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STUDIES OF THE FISHES OF THE ORDER CYPRINO-
DONTES. XV. THE CHARACTERS AND RELA-
TIONSHIPS OF *FURCIPENIS HUBERI*
AND *ALFARO CULTRATUS*BY LUIS HOWELL RIVERO¹ AND CARL L. HUBBS

RECENT studies have indicated that the primitive poeciliid *Furcipenis huberi* and the more specialized *Alfaro cultratum* are apparently closely related, and may be classed together in a distinct subfamily, Alfarinae.

I. *FURCIPENIS HUBERI* (FOWLER)

Furcipenis huberi, one of the peculiar poeciliid fishes of Central America, was described by Fowler (1923: 27) under the name of *Priapichthys huberi*. The two original specimens, the holotype and the female paratype, were collected in "Marceligo Creek, tributary of the Tunky River, at Miranda, Nicaragua." A third specimen, a scarcely developed male, was recorded by Hubbs (1926: 53) from an elevation of 3600 feet at Siquatepeque, Honduras, thus extending the range of the species to the mountains of north-central Honduras. Two females,² more recently collected by Dr. Karl P. Schmidt in

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² Permission to examine and record these specimens was kindly given by the authorities of the Field Museum.

Río Bobós below the railroad bridge at Izabel, in the Río Motagua basin of Guatemala, further extend the range of the species. A series of 29 additional specimens, all females except for 1 undeveloped and 2 fully developed males, was collected by Mr. R. E. Stadelmann, for the Museum of Comparative Zoology in "Brook 'Olomina,' Subirana Valley, Dept. of Yoro, Republic of Honduras" at an elevation of 2800 feet; the only other fish taken at the same locality was *Pseudoxiphophorus bimaculatus taeniatus* Regan (dorsal rays 14 in 7 specimens, 15 in 8 specimens).

GONOPODIUM.—Fowler referred this interesting species to *Priapichthys*, without giving any detailed account of the diagnostic features of the gonopodium. Hubbs at first (1926: 53), having available only an undeveloped male, was unable to place the species generically, but suggested that "it may belong to a distinct genus." Later (1931), after having reexamined the male type, he found characters which justified the erection of a new genus (*Furcipenis*) for *huberi*. *Furcipenis* was regarded as a primitive genus which, on the basis of gonopodial characters, fits well in the Gambusiinae, except that it possesses a membranous swelling on the front of ray 3 (not ray 2 as stated by Fowler), in which respect it resembles the Poeciliinae (Hubbs, 1924). A slight thickening of ray 4a was thought to be possibly ancestral to the "elbow" of the Gambusiini. The absence of serrae, hooks, and processes on the gonopodial rays was regarded as a primitive characteristic. The division of the extreme tip of the gonopodium into 2 pointed projections in the type specimen suggested the name *Furcipenis* and seemed to be especially diagnostic.

The occurrence of two males with completely developed gonopodia in the series from Subirana Valley makes possible a redefinition of the genus, and a more adequate interpretation of its relationships. It now appears that the gonopodium of the holotype is incompletely developed, though it is essentially clear and does show most of the generic features. Unfortunately, the forking of the extreme tip of the gonopodium of the type is now indicated as a probable artifact.

