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BIOGEOGRAFÍA HISTÓRICA DE LA ICTIOFAUNA DE LA MESA DEL NORTE EN MÉXICO

TESIS

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Que presenta la:

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Resumen

México es uno de los países megadiversos, con un alcance considerable en diversidad y mayor grado de endemicidad en la diversidad de peces en comparación con otros países o regiones, incluyendo más de 506 especies descritas, representando aproximadamente 60% de la fauna de peces conocida para toda Norteamérica. Esto es aún más relevante si se toma en cuenta que recientes estudios filogenéticos en especies co-distribuidas de peces de agua dulce ampliamente distribuidos en el Norte de México (*Campostoma ornatum*, *Codoma ornata*, el género *Gila* y *Pantosteus plebeius-nebuliferus*) indican una subestimación de la riqueza de especies, con un importante número de especies aún por describir, además de sugerir que la historia evolutiva de estos grupos podrían tener congruencia geográfica y temporal. Esta tesis doctoral tiene como objetivo general; aplicar métodos probabilísticos para obtener las historias biogeográficas de peces co-distribuidos en la Mesa del Norte y la Sierra Madre Occidental (SMO) en México. Se usarán genes mitocondriales y nucleares para responder cuestionamientos acerca de la historia evolutiva de peces dulceacuícolas habitantes del noroeste de México, específicamente: a) la diversidad genética y los patrones filogeográficos de las poblaciones sureñas de *Pimephales promelas*, así como la inferencia de su historia evolutiva; b) la comparación de las historias biogeográficas de peces dulceacuícolas de amplia distribución en la Mesa del Norte y la SMO: *C. ornata*, *C. ornatum*, el grupo de *Gila* del desierto de Chihuahua (CDGG, por sus siglas en inglés) y *P. plebeius-nebuliferus*.

En el capítulo I, se estudia la diversidad genética en las poblaciones sureñas de *P. promelas* y se aporta información sobre la existencia de cuatro linajes genéticos bien diferenciados (Casas Grandes, Santa María, Yaqui y Nazas+Conchos). La composición y

distribución de los linajes encontrados es consistente con la hipótesis de la fragmentación del sistema ancestral del Río Grande, debido a la influencia de eventos tectónicos y climáticos.

A su vez, en el capítulo 2 se obtienen y comparan las historias evolutivas de *C. ornata*, *C. ornatum*, *P. plebeius-nebuliferus* y el CDGG, buscando patrones evolutivos compartidos en tiempo y espacio. Con base en los resultados obtenidos, la historia biogeográfica de la mayoría de los grupos parece estar más afectada por sus características biológicas o ecológicas que por los eventos paleohidrológicos *per se*. La mayoría de los eventos biogeográficos (compartidos e independientes) que afectaron a los grupos estudiados, parecen estar relacionados con eventos de dispersión y especiación por efecto fundador, asociados con la formación y evolución de la SMO y la acumulación de basaltos alcalinos causada por la actividad tectónica. Esto es congruente con lo que se ha observado en otros peces de agua dulce en el noroeste de México.

La presente tesis doctoral, además, discute la posibilidad de dividir la provincia de la Mesa del Norte en subprovincias acordes a los patrones filogeográficos y biogeográficos encontrados en este trabajo y en trabajos anteriores, de manera que corresponda tanto a la historia evolutiva de los organismos como a la distribución geográfica actual.

Palabras Clave: Filogeografía, peces de agua dulce, noroeste de México, historia evolutiva, patrones concordantes.

Abstract

Mexico is one of the megadiverse countries, with a considerable scope in diversity and a greater degree of endemicity in the diversity of fish compared to other countries and regions, including more than 506 described species, representing approximately 60% of the fish fauna known to all of North America. This is even more relevant if we take into account that recent phylogenetic studies in co-distributed freshwater fish species widely distributed in northern Mexico (*Campostoma ornatum*, *Codoma ornata*, genus *Gila*, and *Pantosteus plebeius-nebuliferus*), indicate an underestimation of species richness, with a significant number of species still to be described, and also suggesting that the evolutionary histories of these groups might have a geographical and temporal congruence. The general objective of this doctoral thesis is to apply probabilistic methods to obtain biogeographic histories in fish co-distributed in the Mesa del Norte and Sierra Madre Occidental (SMO) in Mexico. Mitochondrial and nuclear genes will be used to answer questions about the biogeographic history of freshwater fish inhabitants of northwestern Mexico, specifically: a) the genetic diversity and phylogeographic patterns of the southern populations of *Pimephales promelas*, as well as the inference of his history evolutionary; b) the comparison of the biogeographic histories in freshwater fish of wide distribution in Mesa del Norte and SMO: *C. ornata*, *C. ornatum*, Chihuahuan Desert group of the genus *Gila* (CDGG), and *P. plebeius-nebuliferus*.

Chapter 1 studies the genetic diversity in the southern populations of *P. promelas* provided information on the existence of four well-differentiated genetic lineages (Casas Grandes, Santa Maria, Yaqui, and Nazas+Conchos). The composition and distribution of

the lineages found are consistent with the hypothesis of the fragmentation of the ancestral system of the Río Grande, due to the influence of tectonic and climatic events.

In turn, chapter 2 the evolutionary histories of *C. ornata*, *C. ornatum*, *P. plebeius-nebuliferus*, and the CDGG are obtained and compared with each other, looking for evolutionary patterns shared in time and space. Based on the results obtained, the biogeographic history of these groups seems to be more affected by the biological or ecological characteristic of the groups than the paleohydrological events *per se*. Most of the shared, as well as independent biogeographic events affecting the groups, seem to be linked to dispersal events and founder speciation events associated with the formation and evolution of the SMO and accumulation of alkaline basalts via tectonic activity. This is congruent with what has been observed in other freshwater fishes in northwestern Mexico.

The present doctoral thesis, also, discusses the possibility of dividing the province of Mesa del Norte into subprovinces according to the phylogeographic and biogeographic patterns found in this work and previous works, so that it corresponds to both the evolutionary history of the organisms and the current geographical distribution.

I. Introducción

México es un país mega diverso, con considerable riqueza y representación de la diversidad de peces en el mundo (Espinosa *et al*., 2008). En particular, la ictiofauna dulceacuícola de México incluye más de 506 especies descritas, que a pesar de la extensión de su territorio, representa el 60% de la ictiofauna presente en Norteamérica (Miller *et al*., 2005). Alrededor de 117 (24%) de todas las especies mexicanas son peces dulceacuícolas primarios (Myers, 1938, 1949; Miller *et al*., 2005), 217 (44%) son secundarios y el resto (161 especies, 32%) son periféricos. Dicha riqueza se debe a diferentes factores como, la topografía sumamente variada dentro del territorio mexicano; historia geológica antigua y compleja; amplio intervalo latitudinal (de 32°33'N en el norte hasta 14°33'N en el sur); prolongado aislamiento del Centro de México (que incluye la importante fauna del Río Lerma-Santiago, con un alto porcentaje de endemismo) y a que se encuentra localizado geográficamente en el sistema fluvial más grande de América Central, el Río Grijalva - Usumacinta de México y Guatemala, totalmente tropical y su ictiofauna con alto grado de endemismo; y por encontrarse justo en la zona de transición entre las grandes biotas biogeográficas de origen neártico y neotropical (Miller, 1988; Miller *et al*., 2005). De las 16 ecorregiones dulceacuícolas en Norteamérica, nueve se encuentran en México (Revenga *et al*., 2000). Dentro de éstas regiones figuran por presentar un alto grado de endemismo en peces dulceacuícolas las del Río Colorado, Río Grande y Centro de México (Burr y Mayden, 1992).

Con base en los patrones actuales de distribución de los peces, así como evidencia geológica, climática o fósil (Miller, 1946, 1981; Hubbs y Miller, 1948; Hubbs *et al*., 1974; Miller *et al*., 2005), se han reconocido ocho provincias ictiofaunísticas en México (Miller,

1966; Miller y Smith, 1986; Smith y Miller, 1986). La presente investigación está enfocada la provincia ictiofaunística de la Mesa del Norte o Río Grande, esta provincia incluye además de la cuenca del Río del mismo nombre, un sistema de múltiples cuencas endorreicas que formaron parte de un único paleosistema hidrográfico (Schönhuth *et al*., 2015), llamado sistema ancestral del Río Grande (Fig. 1).

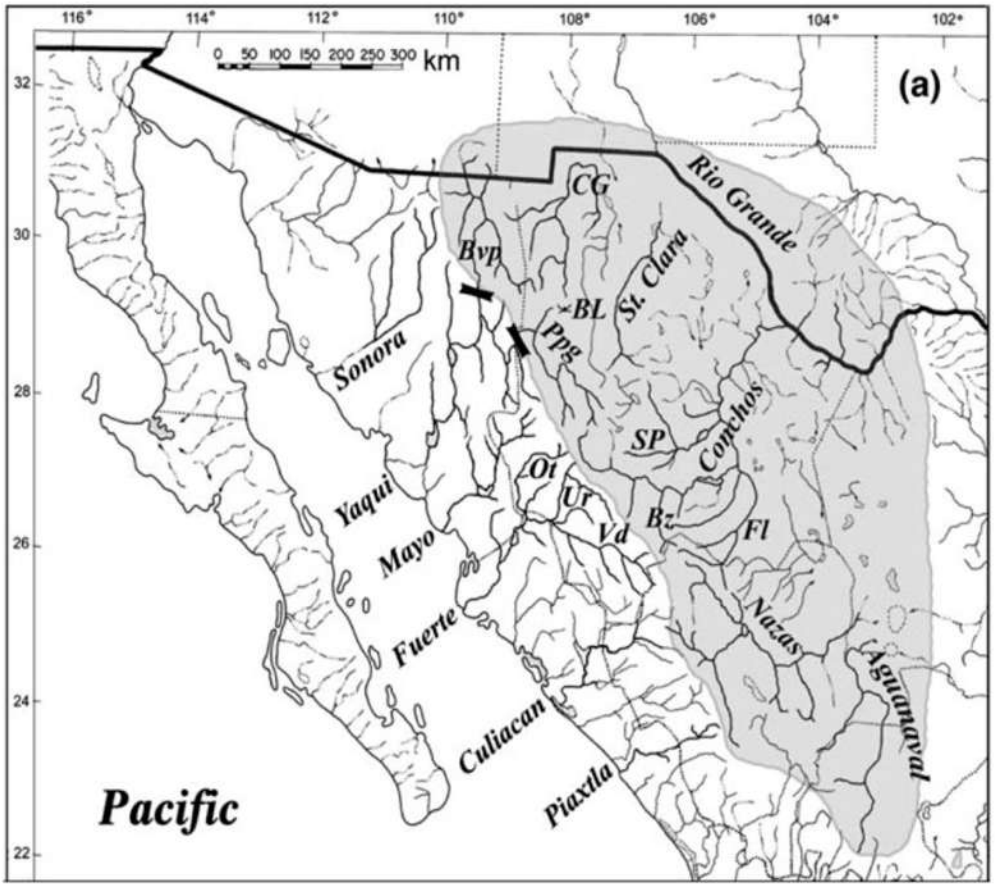

Figura 1. Zona hipotética correspondiente al sistema ancestral del Río Grande, así cómo fue descrito por Schönhuth et al. (2011). Abreviaturas: *CG*, Río Casas Grandes; *Bvp*, Río Bavíspe; *BL*, Laguna Bustillos; *Ppg*, Río Papigochic; *Ot*, Río Oteros; *SP*, Río San pedro; *Ur*, Río Urique; *Vd*, Río Verde; *Bz*, Río Balleza; *Fl*, Río Florido. (Tomado de Schönhuth *et al.,* 2011).

Asimismo, la Mesa del Norte presenta asociaciones (especies compartidas) con distintas cuencas hidrográficas de otras provincias, como es el caso de las cuencas de la vertiente noroeste del Pacífico mexicano (Miller *et al*., 2005). Esta delimitación poco clara, históricamente determinada por su composición ictiofaunística, sugiere que la distribución actual de la ictiofauna en la Mesa del Norte, se explica más claramente con base en las características geológicas históricas de la región que por los patrones hidrográficos modernos (Miller y Smith, 1986; Minckley *et al*., 1986; Smith y Miller, 1986; Miller *et al*., 2005).

Se ha formulado la hipótesis de que los patrones filogenéticos y la distribución geográfica de linajes co-distribuidos de los géneros *Dionda*, *Cyprinodon*, *Campostoma*, *Gila* y *Codoma*, son consistentes con hipótesis geológicas y climáticas que respaldan la existencia y/o fragmentación de un sistema de drenaje ancestral, que conectaba en el pasado a drenajes actualmente independientes en el Norte de México (Mayden *et al.,* 1992; Echelle *et al*., 2005, Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2006, 2011, 2012a, 2014, 2015).

I.1. Norte de México

El Norte de México abarca desde la frontera norte con Estados Unidos hasta aproximadamente la latitud 22ºN en los estados de Zacatecas y San Luis Potosí, abarcando climas calientes semiáridos (Bsh), calientes del desierto (BWh) o fríos semiáridos (BSk) con base en la clasificación climática de Köppen (1936). Con vegetación predominante de matorrales de zonas áridas y semiáridas, selvas secas, pastizales, vegetación halófita o bosques de coníferas o encinos (INEGI, 2008).

En el Norte de México se encuentran dos provincias ictiofaunísticas: 1) La Mesa del Norte (que contiene la extensa área del desierto de Chihuahua en México) y 2) La provincia de las cuencas de la vertiente del Pacífico noroeste (en la zona de la Sierra Madre Occidental y las vertientes del pacífico noroeste). La zona que abarca estas dos provincias ictiofaunísticas está localizada en el centro-norte de México (de 22° a 32° N y de 102° a 112° O), e incluye drenajes importantes como los ríos Yaqui, Mayo, Fuerte y Mezquital en la vertiente del Pacífico de la Sierra Madre Occidental; drenajes endorreicos como los ríos Nazas y Aguanaval, y las subcuencas de la Cuenca de Guzmán y el Río Conchos en la vertiente atlántica (Schönhuth *et al*., 2015).

I.1.1. *Hipótesis paleohidrológica para el Norte de México*

Estudios filogeográficos y biogeográficos en peces de amplia distribución en el Norte de México han mostrado una estrecha relación evolutiva entre las cuencas de la provincia ictiofaunística de la Mesa del Norte y la provincia ictiofaunística de la vertiente del Pacífico noroeste (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011, 2012a, 2014, 2015; Corona-Santiago *et al*., 2018). Relacionada con la existencia de un sistema extendido del Río Grande en la Mesa del Norte y las relaciones de este sistema ancestral con cuencas de la vertiente pacífica a ambos lados de la SMO.

La hipótesis paleohidrológica del paleosistema del Río Grande (Smith y Miller, 1986) menciona que este sistema ancestral surgió durante el Oligoceno al mismo tiempo que la SMO empezó a formarse, su fragmentación habría empezado durante el Mioceno (6.4 Millones de años) relacionada con los eventos tectónicos que dieron como resultado la apertura del Golfo de California (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*.,

2011, 2012a, 2014, 2015; Corona-Santiago *et al*., 2018). La fragmentación del sistema extendido del Río Grande por eventos tecto-volcánicos y climáticos se habría extendido hasta el Plioceno y Pleistoceno. Igualmente se habrían dado relaciones entre cuencas por contactos segundarios y capturas de cuencas durante el Pleistoceno, modelando de esta forma la distribución actual de los peces de agua dulce de la región.

Además de esto, Smith y Miller (1986) propusieron una hipótesis paleohidrológica relacionada con la existencia y fragmentación del paleolago Cabeza de Vaca durante el Pleistoceno. El Lago pluvial Cabeza de Vaca fue una enorme cuenca interior formada por agua y sedimentos del Río Grande y otras corrientes permanentes hacia el sur y el oeste (Axtell, 1977), surgió durante el Cenozoico temprano por eventos tectónicos en Texas, Nuevo México y el Norte de México (Strain, 1970) y se extendía por vastas áreas del sur de Nuevo México, el oeste de Texas y el norte de Chihuahua (Strain, 1970; Axtell, 1977).

El drenaje y fragmentación del paleolago Cabeza de Vaca habría sido causado por eventos tectónicos durante el Pleistoceno medio, (Reeves, 1965; 1969; Strain, 1966; Corona-Santiago *et al*., 2018), formando el curso actual del Río Bravo en México y la formación del Lago Palomas en el noroeste de México (Rosenthal y Forstner, 2014; Wood y Mayden, 2002; Corona-Santiago *et al*., 2018). El Lago pluvial Palomas al fragmentarse por eventos climáticos durante el Pleistoceno, formaría varios ríos endorreicos, lagunas y manantiales (Corona-Santiago *et al*. 2018), entre ellos las actuales subcuencas que hacen parte de la Cuenca de Guzmán en el noroeste de México.

I.2. Peces de agua dulce analizados en este estudio: *Codoma ornata*, *Campostoma ornatum*, *Pimephales promelas*, el grupo de *Gila* del desierto de Chihuahua y *Pantosteus plebeius-nebuliferus*

I.2.1. *Sistemática, taxonomía y características generales de los ciprínidos Codoma. ornata, Campostoma ornatum, Pimephales promelas y el grupo de Gila del desierto de Chihuahua*

Los peces agrupados en este apartado, pertenecen al orden Cypriniformes, uno de los grupos más diversos en especies dentro de Actinopterygii. Dentro del orden Cypriniformes la familia más numerosa es la Cyprinidae, con 3170 especies (Eschmeyer *et al*., 2017), clasificadas en 377 géneros (Eschmeyer y Fong, 2015; Froese y Pauly, 2017; Adeoba *et al*., 2018). Las especies de esta familia se encuentran principalmente en África, Europa, Asia y América del Norte (Thai *et al*., 2007; Adeoba *et al*., 2018), la mayor diversidad de las especies del grupo está en el sureste asiático (Miller *et al*., 2005). La mayoría de los ciprínidos son pequeños, normalmente de 30 a 75 mm de largo, aunque algunos crecen a 2.5 m o más. Todos tienen de una a tres hileras de dientes faríngeos y mandíbulas sin dientes (Miller *et al*., 2005). La familia Cyprinidae está clasificada en dos subfamilias, Leuciscinae y Cyprininae (Cavender y Coburn, 1992; Miller *et al*., 2005), aunque en Norteamérica sólo se encuentran representantes de la subfamilia Leuciscinae (Miller *et al*., 2005).

Codoma ornata, *C. ornatum*, el grupo de *Gila* del desierto de Chihuahua y *Pimephales promelas* pertenece a la subfamilia Leuciscinae, uno de los grupos más grandes y más diversos dentro del suborden Cyprinoidei, con 672 especies clasificados en 90 géneros (Eschmeyer *et al*., 2017; Schönhuth *et al*., 2018), distribuidas en América del Norte

y el norte de Eurasia (Bănărescu y Coad, 1991; Mayden, 1991; Mayden *et al*., 2009; Bufalino y Mayden, 2010).

Se han encontrado registros fósiles de ciprínidos del Paleoceno en Europa y del Eoceno en Asia (Cavender, 1986). En México, los fósiles más antiguos corresponden al Plioceno. Sin embargo, la diferenciación genética y rango de expansión de los géneros del sur; así como el comportamiento reproductivo de los ciprínidos habitantes de tierras subtropicales de la vertiente del Atlántico, más parecidos a las de las carpas del Neártico, sugiere que existieron ciprínidos en México hace más de 5 millones de años postulados (Miller *et al*., 2005).

a. *Codoma ornata*

Codoma ornata (Fig. 2) es un ciprínido endémico de México, en la vertiente del Atlántico y cuencas interiores se distribuye desde el alto y medio Río Conchos hacia el sur hasta los ríos Nazas y Aguanaval), al este de la Sierra Madre Occidental; mientras que en la vertiente del Pacífico, al oeste de la Sierra, en las cabeceras de los ríos Yaqui, Mayo, Fuerte y Mezquital (Miller *et al*., 2005; Schönhuth *et al*., 2015).

Es típico de arroyos de agua clara y frías (7-18°C), de corriente rápida a moderada (puede ser lenta o ausente al final de la época de estiaje), sobre fondos de arena, roca y grava, a profundidades de 1 m aproximadamente, por lo general menos. La vegetación principal consiste en algas verdes sobre rocas. Rara vez se presenta en elevaciones menores de 1500 m, excepto en ríos grandes (Miller *et al*., 2005).

C. ornata fue descrito por Girard en 1856, en el Río Conchos (Río Chihuahua), cerca de la ciudad de Chihuahua, México. A partir de ahí, la clasificación taxonómica y relaciones filogenéticas de *C. ornata* han sido controversiales (Schönhuth *et al*., 2015). En el estudio

realizado por Contreras-Balderas (1975) se determinó a *C. ornata* como un complejo de múltiples subespecies o grupos morfológicos, y retuvo a *ornata* en el género *Notropis*. Estudios morfológicos (Contreras-Balderas, 1975; Mayden, 1989; Coburn y Cavender, 1992) y etológicos (Miller, 1976; Johnston y Vives, 2003) han considerado que el género *Codoma* es cercano a *Pimephales* (Miller, 1976; Miller *et al*., 2005).

Figura 2. *Codoma ornata* Girard 1856. Macho con sus característicos tubérculos nupciales en la época reproductiva. Modificado de http://www.fishbiosystem.ru /CYPRINIFORMES/Cyprinida /Codoma_ornata2.html

El género *Codoma* fue incluido después de su descripción en el género *Notropis* por Woolman (1894) y referido después al subgénero *Cyprinella* por Gibbs (1957). Para

posteriormente ser identificado como un género monotípico por Miller (1976), y Mayden *et al*. (1992).

Estudios morfológicos y de comportamiento reproductivo ubicaron a *Cyprinella* dentro del género *Codoma* (Miller, 1978; Minckley y Vives, 1990). Igualmente, evidencia osteológica y datos moleculares basados en secuencias del gen mitocondrial cyt *b* (Mayden, 1989, 2002), determinaron a *C. ornata* como una especie dentro del género *Cyprinella*.

El género *Codoma* fue agrupado dentro de un mismo clado con otros nueve géneros (*Lythrurus, Luxilus, Pteronotropis, Pimephales, Opsopoeodus, Ericymba, Erimonax, Hybopsis* y *Tampichthys*) (Mayden, 1989; Mayden *et al*., 2006; Schönhuth y Mayden, 2010; Schönhuth *et al*., 2018).

En un estudio molecular reciente (Schönhuth *et al*., 2018) en el que se usaron secuencias de genes mitocondriales (cyt *b* y *COI*) y nucleares (*Rag1* y *IRBP*), se agrupó a *Codoma* dentro de un mismo clado con *Tampichthys* y a este clado, *Codoma-Tampichthys,* como grupo hermano del clado de *Cyprinella* y del clado de *Pimephales-Opsopoeodus*; congruente con estudios anteriores que identificaron a *Codoma* como grupo hermano de *Tampichthys* (Schönhuth *et al*., 2008, 2015; Schönhuth y Mayden, 2010), y a este clado relacionado con *Cyprinella*, *Hybognathus* y *Notropis* del centro y sur de México y *Yuriria* (Schönhuth *et al*., 2006, 2008, 2015; Schönhuth y Mayden, 2010), y *Pimephales* (Schönhuth *et al*., 2015).

Con base en estudios morfológicos, en dónde se distinguen organismos por características como el número de radios de las aletas, tubérculos nupciales, colores de los machos durante la reproducción y forma del cuerpo, se sugirió que aunque el género es monotípico podría presentar tres o más especies (Miller *et al*., 2005).

Actualmente se considera a *Codoma* como un género monotípico (Miller, 1976; Mayden *et al*., 1992; Miller *et al*., 2005; Schönhuth *et al*., 2015), con variaciones genéticas (Schönhuth *et al*., 2008, 2015; Schönhuth y Mayden, 2010), que han sido congruentes con los grupos morfológicos encontrados anteriormente por Contreras-Balderas (1975).

Schönhuth *et al*. (2015) realizaron análisis filogenéticos y de diversidad genética usando genes mitocondriales y nucleares, ratificando que *C. ornata* corresponde a un género monotípico con al menos cuatro linajes genéticos, con divergencias que van desde 0% a 9.8% para cyt *b*, 0.7% a 3.1% en *S7* y 0.2% a 0.8% en *Rag1*. Estos linajes genéticos están agrupados en las principales cuencas en dónde *C. ornata* habita: linaje del Alto Conchos (ríos Conchos, Fuerte, Mayo y Yaqui), linaje del Bajo Conchos + Peñon (ríos San Pedro, Florido y Peñon de Covadonga, y Laguna Bustillos), linaje Nazas (Río Nazas) y linaje del Alto Mezquital (Río Mezquital) (Schönhuth *et al*., 2015). A su vez, resolvieron la población más oriental de *C. ornata* en el Río Peñón de Covadonga (drenaje del Río Nazas) agrupado dentro del linaje Bajo Conchos, contrario a análisis morfológicos previos (Contreras-Balderas, 1975), dónde todas las poblaciones del Río Nazas estuvieron estrechamente relacionadas. Los linajes genéticos en *C. ornata* parecen tener una relación con la teoría de un sistema extendido del Río Grande en el Norte de México, cuya fragmentación por eventos tectónicos y climáticos habría causado la configuración de las cuencas tal y cómo las conocemos hoy en día.

b. *Campostoma ornatum*

C. ornatum o Rodapiedras mexicano (Fig. 3) es un ciprínido que habita una extensa zona que abarca desde el Río Bravo en la región del Big Bend, TX, en Estados Unidos, pasando a través de la cuenca del Río Conchos, las sub-cuencas pertenecientes a la Cuenca

de Guzmán (excepto, el Río Santa María), los ríos Yaqui, Mayo, Fuerte, Piaxtla y Sonora en la vertiente del Pacífico, hasta las cuencas de los ríos Nazas y Aguanaval en México (Miller *et al*., 2005; Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011), y en la parte superior del Río Culiacán (Schönhuth *et al*., 2011), correspondiendo a la población más sureña de las especies del género (Schönhuth *et al*., 2011).

Su hábitat se restringe principalmente a arroyos de pequeño a mediano tamaño de agua clara, con rápidos, caídas y remansos, con fondos de grava o arena (Burr, 1980; Miller *et al*., 2005); siendo común encontrarlo en las cabeceras de ríos y arroyos (Miller *et al*., 2005).

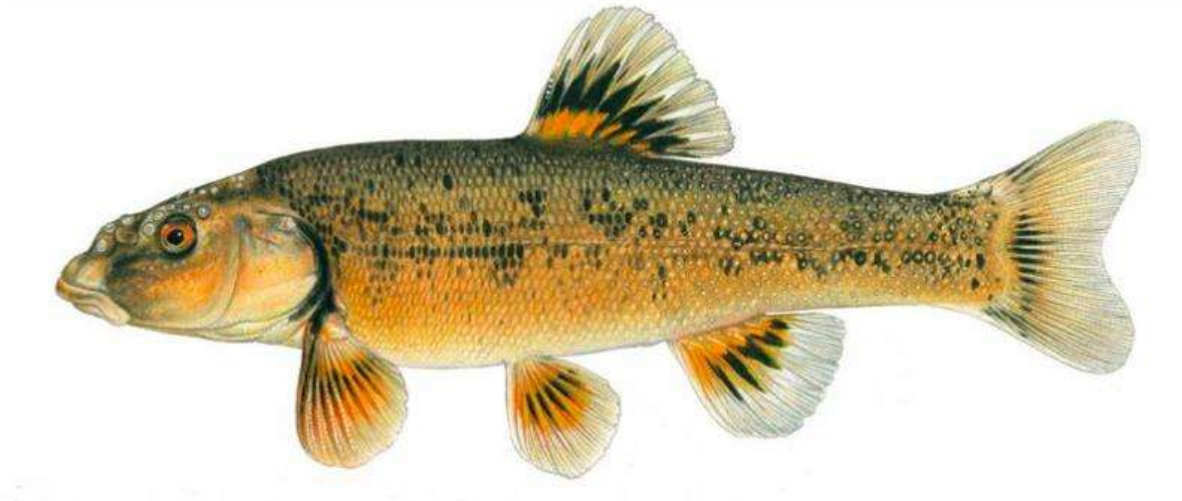

Figura 3. *Campostoma ornatum* Girard, 1856. Tomado de http://www.fishesoftexas.org/taxa /campostoma-ornatum.

El género *Campostoma* fue descrito por Agassiz (1855), quien erigió el género *Campostoma* para incluir *Rutilus anomalous* Rafinesque (1820), *Chondrostoma pullum* Agassiz (1854), así como otras 5 especies que habían sido recientemente descritas (Blum *et*

al., 2008). El género *Campostoma* fue posteriormente expandido, cuándo Girard (1856) incluyó algunos taxones adicionales (Blum *et al*., 2008).

En cuanto a las relaciones filogenéticas del género con otros ciprínidos habitantes de Norte América, se ha recuperado al género *Campostoma* como grupo hermano del género *Nocomis* (Simons y Mayden, 1999; Simons *et al*., 2003; Schönhuth *et al*., 2018). Algunos de los taxones descritos por Girard (1856) fueron sinonimizados con *C. pullum*; y posteriormente, Jordan y Evermann (1896) listaron 11 taxones como sinonimias para *C. anomalum*.

