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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-s*7 (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)].

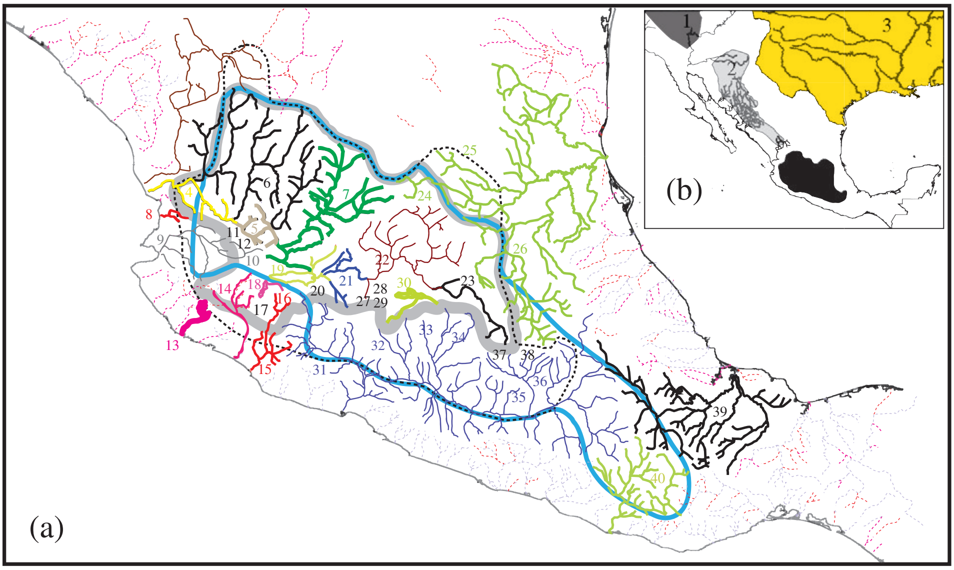

FIG. 1. General distribution pattern of the three groups of fishes. (a) Distribution ranges of Goodeinae (.....), southern notropins (—) and *Algansea* (—) and regional units (river basins) (b) Distribution pattern of western and plateau tracks: —and —areas correspond to the distribution ranges of the 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 $\delta\text{AIC}_{\text{RC}}$ 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

