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BIOGEOGRAFÍA HISTÓRICA DE CUATRO ESPECIES DE PECES DE AGUA DULCE DEL CENTRO DE MÉXICO: *Algansea tincella*, *Notropis calientis*, *Yuriria alta* y *Moxostoma austrinum*

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Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 9 de febrero de 2015, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **PÉREZ RODRÍGUEZ RODOLFO** con número de cuenta **505013592** con la tesis titulada: **"Biogeografía histórica de cuatro especies de peces de agua dulce del centro de México: *Algansea tincella, Notropis calientis, Yuriria alta* y *Moxostoma austrinum*"**, realizada bajo la dirección del **DR. GERARDO PÉREZ PONCE DE LEÓN:**

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Sin otro particular, me es grato enviarle un cordial saludo.

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"POR MI RAZA HABLARA EL ESPIRITU"
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RESUMEN

Se llevó a acabo un estudio de biogeografía histórica de algunos de los principales grupos de peces dulceacuícolas de origen neártico en la región del centro de México, con el propósito de determinar si existen eventos concordantes. Se pretendió inferir si cada uno de los grupos de peces analizados comparten alguna ruta de colonización y si, dentro del centro de México, alguna de las especies más representativas de estos grupos presentan eventos biogeográficos históricos comunes que hayan determinado su distribución actual.

Se abordaron dos enfoques correspondientes a dos niveles biogeográficos: una aproximación de biogeografía histórica, que se implementó para inferir el área ancestral de los grupos de peces neárticos analizados, con el propósito de determinar si se comparten patrones biogeográficos entre ellos. Estos grupos incluyeron: los "Notropinos del Sur" y el género *Algansea*, representantes de las familia Cyprinidae; el "grupo del Sur" del género *Moxostoma*, miembro de la familia Catostomidae, y la diversificada subfamilia Goodeinae, altamente representativa de la región, que presenta una relación cercana con una de las regiones de Norte América. Para ello se emplearon métodos de inferencia filogenética, estimación de tiempos de divergencia, y métodos de análisis de biogeografía histórica. El segundo enfoque consistió en una aproximación a nivel poblacional, en la que se reconocieron los patrones filogeográficos y demográficos históricos de algunas especies de los grupos neárticos, mismos que están codistribuidos en la mayor parte de su área de distribución en el centro de México. Dichos taxa fueron los ciprínidos *Algansea tincella*, *Notropis calientis*, *Yuriria alta*, y el catostómido *Moxostoma austrinum*.

De acuerdo con el enfoque de biogeografía histórica, los Notropinos del Sur, el género *Algansea*, el grupo del Sur de *Moxostoma*, así como la subfamila Goodeinae, presentaron rutas de colonización independientes, en diferentes tiempos. Uno de los primeros en llegar al centro de México fueron los Notropinos del Sur, que utilizaron "la ruta del Altiplano" durante el Mioceno Inferior-Medio; la subfamilia Goodeinae fue el segundo grupo en colonizar la región, a través de "la ruta Oeste" en el Mioceno Medio; luego, utilizando la misma "ruta del Oeste" el género *Algansea* llegó al centro de México

en el Mioceno Superior. Por último, la colonización más reciente en la región, datada en el Plioceno, fue la del grupo del Sur del género *Moxostoma*, que a través de la incorporación de *M. austrinum*, alcanzó la distribución más sureña del género. Asimismo, se determinaron eventos biogeográficos congruentes que se comparten principalmente entre diferentes especies de los Notropinos del Sur, Goodeinae y *Algansea*.

Con respecto al nivel poblacional, se encontró incongruencia entre los patrones filogeográficos de las cuatro especies. Se sugiere que lo anterior está asociado con diferentes tiempos de colonización y expansión en el centro de México de cada una de las especies. Por otro lado, la diferencia en la capacidad de dispersión, debido a los atributos biológicos y ecológicos de cada taxón, estuvo asociada a las diferentes respuestas en relación con barreras a la dispersión, producto de cambios geológicos y climáticos. De acuerdo a lo anterior, la codistribución parcial que muestran las especies analizadas en su área de distribución actual puede ser un reflejo de la historia independiente de cada una de las especies en el centro de México.

ABSTRACT

In order to determine the biogeographic concordance between the main groups of freshwater fishes with Nearctic origin in central Mexico, a study of historical biogeography was carried out. The aim of present study was to infer if each one of the analyzed fish groups shared the same colonization route, determining the current distribution range of the species in central Mexico.

Two approaches, corresponding to different biogeographic levels were followed. A historical biogeography approach, which was used to determine whether the group of fishes share biogeographic patterns. Such groups include the cyprinids contained in the southern notropins clade and the genus *Algansea*; the southern group of the genus *Moxostoma*, a member of Catostomidae, and the diversified subfamily Goodeinae, characteristic component of central Mexico, all of them with affinities to species distributed in North America. Phylogenetic analyses, divergence times inferences, and methods of analysis on historical biogeography were implemented. The other approach consisted in a population approach; phylogeographic and demographic patterns of the some representative species co-distributed in most of their distribution range within central Mexico, were obtained. These taxa included the cyprinids *Algansea tincella*, *Notropis calientis* and *Yuriria alta*, and the catostomid *Moxostoma austrinum*.

The historical biogeographic analyses yielded that the group of fishes analysed, southern notropins, the genus *Algansea*, the southern group of *Moxostoma* and Goodeinae, exhibited colonization routes temporally independent into central Mexico. The southern notropins arrived earlier through the “Plateau route”, during the Early-Middle Miocene; Goodeinae was the second group colonizing the region, using the “Western route” during Middle Miocene; later the genus *Algansea* arrived into central Mexico during Later Miocene, through the “Western route”. The last group to colonized the region was the “southern group” of *Moxostoma*, once the species *Moxostoma austrinum* reached the more austral distribution of genus, during Pliocene. However, the independent routes uncovered

herein exhibit some concordant events, particularly among species of "southern notropins", Goodeinae and *Algansea*.

Regarding the populational approach, incongruence between the four species analysed was uncovered. The main responsible causes are link to the colonization times and expansion periods within the region. Distinct dispersal abilities in the four species, associated to biological and ecological traits, produced a different response for each species to the dispersal barriers, which were promoted by geological and climatic historical changes. Based on the latter arguments, the partial co-distribution range of the four analysed species, reflects the independent history of every species across central Mexico.

1 INTRODUCCIÓN

Las especies de peces dulceacuícolas *Algansea tincella*, *Notropis calientis*, *Yuriria alta* y *Moxostoma austrinum* son especies de procedencia neártica, altamente representativas del centro de México; tienen una amplia distribución a lo largo de la región del centro de México (Miller *et al.*, 2005). Estas especies representan a dos familias de peces neárticas, Cyprinidae (*A. tincella,N. calientis*, *Y. alta*) y Catostomidae (*M. austrinum*). Su área de distribución comprende la principal cuenca hidrológica del centro de México, el sistema Lerma-Chapala, además de otras cuencas aledañas (Miller *et al.*, 2005). Las cuatro especies están codistribuidas en gran parte de su distribución, lo que sugiere que éstas pueden presentar una historia concordante de asociación en las áreas en donde ocurren, determinada por los mismos procesos evolutivos dentro de la región.

Sin embargo, existen algunos elementos teóricos para considerar lo contrario, es decir, que las cuatro especies codsitribuidas presenten historias biogeográficas independientes. Estos peces pertenecen a tres diferentes grupos: el género *Algansea* (Barbour y Miller, 1978); "Notropinos del sur", un clado que incluye varios géneros, con una de las distribuciones más australes de los ciprínidos en Norte America (Schönhuth y Doadrio, 2003), y el género *Moxostoma* representante de la familia Catostomidae (*sensu* Harris *et al.*, 2002). Estos grupos presentan diferencias en la riqueza de sus taxa que puede considerarse como un indicador indirecto de los diferentes tiempos de colonización que éstos tuvieron hacia al centro de México. Así mismo, presentan diferencias en su procedencia inmediata, es decir, cada grupo presenta distintas rutas de colonización del norte al centro de México (Miller y Smith, 1986).

Por otro lado, las especies referidas presentan distintos atributos biológicos y ecológicos que les proveen de capacidades diferentes para adecuarse a los cambios ambientales a través del tiempo, por lo que una falta de congruencia biogeográfica podría estar asociada a diferencias en la respuesta a barreras o gradientes selectivos, niveles de flujo génico, tasas de evolución molecular, tamaño efectivo o tiempo generacional, entre otros (Zink, 1996).

Una aproximación metodológica robusta para determinar los procesos causales comunes que pueden explicar la existencia de patrones homogéneos de distribución es la biogeografía histórica (Zunino y Zullini, 1995). En conjunto con una de sus disciplinas, la filogeografía comparada, considerada por algunos como sinónimo (Arbogast y Kenagy, 2001), es posible abordar diferentes escalas evolutivas, desde encontrar congruencia filogenética en múltiples clados dentro de una región común, hasta eventos de separación dentro grupos de especies codistribuidas (Zink, 2002).

1.1 Área de estudio

La distribución de los grupos de peces del centro de México no presenta límites discretos con respecto a criterios de regionalización que toman en cuenta aspectos geomorfológicos, hidrográficos, altitudinarios y/o bióticos que incluyan distintos taxa (no únicamente peces dulceacuícolas) (Domínguez-Domínguez y Pérez-Ponce de León, 2009). La configuración fisiográfica de la región esta determinada principalmente por cuatro componentes: la Mesa Central (*sensu* Nieto-Samaniego *et al.*, 2005), la Sierra Madre Occidental (SMOc), la Sierra Madre Oriental (SMOr) y la Faja Volcánica Transmexicana (FVTM). La principal cuenca hidrográfica de la región corresponde al sistema Lerma-Chapala, incluyendo las partes altas de algunas cuencas aledañas como son los ríos Balsas, Pánuco, Mezquital, Ameca, Armería y Coahuayana (Fig. 1).

La Mesa Central es una región elevada que se localiza en la parte central del territorio mexicano, que corresponde a la parte sur del altiplano mexicano. Se extiende desde el parteaguas del Río Aguanaval, en el norte, hasta su colindancia con la FVTM, quedando limitada al poniente por la SMOc y al oriente por la SMOr. Comprende los estados de Durango, Zacatecas, San Luis Potosí, Aguascalientes, Jalisco y Guanajuato (Nieto-Samaniego *et al.*, 2005). Comprende los ríos Aguanaval, Turbio y Laja tributarios del Río Lerma, y los ríos Santa María y Santa Catarina-Verde tributarios del Río Pánuco y el Río Verde tributario del Río Grande de Santiago (Fig. 1).

Por su parte, la SMOr es una cadena montañosa situada en el oriente del territorio mexicano, emerge de la planicie costera del Golfo de México, con cumbres que sobrepasan los 2500 metros sobre el nivel del mar (msnm), que descienden hacia el poniente y pasan a un extenso altiplano situado en el centro del país; se extiende a través de los estados de Chihuahua, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, y Puebla (Eguiluz *et al.*, 2000). Las principales cuencas hidrográficas, que en su mayoría drenan hacia el Golfo de México, son el Río Pánuco, Río Soto la Marina, Río San Fernando, así como la cuenca endorreica del Bolsón de Mapimi.

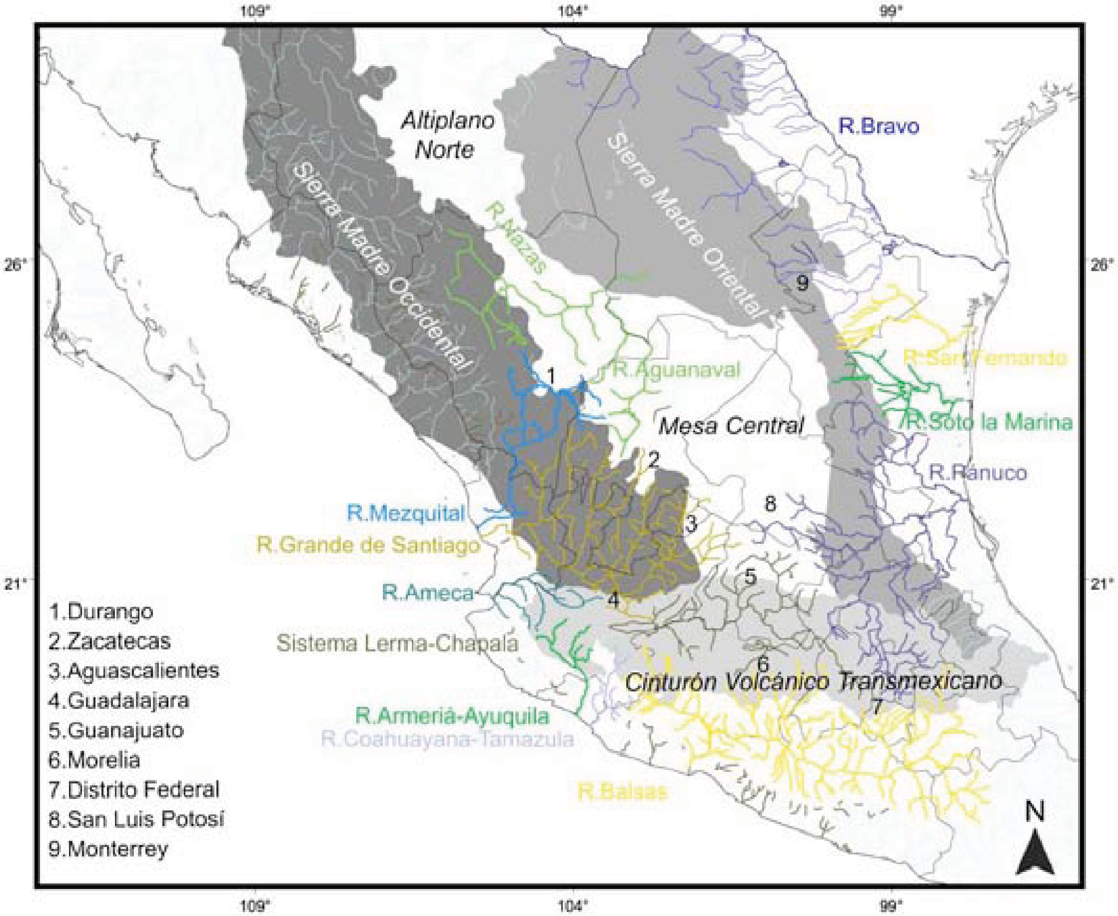

Figura 1. Componentes fisiográficos y cuencas hidrográficas del centro de México.

Al oeste, se encuentra la SMOc, cadena montañosa que se extiende sobre todo el margen noroccidente de México, desde su parte norte en el estado de Sonora, cruza hacia el sur por los estados de Sinaloa, Durango, Nayarit, y el oeste de Jalisco. La cuenca hidrográfica más norteña que guarda relación con el centro de México es el Río Mezquital (Fig. 1), particularmente la parte alta en el Río Tunal. En el límite sur de la SMOc se encuentra el Río Grande de Santiago, con sus tributarios norteños, que de acuerdo a la extensión del sector sur de la SMOc (Ferrarri *et al.*, 2005), drenan la mayor parte de su superficie (Fig. 1). Aunque en menor magnitud, la cuenca del Río Ameca, situada al sur del cauce principal del Río Grande de Santiago (Fig. 1), presenta influencia geológica de la SMOc (Frey *et al.*, 2007).

Por último, la FVTM que es el sistema montañoso que divide a México en dos secciones: al norte, el límite sur del altiplano mexicano, y al sur la cuenca del Balsas; se ubica en el centro de México, en los estados de Jalisco, Michoacán, Oaxaca, Estado de México, Distrito Federal, Puebla, Tlaxcala y Veracruz (Domínguez-Domínguez y Pérez-Ponce de León, 2009). Cuenta con la principal cuenca hidrográfica de la región, el Río Lerma, que desemboca en Chapala. Asociadas al Lerma, se encuentran otras cuencas aledañas, como las de los ríos Ameca, Armería-Ayuquila, Coahuayana-Tamazula, Balsas y Pánuco (Domínguez-Domínguez y Pérez-Ponce de León, 2009), cuyas cabeceras forman parte del FVTM (Fig. 1).

1.2 Configuración fisiográfica del centro de México

La fisiografía del territorio mexicano es el resultado de la interacción de cinco placas tectónicas, la Norteamericana, la del Pacífico, la Rivera, la de Cocos y la del Caribe, cuya acción conjunta ha originado cordilleras por plegamiento (Sierra Madre Oriental, Sierra Madre del Sur) o por vulcanismo (Sierra Madre Occidental, Faja Volcánica Transmexicana); las mesetas (Altiplano central) y depresiones (Balsas y Chiapas) quedaron confinadas entre las cordilleras principales (Espinosa *et al.*, 2008).

La dispersión o colonización a nuevos hábitats en los peces dulceacuícolas están limitadas a la existencia y continuidad de los cuerpos de agua por las conexiones entre cuencas, que a su vez están determinados por la configuración fisiográfica, que es un reflejo de la historia geológica (Bermingham y Martin, 1998). De esta manera las distribuciones actualmente discontinuas de grupos de peces filogenéticamente relacionados, son explicados mediante las asociaciones de la historia geológica o climática de la región, en conjunto con la obtención de patrones biogeográficos.

Puesto que el registro fósil más antiguo de peces dulceacuícolas en el centro de México data del Mioceno (Miller *et al.*, 2005), en la presente sección, solo se describirán los eventos geológicos y climáticos, que influyeron sobre configuración fisiográfica de la región a partir del Mioceno. Como se mencionó previamente, la configuración fisiográfica de la región esta determinada principalmente por cuatro componentes la Mesa Central , la SMOc, la SMOr y la FVTM. El área de la Mesa Central esta altamente influenciada por la actividad geológica del denominado Basin and Range (Israde-Alcántara *et al.*, 2010), y la SMOr es producto de la Orogenia Laramide en el Mesozoico, y la subsecuente tectónica del "Basin and Range" durante el Oligoceno. Estos no han presentado grandes modificaciones en su configuración, con excepción de la actividad puntual del vulcanismo intraplaca independiente que ha ocurrido del Oligiceno al Cuaternario (Aranda-Gómez *et al.*, 2000).

La principal actividad de la FVTM ocurrió hace 12 Ma en su sector centro-oeste, donde se elevaron grandes picos volcánicos, y continuó con la fragmentación de la placa de Norte América (Israde-Alcántara *et al.*, 2010), formando microplacas que generaron grabens, como es el caso del "Jalisco Block", que promovió la activación del sistema de triple-rifts, responsable de la configuración del Occidente del territorio mexicano durante el Mioceno-Plioceno (Garduño-Monroy *et al.*, 1993; Frey *et al.*, 2007).

1.2.1 Paleo-clima en el Plio-Cuaternario (3 Ma)

Como ya se mencionó, uno de los cambios climáticos más bruscos sobre el planeta se presentó en el Plioceno superior-Cuaternario (3 Ma. aprox.) y se caracterizó por la ocurrencia de las grandes glaciaciones del Cuaternario, que teóricamente fueron causadas por la interacción de la variación en la orbita del planeta alrededor del sol que influyeron directamente sobre las corrientes oceánicas (Hewitt, 2000).

Estos grandes cambios climáticos se manifestaron de manera diferente en el planeta debido a las diferencias regionales en la geomorfología, corrientes oceánicas y latitud; para el centro de México predominó un clima frío y condiciones de aridez, pasando de un paisaje densamente cubierto por vegetación a espacios más abiertos caracterizados por pastizales. Con respecto a los ecosistemas acuáticos, estas condiciones fueron un factor importante en la reducción y extensión de los paleo-lagos (Israde-Alcátara *et al*., 2010), y probablemente tuvieron un mismo efecto en otros cuerpos de agua (pantanos, manantiales y ríos) por la disminución de la precipitación.

Durante el Plioceno inferior predominó un clima húmedo en altas latitudes, asociado a un alto nivel del océano, y a su cálida superficie; esto ocasionó altas precipitaciones en el centro de México llevando a una expansión de las cuencas lacustres o paleo-lagos de la región. Sin embargo, después de este periodo que causó el enfriamiento del planeta, comenzaron a predominar condiciones de aridez en la región (Israde-Alcantara *et al*., 2010). Posteriormente, en uno de los periodos interglaciares, el Pleistoceno tardío se caracterizó por presentar altos niveles de humedad, teniendo como resultado que las cuencas lacustres presentaran altos niveles. Es importante señalar que el clima del Cuaternario afectó de manera diferente a la mitad sur y norte del territorio mexicano, puesto que la primera se encuentra dentro de los trópicos y la segunda pertenece a las franjas subtropicales áridas (Cevallos-Ferriz *et al*., 2008). En esta última se ubica principalmente la región del centro de México.

De la misma manera en que fueron afectados los ecosistemas terrestres, los cuerpos de agua epicontinentales fueron fragmentados, reducidos y en algunos casos desaparecidos, ocasionando que poblaciones de organismos acuáticos, como los peces, quedaran aislados en algún refugio que proporcionara las condiciones mínimas para su sobrevivencia, y se desplazaran a un nuevo sitio, si así lo permitía su capacidad de dispersión y se adaptarán a las nuevas condiciones, o de no ser el caso, se extinguieran; esto serían los acontecimientos que podrían suceder durante la etapa de la glaciación.

1.2.2 Actividad tecto-volcánica en el Plio-Cuaternario (3 Ma)

Uno de los principales componentes fisiográficos del centro de México es la FVTM, cuya principal actividad volcánica del arco moderno comenzó a partir del Plioceno superior (3.5 Ma.) (Ferrari, 2003; Cevallos-Ferriz *et al*., 2008).

El vulcanismo durante el Neogeno y Cuaternario causó cambios abruptos en los lagos del centro de México y sus paisajes asociados; sin embargo, se considera que la actividad tectónica fue el factor primario involucrado en la creación y mantenimiento de las cuencas del centro de México (Israde-Alcántara *et al.*, 2010). La combinación de los eventos geológicos (tecto-volcánicos) y paleo-climáticos que ocurrieron en el centro de México durante el Plioceno superior – Pleistoceno, fueron determinantes en los paleo-ambientes. Los ecosistemas dulceacuícolas de la región, representados en su mayor parte por los paleo-lagos y el paleo-cauce del Río Lerma, que para el periodo ya era uno de los principales rasgos en la configuración fisiográfica de la región (Israde-Alcántara *et al.* 2010), estuvieron expuestos a la variación en su volumen de agua a lo largo de este periodo debido principalmente al tectonismo y las fluctuaciones del clima, con una tendencia hacia el establecimiento de condiciones más áridas durante el Pleistoceno.

1.3 Ictiofauna del centro de México

La diversidad ictiofaunística del centro de México o también denominada Mesa Central, conserva el patrón general de diversidad de la biota de México (Espinosa *et al.*, 2008), es decir, presenta la influencia de organismos tanto del norte como del sur del continente, además del elevado número de taxa que se han originado en la región debido a los procesos de vicarianza promovidos por la actividad geológica y climática histórica. Cuenta con alrededor de 78 especies de peces, representando a nueve familias (Petromyzontidae, Cyprinidae, Catostomidae, Ictaluridae, Goodeidae, Poeciliidae, Atherinopsidae, Characidae y Cichlidae) (Miller *et al.*, 2005).

La familia Atherinopsidae, en particular el género *Menidia*, es un relicto de procedencia marina que experimentó una elevada diversificación en la región; otro caso de origen marino son los relacionados con peces anádromos del pacífico, como las dos especies de Lampreas (*Lampetra spadicea* y *L. geminis*), y los representantes fósiles de Salmonidae (géneros *Oncorhynchus* y *Salmo*) (Miller *et al.*, 2005). Existen algunos otros peces de procedencia marina que han tomado residencia en la región, principalmente en las cuencas aledañas al Río Lerma, como es el caso algunos representantes de las familia Gobiescidae, Mugilidae y Atherinopsidae (Miller *et al.*, 2005).

La invasión meridional de la región esta representada por las familias Poeciliidae, Characidae y Cichlidae, que son reconocidas como claras influencias neotropicales (Miller *et al.*, 2005); por su parte, las familias Cyprinidae, Catostomidae, Ictaluridae, incluyendo el registro fósil de Centrarchidae (Miller y Smith, 1986), corresponden a los grupos incorporados de Norte América, o que al menos presentan alguna afinidad, como es el caso de Goodeidae, con la subfamilia Empetrichthynae en el sur-oeste de Norte América, y Goodeinae en el centro de México (Miller *et al.* 2005). De acuerdo con lo anterior, la influencia neártica, incluyendo a Goodeidae, se considera la ictiofauna predominante en esta parte de México. Dentro de éstos destaca Goodeinae, que de acuerdo a la evidencia fósil (Mioceno), se considera uno de los primeros grupos en entrar a esta región (Miller *et al.* 2005), donde esta ampliamente distribuida y presenta la mayor diversidad de todos los grupos presentes (20 géneros y 42 spp. aprox.), así como un elevado nivel de endemismos (Domínguez-Domínguez *et al.* 2006). Además, tomando en cuenta que una de las mayores etapas de actividad geológica en el centro de México, como fue el surgimiento dela Faja Volcánica Trans-Mexicana, que comenzó desde el Mioceno Medio determinando así la configuración fisiográfica, se considera que la diversificación de Goodeinae esta fuertemente asociado a la historia geológica, sugiriendo a este grupo de peces como el mayor representante de la región.

Dentro de la misma influencia neártica, el siguiente grupo de peces más diversificado son los ciprínidos con cinco géneros y 24 spp. (Miller *et al.*, 2005; Mayden *et al.*, 2006; Domínguez- Domínguez *et al.* 2009; Pérez-Rodríguez *et al.* 2009), incluyendo especies ampliamente distribuidas y con altos niveles de endemismo, que también sugieren una larga asociación con la región. Existen dos grupos principales relativamente divergentes entre sí, uno representado por el género *Algansea* (con 8 spp.), y el grupo conocido como "Notropinos del sur" (con 12 spp.), llamado así porque es el grupo más sureño de los notropinos, el clado más diversificado de los ciprínidos de Norte América (Mayden *et al.*, 2006). Este último comprende el complejo de especies "*Notropis calientis*" y otros representantes de *Notropis*, y el género *Yuriria*. Cada uno de estos grupos tiene su respectiva ruta de dispersión al centro de México; *Algansea* presenta una ruta Oeste ó "Western track" que consiste en que la llegada de este género se dio a través de la Sierra Madre Occidental; por otro lado, el arribo del grupo "Notropinos del sur" se dio mediante las conexiones que se establecieron entre el Altiplano y el centro de México; a dicha ruta se le conoce como “Plateau track” (Miller & Smith, 1986).

Con respecto a las familias Catostomidae (Clements *et al.*, 2012) e Ictaluridae (Miller *et al.*, 2005), registran tan solo una especie en el sistema Lerma-Chapala, Armería-Ayuquila y Ameca (*Moxostoma austrinum* e *Ictalurus dugesii*, respectivamente). Así mismo, ambos casos presentan una población correspondiente a la cuenca del Río Grande de Santiago cuya identidad taxonómica no ha sido determinada (Clements *et al.*, 2012; Miller *et al.*, 2005). Por último, aunque solo en registro fósil, también figuran las familias Salmonidae y Centrarchidae, ambas con una especie indeterminada de *Oncorhynchus* sp. y *Moxostoma* sp. encontradas en yacimientos del lago de Chapala (Miller y Smith, 1986).

1.4 Biogeografía histórica y filogeografía comparada

La idea del análisis comparativo de múltiples linajes o taxa codistribuidos se remonta a mediados de la década de los años 1970, con el surgimiento de dos de las corrientes de pensamiento actuales de la biogeografía histórica, la biogeografía *vicariancista* y la *panbiogeografía*. A pesar de su antagonismo, ambas corrientes intentan el reconocimiento de los procesos causales comunes que pueden explicar la existencia de patrones homogéneos de distribución (Zunino y Zullini, 1995). De hecho sus máximos exponentes (León Croizat, Don Rosen, Gareth Nelson, y Norman Platnik), postularon que las distribuciones geográficas concordantes (tracks) entre linajes evolutivamente independientes indican la influencia de una historia geológica compartida (Bermingham y Avise 1986). A partir de este momento se estableció que para cumplir con el paradigma de la vicarianza se necesita la interpretación de distribuciones disyuntas congruentes como resultado de la vicarianza (Strange y Burr, 1997).

La mayoría de los trabajos de biogeografía histórica a mediados de la década de los 1980 comparaba la distribución geográfica de los taxa por encima del nivel de especie, aunque cabe mencionar que a finales de los 70´s y principios 80´s ya había indicios de que poblaciones conespecíficas diferenciadas podían proporcionar información histórica acerca de una región (Bermingham y Avise, 1986). De hecho el primer análisis de múltiple de especiesy/o poblaciones conespecíficas, aparece un año antes de que se acuñara el termino “filogeografía” en 1987 (Avise, 1998). De acuerdo con lo anterior,la filogeografía comparada surge como un elemento metodológico de la filogeografía.

Para la década de los 1990´s se confirmó que en particular la filogeografía comparada tenía un fuerte paralelismo con la biogeografía histórica, llegándose a considerar incluso como sinónimos, puesto que en ambas la explicación más parsimoniosa para múltiples grupos taxonómicos que presentan patrones espaciales comunes de subdivisión evolutiva es que tienen una historia biogeográfica compartida (Arbogast y Kenagy, 2001), y ambas están fundadas o al menos presentan una base importante en los análisis filogenéticos.

Por un lado, el propósito de la biogeografía histórica es encontrar congruencia filogenética en múltiples clados dentro de una región común, cuya interpretación es la fragmentación de una biota ancestral ampliamente distribuida, a causa de una serie de eventos vicariantes sucesivos. A partir de que se aplico por primera vez el método cladista a la biogeografía, han surgido una gran cantidad de métodos basados en la idea que los taxa que comparten patrones filogeneticos y de distribución, presentan una historia biogeográfica común (Ronquist y Sanmartin, 2012). De acuerdo con Ronquist (1995), los métodos de biogeografía filogenetica, que se fundamentan en el principio de parsimonia, se dividen en los métodos “basados en el patrón” y los métodos “basados en el evento”. Los primeros enfatizan y se enfocan mas en los patrones resultantes, que en los procesos de los procesos biogeográficos, es decir, que fueron diseñados para encontrar patrones sin considerar supuestos sobre la base de los procesos evolutivos; estos últimos son inferidos *a posteriori* a partir de la interpretación de los resultados (Buerki *et al.*, 2011). Dentro de estos destacan, el “análisis de parsimonia de Brooks” (BPA por sus siglas en ingles), el “análisis de componentes” y el análisis filogenético de comparación de árboles” (PACT por sus siglas en ingles) (Ronquist y Sanmartin, 2012). Los métodos basados en el evento, además de la topología y la distribución de los taxa (unicamente considerados en los métodos basados en el patrón), incorporan otras fuentes de evidencia previa al análisis biogeográfico; tal es el caso del análisis de dispersión-vicarianza (DIVA por sus siglas en ingles) (Buerki *et al.*, 2011). Dentro de este tipo de métodos, también se han desarrollado las aproximaciones o metodos paramétricos, los cuáles modelan la evolución del área de distribución (el cambio del área geográfica del ancestro al descendiente) como un procesos estocástico con unidades discretas (áreas geográficas) que evolucionan a lo largo de las ramas de la filogenia dada. Los parámetros del modelo son estimados a partir de un conjunto de datos, y utilizando máxima verosimilitud, con el método dispersión-extinción-cladogenesis (DEC), o inferencia bayesiana con los métodos de biogeografía de islas (Buerki *et al.*, 2011) y DIVA-Bayes.

tales como los tiempos de divergencia o la conectividad de areas biogeográficas a traves del tiempo . de manera explicita los costos de los eventos que son ajustados a un modelo biogeográfico dentro los cuáles destacan las aproximaciones paramétricas que……

Por su parte, la filogeografía comparada se define como el estudio de los efectos de la histoia evolutiva y biogeográfica sobre la distribución de la variación genética de especies codistribuidas (Gutiérrez-García y Vázquez-Domínguez, 2011). Consiste en el análisis filogeográfico de dos o más taxa codistribuidos y la comparación de sus patrones (Avise, 2008). En su primera fase busca determinar las relaciones filogenéticas a nivel intraespecífico, diversidad genética, distancias genéticas entre linajes, tamaño efectivo poblacional, flujo génico y el tiempo de los eventos de diversificación. La segunda fase corresponde al componente comparativo que pone a prueba la congruencia de las historias evolutivas y distribución histórica entre cada una de las especies analizadas; esto incluye la validación de hipótesis geográficas, ecológicas y biológicas. El proposito de esta fase es evaluar si las historias evolutivas de las especies analizadas, presentan una respuesta común a los mismos eventos históricos (Gutierrez-García & Vázquez-Domínguez, 2011). Actualmente existe una variedad de técnicas y métodos de análisis que se pueden aplicar de acuerdo a los datos y a la información que se tengan disponible; estos comprenden los métodos gráficos basados en árboles y coalescencia, los estadísticos de resumen (Vázquez-Domínguez *et al.* 2009); los métodos utilizados para evaluar estadísticamente el grado de congruencia de los patrones filogeográficos que incluyen, el método del "superárbol" (*supertree*), una aproximación filogenética que determina el grado de congruencia de las diferentes topologías obtenidas, y por el otro, el método ABC (Aproximate Bayesian Computacional) con modelo jerárquico bayesiano, que determina el grado de congruencia de algunos de los parámetros demográficos, particularmente aquellos asociados a lo tiempos de divergencia en un modelo de coalescencia (Hickerson *et al.* 2010). Asimismo, también se encuentra la estrategia que combina la metodología del modelaje de nicho ecológico y paleodistribución, que incorpora datos de variables ambientales (temperatura, precipitación y topografía) para la reconstrucción y ajuste de posibles escenarios en el pasado a los patrones filogeográficos (Hickerson *et al.* 2010).

Ambas disciplinas tienen la capacidad de revelar la estabilidad histórica de las comunidades (ensamble de clados, grupos de especies) a diferentes escalas de tiempos. Sin embargo, debido a su principal diferencia, la escala temporal evolutiva, presentan un potencial diferente para explicar los posibles patrones que se pueden llegar a obtener. La biogeografía histórica requiere de una hipótesis filogenética resuelta para poder realizar las inferencias históricas, los procesos de dispersión, extinción y los eventos de sobrelapamiento en la historia de la tierra, son susceptibles de ocultar los patrones de biogeografía histórica (Zink, 2002). Por su parte, la filogoegrafía comparada, que trata con eventos relativamente recientes, puede prescindir de una filogenia resuelta. Debido a sus fundamentos teóricos ymétodos de su componente de genética de poblaciones, tiene la capacidadde elaborar estrategias para poder explicar las historias de las especies, independientemente de si sus relaciones filogenéticas no están resueltas (Zink, 2002).

1.5 Planteamiento del problema

La historia geológica y climática del centro de México se debe de considerar como un factor determinante para la expansión y fragmentación del área de distribución de los peces dulceacuícolas. Con base en esto, el patrón de codistribución en su área de distribución compartida de las especies neárticas *A. tincella*, *N. calientis*, *Y. alta* y *M. austrinum*, sugiere que los cuatro taxa pudieron haber experimentado los mismos eventos geológicos y climáticos que promovieron la configuración de los sistemas hidrográficos actuales, que a su vez determinó su distribución actual.

Sin embargo, la historia biogeográfica de las especies dentro de sus respectivos clados, junto con su aparente colonización al centro de México, parecen mostrar diferentes patrones (Miller y Smith, 1986). Por otro lado, la diferencia de atributos biológicos y ecológicos entre las especies, por ejemplo la sensibilidad o tolerancia a diferentes hábitats (Mercado-Silva *et al.*, 2005), la talla que se puede asociar con la capacidad de dispersión

(Rosenfield, 2003), entre otros, permiten cuestionar el que las especies presenten una historia común.

Con base en lo anterior, se considera que una aproximación de biogeografía histórica permitirá, en una primera instancia, reconstruir la historia biogeográfica de cada uno de los clados de los que derivan las especies de estudio, con el fin de determinar la ruta espacial y temporal por la que se dispersó el ancestro común de dichas especies a las cuencas hidrológicas del centro de México. Por otro lado, el análisis filogeográfico de múltiples especies permitiría reconstruir la historia evolutiva las especies en el sistema hidrológico Lerma-Santiago y cuencas aledañas, bajo la hipótesis de que su codistribución actual podría ser resultado de una historia común, teniendo como hipótesis alternativa el que presenten historias no concordantes.