Cuatro especies son reconocidas actualmente: *Campostoma anomalum* (Rodapiedras del centro), *C. oligolepis* (Rodapiedras de gran escala), *C. ornatum* (Rodapiedras mexicano), y *C. pauciradii* (rodapiedras de aletas azules) (Blum *et al*., 2008).

C. ornatum es un ciprínido ampliamente variable merística y morfológicamente (Burr, 1976, 1980; Schönhuth *et al*., 2011), que fue descrito por Girard en 1856, en el Río Conchos (Río Chihuahua) y uno de sus tributarios (Girard, 1856). Dado que las poblaciones estadounidenses de *C. ornatum* son periféricas a su distribución principal, durante un tiempo se clasificó a la población aislada en Rucker Canyon, Montañas Chiricahua, Arizona (Bosque Nacional Coronado), como *Campostoma pricei* Jordan y Thoburn (Jordan y Evermann, 1896). De igual manera Minckley (1973) refirió a este grupo al nivel de subespecie como *C. ornatum pricei*.

Campostoma ornatum parece presentar características consideradas primitivas (e. g. reducción en los tuberculos cefálicos y el intestino rara vez se enrolla alrededor de la vejiga de gas) en comparación con otros miembros del género (Burr, 1976, 1980; Schönhuth *et al*., 2011).

Un estudio de diversidad genética (Buth y Burr, 1978), basado en isoenzimas, ubicó a *C. ornatum* como el miembro basal del género y sugirieron que varios rasgos morfológicos representan estados de carácter ancestrales (Schönhuth *et al*., 2011). Los análisis moleculares realizados por Blum *et al*. (2008) recuperaron a *C. ornatum* como linaje derivado, lo que indica que los rasgos diagnósticos exhibidos por la especie son apomorfías (i.e caracteres derivado de un estado ancestral), en lugar de estados ancestrales (Blum *et al*., 2008; Schönhuth *et al*., 2011).

Por otro lado, la evidencia de la amplia diversidad morfológica y merística (Burr, 1976), y la diferenciación genética mitocondrial (Blum *et al*., 2008) dentro de la especie, sugirió la hipótesis de que la especie podría estar compuesta por más de un linaje evolutivo (Schönhuth *et al*., 2011), hipótesis que fue comprobada por estudios moleculares posteriores usando genes mitocondriales y nucleares (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011).

En trabajos filogenéticos y filogeográficos previos se observó una marcada diferenciación filogenética (4.49-5.59% en cyt *b*, y 0.9-2.3% en *S7*) (Schönhuth *et al*., 2011), entre las poblaciones de *C. ornatum* del sur de la Mesa del Norte (ríos Nazas, Aguanaval, Piaxtla, Culiacán y el Alto Río Balleza) y las poblaciones habitantes de los ríos al Norte (ríos Yaqui, Fuerte, Conchos, Sonora, Ojo de agua, Mayo; así como los ríos Casas Grandes y Santa Clara en la Cuenca de Guzmán, y la Laguna de Bavícora) (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011). Los patrones de variación genética entre las poblaciones de *C. ornatum* parece tener una relación con la existencia y fragmentación del sistema extendido del Río Grande, así como eventos de contactos segundarios y capturas de cuencas en el Norte de México.

c. Grupo de *Gila* del desierto de Chihuahua

El género *Gila* forma un grupo de especies distribuidas en América del Norte y América Central; que aunque morfológicamente similares, presentan una gran variedad de formas corporales, tamaños y hábitats (pequeños arroyos a lagos y grandes ríos), y casos de posible hibridación (Schönhuth *et al*., 2014). *Gila* se ha agrupado junto con otros ciprínidos en el llamado "Clado occidental" (Coburn y Cavender, 1992; Simons y Mayden, 1998), agrupación altamente distintiva de peces que habitan ambientes áridos.

Este Clado Occidental incluye taxones que muestran altos niveles de endemismo y varios géneros monotípicos distintivos morfológicamente (Miller, 1959). La mayoría de las especies pertenecientes a este Clado corresponden al género *Gila* (Baird y Girard, 1853; Schönhuth *et al*., 2014). Posteriormente se hizo una revisión del Clado Occidental (Schönhuth *et al*., 2012b), usando análisis filogenéticos moleculares, y se obtuvo un Clado occidental más reducido que incluía un grupo denominado "linaje de *Gila*". Este linaje incluyó la mayoría de las especies de *Gila*, *Moapa* y *Acrocheilus* (Schönhuth *et al*., 2012b; Schönhuth *et al*., 2014).

Actualmente, se conocen al menos 19 especies descritas de *Gila*; de estas, once especies se distribuyen en el territorio mexicano (*G. diatenia*, *G. eremica*, *G. minacae*, *G. brevicauda*, *G. pulchra*, *G. nigrescens*, *G. conspersa*, *G. sp.*1*, G. modesta*, *G. pandora* y *G. purpurea*) (Schönhuth *et al*., 2014). En un estudio donde analizaron las relaciones filogenéticas del género *Gila* (Schönhuth *et al*., 2014), usando un gen mitocondrial (cyt *b*) y tres genes nucleares (*Rag1*, *S7* y *Rho*), se obtuvo un grupo monofilético con la mayoría de las especies de *Gila* de México (con excepción de *G. diatenia*, *G. eremica*, *G. minacae* y *G. pupurea*). Este grupo fue identificado como "Grupo del desierto de Chihuahua", e incluyó a

seis especies (*G. pulchra*, *G. brevicauda, G. modesta*-*G. pandora*, *G. nigrescens*, *Gila sp*. 1 y *G. conspersa*), los especímenes de *G. modesta* se resolvieron anidados en muestras de *G. pandora*, por lo que se presume que se trata de morfotipos más que de especies válidas (Schönhuth *et al*., 2014). Las seis especies de *Gila* integrantes del grupo monofilético del desierto de Chihuahua, presentaron patrones de distribución similares a los encontrados en estudios previos (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al.*, 2011, 2012a), con poblaciones bien diferenciadas en el norte y sur de la Mesa del Norte y SMO.

Gila sp. 1, recientemente identificada por Schönhuth *et al.* (2014), está restringida al Río del Tunal (cuenca del Río Mezquital). *G. brevicauda* se distribuye en los ríos Yaqui, Fuerte y Mayo, en la vertiente del Pacífico. *Gila nigrescens* es encontrada en el Alto Río Yaqui (Río Papigochic), la Cuenca de Guzmán (ríos Santa María, Del Carmen y Casas Grandes), Río Mimbres y las lagunas Bustillos y Bavícora. *G. conspersa*, se distribuye en las cuencas endorreicas de Nazas y Aguanaval, y en el Río Presidio, en la vertiente pacífica. *G. pulchra* es encontrada en el Río Conchos (especialmente en sus afluentes en el desierto de Chihuahua, Río Florido y Río San Pedro) y en el Río Fuerte (ríos Urique, Verde y Oteros). A su vez, *G. pandora y G. modesta* se distribuyen en los ríos Grande y San Fernando

d. *Pimephales promelas*

Pimephales promelas o la Carpita cabezona (Fig. 4) es un ciprínido distribuido ampliamente desde el Gran Lago de los Esclavos, y la bahía de Hudson en Canadá, el Valle del Misisipi, las Grandes Planicies, los arroyos de la vertiente del golfo en Alabama, y el Río Grande en Estados Unidos (Miller *et al*., 2005); hasta los ríos Yaqui, Conchos,

Nazas, la Cuenca de Guzmán (Meek, 1904; Vandermeer, 1966; Miller *et al*., 2005), y la Laguna Bustillos en México (Vandermeer, 1966; Miller *et al*., 2005).

Habita normalmente remansos lentos y aguas estancadas en arroyos medianos a grandes, de gradiente bajo a moderado, con flujo continuo (Miller *et al*., 2005). Su amplio patrón de distribución está asociado con su capacidad de sobrevivir y reproducirse bajo diferentes condiciones ambientales, incluyendo un amplio rango de temperatura, turbidez y oxígeno en el agua (Miller *et al*., 2005; NatureServe, 2012).

Fue descrito por Rafinesque en 1820, en un estanque cerca de Lexington, Kentucky, en los Estados Unidos. *Pimephales promelas* fue considerado un organismo politípico, con al menos dos especies reconocidas, *promelas* y *confertus* (Vandermeer, 1966). Esta última especie fue descrita por Girard en (1856) como *Hyborhynus confertus*, siendo reclasificada por Gilbert en (1884) como *Pimephales promelas confertus*. Hubbs y Black (1947), mencionaron la importancia de la variación geográfica en la clasificación de *P. promelas*. Dos años después Hubbs y Lagler (1949) clasificaron a *P. promelas* habitantes del Lago Superior en la Isla Royale, Michigan, Estados Unidos, como *Pimephales promelas harveyensis*. Taylor (1954), al analizar estudios morfológicos anteriores, consideró que *P. promelas* correspondía a una sola especie, ya que la variacion observada en esos estudios fue clinal.

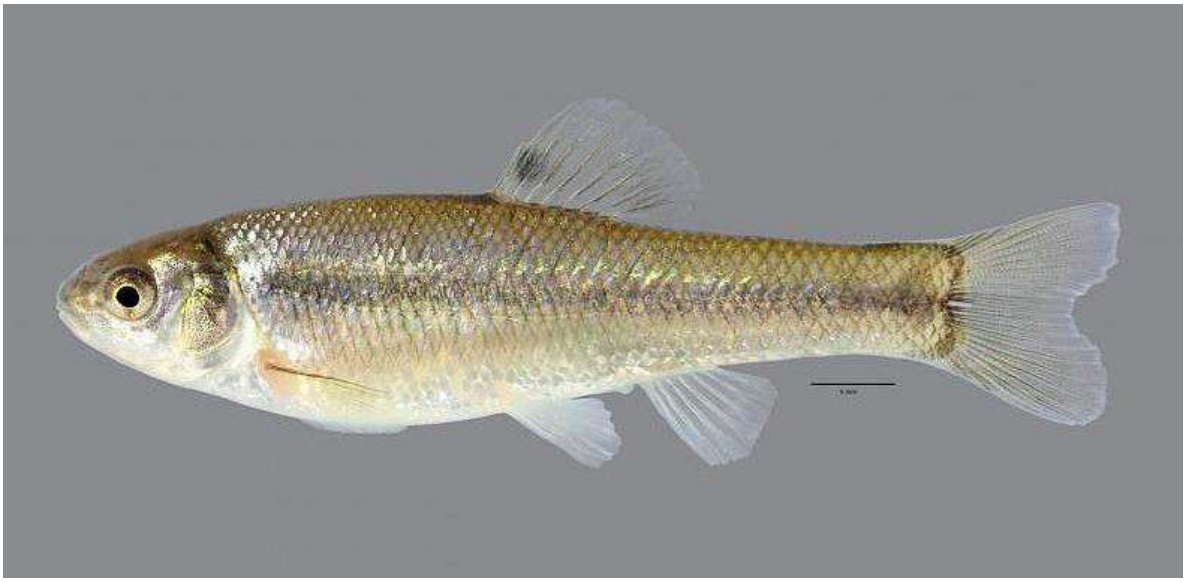

Figura 4. *Pimephales promelas* Rafinesque, 1820. Tomado de http://www.ittiofauna.org/webmuseum/pesciossei/cypriniformes/cyprinidae/pimephales/pimephales_promelas/p_promelas_big_2.htm

En cuanto a las relaciones filogenéticas de *Pimephales* con otros miembros de la familia Leuciscidae, en el estudio realizado por (Schönhuth *et al*., 2018) se incluyó en el clado de *Pimephales* a *Opsopoeodus*. Vandermeer (1966) analizó características morfológicas y merísticas en poblaciones de *P. promelas* en Estados Unidos, encontrando variaciones menores en varios caracteres morfológicos y una clina norte-sur, sugiriendo la presencia de al menos tres subespecies dada la naturaleza de las variaciones y el alto nivel de variabilidad (Vandermeer, 1966).

I.2.2. *Sistemática, Taxonomía y características generales de Pantosteus plebeius-nebuliferus*

El complejo de matalotes *Pantosteus plebeius-nebuliferus* (Fig. 5) fue propuesto por Corona-Santiago *et al*., (2018), siendo un grupo que incluye a dos especies de la familia

Catostomidae, subfamilia Catostominae en México. Este grupo incluye a *Pantosteus plebeius* Baird y Girard, 1854, y *Pantosteus nebuliferus* Garman, 1881, habitantes de la Mesa del Norte y SMO (Sierra Madre Occidental).

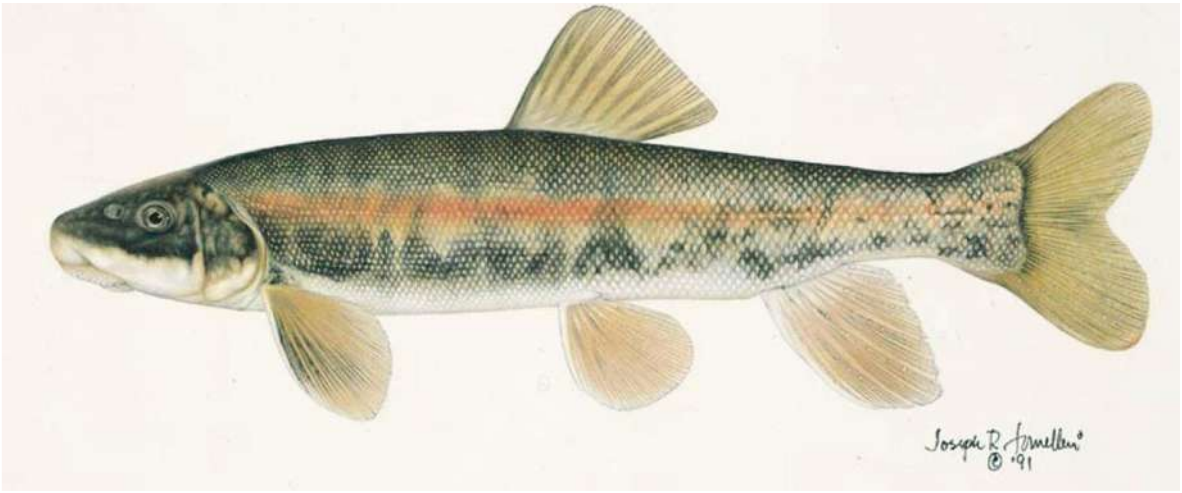

Figure 5. *P. plebeius* Baird y Girard, 1854. Tomado de https://www.fs.usda.gov /Internet/FSE_DOCUMENTS/stelprdb5206797.pdf.

Pantosteus nebuliferus (antes *Catostomus nebuliferus*) fue descrito por Garman 1881, en el Río Nazas, Coahuila, es endémico de las cuencas de los ríos Nazas y Aguanaval. Su hábitat son ríos y arroyos, en remansos y rápidos; anchura de 2 a 25 m; vegetación escasa a abundante, algas verdes a menudo adheridas a las rocas; agua clara (por lo general) a turbia o lodosa; fondos de arena, limo, lodo, grava, rocas, cantos rodados y roca madre; orillas de arcilla o roca (Miller *et al*., 2005).

Por su parte, *P. plebeius* (antes *Catostomus plebeius*) fue descrito por Baird y Girard (1881) en el Río Mimbres, Chihuahua, se encuentra ampliamente distribuido en varias cuencas a través de la SMO: ríos Mezquital, Piaxtla, Fuerte y Yaqui; las subcuencas de la Cuenca de Guzmán (ríos Santa María, Casas Grandes y Del Carmen); el Río Bravo y Río Grande en Estados Unidos; la cuenca del Río Mimbres en Nuevo México, y en el Río Gila

en la Cuenca del Colorado, USA (Miller *et al*., 2005). Su hábitat son remansos y rápidos de arroyos de tamaño pequeño a moderado; los adultos se mueven hacia los rápidos durante la noche (Miller *et al*., 2005).

En el estudio filogenético y filogeográfico realizado por Corona-Santiago *et al*. (2018) para el *Pantosteus plebeius-nebuliferus*, utilizando un gen mitocondrial (cyt *b*) y un gen nuclear (*GHI*), se identificaron cuatro linajes bien diferenciados dentro del complejo de especies, con divergencias que van desde 5.9 a 9.2% para cyt *b* y 0.1% a 0.9% para *GHI*. Los linajes genéticos encontrados en *Pantosteus plebeius-nebuliferus*, fueron correspondientes a las cuencas de drenaje de los ríos Nazas, Mezquital, Fuerte, Casas Grandes y Santa María; existiendo además marcada diferenciación genética entre las poblaciones del sur de la Mesa del Norte (ríos Nazas, Aguanaval, Piaxtla, Culiacán y el Alto Río Balleza) y las poblaciones habitantes de los ríos al Norte (ríos Yaqui, Fuerte, Conchos, Sonora, Ojo de agua, Mayo; así como los ríos Casas Grandes y Santa Clara en la Cuenca de Guzmán, y la Laguna de Bavícora) (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011). La historia evolutiva de *Pantosteus plebeius-nebuliferus* parece estar relacionada con episodios geológicos en la Sierra Madre Occidental y en el centro-norte de México desde el Plioceno, que a su vez causaron la fragmentación del sistema ancestral del Río Grande, el drenaje del paleolago Cabeza de vaca y la fragmentación del Lago Palomas.

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II. Planteamiento del problema

Estudios filogenéticos recientes en especies de peces dulceacuícolas habitantes del Norte de México (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011, 2014, 2015; Corona-Santiago *et al*., 2018), además de revelar una subestimación en la riqueza de especies, sugieren una congruencia geográfica y temporal en la historia evolutiva de algunas especies como *C. ornata*, *C. ornatum,* el CDGG y *Pantosteus plebeius-nebuliferus*, que se encuentran extendidos y co-distribuidos dentro de las cuencas que componen la provincia ictiofaunística de la Mesa del Norte. Ambos patrones, filogenético y de co-distribución, sugieren que estos grupos de peces estuvieron sujetos y además respondieron de forma similar a los mismos eventos geológicos y climáticos, moldeando los procesos de vicarianza o de dispersión que configuraron sus historias biogeográficas. De la misma manera, existen otros peces de amplia distribución, como *P. promelas*, de los que no se cuenta con análisis de diversidad y estructura genética; pero su amplia distribución en la Mesa del Norte y co-distribución con los géneros anteriormente mencionados, hace pensar que podría tener patrones filogenéticos concordantes y posiblemente una historia biogeográfica compartida.

II.1. Preguntas de investigación

¿Cuál es la diversidad genética de las poblaciones sureñas de *P. promelas*?

¿Los patrones filogeográficos de *P. promelas* son compartidos con otras especies dualceacuícolas habitantes de la Mesa del Norte, México?

¿Los patrones filogenéticos y de co-distribución compartidos por peces dualceacuícolas habitantes de la Mesa del Norte, sugieren una historia biogeográfica en común?

III. Hipótesis

La amplia distribución y la compleja historia geológica de la Mesa del Norte sugieren posibles eventos de fragmentación en *P. promelas*, que habrían dado como resultado linajes genéticos.

Los patrones filogenéticos compartidos por las especies de peces dulceacuícolas ampliamente co-distribuidos en la Mesa del Norte, sugieren la existencia de historias biogeográficas en común.

IV. Objetivo general

Realizar un análisis de biogeografía histórica en peces de amplia distribución en la Mesa del Norte, México.

IV.1. Objetivos específicos

- Evaluar las divergencias genéticas utilizando marcadores mitocondriales y nucleares en poblaciones de *P. promelas,* con el fin de obtener las relaciones filogenéticas e inferir la historia evolutiva de las poblaciones mexicanas.
- Obtener y comparar los patrones biogeográficos de *Codoma ornata*, *Campostoma ornatum*, *Pantosteus plebeius-nebuliferus* y el grupo de *Gila* del desierto de Chihuahua, peces dulceacuícolas de amplia distribución en la Mesa del Norte de México.

V. Estructura de la tesis

Con el fin de responder a las preguntas de investigación planteadas, poner a prueba las hipótesis y desarrollar los objetivos propuestos en este trabajo, la presente tesis se estructuró en dos capítulos, cada uno correspondiente a un artículo de investigación.

El primer capítulo tiene como objetivo analizar la variación genética entre poblaciones de *P. promelas* a lo largo de su rango de distribución en México, utilizando un gen mitocondrial y un gen nuclear. Con base en un enfoque de Inferencia Bayesiana y Máxima Verosimilitud, se obtuvieron cuatro linajes genéticos (Casas Grandes, Santa María, Yaqui y Nazas + Conchos) bien soportados, que sugieren que *P. promelas* representa un complejo de especies. La composición y distribución de los linajes encontrados son consistentes con las hipótesis biogeográficas previas para otras especies de peces distribuidos en el noroeste de México, lo que apoya la hipótesis de fragmentación del sistema ancestral del Río Grande a partir del Mioceno (10.9 Millones de años), posiblemente debido a la influencia combinada de eventos tectónicos y aumento en la aridez regional, así como los eventos de intercambio entre cuencas a través de la captura de corrientes.

En el segundo capítulo se realizó una comparación de los patrones biogeográficos de peces de agua dulce de amplia distribución en la Mesa del Norte, México: *C. ornata*, *C. ornatum*, el grupo de *Gila* del desierto de Chihuahua y *Pantosteus plebeius-nebuliferus*. Las secuencias analizadas se obtuvieron en su mayoría de GenBank, correspondientes a estudios filogeográficos previos, sin embargo algunas fueron obtenidas en el presente estudio. Las secuencias corresponden a los principales drenajes en la Mesa del Norte y la vertiente del Pacífico noroeste (Cuenca de Guzmán; y los ríos Yaqui, Conchos, Bravo,

Fuerte, Mayo, Nazas, Aguanaval y Mezquital). La reconstrucción de las áreas ancestrales se realizó con un enfoque de Máxima Verosimilitud utilizando el programa BioGeoBEARS. Se encontró congruencia parcial entre las historias biogeográficas de los organismos analizados, consistente con eventos mayormente de dispersión y especiación por evento fundador, relacionados con tecto-volcanismo y acumulación de basaltos alcalinos durante la formación y evolución de la SMO en México.

V.1. Capítulo 1

PeerJ

Genetic differentiation in the southern population of the Fathead Minnow *Pimephales promelas* Rafinesque (Actinopterygii: Cyprinidae)

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ABSTRACT

The North American cyprinid *Pimephales promelas* is a species with a wide distribution range, occurring in distinct hydrographic basins in Mexico, Canada, and the United States. Previous morphological and meristic analyses of *P. promelas* concluded that at least three subspecies exist in the midwestern and northeast region of the United States. No studies have been carried out on the Mexican population of *P. promelas*, but the findings of cryptic diversity in United States populations of this species, as well as in other codistributed fish species in Mexico could be an indication that Mexican populations of *P. promelas* consist of cryptic species. Using the mitochondrial gene cyt *b* and the first intron of the *S7* ribosomal protein-coding nuclear gene we carried out phylogenetic and phylogeographic analyses of populations of *P. promelas* across its distribution range in northwestern Mexico. Using this information were analyzed the structure and differentiation level between populations of *P. promelas* from distinct river basins in the region in identifying cryptic diversity. Twenty-four sequences were obtained for cyt *b*, and 30 for *S7*, which included the two heterozygous alleles. The results revealed the existence of four well-differentiated lineages: (1) Yaqui in the Pacific slope; (2) Santa Maria, and (3) Casas Grandes in the Guzman Basin; and (4) Nazas+Conchos in Chihuahua state. This challenges the current taxonomy of *P. promelas*. Differences in the relationships between markers and the small sample size for the Santa Maria population ($n = 1$), indicate that our results must be corroborated with more data and morphological analyses. Biogeographic analysis of these findings suggest that the evolutionary history of *P. promelas* is associated with the fragmentation of the ancestral Rio Grande river system since Miocene in northwestern Mexico consistent with findings for codistributed fish species.

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INTRODUCTION

Phylogeographic studies provide useful information that complements biogeographic hypotheses relating to the current distributions of fish species and their link to fragmentation and/or to expansion events (*Devitt, 2006*; *Riddle & Hafner, 2006*; *Vallinoto et al., 2010*; *Schönhuth et al., 2015*).

In North America, tectonic activity and climate changes are the main factors that have contributed to the formation of drainage basins and the evolution of associated species (*Galloway, Whiteaker & Ganey-Curry, 2011*; *Aranda-Gómez et al., 2018*). In northwestern Mexico, the main tecto-volcanic activity since the Oligocene is related to the formation of the Sierra Madre Occidental (SMO) mountain range (*Ferrari, Valencia-Moreno & Bryan, 2007*; *Aguirre-Díaz et al., 2008*). This high level of tectonic activity associated with the SMO has been proposed as responsible for the high level of endemism of flora and fauna in this region of Mexico, and the main force that has shaped the speciation process (vicariance and/or dispersion) in freshwater fishes of the region (*Echelle et al., 2005*; *Hughes, Rinne & Calamusso, 2005*; *Ceballos, Arroyo-Cabrales & Ponce, 2010*; *Morrone, 2010*; *Schönhuth & Mayden, 2010*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2012*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Clements, Bart & Hurley, 2012*). The SMO is also considered an important biogeographic corridor and a Pleistocene refuge (*Hughes, Rinne & Calamusso, 2005*), associated with the expansion and contraction of numerous species ranges in response to climate change during the Pleistocene (*Domínguez-Domínguez et al., 2011*).

Northwestern Mexico is an area including two major physiographic provinces: the highland Chihuahuan desert region in the Mesa del Norte, and the SMO (*Schönhuth et al., 2015*). The Mesa del Norte is located from the United States (US)-Mexico border to Zacatecas and San Luis Potosi states (*Miller, Minkley & Norris, 2005*). These areas include major drainages as Yaqui, Mayo, Fuerte, and Mezquital rivers on the Pacific Slope of the SMO; endorheic drainages as the Nazas and Aguanaval rivers; and the Atlantic drainage Conchos River (*Schönhuth et al., 2015*) (Fig. 1).

Previous studies of fishes in the Mesa del Norte based on molecular data (*Smith & Miller, 1986*; *Mayden, Matson & Hillis, 1992*; *Mayden et al., 1992*; *Echelle et al., 2005*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2012*; *Schönhuth et al., 2015*; *Corona-Santiago et al., 2018*) and geological information (*Galloway, Whiteaker & Ganey-Curry, 2011*), proposed the existence of an extended Rio Grande system that originated in the Oligocene and persisted for more than 10 million years. Extensive zones of the southwestern highlands of the US (Colorado Plateau, in current Utah, Colorado and Arizona), Chihuahuan Desert (New Mexico, Chihuahua, Coahuila and Durango) and the current Lower Grande River Basin were part of the ancient Rio Grande system (*Galloway, Whiteaker & Ganey-Curry, 2011*; *Schönhuth et al., 2015*).This paleo-river system was proposed to have connected drainages in Mexico that are currently independent (*Mayden, Matson & Hillis, 1992*; *Echelle et al., 2005*; *Schönhuth, Doadrio & Mayden, 2007*; *Schönhuth et al., 2011*; *Schönhuth et al., 2015*; *Domínguez-Domínguez et al., 2011*; *Corona-Santiago et al., 2018*), acting as a hydrological corridor for the ancestors of current freshwater fish

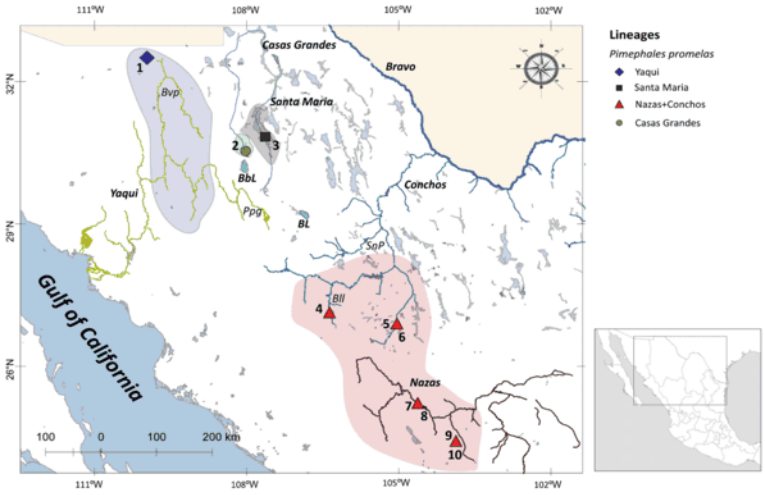

Figure 1 Drainage basins sampled for *P. promelas* and genetic lineages found. Colors and shapes correspond to the four lineages identified in phylogenetic analyses. Numbers and forms indicate different localities where *P. promelas* was collected: 1. Cabullona, (six samples); 2. Casas Grandes, (five samples); 3. Buenaventura, (one sample); 4. Nonoava, (one sample); 5. Villa Coronado, (two samples); 6. Porvenir, (two samples); 7. Jicorica, (two samples); 8. Abasolo, (two samples); 9. Paso Nacional, (two samples); and 10. Covadonga, (two samples), according to the localities in Table S1. Abbreviations: *Bvp*, Bavispe River; *BbL*, Babicora Lagoon; *Ppg*, Papigochic River; *BL*, Bustillos Lagoon; *SnP*, San Pedro River; *Bll*, Balleza River.

