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Systematics of *Cyprinodon higuey* n. sp. and *Cyprinodon jamaicensis* Fowler from the Greater Antilles (Teleostei: Cyprinodontiformes)

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ABSTRACT

The black-and-blue pupfish, *Cyprinodon higuey* n. sp., is described from Laguna de Bávaro, a coastal lake in eastern Dominican Republic, Hispaniola. It is compared to other Antillean pupfishes and diagnosed on the basis of derived characters. The Jamaican pupfish, *C. jamaicensis* Fowler, is found to have low population means for certain meristic

features, but cannot be fully diagnosed from Antillean populations of *C. variegatus* Lacépède, with which it shares other derived characteristics. Low meristic values in the Jamaican population are interpreted as the southern end of a cline and *C. jamaicensis* is synonymized with *C. v. riverendi* Poey.

RESUMEN

El titaco negro y azul, *Cyprinodon higuey* esp. n., se describe de la Laguna de Bávaro de la zona costera oriental de la República Dominicana, Isla Hispaniola. Se compara con otras especies del género en las Antillas y su diagnosis se realiza en base a características derivadas. La especie de Jamaica, *C. jamaicensis* Fowler, posee una media poblacional baja para ciertas características me-

rísticas, pero no puede ser separada completamente de las poblaciones de *C. variegatus* Lacépède de las Antillas, con las cuales comparte otras características derivadas. Los menores valores merísticos en la población de Jamaica se interpretan como el extremo sur de una clina. *C. jamaicensis* se sinonimiza con *C. v. riverendi* Poey.

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INTRODUCTION

Pupfishes of the genus *Cyprinodon* were first recorded from the Caribbean island of Hispaniola by Myers (1935) who described as new the species *C. bondi* from Étang Saumâtre, Haiti. A second Hispaniolan member of the genus, *C. nichollsi*, was recently described from an endorheic hypersaline lagoon on the southwestern coast of the Dominican Republic (Smith, 1989). During a subsequent survey of nonmarine habitats on the southern coast of Hispaniola, an additional species was discovered from a mangrove lake at Laguna de Bávaro, eastern Dominican Republic. It is characterized below.

Determining the species status and relationships of new forms of Antillean *Cyprinodon* is made difficult by extensive variation in *C. variegatus* Lacépède (1803), the most widespread member of the genus. This taxon has been taken most recently to comprise six subspecies (Humphries and Miller, 1981) including populations on the North American mainland and in Cuba, Grand Cayman Island, the Bahamas, and the Turks and Caicos Islands. The Antillean forms have never been characterized in a comparative context, but are known to include populations that are distinct to some degree and that are sometimes recognized as species or subspecies (Hubbs and Miller, 1942; Miller, 1962; Humphries and Miller, 1981). A survey of material from the Antilles and Florida shows that meristic variation is clinal in these populations of *C. variegatus*. We find that the poorly known nominal species *C. jamaicensis* Fowler (1939) can also be interpreted as part of this cline. It is not separated from nearby populations of *C. variegatus*, known as *C. v. riverendi* Poey, by any disjunction in meristic features nor is it diagnosable by other traits.

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METHODS

Measurements were taken as described by Miller (1948) with the addition of several short oblique measurements suggested by Humphries (1984) and with the following exceptions. Body depth is perpendicular to the longitudinal axis at the dorsal-fin origin. Depth of the caudal peduncle is the distance between the first dorsal and ventral procurrent rays of the caudal fin. Mouth width is the greatest distance across the lower dental arcade excluding the lips.

All rays with separate bases were included in fin-ray counts and data from paired fins were taken from the left side. Vertebrae were counted from radiographs and cleared-and-stained specimens; the hypural fan and its half centrum were included as one vertebra. Gill rakers were counted on the first arch of the right side and include all visible rudiments. For meristic characters reported below, the value of the holotype is indicated in boldface. Principal components were extracted from the correlation matrix for the ten meristic characters listed in table 6. Calculations were performed using SAS (Statistical Analysis System).