De acuerdo con lo anterior, se establecieron los siguientes objetivos:

1.1.5.1 Objetivos

Objetivo General

Describir los patrones de biogeografía histórica de cuatro especies de peces representativas de cuencas hidrológicas del centro de México, *A. tincella*, *N. calientis*, *Y. alta* y *M. austrinum*, y discutir los procesos que los determinan.

Objetivos específicos

- Obtener secuencias de genes mitocondriales y nucleares de cuatro especies de peces del centro de México y de sus grupos hermanos, para estimar las relaciones filogenéticas a nivel supraespecìfico.
- Aplicar métodos biogeográficos para, con base en los árboles filogenéticos, describir áreas ancestrales y la historia de diversificación a través de procesos de dispersión y/o vicarianza.

- Estimar los tiempos de divergencia de las cuatro especies y sus grupos hermanos, utilizando secuencias de un gen mitocondrial.
- Comparar los procesos que determinan la biogeografía histórica en los grupos de las cuatro especies peces neárticos de mayor diversificación del centro de México: “notropinos del sur”, género *Algansea*”, y la subfamilia Goodeinae a partir de secuencias de genes mitocondriales y nucleares.
- Correlacionar los procesos de diversificación de las especies de estudio con los eventos que han configurado la hidrografía del centro de México, a partir de su historia geológica y climática.
- Determinar patrones filogeográficos de las poblaciones de las cuatro especies de peces a lo largo de su área de distribución en el centro de México.
- Realizar un análisis de filogeografía comparada entre las poblaciones de las cuatro especies de peces, con base en información sobre estructura genética, tiempos de divergencia y demografía histórica.
- Describir los factores que determinan los patrones filogeográficos observados, asociados con procesos intrínsecos (atributos biológicos y ecológicos) y extrínsecos (historia geológica y climática de la región).

2 MATERIALES Y METODOS

Cada uno de los capítulos describe en detalle la metodología que se utilizó para llevar a cabo cada una de las partes que comprende el presente trabajo; a continuación solo se presenta de manera general el procedimiento que se realizó para completar los tres capítulos que comprenden esta tesis, desde la colecta de material hasta los métodos de análisis empleados.

2.1 Colecta de ejemplares

Con la finalidad de obtener una adecuada representación de las áreas de distribución de las especies, se trató de muestrear al menos una localidad de cada cuenca hidrográfica comprendida dentro del intervalo de distribución de cada una de las especies analizadas. De acuerdo con las regiones geográficas en el centro de México establecidas para peces de agua dulce (Subfamilia Goodeinae; Domínguez-Domínguez *et al.*, 2010), se visitaron localidades específicas dentro de las siguientes 22 cuencas: Lerma Alto, Lerma Medio, Lerma Bajo, Lago Cuitzeo, Lago de Chapala, Lago de Sayula, Lago de Pátzcuaro, Río Verde-Santiago, Río Juchipila-Santiago, Río Bolaños-Santiago, Río Santa María-Pánuco, Río San Juan-Pánuco, Río Ameca, Río Armería-Ayuquila, Río Tamazula, Valle de México y cinco diferentes regiones del Río Balsas (ver detalles en los capítulos I y III). Fuera del centro de México, se incluyeron cuencas hidrográficas tanto del norte como del sur del territorio (Fig. 2).

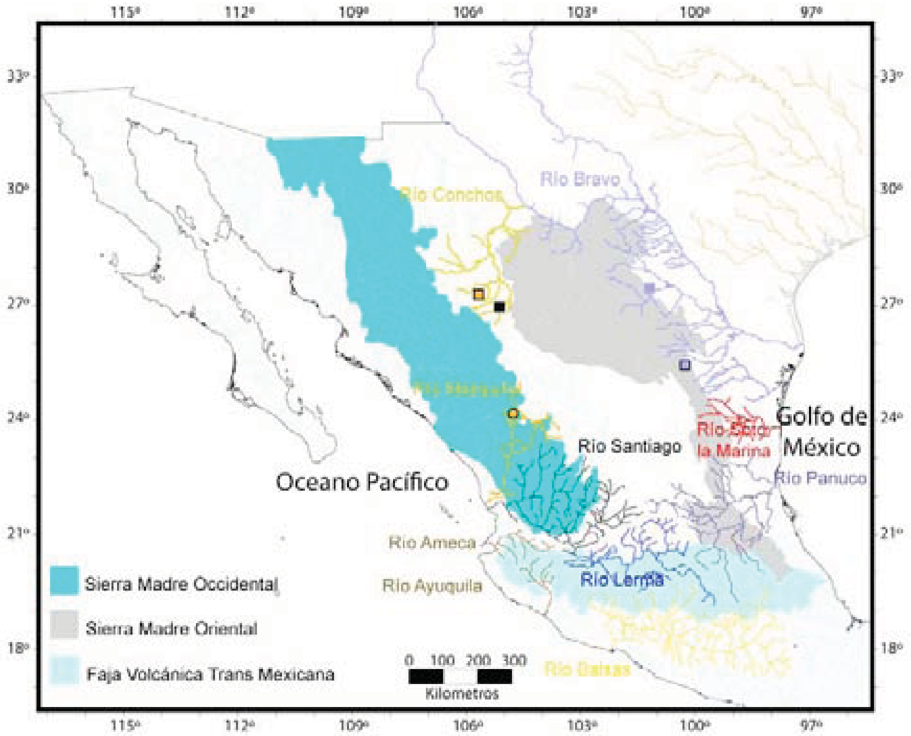

Figura 2. Localidades muestreadas fuera del centro de México y cuencas aledañas. ○ Río el Tunal, ■ Río Florido, □ Río porvenir, ■ Río Ramos y □ Río Nadadores.

2.2 Análisis

2.2.1 *Inferencia filogenética*

En los tres capítulos se llevaron acabo análisis filogenéticos con la finalidad de establecer las relaciones de los diferentes grupos. Se utilizaron los métodos de Máxima verosimilitud con el programa PHYML (Guidon *et al.*, 2010), e Inferencia Bayesiana con el programa MrBayes 3.2.2 (Huelsenbeck & Ronquist, 2001). Para poder llevar acabo ambos métodos, previamente se estimaron los parámetros de modelos de sustitución, para obtener el modelo que más se ajustara a los datos analizados con el programa jModelTest 0.1.1 (Posada, 2008).

2.2.2 *Biogeografía histórica*

En los primeros dos capítulos se utilizaron dos métodos biogeográficos: Phylogenetic Analysis for Comparing Trees (PACT) (Wojcicki & Brooks, 2005) y Dispersal-Extinction-Cladogenesis (DEC) analysis (Ree *et al.*, 2005; Ree & Smith, 2008).

Con la finalidad de detectar patrones biogeográficos concordantes entre tres distintos grupos de peces, Goodeinae, "Notropinos del sur", y el género *Algansea*, se empleo el PACT. Debido a que no hay un programa de cómputo para obtener los cladogramas generales de área, se llevo a cabo un procedimiento manual siguiendo la metodología propuesta por Wojcicki & Brooks (2004; 2005) y Eckstut *et al.*, (2011).

Por otro lado, para inferir el área ancestral del complejo *Moxostoma austrinum*, en el segundo capítulo se utilizó el análisis DEC, con el programa LAGRANGE V. 20130526 (http://code.google.com/p/lagrange; Ree & Smith, 2008).

2.2.3 Red de haplotipos

Con la finalidad de mostrar la relaciones tocogenéticas entre las diferentes poblaciones de cada una de las especies, en el tercer capítulo se realizaron redes de haplotipos. Para la reconstrucción de las redes de haplotipos se utilizó el método "median joining", una combinación de diferentes algoritmos de Parsimonia adecuada para grandes tamaños de muestra y distancias genéticas pequeñas (Bandelt *et al.*, 1999), implementada en el programa Network 4.6.1.3 (http:/www.fluxus-engineering.com).

2.2.4 Estimación de tiempos de divergencia

Para obtener la datación de los diferentes grupos analizados, se llevó a cabo un análisis de reloj molecular relajado, que permite calcular los tiempos de divergencia aunque las tasas de mutación dentro del grupo no sean homogéneas, empleando el paquete de análisis Beast v.1.7 (Drummond, *et al.*, 2007). El archivo de entrada .xml fue creado con el módulo Beauty incluido en Beast. En todos los análisis se hicieron al menos tres corridas independientes que fueron combinadas en el modulo LogCombiner. Por último, se obtuvo el árbol consenso con la ayuda del módulo TreeAnotator. En cada uno de los capítulos se detallan los "priors" para el modelo de sustitución, tasa de reloj molecular así como la calibración empleada.

2.2.5 Estructura genética de la población

Para evaluar la distribución de la variación genética entre las poblaciones se llevó a cabo un Análisis de la Varianza Molecular (AMOVA, por sus siglas en inglés) con el programa Arlequin V. 3.5.1.3 (Excoffier & Lischer, 2010), utilizando 1000 permutaciones.

3 RESULTADOS

En los siguientes tres capítulos se exponen los resultados obtenidos, donde se abordaron las hipótesis planteadas en el presente trabajo. Cada uno de los capítulos se presenta en formato de artículo. En el Capitulo I, documento aceptado para su publicación en la revista *Journal of Fish Biology*, se abordó la historia evolutiva de los grupos de peces a los que pertenecen tres de las especies estudiadas, *A. tincella*, *N. calientis* y *Y. alta*, además de otro de los grupos importantes en el centro de México, la subfamilia Goodeinae. Uno de los objetivos que se logró con este primer documento fue determinar la ruta y tiempo de colonización de los grupos de peces a los que pertenecen *A. tincella*, *N. calientis* y *Y. alta*, con la finalidad de determinar, 1) si tuvieron una historia evolutiva común, 2) hasta que tiempo se remonta y 3) las fuerzas evolutivas que determinaron dicha historia.

En el Capitulo II se abordó la cuarta especie de estudio de manera independiente, *M. austrinum*, de la familia Catostomidae. Debido a su nivel taxonómico básico (especie), y a su mínima riqueza de especies en el centro de México, que en conjunto con el taxón aun no descrito formalmente, *Moxostoma* sp. del Río Santiago, representan los únicos taxa en el centro de México para la familia, sugería otro nivel inferior en la escala temporal, por lo que se decidió tratarla de manera independiente. En este capítulo se analizó la biogeografía histórica del grupo de especies al que pertenece *M.austrinum*, reconocido en el presente capítulo como “southern group”, con la finalidad de establecer la ruta y tiempo de colonización del ancestro común de *M. austrinum*, así como determinar las principales fuerzas evolutivas que influyeron en dicho proceso de dispersión.

El tercer y último capítulo consistió en la comparación directa de las especies de estudio, mediante una aproximación de filogeografía y demografía histórica. El propósito principal de este capítulo fue poner prueba la hipótesis de si la codistribución parcial en la mayor parte del área de distribución de las especies en el centro de México refleja una historia geográfica común, asociada a eventos geológicos y climáticos que afectaron de forma similar a las cuatro especies; o por el contrario, la ausencia de codistribución en el área de distribución de las especies, aunado a la diferencia temporal en la colonización del “ancestro común más reciente” de las cuatro especies, y a los distintos atributos biológicos y ecológicos asociados a la capacidad de dispersión de las mismas, que resulten en patrones filogeográficos no concordantes entre las especies.

CAPITULO I

BIOGEOGRAFIA HISTORICA DE TRES GRUPOS DE PECES NEARTICOS EN EL CENTRO DE MÉXICO

ARTICULO I

Comparative historical biogeography of three groups of Nearctic freshwater fishes across central Mexico

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Comparative historical biogeography of three groups of Nearctic freshwater fishes across central Mexico

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Biogeographic patterns of the three main Nearctic groups of continental fishes inhabiting river drainages in central Mexico (livebearing goodeids, southern Mexican notropins and species of *Algansea*, the last two representing independent lineages of cyprinids) were obtained and compared by following two approaches: an estimate of divergence times and using a well-defined biogeographic method. Three concordant biogeographic events were identified among the three groups, showing some evidence of a partially congruent evolutionary history. The analysed groups show at least three independent colonization events into central Mexico: two western routes, followed by the Goodeinae and members of *Algansea*, and an early Plateau route followed by southern notropins. The most recent common ancestor (MRCA) of each of the three freshwater fish groups diversified in central Mexico in the Late Miocene. The lack of a strong congruence in their biogeographic patterns, and the differences in species richness among the three clades might be evidence for distinct patterns of diversification.

Key words: concordant patterns; Cyprinidae; diversification patterns; Goodeinae; Goodeinae; North America.

INTRODUCTION

The highly dynamic geological history of central Mexico, particularly during the Middle Miocene, led to the formation of the Trans-Mexican Volcanic Belt (TMVB) (Israde-Alcántara *et al.*, 2010). The TMVB along with the southernmost part of the Sierra Madre Occidental (SMOc) and the Sierra Madre Oriental (SMOr) are the major mountain ranges of the region (Morrone, 2005). The formation of such ranges has

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significantly changed the physiography of central Mexico and has determined the geographic distribution pattern and evolution of its biota through time.

The formation of these mountain ranges resulted in biogeographic barriers or dispersal corridors (Marshall & Liebherr, 2000; Mateos, 2005; Ceballos *et al.*, 2010). Continuous geologic activity in the region since the Miocene, combined with the complex climatic history of the past 15 million years (Domínguez-Domínguez *et al.*, 2010), created different surface configurations and contributed to the evolutionary diversification of several animal taxa (Shaffer, 1984; Flores-Villela & Martínez-Salazar, 2009). From a biogeographic point of view, such areas follow a reticulated model (Ronquist & Sanmartín, 2011), which cannot be explained by simple vicariance or dispersal. The occurrence of other processes, such as those considered in taxon pulse dynamics (*e.g.* episodic expansion, geographic colonization, isolation and extinction) have to be invoked on varying temporal and spatial scales (Hoberg & Brooks, 2010).

Freshwater fishes across central Mexico (Domínguez-Domínguez & Pérez-Ponce de León, 2009) present both regionally high species richness and unusual levels of endemism (Guzmán-Arroyo, 1990). In particular, the subfamily Goodeinae, restricted to central Mexico and whose most recent common ancestor (MRCA) is dated to the Miocene (Miller *et al.*, 2005), shows a complex mosaic of biogeographic patterns resulting from high tecto-volcanic activity and climatic history (Domínguez-Domínguez *et al.*, 2010). Goodeins, similar to other freshwater fishes confined to central Mexico, such as the Nearctic cyprinid genus *Algansea* (Miller *et al.*, 2005; Pérez-Rodríguez *et al.*, 2009*a*), are thought to have a western North American origin through the so-called western track (with no panbiogeographic context), which implies that sister group relationships are established with species in the south-western U.S.A. (Miller *et al.*, 2005). Previous studies indicate a common biogeographic history among the goodeins, *Algansea* and the southern notropins; notably, those in central Mexico represent the southernmost distributional range of their North American relatives (Schönhuth & Doadrio, 2003; Mayden *et al.*, 2006; Schönhuth *et al.*, 2008).

Ricklefs *et al.* (2007) suggested that species richness of clades could be a function of age. Some characteristics of the fish groups examined here question this assumption. For instance, goodeins, with around 41 species (Domínguez-Domínguez *et al.*, 2005), are significantly more diverse than cyprinids in this region, with eight or nine species of *Algansea* (Pérez-Rodríguez *et al.*, 2009*b*) and 14 species of southern notropins (Domínguez-Domínguez *et al.*, 2007; Schönhuth *et al.*, 2008), suggesting chronologically distinct origins, and therefore different biogeographic histories. In addition, based on a significant sample of the diversity of North American notropins, Mayden *et al.* (2006) conducted a phylogenetic analysis demonstrating that most lineages derive from eastern North America (Smith & Miller, 1986; Burr & Mayden, 1992), and suggested that southern notropins followed an independent route.

The geological evolution of central Mexico and the geographic confluence of freshwater fishes from distinct areas suggest a taxon pulse model of diversification (Domínguez-Domínguez *et al.*, 2010) as a suitable model to test whether the diversity of each group of fishes is related with the geologic or climatic events of the region (Ritchie *et al.*, 2005; Domínguez-Domínguez *et al.*, 2006, 2010; Pérez-Rodríguez *et al.*, 2009*a*).

This study investigates the potential concordance of biogeographic histories of three co-distributed groups of fishes in central Mexico on a spatio-temporal scale using three dated phylogenies, and the phylogenetic analysis for comparing trees (PACT) biogeographic method (Wojcicki & Brooks, 2005). This method assumes that the history of the context of speciation, dispersal and extinction for any species assemblage, comprises a long and complex combination of a series of events; no single clade contains complete information about its own particular history (Brooks, 2005). Also, the species richness of a clade is related to a particular mode of diversification, rather than clade age. Two phylogenetic approaches for detecting diversification processes were implemented: lineages-through-time (LTT) plots (Nee *et al.*, 1992) and estimates of diversification rates.

The aim of this study was to compare the estimated ages of the MRCAs of three freshwater fish groups in central Mexico, and to describe the biogeographic history and diversification events of each group across river drainages in central Mexico.

MATERIALS AND METHODS

SAMPLING, DNA EXTRACTION, PCR AND SEQUENCING

Phylogenetic relationships for *Algansea* and Goodeinae were based on Pérez-Rodríguez *et al.*, 2009*a* and Domínguez-Domínguez *et al.*, 2010, respectively; for the southern notropins, new sequences of cytochrome *b* (*cytb*) and the *s7 intron 1* were generated in order to obtain a robust phylogenetic hypothesis.

Most of the analysed sequences of the mitochondrial gene *cytb* for the three lineages, and the nuclear locus of the first intron of the *s7* protein gene for cyprinids were obtained from GenBank (Table SI, Supporting Information). In the case of the southern notropins, eight new sequences were generated in this study (KC778801–KC778808; see Table SI, Supporting Information). Tissues consisted of a small piece of caudal-fin and were obtained from the conservation *ex situ* stock of freshwater fishes at Laboratorio de Biología Acuática, Universidad Michoacana de San Nicolás de Hidalgo. DNA extraction and polymerase chain reaction (PCR) protocols followed Doadrio & Domínguez (2004) and Pérez-Rodríguez *et al.* (2009*a*). PCR products were sequenced using DNA Sequencing Services (Macrogen; http://dna.macrogen.com/eng/).

Chromatograms were checked and aligned using BioEdit 7.1.3 (Hall, 1999). Sequences of the complete *cytb* (1140 bp) gene were translated to amino acids to verify the lack of stop codons; because of the lack of indels, the mitochondrial data were aligned manually. Sequences of *s7* were aligned using ClustalW (Thompson *et al.*, 1994), as implemented in BioEdit with default parameter settings; then, alignments were checked visually and corrected manually. The final alignment size of *s7 intron 1* with indels was 825 bp.

TAXON SAMPLING

The subfamily Goodeinae includes 41 valid species (Domínguez-Domínguez *et al.*, 2005); however, molecular studies suggest the need of a major taxonomic revision (D.-K. Corona-Santiago, unpubl. obs.) and highly divergent populations representing potential independent evolutionary lineages (Doadrio & Domínguez, 2004; Domínguez-Domínguez *et al.*, 2010). Therefore, to consider all the available information on the evolutionary history of the three fish groups, operational taxonomic units (OTU) were based on 2% divergence at the *cytb* gene. This operational criterion has been proposed as the lower limit of genetic divergence for several closely related species of vertebrates (Johns & Avise, 1998), including goodeids (Domínguez-Domínguez *et al.*, 2008) and cyprinids (Domínguez-Domínguez *et al.*, 2007, 2009; Pérez-Rodríguez *et al.*, 2009*a*) (see Table SII, Supporting Information). Accordingly, six species of goodeids were actually treated as four OTUs (genetic divergence <1%) (Domínguez-Domínguez *et al.*, 2010); these species were considered as possible synonyms by Doadrio & Domínguez (2004), Domínguez-Domínguez *et al.* (2010) and D.-K. Corona-Santiago (unpubl. data) (Table SII; Supporting Information).

In addition, three populations of goodeins were considered as independent OTUs, because other studies demonstrated their independent evolutionary history (Doadrio & Domínguez, 2004; Domínguez-Domínguez *et al.*, 2010) (Table SII; Supporting Information). Only three species of the 41 goodeins were not sampled in this study, the extinct Parras characodon *Characodon garmani* Jordan & Evermann 1898 (World Conservation Monitoring Centre, 1996) and two members of the genus *Chapalichthys*, the barred splitfin *Chapalichthys peraticus* Álvarez 1963 and the Polka-dot splitfin *Chapalichthys pardalis* Álvarez 1963 (Table SII, Supporting Information).

The southern notropins include the *calientis* species complex (Chernoff & Miller, 1986), referred to as '*Notropis*' in this study, including the sister taxon *Notropis sallaei* (Günther 1868), and the genus *Yuriria*. This cyprinid group accounted for 12 sequences of *cytb* and *s7 intron 1*, corresponding to 11 recognized species and a genetic divergent population, referred to as an undescribed species in Schönhuth & Doadrio (2003), and 12 outgroups (Tables SI and SII, Supporting Information). In this study, the only missing species of the *calientis* complex were the Durango shiner *Notropis aulidion* Chernoff & Miller 1986 and *Notropis calabazas* Lyons & Mercado-Silva 2004, because it was not possible to collect fresh specimens for DNA extraction. Finally, for *Algansea*, seven sequences of *cytb* and *s7 intron 1*, corresponding to seven recognized species and 11 outgroups, were analysed (Table SI, Supporting Information). This includes all recognized species of this genus, except the popoche chub *Algansea popoche* Jordan & Snyder 1899, a species listed as endangered (Jelks *et al.*, 2008).

PHYLOGENETIC ANALYSES

Phylogenetic relationships for *Algansea* and Goodeinae follow previous well-resolved hypotheses (Pérez-Rodríguez *et al.*, 2009*a* and Domínguez-Domínguez *et al.*, 2010, respectively). Phylogenetic relationships of the southern notropins were inferred and based on the concatenated matrix *cytb*-*s7* (Table SI, Supporting Information).

Best-fit models of nucleotide substitution for *cytb* and *s7 intron 1* were obtained using jModelTest 0.1.1 (Posada, 2008) considering both the Akaike information criterion (AIC_c) and the Bayesian information criterion (BIC) (Table I). A summary of the analysed sequences is shown in Table SI (Supporting Information). Phylogenetic relationships were conducted through maximum likelihood (ML) using phylogeneticy maximum likelihood (PhyML; Guidon *et al.*, 2010), with the AIC_c-selected model and parameters. The tree search consisted of initial BIONJ tree estimation followed by a subtree pruning regrafting (SPR) algorithm; node support was assessed using 1000 non-parametric bootstraps. In addition, a Bayesian inference (BI) using MrBayes 3.0.1 (Huelsenbeck & Ronquist, 2001) was conducted based on BIC-selected parameters (Table I); four independent Markov chain Monte-Carlo (MCMC) runs included 10 000 000 generations, sampling every 1000 trees. Convergence and stationarity were verified by an adequate average S.D. of split frequencies (<0·01), and an appropriate effective sample size (ESS) for all parameters (>200) in Tracer 1.5 (Rambaut & Drummond, 2007).

All phylogenetic analyses using both ML and BI were conducted in CIPRES Science Gateway 3.3 portal (www.phylo.org/index.php/portal; Miller *et al.*, 2010).

AGE ESTIMATES

Interlineage divergence times based on *cytb* were estimated for all three groups analysed using BEAST 1.7.5 (Drummond & Rambaut, 2007). BEAST analyses were conducted at the CIPRES Science Gateway portal setting the parameters. The .xml files were generated in BEAST module BEAUti as follows: MCMC consisted of three independent runs for 50 million generations each, sampling every 1000 generations, and using an uncorrelated log-normal relaxed clock model, a Yule process tree prior for the Bayesian hypothesis based on *cytb* as a starting tree for Goodeinae, as well as a concatenated phylogenetic hypothesis as a starting tree for cyprinids were generated. For the goodeins, the calibration point was based on the earliest goodeid fossil species, *Tapatia occidentalis* Álvarez & Arriola-Longoria 1972 from the late Miocene *c.* 9 million years ago (MYA), which was located in the Santa Rosa Canyon in Amatitán, Jalisco, within the Santiago River basin (Álvarez & Arriola-Longoria, 1972; Guzmán

TABLE I. Substitution model and parameters for both the mitochondrial cytochrome *b* (*cytb*) and the *s7 intron 1* (*s7*)

	Goodeidae	Southern notropins			*Algansea*		
	cytb	*cytb*	*s7*	Conc	*cytb*	*s7*	Conc
Number of taxa sampled	42	24	24	24	12	12	12
Size (base pairs)	1140	1140	826	1965	1140	775	1915
Variable sites	555	457	404	861	414	258	672
Parsimony-informative characteristics	467	388	149	537	286	73	359
Model parameters (AIC$_c$)	TVM + I + G	TIM3 + I + G	HKY¨ + G	TIM1 + G	TIM3 + I + G	HKY¨ + G	TIM1 + G
Invariable sites	0·43	0·57	–	–	0·58	–	–
Gamma shape	0·94	1·28	3·07	030	1·77	2·25	030
Model parameters (BIC)	TPM2uf + I + G	TIM3 + I + G	HKY + G	TIM1 + G	TIM3 + I + G	HKY + G	HKY + G
Invariable sites	0·43	0·57	–	–	0·58	–	–
Gamma shape	0·94	1·28	3·07	030	1·77	2·25	030

AIC$_c$, Akaike information criterion; BIC, Bayesian information criterion; conc, Concatenated matrix.

& Polaco, 2009). Because this fossil species demonstrates phylogenetic affinity with members of the tribe Chapalichthyini (Guzmán, 2010), the calibration point was placed in the stem group of Chapalichthyini. Thus, for this node, a mean value of 9 MYA was considered with an S.D. of 0·1 (based on the late Miocene as a range) as a prior with a log-normal distribution. In addition, a *cytb* substitution rate ranging from 0·76 to 2·2% M^{-1} years in teleosts (Berendzen *et al.*, 2008) was incorporated as a prior with a uniform distribution, in order to avoid additional bias to the rate value (Pedraza-Lara *et al.*, 2012). Because the substitution model TPM2uf inferred for Goodeidae is not incorporated in the BEAST configurator module (BEAUti), based on the substitution rates as suggested in jModeltest manual, the model used was Tamura–Nei (TN93).

Due to the lack of suitable fossil records in both cyprinid lineages (*Algansea* and southern notropins), relatively distant calibration points were used. North American cyprinids with a reliable and unambiguous fossil record were included (*i.e. Mylocheilus* spp. and *Richardsonius durranti* Smith 1975, dated at 7 and 3·5 MYA, respectively; Houston *et al.*, 2010) together with southern notropins and *Algansea* in a large matrix; the best-fit substitution model was TN93. Fossil dates were used as the minimum age for the node representing the MRCA (Houston *et al.*, 2010), and were set as a prior with a log-normal distribution. The teleost *cytb* substitution rate was incorporated as *a prior* with a uniform distribution.

Convergence of MCMC was verified by an appropriate ESS for all parameters in Tracer. Sampled trees were merged and summarized with BEAST modules (LogCombiner and TreeAnnotator, respectively). When sampling was reduced to one individual per species, as is required in the Yule process tree prior, the tree topology was altered; in order to maintain the original topology for the three groups, monophyly was enforced.

BIOGEOGRAPHIC ANALYSES

To uncover biogeographic patterns of the three co-distributed groups of freshwater fishes, PACT (Wojcicki & Brooks, 2005) was conducted. The general area cladogram (GAC) constructed by PACT shows multiple clades resulting from a combination of events. Also, GAC might reveal particular events that affect particular clades; finally, PACT allows the incorporation of the taxon pulse hypothesis and shows reticulate area relationships (Domínguez-Domínguez *et al.*, 2010).

In summary, the steps of PACT are (1) convert all phylogenies into area cladograms (AC), (2) choose any AC and determine its elements (areas), then select which will be used as template area cladogram (TAC) and (3) compare (only two trees at the same time) and add a second AC into the TAC (Eckstut *et al.*, 2011). This study was based on the GAC of the subfamily Goodeinae previously generated by PACT (Domínguez-Domínguez *et al.*, 2010). Also, the phylogenetic tree for each cyprinid clade was converted into an AC, and manually combined to form a GAC following Wojcicki & Brooks (2004, 2005) and Eckstut *et al.* (2011). In the case of the southern notropins, the early diverged *Yuriria* clade was nested together with other species occurring in central Mexico.

To investigate diversification processes in both spatial and temporal scales, the molecular clock information was used in the nesting process following Domínguez-Domínguez *et al.* (2010). The only modification made to the template cladogram was the incorporation of the new calibration data for the main nodes.

In order to include the entire distribution range of the three groups of fishes, and also to consider their respective sister taxa, 14 new areas were added to those provided by Domínguez-Domínguez *et al.* (2010) (Fig. 1). Because of differences in the fish fauna composition, the Pánuco area was subdivided into three new regions: Pánuco-Moctezuma, Pánuco-Verde and Pánuco-Santa María del Oro. To include the distribution range of southern notropins, six new areas were added: Papaloapan (*Notropis moralesi* de Buen 1955), Atoyac (*Notropis imeldae* Cortez 1968), Balsas-Mezcala (*Notropis boucardi* Günther 1868 and *Notropis* sp.), Balsas-Amacuzac (*N. boucardi*), Balsas-Cutzamala (*N. sallaei*) and Balsas-Tepalcatepec (*N. moralesi*). The upper Mezquital River was included within the SMOc as it is part of this physiographic component [Fig. 1(b) and Table SI (Supporting Information)].

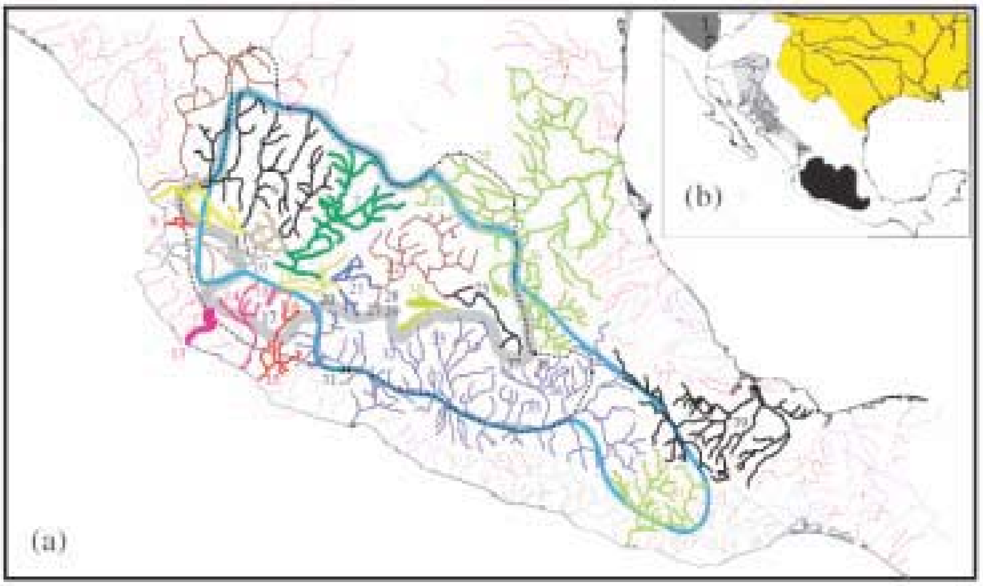

FIG. 1. General distribution pattern of the three groups of fishes. (a) Distribution ranges of Goodeinae (—), southern notropins (—) and *Algansea* (—) and regional units (river basins) (b) Distribution pattern of western and plateau tracks: — and — areas correspond to the distribution ranges of the subfamily Empetrichthyinae (■), genus *Agosia* (□), notropins of south-eastern North America basins (●) and the three groups of fishes from central Mexico (■). Regions and river basins: 1, Great Basin (GBA); 2, Sierra Madre Occidental (SMOc), including the upper Colorado River in the south-western of North America; 3, south-eastern North America basins (SEA); 4, lower Santiago (SAN-L); 5, middle Santiago (SAN-M); 6, upper Santiago (SAN-U); 7, Verde- Santiago (SAN-V); 8, Compostela (COM); 9, lower Ameca (AME-L); 10, upper Ameca (AME-U); 11, Etzatlan-San Marcos (ESM); 12, Magdalena (MAG); 13, Purificación-Marabasco (PUM); 14, Armeria-Ayuquila (AYU); 15, lower Coahuayana-Tamazula (CUT-L); 16, upper Coahuayana-Tamazula (CUT-U); 17, Zapotlán (ZAP); 18, Sayula (SAY); 19, Chapala (CHA); 20, Cotija (COT); 21, lower Lerma (LER-L); 22, middle Lerma (LER-M); 23, upper Lerma (LER-U); 24, Pánuco-Santa María del Río (PAN-S); 25, Pánuco-Verde (PAN-V); 26, Pánuco-Moctezuma (PAN-M); 27, Zacapu (ZAC); 28, Pátzcuaro (PAT); 29, Zirahuén (ZIR); 30, Cuitzeo (CUI); 31, Balsas-Tepalcatepec (BAL-X); 32, Balsas-Cupatitzio (BAL-C); 33, Balsas-Tuxpan (BAL-T); 34, Balsas-Cutzamala (BAL-Z); 35, Balsas-Mezcala (BAL-M); 36, Balsas-Amacuzac (BAL-U); 37, Valle de México; 38, Zempoala (ZEM); 39, Papaloapan (PAP); 40, Atoyac (ATO).

DIVERSIFICATION PATTERNS

Diversification patterns were described by incorporating distinct evolutionary scenarios, such as those resulting from vicariance or dispersal, and these patterns included diversification rates, time and speciation modes. All diversification rate analyses were performed by using the APE (Paradis *et al.*, 2004), GEIGER (Harmon *et al.*, 2008) and LASER (Rabosky, 2006*a*) software packages in R (www.r-project.org). Since incomplete taxon sampling has a non-random effect with a bias towards the decrease of speciation rates, at least 85% of extant species for the three groups of fishes were included in the analyses (Table SII, Supporting Information).

To examine changes in diversification rates over time, semi-logarithmic LTT plots were constructed using chronograms obtained. Analyses considered the inclusion and exclusion of sister taxa (only for Goodeinae and *Algansea*, because of the uncertainty of the sister group relationships of the southern notropins), and re-rooting the trees was carried out in TreeEdit 1.0a10 (Rambaut & Charleston, 2001). Considering the incomplete taxon sampling (85% *Algansea*, 87% southern notropins and 92% Goodeinae of their extant diversity), significant deviations of constancy in diversification rates over time were tested using the gamma statistic corrected by

Monte-Carlo constant rates (MCCR) (Pybus & Harvey, 2000). Birth–death likelihood (BDL) tests were also carried out. To determine the most appropriate diversification model (rate constant or rate variable model) to fit each temporal pattern, a δAIC_{RC} test (Rabosky, 2006*b*) was performed. Finally, to determine any shift point in the rates for specific time intervals, the floating-point Kendall–Moran estimates of diversification were calculated for all of the Miocene and Pliocene subdivisions. To account for effects that extinction may have on the distribution of waiting times or 'pull of the present' as well as incomplete taxon sampling (Pybus & Harvey, 2000; Nagle & Simons, 2012), the time interval-specific diversification rate estimates were compared with null distributions generated by simulating 10 000 birth–death trees, using BDL values of speciation and extinction.

RESULTS

PHYLOGENETIC ANALYSES AND AGE ESTIMATES

For the southern notropins, relationships based on the concatenated matrix [Fig. 2(b)] resulted in a resolved phylogenetic tree. The mean values (95% highest posterior densities) of the MRCA for the three groups of fishes are shown in their respective chronograms (Fig. 2). Goodeinae and southern notropins show a middle Miocene origin, whereas the MRCA of *Algansea* arose in the late Miocene.

BIOGEOGRAPHY

The condensed GAC is shown in Fig. 3. The approach undertaken in PACT showed three concordant events (patterns). In order to explain this complex condensed tree, only those patterns in space (areas) and time (MRCA) were considered, in chronological order (Fig. 3).