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species and permitting their expansion across the drainages in the Chihuahuan Desert (*Smith & Miller, 1986*; *Mayden, Matson & Hillis, 1992*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2015*). This scenario includes the possible transfers and/or integration of headwaters of the Mesa del Norte with drainages from the Pacific slope (Yaqui, Mayo, Fuerte, Piaxtla, Culiacan and Mezquital rivers) (*Minckley, Hendrickson & Bond, 1986*; *Miller, Minkley & Norris, 2005*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Corona-Santiago et al., 2018*) as far south as the Nazas and Aguanaval rivers (*Smith & Miller, 1986*; *Mayden, Matson & Hillis, 1992*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Corona-Santiago et al., 2018*).

One of the most widespread fish species in the Mesa del Norte hydrological basins is the Fathead Minnow *Pimephales promelas*. This species is distributed from eastern North America into Northern Mexico. *P. promelas* ranges from Lake Slave to the Hudson Bay at its northern limit, southward through the Mississippi Valley, the Great Plains and the Gulf slope streams of Alabama and the Grande River basin into the Conchos River. The range of *P. promelas* also includes the endorheic basins of Casas Grandes, Nazas, Del Carmen, Santa Maria, and Bustillos in the Mesa del Norte, as well as the Pacific slope drainage of

the Yaqui River in Mexico (*Vandermeer, 1966*; *Miller, Minkley & Norris, 2005*). Previous morphological analyses of *P. promelas* populations in the United States concluded that at least three subspecies of this widespread species exist in the midwestern and northeast region of the US (*Vandermeer, 1966*). No studies have been carried out in Mexican population, but based on the findings of cryptic diversity in United States populations of this species (*Vandermeer, 1966*), as well as in other codistributed fish species in Mesa del Norte (*Campostoma anomallum* (*Blum et al., 2008*), *Cyprinella lutrensis* (*Schönhuth & Mayden, 2010*), *Campostoma ornatum* (*Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*), *Dionda episcopa* (*Schönhuth et al., 2012*), *Codoma ornata* (*Schönhuth et al., 2015*) and *Pantosteus plebeius* (*Corona-Santiago et al., 2018*) we hypothesize that Mexican populations of *P. promelas* have been taxonomically underestimated.

In accordance with the above, the aim of the present study is to assess the genetic divergences in *P. promelas* populations, to tests the current taxonomic status with molecular data, and determine whether populations from distinct basins correspond to different evolutionary lineages. Based on mitochondrial and nuclear markers, we use both, phylogenetic and phylogeographic approaches to examine the populations of *P. promelas* across its distribution range in northwestern Mexico.

METHODS

Taxon sampling

The specimens of *P. promelas* were collected from five independent drainage basins and ten localities across the Mexican distributional range of the species using electrofishing and seine netting techniques: (1) Cabullona, (6 specimens); (2) Casas Grandes, (5 specimens); (3) Buenaventura, (1 specimen); (4) Nonoava, (1 specimen); (5) Villa Coronado, (2 specimens); (6) Porvenir, (2 specimens); (7) Jicorica, (2 specimens); (8) Abasolo, (2 specimens); (9) Paso Nacional, (2 specimens); and (10) Covadonga, (2 specimens) (Fig. 1; Table S1). For each specimen we fixed a piece of the fin in 95% ethanol for extraction of the DNA, which was then stored at −70 °C. We preserved a maximum of five specimens per site in 5% formalin following the protocols approved by the Mexican Ministry of Environment and Natural Resources (SEMARNAT). We deposited fish and tissue samples in the fish collection of the Universidad Michoacana de San Nicolas de Hidalgo, Mexico (SEMARNAT registration number MICH-PEC-227-07-09). All procedures were reviewed and approved by a committee of Mexican Ministry of Environment and Natural Resources, under collection permit number PPF/DGOPA-362/1. *C. ornata*, *Pimephales notatus*, and *Pimephales tenellus* were used as outgroups (based on prior phylogenetic studies (*Schönhuth et al., 2008*; *Schönhuth et al., 2016*; *Schönhuth et al., 2018*) (Table S1).

DNA extraction, PCR amplification, and sequencing

DNA was extracted using the standard proteinase K/phenol/chloroform protocol (*Sambrook, Fritsch & Maniatis, 1989*). We obtained sequences for a fragment of the mitochondrial cytochrome *b* gene (cyt *b*: 1,049 bp) in twenty-four specimens using the primers LA (5′-GTGACTTGAAAAACCACCGTTG) and HA (3′-CAACGATCTCCGGTTTACAAGAC) (*Dowling et al., 2002*). A subset of eighteen

specimens was selected, accounting for all the variation found for the cyt *b* gene, for amplification of the first intron of the nuclear *S7* ribosomal protein-coding gene (*S7*: 704 bp), with the primers S71F (5′-TGGCCTCTTCCTTGGCCGTC) and S72R (3′-AACTCGTCTGGCTTTTCGCC) (*Chow & Hazama, 1998*).

The final concentrations in each 25 μL polymerase chain reaction (PCR) were: 50 ng template DNA, 10 μM of each primer, 0.7 units of Taq DNA polymerase, 0.25 mM of each dNTP, 2.5 μL of Reaction Buffer and 2.5 mM $MgCl_2$. Thermocycling conditions for amplification of the mitochondrial cyt *b* gene consisted of an initial denaturalization step of 3 min at 94 °C: followed by 35 cycles of 30 s at 94 °C, 1 min at 48 °C, 90 s at 72 °C, and a final 5 min extension step at 72 °C. The *S7* gene was amplified under the following conditions: initial denaturalization step of 3 min at 94 °C, followed by 35 cycles of 45 s at 94 °C, 50 s at 57 °C, 100 s at 72 °C, and a final step of 10 min extension at 72 °C. All PCR products were purified with ExoSAP-IT™. The purified PCR products were sent to Macrogen Korea for sequencing.

The sequences were edited and aligned using the default parameters of Clustal X (*Thompson et al., 1997*) implemented in Mega v6.06 (*Tamura et al., 2013*) and examined using chromatograms. The *S7* sequences were phased with point mutation using DNAsp v5.10 (*Librado & Rozas, 2009*). We evaluated nuclear recombination using the pairwise homoplasy index (PHI) test (*Bruen, Philippe & Bryant, 2006*) as implemented in Splitstree4 (*Huson & Bryant, 2006*). No significant recombination was detected in the nuclear *S7* sequences ($p = 0.3741$). The sequences of *S7* showed heterozygous indels; in this case we performed a manual reconstruction of the two allele phases following the procedure described by *Sousa-Santos et al. (2005)*.

Phylogenetic analyses and haplotype networks

We obtained the evolutionary substitution models, based on the corrected Akaike Information Criterion (AICc), and an optimal partition setting using PartitionFinder v1.1.0 (*Lanfear et al., 2012*). We obtained the optimal partition setting by assigning a substitution model to each gene. The models obtained were the Transitional Model (TIM3) (*Posada, 2003*) + gamma (TIM3+G) for the cyt *b* gene and the Tamura-Nei model (*Tamura & Nei, 1993*) + gamma (TrN+G) for the *S7* gene.

Bayesian Inference (BI) analyses were applied in MrBayes v3.2.1 (*Ronquist et al., 2012*). The sequences were analyzed in two different data sets, one for each gene independently and one for both genes concatenated. We used the two heterozygous alleles for the *S7* gene. The analyses for 10 million generations were run with two independent runs, implementing four Markov Chain Monte Carlo (MCMC) processes and sampling every 500 generations. We evaluated the convergence of the chains with the log-likelihood (-InL) values of the two independent runs on Tracer v1.5 (*Rambaut & Drummond, 2007*), discarding 10% of the generations as burn-in to construct the consensus tree. We visualized the trees in FigTree v1.4.2 (*Rambaut, 2014*).

Maximum Likelihood (ML) trees were constructed in RAxMLGUI v1.3.1 (*Silvestro & Michalak, 2012*; *Stamatakis, 2014*), as implemented in CIPRES (*Miller, Pfeiffer & Schwartz, 2010*), with the default GTR+G+I model using the rapid bootstrap algorithm

with 1000 replicates (CIPRES portal v3.3) at the San Diego Supercomputer Center at http://www.phylo.org/sub_sections/portal/.

For each gene, we constructed unrooted networks under a null hypothesis of no genetic differentiation among populations, using the median-joining method (*Leigh & Bryant, 2015*) as implemented in PopART v1.7 (available at http://popart.otago.ac.nz).

Species tree analysis, genetic distances and divergence times

We estimated a species tree and divergence times for the major nodes in *Pimephales promelas* for both genes (cyt *b* + *S7*) using the Bayesian Method in *BEAST v1.8.1 (*Drummond et al., 2012*). The substitution models were set according to the model selected for each gene by PartitionFinder v1.1.0 (*Lanfear et al., 2012*), the Generalised Time Reversible model (*Tavare, 1986*) + gamma (GTR+G) for the cyt *b* gene and the TN93 model (*Tamura & Nei, 1993*) + gamma (TN93+G) for the individual *S7* gene. We carried out this analysis with a subset of 33 sequences that include all different haplotypes for all genes, and two outgroup sequences (*P. notatus* and *P. tenellus* based on a previous phylogenetic study (*Schönhuth et al., 2018*)) (Table S1). The lineages in the *BEAST analysis were selected according to the lineages recovered on the phylogenetic trees. The model parameters were unlinked across cyt *b* and *S7* genes. Considering that the performance of the strict clock is virtually identical to the lognormal distribution, of the uncorrelated relaxed clock (*Firth et al., 2010*), and the use of uncorrelated relaxed clocks takes the rate variation among lineages into account (*Baele et al., 2012*; *Hasegawa, Kishino & Yano, 1985*), we selected a lognormal relaxed clock (Uncorrelated) model for branch length (*Drummond et al., 2006*). Because of the lack of reliable fossil data, we calibrated the molecular clock using the mutation rate of cyt *b* in teleosts of 0.76–2.2%/million years (*Zardoya & Doadrio, 1999*; *Berendzen, Gamble & Simons, 2008*; *Nagle & Simons, 2012*), applied in a prior with a uniform distribution. Since the mutation rate is not available for the nuclear gene, we included this gene in the analysis without calibration information. We selected the tree prior-species Tree: Yule process model. We ran Markov chain Monte Carlo analysis for 120 million generations, sampled every 1000 generations. We ran analyses in CIPRES Science Gateway v3.3 (http://www.phylo.org/sub_sections/portal/). We assessed whether parameter values had reached effective sample size and convergence in Tracer v1.5 (*Rambaut & Drummond, 2007*), and built the maximum clade credibility tree using Tree Annotator v1.8.1 (*Drummond et al., 2012*), discarding the first 10% of the trees as burn-in. We visualized the tree in FigTree v1.4.2 (*Rambaut, 2014*).

Previous phylogenetic studies in freshwater fishes in northwestern Mexico use uncorrected pairwise (*p*)-distances for generating distance matrices (*Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Corona-Santiago et al., 2018*). In order to be able to compare our results we used *p*-distances, calculated among the recovered monophyletic groups in the phylogenetic trees for both genes independently in Mega v6.06 (*Tamura et al., 2013*).

Bayesian species delimitation test

We conducted Bayesian multilocus species delimitation tests using the concatenated dataset in Bayesian Phylogenetics and Phylogeography (BPP v3.1; *Yang & Rannala, 2010*; *Yang &*

Rannala, 2014; *Yang, 2015*). This method uses a species phylogeny represented by a user-specified guide tree and accommodates lineage sorting due to ancestral polymorphism (*Yang & Rannala, 2010*). To generate the guide tree, each lineage recovered in the concatenated phylogenetic analyses (BI, ML, and species tree) was treated as a terminal taxon in *BEAST (*Drummond et al., 2012*), with the resulting species tree used as a guide for the BPP analyses.

For the BPP analyses of the two concatenated genes, we used the reversible-jump Markov Chain Monte Carlo (rjMCMC) (*Yang & Rannala, 2010*) algorithm to determine whether to collapse or retain nodes throughout the phylogeny. Using the entire dataset coded by each gene, we tested with the Analysis A10 algorithm, in which we used the rjMCMC algorithm to move between species delimitation models that were compatible with a fixed guide tree (*Rannala & Yang, 2013*; *Yang & Rannala, 2010*).

To determine whether lineages could be considered as distinct species under a general lineage species concept, the program assessed the probability of the node separating the species (*De Queiroz, 2007*). We used algorithm 0 with values of 5, 10 and 15 for the fine-tuning parameter in order to ensure that the rjMCMC mixed effectively in the species delimitation models. We conducted analyses with prior distributions on the ancestral population size (θ) and root age (τ_0) (*Leaché & Fujita, 2010*) to discern how these parameters influenced the results. We initially set the gamma prior at θ and τ_0 to the values $\alpha = 1$ and 2, and $\beta = 10$, 100, and 2000; and ran five analyses of each with different starting seeds for two independent chains of 500,000 generations with a burn-in of 50,000 and thinning conducted every five generations.

RESULTS

We obtained 54 sequences for both genes: 24 for cyt *b*, and 30 for *S7*, which included the two heterozygous alleles.

We obtained 16 haplotypes from the 24 sequences of the cyt *b* gene. These haplotypes were defined by 213 polymorphic sites within a 1049 bp sequence fragment (total number of mutations = 240). Sixty-nine of those sites were singletons and 164 substitutions were parsimony informative.

We obtained 18 haplotypes for the *S7* gene. These haplotypes were defined by 43 polymorphic sites (total number of mutations = 45). Twenty-five of those sites were singletons and 18 substitutions were parsimony informative.

Phylogenetic relationships and haplotype networks

Phylogenetic analyses based on the two concatenated genes (cyt *b* +*S7*) (1,753 bp) recovered four well-supported lineages: Santa Maria lineage, clustered one specimen from the Santa Maria River in the Guzman Basin (BS = 100% and PP = 1); Casas Grandes lineage, clustered two specimens from the Casas Grandes River in the Guzman Basin (BS = 100% and PP = 1); Yaqui lineage clustered six specimens from the Yaqui River in the Cabullona locality (BS = 100% and PP = 1); and, Nazas+Conchos lineage, clustered eight specimens from the Nazas and Conchos rivers (BS = 100% and PP = 1) (Fig. 2; Table S1).

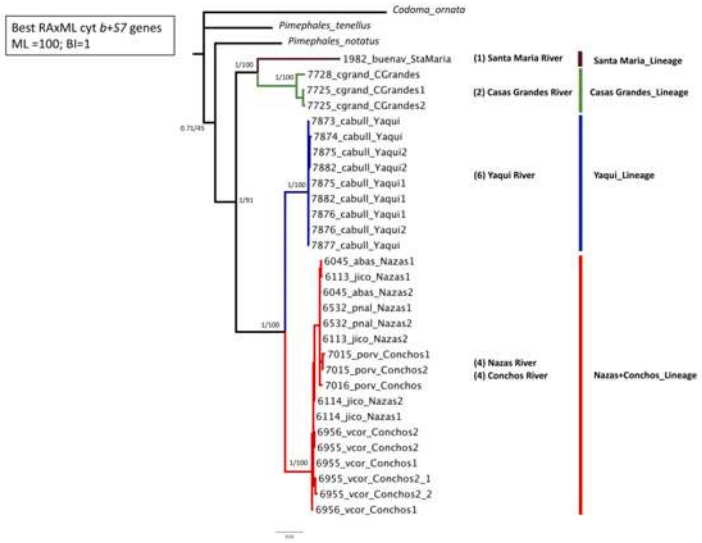

Figure 2 Maximum Likelihood (ML) phylogeny of *P. promelas* based on the concatenated genes (cyt *b* + *S7*), using a GTR+G+I model with ML bootstrap values (based on 1,000 replicates). Numbers on the branches separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Numbers in parentheses correspond to the sample size in each drainage basin. Lineages are color-coded according to the distribution areas in the map (Fig. 1).

Full-size DOI: 10.7717/peerj.6224/fig-2

Phylogenies based on separate analyses for each gene revealed generally consistent results, although they recovered a differing number of lineages. Phylogenies based on cyt *b* and concatenated analyses recovered four major lineages and the same phylogenetic relationships: Santa Maria lineage (BS = 100% and PP = 1); Casas Grandes lineage (BS = 100% and PP = 1); Yaqui lineage (BS = 100% and PP = 1); and Nazas+Conchos lineage, included specimens from localities of the Lower Conchos Drainage (Villa Coronado, El Porvenir and Nonoava), as well as specimens from localities of the Nazas River drainage (Covadonga, Abasolo, Paso Nacional and Jicorica) (BS = 97% and PP = 1) (Fig. 1 and Fig. S1; Table S1). The phylogeny recovered with *S7* identified similar lineages: Casas Grandes, BS = 98% and PP = 1; Santa Maria, BS = 96% and PP = 1; Nazas+Conchos, BS = 97% and PP = 1; and Yaqui, BS = 48% and PP = 0.66. In the *S7* analysis the Santa Maria lineage was recovered as a sister group to a well-supported clade including all three lineages, Casas Grandes, Nazas+Conchos and Yaqui (Fig. S2).

For both genes, the haplotype networks showed the existence of four haplogroups, corresponding to the four lineages found in the phylogenetic analyses: Casas Grandes, Santa Maria, Nazas+Conchos and Yaqui lineages; however, as in the phylogenetic analyses, different relationships were found between the cyt *b* and *S7* groups (Fig. 3).

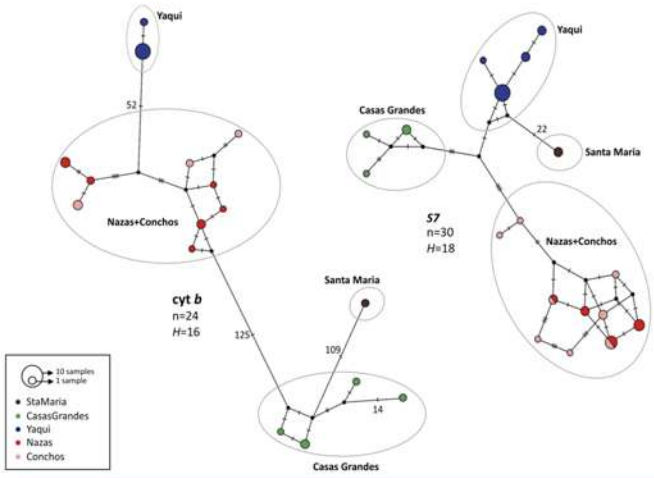

Figure 3 Median-joining haplotype network for mitochondrial (cyt *b*) and nuclear (intron *S7*) genes for *P. promelas*. Each circle represents a different haplotype; circle sizes are proportional to the number of individuals with a particular haplotype. Small black dots represent missing (unsampled or extinct) haplotypes. Lines between circles represent one mutational step, and numbers presented are the number of mutations between haplotypes. Haplogroups are color-coded according to the distribution areas in the map (Fig. 1).

Full-size DOI: 10.7717/peerj.6224/fig-3

For cyt *b* we found 52 mutation steps (MS) between Yaqui and Nazas+Conchos lineages, 109 MS between Casas Grandes and Santa Maria lineages, and 125 MS between Nazas+Conchos and Casas Grandes lineages. For the Nazas+Conchos population we found nine haplotypes: three in Conchos Basin (Villa Coronado, Nonoava and El Porvenir localities), six in Nazas Basin, one in Covadonga and Paso Nacional localities and two in each of the Jicorica and Abasolo localities. For the Yaqui population we found two haplotypes in the Cabullona locality. In the Casas Grandes population we found four haplotypes. In the Santa Maria population we found one haplotype (Fig. 3).

For *S7* we found a mixture of haplotypes among the Nazas and Conchos samples. We found the Santa Maria lineage to be separated by 22 MS from the Yaqui lineage. For the Nazas+Conchos population we found ten haplotypes: six in Conchos Basin (two in the El Porvenir locality and four in the Villa Coronado locality), two in Nazas Basin (Abasolo and Jicorica localities). For the Yaqui population we found four haplotypes in the Cabullona locality. For the Casas Grandes population we found three haplotypes (Fig. 3).

Species tree analysis, divergence times and genetic distances

The species tree analysis with the concatenated dataset (cyt *b* +*S7*) supports the assumption of four lineages of high internal branch-length Bayesian Posterior Probability (>99%), as seen in the cyt *b* and the concatenated (cyt *b* +*S7*) phylogenetic trees. This result is also

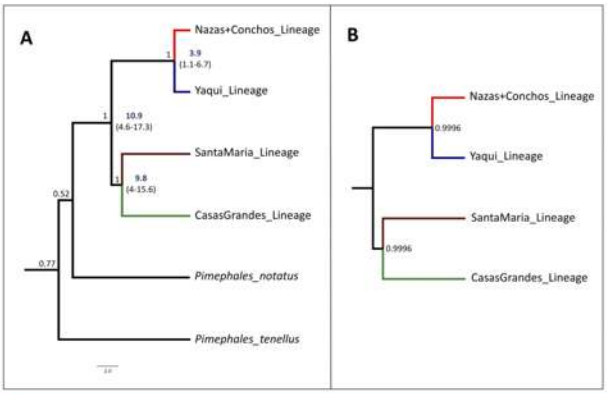

Figure 4 Time-Calibrated Species-Tree and Bayesian species delimitation test results for *P. promelas*. Both nuclear and mitochondrial gene sequences were used. Lineages are color-coded according to the distribution areas in the map (Fig. 1). *(A)* Time-calibrated Species-Tree phylogeny and Divergence Time estimates for nodes based on substitution rates for the cyt *b* gene of 0.76–2.2%/ million of years (*Zardoya & Doadrio, 1999*; *Berendzen, Gamble & Simons, 2008*; *Nagle & Simons, 2012*). Since the mutation rate is not available for the nuclear gene we included in the analysis without calibration information. Numbers in bold and values in parentheses represent the 95% highest posterior density of divergence time estimates. Values on the branches represent the posterior probability. *(B)* Bayesian species delimitation test, assuming four species according to the guide tree obtained from *BEAST. We considered speciation probability values > 0.95 as strong support for a speciation event. For the five analyses, we applied different combinations of θ and t_0 priors: 1. $\theta = (\alpha : 2, \beta : 2000)$, $t_0 = (\alpha : 2, \beta : 20000)$; 2. $\theta = (\alpha : 2, \beta : 20)$, $t_0 = (\alpha : 2, \beta : 200)$; 3. $\theta = (\alpha : 2, \beta : 20)$, $t_0 = (\alpha : 2, \beta : 20000)$; 4. $\theta = (\alpha : 2, \beta : 200)$, $t_0 = (\alpha : 2, \beta : 20000)$ and, 5. $\theta = (\alpha : 2, \beta : 20)$, $t_0 = (\alpha : 2, \beta : 200)$. We obtained strong support (posterior probability ≥ 0.99) in all the five analyses. The number in the nodes correspond to the major posterior probability value obtained in all the five analyses.

Full-size DOI: 10.7717/peerj.6224/fig-4

consistent with the *S7* gene phylogenetic analyses, corresponding to the four recovered lineages (Fig. 4A).

The divergence between the main clades of *P. promelas* was dated to the Mid-Miocene and Mid-Pliocene. The separation of the main clades (Nazas+Conchos and Yaqui *vs.* Santa Maria and Casas Grandes) was dated at *ca.* 10.9 Million years ago (Mya) (95% Highest Posterior Density (HPD): 4.6–17.3) (Fig. 4A). The split between the Santa Maria and Casas Grandes lineages was estimated at *ca.* 9.8 Mya (95% HPD: 4–15.6), whereas the separation event of the Yaqui and Nazas+Conchos lineages was estimated at *ca.* 3.9 Mya (95% HPD: 1.1–6.7) (Fig. 4A).

The maximum genetic distance for both genes occurred between the Nazas+Conchos and Santa Maria lineages (10.6% for cyt *b* and 4.7% for *S7*) (Tables 1A and 1B). The minimum genetic distance for the cyt *b* gene was found between the Nazas+Conchos and Yaqui lineages (3.7%). For *S7* the minimum genetic distance occurred between the Casas Grandes and Yaqui lineages (1.1%). Genetic distances within each lineage ranged from 0% to 0.5% with cyt *b* and 0.1 to 0.4 with *S7* (Tables 1A and 1B).

Table 1 Genetic divergences within *P. promelas*. Ranges of uncorrected pairwise sequence divergence (%) between major lineages within Pimephales promelas. Values in parentheses correspond to the sample size in each lineage. Values in bold correspond to the genetic distance within each lineage. (A) Genetic divergences in mitochondrial cyt *b* gene. (B) Genetic divergences in the first intron of the S7 ribosomal protein-coding gene.

(A) Lineages	Nazas+Conchos (13)	Yaqui (6)	Casas Grandes (5)	Santa Maria (1)
Nazas+Conchos	**0.4%**			
Yaqui	3.7%	**0%**		
Casas Grandes	9.4%	9.6%	**0.5%**	
Santa Maria	10.6%	10.5%	7.8%	–

(B) Lineages	Nazas+Conchos (8)	Yaqui (6)	Casas Grandes (2)	Santa Maria (1)
Nazas+Conchos	**0.4%**			
Yaqui	1.4%	**0.1%**		
Casas Grandes	1.7%	1.1%	**0.3%**	
Santa Maria	4.7%	3.6%	4.4%	–

Bayesian species delimitation test

The speciation model based on the species tree estimate strongly supported the assumption of four putative species. We obtained strong support (posterior probability ≥ 0.99) for the tested speciation model of four *a priori* defined species within Mexican populations of *P. promelas* (Casas Grandes lineage, Santa Maria lineage, Yaqui lineage, and Nazas+Conchos lineage (Fig. 4B)). The BPP was not sensitive to species delimitation, and no alteration of posterior probabilities of the speciation model was observed when we applied different values of root age (τ_0) and population size (θ), demonstrating high posterior probabilities for model tested with the A10 algorithm.

DISCUSSION

The results presented herein revealed that southern populations of *P. promelas* distributed across northwestern Mexico correspond to at least four well-supported independent evolutionary lineages. The four lineages show geographic congruence, with the occurrence of each divergent lineage in independent hydrographic basins, as have been found in other widely distributed fish species (*Blum et al., 2008*; *Schönhuth & Mayden, 2010*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2012*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Corona-Santiago et al., 2018*). This study is consistent with other studies of the freshwater fish species distributed along the Mesa del Norte in Mexico that have found that many species previously considered as a single widespread taxon, are in fact a species complex (e.g., *C. ornatum* (*Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*), and *C. ornata* (*Schönhuth et al., 2015*)). This study is also consistent with other studies of *P. promelas*, such as those carried out on the US populations by *Vandermeer (1966)* with morphological characters, that show the species to be made up of complexes of cryptic species.

Phylogenetic relationships and taxonomic implications

In this study of Mexican *P. promelas* populations the results of the concatenated phylogenetic trees (Fig. 2), species tree (Fig. 4A) and BPP analyses (Fig. 4B), supports a strong genetic differentiation pattern, that corresponds to four well-supported lineages, that must be considered independent evolutionary lineages and even undescribed species (Fig. 4). These four evolutionary lineages were recovered in both genes in spite of the incongruence in the phylogenetic relationships between markers (Figs. S1 and S2) and the small sample size in the case of the Santa Maria Basin ($n = 1$) population. The incongruence found between concatenated and independent genes genealogies could not be attributed to retention of ancestral polymorphisms due to incomplete lineage sorting and/or introgression following secondary contact, since we did not recover shared haplotypes between the four well-differentiated lineages in either of the two genes (Fig. 3, Figs. S1 and S2). But the low sample size in the Santa Maria Basin ($n = 1$) could generate gene trees bias results, (*Satta, Klein & Takahata, 2000*; *Kopp & True, 2002*; *Rokas et al., 2003*; *Rokas & Carroll, 2005*), accordingly we recommend a revaluation of the phylogenetic relationships with a larger sample size and more nuclear loci.

In the case of the genetic divergences, we also found congruences in the differentiation pattern of highly differentiated lineages. For cyt *b* among the four lineages the genetic divergences ranged between 3.7% among the Yaqui and Nazas+Conchos lineages, to 10.6% among populations of the Nazas+Conchos and Santa Maria lineages. These genetic distances are the same or greater than those found among the six species of the Chihuahuan Desert Group of the genus *Gila,* that range from 3.68 to 5.56 (*Schönhuth et al., 2014*) and minimum distances of 1.3% have been found between southwestern species in the *Dionda* genus (*Schönhuth et al., 2008*), 1.9% between species in *Cyprinella*, and 4.7% in species of the genus *Tampichthys* (*Schönhuth & Mayden, 2010*) and 2.1–4.0% between species of *Algansea* (*Pérez-Rodríguez et al., 2009*). Moreover, the *S7* gene showed relatively high genetic differences for a nuclear gene, with minimum genetic distances (*p*-distance 1.1%) found in the comparison between the geographically proximate Casas Grandes and Yaqui lineages, and maximum distances (*p*-distance 4.7%) in the Santa Maria and Nazas+Conchos lineages. A previous study has found similar genetic distances in the *S7* nuclear gene for a species in the Cyprinidae family and in species of the genus *Algansea*, in which interspecific genetic distances between 0.5 to 3.6% were found for *S7* (*Pérez-Rodríguez et al., 2009*).

