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Article *in* Zootaxa · January 2018

DOI: 10.11646/zootaxa.4375.3.5

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Zootaxa 4375 (3): 371–391
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4375.3.5
http://zoobank.org/urn:lsid:zoobank.org:pub:31F06D99-E7DF-4A6E-A24A-781E98385ED6

Redescription of *Vieja hartwegi* (Taylor & Miller 1980) (Teleostei: Cichlidae) from the Grijalva River basin, Mexico and Guatemala, with description of a rheophilic morph

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Abstract

Vieja hartwegi was described by Taylor and Miller in 1980 based on 45 juvenile and sub-adult specimens, but this species shows an enormous variation in coloration patterns during ontogenic development and between individuals. Additionally, morphological data have demonstrated the existence of two forms in *V. hartwegi*: the typical morph of a moderately deep to slightly elongated body shape with midlateral band, and a rheophilic morph with an elongated to slightly deep body shape and lack of midlateral band. Herein we redescribe *V. hartwegi* adding adults and individuals from broad geographic ranges, as well as a rheophilic morph recently discovered in the upper reaches of the Grijalva River basin in Mexico. The set of characters include coloration, meristic, morphometric and osteological features. *Vieja hartwegi* is a polymorphic species whose forms may be segregating because of habitat preferences and food habits.

Key words: Taxonomy, morphological variation, Middle America, Heroini, polymorphism

Resumen

Vieja hartwegi fue descrita por Taylor y Miller en 1980, basada en 45 ejemplares juveniles y subadultos, sin embargo, esta especie muestra una importante variación en sus patrones de coloración durante el desarrollo ontogénico así como entre individuos. Adicionalmente, los datos morfológicos han demostrado la existencia de dos formas en *V. hartwegi*: la forma típica de cuerpo moderadamente profundo o ligeramente alargado provista de una banda mediolateral, y una forma reofílica de cuerpo alargado o ligeramente profundo y carente de banda mediolateral. Presentamos una redescripción de *V. hartwegi*, incluida la talla adulta así como de individuos en todo su ámbito geográfico, y también de la forma reofílica recientemente encontrada en los cursos superiores de la cuenca del río Grijalva. El conjunto de caracteres incluye coloración, merística, morfometría y algunos rasgos osteológicos. *Vieja hartwegi* es una especie polimórfica cuyas formas parecen segregarse en función de sus preferencias de hábitat y alimentarias.

Introduction

The high intra- and interspecific variability within the genus *Vieja* Fernández-Yépez makes it one of the most

Accepted by J. Armbruster: 14 Nov. 2017; published: 25 Jan. 2018

problematic clades within the Neotropical cichlid tribe Heroini. At present, *Vieja* comprises eight valid Middle American species (Eschmeyer *et al.* 2017), with distributional ranges mainly restricted to the Grijalva-Usumacinta, Coatzacoalcos and Papaloapan basins in the Atlantic slope, with the exception of *V. maculicauda*, which extends to the Chagres River in Panama (McMahan *et al.* 2017a), and *V. guttulata* and *V. zonata*, found on the Pacific slope of Middle America, from the Isthmus of Tehuantepec in Mexico to Lake Coatepeque in El Salvador (McMahan *et al.* 2015, Říčan *et al.* 2016). Recently, *Vieja* was rediagnosed by McMahan *et al.* (2015) and Říčan *et al.* (2016); in their works, these authors provide a series of characters that clearly separate the genus from sister and related genera. However, a problem that remains is the availability of enough key characters to accurately separate species at the intrageneric level. The root of this problem often lies with original species descriptions, which do not provide sufficient comparative data, do not contain key diagnostic characters based on coloration patterns, and are often based on juvenile specimens. This is particularly problematic with *Vieja* because members of the genus exhibit extensive intraspecific variability, and many undergo substantial ontogenic changes, creating a systematic and taxonomic ambiguity in this morphologically hyper-variable group of Middle American cichlids (Říčan *et al.* 2005, McMahan *et al.* 2010, 2011, 2017b).

Vieja hartwegi, the tailbar cichlid or mojarra del río Grande de Chiapa, was originally described by Taylor and Miller (1980) as a member of the historical catch-all genus *Cichlasoma* based on 45 juvenile and subadult specimens collected in the Grijalva River basin (or Río Grande de Chiapa) in Chiapas, Mexico. They considered some of their specimens as adult individuals (greater than 93.3 mm standard length [SL]), but none of their specimens were larger than 131.1 mm SL. This is problematic because most species of *Vieja* can reach up to 340 mm SL, likely with the exception of *V. breidohri* (pers. obs.). Besides the inherent problems related to size in descriptions for species of *Vieja*, a second but equally important issue is the fact that it has been common practice to use coloration patterns to diagnose members of this group (Miller *et al.* 2005, McMahan *et al.* 2011). However, it has been demonstrated that color patterns change ontogenetically, with marked differences in coloration between juveniles and adults of the same species, and also, during mating (Říčan *et al.* 2005). This practice has led to taxonomic confusion, especially when trying to separate adult specimens of *V. hartwegi* from its congeners *V. bifasciata* (Steindachner 1864) and *V. breidohri* (Werner & Stawikowski 1987). This is one of the reasons these species have been mis-identified in systematic studies and in museum collections.

Taylor and Miller (1980:8) diagnosed and separated *V. hartwegi* from closely related species by the possession of a "snout and upper jaw usually projecting beyond lower jaw" and "color pattern consisting of lateral blotches or irregular vertical bars associated with a nearly complete, straight, longitudinal stripe on side." Unfortunately, they only had small individuals. Because the original description of *V. hartwegi* presents some limitations, mainly due to the exclusive use of juvenile and subadult individuals and color-based characters, the aim of this study is to present a redescription of *V. hartwegi* based on morphometric, meristic and osteological characters, including examination of adult specimens. We also present a newly discovered rheophilic morph of *V. hartwegi*. Additionally, we include a molecular phylogenetic hypothesis, with increased distributional sampling of specimens to assess genetic variability within *V. hartwegi*.

Material and methods

Morphological data: The holotype, three paratypes and 54 non-type specimens of *V. hartwegi* (including eight specimens of the new rheophilic morph) were examined, as well as related species for comparative material. We examined 21 adult specimens (>120 mm SL, ranging from 122.99 to 176.5 mm). Measurements and counts (Figs. 1 & 2) were based on Taylor and Miller (1980), Kullander (1986), Anseeuw *et al.* (2011), McMahan *et al.* (2011) and Malabarba *et al.* (2015). Only the left side of specimens was considered. Measurements were taken with digital calipers (0.1 mm), made from point to point, except for head length and snout length, which were taken in the same plane along the horizontal axis of the specimen (Kullander 1986). Head measurements do not include the skin fold around the eye. Data are presented and analyzed as percentages of SL, with the exception of the head measurements, which are used as percentages of the head length (HL). Color pattern terminology follows Kullander (1986) and Říčan *et al.* (2005). Bars were counted and numbered posteriorly to anteriorly following Říčan *et al.* (2005). We detail some terms to avoid confusion: a spot is a well defined circular marking; an ocellus is a spot with ring of another color; a blotch is a mark with a poorly defined or irregular border; and a dots is a very

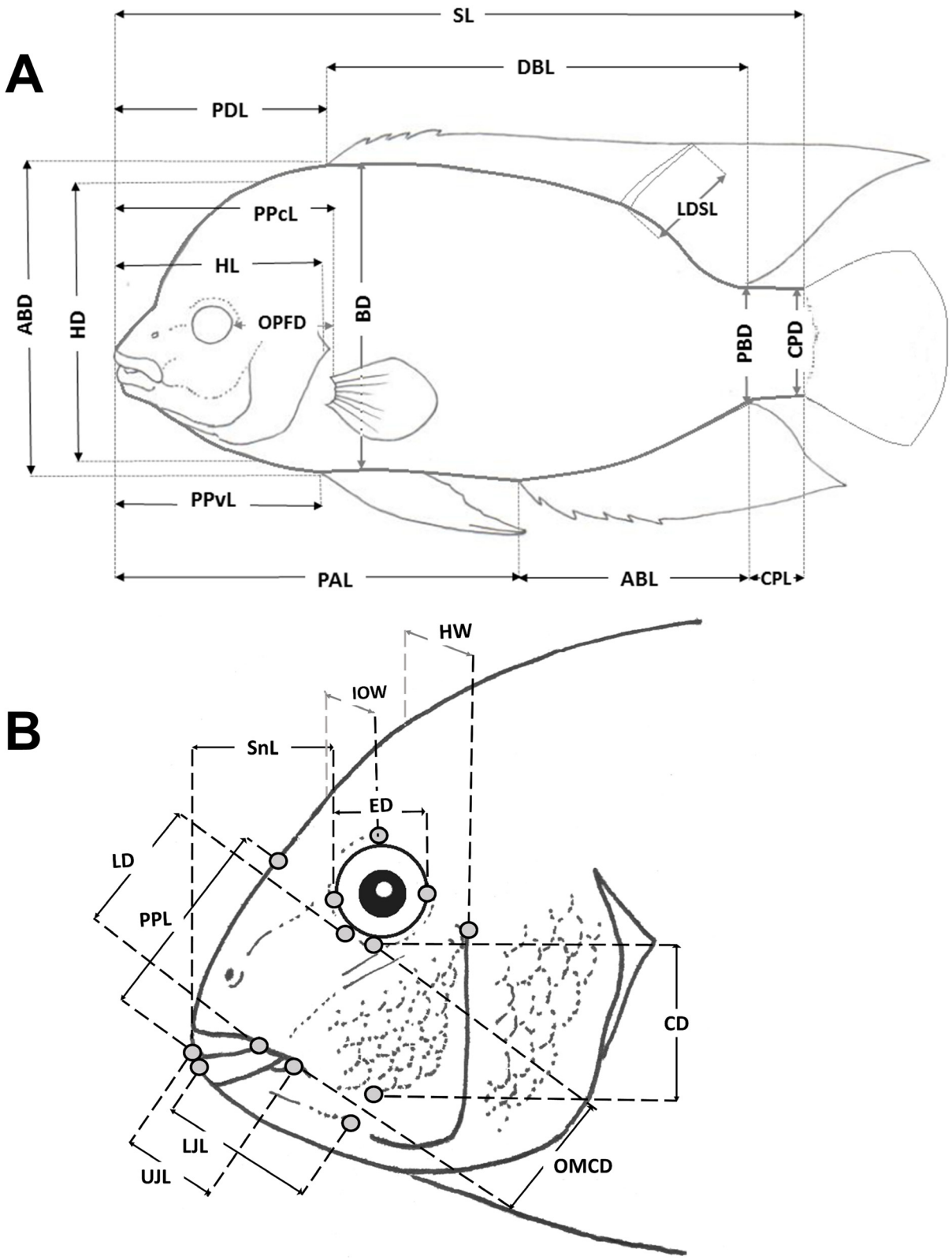

FIGURE 1. Morphometric characters taken on examined specimens. A) Body measurements: standard length (SL), body depth (BD), caudal peduncle length (CPL), caudal peduncle depth (CPD), anterior body depth (ABD), posterior body depth (PBD), predorsal length (PDL), preanal length (PAL), prepelvic length (PPvL), prepectoral length (PPcL), orbit pectoral fin distance (OPFD), head depth (HD), head length (HL), dorsal-base length (DBL), longest (=last) dorsal spine length (LDSL), anal-base length (ABL). B) Head measurements: eye diameter (ED), orbit maxillary cleft distance (OMCD), interorbital (bony) width (IOW), snout length (SnL), upper jaw length (UJL), premaxillary pedicel length (PPL), lower jaw length (LJL), head width (HW), cheek depth (CD), lacrimal depth (LD).