The first uncovered pattern is represented by node A, where the common event is found between the MRCA of '*Xenotoca*' and its basal members, and the MRCA of species in *Algansea* distributed in the Pacific coast drainages (remote chub *Algansea avia* Barbour & Miller 1978, mountain chub *Algansea monticola* Barbour & Contreras-Balderas 1968 and the riffle chub *Algansea aphanea* Barbour & Miller 1978). The second pattern at node B (Fig. 3) involves the upper Ameca area, supported by the presence of *Yuriria amatlana* Domínguez-Domínguez, Pompa-Domínguez & Doadrio 2007 and the goodeids *Allotoca goslinae* Smith & Miller 1987 and the butterfly splitfin *Ameca splendens* Miller & Fitzsimons 1971. The last pattern, node C (Fig. 3), involves several areas within central Mexico whose relationships are supported by widespread species such as *Notropis calientis*, the Jalisco chub *Yuriria alta* Jordan 1880, the spottail chub *Algansea tincella* Valenciennes 1844, jewelled splitfin *Xenotoca variata* Bean 1887, *Chapalichthys encaustus* and the opal allotoca *Allotoca dugesii* Bean 1887. The other branches observed in the AC correspond to independent events for one of the three lineages.

DIVERSIFICATION PATTERNS

LTT plots for empirical trees of the three groups reveal at least two distinct logarithmic curves. For Goodeinae, a convex curve (*i.e.* an initial steep slope that decreases as niche space fills; Crisp & Cook, 2009) is formed [Fig. 4(a)], whereas southern notropins [Fig. 4(b)] and *Algansea* [Fig. 4(c)] show curves with Lyonsanti-sigmoid

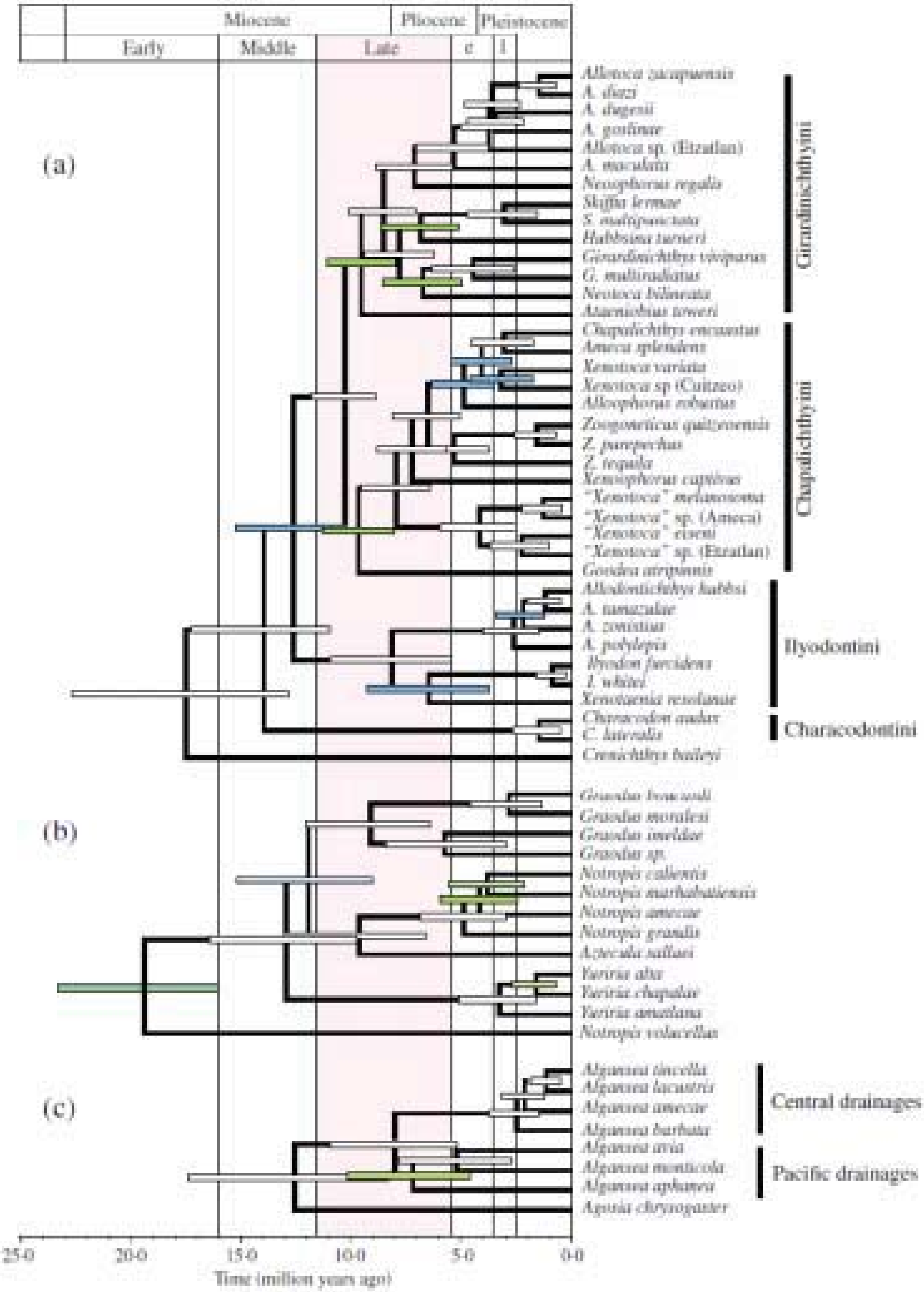

FIG. 2. Phylogenetic relationships and divergence times of the three groups of fishes. (a) subfamily Goodeinae, (b) southern notropins and (c) genus *Algansea*. Bars at nodes, 95% highest posterior density intervals of age estimates; ☐, a node support ≥95% of bootstrap and posterior probabilities; 🟦, a bootstrap support at 85 to 95%; 🟩, a bootstrap support at 75–85%. Phylogenetic relationships of the genus *Algansea* and Goodeinae are based on Pérez-Rodríguez *et al.* (2009*a*) and Domínguez-Domínguez *et al.* (2010).

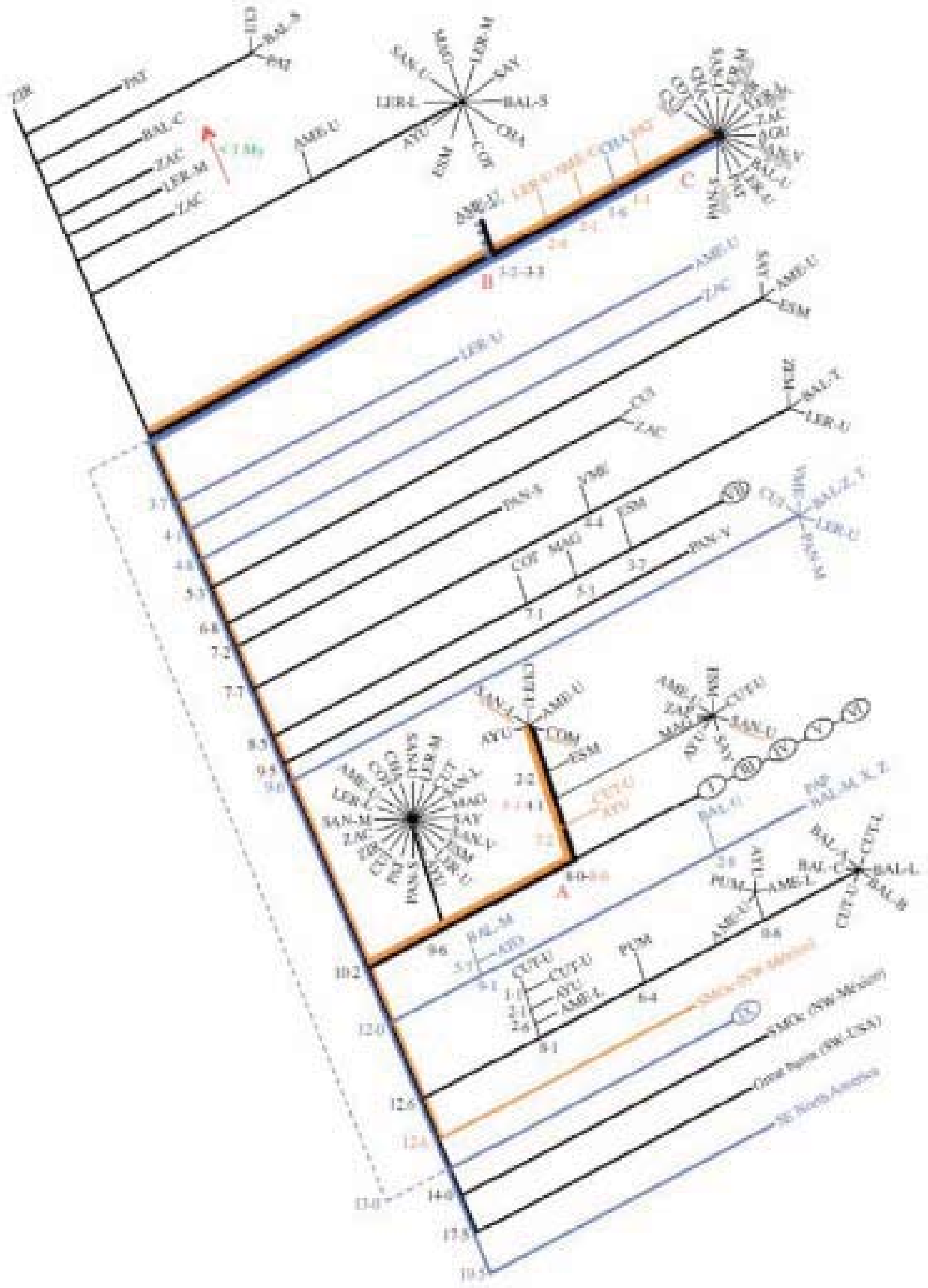

FIG. 3. Condensed general area cladogram (phylogenetic analysis for comparing tree, PACT) of Goodeinae (—). The single clade events are shown as coloured branches. The concondant patterns nested in the template cladogram (Goodeinae) have a node labelled with a red letter (A–C) and a line in color in the co-distribution area. A dashed line represents an insertion of the several monophyletic groups on the main topology following a chronological order. —, Goodeidae; —, genus *Algansea*; —, Southern notropins; - - -, genus *Yuriria*. Area abbreviations corresponds to those in Fig. 1.

trend (*i.e.* a plateau and subsequent sharp upturn; Crisp & Cook, 2009). Corrected values of the gamma statistic, obtained by an MCCR test in the case of Goodeinae, rejected the hypothesis of constant diversification rates; this indicates an early diversification of the group and a decline in speciation rates towards the present by the negative values of gamma and critical values (Table II). In the case of the southern notropins and *Algansea*, a constant diversification rate was not rejected (Table II). In accordance to the $\delta\mathrm{AIC}_{\mathrm{RC}}$ test, Goodeinae have a significant departure from a model of constant rate diversification (Table II); the model with the lowest AIC score is a logarithmic density-dependent model (DDL) (Table II), supporting the convex curve in the LTT plot [Fig. 4(a)]. Conversely, southern notropins and *Algansea* do not significantly follow a variable model (Table II), with anti-sigmoidal curves (Table II). Kendall–Moran estimates of diversification rates across the Miocene, Pliocene and Pleistocene subdivisions show evidence of significant variation through time, only at the late Miocene interval for Goodeinae, resulting in the interval with a higher diversification rate [Fig. 4(a)].

DISCUSSION

BIOGEOGRAPHY

Arrival routes based on molecular data

The condensed AC obtained through PACT, together with the divergence times, appear to indicate three arrival routes from the Nearctic into central Mexico; two lineages followed the western routes and one lineage followed the plateau route. Three northern arrival routes are linked with the last two tectonic phases of the basin and range caused by the intensification of the Farallon subduction under the North American Plate during the Late Oligocene and Miocene, which affected the mountain range of SMOc (Ferrari *et al.*, 2005; Calmus, 2011).

Miller *et al.* (2005) pointed out that the western track consists of a continuous ancestral distribution of the groups of fishes such as goodeids and *Algansea* from the south-western U.S.A. through the western mountain range into central Mexico. Even though these two groups share geographic areas (*i.e.* SMOc), there is a considerable temporal difference: first, between the MRCA of the Goodeinae and *Algansea* with their respective sister groups, and second, between MRCA only of Goodeinae and *Algansea* + *Agosia* (Figs 2 and 3). The time of arrival to central Mexico between these two groups, however, shows differences; in the case of Goodeinae, the MRCA of the tribes Ilyodontini, Chapalichthyini and Girardinichthyini is dated at 12·6 MYA (15·2 to 10·2 MYA), whereas the MRCA of *Algansea* is more recent, estimated at 8·0 MYA (11·0 to 5·1 MYA) [Fig. 2(c)]. Even though Goodeinae and *Algansea* share the same western pattern, divergence times obtained in this study uncover two temporally distinct arrivals [the western route and the plateau route; Fig. 5(a)].

Phylogenetic relationships among the North American notropins remain unresolved, and it is not possible yet to identify their sister groups (Mayden *et al.*, 2006). There is a close relationship, however, between southern notropins and those distributed in the south-eastern river basins across North America, through the Bravo (=Grande) River, the western Gulf of Mexico slope and the Mississippi River (Burr & Mayden, 1992),

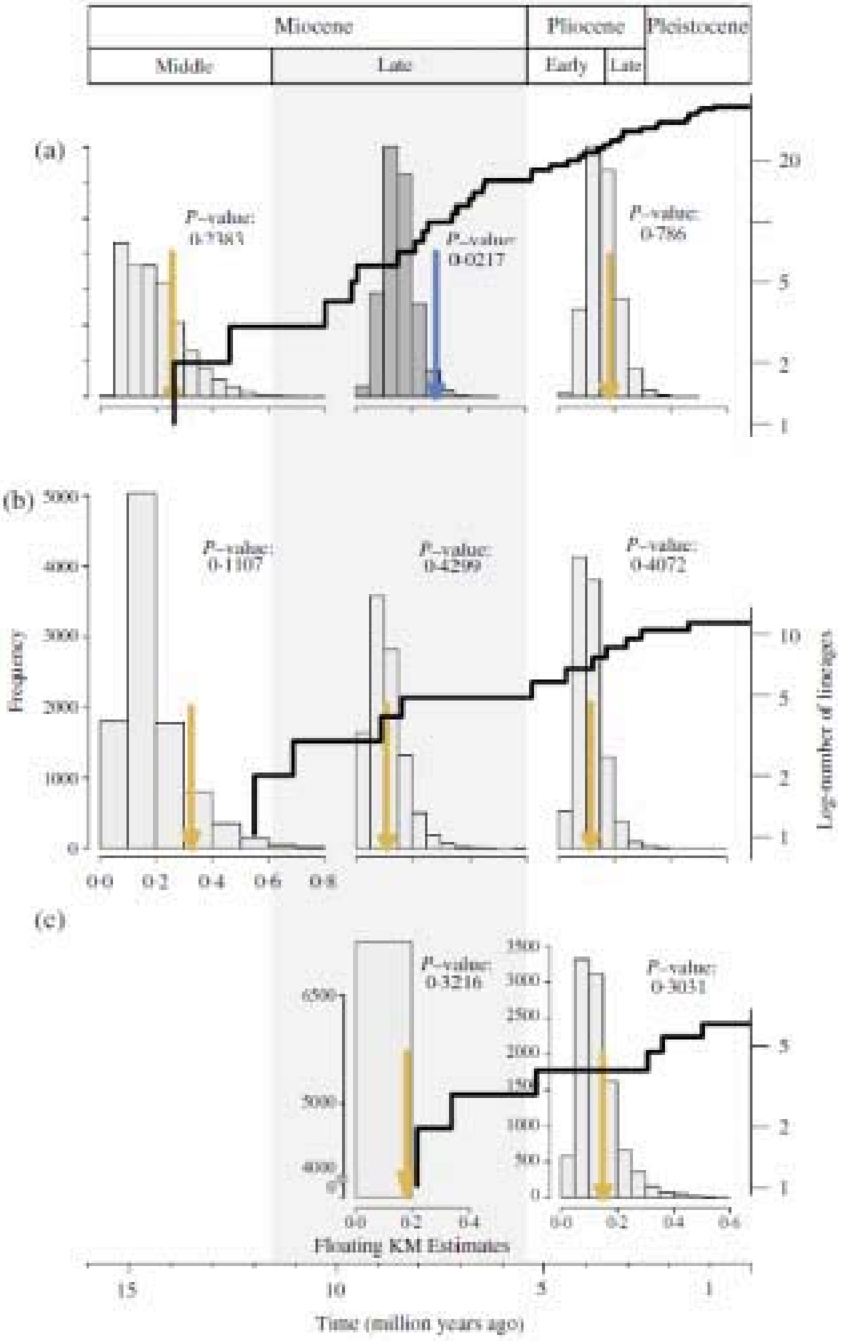

FIG. 4. Diversification pattern of the three groups of fishes: (a) Goodeinae, (b) southern notropins and (c) genus *Algansea*. Ln-transformed accumulations of lineages through time are shown (−); ▬, —, the Kendall–Moran (KM) estimate of a global diversification rate for specified geological time intervals (showing only middle Miocene, late Miocene and Pliocene-Pleistocene); ▨represent the diversification rates simulated (null distribution generated from 10 000 birth–death trees) for the same time intervals; —indicates when the global rate differed significantly from the simulated rate; □, the interval time with the highest geological activity that gave rise to the Trans-Mexican Volcanic Belt (TMVB).

Table II. Model and diversification rates of three freshwater fish groups in central Mexico

Groups	Pure birth	Birth–death	DDL	DDX	Yule-3-rate	MCCR test Richness	MCCR test Sampled	MCCR test Gamma (critical value), *P*-value	δAIC$_{RC}$, *P*-value
Goodeinae; Goodeidae	LH = **−1·32**; −2·97	LH = **−1·32**; −2·97	LH = **3·07**; 0·03	LH = **1·16**; −1·83	LH = **6·04**; 3·10	**40**; 44	**37**; 38	**−2·63 (−1·46), *P* < 0·01**	**6·80, *P* < 0·05**
	AIC = **4·65**; 7·95	AIC = **6·65**; 9·95	AIC = **−2·15**; 3·93	AIC = **1·66**; 7·66	AIC = **−2·09**; 3·79			−2·14 (−1·60), *P* < 0·05	4·16, *P* > 0·05
	r_1 = **0·16**; 0·15	r_1 = **0·16**; 0·15 a = **0·00**; 0·00	r_1 = **0·38**; 0·31 k = **43·35**; 48·45	r_1 = **0·66**; 0·37 x = **0·30**; 0·29	r_1 = **0·34**; 0·27 r_2 = **0·16**; 0·15 r_3 = **0·02**; 0·02 st_1 = **6·44**; 6·44 st_2 = **1·19**; 1·19				
Southern notropins	LH = −13·62	LH = −13·62	LH = −12·02	LH = −12·58	LH = −11·07	**14**	12	**−2·63 (−1·30), *P* > 0·05**	**1·20, *P* > 0·05**
	AIC = 29·25 r_1 = 0·12	AIC = 31·25 r_1 = 0·12 a = 0·00	AIC = 28·05 r_1 = 0·32 k = 12·87	AIC = 29·16 r_1 = 0·60 x = 0·86	AIC = 32·03 r_1 = 0·49 r_2 = 0·16 r_3 = 0·03 st_1 = 11·96 st_2 = 2·83				
Algansea; *Algansea* + *Agosia*	LH = **−8·04**; −10·37	LH = **−8·04**; −10·37	LH = **−7·13**; −10·04	LH = **−7·29**; −10·23	LH = **−7·05**; −9·48	**8**; 9	**7**; 8	**−0·51 (−1·48), *P* > 0·05**;	**−0·16, *P* > 0·05**;
	AIC = **18·09**; 22·74	AIC = **20·09**; 24·74	AIC = **18·26**; 24·09	AIC = **18·59**; 24·46	AIC = **24·10**; 28·96			−2·63 (−1·44), *P* > 0·05	−1·34, *P* > 0·05
	r_1 = **0·14**; 0·11	r_1 = **0·14**; 0·11 a = **0·00**; 0·001	r_1 = **0·47**; 0·23 k = **6·95**; 10·11	r_1 = **1·18**; 0·22 x = **1·14**; 0·44	r_1 = **0·59**; 0·12 r_2 = **0·16**; 0·46 r_3 = **0·07**; 0·06 st_1 = **7·20**; 2·48 st_2 = **2·13**; 2·13				

Values in bold indicate rate estimates not considering the sister group; regular numbers indicate rate estimates including sister group.

AIC$_i$, Akaike information criterion; DDL, logistic density-dependent rate model; DDX, exponential density-dependent rate model; MCCRs, Monte-Carlo constant rates (gamma statistic) test; δAIC$_{RC}$, delta-AIC, the difference in AIC scores between model (*i*) and the overall best-fit model; LH, the log-likelihood under model; r_1, r_2, r_3, net diversification rates (r_1 = initial rate and r_3 = final rate); *a*, the extinction fraction; *k*, the *k*-parameter from DDL model; *x*, the *x*-parameter from the DDX model; st_1, st_2 = shift times (st_1 is always the first shift point). The critical significance level used was *P*-value <0·05.

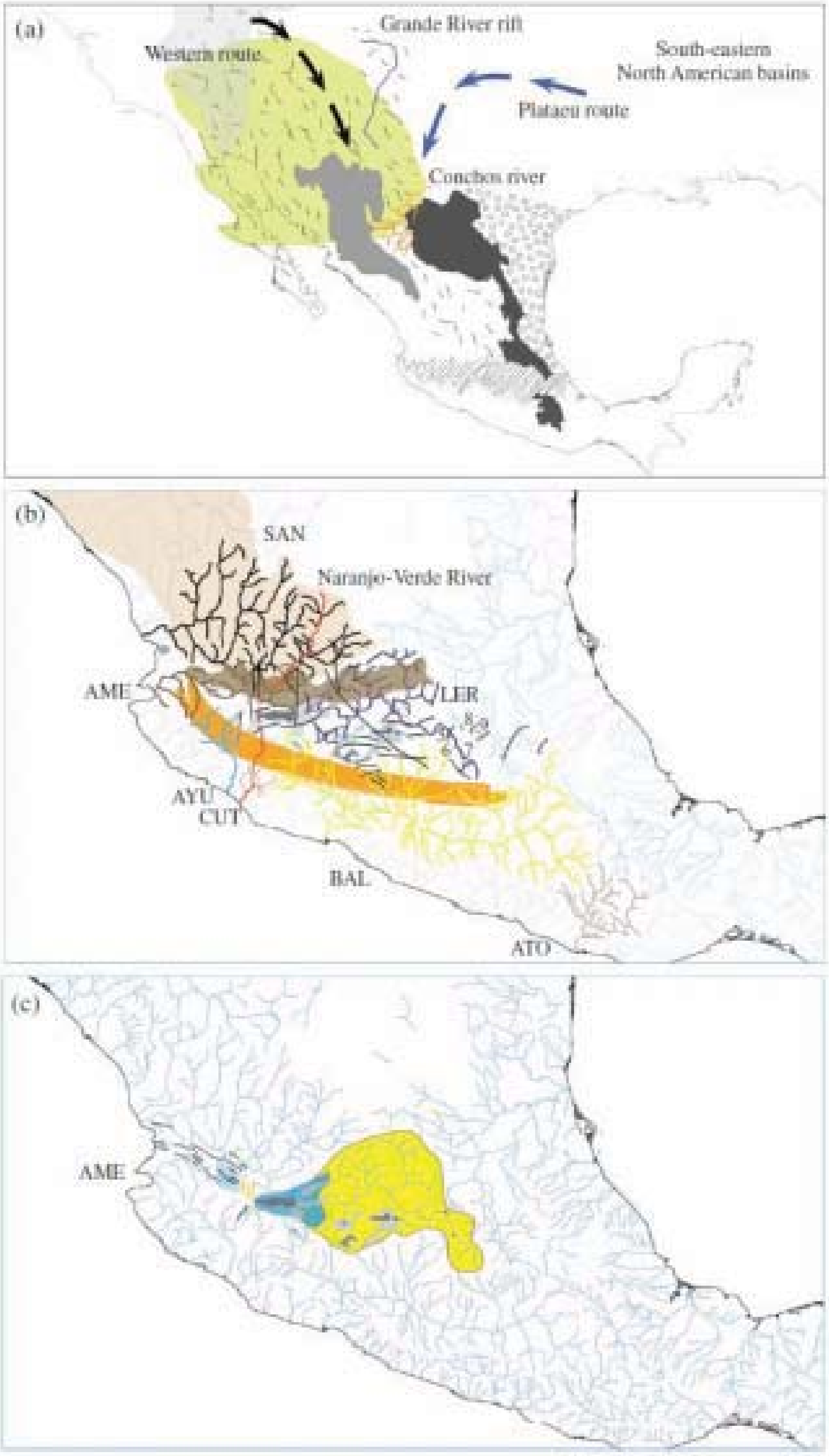

FIG. 5. Legend on next page.

suggesting that southern notropins derive directly from this area [Fig. 5(a)]. There are other freshwater fishes with Nearctic origin such as *Moxostoma* (Catostomidae), *Ictalurus* (Ictaluridae) and *Micropterus* (Centrarchidae), which are represented by species that probably dispersed southwards in the same way as southern notropins did, through the plateau track. These other freshwater fishes consist of groups that occur in central Mexico and have their sister groups in the Bravo River basin, indicating an ancient hydrographic exchange across the presently arid central plateau (Miller & Smith, 1986). In contrast with southern notropins, however, the Catostomidae, Ictaluridae and Centrarchidae are presumably lineages that recently colonized central Mexico, as suggested by the Plio-Pleistocenic fossil evidence (Miller *et al.*, 2005) and by their low species richness in central Mexico, *e.g.* the silver redhorse *Moxostoma austrinum* Bean 1880 and *Moxostoma* sp. (Clements *et al.*, 2012), and the lerma catfish *Ictalurus dugesii* Bean 1880 (Miller *et al.*, 2005).

Geological evidence of a series of events that occurred during the Late Eocene, through the Oligocene and the Early Miocene, indicates that the most likely arrival route was the area of the basin and range province in North Mexico, characterized by the Bolsons (broad desert basins) and isolated ranges of northern and eastern Chihuahua (Hawley, 1969). The early Tertiary Conchos River (King & Adkins, 1946) may have served as a connection to central Mexico [Fig. 5(a)].

Biogeographic patterns

Species of *Algansea* and Goodeinae exhibit the first concordant pattern, which occurred in the late Miocene (8·0 MYA). The southern notropins also show a concordant pattern, particularly with respect to the Goodeinae, occurring around 5–4 MYA, and it was not until *c.* 3·0 MYA that a concordant event among the three groups of fishes took place (node A in Fig. 3).

After several periods of tectonic activity, the uplifting of central Mexico and the formation of the TMVB produced the separation of groups of organisms, defining particular biogeographic events. A magmatic arc evolved in central Mexico between the Miocene and modern times, showing significant changes in its configuration through time (Israde-Alcántara *et al.*, 2010). The uplifting of central Mexico was promoted by the intensification of the tecto-volcanic activity in the southern part of the SMOc (Henry & Aranda-Gómez, 2000), and in the western region of the TMVB, where the eastward migrating pulse of volcanism took place from *c.* 11·5 to *c.* 6 MYA (Ferrari, 2004) [Fig. 5(b)]. Such events were influenced by the Pacific and North American plates that produced the fault systems of Chapala-Tula and Chapala-Ixtlahuaca

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FIG. 5. Geological scenarios through the evolutionary history of the three groups of fishes analysed. (a) Scenario of the Northern routes: ▨, Great basin; ■, Sonoran Desert; ■, early Sierra Madre Occidental (SMOc); ■, Sierra Madre Oriental (SMOr); ▨, Gulf of Mexico coastal plain (GM); ▨, Trans-Mexican Volcanic Belt (TMVB); ▨, Basin and Range province (B&R). (b) Scenario of the uplifting of central Mexico: ■, SMOc middle-late Miocene; ■, TMVB middle-late Miocene; —, Chapala-Tula &Chapala-Ixtlahuaca fault systems; ■, Uplifting of central Mexico; ▨, Ancient lakes; ■, Modern lakes. (c) Scenario of the paleolakes on central Mexico: ▨, Zacoalco paleolake (MRCA of *Ameca splendens*, *Allotoca goslinae* and *Yuriria amatlana*); ■, Chapala-Lerma lower (ancestral area of *Chapalichthys encaustus*, *Allotoca dugesii* and *Yuriria* spp.); ■, Lerma Basin; <, Tepic-Zacoalco Rift; |, San Marcos Fault. LER, Lerma River; SAN, Santiago River; AME, Ameca River; AYU, Ayuquila River; CUT, Coahuayana-Tamazula River; BAL, Balsas River; ATO, Atoyac River.

that roughly follow the Lerma River (Israde-Alcántara *et al.*, 2010) [Fig. 5(b)]. The uplifting of central Mexico, as a widespread event in space and time, caused the disjunction of the Pacific drainages (Ameca, Armeria-Ayuquila, Coahuayana-Tamazula, Balsas-Tepalcatepec and Atoyac) and the drainages that connect to the upper part of the TMVB. This event might have isolated the ancestor of the tribe Ilyodontini (Goodeinae) in the Ameca-Ayuquila River basins and *Notropis* in the Balsas-Atoyac region from their sister groups between 12·6 and 12·0 MYA [Fig. 5(b)]. As a result of the continuous activity of TMVB during the late Miocene to early Pliocene, the isolation of the species within the Pacific clade of *Algansea* and '*Xenotoca*' (node A in Fig. 3) is congruent, in space and time, with the activities of the Santa Rosa fault, Cinco Minas and Colima Grabens. Furthermore, the isolation of the species is concordant with the intensification of volcanism in the areas of Plan de Barrancas, Santa Rosa Dam, Tequila Volcano and Los Altos de Jalisco, also in the upper Miocene, which gave the actual configuration to the Santiago and Tamazula Rivers (Ferrari & Rosas-Elguera, 1999; Ferrari, 2004).

The second pattern (node B) involves the upper Ameca River again, and is supported by the presence of the cyprinid *Y. amatlana* and the goodeins *A. goslinae* and *A. splendens*. This event shows the ancient relationship of the upper Ameca River with drainages in central Mexico, that are associated with the tectonic activity of the San Marcos Fault system that occurred *c.* 3–1 MYA (Ferrari & Rosas-Elguera, 1999) [Fig. 5(c)].

The last pattern, representing node C in Fig. 3, involves several areas within central Mexico with relationships supported by widespread species present in the middle to lower Lerma Basin, Santiago-Verde River and Chapala. The presence of *N. calientis*, *Y. alta*, *A. tincella*, *X. variata*, *C. encaustus* and *A. dugesii* indicates that the aforementioned three basins conform to a single original one, probably reflecting the increase in the extension of palaeolakes due to a wet period in Pleistocene, in addition to the fact that the Lerma Basin maintained flow into the lakes during the Neogene-Quaternary (Israde-Alcántara *et al.*, 2010) [Fig. 5(c)].

DIVERSIFICATION PATTERNS

Evolutionary radiation and constant diversification model

The three groups of fishes show at least two speciation patterns in central Mexico. For instance, goodeins show evidence for an early evolutionary radiation, since they do not follow a constant model of diversification rate, and instead fit a DDL model (Rabosky & Lovette, 2008) and a convex curve (Rabosky & Lovette, 2008; Crisp & Cook, 2009). Density-dependent speciation as a reflection of the decline of the diversification rates is one of the most striking features of the evolutionary radiation; speciation is most likely when there is a relaxation of the interspecific competition in conjunction with the availability of diverse resources, but as radiation progresses, ecological niche space becomes increasingly saturated, yielding fewer opportunities for speciation (Rabosky & Lovette, 2008). Thus, the convex curve reflects a steep slope that decreases as niche space fills (Crisp & Cook, 2009) [Fig. 4(a)]; in addition, the tree shape of the Goodeinae that follows a proportional relationship between branch lengths and the evolutionary change [Fig. 2(a)] reinforces this interpretation (Crisp *et al.*, 2004).

In contrast, southern notropins and *Algansea* show an anti-sigmoidal curve (Harvey *et al.*, 1994; Crisp & Cook, 2009) with considerable gaps in the diversification process [Fig. 2(b), (c)] (Pybus & Harvey, 2000), and a long broom-handle-shaped tree [Crisp *et al.*, 2004; Fig. 2(b), (c)] that may indicate the sole survivor of a near-complete extinction of the stem-group taxa (Crisp *et al.*, 2004). MCCR gamma estimates, however, are above 0·05, indicating that decline in lineage accumulation in cyprinids is non-significant. In addition, the net diversification rates in cyprinids are consistent with a constant model (Table II). These findings suggest that the small clade size affected the significance of the Gamma test and the selection of diversification models in the $\delta\mathrm{AIC}_{\mathrm{RC}}$; thus, a significantly decreasing rate was not obtained.

Likely causes of the diversification mode patterns

The shift in rate of lineage diversification leading to the Goodeinae [Fig. 4(a)] is consistent with Miocene volcanism across central Mexico (Ritchie *et al.*, 2005; Domínguez-Domínguez *et al.*, 2010). Such increases in the diversification rate coincide with the beginning of the period of higher activity in the TMVB in central Mexico, and the development of palaeolakes (Ferrari, 2004; Israde-Alcántara *et al.*, 2010). Findings in this study appear to be in agreement with an overwhelming pattern of evolutionary radiation (Rabosky & Lovette, 2008) in the goodeins. As previously discussed by Ritchie *et al.* (2005) and Domínguez-Domínguez *et al.* (2010), the highly complex geological and climatic history of the region, particularly during the Miocene, promoted a range extension, increasing the geographical range size, and therefore an increase in the probability of vicariant events in one physiographically dynamic region. The two cyprinid groups share a similar evolutionary history with goodeins in central Mexico since the late Miocene [Fig. 2(b), (c)], and their diversification rates were constant through time. A potential explanation for these contrasting patterns could be that goodeins possess several biological traits associated with higher speciation rates, *e.g.* livebearing, that could have improved the survival capability during its diversification in the Miocene.

Some macroecological analyses have demonstrated that small body size (28–40 mm standard length, L_S) associated with small geographical ranges in North American freshwater fishes, birds and mammals confers several advantages for higher speciation rates (Rosenfield, 2002). The relationship between body mass and metabolic requirements determines that large species with small ranges have low population densities that are more likely to be susceptible in a catastrophic event. In addition, body size is also positively correlated with generation time; thus, the shorter generation time of small-bodied species may lead to rapid genetic divergence and speciation in isolation (Pyron, 1999; Rosenfield, 2002).

Body sizes among goodeid species, particularly members of the most diversified groups, excluding the bulldog goodein *Allophorus robustus* (Bean 1892), the blackfin *Goodea atripinnis* Jordan 1880 and the bluetail goodea *Ataeniobius toweri* (Meek 1904), range from 34·0 to 59·0 mm L_S (Domínguez-Domínguez *et al.*, 2005). This range overlaps with the remaining North American freshwater small-bodied fishes (28–40 mm L_S; Rosenfield, 2002), indicating that biological traits associated with small body size, such as high population densities, short generation time or limited dispersal capacity (Rosenfield, 2002), could be significant causes for the observed evolutionary pattern in Goodeinae. Although information on the generation time of goodeins is lacking, the data about the frequency of spawning in some species suggest that some members of the Chapalichthyini and Girardinichthyini tribes have spawning periods during two seasons of the year, indicating that there are at least two generations per year, except the larger *A. robustus* and *G. atripinnis* that reproduce once per year (Moncayo, 1996; Salazar-Tinóco *et al.*, 2010; O. Domínguez-Domínguez, unpubl. data).

Conversely, southern notropins (except the *calientis* complex) and species of *Algansea* may be regarded as medium to moderately large fishes, as they can reach 200–230 mm L_S (Barbour & Miller, 1978; Miller *et al.*, 2005). Moreover, it has been recognized that most species of *Algansea* spawn only once per reproductive season (Barbour & Miller, 1978), suggesting one generation per year. Therefore, the lower and linear diversification rates occurring in this lineage could be associated with the larger body size. Nevertheless, similar to goodeids, the *calientis* complex of the southern notropins are small-bodied fishes ranging from 35·3 to 43·7 mm L_S (Chernoff & Miller, 1986; Lyons & Mercado-Silva, 2004; Domínguez-Domínguez *et al.*, 2009), and it is likely that they possess many of the traits typically associated with a small body, *i.e.* minimum metabolic requirements for high population densities and short generation times, except more than one reproductive season per year, recorded in *N. grandis* (Moncayo, 1996). In accordance with the aforementioned arguments, the only reproductive event per year might determine the non-significant increase of the diversification rate at the origin of the *calientis* complex [Fig. 4(b)].