Accordingly, the Mexican populations of *P. promelas* shows four independent evolutionary lineages that could be recognized as different species. A more integrative taxonomic analysis is pending in order to complement the results presented herein.

Biogeographic implications derived from the cladogenetic pattern

Widespread species are associated with suitable biological and ecological traits that permit a high dispersal ability and an ability to colonize new habitats (*Nathan, 2001*). In the case of freshwater fishes, the discontinuity of aquatic habitats represents the main barrier to range expansion (*Pérez-Rodríguez et al., 2015*). In the case of northwestern Mexico, tecto-volcanic events since the Miocene and Pleistocene, glacial/interglacial cycles, and increasing regional aridity since the Holocene, fragmented the ancestral Rio Grande system

(*Metcalfe, 2006*; *Schönhuth et al., 2015*), effectively isolating different populations and shaping the geographic distribution and phylogenetic relationships of the freshwater fishes of the region (*Smith & Miller, 1986*; *Wood & Mayden, 2002*; *Blum et al., 2008*; *Schönhuth & Mayden, 2010*; *Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*; *Schönhuth et al., 2012*; *Schönhuth et al., 2014*; *Schönhuth et al., 2015*; *Aranda-Gómez et al., 2018*; *Corona-Santiago et al., 2018*).

Our divergences times are in agreement with the paleohydrological history of the region in space and time. Accordingly, in the present study, the most recent common ancestor of the four *P. promelas* lineages and the separation of the Santa Maria and Casas Grandes lineages were dated to the Mid-Miocene (*ca.* 10.9 Mya, 95% HPD: 4.6–17.3; *ca.* 9.8 Mya, 95% HPD: 4.0–15.6 respectively) (Fig. 4A). The most plausible biogeographic scenario for the isolation of these lineages is the fragmentation of the ancestral Rio Grande system (*Smith, Song & Miller, 1984*; *Albritton, 1958*; *Miller & Smith, 1986*; *Minckley, Hendrickson & Bond, 1986*; *Smith & Miller, 1986*; *Schönhuth et al., 2015*), caused by the regional patterns of uplift and subsidence during the Miocene and Pliocene, while an arid climate extended across the western interior, causing the reorganization of drainage configurations (*Galloway, Whiteaker & Ganey-Curry, 2011*; *Schönhuth et al., 2015*) (Fig. 5A). This pattern of isolation has also been proposed for codistributed species such as the genus *Tampichthys* (endemic to central-east Mexico) and its sister group *Codoma* (north-western distribution) occurring during the Mid-Miocene, around 9.17 Mya or 12.19 Mya (*Schönhuth et al., 2015*).

The separation between the Yaqui and the Nazas+Conchos lineages was dated to the Pliocene, approximately 3.9 Mya (95% HPD: 1.1–6.7) (Fig. 4A). This event seems to be related to the tecto- volcanic episodes in SMO evolution, including repeat alkaline basalt events (*Henry & Aranda-Gómez, 2000*; *Aranda-Gómez et al., 2005*; *Ferrari, Valencia-Moreno & Bryan, 2007*), river capture and peripheral isolation (*Ferrari, Valencia-Moreno & Bryan, 2007*; *Aguirre-Díaz et al., 2008*) (Fig. 5B), as has been hypothesized for those Pacific slope rivers that have headwaters extending eastward in the SMO to areas of the Mesa del Norte. Previous studies identified the possible transfers of fish species between drainage basins by integration or fragmentation of drainages, as is the case of the Yaqui River, and have documented closely related lineages on both sides of the SMO, in the Yaqui and Conchos rivers. *Smith & Miller (1986)* suggested that rivers in Northwestern Mexico, draining to the Pacific (Upper Yaqui and Upper Mezquital) across desert regions, originated through headwater capture from the ancestral and extant Rio Grande system, and caused fish dispersal by stream capture events (*Schönhuth et al., 2011*).

A mixture of samples from the current Nazas and Conchos drainage basins was found within the Nazas+Conchos lineage of *P. promelas*. This could be related to a recent connection of both basins via river capture or through pluvial lakes, as shown by the cyt *b* gene, whereas the mixture of haplotypes between both populations in *S7* could be related to incomplete lineage sorting due to the low mutation rate of nDNA. The close relationship between samples of both drainages was previously found in *C. ornatum* populations, a relationship explained by a fish interchange as a result of river capture (*Schönhuth et al., 2011*). Similarly, *Burr (1976)*, in a previous review of *C. ornatum*, hypothesized the formation of a connection between the Nazas River and the Grande River via the Mayran

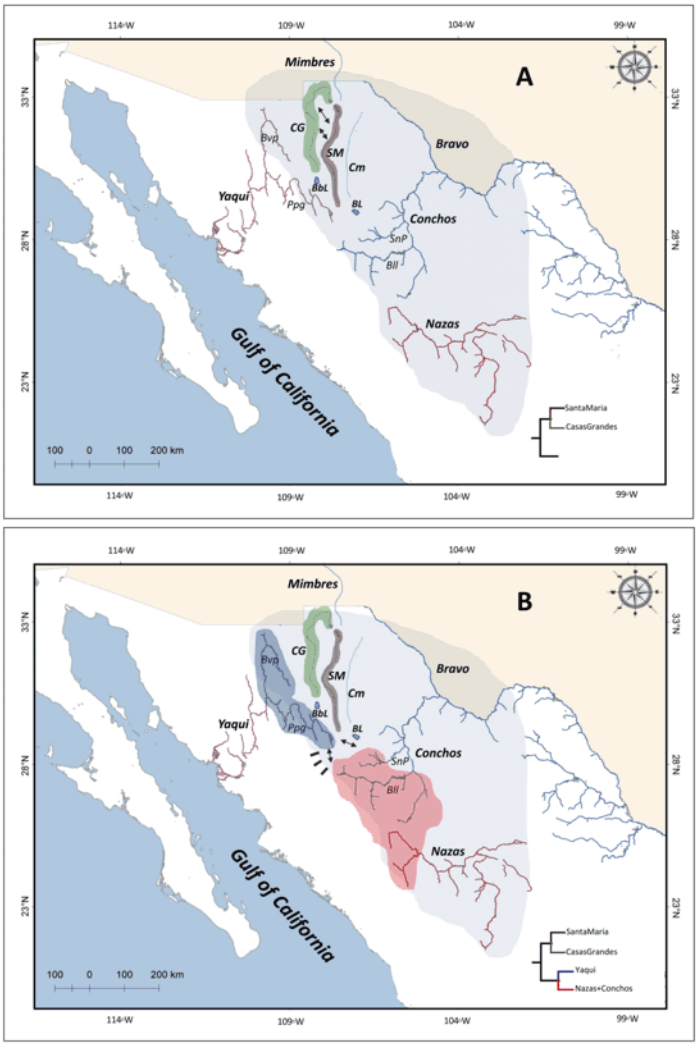

Figure 5 Chronosequence of cladogenetic events, and suggested drainage basin configurations and distributions of the common ancestor of the four *P. promelas* lineages. (A) Ancient 'Rio Grande system'; separation of the Santa Maria Lineage, related to the regional patterns of uplift and subsidence during the Miocene and Pliocene. (B) Hydrological connectivity between areas across the SMO (Yaqui-Conchos rivers); separation between Yaqui *vs.* (continued on next page…)

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Figure 5 (…continued)
Nazas+Conchos lineages, related to the tecto-volcanic episodes in SMO evolution. Green, brown, blue and red shaded correspond to the distribution of the lineages as shown in the phylogenetic trees. Black rectangles represent tecto-volcanic events. Solid arrows represent river capture. The colored shade of light blue represents the hypothetical area of the ancient 'Rio Grande System', as described by *Schönhuth et al. (2011)*. Abbreviations: *CG*, Casas Grandes River; *SM*, Santa Maria River; *Cm*, Del Carmen River; *Bvp*, Bavispe River; *BbL*, Babicora Lagoon; *Ppg*, Papigochic River; *BL*, Bustillos Lagoon; *Bll*, Balleza River; *SnP*, San Pedro River.

and Viesca lagoons (both currently dry) during the Late Pleistocene (*Meek, 1904*; *Burr, 1976*). While a previous biogeographic study in *C. ornata* found a close relationship between the Conchos and Nazas drainage populations, which was attributed to incomplete lineage sorting, no biogeographic scenario was presented (*Schönhuth et al., 2015*).

CONCLUSIONS

The geographic distribution of the four genetic lineages recovered in *P. promelas* (Casas Grandes, Santa Maria, Yaqui, and Nazas+Conchos) is similar to the lineage distributions found in other freshwater fishes in the North of Mexico, such as *C. ornatum* (*Domínguez-Domínguez et al., 2011*; *Schönhuth et al., 2011*), *Rhinichthys cataractae* (*Kim & Conway, 2014*), *C. ornata* (*Schönhuth et al., 2015*), and *P. plebeius* (*Corona-Santiago et al., 2018*). Cladogenic events in *P. promelas* are hypothesized to have been caused by the combined influence of tectonic events and increasing regional aridity; in particular, the fragmentation of the ancestral Rio Grande system and interchange events between basins via stream capture.

The phylogenetic analyses, species tree and Bayesian species delimitation tests results validate the presence of four genetic lineages. In the future, it would be interesting to increase both the sample size and the number of genes, and to evaluate the morphological diversity in the other Mexican populations of *P. promelas*. This would allow the taxonomic status of the genetic lineages found in the present study to be established and the determination of their relationship with other populations of *P. promelas* in North America.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Nayarit E. Ballesteros-Nova conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Rodolfo Pérez-Rodríguez conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft, teaching phylogenetic analysis programs.
- Rosa G. Beltrán-López analyzed the data.
- Omar Domínguez-Domínguez conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

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Data Availability

The following information was supplied regarding data availability:

The raw data are provided in the Supplemental Files and in GenBank: MK821253–MK821306.

Supplemental Information

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Table S1. Sampling localities for the specimens of *Pimephales promelas* and outgroups analyzed in this study. Collection numbers are listed for vouchers stored at institutional collections followed by tissue numbers. Abbreviations: Dr: Drainage. Mex: Mexico. SLUM: Saint Louis University, St. Louis, Missouri, USA. CPUM, Universidad Michoacana de San Nicolás de Hidalgo, Michoacan, Mexico. MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain.

	LOCALITY	BASIN	Cyt *b*	*S7*	*GPS coordinates*
Pimephales promelas	Cabullona River, road Agua Prieta City-Nacozari de García City, Sonora, Mex.	Yaqui	CPUM7882, CPUM7873-CPUM7877 (6)	CPUM7882, CPUM7873-CPUM7877 (6)	31°7'59.5"N, 109°33'51.3"W
	Nazas River, at El Peñasco, San Rafael Jicorica Town, Durango, Mex.	Nazas	CPUM6113-CPUM6114 (2)	CPUM6113-CPUM6114 (2)	25°22'59.7"N, 104°45'54"W
	Abasolo	Nazas	CPUM6044-CPUM6045 (2)	CPUM6045 (1)	--
	Covadonga River, at Peñón Blanco Town, Durango, Mex.	Nazas	CPUM6894-CPUM6895 (2)	--	24°43'55.8"N, 104°5'23.2"W
	Paso Nacional	Nazas	CPUM6531-CPUM6532 (2)	CPUM6532 (1)	25°16'31.6"N, 104°0'57.7"W

	El Porvenir River, at Peñón Blanco Town, Durango, Mex.	Conchos	CPUM7015-CPUM7016 (2)	CPUM7015-CPUM7016 (2)	26°55′23.6″N, 106°19′46.3″W
	Nonoava River, Chihuahua, Mex.	Conchos	BRK02-65 (1)	--	--
	Florido River, at Villa Coronado Town, Chihuahua, Mex.	Conchos	CPUM6955-CPUM6956 (2)	CPUM6955-CPUM6956 (2)	26°44′2.2″N, 105°8′5.2″W
	Casas Grandes River at Hacienda San Diego, S of Casas Grandes City, Chihuahua, Mex.	Casas Grandes	CPUM7728-CPUM7729, CPUM7721-CPUM7722, CPUM7725 (5)	CPUM7725, CPUM7728 (2)	30°14′22.2″N, 107°50′57.5″W
	Buenaventura	Santa María	MNCN1982 (1)	MNCN1982 (1)	--
Outgroups					
Pimephales tenellus	CottonWood River at Emporia, Lyon Co., Neoso River, Kansas, USA.	Kansas	SLUM5542.01	SLUM5542.01	--
Pimephales notatus	Little Vermilion R @ Hwy 63 (upstream) just NW Newport R., Mississippi, Ohio Basin.	Ohio	PN3508	PN3508	--
Codoma ornata	Isolated pool Arroyo de los Alcoces, Conchos Dr., Chihuahua, Mex.	Conchos	BRK02-64	BRK02-64	--

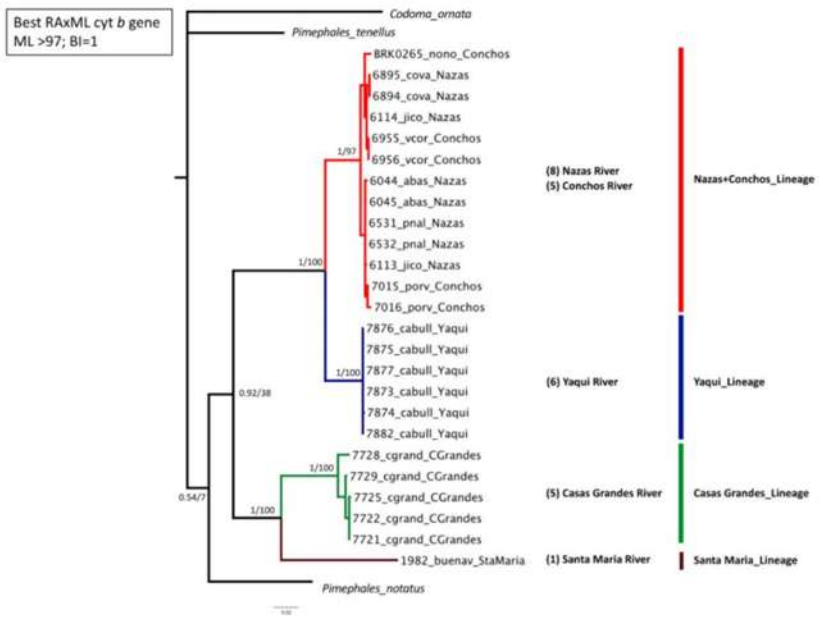

Figure S1. Maximum Likelihood (ML) Phylogeny of *Pimephales promelas* based on the cyt *b* gene, using GTR+G+I model with ML bootstrap values (based on 1000 replicates). Numbers on the branches separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values in parentheses correspond to the sample size in each lineage. Lineages are color-coded according to the distribution areas in the map (Fig. 1).

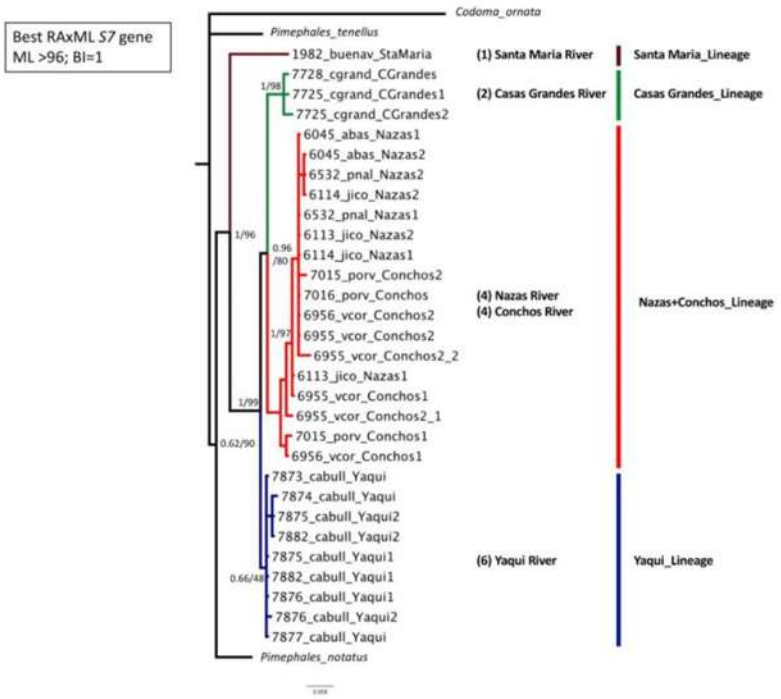

Figure S2. Maximum Likelihood (ML) Phylogeny of *Pimephales promelas* based on the first intron of the *S7* ribosomal protein-coding gene, using GTR+G+I model with ML bootstrap values (based on 1000 replicates). Numbers on the branches separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values in parentheses correspond to the sample size in each lineage. Lineages are color-coded according to the distribution areas in the map (Fig. 1).

V.2. Capítulo 2

Biogeographic patterns of four freshwater fishes of wide distribution in northwestern, México

Running title: Biogeographic patterns in Mexican fishes

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Abstract

Aim

In North America, tectonic activity and climate changes are the main factors that have contributed to the formation of drainage basins and the evolution of associated species. Recent phylogenetic studies in co-distributed species-groups of widely distributed freshwater fish species suggest an underestimation of species richness in northwestern Mexico, and that the evolutionary histories of these groups could have geographical and temporal congruence.

Location

Endo- and exorheic basins in the Mexican Sierra Madre Occidental mountain range system and Mesa del Norte.

Taxa

Codoma ornata, *Campostoma ornatum*, the Chihuahuan Desert Group of the genus *Gila* (CDGG), and *Pantosteus plebeius-nebuliferus*.

Methods

Using phylogenetic information and assessing their geographical ranges, we carried out an ancestral area reconstruction of the distribution of the four co-distributed groups of freshwater fish species in northwestern Mexico. Using this information, we obtained the dates of diversification of the lineages and reconstructed their biogeographical patterns.

Results

Our results showed shared events in the biogeographic history of the four studied groups: 1) A Southern and Northern split in the early radiation of the fourth groups; 2) A shared range in the Yaqui-Guzman Basin; 3) Dispersal events related to Pacific range expansion through river capture. 4) Separation between Nazas +Piaxtla and Mezquital River. 5) Dispersal events between Fuerte and Conchos rivers.

Main conclusion

We found that the biogeographic history of the fish species studied is linked to tecto-volcanic and climatic events from the Miocene, associated with the formation and evolution of the Sierra Madre Occidental.

Keywords: concordant patterns, Mesa del Norte, *BioGeoBEARS,* Cyprinidae, Catostomidae.

1. INTRODUCTION

Historical biogeography can be defined as the study of species distributions over evolutionary time scales. According to biogeographic theory, a group of species coexisting in the same space and time must be subjected to the same events, although they could respond differentially to a particular event (Espinosa, et al., 2008). In the case of northwestern Mexico, geological and climatic process were the main factors that contributed to the evolution of hydrographic drainages and species (Galloway, et al., 2011; Aranda-Gómez, et al., 2018). The biogeographic history of northwestern Mexico is dominated by the tecto-volcanic activity resulting from the formation and emergence of the SMO (Sierra Madre Occidental) mountain range (Ferrari, et al., 2007; Aguirre-Díaz, et al., 2008), driven by the subduction of the Farallon Plate beneath the North America Plate during Cretaceous-Cenozoic periods (Ferrari, et al., 2007; Schönhuth, et al., 2011). Other key biogeographic changes in the region include tecto-volcanic events since the Miocene and Pleistocene periods, glacial/interglacial cycles, and increasing regional aridity since the Holocene period. These events fragmented the ancestral Río Grande drainage system (Metcalfe, 2006; Schönhuth, et al., 2015), isolating different populations and shaping the geographic distribution and phylogenetic relationships of the freshwater fishes of the region (Smith & Miller, 1986; Wood & Mayden, 2002; Blum, et al., 2008; Schönhuth & Mayden, 2010; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2012, 2014, 2015; Aranda-Gómez, et al., 2018; Corona-Santiago, et al., 2018).

Currently, northwestern Mexico comprises two major physiographic provinces: the highland Chihuahuan Desert region in the Mesa del Norte, and the SMO (Schönhuth, et al., 2015). The Mesa del Norte is located from the United States (US)-México frontier to

Zacatecas and San Luis Potosi states (Miller, et al., 2005), whilst the SMO is extends from the southwestern boarder of the US with Mexico down much of the West Coast of Mexico (Miller, et al., 2005). These areas include major drainages such as the Yaqui, Mayo, Fuerte, and Mezquital rivers on the Pacific slope of the SMO in Mexico; endorheic drainages such as the Nazas and Aguanaval rivers; and the Atlantic drainage Conchos-Grande River system (Schönhuth, et al., 2015) (Fig. 1).

Previous studies of fishes in northwestern Mexico based on molecular data (Smith & Miller, 1986; Mayden, Matson, et al., 1992; Mayden, Burr, et al., 1992; Echelle, et al., 2005; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2012, 2015; Corona-Santiago, et al., 2018) and geological information (Galloway, et al., 2011), propose the existence of an extended Río Grande system since the Miocene period, that connected drainages in Mexico; currently independent due to fragmentation over time (Miller & Smith, 1986; Schönhuth, et al., 2015). This ancient Río Grande system acted as a hydrological corridor for the ancestors of current freshwater fish species, and permitted their expansion across the drainages in the Chihuahuan Desert (Smith & Miller, 1986; Mayden, Matson, et al., 1992; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2015). This scenario includes the possible transfer and/or integration of headwaters of the Mesa del Norte with drainages from the Pacific slope of the SMO, permitting range expansion and fragmentation (Yaqui, Mayo, Fuerte, Piaxtla, Culiacan, and Mezquital rivers) (Minckley, et al., 1986; Miller, et al., 2005; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2014, 2015; Corona-Santiago, et al., 2018).

Widespread species are associated with suitable biological and ecological traits that provide high dispersal capabilities and influence their capacity to colonize new habitats (Nathan, 2001). In the case of freshwater fishes, the discontinuity of aquatic habitats

represents the main barrier to range expansion (Pérez-Rodríguez, et al., 2015). The geological history of northwestern Mexico and the geographic congruence of freshwater fish species suggest a taxon pulse model of diversification (Domínguez-Domínguez, et al., 2011) as a suitable model to test whether the diversity of each freshwater fish species is related to the geologic or climatic events in the region (Pérez-Rodríguez, et al., 2009, 2015). The taxon pulse hypothesis is a model of speciation where both vicariance and dispersal are considered, and the distributional ranges of taxa expand and contract around a 'stable center' (Kodandaramaiah & Wahlberg, 2007).

Thus, this study aims to investigate the concordance of biogeographic patterns of four co-distributed groups of freshwater fish species in northwestern Mexico, using an ancestral area reconstruction approach.

2. METHODS

2.1. Taxon sampling and phylogenetic analysis

We analyzed four freshwater fish species groups that inhabit the major drainages in the Mesa del Norte and Pacific northwest slope of the SMO: *Codoma ornata*, *Campostoma ornatum*, the Chihuahuan Desert Group of the genus *Gila* (CDGG), and *Pantosteus plebeius-nebuliferus* (Table S1). We obtained molecular data from museum public research collection specimens and GenBank (Table S1). For each species group, we constructed a molecular concatenated data set using the mitochondrial cytochrome *b* (cyt *b*) gene, the recombination activating gene 1 (*Rag1)*, the first intron of the *S7* ribosomal protein-coding gene (*S7*), and the 3rd nuclear intron of the human growth hormone I (*GHI*) gene (Table S1). We also constructed evolutionary molecular substitution models, based on the corrected Akaike Information Criterion (AICc), and an optimal partition setting by

assessing the best fitting model for each partition as implemented in PartitionFinder v1.1.0 (Lanfear, et al., 2012) (Table S2).

We conducted Bayesian Inference (BI) analyses for phylogenetic reconstruction in MrBayes v3.2.1 (Ronquist & Sanmartín, 2011). For *Codoma ornata* we used *Cyprinella formosa, Erimonax monachus* and *Erimystax dissimilis* as outgroups based on previous phylogenetic studies (Schönhuth, et al., 2015). For the CDGG, we used *Gila cypha* as an outgroup based on a previous phylogenetic study (Schönhuth, et al., 2014). For *Campostoma ornatum* we used *Campostoma pullum* and *Campostoma pauciradii* as outgroups based on a previous phylogenetic study (Schönhuth, et al., 2014), and for *Pantosteus plebeius-nebuliferus* we used *Catostomus catostomus* based on a previous phylogenetic study (Corona-Santiago, et al., 2018) (Table S1). We ran the analyses for 10 million generations, with two independent runs implementing four Markov Chain Monte Carlo (MCMC) processes and sampling every 500 generations. We evaluated the convergence of the chains with the log-likelihood (-InL) values of the two independent runs on Tracer v1.5 (Rambaut & Drummond, 2007), discarding 10% of the generations as burn-in to construct the consensus tree. We visualized the trees in FigTree v1.4.2 (Rambaut, 2014).

We constructed Maximum Likelihood (ML) trees in RAxMLGUI v1.3.1 (Silvestro & Michalak, 2012; Stamatakis, 2014), with the default GTR+G+I model using the rapid bootstrap algorithm with 1000 replicates (CIPRES portal v3.3) at the San Diego Supercomputer Center at http://www.phylo.org/sub_sections/porta

2.2. Species Tree Analysis and Divergence Times

We estimated a species tree and divergence times of the major nodes for each fish species group using the concatenated dataset of genes for each species, with a Bayesian method as implemented in *BEAST v1.8.0 (Drummond, et al., 2012). We set the substitution models according to the best-fit model for molecular evolution, selected for each gene in PartitionFinder v1.1.0 (Lanfear, et al., 2012) (Table S2). Assumptions included a Yule tree prior, piecewise linear and constant root population size model, and the lognormal relaxed molecular clock. The model parameters were unlinked across genes. We conducted the analyses using a mutation rate of cyt *b* of 0.53% per lineage per million years as estimated for North American Cyprinids (Dowling, et al., 2002). Mutation rates for all nuclear markers were estimated, relative to the mitochondrial rate, using a normal prior (mean 0.01, SD 0.05) (Schönhuth, et al., 2015). We selected the lineages in the *BEAST analysis according to the lineages recovered in the phylogenetic trees (*Codoma ornata*, Fig. S1; CDGG Fig. S2; *Campostoma ornatum*, Fig. S3; *Pantosteus plebeius-nebuliferus*, Fig. S4; Table S1). For these analyses we performed a MCMC with 120 million generations, sampled every 1000 generations, in CIPRES Science Gateway v3.3 (http://www.phylo.org/sub_sections/portal/). We assessed convergence with ESSs in TRACER v1.5 (Rambaut & Drummond, 2007). We discarded 20% of the generations as burn-in using the Tree Annotator v1.8.1 (Drummond et al., 2012). We visualized the trees in FigTree v1.4.2 (Rambaut, 2014).

2.3. Historical biogeography

To reconstruct the biogeographic history and ancestral ranges of four freshwater fish species in the Mesa del Norte and Pacific northwest slope of the SMO, we analyzed the ultrametric and dichotomous trees previously obtained in the dating analysis in BEAST,

using the R package BioGeoBEARS (Matzke, 2013a, b). This package uses the likelihood version of the three most common biogeographical history reconstruction methods: dispersal vicariance analysis (DIVA; Ronquist, 1997) as DIVALIKE method, dispersal extinction cladogenesis analysis (DEC; Ree & Smith, 2008), and Bayesian analysis of biogeography (BayArea; Landis, et al., 2013) as BAYAREALIKE method. These traditional models of biogeographic reconstruction assume that the daughter species inherit the distribution or part of the distribution of the ancestor (Matzke, 2013b). We also used a modified version of each model that includes a founder-event speciation (J parameter, or "jump dispersal" parameter), which allows one daughter species to inherit the distribution of the ancestor and another daughter species to disperse to a novel geographic area outside the ancestor's range (Matzke, 2013b, 2014). These models + J are particularly useful an island-like systems, where founder-event speciation is expected (Matzke, 2014).

We compared the fit of the dataset to each of the different models using the Akaike information criterion (AIC) (Matzke, 2013, 2014). We ranked the AIC values for each of the biogeographic models to select the model that yields the smallest values of AIC for inferences. We took ΔAIC values higher than two between the models as evidence that the new parameter (e.g. different dispersal probabilities) is important (Anderson, 2008).We grouped the sampling localities based on the current distribution patterns of the four groups analyzed into the following discrete areas: A) Yaqui River, B) Mayo River, C) Fuerte River, D) Conchos River, E) Nazas River, F) Aguanaval River, G) Mezquital River, H) Piaxtla River, I) Casas Grandes River, J) Santa Maria River, K) Del Carmen River; L) Grande River, M) Lake Palomas (Fig. 1). We allowed for a maximum of two areas at each node. We compared and analyzed the ancestral area reconstructions among fish species for

biogeographical patterns (Van Dam & Matzke, 2016), looking for biogeographic events shared in time and space.

