

El Complejo de Especies de la Mojarra Común en Dos
Lagunas Cratéricas Nicaragüenses

The Midas Cichlid Species Complex in Two
Nicaraguan Crater Lakes



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Descriptions of Three New Species of Cichlid Fishes (Teleostei: Cichlidae) from Lake Xiloá, Nicaragua

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Abstract

Three new species in the *Amphilophus citrinellus* (Günther) species complex from Lake Xiloá are described. Historically, many forms have been recorded that are phenotypically similar to *A. citrinellus* and in the crater lakes of Nicaragua this complex was previously considered to be represented by a single, very variable species. In Lake Xiloá, the three new species mate assortatively, and differ morphologically from each other and from all other described species in the *A. citrinellus* complex.

Introduction

Cichlid nomenclature in Central America is in a state of controversy. Kullander and Hartel (1997) recently discussed the systematic status of the genera *Amphilophus*, *Baiodon*, *Hypsophrys*, and *Parachromis*. They concluded that the name *Amphilophus* is still available as a generic name, but discussed the confusion surrounding *Amphilophus froebelii*, the type species of *Amphilophus*. Essentially, Barlow and Munsey (1976) proposed that the junior synonym of this form, *Amphilophus labiatus* (Günther), should be maintained, since no type material can be found for *A. froebelii*. If the description of *A. froebelii* is adequate, but the type material has been lost, then a neotype can be designated. Kullander and Hartel (1997) suggested that since *A. froebelii* is known from Lake Nicaragua and *A. labiatus* was described from Lake Managua, both names should be maintained since the two lake populations may be heterospecific. If, in fact, these two species are conspecific, article 23.9.1.2 of the ICZN states that a junior synonym may be used as the valid name if "the senior synonym or homonym has not been used as a valid name after 1899" and if "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in

the immediately preceding 50 years and encompassing a span of not less than 10 years."

Jordan *et al.* (1930) referenced *Amphilophus froebelii*, and stated that *Amphilophus* Agassiz has priority over *Astatheros* Pellegrin. Miller (1966) placed the *Astatheros longimanus* (Günther) group in *Amphilophus*. Currently, *Astatheros* and *Amphilophus* are regarded as two different genera. The type species of *Astatheros*, *Astatheros macracanthus* (Günther), was previously regarded as an *Amphilophus citrinellus* (Günther) type cichlid, but Roe *et al.* (1997) placed this species genetically closer to the substrate sifters, *Astatheros alfari/longimanus*. Konings (pers. comm.) has observed *A. macracanthus* in the wild and notes that their behavior and habitat preference resembles more that of *longimanus* than *citrinellus*).

Since *Amphilophus froebelii* has been used since 1899 the validation of the junior synonym, i.e. *A. labiatus* for *A. froebelii*, must be based on the approval of the International Commission on Zoological Nomenclature.

Irrespective of the nomenclatural problems, the genus *Amphilophus* is at best vaguely diagnosed (Bussing and Martin 1975, Kullander and Hartel 1997). Regan (1906-1908) gave several characters of the genus, including: produced snout, maxillary not extending beyond the anterior margin of the eye, long pectoral fins, and presence of 5-9 vertical bars laterally. He did not, however, provide any diagnosis of the genus or speculate on putative synapomorphies.

The confusion surrounding the cichlid nomenclature is further exacerbated when examining *Amphilophus citrinellus* (Günther) and phenotypically similar forms (Gill and Bransford 1877, Günther 1869, Stiassny 1991, Kullander and Hartel 1997, Roe *et al.* 1997). Meek (1907), one of the pioneers to work in Nicaragua, considered *A. citrinellus* by far the most variable species and recognized several forms:

"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. . . 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."

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Subsequently, Barlow and Munsey (1976) recognized three different species within the *A. citrinellus* complex: *A. citrinellus*, *A. labiatus*, and *Amphilophus zaliosus* Barlow. McKaye (1980) concluded that since the morphs of the Midas Cichlid mated assortatively and selected different habitats in which to breed, sympatric speciation of this complex would be possible. In other words, new species could quickly evolve in each of the isolated crater lakes (Stauffer *et al.* 1995, Murry *et al.* 2001, Vivas and McKaye 2001). Nevertheless, through the 80s the prevailing scientific view was that there were two polymorphic species, the Red Devil Cichlid, *A. labiatus*, and the Midas Cichlid, *A. citrinellus*. The specific status of the Arrow Cichlid, *A. zaliosus*, was seriously questioned. Villa (1982), for example, stated that it should be considered “a *labiatum* with ‘normal’ lips.”

In the 1990s, we organized several expeditions and examined the distribution of fishes in eight Nicaraguan

crater lakes (Waid *et al.* 1999), and discovered great morphological variability in this species complex. Detailed behavioral studies using SCUBA in the crater lakes Xiloá and Apoyo (Fig. 1-3) demonstrated that several different forms (but none based on the gold/normal color distinction — Barlow 1976, McKaye and Barlow 1976) were 100% mating assortatively. Our subsequent behavioral and genetic work confirmed that Barlow was correct in determining that the Arrow Cichlid is a valid species (McKaye *et al.* 1998).

Given the great variability in both color and morphology, we have been cautious in assigning specific status to the many newly discovered forms. Instead we have referred to various taxa as Evolutionary Significant Units (ESU) (Stauffer *et al.* 1995). We are now ready to describe three new species in the *A. citrinellus* species complex from Lake Xiloá.



Fig 1. Map of the Pacific region of Nicaragua showing the localities discussed in the text.



Fig 2. View from the eastern shore of Lake Xiloá (photo by Ad Konings).



Fig 3. A composite aerial view of Lake Apoyo (photo by Ad Konings).

Methods and Materials

Lake Xiloá, is located at the center of the volcanic chain of the Pacific Region of Nicaragua, in the Chiltepe peninsula (Fig. 1). This peninsula is an approximately circular protrusion into Lake Managua. Also located in this peninsula is Lake Apoyeque. The area of Lake Xiloá is 3.75 km², and its mean depth and maximum depth are 60 m and 88.5 m, respectively (BANIC, 1977, Waid *et al.* 1999). Lake Xiloá originated by a collapse on the southeastern edge of a volcano around 10,000 years ago (BANIC, 1977). As a result of the way it collapsed, it has two drastically different bottom profiles. At its southeastern end, a low rim rises just above its surface. The bottom profile is a gentle slope, and the bottom consists mostly of silt and sand (McKaye 1984). This end is separated from Lake Managua by 1 km of rather flat terrain. Lake Xiloá was formerly connected to Lake Managua (Villa 1968). At the opposite end (the one closest to Lake Apoyeque) the rim rises to 220 m above the lake surface and the bottom consists of large jumbled boulders and rocky formations descending rapidly to the depths (McKaye 1984). Located at its northern end are sulfurous springs, and the water temperature may reach 37°C in this part of the lake (BANIC, 1977)

Typical of these crater lakes, its waters are alkaline (pH=7.9, hard (443 ppm as CaCO₃), and as the second most saline of the crater lakes (conductivity=5,580 µS Waid *et al.* 1999) Lake Xiloá is a relatively oligotrophic lake. Because of the very low southeastern rim Lake Xiloá is the least wind-protected of the crater lakes, and therefore its waters are very well mixed (Barlow *et al.*, 1976), resulting in significant amounts of dissolved oxygen at great depths (BANIC, 1977).

