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The Red Devil-Midas-Arrow Cichlid Species Complex in Nicaragua

GEORGE W. BARLOW AND JOHN W. MUNSEY

INTRODUCTION

We became involved in the systematics of these fishes through an interest in polymorphism in Nicaraguan cichlids. It soon became evident, however, that there was a formidable problem in identifying the species. Populations in different lakes of apparently the same species were recognizably different. Some of those populations appeared highly variable while others were relatively uniform. Even the occurrence of polychromatism varied radically from lake to lake (Barlow, 1976). Yet the number of names available seemed greater than the number of species, as indicated by Miller (1966: 792).

Since no ichthyologist was able to undertake this problem when we started the research in 1966 we took it upon ourselves to clarify the situation. Specimens were collected from Lake Nicaragua and from four of the nearby crater lakes. We also preserved laboratory specimens to assess the effect of environmental modification.

We have resolved the status of the species and uncovered a new one. In assigning species to the synonymy of the two principal species, we were aided by conversations with Astorqui and later by correspondence with Villa. Once it was determined that only two species were involved, and how to separate them, the synonymy became apparent.

We have also discovered some interesting evolutionary problems. These include apparent introgressive hybridization in two lakes, evidence for character shift (Grant, 1972) involving two of the species, and a possible case of sympatric speciation.

MATERIALS AND METHODS

We gathered data from 197 specimens of three species. From the different populations we chose fish as close to the same size as possible to minimize differences due to allometric growth. Eighteen of the *Cichlasoma citrinellum* had been raised in the laboratory. All specimens are currently housed in the Department of Zoology, University of California, Berkeley, except for the holotype and paratypes of the new species (see below). Four other specimens of *C. citrinellum* (mislabelled *C. labiatum*) were deposited earlier in the British Museum (Natural History); one was collected in Lake Masaya, Nicaragua, and is designated 1968:1.12.1; the other three are laboratory raised fish of Lake Masaya stock, designated 1968:1.12.2-4. Methods of counting and measuring follow those given by Hubbs and Lagler (1958), except as follows:

Face depth — Perpendicular line from dorsal surface to ventral surface of head and tangent to anterior edge of orbit.

Snout - P₁ insertion — Distance from anterior-most tip of

lip to dorsal insertion of pectoral fin when fin held away from body.

Width upper lip — Greatest width, measured at middle of upper lip.

Caudal-fin length — Distance from posterior margin of hypural plate to tip of longest central caudal-fin ray.

Body depth — Perpendicular distance from origin of first dorsal-fin spine to ventral surface of body.

Snout top — Angle formed by two lines, one following profile of snout, other running from tip of premaxilla to top of pectoral-fin insertion.

"Lip corrected" measurements — Some fish had enormously fleshy lips. This created a problem in comparing populations. Measurements of fishes are conventionally converted to proportions of standard length (S.L.), which is the distance from the middle posterior margin of the hypural plate to the anterior-most tip of the upper lip. If two fish are morphologically identical except that one has a large protrusive upper lip, that fish will then have a greater S.L. Consequently, all proportions calculated on that length will appear relatively smaller than those calculated for the fish with the normal lips. Thus instead of differing in one mensural character, they will differ in all of them.

Our solution was to adjust the standard length of the thick lipped fish to that of a fish with thin lips. Using as our reference several normal (thin) lipped fish, we measured in each the standard length, and the standard length minus the lip. The latter is the distance from the top of the hypural plate to the middle of the maxilla just behind the upper lip. We could then calculate the expected standard length for any fish of comparable size, irrespective of lip thickness, by measuring the distance to the maxilla. These "lip corrected" standard lengths facilitate the comparison of populations, revealing the fundamental differences in their morphological traits. For identification, nevertheless, it is useful to have measurements based on traditional S. L. ("lip included"), so both are given in Table 1.

Underwater observations were made in some of the clearer crater lakes. These are reported elsewhere (Barlow, 1976) for *C. citrinellum*, but some other observations are presented here. Observations were also attempted in the Great Lakes and in Lake Masaya, but with no real success because of their great turbidity (Barlow, 1976).

RESULTS

Systematics:

Günther (1864a,b, 1869) described four species from Nicaragua in this complex (see below), one being *Heros citrinellus* and the other three *H. labiatus* and two synonyms of

TABLE 1. Counts and measurements of three species consisting of seven series of specimens. All measurements have been converted to percent of standard length. For each series, the first line gives the mean percent, the second gives \pm two standard deviations, and the third gives the range. "Lip included" and "Lip corrected" are explained under Materials and Methods in the text.

