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Taxonomy and systematics of the herichthyins (Cichlidae: Tribe Heroini), with the description of eight new Middle American Genera

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Abstract

In recent years great strides have been made for improving our understanding of the evolutionary relationships among neotropical cichlids, particularly within the clade Heroini and its crown clade the herichthyins. Most phylogenetic studies have largely converged on congruent topologies for relationships among species and major lineages within the herichthyins. One major aspect missing from previous studies of these cichlids is a formal taxonomic revision, including the redefining of genera. Based on analysis of 52 species and three mitochondrial and two nuclear loci, we generate a Bayesian phylogeny for the herichthyin cichlids, and formally revise the taxonomy for genera within this clade using morphological features. Eight new genera are recognized and a key to all 16 genera of herichthyin cichlids is also presented.

Key words: cichlid, revision, Mexico, Central America, morphology

Resúmen

Grandes pasos se han dado en años recientes en la mejora de nuestro conocimiento de las relaciones evolutivas entre ciclidos Neotropicales, particularmente dentro del clado Heroini. En el clado corona de Heroini están los herichthyins. Los estudios filogenéticos más recientes, han coincidido ampliamente con topologías congruentes para definir las relaciones entre especies y linajes mayores en este clado. La falta de una revisión taxonómica formal de estos ciclidos, es un gran vacío que han dejado estudios anteriores, incluyendo la redefinición de géneros. Basados en un muestreo taxonómico completo y un set de datos molecular casi-completo, nosotros generamos una filogenia para el grupo de ciclidos conocido como los herichthyins, y revisamos formalmente la taxonomía de cada género en este clado usando caracteres morfológicos. Una clave para los 16 géneros de ciclidos herichthyinos es también presentada.

Introduction

Progressive strides have been made in recent years to understand the evolutionary relationships among neotropical cichlids (López-Fernández *et al.* 2010; Říčan *et al*. 2013; Matamoros *et al.* 2015). This is particularly true for the tribe Heroini (subfamily Cichlinae), the second most diverse clade of neotropical cichlids (De la Maza-Benignos *et al*. 2014) that makes up the vast majority of cichlids in Middle America (Mexico, Central America, and the Greater Antilles). Numerous studies, regardless of differences in sampling of genetic markers or slight differences in taxonomic sampling, have recovered largely congruent relationships across some portions of the heroin tree.

The clade of herichthyins (*sensu* Říčan *et al*. 2013) includes some 45 species of heroin cichlids, many of which

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are restricted to northern Middle America (e.g., Mexico and Guatemala). López-Fernández *et al*. (2010) did not include the genera *Herotilapia* and *Tomocichla* in the herichthyins, recognizing them as tomocichlins. Members of the genus *Astatheros* (*sensu* López-Fernández *et al*. 2013) were also recognized as astatheroins, separate from the herichthyins. As these were only clade-based names (i.e., lacking taxonomic definitions/treatments), how one chooses which larger internal clade to refer to the herichthyins is subjective.

Kullander (1983) proposed '*Cichlasoma' incertae sedis* as a placeholder to contain cichlid species of undetermined generic status when he restricted the former catchall genus *Cichlasoma* to just a handful of South American species. Cichlid taxonomists have not always preferred this practice (e.g., Miller *et al*. 2005); however, this taxonomic scenario has at least facilitated the inclusion of these problematic taxa into large-scale phylogenetic studies in an attempt to determine their phylogenetic affinities (e.g., López-Fernández *et al.* 2010; Říčan *et al*. 2013; Matamoros *et al.* 2015). Depending on the authors some of these species, including '*Cichlasoma' grammodes* and '*Cichlasoma*' *festae*, have remained in either the catchall genus *Cichlasoma*, or this placeholder genus '*Cichlasoma'* since their description.

Despite the fact that numerous recent phylogenetic hypotheses for neotropical cichlids have converged on similar topologies (López-Fernández *et al.* 2010; Říčan *et al*. 2013; Matamoros *et al.* 2015), a formal taxonomic revision of the genera within this large diverse group is lacking. Different phylogenetic studies of Cichlinae (neotropical members of Cichlidae) use various generic-level designations for species, such as the use of '*Heros'* instead of '*Cichlasoma'* in Říčan *et al*. (2013) and other studies. All recent large-scale generic-level taxonomic changes proposed have only been topologically-based, thus renaming clades based on the oldest available generic name within that clade (McMahan *et al*. 2010, López-Fernández *et al*. 2010). The purpose of this study is to generate a phylogeny of the herichthyin cichlids with as complete a taxonomic and molecular loci sampling scheme as possible, and to revise the generic-level taxonomy of these cichlids accordingly based on unique combinations of diagnostic features.

Material and methods

A great deal of DNA sequence data exists and is available based on numerous previous phylogenetic studies of neotropical cichlids. Data were compiled from various publications (Chakrabarty 2006; Concheiro-Perez *et al*. 2006; López-Fernández *et al*. 2010; McMahan *et al*. 2010; Říčan *et al*. 2013) and assembled into a dataset consisting of five loci (three mitochondrial genes: cytochrome *b*, 16S, and ND4; two nuclear genes: S7 intron 1 and Rag2). Given that nearly all recent phylogenetic studies of herichthyins converge on similar or congruent topologies, we aimed to fill in as many gaps of missing data (molecular and species sampling) in the matrix as possible, and use this as a framework for a formal taxonomic revision of herichthyin cichlids (only species with questionable identifications were excluded; dataset 82% complete). This taxonomic dataset is identical to that of Matamoros *et al*. (2015) with the addition of three species. The total number of species totals 52.

The five loci used in our analysis are the same set used in López-Fernández *et al*. (2010), which was one of the more complete taxonomic datasets (based on taxonomic sampling and molecular coverage) for neotropical cichlids. Past work has shown that these molecular markers are excellent for determining species-level relationships, and the nuclear loci in particular are well suited for providing apomorphies at higher levels (López-Fernández *et al*. 2010; McMahan *et al*. 2010; Matamoros *et al*. 2015). All available sequence data for a given species on GenBank were compared to assess consistent species identification of sequences in this data repository. Closely related heroin species were used as outgroups (Table 1).

Molecular data were concatenated and phylogenetically analyzed using Bayesian Inference methods following Matamoros *et al*. (2015). For the Bayesian analysis, data were partitioned by gene and a model of evolution selected for each partition in JModelTest (Posada 2008) using the Akaike Information Criterion (AIC) (Posada and Buckley 2004). Estimations of posterior probabilities were calculated using a Metropolis-coupled Markov chain Monte Carlo in MrBayes v.3 (Ronquist and Huelsenbeck 2003). Four runs were performed for 7,000,000 generations with trees sampled every 100 generations. Stationarity was assessed in Tracer v.1.6 (Rambaut *et al.* 2014). Post burn-in trees (65,000) were used to calculate posterior probabilities. Results from four independent runs were also compared to provide corroboration among topologies and posterior probabilities. A 50% majority rule tree was produced from post burn-in trees.

TABLE 1. GenBank accession numbers for individuals used in phylogenetic analyses.

