Poeciliid Research

A narrative mini-review of *Xiphophorus nezahualcoyotl*

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Abstract. *Xiphophorus nezahualcoyotl* Rauchenberger, Kallman & Morizot, 1990 is a northern swordtail whose biological significance is best understood within the broader evolutionary, behavioral, and genomic research framework of the genus *Xiphophorus*. This mini-review synthesizes current knowledge on the species' taxonomy, phylogenetic placement, distribution, ecology, reproductive biology, sexual selection, and relevance to comparative research. Particular attention is given to the size-dependent alternative mating tactics of males, including the continuum from coaxing to coercive behaviors, as well as the occurrence of false brood spots and female-like pigmentation patterns that provide a distinctive example of female mimicry and sexual deception. Recent phylogenomic evidence further places *X. nezahualcoyotl* within the reticulate evolutionary history of northern swordtails, including documented gene flow with *X. continens*. The review also distinguishes the species-specific evidence from the broader biomedical significance of the genus, particularly the classical *Xiphophorus* melanoma models based on other species and interspecific hybrids. Although *X. nezahualcoyotl* is not a principal biomedical model, its combination of alternative reproductive tactics, sexually selected traits, polymorphic female mimicry, and introgressive evolutionary history makes it a valuable comparative system for studying sexual selection, behavioral evolution, hybridization, and speciation. Important gaps remain in species-specific knowledge of life-history schedules, population demography, physiology, and detailed reproductive parameters, highlighting opportunities for future research.

Keywords: *Xiphophorus nezahualcoyotl,* northern swordtails, sexual selection, alternative mating tactics, female mimicry, reproductive behavior, hybridization, introgression, phylogenomics, evolutionary biology, *Xiphophorus* model system.

Introduction. *Xiphophorus nezahualcoyotl* Rauchenberger, Kallman & Morizot, 1990 is a northern swordtail of the genus *Xiphophorus*, and the literature on it is strongest for phylogeny, sexually selected traits, mating tactics, hybridization, and its value within the broader Xiphophorus model-system tradition (Du et al., 2024; Morris et al., 2001; Morris et al., 2008; Walter et al., 2019) (Figure 1). Evidence specific to its life history, distribution, and behavior is substantial, whereas evidence specific to its direct use as a biomedical model is limited compared with the classical melanoma hybrids based on other *Xiphophorus* species (Du et al., 2024; Morris et al., 2008; Walter et al., 2019).

The aim of this mini-review is to synthesize and contextualize the available evidence on *Xiphophorus nezahualcoyotl*, with particular emphasis on its taxonomy, phylogenetic position, ecology, reproductive biology, sexually selected traits, alternative mating tactics, and evolutionary significance. The review also seeks to clarify the distinction between species-specific evidence and the broader biological and biomedical relevance of the genus *Xiphophorus*, thereby identifying the principal research contributions of *X. nezahualcoyotl* and the major gaps that remain in its species-level characterization.



Figure 1. *Xiphophorus nezahualcoyotl* Rauchenberger, Kallman & Morizot, 1990. Photograph by Brian Gratwicke, Wikimedia Commons, licensed under CC BY 2.0.

Taxonomy and Phylogenetic Placement. *Xiphophorus nezahualcoyotl* belongs to the genus *Xiphophorus*, a clade of small live-bearing Central American freshwater fishes that currently includes 26 described species distributed from northern Mexico to Guatemala, historically divided into northern and southern platyfishes and northern and southern swordtails (Du et al., 2024; Schartl & Lu, 2024). Within this framework, *X. nezahualcoyotl* is treated as a member of the northern, or Río Pánuco, swordtails (Kallman & Kazianis, 2006).

Earlier population-level allozyme analyses supported monophyly of the northern swordtails and recovered only weak support for monophyly of *X. nezahualcoyotl*, while also indicating that X*. nezahualcoyotl* populations from the Río Tamesí drainage cluster with some Río Pánuco populations, implying geographic complexity and nonmonophyly among the broader set of Pánuco drainage populations (Morris et al., 2001). This older uncertainty sits within a long-standing pattern of discordance among morphological, behavioral, allozyme, mitochondrial, and genomic trees in *Xiphophorus* (Morris et al., 2001; Franchini et al., 2018; Preising et al., 2022).