	<i>C. labiatum</i> , "Lip included"	Lake Nicaragua "Lip corrected"	<i>C. citrinellum</i> , "Lip included"	Lake Masaya "Lip corrected"	<i>C. citrinellum</i> Lab raised	<i>C. citrinellum</i> Lake Jilóá	<i>C. citrinellum</i> Lake Nicaragua	<i>C. citrinellum</i> Lake Apoyo	<i>C. zaisoum</i> Lake Apoyo
n	30	--	30	--	18	30	30	29	30
Standard length	141.81 \pm 25.62 (119.5-163.6)	138.85 \pm 24.40 (116.3-161.5)	136.33 \pm 22.94 (117.4-160.5)	135.65 \pm 32.02 (117.4-160.5)	136.21 \pm 28.72 (115.0-167.5)	128.94 \pm 32.94 (106.4-171.6)	146.75 \pm 19.62 (133.5-167.0)	123.73 \pm 25.70 (109.0-155.1)	123.57 \pm 22.78 (106.0-163.7)
Body depth	41.30 \pm 2.60 (38.2-43.9)	42.23 \pm 2.52 (39.3-45.2)	47.31 \pm 3.06 (44.3-49.9)	47.53 \pm 2.64 (44.3-49.9)	48.51 \pm 3.46 (46.1-51.1)	44.50 \pm 5.40 (39.0-49.8)	45.50 \pm 3.74 (41.6-48.9)	44.58 \pm 4.54 (41.7-49.7)	37.41 \pm 4.74 (32.2-41.4)
Face depth	24.95 \pm 2.66 (22.2-26.9)	25.51 \pm 2.64 (23.1-28.4)	26.42 \pm 3.60 (23.3-30.1)	26.55 \pm 3.40 (24.1-30.1)	24.85 \pm 2.36 (23.3-26.6)	23.85 \pm 2.84 (21.5-26.1)	25.52 \pm 3.00 (22.5-29.5)	23.39 \pm 4.56 (19.9-27.3)	20.21 \pm 1.94 (18.3-23.2)
Snout length	20.14 \pm 2.72 (17.9-23.3)	--	17.86 \pm 2.10 (15.5-19.5)	--	17.05 \pm 1.58 (15.6-18.4)	15.75 \pm 1.66 (14.1-16.9)	16.43 \pm 2.16 (13.0-18.0)	15.81 \pm 2.24 (13.9-18.0)	13.65 \pm 1.26 (12.4-15.1)
Cheek depth	14.66 \pm 1.54 (13.1-16.2)	14.94 \pm 1.48 (13.4-16.3)	15.73 \pm 1.88 (13.7-17.9)	15.80 \pm 1.78 (13.7-17.9)	15.31 \pm 1.32 (14.1-16.2)	14.63 \pm 1.66 (12.6-16.0)	15.46 \pm 1.64 (13.9-16.3)	15.77 \pm 2.30 (13.9-18.0)	12.44 \pm 1.66 (12.2-15.3)
Inter-orbital space	11.08 \pm 1.60 (9.4-12.2)	11.33 \pm 1.54 (9.7-13.8)	13.61 \pm 2.68 (11.2-17.8)	13.67 \pm 2.58 (11.2-17.8)	14.29 \pm 2.40 (12.2-16.6)	12.46 \pm 2.02 (10.2-14.2)	14.23 \pm 1.58 (12.6-16.3)	12.88 \pm 3.14 (10.5-15.6)	11.02 \pm 1.44 (9.8-12.3)
Caudal ped. depth	13.55 \pm 1.26 (12.0-14.4)	13.89 \pm 1.28 (12.4-15.4)	14.74 \pm 1.44 (12.8-16.2)	14.81 \pm 1.46 (12.8-16.2)	14.89 \pm 0.86 (14.4-15.6)	14.32 \pm 0.74 (13.4-14.9)	14.58 \pm 1.24 (13.6-16.0)	13.92 \pm 1.38 (12.1-15.3)	12.91 \pm 1.42 (11.7-14.5)
Caudal ped. length	12.68 \pm 1.62 (11.2-14.1)	12.98 \pm 1.60 (11.6-14.5)	13.78 \pm 1.52 (12.6-15.0)	13.86 \pm 1.48 (12.6-15.2)	12.58 \pm 1.20 (11.4-13.8)	14.11 \pm 1.42 (12.7-15.5)	13.12 \pm 1.50 (11.3-14.5)	14.03 \pm 2.28 (12.0-16.4)	15.64 \pm 2.60 (13.6-20.0)
Snout-vent	64.10 \pm 4.24 (60.3-67.9)	--	62.35 \pm 4.10 (56.8-68.5)	--	63.77 \pm 4.82 (60.9-70.7)	61.40 \pm 3.10 (57.7-65.0)	58.55 \pm 3.00 (56.7-62.3)	60.87 \pm 3.42 (58.0-66.0)	60.02 \pm 2.70 (58.0-61.7)
Snout-P ₁ insert.	43.38 \pm 2.92 (40.6-45.9)	--	39.97 \pm 3.38 (29.4-43.7)	--	39.79 \pm 1.76 (38.8-41.7)	39.02 \pm 1.32 (36.8-41.8)	37.65 \pm 3.76 (30.9-39.3)	38.19 \pm 4.08 (36.2-43.0)	36.39 \pm 2.18 (34.6-39.0)
Predorsal	45.15 \pm 3.50 (41.0-48.0)	--	44.64 \pm 2.24 (42.1-46.6)	--	43.30 \pm 2.08 (41.8-45.1)	42.41 \pm 3.96 (39.9-49.1)	42.59 \pm 4.12 (38.9-44.6)	42.02 \pm 4.64 (39.1-45.7)	38.59 \pm 2.30 (36.4-42.5)
Head length	40.28 \pm 7.10 (34.1-45.4)	39.38 \pm 2.90 (36.3-41.7)	40.21 \pm 2.08 (38.5-42.2)	39.76 \pm 1.90 (37.5-42.1)	40.24 \pm 1.60 (39.1-40.9)	37.79 \pm 2.06 (36.1-40.9)	37.03 \pm 2.30 (34.8-40.3)	37.20 \pm 3.32 (34.8-41.4)	35.15 \pm 1.90 (33.6-37.6)
Upper-jaw rictus	16.40 \pm 2.72 (12.8-18.7)	16.86 \pm 2.98 (12.8-19.6)	14.77 \pm 2.08 (13.4-17.1)	14.84 \pm 2.34 (14.2-17.6)	13.97 \pm 1.67 (12.2-15.4)	12.96 \pm 1.60 (12.4-14.8)	11.97 \pm 1.96 (7.9-13.1)	12.23 \pm 2.18 (10.7-13.3)	11.30 \pm 1.34 (10.0-12.9)
Width upper lip	7.02 \pm 2.48 (3.7-8.8)	7.20 \pm 2.54 (3.7-9.8)	2.88 \pm 3.74 (1.1-9.4)	2.91 \pm 3.80 (1.1-9.7)	2.29 \pm 0.74 (1.7-3.0)	1.70 \pm 0.58 (0.9-2.3)	2.13 \pm 0.88 (0.9-2.9)	1.87 \pm 0.92 (1.1-2.8)	1.76 \pm 0.58 (1.3-2.4)
Orbit max.	7.73 \pm 0.94 (6.5-8.6)	7.91 \pm 0.94 (6.7-8.8)	8.62 \pm 1.34 (7.5-10.4)	8.65 \pm 1.28 (7.5-10.4)	8.17 \pm 1.14 (7.2-9.0)	8.61 \pm 1.10 (7.5-10.0)	8.07 \pm 1.10 (6.7-8.9)	8.30 \pm 1.66 (7.7-8.9)	8.01 \pm 1.18 (6.9-9.8)

P ₁ length	28.10 ± 3.12 (24.2-30.5)	31.74 ± 3.02 (28.2-34.1)	29.93 ± 2.14 (28.5-31.5)	29.59 ± 2.58 (27.5-33.1)	33.31 ± 2.28 (31.1-35.4)	29.43 ± 4.12 (26.0-33.3)	27.39 ± 3.00 (24.6-30.8)
P ₂ length	30.81 ± 2.94 (26.8-35.6)	37.90 ± 4.88 (31.2-42.3)	37.13 ± 2.60 (34.0-39.3)	30.07 ± 4.22 (29.4-38.1)	35.92 ± 6.14 (27.7-41.9)	31.26 ± 3.58 (27.6-35.1)	27.97 ± 2.66 (24.2-30.8)
C length	27.81 ± 3.14 (25.2-29.0)	31.07 ± 3.90 (27.5-39.6)	31.35 ± 2.88 (28.4-33.7)	30.94 ± 3.18 (28.1-33.1)	33.03 ± 3.02 (29.3-35.0)	31.18 ± 4.08 (27.8-35.6)	28.53 ± 2.64 (26.7-31.1)
Ht. last D spine	14.15 ± 2.30 (12.2-16.3)	14.44 ± 2.20 (12.4-16.5)	15.01 ± 2.14 (12.9-17.2)	16.00 ± 3.26 (14.1-20.2)	16.95 ± 1.66 (14.7-18.7)	14.68 ± 3.04 (12.2-18.4)	13.80 ± 2.18 (12.3-16.8)
Ht. last A spine	14.55 ± 2.32 (12.3-16.6)	14.88 ± 2.38 (12.6-16.9)	15.44 ± 1.88 (13.7-17.7)	16.12 ± 3.00 (13.4-19.4)	17.10 ± 1.54 (15.9-18.6)	14.98 ± 3.38 (12.0-17.6)	13.99 ± 2.20 (11.7-16.4)
D. base	52.40 ± 3.84 (48.8-55.2)	53.58 ± 3.94 (49.8-58.5)	57.15 ± 3.20 (53.1-60.5)	58.05 ± 2.80 (56.0-60.2)	60.07 ± 3.94 (57.5-63.5)	58.37 ± 2.60 (56.1-61.0)	56.73 ± 3.10 (53.5-59.2)
A. base	24.33 ± 2.34 (22.0-26.5)	24.88 ± 2.24 (22.6-28.0)	26.88 ± 2.02 (25.3-29.1)	27.17 ± 1.56 (26.1-29.1)	29.27 ± 2.46 (26.7-31.1)	26.42 ± 2.16 (23.9-28.6)	25.03 ± 2.30 (22.8-27.3)
Lateral line scales	29.5 ± 1.36 (28-30)	--	29.53 ± 1.94 (27-31)	29.43 ± 3.46 (29-31)	29.80 ± 1.22 (28-31)	29.64 ± 1.96 (28-31)	30.56 ± 1.78 (28-33)
Dorsal scales	6.1 ± 0.80 (6-7)	--	5.90 ± 0.96 (5-7)	6.1 ± 0.90 (6-7)	6.40 ± 1.12 (5-7)	5.79 ± 1.10 (5-7)	5.86 ± 0.68 (5-6)
Ventral scales	11.26 ± 1.04 (11-12)	--	11.70 ± 1.40 (10-13)	11.63 ± 1.22 (11-13)	11.63 ± 1.10 (11-13)	11.27 ± 0.90 (11-12)	11.83 ± 1.18 (11-13)
Dorsal fin spines	16.86 ± 0.86 (16-18)	--	16.50 ± 1.24 (15-17)	16.86 ± 0.86 (16-17)	16.66 ± 9.4 (16-17)	16.44 ± 1.26 (15-17)	16.83 ± 1.18 (15-19)
Dorsal fin rays	10.55 ± 1.0 (10-11)	--	11.60 ± 1.54 (10-13)	10.73 ± 1.04 (10-12)	11.60 ± 1.44 (10-13)	10.79 ± 1.10 (10-12)	10.56 ± 1.12 (10-12)
Anal fin spines	6.90 ± 0.60 (6-8)	--	6.96 ± 0.36 (6-7)	6.73 ± 0.88 (6-7)	7.0 ± 0.0 (7)	6.72 ± 1.04 (5-7)	6.73 ± 1.16 (5-8)
Anal fin rays	7.07 ± 0.92 (7-8)	--	8.20 ± 1.42 (7-9)	8.16 ± 1.18 (7-9)	8.36 ± 1.42 (7-9)	8.06 ± 1.30 (5-9)	7.70 ± 1.06 (7-8)
P ₁ elements	15.86 ± 0.68 (15-16)	--	15.73 ± 1.38 (14-17)	15.90 ± 1.08 (15-17)	15.83 ± 0.9 (14-16)	16.27 ± 1.28 (15-18)	16.00 ± 0.0 (16)
Upper gill rakers	3.76 ± 1.34 (3-5)	--	3.72 ± 0.90 (3-4)	3.50 ± 1.00 (3-4)	3.30 ± 0.92 (3-4)	3.51 ± 1.14 (3-4)	3.26 ± 0.88 (3-4)
Lower gill rakers	10.20 ± 1.6 (9-12)	--	10.53 ± 1.46 (9-11)	9.72 ± 1.50 (7-11)	9.70 ± 1.28 (9-11)	8.75 ± 3.18 (7-13)	10.80 ± 1.52 (10-12)

