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Description of two new species of the Midas cichlid complex (Teleostei: Cichlidae) from Lake Apoyo, Nicaragua

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Abstract.—Two species belonging to the *Amphilophus citrinellus* (Günther, 1864) species complex endemic to Lake Apoyo, Nicaragua are described. Both species exhibit unique phenotypic characters that have not been found in other members of the species complex. Furthermore, they breed assortatively in Lake Apoyo and can readily be distinguished in the field from all other described species found in that lake. Including the two herein described species, six species that form a monophyletic species assemblage within the Midas cichlid complex inhabit Lake Apoyo, Nicaragua.

Midas cichlids are monogamous substrate spawners that form pairs only during breeding season, when they aggressively defend their territory and fry. The name Midas cichlid derives from the fact that, in some Nicaraguan lakes, brightly coloured *Amphilophus* individuals can be found that have lost the melanophores that build patterns of black bars, yielding individuals ranging in color from white to orange or red, and collectively termed ‘gold.’ They are found in varying abundance in more turbid lakes but not in Lake Apoyo (Barlow 1976).

The Midas cichlid complex makes an excellent study subject for evolutionary biology and taxonomy. Historically, Barlow & Munsey (1976) recognized only three species in the Midas cichlid complex; however, we are now able to differentiate several species. Field observations using SCUBA, extensive collecting efforts, and proper treatment of collected material for museum collections allowed the description of three endemic species from Lake Xiloá in 2002 and three endemic species from Lake Apoyo in 2008 (Stauffer & McKaye 2002, Stauffer et al. 2008). Findings from molecular genetic studies suggested that both Lake Xiloá and Lake Apoyo contained other undescribed *Amphilophus* and that all examined individuals in one lake are closely related to each other based on microsatellite genotyping of three loci (McKaye et al. 2002). This conclusion was supported by mitochondrial DNA sequence data, which demonstrated that fishes from Lake Apoyo were more closely related to each other than to fishes from other lakes (Barluenga & Meyer 2004, Barluenga et al. 2006).

The recent origins of Lakes Xiloá (<10,000 bp, BANIC 1977) and Apoyo (<23,000 bp; BANIC 1977, Sussman 1985) coupled with their endemic Midas cichlids has inspired biologists to speculate and investigate the possibility of sympatric speciation (Barlow 1976, McKaye et al. 2002, Barluenga et al. 2006,

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but see Schliewen et al. 2006). The small size of Lake Apoyo (20.92 km^2 surface area) and its rather homogeneous habitat with syntopic breeding of its endemic *Amphilophus* species (McCrary & López 2008), support the theory that sympatric speciation has occurred (Wilson et al. 2000, Barluenga et al. 2006).

A complete taxonomic inventory of the region is essential to discover the biologically most meaningful explanations of the phylogenetic history within the Midas cichlid complex. We provide here a description of the fifth and sixth members of Lake Apoyo's endemic species of *Amphilophus*.

Site Description

Lake Apoyo is situated within an almost circular volcanic caldera of 36.32 km^2, about 4 km west of Lake Nicaragua. The lake's water surface occupies 20.92 km^2; its diameter measuring more than 4 km with a maximum depth 178 m (CIRA 2008). The caldera was created by a series of volcanic eruptions, the last one occurred about 23,000 years ago (Sussman 1985). The water level of Lake Apoyo is 70 m above sea level (masl), with effluents limited to subterranean filtration through highly permeable geologic layers toward neighboring Lake Nicaragua (31 masl; 5.4 hm^3 pa). The lake has undergone a 15 m decrease in water level since 1950 (CIRA 2008). The water of oligotrophic Lake Apoyo is warm (27–29.5°C), alkaline (pH = 8.1), and rather saline with a conductivity of 3310 µS and Na^+ of 640 mg/l (Parello et al. 2008).

Compared to some of the smaller volcanic crater lakes in Nicaragua, the fish fauna of Lake Apoyo is depauperate (Waid et al. 1999) and the native forms include: one atherinid *Atherinella sardina*, one poeciliid *Poecilia* cf. *sphenops*, and several cichlids: *Parachromis managuensis* and at least six (four of which have been described) endemic species of the genus *Amphilophus*. *Gobiomorus dormitor* and at least three species of tilapias have been introduced in the past two decades (Waid et al. 1999, McCrary et al. 2007). There are no open-water connections to any other water body; thus, it is speculated that these fishes might have entered the lake via humans, piscivorous birds, and/or climatic events (Stauffer et al. 2008).

Materials and Methods

We collected fishes in three field trips during the dry seasons (Nov–Apr) of 2006/2007, 2007/2008, and 2008/2009. Individuals were caught by SCUBA divers using harpoons following field identification. Fishes were anesthetised, preserved in 10% formalin, individually tagged, and fin-samples taken for molecular genetic studies. Photos of live individuals were taken and notes on coloration made in the field. Fins were pinned, fishes preserved in 10% formalin, and permanently preserved in 70% ethanol. Counts and measurements follow Barel et al. (1977) and Stauffer (1991, 1994), except that head depth was measured from the hyoid symphysis to the top of the head at 90° angle to the horizontal body axis. Measurements are point-to-point using a dial calliper to the nearest 0.01 mm, and taken from the left side of specimens. Following abbreviations are used in the tables:

ADAA—anterior insertion of dorsal fin to anterior insertion of anal fin;
PDPA—posterior insertion of dorsal fin to posterior insertion of anal fin;
ADPA—anterior insertion of dorsal fin to posterior insertion of anal fin;
PDAA—posterior insertion of dorsal fin to anterior insertion of anal fin;
PDVC—posterior insertion of dorsal fin to ventral portion of caudal fin;
PADC—posterior insertion of anal fin to dorsal portion of caudal fin;
ADPV—anterior insertion of dorsal fin to insertion of pelvic fin;
PDPV—posterior insertion of dorsal fin to insertion of pelvic fin.