In summary, in the case of goodeins, small body size and associated traits, in conjunction with sexual selection (that plays an important role in goodein diversification; Ritchie *et al.*, 2007) and the advantages provided by viviparity (particularly matrotrophy, where normally viviparous females produce fewer progeny with a higher survival rate than oviparous progeny; Wourms, 1981; Wourms *et al.*, 1988), could have promoted the highest diversification rate exhibited among the studied fishes. This may have allowed this group of fishes to develop a capacity to confront dynamic environmental conditions generated by the intense geological activity and complex climatic changes of central Mexico during the late Miocene to early Pliocene, and, consequently, increase their ability to colonize new niches. The fragmentation of habitats resulted in vicariant processes that produced an increase in the diversification rate in these fishes.

Meanwhile, despite the small size in the *calientis* complex, the occurrence of one reproductive season per year and the lack of viviparity resulted in a lower capacity to adapt to the environmental challenges generated by the geological activity and climatic fluctuations during the Miocene and Pliocene. This may explain the lower diversification rate in these fishes, with respect to that observed in goodeins. In other fish groups, such as atherinomorphs, it has been demonstrated that viviparous groups are significantly more species-rich than their oviparous sister groups (Mank & Avise, 2005).

Another important implication associated with the distinct diversification patterns of freshwater fishes studied is the relatively low biogeographic concordance. As proposed by Rabosky & Lovette (2008), density-dependent patterns may be explained by diversification models other than ecological opportunity; such is the case of the geographical range size dynamic (increasing-declining) that influences the allopatric speciation. Therefore, this study might be regarded as empirical evidence that geographical range size is positively correlated with diversification rates.

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table S1. Geographic distribution range and the GenBank accession number of the analysed sequences

Table S2. Taxonomic classification

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CAPITULO II

BIOGEOGRAFIA HISTORICA DEL "GRUPO SUREÑO" DEL GENERO *Moxostoma* Y SU COLONIZACIÓN AL CENTRO DE MÉXICO

ARTICULO II

Historical biogeography of the southern group of the sucker genus *Moxostoma*
(Teleostei: Catostomidae), and colonisation of central Mexico

Artículo en**viado a la revista "Zoological Journal of the Linnean Society"**

Historical biogeography of the southern group of the sucker genus *Moxostoma* (Teleostei: Catostomidae), and colonisation of central Mexico.

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Biogeography of the southern group of *Moxostoma*.

ABSTRACT

The historical biogeography of the southern group of *Moxostoma*, a genus of Nearctic freshwater fishes belonging into the Catostomidae, along its entire distribution range in North America was inferred in order to: (1) Determine the biogeographical events responsible for its current pattern of diversity and distribution; (2) Correlate the climatic and geologic history of the region with the biogeographical pattern observed; and (3) Trace the colonisation route into central Mexico, and the western Pacific slope drainages. Sequences of mitochondrial cytochrome *b* and the third intron of the growth hormone were obtained for the members of southern group, and related species of the family Catostomidae. Phylogenetic analyses and relaxed molecular clock analyses were performed to determine the relatedness of species and to estimate divergence times. In order to uncover biogeographical patterns, a Dispersal-Extinction-Cladogenesis analysis (DEC) was conducted. Phylogenetic analyses were consistent with the historical hydrographic scenario in the region. Divergence times show that the southern group evolved during the Pliocene-Plesitocene. DEC analyses, showed that vicariance and dispersal, played an important role in the current distribution patterns of the lineages into central Mexico, allowing us to trace an independent route of colonisation from northern areas of North America, into central Mexico.

ADDITIONAL KEYWORDS: DEC analysis, range extension, dispersal ability, vicariance, molecular clock, hydrographic configuration, cytocrome b, growth hormone.

INTRODUCTION

Biological dispersal is a fundamental process that operates at multiple temporal and spatial scales, encompassing aspects such as the survival, growth and reproduction of individuals, the composition, structure and dynamics of populations and communities, and the persistence, evolutionary history and geographical distribution of species (Nathan, 2001).

Indeed, dispersal ability of an organism is also expected to be a strong determinant for the potential to invade new habitats or areas (Bowler & Benton, 2005); therefore, the redistribution of genotypes by dispersal should be regarded as a process that is closely linked to the evolution of life-history traits (Ronce, 2007).

In species with a limited dispersal capability, such as primary freshwater fishes, the colonisation into new habitats is severely restricted by the extent and continuity of the aquatic ecosystems where they live, which follows geographical patterns (Rosenfield, 2002). In North American freshwater fishes, a positive strong association between geographical range size (home range size and dispersal ability), body size, and habitat or niche breadth has been documented (Pyron, 1999; Rosenfield, 2002). Such is the case of members of the family Catostomidae, commonly known as suckers, whose geographical range size is closely associated to body size and the niche breadth (Pyron, 1999). In this Nearctic fish family, it has been postulated that current allopatric distribution among their species is the result of vicariant speciation (Smith, 1992), even though geographic dispersal appear to be responsible of its wide geographic distribution range, and diversification pattern in North America.

Moxostoma represents a widespread genus of Catostomidae mostly distributed across eastern North America, in southern Canada and the United States (Harris *et al.*, 2002). In previous phylogenetic analyses of the tribe Moxostomatini, species of *Moxostoma* constitutes a monophyletic assemblage, which expand its distribution range southwards into hydrographic systems of central Mexico, and some rivers along the western Pacific slope (Harris & Mayden, 2001; Harris *et al.*, 2002; Clements, Bart & Hurley, 2012). That southern group of *Moxostoma* (previously known as "Western *Scartomyzon*") comprises five differentiated forms: *M. austrinum* Bean 1880, *M. albidum* Girard, 1856 and three undescribed forms (Clements *et al.*, 2012).

Seemingly, the southern group represents a single ancestral dispersal as a result of an allopatric speciation by peripheral isolation from the Mississippi River Basin into drainages of Texas and Mexico (Clements *et al.*, 2012). Previous taxonomic treatments considered this group formed by two species complexes, *Scartomyzon congestus* Baird & Girard, 1854 restricted to the Gulf of Mexico slope drainages, and *S. austrinus* distributed across Conchos River and extending into the Lerma-Santiago hydrographic system in central Mexico, and some river systems across the western Pacific slope (Robins & Raney, 1957; Clements *et al.*, 2012). Currently, since *Scartomyzon* has been recognised as a junior synonym of *Moxostoma*, and the recent finding that two species, *S. congestus* and *S. albidus*, are not closely related (Clements *et al.*, 2012), the species complexes changed to *Moxostoma albidum* for populations inhabiting the Gulf of Mexico slope, and *M. austrinum* for those found in the Conchos, central Mexico and the western Pacific slope. In contrast with other representative groups of freshwater fishes of central Mexico, that arose during Miocene (Pérez-Rodríguez *et al.*, 2015), the Plio-Pleistocene fossil evidence, and the low species richness of members of the southern group suggest a more recent dispersal into central Mexico. Thus, a distinct biogeographical pattern is expected to have occurred for the case of the southern group, implying an independent evolutionary history for the populations occurring in northern and central river basins of Mexico.

Although the members of the southern group and other freshwater fishes endemic to Texas are presumed to have evolved by peripheral isolation from the Mississippi River basin ancestors (Clements *et al.*, 2012), some evidence allow us to consider that dispersal was determinant in the colonisation of these fishes into central Mexico. Such evidence rely on: *i*) the fact that crossing from the Gulf of Mexico coastal streams of Eastern North America, to Pacific drainages has been postulated (Smith, 1992); *ii*) the presence of biological traits in these fish species associated with a high dispersal ability (Pyron, 1999; Rosenfield, 2002), as a relatively large body size (109 mm to 235 mm) (Robins & Raney, 1957; Miller, Minckley & Norris, 2005) and a wide habitat breath (deep pools and riffle habitats in streams, medium and mainstem rivers, with bedrock, gravel, sand and silt substrate) (Robins & Raney, 1957; Lyons & Navarro-Pérez, 1990; Miller *et al.*, 2005), *iii*) the existence of fossil evidence from the Pleistocene (Miller *et al.*, 2005), and *iv*) the wide distribution range of the species *M. austrinum* through several river basins of the region, reflecting a range expansion by ancestral connections across several river basins currently isolated.

The aim of the present study is to use the information from DNA sequences of two molecular markers to describe patterns of historical biogeography and to infer the divergence times for the southern group of *Moxostoma*, to discuss the processes that determined the current geographic distribution of the species complex, and to explain the presence of the southern group in central Mexico, analysing the role that dispersal had in the evolutionary history and current biogeography of this freshwater fish.

MATERIALS AND METHODS

SAMPLING

Tissues samples were obtained from the whole distribution range of the well-delimited monophyletic southern group (Fig. 1, Appendix 1). Fishes were caught by electro-fishing and seine-nets. A piece of caudal fin was cut and stored in micro-tubes with ethanol 96%. Some fishes were fixed in 8% formalin, and later preserved in 70% ethanol. Voucher specimens were deposited at the "Colección de Peces de la Universidad Michoacana de San Nicolas de Hidalgo" (CPUM). Two new records for *M. austrinum* are reported in the present study, which expanded the distribution of this species to a tributary that drains into the southern edge of Chapala lake (Tizapán River), and the Middle Lerma (main channel of Lerma River in Pateo, northeasthern Michoacán) (Fig. 1, Appendix 1). Also, new populations of the species *Moxostoma milleri* Robins & Raney, 1957 were included herein to test the taxonomic hypotheses proposed by Clements *et al.* (2012), that congeners are distributed as follows: *Moxostoma* sp. cf. *austrinum* from Conchos River, *Moxostoma* sp. cf. *austrinum* from Santiago River, and *Moxostoma* sp. cf. *albidum* from Soto la Marina River. According with authors, these are recognized as undescribed forms, thus as independent operational taxonomic units (OTU´s). The remaining OTU´s in that analysis correspond to *M. austrinum*, *M. milleri* and *M. albidum*. To test the phylogenetic hypothesis of Clements *et al.* (2012), sequences used in that study (ingroup and outgroup) were retrieved from the Genbank dataset (Appendix 1) and aligned with the new sequences generated in this study.

DNA SEQUENCING

Prior to DNA extraction, tissues were rinsed with distilled water to remove residual ethanol. Total genomic DNA was extracted from fin-clip tissue using the commercial kit Biosprint15 for tissue and blood (Qiagen). The entire coding region of the mitochondrial cytochrome *b* gene (cytb) (~1140 bp) was obtained using primers GLUDG (5′-TGA CTT GAA RAA CCA YCG TTG-3′; Palumbi, 1996) and H16460 (5′-CGA YCT TCG GAT TAC AAG ACC G-3′; Perdices & Doadrio, 2001), however in order to avoid uncertainity, missing data regions were removed from sequence, resulting in an alignment of 1119 bp. Based on the identification of homologous sequences in the tetraploid genome of catostomids (Clements, 2008; Bart *et al.*, 2010), the 3rd intron of the nuclear Growth Hormone (GHI3) sequences was obtained using primers GHI3F (5′-TCT GCA ACT CTG ACT CCA TAG-3′) and GHI3R (5′-GAC GGT TCC ACT CAA GGT CTG-3′) (Clements, 2008). PCR reactions were performed in a final volume of 25µl containing 2.5µl of 10x PCR buffer with 15mM Magnesium (5PRIME), 10mM dNTP mix, 10 pmol of each primer, and 5 U/µl Taq DNA polymerase (5PRIME). PCR profile program consists of 94°C for 4 min. of denaturation and 35 cycles of 94°C for 45 sec., 46°C for 30 sec. and 72°C for 1.30 min. A final extension of 72°C for 5 min., for cytb; and 94°C for 1 min. of denaturation and 35 cycles of 94°C for 30 sec., 57°C for 30 sec. and 72°C for 1.15 min. A final extension of 72°C for 10 min., for the GHI3. Purification of the PCR products was conducted with ExoSAP-IT (Affymetrix/USB® products).

PHYLOGENETIC ANALYSES

Sequence alignment was carried out using Clustal W (Thompson, Higgins & Gibson, 1994) as implemented in MEGA v.5.05 (Tamura *et al.*, 2011), and were checked and manually corrected. Sequences of GHI3 showed heterozygous positions defined by different base pair or by indels (double-peaks in chromatograms). The former were coded following the IUPAC degenerated code, and for the latter a manual reconstruction of the two allele phases was performed following Sousa-Santos *et al.* (2005).

The substitution models that best fit mitochondrial and nuclear datasets were obtained by jModelTest 0.1.1 (Posada, 2008), considering both, the Akaike information criterion (AICc) and the Bayesian information criterion (BIC) (Table 1). Phylogenetic relationships were inferred with Maximum Likelihood (ML) and Bayesian Inference (BI) for both *loci* independently (cytb and GHI3) and for a concatenated data set. Most of the sequences representative of the family Catostomidae used in Clemments *et al.* (2012) were included herein as outgroups. Maximun likelihood was run in PHYML (Guidon *et al.*, 2010) with the AICc-selected model. The tree search consisted in an initial BIONJ tree estimation followed by a Subtree Pruning Regrafting (SPR) algorithm; node support was assessed using 1000 nonparametric bootstrap. Bayesian analysis was run in MrBayes 3.2.2 (Huelsenbeck & Ronquist, 2001) incorporating BIC-selected model, with four independent MCMCs runs and 10,000,000 generations, sampling every 1000 trees. Convergence and stationary were verified by suitable effective sample size (ESS) for all parameters in Tracer v.1.4.1 (Rambaut & Drummond, 2007). Bayesian Inference was submitted remotely to run at the CIPRES Science Gateway V.3.3 portal (Miller, Pfieffer & Schwartz, 2010). Ten percent of generations were removed (burn-in). Phylogenetic analyses were performed with the separate and concatenated datasets (cytb and GHI3). Indels of nuclear *locus* were coded by simple coding (Simmons & Ochoterena, 2000) using SeqState 1.4.1 (Müller, 2005) and were analysed by BI.

TREE TOPOLOGY TEST

Likelihood-based test for alternative topologies, Approximately Unbiased test (AU) (Shimodaira, 2002), Shimodaira-Hasegawa test (SH) (Shimodaira & Hasegawa, 1999), and the bootstrap and bayesian posterior probabilities for three alignments were performed. Sitewise log-likelihood values were computed with PAUP; tests values including *p* values of the different likelihood-based tests were finally calculated with CONSEL (Shimodaira & Hasegawa, 2001).

GENETIC DISTANCES AND DIVERGENCE TIME ESTIMATES

Overall mean of Maximum Likelihood distances between the species of the southern group based on both *loci*, cytb and GHI3, were estimated with MEGA v.5.05. Divergence times between lineages of the southern group were estimated using a relaxed log-normal clock in BEAST package v.1.7.5 (Drummond & Rambaut, 2007). BEAST analysis was performed including both *loci*, linking the gene trees partition. Two calibration points at internal nodes were used; the oldest (C1) consisted in a geological event that corresponds to the formation and evolution of the Conchos River during Tertiary and Quaternary, that is suggested by the age of the gravels along of the lower Conchos valley (King & Adkins, 1946). Based on above, a uniform prior distribution was specified, placing a hard minimum and a hard maximum bound of 2.6 Myr and 23 Myr, respectively, including the Late Tertiary-Early Quaternary phase. For the second calibration point (C2) a fossil record of *Moxostoma* sp. found in the Chapala lake *ca.* Pliocene-Early Pleistocene (Smith, Cavender & Miller, 1975). That fossil was attributed to the MRCA of *M. austrinum*, and a lognormal prior was used specifying an offset of 1.8 Myr as a hard minimum bound.

The substitution model that best fits for each gene was set. All other parameters used default priors. Three independent MCMC runs were performed for 40,000,000 generations and sampled every 1,000 generations, with a birth-death speciation prior. Only the members of the southern group plus the sister group were included (one individual per species). Analyses were run at the CIPRES Science Gateway V.3.3 portal. Convergence was assessed with estimates of effective sample size (ESS) in Tracer v.1.4.1. and by comparing the marginal posterior distributions for each parameter among independent runs, following the criterion ESS>200 as indicated in the BEAST manual. Ten percent of the generations were discarded (burn-in). The resulting trees were pooled using the LogCombiner in the BEAST Package v.1.7.5. The 95% highest posterior density of divergence times was plotted onto each node of phylogeny using TreeAnnotator in the BEAST Package.

ANCESTRAL AREA RECONSTRUCTION OF THE SOUTHERN GROUP

The historical biogeography of the southern group was assessed through the parametric biogeographical method dispersal-extinction-cladogenesis (DEC) (Ree *et al.*, 2005; Ree & Smith, 2008) using the software LAGRANGE V.20120508 (distributed by the authors from http://code.google.com/p/lagrange; Ree & Smith, 2008). This parametric approach allows estimating the dispersal and extinction rate and the probabilities of range inheritance scenarios using ML inference algorithms, providing a rigorous statistical framework for alternative biogeographic hypotheses (Ree & Smith, 2008; Buerki *et al.*, 2011).

Seven areas were considered in the analysis, corresponding mainly to north-eastern and central-western river drainages across Mexico, encompassing the entire distribution range of the southern group. Because *M. congestum* has been well-supported as the sister group of the southern group (Smith, 1992; Clements *et al.*, 2012), its distribution range was included as the sister group area (Fig. 1). These areas were: A, river drainages of the western Gulf slope of North America (sister group area); Gulf of Mexico slope drainages (GSD), B, Bravo River basin (including the adjacent San Fernando River drainage); C, Conchos River, and D, Soto la Marina River; by other hand, the Pacific Slope Drainages (PSD), E, Mezquital River; F, Santiago River; G, Lerma River including Chapala and Cuitzeo lakes, H, Ameca and Armería-Ayuquila rivers (Fig. 1). *Moxostoma congestum* and *M. austrinum*, occur in more than one area, thus the areas where these species occur were, A, B, and G, H, respectively; the remaining OTU´s exclusively occurred in one area (Fig. 1).

Two possible phylogentic hypotheses were tested by DEC analysis. Chronograms obtained by BEAST analysis were used as input information. Several models were tested; an unconstrained model (M0), which allows geographic ranges to include any combination of hydrographic basins and direct dispersal between any pair.

In addition, based on several paleohydrographic scenarios that have explained the area relationships among some fish groups from the Bravo, Conchos, Nazas, Aguanaval, and Mezquital rivers (e.g., Smith & Miller, 1986), two constrained models were tested with DEC. Such scenarios assumed a freshwater corridor between GSD and PSD by the ancient pluvial lakes in the Mapimi Bolson region (including the headwaters of the Nazas and Aguanaval rivers), which maintained a connection with two tributaries of the Bravo River; likewise, the Tunal River, a tributary of the Mezquital, was part of the headwaters of Nazas-Aguanaval system in the past, before being captured by the Mezquital River. The ancestral isolation of the Conchos River by the accumulation of sediment and the faulting activity along the Conchos valley, also was considered. Finally, a central scenario that consisted in the canyon of Santiago river (Juanacatlán waterfall) located north to the Chapala lake, which represented a barrier for the fish fauna interchange between Santiago and Lerma-Chapala system since their connection at Plio-Pleistocene (Miller *et al.*, 2005), also was considered.

Thus, the constrained model 1 (M1) restricts distribution ranges to include a maximum of two adjacent hydrographic basins. The constrained model 2 (M2), besides to include a maximum of two adjacent hydrographic basins, also considered dispersal constraints between adjacent basins, highlighting the potential dispersal (with a lower probability) through the area between the currently disjuncted Bravo and Mezquital rivers, and the restricted dispersal for the case of the ancestral isolation of the Conchos River (Fig. 1). The canyon of Santiago river was considered as barrier that restricts the dispersal to the Lerma river. See details of dispersal constraints in Appendix 2. File .lagrange.py was built using the Lagrange configurator beta v.2.0.1. interphase available at http://www.reelab.net/lagrange/configurator/index.

RESULTS

TAXON SAMPLING

Seventy sequences were obtained for both genes, 33 for the cytb and 37 for GHI3. In addition, 42 sequences of mitochondrial and 42 sequences of nuclear genes from the Genbank dataset were included in the analyses (Appendix 1). Five heterozygous individuals for indels were identified and included in the analyses (Appendix 1). Substitution models of evolution and other phylogenetic parameters for each *locus* are shown in Table 1.

PHYLOGENETIC ANALYSES

Phylogenetic analyses based on cytb recovered the southern group as a monophyletic assemblage. Both ML and BI analyses, yielded similar topologies, highlighting the ML that resulted with a higher support (Fig. 2). *Moxostoma* cf. *austrinum* from Conchos was supported as the basal group of the complex; although with a short node and lower support, *M. albidum* resulted as the sister taxon of the clade formed by *M.* cf. *albidum* from Soto la Marina and the species from PSD. The species *M. milleri* appear as the sister taxa to a clade formed by *M.* cf. *austrinum* from Santiago and *M. austrinum*, both supported by high bootstrap and posterior probabilities support values (Fig. 2). Genetic divergences were relatively consistent with relationships (Table 2).

Even though the monophyly of the southern group was recovered using GHI3 and both methods, ML and BY, relationships within the complex resulted in a polytomy. *Moxostoma congestum* was recovered as the species with the closest relationship with the complex (Figure S1).

Concatenated hypotheses differed from cytb in the position of *M.* cf. *albidum* from Soto la Marina; with ML analysis this species was related with the other OTU of the GSD, *M. albidum*, but with very low support (Figure S2); BY analysis resulted in a collapsed polytomy with *M. albidum* and the species from PSD (Figure S3). The inconsistency between the cytb and the two concatenated datasets (Figures S2, S3), was due to the variable position of *M.* cf. *albidum* from Soto la Marina; based on above, there are three possible alternative phylogenetic hypothesis: H1) *M.* cf. *albidum* from Soto la Marina as the sister taxon of species from PSD (*M. milleri*, *M.* cf. *austrinum* Santiago and *M. austrinum*, Fig.2); H2) *M.* cf. *albidum* from Soto la Marina as the sister taxon of *M. albidum* (Figure S2), and H3) a true polytomy among *M.* cf. *albidum* from Soto, *M. albidum* and PSD species (Figure S3).

TREE TOPOLOGY TEST

In accordance with the AU test, the hypothesis of the true polytomy is rejected as alternative topology (H3) (Table 3). Otherwise, topology tests indicate that it is not possible to discard between the remaining hypotheses (H1 and H2). Due to the lack of an objective phylogenetic criterion to select the best hypothesis, ancestral area was inferred through DEC analysis considering both hypotheses, including divergence times; thus, the rigorous statistical framework of DEC was used to assess the alternative biogeographical hypothesis corresponding to the H1 and H2, to obtain an objective criteria to choose the biogeographic scenario that best fits.

AGE ESTIMATES

All divergence time estimates at 95% confidence intervals were obtained for the two phylogenetic hypotheses (Fig. 3 A, B). Chronograms shown differences in time estimates and confidence intervals, particularly at basal relationships (Fig. 3 A, B). The MRCA of the southern group was dated in the final part of Middle Miocene using the H1, while using the H2 was dated in the Upper Miocene. *Moxostoma* cf. *austrinum* Conchos is estimated to diverge from remaining species at Upper Miocene, using both H1 and H2. As well, similar dates were record using H1 and H2 for most derived cladogenetic events, as the case of the MRCA of PSD species, that arose at Pliocene, and the MRCA of *M. austrinum* that was dated at Pleistocene.

ANCESTRAL AREA RECONSTRUCTION OF THE SOUTHERN GROUP

The global likelihood scores (-ln$L$) that indicate the highest probability, were obtained for the hypothesis H2, showing significant differences by 2.0 log-likelihood units for several combinations between the two hypotheses (H1 and H2) and three models (M0, M1 and M2) (Table 4). On the other hand, the H2 under the M2 exhibited the less uncertainty at the node areas, with probabilities above 0.9, except for the node F/H that showed 0.8, suggesting that it is the best ancestral area inference. This scenario, H2 under M2 (Fig. 4) indicated that the origin of the southern group was more likely to have occurred at Late Miocene, into an area formed by the Bravo and Conchos (B/BC). The next node area shows a vicariant event into the Bravo River, which gave rise to *M.* cf. *austrinum* Conchos *ca.* 6 Myr. After, the ancestor of remaining members of the southern group showed a range expansion from Bravo area (B) toward the Mezquital area (E). After that, a vicariant post-dispersal event occurred, separating the species from GSD and PSD (B/E). At Late Pliocene occurred the separation of the Mezquital River from the Santiago area (E/F) *ca.* 3.0 Myr, with a posterior range extension from Santiago (F) to Ameca (H). Later at Early Pleistocene, two viacriant events occurred, one corresponded to the separation of *M.* cf. *albidum* from Soto la Marina River (D) and *M. albidum* from the Bravo River (B); the other one, corresponded to the separation of *M.* cf. *austrinum* from Santiago (F) and *M. austrinum* (H). Subsequently, during Pleistocene occurred the dispersal of *M. austrinum* from Ameca (H) to Lerma-Chapala system (G).

DISCUSSION

PHYLOGENETIC ANALYSES

In contrast with the most recent phylogenetic hypothesis of the genus *Moxostoma*, all current known differentiated OTU´s of the southern group (*sensu* Clements *et al*., 2012), including the species *M. milleri* distributed in the Mezquital River basin, were analysed in the present study. In addition, the taxon sampling was increased to include individuals from other populations, and including more populations per species for both *loci* (except for *M.*

cf. *albidum* from Soto la Marina) (Appendix 1). The recovered phylogenetic topology was similar to that obtained by Clements *et al.* (2012), *i.e. M.* cf. *austrinum* from Conchos resulted as the basal group of the complex; taxonomic units from GSD are related with those from PSD, and *M. congestum* occupied a position as the sister taxa of the southern group with the GHI3. These relationships concur with previous hypothesis (Smith, 1992; Clements *et al.*, 2012) and actually, there is a geographical correspondence since *M. congestum* occurs in the Bravo River and the adjacent area, the western gulf slope drainages (Fig. 1).

With the inclusion of *M. milleri* in the analysis, the taxonomic status of this species was confirmed, as previously suggested (Clements *et al.*, 2012); this species is placed as the basal taxon of the OTU´s distributed in PSD. However, the relationships between the differentiated forms from the GSD, *M. albidum* and *M.* cf. *albidum* from Soto la Marina, remained unresolved (Fig. 2, Figures S2, S3). Even though the relationships between these taxa are different under reconstruction methods, the phylogenetic hypothesis H2 under the biogeographical model M2, was the most plausible evolutionary scenario of the southern group. This hypothesis suggests that both members from GSD are closely related and exhibit a major correspondence to drainage boundaries (Fig. 1).

As also found by Clements *et al.* (2012), relationships based on the nuclear GHI3 gene remained unresolved (Figure S1), even though the taxon sampling for this marker was increased in the present study. The low genetic divergences found among the members of the southern group (Table 2) suggest the lack of phylogenetic signal. In addition, the presence of shared haplotypes among species with a disjunct geographical distribution also indicate the lack of phylogenetic signal of the GHI3 gene, probably due to an incomplete lineage sorting process. Based on the aforementioned arguments, the GHI3 is not suitable for reconstructing the phylogenetic history and for establishing a species delimitation criterion among members of the family Catostomidae. Based on previous phylogenetic findings and the results of the present study, a taxonomic revision of this group is considered necessary.

DIVERGENCE TIMES AND RANGE EXTENSION OF THE SOUTHERN GROUP

Origin of the southern group

Ancestral range reconstruction of the H2 under M2, indicated that the MRCA that gave rise to the southern group occurred at the beginning of Late Miocene in an ancient Bravo River basin, where Conchos River drained to the main channel (Fig. 5A). The major geologic feature modeling the Lower Bravo drainage evolution was the "Río Bravo fault" (see Fig. 5A), which was active during the Late Eocene-Oligocene (Flotté *et al.*, 2008), and supports the existence of a former miocenic Bravo River likely inhabited by the MRCA of the species complex. By other hand, the earliest known river deposits of an ancestral Upper Bravo River, in the southern part of the "Río Grande Rift" (Flotté *et al.*, 2008) and the "Hueco Bolson" (Collins & Raney, 1994) are dated at 2.3 and 2.1 Myr, respectively, indicating a more recent event; therefore, the connection between the Bravo River and the Western Gulf Drainages (a) was likely limited through the Lower Bravo, at least before such dates.

On the other hand, the Conchos River drained into the Bravo River allowing the range extension of the MRCA of the complex; a posterior vicariant event indicate the presence of the *M.* cf. *austrinum* from Conchos, explained by the isolation of Conchos valley by the periodic accumulation of sediments that isolated the basin producing an endorheic system named Bolson (King & Adkins, 1946; Hawley, 1969; Fig. 5 A). Thus, the formation of the Mapimi Bolson or a precursor, as indicated by the basin deposits of the valley (King & Adkins, 1946), seems to be responsible for the isolation of the MRCA of *M.* cf. *austrinum* from Conchos during the Late Miocene. This is consistent with the divergence level found in other groups of fishes, as the case of the cyprinid genus *Campostoma* (Domínguez-Domínguez *et al.*, 2011) and the cyprinodontid genus *Cyprinodon* (Echelle *et al.*, 2005).

From the Gulf slope to Pacific slope drainages and central Mexico

Relationships between some fish fauna from the Bravo River and the Nazas, Aguanaval, and Tunal (tributary of the Upper Mezquital) rivers, have been explained by hypothetical connections between the Bravo River and a paleolake that likely formed part of the Mapimi Bolson (Smith & Miller, 1986), which comprises the area of the current Mayran and Viesca temporal lakes (Fig. 5 A). These connections concur with at least two possible outlets of the Bravo River: a first outlet adjacent to the headwaters of the San Juan River, and a second outlet through the Cuatro Ciénegas basin (Fig. 5 A). Although previous studies questioned these connections for some species (Schönhuth *et al.*, 2011), their closure dates (Pliocene-Pleistocene; Arellano, 1951) are concordant with the fragmentation of the Bravo River (B/E) suggested by the DEC analysis (Fig. 4).

Once the MRCA of GSD and PSD was fragmented, populations were isolated in the paleolake and later expanded their distribution, reaching the Nazas and Aguanaval rivers (Fig. 5 A). Subsequently, these two rivers experienced a stream capture by the Mezquital River drainage (Smith & Miller, 1986). Thus, the MRCA arrived to the pacific drainage rivers of the Sierra Madre Occidental (SMOc) (Fig. 5 A). Currently, there are no records of *Moxostoma* for this intermediate area that is represented mainly by the Nazas and Aguanaval system (Fig. 5 A), probably due to the extinction of lineages. This is consistent with the phylogenetic uncertainty in the relationships between GSD and PSD species. With respect to the scenario HI under M2 (Appendix 2), there is no current hydrographic evidence of a connection between the Soto la Marina River and the paleolake.

Evolution of the southern group on the Pacific slope drainages

Once the MRCA of PS clade was established in the region of the Upper Mezquital, at the Tunal River by range expansion, a vicariant event took placed causing the isolation of *M. milleri* on Upper Mezquital (Fig 5 B). Then, a tributary capture by the headwaters of the Santiago River likely produced a range extension of the MRCA of *M.* cf. *austrinum* from Santiago and *M. austrinum* through Santiago and Lerma rivers (Fig. 4; 5 B). This fragmentation is concordant with the last faulting record in the Durango region, as a part of the meridional extension of the Mexican Basin and Range Province during the Pliocene-Quaternary (Aranda-Gómez, Henry & Luhr, 2000).

The formation of the ancient Chapala lake is dated since Late Miocene (11-8 Ma), and is associated to the tectonic activity of triple-rift system in western Mexico (Fig. 5 B), which together with the pliocenic climatic fluctuations reduced the lacustrine habitat (Israde-Alcántara, 1999). The drainage interconnectedness between the main channels of Santiago (F) and Lerma (G) rivers was created by an outlet of the Chapala Lake to the Pacific Ocean through the Santiago River; however, rather than connection, the canyon of the Santiago River (Miller & Smith, 1986) with a depth of 700 m at the first part (Oblatos canyon), represent a biogeographical barrier for the exchange of fish fauna (Fig. 5 B; Miller *et al.*, 2005). Thus, the only possible via through the MRCA of *M. austrinum* colonised central Mexico must have been the Ameca river. This basin is bordered on the north by the Santiago River (Fig. 5 B). Both two river basins are divided by a northwestern trending range, consisting in voluminous volcanic deposits resulted of the tectonic activity of the Tepic-Zacoalco Rift (Frey *et al.*, 2007; Fig. 5 B). The last activity period of the Rift was recorded in the early Pliocene (5.5-3.5 My), with only minor extensional deformation in the Quaternary (Rosas-Elguera & Ferrari, 2000). Because to the proximity between the two basins, is likely a connection between the two rivers occurred in the past, before or during of the last activity period. This is a plausible scenario through the range extension of the MRCA of *M. austrinum* occurred into the Ameca river, with a posterior vicariance event as indicated the DEC analysis (Fig. 4). Once *M. austrinum* reached the Ameca River, it expanded to Chapala Lake by the paleo-channels that connected both basins (Smith *et al.*, 1975) during the Pleistocene, through the region of the Zacoalco-Ameca paleolake (Fig. 4); this was also observed in other fishes like *Zoogoneticus quitzeoensis/purepechus* (Domínguez-Domínguez *et al.*, 2008a; Domínguez-Domínguez, Pérez-Rodríguez & Doadrio, 2008b).

Colonisation of central Mexico by the redhorse suckers of the southern group was confirmed as an independent route. Unlike other Nearctic groups of fishes, as cyprinids and goodeids that colonised central Mexico during Late Miocene (Pérez-Rodríguez *et al.*, 2015), the redhorse suckers arrived to this region later (during the Pleistocene), as the fossil evidence shows, using the same geographic area than miocenic events, the central Plateau, more specifically the region of the Bolsons.

RANGE EXTENSION AND ABILITY TO DISPERSAL

In accordance with Smith (1992), the species of suckers with large-body sizes and a primitive morphology that occur in large water bodies, are regarded as strong swimmers that generally exhibit a large home range and spawning migrations, reflecting a high dispersal ability; likewise, small-bodied catostomid species, morphologically advanced, are less powerful swimmers, and are apparently unable to swim long distances; therefore, gene flow is potentially much more extensive within large-bodied species with large ranges. Members of the southern group (previously considered as the genus *Scartomyzon*) are regarded as the smallest and most specialized within Catostomidae (Smith, 1992). Based on Smith's explanation, besides of watersheds, major streams represent a dispersal barrier for the smaller suckers as the southern group.

However, the occurrence of several members of the southern group on the mainstems of the rivers and their major tributaries (*i.e. M. austrinum*, *M.* cf. *austrinum* Santiago, *M. milleri*, *M.* cf. *austrinum* Conchos and *M. albidum*; Miller *et al.*, 2005; Clements *et al.*, 2012) contradicts Smith's explanation. Moreover, several of the aforementioned species show a high habitat breadth, occurring from small streams and pools at different depths, to large streams with strong rapid currents (Miller *et al.*, 2005), which suggest that such species may be regarded as strong swimmers. Indeed, for the family Catostomidae, the habitat breadth is positively associated with geographical range size, whereas, the relationship between body size and habitat breadth lack such association (Pyron, 1999). With respect to the average size of the North American freshwater fishes (Rosenfield, 2002), the southern group exhibits a medium body size (109 mm to 235 mm standard length; Robins & Raney, 1957; Miller *et al.*, 2005).

Based on above, the wide geographical range size in the southern group, ranging from the Gulf of Mexico drainages in northeastern Mexico, to the western pacific slope drainages, and central Mexico, is associated with the positive relation between habitat breadth and geographical range size, which is promoted by a strong swimming capability, reflected in a high dispersal ability. This is consistent with DEC analysis that showed dispersal events. This could be reflected in the distribution of some species like *M. albidum* and *M. austrinum*, that occur currently in several independent river basin.

