



## A new livebearing fish, *Heterandria tuxtlaensis*, from Lake Catemaco, Veracruz, Mexico (Cyprinodontiformes: Poeciliidae)

JOHN D. MCEACHRAN<sup>1</sup> & THOMAS J. DEWITT<sup>2</sup>

Department of Wildlife & Fisheries Sciences, Texas A&M University, 2258 TAMU, College Station, TX 77843-2258, USA.

E-mail: <sup>1</sup>j-mceachran@tamu.edu, <sup>2</sup>tdewitt@tamu.edu.

### Abstract

A new species of poeciliid fish, *Heterandria tuxtlaensis* **sp. n.**, is described from Lake Catemaco in southern Veracruz, Mexico. Based on traditional and geometric morphometrics, *H. tuxtlaensis* differs most substantially from its likely sister species *H. bimaculata* in possessing short dorsal and caudal fins, a short dorsal fin base composed of fewer fin rays, a more shallow body, and a relatively small basicaudal spot restricted to the area above the mid lateral line. Description of this new species brings the number of known endemics in Lake Catemaco to six. This high level of endemism complements genetic and geological findings suggesting the lake is ancient and well separated from surrounding fish populations.

**Key words:** *Heterandria tuxtlaensis*, Poeciliidae, Lake Catemaco, Lago de Catemaco, Veracruz

### Introduction

Endemism is particularly common in freshwater lakes of ancient origin, and especially for lakes with strong vicariant separation from ancestral populations (Martens *et al.* 1994; McKinnon 2002). Lake Catemaco, which appears to be such a lake, is located in southern Veracruz within the Tuxtlas Mountains. The lake occupies a caldera and was formed up to two million years ago during the Tuxtlas volcanic orogeny that took place in the Pliocene-Pleistocene (West 1964). Lake Catemaco is about 340 m above sea level, resembles an irregular rectangle approximately 9 by 14 km, and has a maximum depth of 22 m (Torres-Orozco *et al.*, 1996; Miller and Conner 1997). Streams to the south and west drain into the lake, and there is only one outlet river, Río Grande de Catemaco, located on the northwest corner of the lake (John Van Conner unpubl. ms.). About 13 kilometers downstream from the lake, at the village of Salto de Eyipantla, the Río Grande flows over a large waterfall. Below the waterfall the Río Grande joins the Río Tuxtla and shortly thereafter the rivers join the San Juan arm of the Río Papaloapan drainage system. The waterfall at Eyipantla isolates the biota of the Lake Catemaco system, the inflowing streams, and the upper section of the Río Grande from that of the remainder of the Papaloapan drainage.

According to Miller and Conner (1997) there are 14 species of fishes in Lake Catemaco. Two species, *Micropterus salmoides* Lacepède and *Oreochromis aureus* Steindachner have been introduced into the lake, and another two species, *Vieja fenestrata* Günther and *Ophisternon aenigmaticum* Rosen & Greenwood, are widespread throughout eastern Mexico and Central America. Of the remaining 10 species, five are endemic to the lake and five may represent undescribed species endemic to the lake (Miller and Conner 1997, Meyer and Scharl 2003). The high rate of endemism suggests that Lake Catemaco has been biogeographically isolated for some time, possibly since its origin up to 2 million years ago. In this paper we describe a new species from

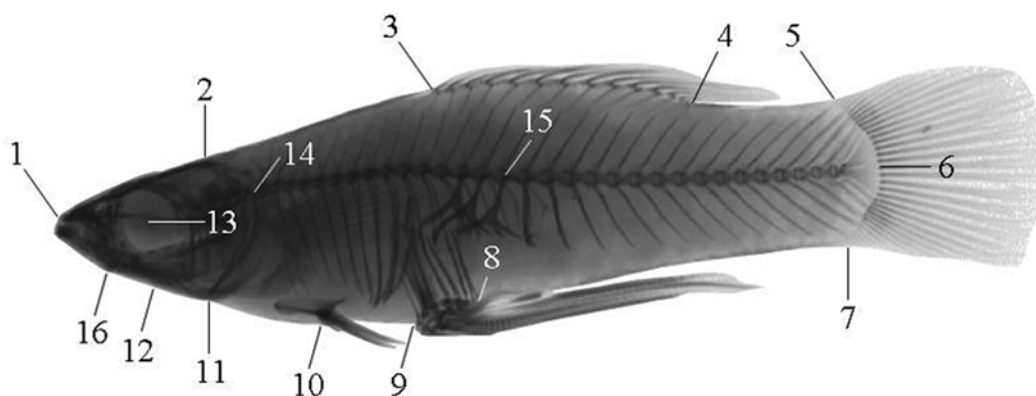
the lake, representing one of the five putative new species, and thus increase the number of endemic species to six.

