Poeciliid Research

Poecilia mexicana as a model of ecological adaptation and convergent evolution across sulfide-rich and cave habitats

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https://doi.org/10.67784/0089

Abstract. *Poecilia mexicana* Steindachner, 1863 has emerged as a powerful model for investigating ecological adaptation, convergent evolution, life-history divergence, and the early stages of ecological speciation. Its exceptional value derives from the repeated occurrence of closely related populations across sharply contrasting habitats, including benign surface waters, hydrogen sulfide-rich springs, nonsulfidic caves, and sulfidic caves, often separated by only a few kilometres. This mini-review synthesizes current knowledge of the taxonomy, phylogenetic relationships, ecological divergence, physiological adaptation, life-history evolution, developmental differentiation, and genomic basis of adaptation in *P. mexicana*. Sulfide-rich habitats impose a particularly strong selective regime because hydrogen sulfide combines acute toxicity with severe hypoxia and disruption of mitochondrial respiration. Populations inhabiting these environments have evolved convergent changes in morphology, trophic ecology, brain organization, reproductive traits, offspring phenotype, and sulfide tolerance. At the mechanistic level, repeated adaptation involves mitochondrial pathways associated with sulfide toxicity, detoxification, and oxygen metabolism, although the genomic routes to similar phenotypes may be only partly parallel. Evidence from common-garden and experimental studies further indicates that many ecological and life-history differences have a substantial genetic basis, while developmental studies demonstrate that similar adult phenotypes can arise through partly distinct developmental trajectories. The occurrence of replicated environmental contrasts across drainages, together with extensive genomic and transcriptomic resources and experimentally tractable populations, makes *P. mexicana* particularly suitable for testing how strong environmental selection translates into phenotypic, physiological, developmental, and genomic divergence. Overall, the species provides an integrated natural framework for understanding how repeated environmental challenges generate convergent functional solutions while retaining lineage-specific evolutionary pathways.

Keywords: *Poecilia mexicana*, Poeciliidae, ecological adaptation, convergent evolution, hydrogen sulfide, hypoxia, sulfide tolerance, cave adaptation, ecological divergence, ecological speciation, life-history evolution, mitochondrial adaptation, genomic convergence.

Introduction. *Poecilia mexicana* Steindachner, 1863 is a livebearing poeciliid fish that has become a major model for studying ecological adaptation, speciation, and convergent evolution because closely related populations repeatedly occupy sharply contrasting habitats, especially hydrogen sulfide-rich springs and caves, over very small geographic scales (Tobler et al., 2018; Kelley et al., 2012). Its research importance also rests on the combination of strong, predictable selection, replicated environmental gradients, reproductive isolation at different stages of divergence, and growing genomic resources that allow links from phenotype to mechanism to be tested directly (Tobler et al., 2018; Kelley et al., 2012; Ryan et al., 2023).

The aim of this mini-review is to synthesize the principal biological features that establish *Poecilia mexicana* as a model system for studying ecological adaptation and

convergent evolution. Particular emphasis is placed on the repeated occupation of sulfide-rich and cave habitats, the resulting morphological, physiological, trophic, life-history, and developmental divergence, and the molecular mechanisms underlying adaptation to hydrogen sulfide and hypoxia. The review also considers how phenotypic convergence relates to genomic parallelism and lineage-specific evolutionary trajectories, highlighting the broader significance of *P. mexicana* for understanding ecological speciation and repeated evolution.

Taxonomy and Phylogeny. *Poecilia mexicana* belongs to the family Poeciliidae and to the subgenus *Mollienesia*, a diverse Middle American lineage whose taxonomy has long been unstable (Tobler et al., 2018; Palacios et al., 2016). Molecular phylogenetic work supports three principal clades within *Mollienesia*: the *P. latipinna*, *P. sphenops*, and *P. mexicana* species complexes (Palacios et al., 2016). That same work found taxonomic inconsistencies and distinct lineages within the *P. mexicana* complex that may represent undescribed species, indicating that diversity in this group is not yet fully resolved (Palacios et al., 2016). Broader phylogeographic analysis of Mexican shortfin mollies further indicates that diversification reflects multiple independent invasions from Middle America, with stronger phylogenetic structure in species south of the Trans-Mexican Volcanic Belt where barriers are greater and lineage persistence appears older (Palacios et al., 2023).