The results of the biogeographic analyses obtained herein, provided empirical evidence to achieve a better understanding of the evolutionary and biogeographical history of the fauna inhabiting a transitional area, as central Mexico, where the boundary between the Nearctic and Neotropical biogeographical regions is established. Findings we presented here contribute to our understanding of the colonisation routes of nearctic fish groups to central Mexico, corroborating that the diversity pattern of the nearctic fish component in the region is resulted of the several independent colonisation events. In particular, for the case of the southern group of *Moxostoma*, the range extension resulted determinant in the colonisation of these fishes into central Mexico, and is related with the high dispersal ability showed by this group. More studies are required on other freshwater taxa to uncover the complex evolutionary patterns of this intricate geographic region.

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TABLES

Table 1. Substitution models and parameters for cyt *b* and GHI3.

	cytb				GHI3	Concatenated
	Unpartitioned	1st position	2nd position	3rd position		
Number of taxa sample	75	75	75	75	79	74
Length	1119	373	373	373	1513	2632
Variable characters	441	11	355	74	76	517
Parsimony-informative characters	410	7	347	56	39	449
Best-fitting model (AIC)	TIM2+I+G	HKY+G	TIM2+I+G	K80+I+G	TIM2+I+G	GTR+G
Best-fitting model (BIC)	TrN+I+G	HKY+G	TIM2+I+G	K80+I+G	HKY+G	TrN+G

Tabla 2. Genetic divergences among the members of the southern group. Likelihood mean genetic distances ± standard error based on cytb (above) and GHI3 (below).

	austrinum	Santiago	*milleri*	*albidum*	Soto	Conchos
M. austrinum		0.025 ± 0.005	0.047 ± 0.009	0.054 ± 0.009	0.063 ± 0.011	0.092 ± 0.014
M. cf. *austrinum* Santiago	0.001 ± 0.000		0.047 ± 0.009	0.061 ± 0.010	0.067 ± 0.011	0.098 ± 0.015
M. milleri	0.000 ± 0.000	0.001 ± 0.000		0.05 ± 0.009	0.065 ± 0.012	0.082 ± 0.013
M. albidum	0.005 ± 0.002	0.005 ± 0.002	0.005 ± 0.002		0.062 ± 0.010	0.080 ± 0.012
M. cf. *albidum* Soto la Marina	0.005 ± 0.002	0.005 ± 0.002	0.005 ± 0.002	0.008 ± 0.003		0.103 ± 0.016
M. cf. *austrinum* Conchos	0.003 ± 0.001	0.003 ± 0.001	0.003 ± 0.001	0.007 ± 0.003	0.007 ± 0.003	

Table 3. *P* values of the approximately unbiased test (AU), Shimodaira-Hasegawa (S-H) test and bootstrap and posterior probabilities of the three topologies obtained.

Trees	-ln likelihood	obs	au	np	bp	pp	sh
1	2985.171	-4.1	0.777	0.724	0.728	0.982	0.828
2	2989.222	4.1	0.268	0.267	0.265	0.017	0.288
3	2992.512	7.3	0.021	0.007	0.006	0.001	0.106

Obs= observed log-likelihood difference to the best topology; au=approximately unbiased; np=bootstrap probability of the topology (i.e. the probability that the given topology has the largest likelihood in 10 scaled sets of 10,000 bootstrap replicates); bp= np with 10 non-scaled sets of 10,000 bootstrap replicates; pp=bayesian posterior probabilities of the model; sh= Shimodeira-Hasegawa. Statistical significant at the 5% level.

Table 4. Inferences about the ancestral area and range evolution parameters of southern group based on the two phylogenetic hypotheses, under DEC models.

Phylogenetic scenarios	Model	-ln(L)	Dispersal	Extinction
H1	M0	24.69	0.09	0.13
	M1	23.54	0.44	0.10
	M2	25.59	0.27	0.07
H2	M0	24.35	0.11	0.17
	M1	22.55	0.25	0.12
	M2	23.35	0.21	0.01

LEGENDS FOR FIGURES

Figure 1. Distribution range of the southern group and sampling localities. Symbols represent the differentiated OTU´s of the southern group. *M. congestum*, *M. albidum*, *M.* cf. *albidum* from Soto la Marina, *M.* cf. *austrinum* from Conchos, + *M. milleri*, *M.* cf. *austrinum* from Santiago, *M. austrinum*, *M. austrinum* (new record).

Figure 2. Pruned phylogenetic hypothesis of southern group based on cytb with Maximum Likelihood (ML). Above node values correspond to Bootstrapp ML support; below node values correspond to bayesian posterior probabilities. GSD= Gulf of Mexico Slope Draianges; PSD= Pacific Slope Drainages.

Figure 3. Chronograms for the southern group based on relaxed-clock Bayesian MCMC methods in BEAST. Error bars on nodes indicarte 95% highest posterior densities around the mean dates. A) shown the phylogenetic hypothesis of the southern group based on H1; B) shown the phylogenetic hypothesis of the southern group based on H2.

Figure 4. DEC analysis of southern group based on H2 under M2. Red lines indicate vicariance events; blue arrows indicate dispersal events.

Figure 5. Ancient scenarios which determined the evolution and the current biegeographic pattern of the southern group. A. Northern scenario; Mapimi Bolson, Mayran-Viesca periodic lakes, Río Bravo Fault zone, Conchos valley, Cuatrocienegas basin, San Juan sub-basin, Ancient connections, Sierra Madre Occidental, Sierra Madre Oriental, and Trans Mexican Volcanic Belt. B. Central-Western scenario; Oblatos canyon, Ancient Chapala lake (previous Late Pliocene-Early Pleistocene), Modern Chapala lake, Zacoalco-Ameca paleolake and Faulting triple-rift system. TZR= Tepic-Zacoalco Rift; ChR= Chapala rift; CR= Colima rift.

FIGURES

Figure 1

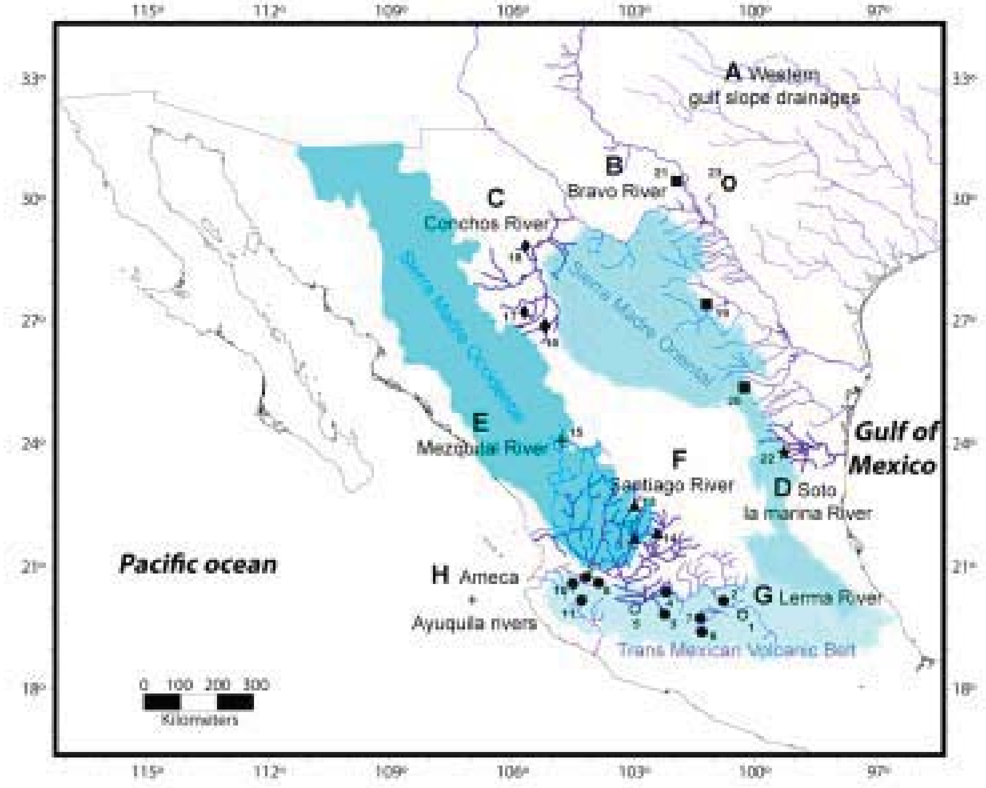


Figure 2

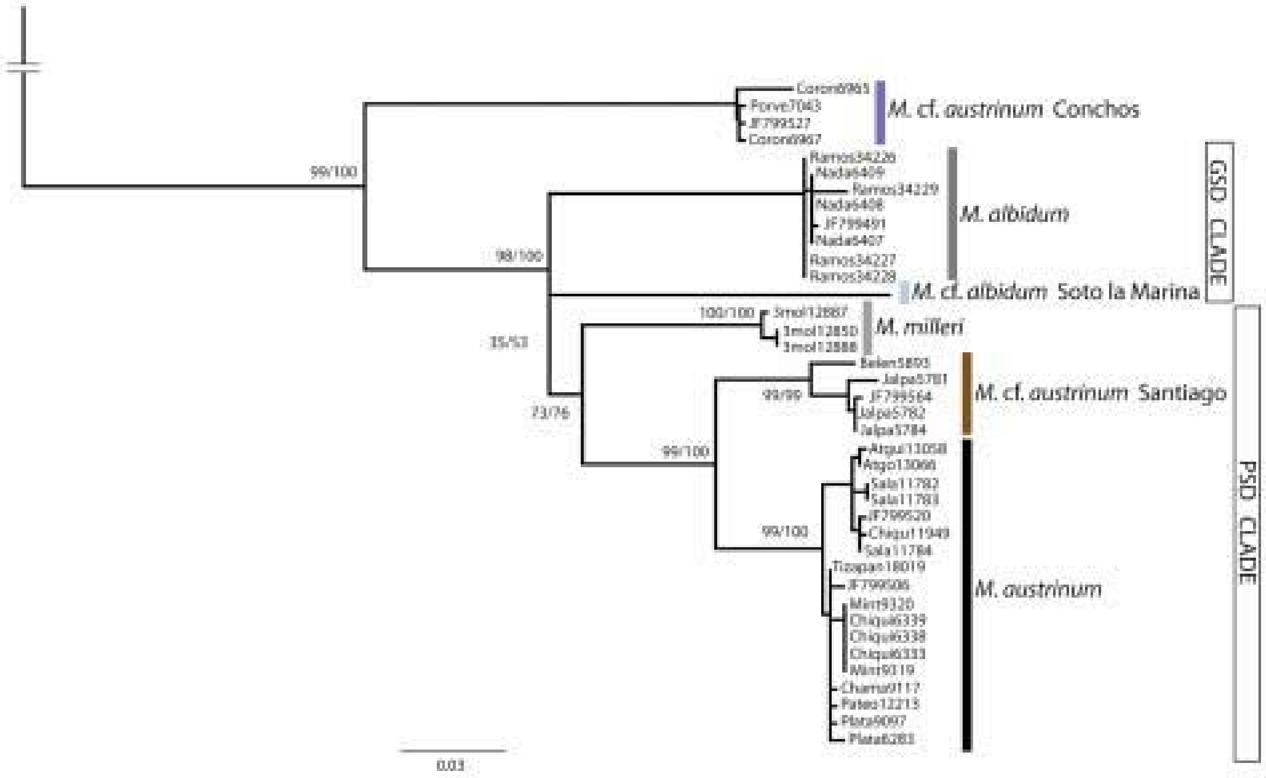

Coron6965
Forve7043
JF799527
Coron6967
M. cf. austrinum Conchos
Ramos34226
Nada6409
Ramos34229
Nada6408
JF799491
Nada6407
Ramos34227
Ramos34228
M. albidum
GSD CLADE
M. cf. albidum Soto la Marina
100/100
3mol12887
3mol12850
3mol12888
M. milleri
Belen5893
Jalpa5781
JF799564
Jalpa5782
Jalpa5784
M. cf. austrinum Santiago
Argu13058
Argo13066
Sala11782
Sala11783
JF799520
Chiqu11949
Sala11784
Tizapan18019
JF799506
Mint9320
Chiqu6339
Chiqu6338
Chiqu6333
Mint9319
Chama9117
Pateo12213
Plata9097
Plata6283
M. austrinum
PSD CLADE
99/100
98/100
35/53
73/76
99/100
99/99
99/100
0.03

Figure 3

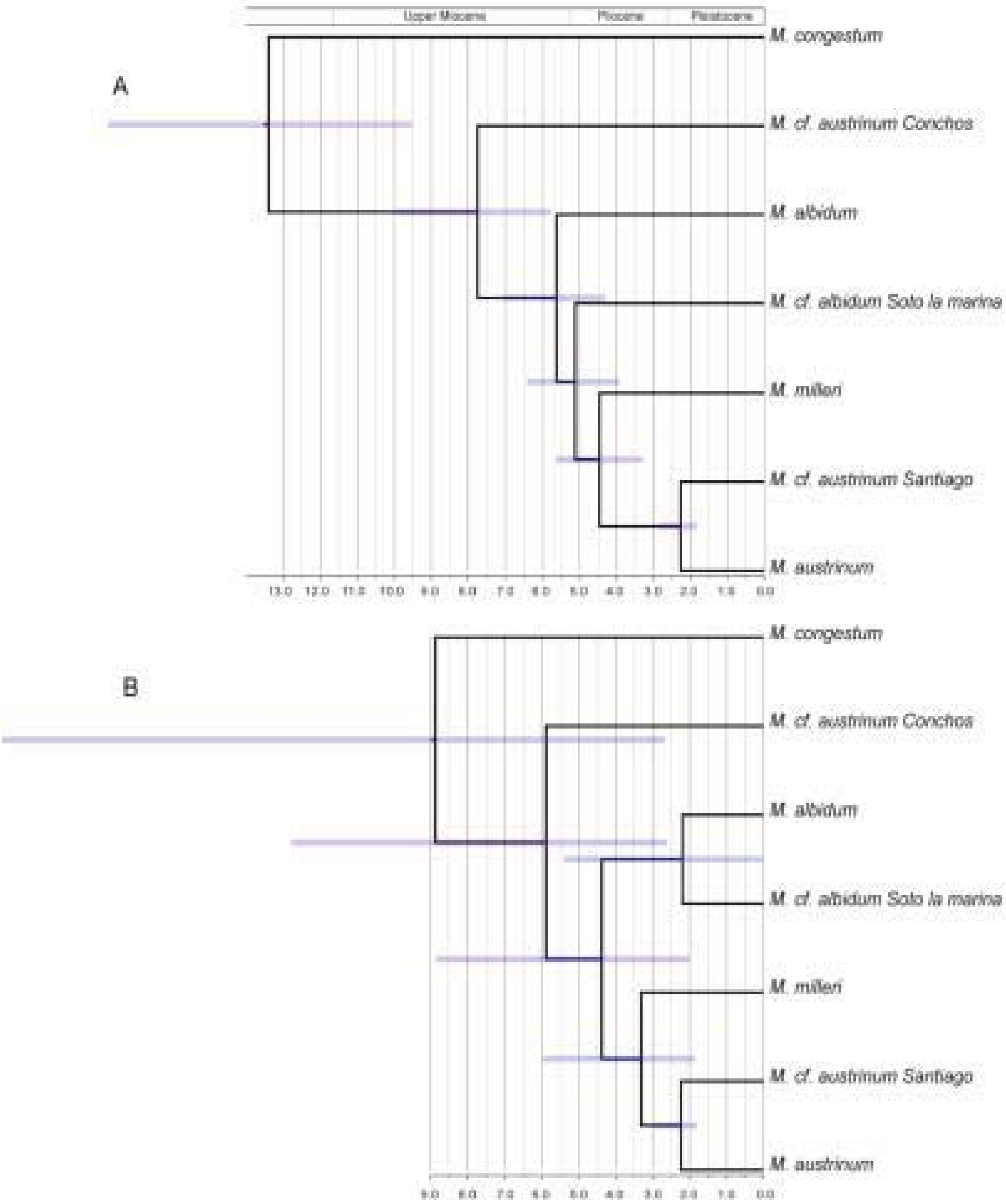

Upper Miocene
Pliocene
Pleistocene
A
M. congestum
M. cf. austrinum Conchos
M. albidum
M. cf. albidum Soto la marina
M. milleri
M. cf. austrinum Santiago
M. austrinum
13.0 12.0 11.0 10.0 9.0 8.0 7.0 6.0 5.0 4.0 3.0 2.0 1.0 0.0
B
M. congestum
M. cf. austrinum Conchos
M. albidum
M. cf. albidum Soto la marina
M. milleri
M. cf. austrinum Santiago
M. austrinum
9.0 8.0 7.0 6.0 5.0 4.0 3.0 2.0 1.0 0.0

Figure 4

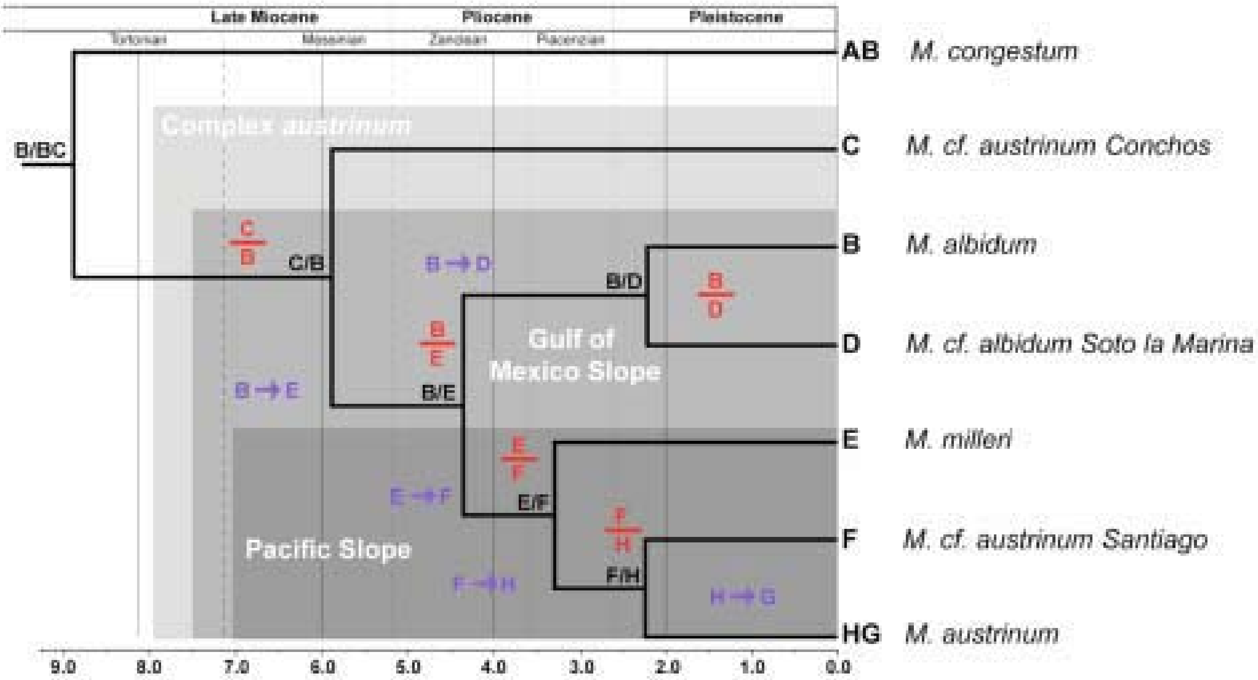
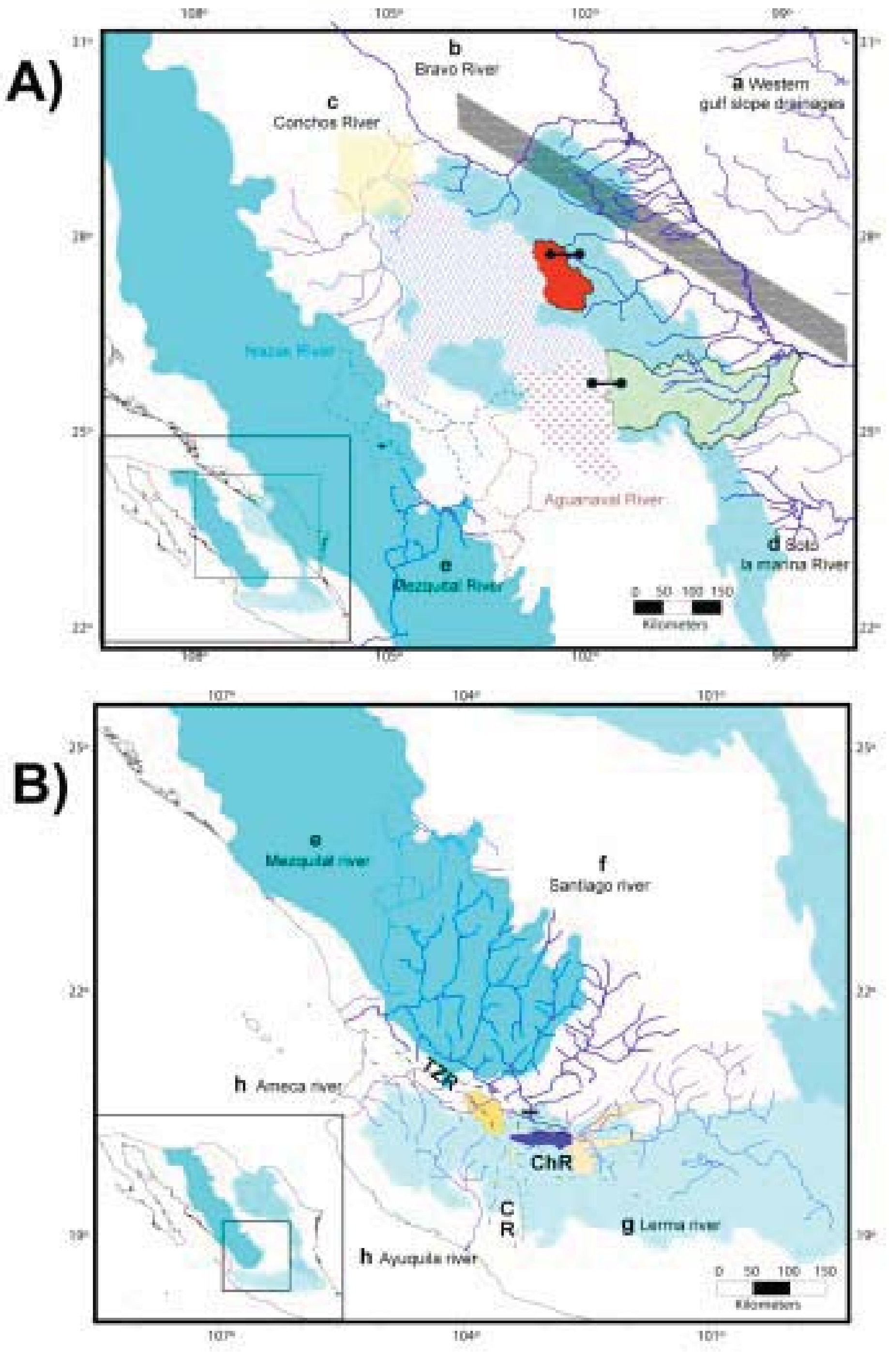

Late Miocene
Pliocene
Pleistocene
Tortonian
Messinian
Zanclean
Piacenzian
Complex *austrinum*
Gulf of Mexico Slope
Pacific Slope
B/BC
C/B
B/E
B/D
E/F
F/H
C/B
B/E
B/D
E/F
F/H
B → D
B → E
E → F
F → H
H → G
AB *M. congestum*
C *M. cf. austrinum Conchos*
B *M. albidum*
D *M. cf. albidum Soto la Marina*
E *M. milleri*
F *M. cf. austrinum Santiago*
HG *M. austrinum*
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0

Figure 5


A)
a Western gulf slope drainages
b Bravo River
c Conchos River
d Soto la marina River
e Mezquital River
f
Nazas River
Aguanaval River
0 50 100 150
Kilometers
108°
105°
102°
99°
31°
28°
25°
22°
B)
e Mezquital river
f Santiago river
g Lerma river
h Ameca river
h Ayuquila river
TZR
ChR
C R
0 50 100 150
Kilometers
107°
104°
101°
25°
22°
19°

Appendices and supporting information

Appendix S1. Geographic distribution range and the genbank accession number of analyzed sequences

	Species	Locality	river basin	*cytb*	GH1 intron 3
	Complex *austrinum*				
1.	*Moxostoma austrinum*	Lerma river, Pateo town, Mich. Mex.	Lerma upper river	KP256238	KP256271
2.		Lerma river, Chamacuaro town, Gto. Mex.	Lerma middle river	KP256239	KP256272
3.		Lerma river, El Platanal town, Mich. Mex.	Lerma lower river	KP256240	KP256273
				KP256241	KP256274
4.		Duero river at bridge crossing on road towards Etucuaro		JF799505	JF799565
5.		Tizapan river, Tizapan el Alto town, Jal., Mex.	Chapala	KP256242	--
6.		Spring "La Mintzita", Morelia, Mich. Mex.	Cuitzeo lake	KP256243	KP256276
				KP256244	KP256276
7.		Stream at Chiquimitio town, Morelia, Mich. Mex.		KP256245	KP256277

				KP256246	KP256278
				KP256247	KP256279
8.		Salado river, Tala town, Jal. Mex.	Ameca River	KP256248	KP256280
				KP256249	KP256281
				KP256250	KP256282
					KP256283*
9.		Chiquito river, Amatlan Town, Nay. Mex.		KP256251	KP256284
10.		Atenguillo river, Los Volcanes town, Jal. Mex.		KP256252	KP256285
				JF799520	JF799566
11.		Atengo river at Ayutla Town, Jal. Mex.		KP256253	KP256286
12.	*Moxostoma cf. austrinum*	Juchipila river, Jalpa town, Zac. Mex.	Santiago-Juchipila river	KP256254	KP256287
					KP256288*
				KP256255	KP256289
					KP256290*
				KP256256	KP256291
13.		Balanos System, Arroyo Chichoco along Hwy 23 N of Momax	Santiago-Bolaños river	JF799528	JF799564
14.		Verde river at Belém town. Jal. Mex.	Santiago-Verde river	KP256257	KP256292
					KP256293*
15.	*Moxostoma milleri*	Tunal river, Tres Molinos, Durango, Dur. Mex.	Santiago-Bolaños river	KP256258	KP256294
					KP256295*
				KP256259	KP256296
				KP256260	KP256297

16.	*Moxostoma cf. austrinum*	Florido river, Villa Coronado, Jimenez, Chi. Mex.	Conchos river	KP256261	KP256298
				KP256262	KP256299
17.		El Porvenir river, Balleza, Chi. Mex.		KP256263	KP256300
18.		Conchos river at Hwy 24 Bridge at Valle de Zaragoza		JF799527	JF799561
19.	*Moxostoma albidum*	Ramos river, Nvo. León, Mex.	Bravo river	KP256264	KP256301
				KP256265	KP256302
				KP256266	KP256303
				KP256267	KP256304
20.		Nadadores river Coah. Mex		KP256268	KP256305
				KP256269	KP256306
				KP256270	KP256307
21.		Devils River, Bakers Crossing Hwy 163 North of Constock Texas, USA.		JF799491	JF799563
22.	*Moxostoma cf. albidum*	Rio San Felipe SW of Ciudad Victoria in the Los Troncones Preserve, Tam., Mex.	Soto la Marina river	JF799526	JF799562
	outgroups				
23.	*Moxostoma congestum*	Pinto creek at Kinney county, Texas, USA	Bravo river	JF799509	JF799564
	Moxostoma rupiscartes			JF799522	JF799558
	Moxostoma cervinum			JF799507	JF799556
	Moxostoma duquesnii			JF799461	JF799554
	Moxostoma poecilurum			JF799481	JF799552

Moxostoma erythrurum	JF799469	JF799550
Moxostoma sp. 'sicklefin redhorse'	JF799488	JF799548
Moxostoma robustum	JF799483	JF799546
Moxostoma valenciennesi	JF799487	JF799543
Moxostoma hubbsi	JF799472	JF799544
Moxostoma breviceps	JF799453	JF799542
Moxostoma macrolepidotum	JF799475	JF799540
Moxostoma pappillosum	JF799477	JF799538
Moxostoma lachneri	JF799519	JF799559
Moxostoma ariommum	JF799501	JF799557
Moxostoma sp. 'brassy jumprock'	JF799525	JF799555
Moxostoma sp. 'Apalachicola redhorse'	JF799485	JF799553
Moxostoma sp. 'Carolina redhorse'	JF799486	JF799549
Moxostoma carinatum	JF799455	JF799547

Moxostoma anisurum	JF799451	JF799537
Thoburnia rhothoeca	JF799532	JF799568
Thoburnia atripinnis	JF799530	JF799569
Thoburnia hamiltoni	JF799531	JF799567
Hypentelium roanokense	JF799442	JF799570
Hypentelium nigricans	JF799441	JF799571
Hypentelium etowanum	JF799440	GU937836
Catostomus conchos	JF799438	JF799534
Catostomus commersonii	JF799435	JF799535
Chasmistes brevirostris	AY219857	GU937825
Deltistes luxatus	AF454870	GU937828
Minytrema melanops	JF799447	JF799536
Cycleptus elongatus	F799439	FJ265028
Ictiobus bubalus	JF799443	JF799533

Ictiobus cyprinellus	JF799444	GU937840
Carpiodes cyprinus	JF799432	GU937849
Myxocyprinus asiaticus	AF036176	FJ265052

*Heterozygous indel individuals

Appendix S2. DEC analysis constraints.

	Gulf slope NA	Bravo	Conchos	Soto la Marina	Mezquital	Santiago	Lerma	Ameca/Armeria
Gulf slope NA	--	1.0	0.001	0.001	0.001	0.001	0.001	0.001
Bravo	1.0	--	0.001	1.0	0.5	0.001	0.001	0.001
Conchos	0.001	0.001	--	0.001	0.001	0.001	0.001	0.001
Soto la Marina	0.001	1.0	0.001	--	0.001	0.001	0.001	0.001
Mezquital	0.001	0.5	0.001	0.001	--	1.0	0.001	0.001
Santiago	0.001	0.001	0.001	0.001	1.0	--	0.001	1.0
Lerma	0.001	0.001	0.001	0.001	0.001	0.001	--	1.0
Ameca/Armeria	0.001	0.001	0.001	0.001	0.001	1.0	1.0	--

1.0 High dispersal; 0.5 moderate dispersal; 0.001 null dispersal.

Dispersal valuse and their theoretical supportment

	Dispersal	Criteria	Authors
1.0	Connection Gulf slope NA and Bravo river	Adjacent basin, which share several fish fauna species, including sister group of *austrinum* complex[1]; interchange of fish fauna between Pecos river (Bravo river tributary) by headwaters from Gulf slope streams[2].	[1]Clements et al. (2012) [2]Smith & Miller (1986)
1.0	Bravo and Soto la Marina	Almost adjacent basins; interchange of fish fauna by SanFernando river, a intermediate drainage	
0.001	Bravo and Conchos	Currently connected basin; the cyclic behaivor as endorheic-open drainage of Conchos valley, caused isolation-connection events	King and Adkins (1946)
0.5	Bravo and Mezquital	Disjunt basins; interchange of fish fauna by Nazas river or paleoBolson of Mapimi	Smith & Miller (1986)
0.001	Soto la Marina and Mezquital	Disjunt basins; interchange of fish fauna by Nazas river or paleoBolson of Mapimi	Smith & Miller (1986)
0.001	Santiago and Lerma	Canyon of Santiago river represented a dispersal barrier	Miller *et al.*, 2005

Figure S1. Phylogenetic hypothesis of "southern group" based on Growth Hormone with Maximum Likelihood. Above node values correspond to Bootstrapp ML support; below node values correspond to bayesian posterior probabilities.

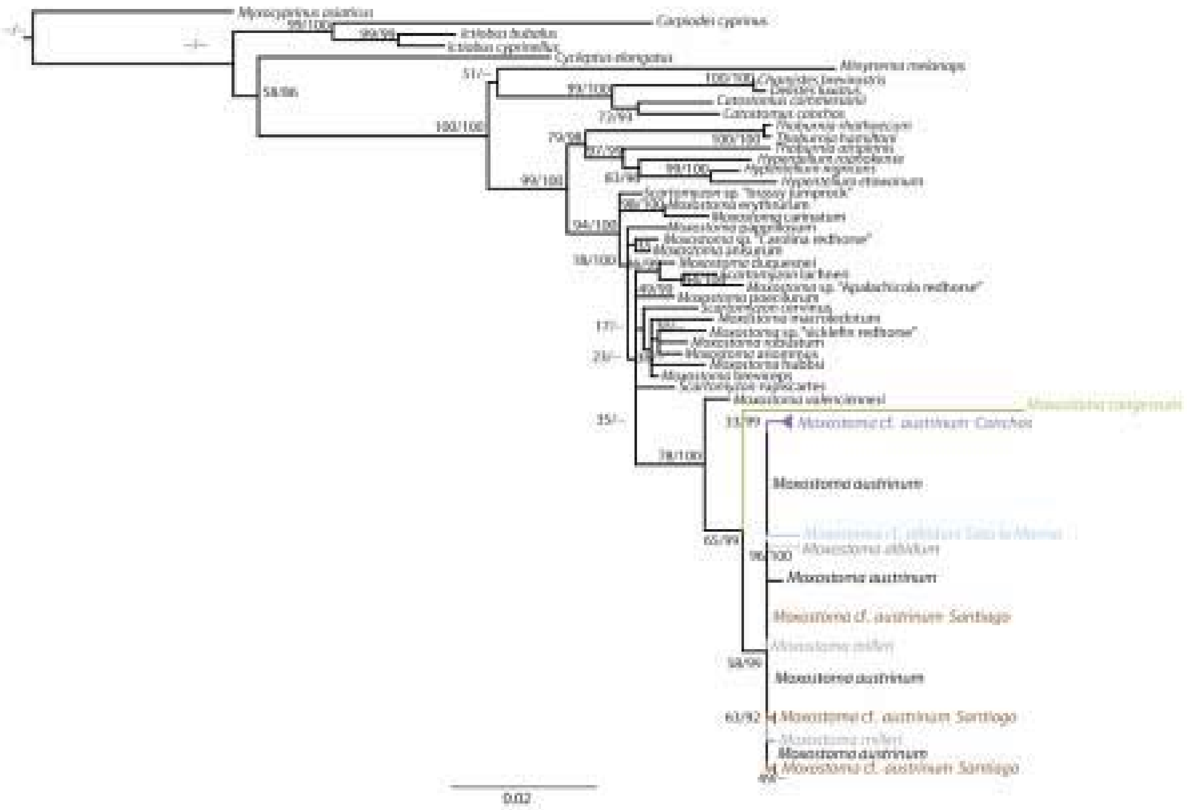


Figure 52. Phylogenetic hypothesis of "southern group" based on concatenated matrix with Maximum Lilelihood (ML). Above node values correspond to Bootstrapp ML support; below node values correspond to bayesian posterior probabilities.