Type specimens were borrowed from several museums (Table 1). Fishes were collected in Lake Xiloá by a diver with SCUBA and a monofilament gill net. Color notes were made on live fish or recently preserved specimens. Specimens were fixed in 10% formalin with their fins pinned and preserved in 70% ethanol.

All measurements were made with dial calipers that were interfaced directly with a computer. External counts and measurements followed Barel *et al.* (1977) and Stauffer (1991), except that head depth was taken along the vertical through the posterior edge of the midpoint of the branchiostegal. The number of scales in the lateral-line series exclude scales in the overlapping portion of the lower and upper lateral lines; pored scales located posterior to the hypural plate were recorded separately. Except for gill-raker meristics, we made all counts and measurements on the left side of the fish. Morphometric values are expressed as percent standard length (SL) or percent head length (HL).

Historically, morphological differences were delimited by meristic and univariate morphometric analysis and many cichlid species were described from one or two specimens. In Nicaraguan lakes, where morphologically similar species occur, such an analysis has led to confusion and controversy concerning taxonomic relationships (Meek 1907, Villa 1976, Barlow and Munsey 1976, Stauffer *et al.* 1995). An approach that utilizes multivariate analysis of shape (e.g., Atchley 1971, Humphries *et al.* 1981, Reyment *et al.* 1984, Bookstein *et al.* 1985) has yielded more reasonable hypotheses (Stauffer and McKaye 2001).

Thus, we analyzed differences in body shape of the new species and the type specimens of previously described species in the *A. citrinellus* complex using sheared principal component analysis (SPCA) of the morphometric data (Humphries *et al.*, 1981; Bookstein *et al.*, 1985). The first principal component of the morphometric data is interpreted as a size component and the sheared components as shape, independent of size (Humphries *et al.*, 1981; Bookstein *et al.*, 1985). Meristic data were analyzed using principal component analysis

Species	Museum	Status	Number
<i>Amphilophus citrinellus</i>	British Museum of Natural History	syntypes	3
<i>Amphilophus dorsatus</i>	Field Museum of Natural History	Paratypes	2
<i>Amphilophus labiatus</i>	British Museum of Natural History	Syntypes	2
<i>Amphilophus erythraeus</i>	British Museum of Natural History	Holotype	1
<i>Amphilophus granadensis</i>	Field Museum of Natural History	Paratype	1
<i>Amphilophus zaliosus</i>	California Academy of Sciences	Paratypes	5

Table 1. Type specimens borrowed from museum for morphological analyses.

Abbreviation	Definition
ADAA	Distance between anterior insertion of dorsal fin to anterior insertion of anal fin.
PDPA	Distance between posterior insertion of dorsal fin to posterior insertion of anal fin.
ADPA	Distance between anterior insertion of dorsal fin to posterior insertion of anal fin.
PDAA	Distance between posterior insertion of dorsal fin to anterior insertion of anal fin.
PDVC	Distance between posterior insertion of dorsal fin to ventral insertion of caudal fin.
PADC	Distance between posterior insertion of anal fin to dorsal insertion of caudal fin.
ADP2	Distance between anterior insertion of dorsal fin to anterior insertion of pelvic fin.
PDP2	Distance between posterior insertion of dorsal fin to anterior insertion of pelvic fin.

Table 2. Definition of abbreviations for selected morphometrics.

Measurements	<i>Amphilophus citrinellus</i>			<i>Amphilophus dorsatus</i>		
	Mean	St. Dev.	Range	Mean	St. Dev.	Range
Standard length, mm	135.2	0.4	130.2-139.5	96.9	18.4	83.9-109.9
Head length, mm	47.7	0.1	46.4-48.9	37.0	6.9	32.1-41.9
<i>Percent of standard length</i>						
Head length	35.2	0.3	35.0-35.6	38.2	0.1	38.1-38.2
Snout to dorsal-fin origin	43.6	0.9	42.7-44.6	45.4	2.0	44.0-46.8
Snout to pelvic-fin origin	42.5	0.7	41.9-43.3	46.1	1.8	44.9-47.4
Caudal peduncal length	11.3	9.6	10.6-12.4	10.1	1.6	9.0-11.3
Least caudal peduncal depth	14.3	4.4	14.0-14.8	13.6	0.1	13.6-13.7
Pectoral-fin length						
Pelvic-fin length						
Dorsal-fin base length	63.3	0.4	63.0-63.9	59.1	2.1	57.6-60.6
ADAA	58.6	0.9	57.6-59.5	55.1	1.0	54.4-55.8
PDPA	16.0	0.5	15.6-16.6	16.1	0.1	16.0-16.2
ADPA	68.5	0.2	68.2-68.7	64.7	0.9	64.1-65.4
PDAA	40.5	1.2	39.2-41.6	37.0	0.3	36.8-37.2
PDVC	17.9	1.4	16.4-19.2	17.1	0	17.1
PADC	181.3	0.7	17.3-18.7	19.0	0.9	18.4-19.7
ADP2	45.9	1.2	44.9-47.3	45.7	1.0	45.0-46.4
PDP2	57.2	0.9	56.6-58.3	56.4	2.0	55.0-57.9
<i>Percent head length</i>						
Horizontal eye diameter	28.8	0.4	28.4-29.2	32.2	1.3	33.9-35.7
Vertical eye diameter	28.4	1.2	27.2-29.6	30.4	0.6	30.0-30.9
Snout length	41.0	0.8	40.4-41.9	34.8	1.3	33.9-35.7
Postorbital head length	37.7	1.6	36.5-39.5	35.7	0.8	35.2-36.3
Preorbital depth	25.6	0.7	25.1-26.4	20.1	3.9	17.4-22.9
Lower-jaw length	42.7	3.9	39.2-41.6	43.5	0.4	43.3-43.8
Cheek depth	32.2	0.5	31.8-32.7	23.9	2.8	22.0-25.9
Head depth	115.7	3.8	111.5-118.9	92.6	3.3	90.3-94.9

Table 3. Morphometric values of *Amphilophus citrinellus* (syntypes, BMNH 1864.1.26.201-3; n=3) and *Amphilophus dorsatus* (paratypes; FMNH 5970; n=2).

