



El Colegio de la Frontera Sur

Análisis de la variación morfológica en cíclidos
mesoamericanos del clado *Theraps-Paraneetroplus* (*sensu*
Řičan 2016)

Tesis

Presentada como requisito para optar al grado de Maestra en
Ciencias en Recursos Naturales y Desarrollo Rural
Con Orientación en Manejo y Conservación en Recursos Naturales

Por

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2021



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San Cristóbal de Las Casas, 14 de julio de 2021.

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AGRADECIMIENTOS Y DEDICATORIA

Al Consejo de Ciencia y Tecnología (CONACYT) y ECOSUR por la beca otorgada durante los estudios de Maestría. Al proyecto “Conectividad y diversidad funcional de la cuenca del río Usumacinta” (Fondo de Investigación Científica y Desarrollo Tecnológico de El Colegio de la Frontera Sur, FID-784), coordinado por la Dra. Rocío Rodiles Hernández.

Agradezco a mi comité tutelar, principalmente al Dr. Alfonso A. González Díaz por toda la confianza, paciencia, apoyo y dedicación que demostró para lograr este trabajo. Al Dr. Omar Mejía por las oportunas revisiones, comentarios asertivos y pertinentes para la mejora de este trabajo. A la Dra. Rocío Rodiles Hernández, por la disposición y tiempo dedicado a cada una de las revisiones de este trabajo.

A Dios. Por permitirme cumplir una meta más en mi vida profesional. Por poner a las personas adecuadas en mi camino, ya que gracias a ellas pude adquirir el conocimiento y herramientas necesarias para culminar este proyecto. Por acompañarme en todo el camino recorrido y continuar siempre conmigo.

A mis padres. Paula Contreras Franco y Porfirio Aguilar Hernández † por todo el apoyo, sacrificio, amor, cariño, consejos brindados y alentándome en momentos de angustia. Gracias por creer en mí, siempre será un privilegio llamarlos padres. Los amo.

A mi familia. Hermanas, sobrin@s y cuñados, por el apoyo incondicional durante estos años de maestría, durante toda mi vida, y siempre celebrando mis metas alcanzadas.

A Limber Sigarroa Gómez por todos los momentos que me otorgaste tu apoyo en todas las etapas de este trabajo y de mi vida. A Yuriria Olvera, Edgar Flores y Aranza García, por apoyarme con sus consejos y mejores deseos. A los amigos que tuve la suerte de conocer en este proceso: Ana Barrientos, Caheri López, Miriam Linares, Cristina Domínguez y David Ucan fue un gusto coincidir chic@s.

Al personal del ECOSUR, por todas las facilidades otorgadas, en especial y principalmente a Susana G. Carpio, por el apoyo otorgado con los trámites administrativos.

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RESUMEN

Los estudios morfológicos son fundamentales para conocer la importancia de los procesos ecológicos y evolutivos en la diversificación de los grupos biológicos. Conocer el origen y los patrones de variación morfológica es particularmente interesante en taxones que han experimentado eventos de diversificación a través de radiaciones adaptativas. Los cíclidos africanos son el ejemplo más claro de especiación a través de este proceso, sin embargo, en los cíclidos neotropicales también existen evidencias de radiaciones adaptativas. Dentro de los cíclidos mesoamericanos, los miembros del clado *Theraps-Paraneetroplus*, han mostrado múltiples cambios taxonómicos debido a su sorprendente variación morfológica convergente, la cual con frecuencia se ha relacionado con la selección del hábitat y el reparto de los recursos alimentarios. Por lo anterior, aún es necesario realizar estudios que permitan entender los procesos evolutivos que intervinieron en los cambios morfológicos de los cíclidos en Mesoamérica. El objetivo de este trabajo fue conocer la variación de la forma del cuerpo entre los miembros del clado *Theraps-Paraneetroplus*, determinar sus relaciones de parecido morfológico y evaluar si la forma del cuerpo muestra señal filogenética. Se encontraron tres grupos morfológicos, los cuales varían principalmente en la longitud y altura del cuerpo, así como en el tamaño de la cabeza, posición de la boca y ojos, *Wajpamheros nourissati* fue la especie morfológicamente más diferente, lo anterior se relaciona con ciertas características asociadas al hábitat y obtención del alimento. Asimismo, se encontró baja señal filogenética en la forma del cuerpo en las especies analizadas.

Palabras clave: Señal filogenética, América central, taxonomía, diversificación, convergencia morfológica.

CAPÍTULO 1. INTRODUCCIÓN

Los peces dulceacuícolas de la familia Cichlidae son considerados de los más diversos a nivel mundial. Esta familia está formada por 251 géneros y 1727 especies válidas que se distribuyen en diversos ambientes acuáticos de África, Medio Oriente, Sur de la India, Centro y Sudamérica (Fricke et al. 2021), es un grupo “modelo” dentro de la biología evolutiva, por ser un ejemplo clásico de radiación adaptativa (Meyer 1993; Kornfield y Smith 2000; Koblmüller et al. 2011; Arbour y López-Fernández 2016). En la región Neotropical, los cíclidos se distribuyen desde la Patagonia hasta Texas, habitando principalmente en ambientes lóticos (Kullander 1998; Kullander 2003; Burress 2014). Se considera que su diversificación es favorecida por el reparto de recursos, particularmente del hábitat y alimento (López-Fernández et al. 2012; Burress 2016; Říčan et al. 2016). Lo anterior se puede observar en la diversidad de formas del cuerpo y especialización trófica (Liem 1973; Meyer 1993; Salzburger 2009; Burress 2016). En particular, Mesoamérica, se considera una región diversa en cuanto a cíclidos, donde se distribuyen alrededor de 124 especies, de las 184 reconocidas para el neotrópico (Říčan et al. 2011).

Sin embargo, aún existen problemas taxonómicos y sistemáticos para algunos grupos de cíclidos mesoamericanos, esto por los cambios frecuentes en su clasificación debido a la gran variación morfológica y la débil señal filogenética de los caracteres diagnósticos (Stiassny 1991; Říčan et al. 2008). Entre las especies que más cambios taxonómicos y de clasificación han experimentado se encuentra el clado *Theraps-Paraneetroplus*, el cual se originó hace aproximadamente 7.3 millones de años (Miller et al. 2009; Říčan et al. 2016). Este grupo de peces está integrado por 25 especies, pertenecientes a 10 géneros, cuya distribución abarca las cuencas hidrológicas de Papaloapan, Coatzacoalcos, Grijalva y Usumacinta, llegando incluso a la parte norte de Belice. En varias localidades de su área de distribución, es frecuente encontrar especies en simpatria (Říčan et al. 2016).

