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Three new species of cichlid fishes (Teleostei: Cichlidae) from Lake Apoyo, Nicaragua

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Abstract.—Three new species of the *Amphilophus citrinellus* (Günther) species complex that are endemic to Lake Apoyo, Nicaragua are described. The new species differ from previously described members of this complex in other lakes, are phenotypically distinct, and assortatively mate in Lake Apoyo. The presence of endemic cichlids in each of the crater lakes suggests that sympatric speciation occurred. A key is presented for the species of *Amphilophus* found in Lake Apoyo.

Closely related animal species appear to be the products of allopatry (Joseph et al. 2004); however, theoretical foundations are well established for non-ecologically driven (Higashi et al. 1999, Lande et al. 2001) and ecologically driven (Doebeli & Dieckmann 2000) sympatric speciation. For example, there is some evidence that speciation of cichlid fishes in small lakes in Cameroon may have been a result of sympatric sexual selection (Schliewen et al. 1994). Similarly, some pelagic forms of Lake Malaŵi fishes may have evolved sympatrically (Shaw et al. 2000).

In contrast to the African rift lakes, the Nicaraguan crater lakes are small endorheic lakes located within a few kilometers of the Nicaraguan Great Lakes. These lakes were formed from volcanic explosions within the past 100,000 years (Waid et al. 1999). Within these crater lakes, sympatric speciation among isolated populations of the Midas cichlid species complex, *Amphilophus* cf. *citrinellus* (Günther) recently has been hypothesized (McKaye et al. 2002, Barluenga et al. 2006). Throughout its range (i.e., Nicaragua and Costa Rica), this species complex is comprised of species that differ morphologically (Stauffer & McKaye 2002) and vary in feeding habits and breeding site selection (Vivas & McKaye 2001). Described species in the *A. citrinellus* species complex include: *A. amarillo* Stauffer & McKaye, *A. citrinellus* (Günther), *A. erythraeus* (Günther), *A. labiatus* Stauffer & McKaye, *A. sagittae* Stauffer & McKaye, *A. xiloaensis* Stauffer & McKaye, and *A. zaliosus* Barlow. *Amphilophus dorsatus* (Meek) and *A. granadense* (Meek) although recognized in the literature are excluded from the *A citrinellus* complex, since they were synonymized with *A. labiatus* and *A. citrinellus*, respectively (Villa 1976).

Although the arrow cichlid, *Amphilophus zaliosus* (Barlow) from Lake Apoyo is phenotypically similar to *Amphilophus sagittae* Stauffer & McKaye from Lake Xiloa, it was diagnosed as being heterospecific (Stauffer & McKaye 2002). The validity of *A. sagittae* is supported by the fact that species of the *Amphilophus citrinellus* species complex within a given

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lake are more closely related, based on molecular genetic analysis, to each other than to similarly shaped forms in different lakes (McKaye et al. 2002). The purpose of this manuscript is to describe three additional species of the *A. citrinellus* species complex endemic to Lake Apoyo.

Site Description

Lake Apoyo lies on the "Ring of Fire" in southwestern Nicaragua. It occupies the crater formed by the most powerful volcanic explosion in the modern geological epoch in the region (Waid et al. 1999), which resulted in a 6-km wide crater extending to more than 130 m below sea level. The volcano that formed Lake Apoyo is approximately 23,000 years old, with the lake probably having a similar age (Sussman 1982). The lake, which is located 4 km west of Lake Nicaragua, is more than 200 m deep and greater than 4 km in diameter. There is no open-water connection of this lake to any other water body. Fishes may have entered this lake via climatic events, piscivorous birds, and/or humans. The water is warm (27–29°C), slightly saline (Na^+ = 640 mg/l), and oligotrophic (Secchi depth > 3 m). It is inhabited by a depauperate native fish fauna, including one atherinid, one poeciliid, the cichlids *Parachromis managuensis* (Günther) and *A. zaliosus*, and at least three undescribed members of the *A. citrinellus* complex.

In 1991, several individuals of *Gobiomorus dormitor* Lacépède from Lake Masaya were transplanted by a local fisherman. The population of these fishes expanded exponentially in the six years following the introduction (Tate et al. 2001). Additionally, approximately 10 years ago the Nile Tilapia, *Oreochromis niloticus* (Linnaeus) escaped from cage culture operations, and successfully established a breeding population (McCrary et al. 2001).