Within the southern Mexican sulfide-spring systems, taxonomy became especially complicated because some sulfide-adapted forms were treated as ecotypes of *P. mexicana*, whereas others were described as endemic species such as *P. sulphuraria* and *P. thermalis* (Palacios et al., 2013). Reassessment of *P. thermalis* showed that its body shape converged with other sulfide-spring forms, but phylogenetic and population genetic analyses placed it as genetically isolated from both *P. mexicana* ecotypes and *P. sulphuraria*, underscoring that similar phenotypes do not necessarily imply close relationship (Palacios et al., 2013). Across the broader species complex, sulfidic springs in southern Mexico were colonized by three different lineages, including two within *P. mexicana* and one represented by *P. sulphuraria*, demonstrating repeated habitat invasion rather than origin from a single sulfide-adapted ancestor (Tobler et al., 2011). A phylogeny of poeciliids inhabiting sulfide springs shows that this ecological transition has occurred across multiple genera, placing the *P. mexicana* complex within a wider comparative framework for repeated evolution.

The species is widely distributed in freshwater habitats along the Atlantic versant from northeastern Mexico into lower Central America (Kelley et al., 2012). Within this broad range, the best-studied populations occur in southern Mexico, where adjacent populations occupy benign surface waters, sulfidic surface creeks, nonsulfidic caves, and sulfidic caves within only a few kilometres of one another (Riesch et al., 2010; Riesch et al., 2016; Plath et al., 2006). In the Cueva del Azufre system, hydrogen sulfide concentrations can exceed 300 μM, and the toxicant is paired with severe hypoxia because H2S interferes with mitochondrial respiration and oxygen transport (Riesch et al., 2016; Tobler et al., 2018). These habitat combinations make *P. mexicana* unusual among evolutionary models because both abiotic toxicity and light regime vary predictably across replicated natural gradients (Riesch et al., 2010; Ryan et al., 2023).

As a poeciliid, *P. mexicana* is viviparous, and male sexual maturation involves transformation of the anal fin into a gonopodium, the intromittent organ used in insemination (Riesch et al., 2016). Female reproductive activity is less obvious externally, and experimental studies have therefore scored maturity through successful brood production (Riesch et al., 2016). The species has also been valuable outside extremophile research: it has been used in work on behaviour, sensory ecology, predator-prey interactions, life-history evolution, and the evolution of sexual reproduction because it is the maternal ancestor of the Amazon molly, *P. formosa* (Kelley et al., 2012). Its native parasite fauna is also increasingly documented, including corrected records and new *Gyrodactylus* species from Mexican poeciliids, which matters for host-parasite ecology and for assessing risks associated with fish translocation (García-Vásquez et al., 2015).

Ecological Divergence and Extremophile Adaptation. Hydrogen sulfide-rich springs impose one of the strongest known abiotic selective regimes on aquatic vertebrates, because H2S is lethal to most metazoans and predictably disrupts mitochondrial energy metabolism (Tobler et al., 2011; Ryan et al., 2023). In response, sulfidic *P. mexicana* populations repeatedly evolved increased H2S tolerance, and ecotoxicological comparisons show convergence toward larger heads, larger gills, and higher sulfide tolerance relative to adjacent nonsulfidic populations (Tobler et al., 2011). Comparative work across poeciliids extends this pattern beyond *P. mexicana*, indicating convergence in morphology, life history, and oxygen-transport genes among independent sulfide-spring lineages (Tobler et al., 2018; Greenway et al., 2020).

