola. Grand Cayman has one species of *Gambusia* and an undescribed form of *Limia*. The Bahamas support a weakly defined species of *Gambusia*. These details can be construed to mean that the earliest poeciliid invaders of the West Indies were the ancestors from Central America of, perhaps first, *Girardinus*, and, later, *Quintana* (see Rosen and Bailey, 1959). Alternatively, *Girardinus* and *Quintana* may have diverged in Cuba from a common ancestral stock from the mainland. In either event the likely dispersal route was from Yucatán to Cuba. This early colonization may then have been followed by two invasions, one by the ancestral stock that gave rise to the endemic West Indian subgenus *Limia*, the other by the subgenus *Poecilia* which resulted in two species on Hispaniola. Both stocks probably entered the Antilles by a route from the Honduras-Nicaragua bulge through Jamaica to Hispaniola. The *Limia* invasion subsequently entered Cuba from the east or south. No species of the subgenus *Poecilia* persists on Jamaica. The fact that a species of *Poecilia* and one of *Gambusia* presently occur on islands off this bulge suggests that this area may have been a principal vantage point from which Middle American stocks made their way to the Greater Antilles. The means of transport may well have been the more or less accidental over-water mechanisms proposed for this route by Darlington (1957). *Limia* may have had its genesis in northern South America; *Poecilia*, in lower Central America.

Gambusia has successfully emigrated from Middle America to the Greater Antilles at least twice and perhaps three times. *Gambusia sexradiata* and *G. luma* from southern Mexico and Guatemala are closely related to *G. punctata* of Cuba. Dispersal from the region of Yucatán to Cuba is indicated, with continued spread from there to southern Florida. *Gambusia beebei* from Lake Miragoâne, Haiti, is apparently related to *punctata* but has much-enlarged jaws. It denotes further differentiation from this line. *Gambusia yucatana* from southern Mexico and northern British Honduras is close structurally to *G. puncticulata* of Cuba and probably represents the stock from which the latter arose. Other intimately allied West Indian species in the same kinship include *howelli* from the Isle of Pines, *baracoana* and *bucheri* from Cuba, *manni* from the Bahamas, and *oligosticta* from Jamaica and, reportedly, Hispaniola. *Gambusia caymanensis* may belong here also. This invasion probably utilized the same route—from Yucatán to Cuba, with subsequent spread in the Antilles. There is strong indication of a third successful Antillean invasion by *Gambusia*, this one stemming from a *nicaraguensis*-like ancestor, crossing from the Nicaragua-Honduras bulge to Jamaica and thence to Hispaniola. To judge from Regan's (1913b) figures, *G. gracilior* and *G. wrayi* from Jamaica and *G. dominicensis* of Hispaniola are involved. *Gambusia melapleura* is perhaps the same as one of the other Jamaican species.

By late Tertiary times, when, according to Rivas, the ancestors of *Girardinus* were making their way over land to Cuba, the present isthmian link connecting the northern and southern continents had been completed (see Woodring, 1954), and strictly fresh-water siluroids and cyprinoids reëntered Central America from north and south (Myers, 1938;

Darlington, 1957). Earlier, the continental bridge had been interrupted through most if not all of the Tertiary. If a land bridge to the Greater Antilles existed in late Tertiary, as contended by Rivas, it is difficult to explain why some of the strictly fresh-water cypriniform fishes did not use it. At any rate, no primary fresh-water fishes occur on the Greater Antilles (Myers, 1938), and aggressive cypriniforms, had they ever reached the Antilles, should still be there. The ichthyological evidence does not offer confirmation of a land connection between the Antilles and the mainland; if such a connection did exist, it must have predated the modern fresh-water fish fauna of the area.

Although there may never have been a land bridge to the Greater Antilles with fresh-water drainage, there may have existed a chain of scattered islands that provided refuge for waifs. Lowered water levels during the Pleistocene, for example, reduced the breadth of water gaps and increased the extent of the West Indian archipelago. Such islands could greatly enhance the dispersal of salt-tolerant cyprinodontiforms and, at the same time, effectively exclude cypriniforms or other strictly fresh-water organisms. Even so, the dispersal of cyprinodontiforms to the Greater Antilles necessitated essentially fortuitous means of transport. The chief role of intervening islands in furthering dispersal may have been through provision of shoreline breeding habitats. Population buildup en route would enhance many-fold the chances of farther penetration toward the Greater Antilles.

EVOLUTIONARY AND DISTRIBUTIONAL FEATURES OF *POECILIA* AND *GAMBUSIA*

There is, at best, an unsubstantial basis for assessing the relative ages of the major groups (genera, tribes, and subfamilies) of poeciliids. A discussion of the problem may be justified on grounds of its heuristic value. Certain empirical evidence can be construed to show that *Gambusia* and *Poecilia* as we know them now are both of relatively more recent date than most other genera. The hypothesis, without support from the fossil record, is predicated on (1) their present pandemic distributions, (2) their speciose character, and (3) the presence in each of many diversely specialized as well as generalized forms. In both genera one finds a mosaic of relationships of the highly specialized members with a central or generalized type, that is, one that contains all the basic modifications of the entire group but that has none of them developed to any great extent.

In *Gambusia*, *G. nicaraguensis*, from Lake Izabal, Guatemala, southward throughout most of Atlantic coastal Central America, may well be a descendant of the original stock that gave rise to the widely distributed northern mainland *affinis*, as well as to *lemaitrei* of Colombia, *myersi* of eastern Mexico, and *yucatana* from southeastern Mexico and northern Central America. Both *nicaraguensis* and *yucatana* appear to represent progenitors for separate fractions of the gambusiin fauna of the Antilles. The *punctata* group from southern Mexico, northern Central America, and the Antilles most likely also evolved from the *affinis* species group and contributed to the West Indian fauna. To the north, in Mexico and southern United States, the *nobilis* group is perhaps derived from the *punctata* group; these groups have similarities in their gonopodia and in pigmentation. From the same general area, the *panuco* and *vittata* groups, each with strong resemblances to the *nobilis* group in pigmentation, body configuration, and suspensorium, but with distinctive gonopodia, are probably interrelated. The immediate relationships of the *rachowi* group of southeastern Mexico are not apparent; the species have retained generalized genitalic features while adding some highly specialized ones.

In *Poecilia*, the Colombian *P. caucana* and the widespread mainland *P. sphenops* complex seem to approximate the generalized structural features expected of an ancestral stock. From this group the West Indian *P. elegans* and *P. montana* may have been derived. In *Poecilia*, which is somewhat better differentiated than *Gambusia*, the outlying, mostly rather specialized components are distributed in a great arc northward and eastward from a possibly northern South American and lower Central American center. In

northeastern South America is a group (subgenus *Lebistes*) notable principally for its pigmentary polymorphism. The subgenus *Pamphorichthys* contains species (*P. minor* from the Amazon basin, *P. hollandi* from the São Francisco system, and *P. heterandria* from Venezuela) that are specialized in gonopodial and pelvic structure. Paralleling *Pamphorichthys* in gonopodial and pelvic characters is the endemic West Indian subgenus *Limia*, which on the islands has split into two, possibly three, distinct species groups. The remaining subgenus *Poecilia*, including the South American *P. vivipara*, is widely represented in northern South America, Hispaniola, Middle America, and the Gulf coastal United States by many species that are all rather generalized, at least in their principal secondary sexual modification. *Poecilia vivipara* appears to provide a link between the subgenera *Poecilia* and *Lebistes*.

Poecilia and *Gambusia* each contain nearly three dozen species, and each is continuously distributed throughout wide areas of tropical America. Judged from the occurrence of some generalized mainland types in the West Indies and in offshore islands, both genera are still actively colonizing. Moreover, both genera are now represented by many diverse morphological types as compared with some impoverished Central and South American genera, four of which are monotypic, and it seems probable that an active evolution of morphologically and ecologically specialized species of *Poecilia* and *Gambusia* is still in progress. This idea is consistent with the lack of stability in number of gonapophyses in the suspensorium of many species of *Gambusia* and of at least three species of *Poecilia*.

Although these speculations presuppose a recent origin of *Gambusia* and *Poecilia*, the groups to which they belong, the Gambusiini and the Poeciliini, are believed to be old, particularly the latter which include also three smaller and, in some ways, rather dissimilar genera (*Xiphophorus*, *Priapella*, *Alfaro*). It may have been from a primitive suspensorium such as that of *Alfaro*, which may have two, three, or four gonapophyses, that the other poeciliin types evolved. That a species of *Gambusia* (*vittata*) and *Belonesox belizanus* have nearly identical gonopodia may indicate that the gonopodial pattern was the primitive type, existing before the two genera had diverged. It is the *G. vittata-B. belizanus* type of genitalium, and the *Belonesox* type of suspensorial gonapophyses, occurring also in some species of *Gambusia*, that find counterparts in *Brachyrhaphis*. *Brachyrhaphis cascajalensis* and *parismina*, as shown above, are remarkably *Gambusia*-like representatives of their genus. Hence, in containing the very primitive species of *Brachyrhaphis*, the Gambusiini appear to be rather old, as do the Poeciliini in embracing *Alfaro*.

Finally, it should be emphasized that members of the Gambusiini and Poeciliini are the only poeciliids thus far known that possess in combination rather short gonopodia, some auxiliary mechanism that is developed from either the pectoral (*Gambusia*) or pelvic (*Poecilia*, *Xiphophorus*) fins to assist gonopodial action, highly polymorphic male pigment patterns, and rather elaborate courtship and mating behaviors (Rosen and Tucker, 1961). Rosen and Gordon (1953) referring chiefly to the groups not thus modified, commented that these [possibly older] genera "... demonstrate a general trend toward elongation of the gonopodium and, at the same time, the reduction of size and effectiveness of the pelvic fins." Rosen and Tucker (1961) observed no pronounced preliminary mating display in any of these latter genera, although the behavioral observations include only a few of them, and the point is therefore not well documented. With the above speculations on the temporal origins of *Poecilia* and *Gambusia*, it is suggested that elaborate mating displays as restricted to the Poeciliini and the Gambusiini are comparatively recent innovations in the family.