Species	ND4	cyt*b*	16S	Rag2	S7-1
Amatitlania nigrofasciata	GU737054	AY843376	GU737208	GU736870	DQ119254
Archocentrus multispinosus	GU737079	AF009942	GU737233	GU736893	GU736788
Astatheros longimanus	GU737057	GU736983	GU737211	GU736873	GU736774
Astatheros macracanthus	GU737076	DQ990695	GU737230	GU736890	GU736785
'Cichlasoma' atromaculatum	-	AY843347	-	-	-
'Cichlasoma' festae	GU737031	AY843351	DQ119187	GU736847	EF433008
'Cichlasoma' grammodes	GU737068	DQ990718	GU737222	GU736883	EF433016
'Cichlasoma' ornatum	-	HQ197729	-	-	-
'Cichlasoma' salvini	GU737065	AY050619	GU737219	GU736880	DQ119258
'Cichlasoma' sieboldii	-	AF009937	DQ119179	-	DQ119266
'Cichlasoma' tuyrense	-	AY84333	DQ119181	-	DQ119268
Herichthys carpintis	GU737071	AY323999	GU737225	GU736886	GU736780
Herichthys cyanoguttatus	GU737072	AY323987	GU737226	GU736887	GU736781
Herichthys deppii	-	DQ990715	GU817217	-	GU946320
Herichthys minckleyi	JN222979	AY323996	-	-	DQ836821
Herichthys tamasopoensis	GU737075	AY324001	GU737229	GU736889	GU736784
Hypsophrys nematopus	GU737081	AF009928	GU737235	GU736895	GU736789
Nandopsis tetracanthus	GU737087	AY998669	GU737241	GU736901	DQ119270
Nosferatu bartoni	GU737074	DQ990721	GU737228	-	GU736783
Nosferatu labridens	GU737073	AY323993	GU737227	GU736888	GU736782
Nosferatu pantostictus	GU737077	AY323988	GU737231	GU736891	GU736786
Nosferatu steindachneri	GU737078	AY324013	GU737232	GU736892	GU736787
Paraneetroplus argenteus	-	DQ494389	GU817232	-	HQ424203
Paraneetroplus bifasciatus	GU737101	GU736989	GU737254	GU736914	GU736802
Paraneetroplus breidohri	-	AY050626	-	-	EF433014
Paraneetroplus bulleri	-	AY324004	-	-	EU620423
Paraneetroplus fenestratus	-	AY324002	-	-	-
Paraneetroplus guttulatus	GU737103	AY324025	GU737258	GU736918	GU736806
Paraneetroplus hartwegi	-	HM193441	-	-	HQ424207
Paraneetroplus maculicauda	GU737105	GU736991	GU737260	GU736919	GU736807
Paraneetroplus melanurus	GU737106	AY843420	GU737261	GU736920	GU736808
Paraneetroplus regani	-	DQ990735	GU817237	-	EF433013
Paraneetroplus zonatus	-	FJ668642	-	-	HQ424211
Rocio octofasciata	GU737062	AY843410	GU737216	GU736877	GU736777
Theraps bocourti	GU737061	GU736984	GU737215	GU736876	GU736776
Theraps coeruleus	-	JX437636	-	-	-
Theraps godmanni	-	AY843428	GU737255	GU736915	GU736803
Theraps heterospilus	-	HQ424213	GU817235	-	HQ424208
Theraps intermedius	GU737102	GU736990	GU737257	GU736917	GU736805
Theraps irregularis	GU737098	DQ494383	GU737251	GU736911	GU736799
Theraps lentiginosus	GU737099	AY843409	GU737252	GU736912	GU736800
Theraps microphthalmus	-	AY843431	-	-	HQ424210

.....continued on the next page

TABLE 1. (Continued)

Species	ND4	cyt*b*	16S	Rag2	S7-1
Theraps nourissati	GU737060	EF436465	GU737214	GU736875	EF433048
Theraps pearsei	-	DQ494388	-	-	DQ836823
Theraps ufermanni	GU737107	GU736992	GU737262	GU736921	-
Thorichthys affinis	GU737094	GU736987	GU737248	GU736907	GU736796
Thorichthys aureus	GU737089	U88859	GU737243	GU736903	DQ119265
Thorichthys callolepis	-	AY324008	-	-	GU946317
Thorichthys maculipinnis	GU737092	AY324011	GU737246	GU736905	GU736794
Thorichthys helleri	GU737093	AY324022	GU737247	GU736906	GU736795
Thorichthys meeki	GU737091	AY843426	GU737245	GU736904	EF433025
Thorichthys pasionis	GU737095	DQ494385	GU737249	GU736908	GU736797
Thorichthys socolofi	-	HM193443	-	GU736909	-
Tomocichla asfraci	GU737096	GU736988	AY662735	GU736909	GU736798
Tomocichla tuba	GU737097	AF009941	GU737250	GU736910	-

Morphological characters exist in several published studies that are quite informative for defining genera as recovered and recognized in the present study. Based on a qualitative evaluation of morphological characters from published studies (Greenfield and Thomerson 1997; Bussing 1998; Miller *et al*. 2005; Chakrabarty 2007), in combination with examination of specimens for corroboration and the search for additional characters, currently recognized genera were rediagnosed based on their new combinations of inclusive species, and new genera were proposed where sufficient morphological differentiation exists to separate species from those in their sister group.

Results

Phylogenetic hypotheses resulting from Bayesian analyses corroborate those of Matamoros *et al*. (2015) and largely that of Říčan *et al*. (2013) (Fig. 1). *Paraneetroplus* (*sensu* López-Fernández *et al*. 2010) was recovered as monophyletic and the sister group to a clade comprising *Herichthys* + *Nosferatu*. *Theraps* was recovered as the sister group of a clade comprising *Paraneetroplus* + (*Herichthys* + *Nosferatu*). A clade consisting only of '*Cichlasoma' grammodes* is the sister group to all aforementioned genera, and *Thorichthys* is the sister clade to all of the above. The South American cichlids '*Cichlasoma' festae*, '*C*.' *ornatum*, and '*C*.' *atromaculatum* are sister to a large clade comprising *Thorichthys* + ('*C*.' *grammodes* + (*Theraps* + (*Paraneetroplus* + (*Herichthys* + *Nosferatu*)))). A clade consisting of *Tomocichla tuba*, *T. asfraci*, and *Archocentrus multispinosus* was recovered at the base of the herichthyins.

Astatheros was recovered as part of a clade that also includes *Rocio*. This clade is sister to the clade of herichthyins. Říčan *et al*. (2013) included this clade as part of the herichthyins; however, we do not recognize *Astatheros* as part of the herichthyins, instead we follow López-Fernández *et al*. (2010) in considering taxa in this clade (*Astatheros* and *Rocio*) as astatheroins. Thus these species are not treated here.

Based on the relationships recovered in this phylogeny (Fig. 1), which are congruent with that of López-Fernández *et al.* (2010), Říčan *et al*. (2013), and Fig. S1 in Matamoros *et al*. (2015), we recognize 15 genera within the herichthyins. Available generic names are rediagnosed and new genera are described where appropriate. The combination of characters given for each genus differentiates it from all other herichthyin genera.