En los cíclidos mesoamericanos, algunas características morfológicas son consideradas convergentes, debido a que especies que no comparten el mismo ancestro muestran formas del cuerpo y estructuras tróficas semejantes. El parecido

morfológico de algunas especies en el clado *Theraps-Paraneetroplus* ha permitido hacer una clasificación ecomorfológica, donde la morfología se puede relacionar con el tipo de hábitat donde se encuentran como lóticos (especies con cuerpo y pedúnculo caudal alargado) y lénticos (peces con cuerpos altos y aleta caudal corta). Esto ha permitido proponer que las formas del cuerpo y tipo de alimentación se relacionan a grupos tróficos particulares, como detritívoros (*Cincelichthys pearsei*, *Maskaheros argenteus*, *Vieja hartwegi*, *Kihnichthys ufermanni* y *Oscura heterospila*) especies con dieta basada en semillas, algas filamentosas y pequeños vertebrados y raspadores (*Wajpamheros nourissati*, *Theraps irregularis*, *Chuco intermedium*, *Rheoheros lentiginosus* y *Paraneetroplus bulleri*), especies que se alimentan de perifiton (Rüber y Adams 2001; Miller et al. 2009; Kerschbaumer y Sturmbauer 2011; Říčan et al. 2016).

Una forma de evaluar la variación morfológica relacionada con procesos de evolución convergente es la comparación morfométrica de organismos que pertenecen a diferentes ambientes (Jaramillo 2011). El analizar y cuantificar dicha variación, ha sido el principal objetivo de la morfometría geométrica, esta herramienta ayuda identificar los cambios en la forma “pura” de los organismos, logrando separar la variación de la posición y tamaño entre los individuos (de una o diferentes especies), por medio de coordenadas cartesianas (x, y) y puntos de referencia, conocidos como “landmarks”, los cuales definen y delimitan de forma exacta los puntos anatómicos de los ejemplares (Toro-Ibacache et al. 2010; Aguirre y Prado 2018).

Estas marcas anatómicas (landmarks) deben ser seleccionados bajo ciertos criterios: a) ser **homólogos**, ubicándolos sobre la misma estructura (parte biológica) que resultan de un ancestro común, ayudando a disminuir el efecto de error en la medición, b) tener una **cobertura adecuada**, ayudando a recrear la forma del organismo utilizando una cantidad adecuada de “landmarks” generando información eficaz y confiable, c) **repetitividad**, donde cada “landmark” se debe localizar de forma fácil y estar claramente definido en todas las imágenes y por último d) la **coplanaridad**, que se refiere a la dimensión de las imágenes, ya que al no tomar

en cuenta este criterio la interpretación puede ser errónea, cuando se trabaja con imágenes bidimensionales que presenten mucha profundidad, la información se debe analizar en el plano posterior de la imagen, para así poder validar la forma del organismo (Bookstein 1991; Toro-Ibacache et al. 2010; Benítez y Püschel 2014).

Una vez obtenido el mapa con las coordenadas, es necesario realizar un proceso de normalización de variables, con el fin de realizar comparaciones entre muestras. Por lo anterior, se utiliza un método conocido como Análisis de Procrusters Generalizado (Rohlf y Slice, 1990), dicho método permite hacer un ajuste de mínimos cuadrados por medio del escalado, rotación y traslación de cada configuración de coordenada, esto con la finalidad de remover aquella información que se relaciona con la orientación, tamaño y posición, donde al final, la forma de los organismos es la única variable para analizar (Torcida y Pérez 2012; Charlin y Llosas 2016). Por último, estos datos son analizados con métodos estadísticos multivariados, los más utilizados en la morfometría geométrica son: **Análisis de componentes principales (ACP)**, análisis exploratorio que ayuda a simplificar una serie de datos, en el cual se observan las direcciones que tienen mayor variación y grafica la distribución de los ejemplares en el espacio, el **análisis de variables canónicas (AVC)**, que es utilizado para conocer la existencia de uno o más grupos de variables que se estén analizando (e. g. especies, grupos de sexos), ya que los ejes canónicos ayudan a establecer y observar que tan separados se encuentran los grupos en el espacio multivariado.

Actualmente, el uso de la morfometría geométrica en peces ha permitido abordar preguntas relacionadas con aspectos ecomorfológicos y funcionales de los taxa (Klingenberg et al. 2003; Cohen et al. 2005; Barrientos-Villalobos et al. 2018; McMahan et al. 2019; Soria-Barreto et al. 2019). Por otro lado, comparar y comprender los procesos de adaptación (selección natural) e historia filogenética (herencia ancestral) de un grupo de especies, ha sido un reto para la biología evolutiva y comparativa. Actualmente la evolución morfológica se puede estudiar a través de los métodos comparativos (Ibáñez y Méndez 2014), donde lo que se

puede evaluar es la importancia de las relaciones filogenéticas y los factores ambientales en la expresión fenotípica de los atributos morfológicos.

Los métodos comparativos son una herramienta que se utiliza para realizar comparaciones entre especies e inferir la significancia adaptativa de un carácter determinado, logrando así explicaciones evolutivas a partir de información ecológica, morfológica y filogenética, reconociendo que las especies a comparar no son independientes, debido a que llegan a compartir caracteres por descender de ancestros comunes (Felsenstein 1985; Pagel y Harvey 1988; Borges et al. 2018). Estos métodos son utilizados con fines estadísticos, para corroborar las explicaciones de fenómenos biológicos.

Existen diferentes modelos para desarrollar los estudios comparativos, tales como el de **contrastes filogenéticamente independientes** (Felsenstein 1985), **análisis de autocorrelación filogenética** (Cheverud et al. 1985), **modelos para la estimación de estados ancestrales** (Morales 2000) y **modelo de máxima verosimilitud** (Schluter et al. 1997). Cada método tiene sus principios teóricos y metodológicos, pero todos buscan analizar la expresión de las características morfológicas desde la perspectiva filogenética. Una de las formas más simples de visualizar los cambios evolutivos de las características morfológicas es a través del mapeo de la forma en la filogenia, donde se hace una comparación de los patrones de variación morfológica de los taxones en el morfoespacio de los análisis multivariados con la estructura de la filogenia.

El uso de los análisis multivariados se ha vuelto una herramienta común en los estudios morfológicos de peces para conocer como varían la forma del cuerpo, cabeza y algunas estructuras relacionadas con la alimentación (mandíbula oral y mandíbulas faríngeas) asimismo han servido para establecer relaciones de parecido morfológico a través de la construcción de dendrogramas (Vergara-Solana et al. 2014; Feilich 2016; Chollet-Villalpando et al. 2019; Price et al. 2019; Pérez-Miranda et al. 2020).

Los métodos morfométricos y comparativos han demostrado su utilidad para conocer el origen, tendencias y evolución de las características morfológicas en diversos grupos de peces.