Adaptation in these habitats is not limited to toxicity tolerance. Sulfidic populations show convergent shifts in trophic ecology, moving from detritus and algae toward sulfur bacteria and invertebrates, together with broader trophic niche width and shorter intestines (Tobler et al., 2015). Common-garden data indicate that intestinal differences are at least partly genetically based (Tobler et al., 2015). Brain anatomy also diverges predictably: H2S-adapted ecotypes have smaller eyes, smaller optic tectum and total brain volumes, but larger corpora cerebelli and hypothalamic volume than fish from nonsulfidic habitats, although some drainage-specific variation remains (Schulz-Mirbach et al., 2016). These patterns show that adaptation reflects the combined effects of toxicity, hypoxia, turbidity, darkness, and altered resource regimes rather than a single-factor response (Tobler et al., 2018; Tobler et al., 2015).

At the mechanistic level, repeated H2S tolerance centers on conserved mitochondrial pathways. Comparative biochemical and physiological analyses found that mitochondrial function is maintained in sulfide-spring *P. mexicana* but not in ancestral nonsulfidic lineages because of convergent modifications in the primary toxicity target, cytochrome c oxidase, and in a key detoxification enzyme of the sulfide:quinone oxidoreductase pathway (Greenway et al., 2020). Across 10 independent sulfide-spring lineages spanning multiple poeciliid genera, tolerance correlates with convergent changes in the modification and expression of genes involved in H2S toxicity and detoxification, in some cases down to the same codons (Greenway et al., 2020). The core physiological pathway underlying this response is illustrated by mitochondrial toxicity and detoxification components and by activity differences in COX and SQR between ecotypes (Figure 1).

Life-history divergence in *P. mexicana* is one of the clearest organismal signatures of adaptation to extreme habitats. Female populations from toxic and dark environments consistently show reduced fecundity and increased offspring size, a pattern interpreted as either direct selection for greater offspring autonomy or a constraint imposed by chronic stress and low resources (Riesch et al., 2010). Across poeciliids, embryo size scales with habitat sulfide concentration, and endemic sulfur-adapted forms show the strongest expression of this shift (Plath & Schlupp, 2011; Riesch et al., 2010). More recent work indicates that this divergence is caused primarily by genetic differentiation rather than maternal effects alone: offspring from sulfidic populations tend to be born larger, mature later, show lower burst swimming performance, and differ behaviorally in exploration and feeding efficiency, while maternal effects are weaker and additive (Coffin et al., 2024).

Male life histories also diverge. Males from extreme habitats show strong site-specific differences in body size, fat content, and gonadosomatic index, and most of these differences persist under common-garden rearing, supporting a genetic component to divergence (Plath & Schlupp, 2011). In cave habitats, size distributions are skewed toward smaller males relative to surface populations (Plath & Schlupp, 2011). Experimental work comparing surface and cave ecotypes also found sex-specific local adaptation: surface females performed best under high food and normal light-dark cycles and showed near-complete reproductive failure in darkness, whereas cave females were comparatively robust across treatments; males showed weaker evidence for local adaptation (Riesch et al., 2016).