SUMMARY

THE FAMILY POECILIIDAE (order Cyprinodontiformes) is divided into three subfamilies, 21 genera, and 138 species. The Tomeurinae and the Xenodexiinae are monotypic; the Poeciliinae contain 19 genera, which are grouped into five tribes. The family, the subfamilies, and the genera are diagnosed, and the distinctive anatomical characteristics of the genera of the Poeciliinae are summarized (table 3). A check list of the species and subspecies in the family incorporates basic synonymies, known geographical ranges, subgenera and species groups, and nomenclatural and anatomical notes. The place of deposit of the types or type series of 80 per cent (207 of 259) of the proposed specific and subspecific names is given.

The present taxonomic arrangement represents a substantial revision of prior classifications. It rests almost wholly on osteological features of the skull and of the sexually modified anal fin (gonopodium) and internal anal-fin supports (gonopodial suspensorium) of the male.

Sexually dimorphic modifications are numerous among the Poeciliidae. Other than size, these include pelvic and pectoral fins and, to a lesser extent, caudal and dorsal fins, mouth parts, dorsicranium, pleural ribs, and color pattern. The anal fin and its suspension are sexually dimorphic in all poeciliids and constitute the primary basis for separating tribes, genera, and species.

The specialized terminal gonopodial structures are produced by specific fields of osteogenic tissue. The hypothesis that the development of a given terminal structure influences that of adjoining ones was tested experimentally in *Xiphophorus*. Removal of the distal half of ray 5 during the growth phase of gonopodium development modifies the underlying ray 4 so that it resembles this ray in *Poecilia*. From such experiments it is inferred that natural deletions may have been an important source of the differences between some poeciliid genera.

Despite differences in length and terminal ornamentation, the functional aspects of most poeciliid gonopodia depend on the same basic mechanical principles. Gonopodial morphogenesis involves the elaboration of a mechanism that allows the rotation and folding of one ray against another as the gonopodium is swung forward. The rotational centers that permit folding of the rays become functional before the terminal specializations are differentiated. In certain species growth may be asymmetrical, so that the rays are actually folded during development and a permanent groove is thereby formed in the sinistral or dextral position. Small developmental asymmetries are of normal occurrence in the gonopodial morphogenesis of all poeciliid species and have evidently led to the evolution of permanently asymmetric gonopodia five times independently in this family.

Permanent folding permits structural modifications to enhance the effectiveness of a mechanism that is normally folded during use, and clearly is potentially adaptive. Permanent gonopodial asymmetry is found only in species with relatively long gonopodia. The action of the short gonopodium during sperm transfer is assisted by the bilaterally modified pectoral and pelvic fins. Thus the absence of asymmetry in species with short gonopodia may indicate canalization of developmental pathways toward the production of bilateral mechanisms such that even slight asymmetric distortions would be inadaptive and quickly eliminated.

During development, the anal-fin suspensorium passes through a period of histolysis that results in the gradual dissolution of the anterior hemal spines. In the developing female, histolysis proceeds unchecked, and as many as four anterior hemal spines may be eliminated. In the maturing male, histolysis is counteracted by the rapid addition of bone, and typically not more than a single hemal is eliminated before osteogenesis sets in. The configuration and orientation of some suspensorial structures appear to be controlled largely by body form and absolute size of the fish. Others transcend such largely mechanical forces and retain a measure of developmental independence. Only the morphological details that show developmental autonomy hold definite promise of aiding phylogenetic analysis.

It is suggested that what matters from the viewpoint of mechanical control of the gonopodium is not the embryological origin of the different suspensorial structures, or even the precise point at which these structures arise, but the total adaptation for the job of suspension. In a sense, all poeciliids may be said to have developed equally an effective suspensory apparatus. Some species have developed it in connection with a long gonopodium, others with a short or an asymmetrical gonopodium, and still others have evolved a gonopodial system that operates in relation to specialized pelvic or pectoral fins. Despite fundamental similarity among the poeciliids in basic structure and morphogenetic plan, each genus presents a relatively distinctive total solution to the problem of gonopodial suspension. With allowances for the influence of size on certain relations, the details of suspensorial morphology thus represent a primary source of taxonomic information in these fishes.

The view expressed by some authors that the specialized terminal structures of the gonopodium are of no adaptive significance is contested. The considerable functional evidence of the definite role these structures play in copulation is reviewed. The real problem is not that the varied terminal modifications in the gonopodia of the poeciliids are indispensable for insemination, but that they probably enhance the effectiveness of the really essential behavioral items that result in precise juxtaposition of the fins and the bodies during mating.

Viviparity in Poeciliidae is reviewed, and theoretical considerations of its significance in the success of the family are considered. It is suggested that a major selective advantage of embryo retention is its involvement as an agent in dispersal. It may have arisen as a heritable capacity for a slightly delayed deposition of eggs while the female sought a favorable environment for them.

The development of a complex external male genitalium in the Poeciliidae is paralleled by anal-fin modification in the New World cyprinodontiform genera *Jenynsia* and *Anableps*, and by that in the Old World genus *Horaichthys*. Modifications associated with viviparity, which is only moderately developed in many poeciliids, are elaborate in the jenynsiids and anablepids as well as in the goodeids of the Mexican plateau. Facultative viviparity, such as that found in the poeciliid genus *Tomeurus*, is approached in *Horaichthys* and *Oryzias*. All other groups of cyprinodontiforms so far as known are oviparous. Hence, an analysis of poeciliid relationships might seem to hinge on the congruence of structure among the actually or potentially viviparous groups. In osteology, however, poeciliids appear to be as close to some oviparous cyprinodontiforms. Obviously, extinction has eliminated many transitional forms in the evolution of viviparous genera, and all the New World groups are now separated by rather abrupt gaps.

In gonopodial modifications poeciliids are most like the Indian genus *Horaichthys*, whereas in their ovarian adaptations for viviparity they are closest to *Anableps*. Resemblances between the probably primitive poeciliid genus *Brachyrhaphis* and the oviparous fundulin *Profundulus* are noted, as are striking similarities in the dorsicrania of *Xenodexia* and the Cyprinodontinae.

The possibility that the relationships of the family are reflected in the similarity between *Tomeurus* and the Old World genus *Horaichthys* is considered. Several major objections to an alliance between these genera are discounted. Nevertheless, it is concluded that present evidence for the affinities of the poeciliids with other Old World or New World cyprinodontiforms is equivocal.

In a check list and in a series of diagnoses and discussions, the supraspecific groupings of the Poeciliidae are analyzed from the standpoint of their natural classification and their zoogeography. The family is broadly defined, and its distribution is given.

The subfamily Tomeurinae is diagnosed, and the anatomy and biology of the single species *Tomeurus gracilis* Eigenmann from northern South America are reviewed in detail.

The sequence of the Poeciliinae is begun with the wide-ranging tribe Poeciliini in which the gonopodial suspensorium is only moderately specialized and the gonopodium is relatively short. The new name *Poecilia montana* is proposed, to resolve a case of homonymy involving an Antillean species. In the South American Cnesterodontini the gonopodium is shifted far forward, with

necessary suspensorial modification, and the gonopodium is elongate. The three remaining tribes are closely interrelated. All are largely Middle American, and all have well-developed supporting processes in the axial elements of their gonopodial suspensorium. The least specialized are the carnivorous Gambusiini, with the gut short and the gonopodium short or moderate. Three species are described as new: *Brachyrhaphis hartwegi*, *Gambusia luma*, and *Gambusia atrora*. The Girardinini have the gut long and coiled and the gonopodium long and complexly modified. The Heterandriini have comparable modifications, although the gonopodial tip is usually simpler, and they are unified by common suspensorial specializations.

A rediagnosis of the subfamily Xenodexiinae is based on osteological study of the single known central Guatemalan species, *Xenodexia ctenolepis* Hubbs. On the basis of skull and suspensorial characters and a unilateral pectoral clasper, perhaps used during mating, *Xenodexia* is regarded as representing a distinct subfamily. That *Xenodexia* may be allied to *Poeciliopsis* (tribe Heterandriini, subfamily Poeciliinae) is regarded as improbable.

The poeciliids have a principally neotropical distribution. They have radiated chiefly from Central America, with lesser centers in the extreme northern Andean region (the Heterandriini), the Brazilian region (the Cnesterodontini), and Mexico, from which a few species have filtered into the subtropical and temperate United States.

Reassessment of the old and new evidence supports the view that poeciliids and other cyprinodontiforms reached the West Indies by essentially fortuitous means; it is unnecessary to hypothesize a land bridge to explain their distribution. Species in each of the five tribes of the Poeciliinae are either euryhaline or can adapt to salt water. *Girardinus* and *Quintana*, endemic and probably old Antillean genera, are reputedly confined to fresh water. However, experiments designed and carried out to test the salt-tolerance of *Girardinus uninotatus* and *Quintana atrizona* showed them both to be highly tolerant to full-strength sea water, 37.6 parts per thousand and 34.4 parts per thousand, respectively. Although a land bridge to the Greater Antilles may never have existed, a chain of scattered islands may have provided refuge for seaborne waifs, perhaps affording a shoreline breeding habitat that would enhance the chances of further penetration toward the Greater Antilles.

Speculations for a relatively recent origin in the family of *Gambusia* and *Poecilia* are predicated on their present pandemic distributions, their speciose character, and the presence in each of many diversely specialized as well as generalized forms. The groups to which they belong, however, the Gambusiini and the Poeciliini, must be of rather old derivation, particularly the latter which include also three smaller and in some ways rather dissimilar genera.