Systematic accounts

Taxonomic revision of herichthyins

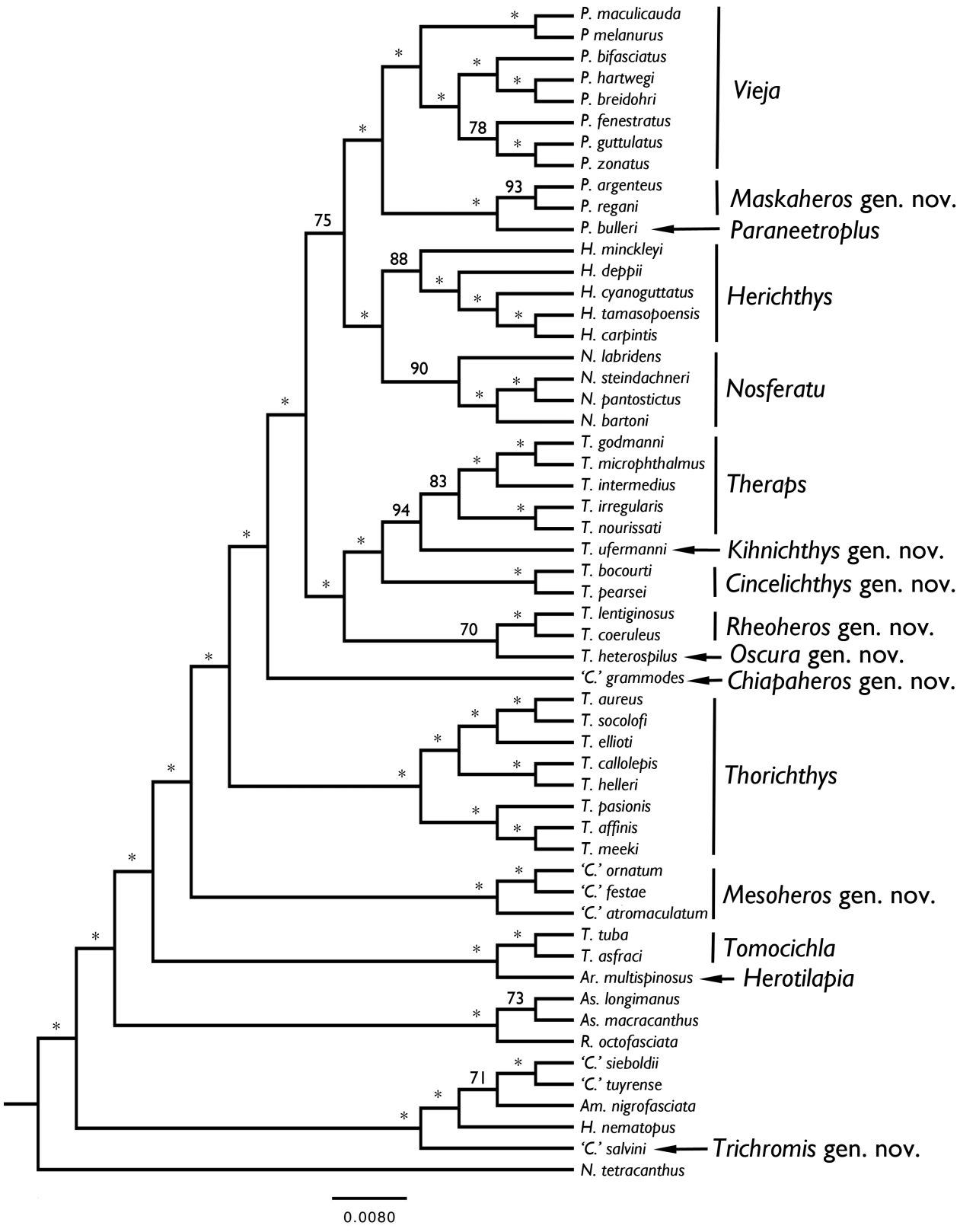

FIGURE 1. Phylogeny of the herichthyins based on Bayesian Inference. * indicates Bayesian posterior probabilities ≥ 95.

Genus *Vieja* Fernández-Yépez 1969
(Fig. 2)

Inclusive species. *V. maculicauda* (type species), *V. bifasciata*, *V. breidohri*, *V. fenestrata*, *V. guttulata*, *V. hartwegi*, *V. melanura*, *V. zonata*

Diagnosis. *Vieja* is diagnosed by the presence of a large round blotch filling the majority of the caudal peduncle. In addition, the lower lateral line runs through the center of this blotch, which in most species (except *V. maculicauda*) continues anteriorly to form a thick, broad dark line running either up to one-half length of the body (as in *V. melanura*) or the entire length of body directly below the lower lateral line (as in all other members of the genus). Members of this genus are relatively elongate to moderately deep-bodied. The presence of the large dark blotch filling most of the caudal peduncle differentiates this genus from other herichthyins, with the exception of *O. heterospila* and *K. ufermanni*; however, *O. heterospila* can be differentiated from *Vieja* based on the absence of a lateral stripe longitudinally down the body and the presence of dark- or black-colored scales and broad bars throughout lateral portions of the body. *Vieja* can be differentiated from *K. ufermanni* by the presence of conical or bicuspid teeth, as opposed to spatulate in *K. ufermanni*.

FIGURE 2. *Vieja maculicauda*, UMMZ 195944, 145.12mm SL.

Distribution. Pacific slope of Middle America from Río Tequistlán in Mexico south to Lago Coatepeque in El Salvador; Atlantic slope of Middle America from Río Chachalacas in Mexico to Río Chagres in Panama. Only *V. maculicauda* extends south past northern Middle America.

Comments. Several studies have all shown a lack of monophyly for the genus *Vieja* as previously recognized (*sensu* Kullander 2003). McMahan *et al*. (2010) specifically aimed to study this genus as recognized at that time and recovered a polyphyletic *Vieja* based on complete taxonomic sampling of all species ever proposed to be in the genus. Species of *Vieja* have previously been considered as members of *Paraneetroplus*, given that the type species of this genus (*P. bulleri*) has consistently been recovered nested within the larger *Vieja* clade and is the older available name. However, substantial morphological differences exist between members of *Paraneetroplus sensu stricto* and *Vieja*. Given this morphological differentiation and the consensus of phylogenetic relationships from several independent studies, we resurrect and rediagnose *Vieja* and restrict *Paraneetroplus* to three riverine species in the Atlantic slope of Mexico.

Material examined. *V. bifasciata*, UMMZ 184634 [n=2, Mexico: Río Grijalva], UMMZ 143879 [n=5, Guatemala: Río San Pedro]; *V. breidohri*, UMMZ 193906 [n=20, Guatemala: Río Grijalva]; *V. fenestrata*, UMMZ 97668 [n=5, Mexico: Río Papaloapan], UMMZ 178578 [n=15, Mexico: Laguna Catemaco], UMMZ 209687 [n=10, Mexico: Río San Carlos]; *V. hartwegi*, UMMZ 159275 [n=1 (Paratype), Mexico: Río Grijalva], 181813

[n=2, Mexico: Río Grande de Chiapa], UMMZ 186388 [n=1 (Paratype), Mexico: Río Grijalva], UMMZ 186407 [n=10 (Paratypes), Mexico: Río Grijalva]; *V. guttulata*, UMMZ 178548 [n=11, Mexico: Río Coatzacoalcos], UMMZ 184759 [n=38, Mexico: Río Coatzacoalcos], UMMZ 188082 [n=7, Guatemala: Río Nahualate], UMMZ 190540 [n=5, Guatemala: Río Grande de Pasaco]; *V. maculicauda*, BMNH 1864.1.26.56-69 [n=4 (Syntypes), Guatemala: Lago Izabal], UMMZ 73279 [n=5, Panama: Gatun Lake], UMMZ 178853 [n=15, Guatemala: Lago Izabal]; *V. melanura*, BMNH 1864.1.26.82 [n=1 (Lectotype), Guatemala: Lago Peten], FMNH 109086 [n=9, Guatemala: Río San Pedro], LSUMZ 16365[n=8, Guatemala: Río La Pasion]; *V. zonata*, FMNH 3776 [n=1 (Holotype), Mexico: Río Niltepec], SLU 5014 [n=3, Mexico: Río Tehuantepec], SLU 5010 [n=5, Mexico: Río Almoloya], UMMZ 168915 [n=4, Mexico: Río Cacaluta].

Genus *Maskaheros* gen. nov. McMahan and Piller 2015

(Fig. 3 and 4)

Inclusive species. *M. argenteus* (type species by designation), *M. regani*

Diagnosis. Species of *Maskaheros* gen. nov. are diagnosed by the presence of small dark, irregularly placed (i.e., not in a consistent pattern of rows) spots along the entirety of the body (often much fainter in *M. regani*), as well as two dark and broad interorbital bars on the head. In addition, these are moderately deep-bodied cichlids (less deep-bodied in overall shape as juveniles), with two to three dark blotches on the body along the upper lateral line. A moderately sized to large dark caudal blotch is present in center of the caudal peduncle but not filling the majority of the caudal peduncle as in *Vieja*. This spot on the caudal peduncle may be smaller in juveniles. Dorsal, caudal, and anal fins are covered in small spots. Teeth are conical and the upper lip hangs slightly over the lower lip. The caudal fin is moderately rounded in shape.