Additionally, we examined the caudal skeletons of ten individuals of each of the six Lake Apoyo species of *Amphilophus* using high-resolution x-ray pictures. We only used specimens with complete and straight caudal-fin rays and counted the number of: principal (segmented) rays, dorsal and ventral procurrent rays (sensu Chakrabarty 2007), procurrent and principal rays inserting at the haemal spine of the preural centrum (sensu De Schepper et al. 2004), principal rays of the parhypural (sensu Chakrabarty 2007), and principal rays inserting in each hypural. We also measured the length of the first ventral principal caudal-fin ray and the length of the lower central caudal-fin ray.

Since sex of Midas cichlids can only be determined by invasive methods or direct observation of breeding pairs, we did not group individuals according to sex and did not test for sexual dimorphism in morphometrics. Institutional abbreviations follow Leviton et al. (1985). Morphometric data were analyzed using sheared principal component analysis (SPCA), which factors the covariance matrix and restricts size variation to the first principal component (Humphries et al. 1981, Bookstein et al. 1985). Meristic data were analyzed using principal component analysis (PCA) in which the correlation matrix was factored. Comparisons among species were illustrated by plotting the sheared second and third principal components (2SPCA, 3SPCA) of the morphometric data or the 2SPCA and first principal components (PCA) of the meristic data. The Statistical Analysis System (SAS) software was used to calculate both PCA and SPCA.

As the monophyly of Lake Apoyo's species of *Amphilophus* flock has been hypothesized previously (Barluenga & Meyer 2004, Barluenga et al. 2006) and tested thoroughly including all known species and the two new species (Geiger et al. pers. obs.), data of the new species were compared to only those species of *Amphilophus* native to Lake Apoyo. To that purpose, we obtained meristic and morphometric data for the holotypes and seven paratypes each of, *A. astorquii*, *A. chancho*, and *A. flaveolus* as well as eight paratypes of *A. zaliosus* (see comparison material).

Results

Amphilophus supercilius, new species
Fig. 1, Table 1

Holotype.—ZSM 38821, adult male, 166.6 mm SL, 27 Feb 2007, Spanish Coast, Lake Apoyo NE shore, Nicaragua, 11°56′5.43″N, 86°00′46.88″W, DNA tag: 247.

Paratypes.—All paratypes were collected from Lake Apoyo, Nicaragua. ZSM 37347, 163.6 mm SL, 11 Feb 2008, rock formation called "los hongos," S shore, 11°54′20.79″N, 86°01′45.40″W, DNA tag: 735. ZSM 37348, 142.4 mm SL, 11 Feb 2008, rock formation called "los hongos," S shore, 11°54′20.79″N, 86°01′45.40″W, DNA tag: 723. ZSM 37351, 2, 157.8–166.7 mm SL, 11 Feb 2008, rock formation called "los hongos," S shore, 11°54′20.79″N, 86°01′45.40″W, DNA tags: 728 & 736. ZSM 38751, 143.2–146.3 mm SL, 22 Jan 2007, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 50 & 164. ZSM 38752, 159.9 mm SL, 17 Apr 2009, Fte Cruz de Mayo, 11°55′29.14″N, 86°03′22.04″W, DNA tag: 629. ZSM 38753, 3, 129.8–148.9 mm SL, 19 Jan 2007, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 39, 42, & 59. ZSM 38754, 150.8 mm SL, same data as for holotype, DNA tag: 250. PSU 4768, 132.5–167.8 mm SL, same data as for holotype, DNA tags: 251 & 252.

Non-type material.—ZSM 38776, 2 (out of 3), 24 Jan 2007, NE shore, Spanish coast, 11°56′04.43″N, 86°00′46.88″W. ZSM 38777, 1, 5 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W. ZSM 38778, 1, 8 Jan 2007, W shore, along

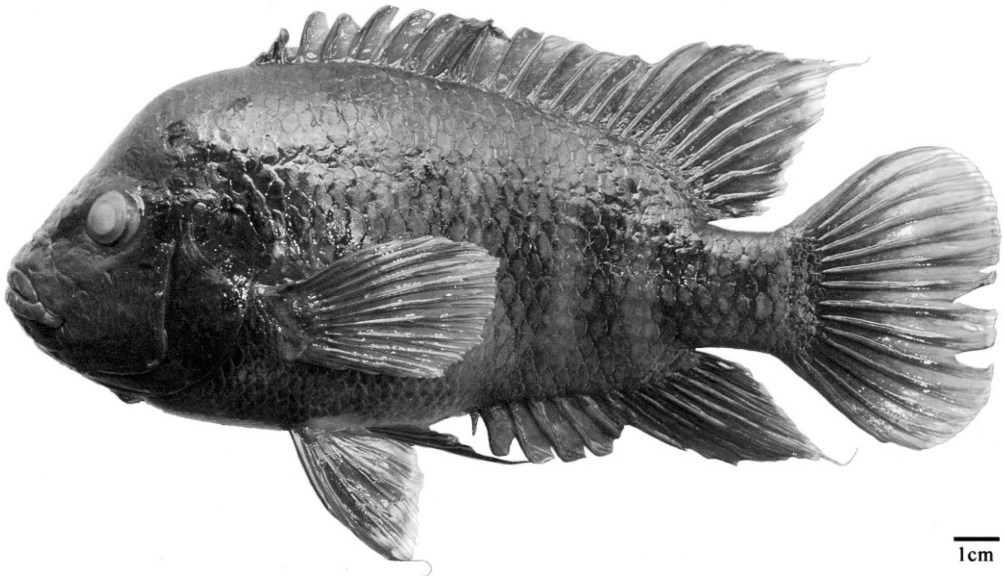

Fig. 1. *Amphilophus supercilius*, holotype, ZSM 38821, adult male, 166.6 mm SL, 27 Feb 2007, Spanish Coast, Lake Apoyo NE shore, Nicaragua 11°56′5.43″N, 86°00′46.88″W, DNA-tag: 247.

public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W. ZSM 38780, 1, 8 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W.

Diagnosis.—*Amphilophus supercilius* can be distinguished from all other described *Amphilophus* by its rounded oval-shaped caudal fin supported by strong and short fin rays; in other species of the complex, caudal fins are subtruncate and more triangular shaped. This is due to the fact that in *A. supercilius* the two outermost principal caudal-fin rays are shorter than in other species of *Amphilophus* from Lake Apoyo (see Figs. 1, 2) and do not reach to the posterior fourth of the caudal fin, thus giving the fin its oval shape.