Counts	<i>Amphilophus citrinellus</i>			<i>Amphilophus dorsatus</i>		
	Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	30	66.7	30-31	31	100	31
Pored scales posterior to lateral line	2	100	2			1-2
Scale rows on cheek	4	100	4	4	100	4
Dorsal-fin spines	17	66.7	16-17	17	100	17
Dorsal-fin rays	12	66.7	11-12	12	100	12
Anal-fin spines	3	100	3	7	100	7
Anal-fin rays	2	66.7	8-9			8-9
Pectoral-fin rays	15	100	15			15-16
Pelvic-fin rays	5	100	5	5	100	5
Gill rakers on first ceratobranchial	9	66.7	9-10	8	100	8
Gill rakers on first epibranchial	2	66.7	2-3	2	100	2
Teeth in outer row of left lower jaw			17-20			8-14
Teeth rows on upper jaw	3	100	3	2	100	2
Teeth rows on lower jaw	3	66.7	3-4	2	100	2

Table 4. Meristic values of *Amphilophus citrinellus* (syntypes, BMNH 1864.1.26.201-3; n=3) and *Amphilophus dorsatus* (paratypes; FMNH 5970; n=2).

	Size	PC ₂
Standard length	0.19	0.05
Head length	0.18	0.17
Snout length	0.23	0.35
Post orbital head length	0.20	0.02
Horizontal eye diameter	0.10	0.04
Vertical eye diameter	0.11	0.10
Head depth	0.24	-0.31
Preorbital depth	0.27	0.55
Cheek depth	0.27	-0.11
Lower jaw length	0.12	0.44
Snout to dorsal-fin origin	0.17	0.19
Snout to pelvic-fin origin	0.17	0.05
Dorsal-fin base length	0.20	-0.08
ADAA	0.21	-0.03
ADPA	0.20	-0.07
PDAA	0.21	-0.07
PDPA	0.22	-0.06
PDVC	0.23	-0.05
PADC	0.20	-0.05
PDP2	0.23	-0.16
ADP2	0.21	-0.21
Caudal peduncle length	0.20	-0.21
Least caudal peduncle depth	0.20	-0.10

Table 5. Variable loadings on the size principal components and second principal components (shape factor) of the morphometric data for the *Amphilophus citrinellus* complex.

Characters	PC ₁
Dorsal spines	0.53
Dorsal rays	-0.14
Anal rays	-0.19
Pectoral rays	-0.33
Lateral-line scales	0.27
Pored scales posterior to lateral line	0.36
Cheek scales	0.28
Gill rakers on first ceratobranchial	0.08
Gill rakers on first epibranchial	0.18
Teeth rows on upper jaw	-0.36
Teeth rows on lower jaw	-0.33

Table 6. Variable loadings on the first principal component of the meristic data for *Amphilophus citrinellus* complex.

(PCA) of the correlation matrix. Differences between species were illustrated by plotting the sheared second principal components of the morphometric data

against the first principal components of the meristic data (Stauffer and Hert, 1992).

Measurements	<i>Amphilophus labiatus</i>			<i>Amphilophus erythraeus</i>	<i>Amphilophus granadensis</i>
	Mean	St. Dev.	Range	Holotype	Holotype
Standard length, mm	135	7.9	129.4-140.6	130	121.3
Head length, mm	52	1.5	51.1-53.2	46.1	41.2
<i>Percent of standard length</i>					
Head length	38.6	1.2	37.8-39.5	35.5	34.0
Snout to dorsal-fin origin	46.7	0.4	46.4-47.0	42.6	41.0
Snout to pelvic-fin origin	45.2	0.9	4.46-4.59	42.8	46.9
Caudal peduncal length	11.1	1.3	10.2-12.0	11.7	10.9
Least caudal peduncal depth	13.6	0.1	13.5-13.7	13.0	15.0
Dorsal-fin base length	55.8	2.1	54.4-57.3	59.0	59.2
ADAA	54.0	2.2	52.5-55.6	54.0	54.6
PDPA	15.7	1.6	14.6-16.9	15.7	16.6
ADPA	61.7	0.2	61.6-61.9	61.7	63.6
PDAA	34.7	2.3	33.1-36.3	34.7	36.8
PDVC	17.4	0.7	16.9-17.9	17.4	19.0
PADC	18.1	0.8	17.5-18.7	18.1	17.8
ADP2	41.8	2.1	40.4-43.3	41.8	43.9
PDP2	54.3	3.7	51.7-56.9	54.3	36.5
<i>Percent head length</i>					
Horizontal eye diameter	25.5	0.4	25.2-25.8	26.9	30.8
Vertical eye diameter	24.6	2.3	23.0-26.3	26.1	30.0
Snout length	43.1	0.4	42.8-43.4	37.8	40.5
Postorbital head length	35.9	0.5	35.6-36.3	35.7	38.5
Preorbital depth	23.4	2.1	22.0-24.9	38.4	23.2
Lower-jaw length	43.4	2.4	41.7-45.1	42.3	41.3
Cheek depth	26.2	2.3	24.6-27.8	27.4	29.4
Head depth	85.4	77.8	79.9-90.9	101.3	108.1

Table 7. Morphometric values of *Amphilophus labiatus* (syntypes, BMNH 1867.9.23:7-8; n=2), *Amphilophus erythraeus* (holotype; BMNH 1865.7.20:33), and *Amphilophus granadensis* (paratype; FMNH 5950).

Counts	<i>Amphilophus labiatus</i>			<i>Amphilophus erythraeus</i>	<i>Amphilophus granadensis</i>
	Mode	% Freq.	Range	Holotype	Holotype
Lateral-line scales	31	100	31	31	30
Pored scales posterior to lateral line	2	100	2	2	2
Scale rows on cheek	4	100	4	4	4
Dorsal-fin spines	17	100	17	17	17
Dorsal-fin rays	11	100	11	12	12
Anal-fin spines	7	100	7	7	7
Anal-fin rays			7-8	8	8
Pectoral-fin rays	14	100	14	15	15
Pelvic-fin rays	5	100	5	5	5
Gill rakers on first ceratobranchial	10	100	10	8	9
Gill rakers on first epibranchial			2-4	3	3
Teeth in outer row of left lower jaw			18-19	16	5
Teeth rows on upper jaw	3	100	3	3	1
Teeth rows on lower jaw	3	100	3	3	1

Table 8. Meristic values of *Amphilophus labiatus* (syntypes, BMNH 1867.9.23:7-8; n=2), *Amphilophus erythraeus* (holotype; BMNH 1865.7.20:33), and *Amphilophus granadensis* (paratype; FMNH 5950).