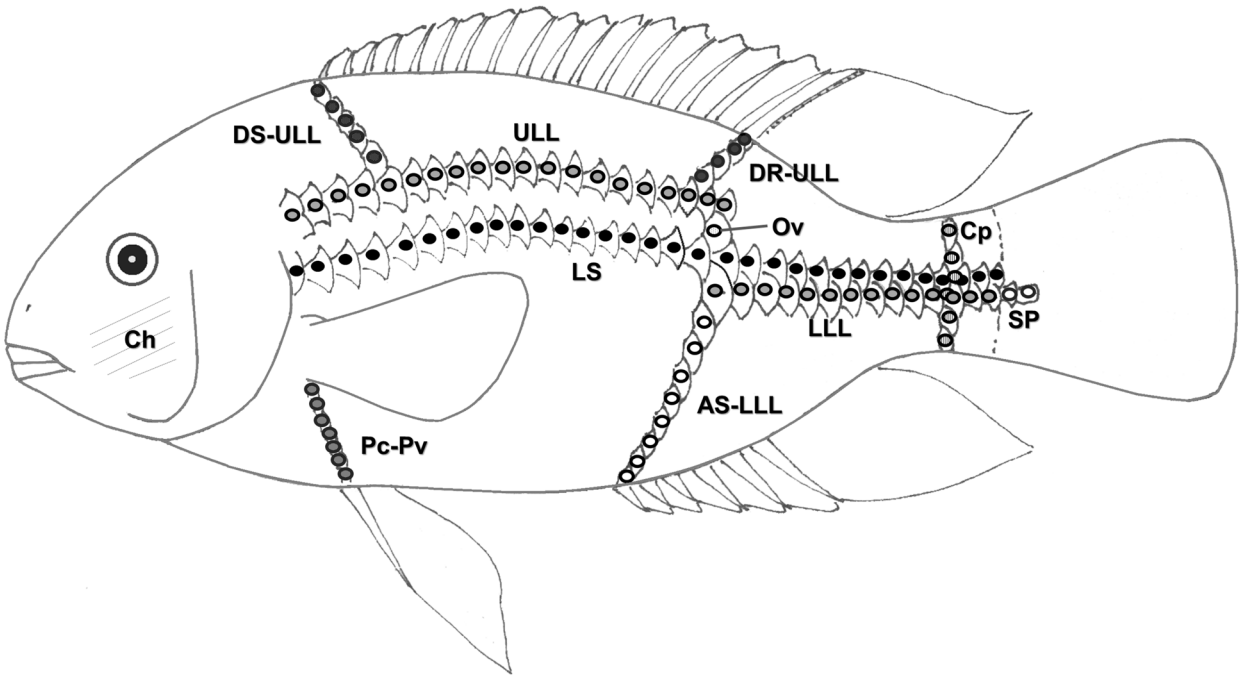

FIGURE 2. Meristic characters in squamation taken on examined specimens: lateral series scales (LS), upper lateral line scales (ULL), lower lateral line scales (LLL), subsidiary pored scales on caudal fin (SP), lateral scale row overlap (Ov), scale cheek rows (Ch), pectoral-pelvic scale rows (Pc-Pv), scale rows from upper lateral line to base of first dorsal-fin ray (DR-ULL), scale rows from upper lateral line to base of first dorsal-fin spine (DS-ULL), scale rows from origin of anal fin to lower lateral line (AS-LLL), circumpeduncular scales (Cp).

fine, little spot. Observations were made on osteological features from standard radiographs and cleared and stained (c&s) specimens. The c&s procedure followed the protocol of Taylor and van Dyke (1985). Institutional abbreviations included: MZUNICACH, Museo de Zoología, Universidad de Ciencias y Artes de Chiapas, Chiapas, Mexico; ECOSC, El Colegio de la Frontera Sur (ECOSUR)-Unidad San Cristóbal, Chiapas, Mexico; FMNH, The Field Museum of Natural History, Chicago, USA; UMMZ, University of Michigan Museum of Zoology, Michigan, USA.

We performed a Principal Component Analysis (PCA) to elucidate differences in body shape between the two morphs of *V. hartwegi* and their related species, *V. bifasciata* and *V. breidohri*. The analysis was implemented in the R 3.0.2. statistical software (R Development Core Team 2013) package 'vegan' (Oksanen *et al.* 2013).

Molecular data: We collected molecular sequence data for a fragment of the mitochondrial Cytochrome *b* (cyt *b*) gene for 34 individuals, including 16 hericthyine species closely related to *V. hartwegi. Chiapaheros grammodes* was included as an outgroup based on its phylogenetic position within the herichthyine clade (McMahan *et al.* 2015, Říčan *et al.* 2016). Our data set included 17 newly produced sequences that were deposited in GenBank (Table 1). DNA was extracted from fin clips using the Qiagen DNeasy Tissue Kit (Qiagen Inc., Valencia, CA). The cyt *b* gene was amplified using the primers and protocols of López-Fernández *et al.* (2010). PCR products were amplified at the Laboratorio Nacional de Biodiversidad (LaNaBio), Instituto de Biología, UNAM. Chromatographs were checked and manually edited using BioEdit v7.2.5 (Hall 1999). We used MUSCLE (Edgar 2004) embedded in MEGA6 (Tamura *et al.* 2013) to align sequences. The final data matrix consisted of 1070 bp. The program jModelTest (Posada 2008) was used to select the best fitting model of sequence evolution under the corrected Akaike Information Criterion (AICc; Akaike 1973), selecting GTR + I + Γ as the best model. The data were analyzed using Bayesian inference methods, using MrBayes v3 (Ronquist & Huelsenbeck 2003). Four runs were performed for two million generations with trees sampled every 1000 generations. We used Tracer 1.5 (Rambaut & Drummond 2009) to check the trace files and ensure the chains had reached convergence. A 50% majority rule consensus tree was obtained from post-burn-in trees.

TABLE 1. GenBank accession numbers for Cyt-b sequences used in this study and locations of the newly sequences. Codes in brackets correspond to individuals of *V. hartwegi* in Fig. 11. ° Sample from near type locality. * Indicates rheophilic morph.

Species	Accession number	Locality	Coordinates
Chiapaheros grammodes	DQ990718	Comalatén River, Mexico (Concheiro-Pérez *et al.* 2007)	
Paraneetroplus bulleri	AY324004	Sarabia River, Mexico (Concheiro-Pérez *et al.* 2007)	
Paraneetroplus gibbiceps	KU854716	Lower Grijalva River, Mexico (Říčan *et al.* 2016)	
Paraneetroplus nebuliferus	KU854702	Papaloapan River, Mexico (Říčan *et al.* 2016)	
Maskaheros argenteus	AY843412	Río de la Pasión, Guatemala (Concheiro-Pérez *et al.* 2007)	
Maskaheros regani	KU854706	Coatzacoalcos River, Mexico (Říčan *et al.* 2016)	
Rheoheros coeruleus	KU854699	Tulijá River, Mexico (Říčan *et al.* 2016)	
Rheoheros lentiginosus	AY843411	Río de la Pasión, Guatemala (Concheiro-Pérez *et al.* 2007)	
Vieja bifasciata	GU736989	Tzendales River, Mexico (López-Fernández *et al.* 2010)	
Vieja breidohri	AY050626	Aquarium stock (Concheiro-Pérez *et al.* 2007)	
Vieja fenestrata	KU854744	Papaloapan River, Mexico (Říčan *et al.* 2016)	
Vieja guttulata	DQ990727	Coatepeque Lake, El Salvador (Concheiro-Pérez *et al.* 2007)	
Vieja hartwegi [FJ]	FJ668645	Grijalva River, Mexico (McMahan *et al.* 2010)	
Vieja hartwegi [KU]	KU854734	Upper Grijalva River, Mexico (Říčan *et al.* 2016)	
Vieja hartwegi [C3]	MG253052	Nezahualcóyotl (Malpaso) Reservoir, Ocozocoautla	17.060841° N, -93.463068° W
Vieja hartwegi [C16]	MG253053	El Zapote River, Chiapa de Corzo	16.596209° N, -92.957935° W
Vieja hartwegi [C26]	MG253054	Grijalva River, Chicoasén	16.971596° N, -93.123953° W
Vieja hartwegi [C49]	MG253057	Los Cocos River, Venustiano Carranza	16.425811° N, -92.718899° W
Vieja hartwegi [C55]	MG253058	Cintalapa River, Cintalapa	16.698514° N, -93.742376° W
Vieja hartwegi [C137]	MG253059	Lagos de Colón, La Trinitaria	15.825549° N, -91.896671° W
Vieja hartwegi [C149]	MG253060	Unnamed Stream at Col. Francisco Villa, Socoltenango	16.273816° N, -92.660069° W
Vieja hartwegi [C152]	MG253061	Belisario Domínguez (La Angostura) Reservoir, La Concordia	16.107326° N, -92.690419° W
Vieja hartwegi [C156]	MG253063	Platanar River, Pichucalco	17.559238° N, -93.290211° W
Vieja hartwegi [C164]	MG253065	La Venta River, Ocozocoautla	16.901944° N, -93.618619° W
Vieja hartwegi [C179]°	MG253066	Santo Domingo River, mouth in Grijalva River, Chiapa de Corzo	16.682453° N, -93.012221° W
Vieja hartwegi [C32]*	MG253055	Tachinua River, Chicomuselo	15.749028° N, -92.280374° W
Vieja hartwegi [C33]*	MG253056	Tachinua River, Chicomuselo	15.749028° N, -92.280374° W
Vieja hartwegi [C155]*	MG253062	Yayahuita River, Chicomuselo	15.748885° N, -92.283614° W
Vieja hartwegi [C185]*	MG253067	Yayahuita River, Chicomuselo	15.748885° N, -92.283614° W
Vieja hartwegi [C186]*	MG253068	Yayahuita River, Chicomuselo	15.748885° N, -92.283614° W
Vieja hartwegi [C158]*	MG253064	Lagos de Colón, La Trinitaria	15.829167° N, -91.886456° W
Vieja maculicauda	GU736991	Monkey River, Belize (López-Fernández *et al.* 2010)	
Vieja melanura	AY843413	Arroyo Comiston, Guatemala (Concheiro-Pérez *et al.* 2007)	
Vieja zonata	FJ668642	Tehuantepec River, Mexico (McMahan *et al.* 2010)	

Results

Redescription of *Vieja hartwegi* (Taylor & Miller 1980)

Figs. 3–8, Tables 2, 3

Cichlasoma hartwegi Taylor & Miller 1980: 8 [original description].
Paratheraps hartwegi (Taylor & Miller 1980)—Werner & Stawikowski 1987: 20 [new combination].
Paraneetroplus hartwegi (Taylor & Miller 1980)—McMahan *et al.* 2010: 1298 [new combination].

