
Abstract

The Neotropic large-eyed and well-pigmented diurnal characid fish *Astyanax* has developed a series of cave populations in Northeastern Mexico. These divide morphologically into a group of strongly eye- and pigment-reduced (SEP) cave populations and another one characterized by variable eye size and pigmentation (VEP cave populations). Molecular and biogeographic data imply that they derive from the Neotropic *Astyanax* surface fish, which were able to invade North America up to the Rio Grande drainage after the closure of the Central American land bridge. Its recent distributional pattern is strongly influenced by Pleistocene climatic changes and is characterized by regional extinction and recolonization from the warmer south and/or survival in climatically buffered refuges. An example of this are the SEP cave fish populations, which according to cytochrome b analysis do not cluster with the surface fish from neighboring rivers and creeks but with fish from a remote location about 500 km away in the Central Mexican Plateau. In line with this, they do not group with either the VEP cave fish or with surface fish from the cave area, and based on microsatellites and SNP studies, they exhibit relation to populations from southern Mexico and Belize. The SEP cave fish and some relic surface fish populations from isolated locations all over Mexico derive from the oldest invasion. In contrast, based on cytochrome b studies, the VEP cave populations cluster with the recent surface fish from the cave area, which is widespread in Northern Mexico. The VEP cave populations derive from a more recent invasion of surface fish into Northern Mexico. In particular, the differing degree of eye reduction between SEP and VEP cave fish reflects the different times of cave entry. Cave colonization in VEP and SEP cave populations took place in parallel and resulted in multiple convergent evolutions.

4.1 *Astyanax* Surface Fish

The characid *Astyanax* is a Neotropical carnivorous midwater fish that possesses large eyes and well-developed pigmentation. It is widespread in all types of freshwater habitats in the coastal lowlands but has also penetrated several streams in the highlands of Mexico as far north as the Rio Grande in Texas and its tributaries (Miller and Smith 1986). Its taxonomy is still under dispute. Based on meristic and morphometric differences as well as on molecular genetic analyses, varying numbers of species have been suggested (Eigenmann 1917; Géry 1977; Reis et al. 2003; Schmitter-Soto 2016), which often do not meet the rules of the International Code of Zoological Nomenclature (e.g. Ornelas-García et al. 2008) (Fig. 4.1) (see Sect. 5.5).

4.2 *Astyanax* Cave Fish

In three separate geographically adjacent limestone ridges located at the eastern margin of the Mexican Sierra Madre Oriental del Norte, the Sierra de El Abra (El Abra populations), Sierra de la Colmena (Rio Subterráneo population), and Sierra de Guatemala (Guatemala populations), a series of cave populations have originated (Table 4.1, Figs. 4.2 and 4.3). Only one *Astyanax* cave population occurs far away from this area, in Central Mexico (Espinasa et al. 2001). Since the discovery of the first blind cave characid *Anoptichthys jordani* (Hubbs and Innes 1936), the Chica fish, about 30 caves inhabited by *Astyanax* cave fish have been detected and explored to date (Mitchell et al. 1977).

The largest number of populations is found in the Sierra de El Abra (Elliott 2015a, b; Gross 2012; Mitchell et al. 1977) (Fig. 4.3). Their most obvious features are external eyelessness caused by the strongly reduced eye rudiments deeply sunken into the eye orbit as well as paleness resulting from decreased numbers of melanophore colour cells and reduced melanin content (Table 4.1) (Mitchell et al.

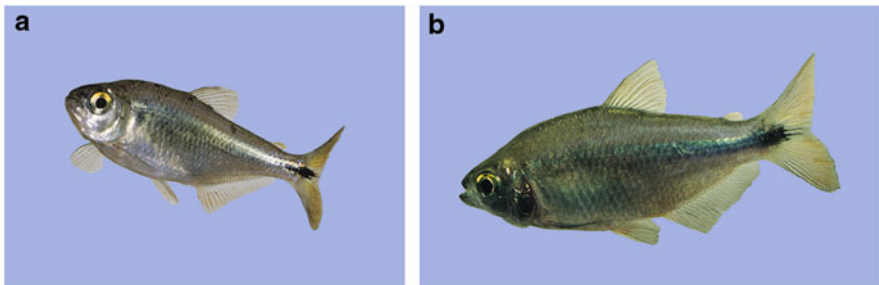


Fig. 4.1 *Astyanax* surface fish from Rio Teapao (Southern Mexico) (cf. “*A. aeneus*”) and Cenote Dzibilchaltún (Yucatán) (cf. “*A. altior*”)

Table 4.1 Distribution and characteristics of the main *Asytanax* cave populations

