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Molecular systematics of the enigmatic Middle American genus *Vieja* (Teleostei: Cichlidae)

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ABSTRACT

The genus *Vieja* represents a group of heroine cichlids (Teleostei: Cichlidae) distributed on the Atlantic and Pacific slopes of North and Central America from southern Mexico to Panama. Sixteen species of *Vieja* are presently recognized; however, based on long-standing taxonomic problems, the genus itself appears to be weakly defined. A number of different generic designations have been proposed for members of *Vieja*, and recent systematic studies of heroine cichlids have not specifically addressed the validity of the grouping and have not included all species in the genus. Therefore, the purpose of this study was to assess the monophyly of the genus *Vieja* by including all nominal species in the genus using the mitochondrial encoded cytochrome *b* gene and nuclear S7-1 intron. Results of Maximum Parsimony, Bayesian inference, and topology tests (constraint tree searches and post-burn-in Bayesian filtering) indicate that the genus is not monophyletic as it is currently recognized. The genus *Herichthys* was recovered as sister to a clade consisting of a number of *Vieja* species (*V. fenestrata, V. guttulata, V. zonata, V. hartwegi, V. bifasciata, V. breidohri, V. argentea, V. regani, V. melanura*, *V. synspila*, and *V. maculicauda*, as well as *Paraneetroplus bulleri*). A clade consisting of *V. intermedia, V. godmanni*, and *V. microphthalma* was recovered sister to *Theraps*. Additionally, *V. heterospila* and *V. tuyrensis* were recovered outside of *Vieja* and *Herichthys* clades. Based on the results of this comprehensive study, we suggest a revised classification of *Vieja* species.

1. Introduction

In recent years, significant advances have been made into better understanding the systematics and taxonomy of New World cichlids (Teleostei: Cichlidae) (Chakrabarty, 2006a; Concheiro Pérez et al., 2007; Hulsey et al., 2004; López-Fernández et al., 2010; Smith et al., 2008); however, a thorough understanding of the generic status and systematic placement for some groups remains uncertain (Nelson, 2006). In fact, Miller et al. (2005) stated that generic treatment of Middle American cichlids is "both chaotic and frustrating," due to the high degree of variation in body morphology between and among groups. One such group is the Middle American cichlid genus *Vieja*.

Vieja represents a group of heroine cichlids that occur on both the Atlantic and Pacific slopes of North America from southern Mexico to Panama (Kullander, 2003). *Vieja*, like many other groups of cichlids, is a taxonomically and systematically difficult group, and a number of different taxonomic designations have been proposed for these fishes (Table 1), with many species belonging to the catch-all genus *Cichlasoma* at some time or another. The genus *Vieja* was proposed in 1969 by Fernández-Yépez and originally included four species. *Vieja panamensis* is the type species but was later recognized as a synonym of *V. maculicauda* (Kullander, 2003). Of the remaining three original species assigned to the genus, *Vieja temporale* is a synonym of *Hypselecara temporalis* (Kullander, 1986), *V. coryphaenoides* is a synonym of *Hypselecara coryphaenoides* (Kullander, 1986), and *V. biocellata* is a synonym of *Rocio octofasciata* (Schmitter-Soto, 2007).

Fernández-Yépez (1969) provided a number of characters to define the genus including the length of the pelvic fin, scale counts, and bifid (bicuspid), as opposed to conical teeth; however, there is considerable overlap between the characters used to define *Vieja*, and those used to define the remaining genera described in the same study: *Chuco*, *Copora*, and *Curraichthys* (Stawikowski and Werner, 1998). *Chuco* is the only other genus of Fernández-Yépez (1969) that includes currently recognized species of *Vieja*. The type species for *Chuco* is *Cichlasoma milleri*, now a synonym of *V. microphthalma* (Kullander, 2003). Fernández-Yépez (1969) assigned three additional species to the genus *Chuco*, including *Cichlasoma globossum*, *Cichlasoma manana*, and *Cichlasoma acutum*. *Cichlasoma globossum* and *C. manana* are synonyms of *Vieja maculicauda*

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Table 1
Summary of alternative generic level groupings for species of *Vieja*. Included studies gave alternative groupings for all recognized species.

Species	Original description	Werner and Stawikowski (1989)	Stawikowski and Werner (1998)		Kullander (2003)
		Paratheraps	*Chuco*	*Vieja*	*Vieja*
V. argentea	*Cichlasoma argentea*			X	X
V. bifasciata	*Heros bifasciatus*			X	X
V. breidohri	*Paratheraps breidohri*	X		X	X
V. fenestrata	*Chromis fenestrata*			X	X
V. godmanni	*Heros godmanni*		X		X
V. guttulata	*Heros guttulatus*			X	X
V. hartwegi	*Cichlasoma hartwegi*	X		X	X
V. heterospila	*Cichlasoma heterospilum*			X	X
V. intermedia	*Heros intermedius*		X		X
V. maculicauda	*Cichlasoma maculicauda*			X	X
V. melanura	*Heros melanurus*			X	X
V. microphthalma	*Heros microphthalmus*		X		X
V. regani	*Cichlasoma regani*			X	X
V. synspila	*Cichlasoma synspilum*			X	X
V. tuyrensis	*Cichlasoma tuyrense*			X	X
V. zonata	*Cichlasoma zonatum*			X	X

(Kullander, 2003), and *Cichlasoma acutum* is a synonym of *Amphilophus robertsoni* (Conkel, 1997).