Material examined. All from Chiapas, Mexico, except FMNH 131457; numbers in parentheses indicate number of specimens examined. ***Vieja hartwegi* (typical morph):** UMMZ 207701 (holotype), Río Grande de Chiapa (= Grijalva River) about 1 km above bridge between Tuxtla Gutiérrez and Chiapa de Corzo; UMMZ 186400 (2 paratypes) Frío River, above mouth of Chiapa River, Acala; FMNH 93578 (1 paratype) Salado River, 1 km from Chiapilla; MZUNICACH 1053 (1), 1065 (2), 1125 (1), 1156 (1) Totopac River, Tecpatán; MZUNICACH 1560 (1), 1639 (1), 7158 (2) La Venta River, Ocozocoautla; MZUNICACH 1789 (2) Malpaso Reservoir, Ocozocoautla; MZUNICACH 3045 (3) Río Grijalva, Chicoasén; MZUNICACH 3145 (5) Grijalva River, Copainalá; MZUNICACH 5947 (1), 6245 (1) Santo Domingo River, Chiapa de Corzo; MZUNICACH 7053 (1) Chiquito River, Chiapa de Corzo; MZUNICACH 7153 (3) Yayahuita River, Chicomuselo; MZUNICACH 6761 (2 c&s), 7154 (8) La Angostura Reservoir, La Concordia; MZUNICACH 7208 (1) Copanó River, Ostuacán; ECOSC 7542 (2), 7544 (1) Blanco River, Venustiano Carranza; ECOSC 7543 (3), 7548 (3) Lagos de Colón, La Trinitaria; FMNH 131457 (2) Lagartero River, Nentón, Huehuetenango, Guatemala. ***Vieja hartwegi* (rheophilic morph):** MZUNICACH 7157 (1 + 1 c&s), 7160 (1), 7166 (1) Yayahuita River, Chicomuselo; MZUNICACH 7159 (1 + 1 c&s) Tachinua River, Chicomuselo; MZUNICACH 7161 (4) Lagos de Colón, La Trinitaria.

Diagnosis. The typical morph of *V. hartwegi* usually possesses a dorsolateral or second stripe thinner and horizontal (parallel) to the midlateral stripe (Fig. 3B-C); in contrast, *V. bifasciata* (Fig. 9A) has a broader second stripe that is slightly angled dorsally. The two stripes are separated by a narrow space (two thirds or half of a scale) or are often fused in *V. hartwegi* (Fig. 5D-J), whereas in *V. bifasciata* the space is broader (one and half or two scales). *Vieja bifasciata* usually has a large dark opercular blotch, extending to the border of the eye (Fig. 9A), whereas *V. hartwegi* has a simple crescent shape (Fig. 3B-C). Additionally, *V. bifasciata* has a much deeper body with a more rounded shape than *V. hartwegi.*

Vieja breidohri can be distinguished from *V. hartwegi* by the presence of molariform or subconical pharyngeal teeth, versus conical. Additionally, lateral blotches or a second stripe above the midlateral stripe are absent in *V. breidohri* (Fig. 9B). The midlateral stripe in *V. breidohri* is markedly disrupted, formed by a series of separated or connected blotches that fade anteriorly, not reaching the opercle (Fig. 9B). Juvenile specimens of *V. hartwegi* often possess a disrupted midlateral stripe below or at the middle of the body; in this case the two species are more difficult to distinguish. *Vieja hartwegi* possesses red spots or blotches on head (Fig. 3A-C), whereas *V. breidohri* has small dark dots on sides of the head (Fig. 9B). *Vieja hartwegi* possesses 29–31 total vertebrae (15 precaudal + 14–16 caudal), and *V. breidohri* has 28 (14 precaudal + 14 caudal).

All other species of *Vieja* with a midlateral stripe along the side of the body (*V. fenestrata, V. guttulata*, and *V. zonata*) can be differentiated from *V. hartwegi* by the absence of the second or dorsolateral stripe.

The rheophilic *V. hartwegi* morph differs from the typical morph and all other species of *Vieja* by a more elongated body shape (Figs. 4 & 6), which contrasts with a deeper body in the typical morph of *V. hartwegi* and other species of *Vieja*. The body shape of specimens is similar to that of other rheophilic herichthyine cichlid species, such as *Paraneetroplus* and *Rheoheros.* The rheophilic morph also differs from all members of *Vieja* by the presence of a simple great spot (Fig. 4A-C) or an ocellus (Fig. 4D) at the center of the base of the caudal peduncle and on the origin of the caudal fin; other species of *Vieja* have a simple caudal spot (*V. maculicauda*) or the caudal spot is fused with the midlateral stripe (the rest of the species; e.g. *V. melanura*). Also, in the rheophilic morph, the midlateral stripe is absent; only a midlateral blotch on the fifth bar is noticeable. This coloration pattern is similar to the syntopic *Chiapaheros grammodes* but can be differentiated by the great spot or ocellus on the caudal peduncle of the rheophilic *V. hartwegi* morph (Fig. 6) versus the simple oblong blotch in *C. grammodes*. This difference is always noticeable between juvenile and adult specimens. The midlateral blotch in *C. grammodes* is on the sixth bar versus the fifth bar in the rheophilic *V. hartwegi* morph. *Chiapaheros grammodes* has a series of thin brownish lines across interorbital region, snout and cheeks (the main character to diagnose this monotypic genus);

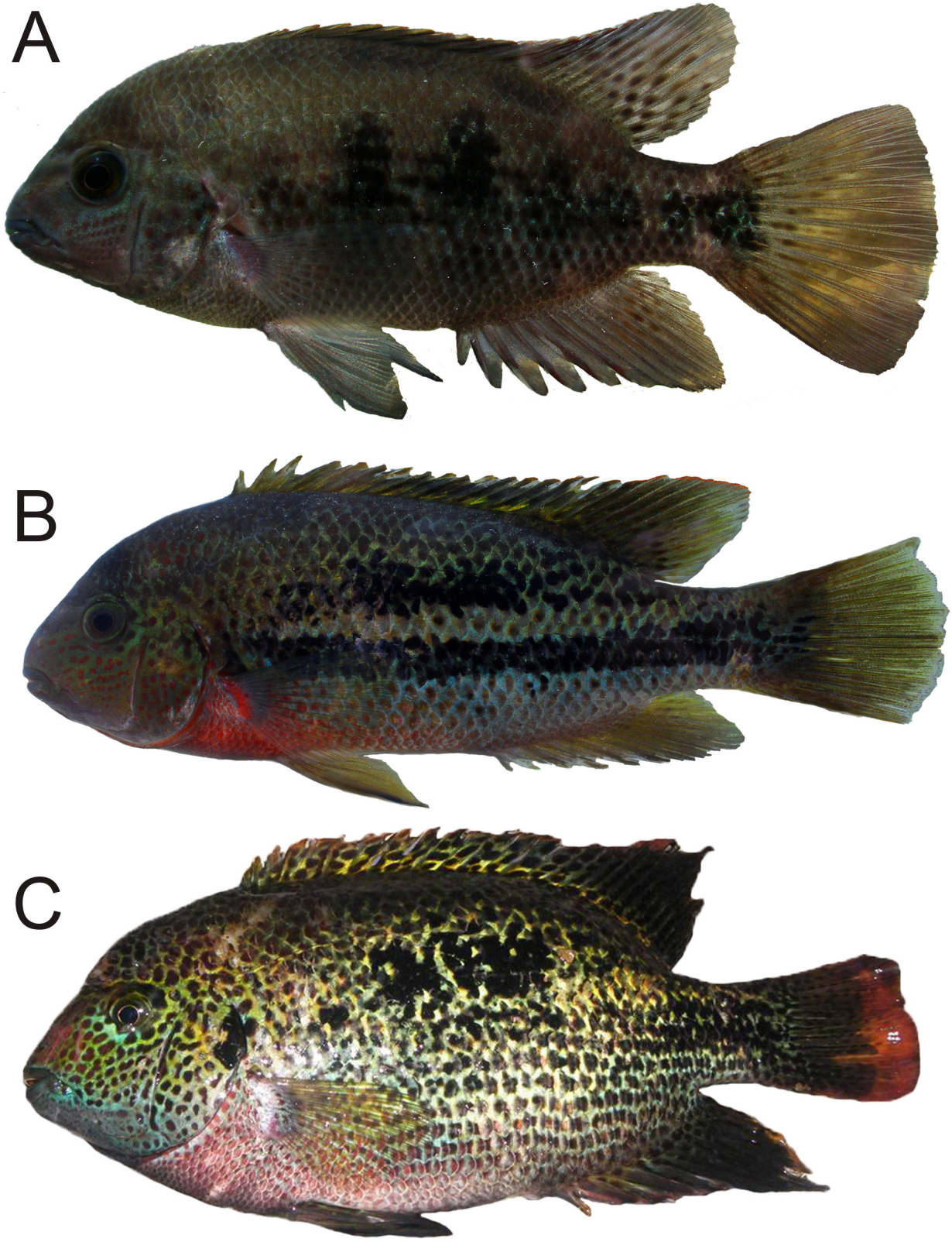

FIGURE 3. Live specimens of the typical morph of *Vieja hartwegi*, showing ontogenic variation in coloration pattern. A) Juvenile, 75 mm SL, MZUNICACH 6761, La Angostura Reservoir, La Concordia, Chiapas. B) Adult, 144 mm SL, aquarium specimen, Cacahuanó River, Ocozocoautla, Chiapas. C) Large adult, 250 mm SL, uncataloged specimen from a fishery, Grijalva River (main channel at Tres Picos), Copainalá, Chiapas (photo by J. M. López-Vila).