## Material and methods

Specimens examined are housed in the following institutions: American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Gulf Coast Research Laboratory (GCRL), Naturhistorisches Museum Wien (NMW), Texas Cooperative Wildlife Collection (TCWC), Tulane University Fish Collection (TU), Universidad Nacional Autónoma de México (UNAM), and University of Michigan Museum of Zoology (UMMZ). Acronyms are according to Leviton *et al.* (1985).

Traditional morphological and meristic data were taken from 40 specimens (20 males and 20 females) of the type series and from 40 specimens (20 males and 20 females) of *H. bimaculata* Heckel (TCWC 759.01), from the village of Sontecomapan about 10 km east of the lake. Counts and measurements follow Rosen and Bailey (1963). Measurements were taken with electronic digital calipers to the nearest 0.01 mm. Vertebral counts are according to Miller (1974) and were made from radiographs.

Additionally, radiographs were used to perform a landmark-based shape analysis to further characterize the new species compared to relatives outside the lake. Fifteen males and females from Lake Catemaco were x-rayed, as were 15 of each sex of *H. bimaculata* from the village of Sontecomapan. In this analysis 16 landmarks were digitized as per Figure 1. Males and females were analyzed separately due to the marked sexual dimorphism in this group of fishes. Landmarks were superimposed (rotated, translated and scaled) into the conformation with minimum least squares deviation from the consensus (average) conformation. Superimposed coordinates were subjected to principle components analysis and 10 principle components, constructed from covariances, were retained for further analysis. These shape variables are equivalent to “relative warps” (with  $\alpha=0$ ; Bookstein 1991, Rohlf 2003a) and accounted for 96.7 and 95.2 % of total shape variance for males and females, respectively. Data reduction through principle components was necessary to prevent having more dependent variables than the number of specimens.



**FIGURE 1.** Radiograph negative of a male *H. tuxtlaensis* showing landmarks used for the body shape analysis. 1—anterio-dorsal-most position on the snout; 2—top of head where skull breaks away from the body outline; 3, 4—origin and insertion of the dorsal fin, respectively; 5—dorsal origin of the caudal fin (anterio-dorsal-most procurent ray); 6—middle of caudal fin base (between hypural plates); 7—ventral origin of caudal fin (anterio-ventral-most procurent ray; 8, 9—insertion and origin of anal fin, respectively; 10—anterior margin of pelvic fins; 11—anterio-ventral corner of interoperculum; 12—first branchiostegal ray at the body outline; 13—center of orbit (eye position); 14—junction between cranium and first vertebral centrum; 15—vertebral centrum bearing third gonapophysis; 16—reticular point of lower jaw.

For both traditional and geometric morphometrics multivariate analysis of covariance (MANCOVA) was used to test for effects due to species, size and the interaction between species and size. To visualize species effects we did not use canonical scores as has become common. Canonical scores are meant to ‘control for’ variance within groups to focus on variance between groups. In practice however, patterns left in error are transferred to the canonical axis, distorting rather than clarifying differences between groups (DeWitt and Papadopoulos, in prep.). Instead, axes for visualization were calculated using the eigenvector of the species effect (SSCP) matrix. Traditional variables were standardized before analysis. Geometric variables were mean-centered only, to prevent distortion of the shape space. No heterogeneity of slopes was found in either the traditional or geometric analyses for either sex, so the size-by-species interaction term was not included in final analyses. Standard length (traditional morphometrics) or centroid size (geometric morphometrics) was used as a covariate to statistically control for multivariate allometry. For the geometric morphometric analysis, the shape axis separating *H. bimaculata* and *H. tuxtlaensis* was visualized using thin plate spline transformation grids, as implemented in the program tpsReg (Rolf 2003b). Discriminant function analysis was conducted for each morphometric approach to provide an intuitive metric of discriminatory ability (% specimens correctly assigned to natal population). For this heuristic examination, data were first regressed with size (standard length or centroid size) and residuals were used to generate the discriminant functions. All statistical analyses were performed in JMP version 5.0 (SAS Inst., 2003) with centered polynomials.

## Results

### Traditional morphometrics

Two males (one of each species) and one female (*H. tuxtlaensis*) could not be included in the multivariate analysis because they did not have complete measurements for all variables. Traditional morphometric measurements differed strongly between species (MANCOVA,  $P < 10^{-7}$  for both sexes; Table 1). Discriminant functions for size-adjusted data correctly classified 81.6 % of males and 100% of females into the correct population of origin. Key features in this discrimination, based on linear axes loadings (species eigenvector weights) from MANCOVA, are as given in Table 2A and are incorporated into the species accounts below.