The chief differences between the fully developed gonopodium of the two adult males at hand (Pl. I) and the imperfectly developed organ of the holotype are as follows: the membranous swelling on the front of ray 3 is enlarged into a large prepuce-like hood, similar to that of the Poeciliini, embracing the tip of the gonopodium. The segments of ray 3 are abruptly constricted in width, length, and thickness distal to the base of the hood, so that the anterior edge of ray 3 is strongly concave distally. The keel-like oblique portion of each of the segments projecting into the base of the hood is definitely spinous (Pl. I and Pl. II, Fig. 1). These segments bearing obliquely antrorse spines grade proximally into wide rectangular segments, keeled along their front edge down to near the middle of the gonopodium; the body of the segments of ray 3 is expanded outward to form lateral keels which are widest and are slightly curved backward opposite the base of the prepuce-like hood. Both branches of ray 4 extend to the extreme pointed tip of the gonopodium, as they are slightly longer than ray 3 and considerably longer than ray 5. The rays are arched forward distally (ray 3 weakly, ray 5 strongly), but the extreme tip of ray 4 shows a tendency to recurve. Ray 5a in the outer half of the gonopodium is strongly dilated laterally, forming a shallow trough containing ray 5p (Pl. II, Fig. 1). Proximally, though not to its extreme base, ray 5p becomes dilated and crenate on its posterior edge because each segment is produced into a rounded protuberance (Pl. II, Fig. 2); distally ray 5p is very slender; toward its tip it becomes enveloped in a dermal keel. The segments of the somewhat swollen ray 6p become modified in the same direction, but to a lesser degree.

Otherwise the gonopodial characters are as described by Hubbs. None of the rays possess serrae. Opposite the base of the prepuce-like hood, ray 4a is somewhat swollen; proximal to the base of the prepuce-like hood, ray 4p shows a more conspicuous but yet simple bulbous swelling; in both of these swellings the sutures remain distinct, straight, and transverse.

Distal to the swelling, the segments of ray 4p are very slender. The distal segments of rays 5a and 5p are elongated rectangles.

The prepuce-like hood and the dilated ray 5 suggest that *Furcipenis* may bear ancestral relationship to the Poeciliinae, as defined by Hubbs (1924: 11). The dilation of ray 5, however, is morphologically different; in *Furcipenis* ray 5a is dilated to form a shallow trough partially surrounding the slender ray 5p (Pl. II, Fig. 1), whereas in the Poeciliinae the two halves of both branches are divided and spread apart to form a trough, so that the left and right halves of ray 5p are widely separated. The prepuce-like hood is remarkably like that of the Poeciliinae, but other evidence suggests that this striking similarity is the product of independent evolution. The pelvic rays of the highly developed males of *Furcipenis* now available do not show the modifications characteristic of the Poeciliinae. The agreement of *Furcipenis* with *Priapichthys* and related genera of the tribe Heterandriini of the subfamily Gambusiinae, in coloration and geographical distribution, suggests that *Furcipenis* is related to that group more closely than to the Poeciliinae.

The slight thickening of ray 4a only faintly approaches the "elbow" of that ray in the tribe Gambusiini. That this resemblance also is probably the result of convergence is suggested by the lack of other points of specific agreement between *Furcipenis* and the Gambusiini, and by the circumstance (Hubbs, 1934) that two other genera, apparently not closely related to each other nor to the Gambusiini, also show a distal thickening of ray 4a.

GONOPODIAL SUSPENSORIUM (Pl. II, Fig. 3).—A further test of the relationships of *Furcipenis* is provided by a study of that portion of the axial skeleton which is specialized for the support of the modified anal fin of the male. The characters furnished by these internal structures, although not utilized by either Regan (1913) or Hubbs (1924 and 1926) in their revisions of the Poeciliidae, were indicated by the researches of Philippi (1908) and Langer (1913) to approach the gonopodial characters in diversity and potential taxonomic value.

As will be further indicated in our forthcoming treatise on these structures, the gonopodial suspensorium of *Furcipenis*, like the gonopodium itself, is very simple, polyisomerous, only minimally different from the homologous structures of the female, and therefore apparently primitive.

The first 3 haemal spines of the male are modified into very simple gonapophyses, somewhat thickened, directed forward and somewhat curved sigmoidally, but not bearing any trace of uncinatoid processes. The tip of each gonapophysis is similarly flattened, transversely, to form a spatulate surface which articulates with the upper ends of the interhaemals. The first gonapophysis ends behind the tip of the fifth interhaemal, against which its spatulate surface is applied; the second and third gonapophyses end respectively behind the tip of the sixth and of the eighth interhaemal.