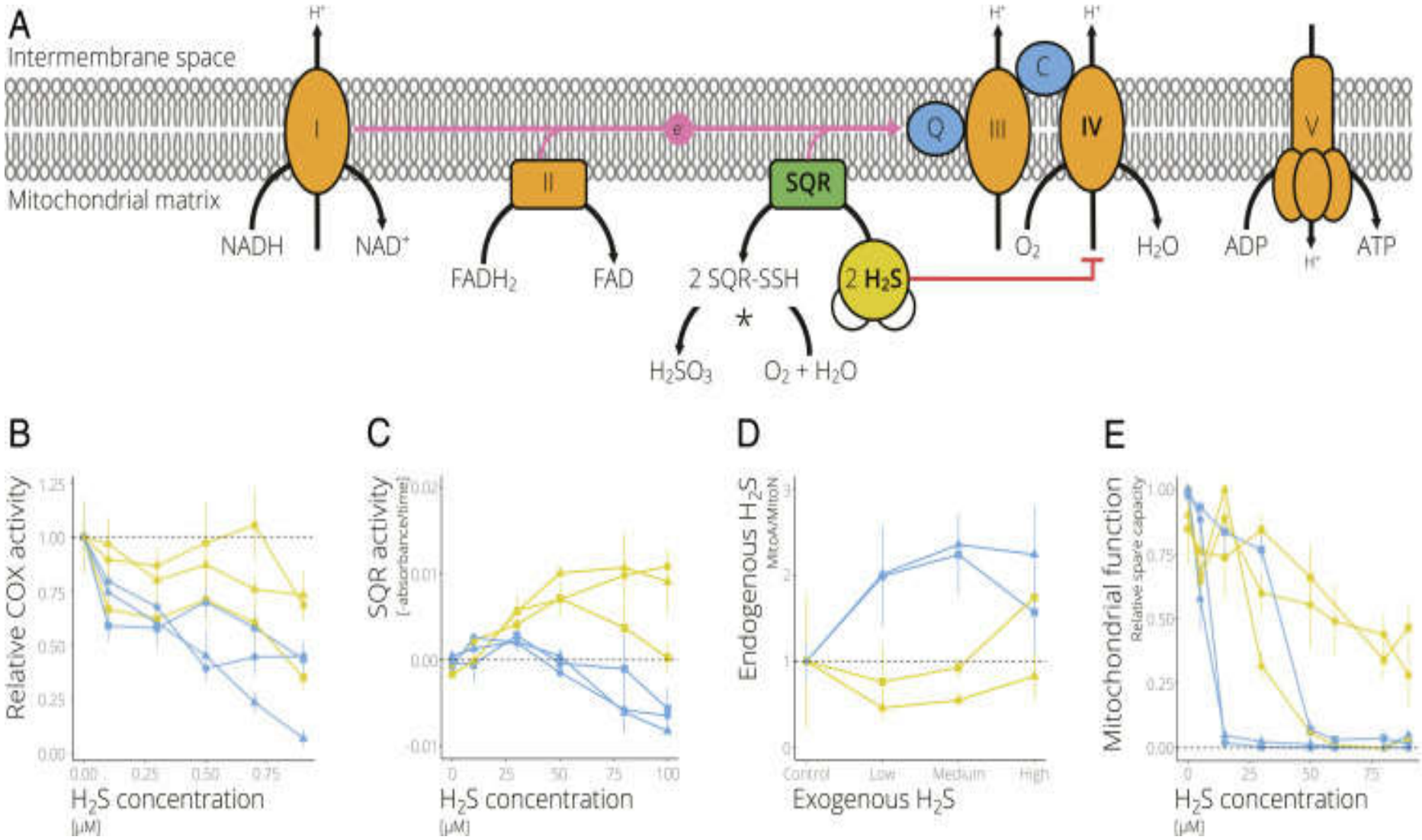


Figure 1. Mitochondrial toxicity and detoxification pathways underlying sulfide tolerance (Greenway et al., 2020).

Embryological comparisons show that convergent adult phenotypes do not always arise through identical developmental routes. In extremophile mollies, embryo mass declines convergently, but patterns of embryonic fat content and ovum or embryo diameter differ among lineages (Schlupp et al., 2011). Relative head size increases through development in both extremophile forms, while eye growth is arrested during mid-stage development in cave mollies but not in surface or sulfur mollies (Schlupp et al., 2011). Cave mollies also show reduced yolk carotenoid signal throughout development, suggesting an additional developmental axis along which adaptation may contribute to reproductive isolation (Schlupp et al., 2011) (Table 1).

Table 1

Comparative summary of core biological dimensions in the species

Dimension	*Main finding*	*Evidence base*
Taxonomic position	Member of Poeciliidae, subgenus *Mollienesia*, within the *P. mexicana* species complex	(Palacios et al., 2016)
Habitat breadth	Occupies benign surface waters, sulfidic springs, nonsulfidic caves, and sulfidic caves	(Riesch et al., 2010; Riesch et al., 2016)
Reproductive mode	Viviparous livebearer with male gonopodium-based insemination	(Riesch et al., 2016)
Life-history shift in extremes	Larger offspring and reduced fecundity in toxic and dark habitats	(Riesch et al., 2010)
Ecological specialization	Diet shifts toward sulfur bacteria and invertebrates; intestines become shorter	(Tobler et al., 2015).