Statements of proportions refer to the specimens of table 1, and comparisons to *C. nichollsi* and *C. bondi* are based on data for those species as reported by Smith (1989). Group

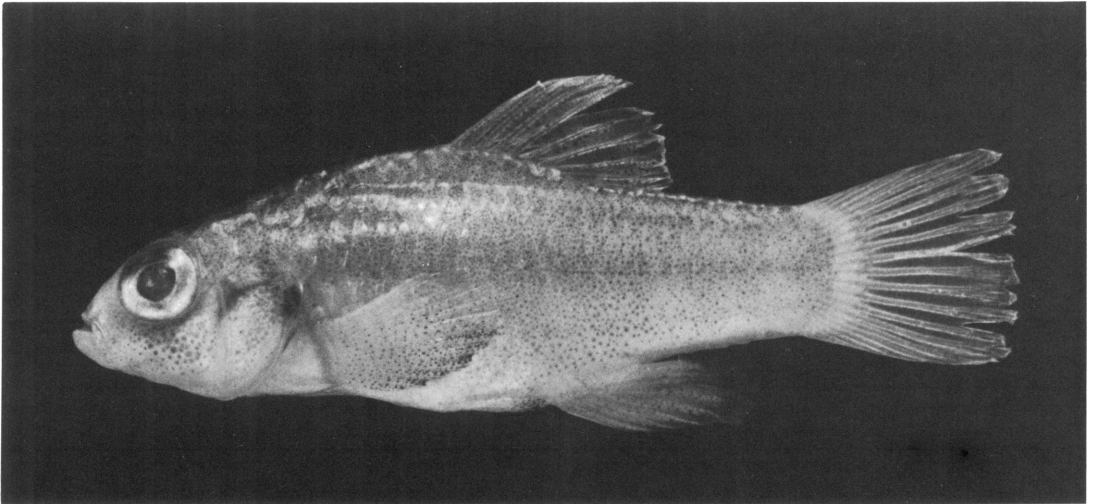


Fig. 1. *Cyprinodon higuey*. AMNH 58623, holotype, male, 23.5 mm standard length.

names within the Cyprinodontiformes are those of Parenti (1981).

SYSTEMATICS

Cyprinodon higuey n. sp.,
Rodríguez and Smith
Black-and-blue pupfish;
Titaco negro y azul
Figures 1, 2; tables 1–5

HOLOTYPE: AMNH 58623, male, 23.5 mm SL, Laguna de Bávaro at village of Cabeza de

Toro, Province of Altagracia, Dominican Republic; C. M. Rodríguez and M. L. Smith, 27 Feb. 1989.

PARATYPES: AMNH 58624, 10 juveniles, males and females, 22.2–28.4 mm SL, including four cleared-and-stained, collected with the holotype. AMNH 58625, 49 juveniles, males and females, 6.8–28.4 mm SL; UF 80375, 10 juveniles, males and females, 9.7–20.0 mm SL; UMMZ 216033, 10 juveniles, males and females, 11.2–23.9 mm SL; roadside pool at southern edge of village of Cabeza de Toro, Province of Altagracia, Do-



Fig. 2. *Cyprinodon higuey*. AMNH 58624, paratype, female, 27.8 mm standard length.

TABLE 1
Proportional Measurements in *Cyprinodon higuey*^a as Thousandths of Standard Length

	9 males				10 females		
	Holotype	Range	Mean	SD	Range	Mean	SD
Standard length, mm	28.2	18.2–28.2			20.5–28.1		
Predorsal length	592.2	554.1–607.3	574.3	15.8	548.1–608.5	584.6	16.7
Prepelvic length	574.5	531.8–582.1	561.6	17.5	528.8–586.2	562.9	15.5
Body depth	397.2	318.7–397.2	354.6	21.3	312.5–387.9	349.5	17.6
Dorsal-fin origin to anal-fin insertion	407.8	351.6–407.8	378.1	16.6	331.7–377.2	355.4	12.4
Pectoral-fin origin to dorsal-fin insertion	436.2	361.6–436.2	395.4	20.6	375.0–423.5	395.3	18.9
Dorsal-fin length	322.7	285.7–328.4	311.6	14.6	260.5–312.5	282.2	14.6
Pectoral-fin length	255.3	239.3–263.7	251.7	6.8	216.4–252.7	233.9	13.0
Anal-fin length	262.4	247.9–298.4	274.3	14.0	194.7–237.4	214.3	11.1
Pelvic-fin length	134.8	109.9–134.8	120.4	7.4	105.8–132.4	116.7	8.7
Caudal-peduncle length	251.8	245.4–277.1	256.0	10.7	243.8–260.5	252.5	5.0
Caudal-peduncle depth	184.4	153.8–184.4	166.6	8.9	149.0–174.4	160.8	6.2
Head length	344.0	325.6–350.8	337.3	6.9	317.3–345.2	338.4	12.8
Head width	230.5	203.5–230.5	216.8	8.6	201.9–243.8	228.8	14.0
Maxilla-end to orbit	78.0	71.4–84.6	78.3	4.2	73.1–81.8	77.1	2.9
Upper-jaw length	113.5	87.9–118.2	108.6	8.8	101.0–118.3	113.1	8.4
Interorbital length	148.9	122.7–148.9	139.5	7.8	132.3–145.0	139.3	4.7
Orbit length	117.0	109.9–120.4	115.6	3.1	103.4–126.0	112.9	7.7
Interorbital width	106.4	85.5–106.4	92.9	8.8	86.5–103.1	95.1	4.8
Snout length	99.3	83.8–99.3	87.9	5.3	76.9–109.5	93.6	8.1
Mouth width	85.1	65.9–85.1	75.4	6.5	67.3–99.6	78.8	8.8