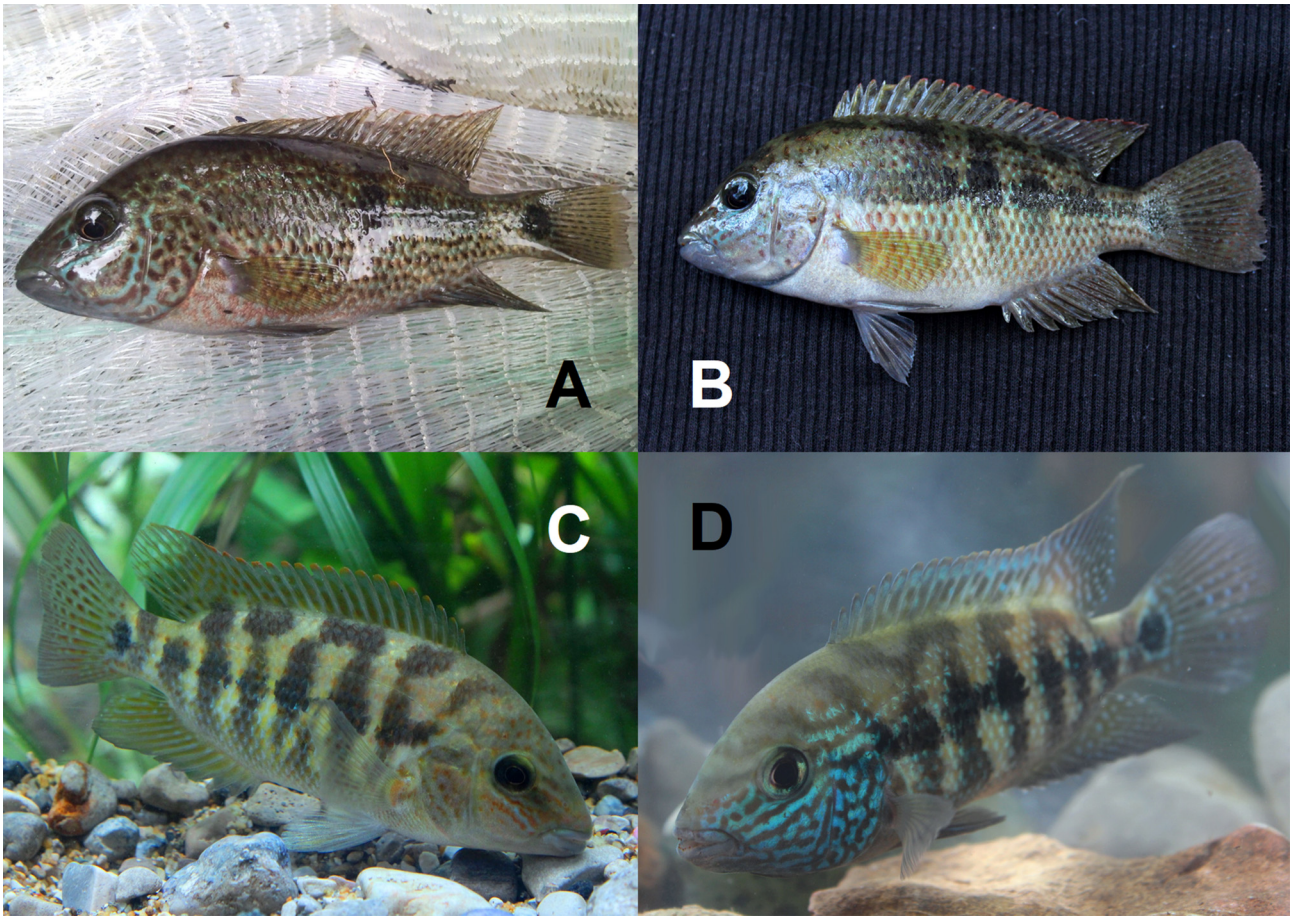

FIGURE 4. Live specimens of the rheophilic morph of *Vieja hartwegi.* A) Adult female in normal coloration, 97 mm SL, MZUNICACH 7161, Lagos de Colón, La Trinitaria, Chiapas (photo by M. A. Peralta-Meixueiro). B) Adult female in stress coloration, 65 mm SL, uncataloged specimen, Lagos de Colón, La Trinitaria, Chiapas. C) Adult female in stress coloration, 91 mm SL, MZUNICACH 7159, Tachinua River, Chicomuselo, Chiapas. D) Adult male in stress coloration, 80 mm SL, MZUNICACH 7157, Yayahuita River, Chicomuselo, Chiapas.

in contrast, the rheophilic morph possesses two dark interorbital bars. Additionally, *C. grammodes* differs notably from the genus *Vieja* by the large head and enlarged snout, a large mouth with prognathous lower jaw. In preserved specimens, the rheophilic morph possesses a horizontal stripe above the middle of the body (Fig. 6), and in live specimens the band is noticeable under stress conditions (Fig. 4B-D). This stripe is similar to the dorsolateral or second stripe of *V. hartwegi* and *V. bifasciata*, formed by the fusion of lateral blotches and always separated from the caudal blotch (Fig. 6). Other members of *Vieja* possess a strong midlateral stripe at level of mid-body (*V. breidohri*), below mid-body (*V. bifasciata, V. fenestrata, V. guttulata, V. zonata*), or variable, as in the typical *V. hartwegi* morph (Figs. 3 & 5).

Description. Morphometric and meristic data summarized in Tables 1–2. Maximum size 340 mm SL with weight of 1028 g in Grijalva River main channel, municipality of Chicoasén, Chiapas (observation from fishery La Cuevita). Meristics for the typical *V. hartwegi* morph (Figs. 3 & 5): *Fins:* D XVI–XVIII (mode 17), 11–14 (mode 12); A VI–VII (mode 6), 8–10 (mode 9); pectoral rays 15–17 (mode 16). *Scales:* Lateral series 30–34 (mode 32); upper lateral line 16–23 (mode 20); lower lateral line 8–15 (mode 12); in one specimen, pored scales of upper lateral line disrupted by non-pored scales (MZUNICACH 7158, specimen 2); subsidiary pored scales on caudal fin, usually 0–3 (mode 2) continuous with lower lateral line or interrupted by one non-pored scale; isolated pored scales (1–3) on the caudal-fin base, usually 1–2 scales above or below the subsidiary pored scales; predorsal squamation pattern irregular; scale row overlap 2–4 (mode 2); pectoral-pelvic scale rows 6–8 (mode 7); scale rows from lateral line to base of first dorsal-fin ray (not including the scaly sheet along the base), 3–4$^1/_2$ (mode 3$^1/_2$); scale rows from lateral line to base of first dorsal-fin spine 5–7 (mode 6); scale rows from origin of anal fin to lower lateral line 8–10 (mode 9); circumpeduncular scales 16–22 (mode 20); scale rows on cheek 5–7 (mode 5), one specimen with

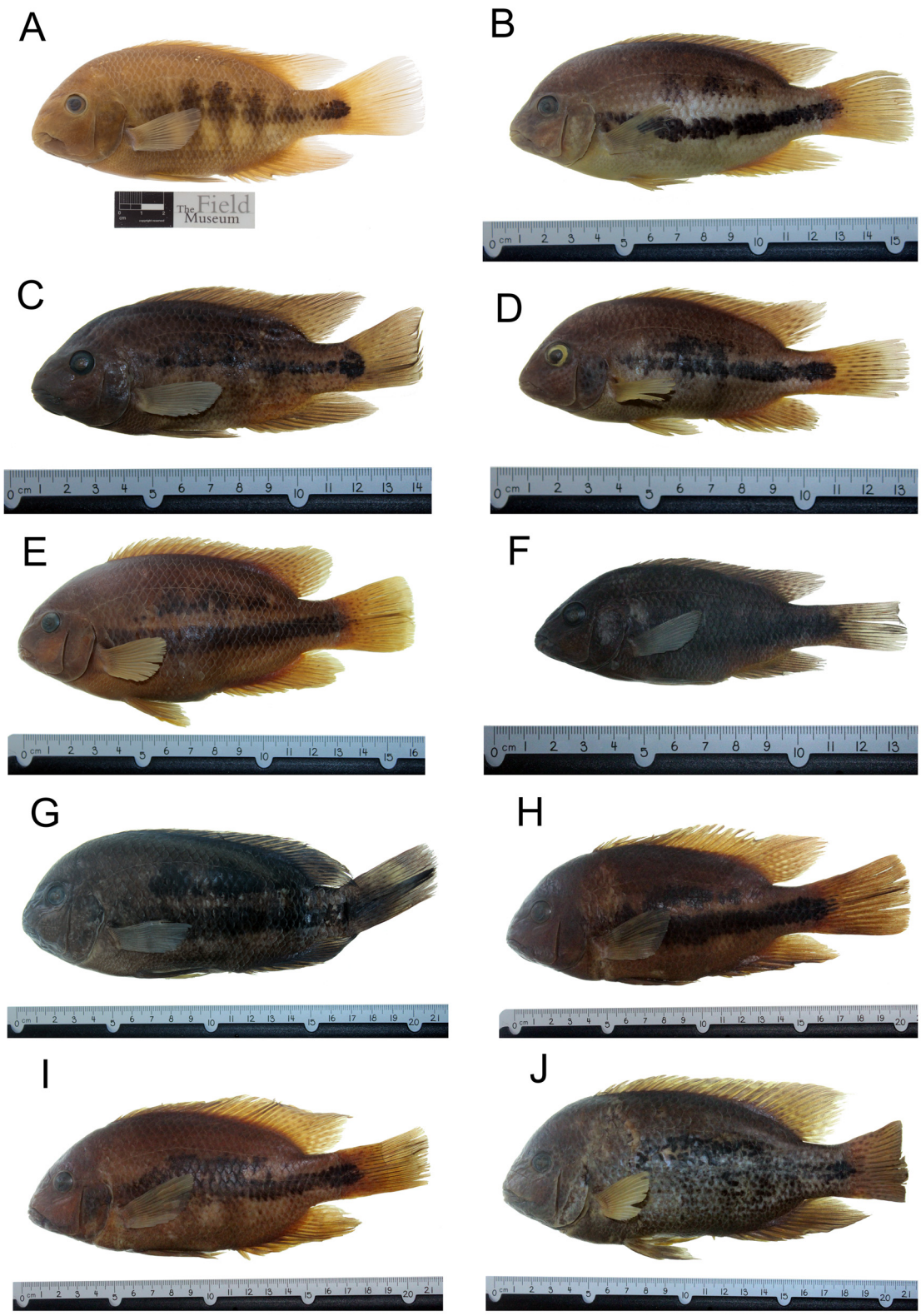

FIGURE 5. Fixed specimens of the typical *Vieja hartwegi* morph, showing the variation in body shape and the ontogenetic and individual variation in coloration patterns. A) Holotype (adult in breeding coloration), UMMZ 207701. B) Chiquito River, Chiapa de Corzo (juv.), MZUNICACH 7053. C) El Zapote River, Chiapa de Corzo (juv.), MZUNICACH 7210. D) La Angostura Reservoir, La Concordia (juv.), MZUNICACH 7154. E) Totopac River, Tecpatán (subadult), MZUNICACH 1053. F) Lagos de Colón, La Trinitaria (subadult), MZUNICACH 7065. G) Copanó River, Ostuacán (adult), MZUNICACH 7208. H-I) Grijalva River (main cannel), Copainalá (adults), MZUNICACH 3145. J) Santo Domingo River, Chiapa de Corzo (adult), MZUNICACH 6245.