3. RESULTS

We constructed a concatenated data set (cyt *b* + *Rag1* + *S7*) of 38 sequences for *Codoma ornata* (Table S1). A concatenated dataset (cyt *b* + *Rag1* + *S7*) of 24 sequences for the CDGG (Table S1). For *Campostoma ornatum*, we obtained a concatenated data set (cyt *b* + *S7*) of 100 sequences. Finally, we obtained a concatenated data set (cyt *b* + *GHI*) of 150 sequences for *Pantosteus plebeius-nebuliferus* (Corona-Santiago, et al., 2018) (Table S1).

3.1. Phylogenetic relationships

Our phylogenies revealed similar results to previous studies (Figs. S1, S2, S3, and S4) (Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2014, 2015; Corona-Santiago, et al., 2018). We recovered four major lineages in *Codoma ornata* (BS= 100% and PP= 1): lineage I (Upper Conchos); lineage II (Lower Conchos + Peñon); lineage III (Nazas); and lineage IV (Upper Mezquital) (Fig. S1; Table S1). In the CDGG, we recovered a monophyletic group in the Chihuahuan Desert composed of six species (BS= 100% and PP= 1): *Gila conspersa*, *Gila sp.* 1, *G. brevicauda*, *G. pulchra*, *G. modesta*, and *G. nigrescens* (Fig. S2; Table S1). We recovered three major lineages for *Campostoma ornatum*: lineage I (Upper Conchos, and Conchos + Grande River), (BS= 88%; PP= 0.99); lineage II (Yaqui + Mayo + Casas Grandes, and Del Carmen), (BS= 98%; PP= 0.98); lineage III (Nazas + Aguanaval + Piaxtla), (BS= 100% and PP= 1) (Fig. S3; Table S1). We recovered four major lineages for *Pantosteus plebeius-nebuliferus* f: lineage I (Guzman: Palomas + Guzman + Santa Maria + Del Carmen), (BS= 77%; PP= 1); lineage II (Upper

Conchos), (BS= 100%; PP= 1); lineage III (Nazas), (BS= 94% and PP= 0.99); lineage IV (Upper Mezquital), (BS= 100%; PP= 1) (Fig. S4; Table S1).

3.2. *Time-calibrated Species Tree analysis:*

In all groups the species tree analyses with the concatenated datasets support the assumption of the lineages recovered in the phylogenetic analyses (Figs. S1, S2, S3, and S4) with high internal branch-length Bayesian Posterior Probability (>99%) (not shown). We dated the divergence between the main clades of *Codoma ornata* to the Pliocene and Pleistocene. We dated the split of the main clades at *ca*. 3.5 million years ago (Mya) (95% Highest Posterior Density (HPD): 1.6-5.4 Mya) (Fig. 2). We estimated the split between the Lower Conchos + Peñon (lineage II) and Upper Conchos (lineage I) at *ca*. 2.9 Mya (95% HPD: 1.4-4.5 Mya). We estimated the split between between Nazas + Piaxtla (lineage III) and Mezquital (lineage IV) at *ca*. 3.0 Mya (95% HPD: 1.2-4.8 Mya) and the separation within the Upper Conchos (lineage I) at *ca*. 1.5 Mya (95% HPD: 0.5-2.5 Mya) (Fig. 2).

We dated the divergence among the species in the CDGG to the Miocene. We dated the separation of *Gila conspersa* at *ca*. 9.8 Mya (95% HPD: 6.2-13.4 Mya) (Figs. 3 and S2); the separation between *Gila sp.*1 and the group of *G. brevicauda*, *G. pulchra*, *G. modesta*, and *G. nigrescens* at *ca*. 8.1 Mya (95% HPD: 4.7-11.6 Mya); the separation between *G. nigrescens*, and the three *G. modesta*, *pulchra*, and *brevicauda* at *ca*. 4.8 Mya (95% HPD: 2.4-7.3 Mya); the separation between *G. modesta*, and the two *G. pulchra* and *G. brevicauda* at *ca*. 4.3 Mya (95% HPD: 2-6.6 Mya); and the split between *G. brevicauda* and *G. pulchra* at *ca*. 2.9 Mya (95% HPD: 1-4.8 Mya) (Figs. 3 and S2).

We dated the divergence between the main clades of *Campostoma ornatum* to the Miocene and Pliocene. We dated the separation of lineages I (Yaqui + Mayo + Guzman +

Del Carmen) and II (Conchos + Grande) with lineage III (Nazas + Aguanaval + Piaxtla) at *ca*. 11.6 Mya (95% HPD: 7-16.3 Mya) (Figs. 4 and S3). We estimated the split between lineage I and lineage II at *ca*. 4.2 Mya (95% HPD: 2.8-5.6 Mya) (Figs. 4 and S3). We estimated the separation within the lineage II (Del Carmen *vs.* Yaqui + Mayo + Guzman) at *ca.* 3.3 Mya (95% HPD: 1.6-5 Mya). Whereas we estimated the separation within lineage I (Upper Conchos *vs.* Grande + Conchos) at *ca.* 1.4 Mya (95% HPD: 0.3-2.6 Mya) (Figs. 4 and S3).

We dated the time divergence between the main clades of *Pantosteus plebeius-nebuliferus* to the Miocene and Pliocene. We dated the separation of lineage I (Guzman) and the other lineages at *ca*. 22.4 Mya (95% HPD: 8.1-36.8 Mya) and the separation between lineage II (Upper Conchos) and the two lineages III (Nazas) and IV (Upper Mezquital) at *ca*. 16.5 Mya (95% HPD: 6.3-26.7 Mya). We estimated the split between lineages III and IV at *ca*. 12.5 Mya (95% HPD: 4.5-20.5 Mya) (Fig. 5). Within lineages we estimated splits at *ca*. 3.5 Mya (95% HPD: 0.6-6.5 Mya) in lineage III (Nazas *vs.* Piaxtla) and within lineage II (Fuerte vs. Conchos) at *ca.* 1.9 Mya (95% HPD: 0.08-3.9 Mya) (Fig. 5). We estimated the separations within lineage I at *ca*. 2.4 Mya (95% HPD: 0.7-4.2 Mya) (Del Carmen *vs.* Santa Maria, Palomas, and Casas Grandes); *ca*. 1.3 Mya (95% HPD: 0.3-2.3 Mya) (Santa Maria *vs.* Palomas and Casas Grandes); and *ca*. 1.1 Mya (95% HPD: 0-2.2 Mya) (Palomas *vs.* Casas Grandes) (Fig. 5).

3.3. Historical biogeography

For *Codoma ornata*, the CDGG, and *Campostoma ornatum* we found that the DIVALIKE + J was the model with the highest likelihood scores and lower AIC values

(Table S3). BAYAREALIKE + J model showed the highest likelihood scores and resulted in the smallest AIC score in *P. plebeius-nebuliferus* (Table S3).

The biogeographic scenario of *Codoma ornata* showed an ancestral area formed by Conchos + Nazas + Mezquital (DEG) rivers for the most recent common ancestor (MRCA) (Figs. 1 and 2). A first vicariant event (1) at the basal node split the ancestral area into two areas, one area comprises the Conchos (D) River, the ancestral distribution of lineages I and II, and the second comprises the Nazas + Mezquital (EG) rivers, the ancestral area of the lineages III and IV (Fig. 2). The second biogeographic event corresponded with a dispersal event (2) related to the secondary contact between Conchos (D) and Nazas (E) rivers, establishing the ancestral area of the lineage II. A founder event was found (3), a result of the invasion of the ancestor of lineage I into the northern Yaqui + Mayo (AB) rivers from Conchos + Nazas (DE) rivers (Fig. 2). Likewise, a second vicariant event (4) split the ancestral area of lineages III and IV in two, one comprised the Mezquital (G) River, the ancestral area of lineage IV, and the second area comprised the Nazas (E) River, followed by a dispersal event (5) to Piaxtla (H) River by the ancestor of lineage III, led to an ancestral area comprising Nazas + Piaxtla rivers (Fig. 2). Inside linage I, we found a second founder event (6) from Yaqui + Mayo (AB) rivers to Fuerte + Conchos (CD) rivers (Fig. 2).

For the CDGG, the historical biogeographic analysis inferred an ancestral area for the MRCA, formed by Yaqui (A) + Casas Grandes (I) + Santa Maria (J) + Del Carmen (K) rivers (Figs. 1 and 3). The first founder event (1) took place from the MRCA to Nazas + Aguanaval (EF) River (Fig. 3). A second founder event (2) from Yaqui (A) + Casas Grandes (I) + Santa Maria (J) + Del Carmen (K) rivers to Mezquital (G) River also occurred (Fig. 3). While the ancestor of *Gila sp.* 1 remained in Mezquital River, a third founder event (3) from Yaqui (A) + Casas Grandes (I) + Santa Maria (J) + Del Carmen (K)

rivers to Grande (L) River occurred (Fig. 3), establishing the distribution of the ancestor of *G. modesta* + *G. pulchra* + *G. brevicauda*, leaving the ancestors of *G. nigrescens* in the Yaqui (A) + Casas Grandes (I) + Santa Maria (J) + Del Carmen (K) rivers. A fourth founder event (4) from the Grande (L) River as an ancestral area to Fuerte (C) River was occured, allowing the differentiation of *G. modesta* and the ancestor of *G. pulchra* + *G. brevicauda* in each river respectively (Fig. 3). A dispersal event (5) from Fuerte (C) to Conchos (D) River, led to the current distribution of *G. pulchra* (Fig. 3). Finally, we found a dispersal event (6) from Fuerte (C) to Yaqui + Mayo (AB) (Fig. 3), resulting in the current distribution of *G. brevicauda* in Fuerte + Yaqui + Mayo rivers (Fig. 3).

The scenario shown by the DIVALIKE + J model in *Campostoma ornatum* inferred an ancestral area formed by Nazas + Aguanaval + Piaxtla (EFH) (Figs. 1 and 4). A first founder event (1) from Nazas + Aguanaval + Piaxtla (EFH) to Conchos River occurred, leading to the current distribution of lineage III (Nazas + Aguanaval + Piaxtla) (Fig. 4). At the same time, a dispersal event (2) from Conchos (D) River to Grande (L) + Fuerte (C) rivers occurred (Fig. 4). A second founder event (3) from Conchos (D) + Grande (L) + Fuerte (C) rivers to Del Carmen (K) River occurred (Fig. 4), followed by a dispersal event (4) from Del Carmen (K) River to Mayo (B) + Yaqui (A) + Casas Grandes (I) rivers (Fig. 4). At the same time, a vicariant event (5) split the Mayo (B) + Yaqui (A) + Casas Grandes (I) rivers (BAI- lineage II area) from Del Carmen (K) River (lineage II area) (Fig. 4). A second vicariant event (6) split the Conchos + Grande (DL) rivers from Conchos + Fuerte (DC) rivers (lineage I area) (Fig. 4).

The biogeographic scenario of *Pantosteus plebeius-nebuliferus* showed an ancestral area of the MRCA formed by Conchos (D) + Fuerte (C) rivers (Figs. 1 and 5). A first founder event (1) from Conchos (D) + Fuerte (C) rivers to Del Carmen (K) River occurred

(Fig. 5). We found widespread sympatry in Conchos (D) + Fuerte (C) rivers, followed by a second founder event (2) from Conchos (D) + Fuerte (C) rivers to Nazas (E) + Piaxtla (H) rivers (Fig. 5). A third founder event (3) from Nazas + Piaxtla (EH) to Mezquital (G) River occurred resulting in the current distribution of lineage IV. The first vicariant event (4) between Nazas (E) and Piaxtla (H) River occurred, resulting in the current distribution of both populations within lineage III (Fig. 5). A fourth founder event (5) from Del Carmen (K) River to Santa Maria (J) River occurred (lineage I area) (Fig. 5). We found a second vicariant event (6) between Fuerte (C) and Conchos (D) rivers (lineage II area) (Fig. 5). A fourth founder event (7) from Santa Maria (J) to Lake Palomas (M) occurred, followed by a dispersal event (8) from Palomas (M) to Casas Grandes (I) River (Fig. 5). A third vicariant event (9) between Palomas (M) and Casas Grandes (I) occurred (lineage I area) (Fig. 5).

4. DISCUSSION

The phylogenetic trees found in *Codoma ornata*, the CDGG, *Campostoma ornatum*, and *Pantosteus plebeius-nebuliferus* recover the same topology as those in previous works (Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2014, 2015; Corona-Santiago, et al., 2018). The divergence times found in *C. ornata* and *C. ornatum* were also similar to those found in previous works (Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2015). Our biogeographic results show a complex history highlighting the role of vicariance, dispersal, and founder events in the diversification and evolution of these four northwestern Mexican freshwater fish clades, with some concordance in biogeographic events in space and time (Figs. 2-5).

4.1. Northern-Southern split

We did not find that the four studied groups shared a common ancestral range, however, we did find a clear Southern (ancestral Nazas-Aguanaval rivers system) and Northern (Conchos and Guzman basins) split in the early radiation of each group: In *Codoma ornata* a vicariant event separated the Nazas-Mezquital ancestral area from Conchos at *ca.* 3.5 Mya (1.6-5.4 Mya) (Fig. 2). In *Gila* a dispersal event from the Yaqui and Guzman paleo system (Casas Grandes, Santa Maria, and Del Carmen) to the Nazas-Aguanaval ancestral area, with a subsequent cladogenesis at *ca.* 9.8 Mya (6.2-13.4 Mya) created the North-South split (Fig 3.). In *Campostoma ornatum* a dispersal event from ancestral Nazas-Aguanaval and Piaxtla to the Conchos River with a subsequent cladogenesis dated at 11.6 Mya (7-16.3 Mya) (Fig. 4) facilitated the split. In *Pantosteus plebeius-nebuliferus* the cause of the split was a dispersal event from Conchos and Fuerte rivers to Nazas and Piaxtla with a subsequent cladogenesis dated at 16.5 Mya (6.3-26.7 Mya) (Fig. 5).

This Northern and Southern paleo-basin split has previously been found in the genera *Cyprinella* (Contreras-Balderas & Lozano, 1994), *Cyprinodon* (Echelle & Echelle, 1998; Echelle, et al., 2005), *Gila* (Miller, et al., 2005), *Ictiobus* (Bart, et al., 2010), and *Campostoma* (Domínguez-Domínguez, et al., 2011), supporting the existence of an ancient paleo-system that connected the Conchos and the Nazas rivers via bolson lakes during the Miocene.

The complex biogeographic history of northwestern Mexico has been associated with the existence of an extended Río Grande system that originated in the Oligocene (Smith & Miller, 1986; Mayden, Matson, et al., 1992; Mayden, Burr, et al., 1992; Echelle, et al., 2005; Galloway, et al., 2011; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2012, 2015; Corona-Santiago, et al., 2018), at the same time that the SMO was increasing in volume and area (Schönhuth, et al., 2015). Extensive zones of the

southwestern highlands of the US (Colorado Plateau, in current Utah, Colorado and Arizona), Chihuahuan Desert (New Mexico, Chihuahua, Coahuila and Durango) and the current Lower Grande River Basin were part of the ancient Río Grande system (Galloway, et al., 2011; Schönhuth, et al., 2015). This system was involved in the possible transfers and/or integration of headwaters of the Mesa del Norte with drainages from the Pacific slope of the SMO (Minckley, et al., 1986; Miller, et al., 2005; Schönhuth, et al., 2015) and stretched as far south as the Nazas and Aguanaval rivers via bolson lakes (Smith & Miller, 1986; Mayden, Matson, et al., 1992; Schönhuth, et al., 2015), and the upper reaches of the Mezquital River (Pacific drainage) (Albritton, 1958; Smith & Miller, 1986; Schönhuth, et al., 2015). This Río Grande system would have acted as a hydrological corridor for the ancestors of current freshwater fish species, permitting their expansion across the drainages (Smith & Miller, 1986; Mayden, Matson, et al., 1992; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2015). The fragmentation of the ancestral Río Grande system (Smith, et al., 1984; Albritton, 1958; Miller & Smith, 1986; Minckley, et al., 1986; Smith & Miller, 1986; Schönhuth, et al., 2015), was caused by regional patterns of uplift and subsidence during the Miocene and Pliocene, while an arid climate extended across the western interior, that caused the reorganization of drainage configurations (Galloway, et al., 2011; Schönhuth, et al., 2015) and the isolation and subsequent cladogenesis of fish species.

4.2. Common events in biogeographic history

Yaqui-Guzman Basin shared range

We found in two of the four studied groups (the CDGG and *Campostoma ornatum*) shared an ancestral range containing the Yaqui River and the Guzman Basin rivers (Casas

Grandes, Santa Maria, and Del Carmen), that was split in to two areas during the Miocene (4.2 to 4.8 Mya). This generated cladogenetic events in the two species. This relationship between the Yaqui and Guzman areas is related to the existence of an ancestral pluvial Lake in the Babicora Lagoon zone (Smith & Miller, 1986). Babcora Lagoon is a current endorheic Basin between the Guzman Basin and the Yaqui River (Papigochic) (Fig. 1) that represents a relic of the ancestral lake (Smith & Miller, 1986). These dispersal events show a biogeographic scenario also congruent with river catchments promoted by alkaline basalts events associated with the volcanism in the Babicora-Bustillos sector (Pérez-Rodríguez, et al., 2016; Corona-Santiago, et al., 2018).

Dispersal events related to the Pacific range expansion through river capture

We found dispersal and founder events in *Codoma ornata*, the CDGG, and *Campostoma ornatum* related to the Pacific range expansion of drainage basins of the Río Grande system (Conchos and Yaqui rivers) to rivers in the Pacific slope of the SMO (Mayo and Fuerte rivers) during the Pliocene-Pleistocene period. These dispersal events support the hypothesis of river capture from the ancestral and the extant Río Grande system, via stream capture events, drainage reversals, and structural integration of sub-basins (Schönhuth, et al., 2011). This biogeographic scenario occurred during the Pliocene and Pleistocene periods and was associated with the tecto-volcanic episodes involved in the origin and formation of the SMO, including repeat alkaline basalt events (Henry & Aranda-Gómez, 2000; Aranda-Gómez, et al., 2005; Ferrari, et al., 2007). These results corroborate previous phylogeographic studies in freshwater fish species (Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2015; Ballesteros-Nova, et al., 2019).

The separation of the Nazas +Piaxtla and Mezquital River

We found a vicariant event related to the separation between Nazas + Piaxtla and Upper Mezquital River (tributary El Tunal, Mezquital Basin) in *Codoma ornata* and *Pantosteus plebeius-nebuliferus*, during the Miocene-Pliocene period. This vicariant event possibly occured as a result of the alkaline volcanic activity occurring in the region at the time, especially south of Laguna Santiaguillo in the Nazas basin, in the southern region of the SMO (Ferrari, et al., 2007; Corona-Santiago, et al., 2018) during Late Miocene and Pliocene (Damon & Nieto-Obregón, 1979; Aguirre-Díaz, et al., 2008; Luhr, et al., 2011).

Dispersal events between Fuerte and Conchos rivers

In the four freshwater fish lineages, a connection and isolation between Conchos River and Fuerte River occurred during the Pliocene and Pleistocene. This biogeographic scenario is related to volcanic activity and headwater erosion in the zone during this time. These events connected and isolated the Conchos River leading it to drain to the east side of the SMO to the Mesa del Norte in the Chihuahuan Desert; while the Fuerte River drained to the west side of the SMO to the Pacific slope (Minckley, et al., 1986; Miller, et al., 2005; Schönhuth, et al., 2015; Ballesteros-Nova, et al., 2019). The combination of tectonic, volcanic, and climatic factors played a major role in the evolution of drainages in the North of Mexico during the Pliocene and Pleistocene period (Galloway, et al., 2011), connecting drainage basins of the Mesa del Norte and the Pacific Slope (Galloway, et al., 2011; Domínguez-Domínguez, et al., 2011; Schönhuth, et al., 2011, 2014, 2015, Corona-Santiago, et al., 2018).

4.3. Codoma ornata an independent history

The biogeographical history of *Codoma ornata* was not temporal congruence with the biogeographic histories of the other three study groups (the CDGG, *Campostoma ornatum* and *Pantosteus plebeius-nebuliferus*). We found that most biogeographic events affecting *Codoma ornata* occured in the Pliocene and Pleistocene, unlike in the other study groups where most of the biogeographic events occurred during the Miocene and Pliocene. This scenario could be linked to the more recent origin of the genus *Codoma* (northwestern of Mexico distribution) compared to the other groups, since this is dated to the Mid-Miocene, between 9.17 to 12.19 Mya (Schönhuth, et al., 2015).

Among the biogeographic events affecting *Codoma ornata* during the Pliocene, we found a secondary contact 3) between Conchos and Nazas rivers at *ca.* 2.9 Mya, similar to the occurrence of Nazas + Conchos lineage in *Pimephales promelas* at *ca.* 3.9 Mya (Ballesteros-Nova, et al., 2019). Is interesting that both, *P. promelas* and *C. ornata,* share reproductive characteristics (e.g. spawn groups of eggs in cavities) (Miller, et al., 2005). This may have helped to protect the eggs of both species during tectonic events, alkaline basalt events, and river capture during the Pliocene, facilitating similar patterns of dispersal in response to such events (Henry & Aranda-Gómez, 2000; Aranda-Gómez, et al., 2005; Ferrari, et al., 2007).

CONCLUSIONS

The results presented herein provide an overview of the biogeographic history of three species (*Codoma ornata*, *Campostoma ornatum,* and *Pantosteus plebeius-nebuliferus*), and the Chihuahuan Desert Group of the genus *Gila*. Our result so not support a common biogeographic history for most of the evolutionary history of the groups.

Codoma. ornata is a most recent species, so the co-distribution with the other

groups have geographic congruence but not time congruence. Alternatively, the other three groups studied have geographic and time congruence, but low biogeographic congruence. Accordingly, the biogeographic history of these groups seems to be more highly affected by the biological or ecological characteristic of the groups than the paleohydrological events *per se*.

Most of the shared, as well as independent biogeographic events affecting the groups seem to be closely linked to dispersal events and founder speciation events associated with the formation and evolution of the SMO and accumulation of alkaline basalts via tectonic activity. This is congruent with what has been observed in other freshwater fishes in northwestern Mexico.

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FIGURES

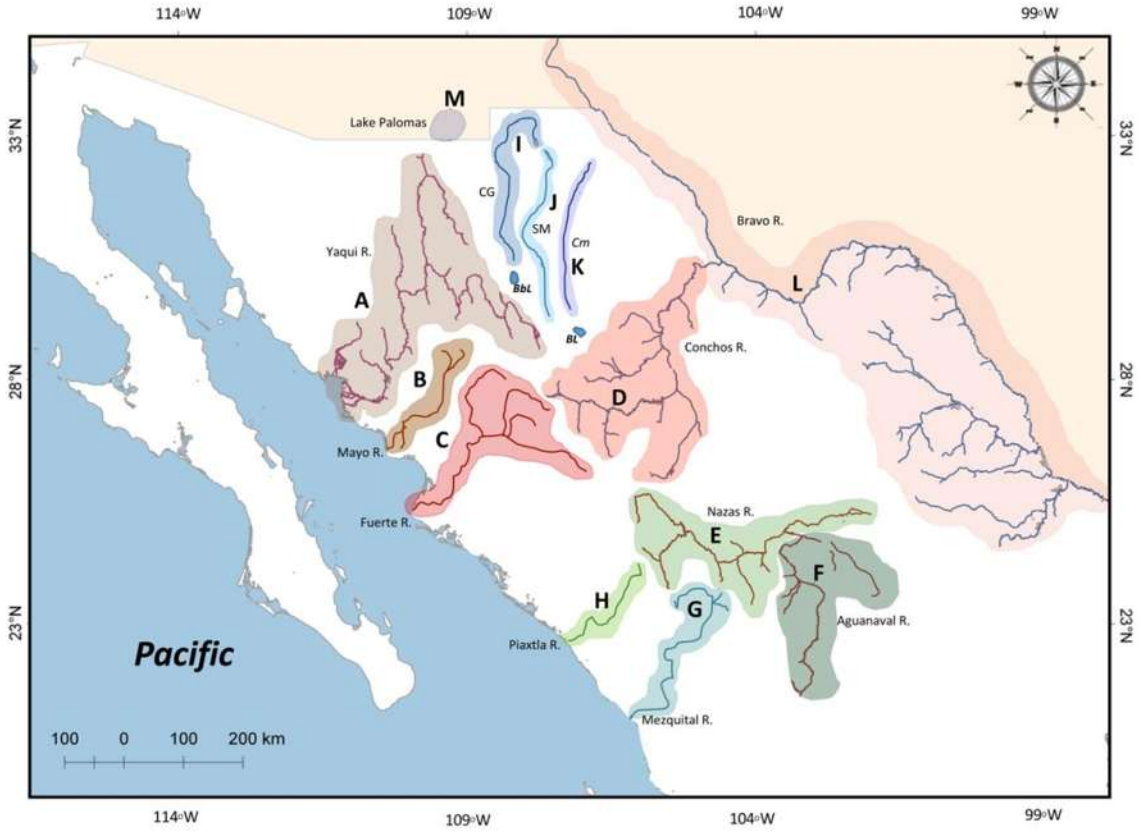

Figure 1. Drainage basins of northwestern Mexico included in this study. Colors and shapes correspond to each drainage basin included to reconstruct ancestral geographical distributions with BioGeoBEARS. Abbreviations: *A*, Yaqui River; *B*, Mayo River; *C*, Fuerte River; *D*, Conchos River; *E*, Nazas River; *F*, Aguanaval River; *G*, Mezquital River; *H*, Piaxtla River, *I*, Casas Grandes River; *J*, Santa Maria River; *K*, Del Carmen River; *L*, Grande River; *M*, Lake Palomas. *CG*, Casas Grandes River; *SM*, Santa Maria River; *Cm*, Del Carmen River; *BbL*, Babicora Lagoon; *BL*, Bustillos Lagoon.

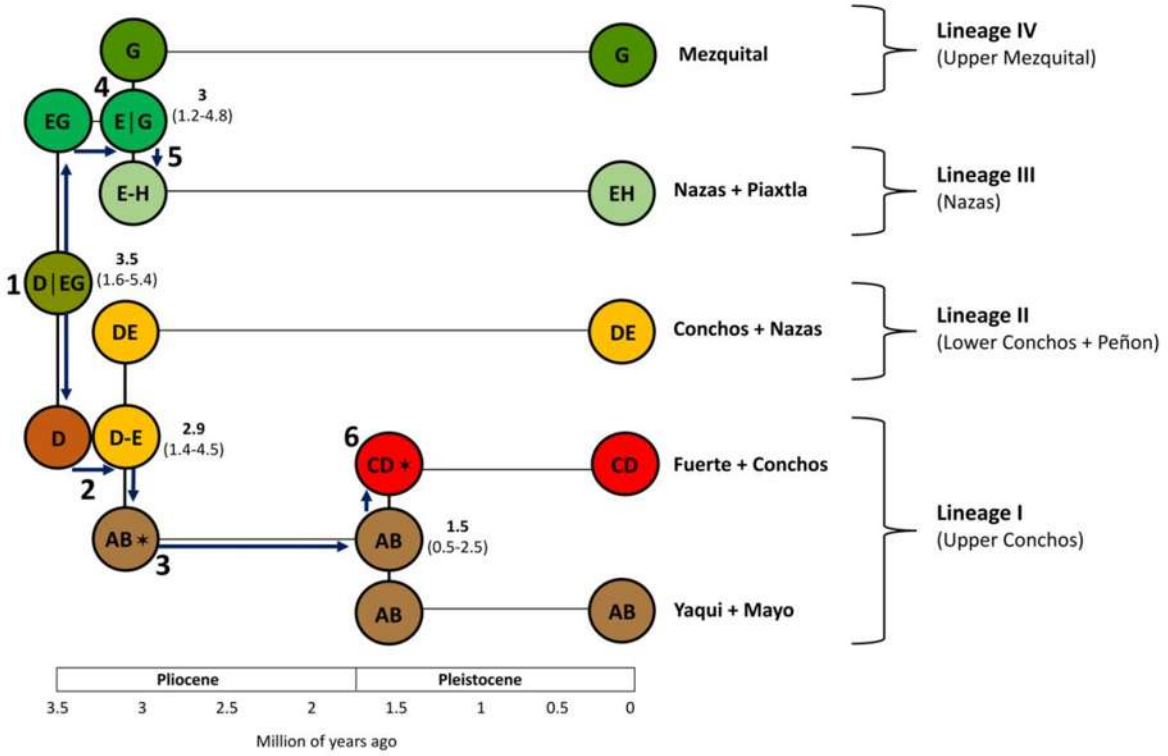

Figure 2. Biogeographic reconstruction (DIVALIKE + J) derived from BioGeoBEARS analysis of the *Codoma ornata* species-group distribution and divergence times estimation. Numbers correspond to major biogeographic events: dispersal events (-), founder-events speciation (*), and vicariant events (|). The geographic areas codes are as follows: *A*, Yaqui; *B*, Mayo; *C*, Fuerte; *D*, Conchos; *E*, Nazas; *G*, Mezquital; *H*, Piaxtla; according to the areas in Figure 1. Values on the right of each node represent the 95% highest posterior density of divergence time estimates obtained in dating BEAST analysis.