A pesar de que la diversificación de los cíclidos mesoamericanos se ha relacionado con la especialización morfológica por el uso del hábitat y los recursos alimentarios, los estudios en este contexto aún son escasos. La mayoría de las investigaciones se han enfocado en aspectos ecomorfológicos relacionados con la alimentación (Soria-Barreto 2011; Pease et al. 2012; Pease et al. 2018). Sin embargo, no existen estudios donde se analice la variación morfológica desde la perspectiva filogenética.

Por lo anterior, los objetivos de este trabajo fueron a partir de 10 especies del clado *Theraps-Paraneetroplus* 1): describir los cambios en la forma del cuerpo, 2): establecer las relaciones de similitud a partir de la variación en la forma del cuerpo y 3): mapear la forma del cuerpo en la filogenia actual y determinar si existe señal filogenética.

Se planteó como hipótesis que, de acuerdo con la perspectiva de la sistemática filogenética y el principio de no independencia evolutiva entre caracteres (Felsenstein 1985), se espera que la forma del cuerpo entre las especies y géneros de este clado tenga un patrón de diversificación compatible con la filogenia molecular (Říčan et al. 2016), donde especies que comparten el mismo ancestro sean morfológicamente más parecidas. En contraste, las especies y géneros más distantes filogenéticamente mostrarán mayores diferencias en la forma del cuerpo.

Artículo enviado a la revista: Acta Ichthyologica et Piscatoria

CAPÍTULO 2. Artículo. Geometric morphometrics analysis of body shape variation in Mesoamerican cichlids of the *Theraps-Paraneetroplus* clade (*sensu* Říčan 2016)

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Summary.

Background. Over the years, the *Theraps-Paraneetroplus* clade have experienced constant changes in their classification due to convergent morphological attributes. Recent studies based on genetic and morphological characters have allowed us to determine their phylogenetic relationships and evolutionary history. The systematics of this group of cichlids is currently stable, which allows us to understand some of the processes involved in their morphological evolution. In this sense, phylogenetic studies have revealed a close relationship between morphology and habitat use. Therefore, the objectives of this work were to understand the patterns of body shape variation and morphological similarity relationships among species of the *Theraps-Paraneetroplus* clade and determine whether body shape exhibits a phylogenetic signal. A total of 209 specimens belonging to 10 species of the *Theraps-Paraneetroplus* clade were used. After photographs of the left side of each specimen were taken, 27 landmarks were set. To identify patterns of body shape variation, a phylogenetic principal component analysis (pPCA) was performed. Then, the phylogenetic signal for body shape was calculated. Finally, to determine the morphological similarity relationships, a dendrogram was constructed using the unweighted pair group method using arithmetic averages (UPGMA). We determined that three morphological groups were formed, which differed mainly in body length and depth, head size, and the position of the mouth and eyes. Based on traits associated with habitat and feeding, *Wajpamheros nourissati* was the most different species. However, no phylogenetic signal was found for body shape. Diversification of the *Theraps-Paraneetroplus* clade was related to habitat use and the exploitation of food resources, as evidenced by the consistently

convergent morphology of the species in this group. Although no phylogenetic signal was found for body shape, there seems to be an ordering associated with phylogeny based on cranial morphology. Therefore, future morphological evolutionary studies should consider cranial structures related to the capture and processing of food.

Keywords

Phylogenetic signal, Middle America, taxonomy, diversification, morphological convergence.

Introduction

In vertebrates, phenotypic variation has been an important attribute for diversification and environmental adaptation. Notably, this relationship has become one of the main topics of study in evolution. A classic example is adaptive radiation, which allows organisms to take advantage of new food resources or diverse environments, thereby facilitating the sudden diversification of species (Simpson 1953; Schluter 2000; Glor 2010). Studies related to morphological diversity have demonstrated that body shape and size variation have been the main axes of diversification for the Pomacentridae, Balistidae, Cichlidae, Anguilliformes, and Labridae groups (Dornburg et al. 2011; Aguilar-Medrano 2013; Frédérick et al. 2013; Reece and Mehta 2013).

In this context, African lake cichlids represent one of the best-described cases since they have revealed great morphological diversity in short periods of time, with body size, fin position, and locomotion strategies being important indicators for the resource exploitation, coexistence, and diversification of species (Rüber and Adams 2001; Hulsey et al. 2013; Colombo et al. 2016).

In the Neotropical region, South American cichlid species have been the most studied. It has been demonstrated that morphological variation determined their diversification, with one of the most notable aspects being the constant presence of morphological convergence between lineages (López-Fernández et al. 2010, 2013; Říčan et al. 2016).

Research on the processes that promoted Mesoamerican cichlid diversification of remains scarce, even in areas considered centers of endemism and high diversity, such as the San Juan and Usumacinta ichthyological provinces (Říčan et al. 2016). Middle America harbors approximately 124 cichlid species (Říčan et al. 2011) and it is assumed that their diversification was promoted by the partitioning of resources—particularly habitat and food (López-Fernández et al. 2012; Burress 2016; Říčan et al. 2016). This is evidenced by the diversity of body shapes and specialization of trophic anatomy (Liem 1973; Meyer 1993; Salzburger 2009; Burress 2016). Notably, this has promoted frequent cases of morphological convergence because lineages have been subjected to the same selective pressures (e.g., habitat use and the exploitation of food resources; Páiz-Medina and Huete-Pérez 2012). The morphological similarity among species and low phylogenetic signal of

diagnostic characters have been the main reasons for the unclear and complex taxonomy of cichlids in Mesoamerica (Stiassny 1991; McMahan et al. 2013; Řičan et al. 2008, 2016).

The *Theraps-Paraneetroplus* clade (*sensu* Řičan 2016) is interesting due to the presence of species with highly variable and frequently convergent morphology, which is mainly evident in their body shapes and characteristics associated with food capture (Soria-Barreto et al. 2008, 2011, 2019). This group of fishes is estimated to have originated under sympatric conditions approximately 7.3 mya (Miller et al. 2009; Řičan et al. 2016). The *Theraps-Paraneetroplus* clade includes 25 species belonging to 10 genera. Moreover, the distribution of this clade is located in the Usumacinta ichthyological province, comprising the hydrological basins Papaloapan, Coatzacoalcos, Grijalva, Usumacinta, and northern Belize (Řičan et al. 2016).

In addition to ecomorphological evidence indicating that the phenotypic expression of morphological attributes in some clade members is associated with habitat type and feeding (Soria-Barreto et al. 2019), studies on the systematics and evolution of Mesoamerican cichlids have demonstrated the existence of convergent morphological characters between several species of the *Theraps-Paraneetroplus* groups (McMahan et al. 2015; López-Fernández et al. 2014; Řičan et al. 2016). Patterns of morphological variation associated with body depth and length are recurrent among species that use similar habitats (McMahan et al. 2015; Řičan et al. 2016). Thus, the existence of lentic and lotic ecomorphological patterns was proposed, where species of the genera *Cinzellichthys*, *Kihnichthys*, *Oscura*, and *Vieja* represent the lentic ecomorphotype, with short and deep bodies. Conversely, the species *Theraps*, *Wajpamheros*, *Chuco*, *Rheoheros*, and *Paraneetroplus* represent the lotic ecomorphotype, with elongated and depressed bodies. An example is represented by members of the genus *Maskaheros*, in which both ecomorphotypes are present (Řičan et al. 2016).