ACKNOWLEDGMENTS

The assistance of many persons facilitated this work. For their generous and varied help we are greatly indebted to Dr. José Alvarez, Dr. James W. Atz, Mrs. Marian K. Bailey, Dr. James E. Böhlke, Dr. Charles M. Breder, Jr., Mrs. Lillian Dempster, Mrs. Myvanwy Dick, Miss Mary G. Dromi, Mr. William I. Follett, the late Dr. Myron Gordon, Mrs. Marion Grey, Drs. P. H. Greenwood, Norman E. Hartweg, Caryl P. Haskins, Prof. Luis Howell-Rivero, Dr. Carl L. Hubbs, Mr. Howard Huddle, Dr. Klaus D. Kallman, Mr. Robert Kanazawa, Dr. Ernest A. Lachner, Mr. R. Elwood Logan, Drs. Giles Mead, Robert R. Miller, George S. Myers, Ross F. Nigrelli, Edward C. Raney, Prof. Luis R. Rivas, Mrs. Carmela B. Rosen, Miss Suzanne Runyan, Mr. Daniel Sable, Drs. Leonard P. Schultz, R. Jack Schultz, C. Lavett Smith, Mr. Ross Socolof, Miss Pearl Sonada, the late Miss Margaret Storey, Drs. Laurence C. Stuart, William Ralph Taylor, Ethelwyn Trewavas, Boyd W. Walker, Miss Margaret Wilson, and Messrs. Gene Wolfsheimer and Loren P. Woods.

The work was carried out in the facilities of the American Museum of Natural History, the Museum of Zoology of the University of

Michigan, the Genetics Laboratory of the New York Zoological Society, and the Florida State Museum of the University of Florida.

Partial financial support of the work was provided by a National Science Foundation grant to the New York Zoological Society, Dr. Myron Gordon, principal investigator (Project: "A Biological Synthesis of the Poeciliid Fishes"), a National Science Foundation post-doctoral fellowship, 1959, to Rosen, and research funds of the Florida State Museum of the University of Florida, of which Rosen is presently a research associate.

LITERATURE CITED

AGASSIZ, J. L. R.

1853. Recent researches of Professor Agassiz. [Extract from a letter to J. D. Dana dated Cambridge, June 9, 1853, detailing some of the results of a rapid tour from Charleston, South Carolina, through Alabama, Mississippi, and Louisiana, thence up the Mississippi to St. Louis, Chicago, and along by the Great Lakes to New York and Massachusetts.] Amer. Jour. Sci., vol. 16, pp. 134–136.

1855. Remarks on Dr. B. Dowler's paper "Discovery of viviparous fish in Louisiana." Amer. Jour. Sci. Arts, ser. 2, vol. 19, pp. 133–136.

AHL, E.

1923. *Gambusia modesta*, sp. n. Bl. Aquar. Terrarienk., vol. 34, no. 10, pp. 220–221.

1925. *Gambusia Myersi* E. Ahl nom. nov. *Ibid.*, vol. 36, pp. 42–43.

ALVAREZ, J.

1948a. Contribución al conocimiento del genero *Priapella* y descripción de una nueva especie (Pisces, Poeciliidae). Rev. Soc. Mexicana Hist. Nat., vol. 9, nos. 3–4, pp. 331–340.

1948b. Descripción de una nueva especie de *Mollienisia* capturada en Baños del Azufre, Tabasco (Pisces, Poeciliidae). An. Esc. Nac. Cien. Biol., vol. 5, nos. 3–4, pp. 275–281.

1952a. Cuatro especies nuevas de peces dulcaecuicolas del sureste de Mexico. Ciencia, vol. 11, nos. 10–12, pp. 281–289.

1952b. Dicerophallini, nueva tribu de Poeciliidae de Chiapas. *Ibid.*, vol. 12, nos. 3–4, pp. 95–97.

1959. Nuevas especies de *Xiphophorus* e *Hyporamphus* procedents del Río Coatzacoalcos. *Ibid.*, vol. 19, pp. 69–73.

ALVAREZ, J., AND F. AGUILLAR

1957. Contribución al estudio de la suspensión gonopodica del genero *Poeciliopsis* con descripción de una nueva especie fosil procedente de El Salvador, Centro America. Rev. Soc. Mexicana Hist. Nat., vol. 18, nos. 1–4, pp. 153–172.

AMEMIYA, I., AND S. MURAYAMA

1931. Some remarks on the existence of developing embryos in the body of an oviparous cyprinodont, *Oryzias* (*Aplocheilus*) *latipes* (Temminck et Schlegel). Proc. Imp. Acad. Japan, vol. 7, no. 4, pp. 176–178.

ARONOWITZ, O., R. F. NIGRELLI, AND M. GORDON

1951. A spontaneous epithelioma in the platyfish, *Xiphophorus* (*Platypoecilus*) *variatus*. Zoologica, vol. 36, pt. 4, pp. 239–242.

BAILEY, R. M., AND R. R. MILLER

1950. *Mollienesia* versus *Mollienisia* as the name for a genus of poeciliid fishes. Copeia, no. 4, p. 318.

BAIRD, S. F., AND C. GIRARD

1853. Descriptions of new species of fishes collected by Mr. John H. Clark, on the U. S. and Mexican Boundary Survey, under Lt. Col. Jas. D. Graham. Proc. Acad. Nat. Sci. Philadelphia, vol. 6 (1852–1853), pp. 387–390.

BAKER, J. A., AND M. S. FERGUSON

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

BARNEY, R. L., AND B. J. ANSON

1921. The seasonal abundance of the mosquito-destroying top-minnow, *Gambusia affinis*, especially in relation to fecundity. Anat. Rec., vol. 22, no. 5, pp. 317–330.

BEHRE, E. H.

1928. A list of the fresh water fishes of western Panama between long. 81° 45′ and 83° 15′ W. Ann. Carnegie Mus., vol. 18, no. 2, pp. 305–328.

BERG, C.

1897. Contribuciónes al conocimiento de los peces Sud-americanos, especialmente de los de la República Argentina. An. Mus. Nac. Buenos Aires, ser. 2, vol. 2, 1896–1897, pp. 263–302.

BIGELOW, H. B., AND W. C. SCHROEDER

1953. Fishes of the Gulf of Maine. Fish. Bull. 74, U. S. Fish and Wildlife Serv., vol. 53, pp. i-viii, 1–577.

BLEEKER, P.

1859. Conspectus systematis cyprinorum. Natuurwetensch. Tijdschr. Nederlandsch-Indië, ser. 4, vol. 20, pp. 421–441.

1860. Ichthyologiae Archipelagi Indici. Vol. II. Cyprini. Acta Soc. Indo-Neerlandicae (Verhandel. K. Natuur. Ver. Nederlandsch-Indië), vol. 7, 492 pp.

BLOCH, M. E., AND J. O. G. SCHNEIDER
1801. Systema ichthyologiae. Berlin, vols. 1, 2, 584 pp.

BOESEMAN, M.
1952. A preliminary list of Surinam fishes not included in Eigenmann's enumeration of 1912. Zool. Meded., vol. 31, no. 17, pp. 179–200.

BOND, J.
1962. Seventh supplement to the check-list of birds of the West Indies (1956). Philadelphia, Academy of Natural Sciences of Philadelphia, pp. 1–11.

BONNER, J. T.
1952. Morphogenesis. An essay on development. Princeton, New Jersey, Princeton University Press, 296 pp.

BOULENGER, E. G.
1912. Notes on the breeding habits of the "Millions" fish (*Girardinus poeciloides*). Proc. Zool. Soc. London, vol. 11, pp. 906–908.

BOULENGER, G. A.
1889. Descriptions of a new snake and two new fishes obtained by Dr. H. von Ihering in Brazil. Ann. Mag. Nat. Hist., ser. 6, vol. 4, no. 22, pp. 265–267.
1897. Viaggio del Dott. Alfredo Borelli nel Chaco Boliviano e nella Repubblica Argentina. III. Poissons. Boll. Mus. Zool. Anat. Comp. Torino, vol. 12, no. 279, pp. 1–4.
1898. Viaggio del Dr. Enrico Festa nell' Ecuador e regioni vicine. Poissons de l'Equateur (Première partie). *Ibid.*, vol. 13, no. 329, pp. 1–13.

BREDER, C. M., JR.
1933. The fishes of Barro Colorado, Gatun Lake, Panama. Zoologica, vol. 9, no. 16, pp. 565–572.
1934. A new *Gambusia* from Andros Island, Bahamas. Amer. Mus. Novitates, no. 719, pp. 1–3.

BRIND, W. L.
1914. Domesticated fish. Part 2. New York, privately printed, pp. 16–22.
1919. *Platypoecilus maculatus*. Aquatic Life, vol. 4, pp. 167–168.

BUEN, F. DE
1940. Sobre una colección de peces de los lagos de Patzcuaro y Cuitzeo. Ciencia, vol. 1, pp. 306–308.
1943a. *Mollienisia sphenops pallida* de Buen, nov. subsp. An. Inst. Biol. Mexico, vol. 14, pp. 251–259.
1943b. *Poeciliopsis* en las cuencas de los Ríos Lerma y Marques, con descripción de dos nuevas especies. *Ibid.*, vol. 14, pp. 261–283.

CAMPO, R. M. DEL
1938. Nota acerca de algunos peces del Lago de Catemaco. An. Inst. Biol. Mexico, vol. 9, nos. 1, 2, pp. 225–226.

CARR, A. F., JR., AND L. GIOVANNOLI
1950. The fishes of the Choluteca drainage of southern Honduras. Occas. Papers Mus. Zool. Univ. Michigan, no. 523, pp. 1–38.

CHAVIN, W.
1956. Pituitary-adrenal control of melanization in xanthic goldfish, *Carassius auratus* L. Jour. Exp. Zool., vol. 133, pp. 1–45.