it. In no case did Günther have more than three specimens in hand when he described a species. His decisions to recognize new species appear to have been guided primarily by the color of the specimens (yellow, orange, red, or greenish yellow), the size and shape of the lips, the length of the eighth spine in the dorsal fin, and the relationship between the length and depth of the free portion of the caudal fin. None of these is a discriminating character when all populations are considered. In his description of *H. lobocheilus*, however, Günther did recognize that the development of the lips may vary with age.

Meek had more material at hand when he studied these fishes, and he had field experience in Nicaragua. His frame of mind, illustrated by the following lengthy quotation about *C. citrinellum*, helps to set the stage for the rest of this article (Meek, 1907:122–123).

“Of all the species (of) fishes in these lakes, this one is by far the most variable. I made many repeated efforts to divide this material . . . in from two to a half-dozen or more species, but in all cases I was unable to find any tangible constant characters to define them. To regard them as more than one species meant only to limit the number by the material at hand, and so I have lumped them all in one.

“The fact that no red forms were found in Lake Tiscapa and Lagoon Jenicero led me to believe that there was possibly one form or species in which rubrism did not occur, but I found myself unable to discover any constant characters to separate it from the others, except on color alone. As to form, some individuals are very deep, others quite elongate. On some with normal color there are well defined lateral bars but no trace of a lateral spot, on other specimens of same size or larger, the lateral blotch is well defined. On some of the more elongate forms (of about 140 mm.) from Lake Nicaragua the nuchal hump is well developed, while on many of the larger individuals it is quite absent. There were no markings or peculiarities that I was able to correlate with sex or size. It is possible that more than one species should be recognized here, and no doubt such will some day be the case, especially if some enthusiastic student of fishes has at his command a far less amount of material than I have had the opportunity to examine.”

Meek was therefore cognizant of the apparently continuous variation. Yet he recognized Günther's species and added two more; these he distinguished on the basis of proportions and coloration.

Two recent reviewers (Astorqui, 1972; Villa, 1976) take as most probable that there are but two species, a thin lipped form *C. citrinellum* and a thick lipped *C. labiatum*. Villa detected other small but overlapping differences between the two, and suggested that they might yet prove to be the same species. Villa has examined most of the type specimens and assigned synonymies based mainly on the lip character.

We now present our view of the situation. We do not provide a traditional description of each species but rather refer to photographs of representative specimens and to extensive counts and measurements (Table 1); nor is a key provided. As will become clear further on, identification from gross morphology requires knowledge of the population from which the specimen has come.

Cichlasoma labiatum

1859. *Amphilophus froebelii* Agassiz, Proc. Boston Soc. Nat. Hist., 6: 408. Locale: Great Lakes of Nicaragua.
 1864. *Heros labiatus* Günther, Proc. Zool. Soc. London, 1864: 27, Pl. 4, Fig. 1. Locale: Lake Managua, Nicaragua.
 1869. *Heros lobocheilus* Günther, Trans. Zool. Soc. London, 6: 457, Pl. 75, Fig. 1. Locale: Lake Managua, Nicaragua.
 1869. *Heros erythraeus* Günther, Trans. Zool. Soc. London, 6: 457, Pl. 75, Fig. 2. Locale: Lake Managua, Nicaragua.
 1907. *Cichlasoma dorsatum* Meek, Field Columb. Mus., Zool. Ser., 7(4): 123. Type: Field Mus. Nat. Hist. 5971. Locale: Managua, Lake Managua, Nicaragua.

Nomenclature — *Amphilophus froebelii* Agassiz was inadequately described and lacks a type specimen (as determined by Karel F. Liem who diligently searched for it at Harvard). It also qualifies as a *nomen oblitum* under Article 23b of the International Code of Zoological Nomenclature since it has remained unused as a senior synonym in the primary zoological literature for more than a half century. It is true that Jordan *et al.* (1930: 422) recognized the genus *Amphilophus* Agassiz, indicating that *A. froebelii* is probably the same species as *Heros labiatus*, of later date. However, they did not synonymize *labiatus* with *froebelii* because of their uncertainty of the identity of Agassiz's species. They did not realize that *C. citrinellum* from the Great Lakes does not develop fleshy lips. *Amphilophus* is a valid supraspecific name by monotypy. Since stability in zoological nomenclature is desirable (Mayr *et al.*, 1971), we regard *A. froebelii* as a *nomen oblitum* and also as a senior synonym of the currently recognized and long-used *C. labiatum*.

Diagnosis — It can be distinguished from those *C. citrinellum* with which it is sympatric, and from other members of the section *Amphilophus* (Miller, 1966) by the combination of large lips, generally more slender body and pointed head, and shorter fins. Laboratory reared specimens of *C. labiatum* tend to have a slightly deeper body and lips only barely enlarged at the midpoint (Fig. 1). Approximately ten percent of the *C. labiatum* lack the species-typical markings and range in color from pink to red, often with irregular black patches. Some of the normal colored morphs also have black patches or, on the other hand, pale splotches (Fig. 1).

Common name — Red devil cichlid; a name used by aquarists. (We would have preferred simply red devil, but that name has been used by Clemens and Wilby (1946) to refer to the cryptocanthodid fish *Lyconectes aleutensis* Gilbert, a totally unrelated marine teleost fish.) In Nicaragua the fishermen seldom distinguish between the various middle sized cichlids, calling them simply *mojarras*. This species, however, is sometimes called *mojarra picuda* (Villa, pers. comm.).