Distribution. Atlantic slope of Mexico and Guatemala in the Río Coatzacoalcos and Río Usumacinta drainages.

Etymology. Gender masculine. The generic epithet *Maskaheros* is derived from the Spanish word “máska” a shortened form of mascara meaning mask, in reference to the mask-like appearance of the broad, dark interorbital bars that diagnose this genus, and “-heros” in reference to the generic name formerly used for many neotropical cichlid species.

FIGURE 3. *Maskaheros argenteus*, UMMZ 143975, 107.86mm SL.

Comments. Recent phylogenetic studies have all recovered a close relationship between *Maskaheros* and *Vieja*/*Paraneetroplus*. In the present phylogeny, *Paraneetroplus* is the sister group to *Maskaheros*, as also recovered in Matamoros *et al*. (2015). The deep body shape, head markings, and caudal spot (see Diagnosis) separate this genus from *Vieja* and *Paraneetroplus*.

Material examined. *M. argenteus*; UMMZ 143975 [n=1, Guatemala: Río San Pedro], UMMZ 143981 [n=5, Guatemala: Río La Pasion], UMMZ 208263 [n=1, Mexico: Río Usumacinta tributary]; *M. regani*; UMMZ 184757 [n=5, Mexico: Río Coatzacoalcos], SLU 5009 [n=1, Río Coatzacoalcos].

FIGURE 4. Close-up of head of *M. argenteus,* showing two broad interorbital bars (mask-like appearance that diagnoses the genus), UMMZ 143975, 107.86mm SL.

Genus *Paraneetroplus* Regan 1905
(Fig. 5)

Inclusive species. *P. bulleri* (type species), *P. gibbiceps*, *P. nebuliferus*

Diagnosis. *Paraneetroplus* is diagnosed by having an elongate body with a narrow, sub-terminal mouth and a caudal peduncle that is longer than it is deep. In addition, the jaw teeth are enlarged anteriorly, and anterior teeth

are conical or spatulate in shape. The lower jaw teeth are oriented more anteriorly as opposed to dorsally in other herichthyin genera. Five or six lateral blotches are present along the sides of the body between the base of the pectoral fin and the posterior end of the dorsal fin; these blotches often appear as a moderately complete longitudinal stripe (as in *P. nebuliferus*). A medium-sized, dorso-ventrally elongate, dark spot is present at the base and center of the caudal peduncle with the lower lateral line continuing through the center of the spot. The caudal fin is truncate or slightly emarginate.

FIGURE 5. *Paraneetroplus bulleri*, FMNH 63937, 183.22mm SL.

Distribution. Atlantic slope of Mexico from the Río Papaloapan to Río Grijalva drainages.

Comments. McMahan *et al*. (2010) recovered *P. nebuliferus* outside of *Paraneetroplus*; however, as pointed out by Paepke *et al*. (2014), this was based on a misidentification of a GenBank sequence of '*Cichlasoma' sieboldii*. Říčan *et al*. (2013) included single samples of both *P. nebuliferus* and *P. omonti* in their phylogeny; however, inclusion of these sole sequences in our dataset was problematic with low support for their phylogenetic positions. Voucher specimens are not reported for these tissue samples, and no other sequence data is available from wild-caught or museum-vouchered specimens of these two species. Given the problematic nature of including these individuals in the present study, they have been excluded. However, morphology of *P. nebuliferus* allies this species with *Paraneetroplus* as currently recognized. Based on examination of the poorly preserved types of *P. omonti*, Miller *et al*. (2005) regarded this species as a synonym of *P. gibbiceps*. Without further evidence or voucher specimens of recently collected individuals from the wild, we follow Miller *et al*. (2005) and do not include the sole *P. omonti* individual from Říčan *et al*. (2013) in our phylogeny, nor do we recognize this species as valid. Several studies have recovered the type species of *Paraneetroplus*, *P. bulleri*, nested within *Vieja*, prompting the naming of the entire mixed group as *Paraneetroplus*, given that *Paraneetroplus* should be recognized as the senior synonym of *Vieja* in this case. However, given the phylogenetic relationships recovered in this study, as well as the morphological distinctiveness of this genus, we rediagnose *Paraneetroplus*, excluding species of *Vieja* and *Maskaheros*.

Material examined. *P. bulleri*; BMNH 1890.10.10.94 [n=1 (Holotype), Mexico: Río de Sarabia], FMNH 63937 [n=2, Mexico: Río Papaloapan], UMMZ 208263 [n=1, Mexico: Río Grijalva-Usumacinta tributary]; *P. nebuliferus*; SLU 8619 [n=3, Mexico: Río Coatzacoalcos].

Genus *Herichthys* Baird and Girard 1854

(Fig. 6)

Inclusive species. *H. cyanoguttatus* (type species), *H. carpintis*, *H. deppii*, *H. minckleyi*, *H. tamasopoensis*, *H. tepehua*, *H. teporatus*.

Diagnosis. *Herichthys* is diagnosed by six to seven vertical bars (often at the posterior of the body) with dark blotches below the upper lateral line. Breeding coloration includes a darkened color ventrally on lateral portions of the body with light- or gray-colored markings on the dorsum. The anteriormost teeth in the upper jaw are spatulate, chisel-like, or bicuspid.

Distribution. Rivers of the Atlantic slope of Mexico and the Río Grande drainage of the United States (Texas) and Mexico.

FIGURE 6. *Herichthys cyanoguttatus*, FMNH 4435, 114.41mm SL.

Comments. Our diagnostic characteristics for *Herichthys* follow De la Maza-Beningnos *et al.* (2015) based on their recent revision of the group. *Herichthys* (before it was divided into *Herichthys* and *Nosferatu*) was largely diagnosed by the shared color pattern of bars and/or blotches along the lateral sides of the body, and a breeding coloration consisting of a dark ventral portion and a lighter dorsal portion of the body (Oldfield *et al*. 2015). As recognized here, following De la Maza-Beningnos *et al*. (2015), the traditional breeding coloration characters delineate these clades, but with slight differences in the extent of coloration between *Herichthys* and *Nosferatu*. Our molecular analysis supports the monophyly of *Herichthys* and its sister relationship with *Nosferatu*. At the species level within *Herichthys*, none of the species in the genus are recovered as monophyletic in De la Maza-Benignos *et al*. (2015). Status and validity of the species within this genus are in need of further study.

Material examined. *H. carpintis*, UMMZ 234903 [n=10, Mexico: Río Paunuco]; *H. cyanoguttata*, UMMZ 92313 [n=4, Mexico: Arroyo Marmolejo], FMNH 4435 [n=9, Mexico: Río Camacho]; *H. minckleyi*, UMMZ 130395 [n=15 (Paratypes), Mexico: Cuatro Cienegas], UMMZ 211734 [n=15, Mexico: Cuatro Cienegas]; *H. tamasopoensis*, UMMZ 193513 [n=15, Mexico: Río Tamasopo], UMMZ 196699 [n=15, Mexico: Río Panuco].

Genus *Nosferatu* De la Maza-Benignos *et al*. 2015

(Fig. 7)

Inclusive species. *N. pame* (type species), *N. bartoni*, *N. labridens*, *N. molango*, *N. pantostictus*, *N. pratinus*, *N. steindachneri*.

Diagnosis. Teeth in anteriormost portion of upper jaw conical and unicuspid, relatively elongate body. Lateral markings variable and irregular (stripe or blotches). Breeding coloration dark ventrally (similar to *Herichthys*), but often not to the extent of members of *Herichthys* in covering most of the body.

Distribution. Rivers of the Atlantic slope of Mexico.

Comments. De la Maza-Benignos *et al*. (2015), in a revision of the *Herichthys,* described the genus *Nosferatu*. Herein we recover *Nosferatu* as monophyletic; however, we lack sequence data for the new species *N. tepehua* described in De la Maza-Benignos *et al*. (2015). As with *Herichthys*, many of the species of *Nosferatu* were not recovered as monophyletic in the phylogenetic analysis of mitochondrial sequences by De la Maza-Benignos *et al*. (2015). Species limits and diversity, as well as interspecific relationships, within *Nosferatu* remain unresolved.