Results

We only measured a subset of the type series of previously described species of the *A. citrinellus* complex

(Tables 2-8); however, based on these data there is no overlap among the minimum polygon clusters when the sheared second principal components (morphometric data) are plotted against the first principal compo-



Figure 4. Holotype (PSU 3448.1) of *Amphilophus amarillo*.



Figure 5. A pair of *Amphilophus amarillo* guarding their offspring in a rocky habitat along the western shore of Lake Xiloá (photo by Ad Konings).

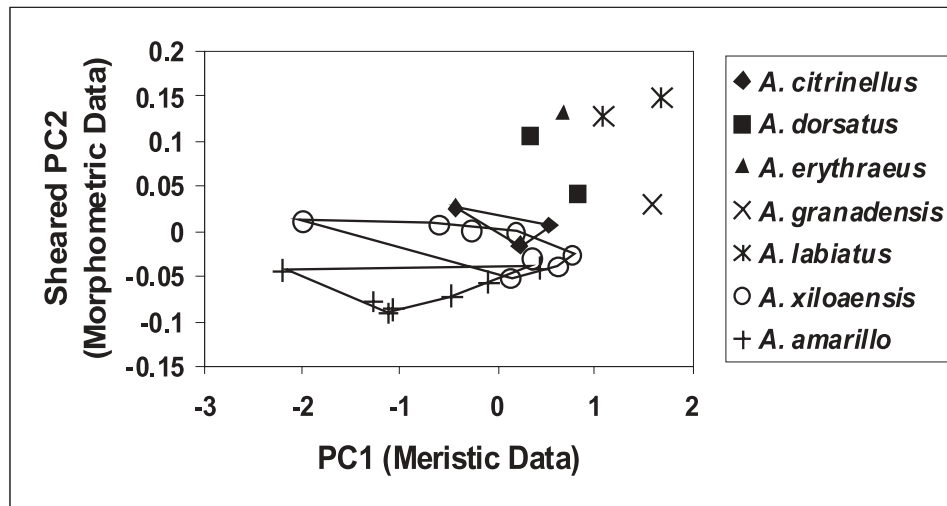


Figure 6. Plot of individual sheared second principal component scores (morphometric data) and the first principle component scores (meristic data) of a subset of the type series of the *A. citrinellus* complex.

nents of the meristic data (Fig. 6). Size accounted for 88.5% and the second principal component accounted for 3.2% of the total variance of the morphometric data. Those variables that had the highest loadings on the sheared second principal component were preorbital depth, lower jaw length, and snout length (Table 5). The parameters that had the highest loadings on the first principal component of the meristic data were dorsal-fin spines, post lateral-line scales, and teeth rows on the upper jaw (Table 6).

Amphilophus amarillo, n. sp.
(Fig. 4)

Holotype. – Penn State University Fish Museum (PSU) 3448.1, adult male, 154.6 mm SL from Agua caliente, Lake Xiloá (N 12° 13,848' W 86° 19,387'); Field No. JRS-93-64, 18 October, 1993 (3-10 m).

Paratypes. – PSU 3448 (6 specimens, 107.6-142.2 mm SL); data as for holotype.

Diagnosis. – *Amphilophus amarillo* has a shorter snout (35.3-40.1% SL) and dorsal-fin base length (57.0-61.9% SL) than *A. citrinellus* (40.4-41.9%, 63.0-63.9% SL, respectively) and a shorter snout than *Amphilophus granadensis* (Meek) (40.5%SL). *Amphilophus amarillo* has a shorter head (34.5-36.8% SL) than *A. dorsatus* (38.1-38.2% SL) and *A. labiatus* (37.8-39.5% SL). Body depth as measured by ADP2 is greater in *A. amarillo* (43.7-49.0% SL) than in either

Amphilophus erythraeus (Günther) (41.8% SL) or *A. granadensis* (36.5% SL).

Description. – Principal morphometric ratios are given in Table 9 and meristic values in Table 10. Both males and females are colored similarly (Fig. 5). Head with green ground coloration with yellow highlights; below cheek head is yellow; anterior portion of gular yellow, posterior portion red/orange. Interorbital region green with two dark green interorbital bars; preopercle green; posterior portion of opercle red/yellow/orange. Dorsally to upper lateral line, green with yellow highlights in some individuals and yellow in others;

middle 1/3 of lateral side yellow; ventral 1/3 green/yellow; 6-8 black bars that appear as extension of mid-black spots, the anterior bars extend into dorsal fin;

Measurements	Holotype	Mean	St. Dev.	Range
Standard length	154.6	125.8	15.9	107.6-154.6
Head length, mm	55.9	44.7	6.2	37.9-55.9
<i>Percent of standard length</i>				
Head length	36.2	35.5	0.75	34.5-36.8
Snout to dorsal-fin origin	43.7	43.0	1.9	40.3-46.7
Snout to pelvic-fin origin	44.2	44.1	1.1	41.8-45.2
Caudal peduncal length	12.8	12.1	1.5	9.9-14.8
Least caudal peduncal depth	13.8	14.1	0.4	13.7-14.7
Dorsal-fin base length	61.1	59.7	1.8	57.0-61.9
ADAA	58.7	55.7	2.6	52.6-60.2
PDPA	16.3	16.2	0.7	15.4-17.4
ADPA	66.9	65.8	1.9	63.5-68.2
PDAA	37.2	37.4	1.3	35.1-39.5
PDVC	19.5	18.1	0.9	16.6-19.5
PADC	18.5	18.8	0.7	18.0-19.6
ADP2	47.7	46.4	1.8	43.7-49.0
PDP2	59.0	57.6	1.1	56.0-59.0
<i>Percent head length</i>				
Horizontal eye diameter	25.8	28.8	2.6	25.8-32.5
Vertical eye diameter	25.9	27.7	1.9	25.6-30.8
Snout length	40.1	37.9	1.7	35.3-40.1
Postorbital head length	40.3	38.1	1.3	35.9-40.3
Preorbital depth	25.3	22.9	1.7	20.6-25.3
Lower-jaw length	36.9	40.6	2.0	36.9-43.3
Cheek depth	33.0	30.1	2.2	26.7-33.3
Head depth	102.8	106	4.2	102-113

Table 9. Morphometric values of *Amphilophus amarillo* (PSU 3448; PSU 3448.1; n=8; mean includes holotype).