Cave population	Location	Phylogenetically		Introgressed by		Eyes			Melanophores			Surface fish in cave	
		Old/SEP	Young/VEP	SEP	VEP	Strongly reduced	Variably reduced	Number reduced	Number reduced	Brown gene	Albino gene		
Pachón	Sierra de El Abra	X			X	X			X	X		X	
Yerbaniz	Sierra de El Abra	X			X	X				X		X	Many
Sabinos	Sierra de El Abra	X				X				X			
Arroyo	Sierra de El Abra	X				X				X			
Tinaja	Sierra de El Abra	X				X				X			
Pichijumo	Sierra de El Abra	X			X	X				X			Few
Piedras	Sierra de El Abra	X				X				X			
Curva	Sierra de El Abra	X				X				X			
Toro	Sierra de El Abra	X				X				X			

(continued)

Table 4.1 (continued)

Cave population	Location	Phylogenetically		Introgressed by		Eyes		Melanophores			Surface fish in cave
		Old/SEP	Young/VEP	SEP	VEP	Strongly reduced	Variably reduced	Number reduced	Brown gene	Albino gene	
Chica	Sierra de El Abra		X	X			X	?	?		? (Few or none)
Cuates	Sierra de El Abra		X	X?			X	?			
Micos	Sierra Colmena		X				X			X ^b	Many
Caballo	Sierra Guatemala		X				X	?			
Molino	Sierra Guatemala		X				X ^a	X		X	

^aOnly genetically variable^bNot manifested

SEP strongly eye- and pigment-reduced, VEP variable eye size and pigmentation, ? uncertain