CLARK, E., L. R. ARONSON, AND M. GORDON
1949. The role of the distal tip of the gonopodium during the copulatory act of the viviparous teleost, *Platypoecilus maculatus*. Bull. Ecol. Soc. Amer., vol. 31, no. 4, p. 64. [Abstract.]
1954. Mating behavior patterns in two sympatric species of xiphophorin fishes: their inheritance and significance in sexual isolation. Bull. Amer. Mus. Nat. Hist., vol. 103, art. 2, pp. 135–226.

CLARK, E., AND R. P. KAMRIN
1951. The role of the pelvic fins in the copulatory act of certain poeciliid fishes. Amer. Mus. Novitates, no. 1509, pp. 1–14.

COPE, E. D.
1870. Partial synopsis of the freshwater fishes of North Carolina. Proc. Amer. Phil. Soc., vol. 11, pp. 448–495.
1880. On the zoological position of Texas. Bull. U. S. Natl. Mus., vol. 17, pp. 1–51.
1894. On the fishes obtained by the Naturalist expedition in Rio Grande do Sul. Proc. Amer. Phil. Soc., vol. 33, pp. 84–108.

CUMMINGS, J. B.
1943. Morphogenesis of the gonopodium in *Mollienisia latipinna*. Jour. Morph., vol. 73, no. 1, pp. 1–17.

CUVIER, M. LE B., AND M. A. VALENCIENNES
1846. Histoire naturelle des poissons. Paris, vol. 18, 505 pp.

DARLINGTON, P. J., JR.
1957. Zoogeography: the geographical distribution of animals. New York, John Wiley and Sons, Inc., 675 pp.

DARNELL, R. M.
1962. Fishes of the Río Tamesí and related coastal lagoons in east-central Mexico. Publ. Inst. Marine Sci., Univ. Texas, vol. 8, pp. 299–365.

DE BEER, G. R.
1937. The development of the vertebrate skull. Oxford, University Press, 552 pp.

DULZETTO, F.
1931. Sviluppo e struttura del gonopodio di *Gambusia holbrookii* (Grd.). Pubbl. Staz. Zool. Napoli, vol. 11, no. 1, pp. 62–85.

EIGENMANN, C. H.
1893. Catalogue of the fresh-water fishes of Central America and southern Mexico. Proc. U. S. Natl. Mus., vol. 16, pp. 53–60.
1894. Notes on some South American fishes. Ann. New York Acad. Sci., vol. 7, pp. 625–637.
1903. The fresh-water fishes of western Cuba. *Extracted from* U. S. Fish Comm. Bull., for 1902, vol. 22, pp. 211–236.
1907. The poeciliid fishes of Rio Grande do Sul and the La Plata Basin. Proc. U. S. Natl. Mus., vol. 32, pp. 425–433.
1909. Reports on the expedition to British Guiana of the Indiana University and the Carnegie Museum, 1908. Some new genera and species of fishes from British Guiana. Ann. Carnegie Mus., vol. 6, no. 1, pp. 4–54.
1910. Catalogue of the fresh-water fishes of tropical and south temperate America. *In* Scott, W. B., Reports of the Princeton University Expeditions to Patagonia 1896–1899. Leipzig, vol. 3, pt. 2, Zoology, pt. 4, pp. 375–511.
1912. Some results of an ichthyological reconnaissance of Colombia, South America. Indiana Univ. Studies, vol. 1, no. 8, pp. 1–27.

EIGENMANN, C. H., AND R. S. EIGENMANN
1891. A catalogue of the freshwater fishes of South America. Proc. U. S. Natl. Mus., vol. 14, no. 842, pp. 1–81.

EIGENMANN, C. H., A. HENN, AND C. WILSON
1914. New fishes from western Colombia, Ecuador and Peru. Indiana Univ. Studies, no. 19, pp. 1–15.

EIGENMANN, C. H., AND A. A. NORRIS
1900. Sobre alguns peixes de São Paulo, Brazil. Rev. Mus. Paulista, vol. 4, pp. 349–362.

ESSENBERG, J. M.
1923. Sex-differentiation in the viviparous teleost, *Xiphophorus helleri* Heckel. Biol. Bull., vol. 45, pp. 46–77.

EVERMANN, B. W., AND H. W. CLARK
1906. New fishes from Santo Domingo. Proc. U. S. Natl. Mus., vol. 30, no. 1478, pp. 851–855.

EVERMANN, B. W., AND W. C. KENDALL
1894. The fishes of Texas and the Rio Grande basin, considered chiefly with reference to their geographical distribution. Bull. U. S. Fish Comm., vol. 12 (for 1892), pp. 57–126.

FILIPPI, F. DE
1861. Note zoologiche. Arch. Zool. Anat. Fisiol., vol. 1, no. 1, pp. 52–76.

FONTAINE, P. A.
1945. Rare guppy reproduction. Aquarium, vol. 13, no. 11, p. 179.

FOWLER, H. W.
1916a. Cold-blooded vertebrates from Costa Rica and the Canal Zone. Proc. Acad. Nat. Sci. Philadelphia, vol. 68, no. 3, pp. 389–414.
1916b. Notes on fishes of the orders Haplomi and Microcyprini. *Ibid.*, vol. 68, no. 3, pp. 415–439.
1920. A list of the fishes of New Jersey. Proc. Biol. Soc. Washington, vol. 33, pp. 139–170.
1923. Fishes from Nicaragua. Proc. Acad. Nat. Sci. Philadelphia, vol. 75, pp. 23–32.
1932. Notes on fresh water fishes from Central America. *Ibid.*, vol. 84, pp. 379–385.
1943. A new poeciliid fish from Honduras. Notulae Nat., no. 117, pp. 1–3.
1949. Results of the two Carpenter African Expeditions, 1946–1948. Part 2.—The fishes. Proc. Acad. Nat. Sci. Philadelphia, vol. 101, pp. 233–275.
1950. Colombian zoological survey. Pt. VI.—Fishes obtained at Totumo, Colombia, with descriptions of two new species. Notulae Nat., no. 222, pp. 1–8.
1954. Os peixes de agua doce do Brasil. Arq. Zool. Estado de São Paulo, vol. 9, pp. 1–400.

FROST, G. A.
1926. A comparative study of the otoliths of the neopterygian fishes (continued)—Orders Haplomi, Heteromi, Iniomi, Lyomeri, Hypostomides, Salmopercae, Synentognathi, Microcyprini, Solenichthyes. Ann. Mag. Nat. Hist., ser. 9, vol. 18, pp. 465–490.

GARDINER, B. G.
1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. Bull. Brit. Mus. (Nat. Hist.), Geol., vol. 4, no. 7, pp. 241–384.

GARMAN, S.
1895. The cyprinodonts. Mem. Mus. Comp. Zoöl., vol. 19, no. 1, pp. 1–179.
1896. Cross fertilization and sexual rights

and lefts among vertebrates. Amer. Nat., vol. 30, p. 232.

GEISER, S. W.
1923. Notes relative to the species of *Gambusia* in the United States. Amer. Midland Nat., vol. 8, nos. 8–9, pp. 175–188.
1924. Sex-ratios and spermatogenesis in the top-minnow, *Gambusia holbrooki* Grd. Biol. Bull., vol. 47, pp. 175–213.

GILL, T.
1876. Notes on fishes from the Isthmus of Panama collected by Dr. J. F. Bransford, U.S.N. Proc. Acad. Nat. Sci. Philadelphia, vol. 28, pp. 335–336.

GIRARD, C.
1859a. Ichthyology of the boundary. *In* United States and Mexican boundary survey, under the order of Lieut. Col. W. H. Emory, Major First Cavalry, and United States Commissioner. Washington, vol. 2, pt. 2, pp. 1–85.
1859b. Ichthyological notices. Proc. Acad. Nat. Sci. Philadelphia, vol. 11, pp. 56–68.
1859c. Ichthyological notices. *Ibid.*, vol. 11, pp. 113–122.

GISTL, J. VON N. F. X.
1848. Naturegeschichte des Thierreichs für höhere Schulen. Stuttgart, pp. i-xvi, 1–216 [4]. [Not seen.]

GOODRICH, E. W.
1930. Studies on the structure and development of vertebrates. New York, Dover Publications, pt. 1, pp. 1–485; pt. 2, pp. 486–837. [Reprinted, 1958.]

GORDON, M.
1932a. Dr. Myron Gordon going on expedition. Aquatic Life, vol. 15, pp. 287–288.
1932b. How fishes get their names. Fish Cult., vol. 12, pp. 87–92.
1940. The ecological isolation factor involved in the failure of *Platypoecilus* and *Xiphophorus* to hybridize in nature. Anat. Rec., vol. 78, no. 4, pp. 171–172. [Abstract.]
1952. Sex determination in *Xiphophorus* (*Platypoecilus*) *maculatus*. III. Differentiation of gonads in platyfish from broods having sex ratios of three females to one male. Zoologica, vol. 37, pt. 2, pp. 91–100.
1953. The use of fishes in the evaluation of heredity in atypical pigment cell growth. Trans. New York Acad. Sci., ser. 2, vol. 15, pp. 192–195.
1955. Those puzzling "little toms." Animal Kingdom, pp. 50–55.

GORDON, M., AND D. E. ROSEN
1951. Genetics of species differences in the morphology of the male genitalia of xiphophorin fishes. Bull. Amer. Mus. Nat. Hist., vol. 95, art. 7, pp. 409–464.

GOSLINE, W. A.
1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus *Fundulus*. Occas. Papers Mus. Zool. Univ. Michigan, no. 519, pp. 1–17.

GOSSE, P. H.
1851. A naturalist's sojourn in Jamaica. London, Longman, Brown, Green, and Longmans, 502 pp.

GREGORY, W. K.
1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Amer. Phil. Soc., vol. 23, art. 2, pp. 75–481.

GREY, M.
1947. Catalogue of type specimens of fishes in Chicago Natural History Museum. Fieldiana: Zool., vol. 32, no. 3, pp. 107–205.

GROBSTEIN, C.
1940. Endocrine and developmental studies of gonopod differentiation in certain poeciliid fishes. I. The structure and development of the gonopod in *Platypoecilus maculatus*. Univ. California Publ. Zool., vol. 47, no. 1, pp. 1–22.