Distribution — Apparently this species is confined to the Great Lakes of Nicaragua and scarcely penetrates the rivers.

Cichlasoma citrinellum

1864. *Heros citrinellus* Günther, Proc. Zool. Soc. London, 1864: 153. Locale: Lake Nicaragua, Nicaragua.
 1877. *Heros basilaris* Gill and Bransford, Proc. Phila. Acad. Nat. Sci., 29: 182. Regan, Ann. Mag. Nat. Hist., 16, ser. 7: 317. Locale: Lake Nicaragua, Nicaragua.

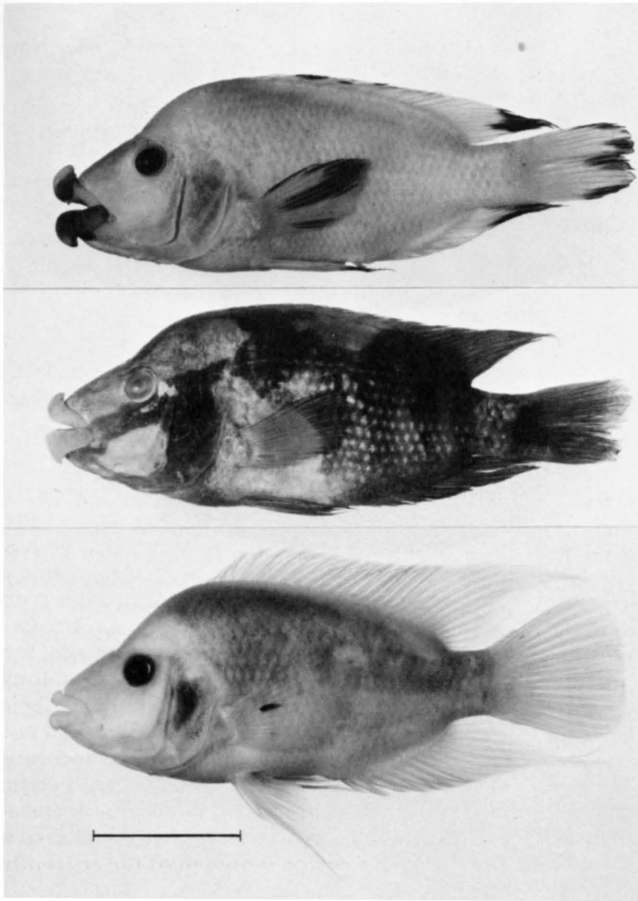


FIG. 1. Three specimens of *C. labiatum*. Top: A red morph from Granada, Nicaragua. Middle: A blotchy specimen from Granada, Nicaragua. Bottom: A red morph raised in the laboratory from parents collected from Lake Nicaragua near Granada. The scale indicates 5 cm.

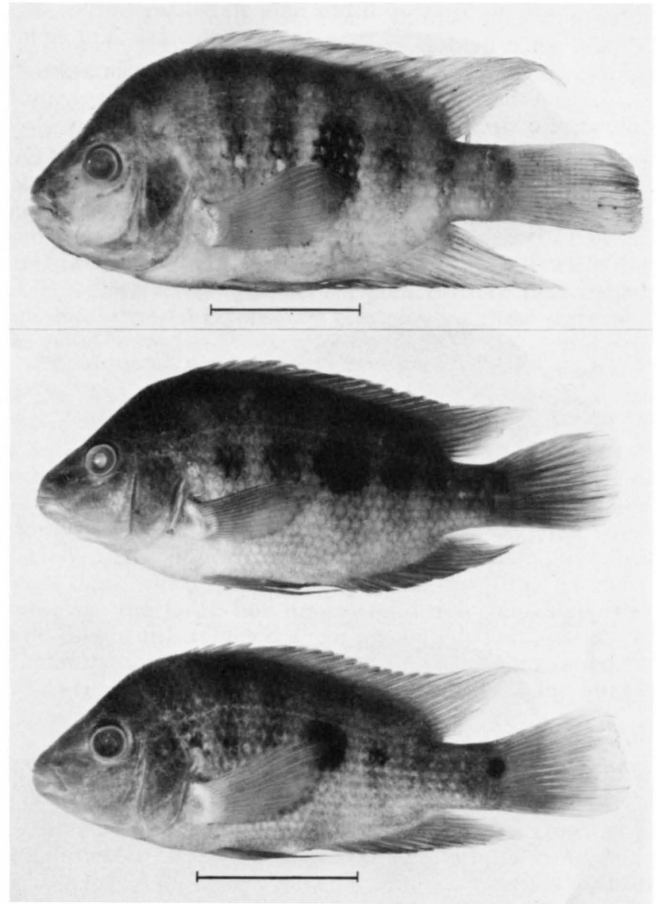


FIG. 2. Three specimens of *C. citrinellum* from, top to bottom, Granada, Lake Jiloá and Lake Apoyo, Nicaragua. The scales indicate 5 cm.

1907. *Cichlasoma granadense* Meek, Field Columb. Mus., Zool. Ser., 7(4): 121. Type: Field Mus. Nat. Hist. 5951. Locale: Granada, Lake Nicaragua, Nicaragua.

Diagnosis — *C. citrinellum* from the Great Lakes of Nicaragua, compared to *C. labiatum*, has thinner lips, a deeper body, steeper forehead, and higher fins; their colorful morphs range from white to yellow through orange (Fig. 2, 3). In the crater lakes, where there are no *C. labiatum*, these differences in morphology and coloration break down in various ways (Table 1, and see below); some individuals have fleshy lips (Fig. 4), more slender bodies and higher fins (Fig. 2), and even red morphs. Some populations are not polychromatic (see Barlow, 1976).

Common name — Midas cichlid, in recognition of the occasional gold morphs.

Distribution — The Midas cichlid is widely distributed in the lakes of Nicaragua but uncommon in the rivers. It is the most ubiquitous cichlid in the lakes where it occurs, and probably makes up the largest biomass of any single cichlid species in those lakes (Barlow, 1976). It has also been taken from coastal lagoons in northwestern Costa Rica (Gilbert and Kelso, 1971).

Cichlasoma zaliosum Barlow sp. nov.

Description of adult specimens — The measurements of 30 specimens (Table 1) plus the photograph of the type specimen (Fig. 5) constitute the bulk of the description. Barlow is responsible for the name and the description.

Dorsal fin XV–XIX, 10–12; anal fin V–VIII, 7–8; pectoral fin 16; lateral scale rows 28–33. Body slender, depth 32 to 41% of standard length; face not deep, 18–23%; head short, 34–38%; paired fins short and median fins low (Table 1).

Teeth in single outer row, conical and brown at tips, largest and most recurved toward front, decreasing rapidly in size and becoming straighter toward side of jaw. Inside this row many small conical teeth with colorless tips only just evident above gums. Tongue free and pointed.

Color of preserved specimen brownish with black markings. Conspicuous spot on body notably wider than high, often fusing with spots ahead of and behind it, when present, to form a stripe. In life, body bluish or greenish gray with black markings. When breeding, seven black vertical bars on a pale body, each bar shaped slightly like an hourglass (Fig. 6).