**TABLE 1.** MANCOVA results for morphometric variation associated with habitat and body size.

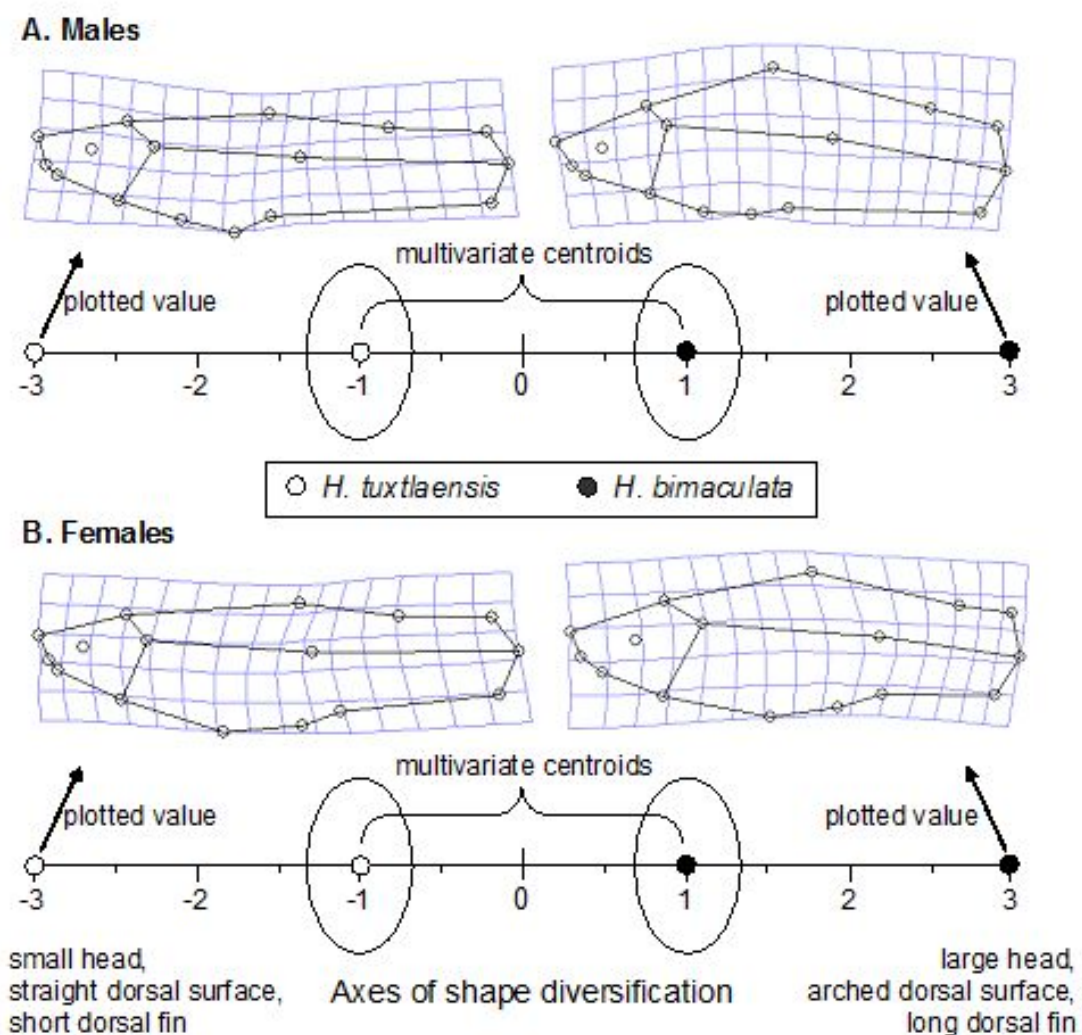
Method	Sex	N	Effect	F	df num	df denom	P	% variance	% discrim.
Geometric	Male	30	Species	20.3	10	18	$< 10^{-7}$	25.9	100
			Centroid size	6.36	10	18	0.0004	3.3	
	Female	30	Species	22.3	10	18	$< 10^{-7}$	28.6	100
			Centroid size	3.28	10	18	0.014	7.5	
Traditional	Male	38	Species	16.5	14	22	$< 10^{-7}$	14.3	81.6
			Std. length	153	14	22	$< 10^{-17}$	49.7	
	Female	39	Species	26.9	16	21	$< 10^{-9}$	19.2	100
			Std. length	502	16	21	$< 10^{-22}$	65.3	

Note: Percent variance is the eigenvalue sum for a given effect (SSCP) matrix divided by the eigenvalue sum of the total variance matrix. Percent discriminated is the percentage of specimens correctly classified to species by discriminant function analysis using size-adjusted shape.