An interesting feature related to the morphology of species in the *Theraps-Paraneetroplus* clade is the contrast with the perspective proposed by phylogenetic systematics and the theory of evolutionary non-independence among characters. It would be expected that body shapes within the species and genera of this clade would have a diversification pattern like phylogeny and taxa sharing the same ancestor being morphologically most similar. Therefore, this study aimed to describe and compare the body shape variation patterns in 10 species of the *Theraps-Paraneetroplus* clade and assess the phylogenetic signal of this trait.

For this purpose, geometric morphometrics and comparative methods were used as analytical tools since they are commonly used to study the evolution of biological morphology. Geometric morphometrics can be used to identify variation in the pure shape of organisms and separate the variation and size of individuals by analyzing shape in multivariate space (Aguirre and Jiménez-Prado 2018). Notably, comparative methods can be used to analyze morphological characteristics and their importance in species diversification from a phylogenetic perspective (Pagel and Harvey 1988; Adams and Collyer 2018; Borges et al. 2019).

Materials and methods

A total of 209 specimens from the Fish Collection of El Colegio de la Frontera Sur, San Cristóbal (ECO-SC-P) were used. We used female and male specimens of similar size that corresponded to 10 species of the *Theraps-Paraneetroplus* clade. To analyze the morphological variation among members of this clade, we considered representative species from each genus: *Theraps irregularis* (Günther 1862), ECOSC 245(2), 817(2), 1255, 1780, 1967, 2133, 2626, 4725, 4729, 4809(8); *Cinzelichthys pearsei* (Hubbs 1936) ECOSC 204, 229(2), 299, 300, 337, 444, 719(4), 849, 1049, 1512(3), 1055, 2352, 2546, 2575, 4422(2), 4436 (2); *Kihnichthys ufermanni* (Allgayer 2002), ECOSC 90, 186, 233, 406, 409, 613, 675, 769, 1729, 1230, 1536(3), 1548, 1557(2), 1867, 1873, 2118(2), 2298, 4687, 7618; *Chuco intermedium* (Günther 1862), ECOSC 103, 314(4), 334, 395(5), 440, 473(3), 815(2), 12747(2), 4892(2); *Wajpamheros nourissati* (Allgayer 1989), ECOSC 532(2), 684(2), 820(2), 893, 1237, 1288(2), 1546(2), 1847, 1289(2), 2082(2), 2105, 2280, 2651, 4744, 4888, 7336, 7453; *Rheoheros lentiginosus* (Stawikowski & Werner 1987), ECOSC 646, 853(3), 869(2), 1471(2), 1503(2), 1874, 1900, 2296(4), 2389, 2515(3), 2549, 2559, 7789, 4695, 12748; *Oscura heterospila* (Hubbs 1936), ECOSC 2338, 2720, 3053, 3054, 3491, 3505, 3777, 4563, 6709, 7826, 8465, 9070, 9080, 9267, 9318, 9816, 9849, 10164, 10165, 13757; *Vieja hartwegi* (Taylor & Miller 1980), ECOSC 4445(3), 4546, 6838, 6857(4), 7468, 7542(4), 7543(4), 7548(2), 7549(2), 12340; *Maskaheros argenteus* (Allgayer 1991), ECOSC 386, 698, 741, 1280, 1448, 1472, 1481, 1502, 1606, 1747, 1771, 1998, 2020, 2163, 2174, 2395, 2555, 2577, 4716, 4747(2), 4806 (2), 4821, 7774; *Paraneetroplus bulleri* (Regan, 1905), ECOSC 12018 (3).

Morphometric analysis

Fishes were photographed on their left side using a Canon (EOS 70D) digital camera. The camera was mounted on a tripod to standardize the distance from the object. A 1-cm scale was placed on each photograph. To perform the body shape description and comparison, a geometric morphometric analysis was performed. We placed 27 landmarks using the configuration provided by Mejía et al. (2015) and two additional landmarks (Fig. 1). Image digitalization and processing were carried out using the software tpsUtil (Rohlf 2018) and tpsDig (Rohlf 2017).

Subsequently, to eliminate variation caused by the size, rotation, and displacement of the organisms, a Generalized Procrustes Analysis (GPA) was performed (Aguirre and Jiménez-Prado 2018). Likewise, the mean body shape configuration of each species was obtained. In both cases, the "gpagen" function of the geomorph library (Adams and Otárola-Castillo 2013; Adams et al. 2016) was used in R software (R Development Core Team 2017).

Shape analysis

To reduce morphological variation related to phylogeny and differences in specimen size, a regression of the Procrustes coordinates and centroid size was conducted using the "phyl.resid" function of the Phytools package in R software (Revell 2009, 2012). Subsequently, to identify body shape variation patterns, a Phylogenetic Principal Component Analysis (pPCA) was performed based on the Procrustes coordinates of the

average configurations of the 10 species. In both instances, the nDNA molecular phylogeny based on ddRAD sequences proposed by Řičan et al. (2016) for Middle American cichlids was used. The body shape variation of the species was displayed on the first three axes of the pPCA. Additionally, deformation grids were obtained to visualize and describe morphological variation among species in morphospace. All analyses were conducted in R software using the Phytools package (Revell 2009, 2012).

Additionally, we computed the phylogenetic signal for body shape by using the Kmult statistic across 1000 permutations via the Geomorph package of the R program (Adams et al. 2021). K values <1 indicate a low phylogenetic signal, while K values >1 indicate a strong phylogenetic signal (Adams 2014). To determine the morphological similarity relationships among the 10 species, we constructed a dendrogram using the unweighted pair group method using arithmetic averages (UPGMA) in Past 4.05 software (Hammer et al. 2001) based on the Mahalanobis distances obtained in MorphoJ 1.07a software (Klingenberg 2011).

Results

The pPCA indicated that the first three components explained 80% of the total variance (PC1: 52.6%; PC2: 17.6%; PC3: 11.6%). Species located on the positive axis of PC1 include *Theraps irregularis*, *Paraneetroplus bulleri*, and *Rheoheros lentiginosus*, while *Oscura heterospila*, *Maskaheros argenteus*, *Cincelichthys pearsei*, and *Kihnichthys ufermanni* were located on the negative axis, and *Chuco intermedium*, *Vieja hartwegi* and *Wajpamheros nourissati*, were in the middle axis (Fig. 2). The deformation grids showed variation among species on the positive axis related to decreased body height and elongation of the caudal peduncle, while the species with a deep body height and shortened caudal peduncle were placed on the negative axis (Fig. 3).