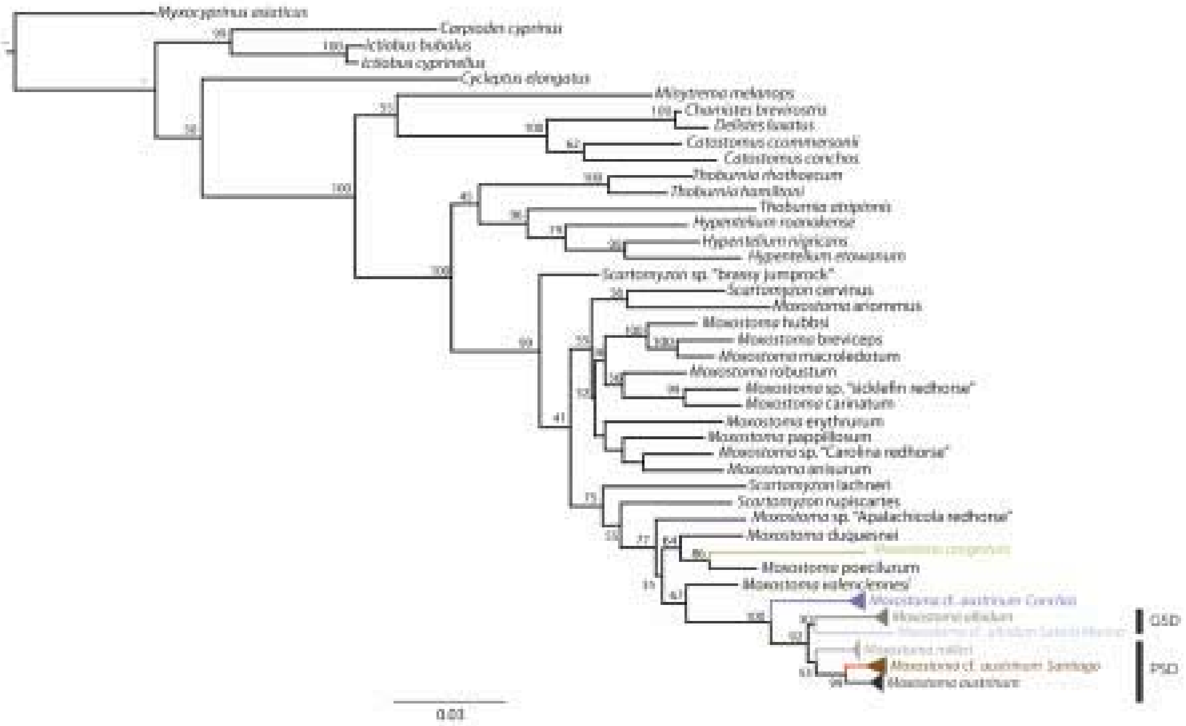
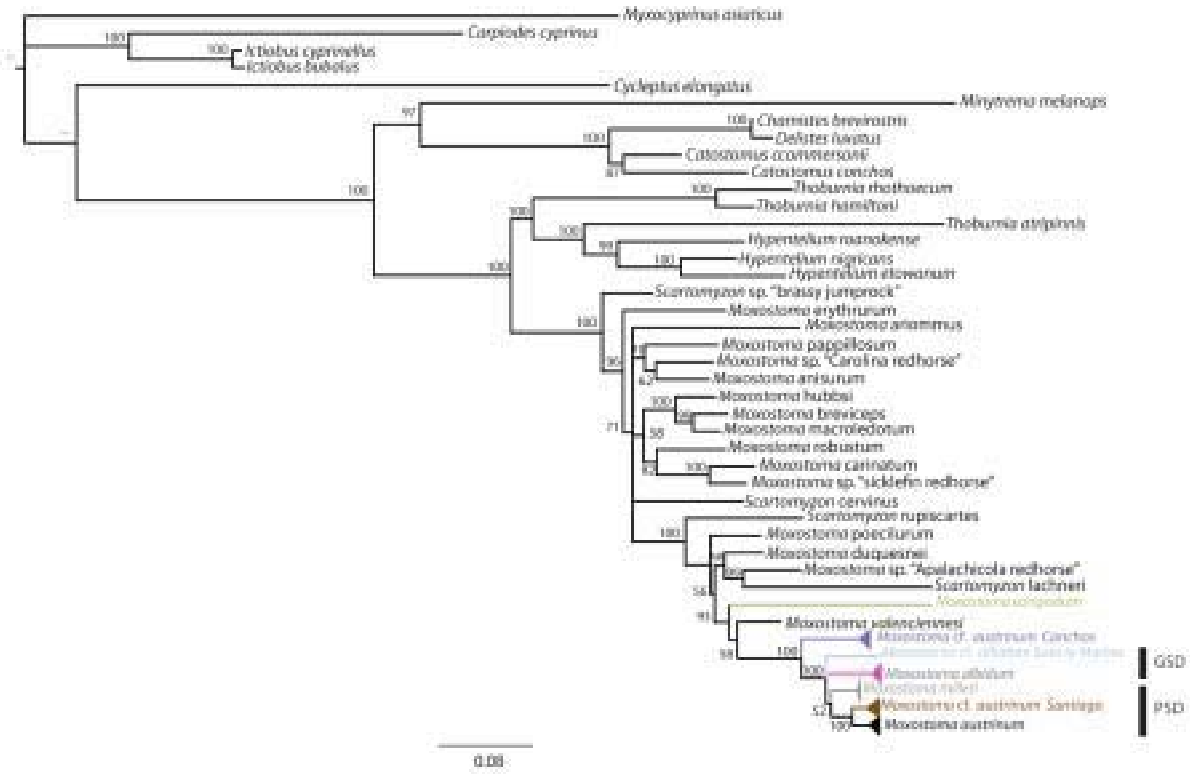


Figure S3. Phylogenetic hypothesis of "southern group" based on Growth Hormone with bayesian inference. Above node values correspond to Bootstrapp ML support; below node values correspond to bayesian posterior probabilities.



CAPITULO III

FILOGEOGRAFIA COMPARADA DE CUATRO ESPECIES DEL CENTRO DE MÉXICO: *Algansea tincella*, *Notropis calientis*, *Yuriria alta* Y *Moxostoma austrinum*

ARTICULO III

Comparative phylogeography of four species of codistributed freshwater fishes in river basins of central Mexico

Artículo en formato para enviar a la revista **“Freshwater Biology”**

Comparative phylogeography of four species of codistributed freshwater fishes in river basins of central Mexico.

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Comparative pylogeography of freshwater fishes

Keywords: comparative phylogeography, freshwater fishes, nearctic, central Mexico, cytochrome *b*.

SUMMARY

1. Central Mexico is a region with an intense geological activity that has greatly influenced the diversification of freshwater fishes. Species codistributed across wide geographical ranges may reflect a common evolutionary history as a result of the presence of the same geobiotic processes.

2. We compared the phylogeographic patterns of four representative species in the region, *Algansea tincella*, *Notropis calientis*, *Yuriria alta* (Actinopterygii: Cyprinidae) and *Moxostoma austrinum* (Actinopterygii: Catostomidae). These species, all with Nearctic affinity are codistributed along most of their distribution range.

3. The most recent common ancestor (MRCA) of each of the fish groups, from which these species emerged, apparently colonised central Mexico in different period; in addition, the four species exhibit distintc natural histories, *i.e.* different biological and ecological traits, as well as different abilities to fit to environmentally changing conditions.

4. Based on a comparative phylogeographic approach, the main aim of this study is to test the hypothesis that the codistribution of these four species of freshwater fishes in central Mexico, is the result of a common evolutionary history.

5. We conducted phylogeographic, demographic and molecular clock analyses, of the four species in central Mexico. The patterns for each species were obtained separately through sequences of the cytochrome b mitochondrial gene, followed by a comparative analysis.

6. Our results revealed a lack of congruence in the phylogeographic patterns of the four species, even though they occurr across the Lerma River drainage (mainstem basin). This is probably the result of spatio-temporal differences related with the original source of the ancestor for each species, producing independent colonisation and isolation events in central Mexico. Also, differential dispersal abilities related with some biological and ecological traits of each species, in conjunction with geological and climatic changes in the area, seem to have influenced their evolutionary, biogeographical and demographic history.

Introduction

The region of central Mexico has been recognized as one of the most important biogeographic provinces in North America for freshwater fishes, mainly due to diversity, species composition and level of endemicity (Burr & Mayden, 1992). The fish fauna of the region comprises about 78 species (Minckley & Norris, 2005), with 63% of endemism (Burr & Mayden, 1992). This region is a particular one because several Nearctic freshwater fish groups have colonised the area at different times, following at least two dispersal routes into central Mexico, where the boundary between the Nearctic and Neotropical biogeographical regions is established (Miller & Smith, 1986; Pérez-Rodríguez *et al.*, 2015). In addition, central Mexico was constantly a changing environment (Israde-Alcántara *et al.*, 2010) leading to a dynamic exchange of fish fauna throughout time, and causing the diversification through vicariance and dispersal speciation events. This dynamic exchange is supported by the presence of Neotropical freshwater fish elements in central Mexico (Miller & Smith, 1986; Mateos, Sanjur & Vrijenhoek, 2002), as well as the adaptative radiation of some fish groups associated to the period of higher tectonic activity in the Trans Mexican Volcanic Belt (TMVB) (Barbour, 1973; Ritchie *et al.*, 2005; Pérez-Rodríguez *et al.*, 2015), and the extinction of ancient components as indicated in the fossil record (Smith, 1981).

Colonisation of new habitats by freshwater fishes is limited by the extent and continuity of their aquatic habitat, and their biotic and abiotic tolerances within that habitat (Rosenfield, 2002). The distribution patterns of the fish fauna across central Mexico include a wide array of possibilities, from microendemic species to native widespread species (Miller & Smith, 1986). In the latter case, some of the species are co-distributed throughout their geographical range, indicating a possible common history resulting from extrinsic forces, such as geological or changing environmental conditions. However, these species show different morphological and ecological traits ranging from small and viviparous species with limited dispersal capabilities, to large and oviparous species with high dispersal abilities (Pérez-Rodríguez *et al.*, 2015). Thus, the different response of fish species to historical events may obscure the pattern of common evolutionary history (Zink, 1996).

Four typically Nearctic freshwater fishes occur in river basins of central Mexico, the cyprinids *Notropis calientis* Jordan & Snyder 1899, *Algansea tincella* Valenciennes 1844, and *Yuriria alta* Jordan 1880, and the catostomid *Moxostoma austrinum* Bean 1880. These species are co-distributed across much of their distribution ranges. The cyprinid fish *Notropis calientis* is a relatively small species that inhabits calm and shallow waters; *A. tincella* possesses a medium size and occurs in small streams and lakes. The species *Y. alta* is a medium size species that occupies several different habitats, including rivers with strong currents. Finally, *M. austrinum* is also a medium species that shows a wide habitat range, although it prefers mainly rivers with strong currents (Miller, Minckley & Norris, 2005).

Our study examines the role that extrinsic and intrinsic factors may have played in the evolutionary history of four co-distributed endemic species of freshwater fishes ocurring in river basins of central Mexico. Comparative phylogeography seeks to find concordant splits within contemporaneous, co-distributed species (Zink, 1996). Both historical biogeography and comparative phylogeography reveal the historical stability of communities (assemblages of clades, groups of species) at different temporal scales (Zink 2002). Thus the aim of this study is to conduct a comparative phylogeographic analysis using sequences of the mitochondrial cytochrome *b* gene (CytB) of fouyr co-distributed species of freshwater fishes in central Mexico, to determine whether or not the co-distribution pattern is associated with a common evolutionary history, in response to the historic changes in the aquatic habitats at the region.

Methods

Sampling

Tissues samples were obtained from specimens across much of the distribution range of each species, *A. tincella*, *N. calientis*, *Y. alta* and *M. austrinum*, in central Mexico. Except for *N. calientis*, the most of hydrographic basins with records of the four species were sampled (Fig. 1). Fishes were caught by electro-fishing and hand-nets. A piece of the caudal fin was cut and stored in micro-tubes with ethanol 96%. A few fishes were fixed in 8% formalin, later preserved in 70% ethanol for identification and deposited at the ichthyologic collection of the Universidad Michoacana de San Nicolas de Hidalgo (CPUM). Sequences obtained were deposited in the GenBank (Accession numbers).

Study area and geographical unit areas

Central Mexico possesses complex physiographic and hydrologic systems promoted by the intense geologic activity and climatic changes since Miocene (Domínguez-Domínguez *et al.*, 2010). The region include a group of several comparmentlised river basins, consisting in a main river basin, the Lerma-Chapala system with several independent basins around this (Barbour, 1973) (Fig. 1).

Geographical units were established as discrete regions, based on their biotic composition and watershed hydrography (following Domínguez-Domínguez *et al.* 2010). Figure 1 shows the areas corresponding to the hydrographic basins encompassed within the distribution range for each species in central Mexico. From the figure is evident that the four species are co-distributed across much of their distribution range (see Miller, Minckley & Norris, 2005; Domínguez-Domínguez *et al.*, 2009; Pérez-Rodríguez *et al.*, 2009a; Clements, Bart & Hurley, 2012).

DNA sequences

DNA extraction, purification and sequencing of the CytB were achieved following the protocols described in detail in Pérez-Rodríguez *et al.* (2009b). The entire coding region of the mitochondrial gene (~1140 bp) was obtained using primers GLUDG (5´-TGA CTT GAA RAA CCA YCG TTG-3´; Palumbi, 1996) and H16460 (5´-CGA YCT TCG GAT TAC AAG ACC G-3´; Perdices & Doadrio, 2001). DNA chromatograms were checked and aligned using Bioedit 7.1.3 (Hall, 1999). Due to the lack of indels in CytB, alignment was carried out manually. In order to avoid uncertainty, missing data regions were removed from sequences, resulting in partial CytB sequences (see Table 1). In addition, several sequences of each species were retrieved from GenBank (Table S1). The substitution models were obtained by jModelTest 0.1.1 (Posada, 2008), considering both, the Akaike information criterion (AICc) (Table 1).

Phylogeographic analyses

Data were tested for neutrality using Tajima´s *D* test, assessing their significance with DnaSP v5.0 (Librado & Rozas, 2009) to produce a null distribution for *D* from 10,000 coalescent simulations. Nucleotide and haplotype diversity parameters were estimated using DnaSP v5.0 both at the species and populational level. Uncorrected-*p* distances between and within populations were also estimated in MEGA v.5.05 (Tamura *et al.*, 2011).

Haplotype networks for the four species were constructed using the median-joining algorithm (Bandelt *et al.*, 1999) implemented in Network 4.6.1.3 (http:/www.fluxus-engineering.com). In order to determine the amount of genetic variability partitioned within and among populations, an analysis of molecular variation (AMOVA) was performed with Arlequin V. 3.5.1.3 (Excoffier & Lischer, 2010); first, overall differences of the whole data sets (one gene pool) were examined; then, several grouping scenarios of the partitioning genetic variation among areas were included and the discrete lineages were also examined. For statistical significance, 10,000 permutations were run.

Divergence times

Divergence times based on the coalescent method were estimated using BEAST package (Drummond & Rambaut, 2007) for the four species separately. Based on the substitution model inferred (Table 1), genealogies were reconstructed with an uncorrelated lognormal tree prior, with a CytB substitution rate ranging from 0.76 - 2.2% per million years in teleost fishes (Berendzen, Gamble & Simons, 2008), using uniform distribution. For each analysis, four runs were conducted for 20,000,000 generations sampling every 1000 generations and in each run, 10% of the initial samples were discarded as burn-in. Analyses were ran at the CIPRES Science Gateway V.3.3 portal (Miller, Pfeiffer & Schwartz, 2010). In order to verify a suitable effective sample size (ESS>200) for convergence and stationary was used Tracer v.1.4.1. (Rambaut & Drummond, 2007). The three MCMC runs were combined and summarised using the modules of BEAST package, Logcombiner and TreeAnnotator.

Historical demography

In order to detect signatures of demographic changes, or selection in the recent history in the four species, Fu's F_S (Fu, 1997) and R_2 (Ramos-Onsins & Rozas, 2002), were tested using 10000 pseudo-replications in DnaSP v5.0. Such tests have high power for revealing demographic growth (Ramos-Onsins & Rozas, 2002). Large negative values of F_S and small positive values of R_2 are indicative of population growth.

In addition, the genealogical coalescent method of Bayesian skyline plots (BSP; Drummond *et al.*, 2005), based on an uncorrelated lognormal relaxed clock, was performed for the whole datasets in each species; appropriate substitution model was selected for each lineage (Table 1); ten piecewise-linear intervals (*m*), and the rate for CytB in teleost ranging 0.76-2.2% (Berendzen, Gamble & Simons, 2008) in a uniform prior were applied. Analyses were conducted with MCMC runs for 40,000,000 generations with a burn-in of 10% generations. Analyses were run at the CIPRES Science Gateway. Convergence was assessed with estimates of effective sample size (ESS) in Tracer following the criterion ESS>200, and finally a BSP for each data set were created.

Results

Sampling

One hundred-thirty seven, 96, 92 and 38 sequences of CytB were obtained for *A. tincella*, *M. austrinum*, *N. calientis* and *Y. alta*, respectively. In addition sequences were retrieved from GenBank (Table S1). The Tajima test for neutrality was rejected for only five populations (see Table S2), detecting positive selection in the data. Substitution models of evolution and other parameters for each *locus* are shown in Table 1.

Genetic structure

Haplotype networks revealed a partial structure for the species, *A. tincella*, *M. austrinum* and *N.calientis*. Populations recovered as discrete lineages in *A. tincella* were those corresponding to the Balsas (with 15 mutational steps), Cuitzeo (four steps), Panuco south (six steps), and Verde-Santiago basins (Fig. 2A). Within the later basin, three different groups are recorded, Verde-Santiago I (VS I, at least eigth steps), Verde-Santiago II (VS II, at least nine steps), and Verde-Santiago III (VS III), corresponding to Guadalupe Victoria, San Julian and Tecolote localities, respectively (Fig.1). VS III area shared haplotypes with the Panuco north (Panuco N) and Middle Lerma (Lerma M) areas (Fig. 2A). Verde-SI, Verde-SII, Panuco S and Cuitzeo, presenting moderate divergences between them, *Dp*=0.5-1.1%, *Dp*=0.6-1.1%, *Dp*=0.6-0.9%, *Dp*=0.5-1.1%, respectively. Five lineages of *A. tincella*, Cuitzeo, Panuco south (Panuco S), and three different groups of Verde-Santiago (VS I, VS II, VS III) exhibited a high population structure through AMOVA, confirming the differentiation between the five haplogroups (Table 2). The population from Balsas showed the highest divergence relative to the other areas (*Dp*=1.7-2.1%), reaching a similar level as the species *Algansea lacustris*, the sister taxon that recorded a divergence of *Dp*=1.7-2.3%. Based on the aforementioned evidence, the population from Balsas was removed from population and demographic analyses.

Concerning *M. austrinum*, two main haplogroups were separated by seven mutational steps. These two haplogroups correspond to the subspecies *Moxostoma austrinum austrinum* and *Moxostoma austrinum mascotae* (*sensu* Robins & Raney 1957; Jenkins, 1980). Significant genetic structure (P<0.01) was found in the four lineages of *M. austrinum*, corresponding to Lerma-Chapala, Cuitzeo, Ameca and Ayuquila basins (Table 2). Although with only two mutational steps (with low genetic divergences, *Dp*=0.2-0.3%), the populations from Cuitzeo basin conformed to a discrete lineage nested in one unique haplotype (Fig. 2b).

The three different basins sampled for *N. calientis*, corresponded to three distinct lineages with high genetic divergences between them, Middle Lerma (*Dp*=0.9-1.0%), Cuitzeo (*Dp*=0.9-1.0%) and Verde-Santiago (*Dp*=0.9-1.1%). Significant genetic structure

(P<0.01) was found in the three lineages of *N. calientis* (Table 2). According with the network obtained, Cuitzeo and Verde-Santiago derivate from Lerma (Fig. 2 C). Otherwise, *Y. alta* presented an unstructured network, with shared haplotypes between Lerma areas as continuous corridor, and remain basins (Fig. 2 D). Highligths the haplogroup from Lerma Upper, that recorded six mutational steps and present a shared haplotype with Lerma Middle. Genetic divergences among populations were *Dp*=0.0-0.9%. Finally, the populations of the cyprinid corresponding to the six areas where this species occurs exhibited significative values of genetic structure only within populations (Table 2).

The species *Algansea tincella*, *M. austrinum* and *N. calientis*, recovered common areas as discrete lineages, as it is the case of the Cuitzeo area (Fig. 2 A, B, C), and the Verde-Santiago area, where *A. tincella* and *N. calientis* recovered at least one discret lineage (Fig. 2 A, C).

Genetic diversity

In accordance with the haplotype and nucleotide diversity values, the highest genetic diversity in *Y. alta* and *A. tincella* was found in populations within the Middle and Lower Lerma (see Table S2). In the case of *M. austrinum*, the population from Ameca River basin recorded the highest genetic diversity of the species (see Table S2). Meanwhile, in *N. calientis*, diversity was moderate and similar across the three areas (see Table S2).

Historical demography

Only for some populations of the cyprinids *A. tincella* (Tigre in Middle Lerma, Zamora-Jacona in Lower Lerma, and G.Victoria in Verde SI) and *Y. alta* (Zamora-Jacona in Lower Lerma, and Tizapan in Chapala), the null hypothesis was rejected in at least one tests, Fu´s *F* s or R_2, indicating population growth (see Table S2). Populations from the remaining two species failed to reject the null hypothesis of a constant population size (see Table S2).

On the other hand, for the species *A. tincella*, *M. austrinum* and *Y. alta*, the coalescent demographic estimates of BSPs with an effective sample size (ESS) for each parameter greater than 200, showed a decrease in the mean effective population size, followed by a sudden increase during the most recent time interval, following a period of slight increase (Fig. 3A, B, D). *Notropis calientis* exhibited a stable population size in the past, with a similar sudden increase near to present (Fig. 3C).

Divergence times

The species with the earliest MRCA in the Lerma basin was the cyprinid *N. calientis* at the Early Pleistocene, followed by *A. tincella*, the catostomid *M. austrinum* and *Y. alta* at the Late Pleistocene (Table 3). The wide confidence intervals of *N. calientis* overlapped with the confidence intervals of the other three species (Table 3). Dates inferred for the MRCA of the Cuitzeo lineage were different for the species, *N. calientis*, *A. tincella* and *M. austrinum*. Also the MRCA of the Verde–Santiago lineages were different in the cyprinids *N. calientis* and *A. tincella* (Table 3).

Discussion

Phylogeographic patterns

Despite of the three taxa, *A. tincella*, *M. austrinum* and *N. calientis* presented well-delimited lineages in a common area (*i.e.* Cuitzeo, and *A. tincella* and *N. calientis* also presented at least one haplogroup in Verde-Santiago basin), the distinct divergence times estimated suggest lack of concordant events (Table 3). Thus, it appears that, for each case, isolation resulted from an independent process. In addition, the two haplogroups in *Y. alta* corresponding, one to the Upper Lerma, and the other corresponding to remaining river basins, discarded any sign of concordance. Rather, the phylogeographic pattern of the latter haplogroup is consistent with a model of recent population expansion as well as the lack of geographic isolation (Zink, 2002) as showed through F_s values in the Lower Lerma population (Table S2), regardless of the fact that some of them occur in independent basins, like Cuitzeo.

Cuitzeo case Ancestral connection between Middle Lerma and Cuitzeo Lake was detected throughout the exorheic Zacapu Lake, via the Angulo River, a tributary of the Lerma Middle (Moncayo-Estrada, Israde-Alcántara & Garduño-Monroy, 2001). This connection is the responsible for the affinity of the fish fauna found between the Lerma Middle and Cuitzeo, pattern also supported by other fish species (Domínguez-Domínguez *et al.*, 2007; Domínguez-Domínguez, *et al.*, 2010).

There are two ancestral connections reported between Cuitzeo and Zacapu lakes, the Villa Morelos and the Chucandiro-Huaniqueo corridors (Fig. 4). Seemingly, both connections were produced by the activity of the Pliocenic Northeast-Southwest fault system of the area (Israde-Alcántara, 1999). Then, in the first corridor, the emergence of the Ventanas volcano produced the separation of both basins at *ca*. 0.7 Ma to 0.5 Ma (Fig. 4; Israde-Alcántara 1999; Moncayo-Estrada, Israde-Alcántara & Garduño-Monroy, 2001). Later, the second connection, the Chucandiro-Huaniqueo corridor, was blocked by the faulting and volcanic activity that produced a difference in the elevation between the lakes, sinking the Cuitzeo basin at the Late Pleistocene-Early Holocene (Fig. 4; Israde-Alcántara 1999; Moncayo-Estrada, Israde-Alcántara & Garduño-Monroy, 2001).

In accordance with the divergence times inferred for the four species (Table 3), Cuitzeo lineages were likely isolated at least in two events. In the case of *N. calientis*, presented closer dates (0.323 Ma) with the rising of the Ventanas volcano (0.5 Ma), therefore the isolation of this population is associated to this event. The isolation of the populations of *A. tincella* in Cuitzeo Lake (0.118 Ma) is congruent with the fragmentation of the Chucandiro-Huaniqueo corridor occurred at Late Pleistocene-Early Holocene. Neverthess it has been found that this last fragmentation event was gradual. In fact, lacustrine transgressions between both lakes have been reported for *ca*. 0.028 Ma to 0.024 Ma (Moncayo-Estrada, Israde-Alcántara & Garduño-Monroy, 2001). Thus, such gradual disruption may have operated as a barrier for *A. tincella* earlier than Cuitzeo lineage of *M. austrinum* (0.043 Ma), likely due to the presence of the biological traits associated to a high dispersal ability in the latter species (Pyron, 1999; Rosenfield, 2002), *i.e.* body size relatively large (109 mm to 235 mm; Robins & Raney, 1957; Miller, Minckley & Norris,

2005) and a wide habitat breath (deep pools and riffle habitats in streams, medium and mainstem rivers, with bedrock, gravel, sand and silt substrate; Robins & Raney, 1957; Lyons & Navarro-Pérez, 1990; Miller, Minckley & Norris, 2005).

In the case of *Y. alta*, its wide distribution range in the region (one of the widest distributed; Fig. 1) could indicate either high dispersal ability, or the occurrence of favourable aquatic corridors. The presence of the biological traits associated to a high dispersal ability, *i.e.* body size relatively large (reaching 200 mm), the wide habitat (streams of clear water to muddy, with moderate to strong current, with bedrock, gravel, sand and silt substrate; Miller, Minckley & Norris, 2005), and the tolerance to the changes in environmental conditions (Mercado-Silva *et al.*, 2005; Ramírez-Herrejón *et al.*, 2012), may turn this species into a good disperser. Thus, such traits may have allowed the genetic flow between Zacapu and Cuitzeo lakes by the Chucandiro-Huaniqueo corridor, even after the fragmentation of *M. austrinum*, that instead, is regarded as a sensitive species to changing environmental conditions; this species require good water and habitat conditions, with water flow constant (Mercado-Silva *et al.*, 2005). Despite these two species are regarded as good dispersers, the tolerance of *Y. alta* to changing environmental conditions (Mercado-Silva *et al.*, 2005), specially in the fluctuating humid conditions in the Holocene (Israde-Alcántara, 1999), may explain the genetic flow in the lineage of *Y. alta*. In this case, the same haplotype shared by Cuitzeo lineages and the other populations (including the neighbour basin of Angulo river; Fig. 4), indicate that the direction flow was from Lerma area to Cuitzeo lake (Fig. 2 D).

Comparisons of phylogeographic patterns among broadly sympatric species may show whether they have responded in parallel to recent isolating events (Zink, 2002). The different responses of *A. tincella*, *M. austrinum* and *Y. alta*, to the second isolation event of Cuitzeo is a clear example of the non concordant isolating events given their dispersal and tolerance to harsh condition. This indicates that Cuitzeo lineages, for the four species, did not share a common history.

Verde-Santiago case The canyon of Santiago river and the Juanacatlán waterfall, located north to the Chapala lake (Fig.1), represents a barrier for the interchange of the fish fauna between Verde-Santiago and Lerma-Chapala system, since their connection at Plio-Pleistocene (Miller, Minckley & Norris, 2005). The most likely connection between these basins could have been the adjacent headwaters of the Laja, Santa María and Cuarenta rivers, which belong to the Middle Lerma, Panuco N and Verde-S I, respectively (Fig. 5). This area is located in the southern limit of the province of the Basin and Range (SBR), where it reaches to central Mexico at the physiographic component knowed as the Mexican Plateau (Barbour, 1973; Aranda-Gómez, Henry & Luhr, 2000). The proximity between the headwaters, and the intermontane plains, that could have operated as corridors in highly humid conditions, suggest that a river capture event is likely to ocurr (Fig. 5). In freshwater fishes, the taxa inhabit headwaters are highly susceptible to river captures, events that represent an important role in the increase of their range, providing genetic change in allopatry (Waters *et al*., 2001; Domínguez-Domínguez *et al*. 2011). This hypothetical conecction has been previously recognized as a dispersal route probably used by the ancestor of the species complex belonging to the atherinopsids silversides (Barbour, 1973).

The species *A. tincella*, *N. calientis* and *Y. alta*, have been found at headwaters, particularly the first two speccies, there are records for the adjacent headwaters of the Laja (Middle Lerma), Santa María (Panuco N) and Cuarenta rivers (Verde-Santiago) (Miller, Minckley & Norris, 2005). The catostomid *M. austrinum* has been recorded at headwaters only for the PSD areas (Miller, Minckley & Norris, 2005), where two important physiographic components, the Sierra Madre Occidental and the Trans-Mexican Volcanic Belt ocurr (Fig. 1).

The earliest isolation event in Verde-Santiago was experienced by the lineage of *N. calientis* dated *ca.* 0.406 Ma, and could be associated with a change of the climatic conditions, from more humid to more mesic ones during the Pleistocene (Israde-Alcántara *et al.*, 2010). Posteriorly, holocenic climatic fluctuations (Israde-Alcántara, 1999) may have promoted a recurring fragmentation-connection process between headwaters again. Likely, such climatic fluctuations influenced the low or null genetic flow of *A. tincella* within Verde-Santiago, causing the isolation of the two lineages detected in the basin, Verde-S I and Verde-S II. By the other hand, the Verde-SIII is located just at the headwaters adjacent to the Panuco N (Santa María River) and Middle Lerma (Laja River) areas (Fig. 1), sharing the same haplotype with these areas (Fig. 2A). This fact is in agreement with the idea that headwater taxa are more susceptible to river capture (Waters *et al.*, 2001), which may suggest a more recent conecction between the three basins. The lineages fragmentation and the holocenic climatic changes may be associated with the fluctuation in the population size during the most recent time interval recorded at *A. tincella* (Fig. 3A).

Otherwise, the high dispersal ability of the *Y. alta*, allowed genetic flow within the Verde-Santiago, well extended in all Santigo River, including Juchipila and Bolaños rivers.

The haplotypes shared with Lower Lerma, indicate a similar pattern as the one found in the Verde-SIII lineage of *A. tincella*, thus suggesting a similar response to connection, at least between Verde-Santiago and Lerma rivers. Recent population expansion exihibited by *Y. alta* suggests that the climatic changes did not played a major role on this species. This expansion may be more related with its high dispersal ability and tolerance to enviromental changes.

Like in the Cuitzeo area, *N. calientis* experienced an isolation event ealier than *A. tincella* and *Y. alta*. The absence of *M. austrinum* is associated mainly to the ancestral area, which may have been other than Lerma River. Thus, when *M. austrinum* arrives to the Lerma-Chapala it may have become difficult to the species to ascend upstream, to the headwaters. The high sensitivity of this species to the habitat changes (Mercado-Silva *et al.*, 2005), represents a low ability to colonise the habitats with harsh conditions (small habitats with null water flow) as the headwaters from central basins. Similar to *A. tincella*, the historical demography of *M. austrinum* is probably associated to the holocenic climatic flutuations (Fig. 3B).

Colonisation from Lerma River

Lerma populations were well represented throughout the haplotype networks, particularly in the *A. tincella*, *N. calientis* y *Y. alta* (Fig. 2 A, C, D), indicating that the MRCA for these three species probably inhabited the Lerma River, which seemingly operates as a mainstem for the dispersal to other basins. Other molecular markers and additional analyses are required to test this hypothesis, but this is in agreement with the configuration of the Lerma

River basin, which developed during Miocene-Pliocene (Israde-Alcántara, *et al*., 2010). It is important to note that the Chapala and Lower Lerma areas were, since the Neogene to the Quaternary, part of a larger lacustrine zone, (Israde-Alcántara, *et al*., 2010), which likely represented a suitable habitat for ancestral populations of *A. tincella* and *Y. alta*.

Due to the lack of *N. calientis* samples from Lower Lerma (Chernoff & Miller, 1986), it is not possible to infer the ancestral population, and its posterior range extension. Nevertheless, the connection of Middle Lerma haplotypes with Cuitzeo and Verde-Santiago areas, may suggest that their respective populations probably derived from Middle Lerma. All populations corresponding to the three areas showed equivalent values of genetic diversity. According with Zink (2002), when two or more populations were separated for a considerable time, genetic diversity should be equivalent in each population. Although with caution, such pattern may result from an old isolation, in Cuitzeo and Verde-S.

Despite of the phylogeographic patterns suggesting that *A. tincella*, *N. calientis* and *Y. alta* lineages all derived from the Lerma area, the differences in divergence times and some haplogroups formed (*i.e. Y. alta*), reject the hypothesis of concordance.

Non-overlapping areas

Concerning the non-overlapping areas, the case of *M. austrinum* must be highlighted, because to the genetic pattern is higly associate with the geographic pattern, which is higly contrasting with the patterns of remaing species. Only for the distribution range of *M. austrinum*, the PSD area corresponding to the Ameca and Ayuquila basins was encompassed. As shown the network (Fig. 2 B), the geographic structure of *M. austrinum*, consisted in two well-differentiated lineages, previously considered as subspecies (*sensu* Robins & Raney 1957): *Moxostoma austrinum austrinum* corresponding to the Lerma-Chapala sytem, and *M. austrinum mascotae* corresponding to the PSD area. There is geologic evidence of the interconnectedness between the west Chapala lake and the adjacent Ameca river basin, that consists at buried channels that present a stream deposition with water moving from Chapala toward Ameca River, dated *ca.* Pliocene-Early Pleistocene; in fact, in theses paleo-channels a fossil record of *Moxostoma* sp. was found in the same area (Smith, Cavender & Miller, 1975).

Such ancestral connection represents the most likely route through MRCA of *M. austrinum* colonised the Lerma-Chapala system, that is considered the tmos plausible route to from Santiago river to Lerma-Chapala system during Pliocene-Early Pleistocene (Pérez-Rodríguez, *et al.*, in press). The divergence times obtained for the separation event of both lineages (0.617 Ma) coincide with the Quaternary extension of the Colima and Tepic-Zacoalco rifts, the main faulting system in this region; activity of both rifts promoted that floors of the northen Colima and Tepic-Zacoalco rifts were lowered by more than 150 m with respect to Chapala lake (Garduño-Monroy *et al.*, 1993), which is likely associated with disruption between Ameca River and Chapala lake.

Thus, the distinct geographic structure pattern obtained in *M. austrinum* was the result of the several colonisation routes followed by their MRCA. In fact, the arrival of *M. austrinum* into central Mexico is considered a relatively recent event in comparison to the arrival of the MRCA of the other three species, *N. calientis*, *Y. alta* and *A. tincella*; these species colonised the area *ca.* 3.7, 3.3 and 2.1 Ma, respectively (Pérez-Rodríguez *et al.*, 2015).

Implications for conservation

The present study provides a multispecies approach to the identification of Operational Conservation Units (OCUs): “a continuous area limited by geographical boundaries and inhabited by one or more populations sharing the same genetic pattern” (Doadrio, Perdices & Machordom, 1996). An integral perspective to delimit conservation units needs to incorporate other factors, *i.e.*, historical and ecological, as well as species distribution data and conservation status, as well as information related with anthropogenic activity (Dodson *et al.*, 1998; Crandall *et al.*, 2000). However, the uncovering of the discrete mitochondrial lineages in the species analysed in this study, is considered as an adequate starting point for a conservation strategy.

One of the benefits of this approach is to uncover the differentiated lineages within a common geographical region, which may have evolved independently from the rest of the populations, as well as the processes that have led to this pattern. Based on the mitochondrial lineages and following a phylogeographic criteria, we identified herein at least four OCUs : 1) Lerma, 2) Cuitzeo, 3) Verde-Santiago and 4) Panuco South. The first and fourth cases were represented by only one species, *N. calientis* and *A. tincella*, respectively.

In the Cuitzeo case, the detection of a differentiated lineage for the species, *A. tincella*, *N. calientis* and *M. austrinum*, and their underlying independent processes, including such intrinsic biological-ecological traits, as well as extrinsic historical geologic and climatic factors, are the elements that support the identification of Cuitzeo basin as an

OCU. These findings are considered a new independent source of information that has to be added to the criteria that were originally used to identify Cuitzeo basin as an OCU by Domínguez-Domínguez *et al.*, (2007), such as: high richness of native species, a critical habitat degradation and therefore a high loss of species, high genetic diversity found in fish, and the environmental impact over the genetic structure of species.

In conclusion, a comparative phylogeographic approach could be regarded as a useful tool to be used, in conjunction with other sources of information, to recognize Operational Conservation Units that may allow the conservation of freshwater fishes in highly impacted areas, such as central Mexico.