Each of the first 3 or gonapophysis-bearing caudal vertebrae has a well developed parapophysis near the tip of which is borne a rib protecting a lobe of the air bladder which extends backward to the fifth haemal spine. The fourth caudal vertebra bears a similar parapophysis to which a short rib is attached; its haemal spine is slightly enlarged and directed slightly forward, but does not contact the interhaemals and can scarcely be termed a gonapophysis.

The first interhaemal is small, thin, and lanceolate. The second, third, and fourth interhaemals are suturally united to form, as usual, a compound interhaemal, in which the second interhaemal is compressed to constitute a strong anterior keel and the fourth is expanded, most widely toward the base, to form a pair of large lateral wings, in the trough of which the rodlike fifth interhaemal is completely concealed except at its extreme base and tip. The following interhaemals are also rodlike, and are evenly spaced. They show an increasing tendency to be curved backward. The fifth to eighth interhaemals are of subequal size and strength, the ninth and tenth are smaller and weaker.

In both the young and gravid female the first 3 haemal spines, although not developed into true gonapophyses, are

very similar in structure to those of the male; all extend down to the interhaemals, as follows: the first of the 3 ends between the fifth and sixth interhaemal; the second, between the seventh and eighth interhaemal; and the third, behind the eighth interhaemal. Each of the first 4 caudal vertebrae, as in the male, bears a parapophysis from which ribs extend outward to protect the posterolateral lobe of the air bladder. The interhaemals are normally developed, as each one is separate and lanceolate.

The gonopodial suspensorium of *Furcipenis* is strikingly unlike that of the Poeciliini, and very much less specialized, as will be shown in our forthcoming paper on these structures. It is, however, very similar to that of the Xiphophorini, especially that of *Xiphophorus*. This resemblance we believe indicates a primitive origin for both *Furcipenis* and *Xiphophorus*, but does not definitely indicate any very close relationship between these genera. The points of similarity merely involve the common lack of specialized features.

OTHER CHARACTERS.—In other than the sexually dimorphic characters described above, the 29 specimens of *Furcipenis huberi* from the Subirana Valley correspond well with Fowler's original description. The dorsal rays are 9 in 27 specimens, 10 in 2; the anal rays number 10 in all (last ray counted as split to base). The scale rows from upper edge of opercle to base of caudal rays number 32, except in 2 specimens having respectively 31 and 33 rows. The caudal fin is almost as long as the head. The length of the gonopodium in the 2 mature males is contained 3.30 and 3.65 times in the standard length. Other proportions in the 3 males, determined by dividing the smaller measurement into the larger one rather than by stepping the measurement over the curve of the head or body, are as follows: head in standard length, 3.42 to 3.93 (average, 3.67); greatest depth of body, 3.47 to 3.62 (3.52); length of snout in head, 2.74 to 3.22 (3.01); length of eye, 2.46 to 3.00 (2.80). Comparable proportions in the females are: head, 3.11 to 3.79 (3.48); depth, 2.95 to 3.67 (3.33); snout, 2.74 to 3.52 (3.10); eye, 2.46 to 3.50

(3.03). The males vary in standard length from 29 to 39 mm., the females from 27.5 to 58.8 mm.; the males vary in total length from 35.8 to 49.0 mm., the females from 34.0 to 72.5 mm.

As noted by Hubbs (1931: 3) "the lower edge of the caudal peduncle, though rounded over, approaches that of *Alfaro* in sharpness." The modification of the squamation on the edge of the peduncle definitely indicates the incipient development of a keel in *Furcipenis*. The scales of the median row, which have been lost in *Alfaro*, still persist, but are much narrowed and pinched in between the scales of either side, which are partially erect and approach one another in such a way that they would form a definite keel if they were somewhat more enlarged and approximated. In other genera of Poeciliidae, *Tomeurus* of course excepted, the median scales on the lower edge of the peduncle remain of normal size, and the scales on either side are normally imbricated.