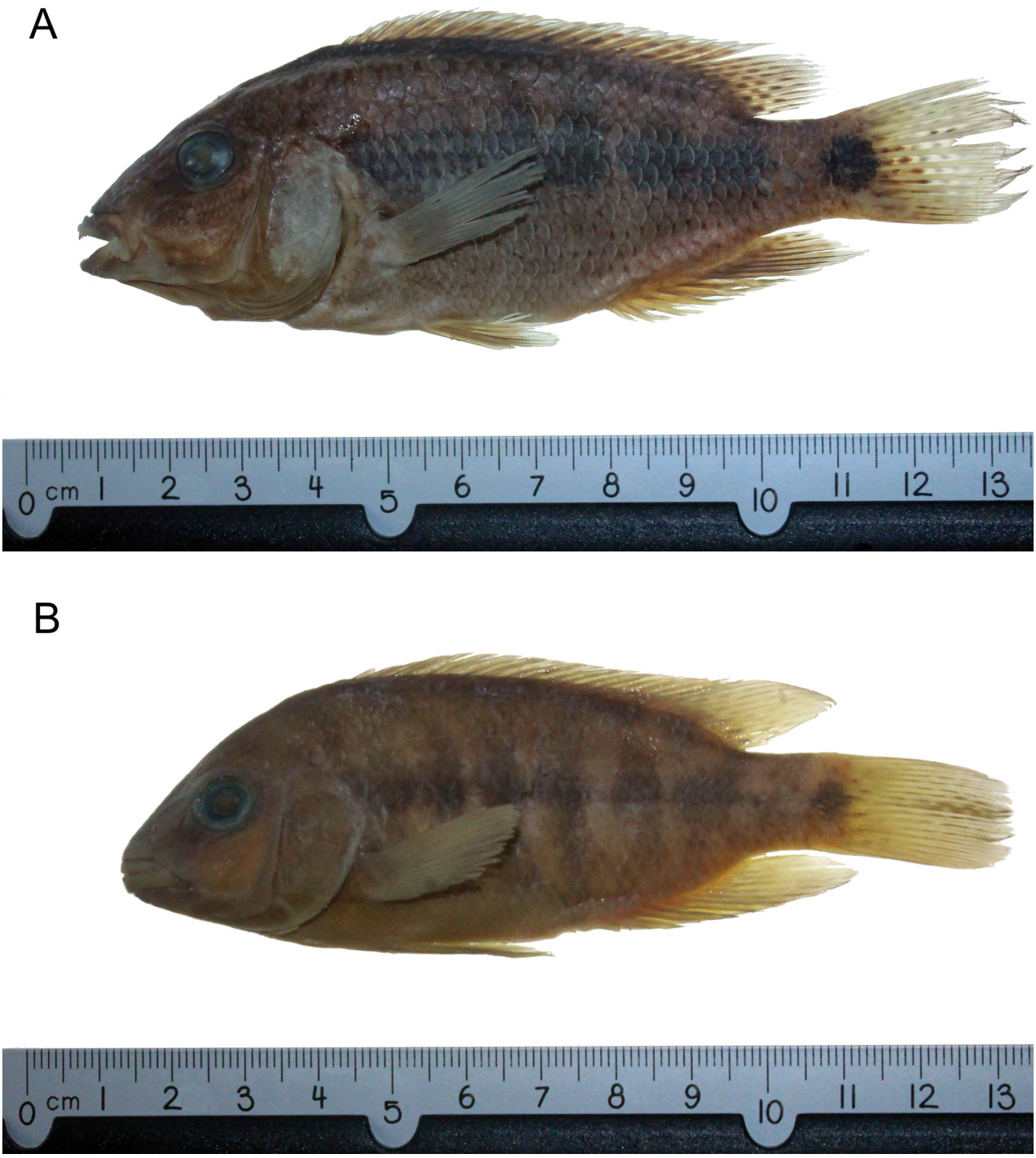

FIGURE 6. Preserved specimens of the rheophilic *Vieja hartwegi* morph. A) Adult female, MZUNICACH 7161, Lagos de Colón, La Trinitaria, Chiapas. B) Adult female, MZUNICACH 7159 [post-mortem fixed specimen], Yayahuita River, Chicomuselo, Chiapas.

irregular pattern, not forming rows (ECOSC 7543, specimen 1). Cheek and opercle fully scaled, scales cycloid; dorsal portion of head and predorsal scales cycloid; base of dorsal and anal fins and scaly sheath along fin bases cycloid; lateral body scales ctenoid; lateral chest scales ctenoid, smaller than lateral body scales; ventral chest scales cycloid.

Body shape moderately deep or slightly slender (Figs. 3 & 5), in very large adults (>200 mm SL) body deeper (Fig. 3C); laterally compresssed; predorsal contour steep, dorsal head profile in front of orbit usually convex in

juveniles, straight or slightly rounded in adults; the individuals with elongated snout, concavity present over the eyes; prepelvic contour gently convex; caudal peduncle short, deeper than long. Mouth small, usually low in position in juveniles and preadults, terminal and slightly oblique in large adults; individuals of upper reaches with more slender bodies, mouth usually terminal (Figs. 5F-G). Upper jaw in juveniles and preadults usually projected beyond lower jaw (Fig. 5A-D), large adults isognathous (Fig. 5G-J). Snout moderately pronounced or sometimes flattish. Lips of both jaws moderately thickened. Frenum well developed. Maxillary cleft position, variable but usually at level of dorsal margin of pectoral fin base.

Gillrakers on first arch: lower limb 7–11 (mode 9), one specimen found in sulphidic environment possessed only two gillrakers (MZUNICACH 1065, specimen 1); upper limb 1–3 (mode 2); total 9–13 (mode 11), one specimen with only 5 (see line above). Gillrakers moderately elongate, shorter and thickened in adults and more elongated in juveniles; tips pointed or rounded, commonly anterior gillrakers on lower limb shorter and rounded and posterior ones larger and pointed. One specimen, with posterior gillrakers bifurcated on lower limb (MZUNICACH 3145, specimen 1). Outer teeth in both jaws recurved, conical; anterior teeth enlarged with small posterior cusp; 3–4 irregular series of inner smaller teeth.

Lower pharyngeal tooth-plate (Fig. 7A), dissected from one specimen (MZUNICACH 6761, 89.3 mm SL), dorsoventrally compressed, with short anterior process and posterior processes slightly enlarged; wider than long; posterior margin concave at center and convex at margins; teeth conical, enlarged posteriorly and shorter anteriorly, with antrorse cusp; second cusp small present at the base; three medial rows on each side, mainly the first, notably bigger and more robust posteriorly than the rest; 26 total (12/14 in each side) teeth in posterior row; 7 and 6 teeth in each near median row. Urohyal bone with posterior edge concave, dorsally slight convex with a short, curved spine (Fig. 7A). Axial skeleton, based on 2 c&s specimens: vertebral counts, 15 precaudal and 14–15 caudal, total 29–30; ribs, 9 epipleurals and 13 pleurals; 2 supraneurals, between the supraoccipital crest and first dorsal pterygiophore; pterygiophores, 27 dorsal and 12–13 anal; the first anal pterygiophore contains 2 or 3 spines (Fig. 8A).

FIGURE 7. Lower pharyngeal tooth plate and urohyal bone of the two morphs of *V. hartwegi.* A) Typical morph, MZUNICACH 6761. B) Rheophilic morph, MZUNICACH 7157 (photos by K. Ramírez-Moreno [pharyngeal tooth plates] and G. Morales-Flores [urohyal bones]).

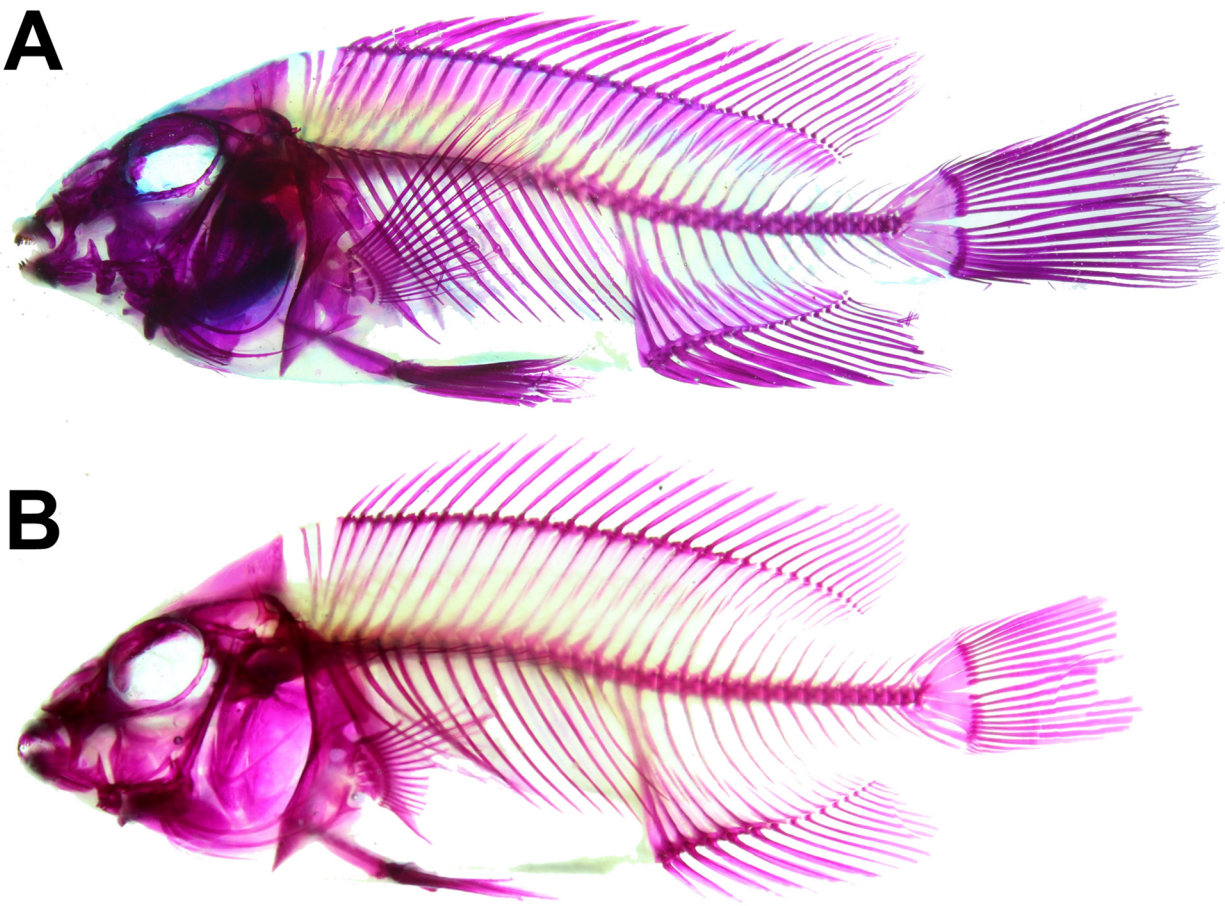

FIGURE 8. Cleared and stained specimens of the two morphs of *V. hartwegi*. A) Typical morph, 89.3 mm SL, MZUNICACH 6761, La Angostura Reservoir, La Concordia, Chiapas. B) Rheophilic morph, 53.2 mm SL, MZUNICACH 7159, Tachinua River, Chicomuselo, Chiapas.

Rheophilic morph smaller, largest known 97.1 mm SL, with following meristic data: *Fins:* D XVIII, 11–13 (mode 11), A V–VII (mode 6), 8–10 (mode 9); pectoral rays 15–16 (mode 16). *Scales:* Lateral series 31–34 (mode 31); upper lateral line 20–21 (mode 21); lower lateral line 9–13 (mode 12), in two cases, pored scales disrupted by non-pored scales and usually 1–3 (mode 2) subsidiary pored scales on caudal fin; isolated pored scales on caudal-fin base, absent; predorsal squamation pattern irregular; scale row overlap 1–3 (mode 2); pectoral-pelvic scale rows 7–8 (mode 7); scale rows from lateral line to base of first dorsal-fin ray 3–$3^1/_2$ (mode $3^1/_2$); scale rows from lateral line to base of first dorsal-fin spine 6–7 (mode 6); scale rows from origin of anal fin to lower lateral line 8–9 (mode 9); circumpeduncular scales 18–21 (mode 20); scale rows on cheek 6–7 (mode 7). Squamation pattern similar to typical morph.