Poecilia mexicana as a Model System. *Poecilia mexicana* is studied so intensively because it unites several features rarely present in one vertebrate system. Extreme habitats are adjacent to benign habitats, environmental differences are sharp and replicated across drainages, and livebearing fish are easy to maintain and breed in the laboratory, which allows field patterns to be tested experimentally (Tobler et al., 2018; Ryan et al., 2023). Adaptation to H2S-rich habitats also spans much of the speciation continuum, from limited differentiation to complete reproductive isolation, making the system especially useful for studying ecological speciation in real time (Tobler et al., 2018; Palacios et al., 2013).

The system is equally important as a model for convergent evolution. Evidence is mixed across biological levels: phenotypic and physiological convergence is strong, but genomic convergence is more nuanced. One study found very little parallelism at the level of SNPs, divergent genomic regions, or genes, with much greater overlap only at the level of metabolic pathways, implying multiple genetic routes to similar functional outcomes (Pfenninger et al., 2015). More recent work, however, identified two mitochondrial sulfide-detoxification genes with signatures of selection in all five sulfidic populations examined and long shared haplotypes among sulfidic populations, supporting a role for standing genetic variation in repeated adaptation (Ryan et al., 2023). Together, these results suggest that repeated evolution in *P. mexicana* is neither wholly deterministic nor wholly contingent: strong selection repeatedly targets the same physiological functions, while the underlying genomic routes can be partly shared and partly lineage-specific (Ryan et al., 2023; Pfenninger et al., 2015; Ryan et al., 2023).

The species' model status is strengthened further by genomic infrastructure. A reference transcriptome identified more than 53,000 putatively unique loci and candidate genes involved in oxidative stress, hypoxia responses, and sulfide metabolism, while also revealing over 100,000 SNPs useful for comparative work (Kelley et al., 2012). These

resources enabled transcriptomic and evolutionary analyses across replicated drainages and across poeciliids more broadly (Kelley et al., 2012; Greenway et al., 2020). Even after long-term captive maintenance, sulfidic populations retain H2S and hypoxia tolerance for roughly 40 generations, which increases their value for experimental evolution, physiology, and conservation-related ex situ studies (Williams et al., 2026).

Conclusions. *Poecilia mexicana* represents an unusually informative model for investigating how strong and replicated environmental selection shapes organismal evolution. Populations exposed to sulfide-rich and cave environments exhibit coordinated divergence across morphology, physiology, trophic ecology, reproduction, life history, development, and behaviour, with hydrogen sulfide toxicity and associated hypoxia acting as major selective pressures. The repeated evolution of sulfide tolerance demonstrates substantial functional convergence, particularly in mitochondrial processes involved in toxicity and detoxification, whereas genomic evidence indicates that similar phenotypes may arise through a combination of shared and lineage-specific genetic mechanisms. Importantly, common-garden and developmental studies show that ecological divergence is not restricted to environmentally induced plasticity but can involve heritable changes expressed across multiple levels of biological organization. The coexistence of replicated natural contrasts, variable degrees of reproductive isolation, and extensive experimental and genomic resources makes *P. mexicana* a particularly powerful system for examining the transition from ecological divergence to evolutionary differentiation. More broadly, this species illustrates how repeated environmental challenges can constrain functional outcomes while still permitting multiple evolutionary routes to adaptation.

Acknowledgements. An AI-powered search engine for research - https://consensus.app – Consensus NLP, Inc – was used to summarize data in tables.

Authors Contributions. ZAG and BM wrote the manuscript; MP read and revised the manuscript.

Conflicts of Interest. The authors declare that there is no conflict of interest.

Data Availability. Not applicable.

Funding. This research received no external funding.

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Received: 13 March 2026. Accepted: 22 June 2026. Published online: 21 October 2026.
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How to cite this article:
Grabán, Z. A., Moldovan, B., Popescu M. (2026). *Poecilia mexicana* as a model of ecological adaptation and convergent evolution across sulfide-rich and cave habitats. *Poeciliid Research*, *16*(1), 47-54. https://doi.org/10.67784/0089