II. *ALFARO CULTRATUS* (REGAN)

The synonymy of the odd Central American poeciliid genus *Alfaro*, and of its type species *A. cultratus*, has been given by Regan (1913: 981). We now agree with Myers (1927: 117) in doubting the occurrence of this genus in the faunally different waters of Brazil, and suppose that the types of *Petalosoma* (= *Alfaro*) *amazonum* were aquarium specimens of *A. cultratus* which originated in Central America rather than the Amazon region. Previously we have recognized *A. amazonus* as distinct on the basis of Regan's work.

GONOPodium.—It is true that Regan's figure (1913: Fig. 169F on p. 990) of the gonopodium of "*Alfaro amazonum*" does not agree well with the gonopodia of our specimens of *A. cultratus*, briefly described by Hubbs (1926: 79). Regan's figure, however, having been drawn before the refinement of the study of the gonopodial structures, omits details of real systematic value.

The developed gonopodium of *Furcipenis* on examination clearly recalled that of *Alfaro*. On close comparison, the

resemblance was found to be very striking. In *Alfaro* as in *Furcipientis* the sutures between the broad segments of ray 3 are obliquely angulated at the base of the well developed prepuce-like hood, the tip of the organ has a similar flexure, none of the rays bear serrae, and rays 4a and 4p are similarly swollen.

The differences between the gonopodia of *Alfaro* and *Furcipientis* are minor. The segments of ray 3 though similarly angulated at the base of the hood are not spinous. This ray is less dilated basal to the hood, but beyond that point develops on each side a broad, flaring keel in which the segments are angulated retrorsely. The halves of ray 5p are broadly divided by the trough on the posterior face of the gonopodium, as in the Poeciliini, and are most widely dilated near the middle of their length; nowhere is ray 5p crenate, nor inclosed in a median, fleshy keel.

GONOPODIAL SUSPENSORIUM.—In the axial skeleton of the male, *Alfaro* also agrees very closely with *Furcipientis*. The gonapophyses as in that genus are only slightly modified haemal spines. The interhaemals are essentially similar in structure and form, and in their relation to the gonapophyses. The most striking difference is the circumstance that 6 instead of 4 caudal vertebrae bear ribs, but this merely reflects the more advanced position of the anal fin and the consequently greater penetration of the urosomè by the air bladder. Minor differences include a lesser transverse dilation of the tips of the gonapophyses in *Alfaro*, and the bare connection between the third gonapophysis and the eighth interhaemal. The suspensorium of *Alfaro cultratus* has been briefly described and diagrammatically figured by Langer (1913: 264, Fig. 87) under the name of *Petalosoma cultratum*.

III. THE SUBFAMILY ALFARINAE (NEW NAME)

The genus *Alfaro* has been shifted from one group to another in the modern classification of the Poeciliidae. Regan (1913: 979) classed it with *Tomeurus* in an unnamed division distinct from all other genera in the group, on the basis of

the sharp lower edge of the caudal peduncle without a median series of scales, and a similar jaw and tooth structure. Hubbs (1924: 11) applied Eigenmann's subfamily name Tomeurinae to this group, but recognized the striking divergence of the two genera by placing each in a separate tribe (Alfarini and Tomeurini). After comparing the two aberrant genera, Hubbs (1926: 78) concluded that they are apparently not directly related. He then reserved the subfamily name Tomeurinae for *Tomeurus*, and stated that the tribe Alfarini, with its one genus *Alfaro*, is apparently placeable in the subfamily Poeciliinae, with which it agrees in the diagnostic features given in his 1924 paper (p. 10). Myers and Hubbs intend to point out in the near future conclusive evidence that *Tomeurus* must be classified by itself.