### Geometric morphometrics

The geometric morphometric analysis also demonstrated a strong species effect (MANCOVA,  $P < 10^{-7}$  for both sexes and correctly discriminated 100% of both males and females into the population of origin (Table

1). Correlations of superimposed landmark positions and the linear discriminatory axis from the MANCOVA are given in Table 2B. The shape axis is illustrated using thin plate spline transformation grids in Figure 2. Because “magnification” of such grids is as much a matter of statistical power as it is about actual differences between groups, it is also helpful to see images of fish from the sample (i.e. the true “observed range” of phenotypic difference between species). To this end we have given in Figure 3 the images of males at the most extreme ends of the species shape gradient. This illustrates the maximum shape difference found in the sample of 30 fish. The strongest shape difference noted from the geometric morphometric analysis was the short and more posterior dorsal fin and narrower peduncle of *H. tuxtlaensis* relative to *H. bimaculata*. Further differences between species are elaborated upon in the species accounts.



**FIGURE 2.** Shape difference between *H. tuxtlaensis* from Lake Catemaco and *H. bimaculata* from Sontecomapan. Transformation grids show the linear regression of shape on habitat controlling for allometry. A) Males. The shape gradient for males explained 29.6 % of total shape variance. B) Females. The gradient for females explained 30.5 % of total shape variance. Multivariate least squares means (i.e. group centroids) are plotted and their 95 % confidence limits are given as ellipses.

**TABLE 2.** Species axis loadings for traditional and geometric morphometrics. A. Partial regression coefficients of traditional morphometric characters regressed on species. B. Correlations of superimposed landmark coordinates with the shape gradient separating species.

A. Trait	Sex		B. Trait	Sex	
	males	females		males	females
Depth	-0.515	-0.247	X1	0.475	0.837
Predorsal length	-0.044	0.015	Y1	0.797	0.469
Dorsal-caudal peduncle	-0.208	-0.082	X2	0.194	0.235
Anal-caudal peduncle	--	0.111	Y2	-0.790	-0.619
Head length	-0.104	-0.144	X3	0.491	0.735
Head width	-0.221	-0.266	Y3	-0.960	-0.838
Snout length	-0.374	-0.363	X4	-0.815	-0.805
Peduncle depth	-0.276	-0.094	Y4	-0.635	-0.423
Dorsal base length	-0.400	-0.400	X5	-0.124	0.178
Depressed dorsal length	-0.457	-0.505	Y5	0.525	0.538
Depressed anal length	--	-0.311	X6	0.699	0.865
Caudal length	-0.877	-0.762	Y6	0.900	0.780
Dorsal rays	-1.021	-0.892	X7	0.803	0.926
Pectoral rays	0.537	0.537	Y7	0.931	0.782
Lateral line scales	0.465	0.752	X8	-0.105	-0.350
Vertebrae number	-0.554	0.331	Y8	-0.279	-0.549
			X9	-0.009	-0.109
			Y9	-0.549	-0.511
			X10	-0.089	-0.669
			Y10	-0.126	-0.147
			X11	-0.543	-0.098
			Y11	0.418	0.677
			X12	-0.489	0.113
			Y12	0.822	0.820
			X13	0.336	-0.384
			Y13	0.434	0.240
			X14	0.433	-0.530
			Y14	-0.891	-0.731
			X15	-0.614	-0.778
			Y15	-0.789	-0.633
			X16	-0.211	0.788
			Y16	0.749	0.601

Notes: A. In this table negative values indicate that *H. tuxtlaensis* sp. n. has smaller size-adjusted trait values compared to *H. bimaculata*. Values rounding to = |0.5| are given in bold. B. In this table negative values imply lesser character values in *H. tuxtlaensis* sp. n. Correlations = |0.8| are given in bold. For both tables, trait labels are given in bold if the trait's loadings were bold for both sexes. The correlations of loadings across sexes are 0.85 for Table A and 0.82 for Table B.

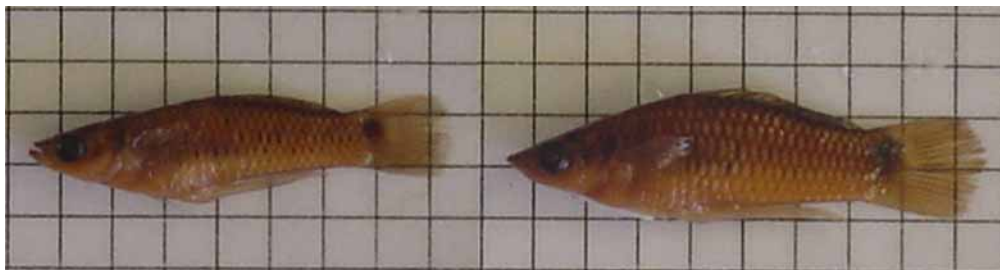
***Heterandria tuxtlaensis* sp. nov.**

(Figs. 1–4, Tables 1–3)

*Heterandria bimaculata* [non *Xiphophorus bimaculatus* Heckel] Rosen, 1979 (in part, specimens listed as *H. bimaculata*)

from Arroyo Esciunopan, USNM 214151)  
*Heterandria cf. jonesi* Miller and Conner, 1997

**Holotype:** UMMZ 248620, 44.0 mm SL, mature male; Veracruz: Laguna Catemaco, south shore near Min-iagua; J.V. Conner and J.R. Mayer, 11 Aug. 1964.