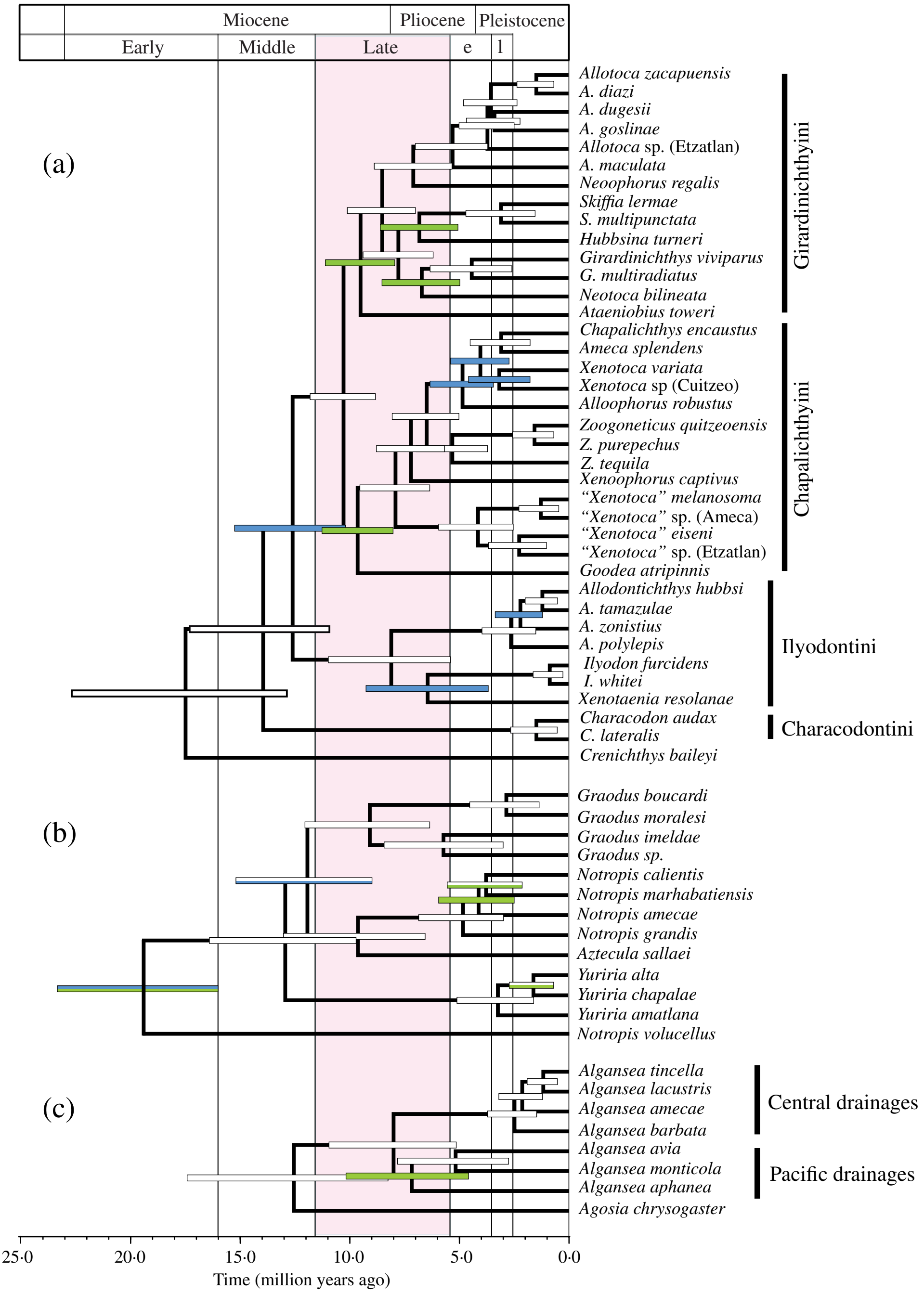

FIG. 2. Phylogenetic relationships and divergence times of the three groups of fishes. (a) subfamily Goodeinae, (b) southern notropins and (c) genus *Algansea*. Bars at nodes, 95% highest posterior density intervals of age estimates; □, a node support ≥95% of bootstrap and posterior probabilities; 🟦, 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).