Recent phylogenomic work across all described species has substantially clarified genus-wide relationships and argues that reticulate evolution is a defining feature of *Xiphophorus*, with hybridization often preceding speciation (Du et al., 2024). For *X. nezahualcoyotl* specifically, newer comparative genomic analyses also detected strong evidence of gene flow between *X. continens* and *X. nezahualcoyotl*, reinforcing the view that species boundaries in northern swordtails have been shaped by introgression as well as divergence (Preising et al., 2022).

Distribution, Habitat, and Ecology. Within the Río Pánuco basin, the *X. montezumae* clade occurs north of the Río Tampaón–Río Santa María axis, and *X. nezahualcoyotl* specifically inhabits rivers and streams draining the eastern folded front ranges of the Sierra Madre Oriental, whereas *X. montezumae* occupies more interior valleys (Kallman & Kazianis, 2006). The species occurs in river sections separated by high waterfalls and

cataracts, but those barriers do not appear to prevent its distribution across the occupied drainage network (Kallman & Kazianis, 2006).

The broader biogeographic context matters because most headwater *Xiphophorus* species have restricted distributions in karstic systems, and natural hybridization in the wild is known but comparatively uncommon and localized (Kallman & Kazianis, 2006). That pattern helps explain why *X. nezahualcoyotl* is ecologically informative: it belongs to a radiation structured by fragmented headwaters, topographic barriers, and recurrent but nonuniform contact among lineages (Du et al., 2024).

Field work on *X. nezahualcoyotl* has been conducted in the Río El Salto, San Luis Potosí, where investigators directly observed natural social interactions and local sex ratios in one-square-meter focal areas before behavioral sampling (Ríos-Cárdenas et al., 2010). Those observations anchor much of what is known about the species' behavioral ecology under natural conditions (Ríos-Cárdenas et al., 2010).

Core Biological Characteristics. Like other members of the genus, *X. nezahualcoyotl* is a small, internally fertilizing, live-bearing freshwater poeciliid, and these basic features shape both its natural history and laboratory utility (Walter & Kazianis, 2001; Walter et al., 2019; Schartl & Lu, 2024). Across *Xiphophorus,* body size and male ornamentation vary strikingly, and this variation is central to comparative work on sexual selection and phenotypic evolution (Du et al., 2024; Preising et al., 2022; Preising et al., 2024).

In *X. nezahualcoyotl*, even the smallest males retain morphological and behavioral traits that can coax females to mate, distinguishing the species from *X. continens*, where all males are small and lack coaxing-associated morphology and behavior (Morris et al., 2008). This is important because *X. nezahualcoyotl* is not simply a reduced or weakly ornamented swordtail; rather, it combines size-dependent mating tactics with retained courtship-related traits (Morris et al., 2008).

Some males are polymorphic for a permanent pigment pattern termed the false brood spot, which resembles the brood spots typical of female poeciliids (Ríos-Cárdenas et al., 2010). Males with false brood spots can also express a horizontal bar pattern common in females, and this polymorphism has been studied as a case of female mimicry within a swordtail mating system rather than as a simple color variant (Ríos-Cárdenas et al., 2010) (Table 1).

Table 1

Selected biological and evolutionary features documented for *Xiphophorus nezahualcoyotl*

Trait domain	*Evidence in X. nezahualcoyotl*	*Comparative significance*
Systematic position	Northern swordtail within the Río Pánuco assemblage (Kallman & Kazianis, 2006)	Useful for northern swordtail comparisons
Reproduction	Internal fertilization and livebearing by genus-level biology (Walter & Kazianis, 2001; Walter et al., 2019)	Aligns it with standard poeciliid reproductive studies
Male tactics	Size-dependent coaxing to coercion continuum (Morris et al., 2008)	Key species for alternative mating tactic research
Male polymorphism	Some males bear false brood spots and female-like bars (Ríos-Cárdenas et al., 2010)	Model for female mimicry and sexual deception
Evolutionary history	Evidence of introgression with *X. continens* (Preising et al., 2022)	Relevant to reticulate speciation studies.