In PC2, species found in the positive region included *Cincelichthys pearsei*, *Kihnichthys ufermanni*, *Chuco intermedium*, *Theraps irregularis*, and *Vieja hartwegi*, while *Oscura heterospila*, *Wajpamheros nourissati*, *Rheoheros lentiginosus*, *Maskaheros argenteus*, and *Paraneetroplus bulleri* were found on the negative axis (Fig. 2). The deformation grids showed that the most remarkable deformation occurred in the cephalic region. On the positive axis, the species exhibited heads with straight profiles and mouths in a terminal position, while the eyes were displaced posteriorly. On the negative axis, the species showed rounded heads and a ventral mouth position, while the position of the eyes was displaced anteriorly (Fig. 3).

In PC3, *Wajpamheros nourissati* was the most differentiated on the positive axis, showing accentuated variation in the cephalic region with increased head size and a notable anteroventral displacement of the mouth. Additionally, the eyes and pectoral fins were displaced posteriorly. In the opposite direction, the remaining species were equally distributed located with short heads, rounded profiles, and small mouths (Figs. 3-4).

The dendrogram based on the distances of Mahalanobis showed that *Chuco intermedium* and *Cincelichthys pearsei* differed the most in body shape, respectively. The

remaining species formed two groups: one composed of *Paraneetroplus bulleri*, *Rheoheros lentiginosus*, and *Theraps irregularis* and another composed of *Maskaheros argenteus*, *Oscura heterospila*, which associate with *Wajpamheros nourissati*, *Vieja hartwegi*, while *Kihnichthys ufermanni* was the most different species of the group. Finally, the phylogenetic signal value of the K_{mult} statistic was 0.76466, with a significance value of $P=0.3078$ and no significant effect of phylogeny in body shape under the Brownian motion evolutionary model (Fig. 5).

Discussion

In the pPCA, species were mainly placed in morphospace based on body length and depth, followed by variation in the cephalic region, with changes in head size and profile, mouth position and size, and eye position. Additionally, some morphological changes were evident in the position and size of the fins. The variation observed in these morphological characteristics has been closely associated with the environment, locomotion, and feeding of fish (Wootton 1990; Fugi 1993; Muschick et al. 2012). In African and South American cichlids, variation in these morphological characteristics has been fundamental to adaptive radiation events because it allowed phenotypic and lineage diversification through the exploitation of ecological opportunities (Kocher et al. 1993; Cooper et al. 2010; Muschick et al. 2014; Arbour and López-Fernández 2016). The morphological body variation patterns observed in South American cichlids are like variation patterns observed in species of the *Theraps-Paraneetroplus* clade, thereby supporting the hypothesis of Mesoamerican cichlid diversification via ecological opportunity proposed in several previous works (Arbour and López-Fernández 2016; Říčan et al. 2016).

In the morphospace and similarity analysis, the most evident groupings were *Theraps irregularis*, *Rheoheros lentiginosus*, and *Paraneetroplus bulleri*, which present an elongated body and caudal peduncle as well as pelvic fins positioned ventrally. Ecomorphological studies have reported their characteristics being functionally associated with environments where the current velocity is high (Lowe-McConnell 1991; Pease et al. 2012). Elongated bodies are more hydrodynamic and fins in a ventral position permit fish to remain attached to the substrate and have more stability (Gatz 1979; Pease et al. 2012). Soria-Barreto and Rodiles-Hernández (2008) reported the same morphological pattern for *Theraps irregularis* and *Rheoheros lentiginosus* in the Lacandon rainforest (Montes Azules Biosphere Reserve, Mexico). Additionally, the mouth positions of the three species tend to be sub-terminal or ventral, which is associated with foraging for algae and invertebrates on the bottom, particularly on the surfaces of rocks with silt and sand substrates (Keast and Webb 1966; Miller et al. 2009; Artigas-Azas 2005b).

The group comprising *Oscura heterospila*, *Kihnichthys ufermanni*, *Maskaheros argenteus*, and *Cincelichthys pearsei* occupies another part of the morphospace. These species displayed deep bodies, short heads, shortened caudal peduncles, and mouths that were generally in a terminal position. These morphological characteristics are associated with environments where current velocity ranges from medium to slow, with different types of substrates (i.e., rock, gravel, sand, and mud). Although these species are generally

herbivorous and omnivorous, some may be detritivores (Miller et al. 2009; Soria-Barreto and Rodiles-Hernández 2008; Říčan et al. 2016). Among those previously described with an intermediate morphology, *Vieja hartwegi*, *Chuco intermedium*, and *Wajpamheros nourissati* present shallow elongated bodies and shortened caudal peduncles except for *Vieja hartwegi*, which has a deep body and moderately elongated caudal peduncle.

However, these species generally share the same distribution patterns and inhabit areas where the current velocity is high to moderate (Miller et al. 2009; Pease et al. 2012; McMahan et al. 2015; Říčan et al. 2016). Additionally, these species present more ventral snouts that facilitate feeding on aquatic invertebrates, detritus, algae, and vegetation (Soria-Barreto and Rodiles-Hernández 2008).

The case of *Wajpamheros nourissati* is very interesting because it is the only species that has long and thick lips, which is a characteristic associated with feeding between cracks, on rock surfaces, and the substrate (Winemiller et al. 1995; Artigas-Azas 2005a; López-Fernández 2014; Říčan et al. 2016). This characteristic has been reported in the cichlids of Middle and South America, which feed on benthic components and live in habitats with a variety of substrates including sand, silt, and organic matter in fine and coarse particles (Barlow and Munsey 1976; Moreira and Zuanon 2002; Hahn and Cunha 2005; Elmer et al. 2010; López-Fernández et al. 2012). Additionally, *W. nourissati* has well-developed pectoral fins that help to provide stability in habitats with currents of moderate velocity (Allgayer 1989).

Although body shape low phylogenetic signal and its expression is associated with ecological factors, it is interesting that species of both clades (*Theraps-Paraneetroplus*) mainly exhibited high convergence in the variation associated with body length and depth. The only exceptions to this were *Oscura heterospila* and *Theraps irregularis*, which were positioned at the extremes of the morphospace, while the remaining species showed a low margin of variation (Figures 2 and 3). Elmer et al. (2010) reported on the ecological, morphological, and phylogenetic diversification associated with two species of cichlids inhabiting Lake Apoyeque in Nicaragua. In this study, the genetic differentiation between the two species indicated that genetic differentiation was weak and ecomorphological characteristics (i.e., body shape, head width, size, pharyngeal jaw shape, and stomach contents) differed considerably, thereby suggesting that these species occupy different ecological niches. Additionally, in cichlids of the tribe Eretmodini from Lake Tanganyika, tooth morphology is associated with differences in diet and behavior (Rüber et al. 1999). Furthermore, studies of other fish groups reported that morphological variation shows a high phylogenetic signal, which suggests that the evolutionary history of these groups is shared among lineages (Tavera-Vargas 2012).