Counts	Holotype	Mode	% Freq.	Range
Lateral-line scales	30	30	50	30-32
Pored scales posterior to lateral line	2	2	75	1-2
Scale rows on cheek	4	4	87.5	3-4
Dorsal-fin spines	17	17	62.5	16-17
Dorsal-fin rays	11			11-12
Anal-fin spines	7	7	87.5	6-7
Anal-fin rays	8	8	75	7-9
Pectoral-fin rays	15	15	62.5	15-16
Pelvic-fin rays	5	5	100	
Gill rakers on first ceratobranchial	7	7	62.5	7-8
Gill rakers on first epibranchial	2	2	75	1-3
Teeth in outer row of left lower jaw	11	11	50	11-13
Teeth rows on upper jaw	3	3	87.5	2-3
Teeth rows on lower jaw	3	3	50	2-4

Table 10. Meristic values of *Amphilophus amarillo* (PSU 3448.1; PSU 3348; n=8; mode includes holotype).

black caudal spot that extends onto caudal fin. Belly yellow-green with black highlights. Dorsal fin green/gray; posterior rays orange in some individuals. Caudal fin with gray rays and clear membranes with orange highlights. Distal portion of anal-fin spines black, majority of anal-fin membranes green/gray with pos-

Measurements	Holotype	Mean	St. Dev.	Range
Standard length	141.6	145.9	15.0	124.3-170.5
Head length, mm	52.6	52.2	4.9	45.1-58.7
<i>Percent of standard length</i>				
Head length	35.6	35.8	0.92	34.2-37.0
Snout to dorsal-fin origin	43.3	42.9	1.5	39.9-44.1
Snout to pelvic-fin origin	41.4	44.1	1.4	41.4-45.4
Caudal peduncal length	12.0	11.6	0.6	11.0-12.5
Least caudal peduncal depth	13.8	14.4	0.4	13.8-15.2
Dorsal-fin base length	62.2	61.3	2.5	58.2-65.3
ADAA	54.9	57.7	3.1	53.5-62.2
PDPA	17.3	17.0	0.5	16.4-17.6
ADPA	66.3	67.0	2.4	64.4-71.0
PDAA	38.9	38.9	1.1	37.3-40.1
PDVC	18.1	18.7	0.9	17.6-19.9
PADC	19.7	19.2	0.8	18.1-20.3
ADP2	45.5	48.8	2.4	45.5-52.1
PDP2	58.8	60.9	1.8	58.8-63.5
<i>Percent head length</i>				
Horizontal eye diameter	26.8	26.8	0.3	26.6-27.3
Vertical eye diameter	25.3	25.4	0.6	24.4-26.1
Snout length	41.9	39.5	2.2	36.1-42.5
Postorbital head length	36.6	38.4	2.0	36.6-47-1.7
Preorbital depth	22.9	24.1	1.0	22.9-25.8
Lower-jaw length	37.9	36.6	1.3	33.9-37.9
Cheek depth	29.2	31.1	2.1	28.6-34.1
Head depth	115.2	118.6	6.4	113.5-131.6

Table 11. Morphometric values of *Amphilophus xiloaensis* (n=7 and includes holotype).

terior portion orange. Pelvic fins green/gray with first ray black. Pectoral fins with clear membranes and rays with faint yellow markings on rays.

Etymology. – Specific epithet from Spanish meaning yellow to denote the yellow highlights throughout. A noun in apposition.

Amphilophus xiloaensis, n. sp.
(Fig. 7)

Holotype. – PSU3381.1, adult male, 147.6 mm SL from the southeastern shore of Lake Xiloá (N 12° 12,793' W 86° 19,028'), Field No. JRS-00-121, 18 December, 2000 (2-8 m)

Paratypes. – PSU3381, data as for holotype, (1 specimen, 124.3 mm); PSU3384, (5 specimens, 137.2-158.6 mm) Lake Xiloá, in front of Club Nautico (N 12° 12,907' W 86° 19,418'), Field No. JRS-93-67, 19 October, 1993.

Diagnosis. – *Amphilophus xiloaensis* has a smaller eye (HED – 26.6-27.3%SL; VED – 24.4-26.1%SL) than *A. citrinellus* (HED – 28.4-29.2%SL; VED – 27.2-29.6%SL), *A. dorsatus* (HED – 33.9-35.7%SL; VED – 30.0-30.9%SL) and *A. granadensis* (HED – 30.8%SL; VED – 30.0%SL). *Amphilophus xiloaensis* (34.2-37.0%SL) has a shorter head than *A. labiatus* (37.8-39.5%SL). *Amphilophus xiloaensis* has a deeper body as evidenced by ADPA (64.4-71.0%SL) and PDAA (37.3-40.1%SL) than either *A. erythraeus* (ADPA – 61.7%SL; PDAA – 34.7%SL) or *A. granadensis* (ADPA – 63.6%SL; PDAA 36.8%SL). *Amphilophus xiloaensis* has 9-11 gill rakers on the first ceratobranchial, while *A. amarillo* has 7-8.

Description. – Principal morphometric ratios are given in Table 11 and meristic values in Table 12. Both males and females are colored similarly (Fig. 8), and there are gold morphs (Figs. 9-10) of both sexes. Some forms have a gray/green head with single black interorbital bar and red gular. Laterally gray ground color with six black vertical bars and caudal spot that extends onto caudal fin; white belly. Dorsal, caudal, and anal fins gray with lighter spots. Pelvic fins gray with black leading edge. Pectoral fins clear. Other colored forms with yellow head and white cheek, white opercle with yellow/green highlights, and white gular with red blotches. Laterally bright orange with white shoulder. Dorsal fin orange with



Figure 7. Holotype (PSU3381) of *Amphilophus xiloaensis*.



Figure 8. A pair of *Amphilophus xiloaensis* defending their offspring in Lake Xiloá (Photo by Ad Konings).



Figure 9. A mixed gold/normal pair of *Amphilophus xiloaensis* in Lake Xiloá (photo by Ad Konings).



Figure 10. Gold pair of *Amphilophus xiloaensis* protecting their brood in Lake Xiloá (photo by Ad Konings).

Counts	Holotype	Mode	% Freq.	Range
Lateral-line scales	32	30	57.1	30-32
Pored scales posterior to lateral line	2	2	57.1	0-2
Scale rows on cheek	4	4	100	
Dorsal-fin spines	17	16	71.4	16-17
Dorsal-fin rays	12	12	71.4	11-12
Anal-fin spines	7	7	57.4	6-7
Anal-fin rays	8	8	71.4	8-9
Pectoral-fin rays	15	15/16	42.9	15-17
Pelvic-fin rays	5	5	100	
Gill rakers on first ceratobranchial	9	9	85.7	9-11
Gill rakers on first epibranchial	3	3	85.7	2-3
Teeth in outer row of left lower jaw	14	11	42.9	10-14
Teeth rows on upper jaw	4	4	71.4	3-4
Teeth rows on lower jaw	4	4	85.7	3-4

Table 12. Meristic values of *Amphilophus xiloaensis* (n=7 and mode includes holotype).

white patches. Caudal fin orange with white tips. Anal fin orange with white lappets. Pectoral fins orange with posterior one-quarter white. Pelvic fins orange, with spine and 1st ray white and 2nd ray red. Other individuals mostly white with orange blotches, while others were bright orange.