Additionally, it differs from *A. zaliosus* by a greater body depth (44.4–49.4% SL vs. 34.9–41.1% SL), a greater PDAA (36.1–40.1% SL vs. 32.5–35.2% SL), and a greater ADPV (43.4–49.4% SL vs. 34.6–42.8% SL). The dark green/black head of *A. supercilius* and dark violet breast and throat distinguish it from *A. chancho* and *A. flaveolus*, which have a yellow/green head, and in *A. chancho* a bright lemon yellow throat. Pectoral-fin rays in *A. supercilius* are yellow and in *A. astorquii* they are usually gray.

Description.—Jaws isognathus (Fig. 1), scale rows on cheek 4 in holotype, 4–6 in paratypes; scales along lateral line ctenoid; holotype with 33 lateral-line scales, paratypes with 27–33; pored scales posterior to hypural plate 0–2. Head deep (91.1–117.2% HL); head length 33.8–36.7% SL. Eye small; horizontal eye diameter 22.6–25.5% HL; vertical eye diameter 22–26.5% HL. Mouth small (lower jaw length 37.1–43.1% HL) and not extending to anterior edge of orbit. Morphometric ratios and meristics in Table 1.

Live males and females with similar color. Breeding individuals with nearly black to dark green ground color dorsally, black to dark gray laterally with five strong, black, vertical bars under dorsal fin. One additional vertical bar extending pre-dorsal to pectoral-fin origin, another strong black bar on the caudal peduncle and one black blotch on caudal-fin base. Belly and breast dark with violet shine.

Table 1.—Morphometric and meristic values of *Amphilophus supercilius* collected from Lake Apoyo, Nicaragua. Means, standard deviation, and range include holotype ($n = 14$). See Materials and Methods for explanation of abbreviations. Holotype ZSM catalog number: 38821. Paratype catalog numbers: ZSM 37347, ZSM 37348, ZSM 37351–38754; PSU 4768.

Variable	Holotype	$\bar{X}$	*SD*	Range
Standard length	166.6	150.1	12.5	129.8–167.8
Head length	58.5	53	5	46.2–60.9
Percent standard length				
Head length	35.1	35.4	0.8	33.8–36.7
Body depth	47.5	46.9	1.3	44.4–49.4
Snout to dorsal-fin origin	41.2	42.2	1.3	40.2–44.4
Snout to pelvic-fin origin	41.6	42.6	1	40.7–44.5
Caudal peduncal length	12.5	12	0.7	11.1–13.1
Least caudal peduncle depth	15.7	15.4	0.5	14.3–16.2
Dorsal-fin base length	61.5	58.3	1.7	55.9–61.5
ADAA	52.6	53.2	1.2	51–55.2
PDPA	17.2	17.1	0.4	16.2–17.6
ADPA	67.4	64.8	1.4	62.9–67.4
PDAA	39.2	37.8	1.1	36.1–40.1
PDVC	20.2	19.5	0.7	18.2–20.6
PADC	19.7	20	0.8	18.6–21.6
ADPV	47.2	46.5	1.6	43.4–49.4
PDPV	59.6	59.1	1.1	57.2–61.1
Percent head length				
Horizontal eye diameter	24.7	24.4	1	22.6–25.5
Vertical eye diameter	22.7	24	1.6	22–26.5
Snout length	36.5	38.8	1.9	36.3–42.5
Postorbital head length	40.5	38.8	1.4	36.4–40.5
Preorbital depth	28.6	25.5	1.9	22.5–28.6
Lower-jaw length	41.9	40.7	2	37.1–43.1
Cheek depth	34.1	29.6	2.2	26.7–34.1
Head depth	110.2	104.1	8.2	91.1–117.2
Counts		Mode	Frequency	Range
Dorsal-fin spines	17	17	50	16–17
Dorsal-fin rays	10	11	57.1	10–11
Anal-fin spines	7	7	92.9	6–7
Anal-fin rays	8	8	50	7–8
Pelvic-fin rays	5	5		
Pectoral-fin rays	14	15	50	14–15
Lateral-line scales	33	31	35.7	27–33
Pored scales post. lat line	2	1	57.1	0–2
Scale rows cheek	4	4	50	4–6

Pectoral fin with yellow/golden rays and transparent membrane. Dorsal, anal, and pelvic-fin membranes sooty transparent with greenish shine. Caudal-fin membrane with dark sooty anterior half fading into lighter reddish/violet transparent posterior half. Iris with golden rim. Preserved specimens almost uniformly black. Dorsal one-third of lateral side black or dark gray, fading to dark violet/gray ventrally; black lateral bars very faint or absent. Black caudal spot on post hypural onto caudal fin. Breast and belly black or dark brown.

Etymology.—Specific epithet is an adjective from the Latin word meaning eyebrow or "frowning being," referring to the strongly developed portion of the

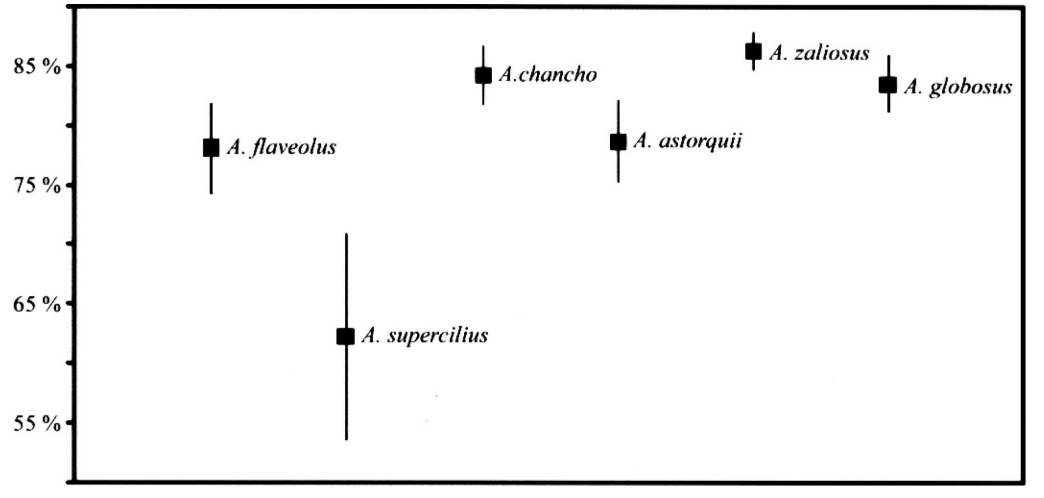

Fig. 2. Mean with 95% confidence interval of length of first principal ventral caudal-fin ray in caudal-fin length ratio of ten individuals of each of the six Lake Apoyo *Amphilophus* species.