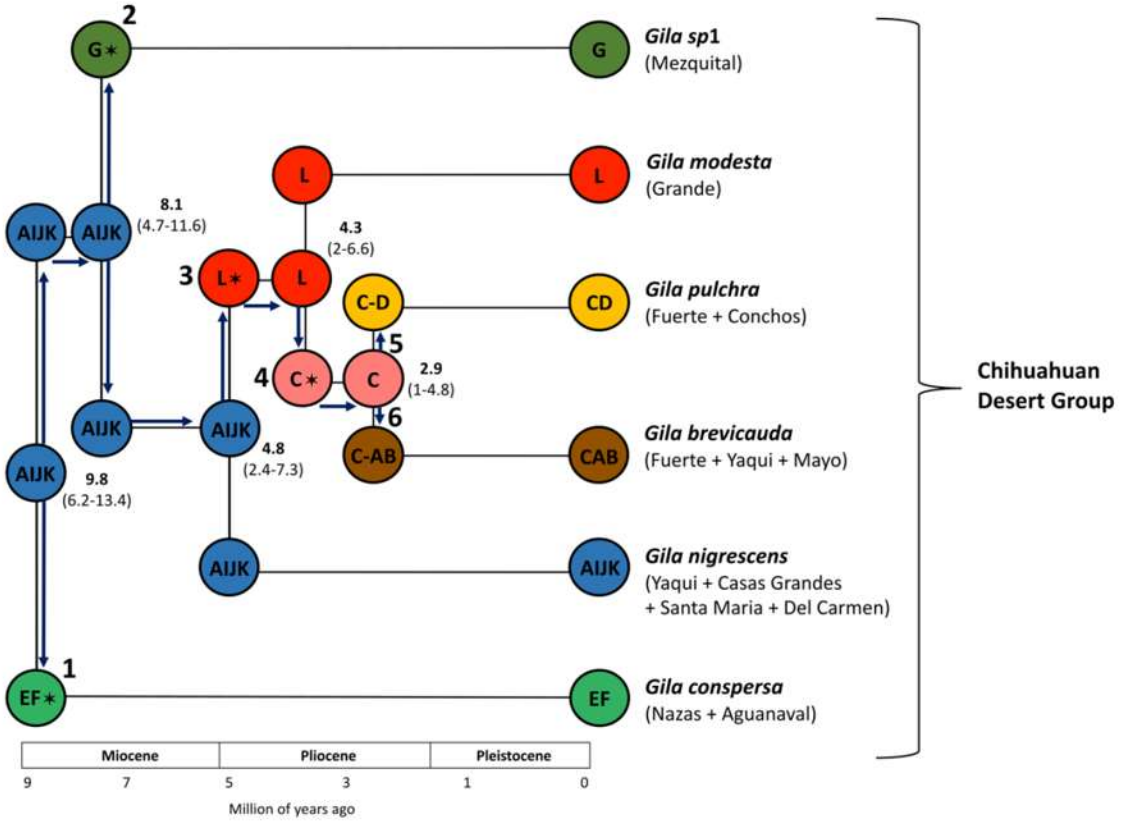

Figure 3. Biogeographic reconstruction (DIVALIKE + J) derived from BioGeoBEARS analysis of the Chihuahuan Desert Group of the genus *Gila* distribution and Divergence times estimation. Numbers correspond to major biogeographic events: dispersal events (-), founder-events speciation (*), and vicariant events (|). The geographic areas codes are as follows: *A*, Yaqui; *B*, Mayo; *C*, Fuerte; *D*, Conchos; *E*, Nazas; *F*, Aguanaval; *G*, Mezquital; *I*, Casas Grandes; *J*, Santa Maria; *K*, Del Carmen; *L*, Grande; according to the areas in Figure 1. Values on the right of each node represent the 95% highest posterior density of divergence time estimates obtained in dating BEAST analysis.

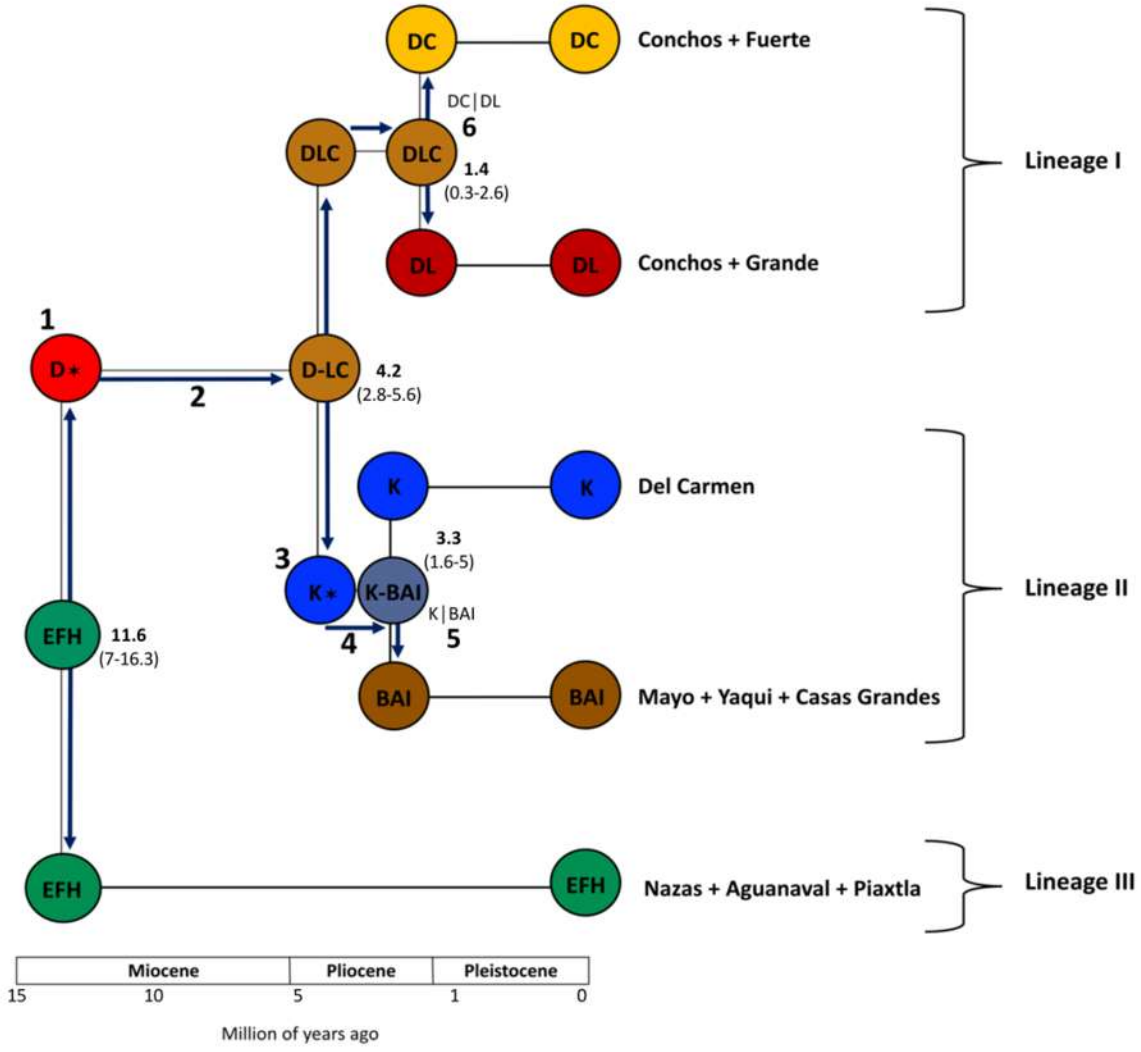

Figure 4. Biogeographic reconstruction (DIVALIKE + J) derived from BioGeoBEARS analysis of *Campostoma ornatum* distribution and Divergence times estimation. Numbers correspond to major biogeographic events: dispersal events (-), founder-events speciation (*), and vicariant events (|). The geographic areas codes are as follows: *A*, Yaqui; *B*, Mayo; *C*, Fuerte; *D*, Conchos; *E*, Nazas; *H*, Piaxtla; *I*, Casas Grandes; *K*, Del Carmen; *L*, Grande; according to the areas in Figure 1. Values on the right of each node represent the 95% highest posterior density of divergence time estimates obtained in dating BEAST analysis.

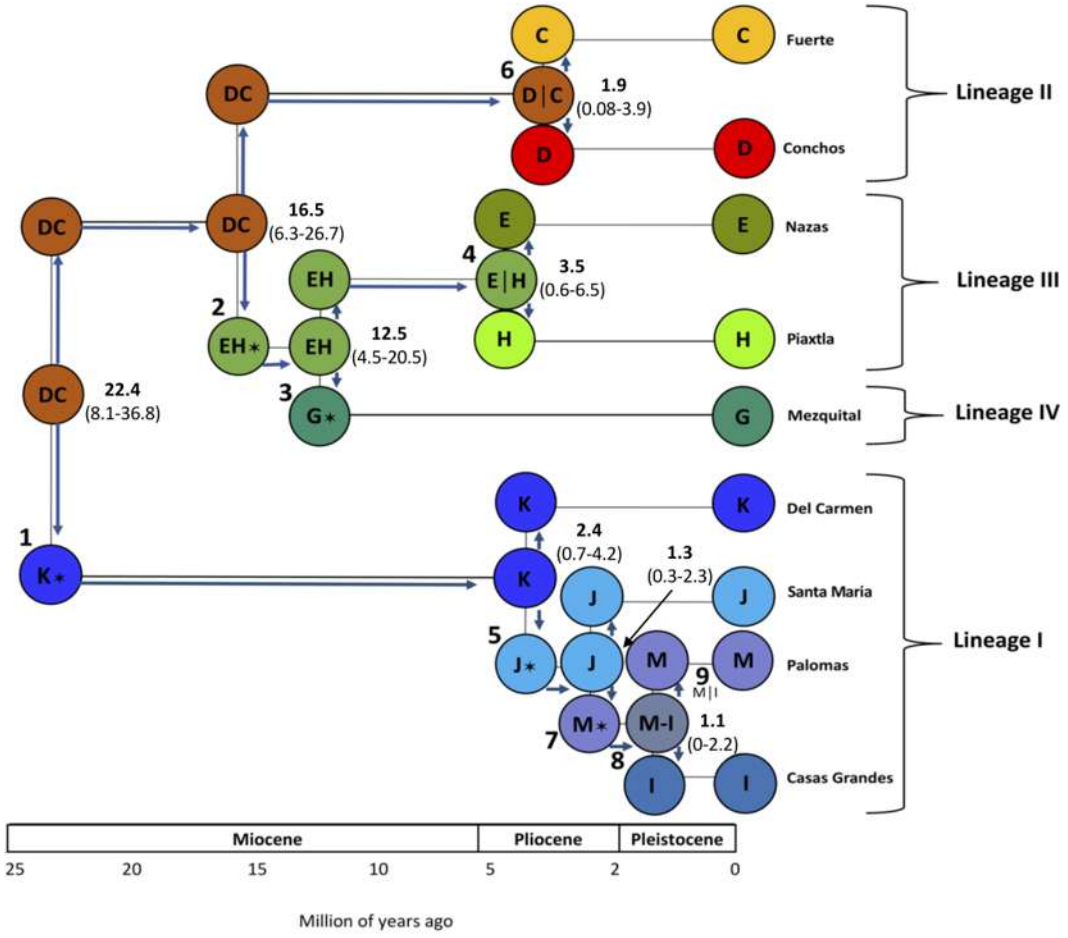

Figure 5. Biogeographic reconstruction (BAYAREALIKE + J) derived from BioGeoBEARS analysis of the of the *Pantosteus plebeius-nebuliferus* species-group distribution and Divergence times estimation. Numbers correspond to major biogeographic events: dispersal events (-), founder-events speciation (*), and vicariant events (|). The geographic areas codes are as follows: *A*, Yaqui; *B*, Mayo; *C*, Fuerte; *D*, Conchos; *E*, Nazas; *G*, Mezquital; *H*, Piaxtla; *I*, Casas Grandes; *J*, Santa Maria; *K*, Del Carmen; *L*, Grande; *M*, Palomas; according to the areas in Figure 1. Values on the right of each node represent the 95% highest posterior density of divergence time estimates obtained in dating BEAST analysis.

SUPPLEMENTARY MATERIAL

Table S1. Sampling localities for the specimens and outgroups analyzed in this study. Collection numbers are listed for vouchers stored at institutional collections followed by tissue numbers. Abbreviations: Dr: Drainage. Mex: México. SLUM: Saint Louis University, St. Louis, Missouri, USA. CPUM, Universidad Michoacana de San Nicolás de Hidalgo, Michoacán, México. MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain. MSB, Museum of Southwestern Biology. IBUNAM, Instituto de Biología-UNAM. UANL, Universidad Autónoma de Nuevo León. UAIC, University of Alabama Ichthyological Collection. Also include the accession number of the samples downloaded from GenBank.

	Drainage	**Sample ID**	**Cyt *b***	***Rag 1***	***S7***	***GHI***
Codoma ornata						
Lineage I						
Upper Conchos	Conchos	UAIC 15292.02	CD0907	CD0907	CD0907	
	Conchos	UANL 21646 (UANL350)	T0350	T350	T350	
	Conchos	SLUM 1647.01 (CD1647)	CD1647	CD1647	CD1647	
	Fuerte	(CD0270)	CD0270	CD270	CD270	
	Fuerte	IBUNAM-P15683 (CDH922)	CDH922	CDH922	CDH922	
	Fuerte	UAIC 15295.02 (CD0911)	CD0911	CD0911	CD0911	
	Fuerte	UANL 21604 (CD206)	CD206	CD206	CD206	
	Yaqui	UAIC 15291.02 (N0906)	CD0906	CD906	CD906	

	Yaqui	UAIC 15001.02 (CD0507)	CD0507	CD0507	CD0507	
	Yaqui	UAIC14992.02 (CD0515)	CD0515	CD515	CD515	
	Yaqui	UAIC 14996.03 (CD0514)	CD0514	CD514	CD514	
	Mayo	UAIC 15308.02 (CD0926)	CD0926	CD0926	CD0926	
Lineage II						
Lower Conchos + Peñon	Mayo	UAIC 14991.04 (CD6492)	CD6492	CD6492	CD6492	
	Nazas	(CPUM1659)	1659	1659	1659	
	Nazas	UANL 21593 (CO220, CD221)	CD220, CD221	CD220, CD221	CD220, CD221	
	Conchos	UANL 18913 (G065)	G065	G065	G065	
	Conchos	UANL 18921 (G096)	G096	G096	G096	
	Conchos	UANL 21617 (T0368)	T0368	T0368	T0368	
	Florido	UAIC 15376.02 (CD2061-2)	CD2062	CD2062	CD2061	
	Bustillos Lagoon	UAIC15392.01 (CD10261-2)	CD10261	CD10261	CD10261	
Lineage III						
Nazas	Nazas	UANL 19265 (G195)	G195A	G195	G195	
	Nazas	UANL 19256 (G183)	G183	G183	G183	
	Nazas	UANL19471 (CO292	CO292	CD292	CD292	
	Nazas	UAIC 15391.01 (CD2276, NSP2278)	CD2276	CD2276	CD2276	
	Nazas	(CPUM8961)	8961	8961	8961	
	Nazas	(CPUM8967)	8967	8967	8967	
	Nazas	(CPUM8968)	8968	8968	8968	
	Nazas	(CPUM8969)	8969	8969	8969	
Lineage IV						

Upper Mezquital	Mezquital	(CPUM 1510)	1510	1510	1510	
	Mezquital	(CPUM 1455)	1455	1455	1455	
	Mezquital	UANL 18741 (G043)	G043	G043	G043	
	Frio	UAIC 15389.01 (CD1022)	CD1022	CD1022	CD1022	
	Caliente	CDH31	CDH31	CDH31	CSPH31	
	Caliente	IBUNAM-P15786 (CDH33, CSPH33)	CSP33	CSPH33	CSPH33	
Outgroups						
Cyprinella formosa		UAIC 7889.03 (CF7889)	CF01	CF01	CF01	
Erimystax dissimilis		UAIC 7922.02 (ED8759)	ED8759	ED8759	ED8759	
Erimonax monachus		STL 888.04 (EM483)	EM483	EM483	EM483	
Chihuahuan desert group of the genus *Gila* (CDGG)						
Gila brevicauda	Fuerte	UAIC 15310.02 (GM0928)	GM0928	GM0928	GM0928	
Gila conspersa	Yaqui	UAIC 14969.03 (BRK514)	BRK514	BRK514	BRK514	
	Nazas	UANL 19267 (G193B)	G193	G193	G193	
	Aguanaval	UANL 18751 (G038)	G038	G038	G038	
	Aguanaval	UANL 18749 (G039)	G039	G039	G039	
	Aguanaval	UANL 18867 (G063)	G063	G063	G063	
	Nazas	UANL 19240 (G166A)	G166A	G166A	G166A	
Gila modesta	Aguanaval	UANL 18853 (G052)	G052	G052	G052	
Gila nigrescens	San Fernando	19274 (G200A-E)	G200A-E	G200A-B	G200A-B	
	Mimbres	MSB 76482 (GN821–GN824)	GN821-GN824	GN821	GN821	

	Yaqui	UAIC 15291.03 (GM399, GM400)	GM399, GM400	GM400	GM400	
	Babicora Lagoon	UAIC 15371.03 (GSP10021, GSP10022)	GSP10021, GSP10022	GSP10021	GSP10021	
	Bustillos Lagoon	UAIC 15373.01 (GN1004, GN2038)	GN1004, GN2038	GN1004	GN1004	
Gila pandora	Yaqui	UAIC 15001.03 (BRK57)	BRK57	BRK57	BRK57	
Gila pulchra	Grande	(GPP21)	GPP21	GPP21	GPP21	
	Fuerte	UAIC 14995.02 (DAN0507)	DAN0507	DAN0507	DAN0507	
	Conchos	UANL 18923 (G090)	G090	G090	G090	
*Gila sp.*1	Conchos	UANL 18914 (G070)	G070	G070	G070	
	Santiaguillo Lagoon	UAIC 15379.01 (GSP10111)	GSP10111	GSP10111	GSP10111	
	Mezquital	UANL 18745 (G040A, B)	G040B	G040B	G040B	
	Mezquital	UANL 19269 (G165)	G165	G165	G165	
	Sauceda	IBUNAM-P15751 (GSPH927, GSPH930, GSPH940, GSPH941)	GSPH930	GSPH930	GSPH930	
	Caliente	IBUNAM-P15785 (GSPH943, GSPH945) IBUNAM-P15769 (GSPH311, GSPH312)	GSPH312	GSPH312	GSPH312	
Outgroup						
Gila cypha	Colorado	SLUM 5521-RLM8306 (GE021)	GE021	GE021	GE021	
Pantosteus plebeius-nebuliferus						
Lineage IV						
Mezquital	Bayas Streem	MG203619.1-MG203706.1 (12855_1)	12855_ArroyoBayas_ Mezquital			12855_1_A_Bayas

	Bayas Streem	MG203620.1-MG203707.1 (12856_1)	12856_ArroyoBayas_Mezquital			12856_1_A_Bayas
	Bayas Streem	MG203621.1-MG203708.1 (12857_1)	12857_ArroyoBayas_Mezquital			12857_1_A_Bayas
	Bayas Streem	MG203622.1-MG203709.1 (12869_1)	12869_ArroyoBayas_Mezquital			12869_1_A_Bayas
	Bayas Streem	MG203625.1-MG203711.1 (12877_1)	12877_ArroyoBayas_Mezquital			12877_1_A_Bayas
	Bayas Streem	MG203624.1-MG203710.1 (12875_1)	12875_ArroyoBayas_Mezquital			12875_1_A_Bayas
	Gertrudis	MG203669.1-MG203770.1 (8901_1)	8901_Santa_Gertrudis_Mezquital			8901_1_S_Gertrudis
	La Barranca	MG203671.1-MG203771.1 (8919_1)	8919_Mezquital			8919_1_La_Barranca
	Bayas Streem	MG203619.1-MG203788.1 (12855)	12855_ArroyoBayas_Mezquital			12855_A_Bayas
	Bayas Streem	MG203620.1-MG203789.1 (12856)	12856_ArroyoBayas_Mezquital			12856_A_Bayas
	Bayas Streem	MG203621.1-MG203790.1 (12857)	12857_ArroyoBayas_Mezquital			12857_A_Bayas
	Bayas Streem	MG203622.1-MG203791.1 (12869)	12869_ArroyoBayas_Mezquital			12869_A_Bayas
	Bayas Streem	MG203625.1-MG203793.1 (12877)	12877_ArroyoBayas_Mezquital			12877_A_Bayas
	Bayas Streem	MG203624.1-MG203792.1 (12875)	12875_ArroyoBayas_Mezquital			12875_A_Bayas
	Gertrudis	MG203669.1-MG203860.1 (8901)	8901_Santa_Gertrudis_Mezquital			8901_S_Gertrudis
	La Barranca	MG203671.1-MG203861.1 (8919)	8919_Mezquital			8919_La_Barranca
Lineage III						
Nazas	Olote	MG203689.1-MG203784.1 (6822_1)	E10_6822			6822_1_El_Olote
	Olote	MG203693.1-MG203786.1 (6823_1)	E9_6823			6823_1_El_Olote
	Olote	MG203686.1-MG203787.1 (6831_1)	C9_6831_El_Olote_Nazas			6831_1_El_Olote

Olote	MG203677.1-MG203794.1 (6004)	6004_El_Olote			6004_El_Olote
Olote	MG203678.1-MG203795.1 (6006)	576804_6006_Nazas			6006_El_Olote
Olote	MG203680.1-MG203734.1 (6836_1)	A7_6836_Cnebuliferus_Nazas			6836_1_El_Olote
Olote	MG203688.1-MG203733.1 (6834_1)	D9_6834_El_Olote_Nazas			6834_1_El_Olote
Olote	MG203683.1-MG203731.1 (6826_1)	B11_6826_El_Olote_Nazas			6826_1_El_Olote
Olote	MG203696.1-MG203730.1 (6824_1)	F9_6824_El_Olote_Nazas			6824_1_El_Olote
Olote	MG203678.1-MG203714.1 (6006_1)	576804_6006_Nazas			6006_1_El_Olote
Olote	MG203677.1-MG203713.1 (6004_1)	6004_El_Olote			6004_1_El_Olote
Olote	MG203701.1-MG203712.1 (6003_1)	6003_ElOlote_Nazas			6003_1_El_Olote
Olote	MG203689.1-MG203811.1 (6822)	E10_6822			6822_El_Olote
Olote	MG203693.1-MG203812.1 (6823)	E9_6823			6823_El_Olote
Olote	MG203686.1-MG203816.1 (6831)	C9_6831_El_Olote_Nazas			6831_El_Olote
Olote	MG203680.1-MG203818.1 (6836)	A7_6836_Cnebuliferus_Nazas			6836_El_Olote
Olote	MG203688.1-MG203817.1 (6834)	D9_6834_El_Olote_Nazas			6834_El_Olote
Olote	MG203683.1-MG203814.1 (6826)	B11_6826_El_Olote_Nazas			6826_El_Olote
Olote	MG203696.1-MG203813.1 (6824)	F9_6824_El_Olote_Nazas			6824_El_Olote
Olote	MG203701.1-MG203869.1 (6003)	6003_ElOlote_Nazas			6003_El_Olote
Torreones	MG203690.1-MG203717.1 (6150_1)	E11_6150_Csp_Arroyo_Torreones_Nazas			6150_1_A_Torreones
Torreones	MG203682.1-	A9_6151_Arroyo_			6151_1_A_Torreone

	MG203717.1 (6151_1)	Torreones_Nazas			
Torreones	MG203679.1-MG203785.1 (6175)	A11_6175_Arroyo_Torreones_Nazas			6175_A_Torreones
Torreones	MG203690.1-MG203798.1 (6150)	E11_6150_Csp_Arroyo_Torreones_Nazas			6150_A_Torreones
Torreones	MG203682.1-MG203798.1 (6151)	A9_6151_Arroyo_Torreones_Nazas			6151_A_Torreones
Torreones	MG203679.1-MG203798.1 (6175_1)	A11_6175_Arroyo_Torreones_Nazas			6175_1_A_Torreones
Atotonilco	MG203697.1-MG203725.1 (6774_1)	G9_6774_Atotonilco_Nazas			6774_1_Atotonilco
Atotonilco	MG203684.1-MG203726.1 (6772_1)	B9_6772_Atotonilco_Nazas			6772_1_Atotonilco
Atotonilco	MG203691.1-MG203727.1 (6775_1)	E7_6775_Cnebuliferus_Atotonilco_Nazas			6775_1_Atotonilco
Atotonilco	MG203695.1-MG203728.1 (6780_1)	F11_6780_Atotonilco_Nazas			6780_1_Atotonilco
Atotonilco	MG203704.1-MG203729.1 (6781_1)	6781_Atotonilco_Nazas			6781_1_Atotonilco
Atotonilco	MG203684.1-MG203806.1 (6772)	B9_6772_Atotonilco_Nazas			6772_Atotonilco
Atotonilco	MG203697.1-MG203807.1 (6774)	G9_6774_Atotonilco_Nazas			6774_Atotonilco
Atotonilco	MG203691.1-MG203808.1 (6775)	E7_6775_Cnebuliferus_Atotonilco_Nazas			6775_Atotonilco
Atotonilco	MG203695.1-MG203809.1 (6780)	F11_6780_Atotonilco_Nazas			6780_Atotonilco
Atotonilco	MG203704.1-MG203810.1 (6781)	6781_Atotonilco_Nazas			6781_Atotonilco
Covadonga	MG203681.1-MG203735.1 (6893_1)	A8_6893_Cnebuliferus_Covadonga_Nazas			6893_1_Covadonga
Covadonga	MG203687.1-MG203736.1 (6903_1)	D11_6903_Covadonga_Nazas			6903_1_Covadonga
Covadonga	MG203681.1-MG203819.1 (6893)	A8_6893_Cnebuliferus_Covadonga_Nazas			6893_Covadonga
Covadonga	MG203687.1-MG203820.1 (6903)	D11_6903_Covadonga_Nazas			6903_Covadonga

	El cuarto	MG203698.1-MG203723.1 (6737_1)	H11_6737_El_Cuarto_Nazas			6737_1_El_Cuarto
	El peñasco	MG203700.1-MG203716.1 (6142_1)	H9_6142_El_Penasco_Nazas			6142_1_El_Penasco
	El peñasco	MG203700.1-MG203797.1 (6142)	H9_6142_El_Penasco_Nazas			6142_El_Penasco
	El peñasco	MG203699.1-MG203715.1 (6141_1)	H12_6141_Csp_El_Penasco_Nazas			6141_1_El_Penasco
	El peñasco	MG203699.1-MG203796.1 (6141)	H12_6141_Csp_El_Penasco_Nazas			6141_El_Penasco
Piaxtla	Las Vegas	MG203673.1-MG203772.1 (9003_1)	9003_LasVegas_Piaxtla			9003_1_Las_Vegas
	Las Vegas	MG203673.1-MG203773.1 (9003)	9003_LasVegas_Piaxtla			9003_Las_Vegas
	Las Vegas	MG203676.1-MG203774.1 (9020_1)	9020_LasVegas_Piaxtla			9020_Las_Vegas
	Las Vegas	MG203676.1-MG203775.1 (9020)	9020_LasVegas_Piaxtla			9020_1_Las_Vegas
	Las Vegas	MG203674.1-MG203862.1 (9010_1)	9010_Piaxtla			9010_Las_Vegas
	Las Vegas	MG203674.1-MG203863.1 (9010)	9010_Piaxtla			9010_1_Las_Vegas
	Las Vegas	MG203675.1-MG203864.1 (9013_1)	9013_Piaxtla			9013_Las_Vegas
	Las Vegas	MG203675.1-MG203865.1 (9013)	9013_Piaxtla			9013_1_Las_Vegas
Lineage III						
Fuerte	El cuarto	MG203698.1-MG203723.1 (6737)	H11_6737_El_Cuarto_Nazas			6737_El_Cuarto
	Oteros	MG203628.1-MG203738.1 (7215_1)	7215_Otero_Fuerte			7215_1_Oteros
	Oteros	MG203629.1-MG203739.1 (7217_1)	7217_Otero_Fuerte			7217_1_Oteros
	Oteros	MG203630.1-MG203740.1 (7218_1)	7218_Csp_Otero_Fuerte			7218_1_Oteros
	Oteros	MG203631.1-MG203741.1 (7219_1)	7219_Csp_Otero_Fuerte			7219_1_Oteros