Materials and Methods

A total of 18–20 adults of each putative species and *A. zaliosus* was collected by SCUBA divers using either monofilament barrier nets or harpoons. Fishes were anesthetized, pinned, preserved in 10% formalin, and permanently preserved in 70% ethanol. Counts and measurements followed Barel et al. (1977) and Stauffer (1991, 1994), except that head depth was measured from the hyoid symphysis to the top of the head (jaws not extended) at a 90° angle to the horizontal body axis. Following abbreviations are used in the tables:

ADAA – anterior insertion of dorsal fin to anterior 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;
PDPA – posterior insertion of dorsal fin to posterior 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;
ADP2 – anterior insertion of dorsal fin to insertion of pelvic fin;
PDP2 – posterior insertion of dorsal fin to insertion of pelvic fin.

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 principal component of the morphometric data against the first principal component of the meristic data.

Genetic evidence shows that the fishes of Lake Apoyo are heterospecific with

Fig. 1. *Amphilophus chancho*, PSU 4404.1, adult male, 207 mm SL, 10 November, 2002, Granada Bajadero, Lake Apoyo, Nicaragua, 11°55.41′N, 86°0.72′W.

members of the *A. citrinellus* species complex that inhabit the other crater lakes of Nicaragua (McKaye et al. 2002, Barluenga et al. 2006). Specifically, McKaye et al. (2002) concluded that similar morphologies between taxa of different lakes are due to convergence. Therefore, data of the new species were compared to only those species of *Amphilophus* indigenous to Lake Apoyo.

Results

Amphilophus chancho, new species
Fig. 1, Table 1

Holotype.—PSU 4500.1, adult male, 207 mm SL, 10 Nov., 2002, Granada Bajadero, Lake Apoyo, Nicaragua, 11°55.41′N, 86°0.72′W.

Paratypes.—All paratypes were collected from Lake Apoyo, Nicaragua. PSU 4500, 1, 213.8 mm SL, 10 Nov., 2002, Granada Bajadero, 11°55.41′N, 86°0.72′W; PSU 4501, 1, 166.3 mm SL, 20 Dec., 2002, Casa Rosal, 11°55.74′N, 86°3.18′W ; PSU 4502, 1, 157 mm SL, 21 Dec., 2002, Casa Rosal, 11°55.74′N, 86°3.18′W; PSU 4503, 1, 242.4 mm SL, 6 Dec., 2003 Fte Ranchos, 11°55.90′N, 86°3.18′W; AMNH 240556, 4, 177–186.6 mm SL, 6 Dec., 2003, Granada Bajadero, 11°55.41′N, 86°0.72′W; PSU 4504 1, 201.9 mm SL, 7 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4505, 1, 173 mm SL, 8 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4506, 1, 230 mm SL, 9 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4507, 1, 189.4 mm SL, 10 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4508, 1, 175.2 mm SL, 11 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4509, 1, 165.4 mm SL, 12 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4510, 1, 168 mm SL, 13 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4511, 1, 147.7 mm SL, 14 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU

Table 1.—Morphometric and meristic values of *Amphilophus chancho* collected from Lake Apoyo, Nicaragua. Means, standard deviation, and range include holotype ($n = 20$). See Materials and Methods for explanation of abbreviations. Holotype PSU Catalog number: 4404.1. Paratype PSU Catalog numbers: 4404, 4407, 4410, 4419, 4420, 4421, 4422, 4423, 4424, 4433.

Variable	Holotype	$\overline{X}$	*SD*	Range
Standard length, mm	207	178.6	33.7	107.6–242.4
Head length, mm	77	65.4	12.5	39.4–90.3
Percent standard length				
Head length	37.2	36.7	0.9	34.6–38.2
Snout to dorsal-fin origin	46.5	44.1	1.6	41.6–47.5
Snout to pelvic-fin origin	44.4	44.2	2.1	41.1–49.1
Dorsal-fin base length	58.3	57.7	1.4	54.9–60.7
ADAA	58.1	54.4	2.6	50.7–58.4
ADPA	64.6	63.9	1.6	61.1–67.5
PDAA	35.4	35.9	1.3	33.8–39.2
PDPA	18.3	17.1	1.1	15.1–19.3
PADC	21.4	19.9	1.1	17.4–21.4
PDVC	18.6	18.5	1	16.5–20.1
PDP2	61.6	59.8	2.1	55.3–63.4
ADP2	52.3	47.9	26	42.9–52.4
Caudal peduncle length	14.6	12.7	1.2	10.2–15.3
Least caudal peduncle depth	15	14.2	0.8	12.3–15.2
Percent head length				
Snout length	46	43.9	3	37.7–49.1
Postorbital head length	41.7	40.5	1.8	37.2–43.8
Horizontal eye diameter	24.1	24.1	2.1	20.4–27.9
Vertical eye diameter	23.4	23.5	2.1	19.9–28.4
Head depth	121.4	103.8	7.7	93.6–121.4
Preorbital depth	26.7	26	2	21.4–30.6
Cheek depth	35.6	31.9	4	22.4–37.7
Lower jaw length	40.6	40.1	1.8	37.2–44.5
Counts		**Mode**	**Frequency**	**Range**
Dorsal-fin spines	17	16	60	16–17
Dorsal-fin rays	10	12	45	10–12
Anal-fin spines	6	7	70	6–8
Anal-fin rays	8	8	55	8–10
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	17	16	50	15–17
Lateral-line scales	29	30	55	28–31
Pored scales post. lat line	1	1	55	0–2
Scale rows cheek	6	4	45	4–6
Gill rakers first ceratobranchial	8	8	45	7–11
Gill rakers first epibranchial	3	3	70	2–4