**FIGURE 3.** Most extreme individuals on the species axis, for males, from our sample of 30 fish. Left: the new species, *H. tuxtlaensis*. Right: the presumed sister taxon *H. bimaculata*. Differences in size are incidental and are not responsible for the shape differences observed. The correlation between the species axis and the axis of allometry was  $r = 0.08$ .

**Paratypes:** AMNH 242324 (15 specimens, 38.4 to 72.2 mm SL), TCWC 762.03 (77 specimens, 15.5 to 69.6 mm SL). UMMZ 248621 (15 specimens, 37.5 to 61.5 mm SL), IBUNAM, 14632 (15 specimens, 34.2 to 60.5 mm SL), and USNM 14632 (15 specimens 29.9 to 59.3 mm SL), same data as holotype.

**Other material:** AMNH 78581 (26 specimens) Veracruz, small stream through a pasture 0.5 km from Lake Catemaco on road beyond Coyame; AMNH 78593 (113 specimens) Veracruz, small stream running into Lake Catemaco, just S of outflow; AMNH 78597 (61 specimens) Veracruz, stream below Sihuanpan flowing into outflow (Río Grande) of Lake Catemaco above falls; AMNH 78604 (44 specimens) Veracruz, small river near Quetzalan flowing into Lake Catemaco; GCRL V71: 6828 (107 specimens) Veracruz, Lake Catemaco, road from San Andres Tuxtla to Tehuantepec, 10 km South of San Andres Tuxtla; TCWC 752.01 (22 specimens) Veracruz, Río Quezelapam, 3 km east of Lake Catemaco; TCWC 756.02 (8 specimens) Veracruz, Río Grande at hydroelectric plant, about 9 km southwest of San Andrés Tuxtla; TCWC 757.02 (30 specimens) Veracruz, Lake Catemaco at dam spillway; TCWC 760.01 (94 specimens) Veracruz, Lake Encantada, 3.0 km northeast of San Andrés Tuxtla; TCWC 762 (139 specimens) Veracruz, Lake Catemaco, south shore of lake; TCWC 775.01 (9 specimens) Veracruz, Río Grande, at spillway below dam, about 1 km west of highway 180; TCWC 776.01 (52 specimens) Veracruz, Río Grande, reservoir of hydroelectric dam, about 1 km west of highway 180; TCWC 809.03 (12 specimens) Veracruz, Lake Catemaco, south shore of lake; TCWC 1847.03 (1 specimen) Veracruz, Lake Catemaco, at Cemolapan; TCWC 1849.02 (2 specimens) Veracruz, Lake Catemaco, at Coyame; TCWC 1850.01 (14 specimens) Veracruz, Lake Chalchoapan, just west of mouth of Río Grande west of Lake Catemaco; TCWC 1854.01 (6 specimens) Veracruz, Lake Catemaco; TU uncat. Veracruz, Lake Catemaco, at outlet of Río San Andres, about 21.8 km east of San Andres, highway 180; UMMZ 178556 (30 specimens) Veracruz, Lake Catemaco at Playa Azul, ca 3 km E of Catemaco; UMMZ 178557 (164 specimens) Veracruz, tributary of Lake Catemaco on hwy 3.2 km SE lake.

**Diagnosis.** The following characters distinguished *H. tuxtlaensis* from the other species of *Heterandria*: body depth in males 23.2 to 27.1% ( $\bar{x}$ =25.3%) of SL; dorsal fin base length 26.5 to 31.3% ( $\bar{x}$ =28.9%) of SL in males and 21.9 to 28.2% ( $\bar{x}$ =25.6%) SL in females; dorsal fin rays 12 or 13 ( $\bar{x}$ =12.7); basicaudal spot relatively small, subcircular to bar-shaped, and limited to area above midlateral line and not extending to dorsal midline; serrae on gonopodial ray 4p arched away from ray 4a; subdistal small segments on gonopodial ray 4a number 5 to 10; and terminal segment on gonopodial ray 4a long and strongly recurved.

**Description.** *Heterandria tuxtlaensis* is a moderate-sized *Heterandria* (up to 49 mm SL for males and 75 mm SL for females). Meristic and morphometric variables are summarized in Table 3. This species is relatively slender, with a short dorsal fin, shallow caudal peduncle, and a short caudal fin. In females head is rela-

tively narrow and anal fin is relatively short. Pectoral fin rays 15 or 16, lateral line scales 28 to 32, and vertebrae 29 to 33 (Fig. 4).