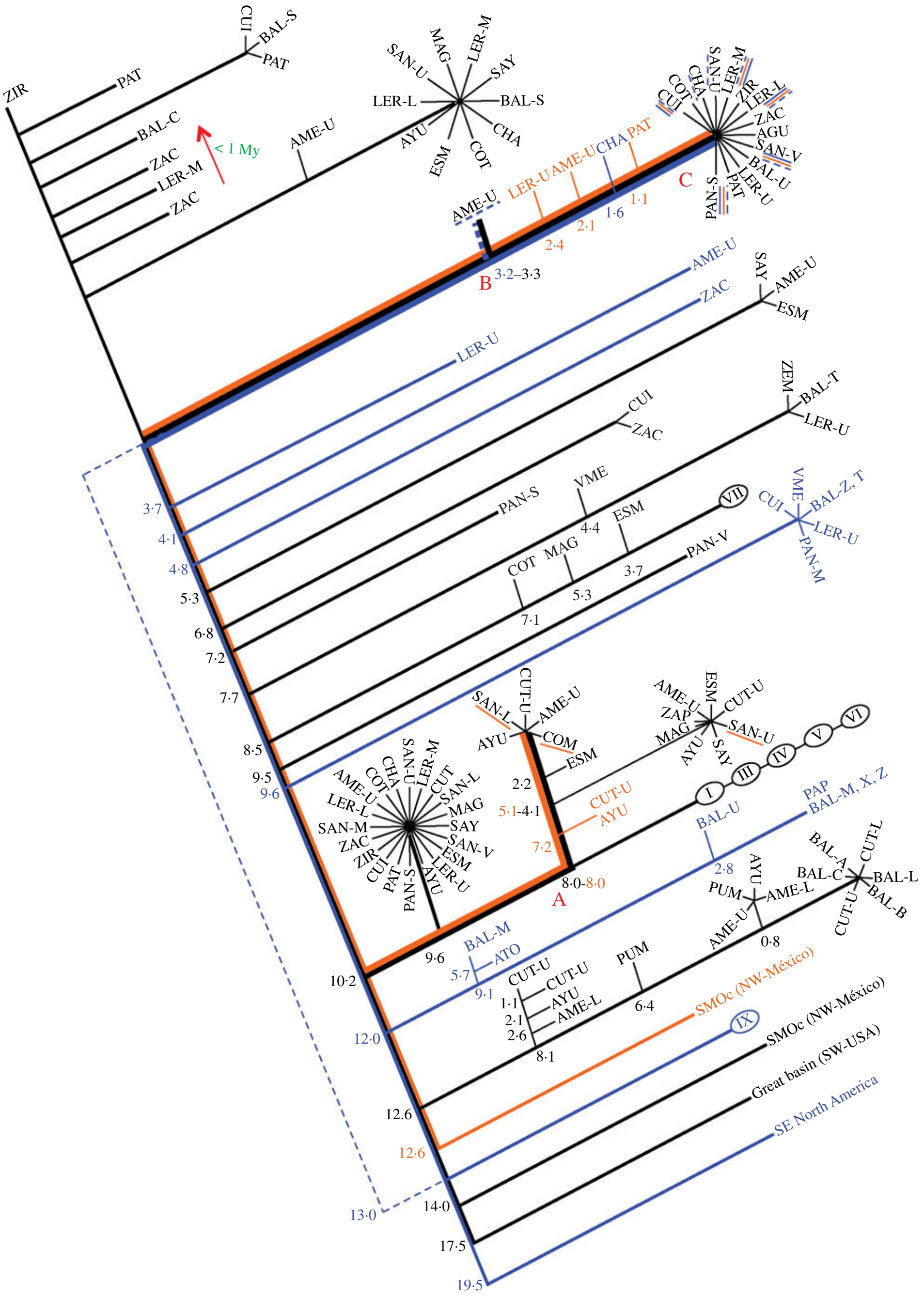

FIG. 3. Condensed general area cladogram (phylogenetic analysis for comparing tree, PACT) of Goodeinae (—). The single clade events are shown as coloured branches. The concordant patterns nested in the template cladogram (Goodeinae) have a node labelled with a red letter (A–C) and a line in color in 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 $\delta\text{AIC}_{\text{RC}}$ 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),

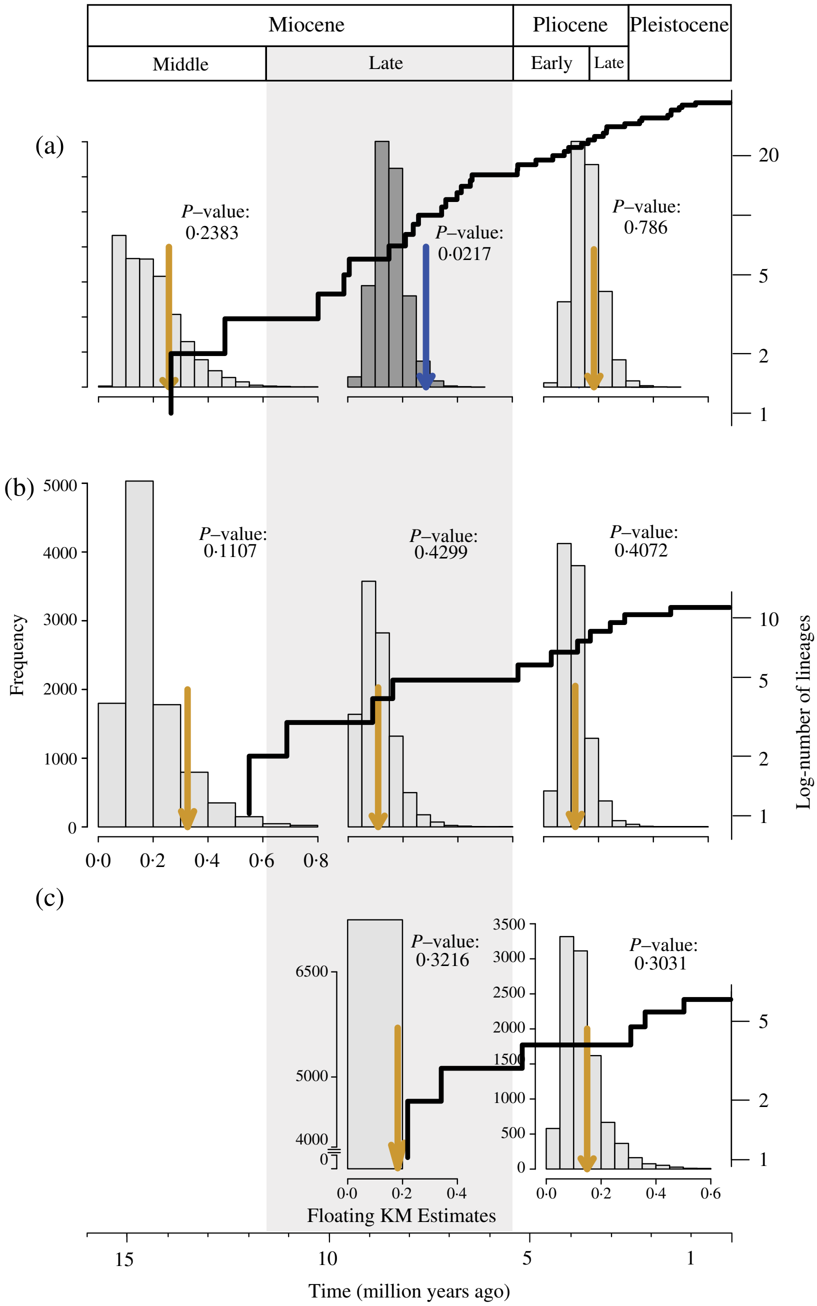

FIG. 4. Diversification pattern of the three groups of fishes: (a) Goodeinae, (b) southern notropins and (c) genus *Algansea*. Ln-transformed accumulations of lineages through time are shown (–): ▬, ←, the Kendall–Moran (KM) estimate of a global diversification rate for specified geological time intervals (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