neurocranium that borders the eye cavity and gives the species the appearance of possessing eyebrows and a frowning appearance.

Notes on biology.—*Amphilophus supercilius* was earlier reported as *A.* 'barlow' in a report on breeding ecology (McCrary & López 2008). This species breeds between September and March during the dry season with peaks in October and February. Breeding pairs can be encountered in depths ranging between 1.5–20 m where rocks form suitable burrows or crevices. It was often found to breed in direct vicinity to *A. zaliosus*, and it is noteworthy to mention that all observed pairs ($n > 30$, MFG pers. obs.) were between conspecifics. Of all the species of *Amphilophus* in Lake Apoyo, *A. supercilius* had the most generalist diet; stomachs contained fish-remains, fish-eggs, molluscs, and the macrophyte *Chara* (McCrary et al. pers. obs.).

Amphilophus globosus, new species
Fig. 3, Table 2

Holotype.—ZSM 38822, adult male, 158.8 mm SL, 17 Apr 2009, Fte Ranchos, Lake Apoyo NW shore, Nicaragua, 11°55′54.00″N, 86°03′10.80″W, DNA tag: 630.

Paratypes.—All paratypes were collected from Lake Apoyo, Nicaragua. ZSM 38755, 106.2 mm SL, 11 Apr 2009, Fte Lorenzo Guerrero, 11°55′13.07″N, 86°03′24.10″W, DNA tag: 618. ZSM 38756, 95.7 mm SL, 17 Apr 2009, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tag: 627. ZSM 38757, 3, 108.7–136 mm SL, 13 Apr 2009, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 621, 622, & 625. ZSM 38758, 3, 110.2–111.2 mm SL, 17 Apr 2009, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 631 & 636. ZSM 38759, 3, 130–135.8 mm SL, 17 Apr 2009, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 640–642. PSU 4742, 6, 87.7–164.6 mm SL, 17 Apr 2009, Fte Cruz de mayo, 11°55′29.14″N, 86°03′22.04″W, DNA tags: 632–635, 638, 639. PSU 4743, 106 mm SL, 17 Apr 2009, Fte Lorenzo Guerrero, 11°55′13.07″N, 86°03′24.10″W, DNA tag: 617. PSU 4744, 2, 97.5–124.7 mm SL, 13 Apr 2009, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W, DNA tags: 623, 624. PSU 4745, 135.4 mm SL, 17 Apr 2009, Fte Escuela, 11°56′14.59″N, 86°03′10″W, DNA tag: 625.

Diagnosis.—*Amphilophus globosus* can be distinguished from all other Lake

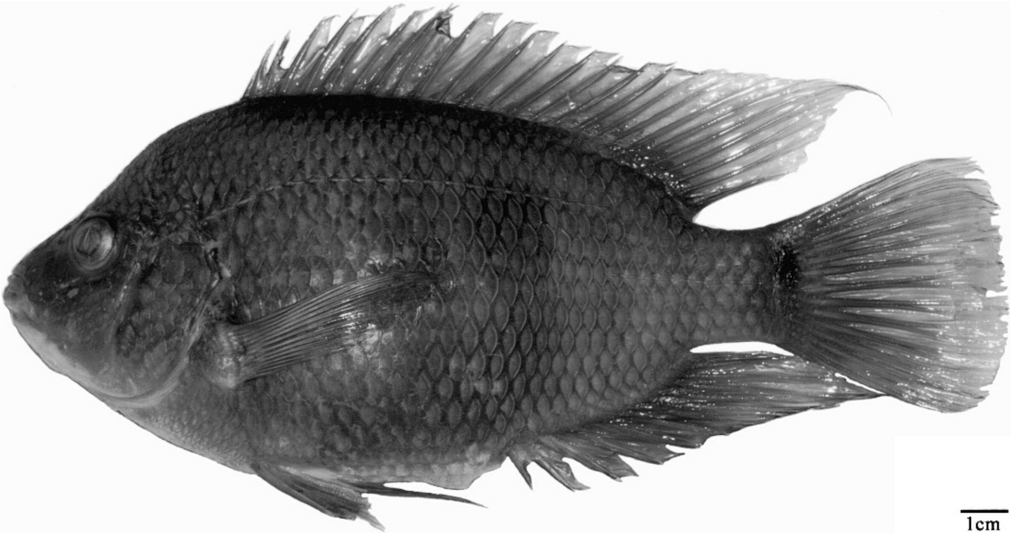

Fig. 3. *Amphilophus globosus*, holotype, ZSM 38822, adult male, 158.8 mm SL, 17 Apr 2009, Fte Ranchos, Lake Apoyo NW shore, Nicaragua, 11°55′54.00″N, 86°03′10.80″W, DNA tag: 630.

Apoyo species *Amphilophus* by its distinctive shape in lateral view, conspicuous bright yellow/greenish coloration, and the absence of clear and continuous dark or black lateral bars in non-breeding coloration.