**TABLE 3.** Traditional morphometrics and meristics of *Heterandria tuxtlaensis* and *H. bimaculata*. Except for SL and meristics, data are given in percentage of standard length.

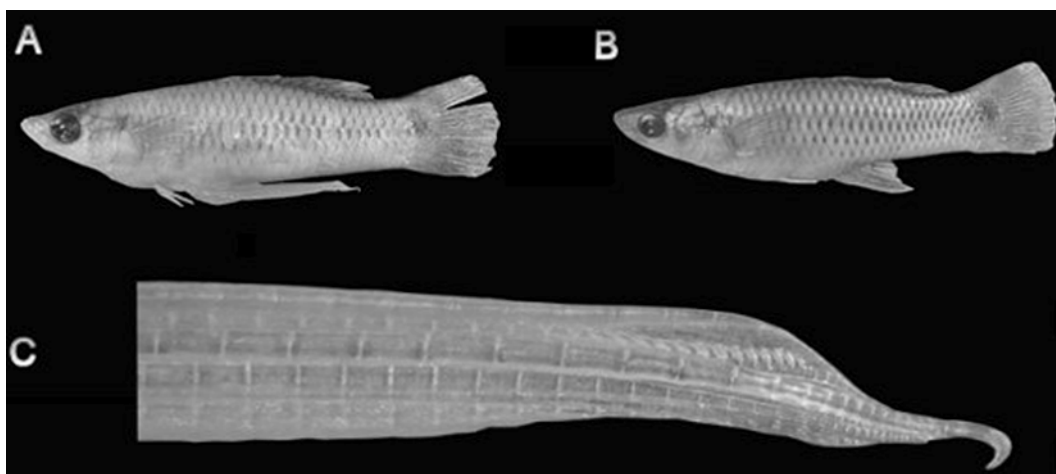
Measurements	Holotype	Paratypes ( <i>H. tuxtlaensis</i> )				Non-types ( <i>H. bimaculata</i> )			
	Male	Males		Females		Males		Females	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean
Standard length	44	31.8–49.4	43	33.7–74.5	55.8	30.1–40.0	36.3	39.6–64.6	52.2
Depth	26.4	23.2–27.1	25.3	23.9–27.6	24.3	26.2–29.9	28.1	25.7–29.5	27.5
Predorsal length	50.9	48.3–53.3	51.1	54.7–58.1	56	49.3–54.2	51.9	53.1–59.6	55.6
Dorsal-caudal peduncle	49.6	45.4–53.6	50.2	44.2–48.5	46	50.0–55.4	52.7	43.5–50.0	47.5
Anal-caudal peduncle	-	-	-	44.5–47.9	46	-	-	43.2–47.6	44.9
Head length	27.1	24.0–27.0	25.5	25.0–27.7	26	25.3–27.9	26.5	26.6–29.9	27.6
Head width	13.5	12.0–14.1	13.3	15.2–16.7	15.8	12.9–15.3	14	16.1–18.2	17.4
Snout length	7.9	5.9–8.4	7.4	6.9–9.7	8.3	7.5–9.2	8.4	8.1–10.4	9.3
Peduncle depth	17.8	15.4–18.1	16.8	14.5–16.4	15.5	16.6–19.1	17.7	15.1–16.7	16
Dorsal base length	28.5	26.5–31.3	28.9	21.9–28.2	25.6	29.8–33.4	31.7	27.1–31.7	29.1
Depressed dorsal length	40.4	38.7–48.8	41.6	33.2–38.2	36	44.7–47.9	46.7	39.3–45.1	42
Depressed anal length	-	-	-	21.0–24.6	22.7	-	-	23.1–27.1	24.7
Caudal length	23.7	21.2–24.9	23.1	19.1–22.8	20.4	25.5–30.8	27.9	23.7–30.2	26.4
Dorsal rays	13	12–13	12.6	12–13	12.9	14–15	14.5	14–15	14.3
Pectoral rays	16	15–16	15.5	15–16	15.3	14–16	14.5	14–16	14.6
Lateral line scales	29	28–32	29.6	28–30	29.2	27–29	27.8	27–29	28
Vertebrae number	33	29–33	30.6	29–31	30.4	30–32	31.2	29–31	30.1

Ray 3 of gonopodium terminating at level of second to last subterminal segment of ray 4a in holotype (terminating at level of last subterminal or terminal segment in male paratypes), distal segments of ray 3 enlarged ventrally to form elbow and running contiguous with ray 4a, segments distal to elbow number 7 to 9 (Fig. 4). Subdistal 7 to 10 segments of ray 4a abruptly shortened, anterior 4 to 6 forming peg-like processes and posterior 3 to 5 squarish. Distal segment of ray 4a greatly elongated, about 5 to 7 times length of proximal squarish segment, and decurved about 110° to 120°. Subdistal 10 to 14 segments of ray 4p bear serrae, distal segments of ray 4p number 5 to 10 and lack serrae. Ray 5a arches downward toward upwardly arched ray 4p and terminates medial to tip of ray 4a.