Material examined. *N. bartoni*, UMMZ 172193 [n=15, Mexico: Río Verde], UMMZ 202972 [n=15, Mexico: Río Panuco]; *N. labridens*, UMMZ 203203 [n=10, Mexico: Río Tamesi], UMMZ 203205 [n=2, Mexico: Río

Tamesi]; *N. pantostictus*, UMMZ 170951 [n=8, Mexico: Río Tamesi], UMMZ 209431 [n=2, Mexico: Río Tamesi]; *N. steindachneri*, FMNH 62682 [n=43, Mexico: Río Sabinas], UMMZ 193514 [n=22, Mexico: Río Tamasopo].

FIGURE 7. *Nosferatu steindachneri*, FMNH 62682, 99.71mm SL.

Genus *Theraps* Günther 1862
(Fig. 8)

Inclusive species. *T. irregularis* (type species), *T. godmanni*, *T. intermedius*, *T. microphthalmus*, *T. nourissati*.

Diagnosis. Species of the genus *Theraps* are all elongate (*T. irregularis*) to moderately elongate (other species) cichlids occurring in lotic riverine systems. All species possess bodies that are longer than deep, versus deep-bodied as in *Vieja* and *Maskaheros*. The mouth is small and subterminal, with the upper jaw extending over the lower jaw (more so in *T. irregularis* than in congeners). Spots are present on the dorsal, anal, and caudal fins. This genus is most similar to *Paraneetroplus* and *Rheoheros* gen. nov. Species of *Paraneetroplus* possess lower jaw teeth oriented anteriorly, versus dorsally in *Theraps*. Species of *Rheoheros* gen. nov. possess a freckled appearance across the body, versus the absence of this characteristic in *Theraps*.

Distribution. Atlantic slope rivers of Mexico, Belize, and Guatemala, to lowland tributaries of the Río Motagua drainage in Honduras (only *T. microphthalmus*).

Comments. *Theraps* has always included riverine, elongate to moderately elongate cichlids (Allgayer 1989; Günther 1862). Phylogenetic relationships recovered in the present study, as well as the corroboration of Matamoros *et al*. (2015), support this traditional habitat association, but with some restrictions on the inclusion of other riverine species in this genus (e.g., species of *Rheoheros*). Thus, this riverine ecology and elongate body shape have evolved more than once within the herichthyin cichlids. The Honduran endemic '*C*.' *wesseli* was described as a member of *Theraps* but is not recovered as part of this clade or genus in any phylogenetic study to date. We continue to recognize the species as a member of '*Cichlasoma*' (*incertae sedis*) pending a systematic and taxonomic treatment of this species.

Material examined. *T. godmanni*, BMNH 1864.1.26.49-50 [n=2 (Syntypes), Guatemala: Río Cahabon], UMMZ 146113 [n=22, Guatemala: Río Cahabon]; *T. intermedium*, UMMZ 143744 [n=12, Guatemala: Río La Pasion], UMMZ 161764 [n=24, Mexico: Río Usumacinta]; *T. microphthalmus*, UMMZ 179910 [n=5, Guatemala: Río Motagua], UMMZ 190569 [n=15, Guatemala: Río Motagua], LSUMZ 15614 [n=8, Honduras: Río Motagua]; *T. nourissati*, MNHN 1989-0583 [n=1 (Holotype), Mexico: Chiapas], MNHN 1989-0583 [n=2 (Paratypes), Mexico: Chiapas].

FIGURE 8. *Theraps irregularis*, LSUMZ 16437, 102 mm SL.

Genus *Kihnichthys* gen. nov., McMahan and Matamoros 2015
(Fig. 9 and 10)

Inclusive species. *K. ufermanni* (type by monotypy)

Diagnosis. *Kihnichthys* is diagnosed by the presence of a dark caudal blotch filling the center, posterior portion of the caudal peduncle, as well as the presence of spatulate or chisel-like teeth in the anterior portions of the upper and lower jaws. Species of this genus possess a deep skull and large head with a small mouth. The lower jaw extends slightly beyond the upper jaw. The combination of these characters differentiates this genus from all other herichthyin genera. *Vieja* possesses a similar but larger caudal blotch, but also has conical or bicuspid (versus spatulate) teeth. *Cincelichthys* gen. nov. possesses spatulate teeth but has a small spot on the caudal peduncle (versus a larger spot in *Kihnichthys*).

Etymology. Gender masculine. The genus is named in honor of Herman A. Kihn, who has spent a lifetime studying the fishes of Guatemala. His work has made invaluable contributions to our understanding of the diversity and distributions of fishes in Guatemala.

Comments. Allgayer (2002) placed this enigmatic cichlid in *Vieja* in its original description. Few specimens exist in museum collections for this species, and most material comes from the Río La Pasion system, a tributary to the Río Usumacinta in Peten, Guatemala. Little is known about this cichlid and more comparative material and natural history information are certainly needed.

Material examined. MNHN 2002-1090 [n=1 (Holotype), Guatemala: Río Pucté], MNHN 2002-1091 [n=1 (Paratype), Guatemala: Río Pucté], MNHN 2002-1092 [n=1 (Paratype), Guatemala: Río Pucté].

FIGURE 9. *Kihnichthys ufermanni*, MNHN 2002-1090 (Holotype), 125mm SL.

FIGURE 10. Spatulate or chisel-like teeth of *K. ufermanni*, MNHN 2002-1090 (Holotype), 125mm SL.

Genus *Cincelichthys* gen. nov., McMahan and Piller 2015
(Fig. 11)

Inclusive species. *C. bocourti* (type species by designation), *C. pearsei*

Diagnosis. *Cincelichthys* possess spatulate, chisel-like teeth, and species are deep-bodied and round or oval in overall body shape. Lateral markings appear along the body as wide, irregular bands dorsally to ventrally. Species possess solid black scales dispersed throughout the lateral sides of the body. White- or faint-colored spots are present on the medial and distal portions of the dorsal, caudal, and anal fins. Species possess a small mouth, with the lower jaw extending slightly beyond the upper jaw. The mouth is slightly upturned. A small black spot is present at the center and base of the caudal peduncle. The chisel-like teeth distinguish this genus from all others within the herichthyins except *Kihnichthys*, which also possesses chisel-like teeth, but exhibits a larger blotch filling the caudal peduncle, versus the small spot characteristic of *Cincelichthys*.

Distribution. Atlantic slope of Mexico, Belize, and Guatemala from the Río Grijalva-Usumacinta drainage to Lago Izabal (Río Dulce drainage basin).

FIGURE 11. *Cincelichthys bocourti*, LSUMZ 16455, 152.53 mm SL.

Etymology. Gender masculine. "Cincel-" is the Spanish word for chisel, in reference to the spatulate or chisel-like teeth defining the genus. "-ichthys" is Greek for fish.

Comments. Previous molecular phylogenetic studies have recovered and recognized these two species as members of *Theraps* (McMahan *et al*. 2010; López-Fernández *et al*. 2010). The phylogeny presented here corroborates that of Říčan *et al*. (2013). Sufficient morphological differences (dentition, markings, orientation of the lower jaw) exist to diagnose a new genus for these two species. *Cincelichthys bocourti* was initially described as a member *Neetroplus*; however, this genus is a synonym of *Hypsophrys*, as the type species for *Neetroplus* is *H. nematopus* (Chakrabarty and Sparks 2007). Therefore, *Neetroplus* cannot be used for these species.