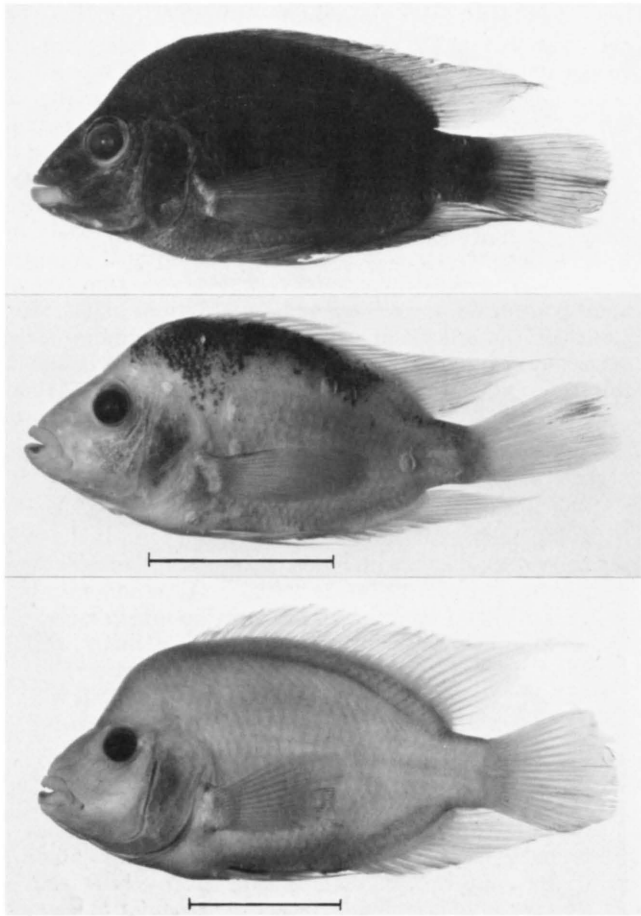


FIG. 3. Three specimens of *C. citrinellum*. Top: A normal morph collected from a region of black lava reefs in Lake Masaya, Nicaragua. Middle: A gold morph from the same collection. Bottom: A gold morph raised in the laboratory from parents collected from the same place. The scales indicate 5 cm.

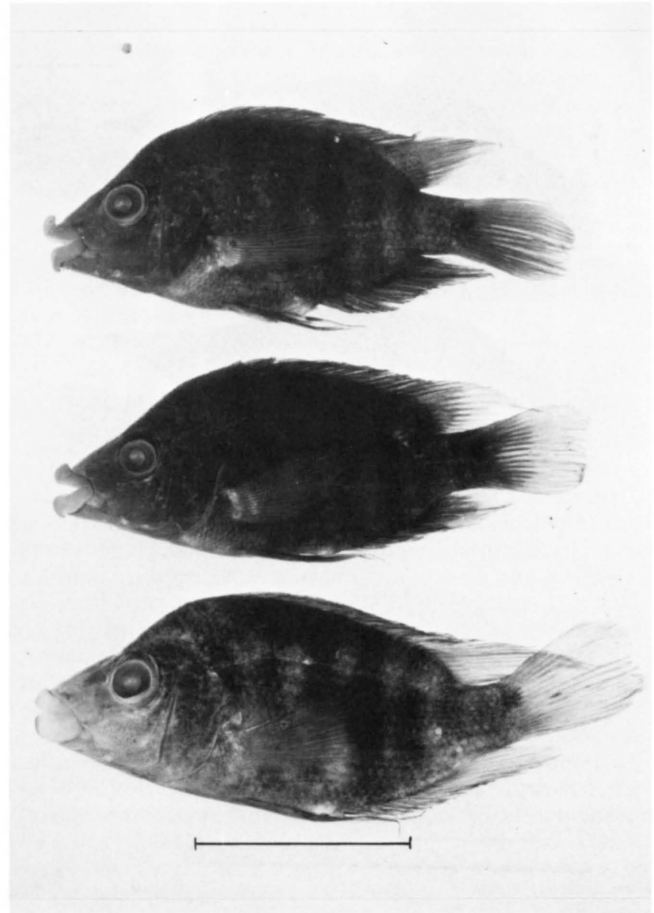


FIG. 4. Three specimens of *C. citrinellum* from the same collection from Lake Masaya, Nicaragua, as the fish in Figure 3. Note the variation in lip morphology and the resemblance in this feature to that of *C. labiatum* (Fig. 1). The scale indicates 5 cm.

Diagnosis — Within *Cichlasoma*, a member of the *Amphilophus* group as designated by Miller (1966: 792; originally as *Astatheros* by Regan, 1906–08: 23). It differs from other species in that group in its very elongate form and the horizontally ovoid dark spot on its side.

Scientific name — *zale* means wave borne, in reference to the open-water habit of this new species; *ios* is for arrow, drawing attention to its most distinctive feature, the unusually slender body.

Common name — Arrow cichlid, for its slender shape.

Holotype — a mature female (Fig. 5), 129.8 mm S.L., collected from Lake Apoyo, Nicaragua, by G. W. Barlow, D. L. G. Noakes, and G. H. Meral, on 2 August, 1969, and deposited at the California Academy of Sciences, San Francisco, as CAS 29104.

Paratypes — Ten specimens, CAS 29105, 111.5 to 130.8 mm S.L., plus ten more from the same collection, deposited in the U.S. National Museum, USNM 212181, 124.0 to 162.0 S.L.

Distribution — This species is apparently confined to Lake Apoyo, Nicaragua. Fish similar in appearance have been seen underwater in Lake Jilpá, but none has been collected from that lake that can be identified as *C. zaliosum*.

Behavior — This is the only cichlid in Central America we know of that has adapted to life in the open-water region of

a lake. It has been observed to strike at the surface in the center of Lake Apoyo (a very deep crater lake of unmeasured depth) where other cichlid species are never seen. It is most abundant, however, just off shore where the water deepens; a diver drifting at the surface there soon attracts a number about him. *Cichlasoma zaliosum* can also be seen near the bottom mingling with *C. citrinellum*. This provides the opportunity to demonstrate a trenchant difference in behavior between the two species: when approached, *C. citrinellum* escapes by swimming toward the bottom and then into crevices, or toward yet deeper water while following the bottom. In contrast, *C. zaliosum* flees by swimming up away from the bottom toward open water.

We have not studied the gut contents or the feeding behavior of *C. zaliosum*. Its relatively small mouth and open-water habits suggest that it feeds on plankton, downed insects, and perhaps occasionally on small fish.

When reproducing, a pair of *C. zaliosum* occupies a small cave in the reef (Fig. 6). The major features of the reproductive behavior are essentially the same as in *C. citrinellum* (Barlow, 1976). While many pairs of *C. citrinellum* were observed breeding in Lake Apoyo only eleven pairs of *C. zaliosum* were found. In every instance each fish was paired with a member of its own species. Moreover, Jeffrey R.

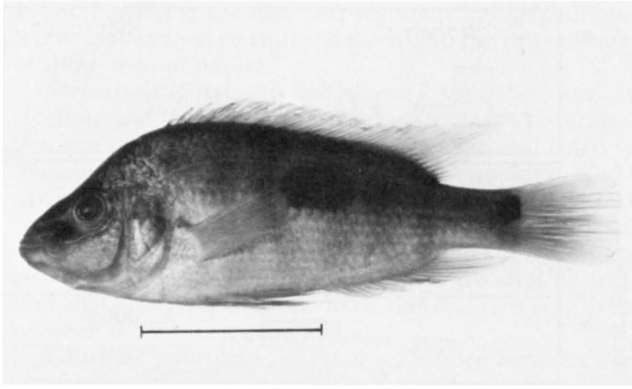


FIG. 5. The holotype of *C. zaliosum* (CAS 29104), collected from Lake Apoyo, Nicaragua. The scale indicates 5 cm.

Baylis has found in this laboratory that, when given a choice, each of the two species mates only with other members of its species. It is possible, however, to force heterospecific pairing when no choice is given. Viable adult hybrids have been produced (Baylis, in prep.).