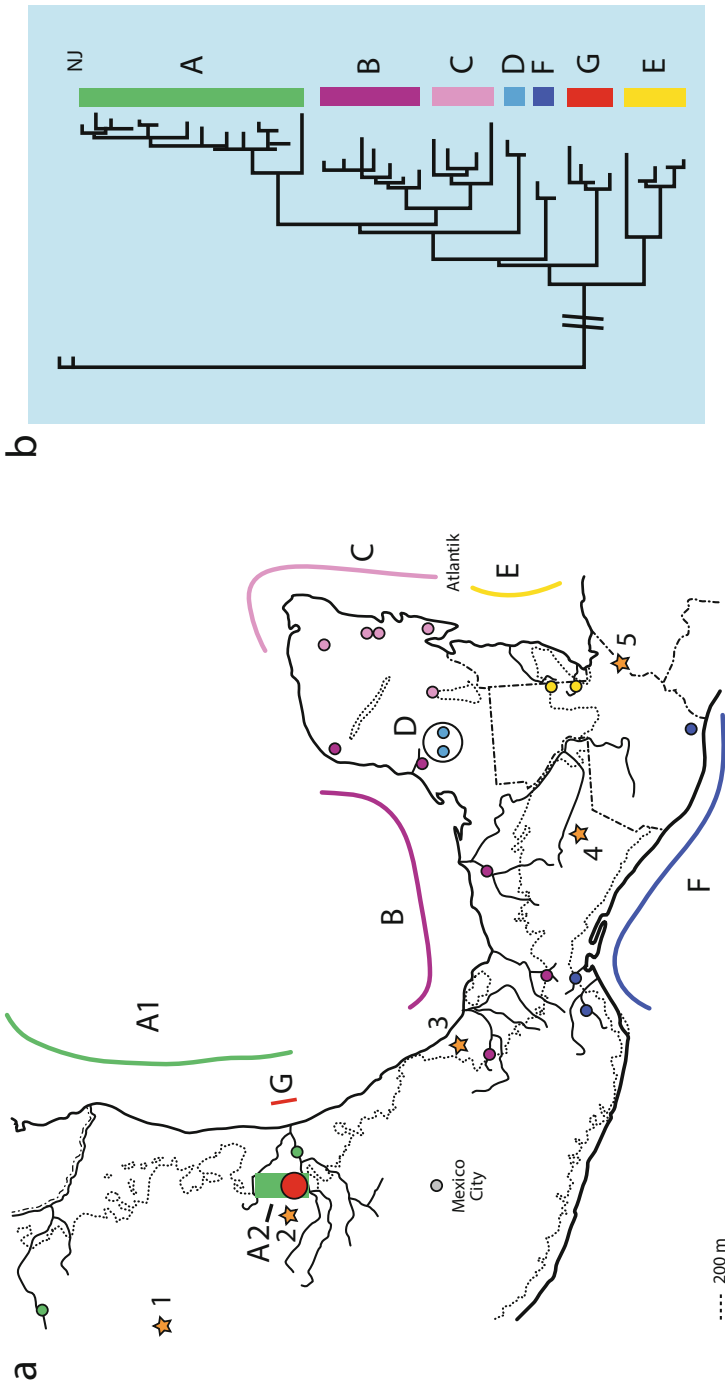


Fig. 4.2 Pattern of geographical distribution of surface and cave *Astyanax* mtDNA lineages occurring in Mexico, Guatemala, and Belize (a) and Bayesian consensus tree (b) illustrating the phylogenetic relationships among 53 cytochrome b mtDNA haplotypes found in 35 *Astyanax* surface and cave populations. The clade A to F include surface populations. The clade from the northern Gulf Coast (A) is split into one subclade (A1) containing all surface populations from the Río Panuco drainage and one haplotype found in a population from the Río Grande system, and the subclade A2 including three of the strongly reduced SEP cave populations Pachón, Pichujmo, and Yerbaniz, as well as the VEP cave populations Molino, Chitea, and Micos. Clade G includes the SEP Piedras, Tinaja, Sabinos, and Curva cave populations. 1–5 = Surface populations from Ríos Aguanaval/Mezquital (1), Rascón/Tamasopo (2), Río Máquinas (3), Lagunas de Montebello (4), Ríos Polochic, Grijalva, Usumacinta (5). *Dotted line* indicates 200 m contour line, *SEP* strongly eye- and pigment-reduced, *VEP* variably eye- and pigment-reduced (adapted from Strecker et al. 2004; Ornelas-García et al. 2008)

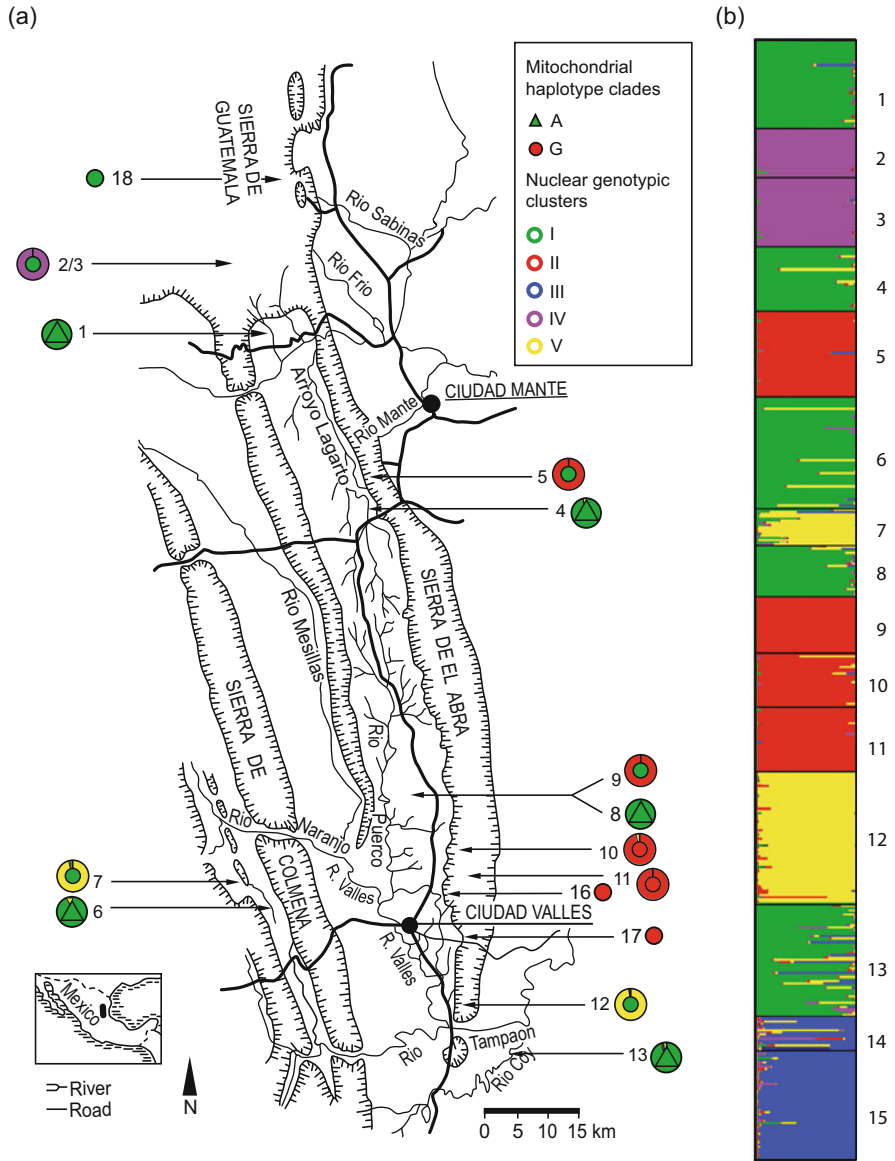


Fig. 4.3 Geographic distribution and genetic variation in Mexican surface and cave *Astyanax* populations. (a) Map of sampling sites in the cave region in Northeastern Mexico. *Outer circles* represent nuclear genotypic clusters delimited using STRUCTURE for $K = 5$; *inner circles and triangles* represent haplotype lineages of cave and surface populations, respectively. (b) Results of the admixture analysis with STRUCTURE for $K = 5$. Numbers refer to populations: 1. Rio Coahuila, 2. Caballo Moro cave fish with sunken eyes, 3. Caballo Moro cave fish with eyes, 4. Pachón surface, 5. Pachón cave, 6. Micos surface, 7. Micos cave, 8. Yerbaniz cave (surface fish washed into the cave), 9. Yerbaniz cave (cave fish), 10. Sabinos cave, 11. Tinaja cave, 12. Chica cave, 13. Rio Coy, 14. Rio Coatzacoalcos drainage, 15. Mahajual (Eastern Yucatán), 16. Piedras cave, 17. Curva cave, 18. Molino cave (adapted from Strecker et al. 2012)