4512; 1, 107.6 mm SL 15 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4513, 1, 107.6 mm SL, 16 Dec., 2003, Fte Ranchos, 11°55.90′N, 86°3.18′W; PSU 4514, 1, 192.8 mm SL, 5 Dec., 2003, Granada Bajadero, 11°55.41′N, 86°0.72′W.

Diagnosis.—*Amphilophus chancho* has a longer head length, as expressed as percent SL (34.6–38.2% SL) than *A. zaliosus* (32.5–34.0% SL). Head color of breeding *A. chancho* is green-yellow while breeding *A. astorquii* have black heads; furthermore *A. chancho* possesses a gray interorbital bar, which is absent in *A. astorquii*. The distance between the snout and the origin of the dorsal fin on average is significantly shorter in *A. flaveolus*

(38.9–42.8% SL) than in *A. chancho* (41.6–47.5% SL).

Description.—Jaws isognathus (Fig. 1); teeth on jaws in 4–6 rows; 8–19 teeth in outer row of left lower jaw. Scale rows on cheek 6 in holotype, 4–6 in paratypes; scales along lateral side ctenoid; holotype with 29 lateral-line scales, paratypes with 28–31; pored scales posterior to hypural plate 0–2. Gill rakers on first ceratobranchial 7–11, with 2–4 on first epibranchial. Head deep (93.6–121.4% HL); head length 34.6–38.2% SL. Eye small; horizontal eye diameter 20.4–27.9% HL; vertical eye diameter 19.9–28.4%HL. Mouth small (lower jaw length 37.2–44.5% HL) and not extending to anterior edge of the orbit. Body deep [ADP2 (42.9–52.4% SL)]. Principal morphometric ratios and meristics in Table 1.

Live males and females with similar color. Breeding individuals with green ground color dorsally, light gray laterally, with five faint, dark, vertical bars. Pectoral fin with light yellow highlights. Distinct caudal spot. Head yellow/green; gray/green interorbital, cheek, dorsal portion of opercle, preopercle, and preorbital. Bright lemon yellow on ventral opercle and throat; opercle with one dark vertical bar. Non-breeding individuals with light vertical bars over bright lemon/yellow ground color; with dark spots on dorsal portion. White patches on belly. Dark caudal spot. Iris lemon/yellow with dark vertical eye bar. White patches on lower mandible.

Preserved specimens with gray interorbital; gular light brown. Dorsal one-third of lateral side dark gray, fading to light brown ventrally; six or seven black lateral spots with extensions of these spots forming gray lateral bands. Breast and belly light brown.

Etymology.—Specific epithet is a noun in apposition, from the Spanish *chancho*, meaning pig, which refers to the local common name for this taxon.

Amphilophus flaveolus, new species
Fig. 2, Table 2

Holotype.—PSU 4515.1, adult male, 126.9 mm SL, 10 Dec., 2003, Otro Lado, Lake Apoyo, Nicaragua 11°54.22′N, 86°1.72′W.

Paratypes.—All paratypes were collected from Lake Apoyo, Nicaragua. PSU 4517, 8, 112.7–136.4 mm SL, 28 Nov., 2003, Otro Lado, 11°54.22′N, 86°1.72′W; PSU 4515, 2, 92.2–130.3 mm SL, 10 Dec., 2003, Otro Lado, 11°54.22′N, 86°1.72′W; AMNH 240555, 6, 112.7–129.7 mm SL, Granada Bajadero, 11°55.41′N, 86°0.72′W.