						MCCR test			
Groups	Pure birth	Birth–death	DDL	DDX	Yule-3-rate	Richness	Sampled	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 (−1·08), *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$_c$, 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.

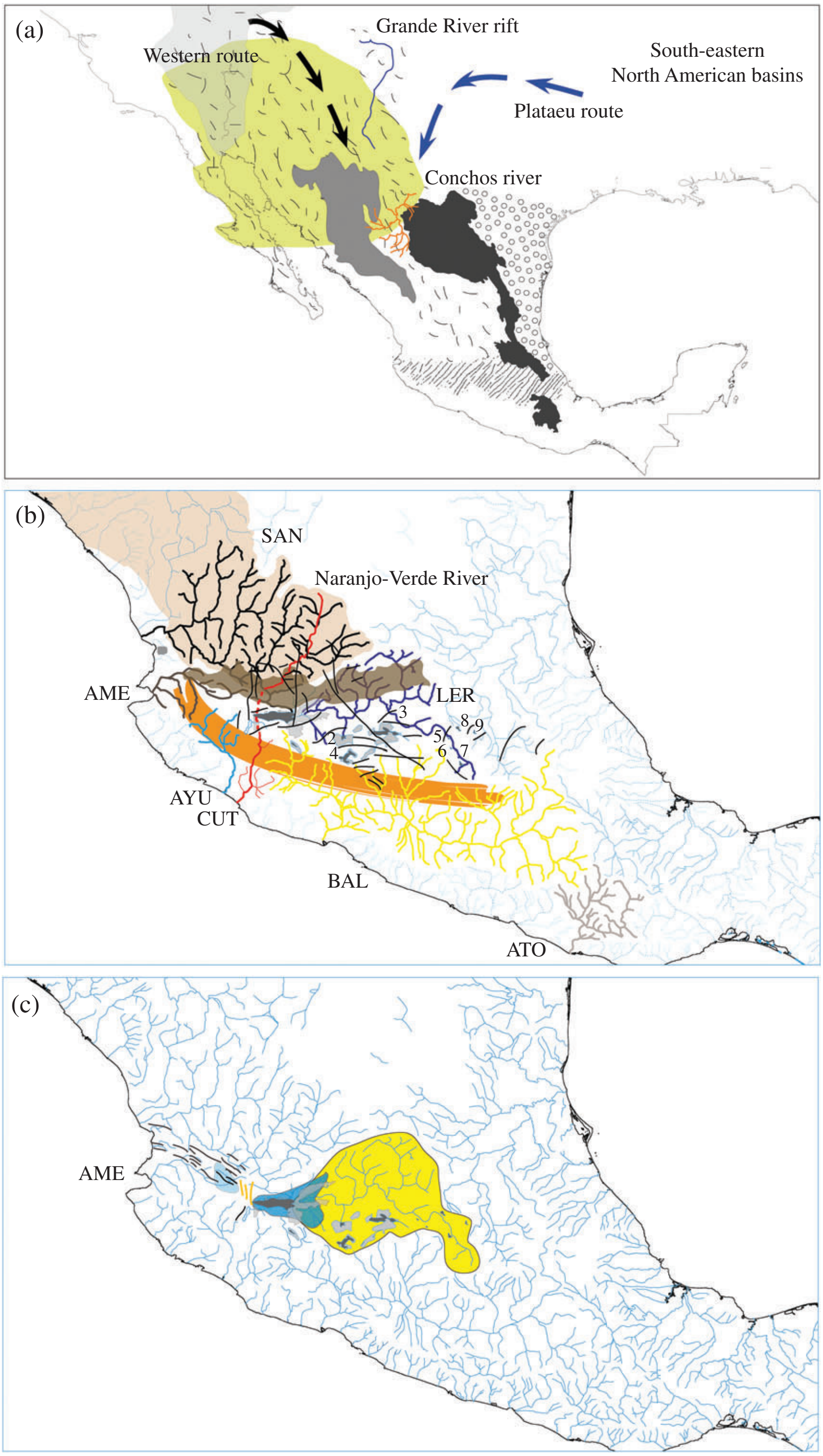

FIG. 5. Legend on next page.

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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