The extremely close resemblance between *Furcipientis* and *Alfaro* indicates, we believe, that they are closely related. The characters of both the gonopodium and the gonopodial suspensorium are almost identical, except for minor differences, as pointed out above. Though lacking the well developed scaly keel on the ventral edge of the caudal peduncle characteristic of *Alfaro*, *Furcipientis* shows an incipient keel involving a definite modification of the squamation.

The resemblance between the two genera extends to certain external features, and particularly to the dentition: in both genera the teeth of both the outer and the inner row are considerably enlarged, and are separated by 2 or 3 rows of smaller teeth. *Furcipientis* is seemingly very close to the ancestral type from which *Alfaro* arose. Since *Furcipientis* appears to be related to the primitive tribe Heterandriini of the subfamily Gambusiinae (see p. 4), the combined group of *Alfaro* and *Furcipientis* would seem to represent a distinct line of evolution, originating earlier in the phylogeny of the viviparous cyprinodonts. The lack of serrae on ray 4 is seemingly a primitive feature peculiar to *Furcipientis* and *Alfaro*, otherwise exhibited only by the Cuban genus *Toxus*, in which these serrae have apparently been replaced by very strong serrae on ray 5.

On this basis of reasoning the prepuce-like hood of *Furcipenis* and *Alfaro* would seem to have had an origin independent from that of the similar structure in the Poeciliinae. One point of divergence in ray 3 is that the spines or similar angulations of the segments of ray 3 are antrorse, instead of retrorse (Poeciliini) or straight (Xiphophorini). The trough formed by ray 5 is much alike in *Alfaro* and the Poeciliinae, but is morphologically different in *Furcipenis*. The modification of the pelvic fins in *Alfaro* (and *Furcipenis*) is so slight as hardly to indicate relationship with the Poeciliinae, in which the short, first pelvic ray becomes swollen, and the second ray swollen and elongated in the breeding males.

Carrying these conclusions into nomenclatorial practice, we propose to place *Furcipenis* in the same group with *Alfaro*, to remove the tribe Alfarini from the Poeciliinae, and to elevate the Alfarini to subfamily rank. The subfamily **Alfarinae** (new name) may be thus characterized:

Lower edge of caudal peduncle with an incipient or well developed scaly keel. Pelvic fins scarcely modified in adult males. Gonopodium short; the halves of ray 5p either conjoined or separated; tip of gonopodium inclosed in a large prepuce-like hood; segments of ray 3 angulated-antrosely into base of hood; none of the gonopodial rays with serrae. Gonopodial suspensorium relatively simple; gonapophyses without uncinatoid processes.

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Luis Howell Rivero and Carl L. Hubbs

PLATE I

Gonopodium of *Furcipenis huberi*. Drawn by Luis Howell Rivero. Line *A-A'* is the base of the cross section diagram shown in Plate II, Figure 1. The anal rays are numbered 3 to 5, and the anterior and posterior branches are lettered *a* and *p*.