Diagnosis.—*Amphilopus flaveolus* on average has a greater PDPA (15.2–16.9% SL) and ADP2 (41.5–46.1% SL) than *A. zaliosus* (PDPA = 13.7–15.5% SL; ADP2 = 36.8–41.5% SL). The distance between the snout and the origin of the dorsal fin on average is significantly shorter in *A. flaveolus* (38.9–42.8% SL) than in *A. chancho* (41.6–47.5% SL. The caudal peduncle and head of *A. flaveolus* is yellow or green (see Figs. 17, 18 in McKaye et al. 2002), while the head of *A. astorquii* is black.

Description.—Jaws isognathous (Fig. 2); teeth on jaws in 4–7 rows; 11–21 teeth in outer row of left lower jaw. Scale rows on cheek 5 in holotype, 3–5 in paratypes; scales along lateral side ctenoid; holotype with 30 lateral-line scales, paratypes with 29–32; pored scales posterior to hypural plate 0–2. Gill rakers on first ceratobranchial 7–11, with 2–4 on first epibranchial. Head deep (83.2–111.8% HL); head length 32.7–37.8% SL. Eye large; horizontal eye diameter 24.7–30.1% SL; vertical eye diameter 24.9–31.6% SL. Mouth small (lower jaw length 37.6–44.6% HL) and not extending to anterior edge of the orbit. Principal morphometric ratios and meristics in Table 2.

Males and females with similar color. Breeding individuals with six or seven vertical bars over green/yellow ground color; green/yellow dorsally to yellow ventrally; yellow/white belly and breast.

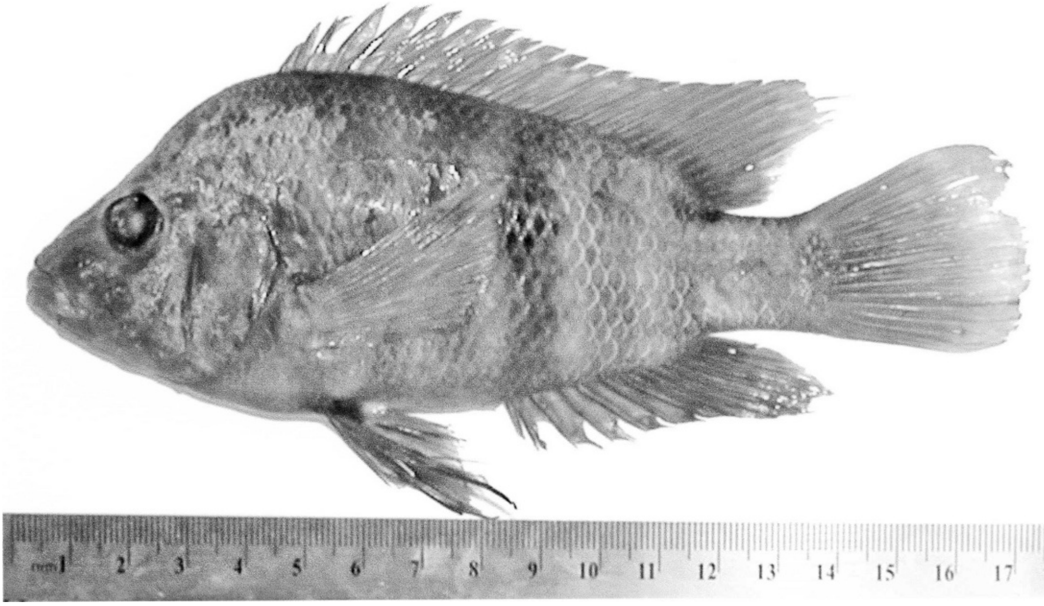

Fig. 2. *Amphilophus flaveolus*, PSU 4425.1, adult male, 126.9 mm SL, 10 December, 2003, Otro Lado, Lake Apoyo, Nicaragua 11°54.22′N, 86°1.72′W.

Iris dark gold. Caudal spot prominent and does not extend onto caudal fin. Fins gray with green highlights.

Preserved specimens with black/dark gray interorbital; gular gray. Lateral side dark light brown; six or seven black/gray bars; posterior four bars with dark middle areas that appears as a spot in some bars. Prominent black caudal spot. Breast and belly light brown.

Etymology.—Specific epithet is an adjective from the Latin word meaning yellowish, referring to the yellow-base color throughout.

Amphilophus astorquii, new species
Fig. 3, Table 3

Holotype.—PSU 4518.1, adult male, 107.7 mm SL, 10 Nov., 2002, Casa Rosal, Lake Apoyo, Nicaragua 11°55.74′N, 86°3.18′W.