^a AMNH 58623, 58624, 58625.

TABLE 2
Frequency Distribution of Vertebrae in Five Species of *Cyprinodon*

Species Locality	Precaudal					Caudal					Total					
	10	11	12	13	Mean	13	14	15	16	Mean	24	25	26	27	28	Mean
<i>variegatus</i> ^a																
1. Cedar Keys, FL		14	17		11.6		4	18	9	15.2			12	16	3	26.7
2. Jupiter, FL			3	12	11.8		6	7	2	14.7			7	8		26.5
3. Florida Keys	2	14	3		11.0	4	11	4		14.3	1	16	2			25.1
4. Cuba	1	15	2		11.1		9	9		14.5	1	6	11			25.6
5. Great Inagua		20			11.0	3	14	3		14.0	3	14	3			25.0
6. Grand Cayman	1	29			11.0	3	23	4		14.0	4	23	3			25.0
7. Jamaica	16	4			10.2		5	15		14.8	2	17	1			25.0
<i>laciniatus</i>																
Bahamas			14	1	12.1		3	12		14.8			2	13		26.9
<i>bondi</i>																
Hispaniola	1	60	11		11.1		2	27	43	15.6			20	52		26.7
<i>nichollsi</i>																
Hispaniola	1	44	11		11.2	8	37	11		14.1	5	35	16			25.2
<i>higuey</i>																
Hispaniola	1	14	11		11.4		5	14	7	15.1			15	10	1	26.5

^a Localities are arranged north to south and numbered as in figure 3.

TABLE 3
Frequency Distribution of Dorsal- and Anal-fin Rays in Two Species of *Cyprinodon*

Species Locality	Dorsal fin						Anal fin			
	10	11	12	13	14	Mean	10	11	12	Mean
<i>variegatus</i>										
1. Cedar Keys, FL			10	14	1	12.6		16	9	11.4
2. Jupiter, FL		4	11			11.7	2	13		10.9
3. Florida Keys		6	13			11.7	2	16	1	11.0
4. Cuba		5	4			11.4		9		11.0
5. Great Inagua	3	16	1			10.9	4	16		10.8
6. Grand Cayman		21	9			11.3	1	27	2	11.0
7. Jamaica		19	1			11.0		17	3	11.2
<i>higüey</i>										
Hispaniola		22	9			11.3	14	17		10.6

minican Republic; C. M. Rodríguez and M. L. Smith, 27 Feb. 1989.

DIAGNOSIS: A small *Cyprinodon* (to 28 mm SL) distinguished from all other pupfishes by the black dorsal fin with a blue border in males. Lateral bars absent in males, mouth wide, first pharyngobranchial toothplate absent, pectoral fin reaching beyond the pelvic-fin origin, usually 15 pectoral-fin rays, 13–16 circumpeduncular scales, 24–26 lateral-series scales, scales entire or slightly crenate. Comparisons to particular congeners are given in the discussion.

ETYMOLOGY: The new species is named for the Higüey people who originally inhabited eastern Hispaniola. The epithet is treated as a noun in apposition.