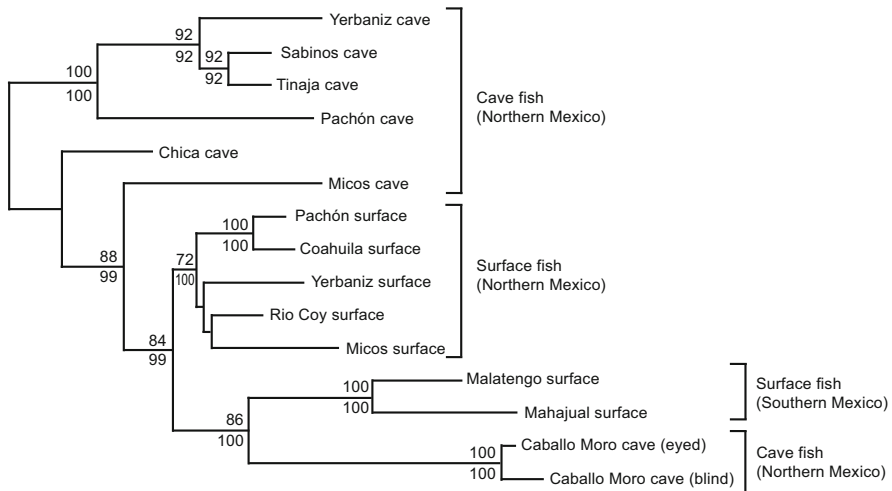


Fig. 4.4 Neighbour joining tree based on Nei's D_A distance from six microsatellite loci of *Astyanax* cave and surface fish from Northeastern Mexico and surface fish from Southern Mexico. Values along branches indicate bootstrap values either based on D_A distances (*above*) or F_{ST} values (*below*) (adapted from Strecker et al. 2012)

1977; Wilkens 1988, 2007). They were therefore denominated strongly eye- and pigment-reduced (SEP) populations (Strecker et al. 2004, 2012; Wilkens 1988) and based on cytochrome b studies classified as phylogenetically old. According to microsatellite analysis, the El Abra populations build a cluster of their own (Bradic et al. 2012; Strecker et al. 2012) (Fig. 4.4).

A second group exhibits variability in the size of their eyes (which, except for the Molino cave fish, are not or just slightly overgrown by body tissue and are still visible externally) and the dark melanin pigmentation. Because of their variability of eyes and pigmentation they are called VEP populations (Strecker et al. 2004). Except for the Chica and probably also the geographically adjacent Los Cuates populations, all others are found outside the Sierra de El Abra in the S. de Colmena (Micos or Rio Subterraneo population) and the S. de Guatemala (e.g. Caballo Moro and Molino population) (Table 4.1). All were originally designated 'mixed fish populations' by Mitchell et al. (1977), because it was believed that these populations were composed of surface fish, cave fish, and their hybrids. In contrast to this, the variability of eyes and pigmentation was alternatively interpreted as resulting from their phylogenetically young age (Table 4.1) (Kosswig 1965; Strecker et al. 2003, 2004, 2012; Wilkens 1988).

4.3 Phylogeography and Speciation of Surface and Cave *Astyanax*

4.3.1 Invasion of Surface *Astyanax* from South America and Origin of the Cave Forms

It is assumed that surface *Astyanax* as a Neotropic primary freshwater fish could not invade North America before the closure of the Middle American land bridge in the late Pliocene (Bussing 1985; Bermingham and Martin 1998; Myers 1966; Perdices et al. 2002; Reeves and Bermingham 2006). Phylogeographic studies based on mtDNA revealed several distinctive haplotype lineages in *Astyanax* surface fish in Northern Central America, which mainly represent geographical patterns of distribution (Strecker et al. 2004; Ornelas-García et al. 2008) (Fig. 4.2). Some cover a broad geographic range like lineages A and B, north and south of the Trans-Mexican Volcanic Belt (TMVB), respectively, whereas others are locally restricted as, for example, lineage D on Yucatán or Montebello (4 in Fig. 4.2). Interestingly, in Northeastern Mexico the SEP cave populations (clade G) do not cluster with their neighbouring surface populations (clade A2), nor do the Belizean populations (clade E) group with their geographic neighbours from the Yucatán (clades B, C and D) or with *Astyanax* from locations 4 and 5 (Strecker et al. 2004; Ornelas-García et al. 2008) (Fig. 4.2).