Material examined. *C. bocourti*; MNHN 1894-0241 [n=1 (Holotype), Guatemala: Lago Izabal], LSUMZ 16455 [n=11, Guatemala: Lago Izabal], FMNH 100620 [n=1, Belize: Belize District]; *C. pearsei*; FMNH 109053 [n=1, Guatemala: Río San Pedro], FMNH 109054 [n=3, Guatemala: Río San Pedro], FMNH 109055 [n=1, Guatemala: Río Usumacinta], UMMZ 144088 [n=10, Guatemala: Río San Pedro], LSUMZ 16227 [n=4, Guatemala: Río La Pasion], UMMZ 144088 [n=10, Guatemala: Río San Pedro].

Genus *Rheoheros* gen. nov. McMahan and Matamoros 2015

(Fig. 12)

Inclusive species. *R. lentiginosus* (type species by designation), *R. coeruleus*

Diagnosis. *Rheoheros* gen. nov. is diagnosed by possessing the combination of an elongate body shape and a unique pattern of dark blotches and/or bars down the body. Markings extending from the first (dorsal-most) blotch often transverse the head anterior to the dorsal fin. Blotch and bar markings are always present at and dorsal to the middle of the body, but not ventral. The genus is most similar to *Paraneetroplus*; however, the freckled appearance in species of *Rheoheros* is absent in *Paraneetroplus*. Additionally, *Paraneetroplus* possesses a much deeper skull (i.e., head depth) than *Rheoheros*.

Distribution. Atlantic slope of Mexico and Guatemala in the Río Grijalva-Usumacinta system.

Etymology. Gender masculine. "Rheo" is from a form of the Greek verb "to flow" in reference to the preferred habitat of species in this genus. "-heros" is in reference to the generic name formerly used for many neotropical cichlid species.

Comments. *Rheoheros coeruleus* was included in the analysis of Říčan *et al*. (2013) with no voucher specimen reported, and there appear to be few lots of specimens for this species in collections (beyond the type series) as we are aware. Miller *et al.* (2005) considered *R. coeruleus* to be a synonym of *R. lentiginosus*, but provided no evidence for this assertion. Additional material of this species for comparative examination is certainly needed.

Material examined. *R. lentiginosus*, LSUMZ 16436 [n=6, Guatemala: Río Machaquilaito], FMNH 109002 [n=29, Guatemala: Río San Pedro], FMNH 109001 [n=38, Guatemala: Río San Pedro].

FIGURE 12. *Rheoheros lentiginosus*, FMNH 109002, 95.52mm SL.

Genus *Oscura* gen. nov., McMahan and Chakrabarty 2015
(Fig. 13)

Inclusive species. *O. heterospila* (type by monotypy).

Diagnosis. *Oscura* is diagnosed by a large, round or oblong, dark blotch filling the entirety (or nearly the entirety) of the caudal peduncle and the presence of small black spots on scales covering the sides of the body. Species of this genus possess an overall dark body coloration. This genus is most similar to *Vieja*; however, *Oscura* possesses dark bars down the body (typically five) and a blotch that fills the entirety of the caudal peduncle, versus the absence of broad bars down the body and a caudal blotch not filling the entirety of the caudal peduncle in members of *Vieja*.

FIGURE 13. *Oscura heterospila*, FMNH 108978, 98.79mm SL.

Distribution. Atlantic slope of Mexico and Guatemala in the Río Usumacinta drainage.

Etymology. Gender feminine. "Oscura" is the Spanish word for dark, in reference to the overall dark coloration that is characteristic of members of this genus.

Comments. The body shape and large, dark caudal blotch of this species initially allied this species in *Vieja,* but all phylogenetic studies to date have recovered them to be distantly related. The increased taxon sampling of the present study, as well as the analysis of Říčan *et al*. (2013) recovered this species in its own clade and the sister group to *Rheoheros*. Given the recovered phylogenetic position and the morphological distinctiveness of this species compared to its closest relatives (*R. lentiginosus* and *R. coeruleus*), we recognize this species in its own (monotypic) genus.

Material examined. LSUMZ 16229 [n=5, Guatemala: Río La Pasion], LSUMZ 16471 [n=1, Guatemala: Río La Pasion], UMMZ 144313 [n=5, Guatemala: Río San Pedro], FMNH 108978 [n=1, Guatemala: Río San Pedro], FMNH 108993 [n=18, Guatemala: Río Usumacinta], FMNH 108990 [n=3, Guatemala: Río Usumacinta].

Chiapaheros gen. nov. McMahan and Piller 2015

(Fig. 14 and 15)

Inclusive species. *Chiapaheros grammodes* (type by monotypy)

Diagnosis. *Chiapaheros* is diagnosed by the presence of thin dark lines (typically seven) running across the side (cheeks) of the head, in combination with an elongated predorsal profile and head. The presence of these lines along the head was one of the key diagnostic characters in the description of this species, and this character also works effectively to separate this genus from all other herichthyin (and heroin) genera. A relatively dorsoventrally oblong black spot is present at the base and center of the caudal peduncle. *Chiapaheros* is morphologically similar to the "guapotes" of the genera *Parachromis* and *Petenia*. In addition to the cephalic lines present in *Chiapaheros*, this genus can be differentiated from *Parachromis* and *Petenia* by the possession of a maxilla that does not extend to the anterior portion of the orbit.

Distribution. Atlantic slope of Mexico and western Guatemala in the Río Grijalva drainage.

Etymology. Gender masculine. The generic name is in recognition of Río Chiapa, the type locality of *C. grammodes* in Chiapas, Mexico. Additionally, this generic epithet appears to have been recorded in a GenBank submission by the late Gustavo Concheiro-Pérez, with sequence data corresponding to Concheiro-Pérez *et al*. (2006). This name is also in memory of Gustavo Concheiro-Pérez and his recognition of the distinctiveness of this species.

Comments. The sole member of this genus has been recovered in its own clade in every taxonomically well-sampled phylogeny of neotropical Cichlidae to date. The species was described as a member of *Cichlasoma*, and besides being regarded as belonging temporarily to '*Cichlasoma'* (*incertae sedis*), this species has never been placed in a separate genus.

Material examined. UMMZ 181815 [n=12 (Paratypes), Mexico: Río Grande de Chiapa], FMNH 93577 [n=9 (Paratypes), Mexico: Río Grijavla].

FIGURE 14. *Chiapaheros grammodes*, UMMZ 181815 (Paratype), 70.62mm SL.

FIGURE 15. Close-up of the markings along the side of the head of *C. grammodes*, UMMZ 181815 (Paratype), 70.62mm SL.

Genus *Thorichthys* Meek 1904
(Fig. 16)

Inclusive species. *T. ellioti* (type species; synonym of *T. maculipinnis*), *T. affinis*, *T. aureus*, *T. callolepis*, *T. helleri*, *T. meeki*, *T. pasionis*, *T. socolofi*.

Diagnosis. All species in the genus *Thorichthys* are relatively small cichlids with five mandibular pores along the dentary, with all other herichthyin genera possessing four mandibular pores. Species possess an elongate and moderately to strongly angular head profile with a small terminal mouth. Scales are not present on the base of the soft dorsal or anal fin. Pectoral fins are elongate, tapering posteriorly, typically to a moderately defined point (i.e., non-rounded edge) and extending to around one-fourth of the anal fin. The posterior edge of the dorsal and anal fins often have elongated tips.

Distribution. Atlantic slope of Middle America from Río Chachalacas area in Mexico, south to the Río Motagua drainage in Guatemala and Honduras.

Comments. The genus was first described by Meek (1904) but subsequently regarded as a subgenus of *Cichlasoma*. The genus is readily diagnosed; however, relationships among, and morphological variation within,

species are problematic. Miller and Nelson (1961) gave nine characters to generally diagnose the genus, although it was then recognized as a species group within *Cichlasoma*. *Thorichthys ellioti* is currently regarded as a synonym of *T. maculipinnis*, and more work is needed to examine the validity of this species and its potential separation from *T. maculipinnis*.