DESCRIPTION: General morphology and pigmentation of preserved specimens are shown in figures 1 and 2, and proportional measurements are given in table 1. Body in

TABLE 4
Frequency Distribution of Pectoral-fin Rays in Three Species of *Cyprinodon*

Species Locality	Pectoral-fin rays						
	13	14	15	16	17	18	Mean
<i>bondi</i>							
E. Saumatre			4	19	25	2	16.5
<i>nichollsi</i>							
L. Oviedo			6	28	16		16.2
<i>higüey</i>							
L. Bavaro	1	4	25	1			14.8

males strongly compressed, but only moderately deep for a *Cyprinodon*. Predorsal profile straight or moderately convex, not greatly arched as in *C. nichollsi* and many North American species. Dorsal-fin origin slightly behind midbody, opposite pelvic-fin origin. Mouth wide and terminal, its cleft oblique. First dorsal-fin ray slender and short, never spinelike as in Antillean populations of *C. variegatus*. Pelvic-fin rays 6(10), 7(21). Branched caudal-fin rays 12(19), 13(6), 14(5), 15(1). Branchiostegal rays 6(10). Gill rakers 20(4), 21(14), 22(11), 23(3). Scales around caudal peduncle 13(1), 14(6), 15(5), 16(14). Other meristic characters are given in tables 2–5. Pectoral fins narrow and long, surpassing the pelvic-fin origin in individuals of all sizes. Breast and prepelvic area fully scaled. Exposed scale margins usually entire, occasionally slightly crenate on crests of the caudal peduncle, never lacinate. Interpelvic scaly appendage absent. Scapular scale moderately enlarged compared to first scales in lateral series; the underlying cleithral process broad, expanded posteriorly beyond the pectoral-fin radials, not greatly enlarged as in *C. nazas* and *C. variegatus*.

Number of pores in cephalic acoustico-lateralis system: mandibular 0(5), 2(27); preopercular 7(30), 8(2); preorbital 0(1), 2(1), 3(8), 4(22). In specimens with no mandibular or preorbital pores, a developing canal is present. The supraorbital canal is uninterrupted and opens to the surface through seven pores.

SEXUAL DIMORPHISM: External differences

TABLE 5
Frequency Distribution of Lateral-series Scales in Five Species of *Cyprinodon*

Species Locality	Lateral-series scales								
	22	23	24	25	26	27	28	29	Mean
<i>variegatus</i>									
1. Cedar Keys, FL				6	7	2			25.7
2. Jupiter, FL			3	12					24.8
3. Florida Keys		2	13	4					24.1
4. Cuba			5	4					24.4
5. Great Inagua		4	13	3					24.0
6. Grand Cayman		13	16	1					23.6
7. Jamaica	2	17	1						23.0
<i>laciniatus</i>									
Bahamas				1	5	7	2		26.7
<i>bondi</i>									
Hispaniola				1	13	20	11	2	27.0
<i>nichollsi</i>									
Hispaniola		3	26	18	3				24.4
<i>higuey</i>									
Hispaniola			8	16	7				25.0