Etymology. – Specific epithet references the type locality Lake Xiloá. An adjective.

Amphilophus sagittae, n. sp.

(Fig. 11)

Holotype. – PSU3386.1, adult male, 157.2 mm SL from from Agua caliente Lake Xiloá (N 12° 13,848' W 86° 19,387'), Field No. JRS-93-64, 18 October, 1993 (3-10 m).

Paratypes. – PSU 3386, (5 specimens, 144.0-159.1 mm SL), data as for holotype; PSU3383 (2 specimens 129.6-159.8 mm SL), Field No. JRS-00-121, 17 December, 2000; PSU82 (5 specimens 121.2-160.3 mm SL), Field No. JRS-00-122, 18 December, 2000; from Lake Xiloá (N 12° 12,793' W 86° 19,028').

Diagnosis. – *Amphilophus sagittae* has a more streamlined body, as indicated by the smaller snout to dorsal-fin origin (38.6-41.9%SL) and ADAA (49.7-53.8%SL) (Table 14) than *A. citrinellus* (42.7-44.6%SL; 57.6-59.5%SL), *A. dorsatus* (44.0-46.8%SL; 54.4-55.8%SL), *A. labiatus* (46.4-47.0%SL; 52.5-55.6%SL), *A. erythraeus* (42.6%SL; 54.0%SL), *A. granadensis* (41.0%SL; 54.6%SL), and *A. amarillo* (40.3-46.7%SL; 52.6-60.2%SL). *Amphilophus sagittae* has a longer caudal peduncal length (11.4-

14.0%SL) than *A. granadensis* (10.9%SL). *Amphilophus sagittae* has a smaller ADP2 (39.3-43.4%SL) than *A. xiloaensis* (45.5-52.1%SL). *Amphilophus sagittae* morphologically resembles *Amphilophus zaliosus* Barlow from Lake Apoyo. The PDPA for *A. sagittae* (15.4-17.9%SL) is greater than that of *A. zaliosus* (13.7-15.5%SL; Table 15 & 16).

Description. – Principal morphometric ratios are given in Table 13 and meristic values in Table 14. Both males and females are colored similarly (Figs. 14, 15). Head is dark green dorsally, black laterally and with a black gular, although some specimens with a red gular. Laterally black with green highlights and 5 black bars. Ventrally black anterior to P2 and white posterior to P2. Dorsal, caudal, anal, and pelvic fins black. Pectoral fins with black rays and clear membranes.

Etymology. – Specific epithet is a noun in apposition, from Latin sagitta or sagittae meaning arrow, which denotes the slender shape of this species when compared to other *Amphilophus* species found in Lake Xiloá.

Measurements	Holotype	Mean	St. Dev.	Range
Standard length	157.2	150.9	12.7	121.2-163.1
Head length, mm	53.8	51.8	4.3	42.8-55.8
<i>Percent of standard length</i>				
Head length	34.2	34.4	0.7	33.1-35.3
Snout to dorsal-fin origin	39.1	40.3	1.0	38.6-41.9
Snout to pelvic-fin origin	40.8	42.0	2.5	38.7-47.5
Caudal peduncal length	12.7	12.6	0.7	11.4-14.0
Least caudal peduncal depth	14.5	14.0	0.4	13.5-14.9
Dorsal-fin base length	60.3	59.9	1.5	55.4-61.7
ADAA	52.2	52.1	1.3	49.7-53.8
PDPA	16.6	16.7	0.7	15.4-17.9
ADPA	65.3	64.7	1.9	59.4-66.8
PDAA	36.7	37.4	1.8	31.9-39.6
PDVC	18.9	18.2	0.9	16.4-19.3
PADC	19.2	19.4	0.6	18.5-20.6
ADP2	40.7	41.8	1.3	39.3-43.4
PDP2	55.8	58.0	1.9	54.0-60.1
<i>Percent head length</i>				
Horizontal eye diameter	27.0	27.1	1.3	25.0-29.1
Vertical eye diameter	26.9	25.6	1.5	23.2-27.4
Snout length	39.7	38.5	2.0	35.0-42.2
Postorbital head length	39.8	39.4	1.6	37.1-42.1
Preorbital depth	23.5	22.8	1.0	21.2-24.2
Lower-jaw length	35.0	38.4	1.9	35.0-42.0
Cheek depth	29.1	28.7	2.0	24.9-31.7
Head depth	97.7	105.0	3.8	97.7-110.5

Table 13. Morphometric values of *Amphilophus sagittae* (n=13 and includes holotype).

Counts	Holotype	Mode	% Freq.	Range
Lateral-line scales	30	31	38.5	30-35
Pored scales posterior to lateral line	1	2	92.3	1-2
Scale rows on cheek	5	5	76.9	4-5
Dorsal-fin spines	17	17	69.2	16-17
Dorsal-fin rays	11	11	61.5	11-12
Anal-fin spines	6	7	67.5	6-7
Anal-fin rays	9	9	53.8	8-10
Pectoral-fin rays	5	16	38.5	14-17
Pelvic-fin rays	15	5	100	
Gill rakers on first ceratobranchial	10	11	46.2	8-12
Gill rakers on first epibranchial	3	2	76.9	2-3
Teeth in outer row of left lower jaw	11	12	46.2	10-12
Teeth rows on upper jaw	4	4	92.3	3-4
Teeth rows on lower jaw	4	4	61.5	3-5

Table 14. Meristic values of *Amphilophus sagittae* (n=13 and mode includes holotype).