GÜNTHER, A.
1866. A catalogue of the fishes in the British Museum. London, vol. 6, 368 pp.
1868. An account of the fishes of the states of Central America, based on collections made by Capt. J. M. Dow, F. Godman, Esq. and O. Salvin, Esq. Trans. Zool. Soc. London, vol. 6, pt. 7, pp. 377–494.
1874. Descriptions of new species of fishes in the British Museum. Ann. Mag. Nat. Hist., ser. 4, vol. 14, pp. 368–371.

GUICHENOT, A.
1853. Zoologie. Poissons. *In* Ramón de la Sagra, D., Histoire physique, politique et naturelle de l'Île de Cuba. Paris, vol. 2, 206 pp.
1855. Atlas (Pisces). *In* Ramón de la Sagra, D., Histoire physique, politique et naturelle de l'Île de Cuba. Paris [to accompany vol. 2, Zoologie, Poissons, 1853].

GUIMARAES, J. R. A.
1930. Evolução dos poeciliideos (guarú-guarú ou barrigudinho). Rev. Indus. Animal, São Paulo, vol. 1, no. 7, pp. 783–791.

HAGAN, H. R.
1951. Embryology of the viviparous insects. New York, Ronald Press Co., 472 pp.

HARLEMAN, G. P. VON
1916–1917. Holbrook's gambusia. Aquatic Life, vol. 2, no. 7, March, 1917, pp. 99–100.

HARRINGTON, R. W., JR.
1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonymy of teleost skull bones. Copeia, no. 4, pp. 267–290.

HASEMAN, J. D.
1911. Some new species of fishes from the Rio Iguassú. Ann. Carnegie Mus., vol. 7, nos. 3–4, pp. 374–387.

HASKINS, C. P., E. F. HASKINS, AND R. E. HEWITT
1960. Pseudogamy as an evolutionary factor in the poeciliid fish *Mollienisia formosa*. Evolution, vol. 14, pp. 473–483.

HECKEL, J.
1848. Eine neue Gattung von Poecilien mit rochenartigem Anklammerungs-Organe. Sitzber. K. Akad. Wiss. Wien, Math. Nat. Cl., vol. 1, pp. 289–303.

HENN, A. W.
1916. On various South American poeciliid fishes. Ann. Carnegie Mus., vol. 10, nos. 1–2, art. 9, pp. 93–142.

HENSEL, R.
1868. Beiträge zur Kenntniss der Wirbelthiere Sudbrasiliens. (Contribution to the knowledge of the vertebrates of southern Brazil.) Arch. f. Naturgesch., vol. 34, pp. 356–375.

HILDEBRAND, S. F.
1917. Notes on the life history of the minnows *Gambusia affinis* and *Cyprinodon variegatus*. Rept. U. S. Comm. Fish., 1917, app. 6, pp. 3–14.
1925. Fishes of the Republic of El Salvador, Central America. Bull. Bur. Fish., Washington, vol. 41, doc. no. 985, pp. 237–287.
1938. A new catalogue of the fresh-water fishes of Panama. Field Mus. Nat. Hist., zool. ser., vol. 22, no. 4, pp. 217–359.

HILGENDORF, F.
1889. Fischsammlung von Haiti, welche 2 neue Arten, *Poecilia* (subg. n. *Acropoecilia*) *tridens* und *Eleotris maltzani*, enthält. Sitzber. Gesell. Naturf. Fr. Berlin, no. 2, pp. 51–55.

HOLMBERG, E. L.
1884. Peces. *In* Holmberg, E. L., Viajes á las Sierras del Toldil y de La Tinto. Actas Acad. Nac. Cien. Exactas Córdoba, vol. 5, no. 2, pp. 99–108.

HOPPER, A. F.
1949. Development and regeneration of the anal fin of normal and castrate males and females of *Lebistes reticulatus*. Jour. Exp. Zool., vol. 10, no. 2, pp. 299–318.

HOUSSAY, B. A.
1930. Acción sexual de la hipófisis en los peces y reptiles. Rev. Soc. Argentina Biol., vol. 6, pp. 686–688.
1931. Action sexuelle de l'hypophyse sur les poissons et les reptiles. Compte Rendus Soc. Biol., Paris, vol. 106, pp. 377–378.

HOWELL-RIVERO, L., AND C. L. HUBBS
1936. Studies of the fishes of the order Cyprinodontes. XV. The characters and relationships of *Furcipenis huberi* and *Alfaro cultratus*. Occas. Papers Mus. Zool. Univ. Michigan, no. 339, pp. 1–11.

HOWELL-RIVERO, L., AND L. R. RIVAS
1944. Studies of cyprinodont fishes. Two new genera of the tribe Girardinini, from Cuba. Torreia, no. 12, pp. 3–19.

HUBBS, C.
1957. *Gambusia heterochir*, a new poeciliid fish from Texas, with an account of its hybridization with *G. affinis*. Tulane Studies Zool., vol. 5, no. 1, pp. 3–16.
1958. *Gambusia senilis* from the Devil's River, Texas, an addition to the fish fauna of the United States. Copeia, no. 3, p. 239.

HUBBS, C., G. E. DREWRY, AND B. WARBURTON
1959. Occurrence and morphology of a phenotypic male of a gynogenetic fish. Science, vol. 129, pp. 1227–1229.

HUBBS, C., AND V. G. SPRINGER
1957. A revision of the *Gambusia nobilis* species group, with descriptions of three new species, and notes on their variation, ecology, and evolution. Texas Jour. Sci., vol. 9, no. 3, pp. 279–327.

HUBBS, C. L.
1924. Studies of the fishes of the order Cyprinodontes. Misc. Publ. Mus. Zool. Univ. Michigan, no. 13, pp. 1–31.
1926. Studies of the fishes of the order Cyprinodontes. VI. *Ibid.*, no. 16, pp. 1–86.
1927. Studies of the fishes of the order Cyprinodontes. VII. *G. manni*, a new species from the Bahamas. Copeia, no. 164, pp. 61–65.
1929. Studies of the fishes of the order Cyprinodontes. VIII. *Gambusia gaigei*, a new species from the Rio Grande. Occas. Papers Mus. Zool. Univ. Michigan, no. 198, pp. 1–11.
1931. Studies of the fishes of the order Cyprinodontes. IX. A new and primi-

tive genus of Poeciliidae from Central America. *Ibid.*, no. 230, pp. 1–3.

1933. Species and hybrids of *Mollienisia*. Aquarium, vol. 1, no. 10, pp. 263–268, 277.

1934. Studies of the fishes of the order Cyprinodontes. XIII. *Quintana atrizona*, a new poeciliid. Occas. Papers Mus. Zool. Univ. Michigan, no. 301, pp. 1–8.

1935a. Studies of the fishes of the order Cyprinodontes. XIV. *Plectrophallus* regarded as a distinct genus. *Ibid.*, no. 302, pp. 1–3.

1935b. Fresh-water fishes collected in British Honduras and Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, no. 28, pp. 1–22.

1936. Fishes of the Yucatan Peninsula. Publ. Carnegie Inst. Washington, no. 457, pp. 157–287.

1937. Fishes from the San Carlos Mountains. Univ. Michigan Studies, sci. ser., vol. 12, pp. 295–297.

1941. A new family of fishes. Jour. Bombay Nat. Hist. Soc., vol. 42, no. 2, pp. 446–447.

1950. Studies of cyprinodont fishes. XX. A new subfamily from Guatemala, with ctenoid scales and a unilateral pectoral clasper. Misc. Publ. Mus. Zool. Univ. Michigan, no. 78, pp. 1–28.

1955. Hybridization between fish species in nature. Syst. Zool., vol. 4, no. 1, pp. 1–20.

1961. Isolating mechanisms in the speciation of fishes. *In* Blair, William Frank, Vertebrate speciation, a University of Texas symposium. Austin, University of Texas Press, pp. 5–23.

HUBBS, C. L., AND M. GORDON

1943. Studies of cyprinodont fishes. XIX. *Xiphophorus pygmaeus*, new species from Mexico. Copeia, no. 1, pp. 31–33.

HUBBS, C. L., AND L. C. HUBBS

1932. Apparent parthenogenesis in nature, in a form of fish of hybrid origin. Science, vol. 76, no. 1983, pp. 628–630.

1945. Bilateral asymmetry and bilateral variation in fishes. Papers Michigan Acad. Sci., Arts, Lett., vol. 30 (1944), pp. 229–310.

1946. Experimental breeding of the Amazon molly. Aquarium Jour., Oct., 2 pp.

HUBBS, C. L., AND R. R. MILLER

1954. Studies of cyprinodont fishes. XXI. *Glaridodon latidens*, from northwestern Mexico, redescribed and referred to *Poeciliopsis*. Zoologica, vol. 39, no. 1, pp. 1–12.

HUMBOLDT, M. M. DE, AND M. A. VALENCIENNES

1821. Recherches sur les poissons fluviatiles d l'Amerique equinoxiale. *In* Humboldt, F. H. A. von, and A. J. A. Bonpland, Voyage aux régions equinoxiales du nouveau continent, fait en 1799–1804. Pt. 2, Recueil d'observations de zoologie et d'anatomie comparée. Paris, vol. 2, no. 4, pp. 145–216.

IHERING, H. VON

1883. Zur Kenntnis der Gattung *Girardinus*. Zeitschr. f. Wiss. Zool., vol. 38, pp. 468–490.

IHERING, R. VON

1930. Notas ecologicas referentes a peixes d'agua doce do Estado de S. Paulo e descripçao de 4 especies novas. Arch. Inst. Biol. São Paulo, vol. 3, pp. 93–104.