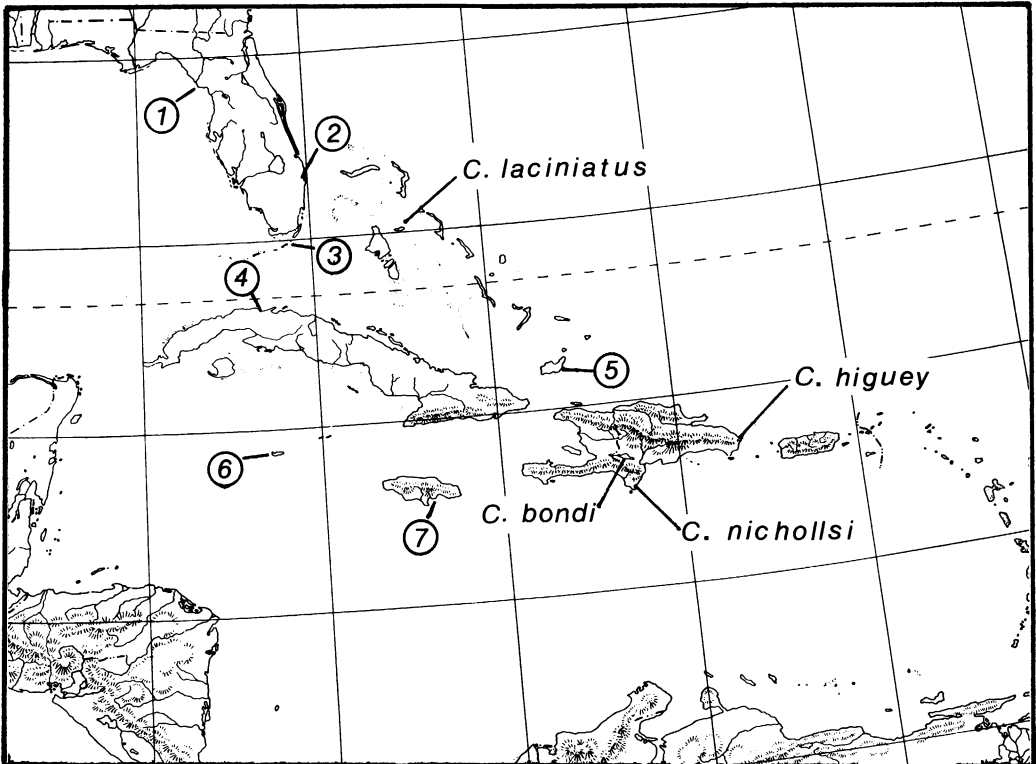


Fig. 3. Localities of material listed in tables 2 and 3. Localities for *Cyprinodon variegatus* are numbered from north to south as follows: (1) AMNH 20584, Cedar Keys, Levy Co., Florida; (2) UF 62653,

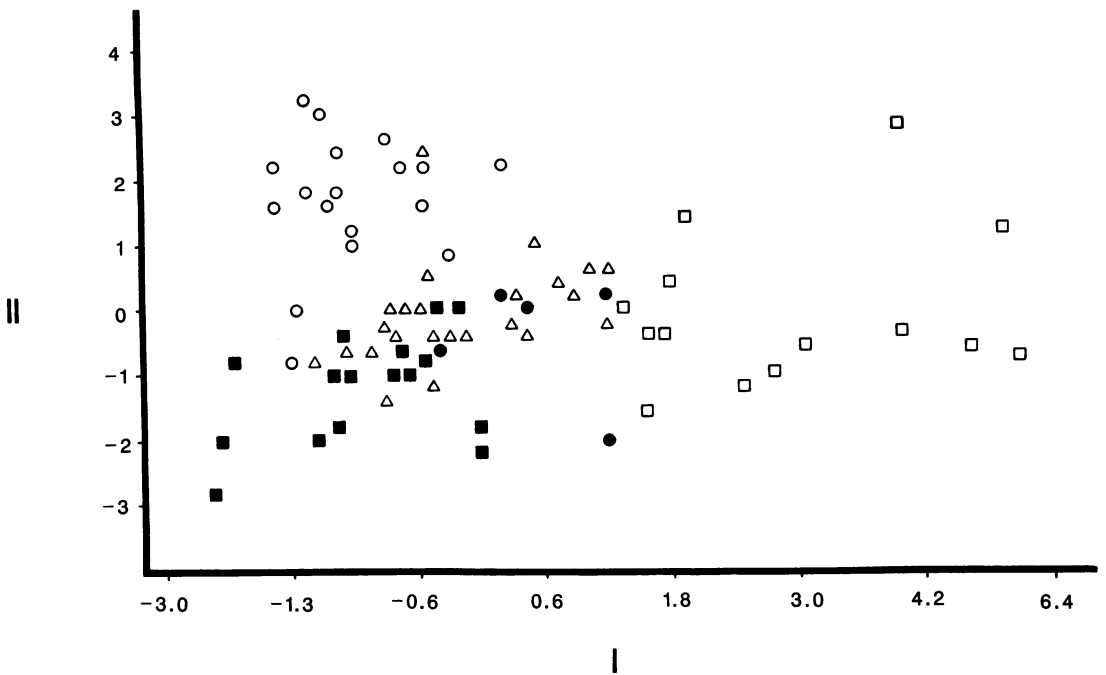


Fig. 4. Scatter diagram of principal components scores of Antillean *Cyprinodon variegatus*. Open squares, Cedar Keys, Florida. Solid squares, Great Inagua. Open circles, Jamaica. Solid circles, northern Cuba. Triangles, Grand Cayman Island. Material as in fig. 3.

between the sexes are pronounced in *Cyprinodon higuery*. The median fins, particularly the anal fin, are longer in males than in females (table 1). Large males become moderately deep-bodied and laterally compressed compared to females (figs. 1, 2). Ciliate scales are present on the sides of the head and body in breeding males, which also bear contact organs on the first seven rays of the anal fin. As in all *Cyprinodon* species, the fifth and sixth anal-fin rays of males are swollen compared to the fourth and eighth rays. The sexes are also readily distinguished by breeding colors as described below.