Some specimens from Lake Apoyo are difficult to assign to one species or the other, suggesting the possibility of hybrids. At small sizes the two species are extremely difficult to distinguish from one another because the juveniles

of *C. citrinellum* are slender and thus more similar in body shape to *C. zaliosum*.

Comparisons across species and populations:

Effect of environment. — Laboratory raised specimens of *C. citrinellum* from Lake Masaya stock differ from fish collected in Lake Masaya, but not greatly (Table 1). For example, the laboratory raised fish tend to have a deeper body, not so deep head, smaller mouth, lips and eyes, generally shorter elements in the pectoral fins, and a longer base of the dorsal fin. There was surprisingly little difference in the meristic characters. Parallel differences were detected in laboratory raised *C. labiatum* (Fig. 1), but these were not analyzed in detail.

The most conspicuous effect of captivity is that on the fleshy lips. In nature all *C. labiatum* have fleshy lips, although the degree of development varies considerably (Fig. 1, 7). In some populations of *C. citrinellum*, but not those of the Great Lakes, a few individuals have fleshy lips (Fig. 4, 7). When such fish were brought into the laboratory the lips slowly regressed. In *C. citrinellum* the lips receded completely; fleshy lipped individuals became indistinguishable from those which had always had thin lips. In *C. labiatum*, however, the large lips never completely regressed; the wild-caught fish retained a just perceptible knob-like swelling at the midpoint of the upper lip. Laboratory raised *C. labiatum* also possess a slight knob on the upper lip, but *C. citrinellum* do not.

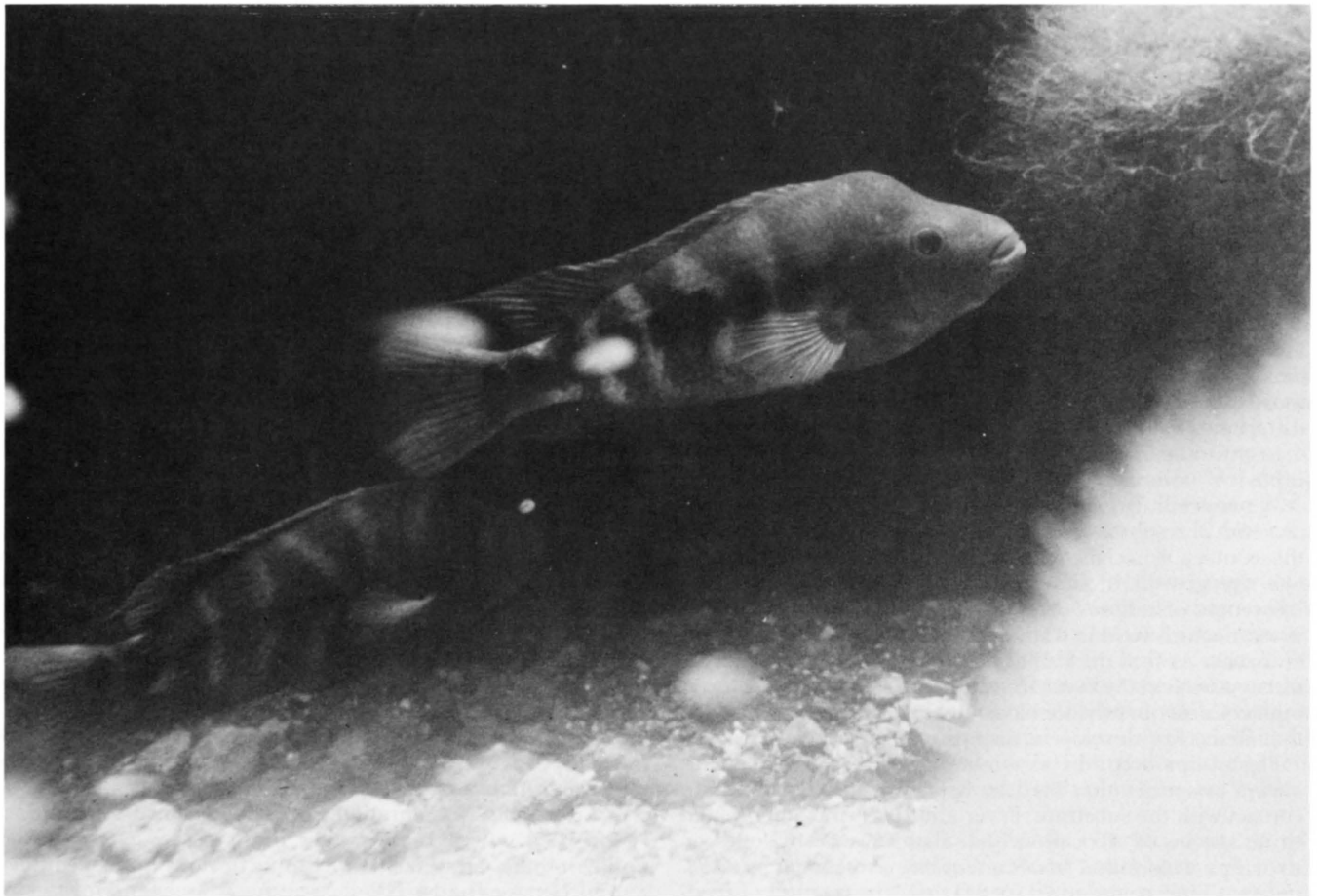


FIG. 6. A pair of *C. zaliosum* guarding their free-swimming young in Lake Apoyo, Nicaragua. The male is the upper right fish with the visible nuchal hump.

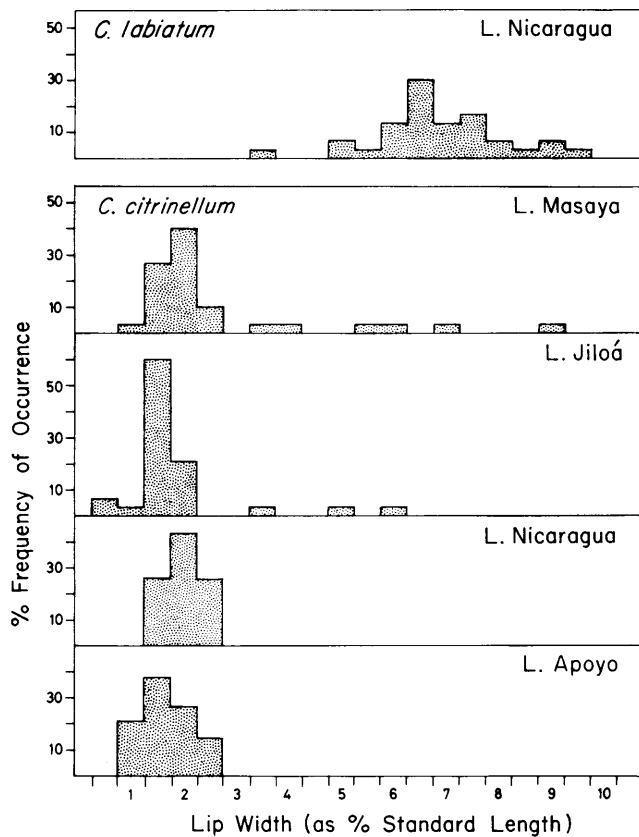


FIG. 7. Histograms comparing the frequency of occurrence, as percentages, of lips of different relative thickness for one population of *C. labiatum* and four of *C. citrinellum*. Each population is identified by the name of the lake, to the right.