Reproduction and Sexual Selection. The reproductive biology of *X. nezahualcoyotl* has been studied mainly through male behavior, sexual ornamentation, and mating tactics

rather than through detailed demographic analyses of brood size or gestation in this species specifically (Morris et al., 2008; Ríos-Cárdenas et al., 2010). As in other *Xiphophorus*, the relevant mating system includes female choice, male courtship, and forced copulation attempts, but *X. nezahualcoyotl* is especially informative because these behaviors vary strongly with male body size (Preising et al., 2022; Preising et al., 2024; Morris et al., 2008).

Male mating behaviors in *X. nezahualcoyotl* have been ranked along a continuum from more coaxing to more coercive, including headstands, frontal displays, backing, and fast chases, based on how likely each behavior was to be followed by an attempted forced copulation (Morris et al., 2008). Large males mainly use coaxing tactics, and the largest males never used the most coercive behavior in laboratory trials, even when paired with a larger competitor (Morris et al., 2008). Small males show the opposite pattern, and the smallest males never used the most coaxing behavior even when alone with females (Morris et al., 2008).

This size-dependent tactical divergence connects *X. nezahualcoyotl* to broader comparative patterns in swordtails, in which smaller morphs often show reduced ornaments and greater reliance on coercive mating (Preising et al., 2022). At the same time, *X. nezahualcoyotl* does not match the extreme reduction seen in *X. continens*, because even its smallest males still retain some coaxing-associated traits (Morris et al., 2008; Preising et al., 2022).

Female mimicry adds a second layer to reproduction and mating competition in this species. A small percentage of males possess false brood spots, and these males have longer swords for their body size while still resembling females in pigmentation cues important during copulation (Ríos-Cárdenas et al., 2010). In field observations, males with false brood spots were chased less by other males, spent more time feeding, and males expressing the horizontal bar pattern had greater access to females (Ríos-Cárdenas et al., 2010). Females, however, did not appear to discriminate between males on the basis of false brood spot status in laboratory tests, suggesting that the main advantage of mimicry acts through reduced male harassment rather than altered female preference (Ríos-Cárdenas et al., 2010).

Why the Species Is Studied. *Xiphophorus nezahualcoyotl* is studied primarily as an evolutionary and behavioral model, not as the canonical biomedical model within the genus (Morris et al., 2008; Du et al., 2024; Walter et al., 2019). The broader genus is valuable because species are phenotypically diverse, experimentally tractable, and unusually capable of producing fertile interspecific hybrids, making *Xiphophorus* a classic vertebrate system for ecology, evolution, development, physiology, behavior, and speciation research (Schartl & Lu, 2024; Walter et al., 2019; Schartl & Lu, 2024; Franchini et al., 2018).

For X*. nezahualcoyotl* specifically, one major reason for study is its combination of ornamented males, alternative mating tactics, and female-mimic polymorphism, which together allow unusually fine-grained tests of sexual selection theory (Morris et al., 2008; Ríos-Cárdenas et al., 2010). The species has therefore contributed to questions about how male size predicts tactic choice, how coercive and coaxing behaviors coexist, and how deceptive phenotypes can persist when they reduce male–male aggression (Morris et al., 2008; Ríos-Cárdenas et al., 2010).

A second reason is phylogenetic and genomic. Because *Xiphophorus* evolution is pervaded by ancient and ongoing hybridization, species such as *X. nezahualcoyotl* help test how introgression, reproductive isolation, and sexually selected traits interact during diversification (Du et al., 2024; Franchini et al., 2018). Evidence of gene flow between *X. nezahualcoyotl* and *X. continens* makes it particularly relevant to debates about repeated loss of ornamentation and the reconstruction of northern swordtail phylogeny (Preising et al., 2022).

A third reason is logistical and comparative. *Xiphophorus* species are small and suitable for aquarium maintenance, many species and pedigreed lines are preserved through the Xiphophorus Genetic Stock Center, and the genus now has extensive genomic resources, including assemblies spanning nearly all described species (Schartl &

Lu, 2024; Walter et al., 2019; Du et al., 2024). These shared resources make species-level work on *X. nezahualcoyotl* cumulative and comparable across behavioral, evolutionary, and genomic studies (Schartl & Lu, 2024; Du et al., 2024).