Body shape slender or moderately deep (Figs. 4 & 6); predorsal contour slightly steep, dorsal head profile in front of orbit usually straight or slightly convex; prepelvic contour gently convex; caudal peduncle short, deeper than long. Mouth small, terminal and isognathous in all sizes. Snout moderately pronunced. Lips of both jaws moderately thickened. Frenum well developed. Maxillary cleft position, usually ventral or sometimes at level of dorsal margin of the pectoral-fin base.

Gillrakers on first arch: lower limb 8–10 (mode 9); upper limb 3–4 (mode 3); total 11–13 (mode 13). Gillrakers moderately elongated; tips pointed or rounded, commonly anterior gillrakers on lower limb shorter and rounded, and posterior larger and pointed. Outer teeth in both jaws recurved and longer than typical morph, with posterior little cusp, anteriorly increasing in size; 3–4 irregular series of inner smaller teeth.

Lower pharyngeal tooth-plate (Fig. 7B) dissected from two specimens (MZUNICACH 7157, 61.2 mm SL; 7159, 53.3 mm SL), dorsoventrally compressed, with short anterior process and posterior processes slightly enlarged; wider than large; posterior margin concave at center and very convex at margins; teeth conical, enlarged

posteriorly and shorter anteriorly, with antrorse cusp; second cusp small but strong, present at the base; four or three medial rows, mainly the first, notably larger and more robust posteriorly than the rest; 22–24 (11/11 and 12/12 in each side) total teeth in posterior row; 8/7 and 6/7 teeth in near median rows. Urohyal bone with posterior edge concave, dorsally convex with a strong curved spine (Fig. 7B). Axial skeleton, based on two c&s specimens and one radiograph: vertebral counts, 15 precaudal and 15(1)–16(2) caudal, total 30(1)–31(2); ribs, 12 epipleurals and 13 pleurals; 2 supraneurals, between the supraoccipital crest and first dorsal pterygiophore; pterygiophores, 30 dorsals and 15 anals; the first anal pterygiophore contains 2 spines (Fig. 8B).

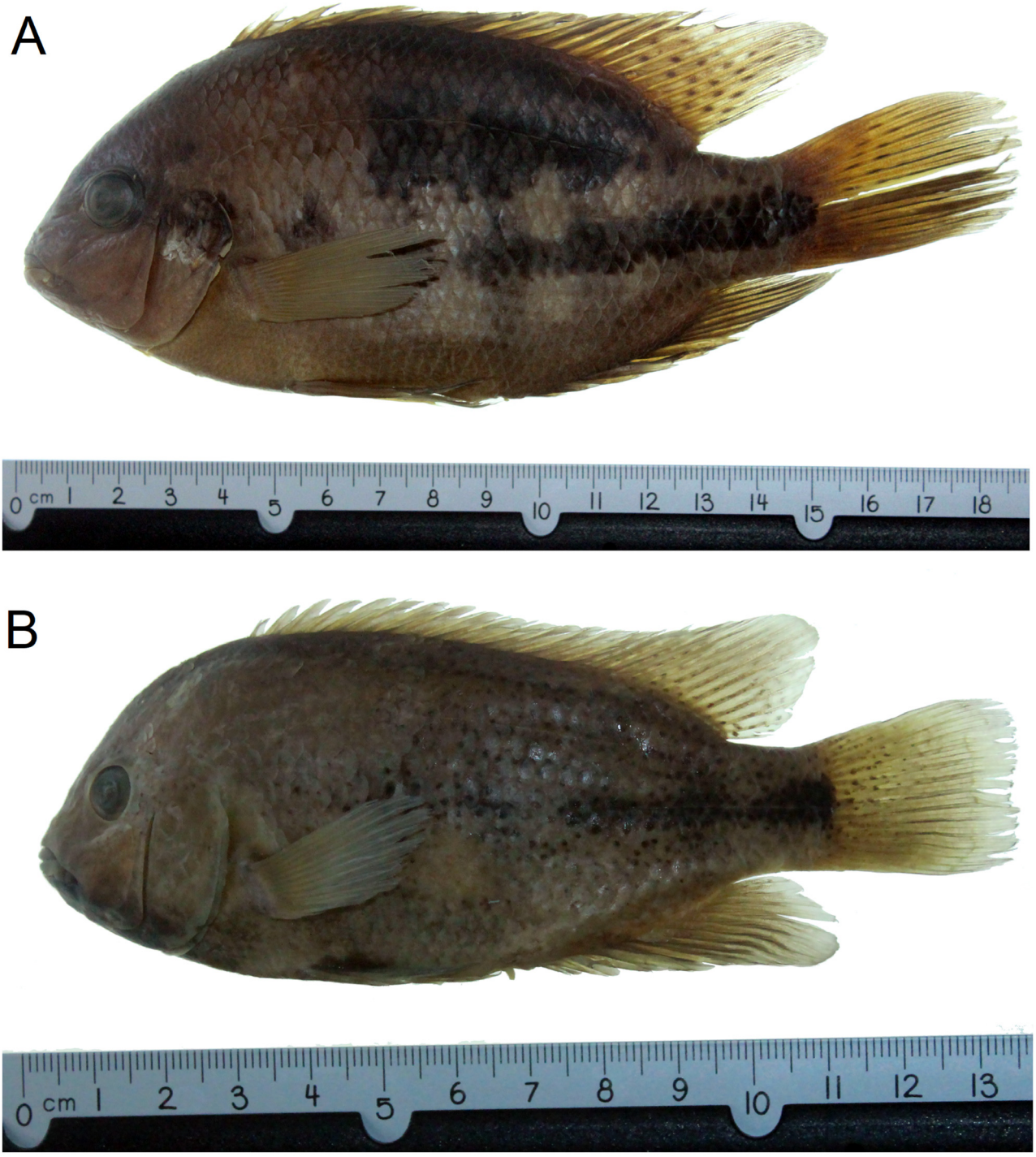

FIGURE 9. Comparison to species closely related to *V. hartwegi*: A) *V. bifasciata,* 140 mm SL, ECOSC 4677, Tzendales River, Ocosingo, Chiapas. B) *V. breidohri,* 105 mm SL, MZUNICACH 7065, Lagos de Colón, La Trinitaria, Chiapas.

Coloration in preserved specimens. *Vieja hartwegi* has grayish background color, turning to brownish depending on time since preservation. Head usually somewhat darker than body. Ventral portion uniformly lighter. Typical morph with distinctive midlateral stripe extending from caudal-fin base to opercle, running at level (Fig. 5A, C-D) or usually below mid-body (Fig. 5B, E-J); a well-developed dorsolateral or second stripe slightly separated (Fig. 5E, G, J), partially fusioned anteriorly (Fig. 5H) or sometimes fully fused (Fig. 5D, I) with midlateral stripe in adults. In adults, second stripe formed by the fusion of blotches. In juveniles and subadults, midlateral stripe usually disrupted; commonly three to five irregular blotches above midlateral stripe (Fig. 5B-C, F) or rarely absent in some specimens; in small juveniles, cross-bars arranged along midlateral stripe. Adults in breeding coloration presents five cross-bars along midlateral stripe, lower jaw and belly darker (as the holotype, Fig. 5A). Interorbital bars commonly not evident in fixed specimens. Black crescent-shaped operculum marking present in adults, in juveniles and preadults usually weak or absent. In some specimens, brown spots present on cheeks. Soft portions of dorsal and anal fins and caudal fin, dark brown spotted in both morphs.

Rheophilic morph with distinctive dorsolateral stripe present above of the middle of the body, extending from margin of the opercle to the level of dorsal fin posterior end (Fig. 6A); this stripe is similar to dorsolateral or second stripe in typical morph, formed by the fusion of lateral blotches. Great rounded spot at center of caudal peduncle and base of caudal fin, often disrupted with dorsolateral stripe or sometimes confluent, but always remarkable (Fig. 6). Eight diffuse bars along the body, usually six bars notable, especially in juveniles (Fig. 6B). Usually, series of 4–6 dark dots below dorsolateral stripe.

Coloration in life. *Vieja hartwegi* exhibits a highly variable coloration throughout its distributional range. Populations in upper Grijalva show background color that varies from silver-gray to olive-gray; in middle and lower Grijalva it varies from olive-gray to yellowish (see Conkel 1993: 58). Head dorsally olive-gray to yellowish; in juveniles and sub-adults red spots present on preoperculum, operculum, cheek, and lachrymal (Fig. 3A); in adults red blotches cover entire head (Fig. 3B-C). Side of head bluish and iridescent base color, more vibrant in sub-adults and adults. Two dark interorbital bars present. In large adults red dots at the center of the scales cover all of the body continuing onto dorsal, anal, and caudal fins (Fig. 3C). Belly usually red in adults. In juveniles and subadults, dots along the body brownish red. Midlateral and dorsolateral (or blotches) stripes black; sometimes the two bars fully fused. Pectoral fins transparent or slightly yellowish; pelvic fins grayish. Dorsal and anal fins gray translucent in juveniles and sub-adults and yellowish in adults. In very large adults, spiny portion of the dorsal fin, golden. Border of dorsal fin red and anal fin dark. Caudal fin gray and translucent, with red border in large adults (Fig. 3C). Breeding coloration is shown in Werner and Stawikowski (1987: 23).

Rheophilic morph has olive gray base color. Head olive gray dorsally with red or brownish orange spots or blotches. Two dark interorbital bars evident. Side of head bluish and iridescent, covered by variable brownish orange or reddish spots or blotches (usually forming a reticular pattern) all over opercle, preopercle, cheek, and lachrymal (Fig. 4). In some specimens, bluish iridescent horizontal stripe prominent below eye (Fig. 4C). In normal coloration, two dark marks notable: a great rounded spot at center of the caudal peduncle and base of caudal fin (Fig. 4A-C; some specimens present an ocellus, with iridescent light blue around the spot, probably a sexual dimorfism in males Fig. 4D) and irregular blotch on the middle of the body. Under stress, coloration consists of dark vertical bars along the body and series of seven blotches along the bars, forming a general dorsolateral stripe above the middle of the body with no fusion of caudal spot or ocellus (Fig. 4B-D). Distal portions of lateral scales reddish or brownish orange, whereas proximal portions iridescent light blue, forming regular series of longitudinal stripes along each scale row. Pectoral fins transparent or slightly yellowish; pelvic fins pale or dark grayish. Dorsal and anal fins brownish or yellowish and translucent with bluish iridescent dots. Border of dorsal fin red with bluish line below the red and across the spiny portion of the fin. Border of anal fin dark; caudal fin gray and translucent with regular series of brownish and sometimes bluish iridescent dots.

Distribution and habitat. Found on the Atlantic slope of Chiapas, Mexico and Guatemala, endemic to the Grijalva River basin. Miller *et al.* (2005) considered its distribution only in the middle and upper portions of the Grijalva. Gómez-González *et al.* (2015) documented its presence in the lower Grijalva in Ángel Albino Corzo or Peñitas reservoir and tributaries. It also inhabits the upper reaches of the lower Grijalva outside of reservoirs (Fig. 10). Elevations typically range from 100 to 700 m; however, an exceptional record exists from 1600 m in the isolated Laguna Verde, municipality of Coapilla, Chiapas (MZUNICACH 1239, 1242). The rheophilic morph is restricted to tributaries of the far upper Grijalva River basin, only known in Lagartero River, near the Guatemalan border, and the Tachinua and Yayahuita rivers in Chiapas, Mexico (Fig. 10).