Paratypes.—All paratypes were collected from Lake Apoyo, Nicaragua. PSU 4519, 4, 107.1–114.8 mm SL, 10 Nov., 2002, Casa Rosal 11°55.74′N, 86°3.18′W; AMNH 240557, 4, 101.6–118.3 mm SL, 10 Nov., 2002, Casa Rosal 11°55.74′N, 86°3.18′W; PSU 4520, 1, 108.4 mm SL, 20 Dec., 2002, Bajadero Granada, 11°55.41′N, 86°0.72′W; PSU 4521, 1, 138.8 mm SL, 20 Dec., 2002, Lado Este OL, 11°54.54′N, 86°0.50′W; PSU 4523, 1, 118.6 mm SL, 21 Dec., 2002, Bajadero Granada, 11°55.41′N, 86°0.72′W; PSU 4521, 1, 119.6 mm SL, 21 Dec., 2002, Lado Este OL, 11°54.54′N, 86°0.50′W; PSU 4525, 1, 109.7 mm SL; 22 Dec., 2002, Casa Rosal, 11°55.74′N, 86°3.18′W; PSU 4526, 1, 154.6 mm SL, 22 Dec., 2002, Lado Este OL, 11°54.54′N, 86°0.50′W; PSU 4527, 1, 85.5 mm SL, 24 December, 2002, Casa Rosal, 11°55.74′N, 86°3.18′W; PSU 4528, 1, 129.7 mm SL, 24 Dec., 2002, Lado Este OL, 11°54.54′N, 86°0.50′W; PSU 4529, 1, 137.7 mm SL, 25 December, 2002, Lado Este OL, 11°54.54′N, 86°0.50′W.

Diagnosis.—The caudal peduncle and head of *A. astorquii* are completely black in breeding adults, while the head and caudal peduncle of *A. chancho* and *A.*

Table 2.—Morphometric and meristic values of *Amphilophus flaveolus* collected from Lake Apoyo, Nicaragua. Means, standard deviation, and range include holotype ($n = 18$). See Materials and Methods for explanation of abbreviations. Holotype PSU Catalog number: 4425.1, Paratypes PSU Catalog numbers: 4418, 4425, 4434.

Variable	Holotype	$\bar{X}$	*SD*	Range
Standard length, mm	126.9	123.1	10.8	92.2–136.4
Head length, mm	45	43.9	4.06	33.0–50.6
Percent standard length				
Head length	35.5	35.6	1.3	32.7–37.8
Snout to dorsal-fin origin	42.3	41.3	1.2	38.9–42.8
Snout to pelvic-fin origin	42.4	43.1	2.1	39.5–47.5
Dorsal-fin base length	59.7	59.5	1.4	56.9–61.7
ADAA	51.2	51.2	1.1	48.3–53.4
ADPA	65	64.5	1.2	62.6–66.8
PDAA	37.5	37.3	1.3	34.7–39.2
PDPA	16.2	16.1	0.5	15.2–16.9
PADC	20.2	19.6	0.7	18.5–20.9
PDVC	19	18.2	0.8	17.2–19.6
PDP2	56.6	58.3	1.7	54.1–61.0
ADP2	43.5	44.1	1.2	41.5–46.1
Caudal peduncle length	11.4	12.5	0.8	11.1–13.8
Least caudal peduncle length	14.1	13.6	0.5	12.8–14.6
Percent head length				
Snout length	41.8	39.8	1.6	37.2–42.5
Postorbital head length	37.3	38.1	1.1	36.2–41.1
Horizontal eye diameter	25.2	27.5	15.7	24.7–30.1
Vertical eye diameter	25	27.4	2.1	24.9–31.6
Head depth	96.7	94.9	6.1	83.2–111.8
Preorbital depth	23.3	23.8	1.5	21.3–27.1
Cheek depth	24.9	26	2.1	21.1–29.6
Lower jaw length	40.4	40.7	1.6	37.6–44.6
Counts		**Mode**	**Frequency**	**Range**
Dorsal-fin spines	17	17	83.3	16–17
Dorsal-fin rays	11	11	72.2	11–12
Anal-fin spines	7	7	72.2	6–7
Anal-fin rays	9	9	77.8	8–9
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	16	16	77.8	15–17
Lateral-line scales	30	30	72.2	29–32
Pored scales post. lat line	1	1	83.3	0–2
Scale rows cheek	5	4	61.1	3–5
Gill rakers first ceratobranchial	10	8	55.6	7–11
Gill rakers first epibranchial	3	3	83.3	2–4

flaveolus are yellow or green (see Figs. 14, 17, 18 in McKaye et al. 2002). *Amphilophus astorquii* differs from *A. zaliosus* by a larger snout to dorsal-fin origin (41.1–47.9% SL vs. 37.3–40.1%SL).