COLORATION: Live adult males are olive on the back and upper sides. During courtship or defense of territories, breeding males develop an intense yellow or orange color that extends from the snout over the cheeks and lower sides of the head, breast, and periproct;

TABLE 6
Principal Components Analysis Using Correlation Matrix of 10 Meristic Variables of *Cyprinodon*

	PCI	PCII
Eigenvalue	3.03	1.68
% variance	30.3	16.8
Dorsal-fin rays	0.47	0.04
Anal-fin rays	0.26	0.27
Pectoral-fin rays	0.07	0.41
Branched caudal-fin rays	0.14	0.22
Pelvic-fin rays	0.18	-0.31
Lateral-series scales	0.50	-0.24
Circumpeduncular scales	0.39	-0.03
Precaudal vertebrae	0.31	-0.54
Caudal vertebrae	0.30	0.41
Gill rakers	0.26	0.30

←
near Jupiter, Palm Beach Co., Florida; (3) UF 77215, Islamorada, Monroe Co., Florida; (4) GCRL V6224, Matanzas, Cuba; (5) AMNH 43282, Great Inagua, Bahamas; (6) AMNH 59045, Palmetto Point, Grand Cayman Island; (7) AMNH 59046, Port Royal Causeway, Jamaica.

the bases of the pectoral, pelvic, and anal fins are also yellow-orange. The caudal, anal, and paired fins are outlined by a terminal black margin which, on the caudal fin, is as wide as the pupil. The dorsal fin is black at the base with a contrasting light blue border on the trailing edge. The vertical bars that are typical of most *Cyprinodon* species are absent in males, a feature shared with *C. alvarezii* and *C. meeki* of interior Mexico. Courting males become dusky or black above the midline and develop an intense iridescent blue band on both sides of the nape. Orange and blue coloration disappears in specimens preserved in ethanol.

Live adult females are mostly silvery on the sides and venter and olive on the back. The area between the opercular cleft and the caudal-fin base is crossed by 7 to 14 irregular vertical bars similar to those of *C. variegatus*. Fins are clear except for a black and white ocellus at the posterior base of the dorsal fin. A cluster of melanophores forms a small dark patch below the eye. Markings in ethanol are similar except that silver and white areas are reduced.

HABITAT: *Cyprinodon higuey* is reported only from Laguna de Bávaro and a nearby roadside pool. The lake is 2.5 km in its major dimension and is situated 0.5 km inland from the tide line. The shoreline at the collection site and around most of the perimeter is mangrove forest. Specimens were collected over plant debris in water 3.0–15.0 cm deep at a water temperature of 27°C. Salinity was 2 ppt as measured with a YSI salinity meter.

DISCUSSION: The new species is classified in the genus *Cyprinodon* with which it shares thickened rays 5 and 6 in the male anal fin and a terminal black band on the male caudal fin. Thickened anal-fin rays also occur in some males of *Floridichthys* and *Megupsilon* (although only in the largest individuals), which may be evidence of their close relationship to *Cyprinodon*. This character is unknown among other Cyprinodontoidei and is therefore inferred to be derived. The thickening of rays 5 and 6 is pronounced in mature males of all species of *Cyprinodon*, including the new species.

The terminal black band on the caudal fin of males in *Cyprinodon* is probably the best evidence for the monophyly of the genus. Al-

though variable among species in width and intensity, it occurs in all *Cyprinodon* and in no cyprinodontine outside the genus. The caudal-fin band of *C. higuey* is typical of the group.

Cyprinodon higuey resembles *C. bondi* of Hispaniola and *C. laciniatus* Hubbs and Miller (1942) of New Providence Island, Bahamas, in having vertebral counts that are higher than in other Antillean pupfishes (table 2). However, high numbers of vertebrae are general among cyprinodontines and probably do not indicate close relationship. *C. higuey* differs from *C. bondi* and *C. laciniatus* in having fewer circumpeduncular scales (13–16 vs. 18–22) and is further distinguished from *C. bondi* in having no toothplate or teeth in the position of the first pharyngobranchial bone, fewer pectoral-fin rays (table 4), and a rectangular rather than strongly tapered caudal peduncle. *C. higuey* differs from its remaining Hispaniolan congener, *C. nichollsi*, in having intense orange coloration of the breast and lower head in breeding males, more numerous vertebrae (table 2), fewer pectoral-fin rays (table 4), and a long narrow pectoral fin that surpasses the pelvic-fin origin.