In contrast, the variation associated with the cephalic region revealed that most species occupy a position in the morphospace that corresponds to the clade to which they belong. For example, members of the *Theraps* clade (i.e., *Cinzelichthys pearsei*, *Chuco intermedium*, *Kihnichthys ufermanni*, and *Theraps irregularis*) are positioned toward the superior part of the morphospace, while members of the *Paraneetroplus* clade (i.e.,

Maskaheros argenteus, *Oscura heterospila*, *Paraneetroplus bulleri*, and *Rheoheros lentiginosus*) are located toward the lower region. However, the convergence between the two clades was also observed here, mainly in the variation of the cephalic characteristics of *Vieja hartwegi* and *Wajpamheros nourissati*. Comparative studies are revealing patterns of rapid diversification between lineages and phenotypes through habitat- and diet-related morphological diversity (Arbour and Lopez-Fernandez 2016). Furthermore, it has been shown that the early radiation of certain Neotropical cichlid tribes in South America occurred rapidly, which resulted in a pattern of conflicting divergence (López-Fernández 2013; Astudillo-Clavijo et al. 2015).

Based on the analysis of body shape and head features, the absence of congruence in the ordering of species in the morphospace supports the ecomorphological classification described by Říčan et al. (2016). However, functional independence between the cephalic and postcranial regions was identified for Middle American cichlids. For the cephalic region, the occurrence of five ecomorphs associated with feeding behavior was identified. Meanwhile, the postcranial region showed the lentic and lotic ecomorphs associated with the environment. In both instances, molecular phylogeny proved the recurrent evolution of diverse cephalic and postcranial ecomorphs among Mesoamerican cichlids (Říčan et al. 2016). Additionally, modularity has been considered an evolutionary factor leading to patterns of variation among cichlids. Modularity studies in African cichlids have centered on modules associated with feeding, where those species that feed by suction have functional modules and those that feed by foraging have developmental modules (Parsons et al. 2012).

Based on the results, species of the *Theraps-Paraneetroplus* clade show highly varied and convergent morphologies that are largely promoted by ecological factors associated with habitat and feeding preferences (Albertson and Kocher 2001; McKaye et al. 2002; Kassam et al. 2003; López-Fernández et al. 2013; Říčan et al. 2016). Body size and depth are features that seem undetermined by phylogenetic relationships, whereas the head features of most species exhibit patterns of variation associated with their phylogeny. However, further analyses of the shape, role, and evolution of these morphological attributes are necessary to understand their significance in the diversification of Mesoamerican cichlids.

Conclusions

The morphological variation of the *Theraps-Paraneetroplus* clade was divided into three groups within the morphospace. These variations are related to body length, body height, head, position, mouth, and eye size. Notably, *Wajpamheros nourissati* was the most different species due to its feeding-related characteristics. No phylogenetic signal was found for body shape, which is evident when considering body size and height as the variables that describe the position of the species in the morphospace. Future morphological evolution studies should consider cranial structures related to the capture and processing of food.

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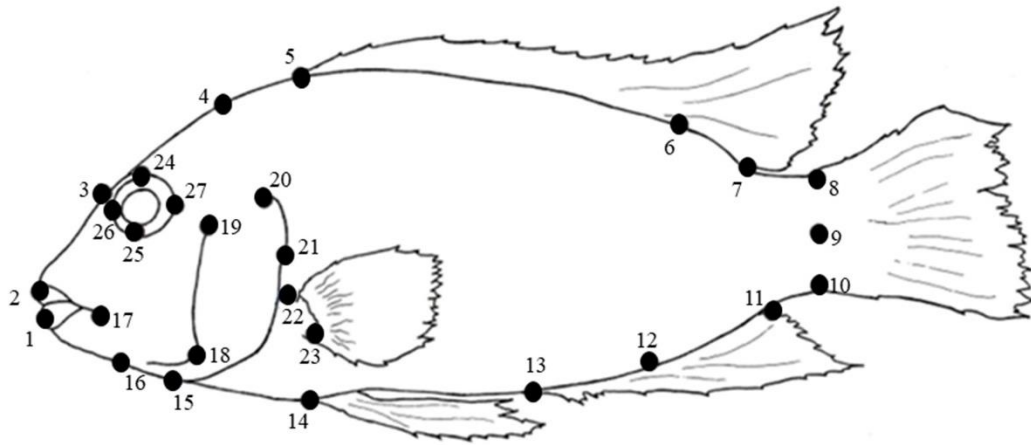


Figure 1. Location of landmarks in species of the *Theraps-Paraneetroplus* clade (image taken from Mejia et al. 2015). 1. Anterior end of the lower maxilla 2. Anterior end of the upper maxilla 3. Length of the ascending premaxillary process 4. End of the supraoccipital bone 5. Start of the dorsal fin 6. Last spine of the dorsal fin 7. End of the dorsal fin 8. Upper boundary of the caudal fin 9. Center of the caudal fin 10. Base of the caudal fin 11. End of the anal fin 12. Last spine of the anal fin 13. Origin of the anal fin 14. Origin of the pelvic fin 15. Lower end of the operculum 16. Posterior end of the lower maxilla 17. Posterior end of the upper lip 18. Maximum point of curvature at the preoperculum 19. Upper end of the preoperculum 20. Upper end of the operculum 21. Most posterior end at the operculum 22. End of the pectoral fin 23. Origin of the pectoral fin 24. Upper extreme of the sphenotic orbit 25. Base of the sphenotic orbit 26. Left extreme of the sphenotic orbit 27. Right extreme of the sphenotic orbit.