FIGURE 10. Map showing distribution of the two morphs of *V. hartwegi* in the Grijalva River basin, Mexico and Guatemala. The white square represents the type locality, black circles are localities of the typical morph and white circles are localities of the rheophilic morph.

The typical *V. hartwegi* morph inhabits a great variety of habitats. Large adults prefer deeper zones of the main river channel (>2 m depth) with variable but mainly moderate current and rocky or sandy substrates, usually without aquatic vegetation. Juveniles and subadults prefer shallow waters with rocky bottoms, sand, silt and mud in rivers and streams with swift to slow currents, usually without aquatic vegetation but covered by riverine vegetation. Also inhabits lakes and reservoirs. The species is also tolerant to sulphidic environments; it has been recorded in El Azufre and Baños del Carmen, municipalities of Tecpatán and Venustiano Carranza, respectively, both in Chiapas, Mexico.

The rheophilic morph primarily inhabits rocky bottoms covered with boulders and rocks of various sizes and wooden debris, aquatic vegetation absent, in depths of 30–100 cm; moderate to fast currents, with clear or slightly murky waters. This morph of *V. hartwegi* is sympatric with the typical morph; however, the two forms are likely segregated because of habitat preferences and food habits. There are too few specimens to robustly analyze the food preferences, but slight differences in pharyngeal jaw dentition may be related to diet. Additionally, *V. breidohri* and *C. grammodes* are found in sympatry with this morph.

TABLE 2. Morphometric data for the two morphs of *Vieja hartwegi* and related species. Measurements are presented as percent of standard length or percent of head length. SD= standard deviation, Min= Minimum, Max= Maximum.

Morphometrics	Holotype	Paratypes (N= 3)				Typical morph (N= 46)				Rheophilic morph (N= 8)				*V. bifasciata* (N= 16)				*V. breidohri* (N= 21)			
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Standard Length (SL)	129.9	99.6	33.7	73.6	138	118	32	58.1	177	68.7	18.5	48.3	97.1	141	24.5	112	186	88.3	23.8	51.9	127
	Percent of standard length (SL)																				
Body Depth (BD)	44.2	46.2	3.9	49.9	42.2	43.6	2.5	38.9	50.5	39.4	1.7	36.6	50.5	49.2	3.4	42.8	53.9	43.3	2.1	37.2	46.0
Caudal Peduncle Length (CPL)	10.9	14.7	0.6	15.3	14.1	10.5	0.8	8.7	12.0	10.1	0.8	8.7	12.0	9.9	1.0	8.3	12.1	9.6	0.7	7.9	10.8
Caudal Peduncle Depth (CPD)	15.1	17.7	1.8	19.1	15.7	14.3	0.7	12.8	15.5	13.5	0.6	12.3	15.5	15.0	0.7	13.7	16.2	14.5	0.5	13.7	15.3
Anterior Body Depth (ABD)	43.4	47.0	3.3	50.2	43.7	42.3	2.1	38.5	47.5	39.3	1.8	35.3	47.5	47.2	2.8	42.0	51.2	43.0	1.8	37.7	45.7
Posterior Body Depth (PBD)	16.3	18.6	1.4	19.8	17.1	16.7	0.8	15.0	18.2	15.7	0.8	14.4	18.2	17.7	0.9	16.6	19.9	17.4	0.9	14.8	18.6
Predorsal Length (PDL)	43.1	44.6	3.2	47.8	41.5	40.9	3.1	37.4	59.6	41.2	1.0	39.2	59.6	41.1	1.7	37.4	43.7	41.6	1.6	39.3	46.1
Preanal Length (PAL)	64.1	62.0	3.4	64.4	59.6	67.2	1.7	62.8	71.1	68.0	2.3	64.6	71.1	67.0	1.9	62.3	70.1	68.0	1.5	65.1	71.3
Prepelvic Length (PPvL)	37.4	41.4	2.5	44.3	39.8	38.3	1.2	35.3	41.1	42.5	4.7	38.1	41.1	40.1	2.0	36.9	43.0	40.3	1.5	38.4	44.8
Prepectoral Length (PPcL)	32.7	35.2	2.8	38.1	32.5	33.3	1.5	30.4	36.1	39.0	2.7	35.3	36.1	34.3	1.8	31.0	37.0	36.2	1.6	33.9	39.3
Orbit Pectoral Fin Distance (OPFD)	14.6	18.4	1.5	19.6	16.7	15.9	0.9	14.4	18.5	18.5	1.7	16.3	18.5	16.5	1.4	14.3	19.9	18.3	0.7	16.6	19.4
Head Depth (HD)	36.9	34.6	3.7	38.0	30.8	36.3	1.6	33.4	39.5	34.7	1.4	32.5	39.5	40.0	2.1	35.8	42.6	38.1	1.1	35.4	39.9
Head Length (HL)	29.4	33.8	2.6	36.7	32.0	28.3	1.3	24.6	31.1	34.3	5.4	30.7	31.1	28.3	1.5	25.3	30.6	30.4	1.2	28.3	32.3
Dorsal-Base Length (DBL)	59.0	37.2	32.3	57.8	0.0	60.0	1.7	56.6	63.8	55.4	1.5	52.5	63.8	63.3	2.2	59.9	67.3	59.5	1.9	54.4	63.2
Longest (=Last) Dorsal Spine Length (LDSL)	15.0	15.5	1.7	16.6	13.6	14.2	2.0	10.1	19.4	13.5	0.9	12.5	19.4	17.5	2.9	12.4	21.8	15.0	1.6	12.4	18.8
Anal-Base Length (ABL)	26.7	26.8	2.7	28.8	23.8	24.5	1.6	20.8	29.7	23.5	1.2	21.9	29.7	27.0	2.0	24.3	30.2	23.5	0.6	22.4	25.3
	Percent of head length (HL)																				
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Eye Diameter (ED)	23.5	23.2	1.6	24.5	21.4	26.8	2.6	21.3	32.4	28.1	5.3	16.9	34.6	26.8	2.0	22.7	29.8	28.4	4.6	22.7	37.0
Orbit Maxillary Cleft Distance (OMCD)	26.7	32.4	1.0	33.6	31.6	29.3	3.4	23.1	34.8	21.0	3.1	17.4	25.6	33.4	7.2	26.8	58.4	25.0	4.1	16.9	32.6
Interorbital Bony Width (IOBW)	43.2	39.8	1.7	41.6	38.2	40.8	3.8	33.6	48.0	25.4	4.0	16.9	29.6	45.4	5.3	28.7	50.8	39.6	3.0	33.7	45.8
Snout Length (SnL)	38.8	42.9	1.6	44.4	41.3	37.4	3.7	28.0	47.6	32.8	3.4	28.3	37.2	36.0	3.5	31.5	44.2	31.0	4.1	23.3	37.0
Upper Jaw Length (UJL)	31.1	22.9	2.9	26.2	20.9	32.8	2.1	28.7	37.7	29.0	5.5	20.5	36.7	32.0	2.0	28.7	34.9	32.4	1.9	29.6	37.2
Premaxillary Pedicel Length (PPL)	46.7	43.3	2.1	45.6	41.8	43.5	3.8	34.3	50.6	43.8	5.8	32.1	49.8	43.0	3.3	36.7	50.4	43.0	2.4	37.9	47.0
Lower Jaw Length (LJL)	40.6	28.4	4.8	31.2	22.9	42.6	3.0	36.3	50.5	37.2	5.1	29.4	44.4	40.9	2.2	35.3	43.8	40.4	3.0	34.6	45.8
Head Width (HW)	61.7	57.3	4.5	62.5	54.2	62.0	4.0	56.1	80.4	50.4	5.9	37.0	54.5	63.2	2.9	59.2	67.2	61.1	3.9	52.0	67.7
Cheek Depth (CD)	31.6	26.3	0.5	26.9	25.8	32.8	3.2	27.7	39.7	24.7	4.1	18.8	30.7	35.9	2.5	31.6	40.9	32.0	4.2	21.2	41.5
Lacrimal Depth (LD)	30.1	27.3	0.9	28.3	26.7	31.7	3.4	25.0	37.5	20.7	2.8	17.9	24.6	31.9	2.8	27.2	36.6	26.6	3.3	20.5	33.9

Dicussion

Phylogenetic hypothesis. Results of the Bayesian analysis recovered a consensus tree in which individuals of the rheophilic morph are nested within a single clade along with the typical *V. hartwegi* morph, and sister to congener *V. breidohri*, and this clade sister to *V. bifasciata*. In this analysis, the rheophilic morph of *V. hartwegi* is not recovered as monophyletic (Fig. 11). Nevertheless, the genetic distances between species are low, but a range wide population analysis of the entire clade (*V. bifasciata, V. breidohri* and *V. hartwegi*) and the addition of more molecular markers are necessary to clarify populations and taxonomic status.