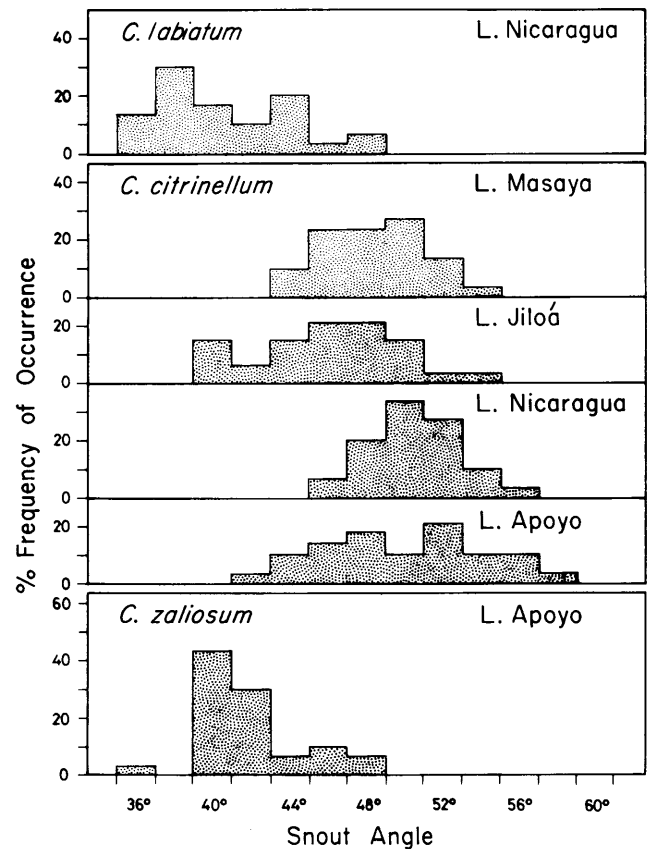


FIG. 8. Histograms comparing the frequency of occurrence, as percentages, of different snout angles for one population of *C. labiatum*, four of *C. citrinellum*, and one of *C. zaliusum*. Each population is identified by the name of the lake, to the right.

Other kinds of fishes show comparable changes in morphology in captivity. For example, a sea horse loses its dermal cirri when put into an aquarium (Herald and Rakowitz, 1951). The pharyngeal mill of an African cichlid, *Astatoreochromis alluadi*, reared in captivity differed radically from those of wild fish (Greenwood, 1965). The reasons for these differences are not known, but in the case of *A. alluadi* it was thought to be associated with different textures of food in captivity.

When feeding, *C. labiatum* bring their mouths into contact with the substrate, often vigorously. We reasoned that this contact, especially with abrasive material, might stimulate the growth of lips, much as friction stimulates development of calluses on human hands. Experiments were done in which food in a stiff agar mix was applied to rough lava rock. At first the fish abraded their lips, but soon they learned to strip the food from the lava rapidly and without injury. Consequently, we have not been able to demonstrate that fleshy lips develop in response to irritation.

Fleshy lips occur in a number of kinds of fishes, and always in species that feed by bringing their mouths into contact with the substrate. Fryer and Iles (1972) mentioned three species of African cichlids that have fleshy lobes on their lips (*Lobochilotes labiatus*, *Haplochromis euchilus*, and *H. chilotes*). They commented (p. 81) that "the manner of feeding of *H. euchilus* leaves little doubt that (the lobes) are sensitive structures which are used to detect the prey by

touch. When feeding *H. euchilus* places these lobes against the rock, presumably 'feeling' for its food. Once detected, the prey is picked off by the very simple teeth." Greenwood (1973) offered a slightly different explanation for the fleshy lips of *H. chilotes* (which are similar to those of *C. labiatum*). The hypertrophied lips were said to "serve as shock absorbers when the fish forces its snout against the rock or wood surface into which the mayfly larvae had bored."

We propose that the fleshy lips act as a gasket forming a seal around the mouth of the fish when it strikes the substrate so it can better suck up objects there. Note that fish with such lips, that feed from the substrate, include both herbivores and carnivores. We asked J. R. Baylis to observe thick lipped *C. citrinellum* in Lake Jiloá with this point in mind. He reported that such individuals fed predominantly by thrusting their snouts into crannies. Such behavior is consistent with the hypotheses suggested by Fryer and Iles, by Greenwood, and by us. All three factors could be operating. We favor the gasket hypothesis because it also explains hypertrophied lips in algae-scraping species.

Coloration. — Coloration, too, changes in captivity (Barlow, 1976). In all three species, orange fades to lemon, and red to pink, but the change is only obvious in the red devil and Midas cichlids. This change is a consequence of lack of pigments in the diet. The orange color derives from carotene and red from two canthaxanthins (Webber *et al.*,

1973). Fortifying the diet with pigments has helped, but it has not maintained or restored the fish to the full saturation of those seen in nature.

Comparisons of sympatric and allopatric populations of C. citrinellum and C. labiatum. — The most obvious conclusion that emerges when comparing these two species (Table 1) is that they are least alike where they are sympatric. The *C. citrinellum* from Lake Nicaragua differ most from *C. labiatum*, all populations considered, in sixteen of thirty-one characters. They differ primarily in the thickness of lips but also appreciably in the shorter snout to pectoral-fin insertion of *C. citrinellum*. Even here there is overlap, except between the sympatric populations.

A further point of maximum difference between these two species in the Great Lakes is that the bases of the dorsal and of the anal fin are longer in *C. citrinellum*. Using these two characters we have calculated an index that accentuates the differences: the distance from the snout to the insertion of the pectoral fin can be expressed as a percentage of the base of the dorsal fin (Table 2). There is some overlap when one calculates the maximum and minimum possible values, although the sympatric populations do not overlap. In practice, the index identifies most but not all allopatric specimens. Use of the index has to be tempered with a consideration of other characters and geographic source.

Table 1 shows that sympatric *C. citrinellum* tend toward a wider (interorbital space), shorter head and deeper body, smaller mouth (shorter jaw), fewer gill rakers, and longer fin elements. There are differences, too, in the hues expressed in polychromatism: *C. citrinellum* in the Great Lakes shows white through yellow and orange whereas *C. labiatum* exhibits pink through red.

The population of *C. citrinellum* the next most different from *C. labiatum* is the one from Lake Masaya. It shows greater depths of body, face, and cheek. Yet some *C. citrinellum* from Lake Masaya, and also from Lake Jiloá, have features in common with *C. labiatum*. For example, a few individuals have fleshy lips (Fig. 4, 7) and low foreheads (Fig. 4, 8). In Lake Masaya there are also a few red morphs. Some of the *C. citrinellum* of Lake Masaya, and some from Lake Jiloá, almost grade into *C. labiatum*. But we have found no specimens from either of those two lakes that are clearly assignable to *C. labiatum*.

Comparisons of C. zaliosum with C. labiatum and C. citrinellum. — *Cichlasoma zaliosum* resembles *C. labiatum* without big lips (Fig. 1, 5). Both are elongate, have low snout angles (Fig. 8), and reduced lengths of fin elements. Nonetheless, compared to all species and populations, *C. zaliosum* differs most from *C. labiatum* in twelve of thirty-one characters. In contrast, *C. zaliosum* differs most from *C. citrinellum* from Lake Nicaragua in only seven characters, and from those in Lake Masaya in six. Most surprisingly, *C. zaliosum* differs most from sympatric *C. citrinellum* in only two of the thirty-one traits, namely, width of cheek and number of gill rakers. In spite of its elongate form, *C. zaliosum* has the basic body plan and meristics of *C. citrinellum* (Table 1, 2).

A rather surprising difference between *C. zaliosum* and *C. citrinellum* is in their palatability. The flesh of *C. citrinellum* is firm, white, and tasty; that of *C. zaliosum* is soft, darker, and of inferior flavor.