Amphilophus globosus differs in a number of morphometric measurements from the remaining species of *Amphilophus* in Lake Apoyo: it differs from *A. zaliosus* by a smaller caudal-peduncle length (9.6–12.3% SL vs. 12.7–14.5% SL), a greater dorsal-fin base length (59–63.4% SL vs. 55.2–58.2% SL), greater PDAA (36.9–40.5% SL vs. 32.5–35.2% SL), greater ADPV (44–47.9% SL vs. 34.6–42.8% SL), greater PDPV (61–67.4% SL vs. 53.3–58.6% SL) and a smaller lower-jaw length (35.3–40.1% HL vs. 40.8–43.3% HL). *Amphilophus globosus* has a smaller least caudal-peduncle depth than *A. supercilius* (12.6–14.3% SL vs. 14.3–16.2% SL) and a greater PDPV (61–67.4% SL vs. 57.2–61.1% SL). *Amphilophus globosus* can be distinguished from *A. chancho* by a greater dorsal-fin base length (59–63.4% SL vs. 54.7–58.1% SL), and shorter head length (31.1–34.3% SL vs. 35.7–38.1% SL). It differs from *A. flaveolus* by a greater PDPV (61–67.4% SL vs. 56.7–59% SL. Compared to *A. astorquii* the new species has a shorter head length (31.1–34.3% SL vs. 34.5–38.9% SL).

Description.—Jaws isognathus (Fig. 3), scale rows on cheek 5 in holotype, 4–6 in paratypes; scales along lateral line ctenoid; holotype with 30 lateral-line scales, paratypes with 28–35; pored scales posterior to hypural plate 1–2. Head depth 75.1–98.8% HL; head length 31.1–34.3% SL. Eye small; horizontal eye diameter 22.1–28% HL; vertical eye diameter 22.5–28.5% HL. Mouth small (lower jaw length 35.3–40.1% HL) and not to anterior edge of orbit. Morphometric ratios and meristics in Table 2.

Live males and females with similar color. Breeding adults greenish yellow background color in the dorsal region and head, yellow in the abdomen and ventral region, broken by seven dark vertical bars plus dark caudal spot. Pectoral fin transparent and yellowish, other fins dark. Non-breeding adults with very faint vertical bars, usually imperceptible in the field, over yellow/greenish ground color dorsally, yellow laterally with one characteristic, strong, black

Table 2.—Morphometric and meristic values of *Amphilophus globosus* collected from Lake Apoyo, Nicaragua. Means, standard deviation, and range include holotype ($n = 22$). See Materials and Methods for explanation of abbreviations. Holotype ZSM catalog number: 38822. Paratype catalog numbers: ZSM 38755–38759; PSU 4742–4745.

Variable	Holotype	$\bar{X}$	*SD*	Range
Standard length	158.8	120.6	19.8	88.5–166.7
Head length	50.9	39.3	5.8	30.2–51.9
Percent standard length				
Head length	32.1	32.7	0.9	31.1–34.3
Body depth	49	48.5	1.4	45.4–51.6
Snout to dorsal-fin origin	38.5	38.6	0.9	37.1–40.4
Snout to pelvic-fin origin	41.9	41.5	1.1	39.6–43.6
Caudal peduncal length	10.5	10.7	0.7	9.5–12.3
Least caudal peduncle depth	14.3	13.5	0.5	12.6–14.3
Dorsal-fin base length	59.9	60.9	1.1	59–63.4
ADAA	56.2	55.2	1.3	52.8–57.2
PDPA	17.5	17	0.5	16.1–17.7
ADPA	66.3	66.4	1.1	64.7–69.2
PDAA	37.8	38.5	1	36.9–40.5
PDVC	19.1	18.4	0.7	16.9–19.7
PADC	19.2	18.3	0.8	16.7–19.4
ADPV	47.4	46.1	1.2	44–47.9
PDPV	64.7	63	1.5	61–67.4
Percent head length				
Horizontal eye diameter	22.9	24.8	1.4	22.1–28
Vertical eye diameter	23.2	25.2	1.7	22.5–28.5
Snout length	38.9	36.2	1.6	33.4–38.9
Postorbital head length	42.2	40.1	1.5	36.5–42.2
Preorbital depth	25.1	22.7	1.7	20–26.7
Lower-jaw length	37.7	37.6	1.2	35.3–40.1
Cheek depth	29.8	26.7	2.6	22.1–32.6
Head depth	98.8	85	6.1	75.1–98.8
Counts		Mode	Frequency	Range
Dorsal-fin spines	17	17	68.2	17–18
Dorsal-fin rays	10	10	81.8	10–11
Anal-fin spines	6	7	90.9	6–8
Anal-fin rays	7	8	54.5	7–8
Pelvic-fin rays	5	5		
Pectoral-fin rays	14	14	68.2	13–15
Lateral-line scales	30	32	40.9	28–35
Pored scales post. lat line	2	2	63.6	1–2
Scale rows cheek	5	4	72.7	4–6

blotch usually on third bar under dorsal fin (“spotted,” sensu Barlow 1976). One black blotch on caudal-fin base. Head yellow/green. Belly and breast bright yellow/olive-green, gular cream white. Pectoral fin with transparent rays and membrane. Dorsal, anal, and pelvic-fin membranes transparent with yellow/orange shine. Caudal-fin membrane transparent or yellowish. Iris with golden/orange rim and dark vertical bar.

Preserved specimens dark brown dorsally, lighter ventrally. Gular white; belly light brown. Lateral bars very faint or absent. Black spot laterally instead of third bar, caudal spot on post-hypural onto caudal fin usually in area above lateral line.

Etymology.—Specific epithet is an adjective from the Latin word meaning round or globated, referred to the general appearance of this high-bodied species.

Notes on biology.—*Amphilophus globosus* was previously not identified as a distinct species and thus its breeding ecology was not catalogued separately. It has been observed breeding with conspecifics over *Chara* vegetation at 4–8 m depth, in March 2009 and in January 2010 ($n = 5$; JKM pers. obs.). Interestingly, while at least some individuals of the other Lake Apoyo species of *Amphilophus* had molluscs in their stomachs, in the ten radio-graphed *A. globosus* individuals, we did not observe any molluscs or shell remains.