	Oteros	MG203633.1-MG203742.1 (7222_1)	7222_Otero_Fuerte			7222_1_Oteros
	Oteros	MG203634.1-MG203743.1 (7223_1)	7223_Otero_Fuerte			7223_1_Oteros
	Oteros	MG203635.1-MG203744.1 (7226_1)	7226_Otero_Fuerte			7226_1_Oteros
	Oteros	MG203627.1-MG203783.1 (7213_1)	7213_Csp_Otero_Fuerte			7213_1_Oteros
	Oteros	MG203627.1-MG203821.1 (7213)	7213_Csp_Otero_Fuerte			7213_Oteros
	Oteros	MG203628.1-MG203823.1 (7215)	7215_Otero_Fuerte			7215_Oteros
	Oteros	MG203629.1-MG203824.1 (7217)	7217_Otero_Fuerte			7217_Oteros
	Oteros	MG203630.1-MG203825.1 (7218)	7218_Csp_Otero_Fuerte			7218_Oteros
	Oteros	MG203631.1-MG203826.1 (7219)	7219_Csp_Otero_Fuerte			7219_Oteros
	Oteros	MG203633.1-MG203827.1 (7222)	7222_Otero_Fuerte			7222_Oteros
	Oteros	MG203634.1-MG203828.1 (7223)	7223_Otero_Fuerte			7223_Oteros
	Oteros	MG203635.1-MG203829.1 (7226)	7226_Otero_Fuerte			7226_Oteros
Conchos	Conchos	MG203637.1-MG203746.1 (7295)	7295_Conchos			7295_Conchos
	Conchos	MG203637.1-MG203831.1 (7295_1)	7295_Conchos			7295_1_Conchos
Lineage I						
Santa Clara	Santa Clara	MG203659.1-MG203760.1 (7694_1)	7694_SantaClara_DelCarmen			7694_1_Santa_Clara
	Santa Clara	MG203660.1-MG203761.1 (7696_1)	7696_Cplebeius_Santa_Clara			7696_1_Santa_Clara
	Santa Clara	MG203661.1-MG203762.1 (7698_1)	7698_SantaClara_DelCarmen			7698_1_Santa_Clara

	Santa Clara	MG203662.1-MG203763.1 (7700_1)	7700_DelCarmen			7700_1_Santa_Clara
	Santa Clara	MG203663.1-MG203764.1 (7701_1)	7701_DelCarmen			7701_1_Santa_Clara
	Santa Clara	MG203664.1-MG203765.1 (7703_1)	7703_SantaClara_DelCarmen			7703_1_Santa_Clara
	Santa Clara	MG203665.1-MG203766.1 (7704_1)	7704_Santa_Clara			7704_1_Santa_Clara
	Santa Clara	MG203666.1-MG203767.1 (7706_1)	7706_SantaClara_DelCarmen			7706_1_Santa_Clara
	Santa Clara	MG203658.1-MG203776.1 (7693_1)	7693_Santa_Clara			7693_1_Santa_Clara
	Santa Clara	MG203658.1-MG203849.1 (7693)	7693_Santa_Clara			7693_Santa_Clara
	Santa Clara	MG203659.1-MG203850.1 (7694)	7694_SantaClara_DelCarmen			7694_Santa_Clara
	Santa Clara	MG203660.1-MG203851.1 (7996)	7696_Cplebeius_Santa_Clara			7696_Santa_Clara
	Santa Clara	MG203661.1-MG203852.1 (7698)	7698_SantaClara_DelCarmen			7698_Santa_Clara
	Santa Clara	MG203662.1-MG203853.1 (7700)	7700_DelCarmen			7700_Santa_Clara
	Santa Clara	MG203663.1-MG203854.1 (7701)	7701_DelCarmen			7701_Santa_Clara
	Santa Clara	MG203664.1-MG203855.1 (7703)	7703_SantaClara_DelCarmen			7703_Santa_Clara
	Santa Clara	MG203665.1-MG203856.1 (7704)	7704_Santa_Clara			7704_Santa_Clara
	Santa Clara	MG203666.1-MG203857.1 (7706)	7706_SantaClara_DelCarmen			7706_Santa_Clara
Santa Maria	Buenaventura	MG203650.1-MG203756.1 (7627_1)	7627_Buenaventura_SantaMaria			7627_1_Buenaventura
	Buenaventura	MG203652.1-MG203757.1 (7630_1)	7630_Buenaventura_SantaMaria			7630_1_Buenaventura
	Buenaventura	MG203653.1-MG203758.1 (7631_1)	7631_Buenaventura_SantaMaria			7631_1_Buenaventura

	Buenaventura	MG203656.1-MG203759.1 (7641_1)	7641_Buenaventura_SantaMaria			7641_1_Buenaventura
	Buenaventura	MG203657.1-MG203777.1 (7642_1)	7642_Buenaventura_SantaMaria			7642_1_Buenaventura
	Buenaventura	MG203655.1-MG203778.1 (7639_1)	7639_Buenaventura_SantaMaria			7639_1_Buenaventura
	Buenaventura	MG203651.1-MG203779.1 (7628_1)	7628_Buenaventura_SantaMaria			7628_1_Buenaventura
	Buenaventura	MG203654.1-MG203782.1 (7638_1)	7638_SantaMaria			7638_1_Buenaventura
	Buenaventura	MG203651.1-MG203842.1 (7628)	7628_Buenaventura_SantaMaria			7628_Buenaventura
	Buenaventura	MG203652.1-MG203843.1 (7630)	7630_Buenaventura_SantaMaria			7630_Buenaventura
	Buenaventura	MG203653.1-MG203844.1 (7631)	7631_Buenaventura_SantaMaria			7631_Buenaventura
	Buenaventura	MG203654.1-MG203845.1 (7638)	7638_SantaMaria			7638_Buenaventura
	Buenaventura	MG203655.1-MG203846.1 (7639)	7639_Buenaventura_SantaMaria			7639_Buenaventura
	Buenaventura	MG203656.1-MG203847.1 (7641)	7641_Buenaventura_SantaMaria			7641_Buenaventura
	Buenaventura	MG203657.1-MG203848.1 (7642)	7642_Buenaventura_SantaMaria			7642_Buenaventura
	Buenaventura	MG203650.1-MG203867.1 (7627)	7627_Buenaventura_SantaMaria			7627_Buenaventura
Casas Grandes	Casas Grandes	MG203644.1-MG203750.1 (7602_1)	7602_CasasGrandes			7602_1_Casas_Grandes
	Casas Grandes	MG203667.1-MG203768.1 (7748_1)	7748_CasasGrandes			7748_1_Casas_Grandes
	Casas Grandes	MG203668.1-MG203769.1 (7749_1)	7749_CasasGrandes			7749_1_Casas_Grandes
	Casas Grandes	MG203642.1-MG203780.1 (7597_1)	7597_CasasGrandes			7597_1_Casas_Grandes
	Casas Grandes	MG203642.1-MG203835.1 (7597)	7597_CasasGrandes			7597_Casas_Grandes
	Casas	MG203644.1-	7602_CasasGrandes			7602_Casas_Grandes

Grandes	MG203837.1 (7602)				
Casas Grandes	MG203667.1-MG203858.1 (7748)	7748_CasasGrandes			7748_Casas_Grandes
Casas Grandes	MG203668.1-MG203859.1 (7749)	7749_CasasGrandes			7749_Casas_Grandes
Zaragoza	MG203638.1-MG203747.1 (7593_1)	7593_Csp_Ignacio_Zaragoza			7593_1_I_Zaragoza
Zaragoza	MG203638.1-MG203832.1 (7593)	7593_Csp_Ignacio_Zaragoza			7593_I_Zaragoza
Zaragoza	MG203641.1-MG203749.1 (7596_1)	7596_Csp_Ignacio_Zaragoza			7596_1_I_Zaragoza
Zaragoza	MG203645.1-MG203751.1 (7605_1)	7605_IgnacioZaragoza			7605_1_Zaragoza
Zaragoza	MG203646.1-MG203752.1 (7606_1)	7606_Ignacio_Zaragoza			7606_1_I_Zaragoza
Zaragoza	MG203647.1-MG203753.1 (7607_1)	7607_IZaragoza_CasasGrandes			7607_1_I_Zaragoza
Zaragoza	MG203648.1-MG203754.1 (7608_1)	7608_IZaragoza_CasasGrandes			7608_1_I_Zaragoza
Zaragoza	MG203649.1-MG203755.1 (7609_1)	7609_IZaragoza_CasasGrandes			7609_1_I_Zaragoza
Zaragoza	MG203643.1-MG203781.1 (7599_1)	7599_IZaragoza_CasasGrandes			7599_1_I_Zaragoza
Zaragoza	MG203640.1-MG203833.1 (7595)	7595_Csp_Ignacio_Zaragoza			7595_I_Zaragoza
Zaragoza	MG203641.1-MG203834.1 (7596)	7596_Csp_Ignacio_Zaragoza			7596_I_Zaragoza
Zaragoza	MG203643.1-MG203836.1 (7599)	7599_IZaragoza_CasasGrandes			7599_I_Zaragoza
Zaragoza	MG203645.1-MG203838.1 (7605)	7605_IgnacioZaragoza			7605_I_Zaragoza
Zaragoza	MG203646.1-MG203839.1 (7606)	7606_Ignacio_Zaragoza			7606_I_Zaragoza
Zaragoza	MG203647.1-MG203840.1 (7607)	7607_IZaragoza_CasasGrandes			7607_I_Zaragoza
Zaragoza	MG203648.1-MG203841.1 (7608)	7608_IZaragoza_CasasGrandes			7608_I_Zaragoza

	Zaragoza	MG203649.1-MG203866.1 (7609)	7609_IZaragoza_CasasGrandes			7609_I_Zaragoza
	Zaragoza	MG203640.1 - MG203748.1 (7595_1)	7595_Csp_Ignacio_Zaragoza			
Palomas	Palomas	KJ441237.1-GU937833.1	KJ441237.1			GU937833.1
Outgroup						
Catostomus catostomus		AF454871.1-GU937824.1	AF454871.1			GU937824.1
Campostoma ornatum						
Lineage I						
Conchos + Fuerte	Conchos	HQ608664.1-HQ608553.1 (STL 1438.01_a)	STL 1438.01_a		STL 1438.01_a	
	Conchos	HQ608665.1-HQ608554.1 (STL 1438.01_b)	STL 1438.01_b		STL 1438.01_b	
	Conchos	HQ608645.1-HQ608556.1 (UAIC 15000.02_a)	UAIC 15000.02_a		UAIC 15000.02_a	
	Conchos	HQ608640.1-HQ608557.1 (UAIC 15006.02_a)	UAIC 15006.02_a		UAIC 15006.02_a	
	Conchos	HQ608639.1-HQ608558.1 (UAIC 15006.02_b)	UAIC 15006.02_b		UAIC 15006.02_b	
	Conchos	HQ608650.1-HQ608555.1 (UAIC 15413.01_b)	UAIC 15413.01_b		UAIC 15413.01_b	
	Conchos	JF343045.1-JF343106.1 (BCY7231)	CPUM7231		BCY7231	
	Conchos	HQ608654.1-HQ608563.1 (UAIC 15414.01_b)	UAIC 15414.01_b		UAIC 15414.01_b	

Fuerte	HQ608798.1-HQ608577.1 (STL 1635.01_b)	STL 1635.01_b		STL 1635.01_b	
Fuerte	HQ608804.1-HQ608578.1 (UAIC 14998.01_b)	UAIC 14998.01_b		UAIC 14998.01_b	
Fuerte	HQ608816.1-HQ608574.1 (UAIC 14964.02_c)	UAIC 14964.02_c		UAIC 14964.02_c	
Fuerte	HQ608814.1-HQ608575.1 (UAIC 14964.02_a)	UAIC 14964.02_a		UAIC 14964.02_a	
Fuerte	HQ608815.1-HQ608576.1 (UAIC 14964.02_b)	UAIC 14964.02_b		UAIC 14964.02_b	
Conchos	HQ608678.1-HQ608549.1 (UAIC 15376.04)	UAIC 15376.04		UAIC 15376.04	
Conchos	HQ608671.1-HQ608671.1 (UANL 18929_a)	UANL 18929_a		UANL 18929_a	
Conchos	HQ608666.1-HQ608550.1 (UAIC 14957.02)	UAIC 14957.02		UAIC 14957.02	
Conchos	HQ608667.1-HQ608551.1 (UAIC 14959.01_a)	UAIC 14959.01_a		UAIC 14959.01_a	
Conchos	HQ608668.1-HQ608552.1 (UAIC 14959.01_b)	UAIC 14959.01_b		UAIC 14959.01_b	
Conchos	HQ608677.1-HQ608537.1 (UAIC 14958.01_b)	UAIC 14958.01_b		UAIC 14958.01_b	
Conchos	HQ608655.1-HQ608537.1 (UAIC 15415.01_a)	UAIC 15415.01_a		UAIC 15415.01_a	
Conchos	JF343066.1-JF343104.1	CPUM1956		OCA1956	

		(CPUM1956)				
	Conchos	JF343055.1-JF343107.1 (CPUM6911)	CPUM6911		COR6911	
	Grande	HQ608679.1-HQ608564.1 (STL 1318.01_a)	STL 1318.01_a		STL 1318.01_a	
	Grande	HQ608680.1-HQ608566.1 (STL 1318.01_b)	STL 1318.01_b		STL 1318.01_b	
	Grande	HQ608681.1-HQ608565.1 (STL 1318.01_c)	STL 1318.01_c		STL 1318.01_c	
	Grande	HQ608684.1-HQ608567.1 (STL 1319.01_a)	STL 1319.01_a		STL 1319.01_a	
	Grande	HQ608685.1-HQ608568.1 (STL 1319.01_b)	STL 1319.01_b		STL 1319.01_b	
	Grande	HQ608686.1-HQ608569.1 (STL 1319.01_c)	STL 1319.01_c		STL 1319.01_c	
	Grande	HQ608687.1-HQ608570.1 (UANL 19270)	UANL 19270		UANL 19270	
	Grande	HQ608688.1-HQ608571.1 (UANL 19271)	UANL 19271		UANL 19271	
	Grande	HQ608689.1-HQ608572.1 (UANL 19272)	UANL 19272		UANL 19272	
	Grande	HQ608690.1-HQ608573.1 (UANL 19273)	UANL 19273		UANL 19273	
Lineage II						
Del Carmen	Del Carmen	JF343050.1-JF343102.1 (CPUM7643)	CPUM7643		CLA7643	

	Del Carmen	HQ608750.1-HQ608620.1 (UAIC 14980.01_a)	UAIC 14980.01_a		UAIC 14980.01_a	
	Del Carmen	HQ608749.1-HQ608618.1 (UAIC 14980.01_b)	UAIC 14980.01_b		UAIC 14980.01_b	
	Del Carmen	HQ608748.1-HQ608619.1 (UAIC 14980.01_c)	UAIC 14980.01_c		UAIC 14980.01_c	
Yaqui+Mayo+ Casas Grandes	Mayo	HQ608728.1-HQ608580.1 (STL 1658.02_a)	STL 1658.02_a		STL 1658.02_a	
	Mayo	HQ608729.1-HQ608581.1 (STL 1658.02_b)	STL 1658.02_b		STL 1658.02_b	
	Mayo	HQ608731.1-HQ608582.1 (MNCN 277141)	MNCN 277141		MNCN 277141	
	Mayo	HQ608732.1-HQ608583.1 (MNCN 277142)	MNCN 277142		MNCN 277142	
	Mayo	HQ608733.1-HQ608583.1 (MNCN 277143)	MNCN 277143		MNCN 277143	
	Mayo	HQ608735.1-HQ608585.1 (MNCN 277137)	MNCN 277137		MNCN 277137	
	Mayo	HQ608734.1-HQ608586.1 (MNCN 277136)	MNCN 277136		MNCN 277136	
	Mayo	HQ608736.1-HQ608588.1 (MNCN 277138)	MNCN 277138		MNCN 277138	
	Mayo	HQ608737.1-HQ608587.1 (MNCN 277139)	MNCN 277139		MNCN 277139	
	Yaqui	HQ608792.1-	UAIC 14280.01_a		UAIC 14280.01_a	

	HQ608591.1 (UAIC 14280.01_a)				
Yaqui	HQ608793.1-HQ608589.1 (UAIC 14280.01_b)	UAIC 14280.01_b		UAIC 14280.01_b	
Yaqui	HQ608794.1-HQ608590.1 (UAIC 14280.01_c)	UAIC 14280.01_c		UAIC 14280.01_c	
Yaqui	HQ608758.1-HQ608594.1 (MNCN 277119)	MNCN 277119		MNCN 277119	
Yaqui	HQ608759.1-HQ608595.1 (MNCN 277132)	MNCN 277132		MNCN 277132	
Yaqui	HQ608760.1-HQ608596.1 (MNCN 277133)	MNCN 277133		MNCN 277133	
Yaqui	HQ608765.1-HQ608597.1 (UAIC 14272.02)	UAIC 14272.02		UAIC 14272.02	
Yaqui	HQ608766.1-HQ608599.1 (UAIC 14281.03_a)	UAIC 14281.03_a		UAIC 14281.03_a	
Yaqui	HQ608767.1-HQ608598.1 (UAIC 14281.03_b)	UAIC 14281.03_b		UAIC 14281.03_b	
Yaqui	HQ608768.1-HQ608600.1 (UAIC 14281.03_c)	UAIC 14281.03_c		UAIC 14281.03_c	
Yaqui	HQ608764.1-HQ608601.1 (UAIC 14278.04)	UAIC 14278.04		UAIC 14278.04	
Yaqui	HQ608763.1-HQ608602.1 (UAIC 14275.02)	UAIC 14275.02		UAIC 14275.02	
Yaqui	HQ608790.1-HQ608604.1 (UAIC	UAIC 7890.04_a		UAIC 7890.04_a	

	7890.04_a)				
Yaqui	HQ608788.1-HQ608605.1 (UAIC 15003.01_a)	UAIC 15003.01_a		UAIC 15003.01_a	
Yaqui	HQ608754.1-HQ608606.1 (UAIC 15302.01)	UAIC 15302.01		UAIC 15302.01	
Yaqui	HQ608786.1-HQ608607.1 (UAIC 15001.01_b)	UAIC 15001.01_b		UAIC 15001.01_b	
Yaqui	HQ608785.1-HQ608608.1 (UAIC 15001.01_c)	UAIC 15001.01_c		UAIC 15001.01_c	
Yaqui	HQ608755.1-HQ608610.1 (UAIC 15005.01_a)	UAIC 15005.01_a		UAIC 15005.01_a	
Babicora Lagoon	HQ608752.1-HQ608611.1 (UAIC 15371.01_a)	UAIC 15371.01_a		UAIC 15371.01_a	
Babicora Lagoon	HQ608753.1-HQ608612.1 (UAIC 15371.01_b)	UAIC 15371.01_b		UAIC 15371.01_b	
Casas Grandes	HQ608744.1-HQ608613.1 (UAIC 14270.01_d)	UAIC 14270.01_d		UAIC 14270.01_d	
Casas Grandes	HQ608745.1-HQ608614.1 (UAIC 14270.01_e)	UAIC 14270.01_e		UAIC 14270.01_e	
Casas Grandes	HQ608741.1-HQ608615.1 (UAIC 14270.01_a)	UAIC 14270.01_a		UAIC 14270.01_a	
Casas Grandes	HQ608743.1-HQ608616.1 (UAIC 14270.01_c)	UAIC 14270.01_c		UAIC 14270.01_e	
Casas Grandes	HQ608742.1-HQ608617.1 (UAIC 14270.01_b)	UAIC 14270.01_b		UAIC 14270.01_b	

	Sonora	JF343067.1-JF343108.1 (CPUM7827)	OJO7827		CPUM7827	
	Sonora	HQ608626.1-HQ608540.1 (UAIC 15410.01_c)	UAIC 15410.01_c		UAIC 15410.01_c	
	Sonora	HQ608623.1-HQ608541.1 (UAIC 15410.01_e)	UAIC 15410.01_e		UAIC 15410.01_e	
	Sonora	HQ608625.1-HQ608542.1 (UAIC 15410.01_b)	UAIC 15410.01_b		UAIC 15410.01_b	
	Sonora	HQ608627.1-HQ608543.1 (UAIC 15410.01_d)	UAIC 15410.01_d		UAIC 15410.01_d	
	Sonora	HQ608629.1-HQ608545.1 (UAIC 15297.01_b)	UAIC 15297.01_b		UAIC 15297.01_b	
	Sonora	HQ608628.1-HQ608544.1 (UAIC 15297.01_a)	UAIC 15297.01_a		UAIC 15297.01_a	
	Yaqui	HQ608630.1-HQ608546.1 (USON 01251.01_a)	USON 01251.01_a		USON 01251.01_a	
	Yaqui	HQ608631.1-HQ608547.1 (USON 01251.02_b)	USON 01251.02_b		USON 01251.02_b	
	Yaqui	JF343048.1-JF343100.1 (CPUM7845)	CPUM7845		CAB7845	
	Yaqui	JF343076.1-JF343101.1 (CPUM7328)	CPUM7328		PAP7328	
Lineage III						
Nazas+Piaxtla+ Aguanaval	Culiacan	HQ608722.1-HQ608538.1 (UAIC 15380.01_c)	UAIC 15380.01_c		UAIC 15380.01_c	
	Culiacan	HQ608723.1-HQ608539.1 (UAIC 15380.01_d)	UAIC 15380.01_d		UAIC 15380.01_d	

Nazas	JF343058.1-JF343112.1 (CPUM1530)	CPUM1530		CUA1530	
Nazas	HQ608699.1-HQ608523.1 (UAIC 7892.06_a)	UAIC 7892.06_a		UAIC 7892.06_a	
Nazas	HQ608691.1-HQ608524.1 (UANL 19252)	UANL 19252		UANL 19252	
Nazas	HQ608692.1-HQ608525.1 (UANL 19254)	UANL 19254		UANL 19254	
Nazas	HQ608693.1-HQ608526.1 (UANL 19257)	UANL 19257		UANL 19257	
Nazas	HQ608694.1-HQ608527.1 (UANL 19258)	UANL 19258		UANL 19258	
Nazas	HQ608695.1-HQ608528.1 (UANL 19261)	UANL 19261		UANL 19261	
Nazas	HQ608696.1-HQ608529.1 (UANL 19264)	UANL 19264		UANL 19264	
Piaxtla	HQ608717.1-HQ608530.1 (UAIC 14994.01_a)	UAIC 14994.01_a		UAIC 14994.01_a	
Piaxtla	HQ608718.1-HQ608531.1 (UAIC 14994.01_b)	UAIC 14994.01_b		UAIC 14994.01_b	
Piaxtla	HQ608713.1-HQ608532.1 (UAIC 15409.01_a-UAIC 15409.01)	UAIC 15409.01_a		UAIC 15409.01	
Aguanaval	HQ608712.1-HQ608533.1 (UAIC 15408.01_a-UAIC 15408.01)	UAIC 15408.01_a		UAIC 15408.01	

	Nazas	HQ608706.1-HQ608534.1 (UAIC 7895.01_b-UAIC 7895.01)	UAIC 7895.01_b		UAIC 7895.01	
	Nazas	JF343057.1-JF343109.1 (CPUM6889)	CPUM6889		COV6889	
	Nazas	JF343070.1-JF343111.1 (CPUM6838)	CPUM6838		OLO6838	
Outgroups						
Campostoma pullum		EU082477.1-EU082702.1 (MEX 27)	MEX 27		MEX27	
Campostoma pauciradii		DQ324065.1-EU082704.1 (UAIC 10858.01)	UAIC 10858.01		UAIC 10858.01	

Table S2. Evolutionary substitution models and parameters by Corrected Akaike Information Criterion estimated for *Codoma ornata*, the Chihuahuan Desert Group of the genus *Gila*, *Campostoma ornatum* and *Pantosteus plebeius-nebuliferus*.

	Gene	Evolutive model	InL	Gamma	PropInv
Codoma ornata	Cyt *b*	TIM3+I+G	-3264.24	1.666	0.613
	Rag 1	K80+G	-2830.7283	0.174	
	S7	TPM3uf	-2805.493		
Campostoma ornatum	Cyt *b*	TIM3+G	-3657.273	0.171	
	S7	HKY+G	-2003.962	0.32	
Pantosteus plebeius-nebuliferus	Cyt *b*	GTR+G	-638.643	0.17	
	GHI	TrN+G	-1453.496	0.33	
Chihuahuan Desert Group of *Gila*	Cyt *b*	TIM2+I	-2693.6131		0.771
	Rag 1	JC+G	-2157.1206	0.029	
	S7	TVM+G	-1456.385	0.024	

InL= Log Likelihood.

Table S3. Scores of model comparisons for the BioGeoBEARS analysis.

Codoma ornata																
Alt	Null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval	test	Tail	AIC1	AIC2	AICwt1	AICwt2	AICwt_ratio_model1	AICwt_ratio_model2
DEC+J	DEC	-12.37	-16.09	3	2	1	7.45	0.0063	chi-squared	one-tailed	30.73	36.18	0.94	0.061	15.26	0.066
DIVALIKE+J	**DIVALIKE**	**-12.37**	**-16.41**	**3**	**2**	**1**	**8.08**	**0.0045**	**chi-squared**	**one-tailed**	**30.73**	**36.82**	**0.95**	**0.046**	**20.95**	**0.048**
BAYAREALIKE+J	BAYAREALIKE	-12.37	-18.05	3	2	1	11.37	0.0007	chi-squared	one-tailed	30.73	40.11	0.99	0.0091	108.4	0.0092
Chihuahuan Desert Group of the genus *Gila*																
Alt	Null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval	Test	Tail	AIC1	AIC2	AICwt1	AICwt2	AICwt_ratio_model1	AICwt_ratio_model2
DEC+J	DEC	-25.34	-29.32	3	2	1	7.96	0.0048	chi-squared	one-tailed	56.68	62.63	0.95	0.048	19.68	0.051
DIVALIKE+J	**DIVALIKE**	**-25.34**	**-27.53**	**3**	**2**	**1**	**4.38**	**0.036**	**chi-squared**	**one-tailed**	**56.68**	**59.05**	**0.77**	**0.23**	**3.28**	**0.30**
BAYAREALIKE+J	BAYAREALIKE	-28.24	-28.29	3	2	1	0.097	0.76	chi-squared	one-tailed	62.48	60.57	0.28	0.72	0.39	2.59
Campostoma ornatum																
Alt	Null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval	Test	Tail	AIC1	AIC2	AICwt1	AICwt2	AICwt_ratio_model1	AICwt_ratio_model2
DEC+J	DEC	-18.95	-20.72	3	2	1	3.54	0.060	chi-squared	one-tailed	43.89	45.44	0.68	0.32	2.16	0.46
DIVALIKE+J	**DIVALIKE**	**-18.63**	**-18.83**	**3**	**2**	**1**	**0.41**	**0.52**	**chi-squared**	**one-tailed**	**43.25**	**41.66**	**0.31**	**0.69**	**0.45**	**2.21**
BAYAREALIKE+J	BAYAREALIKE	-18.95	-22.15	3	2	1	6.41	0.011	chi-squared	one-tailed	43.89	48.3	0.90	0.099	9.06	0.11
Pantosteus plebeius-nebuliferus																
Alt	Null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval	Test	Tail	AIC1	AIC2	AICwt1	AICwt2	AICwt_ratio_model1	AICwt_ratio_model2
DEC+J	DEC	-27.63	-31.68	3	2	1	8.1	0.0044	chi-squared	one-tailed	61.27	67.37	0.95	0.045	21.09	0.047
DIVALIKE+J	DIVALIKE	-30.31	-31.89	3	2	1	3.17	0.075	chi-squared	one-tailed	66.61	67.78	0.64	0.36	1.79	0.56
BAYAREALIKE+J	**BAYAREALIKE**	**-21.07**	**-31.31**	**3**	**2**	**1**	**20.49**	**6.0e-06**	**chi-squared**	**one-tailed**	**48.13**	**66.63**	**1**	**9.6e-05**	**10365**	**9.6e-05**

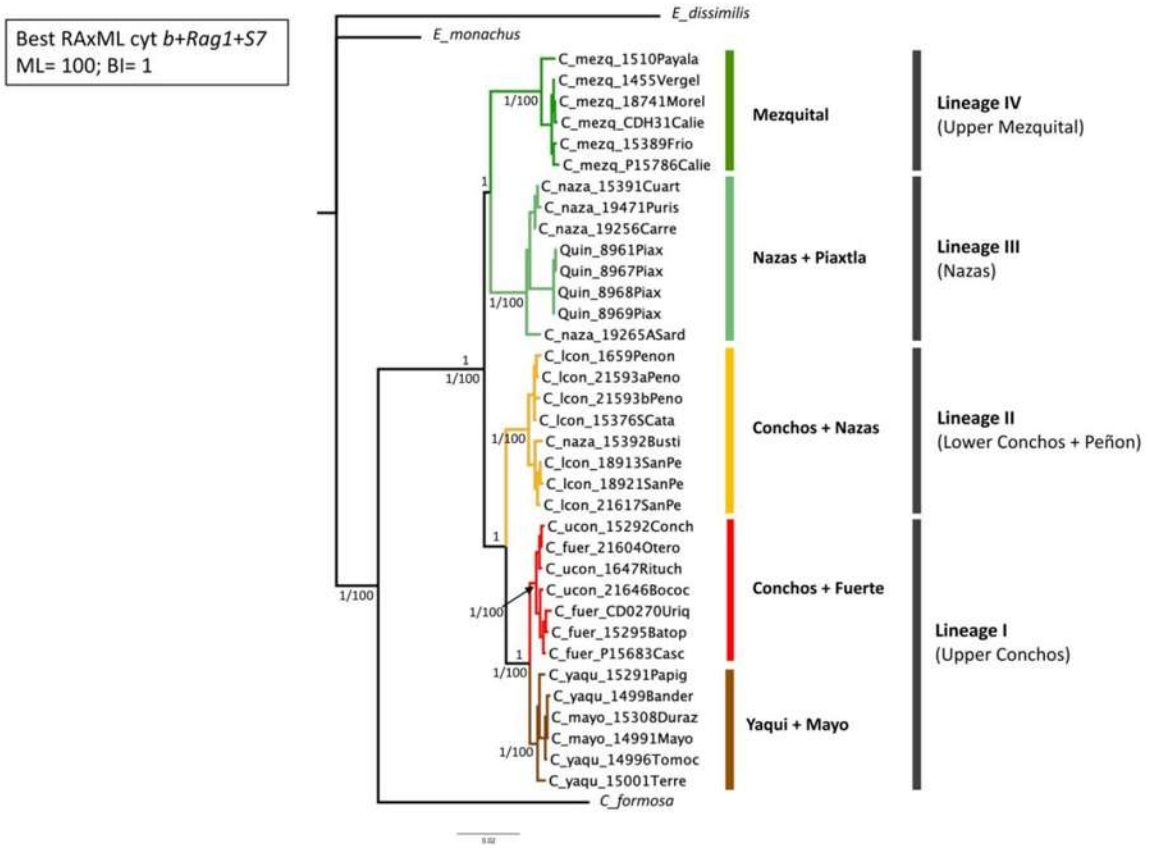

Figure S1. Maximum Likelihood (ML) phylogeny of *Codoma ornata* based on the concatenated genes (cyt *b* + *Rag 1*+ *S7*), using a GTR + G + I model with ML bootstrap values (based on 1000 replicates). Divergence time estimates for nodes based on mutation rate of 0.53% per lineage per million years as estimated for North American Cyprinids. Mutation rates for all nuclear markers were estimated, relative to the mitochondrial rate, using a normal prior (mean 0.01, SD 0.05). Numbers separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values on the branches represent the highest posterior probability.