1931. Cyprinodontes Brasileiros (Peixes "Guarús"). Systematica e informacões biologicas. I. *Ibid.*, vol. 4, pp. 243–280.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

1959. Opinion 569. Use of the plenary powers to set aside first reviser selections made for the generic name *Selene* Lacépède, 1803, and for the specific names *rostrata* LeSueur, 1817 (*Muraena*); *latipinna* LeSueur, 1821 (*Mollienesia*); and *fuscus* Storer, 1839 (*Syngnathus*) (class Pisces). Bull. Zool. Nomenclature, vol. 17, pp. 92–94.

JENYNS, L.

1843. Fish. *In* Darwin, Charles (ed.), The zoology of the voyage of H.M.S. "Beagle," during the years 1832–1836. London, pt. 4, 172 pp.

JORDAN, D. S.

1878. A catalogue of the fishes of the fresh-waters of North America. Bull. U. S. Geol. and Geogr. Surv. Territories, vol. 4, pp. 407–442.

1883. Description of a new cyprinodont (*Zygonectes inurus*) from southern Illinois. Proc. U. S. Natl. Mus., vol. 5 (for 1882), pp. 143–144.

1885. List of fishes collected in Lake Jessup and Indian River, Florida, by Mr. R. E. Earll, with descriptions of two new species. *Ibid.*, vol. 7 (for 1884), pp. 322–332.

1887. A preliminary list of the fishes of the West Indies. *Ibid.*, vol. 9 (for 1886), pp. 561–576.

1889. List of fishes collected by Alphonse Forrer about Mazatlan, with descrip-

tion of two new species—*Heros beani* and *Poecilia butleri*. *Ibid.*, vol. 11 (for 1888), pp. 329–334.

1895. The fishes of Sinaloa. Proc. California Acad. Sci., ser. 2, vol. 5, pt. 1, pp. 377–514.

JORDAN, D. S., AND A. W. BRAYTON

1878. On the distribution of the fishes of the Allegheny region of South Carolina, Georgia, and Tennessee, with descriptions of new or little known species. Contributions to North American ichthyology, III. B. *In* Contributions to North American ichthyology. Based primarily on the collections of the U. S. National Museum. Bull. U. S. Natl. Mus., no 12, pp. 1–95.

JORDAN, D. S., AND H. E. Copeland

1876. Check list of the fishes of the fresh waters of North America. Bull. Buffalo Soc. Nat. Sci., vol. 3, pp. 133–164.

JORDAN, D. S., AND B. W. EVERMANN

1896–1900. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Bull. U. S. Natl. Mus., no. 47, pts. 1–4, pp. i–lx, 1–3313.

JORDAN, D. S., B. W. EVERMANN, AND H. W. CLARK

1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rept. U. S. Comm. Fish., for 1928, app. 10, 670 pp.

JORDAN, D. S., AND C. H. GILBERT

1883. Synopsis of the fishes of North America. Bull. U. S. Natl. Mus., no. 16 (for 1882), pp. 1–1018.

JORDAN, D. W., AND J. O. SNYDER

1900. Notes on a collection of fishes from the rivers of Mexico, with description of twenty new species. Bull. U. S. Fish Comm., for 1899, pp. 115–147.

KALLMAN, K. D.

1962. Gynogenesis in the teleost, *Mollienesia formosa* (Girard), with a discussion of the detection of parthenogenesis in vertebrates by tissue transplantation. Jour. Genetics, vol. 58, no. 1, pp. 7–21.

KNER, R.

1860. Über *Belonesox belizanus*, nov. gen. et spec. aus der Familie der Cyprinodonten. Sitzber. K. Akad. Wiss. Wien, Math. Nat. Cl., vol. 40, no. 10, pp. 419–422.

KNER, R., AND F. STEINDACHNER

1864. Neue Gattungen und Arten von Fischen aus Central-Amerika; gesammelt von Prof. Moritz Wagner. Abhandl. Bayerischen Akad. Wiss., Math. Phys. Cl., vol. 10, no. 1, pp. 1–62.

KOSSWIG, C.

1948. Homologe und analoge Gene. Commun. Fac. Sci. Univ. Ankara, vol. 1, pp. 127–177.

1959. Phylogenetische Trends genetisch betrachtet. Zool. Anz., vol. 162, no. 7/8, pp. 208–221.

KOSTER, W. J.

1957. Guide to the fishes of New Mexico. Albuquerque, University of New Mexico Press, pp. i–vii, 1–116.

KRUMHOLZ, L. A.

1948. Reproduction in the western mosquitofish, *Gambusia affinis affinis* (Baird & Girard), and its use in mosquito control. Ecol. Monogr., vol. 18, no 1, pp. 1–43.

KULKARNI, C. V.

1940. On the systematic position, structural modifications, bionomics and development of a remarkable new family of cyprinodont fishes from the province of Bombay. Rec. Indian Mus., vol. 42, pt. 2, pp. 379–423.

1948. The osteology of Indian cyprinodonts. Part I.—Comparative study of the head skeleton of *Aplocheilus*, *Oryzias* and *Horaichthys*. Proc. Natl. Inst. Sci. India, vol. 14, no. 2, pp. 65–119.

LAHILLE, F.

1895. Faunas locales Argentinas. I. Lista de los pescados recogidos en los alrededores de la Plata (Provincia de Buenos Aires). Rev. Mus. La Plata, vol. 6, pp. 267–276.

LANGER, W. F.

1913. Beiträge zur Morphologie der viviparen Cyprinodontiden. Morph. Jahrb., Leipzig, vol. 47, pp. 193–307.

LESUEUR, C. A.

1821. Description of a new genus, and several species of fresh water fish, indigenous to the United States. Jour. Acad. Nat. Sci. Philadelphia, vol. 2, pt. 1, pp. 2–8.

LIDTH DE JEUDE, T. W. VAN

1887. On a collection of reptiles and fishes from the West Indies. Notes Leyden Mus., vol. 9, pp. 129–139.

LINDBERG, G.

1934. [The systematics of *Gambusia*.] Mag. Parasit. Leningrad, vol. 4, pp. 351–367. [In Russian.]

MAYER, F.
1948. A contribution to the *Micropoecilia* problem. Aquarium, pp. 172–174.

MAYR, E.
1942. Systematics and the origin of species. New York, Columbia University Press, 334 pp.

MEEK, S. E.
1902. A contribution to the ichthyology of Mexico. Publ. Field Columbian Mus., zool. ser., vol. 3, no. 6, pp. 63–128.
1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec. *Ibid.*, zool. ser., vol. 5, pp. v–lxiii, 1–252.
1907. Notes on freshwater fishes from Mexico and Central America. *Ibid.*, zool. ser., vol. 7, no. 5, pp. 133–157.
1909. New species of fishes from tropical America. *Ibid.*, zool ser., vol. 7, no. 7, pp. 207–211.
1912. New species of fishes from Costa Rica. *Ibid.*, zool. ser., vol. 10, no. 7, pp. 69–75.
1914. An annotated list of fishes known to occur in the fresh waters of Costa Rica. *Ibid.*, zool. ser., vol. 10, no. 10, pp. 101–134.

MEEK, S. E., AND S. F. HILDEBRAND
1913. New species of fishes from Panama. Publ. Field Mus. Nat. Hist., zool. ser., vol. 10, no. 8, pp. 77–91.
1916. The fishes of the fresh waters of Panama. *Ibid.*, zool. ser., vol. 10, no. 15, pp. 217–374.

MEINKEN, H.
1934. Über einige, in letzter Zeit eingeführte Fische III. 9. *Platypoecilus maculatus* Günther var. *cyanellus* n. var. Der "Blanue Platy." Bl. Aquar. Terrarienk., vol. 45, no. 14, pp. 261–263.

MEYER, H.
1938. Investigations concerning the reproductive behavior of *Mollienisia "formosa."* Jour. Genetics, vol. 36, pp. 329–366.

MILES, C. W.
1943. Estudio economico y ecologico de los peces de agua dulce del Valle del Cauca. Publ. Sec. Agr. y Fom. Dept., Colombia, pp. 7–97.

MILEWSKI, A. W.
1920. Zur Biologie, Morphologie und Anatomie der lebendgebärenden Zahnkarpfen. Internatl. Rev. Ges. Hydrobiol. u. Hydrograph., vol. 8, pp. 592–625.

MILLER, N.
1907. The fishes of the Motagua River, Guatemala. Bull. Amer. Mus. Nat. Hist., vol. 23, art. 2, pp. 95–123.

MILLER, R. R.
1957. Utilization of X-rays as a tool in systematic zoology. Syst. Zool., vol. 6, no. 1, pp. 29–40.
1960. Four new species of viviparous fishes, genus *Poeciliopsis*, from northwestern Mexico. Occas. Papers Mus. Zool. Univ. Michigan, no. 619, pp. 1–11.

MILLER, R. R., AND W. L. MINCKLEY
1963. *Xiphophorus gordoni*, a new species of platyfish from Coahuila, Mexico. Copeia, no. 3, pp. 540–548.

MINCKLEY, W. L.
1962. Two new species of fishes of the genus *Gambusia* (Poeciliidae) from northeastern Mexico. Copeia, no. 2, pp. 391–396.

MIRANDA-RIBEIRO, A. DE
1905. Vertebrados do Itatiaya (peixes, serpentes, saurios, aves e mammiferos). Arch. Mus. Nac. Rio de Janeiro, vol. 13, pp. 167–190.

MOHSEN, T.
1960. Sur les variations de structures au niveau du système suspensorial du gonopode dans les différentes souches de *Lebistes reticulatus* R. Comptes Rendus Soc. Biol., Paris, vol. 155, no. 2, pp. 399–401.
1961a. Sur la prèsence d'un organe copulateur interne, très évolué chez *Skiffia lermae* (Cyprinodonte Goodeidae). Compte Rendus Acad. Sci., Paris, vol. 252, pp. 3327–3329.
1961b. Sur le dimorphisme sexuel et la présence d'un organe copulateur très évolué chez le cyprinodonte Goodeidae *Skiffia lermae* Meek. Ann. Fac. Sci. Univ. Dakar, vol. 6, pp. 163–180.
1962. Sur le dimorphisme sexuel au niveau de la nageoire anale et de son système suspensorial chez le cyprinodonte ovipare *Tomeurus gracilis* Eigenmann. Bull. Aquatic Biol., Amsterdam, vol. 3, no. 27, pp. 61–64.