Discussion

George Barlow († 14 Jul 2007) first noted the higher variability in certain characters in *Amphilophus* from Lake Apoyo compared to those from other lakes in Nicaragua (Barlow 1976). We agree with him that Lake Apoyo's depauperate fish fauna and the lack of potential competitors probably have lead to character release which might have favored the observed diversification. Nicaragua's crater lakes offer a unique possibility to study such processes. Several isolated crater lakes with differing species assemblages have most probably been seeded by independent source populations of *Amphilophus* given the geographic conditions (Waid et al. 1999). All morphometric, ecological, and genetic results to date in Lake Apoyo and in Lake Xiloá strongly suggest that the original founder stocks have evolved into multi-species lineages under sympatric conditions. In our view, it is more parsimonious to assume independent parallel sympatric speciation in those isolated crater lakes than to accept the idea that the now endemic species of *Amphilophus* in each respective water body would have had wider distributions and undergone subsequent local extinctions.

Amphilophus supercilius and *A. globosus* are morphologically distinct from each other and from the four other species of *Amphilophus* inhabiting Lake Apoyo (Figs. 1, 3, 7). We conducted multivariate analysis of the morphometric and meristic data to support the heterospecificity of all six described species.

The plot of the sheared second principal component of the morphometric data (SPC2) versus the sheared third principal component of the morphometric data (SPC3, Fig. 4) clearly demonstrates that the minimum polygon cluster of *A. globosus* is distinct from those of the remaining species of *Amphilophus* from Lake Apoyo and that the minimum polygon cluster of *A. supercilius* is distinct from that of *A. zaliosus* and *A. chancho*. Size accounts for 93.3%, the sheared second principal component for 2.7%, and the sheared third principal component for 1.4% of variation. Variables with the highest loadings on the sheared second principal component in decreasing order of importance are head depth (−0.37), body depth (0.33), PDPV (0.32) and lower-jaw length (−0.28). Variables with the highest standardized scoring coefficients on the sheared third principal component are caudal-peduncle length (0.64), head depth (−0.38) and cheek depth (−0.28).

The plot of the first principal component of the meristic data (PC1) versus the SPC2 (Fig. 5) shows that the minimum polygon clusters of *A. astorquii* and *A. supercilius* do not overlap. Size accounts for 93.1% and the second principal component for 1.9% of total variation. Variables with the highest loadings on the sheared second principal component in decreasing order of importance are cheek depth (−0.52), preorbital depth (−0.42) and head depth (−0.35). The first principal component of the meristic data accounts for 21.6% of the total variation.

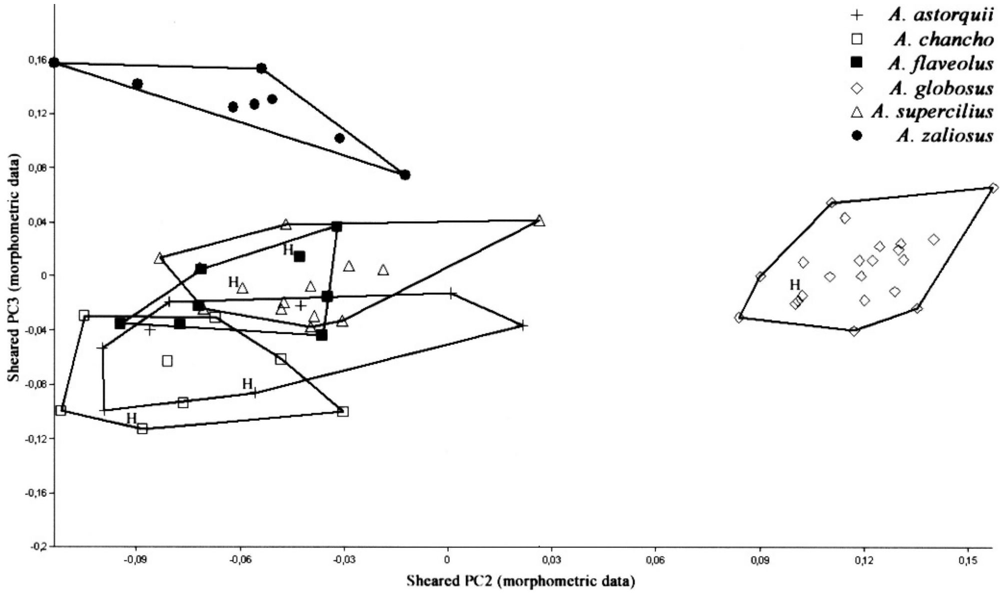

Fig. 4. Plot of the sheared second and third principal component of the morphometric data of *Amphilophus astorquii*, *A. chancho*, *A. flaveolus*, *A. globosus*, *A. supercilius*, and *A. zaliosus*. H demarks the position of the holotype of each species, except for *A. zaliosus*.

Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are dorsal-fin rays (0.61), pored scales posterior to lateral line (−0.50) and anal-fin rays (0.44).

When the data for *A. flaveolus* and *A. supercilius* are analyzed separately, the