Discussion

The SPCA of the morphometric data and PCA of the meristic data of the known species in the *A. citrinellus* species complex result in the minimum polygon clusters shown in Fig. 12. *Amphilophus sagittae* is quite distinct from the other forms; thus, the minimum polygon clusters of the other two newly described species

Measurements	Mean	St. Dev.	Range
Standard length	119.2	6.6	110-124
Head length, mm	39.8	2.6	36.2-42.3
<i>Percent of standard length</i>			
Head length	33.4	0.7	32.5-34.0
Snout to dorsal-fin origin	38.8	1.1	37.3-40.1
Snout to pelvic-fin origin	41.5	0.8	40.6-42.6
Caudal peduncal length	14.6	1.2	13.3-16.3
Least caudal peduncal depth	12.7	1.7	11.2-15.5
Dorsal-fin base length	57.4	1.7	55.8-59.8
ADAA	48.7	2.9	45.7-53.3
PDPA	14.2	0.9	13.7-15.5
ADPA	60.9	2.5	57.1-64.1
PDAA	32.9	0.6	32.0-33.7
PDVC	18.4	1.1	17.1-20.0
PADC	18.3	1.0	16.8-19.5
ADP2	39.2	2.0	36.8-41.5
PDP2	54.4	17.0	51.6-56.2
<i>Percent head length</i>			
Horizontal eye diameter	27.6	1.8	25.6-29.9
Vertical eye diameter	27.0	1.9	24.9-29.2
Snout length	36.3	1.1	35.2-37.8
Postorbital head length	37.9	0.8	37.1-39.2
Preorbital depth	21.2	1.0	20.0-22.4
Lower-jaw length	37.8	1.7	35.2-39.5
Cheek depth	26.7	0.4	26.3-27.3
Head depth	96.1	10.5	81.2-108.4

Table 15. Morphometric values of *Amphilophus zaliosus* (paratypes, CAS29105; n=5).

overlap with each other. When the data for *A. sagittae* is removed from the analysis, the two other new species from Lake Xiloá are closely grouped with *A. citrinellus*. When *A. citrinellus*, *A. amarillo*, and *A. xiloaensis* are analyzed separately the minimum polygon clusters among the species do not overlap (Fig. 13). Size accounted for 90% and the second principal component for 2.9% of the total variance of the morphometric data. Those variables that had the highest loadings on the sheared second principal component were caudal peduncle length and head depth (Table 17). The characters that had the highest loadings on the first principal component of the meristic data were gill rakers and teeth rows (Table 18).

Amphilophus sagittae from Lake Xiloá closely resembles *A. zaliosus* from Lake Apoyo. The minimum polygon clusters formed by plotting the sheared second principal components of the morphometric data against the first principal components of the meristic data do not overlap (Fig. 16). Size accounted for 94% and the second principal component accounted for 2.3% of the total variance of the morphometric data. Those variables that had the highest loadings on the sheared second principal component are least caudal peduncle depth, dorsal-fin base length, and PDPA (Table 19). The parameters that had the highest loadings on the first principal component of the meristic data were dorsal-fin elements and gill rakers (Table 20).

More research on the *Amphilophus* species in the lakes of Nicaragua is desperately needed. Waid *et al.* (1999) reported the presence of *A. citrinellus* in eight crater lakes in the Great Lakes Basin of Nicaragua. It may be

Counts	Mode	% Freq.	Range
Lateral-line scales	32	60	31-32
Pored scales posterior to lateral line	2	80	2-3
Scale rows on cheek	5	80	5-6
Dorsal-fin spines	17	60	16-17
Dorsal-fin rays	12	60	11-13
Anal-fin spines	7	60	6-7
Anal-fin rays	8	60	8-9
Pectoral-fin rays	15	80	13-15
Pelvic-fin rays	5	100	
Gill rakers on first ceratobranchial	11	80	10-11
Gill rakers on first epibranchial	3	60	2-3
Teeth in outer row of left lower jaw	15	40	12-16
Teeth rows on upper jaw	4	100	
Teeth rows on lower jaw	3	80	3-4

Table 16. Meristic values of *Amphilophus zaliosus* (paratypes, CAS29105; n=5).



Figure 11. Holotype (PSU3386.1) of *Amphilophus sagittae*.

	Size	PC ₂
Standard length	-0.19	0.06
Head length	-0.19	0.02
Snout length	-0.24	-0.13
Post orbital head length	-0.20	0.07
Horizontal eye diameter	-0.12	0.20
Vertical eye diameter	-0.14	0.06
Head depth	-0.18	-0.32
Preorbital depth	-0.27	-0.17
Cheek depth	-0.24	-0.16
Lower jaw length	-0.17	-0.03
Snout to dorsal-fin origin	-0.17	-0.12
Snout to pelvic-fin origin	-0.19	0.04
Dorsal-fin base length	-0.20	-0.13
ADAA	-0.22	-0.12
ADPA	-0.21	-0.09
PDAA	-0.20	-0.16
PDPA	-0.23	0.04
PDVC	-0.25	0.05
PADC	-0.21	0.21
PDP2	-0.21	0.04
ADP2	-0.21	-0.08
Caudal peduncle length	-0.21	0.80
Least caudal peduncle depth	-0.20	0.01

Table 17. Variable loadings on the size principal components and second principal components (shape factor) of the morphometric data for *Amphilophus citrinellus*, *Amphilophus amarillo*, and *Amphilophus xiloaensis*.

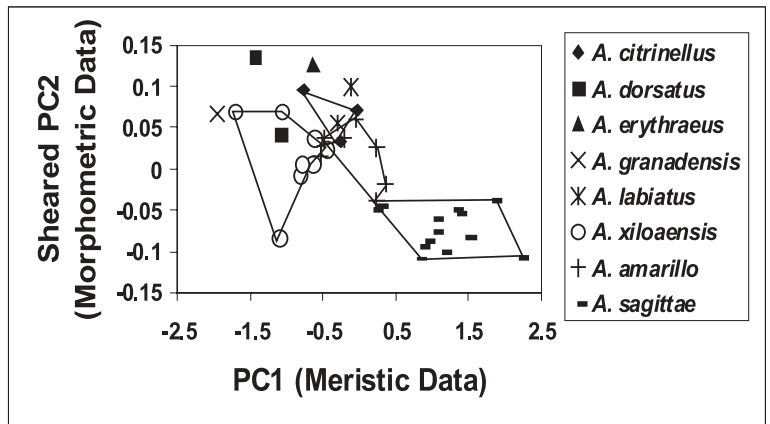


Figure 12. Plot of individual sheared second principal component scores (morphometric data) and the first principle component scores (meristic data) of a subset of the type series of the *A. citrinellus* complex, including *Amphilophus sagittae*.

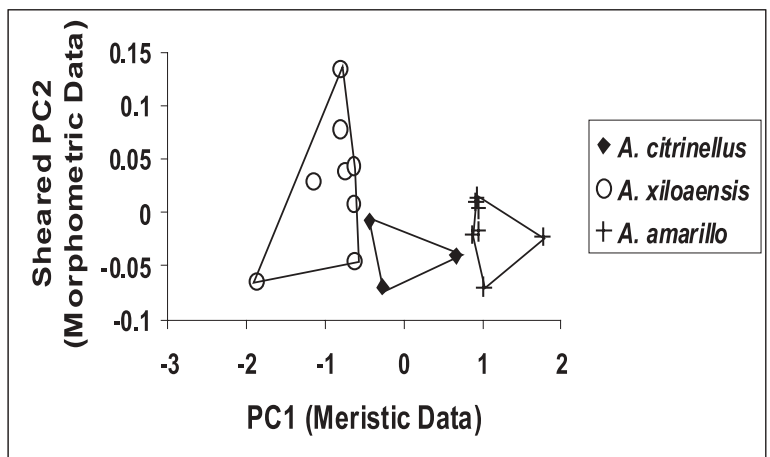


Figure 13. Plot of individual sheared second principal component scores (morphometric data) and the first principle component scores (meristic data) of a subset of the type series of the *Amphilophus citrinellus*, *Amphilophus xiloaensis*, and *Amphilophus amarillo*.