MÜLLER, J., AND F. H. TROSCHEL
1844. Bericht über die zur Bekanntmachung geeigneten. Verhandlungen der Königl. Preuss. Akademie der Wissenschaften zu Berlin im Monat Februar 1844. Monatsber. K. Preussischen Akad. Wiss. Berlin, pp. 35–36.

MYERS, G. S.
1922. The aquarium and its denizens. Jersey City, New Jersey, Hudson County Aquarium Society, pp. 1–22.
1925. Results of some recent studies on the

American killifishes. Fish Cult., vol. 4, pp. 370–371.

1931. The primary groups of oviparous cyprinodont fishes. Univ. Ser. Stanford Univ. Publ. Biol. Sci., vol. 6, no. 3, pp. 243–254.

1935. An annotated list of the cyprinodont fishes of Hispaniola, with descriptions of two new species. Zoologica, vol. 10, no. 3, pp. 301–316.

1938. Fresh-water fishes and West Indian zoogeography. Ann. Rept. Smithsonian Inst., for 1937, pp. 339–364.

1947. The Amazon and its fishes. Aquar. Jour., vol. 18, no. 5, pp. 7–13.

NEEDHAM, J.

1942. Biochemistry and morphogenesis. Cambridge, Cambridge University Press, 787 pp.

NICHOLS, J. T.

1915. On *Heterandria zonata* sp. nov. and *Heterandria versicolor* (Günther) from the Island of Santo Domingo. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 20, pp. 603–604.

NICHOLS, J. T., AND G. S. MYERS

1923. A new *Limia* from San Domingo. Amer. Mus. Novitates, no. 79, 2 pp.

NIKOL'SKII, G. V.

1954 (1961). Chastnaya ikhtiologiya. (Special ichthyology). Translated from Russian by Israel Program for Scientific Translations. Jerusalem, second edition, 1961, 538 pp.

NORDEN, C. R.

1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny. Jour. Fish. Res. Bd. Canada, vol. 18, no. 5, pp. 679–791.

PELLEGRIN, J.

1901. Poissons recueillis par M. L. Diguet, dans l'État de Jalisco (Mexique). Bull. Mus. Natl. Hist. Nat., Paris, vol. 7, no. 5, pp. 204–207.

PERUGIA, A.

1891. Appunti sopra alcuni pesci sud-americani conservati nel Museo Civico di Storia Naturale di Genova. Ann. Mus. Civ. Stor. Nat. Genova, ser. 2, vol. 10, pp. 604–657.

PETERS, C. H.

1933. *Platypoecilia variatus* variations. Home Aquar. Bull., vol. 2, no. 12, pp. 9–10.

PETERS, W.

1859. Hr. W. Peters legte eine neue von Hrn. Jagor im atlantischen Meere gefangene Art der Gattung *Leptocephalus* vor und fügte Mittheilungen über einige andere neue Fische des zoologischen Museums hinzu. Monatsber. K. Preussischen Akad. Wiss., Berlin, pp. 411–412.

PHILIPPI, E.

1904. Ein neuer Fall von Arrhenoidie. Sitzber. Ber. Gesell. Naturf. Fr. Berlin, pp. 196–197.

1906. Kurzer Beitrag zur Kenntnis der Teleostiergenera *Glaridichthys* Garman und *Cnesterodon* Garman (Familie Cyprinodontidae s. Poeciliidae). *Ibid.*, no. 8, pp. 229–232.

1909. Fortpflanzungsgeschichte der viviparen Teleosteer *Glaridichthys januarius* und *G. decem-maculatus* in ihrem Einfluss auf Lebensweise, makroskopische und mikroskopische Anatomie. Zool. Jahrb., vol. 27, pp. 1–94.

PICKFORD, G. E., AND J. W. ATZ

1957. The physiology of the pituitary gland of fishes. New York, New York Zoological Society, 613 pp.

POEY, F.

1854. Los guajacones, pecesillos de agua dulce. *In* Poey, F., Memorias sobre la historia natural de la Isla de Cuba. Havana, vol. 1, pp. 374–392.

1860. Poissons de Cuba, espèces nouvelles. *In* Poey, F., Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios latinos y extractos en frances. Havana, vol. 2, pp. 115–356.

1868. Synopsis piscium cubensium. *In* Poey, F., Repertorio fisico-natural de la Isla de Cuba. Havana, vol. 2, pp. 279–484.

1876. Enumeratio piscium cubensium. An. Soc. Española Hist. Nat., Madrid, vol. 5, pt. 2, pp. 89–176.

RACHOW, A.

1932. *Mollienisia formosa* (Girard). Wochenschr. Aquar. Terrarienk., vol. 29, no. 45, pp. 705–707.

1936. Fam. Poeciliidae Unterfam.: Poeciliinae *Platypoecilus variatus* S. E. Meek. *In* Holly, Maximilian, Herm Meinken, and Arthur Rachow, Die Aquarienfische in Wort und Bild. Stuttgart, lief. 13–14, sheets 145–146 (18C, c. 16).

RAMASWAMI, L. S.

1945. The chondrocranium of *Gambusia* (Cyprinodontes) with an account of the osteocranium of the adult. Jour. Mysore Univ., sect. B, vol. 6, no. 1, pp. 19–45.

1946. A comparative account of the skull of *Gambusia*, *Oryzias*, *Aplocheilus* and

Xiphophorus (Cyprinodontes: Teleostomi). Spolia Zeylanica, vol. 24, pt. 3, pp. 101–192.

RAYNER, D. M.
1951. On the cranial structure of an early palaeoniscid, *Kentuckia*, gen. nov. Trans. Roy. Soc. Edinburgh, vol. 62, pt. 1, no. 3, pp. 53–83.

REGAN, C. T.
1904. Description of new or little-known fishes from Mexico and British Honduras. Ann. Mag. Nat. Hist., ser. 7, vol. 13, pp. 255–259.
1905. A collection of fishes made by Dr. H. Gadow in southern Mexico. *Ibid.*, ser. 7, vol. 16, pp. 361–363.
1906–1908. Pisces. *In* Godman, F. DuC., and O. Salvin, Biologia Centrali-Americana. London, pt. 193, pp. 1–203.
1907a. Diagnoses of new Central American freshwater fishes of the families Cyprinodontidae and Mugilidae. Ann. Mag. Nat. Hist., ser. 7, vol. 19, pp. 64–66.
1907b. Descriptions of six new freshwater fishes from Mexico and Central America. *Ibid.*, ser. 7, vol. 19, pp. 258–260.
1908. A collection of fresh water fishes made by Mr. C. F. Underwood in Costa Rica. *Ibid.*, ser. 8, vol. 2, pp. 455–464.
1909. Descriptions of three new freshwater fishes from South America presented to the British Museum by Herr J. Paul Arnold. *Ibid.*, ser. 8, vol. 3, pp. 234–235.
1911a. On some fishes of the family Poeciliidae. *Ibid.*, ser. 8, vol. 8, pp. 373–374.
1911b. A new poeciliid fish from the Amazon, with notes on the genera *Petalosoma* and *Tomeurus*. *Ibid.*, ser. 8, vol. 8, pp. 659–660.
1912. A revision of the poeciliid fishes of the genera *Rivulus*, *Pterolebias* and *Cynolebias*. *Ibid.*, ser. 8, vol. 10, pp. 494–509.
1913a. The fishes of the San Juan River, Colombia. *Ibid.*, ser. 8, vol. 12, pp. 462–473.
1913b. A revision of the cyprinodont fishes of the subfamily Poeciliinae. Proc. Zool. Soc. London, vol. 11, pp. 977–1018.
1914a. Description of a new cyprinodont fish of the genus *Mollienisia* from Yucatan. Ann. Mag. Nat. Hist., ser. 8, vol. 13, p. 338.
1914b. Descriptions of two new cyprinodont fishes from Mexico, presented to the British Museum by Herr A. Rachow. *Ibid.*, ser 8, vol. 14, pp. 65–67.

RIVAS, L. R.
1944a. Contributions to the study of the poeciliid fishes of Cuba. I. Descriptions of six new species of the subfamily Gambusiinae. Proc. New England Zool. Club, vol. 23, pp. 41–53.
1944b. Contribuciones al estudio de los peces Cubanos de la familia Poeciliidae. II. *Glaridichthys atherinoides*, nueva especie de la Provincia de Camaguey. Contrib. Ocas. Mus. Hist. Nat. Colegio "De La Salle," Havana, no. 2, pp. 1–7.
1958. The origin, evolution, dispersal, and geographical distribution of the Cuban poeciliid fishes of the tribe Girardinini. Proc. Amer. Phil. Soc., vol. 102, no. 3, pp. 281–320.
1962. *Cichlasoma pasionis*, a new species of cichlid fish of the *Thorichthys* group, from the Rio de la Pasion, Guatemala. Quart. Jour. Florida Acad. Sci., vol. 25, no. 2, pp. 147–156.
1963. Subgenera and species groups in the poeciliid fish genus *Gambusia* Poey. Copeia, no. 2, pp. 331–347.

RIVAS, L. R., AND G. S. MYERS
1950. A new genus of poeciliid fishes from Hispaniola, with notes on genera allied to *Poecilia* and *Mollienesia*. Copeia, no. 4, pp. 288–294.