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Tables

Table 1 Substitution models and parameters for cyt *b*

	A. tincella	*M. austrinum*	*N. calientis*	*Y. alta*
Number of taxa	140	96	45	92
Length	1055	1121	1121	1121
Variable characters	56	26	47	27
Parsimony-informative characters	46	20	29	21
Best-fitting model AIC	TrN+G	TrN+G	TPM1uf+G	TrN+G

Table 2. Results of the AMOVA analyses. Intraspecific genetic structure for *A. tincella*, *M. austrinum*, *N. calientis* and *Y. alta*. F_{ST}, F_{CT}, and F_{SC} indicate the proportion of total variance among populations, among groups, and among populations within groups, respectively. * indicates significant p-values <0.05.

Species		Variance	% of variation	*F* statistics	P-value
A. tincella					
One gene pool	Among populations	2.363	79.90	*Fst*: 0.798	0.000*
	Within populations	0.594	20.10		
Regions					
five gene pools (Verde-Santiago, Pánuco, Lerma M, Lerma L and Cuitzeo)	Among groups	0.813	26.31	*Fct*: 0.263	0.012*
	Among populations within groups	1.683	54.46	*Fsc*: 0.739	0.000*
	Within populations	0.594	19.23	*Fst*: 0.807	0.000*
Lineages					
Five gene pools (V-SI, V-SII, Panuco S, Cuitzeo and Lerma M)	Among groups	2.590	57.88	*Fct*: 0.578	0.000*
	Among populations within groups	1.096	27.31	*Fsc*: 0.648	0.000*
	Within populations	0.601	14.81	*Fst*: 0.851	0.000*
M. austrinum					
One gene pool	Among populations	2.727	85.68	*Fst*: 0.856	0.000*
	Within populations	0.379	14.32		
Regions					
Five gene pools	Among groups	2.140	71.26	*Fct*: 07.12	0.000*

	Among populations within groups	0.482	16.08	*Fsc*: 0.559	0.000*
	Within populations	0.380	12.65	*Fst*: 0.873	0.000*
Lineages					
Four gene pools (Lerma, Cuitzeo, Ameca, Ayuquila)	Among groups	2.252	71.83	*Fct*: 0.718	0.000*
	Among populations within groups	0.503	16.06	*Fsc*: 0.570	0.000*
	Within populations	0.379	12.11	*Fst*: 0.878	0.000*
N. calientis					
One gene pool	Among populations	3.777	72.06	*Fst*: 0.720	0.000*
	Within populations	1.464	27.94		
Regions = Lineages					
Three gene pools	Among groups	3.470	63.03	*Fct*: 0.630	0.166
	Among populations within groups	0.570	10.36	*Fsc*: 0.280	0.159
	Within populations	1.464	26.61	*Fst*: 0.733	0.000*
Y. alta					
One gene pool	Among populations	1.330	70.01	*Fst*: 0.700	0.000*
	Within populations	0.569	29.99		
Regions					
Six gene pools	Among groups	0.461	23.25	*Fct*: 0.232	0.136
	Among populations within groups	0.953	48.03	*Fsc*: 0.625	0.000*
	Within populations	0.569	28.71	*Fst*: 0.712	0.000*

Table 3 Coalescence times for major lineages of the four species. The mean and 95% highest probability density (HPD) interval of posterior probability distribution are given in units of million of years (Ma) ago.

Species	MRCA	Mean	95% HPD
N. calientis	All lineages	2.145	0.437-5.167
	Cuitzeo	0.332	0.058-0.785
	Verde-Santiago	0.429	0.061-2.288
A. tincella	All lineages	0.902	0.354-1.658
	Cuitzeo	0.130	0.023-0.258
	Verde-Santiago I	0.103	0.016-0.203
	Verde-Santiago II	0.097	
			0.012-0.203
	Panuco South	0.048	0.001-0.103
Y. alta	All lineages	0.679	0.207-1.271
M. austrinum	All lineages	0.630	0.226-1.150
	Lerma-Chapala	0.237	0.034-0.264
	Pacific slope drainages	0.278	0.068-0.463
	Cuitzeo	0.047	0.007-0.104

Figure 1. Distribution range and sampled localities of the four fish species using in the study. Dark gray, light gray, solid green and dashed black lines correspond to distribution ranges of *A. tincella*, *N.calientis, M. austrinum*, and *Y. alta*.

Figure 2. Median-joining haplotype networks of the four species, A) *A. tincella*, B) *M. austrinum*, C) *N. calientis* and D) *Y. alta*. Geographic location is indicated by colours.

Figure 3. Bayesian skyline plots of the species, *A. tincella*, *M. austrinum*, *N. calientis* and *Y. alta* using cyt *b* sequences. Along the y-axis is the expressed population size estimated in units of $N_e\mu$ (N_e: effective population size, μ: mutation rate per haplotype per generation). The x-axis is in a log-scale. Solid lines represent median estimates and shaded areas represent confidence intervals.

Figure 4. Geologic scenarios for the Cuitzeo lineages of the four speceies *A. tincella*, *M. austrinum*, *Y. alta* and *N calientis*.

Figure 5. Headwater corridors representing ancestral connections between Verde-Santiago, Pánuco and Middel Lerma rivers.

Figures

Figure 1

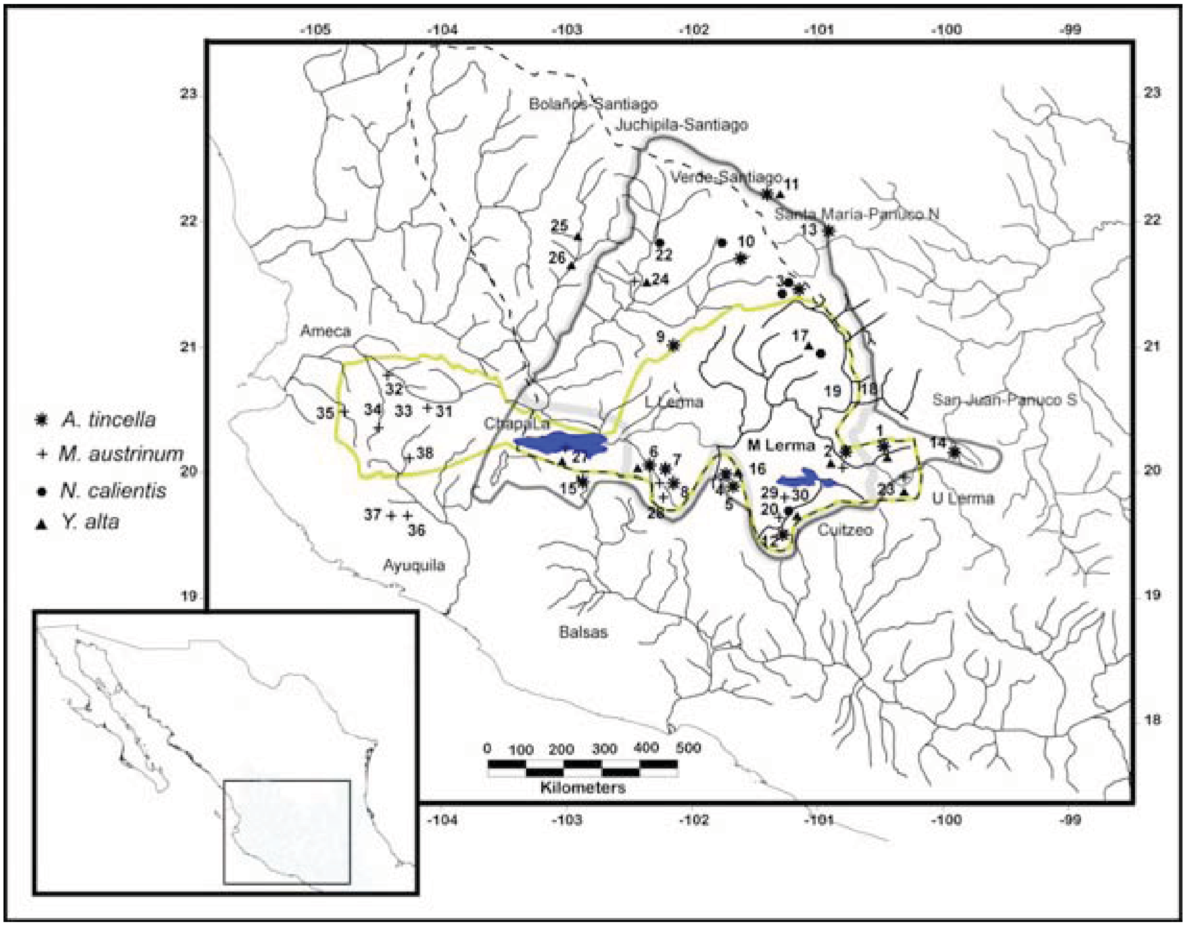


Figure 2

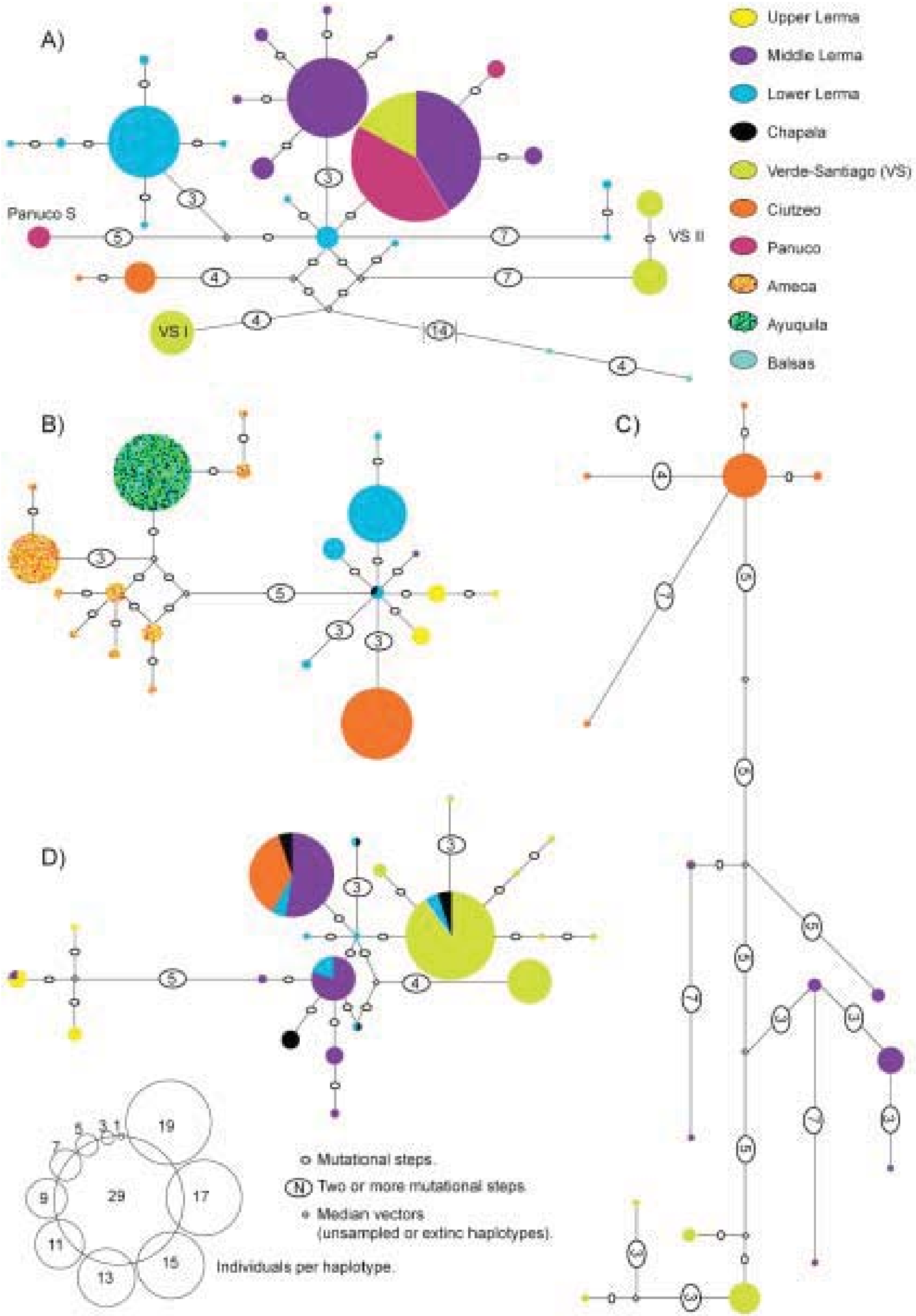

A)
Upper Lerma
Middle Lerma
Lower Lerma
Chapala
Verde-Santiago (VS)
Ciutzeo
Panuco
Ameca
Ayuquila
Balsas
Panuco S
3
3
5
7
VS II
4
7
VS I
4
14
4
B)
C)
3
5
3
3
D)
3
3
5
4
19
5
3
1
7
9
29
17
11
13
15
Mutational steps.
N
Two or more mutational steps.
Median vectors
(unsampled or extinc haplotypes).
Individuals per haplotype.

Figure 3

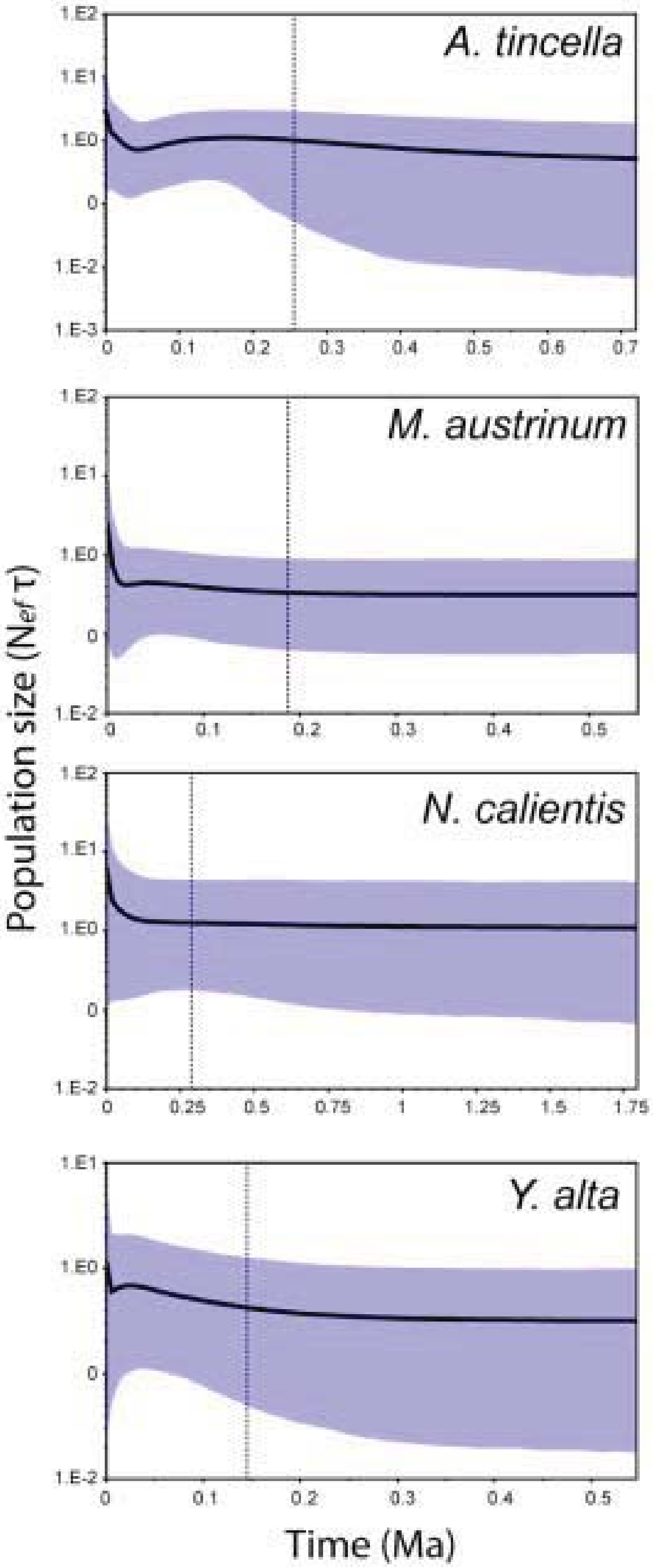

A. tincella
1.E2
1.E1
1.E0
0
1.E-2
1.E-3
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
M. austrinum
1.E2
1.E1
1.E0
0
1.E-2
0
0.1
0.2
0.3
0.4
0.5
N. calientis
1.E2
1.E1
1.E0
0
1.E-2
0
0.25
0.5
0.75
1
1.25
1.5
1.75
Y. alta
1.E1
1.E0
0
1.E-2
0
0.1
0.2
0.3
0.4
0.5
Population size (Nef τ)
Time (Ma)

Figure 4

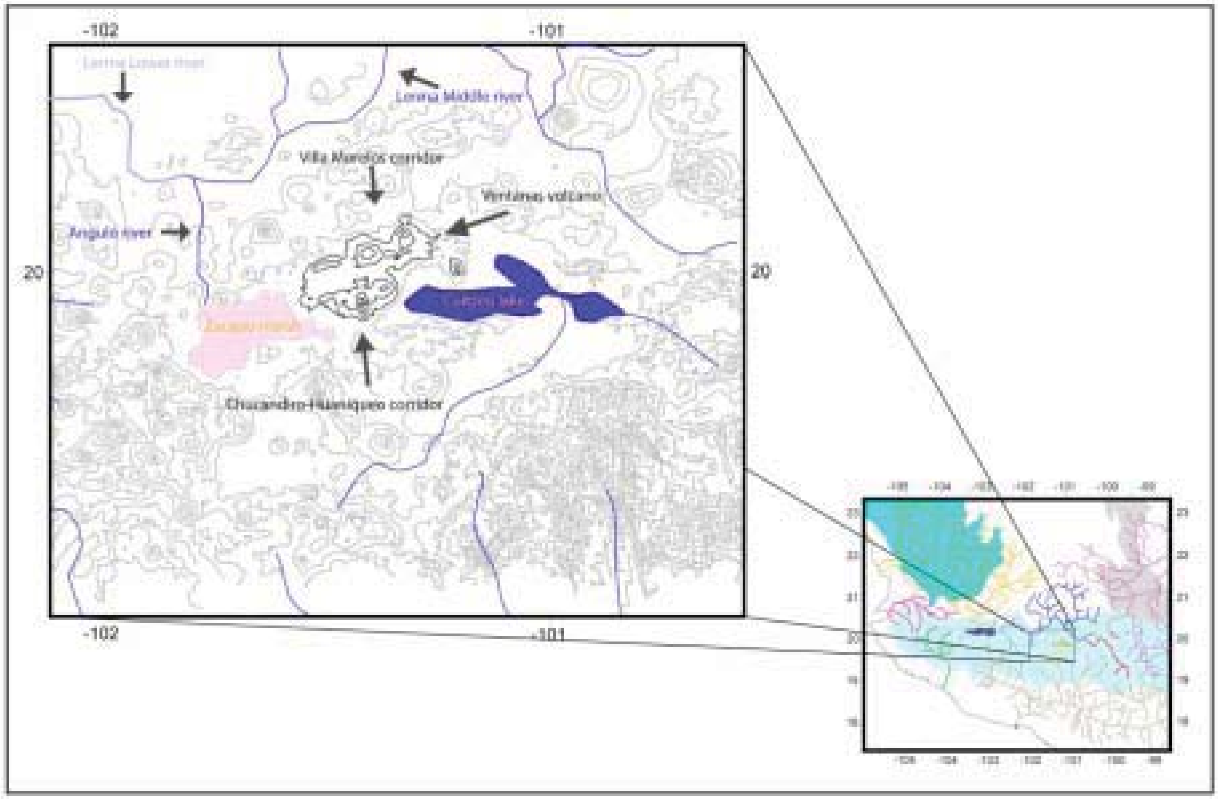
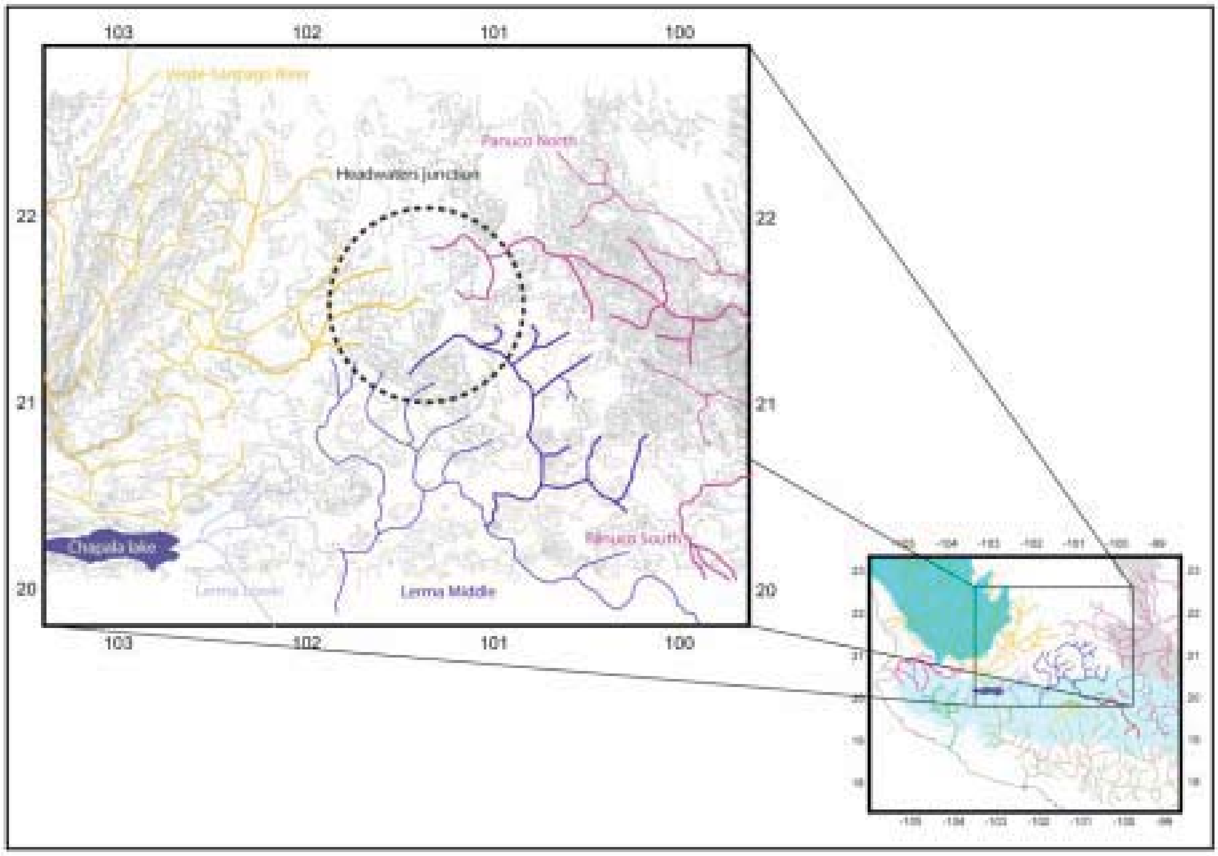

-102
-101
Lerma Lower river
Lerma Middle river
Villa Morelos corridor
Ventanas volcano
Angulo river
20
20
Zacapu marsh
Cuitzeo lake
Chucandiro-Huaniqueo corridor
-102
-101
-105
-104
-103
-102
-101
-100
-99
23
22
21
20
19
18

Figure 5


103
102
101
100
22
21
20
Verde-Santiago River
Panuco North
Headwaters junction
Chapala lake
Lerma lower
Lerma Middle
Panuco South

Supporting information

Table S1. Geographic distribution range and the genbank accession number of analyzed sequences

	Species	Locality	river basin	cytb
1.	*Algansea tincella*	1. Tigre river, Jerecuaro town, Gto. Mex.	Lerma Upper	9339
2.				9340
3.				9341
4.				9342
5.				9343
6.				9345
7.				9346
8.				9347
9.				9349
10.				9350
11.				9351
12.		2. Lerma river, Chamacuaro town, Gto. Mex.	Lerma Middle	9118
13.				9119
14.				9120
15.				9121
16.				9122
17.				9123
18.				9125
19.		3. Bravo river, San Felipe town, Gto. Mex.		4922

20.		4925
21.		8762
22.		8763
23.		8764
24.		8765
25.		8766
26.		8767
27.		8773
28.		8774
29.		8775
30.		12817
31.		12819
32.	4. Angulo river, Botello town, Mich. Mex.	9182
33.		9183
34.		9184
35.		9186
36.		9187
37.		9188
38.		9189
39.		9190
40.		9191
41.		9193
42.	5. La Patera stream, Villa Jiménez town, Mich. Mex.	16850
43.		16851
44.		16852
45.		16853
46.		16854

47.			16855
48.			16856
49.	6. Duero river, Zamora city, Mich., Mex.	Lerma Lower	9237
50.			9238
51.			9239
52.			9240
53.			9241
54.			9242
55.			9243
56.			9245
57.			9246
58.			9247
59.			9248
60.			9249
61.			9251
62.			9252
63.			9253
64.			9254
65.	7. Orandino spring, Jacona town, Mich., Mex.		6227
66.			6228
67.			6229
68.			6230
69.			6231
70.			6232
71.			6235
72.			6236
73.			6237

74.			6238
75.	8. Lerma river, El Platanal town, Mich. Mex.		6269
76.			6270
77.			6271
78.			6276
79.			6278
80.			6279
81.			6280
82.	9. San Julian, Jal., Mex.	Verde-Santiago river	5921
83.			5922
84.			5923
85.			5924
86.			5925
87.			5926
88.			5927
89.			5928
90.			5929
91.			5932
92.			5933
93.			5937
94.			5938
95.			5939
96.	10. Stream at Guadalupe Victoria town, Ojuelos Jal., Mex.		5861
97.			5862
98.			5863
99.			5864

100.			5865
101.			5866
102.			5867
103.			5868
104.			5869
105.			5870
106.	11. Tecolote Dam, Pinos, Zac. Mex.		FJ913805
107.			5686
108.			5687
109.			5688
110.	12. San Carlos river, Morelia, Mich., Mex.	Cuitzeo lake	9327
111.			9328
112.			9329
113.			9330
114.			9331
115.			9332
116.			9333
117.			9334
118.	13. Stream at Jesus María town, SLP., Mex.	Panuco river	5647
119.			5648
120.			5649
121.			5650

122.				5651
123.				5652
124.				5654
125.				5655
126.				5656
127.				5657
128.				5658
129.				5659
130.				5660
131.				5662
132.				5663
133.				5664
134.		14. San Ildefonso stream, San Juan del Río, Qro., Mex.		8743
135.				9112
136.				9113
137.				9114
138.				9116
139.		15. river, Quitupan town, Jal., Mex.		genbank
140.				genbank
141.	*Algansea lacustris*	16. Patzcuaro lake, Patzcuaro town, Mich., Mex		9706
142.	*Notropis calientis*	3. Bravo river, San Felipe town, Gto., Mex.	Lerma Middle	4928
143.				4929
144.				4930
145.				12814

146.			12815
147.			12816
148.			12818
149.			12820
150.			12821
152.			12825
153.	17. Xoconoxtle stream, Dolores Hidalgo, Gto., Mex.		12791
154.			12792
155.			12793
156.			12794
157.			12796
158.	18. San Juan Rayas, Qro., Mex.		AF469137
159.	19. Charco del Ingenio, San Miguel de Allende, Gto., Mex.		AF469143
160.	20. Mintzita dam, Morelia, Mich., Mex.	Cuitzeo lake	9289
161.			9291
162.			9292
163.			9293
164.			9295
165.			9297
166.			9301
167.			9303
168.			9304
169.			9305
170.			10161
171.			10162
172.			10163
173.			GQ249853

174.				AF469138
175.		21. Presa de La Paz, Ojuelos, Jalisco, Mex.	Verde-Santiago	5813
176.				5817
177.				5825
178.				5827
179.				5828
180.				5829
181.				5830
182.				5831
183.				5832
184.				5833
185.				GQ249851
186.				GQ249852
187.		22. Mazcua river, 8 Km W Teocaltiche, Jal. Mex.		EU082473
188.	*Yuriria alta*	23. Lerma river, Pateo town, Mich., Mex.	Alto Lerma	12226
189.				12227
190.				12228
191.				12229
192.				12230
193.				12231
194.				12232
195.		1. Tigre river, Jerecuaro town, Gto., Mex.		9352
196.				9353
197.				9355
198.		2. Lerma river, Chamacuaro town river, Gto., Mex.	Medio Lerma	9124

199.			9126
200.			9127
201.			9128
202.			9129
203.			9130
204.			9131
205.			9132
206.			9133
207.			9134
208.	17. Xoconoxtle stream, Dolores Hidalgo, Gto., Mex.		12795
209.			12797
210.			12798
211.	4. Angulo river, Botello town, Mich., Mex.		9196
212.			9197
213.			9198
214.			9199
215.			9200
216.			9201
217.			9202
218.			9203
219.			9204
220.			9205
221.	6. Duero river, Zamora, Mich., Mex.	Bajo Lerma	9218
222.			9228
223.			9229
224.			9231
225.			9233
226.			9234

227.			9235
228.			9236
229.	20. dam, Morelia, Mich., Mex.	Cuitzeo	9307
230.			9308
231.			9310
232.			9311
233.			9314
234.			9315
235.			9316
236.	24. Verde river, Belen del Refugio town, Jal,. Mex.		5882
237.			5883
238			5884
239.			5885
240.			5886
241.			5887
242.			5888
243.			5889
244.			5890
245.			5891
246.	11. Tecolote dam, Pinos town, Zac., Mex.		5672
247.			5673
248.			5674
249.			5676
250.			5677
251.			5678
252.			5679
253.			5680

254.			5681
255.			5682
256.			5683
257.			5684
258.	25. Juchipila river, Tabasco town, Zac., Mex.		5725
259.			5726
230.			5727
231.			5729
232.			5731
233.	26. Juchipila river, Jalpa town, Zac.., Mex.		5772
234.			5773
235.			5774
236.			5775
237.			5776
238.			5777
239.			5778
240.			Yuri864
241.			Yuri865
242.			EU082475
243.	27. Tizapan river, Tizapan el Alto town, Jal., Mex.	Chapala	17999
244.			18000
245.			18001
246.			18002
247.			18004
248.			18006
249.			18007
250.			18008

251.	*Moxostoma austrinum*	23. Lerma river, Pateo town, Mich. Mex.	Lerma upper river	9337
252.				12212
253.				12213
254.				12214
255.				12215
256.				12216
257.				12217
258.				12218
259.				12221
260.				12222
261.		2. Lerma river, Chamacuaro town, Gto. Mex.	Lerma middle river	9117
262.		8. Lerma river, El Platanal town, Mich. Mex.	Lerma lower river	6282
263.				6283
264.				6284
266.				6285
267.				9097
268.				9098
269.				9099
270.				9102
271.				9103
272.				9104
273.		28. Celio river, Jacona town, Mich. Mex.		4888
274.				4889
275.				4890
276.				4891
277.				6245

278.			6246
279.			6247
280.			6248
281.			6249
282.			6250
283.			6251
284.	29. Duero river at bridge crossing on road towards Etucuaro		JF799505
285.			JF799506
286.	20. Spring “La Mintzita”, Morelia, Mich. Mex.	Cuitzeo lake	9306
287.			9318
288.			9319
289.			9320
290.			9321
291.			9322
292.			9323
293.	29. Stream at Chiquimitio town, Morelia, Mich. Mex.		6296
294.			6333
295.			6334
296.			6336
297.			6337
298.			6338
299.			6339
300.			6340
301.	30. Arroyo San Marcos near Morelia, Mich. Mex.		JF799503
302.	27. Tizapan river, Tizapan el alto town, Jal. Mex	Chapala lake	1809

303.	31. Salado river, Tala town, Jal. Mex.	Ameca river	11782
304.			11783
305.			11784
306.			11785
308.			11796
309.	32. Chiquito river, Amatlan Town, Nay. Mex.		11948
310.			11949
311.			11951
312.			11952
313.			11953
314.	33. Puente Grande stream, Ameca, Jal. Mex.		9926
315.			9927
316.			9928
317.			9929
318.			9930
319.			9931
320.			9932
321.			JF799521
322.	34. Atenguillo river, Los Volcanes town, Jal. Mex.		13051
323.			13058
324.			13059
325.			13060
326.			JF799520
327.	35. Stream at Ahuilota pharm, Mascota, Jal. Mex		18939
328.			18940
329.			18941
330.			18942
331.			18943

332.	36. Stream at Ahuacapan town, Ahuacapan, Jal. Mex.	Armería-Ayuquila river	8807
333.			8808
334.			8809
335.			8810
336.			8811
337.			JF799502
338.	37. Ayuquila river at Las Ventanas town, El Grullo, Jal. Mex.		18955
339.			18956
340.			18957
341.			18958
342.			18960
343.	38. Atengo river at Ayutla Town, Jal. Mex.		13066
344.			13067
345.			13068
346.			13069
347.			13070
348.			13073

Table S2. Diversity and demography genetic data. All demographic results failed to reject the null hypothesis of constant population size (all P values > 0.05).