Variation of gill rakers in C. citrinellum from Lake Apoyo. — Counting gill rakers of fish from various lakes presented no problem until we encountered fish from Lake Apoyo. The adult's typical count would be 4 + 9. Exceptional adults were found with low number of gill rakers; the anterior-

TABLE 2. The snout to pectoral-fin distance, expressed as percent of length of dorsal-fin base. Minima and maxima were calculated from the ranges of each population, *not* from individual fish.

Population	Mean	Minimum	Maximum
<i>C. labiatum</i>			
Lip included	83	73	94
lip corrected	81	69	92
<i>C. citrinellum</i>			
Lake Masaya			
lip included	71	49	82
lip corrected	69	49	82
lab raised	66	62	71
Lake Jiloá	67	61	75
Lake Nicaragua	63	48	68
Lake Apoyo	65	59	77
<i>C. zaliosum</i>			
	63	59	73

most gill rakers are not evident, producing low counts, e.g., 3 + 6. The other gill rakers in such individuals are neither as large nor as complexly developed as in fish with typical counts.

Another type of variation lies in the tendency to develop spatulate gill rakers. Specimens less than 130 mm S.L. usually have rather lance-shaped gill rakers. The counts were usually slightly lower in the fish with spatulate gill rakers (e.g., 3.22 + 8.55 = 11.77 for spatulate vs. 3.65 + 8.85 = 12.50 for lanceolate fish in two small samples). Comparing a number of specimens, we found evidence of fusing or joining of rakers in the spatulate condition.

The gill-raker counts in the Lake Apoyo Midas cichlids, therefore, may be lessened in two ways. One is through reduction and the other through fusion. The adaptive significance of this phenomenon, and of the shift from lanceolate to spatulate gill rakers with growth, is not understood (for an interesting discussion of the variability of structures associated with feeding, see Rothstein, 1973).

DISCUSSION

One of the more interesting findings in this investigation is the apparent character shift (Grant, 1972) revealed by comparing the sympatric populations of *C. citrinellum* and *C. labiatum* in the Great Lakes of Nicaragua. While *C. labiatum* is restricted to the Great Lakes, *C. citrinellum* occurs in many other lakes. But the differences between the two species are most pronounced where they are sympatric, and most strikingly so with regard to the fleshy lips of *C. labiatum*. This doubtless reflects the separation in feeding habits between the two species there. *C. citrinellum* is a generalized feeder (Barlow, 1976), whereas *C. labiatum* probably feeds more from crannies.

It would be especially rewarding to determine what stimulates the lips to hypertrophy. We could then explain the variation in fleshiness both in *C. labiatum* and in *C. citrinellum*. Particularly intriguing would be an appreciation of the extreme variation in some populations of the Midas cichlid: Do all the fish in those populations have the capacity to develop big lips, but only some feed in a way that stimulates their growth? Or do only some individuals have the genetic potential for such a response (see comments on hybrids, below)?

The *C. citrinellum* in Lake Apoyo exist in a contrastingly different situation. While the Great Lakes have a relatively rich and diversified fish fauna, including several species of cichlids, Lake Apoyo is depauperate and lacks potential competitors with *C. citrinellum* (Barlow, 1976). There is

some evidence of character release (Grant, 1972), although admittedly it is not impressive. The *C. citrinellum* there are more variable in their gill-raker counts and also in their head profile (Fig. 8).

The populations of *C. citrinellum* in Lakes Masaya and Jiloá present a different problem. They coexist with a number of other potentially competing cichlids. But instead of reduced variability, they show, in many traits, the greatest variability of any of the populations. However, all of these variable traits are ones in which they most resemble *C. labiatum*, as for example in the sporadic occurrence of fleshy lips (Fig. 7), low snout angle (Fig. 8), certain body proportions (Table 2) and, in Lake Masaya, red morphs.

The evidence suggests introgressive hybridization. We suspect that both Apoyo and Jiloá were settled by the two species but that a relatively small number of *C. labiatum* was present, and that these hybridized with *C. citrinellum*. There may also be environmental differences in the crater lakes that work against *C. labiatum*. However there is apparently no strong selective pressure against the genes of *C. labiatum*; their presence at a low frequency may even be favored.

There is also the question of the affinity of *C. zaliosum*. Superficially it resembles *C. labiatum* with its elongate body, pointed head, and low median fins. This resemblance, however, appears to be a consequence of convergence, such changes in morphology being adaptive to greater mobility and thus life in open waters. The arrow cichlid has a body plan, nonetheless, that is fundamentally like that of the Midas cichlid. Were it not so elongate, it would be extremely difficult to distinguish from *C. citrinellum* in Lake Apoyo. Beyond body shape, the two species differ most in the shape and number of gill rakers (although they overlap), which may reflect some partitioning of the trophic resources. They also differ in details of their color patterns.

We have no compelling evidence bearing on the origin of *C. zaliosum*. The obvious alternatives are successive invasions of Lake Apoyo, perhaps aided by humans (Astorqui, pers. comm.), or sympatric origin. But if the two species had originated in different lakes we might expect them to differ more from one another. Instead, they are the most alike. Because of this, we hypothesize that the Midas cichlid in Lake Apoyo became polymorphic as it occupied the various and diverse habitats there in the absence of competitors. Disruptive selection (see review by Thoday, 1972) then came into operation as the intermediate phenotypes were selected against. Because a few intermediates are still occasionally encountered, *C. zaliosum* appears to be in the terminal phase of coming into being, although it clearly warrants being recognized as a separate species.

A few words are in order about the generic allocation of the species considered here. Obviously the genus *Cichlasoma* needs revision into genera or subgenera of manageable sizes but ones that also reflect natural assemblages. The three species we have treated are doubtless congeneric because they are so similar that it is difficult to identify specimens without knowledge of the population from which they came. Yet some ichthyologists have divided these species into separate genera (see comments in Villa, 1976). Since the three species considered here may be closely allied to yet other species outside Nicaragua and hence beyond the reach of our work, there is no point at this time in attempting generic allocation at a finer level than *Cichlasoma*.

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SUMMARY

Within this group (section *Amphilophus*) of Nicaraguan cichlid fishes, we recognize two of the eight named species, *Cichlasoma labiatum* (Günther) and *C. citrinellum* (Günther). A new species from Lake Apoyo, *C. zaliosum* Barlow, is described. The red devil cichlid (*C. labiatum*) occurs only in the Great Lakes, but the Midas cichlid (*C. citrinellum*) is found in most of the surrounding lakes as well, and also in Costa Rica; where the two species are sympatric they differ most from one another. In Lakes Masaya and Jiloá some individuals of *C. citrinellum* show features of *C. labiatum*, apparently as a result of introgressive hybridization. *Cichlasoma zaliosum* bears a superficial resemblance to *C. labiatum* due to elongation, but a detailed analysis of morphometric features indicates a closer relationship to sympatric *C. citrinellum*.

RESUMEN

Dentro de este grupo (sección *Amphilophus*) de cíclidos nicaragüenses reconocemos dos de las ocho especies nominales, *Cichlasoma labiatum* (Günther) y *C. citrinellum* (Günther), y se describe una nueva especie de la Laguna de Apoyo, *C. zaliosum* Barlow. *C. labiatum* se encuentra solamente en los grandes lagos, pero *C. citrinellum* se encuentra también en los lagos vecinos, y en Costa Rica. Donde ambas especies son simpátricas es donde más difieren entre sí. En las lagunas de Masaya y Jiloá algunos ejemplares de *C. citrinellum* presentan características de *C. labiatum*, aparentemente debido a hibridación introgresiva. *Cichlasoma zaliosum* se asemeja superficialmente a *C. labiatum*, pero un análisis morfométrico detallado indica que está más relacionado a los ejemplares simpátricos de *C. citrinellum*.

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