Material examined. *T. affinis*; LSUMZ 16248 [n=3, Guatemala: Lago Peten-Itza], LSUMZ 16376 [n=73, Gutemala: Laguna Sacnab, Lago Yaxhá]; *T. aureus*; LSUMZ 16278 [n=5, Guatemala: El Paraiso], LSUMZ 16394 [n=6, Guatemala: Río Dulce], FMNH 82060 [n=6, Belize: Temash River]; *T. maculipinnis*; FMNH 5533 [n=11, Guatemala: El Rancho]; *T. helleri*; LSUMZ 16262 [n=4, Guatemala: Río La Pasion], LSUMZ 16476 [n=3, Guatemala: Las Pozas], FMNH 4615 [n=23, Mexico: Rio Otopa]; *T. meeki*; LSUMZ 16346 [n=14, Guatemala: Río La Pasion], LSUMZ 16439 [n=2, Guatemala: Río Machaquilaito], FMNH 109029 [n=3, Guatemala: Peten]; *T. pasionis*; LSUMZ 16261 [n=3, Guatemala: Río La Pasion], LSUMZ 16368 [n=8, Guatemala: Río La Pasion], FMNH 109052 [n=8, Guatemala: Río San Pedro].

FIGURE 16. *Thorichthys ellioti*, FMNH 4627 (Holotype), 103.18mm SL.

Genus *Mesoheros* gen. nov. McMahan and Chakrabarty 2015
(Fig. 17)

Inclusive species. *M. festae* (type by designation), *M. atromaculatus*, *M. ornatus*

Diagnosis. The genus *Mesoheros* is diagnosed by an elongate body with a moderately small mouth that does not reach the anterior margin of the orbit. Seven (rarely six) dark spots (including bars in *M. festae*) are present along the lateral sides of body. All other genera of herichthyin cichlids with a small mouth possess a deeper body with angular heads, and lack this number of spots and bar-type markings along the body. The caudal fin is relatively truncate to rounded, and a well-defined, round, black spot is present on the dorsal portion of the caudal peduncle sitting directly above (often resting upon) the lower lateral line. Scale rows continue onto the base of the dorsal and anal fins. Spots are present on the dorsal, caudal, and anal fins.

Distribution. Colombia, Ecuador, and Peru; Río Atrato, Río San Juan, and Río Baudó in the Atlantic, Río Patia (Colombia) to Río Esmeraldas and Río Tumbes in the Pacific.

Etymology. Gender masculine. The generic epithet *Mesoheros* is based on "Meso-" which is Spanish for middle, for Middle America, given that this South American cichlid is one of the only species phylogenetically nested in a derived Middle American cichlid clade. "-heros" is in reference to the generic name formerly used for many neotropical cichlid species.

Comments. This is the only genus of South American cichlids that is part of the Middle American herichthyin clade as recovered in the present phylogeny. This relationship has been recovered consistently in molecular phylogenetic studies of neotropical cichlids (Chakrabarty 2006; López-Fernández *et al*. 2010; Říčan *et al*. 2013; Matamoros *et al*. 2015) and these three species are recovered as the sister group to the northern Middle American

herichthyins. Thus, we recognize these three species in their own genus, *Mesoheros*, based on morphological distinctiveness and phylogenetic position.

Material examined. *M. festae*; FMNH 122434 [n=4, Ecuador: El Oro, Santa Rosa], FMNH 122420 [n=3, Ecuador: El Oro, Santa Rosa]; *M. atromaculatus*; FMNH 58600 [n=5, Colombia: Istmina], FMNH 58606 [n=2, Colombia: Quibdo]; *M. ornatus*; FMNH 58609 [n=3, Colombia: Río Telembi].

FIGURE 17. *Mesoheros festae*, FMNH 122420, 82.2mm SL.

Genus *Tomocichla* Regan 1908

(Fig. 18)

Inclusive species. *T. tuba* (type species), *T. asfraci*

Diagnosis. *Tomocichla* is diagnosed by the presence of conical but compressed teeth in the anterior of the upper jaw, and strongly pronounced rounded posterior edges of the dorsal and anal fins. These species possess an overall elongate body, but the body and head depth are higher than that of most members of *Theraps* or *Rheoheros*. The number of anal-fin spines is four or five, and the mouth is subterminal with large lips. Pigmentation is largely dark in dorsal portions of the body and white, gray, or cream colored ventrally. *Tomocichla* is most similar to *Paraneetroplus* but does not possess the anterior-facing (horizontally-positioned anterior) dentary teeth present in *Paraneetroplus*.

Distribution. Atlantic slope of Middle America from the Río Escondido drainage in Nicaragua to the rivers of Bocas del Toro, Panama.

FIGURE 18. *Tomocichla tuba*, FMNH 7734, 135mm SL. Right side photographed as left side has been dissected away in this specimen.

Comments. *Tomocichla* was initially considered part of the Regan's *Theraps* section of *Cichlasoma*. Species of *Tomocichla* occur in fast-flowing rivers and is one of the few genera of herichthyin cichlids found outside of northern Middle America. Regan (1908) initially proposed *Tomocichla* based on the posterior placement of the pelvic fins. Bussing (1975) offers information on aspects of the taxonomy and biology of *Tomocichla* such as comparisons with similar species and morphological variation.

Material examined. *T. tuba*, FMNH 7734 [n=2, Costa Rica: Río Matina], LSUMZ 14684 [n=1, Costa Rica: Río Barranca], LSUMZ 14729 [n=1, Costa Rica: Río Sarapiquí].

Genus *Herotilapia* Pellegrin 1904
(Fig. 19)

Inclusive species. *H. multispinosa* (type by monotypy)

Diagnosis. *Herotilapia* can be distinguished from all other herichthyin genera based on the presence of tricuspid teeth (an adaptation for feeding on filamentous algae). This is also one of the smaller-sized Middle American cichlids. The species is deep-bodied, with an oval or round overall body shape and small, terminal mouth. A moderately round to square-like or rectangular-like blotch is present below the upper lateral line just past the midpoint of the body. A stripe connects this blotch to the operculum around the horizontal through the midpoint of the eye.

Distribution. Atlantic slope of Honduras, Nicaragua, and Costa Rica from Río Patuca (Honduras) south to Río Matina (Costa Rica); Pacific slope of Nicaragua and Costa Rica from Río Guasaule south to Río Tempisque. Specimens are also reported from the Río Choluteca in the Pacific of Honduras (USM-31494).

Comments. Schmitter-Soto (2007) synonymized *Herotilapia* with the genus *Archocentrus* based on his phylogenetic analysis of morphological characters. Our molecular phylogeny, as well as all other recent phylogenetic hypotheses, recover *H. multispinosa* as distantly related to *Archocentrus*. In the present study, *H. multispinosa* is recovered as the sister group to *Tomocichla*. Sufficient morphological differentiation exists between these two clades (dentition, body shape, markings), which warrants distinct generic recognition for both. Thus, we recognize *Herotilapia* as valid, resurrecting it from synonymy.

Material examined. LSUMZ 14721 [n=2; Costa Rica: Río Sarapiquí], LSUMZ 15454 [n=4; Nicaragua: Granada], LSUMZ 15471 [n=2; Nicaragua: Lago Managua], FMNH 84975 [n=5; Honduras: Brus Lagoon, La Mosquitia].

FIGURE 19. *Herotilapia multispinosa*, LSUMZ 15445, 72.6mm SL.

Genus *Trichromis* gen. nov. McMahan and Chakrabarty 2015
(Fig. 20)

Inclusive species. *T. salvini* (type by monotypy)

Diagnosis. *Trichromis* is diagnosed by the presence of two dark lines down the length of the body, one just above the distal tip of the pectoral fin, and the other right below the dorsal fin. The mouth is small and terminal and the overall body shape is oval or oblong. Dark, narrow bars or lines are present, typically three or four, from in between the eyes to the predorsal region anterior to the dorsal fin. The interorbital markings are not as broad as those in *Maskaheros*. Both sexes of species within this genus are colorful (yellow, red, blue/green), and coloration becomes more vivid during breeding.