**Coloration in alcohol.** Body is tan, with edges of scale pockets dark brown producing cross hatching pattern on dorsal and lateral surfaces, dark pigment thickest along center of scale pockets. Scale pockets, except for ventral most, are about equally pigmented and mid lateral stripe is absent. Single irregular dark spots are located on upper anterior aspect of operculum and on flank above base of operculum. Dark pigment spots along basal section and mid section of dorsal fin membranes produce two irregular dark stripes on fin. Dark spots located on anal fin membranes of females produce streak-like patterns. Subcircular to bar-shaped dark spot (basicaudal spot) is located on caudal peduncle and base of caudal fin, it is restricted to area above lateral midline and fails to reach dorsal midline.

**Etymology.** Named for the type and only known locality of the species the Tuxtla Mountains of Veracruz, Mexico.

**Distribution.** This species is endemic to Lake Catemaco and tributaries of the lake and the Río Grande de Catemaco above the falls at El Salto de Eyipantla.



**FIGURE 4.** *Heterandria tuxtlaensis*. A. Mature male (Holotype, UMMZ 248620, 44.0 mm SL). B. Mature female (Paratype, TCWC 762.03, 41.3 mm SL). C. Gonopodium tip of Holotype.

**Comparison and relationships.** Within *Heterandria*, *H. tuxtlaensis* is most similar to *H. bimaculata* and can be identified as this species in Rosen's (1979) key to species of *Heterandria*. Interestingly, however, the state of the basicaudal spot does not agree with the states of this character in any of the other species of *Heterandria*. The basal caudal spot of *H. tuxtlaensis* is not diffuse, pale, or obsolescent as in the case of *H. attenuata*, is not bordered by a clear area and broken dark pigment as in the case of *H. litoperas*, is not elongated as in the case of *H. obliqua*, does not have ventral and posterior comet-like extensions as in the case of *H. anzuetoii*, is not irregular and horizontally elongated as in the case of *H. cataractae*, and is not large and round as in the case of *H. dirempta* and *H. bimaculata*. However, the other character states in the key, e.g. body depth, head width, caudal peduncle depth, number of lateral line scales, number of pectoral fin rays, vertebral number, and gonopodial traits are more similar to the states in *H. bimaculata* than to the states in any of the other species of *Heterandria*. The gonopodium of *H. tuxtlaensis* cannot be distinguished from that of *H. bimaculata*. Rosen (1979) also provides 12 tables comparing meristic and morphometric values of the species of *Heterandria* and *H. tuxtlaensis* falls within the ranges of *H. bimaculata*, with exception of values related to size and position of the dorsal fin, the number of pectoral fin rays, and width of the head in females. *Heterandria tuxtlaensis* has fewer than the modal number of dorsal fin rays of *H. bimaculata*, although the dorsal fin ray counts for *H. tuxtlaensis* are within the lower part of the range of values for *H. bimaculata* from Mexico. Dorsal fin rays counts for Mexican *H. bimaculata* given by Rosen are from Miller (1974). Specimens of *H. bimaculata* from Miller's study are from Veracruz and Oaxaca, and include specimens from the Río Papaloapan but not from Lake Catemaco. *Heterandria tuxtlaensis* has a smaller range and mean number of dorsal fin rays than any of the 50 collections of *H. bimaculata* examined in this study. *Heterandria tuxtlaensis* can be further distinguished from *H. bimaculata* by its shorter and more forwardly placed dorsal fin base, greater number of pectoral fin rays, narrower head width in female specimens, and smaller size of the basicaudal spot. Furthermore the specimens of *H. bimaculata* from the Río San Juan of the Papaloapan Drainage below the falls of the Río Grande at Eyipantla, the remainder of the Río Papaloapan drainage, and the coastal drainages of the Tuxtlas are deeper bodied, have a longer dorsal fin base, longer depressed dorsal fin, longer caudal fin, higher dorsal fin ray count and a basicaudal spot typical of *H. bimaculata* (Tables 2, 3; Figs. 2, 3). These differences may have led Miller and Conner (1997) to consider the Lake Catemaco population to be close to or identical with *H. jonesi* rather than a species most similar to *H. bimaculata*. Apparently they based this decision on a collection of *H. tuxtlaensis* (UMMZ 178556) that lacks mature males. Thus they were unaware of the gonopodial characters of the species.