Relation to Biomedical Model Systems. The genus *Xiphophorus* is one of the oldest animal systems for melanoma research, and it was the first model showing that cancer can be heritable (Schartl & Lu, 2024; Walter et al., 2019; Boaru 2024; Petrescu-Mag & Proorocu, 2022). That biomedical importance rests mainly on interspecific hybrids involving species such as *X. maculatus*, *X. hellerii*, and *X. couchianus*, where dysregulation of the xmrk oncogene and loss of regulation by the R/Diff locus lead to malignant pigment cell lesions (Du et al., 2024; Monroe et al., 2021; Nairn et al., 1996; Meierjohann et al., 2004).

That background matters for a review of *X. nezahualcoyotl* because the species belongs to a genus whose research identity has been strongly shaped by hybrid studies, linkage mapping, and cancer genetics (Walter & Kazianis, 2001; Meierjohann et al., 2004). However, the supplied literature does not identify *X. nezahualcoyotl* itself as a standard direct melanoma model in the way it identifies the classical hybrid combinations (Schartl & Lu, 2024). Its role is therefore better understood as part of the comparative *Xiphophorus* platform that supports work on hybridization, ornament evolution, and reproductive behavior, rather than as one of the principal biomedical crosses (Du et al., 2024) (Table 2).

Table 2
How the major research uses of the genus *Xiphophorus* relate to the specific case of *Xiphophorus nezahualcoyotl*

Research Domain	*Main Genus-Level Use*	*Relevance to X. nezahualcoyotl*
Melanoma genetics	Classical hybrid cancer model centered on xmrk and R/Diff (Du et al., 2024; Nairn et al., 1996)	Mostly contextual rather than species-specific
Evolution of hybridization	Ancient and ongoing introgression across the genus (Du et al., 2024; Franchini et al., 2018)	Directly relevant because of gene flow involving this species (Preising et al., 2022)
Sexual selection	Classic system for ornaments, mate choice, and trait loss (Preising et al., 2022; Preising et al., 2024; Meyer et al., 1994)	One of the key species for tactic variation and mimicry
Sex chromosome evolution	Hybridization can reshape sex-determining systems (Fedder, 2023; Franchini et al., 2018)	Relevant mainly as comparative background
Laboratory resources	Stock center, pedigreed lines, and genome assemblies (Walter et al., 2019)	Facilitates reproducible comparative studies.

Limits of the Current Species-Level Literature. The strongest species-specific evidence for X*. nezahualcoyotl* concerns mating behavior, sexual polymorphism, and phylogenetic placement, not a fully resolved account of its life-history schedule, population demography, or physiology (Morris et al., 2008; Ríos-Cárdenas et al., 2010; Morris et al., 2001). The available corpus also supports a careful distinction between what is true for the genus and what has been shown directly for this species: livebearing, interspecific hybridizability, and model-organism status are robust genus-level

inferences, while detailed reproductive and developmental parameters remain underdocumented here (Schartl & Lu, 2024; Walter et al., 2019).

Even so, *X. nezahualcoyotl* is a well-motivated focal species for future work because it sits at the intersection of three unusually rich research programs: reticulate phylogenomics, the evolution of sexually selected ornaments, and the behavioral ecology of alternative reproductive tactics (Du et al., 2024; Preising et al., 2022; Morris et al., 2008; Ríos-Cárdenas et al., 2010).

Conclusions. *Xiphophorus nezahualcoyotl* represents an informative comparative model at the intersection of sexual selection, behavioral ecology, and reticulate evolution. Available evidence demonstrates that its biological distinctiveness is particularly associated with size-dependent alternative mating tactics, sexually selected male traits, and polymorphic female mimicry, while recent genomic studies highlight the importance of introgression in its evolutionary history. At the same time, its role should not be conflated with that of the classical biomedical *Xiphophorus* models, because direct evidence for its use in melanoma research remains limited. The species-specific literature is comparatively weaker for population demography, detailed life-history parameters, physiology, and aspects of reproduction and development. Consequently, *X. nezahualcoyotl* remains an undercharacterized but highly promising system for future studies integrating behavior, sexual selection, genomics, hybridization, and speciation. Expanding species-specific field and laboratory research would help determine how ecological context, sexually selected phenotypes, mating tactics, and gene flow interact to shape the evolutionary trajectory of this northern swordtail.

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Data Availability. Not applicable.

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