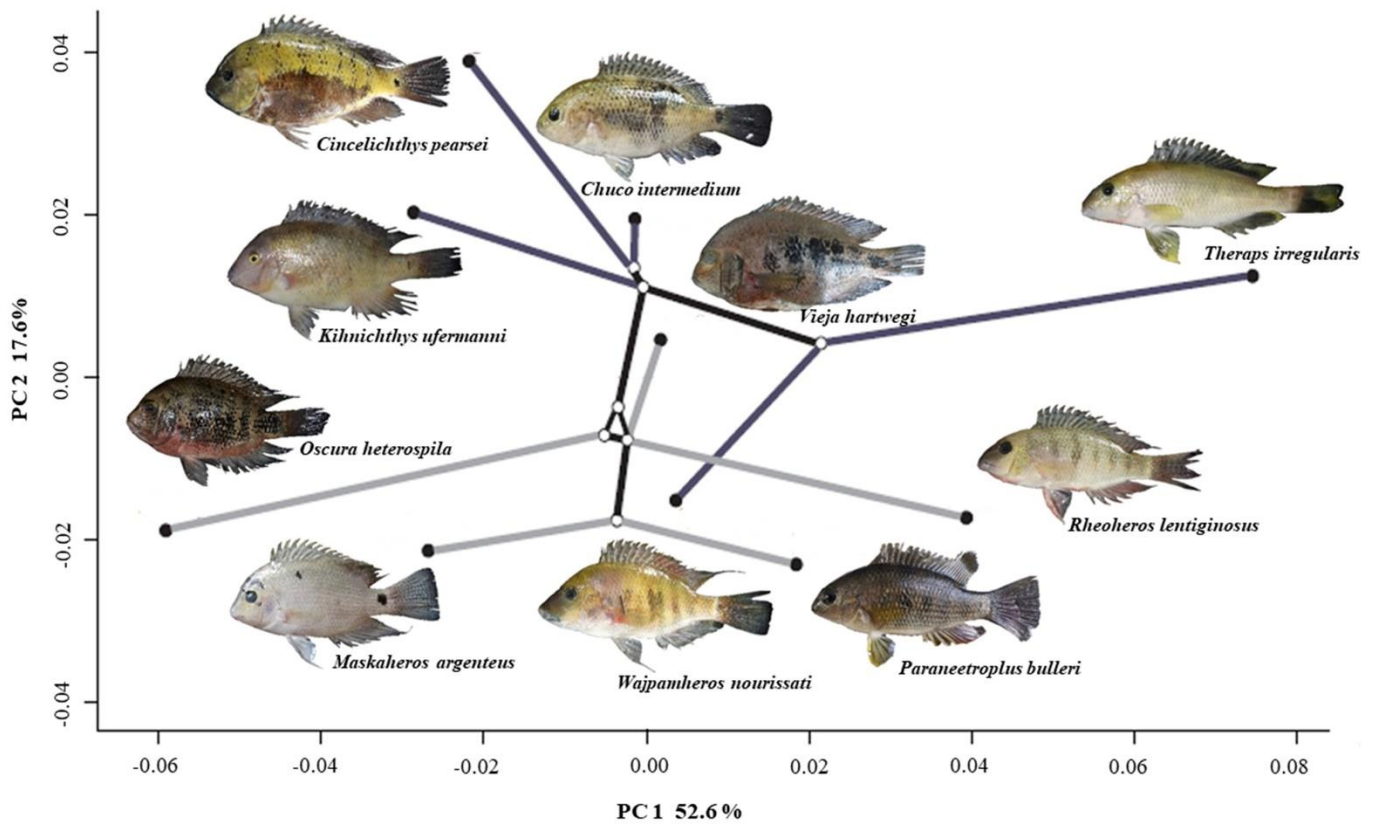


Figure 2. Principal component analysis 1 and 2. Species with elongated body located in the positive part of component 1, while in the positive part of component 2 species with deep body located in the positive part of component 2.

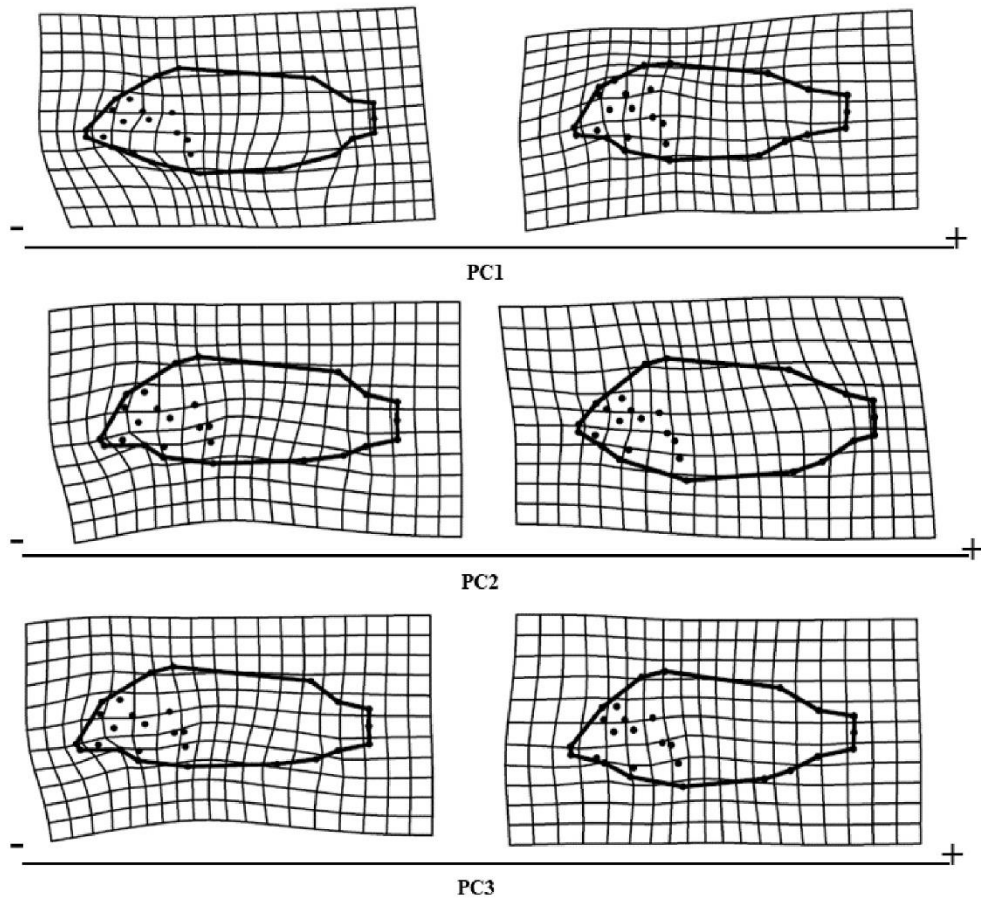


Figure 3. Deformation grids of principal components 1, 2 and 3. Left side negative and right side positive, changes were observed in the anterior part of the body.