Fig 14. A fry-guarding pair *Amphilophus sagittae* in Lake Xiloá (photo by Ad Konings).



Fig 15. A gold-colored pair *Amphilophus sagittae* leading their offspring in Lake Xiloá (photo by Ad Konings).

Characters	PC ₁
Dorsal spines	-0.15
Dorsal rays	0.14
Anal rays	0.16
Pectoral rays	0.20
Lateral-line scales	0.04
Pored scales posterior to lateral line	-0.17
Cheek scales	0.29
Gill rakers on first ceratobranchial	0.48
Gill rakers on first epibranchial	0.49
Teeth rows on upper jaw	0.41
Teeth rows on lower jaw	0.37

Table 18. Variable loadings on the first principal component of the meristic data for *Amphilophus citrinellus*, *Amphilophus amarillo*, and *Amphilophus xiloaensis*.

that we are observing multiple species within each of the crater lakes. For example, *A. zaliosus*, the Arrow Cichlid from Lake Apoyo, is piscivorous and morphologically resembles *A. sagittae*; however, it appears to be genetically closer to all other species in Lake Apoyo than to the *A. sagittae* in Lake Xiloá (McKaye *et al.*, 1998). Our genetic data (Stauffer *et al.* 1995, McKaye *et al.* 1998) indicate that all of the species within both Lake Xiloá and Lake Apoyo are more closely related to each other than to the phenotypically similar forms in the different lakes. This suggests that the similar morphologies are due to convergence (Kocher *et al.* 1993), and that sympatric speciation may indeed be occurring in each of the crater lakes (McKaye 1980). McKaye *et al.* (1998) reported on the genetic similarity of these cichlids in the two lakes and these results have been supported by subsequent research (Wilson *et al.* 2000).

Nicaragua is of geologically recent origin. The region was formed in the late Cretaceous or early Paleocene (Villa, 1982). This implies that the great basin of Nicaraguan lakes (Fig.1), is of recent formation, and so its ichthyofauna. Rapid allopatric and intralacustrine speciation might be taking place within this species group. Further careful research examining the behavior, morphology and genetics of these fishes is required to determine the phylogeny and species composition of this species complex. McKaye *et al.* (this volume) compares and contrasts behavioral and genetic information of the Lake Xiloá species.

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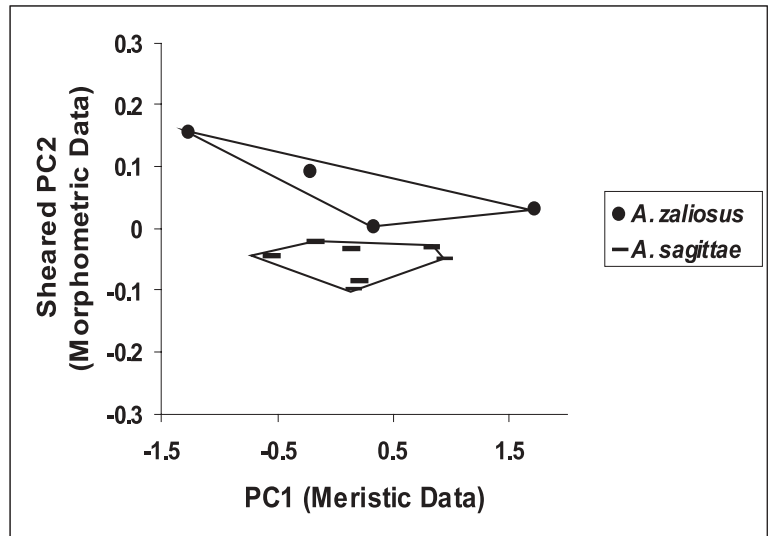


Figure 16. Plot of individual sheared second principal component scores (morphometric data) and the first principle component scores (meristic data) of a subset of the type series of the *Amphilophus zaliosus* (also in the legend above) and *Amphilophus sagittae*.

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	Size	PC ₂
Standard length	-0.20	0.10
Head length	-0.18	0.10
Snout length	-0.27	0.27
Post orbital head length	-0.19	-0.08
Horizontal eye diameter	-0.10	-0.26
Vertical eye diameter	-0.13	-0.17
Head depth	-0.21	-0.35
Preorbital depth	-0.25	0.22
Cheek depth	-0.26	0.18
Lower jaw length	-0.20	0.10
Snout to dorsal-fin origin	-0.20	0.20
Snout to pelvic-fin origin	-0.19	0.13
Dorsal-fin base length	-0.19	-0.60
ADAA	-0.23	0.02
ADPA	-0.23	0.08
PDAA	-0.20	-0.15
PDPA	-0.18	-0.38
PDVC	-0.27	0.29
PADC	-0.19	-0.04
PDP2	-0.19	-0.12
ADP2	-0.21	-0.12
Caudal peduncle length	-0.14	0.25
Least caudal peduncle depth	-0.17	-0.43

Table 19. Variable loadings on the size principal components and second principal components (shape factor) of the morphometric data for *Amphilophus sagittae* and *Amphilophus zaliosus*.

Characters	PC ₁
Dorsal spines	0.51
Dorsal rays	0.36
Anal rays	0.32
Lateral-line scales	-0.03
Pored scales posterior to lateral line	0.07
Cheek scales	0.37
Gill rakers on first ceratobranchial	0.36
Gill rakers on first epibranchial	-0.48

Table 20. Variable loadings on the first principal component of the meristic data for *Amphilophus sagittae* and *Amphilophus zaliosus*.

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Resumen

Tres especies nuevas en el complejo de especies *Amphilophus citrinellus* (Günther) de la laguna de Xiloá son descritas. Historicamente, muchas formas han sido documentadas que son fenotípicamente similares a *A. citrinellus*, y en las lagunas cratéricas de Nicaragua, este complejo fue previamente considerado ser representado por una sola, ampliamente variable especie. En la laguna de Xiloá, las tres especies se aparean asociativamente, y difieren morfológicamente una de otra y de todas las especies previamente descritas en el complejo *A. citrinellus*.