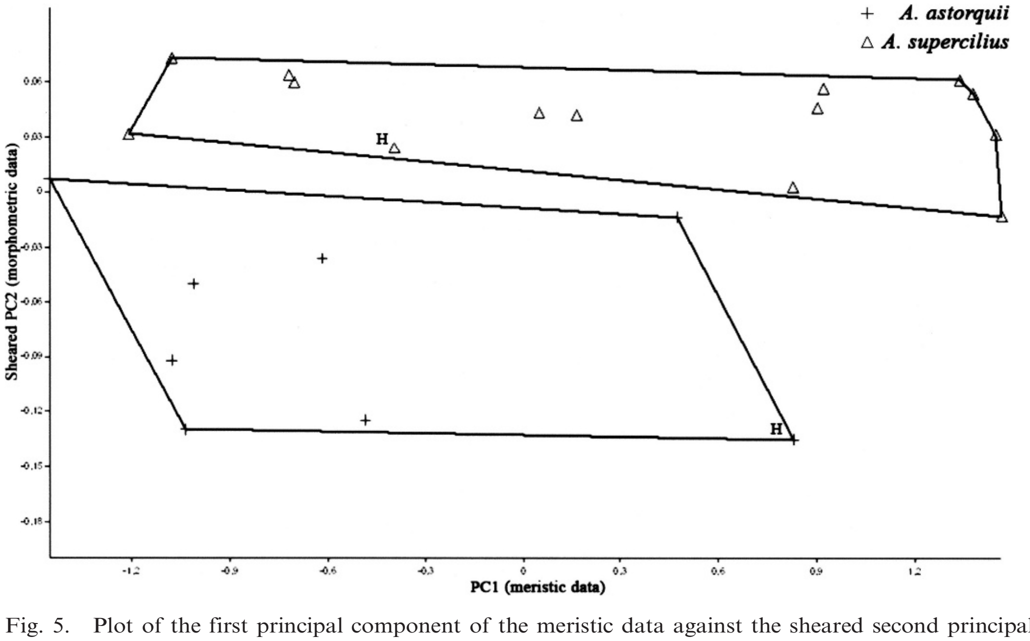

Fig. 5. Plot of the first principal component of the meristic data against the sheared second principal component of the morphometric data of *Amphilophus astorquii* and *A. supercilius*. H demarks the position of the holotype of each species.

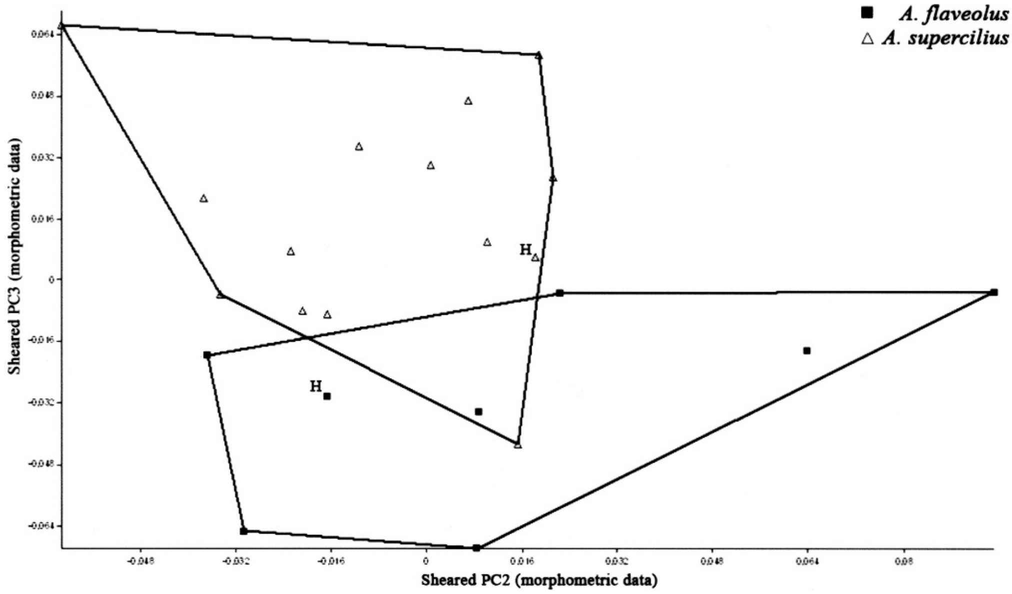

Fig. 6. Plot of the sheared second and third principal component of the morphometric data of *Amphilophus flaveolus* and *A. supercilius*. H demarks the position of the holotype of each species.

minimum polygon clusters between the species show almost no overlap (Fig. 6), only one individual of *A. supercilius* clusters within the polygon of *A. flaveolus*. Size accounts for 94.6%, the sheared second principal component for 1.1% and the sheared third principal component for 1.0% of total variation. Parameters with the highest loadings on the second principal component are cheek depth (0.56), horizontal eye diameter (0.39) and vertical eye diameter (0.31). Those variables that loaded highest on the third principal component are head depth (−0.61) and vertical eye diameter (0.40).

Comparison of the caudal-fin skeleton between the six species endemic to Lake Apoyo revealed only very little structural variation (Table 3) most likely reflecting the recent (<20,000 yr) origin of this species assemblage. In all examined individuals, the caudal-fin base consists of

Table 3.—Meristic values of the caudal-fin skeleton for ten radio-graphed individuals of each of the six Lake Apoyo species of *Amphilophus*. Princ.: principal (segmented); proc.: procurrent (non-segmented); HSP: haemal spine of the preural centrum.

	A. astorquii		*A. chancho*		*A. flaveolus*		*A. globosus*		*A. supercilius*		*A. zaliosus*	
Character	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Princ. caudal-fin rays	16	16	16	16	16	16	16	16	16	16	16	16
Ventral proc. rays	3	3	3	3	3	4	3	4	3	4	2	3
Dorsal proc. rays	3	4	3	4	3	4	4	4	3	5	3	4
Proc. rays HSP	1	1	1	1	1	1	1	1	1	1	1	1
Princ. rays HSP	1	1	1	1	1	1	1	1	1	1	1	1
Parhypural princ. rays	2	2	2	2	2	2	2	2	2	2	1	2
Hypural 1, princ. rays	3	3	3	4	3	4	3	3	3	4	3	4
Hypural 2, princ. rays	2	2	1	2	1	2	2	2	1	2	1	2
Hypural 3, princ. rays	2	3	2	2	2	3	2	3	2	3	2	3
Hypural 4, princ. rays	3	4	4	4	3	5	3	4	3	4	3	4
Hypural 5, princ. rays	2	2	2	2	1	2	2	2	2	3	2	3

Fig. 7. Upper left: *Amphilophus astorquii*; Upper right: *A. chancho*; Middle left: *A. flaveolus*; Middle right: *A. globosus*; Lower left: *A. supercilius*; Lower right: *A. zaliosus*.

five hypuralia, only one individual of *A. supercilius* had the two dorsal hypuralia fused into one plate. It is thus remarkable that in the newly described *A. supercilius* such an 'aberrant' caudal fin with significantly (two-tailed *t*-test, $P < 0.05$) shorter outer principal caudal-fin rays has evolved, despite the observed conservative nature of the caudal skeleton.