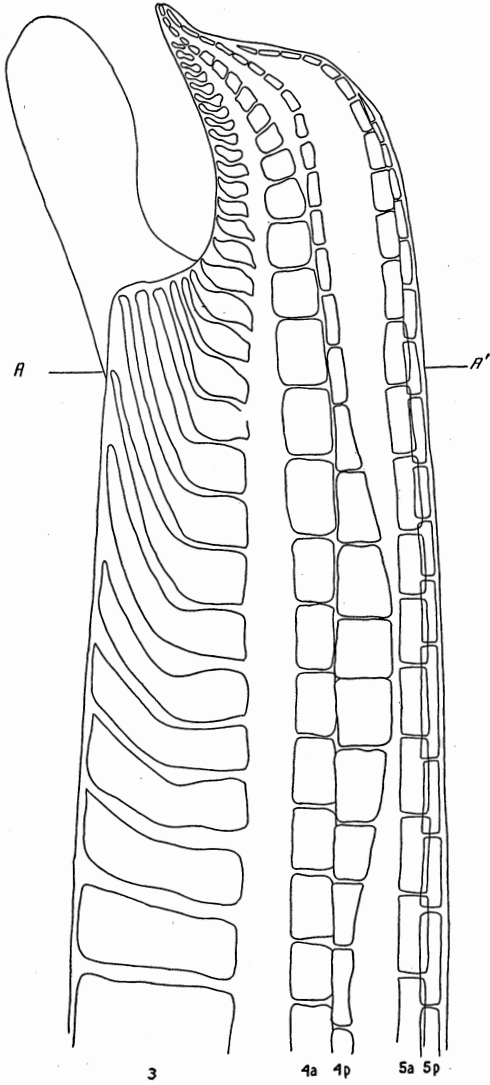


PLATE II

- FIG. 1. Diagrammatic cross section of gonopodium of *Furcipenis huberi*, through line *A-A'* of Plate I, showing the lateral dilation of rays 3 and 5 and the anterior keel on ray 3.
- FIG. 2. Photomicrograph of basal part of gonopodium of *Furcipenis huberi*, showing dilation and crenation of ray 5p and the thickening of ray 6.
- FIG. 3. Gonopodial suspensorium of *Furcipenis huberi*. Drawn by Luis Howell Rivero.

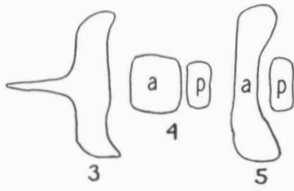


FIG. 1

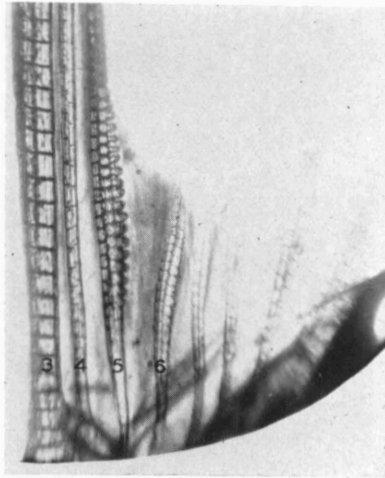


FIG. 2

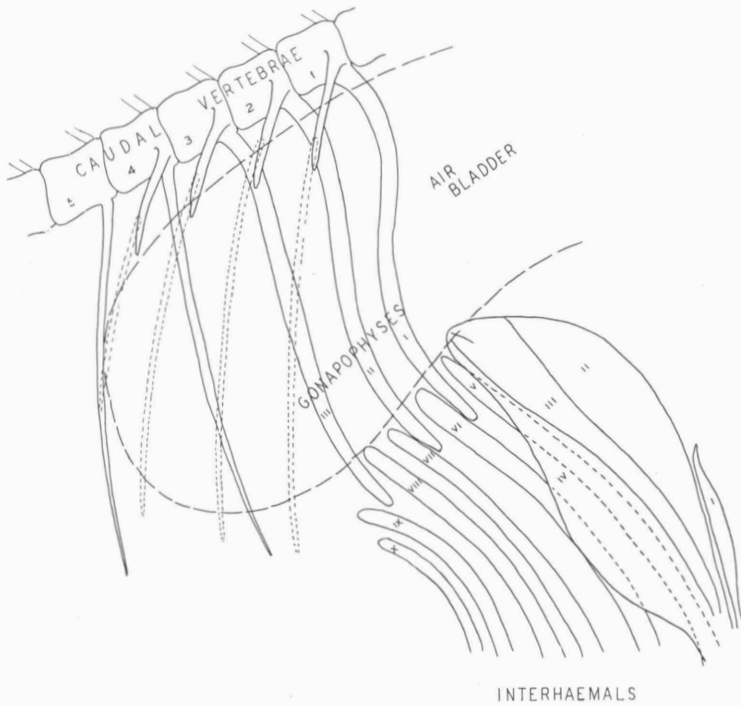


FIG. 3