Description.—Jaws isognathus (Fig. 3); teeth on jaws in 3–6 rows; 10–24 teeth in outer row of left lower jaw. Scale rows on cheek 6 in holotype, 4–6 in paratypes; scales along lateral side ctenoid; holotype with 29 lateral-line scales, paratypes with 26–31; pored scales posterior to hypural plate 0–2. Gill rakers on first ceratobranchial 7–11, with 2–3 on first epibranchial. Head deep (88.2–104.8% HL); head length 34.6–39.5% SL. Eye large; horizontal eye diameter 25.0–31.0% HL; vertical eye diameter

Fig. 3. *Amphilophus astorquii*, PSU 4414.1, adult male, 107.7 mm SL, 10 November, 2002, Casa Rosal, Lake Apoyo, Nicaragua 11°55.74′N, 86°3.18′W.

22.6–30.9% HL. Mouth small (lower jaw length 26.1–41.2% HL) and not extending to anterior edge of the orbit. Principal morphometric ratios and meristics in Table 3.

Males and females with similar color. Breeding individuals with dark greenish/black background, and five dark vertical bars under dorsal fin, plus one anterior to dorsal fin and one on caudal peduncle. Fins gray with dark bars on dorsal fins. Iris gold with dark vertical eye-bar. Non-breeding individuals with light green/gray ground color and dorsal spot, caudal spot, and three or four additional smaller dark spots along lateral line. The belly and breast light gray/white. Fins clear.

Preserved specimens with gray/black interorbital; gular dark brown. Dorsal one-third of lateral side dark brown, fading to brown ventrally; six or seven black lateral bars. Prominent black caudal spot that extends onto caudal fin. Breast and belly brown.

Etymology.—Specific epithet honors Ignacio Astorqui, S. J., a researcher of freshwater fishes in Nicaragua.

Discussion

The Midas cichlid species complex is considered to be primarily lacustrine. All the forms of this species complex are territorial substrate brooders providing biparental care (Barlow 1976). The breeding period for all the Midas cichlid forms in Lake Apoyo is concentrated in the transition from rainy to dry seasons, from November through January. *Amphilophus astorquii* and *A. chancho* nested in dug or adapted preexisting holes in rocky areas at depths ranging from 2–25 m, with *A. astorquii* tending to make and utilize smaller burrows. *Amphilophus flaveolus* nested in sandy/muddy substrates in water less than 2 m deep.

Genetic evidence supports our premise that the fishes of Lake Apoyo are

Table 3.—Morphometric and meristic values of *Amphilophus astorquii* collected from Lake Apoyo, Nicaragua. Means, standard deviation, and range include holotype ($n = 18$). See Materials and Methods for explanation of abbreviations. Holotype PSU Catalog number: 4414.1. Paratype PSU Catalog numbers: 4404, 4405, 4406, 4408, 4409, 4411, 4412, 4413, 4414, 4415, 4416, 4417.

Variable	Holotype	$\overline{X}$	*SD*	Range
Standard length, mm	107.7	116	15.9	85.5–154.6
Head length, mm	39.6	42.1	6.5	30.7–55.6
Percent standard length				
Head length	36.8	36.2	1.3	34.6–39.5
Snout to dorsal-fin origin	43.8	43.7	2	41.1–47.9
Snout to pelvic-fin origin	43.2	43.1	1.5	40.0–45.3
Dorsal-fin base length	61.4	59.2	2.5	54.8–63.3
ADAA	55.3	54.2	2	48.8–57.8
ADPA	67.6	65.5	21.8	61.5–67.9
PDAA	36.3	37.7	2.1	33.7–41.2
PDPA	16.9	16.9	1.1	15.0–19.0
PADC	18.7	19	1.1	16.7–21.3
PDVC	18.2	18.3	1	16.0–20.5
PDP2	60.8	60.2	2.4	56.4–64.5
ADP2	49	46.8	2	42.3–49.0
Caudal peduncle length	10.2	11.5	1	9.8–13.5
Least caudal peduncle length	13.3	13.3	0.6	12.2–14.4
Percent head length				
Snout length	37.7	39.2	2.3	36.2–45.8
Postorbital head length	41	39.1	2.1	34.9–42.5
Horizontal eye diameter	28.4	27.7	1.6	25.0–31.0
Vertical eye diameter	27.2	28	2	22.6–30.9
Head depth	96	95.3	5.2	88.2–104.8
Preorbital depth	25.8	24.2	1.3	22.2–26.5
Cheek depth	27.1	27.6	2.4	22.6–31.9
Lower jaw length	31.9	32.7	4.5	26.1–41.2
Counts		**Mode**	**Frequency**	**Range**
Dorsal-fin spines	17	17	77.8	16–18
Dorsal-fin rays	11	11	72.2	10–12
Anal-fin spines	7	7	66.7	6–7
Anal-fin rays	8	9	61.1	8–9
Pelvic-fin rays	5	5	100	
Pectoral-fin rays	15	16	66.7	15–17
Lateral-line scales	29	29	38.9	26–31
Pored scales post. lat line	1	1	72.2	0–2
Scale rows cheek	6	5	66.7	4–6
Gill rakers first ceratobranchial	9	8	38.9	7–11
Gill rakers first epibranchial	2	2	61.1	2–3