Combining the findings from our morphometric analysis with the observed differences in coloration among taxa (Fig. 7), together with different preferences for time and site of breeding of *A. supercilius* (McCrary & López 2008) strongly support the validity of the newly described species. More basic taxonomic research in Nicaragua is necessary to build the basis for a comprehensive phylogenetic hypothesis for the Midas cichlid complex. To render this species complex a sustainable model system for evolutionary biology and biodiversity, a sound systematic analysis of the whole species assemblage is a necessary prerequisite.

Unfortunately, released exotic tilapias, e.g., *Oreochromis aureus* and *O. niloticus*, in Lake Apoyo (McCrary et al. 2007) threaten the endemic fish fauna. The range of negative consequences is manifold, and it was even suggested that introduced tilapias in Lake Apoyo may have been responsible for the outbreak of blindness in native cichlids (McCrary et al. 2007). The disappearance of submerged vegetation *Chara* sp. (Characeae) for more than five years was clearly correlated with the introduction of tilapias in Lake Apoyo (McCrary et al. 2007). This is especially dramatic since *Chara* beds serve as important nesting sites and refugia for juveniles of certain cichlid species, as well as the preferred habitat for the snail *Pyrgophorus coronatus* which is an essential dietary component of certain species of *Amphilophus* (McCrary et al. 2008). The addition of two new members of the endemic fish fauna of Lake Apoyo underscores the importance of efforts that have been undertaken to protect Laguna de Apoyo Nature Reserve, as a reservoir of endemic species and a study site for sympatric speciation processes.

Comparison Material

Amphilophus astorquii.—Holotype: PSU 4518, 107.7 mm SL, 10 Nov 2002, Casa Rosal, Lake Apoyo, Nicaragua 11°55.74′N, 86°03′10.80″W. Paratypes: PSU 4519, 3 (out of 4), 107.1–114.8 mm SL, 10 Nov 2002, Casa Rosal 11°55.74′N, 86°03′10.80″W; PSU 4520, 1, 108.4 mm SL, 20 Dec 2002, Bajadero Granada, 11°55.41′N, 86°00.72′W; PSU 4523, 1, 118.6 mm SL, 21 Dec 2002, Bajadero Granada, 11°55.41′N, 86°00.72′W; PSU 4525, 1, 109.7 mm SL; 22 Dec 2002, Casa Rosal, 11°55.74′N, 86°03′10.80″W; PSU 4528, 1, 129.7 mm SL, 24 Dec 2002, Lado Este OL, 11°54.54′N, 86°00.50′W. Non-types (x-rays): ZSM 39110, 1 (out of 2), 18 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39111, 2, 19 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39112, 1 (out of 3), 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39114, 1 (out of 5), 23 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39153, 2 (out of 3), 23 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39159, 3, 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39166, 2, 24 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39167, 1 (out of 4), 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W.

Amphilophus chancho.—Holotype: PSU 4500, 1, 207 mm SL, 10 Nov 2002, Granada Bajadero, Lake Apoyo, Nicaragua, 11°55.41′N, 86°00.72′W. Paratypes: PSU 4508, 1, 175.2 mm SL, 11 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4509, 1, 165.4 mm SL, 12 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4511, 1, 147.7 mm SL, 14 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4512, 1, 107.6 mm SL, 15 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4513, 1, 107.6 mm SL, 16 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4423, 1, 228.8 mm SL, 9 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W; PSU 4419, 1, 242 mm SL, 9 Dec 2003, Fte Ranchos, 11°55′54.00″N, 86°03′10.80″W.

Non-types: ZSM 39109, 1 (out of 2), 17 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39128, 1 (out of 2), 17 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39130, 2, 23 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39132, 1, 2 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39168, 1 (out of 2), 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39169, 2, 17 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39175, 1, 17 Feb 2007, S shore, "Diria Bajadero," 11°54′08″N, 86°02′38″W; ZSM 39176, 1, 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39184, 1, 15 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39186, 1, 23 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39187, 1, 12 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W.

Amphilophus flaveolus.—Holotype: PSU 4515, 1, 126.9 mm SL, 10 Dec 2003, Otro Lado, Lake Apoyo, Nicaragua 11°54.22′N, 86°01.72′W. Paratypes: PSU 4515, 2, 92.2–130.3 mm SL, 10 Dec 2003, Otro Lado, 11°54.22′N, 86°01.72′W; PSU 4517, 5 (out of 8), 112.7–136.4 mm SL, 28 Nov 2003, Otro Lado, 11°54.22′N, 86°01.72′W. Non-types: ZSM 39116, 1, 24 Jan 2007, NE shore, "Granada Bajadero," 11°55.41′N, 86°00.72′W; ZSM 39117, 4, 26 Jan 2007, S shore, "Diria Bajadero," 11°54′08″N, 86°02′38″W; ZSM 39133, 1 (out of 2), 24 Jan 2007, NE shore, "Granada Bajadero," 11°55.41′N, 86°00.72′W; ZSM 39134, 2, 27 Feb 2007, NE shore, "Granada Bajadero," 11°55.41′N, 86°00.72′W; ZSM 39135, 1, 14 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39136, 2, 1 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39171, 1, 24 Feb 2007, S shore, "Diria Bajadero," 11°54′08″N, 86°02′38″W.

Amphilophus zaliosus.—Paratypes: CAS 29105, 5 (out of 10), 112.4–126.2 mm SL, 2 Aug 1969, E shore of Lake Apoyo, Nicaragua; USNM 212181, 3 (out of 10), 125.4–141mm SL, 2 Aug 1969, E shore of Lake Apoyo, Nicaragua. Non-types: ZSM 39107, 1, 15 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39108, 1, 6 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39119, 2, 17 Feb 2007, S shore, "Diria Bajadero," 11°54′08″N, 86°02′38″W; ZSM 39125, 1, 16 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39140, 1 (out of 3), 22 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39141, 2, 19 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39142, 1, 24 Jan 2007, NE shore, "Granada Bajadero," 11°55.41′N, 86°00.72′W; ZSM 39172, 1, 1 Feb 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W; ZSM 39173, 1, 23 Jan 2007, W shore, along public beach between Spanish school and bars, 11°56′14.59″N, 86°03′10.00″W.

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