It is likely that the new species shares an ancestor with *H. bimaculata* because of the above listed similarities between the two species and because *H. bimaculata* is the only other species of *Heterandria* found in the Río Papaloapan drainage. Only one other species, *H. jonesi* occurs in Mexico and it has not been reported south of the Río Nautla in central Veracruz (Miller, 1974). The other species of *Heterandria* are either limited to the southern United States (*H. formosa*) or are endemic to Guatemala, and of all of these, the most similar congeners are limited to the Río Senizo in the head waters of the Río Usumacinta drainage, in Alta Verapaz, Guatemala (*H. cataractae*) and the Río Chajmaic, in the headwaters of the Río Usumacinta drainage in Alta Verapaz, Guatemala (*H. dirempta*) (Rosen, 1979).

**Remarks.** *Heterandria tuxtlaensis* constitutes the sixth endemic species of the 12 indigenous fish species of Lake Catemaco. According to Miller and Conner (1997) four of the 12 indigenous fish species in the lake were endemic and that future research might reveal that six of the remaining species were undescribed, and thus also endemic to the lake. One of these six putative new species (*Xiphophorus kallmani*) was described by Meyer and Scharl (2003) and herein we describe the sixth endemic species. Thus endemism within Lake Catemaco lies between 50% and 83%, depending on the status of the possibly new species. This range of endemism is high considering the lake is a maximum of 2 million years old (West, 1964). Mateos *et al.* (2002) investigated the historical biogeography of the poeciliid genus *Poeciliopsis*, which includes a species, *P. catemaco*, endemic to the lake. Based on a molecular clock for *cyt b* divergences, Mateos *et al.* (2002) estimated that *P. catemaco* has been isolated from other members of its *gracilis* species group for 0.75 to 1.5 million years. This estimate is within the age given by West (1964) for the lake and it is reasonable to assume that all of the endemic species to Lake Catemaco are 0.75 to 1.5 million years old.

The endemic fishes in Lake Catemaco are predominantly poeciliids (five species in four genera). The other endemic species is a characid, *Bramocharax caballeri*. The putative new species in the lake include a clupeid of the genus *Dorosoma*, similar to *D. mexicana*, two pimelodids of the genus *Rhamdia*, and a cichlid, similar to *Vieja fenestrata*. This high level of endemism complements genetic and geological findings suggesting the lake is ancient and well separated from surrounding fish populations.

Finally we hope to be indulged to make a methodological point, be it removed from our major goal of describing *H. tuxtlaensis*. We wish to advocate general use of geometric morphometrics in describing new taxa. Such information is a useful addition to traditional measures if reported in a manner to facilitate comparisons among taxa. To this end we report the direction of individual landmark deviations across the species gradient. Correlations of partial warps or principle components with species gradients would not be general, because these variables change in each new analysis. Landmarks retain homology across studies. We also report effect sizes in a manner conducive to comparison with other taxa, and to meta-analysis (Gurevitch and Hedges 2001). Thus we hope this approach can be used or expanded in future work in the valuable service of describing new taxa.

**Other material examined.** *Heterandria bimaculata* (Veracruz, Mexico): FMNH 4601, 3726, TCWC 755.02, 759.01, 779.02, 1852.01, UMMZ 108614, 184547; (Tabasco, Mexico): AMNH 20401, 27489, UMMZ 184718, 209339, 210842; (Oaxaca, Mexico): UMMZ 178533, 178546, 183902, 234799; (Chiapas, Mexico): NMW-59796 (Syntypes of *Heterandria bimaculatus*), AMNH 24649, 59805, 59806, 69807, 59808, UMMZ 163778, 186370, 191730, 196644, 209324, 209353, 209361, 210814, TCWC 3207.01; (Campeche, Mexico): UMMZ 190856, 196612 ; (Yucatan, Mexico): UMMZ 102078 (Holotype of *Heterandria b. peninsulae*), 102079 (Paratype of *H. b. peninsulae*); (Quintana Roo, Mexico): UMMZ 210881; (Belize): AMNH 78703, FMNH 82180, UMMZ 190424, 202737; (Guatemala): AMNH 24584, 24663, 24486, 36339, 36353, 36357, 36361, 36362, 36363.

*Heterandria anzuetoi* (Guatemala): UMMZ 197389 (Paratypes).

*Heterandria attenuata* (Guatemala): UMMZ 197091 (Paratypes).

*Heterandria cataractae* (Guatemala): UMMZ 193888 (Paratypes)

*Heterandria dirempta* (Guatemala): UMMZ 187950 (Paratypes)

*Heterandria litoperas* (Guatemala): UMMZ 197134, 146107 (Paratypes)

*Heterandria obliqua* (Guatemala): UMMZ 197079, 193893 (Paratypes)

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