The current distribution pattern of haplotype lineages can be explained by several invasions of surface *Astyanax* from the South. This was probably caused by Pleistocene climate changes and their concomitants like fluctuating temperatures and precipitation leading to large-scale extinction and distributional fragmentation. During warmer periods, recolonization of different genetic lineages took place either from the South or from isolated refugia within the former distributional area (Hausdorf et al. 2011; Strecker et al. 2004). An example of such glacial refuge may be provided by a warm spring in Northwestern Mexico, which to date, at 2000 m altitude, still represents the highest elevation attained by *Astyanax* surface fish in Mexico north of the TMVB (Miller and Smith 1986). It lies between the endorheic drainage of the Rios Aguanaval or Rio Nazas and the Pacific affluent Rio Mezquital (Fig. 4.2), which contain surface *Astyanax* carrying, beside the widespread haplogroup A, the same haplotype lineage G as the SEP cave fish in caves about 500 km away by air. Similarly, the SEP cave fish (haplotype lineage G) could survive in caves in the Sierra de El Abra because the cave habitat in general is characterized by constancy of temperature enabling species to overcome a temporarily fluctuating climate (Juberthie 2000). This environmental characteristic is proven by the co-occurrence of a series of crustacean cave species like palaemonid shrimps (genus *Trogloxemus*), cirrolanid isopodes (genus *Speocirolana*) (Fig. 3.6), or mysids (genus *Speleomysis*). These species are much older inhabitants in these caves and had already colonized the Pliocene anchialine caves situated along the Sierra de El Abra before the arrival of *Astyanax* surface fish in the cave region (see Sect. 3.2). The SEP cave haplotype lineage G is a sister group of the before-mentioned geographically remote surface populations from Aguanaval and

Mezquital (Fig. 4.2). They are more closely related than either are to two other relic surface populations, Rascón and Tamasopo, found close to the cave area by Ornelas-García et al. (2008).

Additionally, three other lineages occur far south of the TMVB in the drainage systems Polochic-Grijalva-Usumacinta, Lagunas de Montebello, and Río Máquinas (Ornelas-García et al. 2008). These four lineages build a polytomy suggesting that the ancestral lineage spread rapidly across Northern America, as was similarly shown for characiform fish in Mesoamerica (Reeves and Bermingham 2006). The large genetic distance of 12–17 mutations between these lineages indicates a rather old separation. The four haplotype lineages form a basal clade (Fig. 4.2) (Ornelas-García et al. 2008), suggesting that they descended from the first invasion from the South to north of the TMVB (Strecker et al. 2004). This is supported by the high level of troglomorphism found in all SEP populations, given that the degree of troglomorphism and phylogenetic age are correlated (see Chap. 3) (Culver and Wilkens 2000).

The haplotype lineage A is widely spread north of the TMVB and represents a more recent invasion. It includes surface populations as well as SEP and VEP cave fish. As will be shown below, it is suggested that the SEP populations, which are grouping in this lineage, are the result of introgressive hybridization (see Sect. 5.4).

Notably, SEP cave populations like Piedras, Sabinos, Tinaja, and Curva exclusively occur in the Sierra de El Abra and are missing outside it in the geographically separated Sierra de la Colmena and Sierra de Guatemala, where only VEP cave populations and none of the Pliocene crustacean cave genera typical of the Sierra de El Abra have been found as yet. It is hypothesized that this biogeographical difference might be explained by the microclimatic and/or hydrological differences of these Sierras. It is worthwhile considering whether the SEP *Astyanax* cave populations that potentially originally existed in the other Sierras became extinct because of the inflow of cool water from higher altitudes during glacial advances, as is proposed for the cave fauna located south of the TMVB (see Sect. 3.3).

In contrast with the Sierra de la Colmena and de Guatemala, no VEP *Astyanax* cave populations seem to exist in the Sierra de El Abra. However, this is only at first glance. It is proposed that VEP cave populations have also arisen in the Sierra de El Abra, because, in karst, new caves are continuously being formed and can be colonized. Such cave populations may have introgressed and merged with already existing SEP cave populations due to the erosional dynamics of karst. Proof for this is provided by the SEP Pachón and Yerbaniz cave populations, which cluster with the recent surface fish because of mitochondrial capture, but based on their nuclear genotype belong to SEP cave fish (see Chap. 5). As the only exception, Chica can be characterized as a VEP cave fish in the Sierra de El Abra, although in this population too, introgression from an unknown SEP cave population was detected by microsatellite analysis (Strecker et al. 2003) (Fig. 4.3).