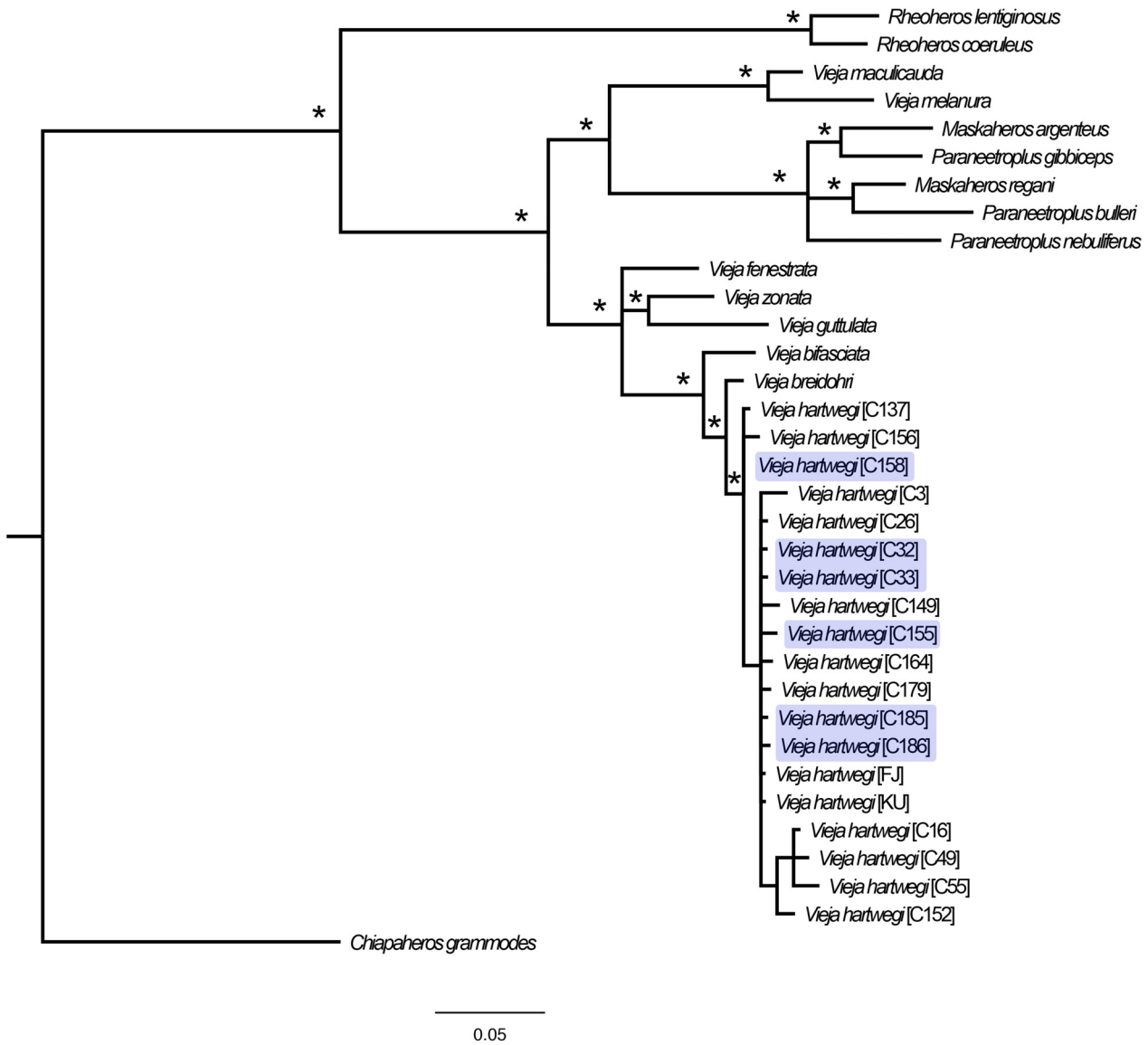

FIGURE 11. Bayesian phylogeny (based on partial sequences of cyt b) showing relationships of the two morphs of *V. hartwegi* with other closely related species. Highlighted specimens specify rheophilic morph. * Indicates posterior probabilities ≥ 95.

Statistical analysis. The results of the PCA based on morphometric characters showed that the body shape is highly variable in *V. hartwegi* (Fig. 12). The two first PC axes explained 58.5% of the variance, with 37.2% corresponding to PC1 and 20.8% to PC2. PC1 was related to premaxillary pedicel length and body depth, with the rheophilic *V. hartwegi* morph occupying the most positive side of the axis. For PC2, the most important characters were snout length and lachrymal depth, but there is not a clear separation between species.

Remarks. Říčan *et al.* (2016) used 15 precaudal and 15 caudal vertebrae to diagnose the entire genus *Vieja*; however, our results indicate these counts are actually quite variable. *Vieja bifasciata* and *V. breidohri* have less total vertebrae (29 and 28, respectively); *V. bifasciata* has 15 precaudal and 14 caudal vertebrae (n=1), and *V.*

breidohri has 14 precaudal and 14 caudal vertebrae (n=3); two individuals of both morphs of *V. hartwegi* (n=5) display the character as given by Říčan *et al.* (2016), but one specimen of the typical morph has 29 and two of the rheophilic morph have 31 total vertebrae. Additionally, Taylor and Miller (1980) report a total of 29–31 total vertebrate in the description of *V. hartwegi*.

Conclusion. The original description of *Vieja hartwegi* does not provide a clear set of characters to identify adults of the species with respect to its closest congeners *V. bifasciata* and, at that time undescribed, *V. breidohri*. Close examination of specimens of all three species shows an important overlap in morphometric and meristic characters (Tables 2–3, Fig. 12). Nonetheless, specimens and tissues of *V. breidohri* are scarce in ichthyological collections and sequences available on Genbank come from aquarium stocks. Coloration, vertebral count, and pharyngeal jaw dentition separate *V. hartwegi* from *V. breidohri*. Only the body depth and pattern arrangement of the two stripes allow separation of *V. hartwegi* from *V. bifasciata*. The molecular phylogeny at the population level provided by Říčan *et al.* (2016) recovered this group as paraphyletic; however, many sequences archived on Genbank and used by these authors have questionable identifications.

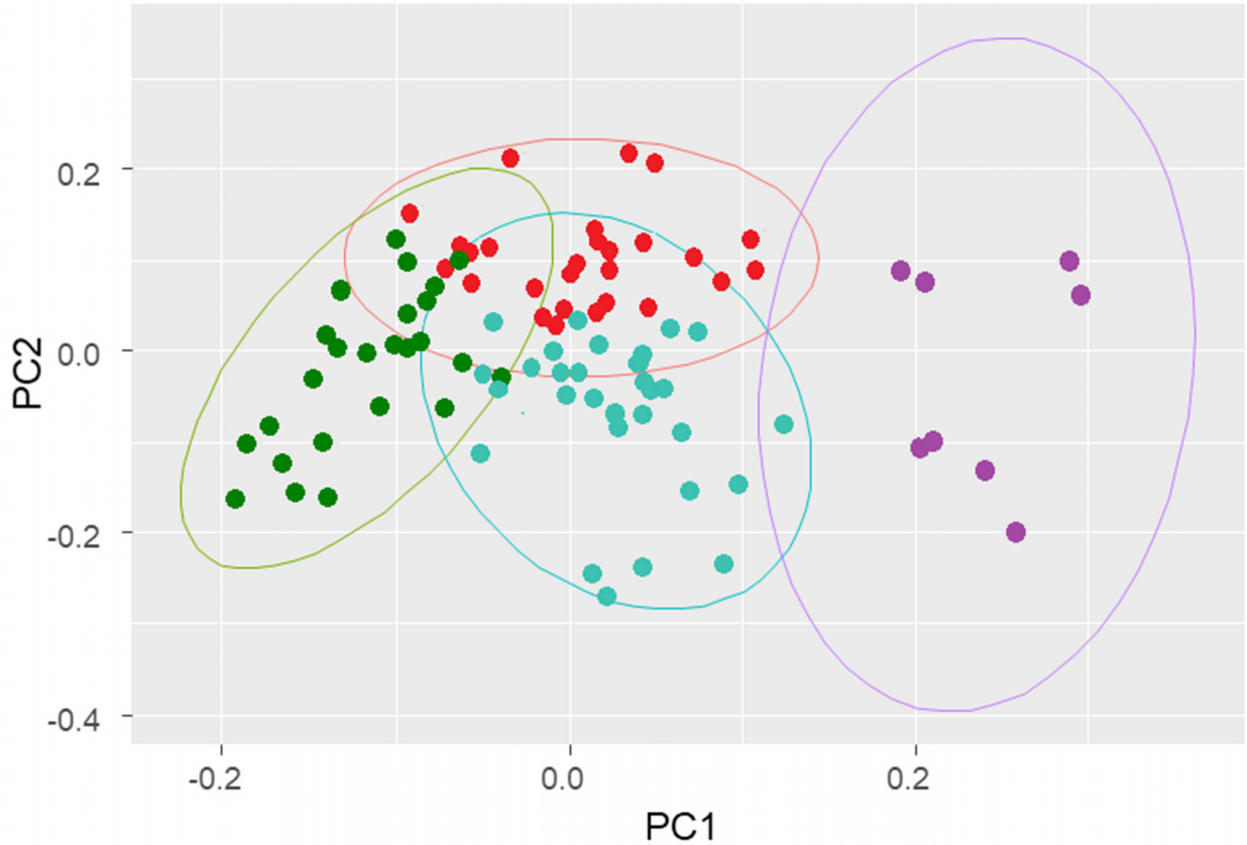

FIGURE 12. Principal component analysis (PCA) for morphometric data between the two morphs of *V. hartwegi* (typical in red and rheophilic in purple) and related species, *V. bifasciata* (green) and *V. breidohri* (turquoise). Ellipses represents 95% confidence intervals.

The discovery of the new rheophilic morph of *V. hartwegi* is evidence of the high morphological variability of this species, our observations show variation in body shape, coloration and some meristic and morphometric features, as well as osteological characters. The molecular data demonstrate this morph is not genetically distinct and it was recovered nested inside other individuals of the species, confirming that this species is extremely polymorphic. Polymorphism in Middle American heroine cichlids has been well documented in other species, e.g. the convict cichlid *Amatitlania nigrofasciata* (McMahan *et al.* 2014, Bagley *et al.* 2016), the Midas cichlid *Amphilophus citrinellus* species complex (Barluenga & Meyer 2004) and the Cuatro Ciénegas cichlid *Herichthys minckleyi* (Kornfield & Taylor 1983, Cohen *et al.* 2005). Some species of the genus *Herichthys* described by De la Maza-Benignos *et al.* (2013) may also be polymophisms (Říčan *et al.* 2016). Based on our findings and the well-documented cases of polymorphisms, taxonomic work with heroine cichlids based only on morphological criteria

may be insufficient, as was suggested by Kornfield and Taylor (1983); descriptions and taxonomic revisions in heroine cichlids should combine morphological and molecular data when possible.

Comparative material

Vieja bifasciata: MZUNICACH 6293 (1), 6655 (1) Tulijá River, Salto de Agua, Chiapas; MZUNICACH 6654 (3) Puyacatengo River, Teapa, Tabasco; ECOSC 3224 (6) Serranal Lagoon, Catazajá, Chiapas; ECOSC 3772 (1), 3878 (1 c&s) El Raizal, Catazajá, Chiapas; ECOSC 4704 (1) San Pedro River, Ocosingo, Chiapas; ECOSC 4746 (2) Tzendales River, Ocosingo, Chiapas; ECOSC 7520 (1) El Salado Stream, Marqués de Comillas, Chiapas. ***Vieja breidohri*:** MZUNICACH 6657 (2 c&s), 6659 (2), 7209 (1) La Angostura Reservoir, La Concordia, Chiapas; MZUNICACH 7065 (12 + 1 c&s), 7212 (6) Lagos de Colón, La Trinitaria, Chiapas.

Acknowledgements

Thanks are extended to the Graduate Program in Biological Sciences of the Universidad Nacional Autónoma de México (UNAM); this paper constitutes a partial fullfillment of the requirements for Graduate Program in Biological Sciences of the UNAM for the first author. The first author thanks the scholarship and financial support provided by the Consejo Nacional de Ciencia y Tecnología (CONACYT) (scholarship number 251569) and the Instituto de Biología (UNAM) for the infrastructure provided. We thank Miguel Peralta Meixueiro, Marco Gómez López and Juan Pérez Castañeda for providing the first specimens of the rheophilic morph and all members of the UNICACH Ichthyology lab for their assistance with field and lab work: Manuel Anzueto Calvo, Christian Narcia Rico, Georgina Morales Flores, Karen García López, Eidylimg Morales Arriaga, Alhelí Basulto Rangel, Jesús Hernández Cruz, Alejandro Jamangapé Ovando, Limber Sigarroa Gómez, Eduardo Urbina Trejo, Ramón Ramos Aguilar and Karem Ramírez Moreno. Special thanks to Juan C. Ojeda Escoto and Eduardo Torres Torres at IBUNAM and Javier Barrientos Villalobos at ECOSUR, for their help in molecular work. Jazmín Terán Martínez at ECOSUR, for her help with osteological work. Eric Moreno Juárez for standard radiographs. Jorge L. Liévano Trujillo for the map. Susan Mochel and Kevin Swagel (FMNH) kindly provided assistance with specimens at FMNH. Elías García López for Figure 1A. Special thanks to Rocío Rodiles-Hernández for facilitating access to the ichthyological collection of ECOSUR-Unidad San Cristóbal.

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