Lineages	***N***	***h***	***#Mut***	***S***	***Hd (std.dev.)***	π	***k***	***D***	***Fs***	R_2
A. tincella	140	28	56	56	0.914(0.012)	0.005(0.003)	5.704	-1.240	-7.448*	0.052
Lerma Middle	48	8	8	8	0.777(0.040)	0.002(0.0001)	2.060	0.400	-0.38	0.127
Tigre	11	4	3	3	0.600(0.154)	0.0006(0.0002)	0.700	-1.113	-1.525*	0.044*
Chamacuaro	7	3	2	2	0.524(0.209)	0.0005(0.0002)	0.571	-1.237*	-0.922	0.225
San Felipe	13	1	0	0	0.000	0.000	0.000	--	--	--
Botello	10	3	5	5	0.733(0.076)	0.002(0.0003)	2.600	1.888	2.679	0.260
Patera	7	3	2	2	0.762(0.115)	0.001(0.0002)	0.952	0.068	-0.056	0.238
Lerma Lower	33	11	18	18	0.748(0.074)	0.003(0.0006)	3.098	-1.019	-8.177*	0.080
Zam-Jac	16	4	5	5	0.442(0.145)	0.001(0.0003)	0.950	-1.217	-0.374	0.096*
Orandino	10	7	14	14	0.933(0.062)	0.005(0.001)	5.111	0.150	-0.684	0.164
Platanal	7	6	13	13	0.952(0.096)	0.004(0.001)	4.571	-0.758	-1.310	0.166
San Julian	14	2	1	1	0.527(0.064)	0.0005(0.00006)	0.527	1.434	1.250	0.263
Gvictoria	14	5	4	4	0.505(0.158)	0.0005(0.0002)	0.571	-1.797*	-3.143*	0.112*
Tecolote	4	1	0	0	0.000	0.000	0.000	--	--	--
Umecuaro	13	4	5	5	0.423(0.164)	0.0008(0.0004)	0.897	0.031*	-0.747	0.147

Jesus Maria	16	2	1	1	0.400(0.114)	0.0004(0.0001)	0.400	0.650	0.871	0.200
San Ildefonso	5	1	0	0	0.000	0.000	0.000	--	--	--
M. austrinum	96	21	26	26	0.905(0.013)	0.004(0.001)	5.000	-0.039	-2.692	0.094
Lerma-Chapala clade	51	10	11	11	0.821(0.032)	0.002(0.0001)	2.097	-0.412	-1.705	0.092
Pateo	10	3	3	3	0.644(0.101)	0.001(0.0001)	1.311	0.850	1.020	0.210
Lerma Lower	23	5	5	5	0.644(0.092)	0.001(0.0002)	1.273	-0.177	-0.315	0.125
Platanal	10	4	4	4	0.733(0.120)	0.001(0.0003)	1.622	0.565	0.137	0.202
Celio	11	2	1	1	0.182(0.144)	0.0001(0.0001)	0.182	-1.128	-0.409	0.287
Cuitzeo	16	1	0	0	0.000	0.000	0.000	--	--	--
Mintzita	7	1	0	0	0.000	0.000	0.000	--	--	--
Chiquimitio	9	1	0	0	0.000	0.000	0.000	--	--	--
PSD clade	45	11	11	11	0.794(0.044)	0.002(0.0001)	2.384	-0.155	-2.208	0.104
Ameca	28	10	11	11	0.820(0.060)	0.002(0.0002)	2.825	-0.001	-1.879	0.122
Salado	5	2	3	3	0.400(0.237)	0.001(0.0006)	1.200	-1.048	1.687	0.400
Chiquito	5	3	2	2	0.800(0.268)	0.001(0.0002)	1.000	0.243	-0.475	0.250
Potrero	8	2	1	1	0.250(0.180)	0.0002(0.0001)	0.250	-1.054	-0.182	0.330
Atenguillo	6	4	7	7	0.800(0.172)	0.002(0.0008)	2.933	-1.124	0.643	0.309
Ahuilota	5	2	1	1	0.400(0.237)	0.0003(0.0002)	0.400	-0.816	0.090	4.000
Ayuquila	17	1	0	0	0.000	0.000	0.000	--	--	--

Ahuacapan	6	1	0	0	0.000	0.000	0.000	--	--	--
Ventanas	5	1	0	0	0.000	0.000	0.000	--	--	--
Atengo	6	1	0	0	0.000	0.000	0.000	--	--	--
N. calientis	45	16	47	47	0.900(0007)	0.008(0.0004)	9.000	-0.600	0.502	0.089
Lerma Middle	17	7	27	27	0.838(0.063)	0.006(0.001)	7.132	-0.432	2.367	0.124
Sfelipe	10	3	14	14	0.600(0.131)	0.005(0.001)	6.000	0.972	5.625	0.204
Xoconoxtle	5	2	7	7	0.600(0.175)	0.003(0.001)	4.200	1.742	4.360	0.300
Cuitzeo (Mintzita)	16	5	11	11	0.533(0.142)	0.001(0.0006)	1.483	-2.087*	-0.440	0.143
Verde-Santiago (Paz)	12	4	7	7	0.636(0.128)	0.001(0.0005)	1.924	-0.664	0.831	0.132
Y. alta	92	21	27	27	0.886(0.018)	0.003(0.0002)	3.577	-0.987	-5.595*	0.064
Lerma Upper (Pateo)	7	3	3	3	0.714(0.127)	0.001(0.0002)	1.429	0.754	0.668	0.223
Lerma Middle	26	6	9	9	0.754(0.053)	0.001(0.0003)	1.972	-0.526	0.131	0.125
Tigre	3	3	7	7	1.000(0.272)	0.004(0.001)	4.667	--	--	--
Chamacuaro	10	3	2	2	0.700(0.104)	0.001(0.0001)	0.911	0.931	0.300	0.227
Xoconoxtle	3	1	0	0	0.000	0.000	0.000	--	--	--
Botello	10	1	0	0	0.000	0.000	0.000	--	--	--
Lerma Lower (ZamJac)	8	7	7	7	0.964(0.077)	0.002(0.0003)	2.036	-1.170	-4.477*	0.101*
Cuitzeo (Mintzita)	7	1	0	0	0.000	0.000	0.000	--	--	--
Santiago	36	8	12	12	0.681(0.063)	0.002(0.0003)	2.659	-0.255	0.019	0.106

Verde-Santiago	22	5	8	8	0.701(0.066)	0.002(0.0002)	3.108	1.366	2.25	0.190
Belen	10	4	3	3	0.711(0.117)	0.001(0.0002)	1.022	-0.129	-0.830	0.169
Tecolote	12	2	5	5	0.303(0.147)	0.001(0.0006)	1.515	-0.312	3.470	0.151
Juchipila-Santiago	14	4	4	4	0.400(0.159)	0.0006(0.0002)	0.692	-1.481*	0.395	0.143
Jalpa	9	4	4	4	0.583(0.183)	0.001(0.0003)	1.056	-1.149	-0.927	0.173
Tabasco	5	1	0	0	0.000	0.000	0.000	--	--	--
Chapala (Tizapan)	8	5	7	7	0.786(0.151)	0.002(0.0004)	2.357	-0.603	-0.800	0.021*

4 DISCUSIÓN GENERAL

De acuerdo con los resultados encontrados en este trabajo, podemos señalar que la dinámica geológica que ha configurado la fisiografía de la región del centro de México, particularmente del Mioceno Medio al presente (Ferrari, 2003), ha determinado en gran medida los procesos o fuerzas evolutivas que han dado como resultado el patrón de diversidad actual de la ictiofauna dulceacuícola dentro esta región. Asimismo, las fluctuaciones climáticas pleistocénicas y holocénicas han influido en la configuración de los sistemas hidrográficos, particularmente del sistema Lerma-Chapala, que es la principal cuenca que abarca casi en su totalidad el centro de México (Domínguez-Domínguez y Pérez-Ponce de León, 2009).

En el presente estudio se analizaron los patrones biogeográficos de los representantes de dos familias de peces de origen neártico, *A. tincella*, *N. calientis* y *Y. alta*, pertenecientes a la familia Cyprinidae, y la especie *M. austrinum* que pertenece a la familia Catostomidae. En una primera aproximación, a nivel de los principales grupos de peces a los que pertenecen dichas especies, se compararon los patrones biogeográficos, incluyendo además a la subfamilia endémica Goodeinae, representativa del centro de México.

4.1 Colonización del componente neártico de peces dulceacuícolas en el centro de México

El componente neártico del centro de México está representado por cuatro familias, Cyprinidae, Catostomidae, Ictaluridae y Centrarchidae, las últimas dos solo como fósiles pleistocénicos (Miller y Smith, 1986). Aunque no estrictamente neártico en su origen, también se encuentra la subfamilia Goodeinae, cuyo grupo hermano, Empetrichthynae, presenta una distribución septentrional que se encuentra en el suroeste de los Estados Unidos. Además, la tribu más basal de Goodeinae, es decir, Characodontini, se encuentra en el norte de México (Parenti, 1981; Doadrio y Domínguez, 2004; Webb *et al.*, 2004; Domínguez-Domínguez *et al.*, 2010).

A diferencia de Goodeinae y Cyprinidae, el resto de los representantes de las familias neárticas en el centro de México presentan una riqueza de especies baja. En el caso de Centrarchidae, sólo esta representado por una especie del género *Micropterus*; Ictaluridae y Catostomidae, ambas presentan un solo género, *Ictalurus* y *Moxostoma*, respectivamente, con dos especies actuales distribuídas en cuencas hidrológicas del centro de México (Miller *et al.*, 2005; Clements *et al.*, 2012) y un representante fósil (Miller y Smith, 1986). Con los resultados obtenidos en los capítulos I y II se corroboró que efectivamente el bajo número de especies del género *Moxostoma*, en relación con Goodeinae, y los ciprínidos formando el denominado grupo "Notropinos del sur", y *Algansea*, esta asociado a la colonización relativamente reciente de los catostómidos al centro de México durante el Pleistoceno. Sin embargo, la relación entre el número de especies y el tiempo evolutivo no fue proporcional para los otros tres grupos, puesto que el más antiguo, "Notropinos del sur" (Mioceno Inferior), no resultó ser el de mayor riqueza taxonómica. Estos grupos, con una mayor escala de tiempo, estuvieron sujetos a otras fuerzas evolutivas como la radiación adaptativa en Goodeinae (ver más adelante).

Para cada uno de los grupos se detectó una ruta de colonización particular al centro de México. La más antigua de éstas es la ruta del "Altiplano", utilizada como corredor por el grupo "Notropinos del sur". Es a través de esta ruta que se ha planteado la dispersión de la ictiofauna derivada del Río Bravo hacia otras cuencas, dentro de las que figura el centro de México (Miller y Smith, 1986). El "Altiplano" corresponde a una amplia llanura elevada contenida entre la Sierra Madre Oriental (SMOr), la Sierra Madre Occidental (SMOc) y la Faja Volcánica Trans Mexicana (FVTM); a partir del parteaguas de las cuencas de los ríos Nazas y Aguanaval se divide en dos regiones (Espinosa *et al.*, 2008), la Mesa del Norte y la Mesa central (Aranda-Gómez *et al.*, 2000), esta última comprendida en el centro de México (Domínguez-Domínguez y Pérez-Ponce de León, 2009). Este componente fisiográfico del "Altiplano" queda dentro de lo que se conoce como la provincia "Basin and Range" de México Sur o extensión de México (Calmus, 2011), cuya formación esta asociada a las últimas dos fases tectónicas del "Basin and Range", causadas por la intensificación de la subducción de la placa de Farallon bajo la Placa Norteamericana *ca.* Oligoceno Superior – Mioceno (Pérez-Rodríguez *et al.*, 2015).

Cronológicamente, continuaron las rutas del "Oeste" que consistieron en dos distintas que se llevaron a cabo a través de la SMOc. La subducción de la placa de Farallón bajo la Placa Norteamericana durante el Oligoceno Superior-Mioceno, se asocia con el cambio en la configuración de la SMOc, por lo que se considera que dicha actividad durante el Mioceno influyó primero sobre la fragmentación de la familia Goodeidae en el Mioceno Medio, y segundo con la fragmentación del ancestro de los géneros *Agosia-Algansea* y la colonización de este último al centro de México en el Mioceno Superior.

Por su parte, la ruta más reciente al centro de México fue la que utilizó el género *Moxostoma*, que consistió en una combinación de ambas rutas, "Altiplano" y "Oeste". La primera parte consistió en el cruce de los linajes del Río Bravo a partir de las cuencas de la vertiente del Golfo de México, hacia las cabeceras de los ríos de la SMOc en la vertiente pacífico, a través del "Altiplano". Dicha dispersión se llevó a cabo mediante dos probables conexiones del Río Bravo (Río San Juan y Cuatro Ciénegas), con los paleoambientes lacustres del "Altiplano" durante el Plioceno-Pleistoceno (Fig. 3). Una vez que el linaje ancestral derivado del Río Bravo alcanzó los paleolagos en la Mesa del Norte, conocidos como "Bolsones", que además estaban conectados con sistemas hidrográficos de la SMOc, se dispersó hacia los ríos de la vertiente Pacífica; una vez ahí experimentó un proceso de dispersión-vicarianza, a través de la vertiente pacífica de la parte centro-sur de la SMOc, por los ríos Mezquital y Santiago, hasta llegar al centro de México durante el Pleistoceno (Fig. 2).

De acuerdo con estas distintas rutas de colonización al centro de México que se diferencian en tiempo y espacio, se reconoce un alto dinamismo en el cambio de la composición ictiofaunística de la región. Esto indica que a partir de que se comenzó a configurar el sistema hidrográfico principal, el Río Lerma, durante el Mioceno (Israde-Alcántara, *et al*., 2010), y de los continuos cambios en su configuración debido a la actividad geológica de la región y a las fluctuaciones climáticas durante el Plioceno, Pleistoceno, incluso el Holoceno (Israde-Alcántara, 1999; Moncayo *et al*., 2001; Israde-Alcántara *et al*., 2010), los intercambios de fauna con otras provincias ictiofaunísticas del Norte (como el Río Bravo) fueron recurrentes. También se consideran eventos tan recientes como la colonización de *Y. alta*, especie representativa del Lerma-Chapala, hacia el Río Santiago y sus tributarios norteños (Fig. 2).

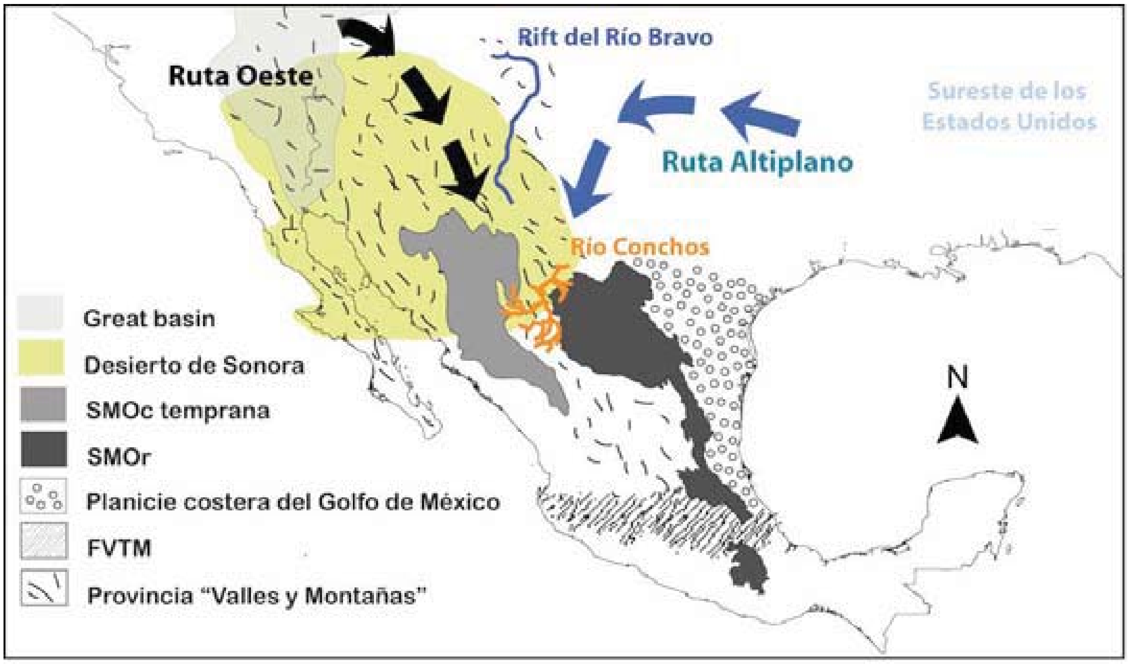


Figura 3. Rutas de colonización al centro de México.

4.2 Origen y dispersión de las especies A. tincella, N. calientis, Y. alta y M. austrinum en el centro de México

Tomando en cuenta al taxón hermano de cada una de las especies analizadas en el presente trabajo, los eventos cladogenéticos de los cuales derivaron estas especies, excepto *M. austrinum*, ocurrieron dentro del sistema Lerma-Chapala.

En el caso de *N. calientis*, la especie más antigua presenta un área de distribución que comprende casi todos los afluentes del Río Verde-Santiago, el Río Santa María, afluente norteño del Pánuco, los ríos Laja y Turbio, afluentes del Lerma Medio, el Río Duero en la parte del Lerma Bajo, algunos tributarios del lago de Chapala y el Río Grande en la cuenca de lago de Cuitzeo (Miller *et al*., 2005; Domínguez-Domínguez *et al*., 2009). Sin embargo, debido a la extirpación de algunas de sus poblaciones por reducción y modificación de su hábitat (Jelks *et al*., 2008), en el presente estudio solo se tuvo la representación de los ríos Encarnación y Mascua que son afluentes del Río Verde-Santiago, Río Laja en el Lerma Medio, y Río Grande en el Lago de Cuitzeo. De acuerdo con la conexión de los haplotipos del Río Laja con los de las otras dos areas, Cuitzeo y Verde-Santiago, se infiere que *N. calientis* colonizó estas dos cuencas a partir del Lerma Medio (Fig. 4 C). Del Plioceno Medio al Pleistoceno Temprano (3.5 - 1.8 Ma) las cuencas lacustres del centro de México se caracterizaron por presentar lagos someros conectados por canales (Israde-Alcántara *et al*., 2010). Durante este periodo se registra un levantamiento del centro de México causado por la actividad tectónica y volcánica de la Faja Volcánica Trans-Mexicana, que promovió la distribución de lagos, ciénegas, manantiales y ríos, lo más cercano al sistema hidrográfico actual, que resultaron en hábitats favorables para la acumulación de vertebrados durante ese periodo (Israde-Alcántara *et al*., 2010). Para una especie de talla pequeña (Chernoff y Miller, 1986; Lyons *et al*., 2004; Domínguez-Domínguez *et al*., 2009), carnívora y altamente sensible a los cambios en las condiciones del ambiente como *N. calientis* (Mercado-Silva *et al*., 2005), este momento fue el adecuado para llevar a cabo la extensión en su área de distribución, previo al episodio de condiciones más áridas que se estableció durante el Cuaternario.

La especie *A. tincella* presenta una de las áreas de distribución más amplias y resultó ser de las más estructuradas genéticamente. De acuerdo con su relativa capacidad de dispersión y tolerancia a los cambios en las condiciones ambientales (Mercado-Silva *et al*., 2005), extendió su intervalo de distribución en condiciones menos favorables a las del Plioceno Medio-Pleistoceno Temprano. La posición central y la alta representación de los haplotipos del Río Lerma (Bajo y Medio Lerma; Fig. 4 A) dentro de la red, sugiere que la población ancestral de esta especie se originó en el Río Lerma. Posteriormente, con las fluctuaciones climáticas en el Holoceno se dieron las fragmentaciones que condujeron a su estructura geográfica. En este caso, el aumento en el área de distribución estuvo relacionado con la cantidad de procesos de fragmentación geográfica.

En el caso de *Y. alta*, una especie que también cuenta con un área de distribución amplia, su más reciente incorporación a la región, junto con su alta capacidad de dispersión Miller *et al.*, 2005) y tolerancia a los cambios en las condiciones ambientales (Mercado-Silva *et al.*, 2005; Ramírez-Herrejón *et al.*, 2012), le permitieron un amplia extensión, a partir de su area ancestral que resultó ser el Río Lerma, como sugiere la posición de y la alta representación de los haplotipos del Lerma (Medio y Bajo; Fig. 4 D). Dichas características no permitieron que se diera aún una estructura geográfica en alguna de las cuencas que actualmente son independientes al sistema Lerma-Chapala.

A pesar de que la conexión del Río Santiago con el sistema Lerma-Chapala data desde el Plio-Pleistoceno, la cascada de Juanacatlán (con 700 m de profundidad aprox.) dentro del cañon del Río Santiago localizada al norte del lago de Chapala, representó desde ese periodo hasta la actualidad una barrera biogeográfica para el intercamio de la ictiofauna entre el Santiago y el sistema Lerma Chapala (Miller *et al.*, 2005). Esto sugiere que la colonización del ancestro mas reciente de *M. austrinum* al centro de México, se dió mediante la cuenca del Río Ameca. El registro fósil de la especie *Moxostoma* sp. encontrado en los paleo canales que conectaron durante el Plio-Pleistoceno, el oeste del lago de Chapala con la cuenca del Río Ameca (Smith *et al.*, 1975), soportan dicha aseveración. Posteriormente, esta especie extendió su área al sistema Lerma-Chapala a finales del Pleistoceno. De acuerdo con la posición y representación de los haplotipos del Río Lerma, se dispersó a lo largo de toda la cuenca, incluyendo el lago de Cuitzeo en el último de sus episodios de conexión con el Lerma Medio (Israde-Alcántara, 1999; Moncayo *et al.*, 2001). Finalmente, una de las fases de aislamiento del lago de Cuitzeo (Moncayo *et al.*, 2001), ocasionó la diferenciación del haplotipo único de Cuitzeo (Fig. 4 B).

De acuerdo a lo anterior, se puede afirmar que el patrón de codistribución parcial, es decir, el no sobrelapamiento entre las áreas de distribución de las cuatro especies, está asociado tanto a factores extrínsecos como intrínsecos. El primer caso, es relativo al tiempo y espacio en el que se originó y se dispersó cada una de las especies, lo que determinó las rutas o corredores disponibles para dispersarse hacia otras áreas. Los factores intrínsecos se refieren principalmente a la capacidad de dispersión y de tolerancia a los cambios en las condiciones ambientales, que implican, en primera instancia la capacidad de traslado, y en segundo, la habilidad para adaptarse a los nuevos sitios con distintas condiciones ambientales.

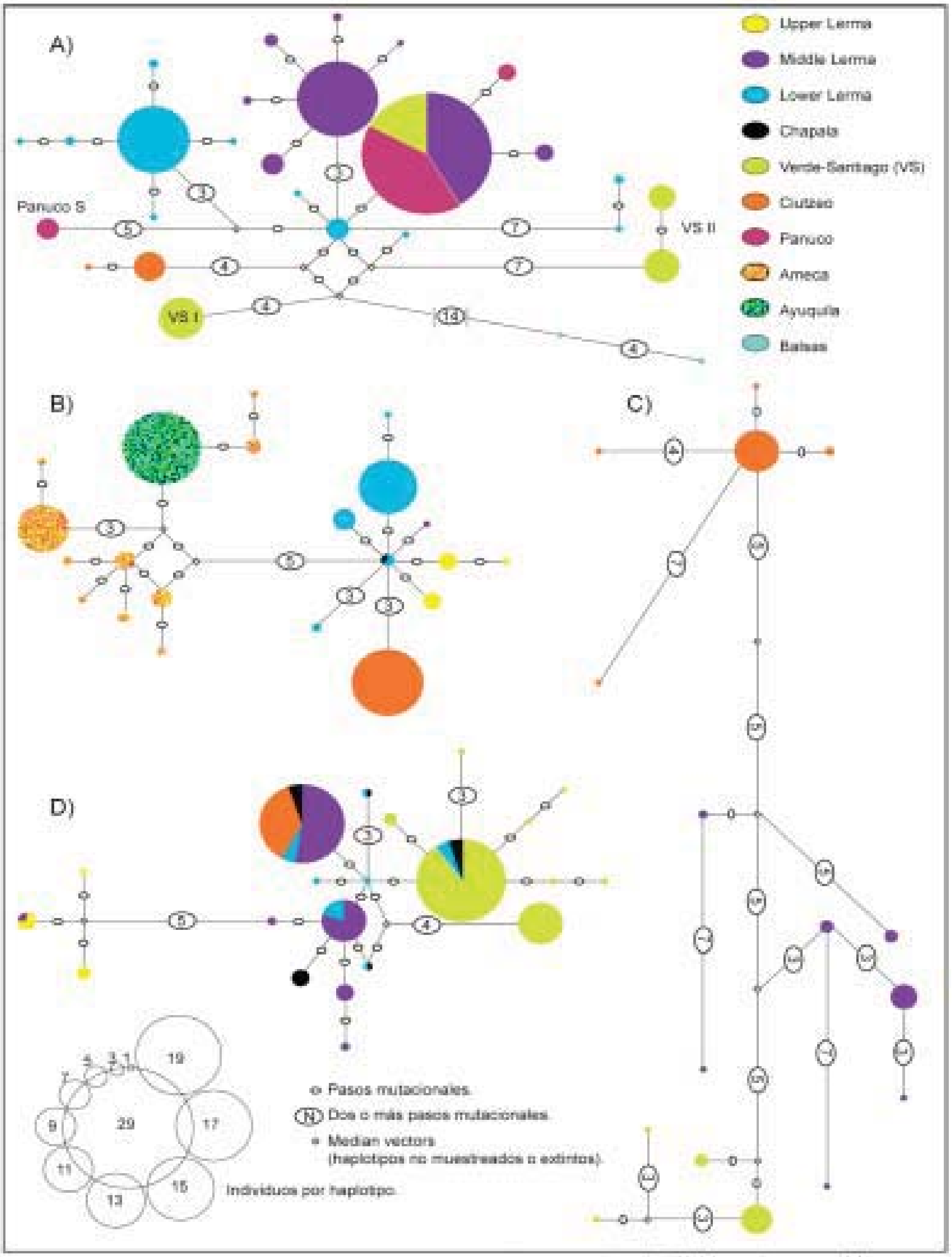


Figura 4. Redes de haplotipos de las especies A) *Algansea tincella*, B) *Moxostoma austrinum*, C) *Notropis calientis* y D) *Yuriria alta*.

4.3 Congruencia biogeográfica

Algunos de los acontecimientos geológicos en la región fueron responsables de eventos vicariantes, que en algunos casos influyeron de la misma manera en distintos grupos de peces. Tal es el caso del levantamiento del centro de México, un evento gradual que ocurrió durante el Mioceno Superior, producto de la actividad tectovolcánica de la parte sur de la Sierra Madre Occidental (Henry y Aranda-Gómez, 2000), y de la migración al este en el pulso magmático de la Faja Volcánica Trans-Mexicana (Ferrari, 2004). En un primer episodio, se produjo la fragmentación entre las cuencas de la vertiente Pacífico, que incluyen de Oeste a Este, el Río Ameca, Río Ayuquila, Río Tamazula, Río Balsas y Río Atoyac, y sus partes altas que quedaron dentro del proto-sistema Lerma-Chapala, ocasionando con ello el aislamiento de la tribu Ilyodontini (Goodeinae) en los ríos Ameca y Ayuquila, y al Género *Notropis* en los ríos Balsas y Atoyac. Es importante señalar que esta es una congruencia únicamente temporal, puesto que a pesar de que los ríos donde quedaron aislados se encuentran en la vertiente pacífica, se localizan en dos regiones distintas, Oeste (Ameca y Ayuquila) y Este (Balsas y Atoyac).

El primer evento de congruencia biogeográfica en tiempo y espacio se registró entre Goodeinae y *Algansea* aproximadamente hace 8 Ma. Este consistió en el aislamiento del género "*Xenotoca*" y el clado Pacífico de *Algansea* (*sensu* Pérez-Rodríguez *et al.*, 2009), en las ríos de la parte Oeste de la vertiente pacífica; por otro lado, los correspondientes taxa hermanos de ambos grupos (el resto de la tribu Chapalichthyini y el clado central de *Algansea*), respectivamente, se quedaron aislados dentro del sistema Lerma-Chapala. Este evento fue promovido de la continua actividad de la FVTM durante el Mioceno Superior-Plioceno Inferior.

Más recientemente, la actividad tectónica del sistema de fallas de San Marcos que ocurrió de 3-1 Ma (Ferrarri y Rosas-Elguera, 1999), produjo la separación de las especies *Yuriria amatlana* (Notropinos del sur), *Allotoca goslinae* (Goodeinae) y *Ameca splendens* (Goodeinae) distribuídas en el la parte alta del Río Ameca, de sus taxa hermanos distribuidos en el Lerma-Chapala *Yuriria chapalae-Y. alta* (Notropinos del sur), *A. dugesii* (Goodeinae) y *Chapalichthys* spp. (Goodeinae), respectivamente.

El último evento de congruencia biogeográfica tiene que ver con el patrón de codistribución de las especies *N. calientis*, *Y. alta*, *A. tincella*, *X. variata*, *C. encaustus* y *A. dugesii*, en las areas del Lerma Bajo, Lerma Medio, Verde-Santiago y Chapala, que esta asociado a la extensión del área de los paleolagos durante un lapso húmedo en el Plesitoceno y a la conexión de estos mediante canales durante el Neogeno-Cuaternario (Israde-Alcántara *et al.*, 2010). Sin embargo, con la aproximación filogeográfica evidenciamos que dicho patrón de codistribución se asocia con una historia independiente en cada una de las especies analizadas, al menos en esta escala de tiempo.

4.4 Implicaciones microevolutivas en los procesos macroevolutivos

En el capítulo tres se muestra que fueron tanto factores extrínsecos como intrínsecos los que determinaron la incongruencia en el patrón de la estructura geográfica a nivel poblacional. Los extrínsecos consistieron básicamente en la diferencia de tiempo y espacio que ocupó el Ancestro Común Mas Reciente (MRCA por sus siglas en inglés) de cada una de las especies (Tabla 3, Capítulo 3). Por su parte, los intrínsecos consistieron en la diferencia entre la historia natural y los rasgos biológico y ecológicos de cada una de las especies comparadas. La presencia o ausencia de estas características determinaron un diferencial en la capacidad para adecuarse a los cambios ambientales que se experimentaron en la región del centro de México, lo cuál se reflejó en las distintas respuestas que tuvieron las especies a un mismo evento geológico-climático. Dichos cambios ambientales en el tiempo tienen que ver básicamente con las modificaciones de las condiciones ambientales de los ecosistemas acuáticos y sus estrategias para adecuarse.

En el caso de la especie *A. tincella*, que presentó mayor estructuración geográfica, tanto el tiempo del MRCA dentro del sistema Lerma-Chapala, como algunas de sus rasgos biológico y ecológicos, fueron igualmente importantes para logar dicha estructura. Mientras que la ocurrencia del MRCA de *A. tincella* dentro del Río Lerma *ca.* 0.5 Ma, permitió a la especie abarcar una amplia área de distribución, debido a que estuvo provista con los atributos biológicos y ecológicos, tales como ser un organismo omnívoro, relativamente tolerante a los cambios en las condiciones ambientales, que habita en una amplia variedad de cuerpos de agua (Mercado-Silva *et al.*, 2005), y se considera medianamente buen dispersor (Miller *et al.*, 2005). De no haber sido por estos atributos, no hubiera podido colonizar distintas áreas, y resistir el aislamiento y todos los procesos que este implica como la fragmentación y degradación de hábitats (Pérez-Rodríguez *et al.*, 2015).

Las ventajas que ofrecen estos atributos, al permitir una extensión en el área de distribución y la tolerancia a las fluctuaciones en las condiciones ambientales, en una escala de tiempo mayor, puede llevar a un proceso macro-evolutivo como la radiación adaptativa, tal y como sucedió en el caso de la subfamilia Goodeinae.

Barbour (1973) destaca la proximidad entre las cabeceras de los ríos Lerma y Verde-Santiago, asociándola a posibles conexiones en el pasado. Se tienen al menos dos puntos de contacto posibles entre estos ríos; el primero consiste en la proximidad entre la cabeceras del Río Laja y el Río Cuarenta, afluentes del Lerma y Verde-Santiago, respectivamente (Miller *et al.*, 2005); el segundo, implica un área donde se encuentran algunos de los arroyos de origen, en las cabeceras de los ríos Irapuato y Turbio, afluentes del Lerma, que corren apenas al sur del Río San Juan de los Lagos, que es otro de los afluentes del Río Verde-Santiago (Miller *et al.*, 2005). De acuerdo a la estructura geográfica que resultó para la especie *A. tincella*, dentro del Río Verde-Santiago se obtuvieron dos linajes diferentes, uno correspondiente al Río San Juan de los Lagos, y el otro asociado al Río Cuarenta. Esto corrobora que efectivamente existieron estas dos conexiones (Fig. 5). A pesar de que el Río Cuarenta finalmente es un tributario del Río San Juan de los Lagos (Fig. 5), el aislamiento genético entre ambas poblaciones debería de estar reflejando un aislamiento físico. Ambas poblaciones se aislaron *ca.* 0.1 Ma, probablemente en respuesta a las fluctuaciones climáticas durante el Holoceno (Israde-Alcántara, 1999).

Por otro lado, durante el Holoceno las mismas fluctuaciones climáticas, posiblemente reactivaron dichas conexiones y de esta manera permitieron el paso de *Y. alta* hacia el Río Verde-Santiago utilizando la conexión Laja-Cuarenta. Una vez, en el Río Verde expandió su intervalo de distribución al resto de la cuenca del Río Santiago, los ríos Juchipila, Bolaños y muy seguramente al Huaynamota (Fig. 5).

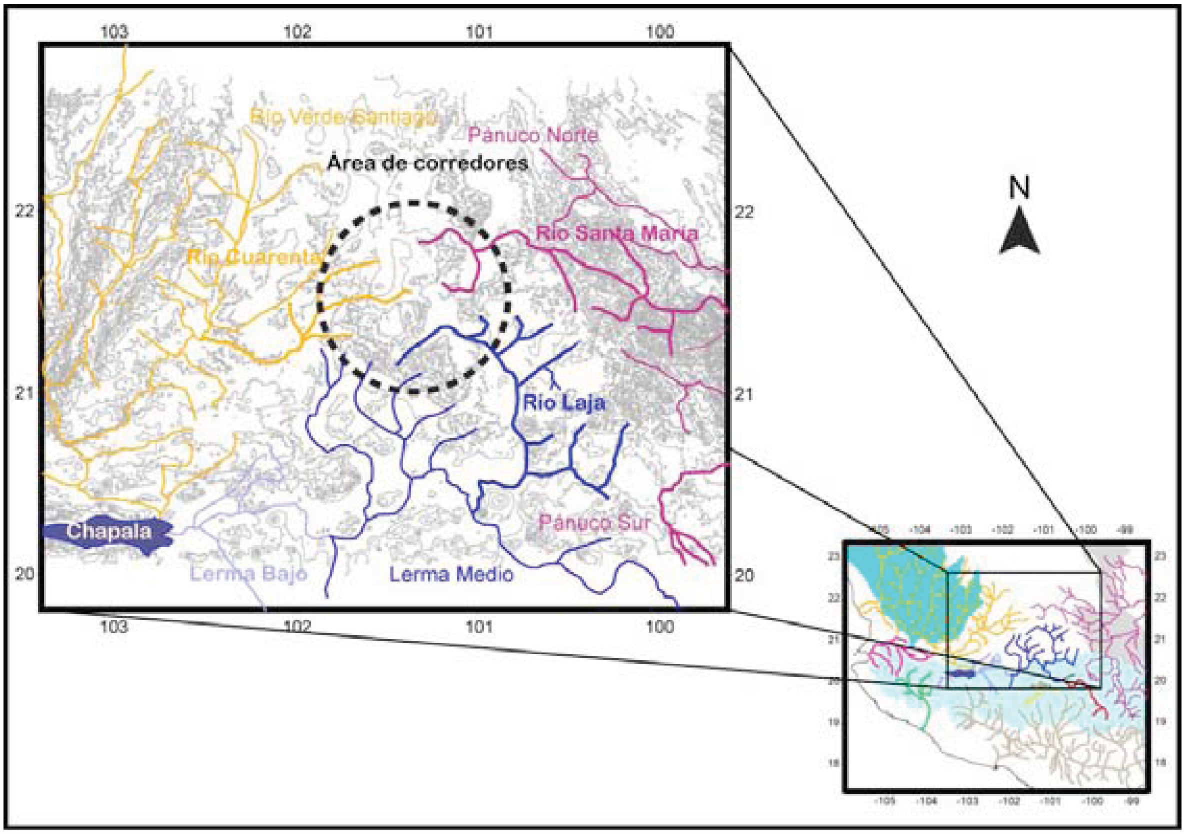


Figura 5. Corredores entre las cabeceras de los ríos Pánuco, Lerma y Verde-Santiago.

5 CONCLUSIONES GENERALES

- La colonización del centro de México del componente neártico de peces dulceacuícolas presentó el siguiente orden cronológico: "Notropinos del sur" a través de la ruta del "Altiplano" durante el Mioceno Temprano; la subfamilia Goodeinae, que aparecen por la ruta "Oeste" a través de la SMOc en el Mioceno Medio; el género *Algansea*, que también utilizó la ruta "Oeste" en el Mioceno Superior, y por último, el género *Moxostoma*, utilizó primero la ruta del "Altiplano" para cruzar del Río Bravo a las cuencas de la vertiente Pacifico, y después la SMOc para arribar al centro de México.

- La dinámica en el cambio de la composición ictiofaunistica en el centro de México desde el Mioceno Inferior hasta el Holoceno, particularmente para el componente neártico, ha sido determinada por factores extrínsecos (configuración de la fisiografía de la cuenca del Río Lerma) e intrínsecos (diferencias en la historia natural y los atributos biológicos y ecológicos como la capacidad diferencial de dispersión y la tolerancia a los cambios ambientales).

- Se describieron cuatro eventos de congruencia biogeográfica de los grupos de peces neárticos en el centro de México, predominando la frecuencia en ocurrencia entre Goodeinae y "Notropinos del sur".

- Con excepción de la especie *M. austrinum*, cuyo origen fue inferido en el Río Ameca en el Pleistoceno, las otras especies, *N. calientis*, *A. tincella* y *Y. alta*, se originaron dentro del sistema Lerma-Chapala *ca.* 2.1, 0.56 y 0.38 Ma, respectivamente.

- El patrón de codistribución parcial entre los intervalos de las cuatro especies es un reflejo de la ausencia de congruencia filogeográfica. Dicho patrón esta asociado a factores tanto extrínsecos como intrínsecos. Los primeros consisten en el tiempo y espacio de origen de cada una de las cuatro especies, mientras que los segundos tienen que ver con la capacidad de dispersión y de tolerancia a los cambios en las condiciones ambientales, que juegan un papel importante en la extensión del área de distribución.

- La presencia de grupos de peces neárticos que actualmente solo estan representados como fósiles en el centro de México, como es el caso del centrárquido, *Micropterus* sp., corrobora la contundencia de los atributos biológicos y ecológicos de las especies para que puedan establecerse, o por el contrario, su desaparición después de los cambios en las condiciones ambientales. Por otro lado, la presencia de estos atributos que permiten el establecimiento y la extensión del área de distribución de las especies, a una mayor escala de tiempo, podrían conducir a una radiación adaptativa, al menos incrementar la tasa de diversificación.

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