heterospecific with members of the *A. citrinellus* species complex that inhabit the other crater lakes of Nicaragua (McKaye et al. 2002, Barluenga et al. 2006). *Amphilophus chancho*, *A. flaveolus*, and *A. astorquii* are morphologically distinct from each other. The heterospecificity of these three species is further supported by multivariate analysis of the morphometric and meristic data. The plot of the sheared second principal component of the morphometric data versus the first principal component of the meristic data (Fig. 4) clearly demonstrates that the minimum polygon of *A. astorquii* is distinct from those of *A. chancho* and *A. flaveolus*. Although there is some overlap, the data for *A. astorquii* are significantly different

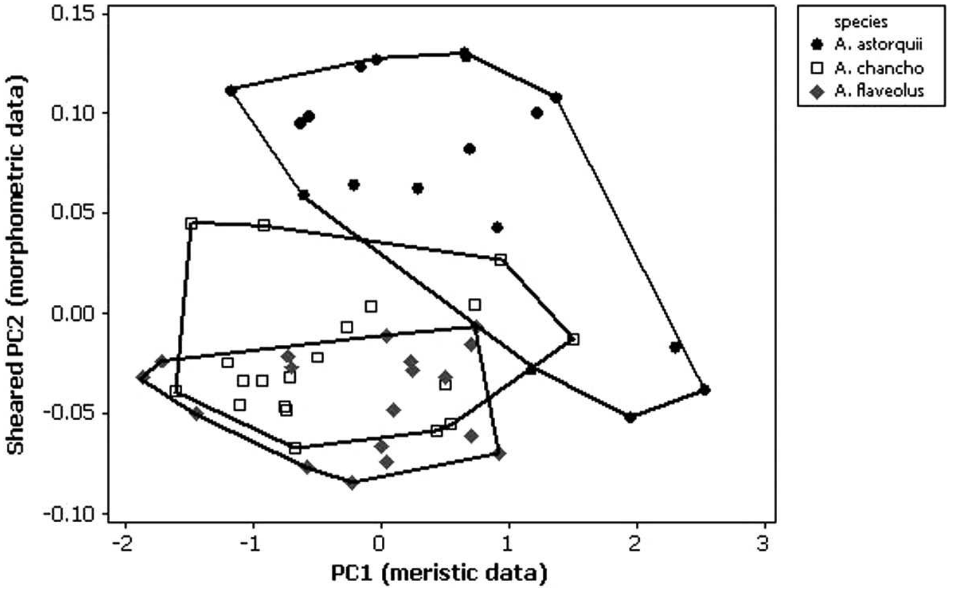

Fig. 4. Plot of the sheared second principal component of the morphometric data and the first principal component of the meristic data of *Amphilophus chancho*, *Amphilophus flaveolus*, and *Amphilophus astorquii*.

along the second sheared principal component (Duncan's Multiple Range Test $p < 0.05$). Size accounts for 98% and the second principal component for 1.1% of the total variation. Variables with the highest loadings on the sheared second principal component in decreasing order of importance are lower jaw length, PDPA, and ADAA. The first principal component of the meristic data accounts for 40.1% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are dorsal-fin rays, dorsal-fin spines, and lateral-line scales.