The date of cave entry of the *Astyanax* cave fish is still unknown and controversial. Based on allozyme variability, the SEP cave populations were calculated to be very young, having a post-Pleistocene age (Avisé and Selander 1972). In contrast, gene differentiation calculations between populations of unequal sizes revealed an

approximate divergence time between $710,000 \pm 460,000$ years ago for the Pachón and $525,000 \pm 330,000$ years ago for the Sabinos cave fish (Chakraborty and Nei 1974).

According to the calibration rate of 1.5% (Zardoya and Doadrio 1999) the cytochrome b analyses of *Astyanax* revealed a divergence time of between 1.8 and 4.5 million years ago (mya) with a mean of 3.1 mya (Strecker et al. 2004), which is a date concurring with that of the final closure of the Middle American land bridge at the end of the Pliocene (Reeves and Bermingham 2006; Picq et al. 2014). This date is also confirmed by the second Neotropic salt intolerant primary freshwater fish genus *Rhamdia* to reach North America, including the *R. laticauda* clade, which is sister species to a series of cave species (Wilkens 2001), followed by a rapid expansion in Central America between 2.9 and 2.5 mya (Perdices et al. 2002).

In contrast, Ornelas-García et al. (2008, 2014) assume an earlier invasion of surface *Astyanax* during the Miocene at about 7.8–8.1 mya using a different calibration rate. However, biogeographical data from the totally karstic Yucatán peninsula, a landscape characterized by the complete absence of surface rivers, support the more recent invasion time as calculated by Strecker et al. (2004). The geographical distribution of the salt-intolerant primary freshwater fish *Astyanax* is exclusively restricted to freshwater habitats situated in the narrow Pleistocene coastal plain (Fig. 4.5). *Astyanax* is not found in the cenotes of the interior of northern Yucatán, where neotropic salt-tolerant secondary freshwater fish species like *Cichlasoma urophthalmus* (Cichlidae) and the live-bearing toothcarp *Gambusia puncticulata* (Poeciliidae) are common, however (Wilkens 1979). This diverging distribution pattern of primary and secondary fish species results from the fact that the salt-tolerant secondary freshwater species had been able to invade North America long before the final uplift of the Middle American land bridge (Myers 1966; Martin and Bermingham 2000). They could already colonize the interior of the present Yucatán peninsula while, during Mio- and Pliocene, the sea slowly retreated from the limestone platform in a northeasterly direction. The exclusive existence of *Astyanax* in the coastal zones demonstrates that this fish was not yet present in North America, while the secondary freshwater fish already were. As an exception, the hepapterid catfish *Rhamdia guatemalensis*, another Neotropic salt-intolerant primary freshwater fish that arrived at the same time as *Astyanax* in North America (Perdices et al. 2002), was able to later reach the cenotes of the interior of Northern Yucatán. In contrast to *Astyanax*, this fish is a nocturnal and troglophile species. It took advantage of the vast aquatic underground pathways characteristic of the karstic Yucatán peninsula for dispersal (Fig. 4.5) (Wilhelm and Ewing 1972; Wilkens 1982, 1986).

Summarizing, it is suggested that *Astyanax* was able to invade North America only after the closure of the land bridge about 3 mya, as is proposed for other tropical primary freshwater fishes (Bermingham and Martin 1998; Reeves and Bermingham 2006; Perdices et al. 2002), whereas salt-tolerant, so-called secondary freshwater fish like cichlids or poecilids could have already dispersed to the North about 8 mya (Martin and Bermingham 2000; Myers 1966).

Thus, based on the assumption that the Neotropic surface *Astyanax* only reached Northern Mexico after the final uplift of the Central American land bridge, cave colonization and origin of the SEP cave forms in Northeastern Mexico can be dated