ROSEN, D. E.
1952. A revision of the fishes of the subfamily Alfarinae in the family Poeciliidae. Zoologica, vol. 37, pt. 3, pp. 151–156.
1958. Evolutionary significance of the axial and appendicular skeletons of viviparous cyprinodonts (Pisces). Anat. Rec., vol. 132, no. 3, pp. 496–497.
1960. Middle-American poeciliid fishes of the genus *Xiphophorus*. Bull. Florida State Mus., biol. sci., vol. 5, no. 4, pp. 57–242.
1962a. Comments on the relationships of the North American cave fishes of the family Amblyopsidae. Amer. Mus. Novitates, no. 2109, 35 pp.
1962b. Egg retention: pattern in evolution. Nat. Hist., vol. 71, no. 10, pp. 46–53.

ROSEN, D. E., AND R. M. BAILEY
1959. Middle-American poeciliid fishes of the genera *Carlhubbsia* and *Phallichthys*, with descriptions of two new species. Zoologica, vol. 44, pt. 1, pp. 1–44.

ROSEN, D. E., AND M. GORDON
1951. A new fish of the genus *Gambusia* from southern Veracruz, Mexico, with a discussion of the tribe Gambusiini Hubbs. Zoologica, vol. 36, pt. 4, pp. 267–272.
1953. Functional anatomy and evolution of

male genitalia in poeciliid fishes. *Ibid.*, vol. 38, pt. 1, pp. 1–47.

ROSEN, D. E., AND K. D. KALLMAN
1959. Development and evolution of skeletal deletions in a family of viviparous fishes (Cyprinodontiformes, Poeciliidae). Quart. Jour. Florida Acad. Sci., vol. 22, no. 4, pp. 169–190.

ROSEN, D. E., AND A. TUCKER
1961. Evolution of secondary sexual characters and sexual behavior patterns in a family of viviparous fishes (Cyprinodontiformes: Poeciliidae). Copeia, no. 2, pp. 201–212.

SANDERS, M., AND M. G. SORET
1954. Cultivation of animal viruses in embryonic teleost cells. Trans. New York Acad. Sci., ser. 2, vol. 17, no. 1, pp. 19–25.

SANGSTER, W.
1948. A study of the quantitative effects of ethynyl testosterone upon the sword and gonopodium of *Xiphophorus hellerii*. Physiol. Zool., vol. 21, no. 2, pp. 134–147.

SANTA MARIA, M. A. DE
1956. Album de Don Carlos de la Torre y Huerta. Acuario, vol. 2, no. 4, pp. 94–97.

SCHINDLER, O.
1959. *Mollienisia sphenops petersi* nov. subsp. eine neue Poeciliiden-Unterart aus Nordwest-Honduras. Opuscula Zool., no. 31, pp. 1–6.

SCHREINER, C., AND A. DE MIRANDA-RIBEIRO
1903. A collecção de peixes do Museu Nacional do Rio de Janeiro. Arch. Mus. Nac. Rio de Janeiro, vol. 12, pp. 67–109.

SCRIMSHAW, N. S.
1944a. Embryonic growth in the viviparous poeciliid, *Heterandria formosa*. Biol. Bull., vol. 87, no. 1, pp. 37–51.
1944b. Superfetation in poeciliid fishes. Copeia, no. 3, pp. 180–183.
1945. Embryonic development in poeciliid fishes. Biol. Bull., vol. 88, no. 3, pp. 233–246.

ŞENGÜN, A.
1949. Experimente zur sexuell-mechanischen Isolation. II. Rev. Fac. Sci. Univ. Istanbul, ser. B, vol. 14, no. 2, pp. 114–128.

SMITH, C. L., AND R. M. BAILEY
1962. The subocular shelf of fishes. Jour. Morph., vol. 110, no. 1, pp. 1–18.

STARKS, E. C.
1904. A synopsis of characters of some fishes belonging to the order Haplomi. Biol. Bull., vol. 7, pp. 254–262.
1926. Bones of the ethmoid region of the fish skull. Univ. Ser. Stanford Univ. Publ. Biol. Sci., vol. 4, no. 3, pp. 139–338.

STEINDACHNER, F.
1863. Beiträge zur Kenntniss der Sciaenoiden Brasiliens und der Cyprinodonten Mejicos. Sitzber. K. Akad. Wiss. Wien, Math. Nat. Cl., vol. 48, no. 1, pp. 162–185.
1864. Beiträge zur Kenntniss der Chromiden Mexico's und Central-Amerika's. Denkschr. K. Akad. Wiss. Wien, vol. 23, pt. 2, pp. 57–74.
1878. Ichthyologische Beiträge (VI). Sitzber. K. Akad. Wiss. Wien, Math. Nat. Cl., vol. 77, no. 1, pp. 379–392.
1880. Zur Fisch-Fauna des Cauca und der Flüsse bei Guayaquil. Denkschr. K. Akad. Wiss. Wien, vol. 42, no. 1, pp. 55–103.

STOLL, N. R., AND OTHERS (EDS.)
1961. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. London.

STORER, D. H.
1846. A synopsis of the fishes of North America. Cambridge, Metcalf and Co., 298 pp.

STOYE, F. H.
1933. Einige neueingeführte Zahnkarpfen, I. Bl. Aquar. Terrarienk., vol. 44, no. 18, pp. 305–309.
1935. Tropical fishes for the home: their care and propagation. Second edition. New York, Carl Mertens, 284 pp.

TAUBLES, J.
1916. Community aquaria. Aquatic Life, vol. 2, p. 16.

THOMPSON, D. W.
1952. On growth and form. Second edition. Cambridge, Cambridge University Press, 2 vols., 1116 pp.

TREWAVAS, E.
1948. Cyprinodont fishes of San Domingo, Island of Haiti. Proc. Zool. Soc. London, vol. 118, pt. 2, pp. 408–415.

TRINKAUS, J. P., AND J. W. DRAKE
1952. Role of exogenous nutrients in development of the viviparous teleost, *Lebistes reticulatus*. Anat. Rec., vol. 112, no. 2, p. 435.

TROEMNER, J. L.
1943. Notes. Fish Cult., vol. 23, no. 1, pp. 1–3.

TROSCHEL, F. H.
1865. Systematisches Verzeichniss der Wirbelthiere Mexico. *In* Muller, J. W., Reisen

in den Vereinigten Staaten, Canada und Mexico. Leipzig, vol. 3, 109 pp.

TURNER, C. L.
1937. Reproductive cycles and superfetation in poeciliid fishes. Biol. Bull., vol. 72, no. 2, pp. 145–164.
1938. The reproductive cycle of *Brachyrhaphis episcopi*, an ovoviviparous poeciliid fish, in the natural tropical habitat. *Ibid.*, vol. 75, no. 1, pp. 56–65.
1939. The pseudo-amnion, pseudo-chorion, pseudo-placenta and other foetal structures in viviparous cyprinodont fishes. Science, vol. 90, no. 2324, pp. 42–43.
1940a. Superfetation in viviparous cyprinodont fishes. Copeia, no. 2, pp. 88–91.
1940b. Pseudoamnion, pseudochorion, and follicular pseudoplacenta in poeciliid fishes. Jour. Morph., vol. 67, no. 1, pp. 59–89.
1940c. Adaptations for viviparity in jenynsiid fishes. *Ibid.*, vol. 67, no. 2, pp. 291–296.
1941. Morphogenesis of the gonopodium in *Gambusia affinis affinis*. *Ibid.*, vol. 69, no. 1, pp. 161–185.
1942a. Morphogenesis of the gonopodial suspensorium in *Gambusia affinis* and the induction of male suspensorial characters in the female by androgenic hormones. Jour. Exp. Zool., vol. 91, no. 2, pp. 167–193.
1942b. Diversity of endocrine function in the reproduction of viviparous fishes. Amer. Nat., vol. 76, pp. 179–190.
1947. Viviparity in teleost fishes. Sci. Monthly, vol. 65, no. 6, pp. 508–518.
1950. Skeletal structure of the gonopodium and gonopodial suspensorium of *Anableps*. Jour. Morph., vol. 86, no. 2, pp. 329–365.

VERDOORN, F. (ED).
1945. Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. i–xxxvii, 1–381. [End papers, vegetation map.]

VIVIEN, J., AND T. MOHSEN
1951. Etapes de la différenciation sexuelle du suspensorium gonopodial chez *Xiphophorus helleri* H. Comptes Rendus Soc. Biol., Paris, vol. 145, pp. 1364–1368.

WHEELER, A. C., AND R. W. INGLE
1953. Fishes of the genus *Mollienesia*. Water Life, Oct., pp. 264–266.

WHITLEY, G. P.
1951. New fish names and records. Proc. Roy. Zool. Soc. New South Wales, for 1949–1950, pp. 61–68.

WICHAND, B.
1906. II. Neuimportierte bezw. erstmalig nachgezüchtete Zahnkarpfen (Poeciliidae). B. Lebendgebärende Zahnkarpfen (Poeciliidae viviparae). *In* Wichand, B., and W. Köhler, Diesjährige Neuheiten in Wort und Bild. Bl. Aquar. Terrarienk., vol. 17, no. 47, pp. 463–469, no. 49, pp. 483–485, no. 50, pp. 495–496, no. 51, pp. 503–504, no. 52, pp. 515–516.

WICKBOM, T.
1943. Cytological studies on the family Cyprinodontidae. Hereditas, vol. 29, nos. 1–2, pp. 1–24.

WOODRING, W. P.
1954. Caribbean land and sea through the ages. Bull. Geol. Soc. Amer., vol. 65, no. 8, pp. 719–732.

WOOLMAN, A. J.
1894. Report on a collection of fishes from the rivers of central and northern Mexico. Bull. U. S. Fish Comm., vol. 14, pp. 55–66.

YAMAMOTO, T.
1961. Progenies of sex-reversal females mated with sex-reversal males in the medaka, *Oryzias latipes*. Jour. Exp. Zool., vol. 146, no. 2, pp. 163–180.

ZOLOTNISKY, N.
1901. Les moeurs du *Girardinus decemmaculatus* poisson vivipare. Arch. Zool. Exp. Gen., ser. 3, vol. 29, no. 5, pp. lxv–lxxi.

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