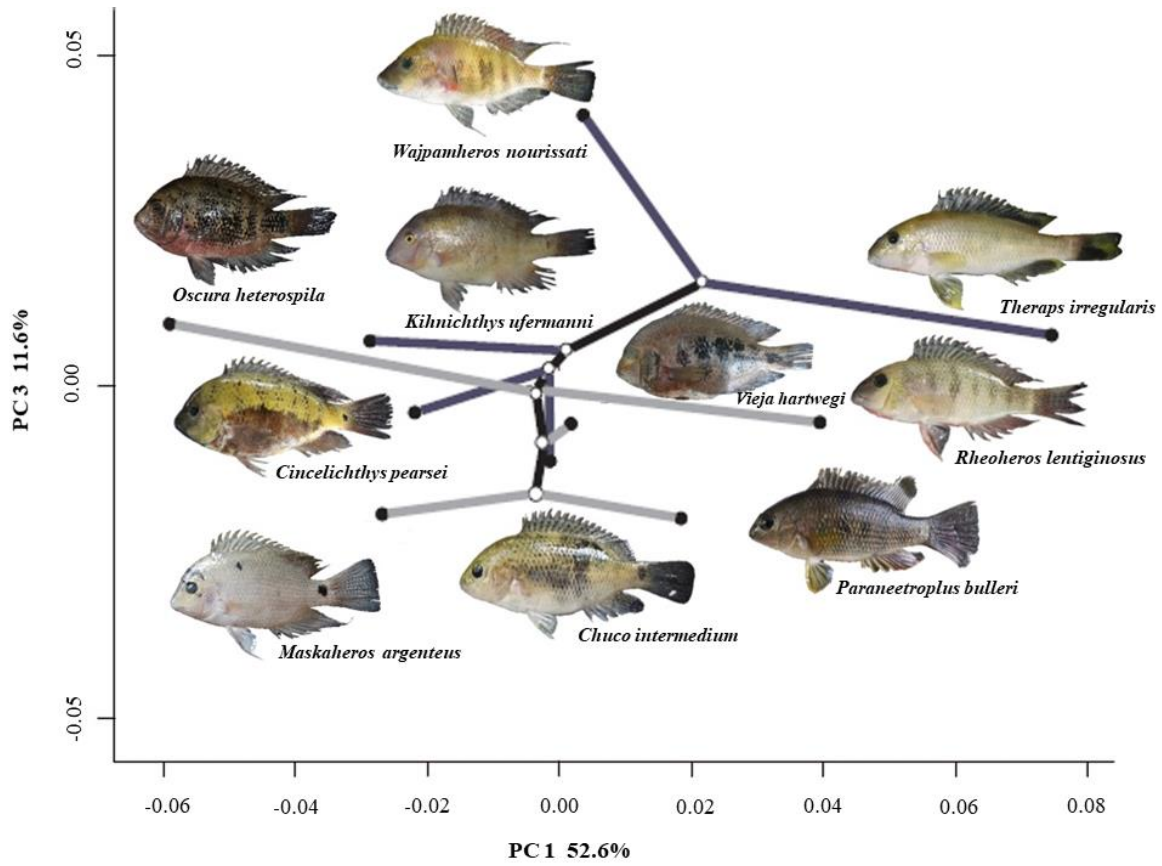


Figure 4. Principal component analysis 1 and 3, in the positive part of component 3 *Wajpamheros nourissati* stands out from the rest of the species.

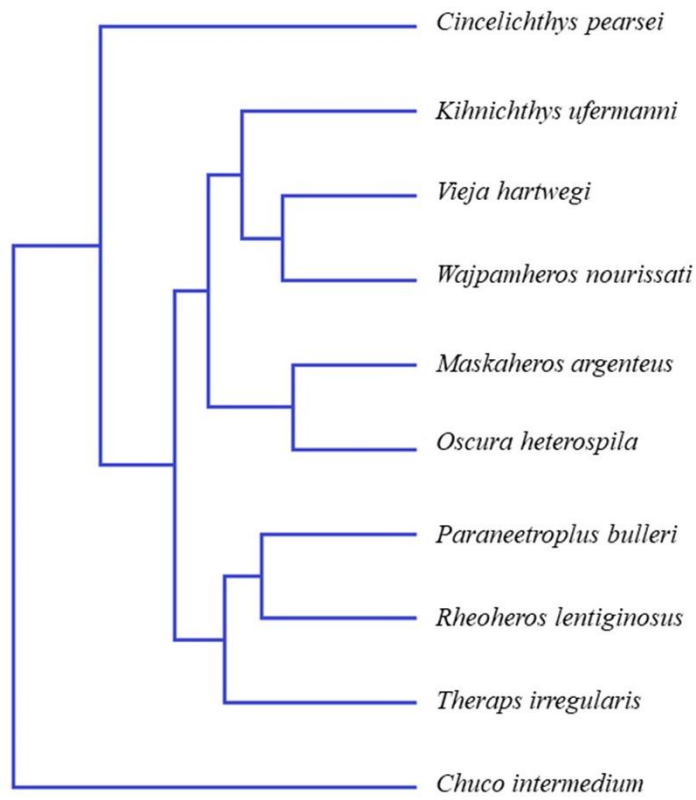


Figure 5. Dendrogram with the species of the *Theraps-Parannetroplus* clade, obtained from the distances of Mahalanobis and UPGMA.

CAPÍTULO 3. CONCLUSIONES

Los cambios morfológicos entre las especies analizadas se presentan en longitud, altura del cuerpo, cabeza, posición, tamaño de boca y posición de los ojos. A partir de esta variación morfológica se lograron distinguir tres grupos principales en el morfoespacio. El primero integrado por *Theraps irregularis*, *Rheoheros lentiginosus* y *Paraneetroplus bulleri*, donde el cuerpo y pedúnculo caudal son alargados. El segundo grupo está formado por *Oscura heterospila*, *Kihnichthys ufermanni*, *Maskaheros argenteus* y *Cincelichthys pearsei*, especies que presentan cuerpo alto, cabeza corta, pedúnculo caudal corto y boca en posición terminal. Por último, *Chuco intermedium*, *Vieja hartwegi* y *Wajpamheros nourissati*, presentando un cuerpo alto y pedúnculo caudal corto a levemente alargado. *Wajpamheros nourissati* representa una forma única, esta especie es morfológicamente muy diferente, sobresale del resto por presentar labios gruesos, característica que se relaciona con la captura del alimento. La morfología del cuerpo entre los grupos encontrados además de ser muy parecida también coincide con el hábitat que las especies ocupan. Las evidencias morfológicas son contundentes, es claro que la diversificación del clado *Theraps-Paraneetroplus* se relacionó con el uso del hábitat y explotación de los recursos alimentarios, lo que se manifiesta en la constante morfología convergente de las especies.

En la forma del cuerpo se encontró baja señal filogenética, ocurre cuando las especies presentan una expresión fenotípica muy diferente. Esto es más evidente al considerar el tamaño y altura del cuerpo como las variables que describen la posición de las especies en el morfoespacio. No obstante, al considerar la morfología craneal, existe un ordenamiento que parece estar asociado a la filogenia. Se recomienda llevar a cabo análisis con otras estructuras morfológicas que ayuden a comprender aún más la forma, función y evolución de dichas características, así como la importancia y diversificación de los cíclidos mesoamericanos. Particularmente, se recomienda realizar estudios de evolución morfológica considerando estructuras craneales relacionadas con la captura y procesamiento del alimento.

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