Furthermore, the plot of the sheared second principal component (SPC2) of the morphometric data versus the first principal component of the meristic data (Fig. 5) show that *A. chancho* and *A. flaveolus* are also delimited. The data for the two species are significantly different along both the morphometric and meristic axes (ANOVA, $p < 0.05$). Size accounts for 97.7% and the second principal component for 0.56% of the total variation. Variables with the highest standardized scoring coefficients on the second principal component of the morphometric data in decreasing order of importance are caudal peduncle length, vertical eye diameter, and horizontal eye diameter. The first principal component of the meristic data accounts for 39.2% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are lateral-line scales, cheek scales, and pectoral-fin rays. Although there is overlap of the minimum polygons (Fig. 5) of *A. chancho* and *A. flaveolus*, the uniqueness of each of these species is supported by differences in coloration. Unique color patterns among cichlids are recognized to be sufficient to diagnose valid species (Barlow 1974, Barel et al. 1977, Stauffer et al. 1995).

Observations, while SCUBA diving, demonstrated that breeding of each species commonly occurs at distances of a few meters of the other respective taxa in Lake Apoyo. Clearly, strong reproductive

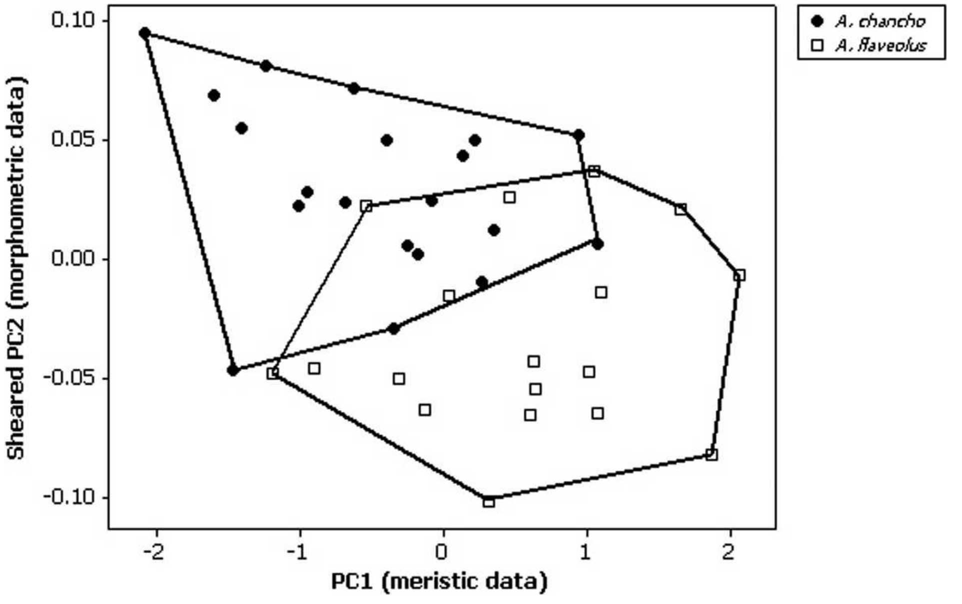

Fig. 5. Plot of the sheared second principal component of the morphometric data and the first principal component of the meristic data of *Amphilophus chancho* and *Amphilophus flaveolus*.

isolation mechanisms have been in place in these lakes. The small species flocks in these lakes apparently evolved in close quarters, as these lakes are small and "ecologically monotonous" (Schliewen et al. 1994). The lack of geographic isolation of any habitat in either lake, combined with the morphometric (Stauffer & McKaye 2002), ecological (Vivas & McKaye 2001, McKaye et al. 2002), behavioral (Murry et al. 2001, McKaye et al. 2002), and genetic (McKaye et al. 2002, Barluenga et al. 2006) data provide strong evidence in favor of sympatric speciation in the Nicaraguan volcanic crater lakes. Given that this lake is not likely more than 23,000 years old and that species within the lake are more closely related to each other than to phenotypically similar but allopatric species, sympatric speciation events are suggested (McCune & Lovejoy 1998).

Key to the *Amphilophus* in Lake Apoyo

1a. Posterior insertion of dorsal fin to anterior insertion of anal fin is less than 33.8% SL or anterior insertion of dorsal fin to insertion of pelvic fin less than 41.6% SL .... *A. zaliosus* Barlow

1b. Posterior insertion of dorsal fin to anterior insertion of anal fin is greater than 33.6% SL or anterior insertion of dorsal fin to insertion of pelvic fin greater than 41.6% SL 2

2a. Caudal spot does not extend onto caudal rays .. *A. flaveolus*, new species

2b. Caudal spot extends onto caudal rays .. 3

3a. Presence of gray interorbital bar .... *A. chancho*, new species

3b. Absence of interorbital bar .... *A. astorquii*, new species

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