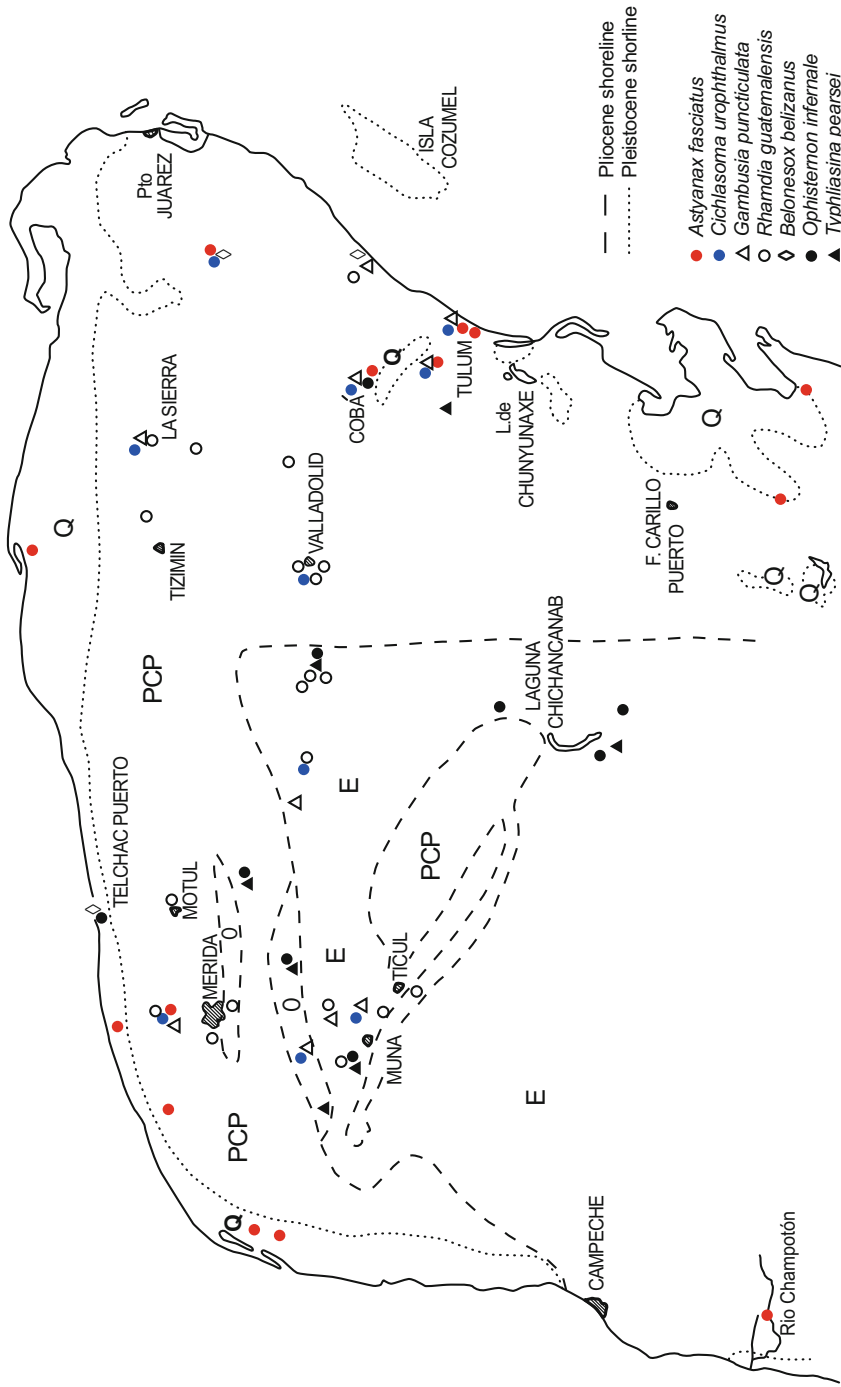


Fig. 4.5 Distribution of the main freshwater fish species in Yucatán. Q Pleistocene, PCP Mio/Pliocene, E Eocene sediments (adapted from Wilkens 1979; Wilhelm and Ewing 1972)

to have taken place around this time, but no earlier. This possibility is corroborated by the co-occurrence with Pliocene marine cave relics, which indicates that surface *Astyanax* in principle could have colonized the caves in the Sierra de El Abra soon after arriving in North America about 3.0 mya. It cannot be ruled out, though, that the marine cave species were better cold adapted than *Astyanax*, which has Neotropical origin. Due to this, cave populations of this fish might have become extinct several times during Pleistocene climatic coolings. In addition, these calculations of cave entry are uncertain, because it can generally be assumed that the cytochrome b calibration data only reveal the splitting time between surface lineages, one of which became the ancestor of the cave forms at an unknown later date (Trontelj et al. 2007).

As concerns the phylogenetically younger *Astyanax* VEP cave populations, the split of lineages for the Micos and the Chica cave fish was calculated as 0.26 and 0.39 mya, respectively (Strecker et al. 2004). However, when comparing the similar intermediate and variable degrees of eye regression of the Micos, Caballo Moro, and Chica cave fish populations with those of the group of lesser eye-reduced fish and crustacea occurring in Mexico south of the TMVB and the Peri-Caribbean islands of the Bahamas (see Chap. 3), it can also be concluded that the VEP populations possibly only originated after the last glacial maximum during Wisconsin at 27,000 to 24,000 years ago, or even only after the Younger Dryas period at 12,900 to 11,700 years ago.

4.3.2 Multiple Origin of Cave Forms

Caves as isolated habitats are usually colonized in parallel by the same widely spread ancestral surface species. As a result, convergent adaptation to cave life starting at the same or even subsequent times may arise. Examples for this have been demonstrated for the freshwater shrimp genus *Macrobrachium* occurring in Mexico south of the TMVB or the crayfish genus *Procambarus* from south of the TMVB and Florida. Also, the hepapterid surface catfish *Rhamdia laticauda* occurring south of the TMVB is sister species to a still rising number of cave species, five of which have as yet been taxonomically described (Weber et al. 2003; Wilkens 2001). In Northeastern Mexico, the ictalurid cave catfish *Prietella phreatophila* and *P. lundbergi*, which both derive from the same surface ancestor, have colonized caves distributed over two geographically separate limestone areas (Hendrickson et al. 2001; Wilcox et al. 2004).