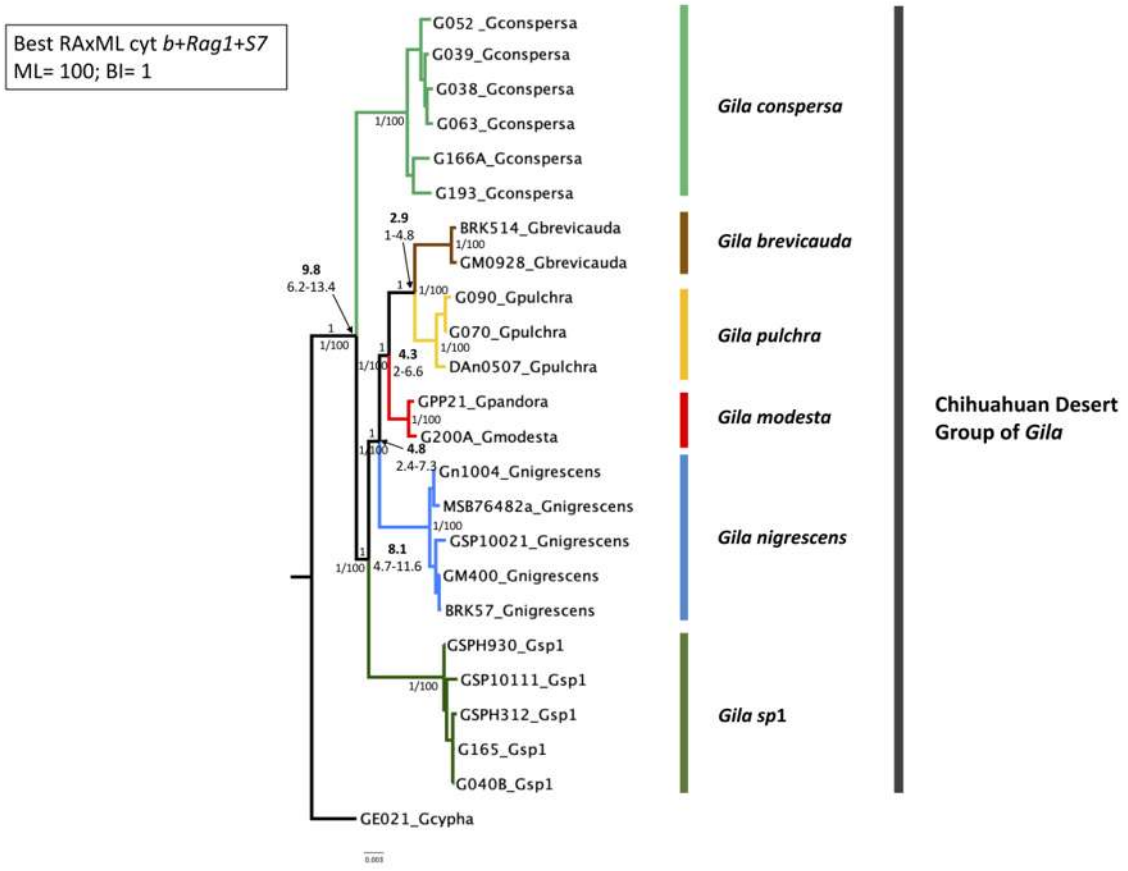

Figure S2. Maximum Likelihood (ML) phylogeny of the Chihuahuan Desert Group of the genus *Gila* based on the concatenated genes (cyt *b* + *Rag1* + *S7*), using a GTR + G + I model with ML bootstrap values (based on 1000 replicates). Divergence time estimates for nodes based on mutation rate of 0.53% per lineage per million years as estimated for North American Cyprinids. Mutation rates for all nuclear markers were estimated, relative to the mitochondrial rate, using a normal prior (mean 0.01, SD 0.05). Numbers separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values on the branches represent the highest posterior probability. Values in the nodes represent the 95% highest posterior density of divergence time estimates.

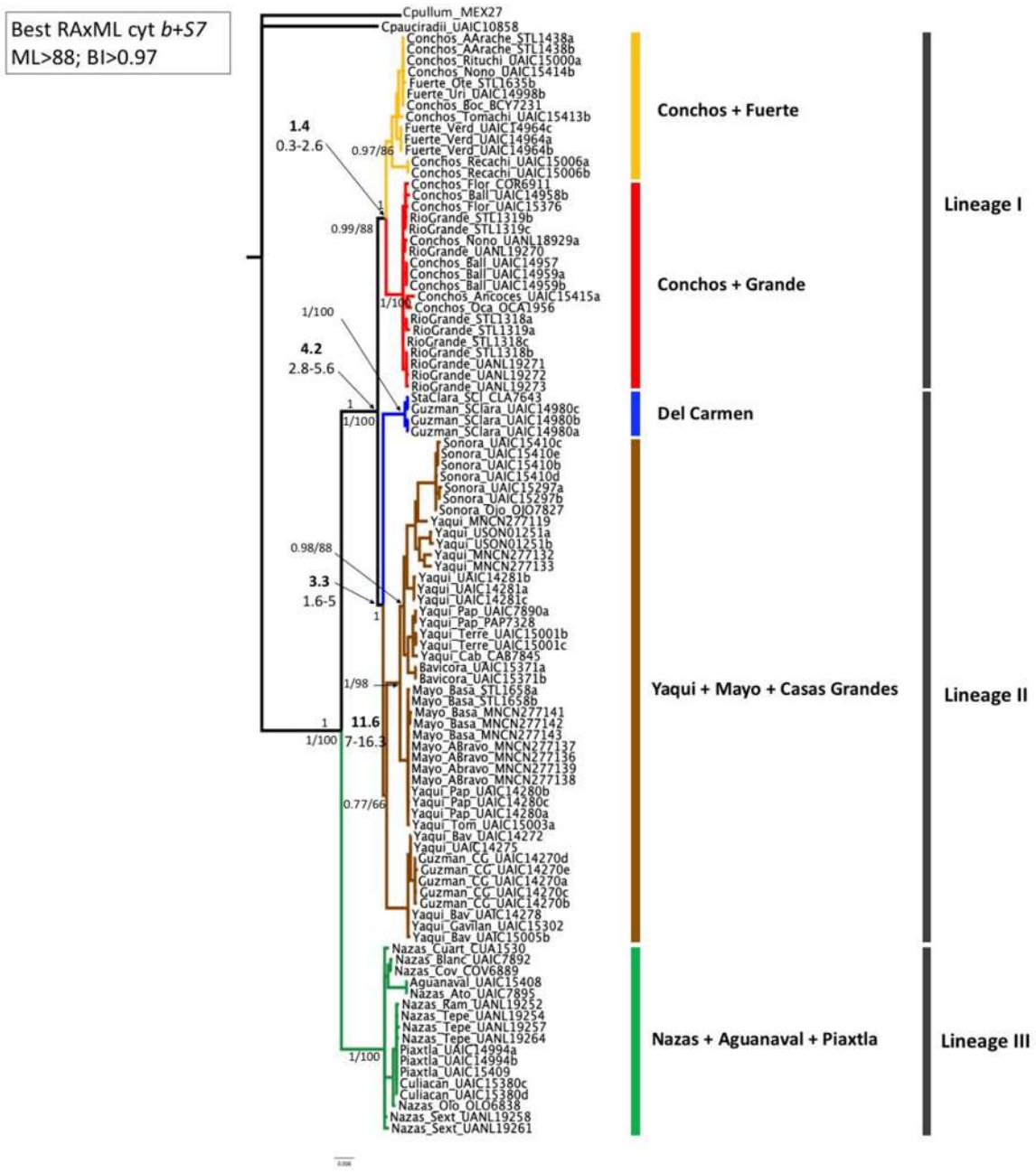

Figure S3. Maximum Likelihood (ML) phylogeny of *Campostoma ornatum* based on the concatenated genes (cyt *b* + *S7*), using a GTR + G + I model with ML bootstrap values (based on 1000 replicates). Divergence Time estimates for nodes based on mutation rate of 0.53% per lineage per million years as estimated for North American Cyprinids. Mutation rates for all nuclear markers were estimated, relative to the

mitochondrial rate, using a normal prior (mean 0.01, SD 0.05). Numbers separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values on the branches represent the highest posterior probability. Values in the nodes represent the 95% highest posterior density of divergence time estimates.

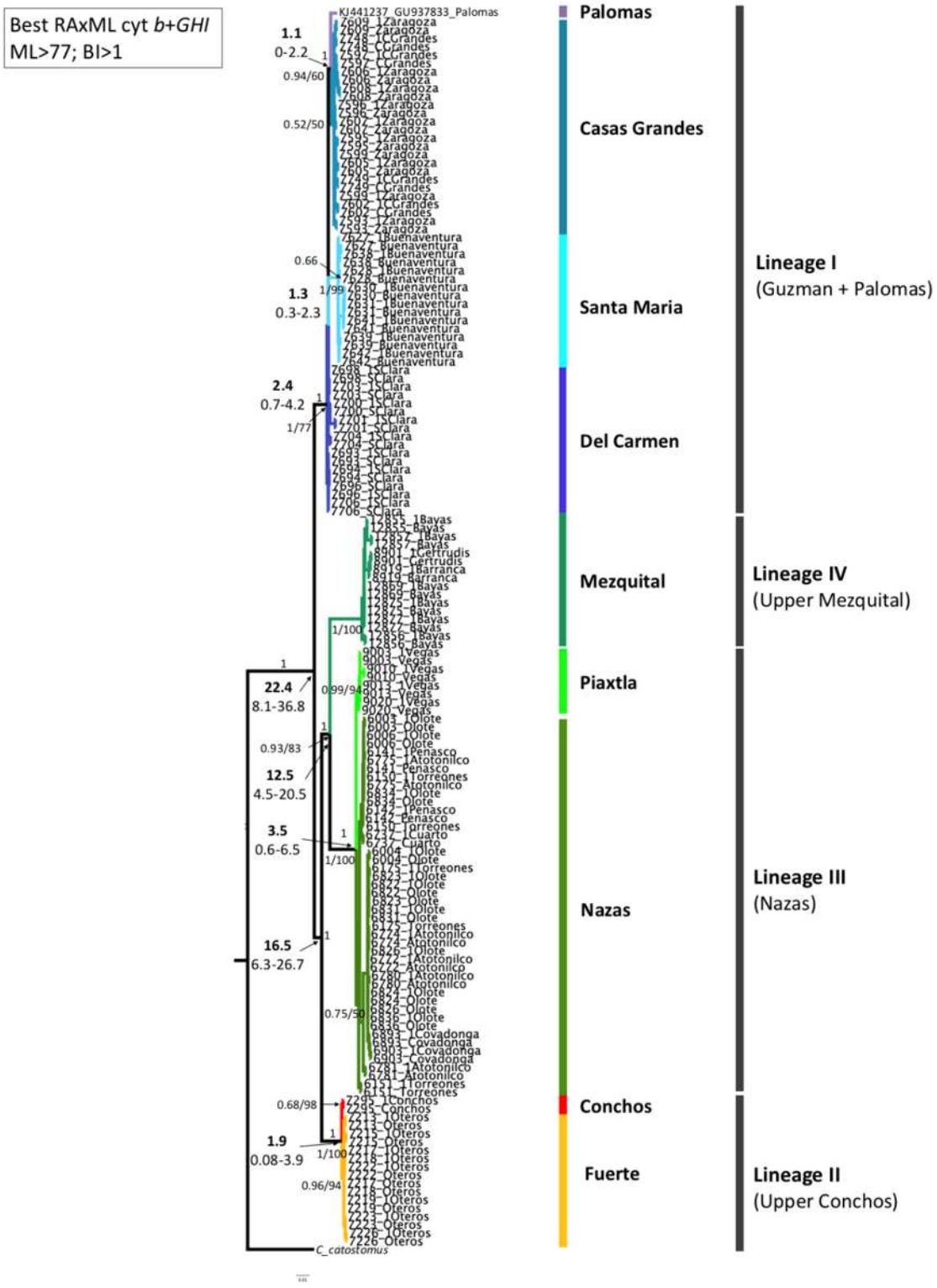
Best RAxML cyt b+GHI
ML>77; BI>1
KJ441237_GU937833_Palomas
1.1
0-2.2
0.94/60
0.52/50
0.66
1.3
0.3-2.3
1/99
2.4
0.7-4.2
1/77
22.4
8.1-36.8
0.99/94
0.93/83
12.5
4.5-20.5
3.5
0.6-6.5
1/100
16.5
6.3-26.7
0.75/50
0.68/98
1.9
0.08-3.9
1/100
0.96/94
C_catostomus
Palomas
Casas Grandes
Santa Maria
Del Carmen
Mezquital
Piaxtla
Nazas
Conchos
Fuerte
Lineage I
(Guzman + Palomas)
Lineage IV
(Upper Mezquital)
Lineage III
(Nazas)
Lineage II
(Upper Conchos)

Figure S4. Maximum Likelihood (ML) phylogeny of *Pantosteus plebeius-nebuliferus* based on the concatenated genes (cyt *b* + *GHI*), using a GTR + G + I model with ML bootstrap values (based on 1000 replicates). Divergence Time estimates for nodes based on mutation rate of 0.53% per lineage per million years as estimated for North American Cyprinids. Mutation rates for all nuclear markers were estimated, relative to the mitochondrial rate, using a normal prior (mean 0.01, SD 0.05). Numbers separated by a diagonal correspond to Bayesian posterior probabilities and Maximum Likelihood bootstrap values. Values on the branches represent the highest posterior probability. Values in the nodes represent the 95% highest posterior density of divergence time estimates.

VI. Discusión general

La biogeografía histórica es una ciencia que estudia la distribución de las especies sobre escalas de tiempo evolutivo (Yu *et al*., 2015). Se basa en elementos filogenéticos y filogeográficos, para analizar los patrones biogeográficos en las zonas de distribución de una o más especies y sus ancestros, buscando eventos de vicarianza o dispersión, lo que puede dar como resultado dos o más especies descendientes y la formación subsecuente de un clado monofilético, para después proveer explicaciones de estos procesos basándose en datos geológicos, climáticos o biológicos (Miller *et al*., 2005).

En el caso de los peces dulceacuícolas, sus ámbitos geográficos parecen preservar la historia filogenética, al menos la más reciente, principalmente porque los peces están aislados en los cuerpos de agua en que habitan. La formación de corredores hidrográficos facilita la dispersión de los peces, cruzando límites entre cuencas sólo cuando se establecen conexiones entre ellas, como es el caso de la captura de cabeceras de río (Miller *et al*., 2005). En ese mismo sentido, el esquema de regionalización para las provincias ictiofaunísticas (Miller *et al*., 2005) se ha basado en las asociaciones actuales de especies con ámbitos ecológicos y geográficos similares (Middlemiss *et al*., 1971; Greenwood, 1983), en general correspondientes con las principales cuencas hidrológicas (Miller y Smith, 1986; Smith y Miller, 1986) y por ende a los patrones hidrográficos más que a los climáticos (Miller *et al*., 2005). Smith y Miller (1986) señalaron que el Norte de México es una región con una compleja historia geológica, siendo su principal componente fisiográfico la Mesa del Norte; cuya corriente principal nace como el Río Grande en el sur de Colorado y fluye hacia el sur y hacia el este a través de cuencas de aluvión dentro de la falla del Río Grande (Miller *et al*., 2005). Los cuerpos de agua actuales en la Mesa del

Norte son parte de la cuenca del Río Bravo o bien son endorreicas (Miller *et al*., 2005). Estas cuencas endorreicas representan partes disyuntas del sistema ancestral del Río Grande, un sistema mucho más antiguo, integrado y extenso (Smith y Miller 1986; Echelle *et al*., 2005), dentro del cual algunas cuencas cerradas se recapturaron posteriormente por afluentes que erosionaron sus cabeceras y otros fueron capturados por ríos pertenecientes a la vertiente del Pacífico (Miller *et al*., 2005; Echelle, 2008; Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011, 2015; Corona-Santiago *et al*., 2018).

En la región semiárida del Norte de México, así como en otras regiones semiáridas con cabeceras de ríos geográficamente próximas, la influencia relativa del aislamiento y el intercambio entre cuencas ha sido poco clara (Hubbs y Miller, 1948; Smith y Miller, 1986; Miller *et al*., 2005; Schönhuth *et al*., 2011). En ese caso, las relaciones filogenéticas entre taxones estrechamente relacionados y patrones geográficos de variación genética intraespecífica pueden servir como registros biológicos de la evolución geomórfica en regiones semiáridas (Smith *et al*., 2002; Echelle, 2008; Schönhuth *et al*., 2008, 2011). Igualmente, es posible inferir el tiempo y la secuencia de los eventos geomórficos a partir de estimaciones de divergencia genética dentro y entre los linajes (Smith y Dowling, 2008; Schönhuth *et al*., 2011). En ese mismo sentido, los análisis filogenéticos y filogeográficos en peces de agua dulce han ido resolviendo relaciones entre la evolución de los drenajes y la estructura de la diversidad de los peces de agua dulce que habitan la zona semiárida del Norte de México. (Schönhuth *et al*., 2007, 2011, 2014, 2015; Echelle, 2008; Domínguez-Domínguez *et al*., 2011; Corona-Santiago *et al*., 2018). Sin embargo, aún falta información sobre otras especies de amplia distribución en esta zona, con el fin de entender a profundidad la compleja historia geomórfica de las regiones del desierto de Chihuahua y la Sierra Madre Occidental (SMO), y sus relaciones con la vertiente del Pacífico noroeste.

En el presente trabajo se estudiaron especies de peces dulceacuícolas de amplia distribución en la SMO y el desierto de Chihuahua en México: *Pimephales promelas*, *Codoma ornata*, el grupo de *Gila* del Desierto de Chihuahua (CDGG), *Campostoma ornatum* y *Pantosteus plebeius-nebuliferus*. Se usaron métodos filogenéticos y filogeográficos para inferir la historia evolutiva de estas especies, en la búsqueda de patrones biogeográficos, que nos permitan obtener hipótesis biogeográficas para el Norte de México (desierto de Chihuahua, Río Grande, SMO y la vertiente del Pacífico noroeste). Usando métodos probabilísticos, se obtuvieron patrones filogenéticos (Inferencia Bayesiana (MrBayes v3.2.1 (Ronquist y Sanmartín, 2011)) y Máxima Verosimilitud (RAxMLGUI v1.3.1 (Silvestro y Michalak, 2012; Stamatakis, 2014)), y patrones biogeográficos (Reconstrucción de Áreas Ancestrales (BioGeoBEARS (Matzke, 2013a, b)). La inferencia de los eventos cladogénicos relacionados con la diversidad en *P. promelas* y los datos obtenidos en los análisis de biogeografía histórica en *C. ornata*, *C. ornatum*, *P. plebeius-nebuliferus* y el grupo de *Gila* del desierto de Chihuahua, muestran una congruencia parcial en sus historias evolutivas, indicando que estos organismos estuvieron sujetos a las mismas fuerzas evolutivas y reaccionaron de la misma forma a estos eventos, así como lo sugería la congruencia en sus patrones filogenéticos. Los métodos probabilísticos utilizados para determinar la historia biogeográfica de los organismos, corroboraron la existencia de eventos de dispersión y/o vicarianza asociados con la formación y evolución de la SMO, acumulación de basaltos alcalinos y cambios climáticos, así como se ha observado en otros peces de agua dulce en el noroeste de México (Smith y Miller, 1986; Echelle, 2008; Schönhuth *et al*., 2007, 2011, 2014, 2015; Corona-Santiago *et al*., 2018).

Se observó una relación entre las áreas en el sur de la Mesa del Norte hacia áreas en el Norte (e.g. Mezquital a Yaqui + Guzman; Nazas + Aguanaval a Guzman; Piaxtla a

Guzmán) durante el Mioceno y Plioceno. Estos eventos de dispersión y relaciones entre cuencas ampliamente separadas geográficamente, son congruentes con la existencia del sistema ancestral del Río Grande (Smith y Miller, 1986; Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011, 2015; Corona-Santiago *et al*., 2018). Este sistema ancestral surgió en el Oligoceno y estuvo relacionado con la acumulación de basaltos alcalinos por la alta actividad volcánica en el Norte de México (Henry y Aranda-Gómez, 2000; Aranda-Gómez *et al*., 2005; Ferrari *et al*., 2007; Corona-Santiago *et al*., 2018). Los patrones biogeográficos compartidos entre la mayoría de los grupos analizados en el presente trabajo, fueron los siguientes: 1) Rango geográfico compartido entre el Río Yaqui y la Cuenca de Guzmán (ríos Casas Grandes, Santa María y Del Carmen). Esta relación entre las áreas de Yaqui y Guzmán está relacionada con la existencia de un lago pluvial ancestral en la zona de la Laguna de Babícora (Smith y Miller, 1986). Este evento de dispersión muestra un escenario biogeográfico también congruente con cuencas fluviales promovidas por eventos de basaltos alcalinos, asociados con el vulcanismo en el sector Babícora-Bustillos (Pérez-Rodríguez, *et al*., 2016; Corona-Santiago, *et al*., 2018). 2) Eventos de dispersión hacia las cuencas en la vertiente del Pacífico (e.g. Yaqui + Mayo a Fuerte + Conchos; Fuerte a Yaqui + Mayo; Guzmán a Mayo + Yaqui) durante el Mioceno tardío y el Plioceno. Estos eventos de ampliación de área hacia las cuencas en la vertiente pacífica, estuvieron relacionadas con capturas de cuencas durante la evolución de la SMO (Henry y Aranda-Gómez, 2000; Aranda-Gómez *et al*., 2005; Ferrari, 2007). 3) Separación entre Nazas + Piaxtla y Mezquital. Estos eventos de vicarianza estuvieron relacionados posiblemente con la alta actividad volcánica alcalina ocurrida en la Laguna de Santiaguillo, cuenca del Nazas, en la región sureste de la SMO (Ferrari, *et al*., 2007; Corona-Santiago, *et al*., 2018) durante el Mioceno tardío y Plioceno (Damon y Nieto-Obregón, 1979; Aguirre-

Díaz, *et al*., 2008; Luhr, *et al*., 2011). 4) Eventos de dispersion del Río Fuerte al Río Conchos durante el Plioceno y Pleistoceno. Estos eventos de dispersion Fuerte-Conchos han sido relacionados en otros trabajos con la alta actividad volcánica y erosión de cabeceras en la SMO durante ese periodo (Schönhuth *et al*., 2011, 2014, 2015, Corona-Santiago *et al*., 2018).

Los resultados presentados en este documento respaldan la existencia de cuatro linajes genéticos bien diferenciados (Yaqui, Nazas+Conchos, Casas Grandes y Santa María) dentro de las poblaciones de estudio de *P. promelas*. Los linajes evolutivos encontrados pueden corresponder a unidades significativas y evolutivas independientes, que deben preservarse para garantizar la conservación a largo plazo de sus diferentes trayectorias evolutivas. El concepto de conservación a nivel de especie utilizando datos moleculares ganó importancia cuando surgió el concepto de Unidades Evolutivas Significativas (UES) (Ryder, 1986; Domínguez-Domínguez y Vázquez-Domínguez, 2009) y, desde entonces, la diversidad genética se reconoció como el nivel de referencia de la biodiversidad (Domínguez-Domínguez y Vázquez-Domínguez, 2009). Una Unidad Significativa Evolutiva (UES) se ha definido como un grupo de individuos o poblaciones que presentan monofilia recíproca para marcadores mitocondriales y divergencias significativas en las frecuencias alélicas en los loci nucleares, considerando a su vez el tiempo de divergencia entre las poblaciones (Moritz, 1994, 2002; Domínguez-Domínguez y Vázquez-Domínguez, 2009). Esta idea de conservación busca identificar las unidades de manejo que forman parte de la historia evolutiva de los linajes dentro de la especie, para crear programas efectivos para su conservación, a fin de preservar los procesos evolutivos, indispensables para la permanencia a largo plazo de la especie. y los factores evolutivos asociados (Avise y Hamrick, 1996; Crandall *et al*., 2000; Moritz, 2002; Pertoldi, Bijlsma y

Loeschcke, 2007; Domínguez-Domínguez y Vázquez-Domínguez, 2009).

De igual forma, se considera en el presente trabajo que sería interesante evaluar la posibilidad de dividir la provincia ictiofaunística de la Mesa del Norte en subprovincias acordes a los patrones filogeográficos y biogeográficos encontrados en este trabajo y en trabajos anteriores (Domínguez-Domínguez *et al*., 2011; Schönhuth *et al*., 2011, 2012a, 2014, 2015; Corona-Santiago *et al*., 2018), de manera que corresponda además de a la distribución geográfica actual, a la historia evolutiva de los organismos. Los patrones biogeográficos encontrados en el presente trabajo sugieren que la Mesa del Norte de México no debería considerarse una provincia biogeográfica. Smith y Miller (1986) establecieron los límites de la Mesa del Norte con base en características fisiográficas y a la distribución de los principales elementos de la fauna ictiológica dulceacuícola (catostómidos y ciprínidos); sin tomar en cuenta eventos geomórficos. Los eventos biogeográficos compartidos por *C. ornata, C. ornatum*, el CDGG y *P. plebeius-nebuliferus*, sugieren que la Mesa del Norte podría dividirse en al menos 4 subprovincias, con base en los patrones geomórficos compartidos que podrían sugerir trayectorias evolutivas en común.

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VII. Conclusiones Generales

Con base en los trabajos realizados en la presente tesis, las conclusiones obtenidas fueron las siguientes:

1. *P. promelas* es un complejo de especies con al menos 4 linajes genéticos (Nazas+Conchos, Yaqui, Casas Grandes y Santa María), que corresponden a los ríos del mismo nombre.
2. Los eventos cladogénicos en las poblaciones de *P. promelas* están relacionados con la fragmentación del sistema ancestral del Río grande durante el Mioceno y Plioceno.
3. Aunque se encontraron eventos biogeográficos compartidos, no se encontró una historia biogeográfica en común para la mayor parte de la historia evolutiva de los 4 grupos analizados. La historia biogeográfica de *C. ornata*, *C. ornatum,* el grupo de *Gila* del desierto de Chihuahua (CDGG) y *P. plebeius-nebuliferus* parece estar más afectada por las características biológicas o ecológicas intrínsecas de cada grupo, que por los eventos paleohidrológicos
4. La mayoría de los eventos biogeográficos (compartidos e independientes) observados en la historias evolutivas de de *C. ornata*, *C. ornatum,* el CDGG y *P. plebeius-nebuliferus*, parecen estar relacionados con eventos de dispersión y especiación por evento fundador, asociados a la formación y evolución de la SMO y a la acumulación de basaltos alcalinos en el Norte de México a partir del Mioceno.
5. Los patrones biogeográficos compartidos por los grupos estudiados sugieren la necesidad de una revisión en la clasificación de la provincia ictiofaunística de la

Mesa del Norte, de manera que se tomen en cuenta además de la distribución geográfica actual de los peces dulceacuícolas, los datos probabilísticos acerca de la historia evolutiva de los peces que allí habitan.