Distribution. Rivers of the Atlantic slope of southern Mexico, Belize, and Guatemala.

Etymology. Gender feminine. "Tri" is Greek for three, in reference to the three vibrant colors defining this genus (red, yellow, and blue). "-chromis" is Greek for fish.

Comments. This species of northern Middle American cichlid has been recovered in several different phylogenetic positions across studies. Most of these discrepancies are likely due to differences in taxonomic sampling among studies. Matamoros *et al*. (2015) recovered this species outside of the herichthyins and sister to *Cryptoheros nanoluteus*. Říčan *et al*. (2013) recovered this species as the sister group to *Thorichthys*, and López-Fernández *et al*. (2010) found this species to be outside of the herichthyin cichlids and the sister group to a large clade of several different genera. In nearly all cases (including the present study), *T. salvini* is recovered in its own clade and not the sister group to any species or clade of species even remotely similar morphologically. Thus, given the phylogenetic position and the morphological distinctiveness of this species, we describe a new genus to contain this species.

Material examined. LSUMZ 16257 [n=2, Guatemala: Lago Peten-Itza], LSUMZ 16366 [n=4, Guatemala: Río La Pasion], LSUMZ 16417 [n=4, Guatemala: Lago Yaxhá], FMNH 109065 [n=18, Guatemala: Río San Pedro].

FIGURE 20. *Trichromis salvini*, FMNH 109065, 69.76mm SL.

Key to the genera of herichthyin cichlids

1a) Presence of four mandibular pores . . . . . *Thorichthys*
1b) Presence of five mandibular pores 2
2a) Teeth tricuspid . . . . . *Herotilapia*
2b) Teeth not tricuspid 3
3a) Teeth spatulate throughout most of mouth 4

3b) Teeth conical or bicuspid throughout most of mouth 5
4a) Round body shape with small dark spot in center base of caudal peduncle . . . . . *Cincelichthys* **gen. nov.**
4b) Large dark spot on caudal peduncle, tall bodied but not round in shape . . . . . *Kihnichthys* **gen. nov.**
5a) Mouth strongly subterminal, median dentary teeth directed anteriorly . . . . . *Paraneetroplus*
5b) Mouth terminal or moderately subterminal, median lower jaw teeth directed dorsally 6
6a) Presence of two broad interorbital bars. . . . . *Maskaheros* **gen. nov.**
6b) Presence of more than two interorbital bars, thin interorbital bars, or absence of bars 7
7a) Presence of thin lines (typically seven) across sides of head . . . . . *Chiapaheros* **gen. nov.**
7b) Absence of thin lines on sides of head 8
8a) Presence of two or three narrow dark interorbital bars and two broad lines down length of body. . . . . *Trichromis* **gen. nov.**
8b) Conditions not as in 8a 9
9a) Elongate to moderately elongate body shape 10
9b) Deep-bodied to moderately deep-bodied body shape, presence of large to moderately sized caudal blotch 11
10a) Presence of dark bars and/or blotches along body, often with freckled pattern of dark spots across body . . . . . *Rheoheros* **gen. nov.**
10b) Absence of characters in 10a. 14
11a) Presence of dark bars and small spots across sides of body . . . . . *Oscura* **gen. nov.**
11b) Absence of dark bars and dark spots across body, although some spots may be present 12
12a) Presence (except in *V. maculicauda*) of dark, broad stripe continuing from caudal blotch to either ¼ to ½ length of body, or entire body . . . . . *Vieja*
12b) Absence of stripe described in 12a 13
13a) Teeth in anteriormost portion of upper jaw conical or unicuspid . . . . . *Nosferatu*
13b) Teeth in anteriormost portion of upper jaw typically spatulate. . . . . *Herichthys*
14a) Spots on dorsal, caudal, and anal fins 15
14b) No spots on dorsal caudal, and anal fins, occurring in lower Middle America (Costa Rica, Panama). . . . . *Tomocichla*
15a) Upper jaw extends over lower jaw . . . . . *Theraps*
15b) Upper jaw not extending over lower jaw, occurs in South America . . . . . *Mesoheros* **gen. nov.**

'Cichlasoma' (*incertae sedis*)

'C.' tuyrense and *'C.' sieboldii*—Numerous phylogenetic studies on neotropical cichlids have now recovered a well-supported sister relationship between the Panama endemic '*C.*' *tuyrense* and Lower Middle American *'C.' sieboldii*. '*Cichlasoma*' *tuyrense* was, at one time, considered a member of the genus *Vieja* (Kullander 2003). McMahan *et al*. (2010) and López-Fernández *et al*. (2010) both recovered this species phylogenetically far outside of the few clades containing species of *Vieja*, as well as quite distantly related to the herichthyins in general. '*Cichlasoma' sieboldii* was once considered a member of the genus *Tomocichla* based on morphological affinities with *T. tuba* and *T. asfraci* (Chakrabarty 2007; Bussing 1998). The species has also been placed in *Theraps*, *Paraneetroplus*, and other genera (see Bussing (1975) for a detailed examination of the taxonomic history of '*C.*' *sieboldii*). All phylogenetic studies clearly illustrate that both of these species are not closely related to the herichthyins.

These two species are also considerably different morphologically, making it difficult to discover anatomical characters that may unite them. Given the nearly complete taxonomic coverage of Middle American (i.e., heroin) cichlids in phylogenetic studies, with the congruent recovery of this relationship regardless of loci used, we continue to recognize these two non-herichthyin species as members of '*Cichlasoma'* (*incertae sedis*) until additional work is presented on morphology of these species.

Conclusions

The majority of named clades discussed in the present study have been recovered in a number of previously published molecular-based phylogenies of neotropical cichlids (López-Fernández *et al*. 2010; McMahan *et al*. 2010; Říčan *et al*. 2013; Matamoros *et al*. 2015). We used nearly complete taxon sampling of the herichthyins, as well as complete sampling for loci whenever possible. Based on our recovered phylogeny, we have revised the generic-level taxonomy of the herichthyins accordingly and now recognize 15 valid genera. Past studies have proposed generic-level names based only on tree topology; however, formal taxonomic revisions, complete with the redefining of genera, are more robust and necessary for these names to be meaningful and taxonomically valid (i.e., with character based diagnoses).

Several new genera are described in this study, and several of these are monotypic or include only a few species. Even though there may be characters that could unite these species into genera of more than one or a few species, the morphological distinctiveness of these species is such that recognition of multiple genera is justified. The generic-level morphological differences proposed here are at par or surpass those between other neotropical cichlid genera (e.g., *Herichthys* and *Nosferatu*, *Geophagus* and *Gymnogeophagus*) or other cichlid genera (e.g., *Katria* and *Ptychochromis*). Recognition of these disparate clades as separate genera is more beneficial in terms of taxonomic utility than lumping of such morphological differentiation into a single generic name.

Given the age (McMahan *et al*. 2013; Říčan *et al*. 2013) and morphological diversity of the herichthyin cichlids, it seems that a substantial amount of extinction in this (once likely far more diverse) Middle American clade has likely occurred. Most of the herichthyin species are distributed in northern Middle America, and many of these species have an origin that can be traced back to this region (Říčan *et al*. 2013; Matamoros *et al*. 2015).

In general, the discrepancies across various phylogenetic studies regarding the relationships of herichthyin species are likely due to taxonomic sampling. Past work has certainly shown the importance of taxonomic sampling for addressing questions of fine-scale cichlid evolutionary relationships (McMahan *et al*. 2010). While future studies can certainly work towards utilization of additional markers or genomic-level datasets, the five loci used here have been shown to work well for resolving relationships among these lineages (López-Fernández *et al*. 2010). This generic-level revision sets up the framework for detailed systematic studies among species within these groups.

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