The *Astyanax* cave populations, too, are characterized by this evolutionary pattern. The caves in the three different limestone ridges, the Sierra de El Abra, S. de Colmena, and S. de Guatemala, are geographically separated from each other, which indicates independent colonization. This was by at least two invasions of surface fish at different times from the South of Mexico, resulting in SEP and VEP cave populations. For the Sierra de El Abra, it has long been debated whether the cave populations occurring in this karst area are the result of secondary dispersal of an already cave-adapted ancestor or if they have multiple origins (Avisé and Selander 1972; Espinasa and Borowsky 2001; Dowling et al. 2002; Mitchell et al.

1977; Strecker et al. 2003). Based on allozyme studies, it was concluded for the cave fish of the Sierra de El Abra that “the eyeless and unpigmented condition is believed to have evolved in whole or part prior to the present-day subdivision of the populations” (Avisé and Selander 1972). In contrast, Mitchell et al. (1977) suggested, on the basis of hydrological data from the Sierra de El Abra, that a multiple colonization hypothesis is more plausible. This was corroborated by molecular studies. It is assumed that the *Astyanax* surface fish invaded different caves separately and were submitted to convergent evolution (Bradic et al. 2012; Coghill et al. 2014; Strecker et al. 2004, 2012).

Confirmation of convergent evolution of the different SEP cave populations was for the first time shown by the development of larger and better differentiated eyes in the F1 crossing between the SEP Pachón and Sabinos cave fish revealing differences of the genetic basis of eye reduction (Wilkins 1971). Similarly, differences in the respective size ranges of the F2 crossings of the SEP Pachón, Yerbaniz, Piedras, and Curva occurring in the Sierra de El Abra with the VEP Molino cave fish from the Sierra de Guatemala demonstrate that even between the four SEP populations found in relatively close proximity in the Sierra de El Abra, eye genes are submitted to different regressive mutations, to a certain extent (Wilkins and Strecker 2003). The same was described for the pigment *albino* (*Oca2*) and *brown* genes (*Mcl1r*) (Protas et al. 2007; Gross et al. 2009; Gross and Wilkins 2013; Stahl and Gross 2015, see Sects. 6.20.2 and 6.20.3). Nonetheless, the fact that introgressive hybridization with mitochondrial capture has taken place makes it probable that in the Sierra de El Abra, due to the dynamic geohydrological development of its karst system, cave populations were submitted to underground migration (Espinasa and Espinasa 2015) and some of them have merged into a single one.

4.3.3 Population Genetic Diversity of Cave Populations

With rare exceptions, as, for example, found in the troglobitic bivalve *Congeria kusceri* (Dreissenidae) (Bilandžija et al. 2013; Stepien et al. 2001), cave species are characterized by low genetic variability (Caccone et al. 2000; Culver 1982; Culver et al. 1995; Culver and Pipan 2009; Kane et al. 1992). This is also valid for the *Astyanax* cave fish in comparison with the surface fish. Low mtDNA variability found in the SEP Curva, Pachón, Yerbaniz, Tinaja, and Sabinos cave fish and in the VEP Molino and Micos cave populations is congruent with previous data obtained from allozymes in the Pachón and Sabinos cave fish (Avisé and Selander 1972; Dowling et al. 2002; Peters et al. 1975; Strecker et al. 2004). Comparable results are provided by microsatellite and transcriptome studies (Bradic et al. 2012; Hinaux et al. 2013; Strecker et al. 2003, 2012). Furthermore, intrapopulation nucleotide difference of opsin genes is the highest in the surface fish and decreases in Micos and Pachón cave fish, in that order (Yokoyama et al. 1995). It is assumed that the low genetic variability of the *Astyanax* cave populations results from repeated population bottlenecks resulting from temporary food scarcity. This is caused by the *Astyanax* caves receiving food input only once a year during the rainy season. At that time, specimens of surface *Astyanax* as well as of other surface species and

plant material are washed into the cave systems. During the rest of the year the creeks at the surface are dry and no water flows from them into the underground caves. At that time, food scarcity arises as is obviously exemplified by the presence of starving *Astyanax* surface fish (see Fig. 5.3). Further proof of periodic bottlenecking in the *Astyanax* caves is provided by the change from polygenic in the surface to monogenic sex determination in the cave fish (see Sect. 6.3) As the only exception, the Chica cave receives rich food input from large bat roosts, which is so ample that even a large number of crayfish can coexist.

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