The orange coloration of breeding males is a striking feature shared by *C. higuey* and *C. variegatus* and is certainly a derived feature of a subgroup of *Cyprinodon*. However, we are uncertain of its character-state distribution among other pupfishes because orange color is not evident in preserved material and, in living specimens, it is a transient state associated with reproductive activity. It may actually define a group that includes several species from mainland North America. *C. higuey* differs from *C. variegatus* in having no vertical bars on the sides of males and a smaller cleithral process. The cleithral scale is only slightly larger than the first lateral-series scale, rather than two or three times as large. *C. higuey* tends to have higher numbers of vertebrae and lateral-series scales, particularly when compared to the nearest populations of *C. variegatus* which occur in Jamaica, Great Inagua, and Grand Cayman Island.

Cyprinodon higuey is distinguished from all other cyprinodontines by the black dorsal fin with a blue margin, a characteristic that is inferred to be autapomorphic.

STATUS OF *CYPRINODON JAMAICENSIS*

Comparison of new Hispaniolan pupfishes to geographically neighboring *Cyprinodon* has led us to a reevaluation of the population on Jamaica. Fowler (1939) first reported a *Cyprinodon* from Jamaica, giving the name *C. jamaicensis*. The nominal species has been mentioned in faunal lists and synonymies (Hubbs and Miller, 1942; Miller, 1962, 1981, 1982; Caldwell, 1966; Humphries and Miller, 1981; Lazara, 1984), but its systematic position has not been determined. Fowler based his description on two specimens sent from an unspecified locality in Jamaica. His characterization of this material is inadequate to diagnose it from the many populations of *C. variegatus* and other pupfishes now known from the Antilles. Unfortunately, the holotype is apparently lost (see below). Examination of meristic characteristics in the surviving paratype and in newly collected material shows that the Jamaican population has mean values for precaudal vertebrae (table 2) and lateral-series scales (table 5) that are extreme among Antillean pupfishes and that might therefore be derived. The number of precaudal vertebrae is the lowest reported in any *Cyprinodon* (cf. Smith and Miller, 1980; Humphries and Miller, 1981; Humphries, 1984; Minckley and Minckley, 1986).

Given that several meristic features show that the Jamaican population is somewhat distinctive, principal components analysis was used to seek combinations of characters, or general factors, that might diagnose the population more fully. This method does not involve prior assignment of specimens to groups. The resulting overall meristic features of *C. variegatus* and the Jamaican population are compared in figure 4. Only the first two axes contributed to group discrimination. On the first principal component, which primarily reflects the number of lateral-series scales and dorsal-fin rays (table 6), the most distinctive cluster comprises specimens from northern Florida. Each Antillean population, including the nominal *C. jamaicensis*, overlaps its geographic neighbors, suggesting a cline. The character that contributes most strongly to the partial separation of the Jamaican population on the second principal

component is the number of precaudal vertebrae (table 6), but variation in this character is also clinal (table 2). We find no single character nor any general factor by which *C. jamaicensis* can be recognized. Although position in a cline could be primitively inherited and therefore unhelpful in determining the systematic position of a population, there are apparently no other characters by which *C. jamaicensis* can be diagnosed. Like other examples of *C. variegatus*, the Jamaican population has the following derived characters: a much expanded cleithral process, an enlarged cleithral scale that is two or three times as large as the first scale in lateral series, and a thickened first dorsal-fin ray. We conclude that *C. jamaicensis* Fowler (1939) is conspecific with Antillean populations of *C. variegatus*. We take the taxonomically conservative position of using the name *C. v. riverendi* Poey (1860) for the Antillean populations until the status of other subspecies of *C. variegatus* has been determined.

TYPES OF *CYPRINODON JAMAICENSIS*: Although the paratype (ANSP 68631) of *Cyprinodon jamaicensis* has been reported missing (Bohlke, 1984), it is actually the holotype (ANSP 68630) that has been misplaced. Fowler (1939) described the holotype as a male, 26.0 mm SL. The specimen found in its jar is a female, 38.0 mm SL, which matches Fowler's description of the paratype and only other specimen known to him. No specimen matching the description of the holotype or paratype was found in a series of 15 aquarium specimens (ANSP 141223), the only other material labeled as *C. jamaicensis* at ANSP.

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