In 1987, Werner and Stawikowski proposed a new genus, *Paratheraps*, which included *P. breidohri*, the type species, and the reassigned *Cichlasoma hartwegi* to *Paratheraps*. Werner and Stawikowski (1987) failed to designate a holotype for this new species and genus, and subsequently published an article correcting the error (Werner and Stawikowski, 1989). *Paratheraps* was later considered to be in synonymy with *Vieja* (Allgayer, 1991; Stawikowski and Werner, 1998), although Stawikowski and Werner (1998) continued to recognize the genus *Chuco* as a valid group. They placed three *Vieja* species into the genus *Chuco*: *V. microphthalma*, *V. intermedia*, and *V. godmanni* and noted that all three of these species have especially large front, middle teeth with rear-facing points, and a small number of lateral scales (32–35).

Kullander (2003) published the most recent checklist of Neotropical fishes and, without a re-diagnosis or formal taxonomic treatment, placed *Chuco* as a synonym of *Vieja*. *Paratheraps* continued to be considered in synonymy with *Vieja*, thereby recognizing 16 species in the genus *Vieja*. Two additional species, *Herichthys pearsei* and '*Cichlasoma*' *ufermanni*, have been recognized as members of *Vieja* (Allgayer, 2002; Miller et al., 2005) although they are not currently (Eschmeyer, 2010; Kullander, 2003).

Recent molecular phylogenetic studies of heroine cichlids (Concheiro Pérez et al., 2007; Hulsey et al., 2004; López-Fernández et al., 2010) have found the genus *Vieja* to be paraphyletic and therefore used alternative taxonomic designations for species within *Vieja*. While we acknowledge that relationships among and within *Vieja* were not the focus of these studies, it is clear that the taxonomic sampling of *Vieja* used for those studies did not allow for a thorough assessment of the genus and subsequent altered generic designations. This is critical, as previous studies have noted the importance of increased taxon sampling on reducing phylogenetic error (Hillis et al., 2003; Rican et al., 2008; Zwickl and Hillis, 2002), which in turn, could result in inaccurate taxonomic changes that may occur as a result of an incomplete phylogeny. Smith et al. (2008) and López-Fernández et al. (2010) specifically note the importance of complete taxon sampling within genera such as *Vieja*.

Two main issues have confounded taxonomy of the genus *Vieja*. First and foremost, the genus was never properly diagnosed such that a set of characters could clearly differentiate *Vieja* from other New World cichlid genera. The original description of the genus is marginal at best, with only a short paragraph to serve as the generic diagnosis. Also, as previously mentioned, many of the characters used by Fernández-Yépez (1969) to diagnose *Vieja* are not exclusive to these fishes. To that extent, the entire genus has never been studied as a whole and with this comes the second issue. Many authors have used a variety of generic names for *Vieja* species without sufficient examination of the entire group (i.e. utilization of all species). While it has been acknowledged for some time that the genus is paraphyletic as currently recognized, arbitrary use of invalid names is counterproductive. For example, many researchers and aquarists have considered a number of *Vieja* species to be in the genus *Paratheraps* (Artigas Azas, 2008; Concheiro Pérez et al., 2007; Hulsey et al., 2004). We find only two *Vieja* species, *V. breidohri* and *V. hartwegi*, to have ever formally been assigned to this genus (Werner and Stawikowski, 1989). Species were assigned to the genus without determining if those species possessed the traits proposed to diagnose *Paratheraps*. Therefore, at present one should not use *Paratheraps* as the generic designation for any additional species. The most recently proposed generic revision of *Vieja* was that of López-Fernández et al. (2010). This study found species formerly assigned to *Chuco* to be within a *Theraps* clade, and *Paraneetroplus bulleri* to be nested well within a clade consisting of the remaining *Vieja* species used in the study. The close relationship of *Vieja* spp. with *P. bulleri* has been shown (Chakrabarty, 2006b; Hulsey et al., 2006, 2004); however, there was little resolution among *Vieja* spp. (Chakrabarty, 2006b).

After nearly 40 years of study, it is clear that the taxonomic status of *Vieja* and its inclusive species remains uncertain. Previous molecular systematic studies (Chakrabarty, 2006a; Concheiro Pérez et al., 2007; Hulsey et al., 2004; López-Fernández et al., 2010; Smith et al., 2008) included a subset of the species that historically have been included in *Vieja*, but were not specifically addressing phylogenetic relationships among species in the genus. Therefore our objective was to utilize available mitochondrial encoded cytochrome *b* and nuclear S7-1 intron sequence data and augment it with additional populations and species to conduct a comprehensive systematic study inclusive of all sixteen species of *Vieja*, to specifically assess the monophyly of the genus and relationships among its species. Complete taxon sampling of the genus renders our study novel and we feel this is a necessity for revision of genera and their respective species. We utilized Kullander (2003) as the most recent taxonomic summary of all recognized species of *Vieja* and *a priori* accept this as the currently valid taxonomy for this genus. Generic names for other herichthyines follow López-Fernández et al. (2010), the most completely sampled Neotropical cichlid phylogeny to date.